



CHICAGO JOURNALS



Conditional Heteroscedasticity as a Leading Indicator of Ecological Regime Shifts.

Author(s): David A. Seekell, Stephen R. Carpenter, Michael L. Pace

Source: *The American Naturalist*, Vol. 178, No. 4 (October 2011), pp. 442-451

Published by: [The University of Chicago Press](#) for [The American Society of Naturalists](#)

Stable URL: <http://www.jstor.org/stable/10.1086/661898>

Accessed: 03/10/2011 09:45

Your use of the JSTOR archive indicates your acceptance of the Terms & Conditions of Use, available at <http://www.jstor.org/page/info/about/policies/terms.jsp>

JSTOR is a not-for-profit service that helps scholars, researchers, and students discover, use, and build upon a wide range of content in a trusted digital archive. We use information technology and tools to increase productivity and facilitate new forms of scholarship. For more information about JSTOR, please contact support@jstor.org.



The University of Chicago Press and *The American Society of Naturalists* are collaborating with JSTOR to digitize, preserve and extend access to *The American Naturalist*.

<http://www.jstor.org>

Conditional Heteroscedasticity as a Leading Indicator of Ecological Regime Shifts

David A. Seekell,^{1,*} Stephen R. Carpenter,² and Michael L. Pace¹

1. Department of Environmental Sciences, University of Virginia, Charlottesville, Virginia 22904; 2. Center for Limnology, University of Wisconsin, Madison, Wisconsin 53706

Submitted March 25, 2011; Accepted June 30, 2011; Electronically published August 25, 2011

Online enhancement: zip file. Dryad data: <http://dx.doi.org/10.5061/dryad.2jr4g>.

ABSTRACT: Regime shifts are massive, often irreversible, rearrangements of nonlinear ecological processes that occur when systems pass critical transition points. Ecological regime shifts sometimes have severe consequences for human well-being, including eutrophication in lakes, desertification, and species extinctions. Theoretical and laboratory evidence suggests that statistical anomalies may be detectable leading indicators of regime shifts in ecological time series, making it possible to foresee and potentially avert incipient regime shifts. Conditional heteroscedasticity is persistent variance characteristic of time series with clustered volatility. Here, we analyze conditional heteroscedasticity as a potential leading indicator of regime shifts in ecological time series. We evaluate conditional heteroscedasticity by using ecological models with and without four types of critical transition. On approaching transition points, all time series contain significant conditional heteroscedasticity. This signal is detected hundreds of time steps in advance of the regime shift. Time series without regime shifts do not have significant conditional heteroscedasticity. Because probability values are easily associated with tests for conditional heteroscedasticity, detection of false positives in time series without regime shifts is minimized. This property reduces the need for a reference system to compare with the perturbed system.

Keywords: regime shift, conditional heteroscedasticity, Lagrange multiplier test, moving-window analysis, leading indicator, ecosystem model.

Introduction

Regime shifts are reorganizations of nonlinear ecological processes that occur when systems pass critical transition points. Ecological regime shifts are sometimes irreversible and can have severe consequences for human well-being through loss of water quality, loss of rangeland or fish production, or loss of species (Carpenter and Brock 2006; Scheffer et al. 2009; Drake and Griffen 2010). Generally, the critical transition point is unknown, and regime shifts

occur with little or no warning (Scheffer et al. 2009). There are a wide variety of approaches to identify regime shifts after they occur, but methods to warn of impending regime shifts are needed if unwanted transitions are to be prevented (Andersen et al. 2009; Biggs et al. 2009; Contamin and Ellison 2009).

Theoretical evidence suggests that statistical anomalies appear in ecological time series prior to regime shifts (e.g., Carpenter and Brock 2006; Carpenter et al. 2008; Scheffer et al. 2009). Increasing autocorrelation (Scheffer et al. 2009), increasing variance (Brock and Carpenter 2006; Carpenter and Brock 2006; Scheffer et al. 2009), shifts to low-frequency variance (Kleinen et al. 2003; Biggs et al. 2009), and changing skewness (Guttal and Jayaprakash 2008) in ecological time series warn of impending regime shifts in theory and are present before regime shifts in simulations of stochastic ecosystem models (e.g., Carpenter et al. 2008; Guttal and Jayaprakash 2008; Scheffer et al. 2009), as well as in laboratory studies (Drake and Griffen 2010). These indicators are thought to represent a general class of early warning signals applicable to a wide variety of regime shifts. However, some common critical transitions are characterized by decreasing variance, decreasing autocorrelation, or no change in symmetry (Berglund and Gentz 2002; Brock and Carpenter 2006; Guttal and Jayaprakash 2008; Carpenter et al. 2009). Hence, leading indicators may have ambiguous interpretations when applied to environmental data if the form of the underlying dynamics is unknown (Brock and Carpenter 2006). An additional challenge is to discern between random and nonrandom changes in indicators (Scheffer et al. 2009). Currently, a reference system is needed to compare to the perturbed system in order to interpret changes in indicators because indicators are not easily associated with probability values (e.g., Drake and Griffen 2010; Carpenter et al. 2011).

Conditional heteroscedasticity is persistence in the error variance of autoregressive time series models (Engle 1982).

* Corresponding author; e-mail: das9xx@virginia.edu.

In time series, conditional heteroscedasticity appears as clustered volatility, such as the periods of high volatility and low volatility seen in plots of stock market returns (Engle 2001). Conditional heteroscedasticity is well known in economics, but tests for conditional heteroscedasticity and related autoregressive conditional heteroscedastic time series models have rarely if ever been applied to ecological time series (Lamoureux and Lastrapes 1990; Engle 2001). We analyzed conditional heteroscedasticity as a potential leading indicator of regime shifts in ecological time series. We use simulated time series from stochastic ecosystem models to evaluate the power of conditional heteroscedasticity to detect impending regime shifts and to evaluate the susceptibility of these tests to false positives. Some of these models use empirically measured large process error, which more adequately mimics nature than small-noise processes generally applied to ecosystem models.

