

Are rapid transitions between invasive and native species caused by alternative stable states, and does it matter?

GRETCHEN J. A. HANSEN,^{1,3} ANTHONY R. IVES,² M. JAKE VANDER ZANDEN,¹ AND STEPHEN R. CARPENTER¹

¹Center for Limnology, University of Wisconsin, 680 North Park Street, Madison, Wisconsin 53706 USA

²Department of Zoology, University of Wisconsin, 250 North Mills Street, Madison, Wisconsin 53706 USA

Abstract. Rapid transitions in ecosystem structure, or regime shifts, are a hallmark of alternative stable states (ASS). However, regime shifts can occur even when feedbacks are not strong enough to cause ASS. We investigated the potential for ASS to explain transitions between dominance of an invasive species, rusty crayfish (*Orconectes rusticus*), and native sunfishes (*Lepomis* spp.) in northern Wisconsin (USA) lakes. A rapid transition from *Lepomis* to rusty crayfish dominance occurred as rusty crayfish invaded Trout Lake, and the reverse transition resulted from an eight-year experimental removal of rusty crayfish from Sparkling Lake. We fit a stage-structured population model of species interactions to 31 years of time-series data from each lake. The model identified water level as an important driver, with drought conditions reducing rusty crayfish recruitment and allowing *Lepomis* dominance. The maximum-likelihood parameter estimates of the negative interaction between rusty crayfish and *Lepomis* led to ASS in the model, where each species was capable of excluding the other within a narrow range of environmental conditions. However, uncertainty in parameter estimates made it impossible to exclude the potential that rapid transitions were caused by a simpler threshold response lacking alternative equilibria. Simulated forward and backward transitions between species dominance occurred at different environmental conditions (i.e., hysteresis), even when the parameters used for simulation did not predict ASS as a result of slow species responses to environmental drivers. Thus, ASS are possible, but by no means certain, explanations for rapid transitions in this system, and our results highlight the difficulties associated with distinguishing ASS from other types of threshold responses. However, whether regime shifts are caused by ASS may be relatively unimportant in this system, as the range of conditions over which transitions occur is narrow, and under most conditions, the system is predicted to exist in only a single state.

Key words: alternative stable states; climate change; drought; invasive species; *Lepomis* spp.; *Orconectes rusticus*; regime shift; rusty crayfish; sunfishes; threshold; time series; water level.

INTRODUCTION

Ecological regime shifts are rapid transitions between states that alter the fundamental nature of ecosystems, often with severe ecological and economic impacts (Scheffer et al. 2001). Many mechanisms can cause regime shifts. Some regime shifts are transitions between alternative stable states (ASS; sensu May 1977), where multiple stable equilibria are possible under identical environmental conditions. However, regime shifts can also occur due to a nonlinear or threshold response in systems for which only one stable state exists for any set of conditions (Scheffer et al. 2001, Andersen et al. 2009). Regime shifts caused by ASS are distinguished by several unique properties of both theoretical and practical interest. Systems containing ASS exhibit hysteresis; that is, backward and forward transitions between states occur at different levels of environmental

drivers (Scheffer et al. 2001, Andersen et al. 2009). This phenomenon relates to the resilience of a given state, i.e., the magnitude of change in environmental drivers needed to cause the shift between states (Walker and Meyers 2004). Practically, hysteresis means that restoring environmental conditions to those that existed immediately before a regime shift will not reverse the change (Suding and Hobbs 2009), while forward and backward shifts between states should occur at the same environmental conditions in cases where no ASS exist. Furthermore, systems with ASS will move toward different end points depending on initial conditions; this is not the case in systems lacking ASS (Scheffer et al. 2001). Despite the importance of identifying whether transitions are caused by ASS, few studies have done so empirically (but see, e.g., Bestelmeyer et al. 2011, Fung et al. 2011, Bestelmeyer et al. 2013), due in part to rigorous data requirements (Collie et al. 2004, Schröder et al. 2005). The strongest approaches to demonstrating ASS combine experiments, observations, and modeling (Carpenter 2003, Scheffer and Carpenter 2003).

Manuscript received 17 January 2013; revised 16 April 2013; accepted 25 April 2013. Corresponding Editor: K. O. Winemiller.

³ E-mail: ghanzen2@wisc.edu

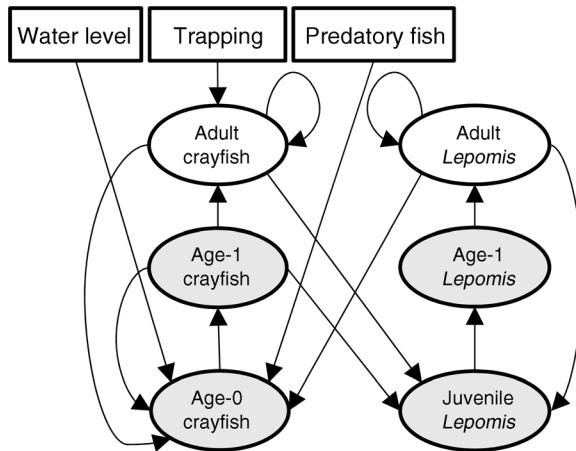


FIG. 1. Conceptual diagram of the time-series model. Ovals represent modeled life stages of rusty crayfish (*Orconectes rusticus*) and native sunfishes (*Lepomis* spp.) in northern Wisconsin (USA) lakes. White ovals indicate stages for which we had observed data and, thus, estimated both process error and measurement error; gray ovals represent life stages for which we had no observed data. Rectangles indicate observed drivers of rusty crayfish abundance. Arrows indicate parameters in the state-space model. Predatory fish include smallmouth bass, largemouth bass, rock bass, and walleye.

Species invasions exhibit several traits consistent with ASS (c.f., Scheffer and Carpenter 2003). Complex food web interactions common to invasive species are known to produce ASS, such as strong interspecific competition (Begon et al. 1986) and life history omnivory (Mylus et al. 2001). Invasive species can produce rapid transitions from a state where invaders exist at low abundance to a state of dominance, and vice versa (e.g., Huxel 1999, Crooks 2005, Strayer et al. 2006), producing jumps in time series consistent with multiple equilibrium states. Invasive species abundances can be spatially and temporally heterogeneous (e.g., Brown and Carter 1998, Simberloff and Gibbons 2004, Roth et al. 2007), producing bimodal frequency distributions also consistent with expectations of two ASS. The outcome of species invasions may depend upon initial conditions, such as the number of invasive propagules (Lockwood et al. 2005) or the state of the invaded community (Case 1990). Finally, restoring communities to pre-invasion states is often impossible, even when the invasive is reduced to extremely low numbers (e.g., Cox and Allen 2008, Zipkin et al. 2009, Firn et al. 2010), suggesting the possibility of hysteresis.

Rusty crayfish (*Orconectes rusticus*) are an invasive species capable of producing rapid transitions in ecosystems, sometimes across multiple trophic levels (Lodge et al. 1994, Wilson et al. 2004). However, some systems resist the negative effects of invasion; rusty crayfish establish populations, but persist at low densities with minimal effects (Garvey et al. 2003, Roth et al. 2007). This variation in rusty crayfish relative abundance could result from variation in predation by

native bluegill and pumpkinseed sunfish (*Lepomis macrochirus* and *L. gibbosus*, respectively; hereafter *Lepomis*; Roth et al. 2007, Tetzlaff et al. 2010) and other predatory fishes in the littoral zone (Mather and Stein 1993, Garvey et al. 2003). The interaction between *Lepomis* and rusty crayfish is complex. *Lepomis* impact rusty crayfish populations when they prey upon juveniles (Roth et al. 2007). At the same time, rusty crayfish can negatively affect *Lepomis* recruitment via two primary mechanisms (Wilson et al. 2004, Roth et al. 2007): by destroying aquatic macrophytes (Olsen et al. 1991, Lodge et al. 1994) that create critical habitat for *Lepomis* juveniles (Mittelbach 1981; see Plate 1) and by consuming *Lepomis* eggs (Dorn and Mittelbach 2004). Thus, interactions between rusty crayfish and *Lepomis* are akin to a competitive relationship, wherein each species negatively affects the recruitment of the other (Fig. 1; Chesson 1986). These interactions could produce ASS, whereby high densities of rusty crayfish reduce macrophytes necessary for the survival of *Lepomis* (Tetzlaff et al. 2010), which in turn reduces predation on rusty crayfish juveniles, allowing further rusty crayfish population growth, and thus, further reducing macrophyte habitat in a positive feedback loop (Roth et al. 2007).

