ORIGINAL PAPER

Evidence of alternate attractors from a whole-ecosystem regime shift experiment

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Abstract Ecosystems sometimes shift between different states or dynamic regimes. Theory attributes these shifts to multiple ecosystem attractors. However, documenting multiple ecosystem attractors is difficult, particularly at spatial and temporal scales relevant to ecosystem management. We manipulated the fish community of a lake with the goal of causing trophic cascades and shifting the food web from a planktivore-dominated state to an alternate piscivore-dominated state. We evaluated evidence that the shifts in the fish community comprise alternate attractors using two complementary approaches. First, we calculated phase space trajectories to visualize the shift between attractors. Second, we computed generalized autoregressive conditional heteroskedasticity (GARCH) models and the Brock–Dechert–Scheinkman (BDS) test for linearity. The reconstructed phase space trajectories show the system departing a point attractor, entering a limit cycle, and then shifting to a new point attractor. The GARCH and BDS results indicate that linear explanations are not sufficient to explain the observed patterns. The results provide evidence for alternate attractors based on high-frequency time series of field measurements.

Keywords Alternate ecosystem attractors · Regime shift · Trophic triangle · Ecosystem experiment · Bifurcation · Nonlinearity · GARCH · BDS test · Phase space

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Introduction

Ecosystems sometimes shift between different states or dynamic regimes (Scheffer et al. 2001; Scheffer and Carpenter 2003). For example, savannas shift to deserts, lakes shift from clear water to algae blooms, and fisheries shift from thriving to collapsed (Scheffer et al. 2001). These shifts are sometimes attributed to shifts among multiple attractors (Holling 1973; Scheffer and Carpenter 2003). Multiple attractors potentially explain sudden, dramatic ecosystem changes as well as failures to predict or reverse unwanted changes (Scheffer et al. 2001; Scheffer and Carpenter 2003; Suding et al. 2004). However, empirical tests for the existence of multiple ecosystem attractors are difficult and consistent evidence remains elusive (e.g., Carpenter and Pace 1997; Scheffer et al. 2003; Schröder et al. 2005; Mittelbach et al. 2006; Persson et al. 2007; Hobbs et al. 2012; Schröder et al. 2012). Laboratory experiments on model systems document multiple attractors (e.g., Fussmann et al. 2000; Dai et al. 2012), but complex patterns and variability in field data have led to disagreement over the existence and importance of multiple attractors in ecosystems (e.g., Carpenter 2001; Biesner et al. 2003; Hsieh et al. 2005; Mittelbach et al. 2006; Mumby et al. 2007; Hsieh et al. 2008; Bruno et al. 2009).

Evidence for existence of multiple ecosystem attractors comes from several types of studies in a variety of systems (Scheffer and Carpenter 2003). For example, Scheffer et al.

(2003) found that drainage ditches demonstrating floating or submerged plant dominance exhibited bimodality and path dependency (when slightly different initial conditions lead to very different ending conditions), both characteristics of a system with more than one attractor (see also Scheffer and Carpenter 2003; Schröder et al. 2005; de Young et al. 2008; Andersen et al. 2009). In other studies, tests for discontinuous response to changing environmental conditions, path dependency, lack of recovery from perturbations, and changes in driver–response relationships are often used to infer alternative attractors (see reviews by Scheffer and Carpenter 2003, and Schröder et al. 2005). These tests are often coupled to ecosystem models with multiple attractors that exhibit the same patterns (e.g., Scheffer et al. 2003; see review by Schröder et al. 2005). The strong empirical evidence from laboratory experiments (Schröder et al. 2005) proves the potential for multiple attractors in ecological systems. In field settings, statistical comparisons of mechanistic models with and without alternative attractors have proven a powerful means of testing for multiple attractors in ecosystems when long-term data are available (Carpenter and Pace 1997; Carpenter 2003; Scheffer and Carpenter 2003; Mumby et al. 2007; Ives et al. 2008; Schooler et al. 2011). Thus, the consistency of models and data in long-term observational studies represents the primary evidence for multiple attractors in ecosystems.

The existence of multiple attractors is due to certain nonlinear processes (Scheffer et al. 2001; Scheffer and Carpenter 2003). However, combinations of linear processes not associated with multiple attractors can also cause shifts in means, bimodality, and changes in driver–response relationships similar to those observed in systems with alternate attractors (Scheffer and Carpenter 2003; Schröder et al. 2005; Scheffer et al. 2003; Hsieh et al. 2005; Daily et al. 2012; Dakos et al. 2012). While patterns such as path dependency, bimodality, and hysteresis are indicative of two or more attractors, these patterns do not reconstruct attractors themselves. Physicists and economists have developed statistical tests and visualization techniques for identification of nonlinear dynamics and shifts between multiple attractors in time series. For instance, tests for linearity can be applied to time series data to evaluate linear dynamical hypotheses (e.g., Brock et al. 1991; Brock et al. 1996; Hsieh et al. 2005). If linear possibilities are eliminated then nonlinear explanations are more plausible (Brock et al. 1991; Brock et al. 1996). In other approaches, lagged values from time series can be plotted in certain combinations to visualize the form of attractors in phase space (Takens 1981; Schaffer 1984). These approaches make no a priori assumptions about ecological processes and are promising for detecting multiple attractors in ecosystems when other approaches are difficult to apply or interpret. Nonetheless, these visualization and statistical approaches are not widely used (Hsieh et al. 2005; Sugihara et al. 2012).

