Massive impacts on ecosystem services and processes due to an invasive species outbreak

By

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To my wife, Naomi. Of any blessing I have received, you are by far the greatest, and I’m honored to be yours. Love you, Beans.

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It is not our part to master all the tides of the world, but to do what is in us for the succour of those years wherein we are set, uprooting the evil in the fields that we know, so that those who live after may have clean earth to till. What weather they shall have is not ours to rule.

- JRR Tolkien (Return of the King)

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Dissertation Abstract

Human driven ecological and environmental change has become the defining characteristic of the planet's current geological age. Climate change, eutrophication, and species invasions have produced novel challenges that affect how ecosystems sustain and improve human well-being. Here, I use the case study of the spiny water flea (*Bythotrephes longimanus*) invasion into the culturally eutrophic Lake Mendota, WI (USA), to investigate how these anthropogenic changes feed back onto human economy. First, I model how natural variation in climate likely drove a high-density outbreak of a low-density population of *Bythotrephes*. I use the model to explore how future warming might affect the persistence of the cool-water zooplankter in Lake Mendota. Second, I investigate how *Bythotrephes* damaged water clarity in Lake Mendota through predation on the native herbivore, *Daphnia pulicaria*, in turn driving enormous economic loss – US$140 million. I estimate that this loss in value could be returned through equally substantial investments in redoubling efforts to reduce phosphorus loading into Lake Mendota. Finally, I show how the future of Lake Mendota may be defined by two apparently diverging elements of water quality - the frequency and intensity of harmful algal blooms and water clarity. *Bythotrephes* invasion coincided with a substantial reduction in the concentration of phosphorus in the lake's surface waters. Despite declines in *D. pulicaria* and clarity, I observe no change in the summer biomass of cyanobacteria or the frequency of Lake Mendota beach closures due to cyanobacteria blooms. Future research should address the fate of 30% of Lake Mendota's epilimnetic total phosphorus and the implications of that loss for water quality. *Bythotrephes* invasion of Lake Mendota presents a unique case study to investigate the interrelated roles played by anthropogenic changes in an ecosystem. The invasive *Bythotrephes* intensified one of the harmful effects of eutrophication in Lake Mendota, but may be negatively affected by future warming. Further change in the watershed via nutrient load management, warming and elevated precipitation, and new invasive species will continue to play a central role in the functioning of Lake Mendota and, in turn, the delivery of its valuable services.

Introduction: Invasion through a long-term lens

Species invasions and global change

Invasive species are profoundly changing the biological make-up and functioning of world ecosystems (Clavero and García-Berthou 2005, Ehrenfeld 2010); often with costly implications for human well-being (Pimentel et al. 2005, Charles and Dukes 2007, Keller et al. 2009, Pejchar and Mooney 2009, Rothlisberger et al. 2012). Invasive species' impacts radiate into ecosystem processes and services through food webs. These complex pathways of an invasive species' impact are conceptualized as the product of an invasive species' range; i.e., the number of systems it has invaded, its abundance distribution, and its per capita effect (Yokomizo et al. 2009, Thiele et al. 2010). While this simplifies conceptualizing invasive species' impact at broad spatial scales, the reality is that each of these components changes through time.

This dynamic nature of invasive species' impact plays out through each component of this conceptual impact model. Invasive species initially spread across landscapes, increasing their range. Even within their geographical range, new systems are colonized. Similarly, invasive populations will change in response to long-term changes in ecosystems. These changes are intensified in systems where invasive populations have yet to equilibrate and stabilize. Finally, invasive species' impact is the complex realization of a large number of ecological interactions. Therefore, as invasive species spread or as ecosystems change, per capita effect is also likely to change as invasive species encounter new ecological interactions. Because of variation in each of these three components, invasion ecology is and will continue to be a critical component of conservation and global ecosystem management (Rahel and Olden 2008, Strayer 2012).

For example, secondary invasion or spread multiplies invasive species' impacts at the continental scale. This is intuitive as an invasive species' total impact increases with its range and the number of systems it affects. However, as invasive species spread they encounter new ecological interactions and new anthropogenic stressors, resulting in new pathways of impact. So as an invasive species spreads, its impact is not only modulated by the additional ecosystems it invades and impacts, but also by these new pathways. Here I investigate how a relatively benign invasive species tripped an "ecological landmine" when it spread into a lake nested in an agricultural landscape; leading to unprecedented ecological and economic impacts.

Similarly stemming from this state of disequilibrium are gradual or abrupt changes in invasive populations. As an invasive species is "pinned" at the edge of its invaded range (Keitt et al. 2001), long-term population dynamics and the factors that drive them become a critical component of understanding invasive species impact. In this phase of the invasion process, outbreaks of invasive populations are often mistaken for new invasions or, more tragically, for low-density populations that are thought to be unlikely to have large impacts within ecosystems (Crooks and Soule 1999, Crooks 2005). While there are many cases of how long-term ecological change affects invasive populations (Manca et al. 2007, Aikio et al. 2010, Witte et al. 2010, Larkin 2012, Aagaard and Lockwood 2014), here I show how even short-term variation in climate can abruptly transition low-density invasive populations to outbreaks of populations shifting to higher density states.