Rusty crayfish interactions with *Lepomis* are further complicated by the influence of climate on crayfish habitat in lakes. In recent years, regional drought has resulted in the lowest water levels on record in the temperate seepage lakes of northern Wisconsin, USA (water-level data available online),⁴ dramatically reducing littoral cobble habitat used by juvenile rusty crayfish to avoid predation (Kershner and Lodge 1995). Because drought reduces cobble habitat, it has the potential to increase predation on juvenile rusty crayfish that depend upon cobble for shelter (Garvey et al. 2003), and the positive feedback between rusty crayfish and *Lepomis* may be influenced by climate-driven fluctuation in water levels.

Using an ecosystem manipulation, observational data, and modeling, we evaluated evidence for ASS to explain transitions between invasive rusty crayfish and native *Lepomis*. We used 31 years of time-series data from each of two lakes. In one lake, we conducted an eight-year experimental crayfish removal, resulting in a rapid transition from rusty crayfish to *Lepomis* dominance. In the second lake, we observed the reverse transition as rusty crayfish invaded. Our objectives were to (1) quantify empirical relationships between rusty crayfish, native fishes, and water level; (2) evaluate the evidence for alternate stable states vs. a threshold response that does not include ASS; and (3) identify conditions that cause rapid transitions between rusty crayfish and *Lepomis* dominance, regardless of whether ASS are predicted.

⁴ www.lter.limnology.wisc.edu

MATERIALS AND METHODS

Study systems

To quantify relationships between rusty crayfish, fish, water levels, and trapping (Fig. 1), we used time-series data collected from 1981 to 2011 in two lakes, both part of the North Temperate Lakes Long Term Ecological Research (NTL-LTER) site in Vilas County, Wisconsin, USA (more information *available online*; see footnote four). Sparkling Lake (46°00' N, 89°42' W) is a 64-ha mesotrophic seepage lake (20 m maximum depth). Rusty crayfish invaded Sparkling Lake in the 1970s (Capelli 1982), and data collection in Sparkling Lake began after rusty crayfish established. Adult rusty crayfish were removed from Sparkling Lake from 2001 to 2008 via experimental trapping and changes in fishing regulations to increase predation on juvenile crayfish (Hein et al. 2006); rusty crayfish abundance declined by two orders of magnitude during the removal (Hein et al. 2007, Hansen et al. 2013). Water levels declined in Sparkling Lake from 2005 to 2009, and the water level in 2009 was the lowest on record (Fig. 2). The littoral zone of Sparkling Lake contains cobble located primarily in the shallow nearshore areas (Hein et al. 2006), and most of this cobble was exposed when the water level fell. Consequently, much of the habitat that provided juvenile crayfish with refuge from predation was eliminated.

For data on the initial phase of invasion, we used nearby Trout Lake (46°2' N, 89°40' W), a 1608-ha mesotrophic drainage lake (36 m maximum depth). Rusty crayfish invaded Trout Lake in the 1970s, but did not disperse around the entire lake for over two decades (Wilson et al. 2004). Trout Lake is a stream-fed, low-lying lake, and the littoral zone habitat consists mainly of cobble (Roth et al. 2007); therefore, neither water levels nor area of cobble have been affected by recent drought conditions (NTL-LTER; information *available online*, see footnote 4). Neither rusty crayfish nor fishing regulations were manipulated in Trout Lake during our study period.

Data collection

Data, methods, and equipment descriptions are *available online* (see footnote four). Abundances of rusty crayfish, *Lepomis*, and other predatory fishes were indexed using annual catch per unit effort (CPUE) data from 1981 to 2011. Annual mean and standard error of CPUE were calculated using the catch per trap for rusty crayfish, and catch per fyke net of *Lepomis* and other predatory fish (including largemouth bass, *Micropterus salmoides*; smallmouth bass, *M. dolomieu*; rock bass, *Ambloplites rupestris*; and walleye, *Sander vitreus*) greater than 80 mm total length. Annual counts of zero were replaced by one-half of the lowest nonzero value recorded for the population. Rusty crayfish and *Lepomis* CPUE were log_e-transformed, and all CPUE data were standardized to have mean = 0 and variance = 1 to

facilitate comparisons of parameter effect sizes. Mean annual water level in Sparkling Lake was calculated from observed LTER data from 1984 to 2011. To generate water-level data prior to 1984, we interpolated from the linear relationship ($r = -0.92$) between the water level in Sparkling Lake and the annual mean depth of a nearby United States Geological Survey groundwater well (45°55'17" N, 89°14'40" W; Groundwater Watch, *available online*).⁵

Time-series model

To investigate the transitions between rusty crayfish and *Lepomis* abundance, we used an age-structured time-series model fit to data from both lakes simultaneously. Therefore, the data include both the invasion phase of rusty crayfish (Trout Lake) and the declining phase caused by experimental crayfish removal (Sparkling Lake). Our model has the potential to produce ASS, but their existence depends on parameter estimates (cf., Collie et al. 2004, Steele 2004); the model thus provides an opportunity to evaluate statistically whether ASS explain observed dynamics. The model has a nonlinear state space form (Harvey 1989) and accounts for process errors (due to stochasticity caused by environmental drivers not included in the model) and observation errors (due to sampling variability). The model is based on three sets of equations: one for the biological processes driving rusty crayfish dynamics, one for the biological processes driving *Lepomis* dynamics, and one to describe the sampling used to generate observed data. Analyses were run in Matlab v.8.0 (MathWorks 2012).

To model the dynamics of rusty crayfish, we used the following set of equations:

$$\begin{aligned} x_1(t) &= f_x(x_2(t-1) + x_3(t-1)) \\ &\quad \times \exp\left[-k_x(x_2(t-1) + x_3(t-1))\right. \\ &\quad \left.- a_x y_3(t-1) - cu_2(t)^q - vu_3(t)\right] \\ x_2(t) &= s_x x_1(t-1) \\ x_3(t) &= s_x [x_2(t-1) + (1 - mu_1(t))x_3(t-1)] \\ &\quad \times \exp[\epsilon_x(t)] \end{aligned} \quad (1)$$

where the variates $x_1(t)$, $x_2(t)$, and $x_3(t)$ denote the densities of young-of-year, one-year-old, and adult (trappable) crayfish in year t , respectively. Covariates $u_1(t)$, $u_2(t)$, and $u_3(t)$ give the trapping pressure on adult rusty crayfish, lake level, and the density of predatory fish in year t , respectively. Trapping pressure $u_1(t)$ was