Application of novel techniques such as tests for linearity and phase space reconstructions has been identified as a priority in efforts to evaluate multiple attractors, particularly at spatial and temporal scales relevant to ecosystems (Scheffer and Carpenter 2003; Hsieh et al. 2005). We previously reported a whole-ecosystem experiment where we manipulated the fish community in a small lake with the purpose of testing for early warning indicators of a regime shift (Carpenter et al. 2011; Seekell et al. 2012; Pace et al. 2013). Here, we use a unique 4-year high-resolution time series derived from this experiment to test the hypothesis that this change comprised a shift between two alternate attractors. We examine phase plots for patterns consistent with a transition between two attractors and test for bursts of variance not explained by linear time series models, which should accompany a transition between attractors.

Background and Theory

We manipulated Peter Lake, a small (area: 2.6 ha; max depth: 19.6 m) oligotrophic lake in the Upper Peninsula of Michigan (89°32′ W, 46°13′ N). The lake was minnow dominated from 1991 onward due to earlier experiments that removed much of a predatory largemouth bass *Micropterus salmoides* population (Carpenter et al. 2001). By the time the present study began the prey fish community consisted of a mixture of minnows including golden shiner *Notemigonus crysoleucas*, fathead minnow *Pimephales promelas*, dace *Phoxinus* spp., brook stickleback *Culaea inconstans*, central mudminnow *Umbra limi* and pumpkinseed *Lepomis gibbosus*. These small fishes dominated Peter Lake and there was only a small population of predatory adult (>150 mm) largemouth bass (Carpenter et al. 2011). The minnow dominance prior to the experiment was maintained because large numbers of prey fish suppress growth of juvenile largemouth bass, increasing juvenile largemouth bass vulnerability to predation or other stressors and thereby preventing growth and recruitment of juveniles into the adult largemouth bass population (Walters and Kitchell 2001; Carpenter et al. 2008; Carpenter et al. 2011).

We expected that slowly adding adult largemouth bass would shift the food web from minnow dominance to largemouth bass dominance. We hypothesized that if the abundance of adult predators increased past a critical point, adult predators would dramatically reduce the prey population (Carpenter et al. 2008). The resulting reduction in competition should allow juvenile predators to grow and subsequently recruit into the adult population. The feedback maintaining minnow dominance (minnows cause a recruitment bottleneck for largemouth bass) consequently shifts to a feedback maintaining largemouth bass dominance (largemouth bass continue suppressing minnows such that their juveniles can continue recruiting into the adult population, causing further suppression of the minnows).

Our expectations for the existence of alternate ecosystem attractors in this system and the ability of largemouth bass additions to shift the system between alternate attractors derive from a mathematical model of the Peter Lake food web, which was solved to show that altering largemouth bass abundance creates multiple ecosystem attractors (see Carpenter et al. 2008). The specific ecological mechanism for the alternate attractors is the existence of trophic triangles—a set of predator–prey relationships where positive feedbacks can drive either predators or prey to dominance—in fish communities, including the Peter Lake fish community (Walters and Kitchell 2001; Carpenter 2003; Carpenter et al. 2008; Carpenter and Scheffer 2009).

A shift between alternate attractors due to nonlinear dynamics is not the only possible mechanism for change due to largemouth bass additions (Carpenter et al. 2011). For instance, largemouth bass additions could cause step-change reductions in minnow abundance without changing feedbacks within the food web. This would happen if, for example, sudden increases adult largemouth bass simply forced minnows into short-term refuges without eliminating the largemouth bass recruitment bottleneck. Such a change could be intrinsically linear and not associated with alternate ecosystem attractors. Previous fish community manipulations in this and nearby lakes did not attempt to discriminate between linear and nonlinear dynamics and these previous studies were based on low-frequency time series suitable for linear analyses but unsuitable for statistical tests to reject linear dynamics (He et al. 1993; Carpenter et al. 2001). In the present analysis, we leverage high-frequency measurements to discriminate between these linear and nonlinear possibilities.

