Turning back from the brink: Detecting an impending regime shift in time to avert it

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Ecological regime shifts are large, abrupt, long-lasting changes in ecosystems that often have considerable impacts on human economies and societies. Avoiding unintentional regime shifts is widely regarded as desirable, but prediction of ecological regime shifts is notoriously difficult. Recent research indicates that changes in ecological time series (e.g., increased variability and autocorrelation) could potentially serve as early warning indicators of impending shifts. A critical question, however, is whether such indicators provide sufficient warning to adapt management to avert regime shifts. We examine this question using a fisheries model, with regime shifts driven by angling (amenable to rapid reduction) or shoreline development (only gradual restoration is possible). The model represents key features of a broad class of ecological regime shifts. We find that if drivers can only be manipulated gradually management action is needed substantially before a regime shift to avert it; if drivers can be rapidly altered aversive action may be delayed until a shift is underway. Large increases in the indicators only occur once a regime shift is initiated, often too late for management to avert a shift. To improve usefulness in averting regime shifts, we suggest that research focus on defining critical indicator levels rather than detecting change in the indicators. Ideally, critical indicator levels should be related to switches in ecosystem attractors; we present a new spectral density ratio indicator to this end. Averting ecological regime shifts is also dependent on developing policy processes that enable society to respond more rapidly to information about impending regime shifts.

early warning indicator | ecological threshold | spectral density ratio

Ecological regime shifts are large, sudden changes in ecosystems that last for substantial periods of time (1, 2). Regime shifts are a source of growing concern as rising human impacts on the environment are increasing the likelihood of ecological regime shifts at local to global scales (3–5). Accumulating evidence suggests that regime shifts can occur in diverse ecosystems: They have been documented in oceans (6–8), freshwaters (2, 9, 10), forests (11), woodlands (12), drylands (13), rangelands (14–16), and agroecosystems (17–19). Ecological regime shifts are widely regarded as undesirable as they often have considerable impacts on human well-being. For example, the collapse of Canada's Newfoundland cod fishery in the early 1990s directly affected the livelihoods of some 35,000 fishers and fish-plant workers, led to a decline of over $200 million dollars per annum in revenue from cod landings (20) and had significant indirect impacts on the local economy and society (21). Ecological regime shifts are also undesirable because they may be very costly or impossible to reverse (1, 2, 22). Regime shifts entail changes in the internal dynamics and feedbacks of an ecosystem that often prevent it from returning to a previous regime, even when the driver that precipitated the shift is reduced or removed (1, 2). For instance, despite a moratorium on the Canadian cod fishery for >15 years, the fishery has shown little sign of recovery (20).

Avoiding unintentional regime shifts is widely regarded as desirable (3, 4). However, ecological regime shifts are notoriously difficult to predict. Most regime shifts come as surprises, and the conditions and mechanisms leading to them only become clear once the shift has occurred (1, 2). Regime shifts typically result from a combination of gradual changes in an underlying driving variable (or set of variables), combined with an external shock, such as a storm or fire (23, 24). Gradual changes in underlying drivers usually have little or no apparent impact up to a certain point, and then unexpectedly lead to a regime shift when that threshold is crossed. Once an ecosystem is close to a threshold, a shift is often precipitated by a shock that under previous conditions had no dramatic consequences (1, 2). Slow underlying drivers that push ecosystems toward thresholds often go unnoticed and are frequently associated with increased economic benefits. In the absence of known thresholds and impacts, it is very difficult to constrain such drivers. Rising demands on the world's ecosystems are therefore expected to increasingly push ecosystems toward ecological thresholds (3–5). To avoid large-scale disruptions to human societies, there is accordingly an urgent need to improve our ability to anticipate and avert ecological regime shifts.

The need to better anticipate regime shifts has sparked much recent research (25–33). Most of this work has been based on mathematical models of ecosystems with multiple stable states (34, 35). The focus has been on generic changes in system behavior that might enable one to predict regime shifts across a diverse range of ecosystems, rather than experimental or model-based methods that focus on better understanding the mechanisms of particular regime shifts in specific ecosystems. It turns out that although little change may be evident in the average condition of an ecosystem as a regime shift is approached, there may be detectable changes in other properties of monitoring data. Specifically, time series data may show increased variability (25), changes in skewness (27), higher correlation through time (29, 33), and slower rates of recovery from disturbances (32) in advance of regime shifts. Such changes in the ways ecosystems behave hold substantial promise as early warning indicators of regime shifts, although there are as yet few empirical tests (25, 27, 29, 32, 33). However, given their potential use as early warning indicators, a critical question is: Would such changes in ecosystem behavior provide sufficient advance warning to adapt management to avoid a regime shift? Or are the lags and momentum of change in the ecosystem so great that by the time these changes are detected the system is already committed to a shift? Answers to these questions clearly impact whether attempts to employ such early warning indicators are worthwhile, and whether use of these indicators may be a viable strategy for avoiding undesirable regime shifts.

