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Outbreak of an undetected invasive species triggered by a climate anomaly

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Abstract. When an invasive species appears at a new location, we typically have no knowledge of the population dynamics leading up to that moment. Is the establishment of invasive propagules closely followed by the appearance of the population? Or alternatively, was there an established low-density population that was released from a constraint and crossed the detection threshold? The early stages of the invasion process are a critical gap in our knowledge, yet vitally important for the detection and management of invasions. Here, we present multiple lines of evidence supporting the lag scenario for an invasive species outbreak. The invasive predatory zooplankton, spiny water flea (*Bythotrephes longimanus*), was detected in Lake Mendota, Wisconsin (USA), in summer of 2009 and rapidly reached and sustained exceptionally high densities. To evaluate whether *Bythotrephes*' outbreak immediately followed introduction or erupted from an established low-density population, we constructed a population model of *Bythotrephes* in Lake Mendota. In the model, *Bythotrephes* persisted indefinitely at low levels until favorable thermal conditions in 2009, the coolest July since at least 1895, allowed it to erupt to high densities and establish a large egg bank in the lake sediments. The egg bank stabilized the population in the high-density state despite a return to nonfavorable thermal conditions, which is further supported by demographic data suggesting a constant contribution from the egg bank during the year. The prolonged lag scenario is corroborated by the detection of two individual *Bythotrephes* in pre-2009 archived samples, and the detection of *Bythotrephes* spines in lake sediment core layers dating back to 1994 (±5 yr). Together, our results suggest that *Bythotrephes* persisted for at least a decade below the detection limit, until optimal thermal conditions triggered a population outbreak. This work highlights the potential for environmental conditions to trigger invasive species outbreaks from low-density populations.

Key words: abrupt transitions; *Bythotrephes longimanus;* invasive species; outbreaks; prolonged lags.

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Introduction

Nonnative species have been widely dispersed due to human activities (García-Berthou et al. 2005, Hulme 2009). A subset of these nonnative species are considered invasive due to a tendency to spread to new sites, reach exceptionally high abundances, and produce undesired ecological and economic impacts (Mack et al. 2000).

Imagine a case where an invasive species has spread to a new site, establishes, and has been detected. For this to happen involves multiple steps: (1) Invasive species propagules are transported and introduced, (2) the population

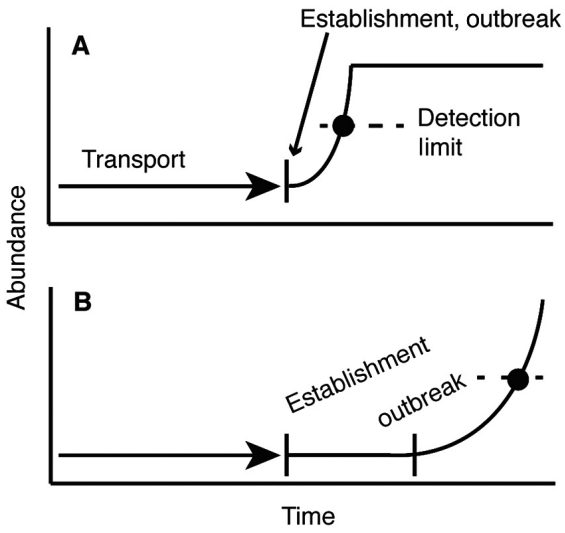

Fig. 1. Two possible scenarios of invasive species population establishment and outbreak timing. (A) An invasive species establishes after some number of introduction events and becomes abundant soon after, passing a detection limit. (B) Establishment and outbreak are separated in time. As a result, the established population is detected much later.

establishes and becomes self-sustaining, and (3) the population crosses a detection threshold (Fig. 1A; e.g., Kowarik 1995, Costello and Solow 2003, Vander Zanden and Olden 2008). In many cases, an invasive species may not be detected until it becomes quite abundant, often referred to as a population outbreak or eruption (Solow and Costello 2004, Costello et al. 2007, Liebhold and Tobin 2008, Aikio et al. 2010).

Once established, a population can persist for a long period of time at low abundance. Such a population would likely remain undetected. But at some point, environmental or ecological conditions may allow or trigger a population eruption (Crooks and Soule 1999, Takimoto 2009, Fig. 1B). Such events are often described as a change in equilibrium, whereby the environment becomes more favorable or an organism adapts to its new environment (i.e., prolonged lag sensu Crooks 2005). There are numerous examples for plants where a gradual or step-change in an external driver or adaptation to that driver allows a low-density invasive species population to erupt (e.g., Geerts et al. 2013, Donaldson et al. 2014, Flores-Moreno et al. 2015). In contrast, examples of invasive animal populations erupting in response to directional environmental change are relatively rare (Aagaard and Lockwood 2014).

Little is known about how nonnative species' life histories stabilize population responses to short-term temporal variation in an external driver. For example, nonnative species may be able to capitalize on temporary favorable conditions, thereby transitioning to a high-density state that persists when conditions return to normal (similar to endemic and epidemic equilibria; Anderson and May 1992). Understanding how invasive species populations respond to short-term change in drivers is critical to understanding when and how invasive species populations erupt. It also has important implications for how we manage biological invasions, whether to focus on preventing the spread of propagules, vs. managing the environmental conditions that result in a population eruption (Taylor and Bothwell 2014).

In this study, we present the case of the invasion of the predatory zooplankton, *Bythotrephes longimanus* (the spiny water flea), into Lake Mendota, Wisconsin (USA). *Bythotrephes* was detected in 2009 at previously unrivaled densities, which caused large ecological and economic impacts on water quality (Walsh et al. 2016). Further, Lake Mendota is one of the most well-studied lakes in the world, and its zooplankton community has been sampled fortnightly in the open water season of each year since 1976, well before *Bythotrephes* detection in the Laurentian Great Lakes in 1984.

Bythotrephes' invasion into Lake Mendota provides a unique opportunity to investigate the mechanism of invasive species population eruption. Did *Bythotrephes* erupt soon after (presumably in the same year) it was introduced to Lake Mendota (Fig. 1A)? Or did an existing low-density, but undetected population erupt suddenly due to some sort of trigger in 2009 (Fig. 1B)? Further, what environmental drivers or internal feedbacks in *Bythotrephes* facilitated its eruption? Answering these questions and piecing together the invasion history of *Bythotrephes* in Lake Mendota will help lay the groundwork to address the broader challenges posed by these sudden high-density outbreaks.

