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Early Warnings of Regime Shifts: A Whole-Ecosystem Experiment

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Catastrophic ecological regime shifts may be announced in advance by statistical early warning signals such as slowing return rates from perturbation and rising variance. The theoretical background for these indicators is rich, but real-world tests are rare, especially for whole ecosystems. We tested the hypothesis that these statistics would be early warning signals for an experimentally induced regime shift in an aquatic food web. We gradually added top predators to a lake over 3 years to destabilize its food web. An adjacent lake was monitored simultaneously as a reference ecosystem. Warning signals of a regime shift were evident in the manipulated lake during reorganization of the food web more than a year before the food web transition was complete, corroborating theory for leading indicators of ecological regime shifts.

Massive ecosystem changes affect water supplies, fisheries, productivity of rangelands and forests, and other ecosystem services (*1*, *2*). Nonlinear regime shifts often come as surprises. However, recent research has revealed statistical signals that precede some nonlinear transitions, such as rising autocorrelation, steep increases in variance, and extreme changes in skewness and shift in variance spectra toward low frequencies (*3–7*). If the transition is approached slowly and the right variables are sampled frequently, warnings may be evident well before the regime shift is complete. Empirical evidence for early warnings of environmental regime shifts comes from a time series of major changes in paleoclimate (*8*), spatial pattern of dryland vegetation during desertification (*9*), variability of exploited fisheries (*10*, *11*), and laboratory studies (*12*). Here, we present a test of early warning indicators from a large-scale multiyear field experiment using a manipulated and a reference ecosystem.

Gradual addition or removal of top predators destabilizes food webs, and extreme manipulations of predators cause trophic cascades, a type of regime shift that alters food web structure and ecosystem processes such as primary production, ecosystem respiration, and nutrient cycling (*13*, *14*).

Predator-driven transitions in lakes involve nonlinear dynamics of fish, zooplankton, and phytoplankton populations (*15*). Over 3 years, we gradually added a top predator, largemouth bass (*Micropterus salmoides*), to a lake dominated by planktivorous fishes to destabilize the food web and induce a trophic cascade leading to dominance of the food web by piscivores (*16*). A nearby lake, dominated by adult largemouth bass, was not manipulated and served as a reference ecosystem. The reference ecosystem allows us to evaluate the possibility that responses were caused by external drivers rather than the manipulation (*15*). Planktivorous fishes, zooplankton, and phytoplankton were monitored daily in both lakes for 3 years of summer stratification (2008 to 2010) (*16*).

Predicted responses of the food web follow from previous experiments in these lakes (*15*) and an ecosystem model calibrated for the manipulated lake (*17*). Before manipulation, the manipulated ecosystem was dominated by a variety of small fishes [hereafter planktivores (*16*)], and largemouth bass were few. We expected that the addition of largemouth bass would trigger recruitment of juvenile bass that were planktivorous initially but became omnivorous, adding benthos and fish to their diets, as they grew. Piscivory by largemouth bass would cause planktivorous fishes to seek refuge from predation by occupying littoral refugia and shoaling (aggregating). Eventually piscivory would drive planktivorous fishes to low densities. As planktivory declined in the open water, larger-bodied zooplankton (including migratory *Daphnia pulex*) would increase in relative abundance. Increased grazing would lead to cyclic oscillations of zooplankton and phytoplankton biomass. Thus, the food web transition would exhibit a sequence of nonlinear changes resulting from shoaling and diel movements of consumers, species replacement, and predator-prey cycles as the manipulated ecosystem became more similar to the reference ecosystem. We hypothesized that dynamics during this transitional period would generate early warning signals of a regime shift toward a piscivore-dominated food web.

Transitional dynamics of the food web were consistent with our expectations (Fig. 1). In the manipulated lake, 39 adult largemouth bass were present at the beginning of the experiment. We added 12 largemouth bass on day 193 of 2008, and 15 largemouth bass on each of days 169 and 203 of 2009. Enhancement of adult largemouth bass triggered a recruitment event in 2009, leading to 1281 young-of-year largemouth bass (95% confidence interval of 1088 to 1560) by day 240 of 2009. Numbers of this cohort (1+ in Fig. 1C) declined through 2010, whereas surviving individuals grew in body mass and became piscivorous. Planktivore numbers in the manipulated lake declined through the study as piscivory increased and were similar to those of the reference lake by about day 230 of 2010 (Fig. 1F).

