Early Warnings of Regime Shifts: A Whole-Ecosystem Experiment

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Abstract

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 three 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.

Main Text

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, 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 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 multi-year 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 three 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 three years of summer stratification (2008-2010) (*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*). Prior to manipulation, the manipulated ecosystem was dominated by a variety of small fishes (hereafter planktivores, *16*) and largemouth bass were few. We expected that addition of largemouth bass would trigger recruitment of juvenile bass that were planktivorous initially but become 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 due to 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% CI 1088-1560) by day 240 of 2009. Numbers of this cohort (1+ in Fig. 1C) declined through 2010 while 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 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 *Daphnia 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 (*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 expect 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 is 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 three years prior to manipulation (Table S2).

High frequency measurements of chlorophyll (every 5 minutes) 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 panels 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 185-210) 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 180-215 of 2009 and until about day 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 BDS test on AR and GARCH 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 due to 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 to 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 influences. Both the manipulated and reference ecosystems were sampled at high frequency using identical methods, leading to relatively large datasets 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 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 prior to regime shifts in aquatic or terrestrial ecosystems as well as other 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 US Long Term Ecological Research network (http://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 if 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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38. This research was supported by the National Science Foundation. Chase Brousseau, Matt Dougherty, Andy Farrell, Robert Johnson, Steve Klobucar, Jason Kurtzweil, Katie Lee, Tony Matthys, Kevin McDonnell, Haley Pack, Tim Walsworth and Lee Zinn provided technical help. We thank the staff of the University of Notre Dame Environmental Research Center for assistance.