Methods

Study site

Lake Mendota is a eutrophic, 39.6 km^2 lake in south central Wisconsin, at the southwestern edge of *Bythotrephes*' invasive range. Lake Mendota is dimictic, mixing in the spring and fall, and heats to peak temperatures in the roughly 10 m mixed layer in July and August (Fig. 2) that consistently exceed *Bythotrephes*' thermal optimum of 25°C (Kim and Yan 2010) and observations of thermal conditions from *Bythotrephes* reported range (e.g., Kerfoot et al. 2011). Moreover, in the mid-summer, the top of the metalimnion will consistently heat past 25°C and the lake bottom (25.3 m maximum depth and 12.7 m mean depth) becomes anoxic (<0.5 mg/L) in early June. On average, anoxia extends from the lake bottom to 10 m below the surface by mid-July, which persists through October, constricting the potential vertical distribution of cool-water aquatic organisms like *Bythotrephes* (D.O. tolerance of 2.0 mg/L; Sorensen and Branstrator 2016). As anoxia in lake bottom nearly always limits predicted suitable habitat for *Bythotrephes* in the summer, we believe that variation in surface temperatures, which is only periodically limiting, will determine whether *Bythotrephes* is able to successfully persist through summer in Lake Mendota.

While Lake Mendota has been consistently monitored since 1976, half of NTL-LTER zooplankton samples are archived for long-term storage without being processed. Therefore, we processed the entirety of each archived sample starting in 2008, the year before *Bythotrephes* detection, working backward and counting all samples through 2003 and September through December samples from 1997 to 2002.

Bythotrephes *demography—data collection*

Bythotrephes has been a highly researched model invader, making possible a detailed investigation of the environmental factors that influence its population growth (Yan et al. 2011). Further, *Bythotrephes*' range expansion is limited by temperature-dependent propagule pressure (Wittmann et al. 2011), revealing the importance of climatic drivers in limiting *Bythotrephes* growth. *Bythotrephes* reproduces through cyclic parthenogenesis whereby the population grows primarily through asexual reproduction but will periodically produce males in response to environmental cues prior to harsh conditions, allowing for the sexual production of resting eggs (Yurista 1992). Asexual reproduction allows for rapid, opportunistic growth. In contrast, sexually produced resting eggs allow for persistence through harsh conditions and genetic recombination.

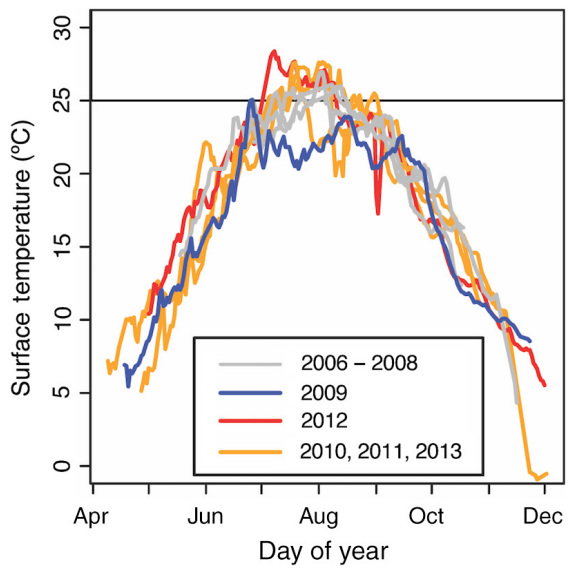

Fig. 2. Daily surface water temperature in Lake Mendota from before *Bythotrephes*' detection (2006–2008; grey lines), the year of outbreak (2009; blue line), and the years since the detection (2010–2013; orange lines with 2012 in red). *Bythotrephes*' thermal optimum of 25°C is marked with a black line.

To obtain *Bythotrephes*' demographic information in Lake Mendota, we conducted fortnightly sampling of the water column using three tows from a zooplankton net (150 μm mesh, 0.5 m diameter, and 1.5 m net length) lowered to 20 m at the deepest point in the lake (Z_{max} = 25.3 m) and 15 m at four additional sites located around the lake. Sampling occurred during the open water season (roughly April through December) from 2009 to 2013. Samples were processed in their entirety to estimate volumetric density of *Bythotrephes* in the lake. Thirty randomly selected individuals from each site (~150 individuals per day in total) were set aside to obtain gender, instar stage, reproductive state (carrying asexually produced embryos or sexually produced resting eggs), clutch size (number of embryos or

eggs), and the presence of a "kink" or "s-bend" in the tail spine to identify sexually (no s-bend) and asexually (s-bend) produced individuals (Yurista 1992).

Sediment coring and dating

Sediments are archives of biological activity in lakes and deposited *Bythotrephes* tail spines preserve well in lake sediments (Beranek 2012). To investigate long-term population dynamics of *Bythotrephes* in Lake Mendota using lake sediments and deposited tail spines, we collected a 115 cm sediment core from the deep hole (43.10667° N, 89.42472° W, water depth = 25 m) of Lake Mendota through ice cover in March 2015 using a Livingstone-Wright piston corer with a Bolivia adapter attached to a 7 cm diameter PVC tube. The sediment–water interface at the core top was stabilized using the superabsorbent powder Zorbitrol and kept upright for two weeks in cold (5°C) storage to minimize disturbance to the upper-most sediment stratigraphy. The sediment core was split longitudinally, imaged, described, and sub-sampled at 1 cm intervals at the National Lacustrine Core Facility (LacCore) at the University of Minnesota. Every other 1 cm sub-sample (n = 56) was freeze-dried and sent to the St. Croix Watershed Research Station for ^{210}Pb alpha spectrometry to constrain the ages of the upper-most sediments (a large enough subset of total samples, n = 16, was processed to create a reliable ^{210}Pb age model). The ^{210}Pb chronology formed the basis of a Bayesian age model constructed using bacon v.2.2 (Blaauw and Christen 2011), which iteratively simulates sedimentation in the lake to provide an age-depth model with robust uncertainty estimates. Finally, each 1 cm sub-sample (~16 cc of sediment material) was sieved at 150 μm, rinsed, and tail spine fragments of *Bythotrephes* were counted under a dissecting microscope following the methods described in Beranek (2012).

Model—general structure

We built a stage-structured, temperature-dependent population model that allowed us to input lake temperature profile data into a population model containing *Bythotrephes*' life-history characteristics and processes that influence population growth. The model is structured into an active portion of the population in the water column composed of three instar stages (immature stages S_1 and S_2 and mature stage S_3), as well as a resting portion of the population in the egg bank in the lake's sediment that seeds and sustains population growth in Lake Mendota (Fig. 3, Table 1). Additional detail on the construction of the model and model sensitivity analyses can be found in the Appendix S1. All computation, component derivation, and model simulations are conducted using the statistical program R (R Development Core Team 2014).