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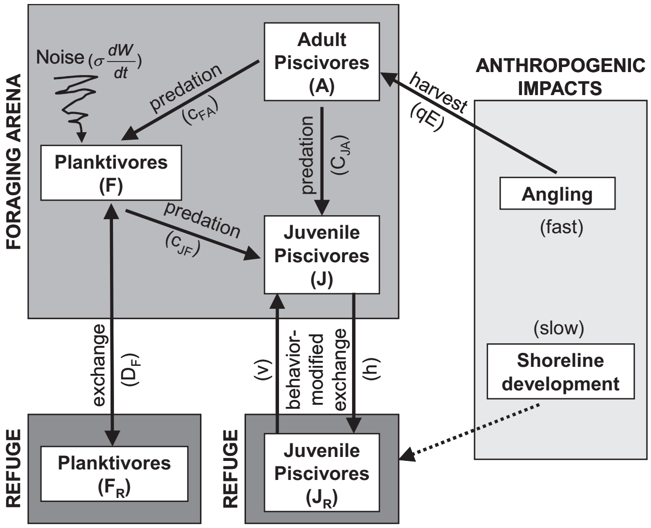

Fig. 1. The fisheries food web model used to explore the use of regime shift indicators in averting ecological regime shifts. Regime shifts are driven by angling or shoreline development. Angling directly affects the populations of adult piscivores through harvesting (*qE*). Shoreline development affects the amount and quality of refuge habitat, and thus the rate at which juvenile piscivores hide from predators (*h*).

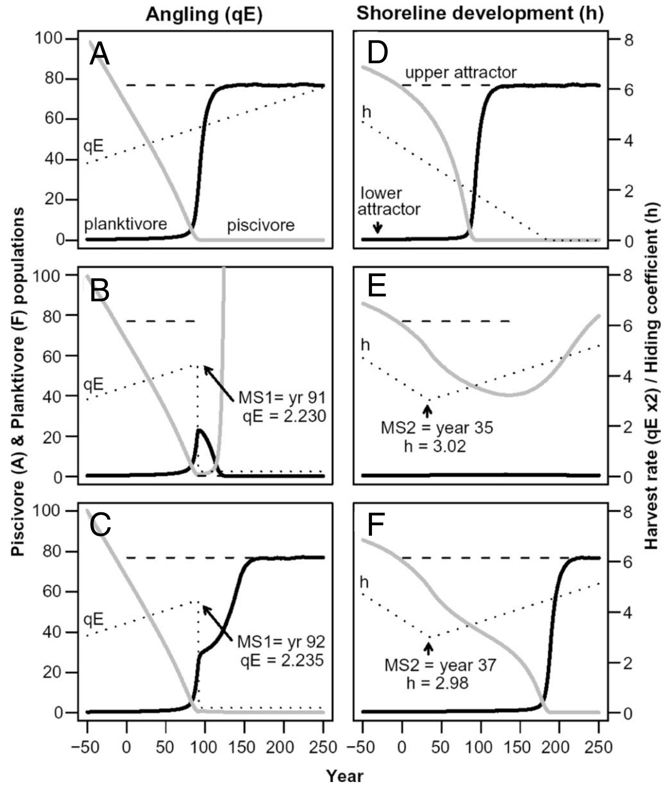

Fig. 2. The attainable proximity to a regime shift is much greater for driving variables that can be rapidly manipulated (angling) than for variables that can only be manipulated gradually (shoreline development). Year 0 is defined as the year in which the switch from the lower ($F = 0.34$) to the upper ($F = 76.92$) planktivore attractor occurs. (*A*) In the absence of policy action, a harvest-driven shift occurs in years 81 to 95. The switch in attractors occurs at $qE = 1.78$. (*B*) The window for averting a regime shift by implementing harvest-reduction policy MS1 lasts to year 91, well within the regime shift. (*C*) However, instituting MS1 just a year later cannot avert a regime shift. (*D*) In the absence of policy action, a shoreline development-driven shift occurs between years 80 and 95, and the switch in attractors occurs at $h = 3.7$. (*E*) To avert a regime shift, shoreline restoration policy MS2 has to be implemented substantially before the shift, by year 35. (*F*) Taking action slightly later (year 37) cannot avert a regime shift, although it is substantially delayed.

To examine these questions, we use a fisheries food web model to explore (*i*) how close an ecosystem can get to an ecological threshold and still avert a regime shift by implementing changes in management, and (*ii*) which regime shift indicators might give warning before this "point of no return." Regime shifts in the model can be triggered by 2 mechanisms: (*i*) angling, which is amenable to relatively fast manipulation through management action, or (*ii*) shoreline development, which can only be manipulated gradually. This enables us to investigate the potential avoidance of regime shifts for fast versus slow management variables. We use a modeling approach to explore the use of regime shift indicators under the most favorable possible conditions, where the signal from the indicators is not obscured by environmental variability and management changes can be implemented without delay. If the indicators provide insufficient warning under these conditions they hold little promise as tools for avoiding regime shifts in practice. However, if they perform adequately further investigations into the generality of the indicators, their detection in the field, and suitable policy instruments for management response are warranted.