Methods

Conditional Heteroscedasticity

Constant residual variance (homoscedasticity) is a fundamental assumption of ordinary least squares regression analysis. Methods for dealing with violation of the constant variance assumption (heteroscedasticity) are well studied and include weighted least squares regression, data transformations, and heteroscedastic consistent covariance estimators (e.g., Box and Cox 1964; White 1980). Similarly, stationary residual variance is also an assumption of many time series analysis methods, and many time series are heteroscedastic, with periods of high and low volatility (Engle 1982, 2001; Lamoureux and Lastrapes 1990). These time series are described as conditionally heteroscedastic, meaning that the variance at a time step is dependent or conditional on the variance at the time step before. High volatility is likely to follow high volatility, and low volatility is likely to follow low volatility, leading to a characteristic clustering of variances.

Variance increases in the vicinity of an impending regime shift due to flickering or squealing (Taylor et al. 1993; Carpenter and Brock 2006; Scheffer 2009; Brock and Carpenter 2010). Flickering occurs when stochastic forcing moves a system between two states but not permanently from one state to another (Scheffer 2009; Brock and Carpenter 2010). These back and forth changes in state variables create increased variance that can be viewed as an early warning because environmental conditions have not changed enough to force the system into one state (Scheffer 2009). Squealing occurs when variance builds in vicinity of a regime shift because the system does not recover from random environmental perturbations rapidly due to reduced return rate to equilibrium (Scheffer 2009; Scheffer

et al. 2009; Brock and Carpenter 2010). Because of flickering and squealing, the region of time series near a critical transition might be a cluster of high volatility, and the region of time series more distant from the critical transition point might be a cluster of low volatility. Thus, significant conditional heteroscedasticity is expected to appear as a system approaches a critical transition point because high volatility will appear to cluster. If an impending regime shift is characterized by declining variance prior to the critical transition point, conditional heteroscedasticity will still appear because there is still a clustering of, in this case, low variance prior to the shift. There should be no significant conditional heteroscedasticity in time series without a critical transition. Figure 1 is an example of conditional heteroscedasticity. The figure consists of squared residuals from an autoregressive lag-1 time series model applied to 200 time steps of simulated planktivore biomass prior to a regime shift in a temperate-lake food web model plotted by the squared residual at the previous time step. The strong positive relationship between squared residuals and the squared residuals at the previous time step is characteristic of conditional heteroscedasticity. The regression line would be horizontal if there were no conditional heteroscedasticity and variance at one time step was not dependent on variance at the previous time step.

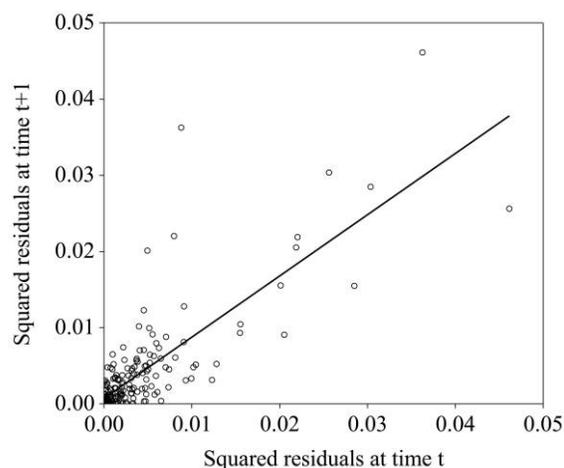


Figure 1: Squared residuals from an autoregressive lag-1 model applied to the 200 time steps prior to regime shift in the planktivore biomass time series from the temperate-lake food web model plotted by the previous squared residual. The strong positive relationship is indicative of conditional heteroscedasticity because there is a relationship between the error variance at a given time step and the error variance at the previous time step. If the regression line was horizontal, error variance would have no relationship with error variance at previous time steps, and there would be no conditional heteroscedasticity.

Analytical Approach

We used simulated time series with and without regime shifts to evaluate conditional heteroscedasticity as a leading indicator. Simulated data are well suited to evaluation of leading indicators because the locations of regime shifts due to changes in the control parameter are known exactly. The power of conditional heteroscedasticity as a leading indicator can be assessed at different distances preceding the simulated regime shift, and the indicator can be applied to simulated time series without regime shifts to evaluate its susceptibility to returning false positives. We selected four models from the literature to generate time series (table 1) representing discrete- and continuous-time approaches with various magnitudes of noise. The models are formed from systems of stochastic difference equations or stochastic differential equations and are calibrated to either long-term observations or experimental results. The stochastic difference equations include empirically measured large process errors. The stochastic differential equations contain small-noise perturbations typical of leading indicator simulation studies (e.g., Carpenter et al. 2008). These noise terms represent environmental stochasticity but not independent random observation error due to measurement error (Carpenter 2003). The stochastic differential equations were integrated numerically using the Euler-Maruyama method for Ito calculus. The models were run in R (<http://www.r-project.org>) and Maple 13 (<http://www.maplesoft.com>).

Models

The models used in this study have been described in detail elsewhere and are described only briefly here (table 1). The first model is a stochastic Ricker population dynamics model (May 1976; Ponciano et al. 2005) that is widely used to describe discrete-time, density-dependent population dynamics (e.g., Beard et al. 2003; Ponciano et al. 2005). Model parameters, including process error, were derived from laboratory cultures of *Escherichia coli*, using maximum likelihood methods by Ponciano et al. (2005). When the model growth rate (see table 1) is raised past the critical transition point, the system undergoes a period-doubling (pitchfork) bifurcation. We simulated 2,000 time steps at a stable point as a reference series with no regime shift. We then simulated 2,000 time steps with slowly increasing population growth rate so that the system would pass the critical transition point at time step 1,500.

The second model describes the discrete-time dynamics of a midge-algae-detritus food web in Lake Myvatn, Iceland (Ives et al. 2008). The model parameters, including process error, were derived from long-term data, using maximum likelihood methods by Ives et al. (2008). We

generated a reference series of midge biomass with no regime shift by setting the algal growth rate low so that midge dynamics remained at a stable point. We simulated a 2,000-step time series of midge biomass with regime shift by slowly increasing the algal growth rate to mimic eutrophication, with the result that the critical transition point is crossed at step 1,500. We applied conditional heteroscedasticity tests to the resulting midge time series. To find the transition point, we simulated the deterministic skeleton of the model and labeled the point just before oscillations begin as the critical transition point. After the critical transition point is crossed, this equation undergoes a supercritical Neimark-Sacker bifurcation (a discrete-time Hopf bifurcation), which is characteristic of a system that loses fixed-point stability and moves toward periodic or quasi-periodic behavior (Ives et al. 2008).