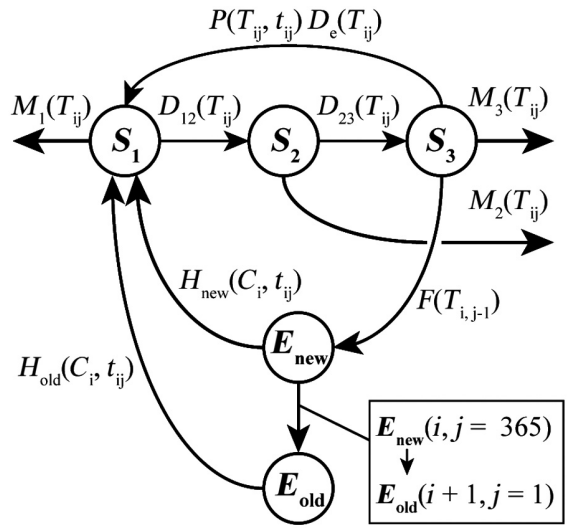

Fig. 3. Flow model describing the stage-structured *Bythotrephes*' population model. The active population in the water column (S_1–S_3) and resting egg bank in sediment (E_{old}, E_{new}) are stages (depicted as circles) in the model governed by temperature-dependent (T or C in the case of time since a thermal cue) and time (t)-dependent processes (depicted as arrows): development (D), reproduction (P, asexual, and F, sexual), mortality (M), and hatching from the egg bank (H).

In the model, developmental, reproductive, and mortality rates are temperature dependent, changing with inputted surface water temperatures. Temperature-dependent development rates (D; Fig. 3, Table 1) are obtained from Lehman et al. (1997) and fitted to sigmoidal curves (developed in Logan et al. 1985) to account for surface water temperatures outside of the range described in *Bythotrephes*' development literature (described up to 22°C) that are reached annually in Lake Mendota. *Bythotrephes*' development rates decline rapidly with increasing temperature

Table 1. Model components, units, descriptions, and references from Fig. 1.

Symbol	Units	Description	Sources
Time (t)			
j	Day of year	Day at timestep $t_{i,j}$	
i	Year	Year at timestep $t_{i,j}$	
Temperature			
T	°C	Surface temperature	NTL-LTER
C	Day of year	First day of thermal hatching cues at lake bottom in year i	Bottom temp. NTL-LTER Hatching cues, dormancy time (only for E_{new})—Herzig (1985)
Instar stage and egg density			
S	ind/m^3	Instar stage x density	Model output
E	ind/m^3	Egg bank density. E_{new} is the same-year egg bank, and E_{old} is the previous year egg bank	Model output
Rates			
D	d^{-1}	Temperature-dependent developmental rates. D_{xy} is the development rate from stage x to stage y. D_e is the embryonic development rate	*Bythotrephes'* development rates—Lehman et al. (1997) Sigmoidal development rate shape—Logan et al. (1985) *Bythotrephes'* optimal thermal range—Kim and Yan (2010)
P	Embryos ind^{-1}·d^{-1}	Temperature- and time (day of year)-dependent asexual reproduction rate of embryos per S_3 female	L. Mendota Pop. Data (GAM function of temp., day of year)
F	Eggs ind^{-1}·d^{-1}	Temperature-dependent sexual reproduction rate of eggs per S_3 female	L. Mendota Pop. Data (GAM function of temp.)
H	% d^{-1}	Daily percentage of hatching. Percentage of $E_{old}(i, j = 1)$ for E_{old} and percentage of $E_{new}(i, j - 1)$ for E_{new} p—constant proportion hatching from E_{new} (maximum hatching rate from Yurista [1992])	Hatching rates at 6°C—Yurista (1992) Total % Hatched—Brown (2011)
M	Deaths ind^{-1}·d^{-1}	Temperature-dependent daily per capita mortality	L. Mendota Pop. Data Mortality calculation—Brown et al. (2012) Polynomial function of temp.

from maximum development at 25°C and to zero development at 30°C (Kim and Yan 2010). Temperature-dependent reproductive rates (P and F; Fig. 3, Table 1) are developed using our own demographic data fitted to generalized additive models of temperature-dependent reproduction (Wood 2015). Temperature-dependent mortality (M; Fig. 3, Table 1) is estimated by applying the methods outlined in Brown et al. (2012) to our own demographic data to estimate daily per capita mortality as the difference between observed population densities and expected population densities predicted by population growth rates under temperature and demographic data from a previous timestep (additional detail in Appendix S1). These daily estimates of mortality are then fitted to a quadratic function of temperature ($M = B_0 + B_1 \times T + B_2 \times T^2$) for each instar stage using nonlinear least squares regression.

Hatching rates out of the resting egg bank (H_{old} and H_{new}) are dependent on the timing of thermal cues at the sediment–water interface (C; Fig. 3, Table 1). These hatching rates are obtained from Yurista (1992) and are a function of the number of days since the onset of a thermal hatching cue in the bottom of the lake. Same-year hatching from the newly established egg bank (H_{new}) starts at a constant rate (p = 3% d^{-1}; peak hatching from Yurista) after a period of dormancy (114 days mean observed dormancy; Herzig 1985) after the first day of the onset of the hatching cue (C_{first}) and ends a period of time

equal to the minimum observed dormancy (66 days minimum observed dormancy; Herzig 1985) before the last day of the hatching cue (C_{last}). Model simulations are seeded with 10 resting eggs/m^3 in $E_{old}(t_{j=1})$ in 1999 to fit the range of modeled densities to observed densities. The density of the model seed does not impact the shape of model dynamics (there is no density-dependence or carrying capacity in the model), only the relative densities at which they occur. Therefore, the relative dynamics of the model (e.g., long-term, annual, and seasonal variation) are more useful for understanding *Bythotrephes*' population than the modeled size of the population.

Lake temperature data

For temperature-dependent rates, we obtained lake temperature data from 1995 through 2013 from the NTL-LTER program database (North Temperate Lakes Long-Term Ecological Research 2014). We calculated mean surface temperature as the mean temperature from 0 to 5 m. Though the mixed layer extends to 10 m depth in the summer in Lake Mendota, roughly the same depth as the top of the anoxic zone in the summer, this range corresponds to depths that contain the majority of the *Bythotrephes*' population (E. Vennie-Volrath, *unpublished data*; J. R. Walsh, *unpublished data*). We obtained daily estimates of surface temperature through linear interpolation between consecutive sampling dates including during the ice cover period. We compare these estimates to daily observations of surface temperature taken by the NTL-LTER high frequency data logging buoy from 2006 to 2013 (Fig. 2).

To observe model dynamics under a wider range of lake thermal conditions, we used the predictive model of Sharma et al. (2007) to estimate lake daily surface water temperature from July air temperature (Model 2 from Sharma et al. 2007). Modeling water temperature from air temperature allows us to scale up and generalize the model more easily as air temperatures are widely available. Using this model, we estimated daily lake surface water temperature across a broad range of mean July air temperatures (0–30°C, 1°C increments).