Model

The fisheries food web model is derived from refs. 26 and 36 and involves a trophic triangle where adult piscivorous fish (*A*) prey on planktivorous fish (*F*), which in turn prey on juvenile piscivores (*J*) (Fig. 1). The model includes movement between refugia and foraging arenas by planktivores and juvenile piscivores (37). Two possible regimes exist: a piscivore-dominated regime and a planktivore-dominated regime. Nonlinear shifts between the regimes are precipitated by harvesting of adult piscivores (*qE*) or through shoreline development. Shoreline development impacts refuge habitat (fallen trees in shallow water), and hence affects the rate at which juvenile piscivores move from the foraging to the refuge arenas (*h*). This in turn impacts the predation of juvenile piscivores and affects recruitment. See the Methods section for further details.

We used 2 management scenarios in our simulations: (*i*) Immediate reduction in harvest to a level of $qE = 0.1$ (policy MS1), and (*ii*) gradual restoration of shoreline habitat, such that $h = +0.01$/year (policy MS2). In reality, political tradeoffs and bureaucratic delays mean that management responses will usually be substantially weaker and tardier than MS1 and MS2. In accordance with our aims, we chose optimistic management scenarios to explore the use of regime shift indicators under highly favorable conditions.

Results

We defined a regime shift as the period over which the annual increase in the planktivore (*F*) population exceeded 10%. In the model, regime shifts have a typical duration of ≈15 years, reflecting plausible limits on the growth rate of *F*.

How Close to a Regime Shift Can the Ecosystem Get and Still Avert a Shift? Dramatic differences are evident in the proximity to a regime shift that can be reached where management action focuses on angling (MS1) as opposed to shoreline development (MS2). For the angling-induced regime change, a regime shift can be well underway (10 years into the shift) and a permanent change still averted by reducing harvest as per scenario MS1. In contrast, for a regime shift driven by shoreline development, habitat restoration according to scenario MS2 has to be initiated at least 45 years before the onset of the shift to avert it (Fig. 2). Under these management options, avoiding a regime shift driven by shoreline development therefore requires much earlier detection and action than avoiding a shift driven by angling. Sensitivity analyses show that the attainable proximity to a regime shift is reduced if the management response is weaker or if the system is subject to greater levels of stochastic variation, but is unaffected by the rate of change in the variable driving the regime shift (Fig. S1).

We also explored manipulation of angling to avert a shoreline development-driven shift, and shoreline restoration to address an angling-induced shift. For the shoreline-driven shift, harvest-reduction policy MS1 (with h fixed at its level at the time of policy implementation) enabled a much greater proximity to the regime shift (8 years into the shift) than policy MS2 (45 years before the shift). A proximity equivalent to MS1 alone was attained if MS1 and MS2 were implemented simultaneously. Analogous results were found for the angling-driven shift and a regime shift driven by concurrent changes in qE and h (Table S1). The attainable proximity to a regime shift is therefore determined by the nature of the management variables: Where pressure on the ecosystem can be immediately reduced (angling), a shift can be averted by taking action even once a regime shift is underway, whereas, if pressure can only be gradually reduced (restoration of shoreline habitat), action needs to be taken substantially in advance of a shift. The remainder of our analyses focus on the scenarios in Fig. 2, because these capture the essential differences between fast and slow management variables in the model.

Two further features are evident in Fig. 2. First, there is a very clear and abrupt end to the window in which management action to avert a regime shift is possible. For instance, for the angling-induced regime shift, management action MS1 in year 91 leads to a rapid recovery of the piscivore population. However, the same management action just a year later is unable to prevent the regime shift, and the piscivore population never recovers despite a prolonged reduction in harvest.

Second, in transient settings such as those characterized in Fig. 2, the actual regime shift occurs substantially later than the switch to the alternate attractor. Consequently, there is a considerable lag between the point at which the long-term sustainable level of qE or h necessary to maintain a particular regime is surpassed, and the point at which a regime shift occurs. For instance, in the case of shoreline development the critical level at which the lower planktivore attractor disappears is $h = 3.7$. However, it is not until 80 years later when h has been reduced to $h = 2.1$ that a regime shift occurs. This may lead to the mistaken inference that the long-term sustainable level of h is close to the level at which the regime shift is initiated. More encouragingly, such lags provide room for "overshoot error": It is possible to substantially exceed long-term critical levels and still avert a regime shift. For instance, although the critical long-term harvest level is $qE = 1.78$, there is a window of 90 years, during which qE can be further increased to as much as 2.23, when it is still possible to avert a regime shift by implementing response MS1.