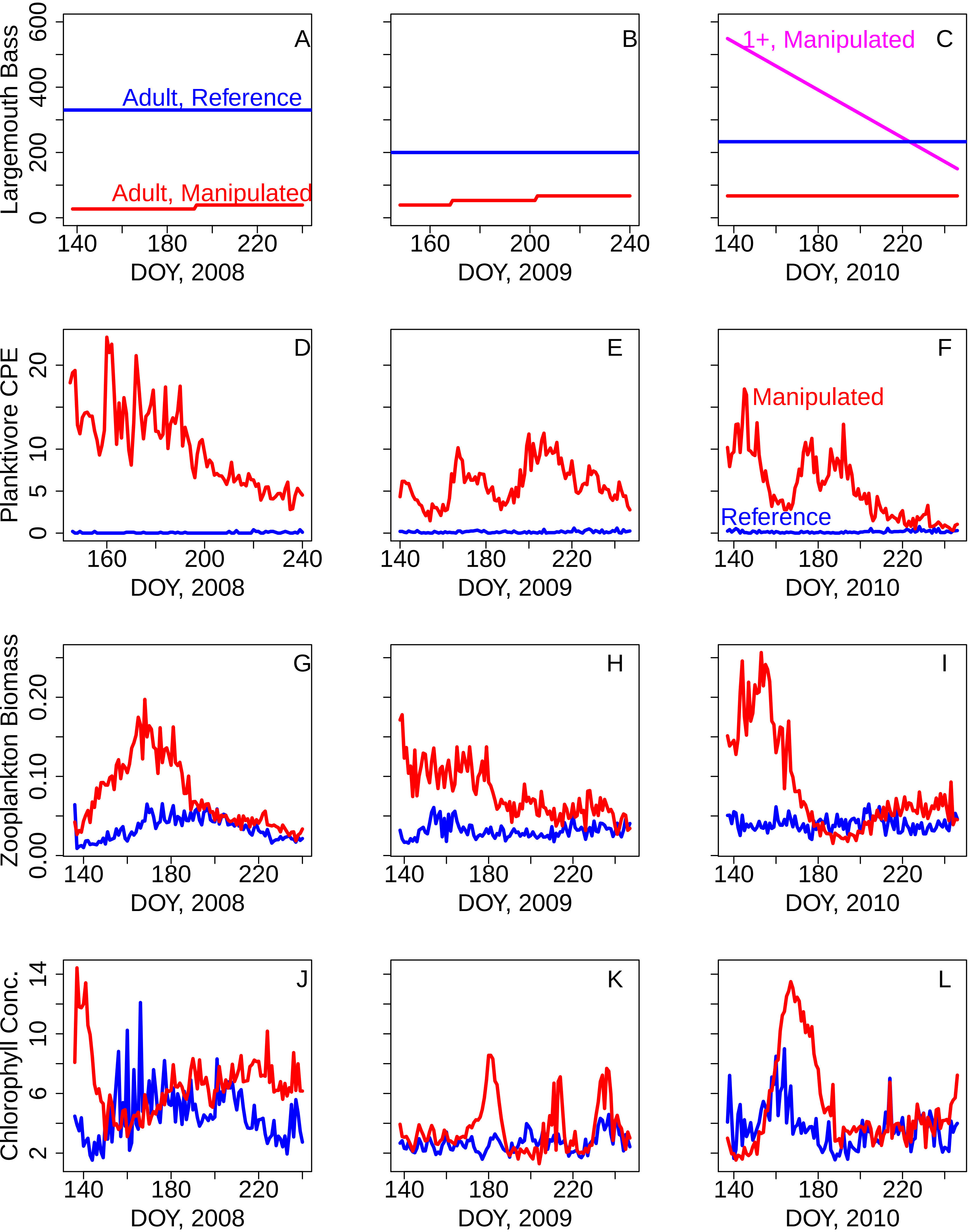
Figure Captions

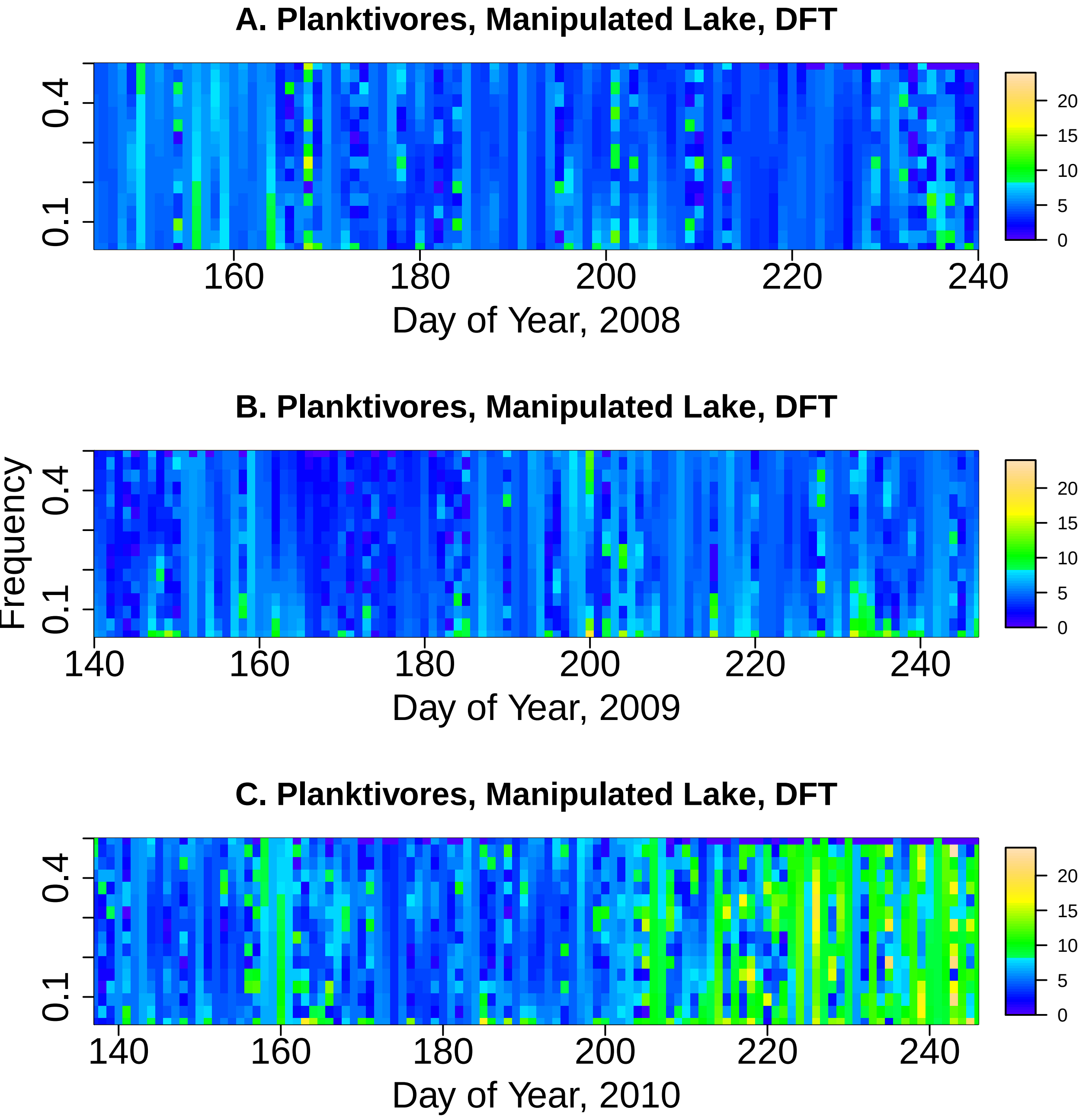
Fig. 1. Time series of the food webs in manipulated (red) and reference (blue) lakes in 2008-2010 . A-C: Largemouth bass adult population (fish/lake) in each lake. For the manipulated lake in 2010, numbers of year 1+ bass (recruited in 2009) are shown in magenta. D-F: Planktivorous fish density (animals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

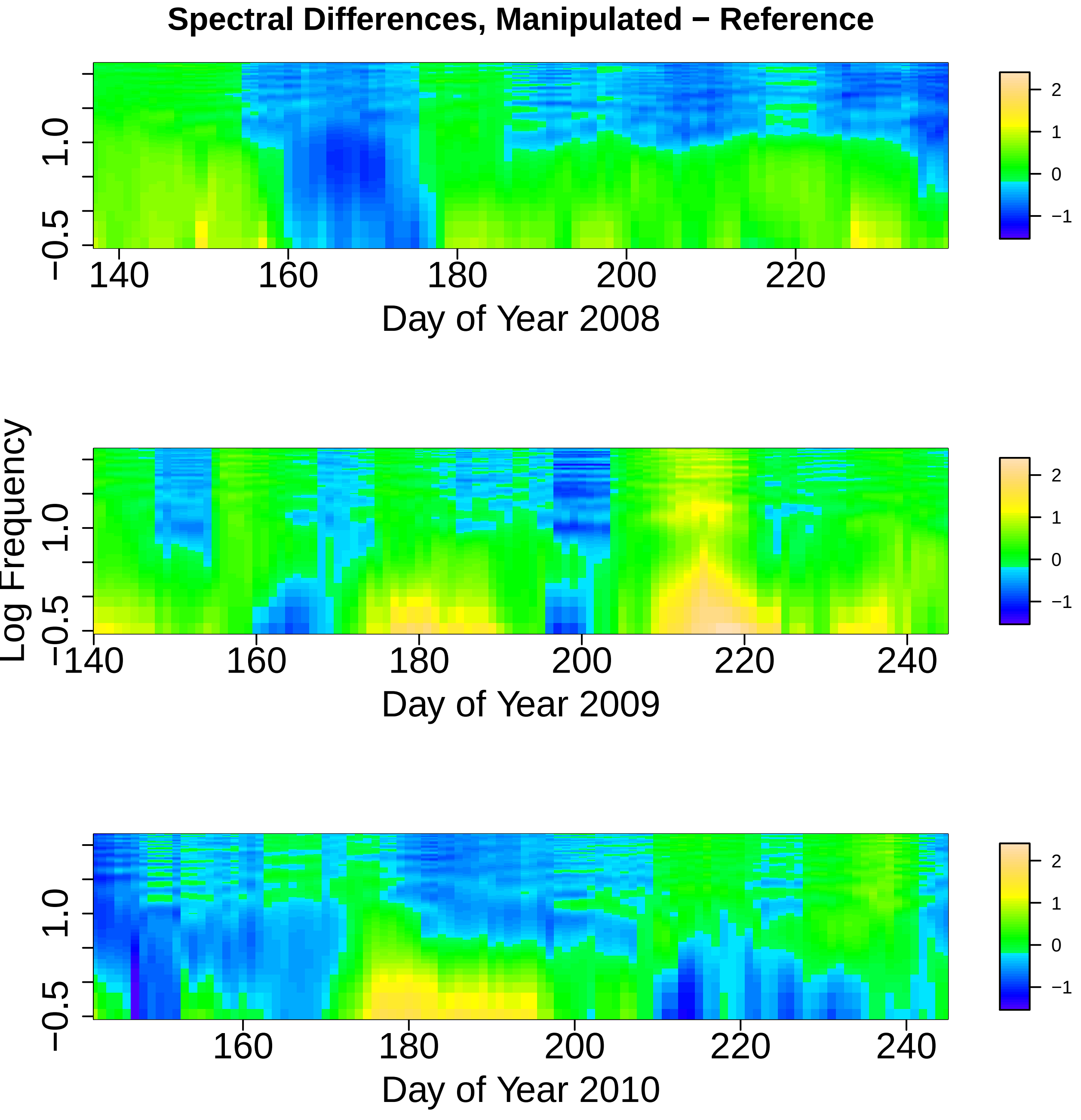
Fig. 2. Discrete Fourier transform (DFT) of the spatial sequence of minnow (planktivorous fish) trap catches around the perimeter of the manipulated lake on each day of sampling in 2008 (A), 2009 (B) and 2010 (C). Spatial frequency (per trap) is plotted versus day of the year, with DFT ordinate (a measure 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 once 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 (A), 2009 (B) and 2010 (C). On each date in each lake, spectra were computed for the preceding 7 days using observations recorded every 5 minutes 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*).

