ESSAY

ECOLOGY AND ENVIRONMENT

Passing the point of no return

Early warning signals indicate impending ecosystem regime changes

By **David Seekell**

In the field of ecology, regime shifts are massive changes in function and character that occur when an ecosystem passes a tipping point. Regime shifts sometimes have severe consequences for human well-being through losses of ecosystem services, including desertification in arid regions and marine fisheries collapses (*1*, *2*). These changes are difficult to predict and sometimes impossible to reverse (*2*). For these reasons, understanding how to anticipate and prevent regime shifts is one of the most important challenges faced by environmental scientists (*1*–*3*).

Theoretical analyses have identified statistical anomalies, such as increased autocorrelation and variance in time series before regime shifts (*1*, *2*). These patterns are a manifestation of "critical slowing down"—when return rate from perturbation to equilibrium progressively declines before a tipping point (*1*). My dissertation research evaluated these anomalies as potential early warning indicators for ecosystem regime shifts.

This research was centered around a whole-lake experiment conducted with collaborators on two small lakes in the Upper Peninsula of Michigan. We manipulated the fish community of one lake to cause a trophic cascade—a type of regime shift—and made measurements throughout the food web to determine whether early warning indicators were detectable before the tipping point (*2*, *4*–*6*). An adjacent reference lake was monitored for comparison.

The experimental lake and reference lake had similar fish communities, with piscivorous largemouth bass (*Micropterus*

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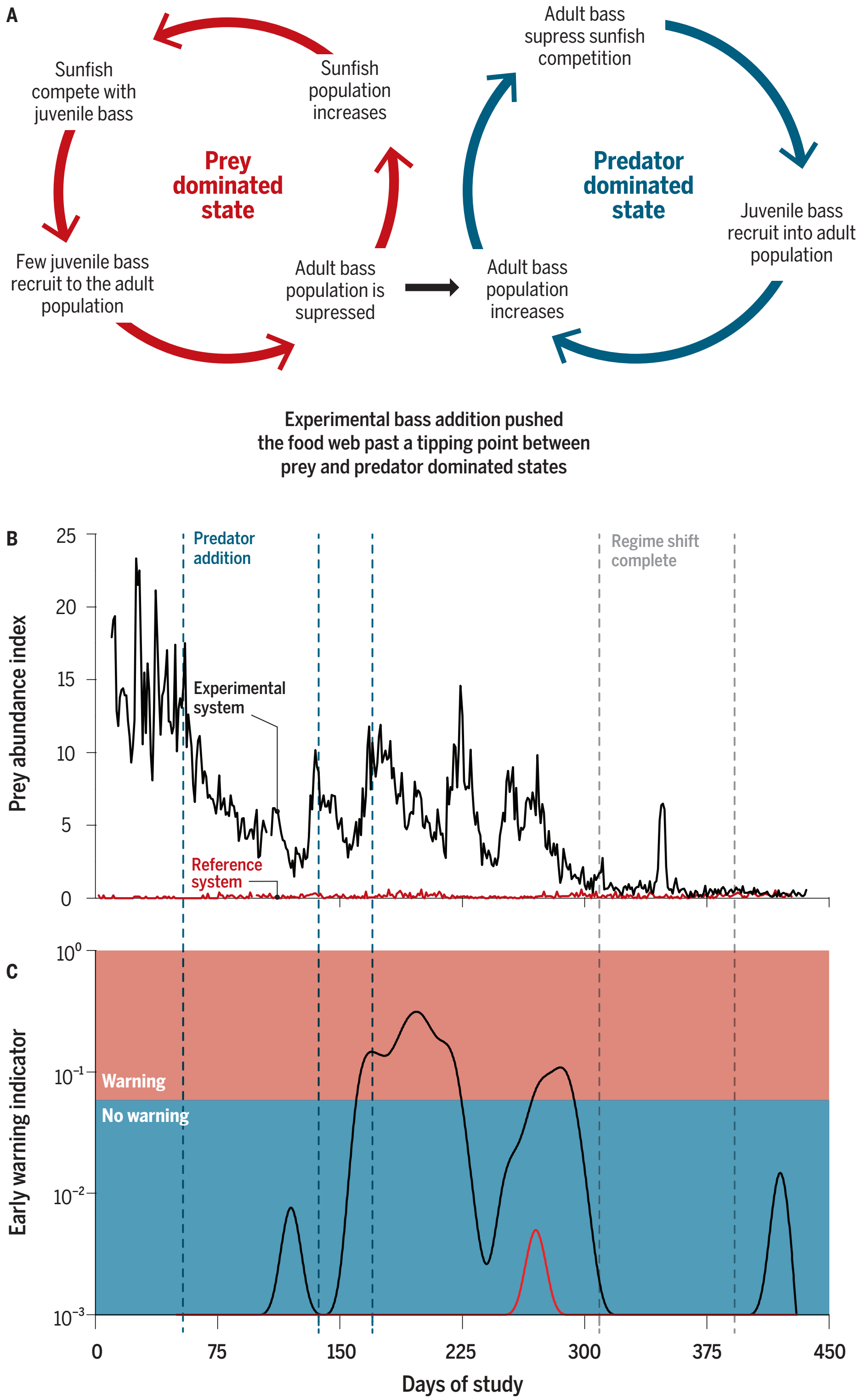