⁵ <http://groundwaterwatch.usgs.gov/AWLSites.asp?S=455517089144001&ncd>

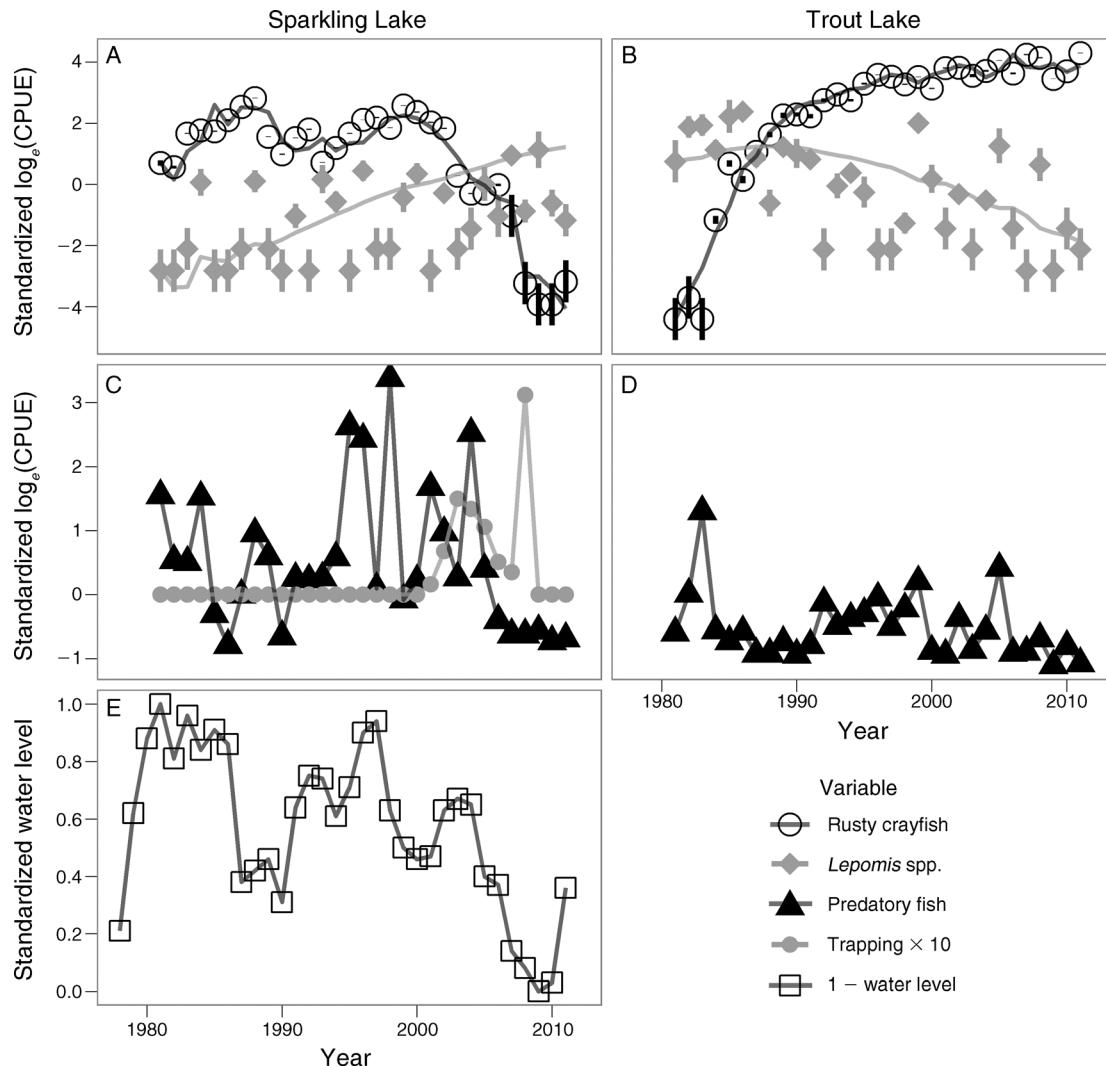


FIG. 2. Data used in the state-space model. (A, B) Standardized \log_{10} (CPUE) (catch per unit effort) of rusty crayfish (black-outlined, open circles) and *Lepomis* spp. (gray-filled diamonds) in (A) Sparkling Lake and (B) Trout Lake; error bars are standard errors. Values from the fitted model (lines) are the updated estimates of population abundances from the extended Kalman filter. (C, D) Standardized values of predatory fish CPUE (smallmouth bass, rock bass, and walleye; solid black triangles), $10 \times$ removal trapping effort (solid gray circles), in (C) Sparkling Lake and (D) Trout Lake. (E) Standardized water level (open squares) in Sparkling Lake (measured in meters above sea level before standardization). Water level for Trout Lake was set to 0 for all years (not shown). In panels (C–E), lines connect observed data points. Fish and crayfish abundance data were standardized to have a mean of 0 and variance of 1. Water level was standardized to have a maximum 0 and minimum 1 for model fitting; the reverse is displayed for a more intuitive plot. Trapping effort is the number of adult crayfish removed divided by rusty crayfish CPUE, scaled to have a maximum value of 1.

measured as the number of adult crayfish removed during the manipulation divided by the abundance index of rusty crayfish caught in the same year, scaled to have a maximum value of 1. For Sparkling Lake the value of $u_2(t)$ is the reduction in the water level standardized so that 0 and 1 correspond to the maximum and minimum water level during the study period, respectively; because low lake levels are expected to remove juvenile refuge habitat, greater reductions in water level (higher values of $u_2(t)$) correspond to lower recruitment. For Trout Lake $u_2(t)$ was set to zero, because lake level remained

relatively constant in this system, and Trout Lake contains large areas of cobble (Roth et al. 2007).

The parameter m translates trapping pressure into mortality of adult crayfish due to trapping and is constrained to be between 0 and 1. We assumed that one-year-old females can reproduce, but are generally too small to be trapped effectively (Hein et al. 2006). The recruitment of young-of-year crayfish, $x_1(t)$, depends on the density of one-year-old and adult females from the previous year, $x_2(t - 1)$ and $x_3(t - 1)$, respectively, multiplied by the recruitment rate f_x .

Recruitment is density dependent, with k_x scaling the strength of density-dependent reduction in recruitment. Young-of-year crayfish survival to age 1 in the following year is given by s_x , and adults in year t depend on the density of one-year-olds and adults in year $t - 1$ multiplied by survival s_x . The survival of young-of-year crayfish in a given year is incorporated within the recruitment coefficient f_x .

Lepomis have the potential to negatively influence rusty crayfish survival via both direct predation of juveniles and competition for shared prey (Dorn and Mittelbach 1999), and both effects are combined in the single term a_x . Similarly, the effect of littoral predatory fish density (excluding *Lepomis*) on crayfish recruitment is given by v . Lake level, $u_2(t)$, reduces the number of crayfish recruited by the proportion $\exp[-cu_2(t)^q]$, where c sets the magnitude of effect of lake level on crayfish recruitment, and q allows this effect to be nonlinear.

To account for environmental variability, trappable adults experience lognormal process error described by $\epsilon_x(t)$, a Gaussian random variable with a mean of zero and standard deviation σ_x . We did not include an effect of random environmental fluctuation on young-of-year and one-year-old density, because we lack data on these groups; environmental variability affecting young-of-year and one-year-olds is implicitly included into variability experienced by adults.

Lepomis dynamics were modeled as follows:

$$\begin{aligned}
 y_1(t) &= f_y y_3(t - 1) \times \exp \left[-k_y y_3(t - 1) \right. \\
 &\quad \left. - a_y \left(x_2(t - 1) + x_3(t - 1) \right) \right] \\
 y_2(t) &= s_y y_1(t - 1) \\
 y_3(t) &= s_y \left(y_2(t - 1) + y_3(t - 1) \right) \times \exp[\epsilon_y(t)] \quad (2)
 \end{aligned}$$

where variates $y_1(t)$, $y_2(t)$, and $y_3(t)$ denote the densities of young-of-year, one-year-old, and adult fish in year t . The structure of these equations is similar to those for crayfish, although only fish of age 2 and older reproduce. The recruitment of juvenile fish, $y_1(t)$, depends on the density of adults in the previous year ($y_3(t - 1)$) multiplied by the recruitment rate f_y . The strength of adult-density-dependent reduction in recruitment is scaled by k_y . Rusty crayfish have the potential to influence *Lepomis* survival via both trophic (egg predation) and non-trophic (macrophyte habitat destruction, competition) pathways. Because data on macrophyte habitat were unavailable for the entire time series of the two lakes, both effects of rusty crayfish are combined in the single term a_y . The density of adults depends on the density of one-year-olds and adults in the previous year with survival s_y , and the density of one-year-olds depends on the density of young-of-year in the previous year with survival s_y . Adults experience lognormal process error described by the Gaussian

random variable $\epsilon_y(t)$ that has zero mean and standard deviation σ_y .

The sampling (measurement) process is described by the following set of equations:

$$\begin{aligned}
 X_3(t) &= \log x_3(t) + \alpha_x(t) \\
 Y_3(t) &= \log y_3(t) + \alpha_y(t) \quad (3)
 \end{aligned}$$

where $X_3(t)$ and $Y_3(t)$ are the observed \log_e densities of adult crayfish and *Lepomis*, respectively, and $\alpha_x(t)$ and $\alpha_y(t)$ are Gaussian random variables with mean zero and standard deviations $\sigma_{xx}(t)$ and $\sigma_{yy}(t)$, respectively. Eq. 3 uses information only on adult crayfish and *Lepomis*; Eqs. 1 and 2 describe the dynamics in terms of three age classes, and Eq. 3 maps the dynamics of the adults from these equations onto the observed data (which were collected only for adults). Standard deviations of observed \log_e densities of crayfish and fish in each year were used as estimates of $\sigma_{xx}(t)$ and $\sigma_{yy}(t)$ for each year t . Preliminary analyses suggested that these direct estimates of measurement errors underestimated the true population-level variability in the time series, so we scaled the time-dependent measurement errors as $w_x \sigma_{xx}^2(t)$ and $w_y \sigma_{yy}^2(t)$, where scaling parameters w_x and w_y were estimated in the analysis.

Preliminary analyses showed that several parameters estimates were biased (i.e., maximum-likelihood parameter estimates did not equal mean of bootstrapped parameter estimates) when all parameters were estimated from the data, probably due to correlations among parameter estimates when estimated simultaneously (Appendix A). To reduce this bias, we reduced the number of estimated parameters by obtaining some values from the literature (Table 1). The reduced-parameter model gave the same qualitative results regarding the relative strengths of intra- and interspecific interactions, although parameter estimates differed in some cases. Values of f_y and s_y for *Lepomis* were obtained from Bertschy and Fox (1999); we used fecundity and survival values from Black Lake, which gave the highest intrinsic rate of increase. For survival of crayfish, we used abundance-weighted average survivals of one-, two-, and three-year olds from Hein et al. (2006: Table 2, Method 2) obtained from data of Lorman (1980). The model included 13 remaining coefficients (Table 1) that were estimated from the data using maximum likelihood with an extended (nonlinear) Kalman filter (Harvey 1989). Adult population values at the first time point for each lake were set to the observed values, and juvenile values (that were not measured) were back-calculated assuming the populations were at the stable age distribution. Initial values of the variance in population values for crayfish and *Lepomis* were assumed to be σ_x^2 and σ_y^2 .