Aquatic invasive species and Great Lakes shipping

Many aquatic invasive species are transported through the ballast of transatlantic shipping vessels that were once discharged into the St. Lawrence Seaway of the Laurentian Great Lakes. This common vector of transcontinental aquatic invasions has been identified as one of the major consequences of transatlantic shipping and trade (Taylor and Roach 2009, Rothlisberger et al. 2012). Because of this, huge efforts have been made to improve ballast water management practices as a compromise between closing the St. Lawrence Seaway to these oceanic vessels and preventing future invasions (Transportation Research Board 2008, National Research Council 2011).

Since major ballast water management reform in 2008 there has been no new invasive species in the Great Lakes. However, given the relatively minor cost of closing the seaway to oceanic vessels (US$55M or 6% of a nearly US$1B industry; (Taylor and Roach 2009) and the enormous costs of invasions (Rothlisberger et al. 2012), many scientists are skeptical of practice that “leaves the door cracked open” to future invasions (Egan 2014). This is particularly true for abundant and small invasive species (e.g., invertebrates, phytoplankton, bacteria, viruses, etc.).

Finally, as most of the economic impacts of aquatic invasive species have been assessed on the Great Lakes alone, expanding those analyses to secondary spread will dramatically increase the true cost of Great Lakes’ invasive species that has already been estimated on the order of billions annually (Pimentel et al. 2005, Rothlisberger et al. 2012).

The spiny water flea

One such species, the invasive predatory zooplankter, *Bythotrephes longimanus* (the spiny water flea), was transported to the Laurentian Great Lakes via this pathway in the early 1980s. Since, it has spread to many inland lakes in the Great Lakes Region (Yan et al. 2011). *Bythotrephes* has been shown to have enormous impacts within the zooplankton community, often extirpating zooplankton from lakes (Lehman and Caceres 1993, Dumitru et al. 2001, Strecker and Arnott 2005, Barbiero and Rockwell 2008, Strecker et al. 2011). While predation by *Bythotrephes* is likely to have radiating consequences for food webs, few of such cases have been reported.

In Lake Michigan, *Bythotrephes* nearly extirpated a key grazer and prey resource for pelagic fishes – *Daphnia pulicaria* (Lehman and Caceres 1993, Barbiero and Tuchman 2004). While likely overlooked, this may have played a role in the collapse of the lake's yellow perch fishery, as *Bythotrephes* can consume more zooplankton than fish and invertebrate zooplanktivores *combined* (Bunnell et al. 2011). Similarly, any cascading effects *Bythotrephes* may have had on primary production in Lake Michigan are dramatically overshadowed by many other high impact invasions (e.g., sea lamprey, zebra and Quagga mussels, round goby, and a largely man-made salmon fishery).

Bythotrephes has been most frequently observed in deep, clear, cool, and unproductive lakes; often in the Canadian Shield or along the lakes bordering the southern edge of the Great Lakes in the U.S (Branstrator et al. 2006, Hessen et al. 2011). Therefore, its impact is most often contained within zooplankton communities as the algal production in these lakes is nutrient rather than grazer limited (Strecker and Arnott 2008). However, *Bythotrephes* is still spreading somewhat rapidly in North America, particularly in Wisconsin.

Bythotrephes was detected in Lake Mendota in 2009 at unprecedented densities that it has reached regularly since. Its prey, *D. pulicaria*, has been critical to the lake's food web, supporting its fishery (Johnson and Kitchell 1996) and maintaining clear water through grazing algae (Lathrop et al. 1996, 1999, 2002). The latter service has yielded good or mostly "mesotrophic" (moderate productivity) water clarity despite poor or mostly "eutrophic" (high productivity) nutrient concentrations in the lake due to run-off from the surrounding agricultural watershed (Fig. 1). The detection of *Bythotrephes* was an immediate concern primarily for its potential to reduce top-down pressure on algal growth through predation on large grazers like *D. pulicaria*, in turn degrading water clarity, but also for its potential impact on the lake's fishery which depends heavily on the zooplanktivorous yellow perch and the availability of small zooplanktivorous fishes to larger game fishes.

Lake Mendota was thought to be relatively unsuitable for *Bythotrephes*' establishment, yet it supports the largest known population of the invader in its native or invaded range. Additionally, Lake Mendota is considered one of the most researched lakes in the world and its zooplankton community is surveyed over one dozen times per year. How, then, does an invader go from undetected in a well-monitored lake to unprecedented densities in a single year? Further, how does this happen in a relatively unsuitable lake that annually heats past *Bythotrephes*' thermal optimum?