We used these estimated surface water temperatures as inputs for the *Bythotrephes*' population model, running the model through single-year simulations. For each model run, we calculated the egg bank growth rate (eggs·m^{-3}·yr^{-1}) as a metric of *Bythotrephes*' population persistence under varying temperatures. If modeled annual growth rates in the egg bank are high, then it is likely that *Bythotrephes* would not be temperature limited under such conditions (i.e., persistence is unlikely to be affected by mid-summer temperatures). Conversely, if modeled growth rates in the egg bank are low or negative, then it is more likely that the population would be temperature limited under such thermal conditions. Additionally, we use this metric to model *Bythotrephes* long-term persistence in Lake Mendota using model simulations under varying climate conditions and observing the climate conditions required to return the population to pre-2009 densities below the detection limit (0.7 ind/m^3).

Results

Population outbreak

Bythotrephes appeared in LTER zooplankton samples on 21 July 2009 and erupted to unprecedented densities (300 ind/m^3) during fall of that year (Fig. 4A). *Bythotrephes* maintained high densities (>100 ind/m^3) through 3 December, the last sampling trip before ice-on in the lake. Each year since 2009, *Bythotrephes* has followed a similar pattern of detection in the mid-late summer, rapid growth in the early fall, and high densities through the fall (Fig. 4B–E).

Observed population demography was consistent with a population that both produces and hatches from resting eggs throughout the open water season (Fig. 4F–H). The percentage of males in the population, for the sexual production of resting eggs, was highest during August, September, and October (Fig. 4F), which is reflected in the number of sexually produced resting eggs observed per adult female, which peaks in September (Fig. 4G). December and June are represented by relatively few individuals (30 with 12 adult females over two sampling trips and 53, with 39 adult females over two sampling trips, respectively). Finally, we observed *Bythotrephes* with straight tail spines, indicative of having hatched from the egg bank, at all times of the year, with the highest percentage of straight-spined individuals present in September and October sampling trips (Fig. 4H).

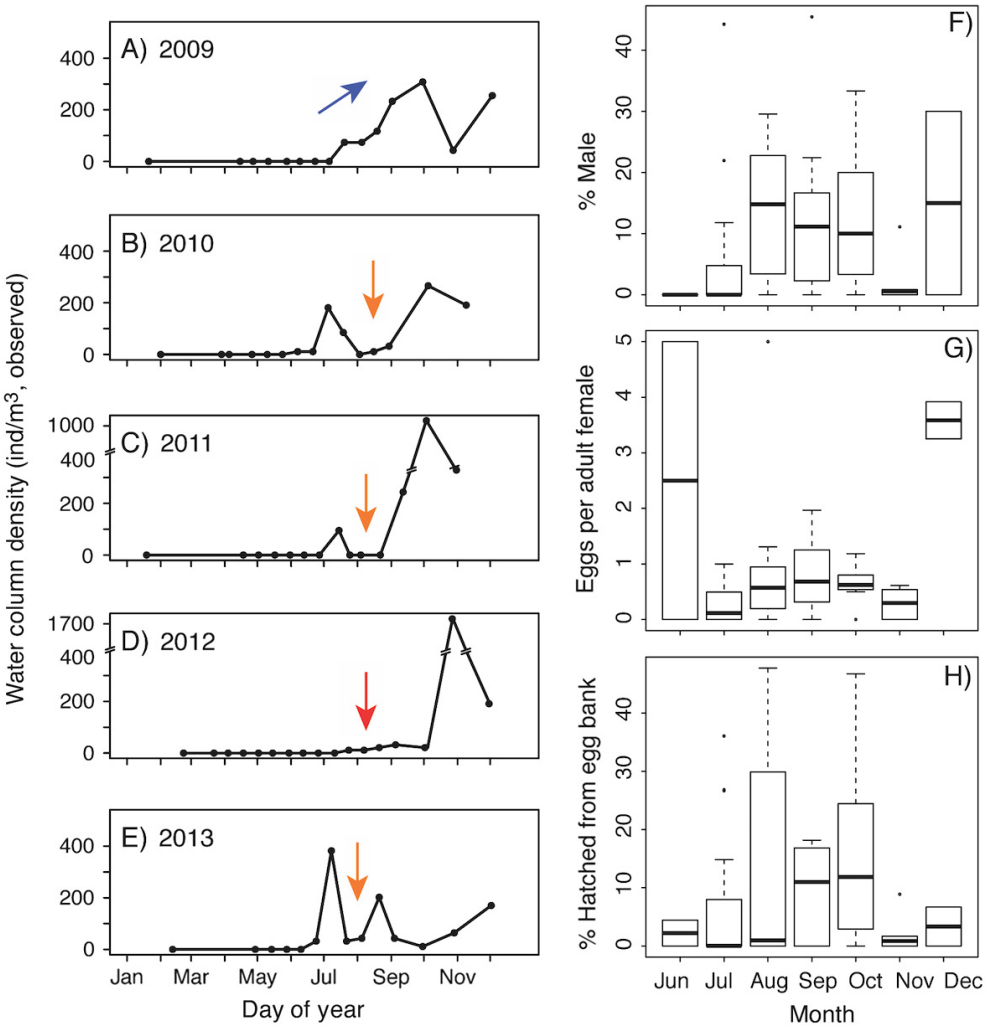

Fig. 4. Annual *Bythotrephes*' population dynamics in Lake Mendota since the 2009 outbreak are plotted in panels A–E. In many years, the population crashes during peak summer surface water temperatures (2010, 2011, 2013; orange arrows). In 2012 (red arrow), population growth was delayed until much later in the fall than normal. Most importantly, in 2009 (blue arrow), there was no summer population crash. Note breaks in the *y*-axes of 2011 (point at 1019 ind/m^3) and 2012 (point at 1719 ind/m^3). Important demographic information observed from 2009 to 2013 is plotted by month in F–H. Male *Bythotrephes* (F) allow for the sexual reproduction of resting eggs (G). Individuals hatched directly from the resting egg bank can be identified by their straight rather than "s-bend" tail spines (H).

Modeled dynamics

The model captured the transition from a low-density population to a high density in 2009 (Fig. 5A). Steady population growth during summer 2009 led to increased production in the egg bank (Fig. 5B). This growth enabled a transition to a high-density state that was stabilized by the high-density egg bank (Fig. 5C). Notably, the model predicts high population densities in the early summer that are not matched by the small, secondary peaks observed in the early summers of 2010 and 2011, and extremely low summer densities in 2012. However, seasonal dynamics are captured relatively well in 2013 (Fig. 5A).