Methods

Food web manipulation

We added 1,200 golden shiners on 28 May 2008 to help prevent the transition to largemouth bass dominance from happening too quickly to be detected by early warning statistics applied in our previous analyses (Carpenter et al. 2011). The number of fish added was <10% of the existing minnow population (Carpenter et al. 2011). Subsequently, we slowly added adult largemouth bass to Peter Lake over the course of four summers (12 on 7 July 2008, 15 on 18 June 2009, 15 on 21 July 2009) to cause trophic cascades and create a transition from a state of prey dominance to predator dominance. The system stabilized in its new condition toward the end of 2010. However, we added additional largemouth bass in 2011 (32 on 23 June 2011) to ensure that the food web structure would not revert due to winterkill, which may occasionally happen in this lake, after the study was complete (Hodgson and Kitchell 1987).

By experimentally increasing the population of adult largemouth bass we attempted to push the system from a minnow dominated point attractor, through a zone of bistability, to a new largemouth bass-dominated point attractor (Carpenter et al. 2008). This design is different than some tests for alternate attractors that induce transitions in experimental systems from one attractor to another within the zone of bistability and with no structural change in the system, then monitor the system for several generations to evaluate persistence at the new attractor (Dudgeon et al. 2010). In other words, our manipulation is not designed to shift the system between attractors within a zone of bistability, but is meant to create structural changes in the system by manipulating a slow moving variable (Walker et al. 2012). This mechanism is consistent with mathematical understanding of multiple ecosystem attractors and is also thought to represent the principal mechanism of change between alternate attractors in ecosystems (Scheffer et al. 2001; Scheffer and Carpenter 2003; Fauchald 2010).

Sampling

We measured prey fish abundance daily with 30 minnow traps (6 mm mesh with two 25 mm openings) spaced approximately equidistant around the perimeter of the lake. All trapped fish were released back into the lake at their capture location. The average number of prey fish caught per trap per day for each summer was concatenated into one time series (cf., Carpenter 1993). The resulting time series was log transformed and differenced once prior to the statistical analysis to ensure normality of time series model (see below) residuals. We only sampled from late May to early September but concatenating these time series is unlikely to affect our analysis because our sampling period encompassed the dominant ecological processes relevant to this study. Further, there were no obvious jumps between years that would suggest dramatic overwinter changes in fish abundance that might adversely affect the statistical analysis (Fig. 1, see also Appendix A).

Statistical analysis

Aggregates of linear processes may cause changes in the mean or variance of a time series and these changes can be mistaken for nonlinear structure by statistical tests for linearity. Time series models commonly applied to ecological data, such as autoregressive moving average models, filter linear structure from the mean, but the residuals could contain linear structures from the error variance that could be mistaken for hidden nonlinear structure. Consequently, we filtered the data through a generalized autoregressive conditional heteroskedasticity (GARCH) time series model (Bollerslev 1986). GARCH models remove linear relationships from the time series by predicting mean values and
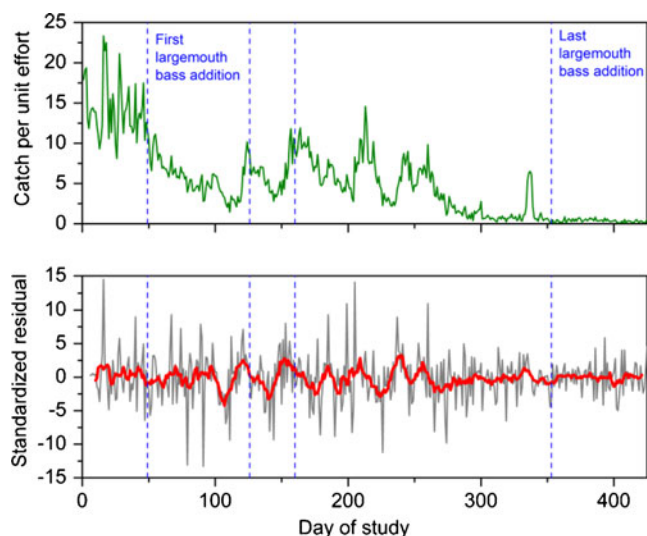
Fig. 1 *Top* Mean catch per day for minnow traps in the manipulation lake for four summers (11 May–27 August 2008; 18 May–4 September 2009; 17 May–3 September 2010; 16 May–3 September 2011). The largemouth bass additions are denoted with *dashed vertical blue lines*. We consider the time before the first addition and after the last addition to be stable. The time between these additions is considered the transition. *Bottom* The *gray line* is the time series of standardized residuals from the GARCH time series model fit to the mean catch-per-day time series. The *red line* is the standardized residuals smoothed using a seven-point moving average