The spatial pattern of planktivores was occasionally patchy in 2008 and 2009, indicated by high values in the discrete Fourier transform (DFT) of spatial data (*16*, *18*) (Fig. 2). Patchy distributions were more frequent and of longer duration in 2010. Patchy distributions indicate shoaling behavior, a likely response to predation risk.

Zooplankton biomass of the manipulated lake declined during the summers of 2008 and 2009 and became strongly oscillatory in 2010 (Fig. 1). Through 2009 and 2010, dominance of the zooplankton shifted toward larger-bodied cladocerans, including *D. pulex*, in the manipulated lake (fig. S1), consistent with previous whole-lake experiments in which body size but not biomass of zooplankton responded to fish manipulations (*15*, *19*). Phytoplankton biomass as measured by chlorophyll a of the manipulated lake displayed strong oscillations in 2009 and the first half of 2010. By day 230 of 2010, manipulated and reference lakes were similar in planktivore numbers, zooplankton biomass, and chlorophyll.

Modeling predicts that early warning indicators would appear after the largemouth bass addition in 2008 and continue until stabilization of a new food web dominated by largemouth bass

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(17). It is not necessary to observe complete convergence of the food webs, because in order to be useful the early warnings must be seen before the food webs converge. Specifically, after 2008 we expected periods of increased variability, return rates near zero, lag-1 autocorrelations near one, skewness far from zero, and shifts in variance spectra toward low frequencies if the theory of early warning indicators was supported. We focused on chlorophyll, which responds strongly to food web fluctuations and can be measured at high frequency and precision (20, 21). Chlorophyll variability was somewhat lower in the manipulated lake than in the reference lake during the 3 years before manipulation (table S2).

High-frequency measurements of chlorophyll (every 5 min) had similar spectra in both lakes in 2008 (Fig. 3). In 2009 and 2010, however, spectral power shifted to low frequencies in the manipulated lake relative to the reference lake (yellow and tan colors in graphs for 2009 and 2010, Fig. 3). This shift toward lower-frequency variance is characteristic of regime shifts (3), including dynamics of chlorophyll in model simulations of trophic cascades in this manipulated lake (17). Early warning indicators calculated for daily chlorophyll concentrations were consistent with theoretical expectations (Fig. 4). In 2009 and 2010, there are times when the variance was much higher in the manipulated lake than in the reference lake, and the return time in the manipulated lake was close to zero. Variance was high in the manipulated lake for most of 2009 and early 2010. The coefficient of variation (standard deviation/mean) was also elevated in the manipulated lake through 2009 and early 2010 (fig. S2). The return rate was close to zero in 2009 (days 185 to 210) and 2010 (until day 206) (Fig. 4). Autocorrelations near one, which are also associated with near-zero return rates, occurred in the manipulated lake from about days 180 to 215 of 2009 and from about days 160 to 210 of 2010 (fig. S2). Skewness, an indicator of asymmetry associated with alternate states (6), reached high values in 2009 and cycled from low to high values in 2010 (Fig. 4). These changes in skewness are consistent with shifts between alternate states (6). The spectral ratio (16), a measure of the strength of the shift in variance from high to low frequencies (22), was elevated in the manipulated lake in late 2008, much of 2009, and the first half of 2010.

Regime shifts are characterized by nonlinear dynamics. A conservative test for nonlinearity [bootstrap Brock-Dechert-Scheinkman test on generalized autoregressive conditional heteroskedasticity residuals for daily chlorophyll data (16)] rejects the hypothesis of linearity for the manipulated lake and does not reject the hypothesis of linearity for the reference lake (23). This result is consistent with nonlinear dynamics because of a regime shift in the manipulated lake but not the reference lake. Diverse nonlinear models have been proposed for dynamics of plankton (24–28). The precise mechanism of the nonlinear transitions is not known for our experiment; it could be

one of the processes proposed in the literature or something else. These early warning signals are expected to occur for a wide class of nonlinear transitions (7). Even though the mechanism is not known, manipulation of an apex predator triggered a nonlinear food web transition that was signaled by early warning indicators more than a year before the food web transition was complete. Thus, the early warning indicators appear to be useful even in cases where the form of the potential regime shift is not known.