The modeled egg bank increased by over 1300% in 2009, with minimal increases and

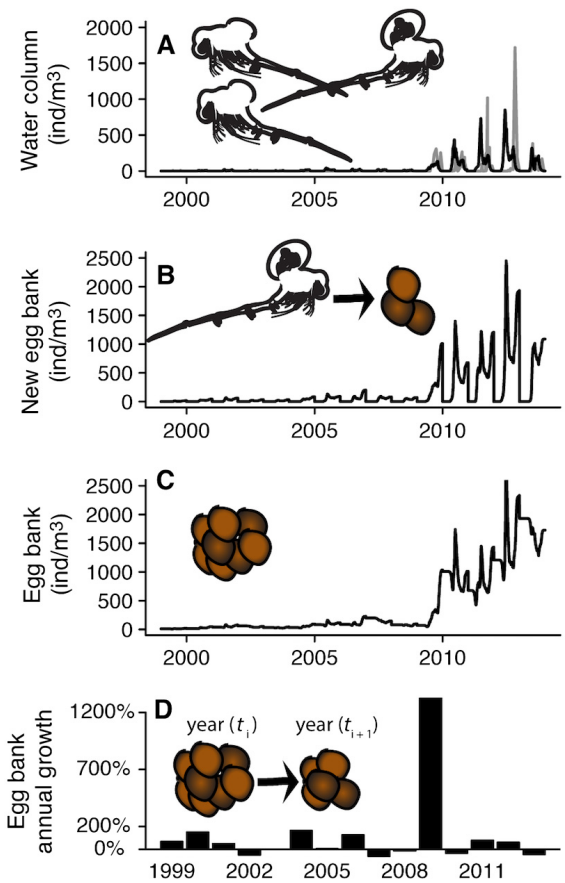

Fig. 5. Model results (black lines) are plotted over time ($t_{i,j}$) in panels A–C, and annual growth in the egg bank is plotted in D. (A) The population in the water column is summed over all three active development stages (S_1–S_3). The model simulation is in black and observed data in gray. (B) Population density in the water column is driven by the new production in the stabilizing egg bank in the lake sediments (modeled egg bank density, E_{new} in black). (C) Steady new growth in the egg bank drove a shift in the total egg bank ($E_{new} + E_{old}$) from a low-density egg bank supporting a low-density population state to a high-density state. (D) Modeled egg bank growth rates (% per yr) in 2009 were exceptionally high relative to other years.

decreases in all other years (Fig. 5D). Further investigation of surface temperatures in Lake Mendota reveals that 2009 was one of only five years (also 1996–1998 and 2004) in the 19-year LTER dataset that did not exceed *Bythotrephes*' thermal optimum (25°C; Fig. 2; 2006–2013 daily surface temperatures) and, thus, 2009 was the only year where there was no mid-summer decline or collapse of either the observed or modeled populations (Figs. 4 and 5). Furthermore, 2009 was the coldest July in Madison since at least 1895 (ncdc.noaa.gov/cag). Despite this, the hatching cue of 4°C in the lake bottom occurred sometime near 1 March, earlier than any year since 1995 other than 1995 and 2011, and 37 days earlier than any other year in which the lake did not warm past 25°C.

These anomalies gave the modeled population an extra month of hatching and growth in the early summer, and moderate, rather than zero, densities (observed in Fig. 4A–C) to produce resting eggs at a relatively high rate (Fig. 4G and Appendix S1: Fig. S2C—observed resting egg production) during mid-summer. In fact, over the 1999–2013 simulation under natural variation in lake temperatures, the modeled egg bank gained +8% (SE = 0.3%) annual growth per day of earlier hatching and lost 14% (SE = 0.5%) annual growth per warm day (annual egg bank growth = $B_1 \times$ [days > 25°C] + $B_2 \times$ [day of hatch] + B_0; $F_{2,12}$ = 4.599, p = 0.03, R^2 = 0.43). The modeled *Bythotrephes*' population eruption in response to this short-term climate anomaly was stabilized by the egg bank (Fig. 6). This apparently sustaining role of the egg bank in the model is supported by the high proportion of sexually produced *Bythotrephes* observed throughout the year in Lake Mendota (Fig. 4H).

Evidence of modeled population dynamics in Lake Mendota sediments

Though *Bythotrephes* was discovered in 2009, examination of uncounted archived NTL-LTER zooplankton samples revealed two individuals in a sample taken in October of 2008. An analysis of spines from sediment cores confirms this finding. Small numbers of spines were detected in core layers dated starting in 1994 (±5 yr, 95% CI) and spine deposition increased sharply in the layer dated 2009 (±4 yr, 95% CI; Fig. 7). Evidence from archived samples and sediment cores is consistent with the modeled eruption dynamics.

The role of lake temperature in modeled dynamics

To further evaluate the general role of temperature in driving *Bythotrephes*' population dynamics, we used our population model to simulate

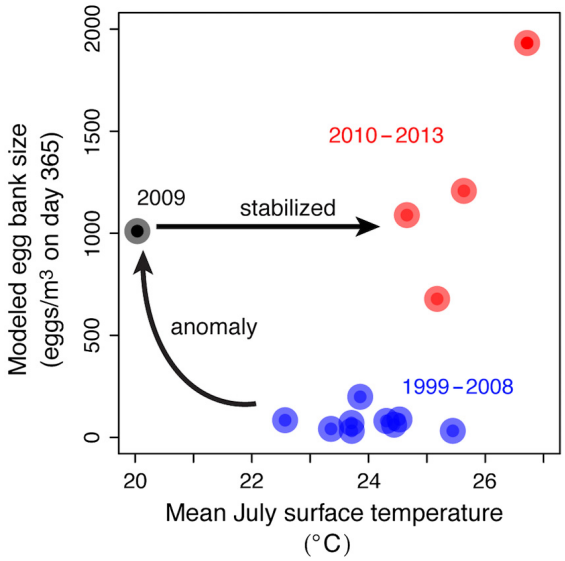

Fig. 6. Short-term variation in a key driver of *Bythotrephes*' population dynamics, surface water temperature, drove a massive increase in the size of *Bythotrephes* modeled egg bank (blue points to black point). This stabilized the population at high densities (red points) despite a return to warm surface water temperatures.

hypothetical growth in *Bythotrephes*' egg bank across a broad range of mean July air temperatures, which we used to simulate lake surface water temperatures (Fig. 8A). Annual growth rates in the egg bank increased with mean July air temperature up to 14°C, beyond which growth in the egg bank decreased, reaching 0 eggs·m^{-3}·yr^{-1} at 22°C and becoming negative above that temperature.

When we simulate consecutive years under warm conditions (+3°C above mean July air temperature), we find that the population would fall back below detection limits after three to four consecutive warm years (Fig. 8B). This increases to four to five consecutive warm years with a single recovery year after consecutive warm years (e.g., 2009 or −3°C below mean July air temperature).