The third model is a simple continuous logistic growth equation that describes *Daphnia magna* population dynamics in a laboratory experiment (Drake and Griffen 2010). Drake and Griffen (2010) progressively decreased food supply to populations of *Daphnia* over the course of several weeks, leading to declines in abundance and eventually extinction. Declines in both population growth rate and system carrying capacity are expected when food supply is diminished (Griffen and Drake 2008; Drake and Griffen 2010). We generated a reference series of *Daphnia* biomass by simulating 2,000 time steps at a stable equilibrium. We generated a series with regime shift by simulating 2,000 time steps with slowly decreasing intrinsic growth rate and decreasing carrying capacity so that the system crosses the critical transition point at time step 1,500 and undergoes a transcritical bifurcation. We did not allow the population to become extinct so that we could continue to apply conditional heteroscedasticity tests to the end of the 2,000-step time series. Small noise was added because process error was not estimated empirically by Drake and Griffen (2010).

The fourth model describes planktivore-zooplankton-phytoplankton food web dynamics in a temperate lake. The model parameters were derived from long-term data by Carpenter et al. (2008). Small noise was added because process error was not estimated empirically (Carpenter et al. 2008). We generated a reference series of planktivore biomass by simulating 2,000 time steps at a stable equilibrium with high predation pressure on planktivores. This system has low planktivore biomass, high zooplankton biomass, and low phytoplankton biomass. We generated a series with regime shift by slowly reducing predation pressure on the planktivores to simulate overfishing of predatory fish. The system crosses the critical transition point for a fold bifurcation at time step 1,500, and there is a trophic cascade characterized by increasing planktivore biomass, declining herbivore biomass, and increasing phy-

Table 1: Ecological models and parameter values used in this study

Description	Model	Parameters
<i>Escherichia coli</i> growth (Ponciano et al. 2005)	$N_{t+1} = N_t \exp(a + bN_t + \sigma^2 z_t)$	N_t (population size at time t), $a = .01782$ (growth rate, control parameter), $b = -.0004802$ (density effect on growth), $\sigma^2 = .0002713$, $z_t = N(0, \sigma^2)$
Midge dynamics in Lake Myvatn, Iceland (Ives et al. 2008)	$x_{t+1} = r_t x_t [1 + (x_t/R_t)]^{-q} \exp(\varepsilon_{1t}),$ $y_{t+1} = [r_2 y_t (1 + y_t)^{-1} - (y_t/R_t)] x_{t+1} + c] \exp(\varepsilon_{2t}),$ $z_{t+1} = [dz_t + y_t - (pz_t/R_t)] x_{t+1} + c] \exp(\varepsilon_{3t}),$ $R_t = y_t + pz_t$	x_t (midge abundance at time t), $r_t = 3.87$ (intrinsic growth rate of midges), $q = .903$ (strength of density-dependent midge dynamics), $\varepsilon_{1t} = N(0, .349)$ (random noise), y_t (abundance of algae at time t), r_2 (intrinsic growth rate of algae, control parameter), $c = 10^{-6.435}$ (input rate of algae and detritus from outside the system), $\varepsilon_{2t} = N(0, .75)$ (random noise), z_t (abundance of detritus at time t), $d = .552$ (retention rate of detritus), $p = .0666$ (quality of detritus relative to algae), $\varepsilon_{3t} = N(0, .75)$ (random noise), R_t (resource abundance at time t)
<i>Daphnia</i> population growth (Drake and Griffen 2010)	$dN/dt = rN[1 - (N/k)] + \sigma(dW/dt)$	N is population abundance (initial value = 35); k is carrying capacity (initial value = 35, control parameter); r is intrinsic rate of increase (initial value = 1, control parameter); $\sigma = 17.5$
Food web dynamics in a northern temperate lake (Carpenter et al. 2008)	$dA/dt = -qEA,$ $dF/dt = D_F(F_R - F) - C_{FA}FA + \sigma_F(dW_F/dt),$ $dJ/dt = -C_{JA}JA - [C_{JP}P/F](h + v + \varepsilon_{PF}),$ $dH/dt = D_H(H_R - H) + \alpha C_{HP}HP - C_{HF}HF + \sigma_H(dW_H/dt),$ $dP/dt = r_P I_P \gamma(L_0, P)P - mP - C_{PH}HP + \sigma_P(dW_P/dt)$	qE (harvest rate, control parameter), A (adult largemouth bass biomass), F (planktivore biomass), J (juvenile largemouth bass biomass), H (zooplankton biomass), $D_F = .1$ (diffusion parameter for planktivores), F_R (refuge reservoir of planktivore biomass), $C_{FA} = .3$ (consumption coefficient of planktivores by adult piscivores), $\sigma_F = \sigma_P = .1$ (standard deviation of stochastic processes, same units as F , H , and P , respectively), $\alpha = .3$ (conversion of consumed phytoplankton phosphorus to zooplankton phosphorus), $C_{JA} = .001$ (consumption coefficient of juvenile piscivores by adult piscivores), $C_{JP} = .5$ (consumption coefficient of juvenile piscivores by planktivores), $v = 1$ (vulnerability parameter for juvenile piscivores), $D_H = .5$ (zooplankton diffusion parameter), $h = 8$ (refuging parameter for juvenile piscivores), $C_{PH} = .25$ (consumption rate of phytoplankton by zooplankton), $L = .6$ (phosphorus load), $\gamma(L_0, P)$ (light function based on surface irradiance $L_0 = 300 \mu\text{E m}^{-2} \text{s}^{-1}$ and phytoplankton biomass), $C_{HP} = .1$ (consumption rate of zooplankton by planktivores), P (phytoplankton biomass), $r_P = 3$ (phytoplankton growth parameter per unit phosphorus load), $m = .1$ (mortality rate of phytoplankton), $H_r = 100$ (density that plankton refuge supports)

Note: The first model is a Ricker population dynamics model (period-doubling bifurcation) of *E. coli* growth. The second model describes midge-algae-detritus dynamics in Lake Myvatn, Iceland (Neimark-Sacker bifurcation). The third model is a logistic population dynamics model (transcritical bifurcation) for *Daphnia magna*. The fourth model describes temperate-lake food web dynamics when predation pressure from apex predators is altered (fold bifurcation).

toplankton biomass. The planktivore biomass time series is used in this analysis of conditional heteroscedasticity. The herbivore biomass time series and phytoplankton biomass time series are considered in further analysis described below.