Which Indicators Provide Warning before the "Point of No Return?" Large annual increases in variance, skewness, kurtosis and the AR1 coefficient of within-year planktivore population only occur once a regime shift is underway (Fig. 3). In the case of the angling-driven shift and response MS1, such increases could provide warning 3–10 years before the end of the policy window in year 91, depending on the sensitivity with which "large annual increase" is defined. However, for a regime shift driven by shoreline development with management restricted to MS2, large annual increases in the indicators do not occur until several decades after the end of the policy window in year 35. "Spikes" associated with regime shifts occur in the variance and AR1 indicators under a wide range of model conditions. In contrast,

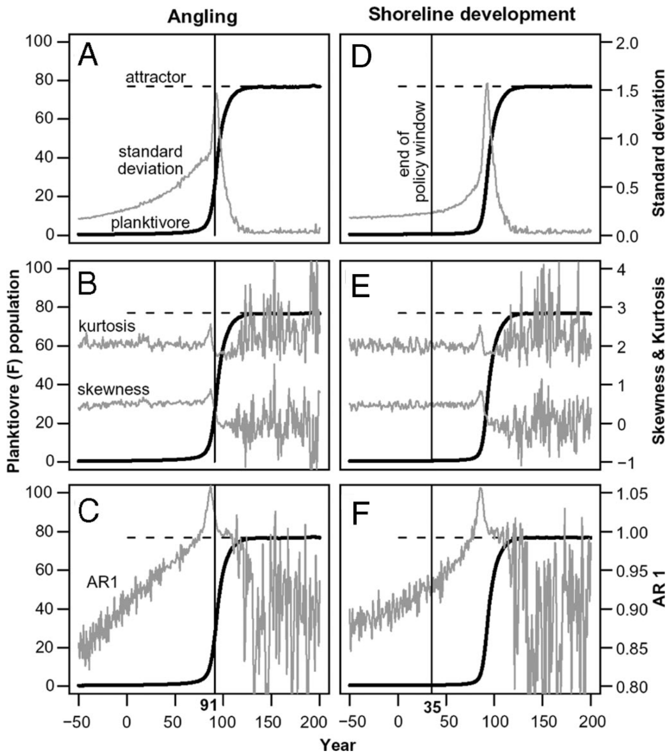

Fig. 3. Large annual increases in the regime shift indicators only occur once a regime shift is underway, which is often too late for management action to avert a shift. Gradual increases in variance (*A* and *D*) and AR1 (*C* and *F*) may occur before a regime shift, but specific thresholds need to be defined to indicate whether or when policy action to avert a shift is required. Indicators are based on the within-year planktivore data and correspond to the changes depicted in Fig. 2 *A* and *D* (vertical lines show the end of the policy windows).

skewness and kurtosis show spikes under some conditions, but not others (such as high levels of environmental noise).

Before the onset of a regime shift, directional changes in angling or shoreline development produce more gradual increases in variance and the AR1 coefficient (Fig. 3). Such increases could potentially provide greater advance warning of a regime shift. However, as apparent in Fig. 3, there are two difficulties associated with using gradual increases as early warning indicators. First, it may be difficult to detect these changes above the inherent variability in the ecosystem unless data were available for a substantial length of time. For instance, no increase in variance or AR1 is detectable in the 30-year period (a considerable time series in most real-world contexts) preceding the end of the policy window for the shoreline-driven shift. Second, detecting a slow increase in variance or the AR1 coefficient provides no information about how close to a regime shift the ecosystem may be. Gradual increases in variance and AR1 simply indicate that there is ongoing, directional change in some driver, and occur even when the driving variables are below the critical long-term levels that would lead to a switch in the attractor. Detecting a gradual increase in variance or AR1 therefore does not indicate whether or when management action is needed to avert a regime shift.

To sustain desirable regimes, indicators of regime shifts should ideally provide warning when the long-term critical qE or h levels are being approached or have been exceeded—i.e., when a switch in the attractor occurs. No marked changes in variance, AR1, skewness, or kurtosis accompany a switch in the attractor (Fig. 3). To investigate signals of a changing attractor, we calculated spectral densities based on the within-year planktivore data. We found clear signs of "reddening" after the switch

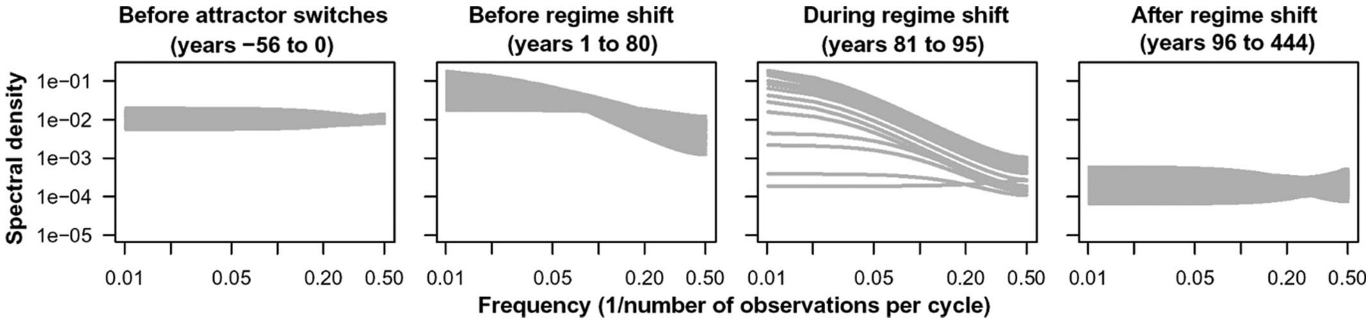

Fig. 4. For the angling-induced regime shift in Fig. 2*A*, clear signs of spectral ''reddening'' are evident after the switch from the lower to the upper planktivore attractor. The spectral density describes how variation in the within-year planktivore population data may be accounted for by cyclic components of different frequencies as determined by Fourier analysis. Each line gives the AR1-based spectral density for 1 year. Analogous spectra exist for the shoreline-driven regime shift.