Discussion

We investigated the early-stage dynamics of the *Bythotrephes*' invasion into Lake Mendota through population modeling. We corroborate our model findings with analysis of archived samples where we found evidence of *Bythotrephes* as early as October 2008 and lake sediment cores where we found evidence of *Bythotrephes* in core layers corresponding to the mid-1990s. Each approach supported the scenario that *Bythotrephes* had persisted undetected and erupted to high densities in 2009 (we note that it is possible that there is a constant source of propagules of *Bythotrephes* into Lake Mendota from Lake Michigan, located over 120 km east, or nearby undiscovered populations). In this case, an undetected low-density population shifted to a high-density state (Fig. 1B), rather than a newly introduced population erupting in the same year of its introduction (Fig. 1A). This outbreak was associated with a climate anomaly, an unusually cool summer. The short-term trigger of this outbreak contrasts with more common findings of population shifts with long-term changes in invaded habitats (Crooks 2005), revealing the importance of life history, in this case a resting egg bank, in stabilizing population responses to short-term variation (Fig. 6).

As we refer to temperature in the following paragraphs, we are referring to both the direct effects of temperature on *Bythotrephes* (e.g., via its thermal optimum and maximum) and the effects of the many variables that are correlated with temperature. For example, temperature indirectly influences the *Bythotrephes* population through consumption rates of predators (e.g., consumption rates of the lakes two dominant zooplanktivores, yellow perch and white bass, peak at 23° and 28°C, respectively; Johnson and Kitchell 1996). Further, calculated mortality is fit to surface temperatures in the model, so modeled mortality includes both the direct and indirect effects of temperature on the population. Finally, while 25°C is the upper limit of *Bythotrephes*' thermal optimum, temperatures are not acutely lethal until past 28°C. As a result, we refer to heat stress in terms of days >25°C, as some period of exposure to rapidly suboptimal temperatures that exceed 25°C would be required to collapse the population or slow population growth.

Bythotrephes' *population dynamics*

Our results suggest that favorable thermal conditions allowed for *Bythotrephes*' transition to a high density in 2009. July of 2009 was the coolest since at least 1895 for both Madison and south

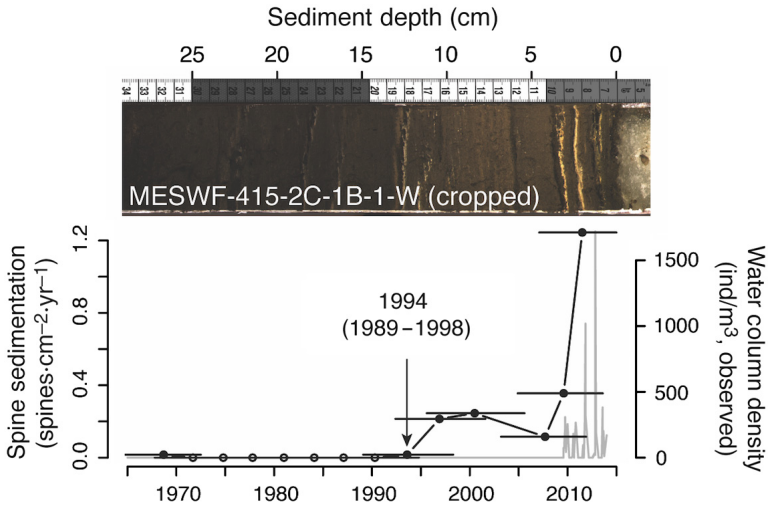

Fig. 7. *Bythotrephes* areal spine sedimentation rates are plotted in black with observed water column density plotted in gray. The *x*-axes are depth in the core (top) and estimated age at core depth (bottom). 95% confidence intervals (horizontal lines) are shown for the median age estimate of each core layer (black circles). The estimated date and 95% confidence interval of *Bythotrephes* arrival into Lake Mendota is shown with a black arrow (i.e., the deepest core layer containing at least one spine—1994). Sediment dates and errors are calculated using the Bayesian modeling program bacon v.2.2 (Blaauw and Christen 2011) constrained by dates derived from ^{210}Pb analysis.

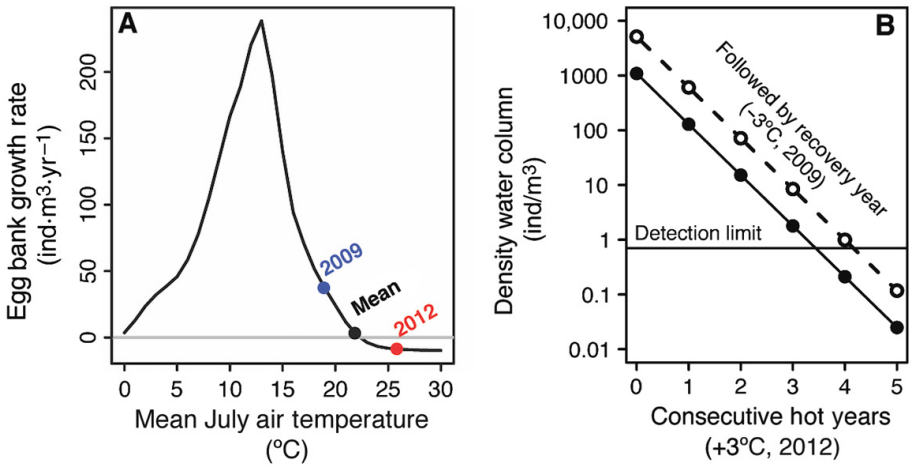

Fig. 8. (A) Annual growth rates (ind·m^{-3}·yr^{-1}) in the egg bank after one simulated year under varying mean July air temperatures (used to simulate lake surface temperature; Sharma et al. 2007) reveal *Bythotrephes*' nonlinear response to surface temperature. Under average conditions in Lake Mendota (black), there is little net change in the egg bank. There is large positive growth in the egg bank under cool years such as 2009 (blue). However, equally warm years such as 2012 (red) do not drive the same magnitude in loss in the egg bank. (B) Simulated consecutive warm years slowly deplete the modeled egg bank, driving down population density in the water column (depicted). Solid lines and circles represent simulation under consecutive hot years, and dashed lines and open circles represent the same simulation followed by a single cool year.

central Wisconsin, reaching mean air temperatures of just 18.7°C compared to average July air temperatures of 21.9°C (ncdc.noaa.gov/cag). This climate anomaly was critical for *Bythotrephes*' population growth as Lake Mendota routinely warms past its thermal optimum (as per individual developmental rate, which declines rapidly after 25°C; Kim and Yan 2010, Kerfoot et al. 2011, Keeler et al. 2015; Fig. 2), thereby crashing the population (Fig. 4A–E). Despite surface waters never warming past 25°C in 2009, lake bottom temperatures warmed to the 4°C hatching cue extremely early. Early hatching and fewer warm (>25°C) days have strong positive effects on modeled growth in the egg bank, even under natural variability in surface temperatures. However, the cool summer of 2009 was a climate anomaly and the lake returned to consistently warm summers. In fact, 2010, 2011, and 2012 were the 16th (+1.5°C), seventh (+2.5°C), and first (+4.0°C) warmest Julys since 1895 (ncdc.noaa.gov/cag). Despite hot summers, the population did not decrease to pre-2009 densities.