Statistical significance of the coefficients was obtained by parametric bootstrapping. Using parameter values estimated from the data, the dynamics of crayfish and *Lepomis* were simulated 1000 times using the full state-

TABLE 1. Parameter descriptions, sources, maximum-likelihood (MLL) estimates, and mean and 95% confidence intervals from parametric bootstrapping (where applicable).

Parameter	Description	Source	MLL estimate	Bootstrap mean	Lower 95% CI	Upper 95% CI
a_x	<i>Lepomis</i> spp. effect on juvenile crayfish	estimated from data	0.79	0.72	0.00	2.30
a_y	crayfish effect on juvenile <i>Lepomis</i>	estimated from data	0.02	0.02	0.00	0.04
c	water level effect on crayfish recruitment (Sparkling Lake)	estimated from data	5.30	5.82	3.00	8.80
f_x	maximum crayfish recruitment rate	estimated from data	58.10	19.08	4.60	184.00
f_y	maximum <i>Lepomis</i> recruitment rate	Bertschy and Fox (1999)	6.00	NA	NA	NA
k_x	rate of adult-density-dependent reduction in crayfish recruitment	estimated from data	0.05	0.06	0.02	0.08
k_y	rate of adult-density-dependent reduction in <i>Lepomis</i> recruitment	estimated from data	0.23	0.28	0.01	0.80
m	effect of trapping on adult crayfish	estimated from data	1.00	0.90	0.35	1.00
q	nonlinearity in effect water level effect on crayfish recruitment	estimated from data	0.26	0.45	0.13	1.25
s_x	survival rate of one-year-old and adult crayfish	Lorman (1980)	0.57	NA	NA	NA
s_y	survival rate of one-year-old and adult <i>Lepomis</i>	Bertschy and Fox (1999)	0.47	NA	NA	NA
v	effect of predatory fish on juvenile crayfish	estimated from data	0.00	0.06	0.00	0.40
w_x	measurement error rescaling for crayfish CPUE	estimated from data	0.93	0.96	0.00	2.70
w_y	measurement error rescaling for <i>Lepomis</i> CPUE	estimated from data	3.90	5.37	2.70	10.20
σ_x	process error standard deviation in adult crayfish survival	estimated from data	0.36	0.39	0.21	0.57
σ_y	process error standard deviation in adult <i>Lepomis</i> survival	estimated from data	0.00	0.00	0.00	0.00

Note: We modeled the dynamics of rusty crayfish (*Orconectes rusticus*) and native sunfishes (*Lepomis* spp.) in northern Wisconsin (USA) lakes. CPUE is catch per unit effort; NA, not applicable.

space model, including process and measurement error (Eqs. 1–3). The state-space model was subsequently fit to each of the 1000 simulated data sets to give 1000 sets of bootstrapped parameter values. The distributions of these parameter values approximate distributions of the estimators of the parameters, thereby giving confidence intervals.

To assess model fit, we calculated the degree of explained variance (R^2) for rusty crayfish and *Lepomis* in two ways. First, we calculated the total R^2 , which provides an estimate of overall model fit. For rusty crayfish

$$R_{\text{total}}^2 = 1 - \text{var}(x_3(t) - X_3(t)) / \text{var}(X_3(t)) \quad (4)$$

where $X_3(t)$ is the observed \log_e abundance of crayfish, and $x_3(t)$ is estimated from the process equation (Eq. 3). We also calculated the prediction R^2 , which represents the ability of the model to predict changes in abundance as follows:

$$R_{\text{prediction}}^2 = \frac{1 - \text{var}(x_3(t+1) - X_3(t+1))}{\text{var}(X_3(t+1) - X_3(t))}. \quad (5)$$

We repeated these calculations for *Lepomis*, substituting $y_3(t)$ for $x_3(t)$ and $Y_3(t)$ for $X_3(t)$.

Water level effects in Sparkling Lake

We structured the model given by Eqs. 1 and 2 to take advantage of the data from Sparkling and Trout Lakes, which together capture both the invasion phase of rusty crayfish dynamics and the declining phase caused by experimental removal. This model formulation is designed to analyze the dynamics of rusty crayfish and *Lepomis* in the general case, and assumes no differences between lakes other than differences in environmental drivers (trapping pressure on adult rusty crayfish, lake level, and the density of predatory fish). However, we were also interested in identifying the effect of changing water levels within Sparkling Lake, which was not possible using Eq. 1. Because we assumed that water levels are always high (good for crayfish recruitment) in Trout Lake, the effect of water level in Sparkling Lake is confounded by differences in crayfish recruitment between lakes not caused by differences in water levels. To assess the effects of water level on crayfish recruitment in Sparkling Lake specifically, we repeated

the analyses while replacing the first line of Eq. 1 with the following:

$$x_1(t) = f_x \left(x_2(t-1) + x_3(t-1) \right) \times \exp \left[-k_x \left(x_2(t-1) + x_3(t-1) \right) - a_x y_3(t-1) - cu_2(t)^q - vu_3(t) + bI_L \right] \quad (6)$$

where I_L is an indicator variable set to 0 for Sparkling Lake and 1 for Trout Lake, and b is an estimated parameter. Thus, b extracts any fixed difference between lakes in crayfish recruitment unrelated to water level, and the parameter c isolates the effect of water level in Sparkling Lake.

Alternative stable states

We used the maximum-likelihood parameter estimates and the 1000 bootstrapped parameter sets to evaluate the evidence for ASS in the rusty crayfish–*Lepomis* system. For each parameter set, we performed an invasibility analysis in which one species was assumed to reach equilibrium, and the per capita population growth rate of the second species was computed mathematically as it invaded (May 1973). Performing this invasibility analysis reciprocally for both species allowed us to categorize the parameter set as: (1) crayfish always exclude *Lepomis*, (2) *Lepomis* always exclude crayfish, (3) both species coexist, and (4) ASS exist in which either species, once established, can thwart the invasion of the other. To investigate ASS over a range of conditions, we decreased the per capita recruitment of crayfish by e^{-U} so that U serves as a generic bifurcation parameter; at low values of U , crayfish have high recruitment and will outcompete *Lepomis*, whereas at high values of U , *Lepomis* will outcompete crayfish. We performed the invasibility analysis for each parameter set with U ranging from -1 to 5 . Biologically, increasing U represents either increasing the (negative) effect of water level $cu_2(t)^q$ or increasing the abundance of predatory fish, $vu_3(t)$; using the generic variable U allows the results to be easily generalized to other potential environmental drivers which may influence per capita recruitment of rusty crayfish. Trapping pressure, $u_1(t)$, was set to zero for the invasibility analysis.

Simulated transitions between rusty crayfish and *Lepomis* dominance

Transitions in dominance of invasive and native species as a function of changing conditions are of both practical and theoretical interest. To visualize these transitions, we simulated rusty crayfish and *Lepomis* CPUE using Eqs. 1 and 2 under two parameter sets: one set predicting alternative stable states (the maximum-likelihood parameter set estimated from the data) and one set predicting coexistence (selected from the bootstrapped parameter estimates). In each of these

parameter sets, two scenarios were explored: the transition from rusty crayfish to *Lepomis* dominance as U increased, and the transition from *Lepomis* to rusty crayfish dominance as U decreased. Simulations were run for 200 years with U changing steadily from -1 to 5 or 5 to -1 over the course of the simulation. The first U value (and simulation year) at which each species comprised at least 99% of total abundance was recorded, and the difference between these threshold values for rusty crayfish and *Lepomis* indicated the duration of the transitions.

RESULTS

Time series model

Rusty crayfish abundance varied over three orders of magnitude in Trout Lake and two orders of magnitude in Sparkling Lake between 1981 and 2011 (Fig. 2A, B). Rusty crayfish abundance increased over time in Trout Lake; in Sparkling Lake rusty crayfish abundance was more variable, with the lowest numbers observed during and following the experimental removal (2003–2011). *Lepomis* populations showed high levels of interannual variation, with a general increasing trend in Sparkling Lake and a decreasing trend in Trout Lake (Fig. 2A, B). Predatory fish exhibited interannual variation in both lakes, but no strong directional trend (Fig. 2C, D). Water level in Sparkling Lake declined from 2005 to 2009, with the lowest observed value in 2009 (Fig. 2E).