Test for Conditional Heteroscedasticity

We tested for conditional heteroscedasticity in the model time series with a simple and widely used Lagrange multiplier test described by Engle (1982; see also Engle et al. 1985). The testing procedure is as follows: (1) fit a lag-1 autoregressive model by using ordinary least squares regression, (2) square the residuals obtained from step 1, (3) lag the squared residuals from step 2 by one time step, (4) regress the squared residuals from step 2 by the lagged squared residuals from step 3, (5) calculate the Lagrange multiplier test statistic as the product of the r^2 value from the auxiliary regression in step 4 and sample size from the auxiliary regression in step 4, and (6) calculate the probability value for the Lagrange multiplier by comparing the Lagrange multiplier test statistic to a χ^2 distribution with 1 df.

Worked examples of the test calculations with and without conditional heteroscedasticity are provided in the appendix, available as a zip file in the online edition of the *American Naturalist*. Generally, leading indicators are applied using moving-window analysis (e.g., Scheffer et al. 2009). Here we apply the Lagrange multiplier test for conditional heteroscedasticity to 200 time step windows. At time t , the value for t and the 199 previous time steps are included in the window. We move the window forward 50 time steps in between each test. In our model analyses, the time series have 2,000 observations so that 37 tests are applied with each test, consisting of 200 observations. We applied these tests in Minitab 15 (<http://www.minitab.com>).

A likely outcome is recording some significant tests even if there is no conditional heteroscedasticity and no impending regime shift. If the critical level of significance for conditional heteroscedasticity tests is 0.05, five significant tests are expected per 100 tests conducted when there is no conditional heteroscedasticity. A Bernoulli expansion may be used in conjunction with the moving-window test results in order to find the probability of returning a given number of significant tests in the total number of tests (Wilkinson 1951; Moran 2003). For example, if there is one significant test in 10 tries, we might not, without other evidence, conclude that there is an impending regime shift because the probability of finding one significant test in 10 is high ($P = .315$). The probability by Bernoulli expansion is calculated as

$$p = \left[\frac{N!}{(N-K)!K!} \right] \times a^K(1-a)^{N-K},$$

where N is the number of tests conducted, K is the number of significant tests, and a is the level of significance (e.g., $a = 0.05$) for the individual conditional heteroscedasticity tests (Moran 2003). Lookup tables for probability values from this equation are available in Wilkinson (1951).

Variable Selection

Leading indicators of regime shifts might be effectively resolved in time series data collected by standardized environmental monitoring programs (Brock and Carpenter 2006). However, environmental monitoring programs cannot record all variables of interest, and it may be difficult to choose variables that may be important for warning of a future regime shift (Lovett et al. 2007). We applied the moving-window Lagrange multiplier test for conditional heteroscedasticity (window width, 200) to the simulated phytoplankton and zooplankton biomass time series from the temperate-lake food web model to evaluate how variable selection from environmental monitoring may affect conditional heteroscedasticity as a leading indicator.

Results

Conditional Heteroscedasticity as a Leading Indicator of Regime Shifts

The discrete-time *Escherichia coli* dynamics model shifts toward chaotic behavior as the growth rate increases past the critical transition point and the data pitchfork, a pattern characteristic of the period-doubling bifurcation (fig. 2A, black dots). The reference series was variable around a stable point and had no long-run change in *E. coli* abundance (fig. 2A, red line). There was significant conditional heteroscedasticity prior to the critical transition in the time series with a regime shift, and significant tests appeared consistently before the transition point (fig. 2B, black line). The cumulative number of significant tests was significant, as judged by Bernoulli expansion ($P < .05$) at time step 450. In the reference time series, there was one significant conditional heteroscedasticity test in 37 applications (fig. 2B, red line). This frequency of occurrence is not significant as judged by Bernoulli expansion.

The midge biomass dynamics from the discrete-time food web model for Lake Myvatn transition from a stable point to oscillating behavior as algal growth rate is slowly increased (fig. 2C, black line). Midge biomass began oscillating prior to algal growth rate being pushed across the critical transition point, indicating that environmental stochasticity plays an important role in determining the state