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 using daily observations (*16*). A-C: Variance; high values are associated with nonlinear transitions. D-F: Return rate from small perturbations computed by autoregressive modeling (*16*). Values near zero are associated with nonlinear transitions. G-I: Coefficient of skewness. Values far from 0 (the value for a normal distribution) are associated with nonlinear transitions. J-L: Spectral ratio ($\log_{10}$ transformed) of power at low frequencies (< once per day) to power at high frequencies (from once per three hours to once per 15 minutes) computed from chlorophyll measurements made every 5 minutes. High spectral ratios are associated with nonlinear transitions (*22*).


Largemouth Bass
0
200
400
600
A
Adult, Reference
Adult, Manipulated
140
180
220
DOY, 2008
B
160
200
240
DOY, 2009
C
1+, Manipulated
140
180
220
DOY, 2010
Planktivore CPE
0
5
10
20
D
160
200
240
DOY, 2008
E
140
180
220
DOY, 2009
F
Manipulated
Reference
140
180
220
DOY, 2010
Zooplankton Biomass
0.00
0.10
0.20
G
140
180
220
DOY, 2008
H
140
180
220
DOY, 2009
I
140
180
220
DOY, 2010
Chlorophyll Conc.
2
6
10
14
J
140
180
220
DOY, 2008
K
140
180
220
DOY, 2009
L
140
180
220
DOY, 2010


A. Planktivores, Manipulated Lake, DFT
0.4
0.1
160
180
200
220
240
Day of Year, 2008
20
15
10
5
0
B. Planktivores, Manipulated Lake, DFT
Frequency
0.4
0.1
140
160
180
200
220
240
Day of Year, 2009
20
15
10
5
0
C. Planktivores, Manipulated Lake, DFT
0.4
0.1
140
160
180
200
220
240
Day of Year, 2010
20
15
10
5
0


Spectral Differences, Manipulated − Reference
Log Frequency
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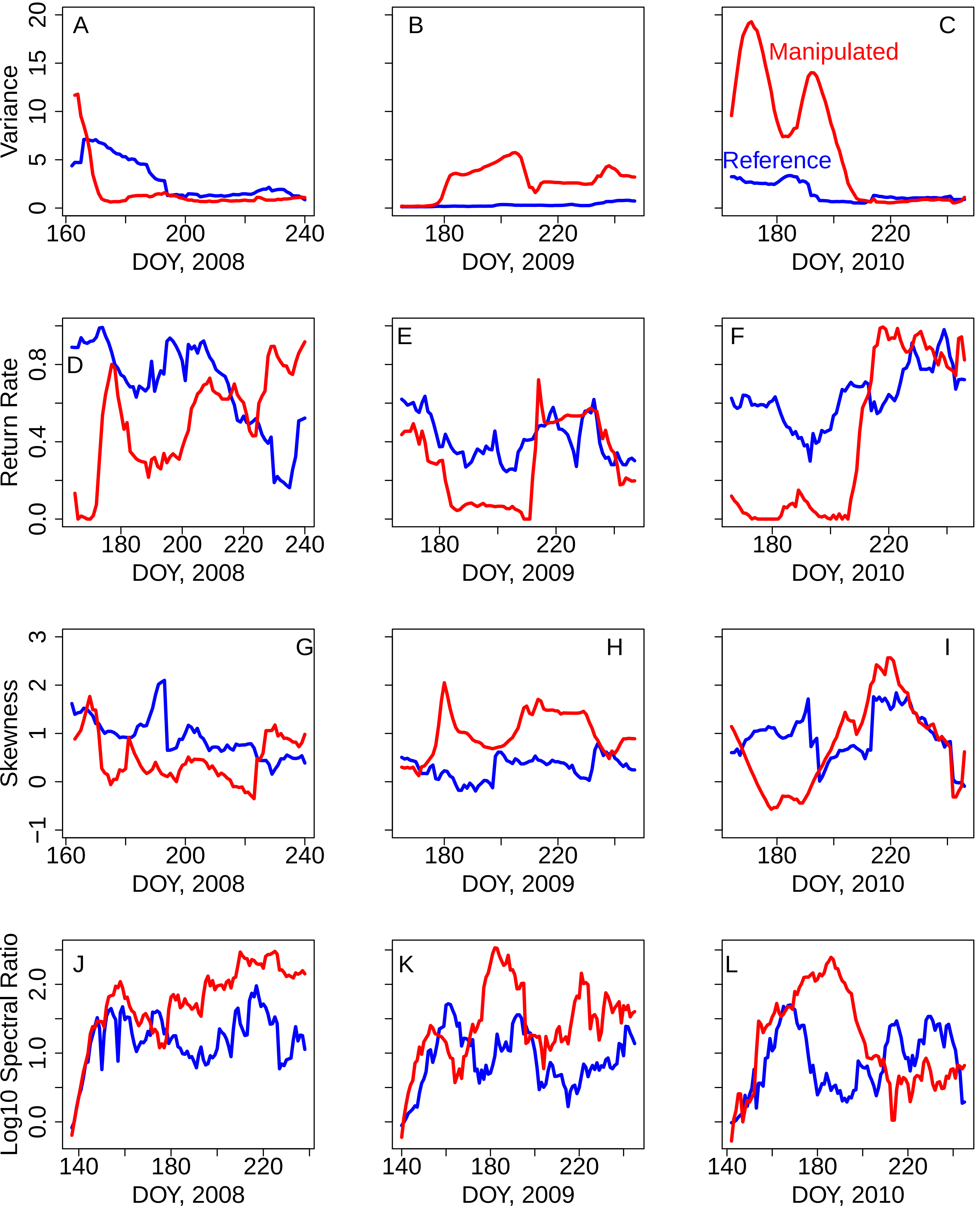
1.0
140
160
180
200
220
Day of Year 2008
240
Day of Year 2009
Day of Year 2010
2
1
0
−1