from the lower to the upper attractor (Fig. 4). Based on the spectra in Fig. 4, we calculated a spectral density ratio to compare the contribution of low to high frequency processes to the total within-year variance in the planktivore population. In our model, the point at which low frequency processes start to dominate (10-year running mean spectral density ratio exceeds 1) provided warning of the disappearance of the lower attractor, for both the angling and shoreline development-driven shifts (Fig. 5). The 10-year running mean threshold also performed well when the system was subject to larger amounts of stochastic variation, or when the rates of change in the driving variables were increased (Fig. S2).

Discussion

Our model focuses on regime shifts precipitated by changes in slow underlying drivers, rather than shifts precipitated by large external shocks (23, 24). Mathematically, regime shifts driven by slow underlying variables involve bifurcations: A small, smooth change in parameter values causes sudden qualitative changes in the long-term behavior of a dynamical system because of the appearance or disappearance of attractors. Ecological models have demonstrated that mathematical bifurcations provide a plausible explanation for regime shifts in a diverse range of ecosystems (34, 35, 38). As human impacts on Earth expand, gradual changes in variables leading to bifurcations are likely to be a major cause of ecological regime shifts (3–5). As in our model, some of these drivers will be amenable to fast manipulation through management action, whereas it will only be possible to manipulate others much more gradually. Although not applicable to all ecological shifts, our model therefore represents key features of a broad class of potential regime shifts. For regime shifts driven by slow underlying variables, our findings relate specifically to: (*i*) the possibility of averting ecological regime shifts, and (*ii*) the use of regime shift indicators to this end.

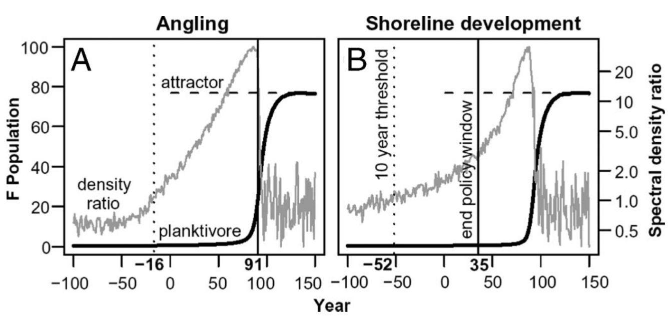

Fig. 5. The point at which the spectral density switches from domination by high to domination by low frequency processes (10-year running mean spectral density ratio exceeds 1 provided warning of a shift in the attractor in our model. We defined the spectral density ratio as the ratio of the spectral density at a frequency of 0.05 (low) to the density at a frequency of 0.5 (high) as given in Fig. 4.

Averting Regime Shifts. Our findings emphasize the need for monitoring and proactive intervention in averting ecological regime shifts (3, 4, 39), especially in cases where underlying drivers cannot be rapidly manipulated. Where it is possible to rapidly and drastically reduce impacts driving a shift (as in the case of angling), our results indicate that regime shifts could potentially be averted even once they are underway. However, bureaucratic inertia, policy compromise (40), and the risk of unforeseen environmental shocks (23, 24), make delaying action until a regime shift is underway a dangerous strategy even where it is theoretically feasible. If the variable driving a regime shift can only be manipulated gradually (as in the case of shoreline development), our results indicate that taking action substantially before the onset of a regime shift is crucial if a shift is to be averted. Proactive intervention is also desirable from the standpoint of cost, because the closer the system has moved to a regime shift, the stronger (and generally more costly and socially disruptive) the action needed to prevent a regime shift (4, 39).

Our results highlight that in systems subject to regime shifts there is often a discrete window for policy action, after which it becomes impossible to avert a shift. The existence of such windows, where the same action in 2 adjacent years could differ radically in its effectiveness, is seldom considered in environmental decision-making processes. Policy windows may help explain why some fisheries have shown rapid recovery when fishing controls were instituted, whereas other fisheries, such as the Newfoundland cod, have shown little recovery despite prolonged reductions in harvest (41, 42). Our findings also underscore the risks being taken by current inaction surrounding climate change. Atmospheric carbon dioxide (CO_2) levels are a variable that cannot be rapidly and drastically reduced. As highlighted by other authors, timely action to avert potential CO_2-induced regime shifts is therefore likely to be critical (4, 39).

Our results underscore the need for developing alternative decision-making processes for systems subject to ecological regime shifts (43, 44). In transient settings, such as those that characterize our simulations and most real-world ecosystems (34, 45), long-term sustainable levels of human impact can easily be exceeded. Switches in system attractors will usually occur substantially before any noticeable effects on ecosystems become evident. By the time adverse environmental effects become apparent it is often too late to avert a regime shift. Trial-and-error approaches that wait for evidence of negative environmental impacts before taking action are therefore ill-advised. However, as evidenced by the issue of climate change justifying restraint of human impacts without evidence of negative environmental effects represents a considerable challenge (4, 39). In such contexts, leading indicators could be a useful tool for policymakers.