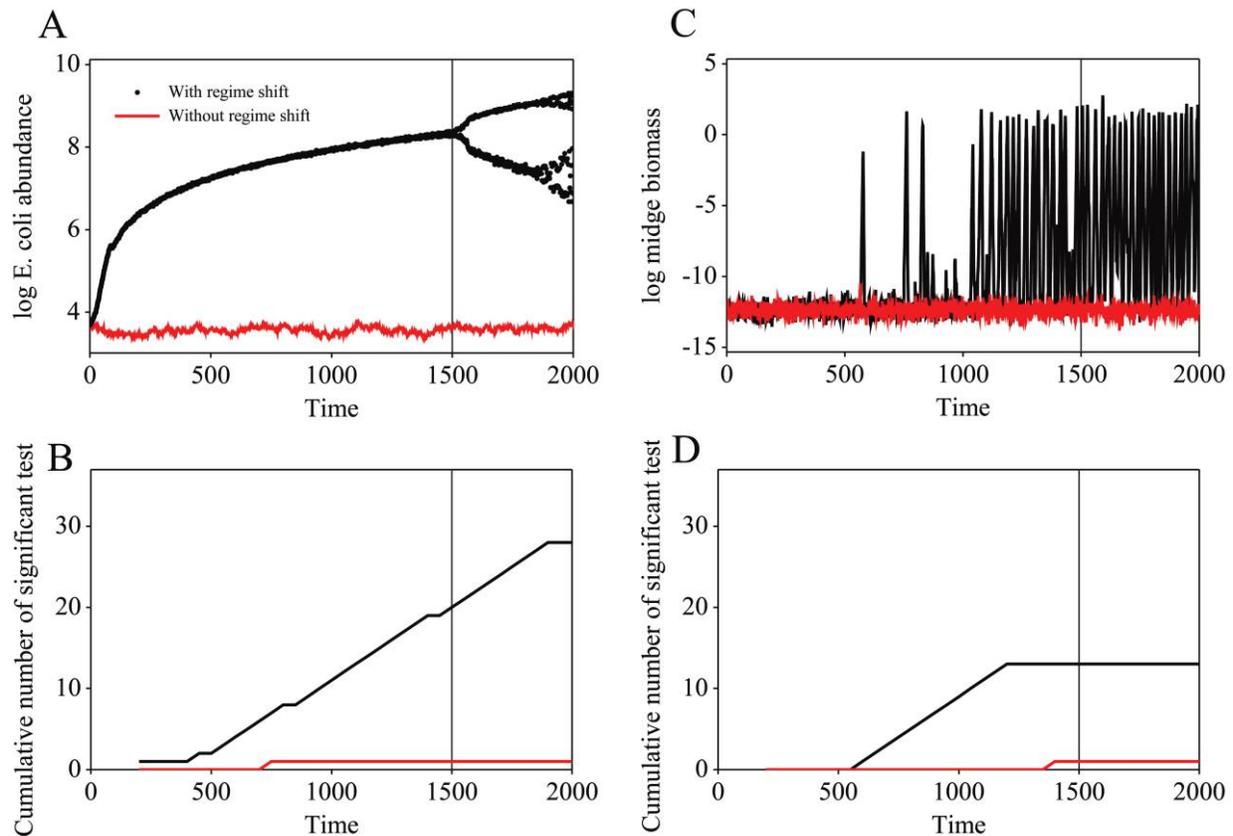


Figure 2: A, Time series from the discrete *Escherichia coli* dynamics model with (black line) and without (red line) a regime shift. B, Cumulative number of significant moving-window Lagrange multiplier tests for conditional heteroscedasticity applied to the discrete *E. coli* dynamics model time series with (black line) and without (red line) regime shift. There are 37 total tests applied to the time series. C, Midge biomass time series from the discrete lake food web model with (black line) and without (red line) a regime shift. D, Cumulative number of significant moving-window Lagrange multiplier tests for conditional heteroscedasticity applied to midge biomass time series from the discrete lake food web dynamics model time series with (black line) and without (red line) regime shift. There are 37 total tests applied to the time series. The vertical gray line at step 1,500 denotes the critical transition point for the control parameter in both models with regime shift.

of the system. Flickering between the stable point and oscillating regimes appears to occur between time steps 500 and 1,000. The reference system had considerable variability but remained about the stable point throughout the time series (fig. 2C, red line). Significant tests accumulated for the transition case, and the frequency of significant tests was significant by time step 700 (fig. 2D, black line). The significant tests occurred mainly while the system was flickering, and there were few or no significant conditional heteroscedasticity tests when the time series was at the stable or oscillating regime. This result underscores the potential importance of flickering in facilitating detection of early warnings of impending regime shifts. There was one significant test in 37 applications to the reference time series (fig. 2D, red line). This frequency of

occurrence is not significant as judged by Bernoulli expansion.

The time series from the continuous *Daphnia* dynamics model with critical transition (fig. 3A, black line) had steady population decline, while the *Daphnia* dynamics time series without critical transition varied around a stable point (fig. 3A, red line). There was a steady increase in cumulative number of significant conditional heteroscedasticity prior to the transition in the series with regime shift. The cumulative number of significant tests was significant, as judged by Bernoulli expansion, by time step 450 (fig. 3B, black line). In the reference time series, there were two significant tests in 37 applications (fig. 3C). This number of significant tests is not significant as judged by Bernoulli expansion.