A
B
C
Manipulated
Reference
Variance
0
5
10
15
20
DOY, 2008
DOY, 2009
DOY, 2010
160
200
240
180
220
D
E
F
Return Rate
0.0
0.4
0.8
G
H
I
Skewness
−1
0
1
2
3
J
K
L
Log10 Spectral Ratio
0.0
1.0
2.0
140

Supporting Online Material for

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This PDF file includes:

SOM Text:
    Field and laboratory methods
    Statistical analyses
Figures S1 to S4
Tables S1 and S2

Supporting online text

Field and laboratory methods

Study Sites and Fish Community Structure - Paul and Peter Lakes, MI (89°32' W, 46° 13' N) located at the University of Notre Dame Environmental Research Center were used as the reference and manipulated systems in this study. The lakes are separated by an earthen dike, with Paul Lake lying slightly upstream of Peter Lake. The lakes have similar morphometry and limnology (*15*). Nutrient concentrations during this experiment are presented in Table S1.

During this study, the fish in the reference lake (Paul) were adult largemouth bass (*Micropterus salmoides*) and a smaller population of pumpkinseeds (*Lepomis gibbosus*). Average total abundance of adult largemouth bass in the reference lake ranged from 200 to 330 individuals over the period 2008 to 2010. At the outset of the study, the manipulated lake (Peter) was dominated by a variety of small-bodied fish species including pumpkinseeds (*Lepomis gibbosus*), golden shiners (*Notemigonus crysoleucas*), fathead minnows (*Pimephales promelas*), dace (primarily *Phoxinos eos* and *Phoxinus neogaeus*), brook stickleback (*Culaea inconstans*), and central mudminnow (*Umbra limi*). These fishes consume a mix of plankton and benthos. We focus here on their effect on chlorophyll through zooplanktivory, and refer to these fishes collectively as planktivores. On day 149 of 2008 we added 1200 golden shiners to Peter Lake to increase the dominance by planktivores. Approximately 39 largemouth bass were present in Peter Lake in early 2008. Over 2008-2010, biomass of largemouth bass increased as a result of our manipulations (see below) and a major recruitment event in 2009. As numbers of 1+ and adult largemouth bass increased, populations of small-bodied planktivorous fishes decreased (see main text).

Food web structure -- Adult largemouth bass, the apex predator in these lakes, feed on benthic invertebrates, zooplankton, terrestrial prey and smaller-bodied fishes, including young-of-year and juvenile largemouth bass Planktivorous fishes in this experiment are listed above and feed on zooplankton as well as benthic invertebrates and in some cases young-of-year fishes. Importantly, planktivorous fishes move between littoral and pelagic habitats and engage in shoaling behavior in response to predation threats and food availability. Responses to bass predators thus diminish planktivory. Zooplankton feed on phytoplankton or in some cases on other zooplankton species. Large-bodied species of *Daphnia* are the most effective grazers in these lakes and are capable of diel vertical migration in the presence of planktivorous fishes. This paper focuses on the interactions of largemouth bass, the full set of planktivorous fishes, pelagic zooplankton and phytoplankton.

Bass addition and population sampling – Adult largemouth bass were added to the manipulated lake on day 193 of 2008, day 169 of 2009, and day 203 of 2009. Twelve largemouth bass were added in 2008 and fifteen were added on each of the two dates in 2009. Adult largemouth bass population size in the manipulated and reference lakes was estimated by mark/recapture sampling using electrofishing and angling (3*2, 33*). Young-of-the-year and age 1+ largemouth bass were sampled using a combination of traps and electrofishing (*15*). Population sizes of these age classes were also estimated in the manipulated lake as they became abundant.

Sampling of small fishes – In the manipulated lake, we deployed a spatially distributed array of 30 littoral and 30 pelagic minnow traps. In the reference lake, we deployed a spatially distributed array of 20 littoral and 20 pelagic minnow traps. Trap mesh size was 6 mm and trap opening diameters were 25 mm in all cases.. These traps were monitored daily in both lakes from late May to early September in each year of the study. The abundance of each species of fish collected in each trap was recorded daily.

Zooplankton biomass – Four replicate vertical net hauls were made daily in each lake with a 153 µm mesh net. Net haul samples were processed by filtering a sample through a 2 mm mesh to remove *Chaoborus* spp. and then concentrating the sample on a pre-weighed filter. The filter with zooplankton concentrate was dried and weighed to get a direct biomass measurement. Visual inspection of the zooplankton concentrate using a stereomicroscope confirmed that the samples were dominated by zooplankton. Further, phytoplankton biomass was a trivial component of total sample weight based on direct measures of chlorophyll in the concentrates.