The state-space model was able to capture crayfish dynamics well (total $R^2 = 0.91$ and 0.31 for rusty crayfish and *Lepomis*, respectively). The prediction $R^2 = 0.11$ for rusty crayfish, and is much lower than the total R^2 owing to the high autocorrelation observed in the data. The prediction $R^2 = 0.30$ for *Lepomis*, similar to the total R^2 . The model ascribed much of the interannual variability in *Lepomis* abundance to measurement error, so that the fitted line appears to average over this variability (Fig. 2A, B). This result is consistent with the large standard errors of estimates of *Lepomis* populations.

The maximum-likelihood parameter estimates contained a positive density-dependent effect on recruitment for both rusty crayfish and *Lepomis* (k_x and k_y , respectively; Table 1), and reciprocal negative effects of rusty crayfish on *Lepomis*, and *Lepomis* on rusty crayfish (a_y and a_x), although the 95% confidence intervals of both interspecific parameters included 0. Removal trapping had a strong negative effect on adult rusty crayfish (m), and the estimated effect of predatory fish on rusty crayfish (v) was zero.

Alternative stable states

The maximum-likelihood parameter estimates predicted ASS at intermediate values of the bifurcation parameter U . For U below 1.24, rusty crayfish always exclude *Lepomis*, whereas, for U greater than 2.04, *Lepomis* always exclude rusty crayfish. Between 1.24 and 2.04, however, ASS exist in which rusty crayfish and

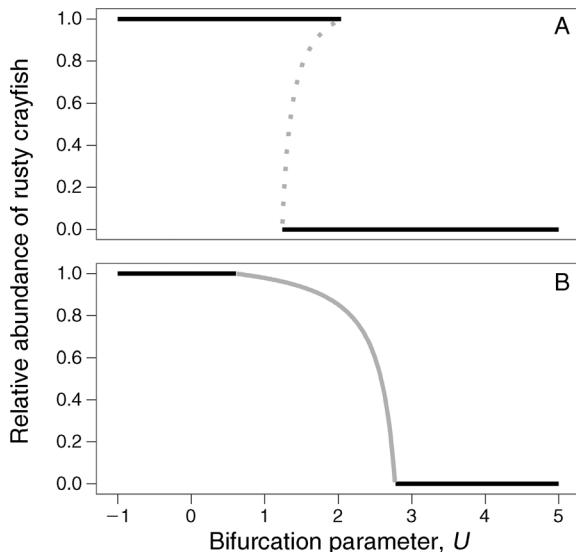


FIG. 3. Relative abundance of rusty crayfish (rusty crayfish CPUE/[rusty crayfish CPUE + *Lepomis* CPUE]) predicted from invasibility analysis as a function of the bifurcation parameter U (reduction in crayfish recruitment). Predicted abundances were generated from invasibility analysis (see *Methods: Alternative stable states*) using (A) the maximum-likelihood parameter estimates, which produce alternative stable states for U values from 1.24 to 2.04 (gray dotted line), and (B) one of the 1000 bootstrapped parameter sets for which no alternative stable states exist and both species coexist for U between 0.62 and 2.77 (gray solid line). Under both parameter sets, rusty crayfish always exclude *Lepomis* at low U values, and *Lepomis* always exclude rusty crayfish at high U values.

Lepomis are each capable of excluding the other, depending on their relative initial abundances (Fig. 3A). Results were similar when Eq. 6 was used to describe rusty crayfish dynamics (Appendix B: Fig. B1).

Because uncertainty exists in parameter estimates (Table 1), we performed an invasibility analysis using the bootstrapped parameter sets to assess the uncertainty in the existence of ASS. For 2.3% of the data sets, rusty crayfish could never invade *Lepomis*, and in 2.8% of the data sets, *Lepomis* could never invade rusty crayfish; these cases correspond to parameter sets for which the estimate of one of the competition coefficients (a_x or a_y) was zero. In the remaining bootstrapped parameter sets, rusty crayfish could exclude *Lepomis* at low values of U , and *Lepomis* could exclude rusty crayfish at high U . Of these cases, 58% predicted ASS at intermediate U values similar to Fig. 3A, and 42% predicted coexistence at intermediate U values (e.g., Fig. 3B).

These results can be summarized by plotting the range of values of the bifurcation parameter U from the point at which *Lepomis* exclude rusty crayfish to the point at which rusty crayfish exclude *Lepomis* (Fig. 4). This range is represented by the gray areas in Fig. 3; negative values give ASS (e.g., Fig. 3A), whereas positive values give coexistence (e.g., Fig. 3B). This range can be conceptualized as a hyperparameter that characterizes

the dynamical structure of the system, with lower values corresponding to a wider region of ASS and higher values corresponding to a wider region of coexistence. For most parameter sets, this hyperparameter was small (mean = 0.25, SD = 2.8), meaning transitions between rusty crayfish and *Lepomis* occurred over small ranges of U . The distribution of this hyperparameter contains zero and shows that, while ASS are consistent with the observed dynamics in this system, their existence is far from certain. Results were similar when Eq. 6 was used (Appendix B: Fig. B2).

Water level effects in Sparkling Lake

From Eq. 1, the effect of water level was large ($c = 5.3$), with the 95% confidence interval (3.0–8.8) far from zero (Table 1). When the model was structured to remove any fixed differences between Sparkling and Trout Lakes (Eq. 6), the water level effect on crayfish recruitment was still large ($c = 3.7$) with the 95% confidence interval again excluding zero (2.4–15.0; Appendix B: Table B1); therefore, the effects of fluctuations in water level on rusty crayfish abundance within Sparkling Lake were statistically significant.

Simulated transitions between rusty crayfish and Lepomis dominance

Simulated transitions between rusty crayfish and *Lepomis* dominance occurred rapidly at intermediate values of the bifurcation parameter U regardless of whether ASS or coexistence was predicted (Fig. 5). On average, transitions required fewer years to complete as

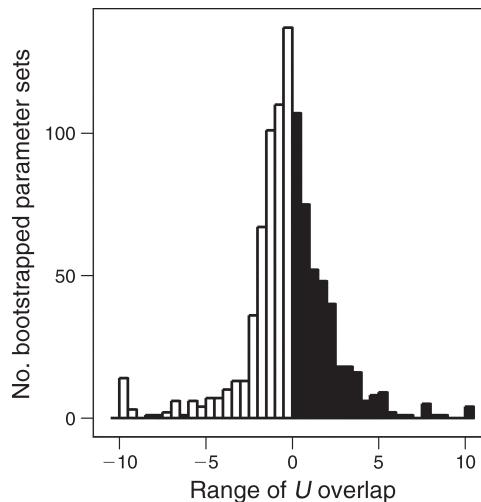


FIG. 4. For the 1000 bootstrapped parameter sets, the range of values of the bifurcation parameter U (reduction of crayfish recruitment) from the point at which rusty crayfish exclude *Lepomis* to the point at which *Lepomis* exclude crayfish. Negative values (white) correspond to alternative stable states in which each species can exclude the other at identical U values, depending on initial conditions (e.g., Fig. 3A); positive values (black) correspond to coexistence parameter sets (e.g., Fig. 3B). Values with absolute values >10 were binned in the maximum (or minimum) bin for clarity of presentation.