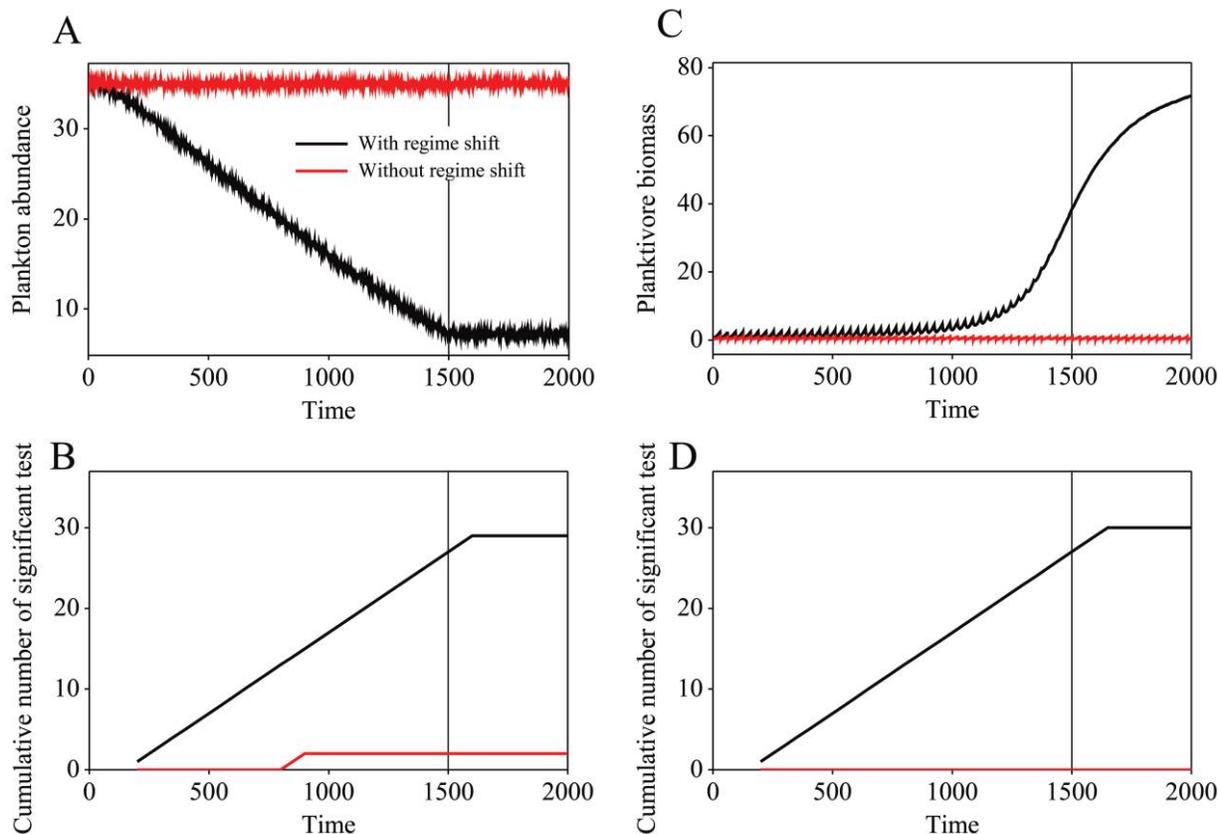


Figure 3: *A*, Time series from the continuous *Daphnia* dynamics model with (black line) and without (red line) a regime shift. *B*, Cumulative number of significant moving-window Lagrange multiplier tests for conditional heteroscedasticity applied to the continuous *Daphnia* dynamics model time series with (black line) and without (red line) regime shift. There are 37 total tests. *C*, Planktivore biomass time series from the continuous lake food web model with (black line) and without (red line) a regime shift. *D*, Cumulative number of significant moving-window Lagrange multiplier tests for conditional heteroscedasticity applied to the continuous lake food web dynamics model time series with (black line) and without (red line) regime shift. There are 37 total tests. The vertical gray line at step 1,500 denotes the critical transition point.

The planktivore biomass time series with critical transition from the continuous lake food web model demonstrated logistic growth and had significant conditional heteroscedasticity throughout the period approaching the regime shift, and the impending regime shift was identified by time step 450 (fig. 3C, 3D, black lines). The reference series varied steadily near an equilibrium value in the reference time series (fig. 3C, red line). There were no significant conditional heteroscedasticity tests in the 37 tests applied to the reference time series (fig. 3D, red line).

Variable Selection

Variable selection for detecting the regime shift was important in the continuous temperate-lake food web model. While there is clear early warning in the planktivore biomass series (fig. 3C), there is no clear early warning in the

zooplankton biomass time series (fig. 4A). Herbivore biomass decreased as planktivore biomass increased (fig. 4A, black line), but there was no consistent significant conditional heteroscedasticity (fig. 4A, red line). Phytoplankton biomass increased as zooplankton biomass decreased (fig. 4B, black line). There was significant conditional heteroscedasticity prior to the critical transition point (in the planktivore time series), but this was not consistent through the time series (fig. 4B, red line). The phytoplankton time series provides early warning as quickly as the planktivore biomass series as judged by Bernoulli expansion; however, the number of significant tests is less compelling than the planktivore series when plotted (fig. 4B). The discrepancy in consistency in returning significant conditional heteroscedasticity tests demonstrates the importance of selecting relevant environmental parameters for long-term monitoring and application of conditional

heteroscedasticity as a leading indicator of regime shifts. Finding appropriate parameters to measure for real systems will be a subjective task based on modeling studies and researchers' expert knowledge of the systems they are studying (e.g., Carpenter et al. 2011).

Discussion

Conditional heteroscedasticity is a powerful leading indicator of impending regime shifts. Cumulative tests for conditional heteroscedasticity warn of regime shifts hundreds of time steps ahead of critical transition points. Conditional heteroscedasticity is robust and is effective for forecasting a variety of forms of regime shift. This is because both increasing and decreasing variance prior to a shift appear as clustered volatility prior to the shift.

Some indicators are ambiguous when the underlying dynamics of the system are unknown (Brock and Carpenter 2006). For instance, variance in water column phosphorus increases prior to the critical transition from an oligotrophic state to a eutrophic state in lake ecosystem models (Carpenter and Brock 2006). However, variance in algal biomass declines in models describing the transition of phytoplankton communities to dominance by toxic cyanobacteria during eutrophication (Carpenter et al. 2009). Hence some understanding of the potential regime shift is necessary to judge the practical importance of increases and decreases in variance. Here, we have shown that a test for conditional heteroscedasticity is effective for warning of a variety of critical transitions and could be applied to systems with increasing or decreasing variance prior to a regime shift. Association with probability values eases interpretation of test results.

Tests for conditional heteroscedasticity require much larger samples than descriptive statistics such as variance and autocorrelation (see Engle et al. 1985). This is unlikely to be problematic for parameters that are easily measured in situ at high frequency, such as chlorophyll-*a* in lakes (Carpenter et al. 2009). However, this sample size requirement could be problematic for properties that cannot be sampled at high resolution, such as fish biomass and many other ecological variables. Hence, conditional heteroscedasticity tests will be practical for application only to some variables and studies with high numbers of observations.

Increased attention will be needed to minimize false positives as the effectiveness of leading indicators is tested in theory and in field applications. False positives are cases where statistics falsely indicate an impending regime shift. False positives could lead to expensive, inconvenient, and unnecessary changes in population or ecosystem management. It is difficult to demonstrate the successfulness of avoiding regime shifts because success is essentially equivalent to no state change (Scheffer 2009). If this difficulty