In Chapter 1 of this thesis, I investigate the mechanism of *Bythotrephes'* outbreak in Lake Mendota through population modeling. In Chapter 2, I address *Bythotrephes*' impact on water clarity in Lake Mendota. As a key ecosystem service, water clarity has economic value to Dane County's citizens that use the lake for a many recreational activities. Therefore, Chapter 2 focuses on how ecological impacts drive economic impacts, which I present alongside the cost of potential restoration options. In Chapter 3, I investigate in more detail how the invasion impacted the lake's biological communities and ecological processes. Here, *Bythotrephes*' cascading impact has differential and possibly even divergent implications for two different components of Lake Mendota's water quality – clarity and the frequency and intensity of harmful cyanobacteria blooms. This work not only informs on a new key driver of Lake Mendota's food web, but also advances understanding of the many complex pathways of invasive species' impacts in a changing world.

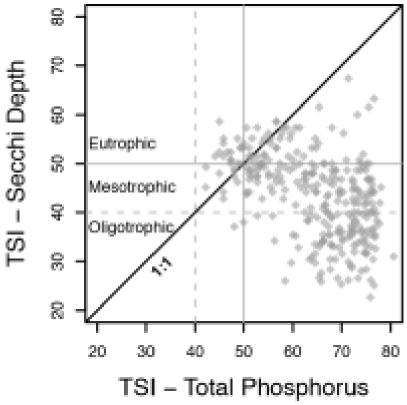

Figure 1. Trophic state index in Lake Mendota from 1995 to 2013 (grey diamonds). Trophic state can be estimated through total phosphorus concentrations (higher TP is more eutrophic) and Secchi depth (lower Secchi depth or clarity is more eutrophic). “Mesotrophic” status ranges from 40 – 50 (bounded by dashed and solid lines along each axis). Note that most points fall beneath the 1:1 line (black solid), signifying that Lake Mendota often has a lower trophic state estimated by clarity than would be predicted by nutrients (TP).

Chapter One: Outbreak of an undetected invasive sleeper cell triggered by climate anomaly

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Co-Authors: Samuel E. Munoz and M. Jake Vander Zanden

Manuscript

Abstract

When an invasive species appears at a new location, we typically have no knowledge of the population dynamics leading up to that moment. Was 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. 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 (+/- 4.6 y). Together, our results indicate 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.

Keywords: invasive species, outbreaks, abrupt transitions, prolonged lags, *Bythotrephes longimanus*

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, and has been detected. For this to happen involves multiple steps: 1) invasive species propagules are transported and introduced, 2) the population establishes and becomes self-sustaining, and 3) the population crosses a detection threshold (Fig. 1A; e.g., 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 (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 animals 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, non-native 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, versus 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 unrivaled densities (Walsh et al. 2016), despite what are generally considered unfavorable ecological conditions in the lake (MacIsaac et al. 2000, Branstrator et al. 2006, Kerfoot et al. 2011). Concomitant with high densities of *Bythotrephes*, there has been a reduction in biomass of the efficient grazer *Daphnia pulicaria*, resulting in an economically costly decline in lake water clarity (Walsh et al. 2016).

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 July and August (Fig. 2) that consistently exceed *Bythotrephes'* thermal optimum of 25°C (Kim and Yan 2010). The lake bottom (25.3 m maximum depth and 12.7 m mean depth) becomes anoxic in summer, further constricting the potential vertical distribution of cool-water aquatic organisms.

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.

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), and clutch size (number of embryos or eggs).

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 subsampled 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 (n = 16 for ^{210}Pb analysis). 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 S1 and S2 and mature stage S3), 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. All computation, component derivation, and model simulations are conducted using the statistical program R (R Core Team 2014).

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 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 2) are developed using our own demographic data fitted to generalized additive models of temperature-dependent reproduction (Wood 2015). Temperature-dependent mortality (*M*; Fig. 2, Table 2) is estimated by applying the methods outlined in Brown et al. (2012) to our own demographic data to estimate daily per capita mortality. These daily estimates of mortality are then fitted to a polynomial function of temperature ($M = B_0 + B_1 \times T + B_2 \times T^2$) for each instar stage using non-linear 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.

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 m – 5 m, which corresponds to depths that contain the majority of the *Bythotrephes* population. 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°C - 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. If growth greatly exceeds 0 eggs m^{-3} yr^{-1} under lake surface temperatures simulated from mean July air temperature, then it is likely that *Bythotrephes* would not be temperature limited in such a lake. Conversely, those that would produce growth rates much lower than 0 eggs m^{-3} yr^{-1} would be unlikely to support *Bythotrephes*. Additionally, we 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. 4). *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. 4).

Modeled Dynamics

The model captured the population dynamics observed in the Lake Mendota *Bythotrephes* population whereby a low density population transitioned 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).

The modeled egg bank increased by over 1,300% in 2009, with minimal increases and 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 (25ºC) (Fig. 2; 2006 –

2013 daily surface temperatures). Furthermore, 2009 was the coldest July in Madison since at least 1895 (ncdc.noaa.gov/cag). The *Bythotrephes* population eruption in response to this short-term climate anomaly was stabilized by the egg bank (Fig. 6).