Phytoplankton biomass - We took daily water samples from 0.5 m in each lake to measure chlorophyll *a* as an indicator of phytoplankton biomass. We filtered 200 ml of water onto GF/F filters which were frozen and subsequently extracted in methanol. Chlorophyll a was measured using standard fluorometric methods (*34*). *In situ* chlorophyll measurements were also made at five minute intervals using a YSI 6600 V2 water quality sondes fitted with chlorophyll probes (model 6025). The probe sensors were calibrated and corrected for variations in fluorescence related to temperature.

Other limnological variables – To characterize lake conditions and plankton communities we measured a variety of variables at a central station in the reference and manipulated lakes weekly from late May through August. Vertical profiles of dissolved oxygen and temperature were made at 0.5 meter depth intervals from surface to bottom at a central station. Light extinction was measured using a LiCor submersible meter. Chlorophyll *a* concentrations were measured at l00%, 50%, 25%, 10%, 5% and 1% light levels following the methods described above. Zooplankton were sampled using calibrated net hauls. Zooplankton were enumerated by taxa from preserved samples using a stereomicroscope. Body lengths of the dominant taxa of crustacean zooplankton were also measured and biomass estimated from length x weight regressions.

Statistical Analyses

Daily time series autocorrelation, variance, CV, skewness and return rate – Within each year in each lake, indicators presented in Figs. 4 and S2 were computed for each date as follows. Daily chlorophyll time series, x_t, were divided into sequential overlapping windows of length h days. For each date t, statistics were computed for the series x_{t-h+1}, x_{t-h+2}, . . . x_t. Statistics were computed for each sampling day after h days of sampling had occurred. Thus each indicator is a "leading indicator" based on data available prior to and including date t. Variance, coefficient of variation, skewness, and lag-1 autocorrelation coefficient were computed using moment functions in R (http://www.r-project.org/). Return rate was computed by linear regression of the vector $[x_{t-h+2} \ldots x_t]'$ on the vector $[x_{t-h+1} \ldots x_{t-1}]'$. The slope b_1 is used to calculate the return rate $1\text{-}b_1$ (*35*). We experimented with h values of 14 to 42 days. Higher h increases precision of the estimates but decreases capacity to resolve events in the time series. We report results based on h=28 days, a compromise between precision and resolution. The overall patterns were similar for h values greater than 21 days. For h less than about 20 days, patterns were noisy and precision was low, especially for autocorrelation and return rate estimators.

Several considerations affect selection of time windows for computing these early warning indicators. Some of the methods used for early warning signals consider all possible windows (e.g. spectral analysis, power laws). In some cases, it may be possible to use nonparametric approaches and associated methods for choosing optimal bandwidths. In many ecological cases, the most practical approach may be to consider a range of different windows, evaluate the tradeoffs between precision and time-resolution of the signal, and consider whether the outcome is sensitive to the choice of window length as we have done here.

Spectral analysis of high frequency chlorophyll measurements – Chlorophyll data measured at 5 minute intervals using sondes were analyzed in sequential overlapping windows of 7 days, the duration of a sonde deployment. For each time window, variance spectra were computed using the 'spectrum' function in R (http://www.r-project.org/). The spectrum was computed from the autoregression function of optimal order selected by AIC. Thus in a year with n sampling dates we computed n-7+1 spectra. These are plotted for each lake in each year in Figs. S3 and S4. Prior to analysis, data points that were missing due to sonde malfunction were replaced with randomly chosen values from the same lake the same year. Malfunction affected less than 0.6% of the observations in the reference lake and less than 0.01% of the observations in the manipulated lake. By replacing the missing observations with random observations from the same lake and year, we maintain the continuity and variability of the time series.

Spectral differences (Fig. 3) were computed by subtracting the reference lake log spectral density from the manipulated lake log spectral density on each date at each frequency. Because differences were taken of log spectral densities, the values reported in Fig. 3 are equivalent to the log of the ratio of spectral densities.

Spectral frequency ratios for each lake on each date were computed as the ratio of the mean spectral density at low frequencies to the mean spectral density at high frequencies. Low frequencies were all frequencies less than once per day. High frequencies were all frequencies between once in 15 minutes and once in 3 hours.

Discrete Fourier Transform of Planktivore Data – In each lake, littoral minnow traps were placed around the perimeter of the lake in a clock-like arrangement. This arrangement is equivalent to a one-dimensional gradient in a closed loop. In this setting, changes in spatial pattern consistent with shoaling of fishes or other nonlinear phenomena can be evaluated using the discrete Fourier transform (DFT) (17). The DFT is a transformation of spatial data into the frequency domain. Pattern is evaluated by plotting the DFT versus frequency, measured in units of 1/trap in this study. A peak in the DFT at a particular frequency is associated with spatial pattern at that frequency. We used the DFT as an indicator of shoaling by fishes (*17*). We computed the DFT for littoral zone traps on each date in the manipulated lake. In the littoral zone of the reference lake, and the pelagic zone of both lakes, the DFT was not computed because catch rates were too often zero .

Brock-Dechert-Scheinkman (BDS) Test for nonlinearity – The early warning signals that we studied are sensitive to nearby regime shifts in models of complex systems, but in field data false signals can be generated by many linear processes that are unrelated to nonlinear transitions. For example, autocorrelation can result from linear processes, and autoregressive conditional heteroskedasticity can produce bursts of variance from linear processes.

Therefore, we tested the daily chlorophyll time series for potential effects of linear processes masquerading as nonlinear ones (*36*). For each lake in each year, we fit an autoregressive model to the time series, choosing the optimal order by AIC. We then fit the AR residuals to a generalized autoregressive conditional heteroskedasticity (GARCH) model. In all cases the order of the GARCH model was (1,1) and higher-order GARCH models did not improve the fit. AR, BDS and GARCH statistics were computed by the corresponding functions in the 'tseries' module of R (http://www.r-project.org/). The residuals of the GARCH model represent pattern that cannot be explained by autoregressive or GARCH processes. Residuals of the GARCH models for a given variate in a given lake were concatenated in a single series spanning all three years for the BDS test (*37*). Concatenation was necessary because of the high sample size requirements of the BDS test. The BDS statistic was referred to a null distribution computed by bootstrapping 10,000 random permutations of the GARCH residuals. For the reference lake, the p-value was 0.184. Thus we cannot reject the null hypothesis that the underlying dynamics are linear in the reference lake. For the manipulated lake the p-value was 0.011. Thus the null hypothesis of linearity is rejected for the manipulated lake.