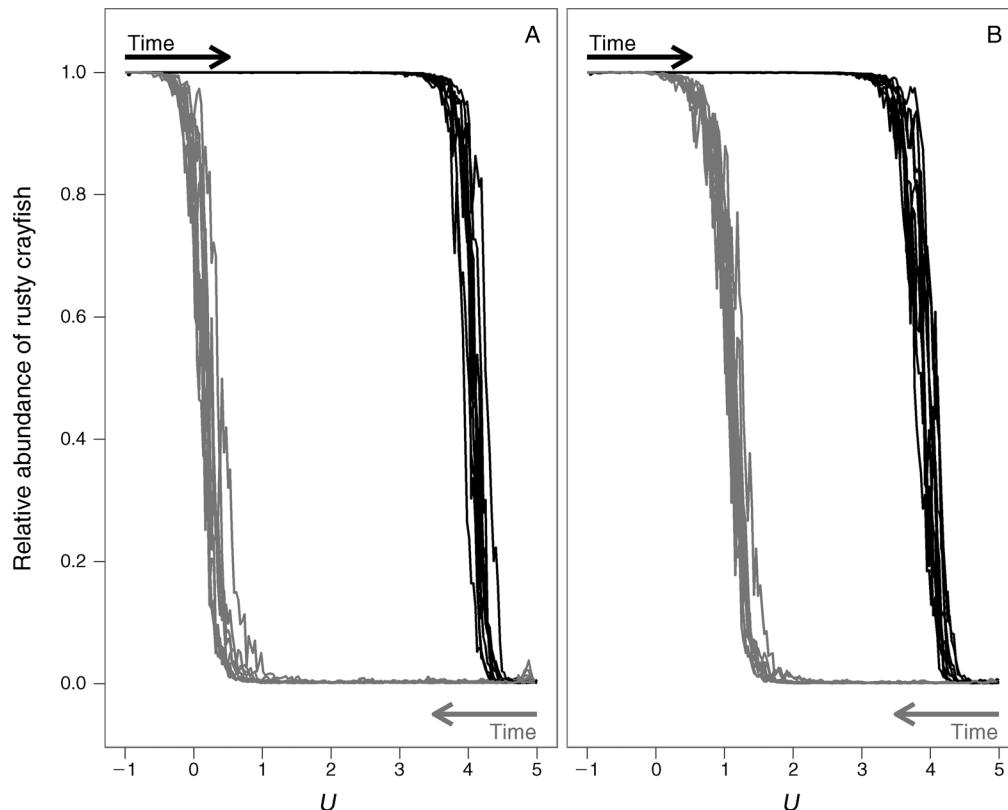


FIG. 5. Simulated relative abundance of rusty crayfish (predicted rusty crayfish CPUE/[predicted rusty crayfish CPUE + predicted *Lepomis* CPUE]) as a function of changing U (reduction in rusty crayfish recruitment rate) over time. Data were simulated using Eqs. 1 and 2, with (A) parameters predicting alternative stable states estimated from the observed data, and (B) parameters predicting coexistence selected from the bootstrapped parameter sets. For both parameter sets, simulations were run for 200 time steps with U either increasing (black lines) or decreasing (gray lines) over time. Multiple lines within a panel represent multiple simulations using the same parameter set; differences are a result of process error in model.

U decreased from high to low and crayfish took over compared to when U increased and crayfish declined. This was true when data were simulated using the both alternative stable state (mean years, high to low = 25; years, low to high = 32) and the coexistence (mean mean years, high to low = 32, years, low to high = 40) parameter sets. Transitions occurred more rapidly under the ASS parameter set regardless of transition direction (Fig. 5A). Interestingly, both parameter sets exhibited hysteresis; the transitions between species occurred at different U values when approached from opposite directions. Transitions occurred on average at lower U values as U decreased compared to when U increased under both the alternative stable state parameters (mean U , high to low = 0.67; U , low to high = 3.62) and the coexistence parameters (mean U , high to low = 1.58; U , low to high = 3.34). When U was changed more gradually, the apparent hysteresis in the coexistence parameter set disappeared, while hysteresis remained in the ASS parameter set (Appendix C: Fig. C1).

DISCUSSION

Our results show rapid transitions between invasive rusty crayfish and native *Lepomis* both empirically (Fig. 2) and through simulations (Fig. 5). These rapid transitions are consistent with evidence for ASS in this system (Roth et al. 2007), but are also consistent with a threshold response that lacks ASS. Food web interactions between invasive and native species were responsible for the observed transitions. Rusty crayfish and *Lepomis* each negatively affected the recruitment of the other (a_y and a_x ; see Table 1). However, the 95% confidence intervals of both interspecific coefficients include zero, indicating uncertainty in this relationship. The influence of rusty crayfish on *Lepomis* in our model includes both the direct effect of predation on *Lepomis* eggs and the indirect effect of macrophyte destruction; because we lack data on macrophyte cover for both lakes, we were unable to distinguish among these two potential mechanisms. Surprisingly, other littoral fishes (smallmouth bass, largemouth bass, rock bass, and walleye) exerted no measurable population-level effect on rusty crayfish ($v = 0$; Table 1). These species are



PLATE 1. Bluegill sunfish (*Lepomis macrochirus*) in a macrophyte bed in Sparkling Lake, Wisconsin, USA. Photo credit: G. A. Hansen.

known to consume rusty crayfish at high rates (Garvey et al. 1994, Vander Zanden et al. 1997), and have been implicated as the drivers of ASS in rusty crayfish dynamics (Horan et al. 2011). The effect of *Lepomis* predation may be greater than that of other littoral fishes, because *Lepomis* greatly increase mortality of juvenile rusty crayfish, which produces a larger population-level effect than adult mortality (Hein et al. 2006).

The reciprocal negative effects of rusty crayfish and *Lepomis* caused rapid transitions in invasive vs. native species dominance that represent fundamental shifts in system states (i.e., regime shifts; Scheffer and Carpenter 2003, Walker and Meyers 2004). Environmental conditions can change the outcome of competitive interactions, such that a superior competitor capable of excluding another species under one set of conditions is inferior and outcompeted under others (e.g., Tilman 1987, Mason et al. 2012). When the range of abiotic conditions favoring one competitor over another is narrow, rapid transitions from one species dominating to another can occur (e.g., Park 1962), because relatively minor changes in environmental conditions can shift the balance from one competitor to another due to positive feedbacks (Connell 1961, Frost et al. 1995, Wilson and Nisbet 1997). Transitions between rusty crayfish and *Lepomis* dominance occurred across small gradients of external factors reducing crayfish recruitment (U ; Fig. 4), and under most conditions, competitive exclusion by either species was predicted regardless of whether ASS exist (Fig. 3). In such cases, the exact type of regime shift may be less critical than identifying drivers of transitions

(Schröder et al. 2005, Andersen et al. 2009). Reduction in water level is one mechanism by which U could increase, but anything that negatively affects recruitment could produce similar dynamics. Conversely, external drivers that increase U (e.g., high water levels) weaken the stability of *Lepomis*-dominated systems and allow rusty crayfish to take over.

Rapid transitions between native and invasive species dominance resulting from changes in a single environmental driver, such as water level, suggest that high water levels in Sparkling Lake may be associated with low resilience of the *Lepomis*-dominated state. In general, gradual changes in habitat features (such as water level or macrophyte cover) alter interaction strengths of fast-acting variables (such as rusty crayfish and *Lepomis* abundance) and thereby change ecological resilience, or the amount of perturbation that a system can absorb and remain in the same state (Scheffer et al. 2001). For example, shifts from coral- to algae-dominated reef systems occur when resilience is lowered by overfishing and coastal eutrophication (Bellwood et al. 2004), and transitions from grassland to shrub or woodland can occur when resilience is lowered due to fire prevention and hunting of herbivores (Folke et al. 2004). Lowered resilience due to environmental degradation may even explain the mass extinction of dinosaur communities following the Chicxulub bolide impact at the end of the Cretaceous period (Renne et al. 2013). Lowered resilience of *Lepomis*-dominated systems is a possible explanation for the capacity of rusty crayfish to invade in the first place; even when at their highest

levels, catch rates of *Lepomis* in our study lakes were below mean catch rates in other northern Wisconsin lakes (J. F. Hansen, Wisconsin Department of Natural Resources, *personal communication*). In the future, prevention of rusty crayfish introduction will likely be most important in systems with high water levels, abundant rusty crayfish habitat, and low *Lepomis* populations.

Transitions between rusty crayfish and *Lepomis* exhibit characteristics consistent with ASS, although our rigorous assessment of parameter uncertainty means that we cannot rule out a simpler, threshold response that allows coexistence. Because ecological time series are generally noisy and often include only one transition between states, estimating model parameters with the degree of precision needed to conclusively demonstrate ASS is exceptionally challenging (Andersen et al. 2009). Experimental manipulation can increase the probability of detecting ASS when they exist (Carpenter 2003). Some large-scale manipulative studies have revealed hysteresis driven by food web interactions (Schmitz et al. 2006, Persson et al. 2007, Schröder et al. 2012), and others have shown reversibility of threshold responses in systems previously believed to contain ASS such as freshwater pelagic (Mittelbach et al. 2006) and arid grassland ecosystems (Bestelmeyer et al. 2013). Our study illustrates the difficulty of demonstrating ASS conclusively even with an extensive data set; we were unable to do so with a long (>30 years) data set on two ecosystems documenting both transitions to *Lepomis* dominance and rusty crayfish dominance, including a whole-lake food web manipulation. Still, the maximum-likelihood parameter estimates and the majority (58%) of bootstrapped parameter sets predict ASS, and simulations demonstrated hysteresis and dependence on initial conditions as expected for ASS (Scheffer and Carpenter 2003). Overall, on a continuum between ASS and a simple linear relationship between variables, rusty crayfish-*Lepomis* dynamics lean toward ASS.