Confirming Modeled Dynamics in Lake Mendota

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 confirm this finding. Small numbers of spines were detected in core layers dated starting in 1994 (+/- 4.6 y, 95% C.I) and spine deposition increased sharply in the layer dated 2009 (+ 4.1 y and – 4.4 y, 95% C.I.) (Fig. 7). Evidence from archived samples and sediment cores are 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 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 (+3ºC above mean July air temperature) we find that the population would fall back below detection limits after 3-4 consecutive warm years (Fig. 8B). This increases to 4-5 consecutive warm years with a single recovery year after consecutive warm years (e.g., 2009 or -3 ºC 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 and lake sediment cores. Each approach supported the scenario that *Bythotrephes* had persisted undetected and erupted to high densities in 2009. 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).

Bythotrephes *Population Dynamics*

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 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), and thereby crashing the population (Fig. 4). 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), 7th (+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.

Bythotrephes' egg bank allowed the population to persist through unfavorable conditions in both its low and high density states. The essential roles of the egg bank and of summer resting egg production are evaluated further in the Appendix. 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. *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 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 stabilizes the population. 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 non-linear response to water temperature allowed the 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°C (i.e., 2009) and 22°C (such as 1984-85, 1990, 1994, 1997-1998, 2000, 2003-2004) or observed surface water temperature that never exceeded 25°C (1996 – 1998, 2004) either a) were not "favorable enough" (e.g., Fig. 8A) to transition the population to a higher density, or b) represent potential times of *Bythotrephes'* initial establishment into Lake Mendota as a low-density population. *Bythotrephes* initial establishment may be constrained by two pieces of evidence presented here. First, in the model, the population persisted from 1999 through 2008 prior to eruption in 2009, and second, surface water temperatures remained below 25°C from 1996 to 1998, and we first detected tail spines in sediment core layers corresponding to 1994.

Future of Bythotrephes *in Lake Mendota*

We found that the modeled population would be unlikely to persist above our detection limit after 3 – 4 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 greater than 22°C. At 22°C mean July air temperatures, 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 greater than 22°C suggests the benefit of the earlier cue does not outweigh the cost of high summer water temperature. 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 will likely have implications for *Bythotrephes* impact on the native grazer, *Daphnia*. *Bythotrephes*' outbreak in 2009 caused massive declines in *D. 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 co-existing 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. 2015), 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 stabilize populations through unfavorable conditions endured during the early stages of an invasion (analagous to invasive plant seed banks; Thompson et al. 1995, Gioria et al. 2012).

Application

This model represents 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. Egg bank growth rates are critical to *Bythotrephes* long-term population dynamics (e.g., Fig. 8A). One could apply 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. In addition, the recent emergence of highly sensitive species detection methods such as environmental DNA (Jerde et al. 2011) will likely shed new light on the low population and eruption dynamics of invasive species.

Acknowledgements

We thank the many in the NTL-LTER program responsible for data collection and curation; Marco Scarasso, Thomas Shannon, Bridget Murphy, Sommer Kuhn, and Henry Schmit for assistance with coring and core processing; UMN LacCore staff, particularly Kristina Brady and Mark Shapley; St. Croix Watershed Research Station and Daniel Engstrom; Laura Josephson, Danielle Gries, Michael Josephson, Jared Burris, Carly Broshat, Steve McMahon, Evan Booth, Ryan Toman, Sam Christel, Brad Benson, Petra Wakker, Olin Halsten, Jennifer Schlobohm, Kaity Taylor, and Sam Neary for assistance collecting and processing *Bythotrephes*; and Emily Stanley, Steve Carpenter, Tony Ives, Randy Jackson, Anthony Ricciardi, and Michael Marchetti for friendly review. This work was funded by the NSF North Temperate Lakes Long-Term Ecological Research Program grants DEB-0217533 and DEB-1440297 and the Wisconsin Department of Natural Resources.

Author Contributions

MJVZ and JRW designed the research regarding population modeling of outbreak. JRW, MJVZ, and SEM designed the research regarding sediment analysis. JRW conducted the research for the population model. SEM and JRW conducted the research for the sediment analysis. JRW completed data analysis for the model and SEM for sediment dating. JRW, SEM, and MJVZ wrote the paper.

Table & Figure Legends

Table 1. Model components, units, descriptions, and references from Figure 1. The structure of the model is described in more detail in the Methods, Appendix, and Table S1.

Figure 1. Two possible scenarios of invasive species population establishment and outbreak timing. A) An invasive species establishes 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.

Figure 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.

Figure 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- (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).

Figure 4. Annual *Bythotrephes* population dynamics in Lake Mendota since the 2009 outbreak. 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 1,019 ind m^{-3}) and 2012 (point at 1,719 ind m^{-3}).

Figure 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 (black line) matches among year variation in observed population density data (grey line) in the water column. 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 (% yr^{-1}) in 2009 were exceptionally high relative to other years.

Figure 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.

Figure 7. *Bythotrephes* areal spine sedimentation rates are plotted in black with observed water column density plotted in grey. 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 & Christen 2011) constrained by dates derived from ^{210}Pb analysis.

Figure 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*' non-linear 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.

Tables & Figures

Table 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 et al. 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 percent hatching. Percent of $E_{old}(i, j=1)$ for E_{old} and percent of $E_{new}(i, j\text{-}1)$ 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.