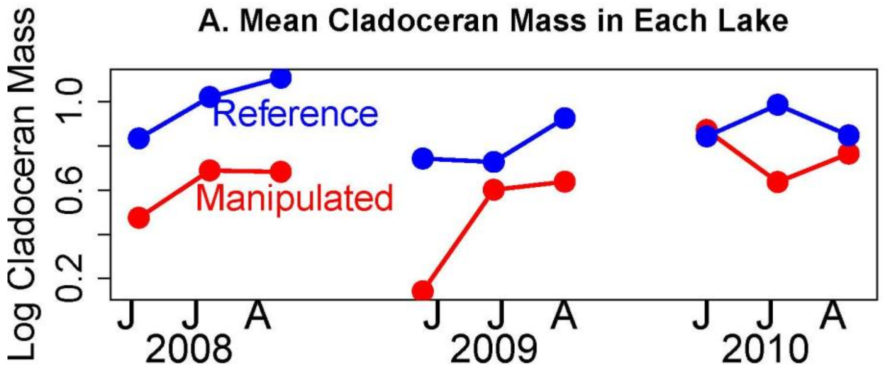
We conclude that the early warning indicators in the manipulated lake cannot be explained by linear processes, and are consistent with a regime shift caused by the manipulation. If a regional driver of nonstationarity, such as variable plankton dynamics related to weather, were involved in the behavior of the manipulated lake, then a similar signal would have been expected in the reference lake, but the BDS test indicates this was not the case.

Figure S1

Cladoceran mass was computed from enumeration of zooplankton species in weekly samples. Measures of individual body sizes of cladocerans are effective indicators of lake food web structure and trophic cascades (*15, 18*). Plots of the log of body mass (which is linearly related to body length) in the reference lake illustrate the typical variability of a piscivore-dominated lake (Fig. S1A). Over time the manipulated lake became more similar to the reference lake (Fig. S1B). The low cladoceran mass in the manipulated lake June 2009 was due to high density of *Bosmina*, a small-bodied genus. Over the three years of the experiment, the mean length of *Daphnia* in the manipulated lake increased from about 0.8 mm to about 1 mm while no change was observed in the reference lake.

Fig. S1-A. Mean cladoceran mass ($\log_{10}$ transformed) for each month of summer stratification in each lake, 2008-2010. In 2009, cladoceran mean mass was decreased by planktivory by young-of year largemouth bass.

Fig. S1-B. Difference in mean cladoceran mass ($\log_{10}$ transformed) between lakes (manipulated – reference values) computed from the data in panel A. Over the course of the experiment, the cladoceran mean mass in the manipulated lake became more similar to that of the largemouth-bass dominated reference lake.



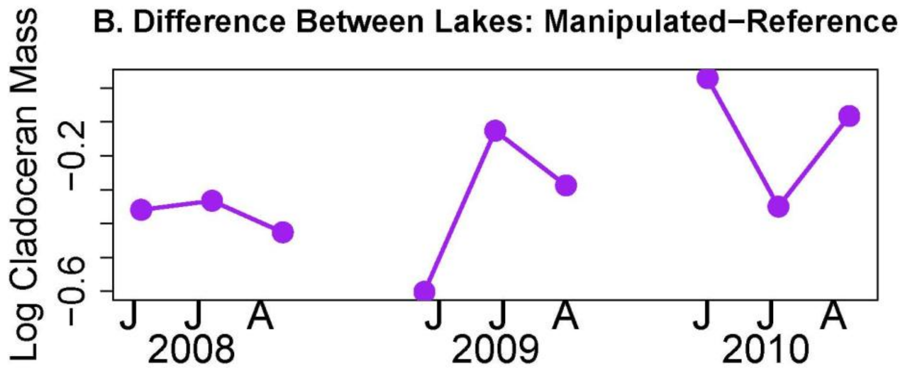
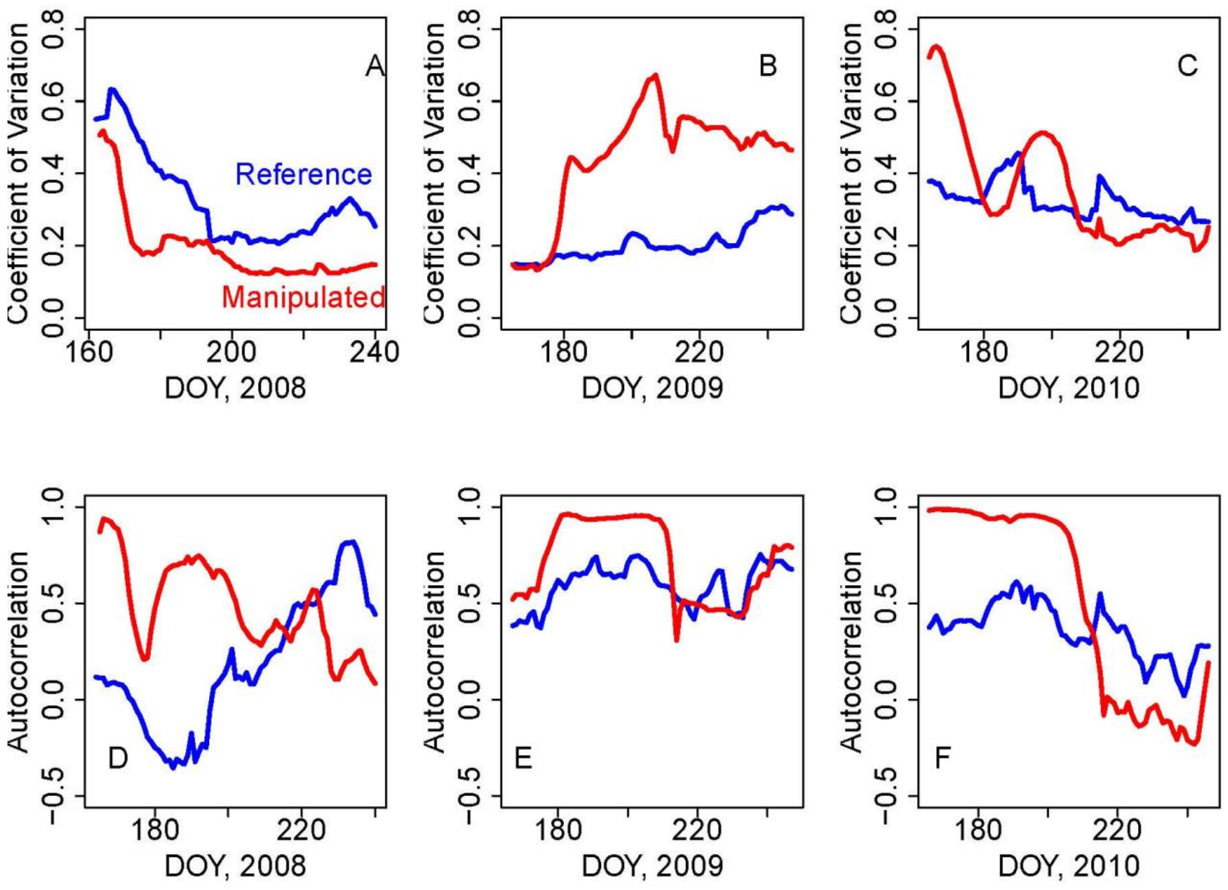