In the model, *Bythotrephes*' egg bank allowed the population to persist through unfavorable conditions in both its low- and high-density states. This supplemental role of the egg bank is supported by observations of a relatively high and constant (rather than pulsed) proportion of newly hatched individuals present in samples throughout each year (Fig. 4H) and by negative calculated death rates in first-instar stage individuals, indicative of a contribution from the egg bank (M. E. Brown, *personal communication*, see Appendix S1 "Mortality Rates"). The essential roles of the egg bank and of summer resting egg production are evaluated further in the Appendix where we show that persistence in Lake Mendota would be highly unlikely in any year, 2009 included, without either summer resting egg production or a secondary hatch from the egg bank in the late summer and fall (Appendix S1: Fig. S6). A peak in resting egg production prior to the harsh conditions of winter is common for cladoceran zooplankton (Kerfoot 1980); however, the secondary peak we observe prior to warm July and August water temperatures for "oversummering" is much less so. Additional work should investigate the drivers of *Bythotrephes* resting egg production in Lake Mendota to tease apart the many possible triggers of resting egg production that are also correlated with temperature (e.g., population density, day length, or predator cues). *Bythotrephes* resting eggs remain viable in the sediment up to three years after they are deposited (Herzig 1985), establishing an egg bank to support and reseed the population after winter and harsh summers. Furthermore, as long as modeled net growth in the egg bank is near zero, which occurs under most annual temperature increases and small temperature decreases in Madison (Fig. 8A), the egg bank and the population in the water column exist in equilibrium. This is likely why the population remained at low densities prior to 2009 and why the high-density population was able to persist through the warm conditions of 2010–2012.

A nonlinear response to water temperature allowed the modeled population to explode in 2009 and persist in subsequent years (Fig. 8A). We found that Lake Mendota surface temperatures did not exceed *Bythotrephes*' thermal optimum in 1996–1998, 2004, and 2009. Further, most mean July air temperatures in Lake Mendota between *Bythotrephes*' discovery in the Great Lakes in 1983 and detection in Mendota in 2009 have been warmer than 20.5°C, which would cause a decline in the egg bank. It is likely that the few years with more favorable July air temperatures between 18.7° (i.e., 2009) and 22°C (such as 1984–1985, 1990, 1994, 1997–1998, 2000, 2003–2004) or observed surface water temperature that never exceeded 25°C (1996–1998, 2004) may not have been "favorable enough" to transition the population to a higher density. For example, hatching would have been cued anywhere from 33 to 43 days later in 1996–1998 and 2004 than it was 2009, possibly precluding a population eruption. However, establishment could have also been influence by factors that are not captured by the model such as interannual variability in predator biomass. Alternatively, these years represent potential times of *Bythotrephes'* initial establishment into Lake Mendota as a low-density population. Timing of *Bythotrephes*' initial establishment may be constrained further by the detection of tail spines in sediment core layers that were dated to be deposited somewhere between 1989 and 1998, which spans favorable thermal conditions observed from 1996 through 1998. Since the only archived evidence was found

in October of 2008, it is worth considering whether 2008 played a role in either *Bythotrephes* establishment or transition to a higher density population.

The modeled *Bythotrephes* population peaks at high densities in the early summer, which is not matched in our observations of the population. While we observed a small peak early in most summers (2010, 2011, and 2013), this discrepancy is most obvious in 2012 when *Bythotrephes* was nearly absent from the water column until October (Fig. 5A). This mismatch between our model, which was derived from an extensive literature on *Bythotrephes*' population dynamics, and reality highlights a key gap in our understanding of *Bythotrephes*' population dynamics.

We have observed a marked difference in the production and hatching of *Bythotrephes* resting eggs in a warm lake (Fig. 4F–H) relative to cooler lakes in the literature. In temperate lakes, zooplankton resting eggs are typically produced and laid prior to winter, and then hatch in spring. In contrast, the model suggests that these eggs could have been laid earlier in the same year that they hatch after a mandatory period of dormancy (114 d; Herzig 1985), which is supported by demographic data (Fig. 4F–H). In the model, reducing this mandatory period of dormancy or increasing the hatching rate of eggs laid within the same year yields modeled seasonal dynamics that more closely match observed dynamics, that is, reduces the relative size of the early season peak to the late season peak (Appendix S1: Fig. S7). Interestingly, bottom temperatures in Lake Mendota in 2009 were very similar to the warm 2012, warming earlier and to a higher degree than any other cool year (e.g., 1996–1998, 2004, or even the slightly warmer 2013). While we have shown that favorable conditions in the lake bottom (earlier hatching) do not offset stressful surface water temperatures (>25°C), it is likely that bottom temperatures play a key role in *Bythotrephes*' population dynamics. This model suggests that the response of the dormant stage to increasing temperatures should be addressed with further study as it could be critical to *Bythotrephes* future in warm lakes.

Future of Bythotrephes *in Lake Mendota*

We found that the modeled population would be unlikely to persist, that is replenish the modeled egg bank at a sustainable annual rate, after three to four consecutive hot years (e.g., 2012, the hottest year on record), with implications for *Bythotrephes* long-term role and persistence in Lake Mendota (Fig. 8B). However, trophic or life-history mismatches due to climate change are most likely to occur in zooplankton when the environmental cues that drive resting egg or diapausing stage emergence (e.g., photoperiod) do not change with the environmental factors that promote favorable population growth (e.g., temperature, resource availability; Winder and Schindler 2004). *Bythotrephes* emergence is likely driven by temperature (Herzig 1985). As a result, earlier favorable thermal conditions may correspond with earlier cues for emergence in the spring. In fact, modeled spring and summer hatching is cued earlier in the lake bottom with warmer air temperatures. Despite this, the modeled *Bythotrephes* population still struggles to replenish its egg bank at mean July air temperatures >22°C. At this temperature, modeled maximum surface water temperatures begin to surpass 25°C, but eggs are cued to hatch just one week earlier than under mean July air temperature of 19°C. Failure to replenish the egg bank in the model at temperatures >22°C suggests the benefit of the earlier cue does not outweigh the cost of high summer water temperature, as observed in the 1999–2013 Lake Mendota simulation. How the relationships between ice break up, early spring warming in the hypolimnion, and summer surface temperatures change with climate will be key to understanding *Bythotrephes* persistence in Lake Mendota.