In practice, regime shifts often involve multiple driving variables (2, 46). Where some of these variables can be manipulated quickly and others only more gradually, it may be possible to "buy time" to ameliorate a slow variable by implementing changes in a variable that can be rapidly manipulated. For instance, if the policy window for preventing a shoreline-induced regime shift through habitat restoration has closed, it may still be possible to avert a shift by reducing angling pressure. This effectively provides additional time to rehabilitate shoreline habitat. Identifying fast management variables that can act as "emergency levers" to extend our opportunity for addressing slow management variables may be critical to avoiding regime shifts. In the case of climate change, such actions could potentially include activities such as large-scale reforestation programs that can help provide the time needed to restructure energy systems (4, 39).

Use of Regime Shift Indicators. Regime shift indicators need to be further developed and refined if they are to detect impending shifts with sufficient warning to avert regime shifts. Rapid increases in variance, skewness and kurtosis, and the AR1 coefficient only occur at the onset of a regime shift. In most cases, such increases occur too late for management action to avert a shift. Although gradual increases in variance and AR1 occur substantially before a shift, these trends are problematic as early warning indicators. First, because the changes are small, detection is only likely in variables monitored over substantial periods of time, where the rate of change in the driving variables is high, or if baseline data from a much earlier period in time were available. Second, even if an increase in variance or AR1 is detected, it provides no indication of how close to a regime shift the ecosystem is, or even whether the long-term sustainable levels of the underlying drivers have been exceeded or not.

To provide useful early warnings, it is necessary to determine specific values of the regime shift indicators that should trigger management action, rather than simply detecting trends. Ideally, critical warning levels should be related to the point at which switches in the attractor occur, because this is the impact level of concern for longer-term sustainability. We have attempted to define such an indicator by means of a spectral density ratio. For our model, it appears that a shift from dominance by high frequency processes (spectral ratio <1) to dominance by low frequency processes (spectral ratio >1) provides a robust indicator of a switch in the attractor. These ratios need to be tested across a broader set of models and field data to assess the degree to which they are ecosystem-specific. Critical indicator levels could also be defined in terms of variance or AR1, but our analyses suggest that such critical levels will tend to vary with environmental conditions.

An advantage of defining critical levels in absolute terms is that the possibility of impending regime shifts can then be assessed from intensive time series data collected over a relatively short period. With the rapid growth in high frequency environmental monitoring equipment, intensive time series are becoming available for a wide range of ecosystems (47, 48). Nevertheless, determining critical indicator levels may be challenging and will need to draw heavily on model simulations, experimental manipulations and long-term observation of particular ecosystems. Given research constraints, the degree to which critical levels turn out to be ecosystem-specific will largely determine their potential use for helping avert regime shifts. However, it may be possible to select or define indicators that have critical levels that are relatively transferable between ecosystem types or subtypes. This is an important area for future research.

In conclusion, our results indicate that regime shift indicators cannot at present be relied upon as a general means for detecting and avoiding ecological regime shifts. It is as yet unclear whether use of regime shift indicators for this purpose is achievable, but to the extent that it may be, our work suggests that it would rely on: (*i*) defining critical levels of the regime shift indicators, (*ii*) linking these critical levels to long-term sustainable impact levels, and (*iii*) finding or developing indicators that have critical levels that are relatively transferable across different ecosystem types. In addition, our results highlight the need for research on policy processes that are better suited to managing complex systems subject to regime shifts. Such processes would reduce inertia and enable society to respond more rapidly to information about impending regime shifts, better account for the existence of policy windows when planning management interventions, and rely on leading indicators, rather than adverse environmental impacts, as triggers for management action. While this research develops, management for unwanted regime shifts will depend on existing approaches that hedge, avoid risk, maintain ecological resilience, or build social resilience to cope with unexpected change (2, 43, 44).

Methods

Model specification. Changes in the populations of adult piscivores (A), planktivores (F) and juvenile piscivores (J) are modeled on 2 times scales (26, 36). The dynamics over the shorter "monitoring interval" (taken as 1/50th of a year) are given by:

$$\frac{dA}{dt} = -qEA$$

$$\frac{dF}{dt} = D_F(F_R - F) - c_{FA}FA + \sigma\frac{dW}{dt}$$

$$\frac{dJ}{dt} = -c_{JA}JA - \frac{c_{JF}vFJ}{h + v + c_{JF}F}$$

with parameters catchability (q), effort (E), exchange rate of F between the foraging arena and a refuge (D_F), refuge reservoir of F (F_R), consumption rate of F by A (c_{FA}), additive noise (σ), control of J by A (c_{JA}), consumption rate of J by F (c_{JF}), rate at which J enter the foraging arena (v), and rate at which J seek refuge (h). The harvest rate is the product qE and dW/dt is a Wiener stochastic process. It can be shown analytically that up to the level of small noise expansion and linearization of the above system, the choice of where to incorporate stochasticity in the model, or including stochasticity in multiple places, does not affect the generality of our results in the sense that the behavior of the variance-covariance matrix of the linear approximation still signals an impending bifurcation (*SI Appendix*, *General Analysis of Early Warning Signals of Impending Bifurcations*).