Whether ASS exist may be relatively unimportant to the understanding and managing invasive rusty crayfish. One reason for distinguishing between ASS and simpler threshold responses is the difficulty of reversing thresholds associated with ASS due to hysteresis (Suding and Hobbs 2009, Fung et al. 2011). However, we observed hysteresis and time lags in reversibility of threshold responses even under parameter sets for which only one equilibrium was possible for any given set of conditions (Fig. 5). This apparent hysteresis in the absence of ASS is expected in cases where the response variable changes at approximately the same rate as the control variable (Scheffer and Carpenter 2003), as is the case here in which rusty crayfish, *Lepomis*, and the bifurcation parameter (U) changed annually. In such systems, the return time to previous states can be long, even though regime shifts are ultimately reversible (Schröder et al. 2005, Frost et al. 2006) and processes that affect recovery rates, such as changes in water level, may be

more important for conservation and management than the existence of ASS (Knowlton 2004). Overall, the difficulty of reversing regime shifts regardless of the underlying mechanism provides support for a precautionary approach to management, whereby critical transitions are avoided whenever possible (van Nes and Scheffer 2004, Bestelmeyer et al. 2013).

There is growing recognition that impacts of climate change extend beyond the direct effects of altered abiotic regimes to changes in species interactions (Suttle et al. 2007, Tylianakis et al. 2008, Gilman et al. 2010). Although some evidence suggests that native species are more adversely affected by climate change than nonnative species (Mason et al. 2012, Sorte et al. 2013), we show that climate-driven reductions in water level can be favorable to native species (see also Messner et al. 2013). Climate projections predict more frequent droughts in the study region (WICCI 2009), which may present opportunities for control of rusty crayfish populations. Our study highlights the complexity of interactions between species invasions and climate trends that can lead to distinctive changes in community structure that affect human use of ecosystems, regardless of whether ASS exist. If current trends in climate and species invasions continue, we may expect to see more transitions of this nature in the future. Determining whether these transitions are caused by ASS, and whether it matters, should be an important research priority.

ACKNOWLEDGMENTS

We thank the NSF-supported North Temperate Lakes Long Term Ecological Research site for funding (DEB-9632853) and data. We gratefully acknowledge John Magnuson, Tim Kratz, Katie Hein, and Brian Roth for their leadership of the Sparkling Lake experiment, and Tim Meinke, Pam Montz, and countless others who collected data for NTL-LTER. Thanks to two anonymous reviewers, Katie Hein, Brian Roth, and Jereme Gaeta for comments that greatly improved the quality of the manuscript.

LITERATURE CITED

- Andersen, T., J. Carstensen, E. Hernandez-Garcia, and C. M. Duarte. 2009. Ecological thresholds and regime shifts: Approaches to identification. *Trends in Ecology and Evolution* 24:49–57.
- Begon, M., J. L. Harper, and C. R. Townsend. 1986. *Ecology. Individuals, populations and communities*. Blackwell Scientific, Oxford, UK.
- Bellwood, D. R., T. P. Hughes, C. Folke, and M. Nystrom. 2004. Confronting the coral reef crisis. *Nature* 429:827–833.
- Bertschy, K. A., and M. G. Fox. 1999. The influence of age-specific survivorship on pumpkinseed sunfish life histories. *Ecology* 80:2299–2313.
- Bestelmeyer, B. T., M. C. Duniway, D. K. James, L. M. Burkett, and K. M. Havstad. 2013. A test of critical thresholds and their indicators in a desertification-prone ecosystem: More resilience than we thought. *Ecology Letters* 16:339–345.
- Bestelmeyer, B. T., A. M. Ellison, W. R. Fraser, K. B. Gorman, S. J. Holbrook, C. M. Laney, M. D. Ohman, D. P. C. Peters, F. C. Pillsbury, and A. Rassweiler. 2011. Analysis of abrupt transitions in ecological systems. *Ecosphere* 2:129.

- Brown, J. R., and J. Carter. 1998. Spatial and temporal patterns of exotic shrub invasion in an Australian tropical grassland. *Landscape Ecology* 13:93–102.
- Capelli, G. M. 1982. Displacement of northern Wisconsin crayfish by *Orconectes rusticus* (Girard). *Limnology and Oceanography* 27:741–745.
- Carpenter, S. R. 2003. Regime shifts in lake ecosystems: Pattern and variation. Excellence in Ecology Series 15. International Ecology Institute, Oldendorf/Luhe, Germany.
- Case, T. J. 1990. Invasion resistance arises in strongly interacting species-rich model competition communities. *Proceedings of the National Academy of Sciences USA* 87: 9610–9614.
- Chesson, P. L. 1986. Environmental variation and the coexistence of species. Pages 240–256 in J. Diamond and T. J. Case, editors. *Community ecology*. Harper and Row, New York, New York, USA.
- Collie, J. S., K. Richardson, and J. H. Steele. 2004. Regime shifts: Can ecological theory illuminate the mechanisms? *Progress in Oceanography* 60:281–302.
- Connell, J. H. 1961. Effects of competition, predation by *Thais lapillus*, and other factors on natural populations of the barnacle *Balanus balanoides*. *Ecological Monographs* 31:61–104.
- Cox, R. D., and E. B. Allen. 2008. Stability of exotic annual grasses following restoration efforts in southern California coastal sage scrub. *Journal of Applied Ecology* 45:495–504.
- Crooks, J. A. 2005. Lag times and exotic species: The ecology and management of biological invasions in slow-motion. *Ecoscience* 12:316–329.
- Dorn, N. J., and G. G. Mittelbach. 1999. More than predator and prey: A review of interactions between fish and crayfish. *Vie et Milieu* 49:229–237.
- Dorn, N. J., and G. G. Mittelbach. 2004. Effects of a native crayfish (*Orconectes virilis*) on the reproductive success and nesting behavior of sunfish (*Lepomis* spp.). *Canadian Journal of Fisheries and Aquatic Sciences* 61:2135–2143.
- Firn, J., A. P. N. House, and Y. M. Buckley. 2010. Alternative states models provide an effective framework for invasive species control and restoration of native communities. *Journal of Applied Ecology* 47:96–105.
- Folke, C., S. Carpenter, B. Walker, M. Scheffer, T. Elmqvist, L. Gunderson, and C. S. Holling. 2004. Regime shifts, resilience, and biodiversity in ecosystem management. *Annual Review of Ecology, Evolution, and Systematics* 35:557–581.
- Frost, T. M., S. R. Carpenter, A. R. Ives, and T. K. Kratz. 1995. Species compensation and complementarity in ecosystem function. Pages 224–239 in C. G. Jones and J. H. Lawton, editors. *Linking species and ecosystems*. Chapman and Hall, New York, New York, USA.
- Frost, T. M., J. M. Fischer, J. L. Klug, S. E. Arnott, and P. K. Montz. 2006. Trajectories of zooplankton recovery in the Little Rock Lake whole-lake acidification experiment. *Ecological Applications* 16:353.
- Fung, T., R. Seymour, and C. Johnson. 2011. Alternative stable states and phase shifts in coral reefs under anthropogenic stress. *Ecology* 92:967–982.
- Garvey, J. E., J. E. Rettig, R. A. Stein, D. M. Lodge, and S. P. Klosiewski. 2003. Scale-dependent associations among fish predation, littoral habitat, and distributions of crayfish species. *Ecology* 84:3339–3348.
- Garvey, J. E., R. A. Stein, and H. M. Thomas. 1994. Assessing how fish predation and interspecific prey competition influence a crayfish assemblage. *Ecology* 75:532–547.
- Gilman, S. E., M. C. Urban, J. Tewksbury, G. W. Gilchrist, and R. D. Holt. 2010. A framework for community interactions under climate change. *Trends in Ecology and Evolution* 25:325–331.
- Hansen, G. J. A., C. L. Hein, B. M. Rotn, M. J. Vander Zanden, J. W. Gaeta, A. W. Latzka, and S. R. Carpenter. 2013. Food web consequences of long-term invasive crayfish control. *Canadian Journal of Fisheries and Aquatic Sciences* 70:1109–1122.
- Harvey, A. C. 1989. *Forecasting structural time series models and the Kalman filter*. Cambridge University Press, Cambridge, UK.
- Hein, C. L., B. M. Roth, A. R. Ives, and M. J. Vander Zanden. 2006. Fish predation and trapping for rusty crayfish (*Orconectes rusticus*) control: A whole-lake experiment. *Canadian Journal of Fisheries and Aquatic Sciences* 63: 383–393.
- Hein, C. L., M. J. Vander Zanden, and J. J. Magnuson. 2007. Intensive trapping and increased fish predation cause massive population decline of an invasive crayfish. *Freshwater Biology* 52:1134–1146.
- Horan, R. D., E. P. Fenichel, K. L. S. Drury, and D. M. Lodge. 2011. Managing ecological thresholds in coupled environmental-human systems. *Proceedings of the National Academy of Sciences USA* 108:7333–7338.
- Huxel, G. R. 1999. Rapid displacement of native species by invasive species: Effects of hybridization. *Biological Conservation* 89:143–152.
- Kershner, M. W., and D. M. Lodge. 1995. Effects of littoral habitat and fish predation on the distribution of an exotic crayfish, *Orconectes rusticus*. *Journal of the North American Benthological Society* 14:414–422.
- Knowlton, N. 2004. Multiple “stable” states and the conservation of marine ecosystems. *Progress in Oceanography* 60: 387–396.
- Lockwood, J. L., P. Cassey, and T. Blackburn. 2005. The role of propagule pressure in explaining species invasions. *Trends in Ecology and Evolution* 20:223–228.
- Lodge, D. M., M. W. Kershner, J. E. Aloï, and A. P. Covich. 1994. Effects of an omnivorous crayfish (*Orconectes rusticus*) on a freshwater littoral food web. *Ecology* 75:1265–1281.
- Lorman, J. G. 1980. *Ecology of the crayfish Orconectes rusticus in northern Wisconsin*. Dissertation. University of Wisconsin, Madison, Wisconsin, USA.
- Mason, T. J., K. French, and K. Russell. 2012. Are competitive effects of native species on an invader mediated by water availability? *Journal of Vegetation Science* 23:657–666.
- Mather, M. E., and R. A. Stein. 1993. Direct and indirect effects of fish predation on the replacement of a native crayfish by an invading congener. *Canadian Journal of Fisheries and Aquatic Sciences* 50:1279–1288.
- MathWorks. 2012. *Matlab*. Version 8.0. MathWorks, Natick, Massachusetts, USA.
- May, R. M. 1973. *Stability and complexity in model ecosystems*. First edition. Princeton University Press, Princeton, New Jersey, USA.
- May, R. M. 1977. Thresholds and breakpoints in ecosystems with a multiplicity of stable states. *Nature* 269:471–477.
- Messner, J. S., M. M. MacIennan, and R. D. Vinebrooke. 2013. Higher temperatures enhance the effects of invasive sportfish on mountain zooplankton communities. *Freshwater Biology* 58:354–364.
- Mittelbach, G. G. 1981. Foraging efficiency and body size: A study of optimal diet and habitat use by bluegills. *Ecology* 62: 1370–1386.
- Mittelbach, G. G., E. A. Garcia, and Y. Taniguchi. 2006. Fish reintroductions reveal smooth transitions between lake community states. *Ecology* 87:312–318.
- Mylius, S. D., K. Klumpers, A. M. de Roos, and L. Persson. 2001. Impact of intraguild predation and stage structure on simple communities along a productivity gradient. *American Naturalist* 158:259–276.
- Olsen, T. M., D. M. Lodge, G. M. Capelli, and R. J. Houlihan. 1991. Mechanisms of impact of an introduced crayfish (*Orconectes rusticus*) on littoral congeners, snails, and macrophytes. *Canadian Journal of Fisheries and Aquatic Sciences* 48:1853–1861.