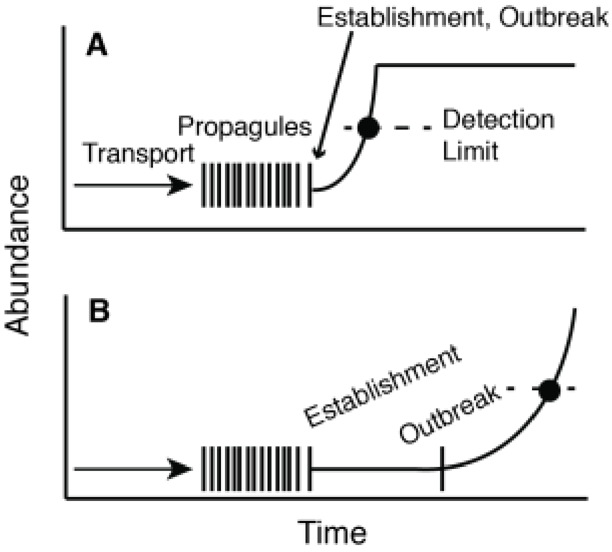
A
Establishment, Outbreak
Propagules
Transport
Detection
Limit
Abundance
B
Establishment
Outbreak
Time

Figure 1.

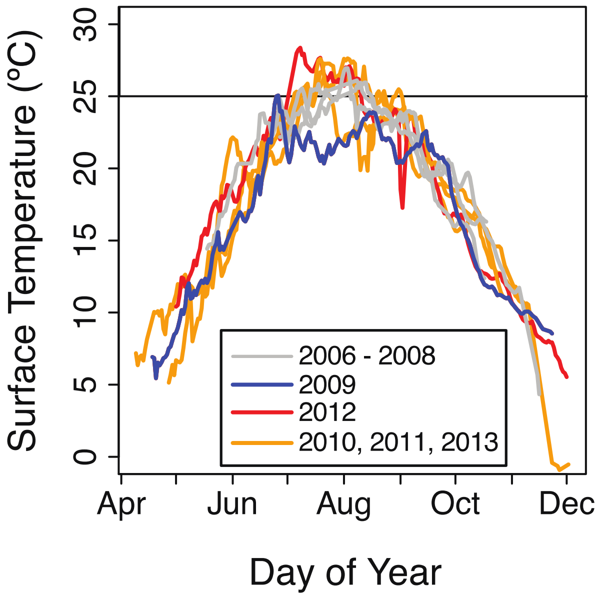
Surface Temperature (°C)
30
25
20
15
10
5
0
2006 - 2008
2009
2012
2010, 2011, 2013
Apr
Jun
Aug
Oct
Dec
Day of Year

Figure 2.

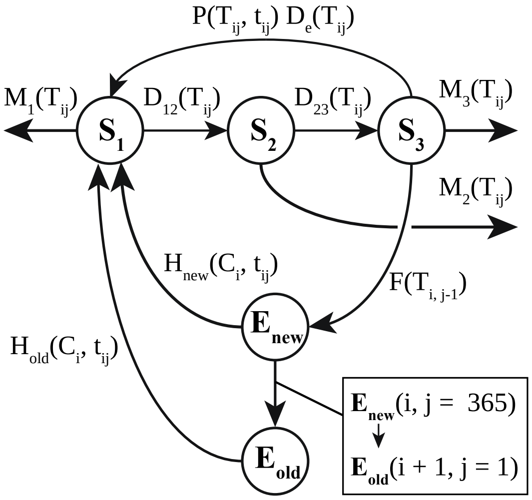
P(T_ij, t_ij) D_e(T_ij)
M_1(T_ij)
D_12(T_ij)
D_23(T_ij)
M_3(T_ij)
S_1
S_2
S_3
M_2(T_ij)
H_new(C_i, t_ij)
F(T_i, j-1)
E_new
H_old(C_i, t_ij)
E_new(i, j = 365)
E_old(i + 1, j = 1)
E_old

Figure 3.