Dynamics over the longer "maturation interval" (nominally 1 year; may be longer for species with slower maturation) are given by:

$$A_{t+1} = A_{t+1;1} = s(A_{t;n} + J_{t;n})$$

$$F_{t+1} = F_{t+1;1} = F_{t;n}$$

$$J_{t+1} = J_{t+1;1} = fA_{t+1}$$

where t in $A_{t;n}$ denotes the maturation interval and n denotes the monitoring interval. s is survivorship between maturation intervals and f is the fecundity rate of A. Parameter values are given in Table S2, and are based on the literature and whole lake experiments (26, 49, 50). Phase diagrams for equilibrium conditions under different combinations of qE, h and initial A are given in Fig. S3.

Simulations. Our simulations focus on transient conditions. Simulations were initiated near steady-state values corresponding to $qE = 1.5$ and $h = 8$ and run for a burn-in period of 500 years to ensure convergence. The transient results reported in this article were simulated over an additional 500 year period by slowly increasing qE (at a rate of $+0.005$/year) or decreasing h (at a rate of -0.02/year until $h = 0$). These parameter values were chosen for illustrative purposes; other values gave analogous results. Simulations were performed in R (51).

Regime Shift Indicators. All indicators were calculated from the 50 simulated ''monitoring'' data points for F within each year. We calculated variance, skewness, and kurtosis, using the R Moments package (51), and mean-detrended OLS autoregressive lag 1 (AR1) coefficients and the spectral density ratio, using R functions. We did not use return time to equilibrium because our simulations involve ongoing changes in qE and h. The spectral density ratio was derived from spectral densities based on an AR1 fit to first-difference detrended F data (52, 53). We calculated the spectral density ratio as the ratio of the spectral density at a frequency of 0.05 (low) to the density at a frequency of 0.5 (high). For more details, see *SI Appendix*, *Calculation of the Spectral Density Ratio*.