- Park, T. 1962. Beetles, competition, and populations. *Science* 138:1369–1375.
- Persson, L., P.-A. Amundsen, A. M. De Roos, A. Klemetsen, R. Knudsen, and R. Primicerio. 2007. Culling prey promotes predator recovery: alternative states in a whole-lake experiment. *Science* 316:1743.
- Renne, P. R., A. L. Deino, F. J. Hilgen, K. F. Kuiper, D. F. Mark, W. S. Mitchell, L. E. Morgan, R. Mundil, and J. Smit. 2013. Time scales of critical events around the cretaceous-paleogene boundary. *Science* 339:684–687.
- Roth, B. M., J. C. Tetzlaff, M. L. Alexander, and J. F. Kitchell. 2007. Reciprocal relationships between exotic rusty crayfish, macrophytes, and *Lepomis* species in northern Wisconsin lakes. *Ecosystems* 10:75–86.
- Scheffer, M., and S. R. Carpenter. 2003. Catastrophic regime shifts in ecosystems: Linking theory to observation. *Trends in Ecology and Evolution* 18:648–656.
- Scheffer, M., S. Carpenter, J. A. Foley, C. Folke, and B. Walker. 2001. Catastrophic shifts in ecosystems. *Nature* 413:591–596.
- Schmitz, O. J., E. L. Kalies, and M. G. Booth. 2006. Alternative dynamic regimes and trophic control of plant succession. *Ecosystems* 9:659–672.
- Schröder, A., L. Persson, and A. M. De Roos. 2005. Direct experimental evidence for alternative stable states: a review. *Oikos* 110:3–19.
- Schröder, A., L. Persson, and A. M. de Roos. 2012. Complex shifts between food web states in response to whole-ecosystem manipulations. *Oikos* 121:417–427.
- Simberloff, D., and L. Gibbons. 2004. Now you see them, now you don't!: Population crashes of established introduced species. *Biological Invasions* 6:161–172.
- Sorte, C. J. B., et al. 2013. Poised to prosper? A cross-system comparison of climate change effects on native and non-native species performance. *Ecology Letters* 16:261–270.
- Steele, J. H. 2004. Regime shifts in the ocean: Reconciling observations and theory. *Progress in Oceanography* 60:135–141.
- Strayer, D. L., V. T. Eviner, J. M. Jeschke, and M. L. Pace. 2006. Understanding the long-term effects of species invasions. *Trends in Ecology and Evolution* 21:645–651.
- Suding, K. N., and R. J. Hobbs. 2009. Threshold models in restoration and conservation: A developing framework. *Trends in Ecology and Evolution* 24:271–279.
- Suttle, K. B., M. A. Thomsen, and M. E. Power. 2007. Species interactions reverse grassland responses to changing climate. *Science* 315:640–642.
- Tetzlaff, J. C., B. M. Roth, B. C. Weidel, and J. F. Kitchell. 2010. Predation by native sunfishes (*Centrarchidae*) on the invasive crayfish *Orconectes rusticus* in four northern Wisconsin lakes. *Ecology of Freshwater Fish* 20:133–143.
- Tilman, D. 1987. On the meaning of competition and the mechanisms of competitive superiority. *Functional Ecology* 1:304–315.
- Tylianakis, J. M., R. K. Didham, J. Bascompte, and D. A. Wardle. 2008. Global change and species interactions in terrestrial ecosystems. *Ecology Letters* 11:1351–1363.
- Vander Zanden, M. J., G. Cabana, and J. B. Rasmussen. 1997. Comparing trophic position of freshwater fish calculated using stable nitrogen isotope ratios ($\delta^{15}N$) and literature dietary data. *Canadian Journal of Fisheries and Aquatic Sciences* 54:1142–1158.
- van Nes, H. Egbert and M. Scheffer. 2004. Large species shifts triggered by small forces. *American Naturalist* 164:255–266.
- Walker, B., and J. A. Meyers. 2004. Thresholds in ecological and social ecological systems: A developing database. *Ecology and Society* 9(2):3.
- WICCI [Wisconsin Initiative on Climate Change Impacts]. 2009. Maps of recent and projected climate change in Wisconsin. WICCI, Madison, Wisconsin, USA. http://www.wicci.wisc.edu/resources/wicci_climate_change_maps.pdf
- Wilson, K. A., J. J. Magnuson, D. M. Lodge, A. M. Hill, T. K. Kratz, W. L. Perry, and T. V. Willis. 2004. A long-term rusty crayfish (*Orconectes rusticus*) invasion: Dispersal patterns and community change in a north temperate lake. *Canadian Journal of Fisheries and Aquatic Sciences* 61:2255–2266.
- Wilson, W. G., and R. M. Nisbet. 1997. Cooperation and competition along smooth environmental gradients. *Ecology* 78:2004–2017.
- Zipkin, E. F., C. E. Kraft, E. G. Cooch, and P. J. Sullivan. 2009. When can efforts to control nuisance and invasive species backfire? *Ecological Applications* 19:1585–1595.

SUPPLEMENTAL MATERIAL

Appendix A

Parameter estimates (maximum-likelihood and mean \pm 95% confidence intervals from parametric bootstrapping) of the unconstrained model, in which all parameters were estimated from the data ([Ecological Archives E094-205-A1](#)).

Appendix B

Model results when Eq. 6 was used to describe rusty crayfish abundance, separating effects of water level on crayfish recruitment from other lake-specific effects ([Ecological Archives E094-205-A2](#)).

Appendix C

Simulation of transitions between rusty crayfish and *Lepomis* dominance as a function of the bifurcation parameter U (reduction in recruitment of rusty crayfish) changing gradually over 10000 time steps ([Ecological Archives E094-205-A3](#)).