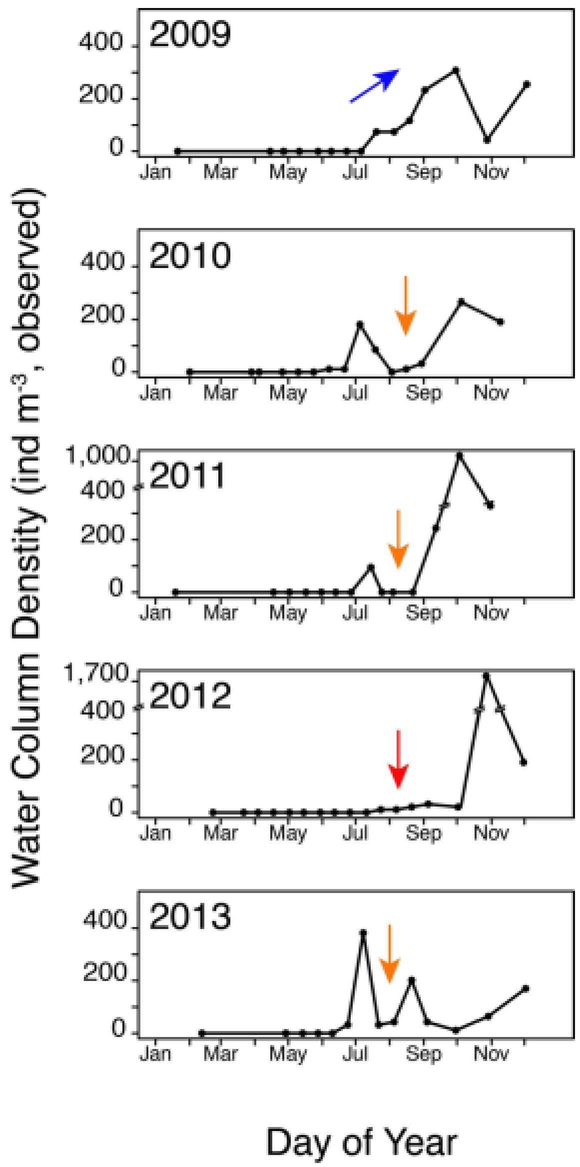
2009
2010
2011
2012
2013
400
200
0
1,000
1,700
Jan
Mar
May
Jul
Sep
Nov
Water Column Denstity (ind m^{-3}, observed)
Day of Year

Figure 4.

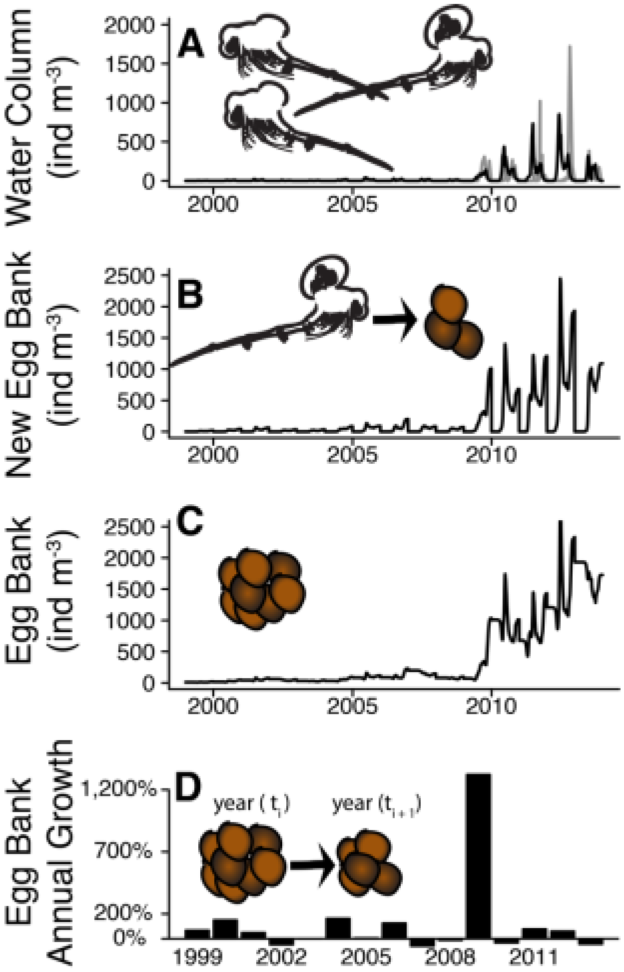
A
Water Column (ind m-3)
2000
1500
1000
500
0
2000
2005
2010
B
New Egg Bank (ind m-3)
2500
2000
1500
1000
500
0
2000
2005
2010
C
Egg Bank (ind m-3)
2500
2000
1500
1000
500
0
2000
2005
2010
D
Egg Bank Annual Growth
year (t_i)
year (t_i+1)
1,200%
700%
200%
0%
1999
2002
2005
2008
2011

Figure 5.

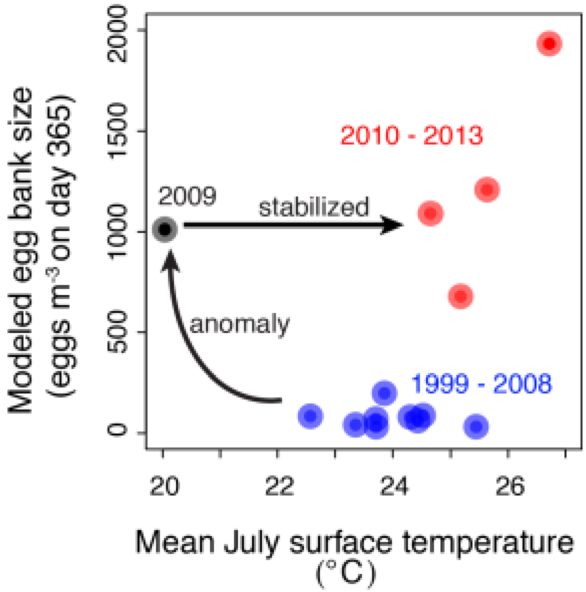
Modeled egg bank size
(eggs m-3 on day 365)
0
500
1000
1500
2000
20
22
24
26
Mean July surface temperature
(°C)
2010 - 2013
2009
stabilized
anomaly
1999 - 2008

Figure 6.