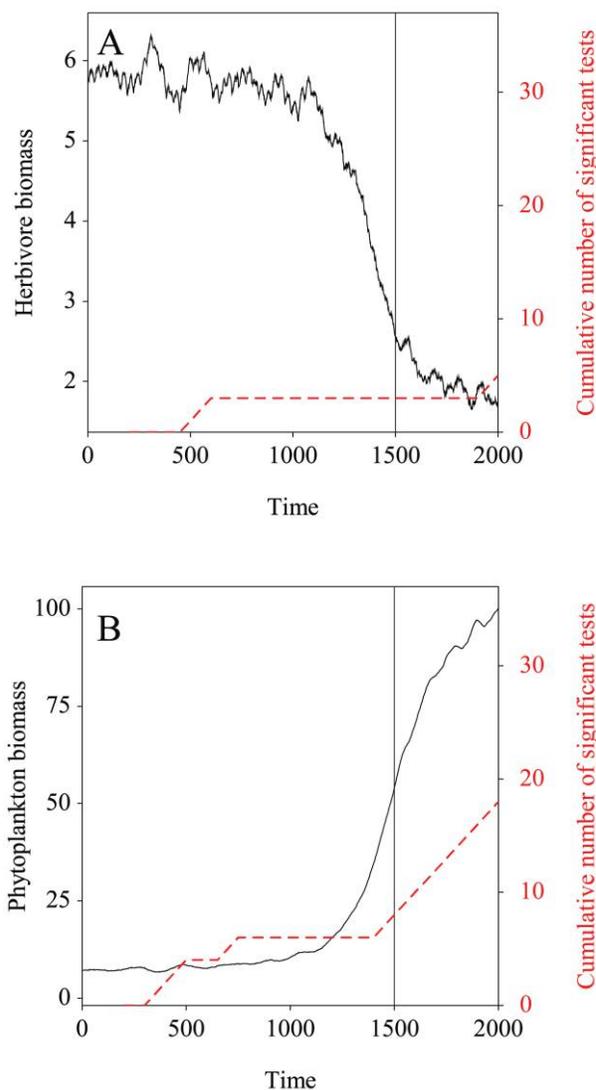


Figure 4: A, Zooplankton (herbivore) biomass from the continuous lake food web dynamics model with regime shift (black line). B, Phytoplankton biomass from the continuous lake food web dynamics model with regime shift (black line). The cumulative numbers of significant moving-window conditional heteroscedasticity tests are the red dashed lines. The vertical gray lines denote the location of the critical transition in the planktivore dynamics. A total of 37 tests were applied to each time series.

is combined with an abundance of false positives, policy makers and public confidence in the usefulness of programs designed to inhibit regime shifts could erode. Thus, while these indicators should be pursued, future evaluations of regime shift indicators should include time series without regime shifts to evaluate the potential susceptibility of indicators to returning false positives. In this study, by associating probability values with the condi-

tional heteroscedasticity indicator, we were able to minimize false positives due to chance. However, false positives may also be triggered by confounding trends in external perturbations (Scheffer 2009). Thus, field studies are necessary to more adequately evaluate leading indicators.

In simulation, leading indicators should be evaluated against models with empirically measured process error to better mirror real-world perturbations. Such models may have interesting and unexpected dynamics. For instance, the midge biomass time series we used contains flickering and an unexpected early transition to the oscillating state due to environmental stochasticity. Such complex dynamics, not seen in the other models in this analysis, may be more adequately captured in models with more realistic large noises. Further, the response of some indicators may vary considerably, depending on the magnitude of noise in the system (Berglund and Gentz 2002). Thus, indicators should also be evaluated against models with a variety of magnitudes of noise.

Observation errors and biases may also be added to simulated data to more adequately mimic field data (Carpenter 2003). Parameters are associated with unique levels of observational error, and this may reduce the power of some indicators to identify impending regime shifts (Carpenter 2003). Magnitude of observation error may be dependent on sampling frequency, and high-frequency measurements (e.g., every 5 min) may be superior for practical application because they may record at a more ecologically relevant timescale than low-frequency measurements (e.g., weekly). Improved statistical power due to increased sampling size with high-frequency data will likely offset any decreased power to identify impending regime shifts due to observation error. In an experimentally induced ecosystem regime shift, Carpenter et al. (2011) found strong early warning signals in high-frequency data, and large data sets may be needed to uncover nonlinear dynamics in all complex systems.

Leading indicators such as conditional heteroscedasticity may fail to provide early warning of regime shifts (false negative) if the system is driven rapidly across the critical transition point or if an unlikely and large shock pushes the system from one stable equilibrium to another (Scheffer et al. 2009). The mechanics of the system may also cause leading indicators to fail, and it may be impossible in practice to know whether this is the case prior to a regime shift occurring. However, models thought to adequately represent nonlinear ecosystem dynamics are characterized by leading indicators prior to a regime shift (e.g., van Nes and Scheffer 2007; Carpenter et al. 2008; Scheffer et al. 2009). Laboratory (Drake and Griffen 2010) and whole-ecosystem (Carpenter et al. 2011) experimental regime shifts, as well as paleoclimate records (Dakos et al. 2008), are characterized by dynamics with early warnings

prior to a regime shift. Given that conditional heteroscedasticity is expected prior to shifts, the probability of false negatives will be determined largely by the sample size that each test is applied to (Engle et al. 1985).

Leading indicators of regime shift have been successfully applied to reconstructed time series of climate transitions in the ancient past (Dakos et al. 2008). However, the true utility of regime shift indicators will not be established until they are adequately evaluated on transitions that occur at temporal and spatial scales that are relevant to policy makers and the public (e.g., Carpenter et al. 2011). Field studies that experimentally induce regime shifts are necessary to examine the advantages and limitations of different indicators and to resolve potential discrepancies in their practical interpretations.

Acknowledgments

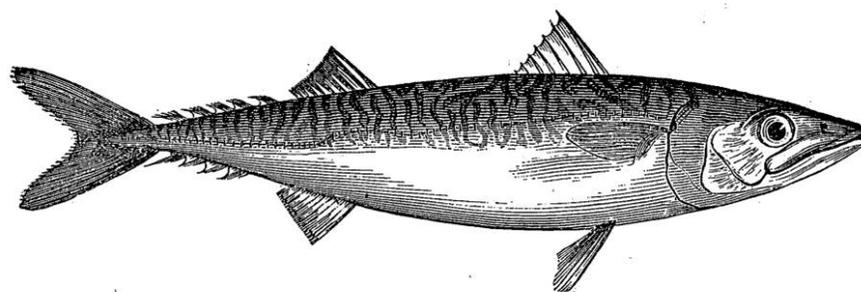
This work was supported by the National Science Foundation (grants DEB-0716869 and DEB-0917696) and the Department of Environmental Sciences, University of Virginia. W. Brock, A. Ellison, K. Hondula, and an anonymous reviewer provided helpful comments that improved this manuscript.