This experiment created ideal conditions for detection of early warning indicators under field conditions in a whole ecosystem. The regime shift was driven at a slow rate compared with the frequency of sampling and the response rate of the plankton. A reference system was used to assess the indicators in an unmanipulated system subject to the same weather and watershed in-

fluences. Both the manipulated and reference ecosystems were sampled at high frequency by using identical methods, leading to relatively large data sets for evaluation of the indicators. In other situations, it may be difficult to identify meaningful changes in the indicators. Modeling studies have pointed out a number of limitations of these early warning indicators (7, 18, 22, 29, 30). False early warnings can be generated by aggregation of linear processes or by exogenous shocks. Errors of this kind are not likely in our experiment because the regime shift was induced experimentally, multiple indicators are consistent in the manipulated lake, the reference lake shows no indications of exogenous shocks (e.g., regional weather events), and a conservative statistical test is consistent with nonlinear dynamics in the manipulated but not the reference lake. Early warnings, however, may fail in cases where
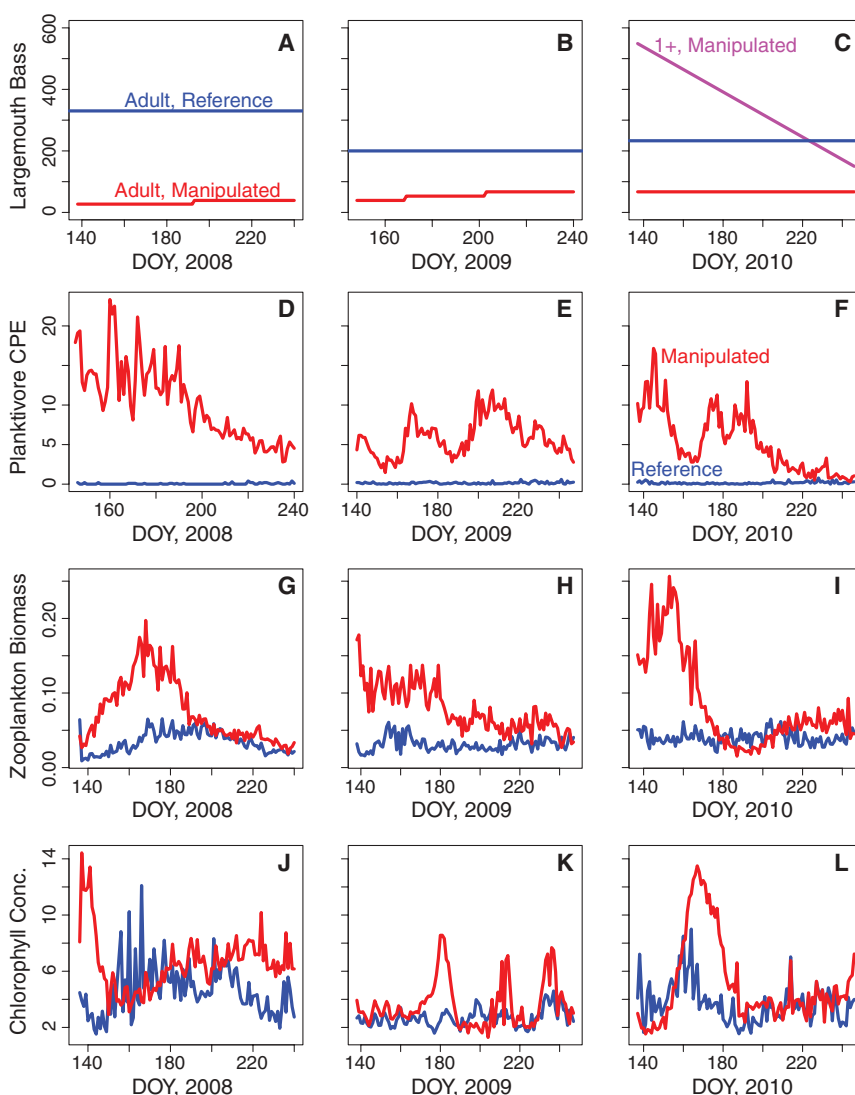