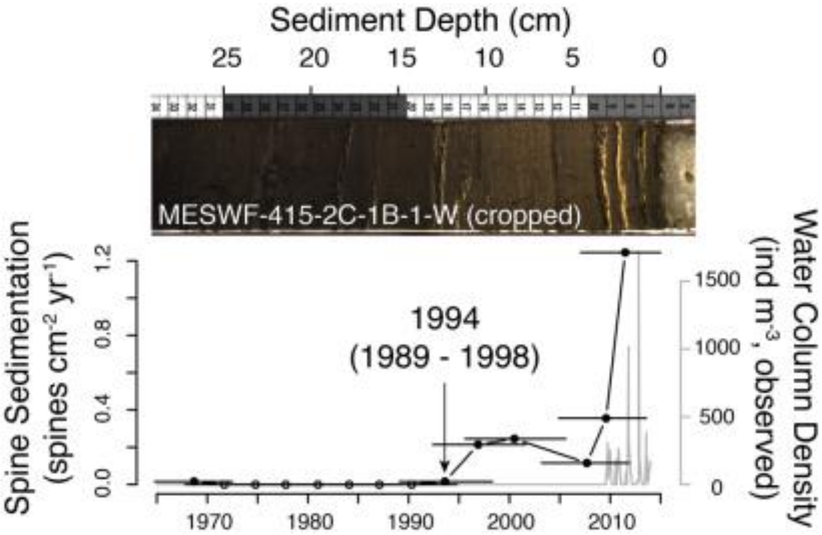
Sediment Depth (cm)
25
20
15
10
5
0
MESWF-415-2C-1B-1-W (cropped)
Spine Sedimentation (spines cm^{-2} yr^{-1})
0.0
0.4
0.8
1.2
1994
(1989 - 1998)
1970
1980
1990
2000
2010
Water Column Density (ind m^{-3}, observed)
0
500
1000
1500

Figure 7.

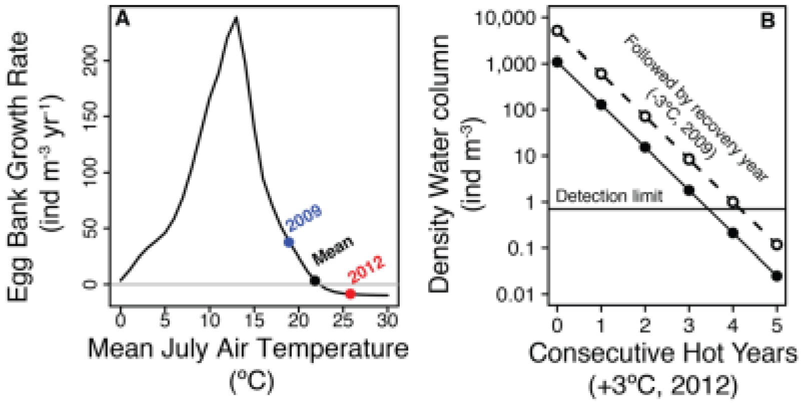
A
Egg Bank Growth Rate
(ind m-3 yr-1)
0
50
100
150
200
2009
Mean
2012
0
5
10
15
20
25
30
Mean July Air Temperature
(°C)
B
Density Water column
(ind m-3)
10,000
1,000
100
10
1
0.1
0.01
Followed by recovery year
(-3°C, 2009)
Detection limit
0
1
2
3
4
5
Consecutive Hot Years
(+3°C, 2012)

Figure 8.

Appendix

Supplementary Information

Outbreak of an undetected invasive species triggered by climate anomaly

Jake R. Walsh, Samuel E. Munoz, and M. Jake Vander Zanden

Contents:

Methods – Detailed description of model component derivation

Results & Discussion – Investigating the early summer peak in modeled density

Results & Discussion – Effects of same-year hatching from the resting egg bank

Results & Discussion – Effects of secondary peak in resting egg production

Methods

Developmental Rates

Developmental rates (D; Fig. S1) are derived from the functions describing embryonic and post-embryonic development rates provided in Lehman et al. (1997) and fitted to sigmoidal development curves with upper thermal boundaries developed in Logan et al. (1985) for each *Bythotrephes*' instar stage (Fig. S1):

$$D = C \times \left[\frac{1}{1 + e^{k_1 + k_2 T}} - e^{-\frac{T_m - T}{DT}} \right]$$

A sigmoidal function was selected because each summer Lake Mendota reaches surface temperatures outside of the experimental range in Lehman et al. (1997), where development was evaluated from 12°C to 22°C. Output from these functions was fitted to the sigmoidal function using non-linear least squares to provide estimates of k_1 (2.88, std. error = 0.105, t = 27.43, $p << 0.0001$) and k_2 (-0.165, std. error = 0.0068, t = -24.08, $p << 0.0001$) which are constants and equal across stages that determine the approach to the asymptote of maximum development rate, C (the stage-specific development rates from Lehman et al. at 25°C). The temperature of maximum development rate (25°C) and T_m, the temperature at which no development occurs (30°C), were obtained from laboratory culture experiments (Kim and Yan 2010). In these rearing experiments, peak developmental rates were obtained at 25°C (though peak development rate without mortality over 96 hours was obtained at 22°C) and 90% mortality was reached in 24 hours at 32°C (100% at 48 hours) and 70% mortality was reached in 96 hours at 28°C. DT, the width of the upper boundary of the sigmoidal curve, was chosen as the value that provided the most gradual approach to T_m without altering the temperature at which maximum development occurs (DT = 3°C).