error variances based on linear terms (Bollerselev 1986; Hsieh 1991). Structure in the residuals of such models is likely due to nonlinear processes affecting either the mean or the variance that are not removed by the GARCH model. We fit the models using maximum likelihood in an approach that is typical for application of GARCH models. This approach is described in detail in Appendix A. We standardized the residuals from the GARCH model by dividing by the conditional variance (Hsieh 1991). We plotted ecosystem phase space trajectories based on the standardized GARCH residuals to identify the form of the nonlinear relationship. Ecosystem trajectories for standardized GARCH residuals are created by plotting in three dimensions a state variable $x(t)$ by $x(t+T)$ by $x[t+(m-1)T]$, where m is an embedding dimension and T is a time lag (Schaffer 1984). The resulting plot contains the dynamical properties of the system and the patterns formed are diagnostic of different types of nonlinear dynamics and attractors (Takens 1981; Schaffer 1984). Some types of stochastic variation may alter the nature of nonlinear dynamics and a limitation of plotting the ecosystem trajectories is that the lagged variables approach is not designed to handle this (Horsthemke and Lefever 1984). However, the noise in this system is thought to be additive (see Carpenter et al. 2008) and while this type of noise may cause variability in phase plots such that it is more difficult to discern patterns, additive noise should not alter the underlying dynamics

recovered in the plot. To minimize these effects, we smoothed the standardized GARCH residuals using a seven-point moving average and plotted the resulting trajectories as B-splines (cf., Schaffer 1984). We also created phase plots in the original state space of the data (i.e., using unfiltered data) for comparison. We display each phase plot in two dimensions for ease of viewing. For each plot, the X ($x(t)$) and Z ($x[t+(m-1)T]$) axis are the abscissa and ordinate, respectively. Each phase plot uses an embedding dimension $m=2$ and lag $T=3$.

We tested the standardized residuals for departure from being independent and identically distributed (IID) using the Brock–Dechert–Scheinkman (BDS) test (Brock et al. 1991; 1996; see Lai 1996; Carpenter et al. 2011, and Dakos et al. 2012 for applications of the BDS test in ecological contexts). The standardized GARCH residuals are IID if linear processes determine the ecosystem dynamics (Hsieh 1991). For some nonlinear processes, including the ones we are interested in, the standardized GARCH residuals are not IID (Hsieh 1991; Dakos et al. 2012). The BDS test can be thought as a statistical test for spatial correlation of time series histories in phase space (Brock et al. 1991; 1996). After GARCH filtering, linear dynamics will create a random pattern in phase space whereas nonlinear dynamics will be patterned (correlated) in phase space (Brock et al. 1991; Schaffer 1984). The GARCH model can approximate and remove some nonlinear dynamics (Engle 1982; Granger 1991). Hence in our application, the BDS test applied to the standardized GARCH residuals is a conservative way to screen out linear mechanisms that could otherwise appear to be nonlinear dynamics (Granger 1991; Brock et al. 1996; Dakos et al. 2012). We calculated probability values for the BDS test by bootstrapping ($n=10,000$ permutations) the standardized GARCH residuals (Brock et al. 1996; Carpenter et al. 2011). We did not use asymptotic probability values for the BDS test because they deviate considerably from the normal distribution if the GARCH model is not correctly specified (Brock et al. 1991; Brooks and Heravi 1999). The bootstrapped probability values are robust to potential misspecification errors (Brock et al. 1991).

The BDS test has two free parameters, the embedding dimension and the radius, used to determine if the history of points in the system trajectory are near each other in phase space. We calculated the BDS test with a variety of embedding dimensions and radius parameters because there is no theoretically optimal parameter choice (Brock et al. 1991; 1996; Hsieh 1991). Significant BDS tests for a wide variety of combinations of embedding dimensions and radii indicate a robust conclusion (i.e., indicating nonlinear vs. linear dynamics). We applied the BDS test instead of other tests (e.g., the S-map procedure used by Hsieh et al. 2005) because BDS is well vetted and has good power for a variety of types of dynamics (Hsieh 1991; Brock et al. 1991). Other

linearity tests (e.g., S-map or Tsay's test; see Hsieh et al. 2005 and Tsay 1986, respectively) may be more powerful than the BDS test for certain narrowly specified hypotheses, but we do not assume one type of dynamic a priori and hence a more general test is appropriate for our application (Brock et al. 1991; Brooks and Henry 2000).

The two approaches we apply to identify alternate attractors are complementary. The phase space plots are the main results of the analysis and represent a unique case where a transition between ecosystem attractors can be visualized in phase space. The BDS test is a supporting result that does not identify alternate attractors directly, but rules out spurious linear explanations for the patterns observed in the phase plots.

Results

Prior to the first largemouth bass addition to Peter Lake, small prey fishes were abundant based on trap catches and there was high day-to-day variability (Fig. 1, top panel). After the first largemouth bass addition, catches immediately declined. Variability shifted to lower frequencies—meaning from high day-to-day variability to longer-term oscillations. By the time of the last largemouth bass addition, daily catches were low and stable (Fig. 1, top panel).