Fig. 1. Time series of the food webs in manipulated (red) and reference (blue) lakes in 2008 to 2010. DOY indicates day of the year. (**A** to **C**) Largemouth bass adult population in each lake. For the manipulated lake in 2010, numbers of year 1+ bass (recruited in 2009) are shown in magenta. (**D** to **F**) Planktivorous fish density (animals caught per trap per hour) estimated as catch per effort (CPE) in minnow traps deployed in the littoral zone. (**G** to **I**) Zooplankton biomass (g m^{-2}). (**J** to **L**) Chlorophyll concentration (mg m^{-3}) in the mixed layer.

the system is forced too fast across a critical threshold, where observation errors are large, or where signals are dampened by interactions among multiple nonlinear processes. Our experiment was designed to minimize these limitations and thereby maximize the possibility of detecting early warnings.

Theory indicates that early warning signals should be discernible before regime shifts in aquatic or terrestrial ecosystems as well as other

Fig. 2. DFT of the spatial sequence of minnow (planktivorous fish) trap catches around the perimeter of the manipulated lake on each day of sampling in 2008 (**A**), 2009 (**B**), and 2010 (**C**). Spatial frequency (per trap) is plotted versus day of the year, with DFT ordinate [a measure of variance (16)] shown by colors (see legend). High ordinates indicate clustering of planktivores at a particular spatial frequency (18). Spatial frequency is inversely related to spatial extent; for example, a frequency of 0.1 corresponds to 1 in 10 traps or a total of 3 traps in our array of 30 traps. In the reference lake, catch numbers were too small to estimate the DFT.
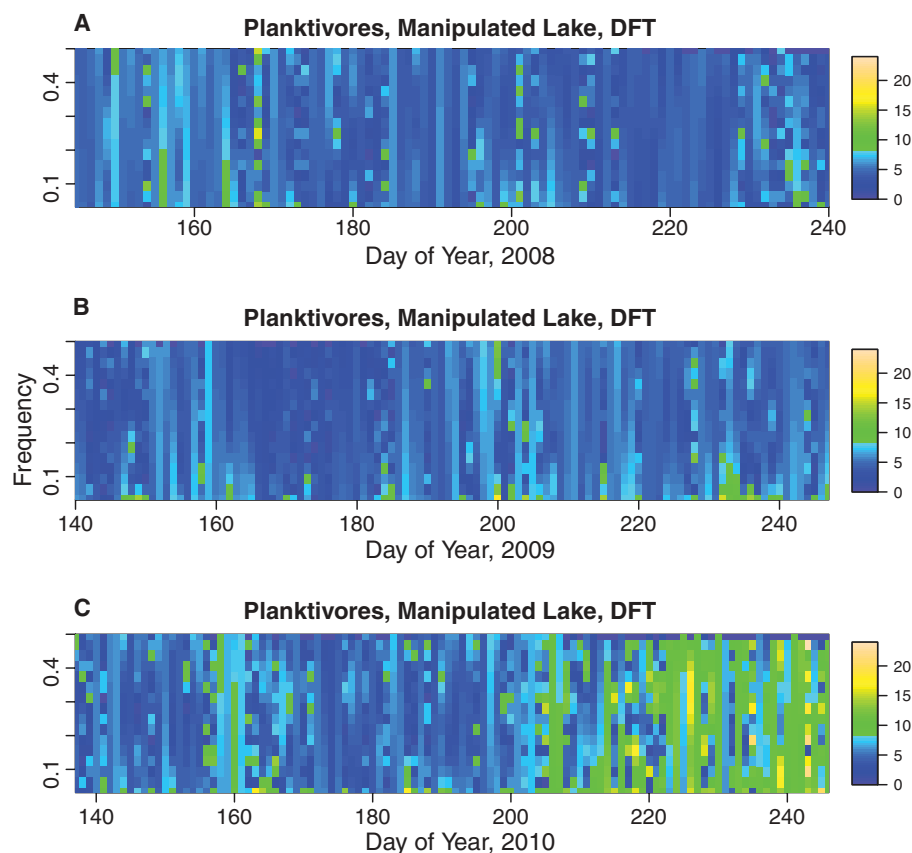