Figure S2

The variance (Fig. 4 A-C) and return rate from small perturbations (Fig. 4 D-F) are closely related to the coefficient of variation and autocorrelation, respectively. The coefficient of variation (CV, standard deviation / mean) is a measure of variability that adjusts for possible correlation of the variance and mean. High values are associated with nonlinear transitions. Autocorrelation near one is widely used as a measure of slow return rate associated with nonlinear transitions (*5*). These additional early warning indicators are presented here. Expectations for early warnings in the manipulated lake are consistent with the high CV in 2009 and early in 2010 and the intervals of autocorrelation near one in 2009 and early 2010.

Fig. S2. Potential early warning indicators computed from daily chlorophyll time series in the mixed layer of 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 using daily observations. Regime shifts are associated with high CV and autocorrelation close to one. A-C: coefficient of variation. D-F: autocorrelation.



Figures S3 and S4

To assess changes in variance spectra of the manipulated lake versus the reference lake, we calculated differences in spectra based on high-frequency chlorophyll measurements (Fig. 3). To assess potential shifts in variance spectra toward low frequencies, we calculated spectral frequency ratios for both lakes (Fig. 4 J-L). Both of these indicators are based on the spectra for the individual lakes. We present these spectra in Figs. S3 and S4.

Fig. S3. Variance spectra for high-frequency chlorophyll observations from sondes in the reference lake. On each date, spectra were computed for the preceding 7 days using observations recorded every 5 minutes. Frequency (per day, $\log_{10}$ transformed) is plotted versus day of the year, and spectral density ($\log_{10}$ transformed) is indicated by the colors. High spectral density at low frequencies is associated with nonlinear transitions. A: 2008. B: 2009. C: 2010.