The standardized GARCH residuals are displayed in the bottom panel of Fig. 1 (gray line). Tabular results from the model selection procedure and parameter values of the best fitting GARCH model used to produce the residuals are given in Appendix A. The smoothed values (red line) are steady before and after the first and last largemouth bass additions, consistent with linear dynamics at a point attractor. However, there are oscillations during the transition between point attractors (the time between the first and last largemouth bass addition), indicating that the oscillations in the unfiltered catch time series are likely due to nonlinear dynamics. The oscillations in the standardized GARCH residuals are of approximately the same amplitude, suggestive of limit cycle dynamics. There were no oscillations prior to the first largemouth bass addition that would suggest nonlinearity due to the early golden shiner addition. The bootstrap BDS test applied to the raw (gray line, bottom panel Fig. 1) standardized GARCH residuals was significant over a wide range of parameter values. Twenty one of 24 tests were significant at the 0.05 level of significance and two additional tests were significant at the 0.1 level. Only one BDS test was not significant. The large number of tests with low probability values, especially considering that the BDS test is conservative when applied to GARCH residuals (Granger 1991; Brock et al. 1996), indicates that the oscillations in standardized GARCH residuals cannot be explained by linear processes and can plausibly be attributed

to nonlinear dynamics such as those associated with alternate attractors (Table 1).

Figure 2 is the phase portrait for the Peter Lake minnow trap time series prior to GARCH filtering. The line represents the trajectory of the prey fish community over time as it moves to different parts of the phase space. The mean catch declines during the study and the system dynamics change as the mean catch does. The blue portion of the line is the system varying around an attractor, prior to the first largemouth bass addition. The gray line is the trajectory during the transition period (between the first and last largemouth bass additions). The circular pattern is consistent with the fish entering into a limit cycle (May 1972). The red line is the trajectory during the period after the last largemouth bass addition. There is considerably less variability after the transition period than before the transition.

Figure 3 is the phase portrait for the Peter Lake minnow trap time series based on standardized GARCH residuals. The same basic dynamics are present as in the raw data, but the form of the attractors is clearer. Prior to the first largemouth bass addition (blue portion of the trajectory), the system is varying around a point attractor. The system has some excursions away from the attractor towards the upper right quadrant of the figure, but the trajectory returns around the same point attractor. The transition period (gray portion of the trajectory) retains its circular pattern consistent with a limit cycle dynamic. After the transition period (red line portion of the trajectory) the system varies around a point attractor with some excursions to the bottom left quadrant. The magnitude of variability around the two point attractors is much more similar in the phase plot based on standardized GARCH residuals (Fig. 3) than in the phase plot based on the raw data (Fig. 2).

The two point attractors in Fig. 3 appear to overlap in phase space. This is because the figures are drawn from standardized GARCH residuals, which are centered on zero. Hence, the two point attractors are centered at zero. To clarify the dynamics and emphasize that these are unique point attractors, we replotted the trajectories before and after the first and last

Table 1 Probability values from bootstrapped (n=10,000) BDS tests on the standardized GARCH residuals. We experimented with a variety of radiuses (ε=0.25–2×σ, where σ is the standard deviation of the standardized GARCH residuals) and embedding dimensions (m=2–5)

ε	m=2	m=3	m=4	m=5
0.25×σ=0.858	0.0079	0.0046	0.0057	0.0053
0.50×σ=1.716	0.0041	0.0007	0.0004	0.0002
0.75×σ=2.574	0.0031	0.0017	0.0002	0.0000
1.00×σ=3.433	0.0117	0.0056	0.0061	0.0059
1.50×σ=5.149	0.1025	0.0127	0.0093	0.0089
2.00×σ=6.865	0.4064	0.0733	0.0203	0.0146
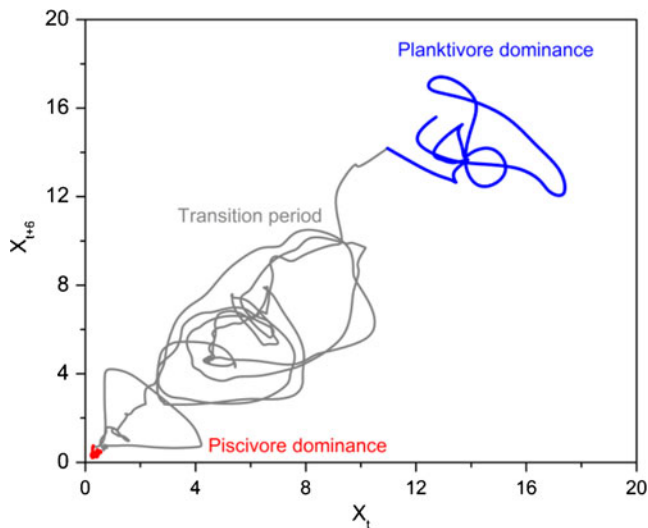
Fig. 2 Phase space plot of the Peter Lake minnow trap time series (untransformed and unfiltered). The *blue trajectory* is the period prior to the first largemouth bass addition. The *gray trajectory* is the transition period. The *red trajectory* is the period after the last largemouth bass addition. The system is initially at a point attractor, but enters into a limit cycle after the first largemouth bass addition. The system has returned to a new point attractor by the time of the last largemouth bass addition