Fig. 3. Difference between manipulated and reference lakes in spectra for high-frequency chlorophyll observations in 2008 (**top**), 2009 (**middle**), and 2010 (**bottom**). On each date in each lake, spectra were computed for the preceding 7 days by using observations recorded every 5 min by floating sensors (16). Frequency (per day, $\log_{10}$ transformed) is plotted versus day of the year, with differences in spectra ($\log_{10}$ transformed) indicated by colors (see legend). Green colors indicate little difference in spectral power between lakes, blue colors indicate that spectral power of the manipulated lake was lower than that of the reference lake, and yellow or tan colors indicate that the spectral power of the manipulated lake was greater than that of the reference lake. High spectral power at low frequencies is associated with nonlinear transitions (3, 17, 22).
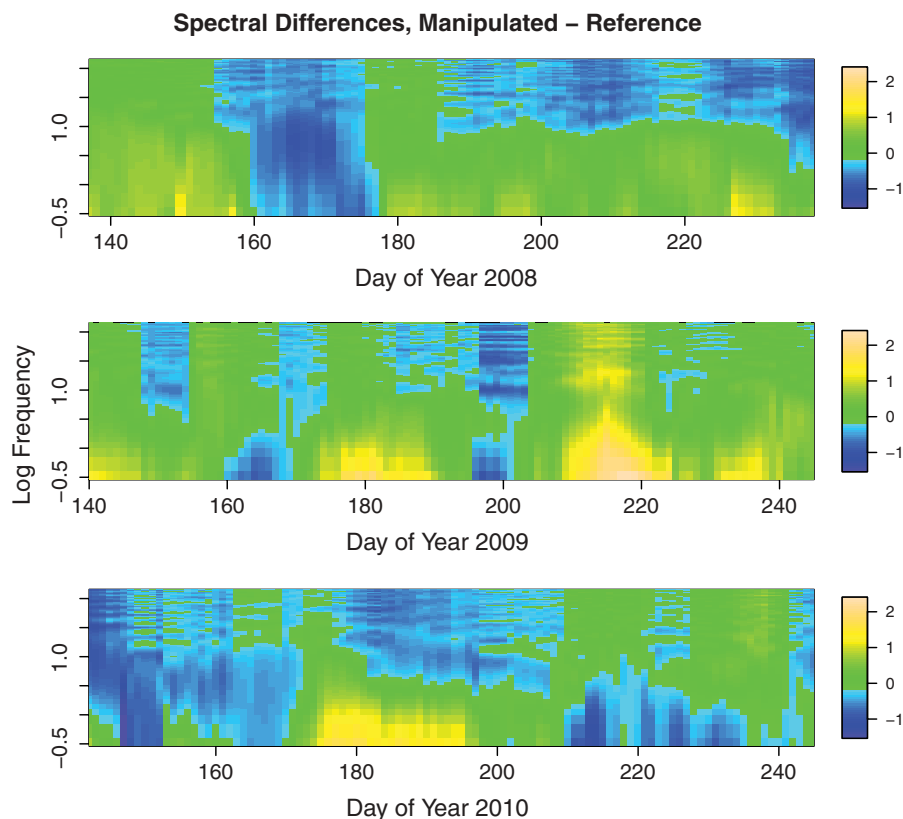
types of nonlinear systems, even in cases where the driver is not known [7]. Spatial statistics may prove especially useful for terrestrial or benthic habitats [7, 9, 17]. Expanding availability of automated sensors and remote sensing increases opportunities for measuring early warning signals. Comparison with a reference ecosystem was important for discerning changes in our experiment. Networks for long-term ecological observation, such as the U.S. Long-Term Ecological Research network (www.lternet.edu), increase the possibility of detecting early warnings through comparisons across sites and among regions.

Early warning signals are potentially useful for managing ecosystem services that are subject to catastrophic change, such as unwanted shifts in freshwater quality or production of fisheries and rangelands. In our experiment, early warnings were discernible while a transition was underway, but the experiment was not designed to assess whether a regime shift could be reversed by intervention after detection. Modeling suggests that some but not all regime shifts can be reversed by prompt intervention after early warnings are detected [22, 31]. Reversibility through detection of signals and subsequent intervention is a key question for future field experiments.