Lake fish regime shift. (**A**) Positive feedbacks can push either predators (largemouth bass) or prey (pumpkinseed sunfish) to dominance in the study lakes. (**B**) Average number of fish caught in minnow traps distributed around the edge of the experimental (black line) and reference (red line) lakes. This is an index of prey abundance. The study occurred during four consecutive summers, but here the data are concatenated into a continuous time series for aesthetic reasons. (**C**) Early warning of the regime shift based on moving-window conditional heteroskedasticity tests applied to chlorophyll-a concentrations from four summers concatenated into a single time series (*5*, *8*, *9*). Chlorophyll-a concentration is an index of phytoplankton biomass that strongly reflects the variability generated by the regime shift in the fish community (*2*, *5*). There was early warning for the entire summer the year before the regime shift and until the tipping point was passed during the year of the regime shift.

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CATEGORY WINNER: ECOLOGY AND ENVIRONMENT

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David Seekell is an environmental scientist based in Sweden. He holds a Bachelor of Science in Natural Resources from the University of Vermont, and a Ph.D. in Environmental Sciences from the University of Virginia. In his Ph.D. research, Seekell developed statistics to provide early warning that an ecosystem is passing a tipping point and is about to undergo a regime change. He is currently an assistant professor of Ecology in the Department of Ecology and Environmental Science at Umeå University. In 2015, he became a Wallenberg Academy Fellow, and in 2016, he received a Science for Solutions Award from the American Geophysical Union.

salmoides) and planktivorous pumpkinseed sunfish (*Lepomis gibbosus*) being most abundant. The competitive interactions between these species form a trophic triangle—a food web configuration where positive feedback can push either the predator (largemouth bass) or the prey (pumpkinseed sunfish) species to dominance (*4*).

Before the experiment, pumpkinseed sunfish dominated the fish community in the experimental lake, and largemouth bass dominated the fish community in the reference lake. We slowly added largemouth bass to the experimental lake over the course of 4 years in an attempt to push the food web past a tipping point where positive feedback would move the system from a sunfish-dominated regime to a bass-dominated regime [see the figure (A)].

The experimental lake passed a tipping point during the third year of the study [see the figure (B)]. Pumpkinseed sunfish competed with juvenile bass, and the tipping point occurred when the adult bass population became sufficiently large that it could suppress the sunfish, and juvenile bass could reach maturity and increase the size of the adult population (see the figure, A). This created feedback that promoted bass dominance (*2*, *4*–*6*). Variability from this shift propagated throughout the lake, and early warning indicators based on autocorrelation and variance responded strongly. Early warning signals were recorded up to a year and a half before the tipping point and were present throughout the food web including in time series of prey fish abundance, zooplankton biomass, and phytoplankton biomass (*2*, *4*–*7*). There were no early warning signals in the reference system.

This was the first ecosystem-scale proof-of-concept that early warning indicators can be detected before tipping points. These results suggest that ecosystem managers may one day be able to use adaptive management to avert unwanted regime shifts.

A specific contribution of my dissertation was to evaluate the efficacy of tests for conditional heteroskedasticity (clustered variability in time series) as early warning indicators. Conditional heteroskedasticity is widely studied by economists but almost never examined by ecologists. A key observation in my dissertation was the presence of conditional heteroskedasticity in time series from ecosystems approaching tipping points but not from stable ecosystems (*8*, *9*).

This observation has great practical importance. Most early warning indicators are interpreted by comparison with indicators from a pristine reference system. Such pristine systems are in short supply given the global nature of many environmental changes, such as climate warming. Conditional heteroskedasticity tests have thresholds that make clear distinctions between "warning" and "no warning" conditions, reducing the need for pristine reference systems (*5*, *8*) (see the figure, C). In the whole-lake experiment, conditional heteroskedasticity was the most powerful early warning indicator we tested but also the best at minimizing false-positive warnings due to the inclusion of thresholds (*5*).

Critical slowing down is a generic phenomenon that is not restricted to ecosystems. After our experiment, other research groups identified early warning indicators before regime shifts in a variety of complex systems, including in economic records before the subprime housing loan crisis (*10*), before the self-termination of epileptic seizures (*11*), and before shifts in social networking activity on Twitter (*12*). Hence, although my dissertation focused on lake ecology, the project is exemplary of how fundamental ecological research can generate tools and concepts that provide diverse benefits to society. ■

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