largemouth bass additions with vectors for each point in time to denote the direction of the system trajectory (Fig. 4). The trajectory during the transition period is excluded for clarity. These vectors show the trajectories almost always returning to
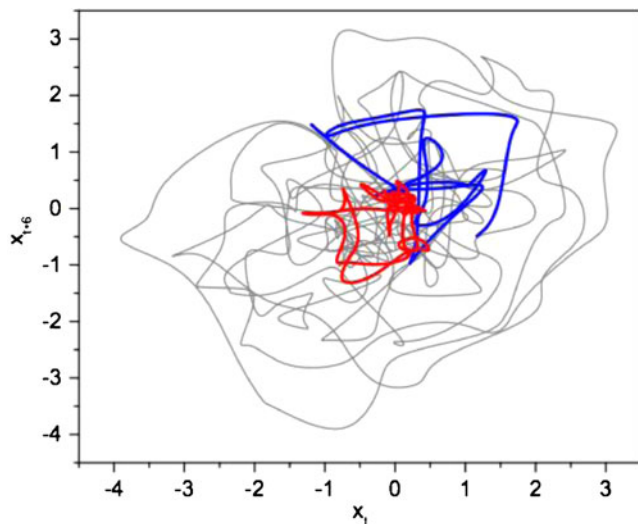

Fig. 3 Phase space plot of standardized GARCH residuals for the Peter Lake minnow trap time series. The *blue trajectory* is the period prior to the first largemouth bass addition. The *gray trajectory* is the transition period. The *red trajectory* is the period after the last largemouth bass addition. The system is initially at a point attractor, but enters into a limit cycle after the first largemouth bass addition. The system has returned to a new point attractor by the time of the last largemouth bass addition. The two point attractors appear very close to each other because they are based on the standardized GARCH residuals that are centered at zero

the point attractors. However, when there are large excursions, the trajectories before the first and after the last largemouth bass addition "spin" back to the attractors in opposite directions (Fig. 4), indicating that the attractors are unique even though they overlap in phase space.

Discussion

Our analysis provides evidence of two point attractors in a food web. The system began oscillating and the transition began soon after the first largemouth bass addition. These oscillations continued for 2 years until the system converged to a new, predator-dominated attractor. The BDS test ruled
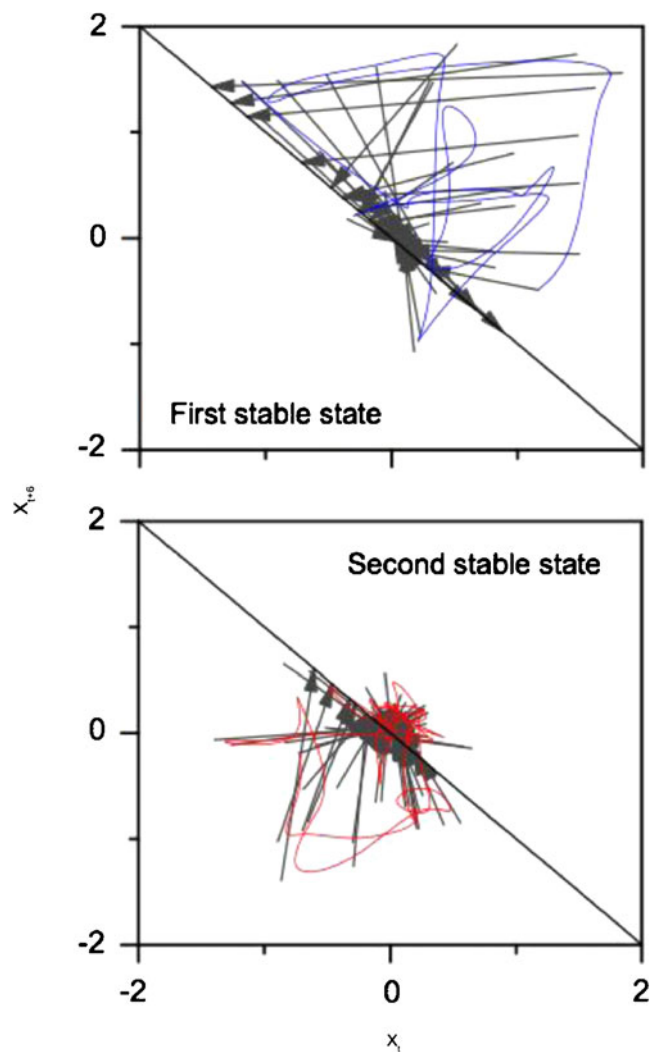
Fig. 4 Vector plots for the manipulation lake minnow trap time series trajectories before the first (*top*) and after the last (*bottom*) largemouth bass additions when the manipulation lake varied around point attractors. The point attractors appear close to each other because the time series are center around zero. However, the system diverts and varies around these states in different directions, indicating that they are distinct

out linear explanations for these patterns suggesting that the manipulation represents a true nonlinear regime shift between alternative attractors.