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1. Scheffer M, Carpenter SR, Foley JA, Folke C, Walker BH (2001) Catastrophic shifts in ecosystems. *Nature* 413:591–596.
2. Carpenter SR (2003) *Regime Shifts in Lake Ecosystems: Pattern and Variation* (International Ecology Institute, Oldendorf, Germany).
3. MA (2005) *Ecosystems and Human Well-Being: Synthesis* (Island, Washington DC).
4. IPCC (2007) *Climate Change 2007: Synthesis Report* (IPCC, Geneva).
5. Steffen WL, *et al.* (2004) *Global Change and the Earth System: A Planet Under Pressure* (Springer, Berlin, Germany).
6. Knowlton N (1992) Thresholds and multiple stable states in coral reef community dynamics. *Am Zool* 32:674–682.
7. Hare SR, Mantua NJ (2000) Empirical evidence for North Pacific regime shifts in 1977 and 1989. *Prog Oceanogr* 47:103–145.
8. Jackson JBC, *et al.* (2001) Historical overfishing and the recent collapse of coastal ecosystems. *Science* 293:629–637.
9. Scheffer M (1997) *The ecology of shallow lakes* (Chapman and Hall, London).
10. Scheffer M, van Nes EH (2007) Shallow lakes theory revisted: Various alternative regimes driven by climate, nutrients, depth and lake size. *Hydrobiologia* 584:455–466.
11. Ludwig D, Jones D, Holling CS (1978) Qualitative analysis of insect outbreak systems: The spruce budworm and the forest. *J Anim Ecol* 47:315–332.
12. Dublin HT, Sinclair AR, McGlade J (1990) Elephants and fire as causes of multiple stable states in the Serengeti-Mara woodlands. *J Anim Ecol* 59:1147–1164.
13. Foley JA, Coe MT, 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.
14. Walker BH, Ludwig D, Holling CS, Peterman RM (1981) Stability of semiarid savanna grazing systems. *J Ecol* 69:473–498.
15. van de Koppel J, Rietkerk M, Weissing FJ (1997) Catastrophic vegetation shifts and soil degradation in terrestrial grazing systems. *Trends Ecol Evol* 12:352–356.
16. Laycock WA (1991) Stable points and thresholds of range condition on North American rangelands: A viewpoint. *J Range Manage* 44:427–433.
17. Anderies JM, Ryan P, Walker BH (2006) Loss of resilience, crisis and institutional change: Lessons from an intensive agricultural system in southeastern Australia. *Ecosystems* 9:865–878.
18. Cramer VA, Hobbs RJ (2005) Assessing the ecological risk from secondary salinity: A framework addressing questions of scale and threshold responses. *Austral Ecol* 30:537–545.
19. Gordon LJ, Peterson GD, Bennett EM (2008) Agricultural modifications of hydrological flows create ecological surprises. *Trends Ecol Evol* 23:211–219.
20. DFO (2004) Fish landings and landed values (Department of Fisheries and Oceans, Ottawa, Ontario, Canada). Available at www.nfl.dfo-mpo.gc.ca.
21. Finlayson AC, McCay BJ (1998) in *Linking Social and Ecological Systems: Management Practices and Social Mechanisms for Building Resilience*, eds Berkes F, Folke C (Cambridge Univ Press, Cambridge, UK), pp 311–337.
22. Meijer ML (2000) Biomanipulation in the Netherlands: 15 years of experience. (Wageningen University, Wageningen, The Netherlands).
23. Scheffer M, Carpenter SR (2003) Catastrophic regime shifts in ecosystems: Linking theory to observation. *Trends Ecol Evol* 18:648–656.
24. Beisner BE, Haydon DT, Cuddington K (2003) Alternative stable states in ecology. *Front Ecol Environ* 1:376–382.
25. Carpenter SR, Brock WA (2006) Rising variance: A leading indicator of ecological transition. *Ecol Lett* 9:311–318.
26. Carpenter SR, Brock WA, Cole JJ, Kitchell JF, Pace ML (2008) Leading indicators of trophic cascades. *Ecol Lett* 11:128–138.
27. Guttal V, Jayaprakash C (2008) Changing skewness: An early warning signal of regime shifts in ecosystems. *Ecol Lett* 11:450–460.
28. Oborny B, Meszéna G, Szabó G (2005) Dynamics of populations on the verge of extinction. *Oikos* 109:291–296.
29. 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 Dynam* 53:53–63.
30. van Nes EH, Scheffer M (2003) Alternative attractors may boost uncertainty and sensitivity in ecological models. *Ecol Model* 159:117–124.
31. Rietkerk M, Dekker SC, de Ruiter PC, van de Koppel J (2004) Self-organized patchiness and catastrophic shifts in ecosystems. *Science* 305:1926–1929.
32. van Nes EH, Scheffer M (2007) Slow recovery from peturbations as a generic indicator of a nearby catastrophic shift. *Am Nat* 169:738–747.
33. Dakos V, *et al.* (2008) Slowing down as an early warning signal for abrupt climate change. *Proc Natl Acad Sci USA* 105:14308–14312.
34. Holling CS (1973) Resilience and stability of ecological systems. *Annu Rev Ecol Syst* 4:1–23.
35. May RM (1977) Thresholds and breakpoints in ecosystems with a multiplicity of stable states. *Nature* 269:471–477.
36. Carpenter SR, Brock WA (2004) Spatial complexity, resilience and policy diversity: Fishing on lake-rich landscapes. *Ecol Soc* 9:8.
37. Walters CJ, Martell SJD (2004) *Fisheries Ecology and Management* (Princeton Univ Press, Princeton).
38. Ludwig D, Walker BH, Holling CS (1997) Sustainability, stability and resilience. *Conserv Ecol* 1:7.
39. Stern N (2006) The economics of climate change: The Stern review (Cambridge Univ Press, Cambridge, UK).
40. Kingdon JW (1995) *Agendas, Alternatives, and Public Policies* (Harper Collins, New York).
41. Hilborn R (2007) Reinterpreting the state of fisheries and their management. *Ecosystems* 10:1362–1369.
42. Beddington JR, Agnew DJ, Clark CW (2007) Current problems in the management of marine fisheries. *Science* 316:1713–1716.
43. Waltner-Toews D, Kay JJ, Lister NME eds (2008) *The Ecosystem Approach: Complexity, Uncertainty, and Managing for Sustainability* (Columbia Univ Press, New York).
44. Norberg J, Cumming GS eds (2008) *Complexity Theory for a Sustainable Future* (Columbia Univ Press, New York).
45. Hastings A (2004) Transients: The key to long-term ecological understanding? *Trends Ecol Evol* 19:39–45.
46. Kinzig A, *et al.* (2006) Resilience and regime shifts: Assessing cascading effects. *Ecol Soc* 11:20.
47. Jeong Y, Sanders BF, Grant SB (2006) The information content of high-frequency environmental monitoring data signals pollution events in the coastal ocean. *Environ Sci Technol* 40:6215–6220.
48. DeFries RS, Townshend JRG (1999) Global land cover characterization from satellite data: From research to operational implementation? *Global Ecol Biogeogr* 8:367–379.
49. Carpenter SR, *et al.* (2001) Trophic cascades, nutrients and lake productivity: Whole-lake experiments. *Ecol Monogr* 71:163–186.
50. Carpenter SR, Kitchell JF eds (1993) *The Trophic Cascade in Lakes* (Cambridge Univ Press, Cambridge, UK).
51. R Development Core Team (2006) R: A language and environment for statistical computing (R Foundation for Statistical Computing, Vienna, Austria). Available at www.R-project.org.
52. Wei WWS (1990) *Time Series Analysis: Univariate and Multivariate Methods* (Addison-Wesley, Redwood City, CA).
53. Chatfield C (1989) *The Analysis of Time Series: An Introduction* (Chapman and Hall, London).