Ecosystems are subject to increasing human pressures that can lead to drastic changes, including shifts to unwanted states [2]. In this whole-lake field experiment, early warnings were detected in a food web undergoing a regime shift. Statistical indicators related to variability, autocorrelation, and recovery time provide new tools for empirical studies of nonlinear dynamics in field studies of ecosystems or other complex systems. Thus, our findings should prompt further field experiments to evaluate early warnings for massive change in ecosystems and other complex systems. This research could reveal new indicators of vulnerability to large environmental changes and thereby improve ecosystem management in a rapidly changing and interconnected world.
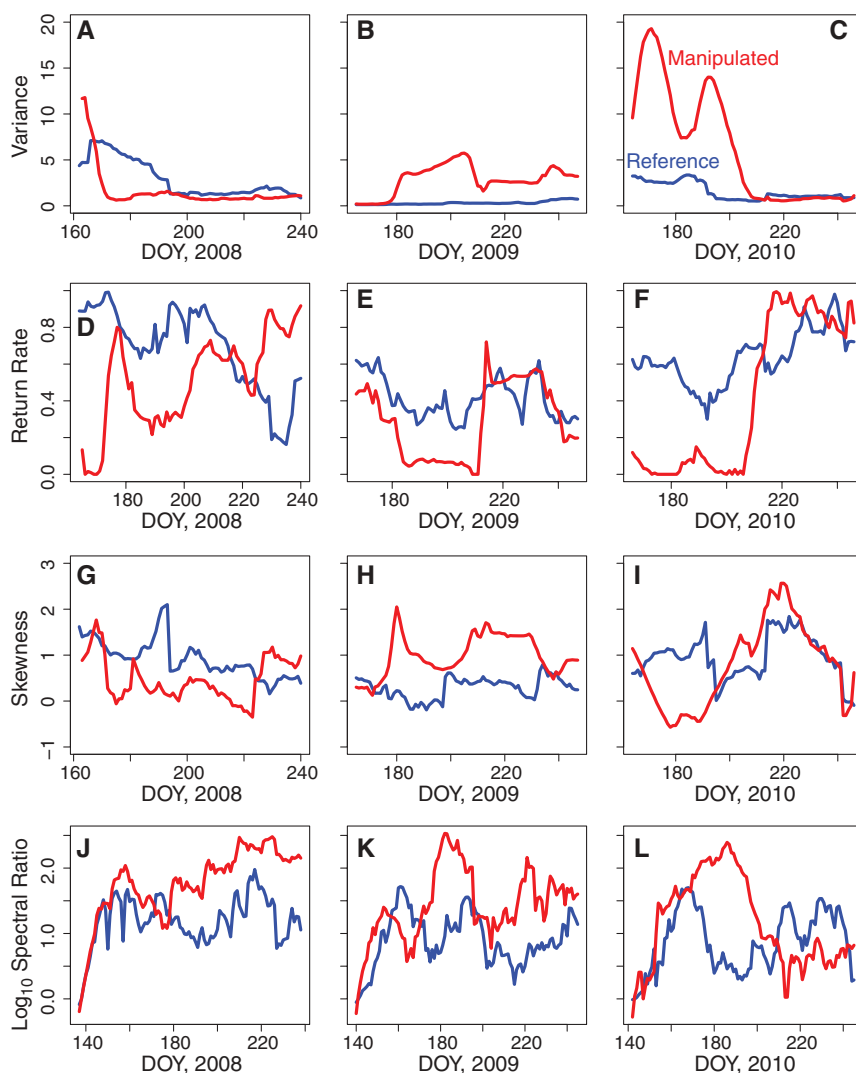
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Fig. 4. Potential early warning indicators computed from daily chlorophyll time series in the mixed layer in the manipulated (red) and reference (blue) lakes in 2008, 2009, and 2010. On each date in each lake, statistics were computed for the preceding 28 days by using daily observations [16]. (**A** to **C**) Variance; high values are associated with nonlinear transitions. (**D** to **F**) Return rate from small perturbations computed by autoregressive modeling [16]. Values near zero are associated with nonlinear transitions. (**G** to **I**) Coefficient of skewness. Values far from zero (the value for a normal distribution) are associated with nonlinear transitions. (**J** to **L**) Spectral ratio ($\log_{10}$ transformed) of power at low frequencies (less than once per day) to power at high frequencies (from once per 3 hours to once per 15 min) computed from chlorophyll measurements made every 5 min. High spectral ratios are associated with nonlinear transitions [22].

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