Literature Cited

- Andersen, T., J. Carstensen, E. Hernández-García, and C. M. Duarte. 2009. Ecological thresholds and regime shifts: approaches to identification. *Trends in Ecology & Evolution* 24:49–57.
- Beard, T. D., M. J. Hansen, and S. R. Carpenter. 2003. Development of a regional stock-recruitment model for understanding factors affecting walleye recruitment in northern Wisconsin lakes. *Transactions of the American Fisheries Society* 132:382–391.
- Berglund, N., and B. Gentz. 2002. Beyond the Fokker-Planck equation: pathwise control of noisy bistable systems. *Journal of Physics A* 35:2057–2091.
- Biggs, R., S. R. Carpenter, and W. A. Brock. 2009. Turning back from the brink: detecting an impending regime shift in time to avert it. *Proceedings of the National Academy of Sciences of the USA* 106:826–831.
- Box, G. E. P., and D. R. Cox. 1964. An analysis of transformations. *Journal of the Royal Statistical Society B* 26:211–252.
- Brock, W. A., and S. R. Carpenter. 2006. Variance as a leading indicator of regime shift in ecosystem services. *Ecology and Society* 11(2):9.
- . 2010. Interacting regime shifts in ecosystems: implication for early warnings. *Ecological Monographs* 80:353–367.
- Carpenter, S. R. 2003. Regime shifts in lake ecosystems: patterns and variation. International Ecology Institute, Oldendorf.
- Carpenter, S. R., and W. A. Brock. 2006. Rising variance: a leading indicator of ecological transition. *Ecology Letters* 9:311–318.
- Carpenter, S. R., W. A. Brock, J. J. Cole, J. F. Kitchell, and M. L. Pace. 2008. Leading indicators of trophic cascades. *Ecology Letters* 11:128–138.
- Carpenter, S. R., W. A. Brock, J. J. Cole, and M. L. Pace. 2009. Leading

- indicators of phytoplankton transitions caused by resource competition. *Theoretical Ecology* 2:139–148.
- Carpenter, S. R., J. J. Cole, M. L. Pace, R. Batt, W. A. Brock, T. Cline, J. Coloso, et al. 2011. Early warnings of regime shifts: a whole-ecosystem experiment. *Science* 332:1079–1082.
- Contamin, R., and A. M. Ellison. 2009. Indicators of regime shifts in ecological systems: what do we need to know and when do we need to know it? *Ecological Applications* 19:799–816.
- Dakos, V., M. Scheffer, E. H. van Nes, V. Brovkin, V. Petoukhov, and H. Held. 2008. Slowing down as an early warning signal for abrupt climate change. *Proceedings of the National Academy of Sciences of the USA* 105:14308–14312.
- Drake, J. M., and B. D. Griffen. 2010. Early warning signals of extinction in deteriorating environments. *Nature* 467:456–459.
- Engle, R. F. 1982. Autoregressive conditional heteroskedasticity with estimates of the variance of United Kingdom inflation. *Econometrica* 50:987–1008.
- . 2001. GARCH 101: the use of ARCH/GARCH models in applied econometrics. *Journal of Economic Perspectives* 15:157–168.
- Engle, R. F., D. F. Hendry, and D. Trumble. 1985. Small-sample properties of ARCH estimators and tests. *Canadian Journal of Economics* 18:66–93.
- Griffen, B. D., and J. M. Drake. 2008. Effects of habitat quality and size on extinction in experimental populations. *Proceedings of the Royal Society B: Biological Sciences* 275:2251–2256.
- Guttal, V., and C. Jayaprakash. 2008. Changing skewness: an early warning signal of regime shifts in ecosystems. *Ecology Letters* 11: 450–460.
- Ives, A. R., A. Einarsson, V. A. A. Jansen, and A. Gardarsson. 2008. High-amplitude fluctuations and alternative dynamical states of midges in Lake Myvatn. *Nature* 452:84–87.
- 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.
- Lamoureux, C. G., and W. D. Lastrapes. 1990. Heteroskedasticity in stock return data: volume versus GARCH effects. *Journal of Finance* 45:221–229.
- Lovett, G. M., D. A. Burns, C. T. Driscoll, J. C. Jenkins, M. J. Mitchell, L. Rustad, J. B. Shanley, G. E. Likens, and R. Haeuber. 2007. Who needs environmental monitoring? *Frontiers in Ecology and the Environment* 5:253–260.
- May, R. M. 1976. Simple mathematical models with very complicated dynamics. *Nature* 261:459–467.
- Moran, M. D. 2003. Arguments for rejecting the sequential Bonferroni in ecological studies. *Oikos* 100:403–405.
- Ponciano, A. M., F. P. J. Vandecasteele, T. F. Hess, L. J. Forney, R. L. Crawford, and P. Joyce. 2005. Use of stochastic models to assess the effect of environmental factor on microbial growth. *Applied and Environmental Microbiology* 71:2355–2364.
- Scheffer, M. 2009. *Critical transitions in nature and society*. Princeton University Press, Princeton, NJ.
- Scheffer, M., J. Bascompte, W. A. Brock, V. Brovkin, S. R. Carpenter, V. Dakos, H. Held, E. H. van Nes, M. Rietkerk, and G. Sugihara. 2009. Early-warning signals for critical transitions. *Nature* 461:53–59.
- Taylor, K. C., G. W. Lamorey, G. A. Doyle, R. B. Alley, P. M. Grootes, P. A. Mayewski, J. W. C. White, and L. K. Barlow. 1993. The “flickering switch” of late Pleistocene climate change. *Nature* 361: 432–436.
- van Nes, E. H., and M. Scheffer. 2007. Slow recovery from perturbations as a generic indicator of a nearby catastrophic shift. *American Naturalist* 169:738–747.
- White, H. 1980. A heteroskedasticity-consistent covariance matrix estimator and a direct test for heteroskedasticity. *Econometrica* 48: 817–838.
- Wilkinson, B. 1951. A statistical consideration in psychological research. *Psychological Bulletin* 48:156–158.

Associate Editor: Daniel I. Bolnick
 Editor: Mark A. McPeck



The Mackerel, *Scomber vernalis*.

Mackerel *Scomber vernalis*. “Some seasons they will be very plentiful, and schools of them may be seen near the surface of the water one or two miles in extent. When seen thus maneuvering in such great abundance they will not allow themselves to be taken with the hook very extensively.” From “The Habits and Migrations of Some of the Marine Fishes of Massachusetts” by James H. Blake (*American Naturalist*, 1870, 4:513–521).