The transitional dynamics were due to the interaction of fast and slow ecological processes. Largemouth bass abundance is a slow changing variable (Walker et al. 2012), driven by our experimental additions and the annual reproductive cycles of this species. Minnow catch is a fast-changing variable where large magnitude intra-annual variability is driven by behavior, specifically the decisions to move between foraging zones and refuges as well as shoaling in response to predation risk (Carpenter et al. 2011). We interpret the oscillations in our analysis as resulting from delays due to annual reproductive cycles. The largemouth bass had a large year class in 2009 and direct and indirect predation risk suppressed competition from minnows such that many of these young-of-year largemouth bass survived through the winter into 2010 (cf. Post et al. 1998). The juvenile largemouth bass grew rapidly and were able to prey on small minnows midway through 2010. The largemouth bass spawned again in 2010 and the system was pushed out of an oscillatory phase to the largemouth bass-dominated point attractor. The extended delay between annual reproductive cycles of largemouth bass allowed time for cycles to form in minnow dynamics due to behavior. Eventually, largemouth bass dominance suppressed minnow cycles as the system settled to the alternate attractor.

Recent theoretical and field studies have identified early warning signals such as increased variance and increased autocorrelation that occur in ecological time series prior to shifts between alternate attractors (van Nes and Scheffer 2007; Carpenter et al. 2008; Scheffer et al. 2009; Carpenter et al. 2011). Autocorrelation and variance will often increase together prior to a critical transition between alternate attractors driven by a slow variable (Brock and Carpenter 2012), but these indicators do not increase simultaneously if noise perturbs the system from one attractor to another or if there is no shift between attractors (Ditlevsen and Johnsen 2010; Wang et al. 2012). The indicators will also not respond to step changes in control variables, for instance if the largemouth bass additions suddenly pushed the system to a new attractor without allowing for changes in internal feedback mechanisms (Carpenter et al. 2011). We previously reported increased variance and autocorrelation in chlorophyll-a concentration and zooplankton biomass prior to a suspected shift between alternate attractors in this experiment (Carpenter et al. 2011; Seekell et al. 2012; Pace et al. 2013). These increases occurred during the transition period and dissipated after the shift between attractors. The early warning indicators provide strong corroborating evidence of the nonlinear dynamics identified in our present analysis because variance and autocorrelation would not have increased simultaneously if the food web had not shifted from one attractor to another or if the transition was caused by a strong perturbation and not our experimental manipulation. Further,

these indicators would not have returned to low levels after the transition if the system remained in an unstable condition as opposed to converging to a new attractor.

How long will the system persist in the predator-dominated state? This is difficult to predict. Some shifts between attractors are essentially permanent, at least at time scales relevant to humans (e.g., desertification; species extinctions), but others are not (e.g., trophic cascades). While we cannot predict with certainty how long the system will stay in the predator-dominated state, we do know that it is possible for largemouth bass-dominated states to persist for long periods. For instance, an adjacent lake (Paul Lake) has been dominated by largemouth bass for at least 30 years (Carpenter et al. 2001). Peter Lake had a similar largemouth bass-dominated fish community prior to 1991 and this suggests that a largemouth bass-dominated state in Peter Lake could also persist for an extended period of time (Carpenter et al. 2001). However, largemouth bass are cannibalistic and this can lead to large oscillations in adult largemouth bass abundance over time. For instance, in Paul Lake, adult largemouth bass populations vary by fivefold in 8- to 10-year cycles (Post et al. 1998). If the largemouth bass in Peter Lake enter into cyclical population dynamics, the probability of a sudden reverse transition will increase during the minima of these cycles, when stochastic events (such as winterkills) might push the largemouth bass population below the critical threshold for dominance, causing a reverse transition to small fish dominance (Rosenzweig 1971). Hence, while the predator–prey role reversal associated with the transition between point attractors occurred very rapidly in this study (relative to the lifespan of the organisms: ~10 years for largemouth bass), the longer-term dynamics are not clear and will depend both on the life history of the fish (the ability to develop strong cohort dynamics) and on the occurrence of strong random shocks to the system. In addition, the small fish populations in Peter Lake were not driven to extinction during the 4 years of this study but may be in the longer term. Under such conditions, piscivore dominance might be more sustained and less subject to reversal to the alternate attractor of small fish dominance.