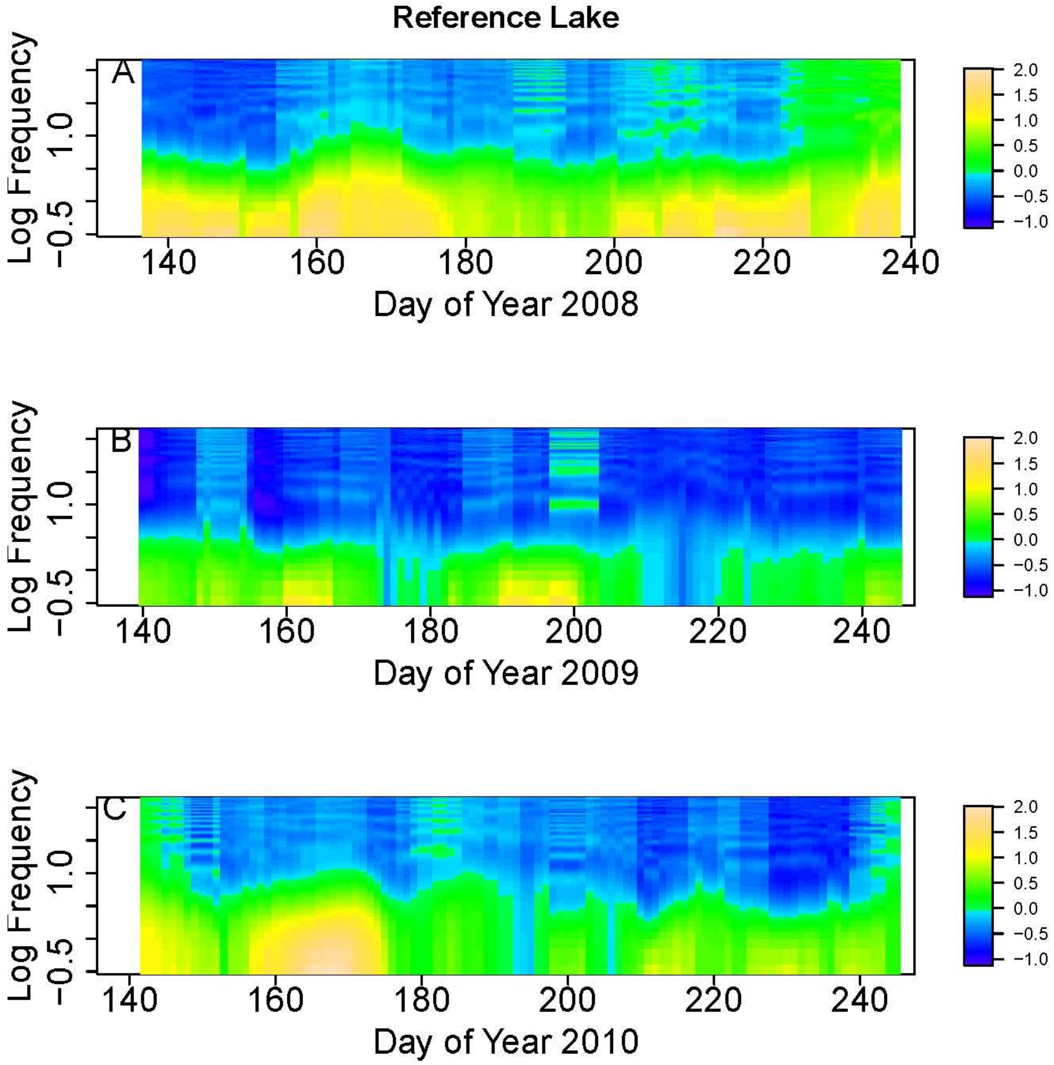


Fig. S4. Variance spectra for high-frequency chlorophyll observations from sondes in the manipulated lake. On each date, spectra were computed for the preceding 7 days using observations recorded every 5 minutes. Frequency (per day, $\log_{10}$ transformed) is plotted versus day of the year, and spectral density ($\log_{10}$ transformed) is indicated by the colors. High spectral density at low frequencies is associated with critical transitions. A: 2008. B: 2009. C: 2010.

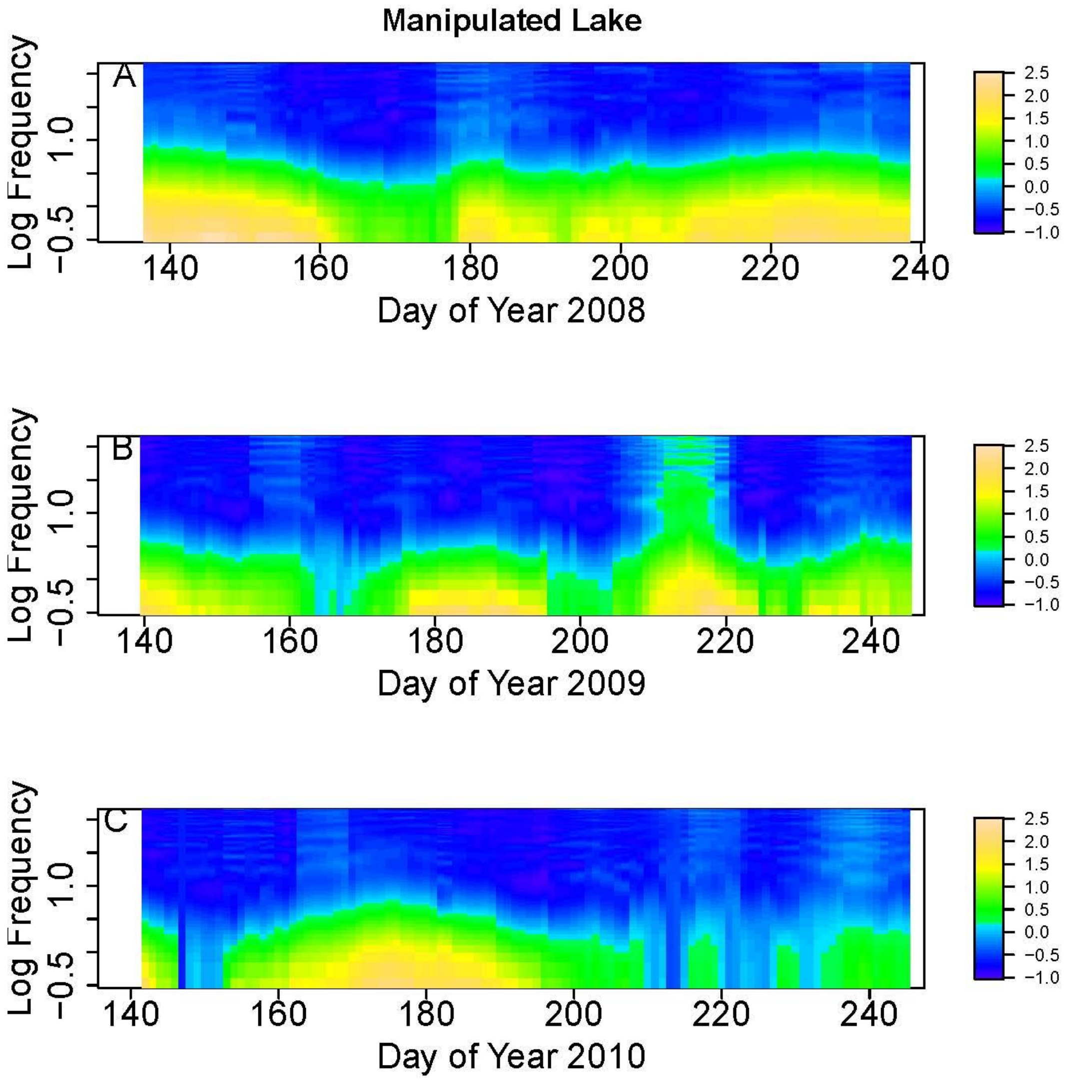


Table S1. Nutrient data for 2008-2010. Each value is based on 15 weekly samples during summer stratification from the epilimnion of each lake.

Year	Lake	Total P (mg m^{-3})		Total N (mg m^{-3})	
		Mean	SD	Mean	SD
2008	Ref	6.40	3.39	283	45.6
	Manip	6.67	2.79	344	47.7
2009	Ref	3.65	2.83	303	58.9
	Manip	5.60	2.57	353	41.0
2010	Ref	3.85	1.76	224	31.9
	Manip	4.37	2.04	302	39.6

Table S2. During three years prior to this experiment, chlorophyll concentration in the manipulated lake was less variable than chlorophyll concentration in the reference lake in two years out three based on standard deviation, and three years out of three based on coefficientof variation (SD/mean). However the differences between lakes in chlorophyll variability were small compared to those observed during the experiment in 2009 and 2010. The table below presents chlorophyll mean, standard deviation and coefficient of variation based on 15 weekly samples from the epilimnion during summer stratification in each of three years prior to manipulation, 2005-2007.

Year	Lake	Chl Mean (mg/m3)	Chl SD	Chl CV
2005	Ref	3.16	1.94	0.613
	Manip	5.13	2.20	0.428
2006	Ref	4.20	2.44	0.580
	Manip	4.16	1.45	0.349
2007	Ref	4.17	1.54	0.369
	Manip	4.94	1.28	0.259