This temperature-dependent population dynamic may have implications for *Bythotrephes'* impact on the native herbivore, *Daphnia*. *Bythotrephes*' outbreak in 2009 caused massive declines in *Daphnia pulicaria* (Walsh et al. 2016). Intense predation in the fall affected *D. pulicaria* dominance in spring 2010, where it shared dominance with other zooplankton for the first time in nearly three decades. However, this lingering spring effect was not as strong after the warm summers of 2010–2012 (i.e., in the springs of 2011–2013). In contrast, air temperatures in July 2014 were the fourth coolest on record (1.4°C below long-term average mean July air temperatures) and surface water temperature remained low. In fall 2014, the entire *Daphnia* community

collapsed, including species such as *D. galeata mendotae,* which had been more successful at coexisting with *Bythotrephes*. This *Daphnia* collapse lasted over 250 days, delaying and muting the spring 2015 clear water phase, as observed in 2010 and 2014. As warm summers seem to improve the overwintering success of *D. pulicaria* and its population growth in the following spring, additional research should target how *Bythotrephes*' impact might change with a warming climate.

Invasion ecology of prolonged lags

Low-density population outbreaks may be more likely to occur along the edge of an invading species' range as a result of invasion pinning, the slowing or halting of range expansion as an invasive species reaches ecological limits in geographical space (Keitt et al. 2001, Crooks 2005). Expansion is slowed along this edge as established populations in favorable environments seed nearby populations in less favorable environments. When conditions in these new habitats become favorable, either temporarily as we present here or over time with ecological change (Kowarik 1995, Rilov et al. 2004, Witte et al. 2010), low-density populations can shift to higher densities (Takimoto 2009), resulting in undesired impacts. Thus, understanding the mechanism of invasive species population outbreaks will be an important endeavor in invasion ecology, even for species that are already widespread.

Abrupt regime shifts provide unique challenges to the management of ecosystems (Scheffer and Carpenter 2003, Bestelmeyer et al. 2011) and invasive species in particular (Takimoto 2009). We show how an abrupt transition in an invasive population from a low-density to high-density state can be triggered by temporary environmental conditions. While regime shifts, even those due to singular stochastic events, are commonly reported (e.g., Bertani et al. 2016), reports of abrupt transitions in invasive populations due to temporary anomalies, rather than gradual or step-change in population equilibrium, such as this are rare. Further, the *Bythotrephes* eruption in Lake Mendota had significant effects on the ecosystem (Walsh et al. 2016), further revealing how changes in established invasive populations can have lasting effects on ecosystem functioning (Strayer 2012).

The early-stage dynamics of invasions remain a key challenge to invasion ecologists (Severns et al. 2015) and managers. For example, at their invasion front, gypsy moth populations cycle through periods of high and low abundance, which affects both dispersal and the detection of new outbreaks (Walter et al. 2015). Similarly, in cases where outbreaks are triggered by anomalies, the ecology of endemic and epidemic equilibria may shed light on these dynamics (Anderson and May 1992). Endemic populations can be pushed into a higher density, stabilized epidemic state through short-term variation in environmental conditions. If the *Bythotrephes*' population dynamics in Lake Mendota can be approximated by epidemic dynamics, then managers may target solutions that stabilize the endemic equilibrium rather than more intensive eradication solutions.

Further, the role of climate in triggering outbreaks of native nuisance species is well established (e.g., Todd et al. 2002, Tian et al. 2011, Greenville et al. 2013, Taylor and Bothwell 2014). Climate has also been a key trigger of invasive outbreaks indirectly through pathways such as resource pulses (Holland et al. 2015) and adaption to newly encountered pathogens (Wendling and Wegner 2015), as well as directly through driving eruptive dynamics in invasive forest-defoliating insects (Jepsen et al. 2008) and invasive kelp-defoliating bryozoans (Saunders et al. 2010). These outbreaks reveal the importance of early detection coupled with understanding of the triggers of population outbreaks.

Finally, resting or diapausing stages are a key vector of aquatic species invasions. Resting eggs in particular are innately equipped to handle harsh environmental conditions and are more likely to endure the harsh conditions of transport (Panov et al. 2004, Kerfoot et al. 2011). We add to this literature by noting that resting egg banks may stabilize populations through unfavorable conditions endured during the early stages of an invasion (analogous to invasive plant seed banks; Thompson et al. 1995, Gioria et al. 2012).

Application

This model represents the foundation of a potential mechanistic tool to use in modeling the ecological niche of *Bythotrephes* and, in turn, predicting where and when it is likely to be abundant. While a discrepancy exists between the early

summer dynamics of modeled and observed populations, this highlights a key gap in our understanding of *Bythotrephes*' population growth and range expansion in warm climates. Nevertheless, egg bank growth rates are critical to *Bythotrephes* long-term population dynamics (e.g., Fig. 8A). As is, the model could help identify regions where the dynamics that occurred in Lake Mendota may repeat, possibly helping to identify lakes where population dynamics may preclude detection by traditional means but still may be ecologically harmful given temporarily favorable conditions in the future. One could apply a more complete version of this model to lakes across North America, observing where egg bank growth may be limited by temperature (e.g., via model simulation under observed mean July air temperature from WorldClim). Also, this model could be used to predict prolonged lags, which occur in systems with near neutral growth rates under mean annual conditions (e.g., ~0 eggs·m^{-3}·yr^{-1}) but which have the potential to erupt under cool years (e.g., >10–20 eggs·m^{-3}·yr^{-1}). This model could also be used to model *Bythotrephes*' range and population dynamics under climate change scenarios (e.g., Fig. 8B at broad spatial scales).

Conclusion

When an invasive species suddenly appears at a site, is it the result of a recent introduction? Or is it the result of a previously established but undetected, low-density population undergoing a population eruption and/or crossing a detection threshold? We generally have no information regarding the situation preceding the eruption of an invasive species, due to the near-impossibility of studying population dynamics of species at densities below the detection limit. While it is convenient to assume that the introduction of invasive species propagules and the detection of a population are closely coupled in time, our work highlights the potential for invasive species propagules to be introduced and subsequently persist at low densities for a prolonged period of time, until a population eruption is triggered by environmental conditions. In our case, the trigger was a temporary climate anomaly, and the invasive species population was stabilized by the existence of a resting egg bank. Moreover, the possibility of such dynamics has important implications for invasive species management, since the standard programs aimed at preventing invasive species propagule transport may be futile if a population is already established and persisting at low levels at a site. Our work highlights the need for more rigorous detection methods and real-time processing of nonnative species sampling efforts.

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Supporting Information

Additional Supporting Information may be found online at: http://onlinelibrary.wiley.com/doi/10.1002/ecs2.1628/full