Our analytical approach is well suited for identifying the existence of alternate attractors in ecosystems. However, our approach is unable to resolve some parallel problems that are particularly relevant for ecosystem management. For instance, we are unable to calculate a threshold value for the transition between states from our analysis. Environmental stochasticity creates a range of possible transitions depending on the magnitude of perturbations and hence it is difficult to know what the critical point will be prior to reaching it (Guttal and Jayaprakash 2007). We are also unable to calculate the probability that the transition is or is not reversible through management (Carpenter and Lathrop 2008). These questions are probably best addressed with a correctly specified mechanistic model of the system. Despite this limitation, confirmation of

the existence of alternate ecosystem states has profound management implications because the ability to switch between states is known, even if thresholds are unknown (Carpenter et al. 1999; Carpenter 2001; Peterson et al. 2003).

The magnitude and variability in phase space trajectories was different between the standardized GARCH residuals and the raw minnow trap catch time series (compare Figs. 2 and 3). There is much more variability in the raw data in the period prior to the transition than in the period after the transition. This is because mean catch is tightly correlated with the variance and skewness of the distribution of catch (cf., Seekell 2011; Seekell et al. 2011a). The high variance at the first attractor in the raw data is a function of the inherent high variability when fish catch is high. Likewise, the low variability at the second attractor is because there is inherently low variability when mean catch is low. This high and low variability is not due to the regime shift but rather the decline in minnow populations resulting from increased predator abundance. These changes in variability are not present in the phase plot for standardized GARCH residuals (Fig. 3). For standardized GARCH residuals, the two attractors have similar variability because the GARCH model removed changes in variance due to linear dynamics (i.e., due simply to the reduced size of minnow populations caused by the predator additions). Further, the magnitude of variability during the transition is greater than the variability around the attractors in Fig. 3. This is consistent with theoretical expectations for lake food webs (see Carpenter et al. 2008), indicating that the GARCH filtering isolated nonlinear dynamics associated with the regime shift (i.e., the results are not simply due to a linear reduction in prey due to predator additions).

The significant GARCH terms in our model indicate time-varying variance. While the application of GARCH models is extremely common in some disciplines (e.g., economics), we know of no prior applications to ecological data. Hence, it is difficult to know the prevalence and potential implications of GARCH type processes in ecosystems. The GARCH dynamics in this system are consistent with a system approaching a transition between alternate attractors (Seekell et al. 2011b; Seekell et al. 2012). GARCH dynamics in stable systems could provide false positive early warnings of transitions between ecosystem attractors. However, GARCH dynamics are not typically present in models of stable ecosystems (Seekell et al. 2011). Further, the significance of BDS tests here and in our previous analyses (see Carpenter et al. 2011) indicate potential nonlinearities beyond GARCH processes and this is consistent with expectations for early warning indicators (Carpenter et al. 2011; Dakos et al. 2012). Further application of these types of models to ecological data is necessarily to better understand the prevalence of GARCH dynamics in ecosystems.

The potential for transition between point attractors is widely discussed in ecology but the evidence for and approaches to detecting these attractors in ecosystems have been disputed (e.g., Connell and Sousa 1983; Sutherland 1990; Scheffer and Carpenter 2003; Schröder et al. 2005; Dudgeon et al. 2010). Tests for hallmark patterns of alternate attractors such as hysteresis, path dependence, and bimodality have provided evidence for the existence of alternate attractors in a wide variety of systems including laboratory model systems, oceans, lakes, and forests, at a variety of scales—from competition between two species (e.g., between floating and submerged vegetation, Scheffer et al. 2003) to huge changes in regional structure (e.g., collapse of Saharan vegetation between 5000 and 6000 years ago, deMenocal et al. 2000; Scheffer and Carpenter 2003). However, these results are often based on observational records and a review of experimental tests for alternative attractors by Schröder et al. (2005) revealed that ecosystem-scale studies and studies involving long-lived organisms such as fish typically do not find evidence of alternative attractors. This has led concern over the generality of the concept of alternative attractors (Schröder et al. 2005). For instance, there is disagreement over the applicability of the concept of alternative states to the highly visible and dramatic shift from hard coral to algal dominance in Caribbean coral reefs where ecosystem-scale experiments are difficult or impossible to conduct and long-term data is both rare and potentially confounded by changing baseline conditions (Mumby et al. 2007; Dudgeon et al. 2010). Our result relative to alternate attractors is specific to the fish community dynamics in one lake analyzed in this study, but is a consequence of relatively general ecosystem phenomena (trophic triangles, trophic cascades). Our results show empirically that alternate attractors can exist at the ecosystem scale and that these attractors can be reconstructed and evaluated from high-resolution time series.

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