Reproductive Rates

Asexual production of embryos (P; Fig. S2A-B) is calculated by multiplying the proportion of females reproducing sexually by the mean clutch size (number of embryos) of asexually reproducing females (2.8 embryos per adult female). The proportion of females reproducing asexually is a function of temperature, T, and the day of the year, j, calculated from a generalized additive model (GAM; Wood 2015) fitted to the relationship (Fig. S2A-B; $edf_T = 1.87$, $F_T = 4.72$, $p_T = 0.011$; $edf_j = 2.03$, $F_j = 5.58$, $p_j = 0.0042$; $R^2 = 0.29$). $P(T_j, j)$ is multiplied by the developmental rate of embryos in the brood pouch and the density of S_3 individuals to obtain the daily rate of embryonic production contributing to S_1.

Similar to P, sexual production of resting eggs (F; Fig. S2C) is calculated by multiplying the proportion of females reproducing sexually by the mean clutch size (number of eggs) of sexually reproducing females (4.0 eggs per adult female). This product, the number of resting eggs per adult female, is a function of temperature, T, calculated from a GAM fitted to the relationship (Fig. S2C; $edf_T = 8.15$, $F_T = 6.65$, $p_T << 0.0001$; $R^2 = 0.64$). $F(T_j)$ is multiplied by the density of S_3 individuals to obtain the daily rate of resting egg production contributing to E_{new}.

Mortality Rates

Observed daily per capita mortality rates were calculated using the methods in Brown et al. (2012) developed for estimating *Bythotrephes*' mortality in Island Lake Reservoir (MN, USA).

Death rates between weekly sampling dates are estimated by subtracting observed population densities at a time step from modeled population densities at the previous time step. Modeled densities at the previous time-step are dependent on temperature-dependent development, observed instar stage structure, and observed asexual reproduction. We observed second and third instar stage daily per capita mortality estimates that were much larger than those found in Island Lake (0.99 third stage and 0.10 second stage deaths ind^{-1} d^{-1} in Lake Mendota versus 0.27 and 0.07 deaths ind^{-1} d^{-1} in Island Lake, respectively) and negative - often to a large degree - mortality in first instar stage daily per capita mortality compared to large (0.18 ind^{-1} d^{-1}) mortality in the first instar from Island Lake. While differences in the food web stages (planktivory index from Brown et al. 2012 – ratio of piscivores to planktivores in gill net data: 0.8 Island, 0.1 Mendota) and thermal regimes (peak summer surface water temperature: ~18°C Island, 28°C Mendota) among the two lakes may describe the elevated mortality in second and third instar, the negative mortality is more likely associated with large contributions from the egg bank (Brown, *personal communication*).

For each stage, estimated mortality rates were fitted to a polynomial function of surface temperature using non-linear least squares regression and the best formulation of the polynomial function was selected using AIC (Fig. S3):

$$M = B_0 + B_1 \times T + B_2 \times T^2$$

In addition to providing the best fit to mortality as a function of temperature, the polynomial function was selected to model sources of mortality that are likely to increase rapidly with temperature: predation by planktivorous fishes (yellow perch dominate Lake Mendota planktivory and predation rates increase with temperature; Johnson and Kitchell 1996), thermal stress (Kim and Yan 2010), and cladoceran prey scarcity (North Temperate Lakes Long-Term Ecological Research 2014).

To account for negative mortality in the first instar stage, we add a small value (*b*; ranging from -0.2 to 0.2, 0.034 offsets all negative first instar stage mortality) to the B_0 intercept of the M_1 polynomial function. This also allows us to adjust overall mortality relative to population growth in order to adjust model performance using different model formulations to observe the presence or absence of the prolonged lag dynamic in 2009. Annual mortality increases linearly with *b* and, therefore, *b* is incredibly important for model dynamics (Fig. S4A) and annual growth rates in the egg bank (Fig. S4B). Values of *b* that are too small relative to population growth lead to exponential growth in the model with an increase in exponential growth rates in 2009, values of *b* that are too large lead to population crashes with recovery in 2009, and values of *b* that are much too large lead to population crashes and no recovery (Fig. S4).

Hatching Rates

Early season hatching from the "old" egg bank established in the previous year, *i* – 1, was obtained from Yurista (1992) for hatching rates at 6°C (Fig. S5):

$$h(C_i, t_{i,j}) = x / (1 + e^{y*(t_{i,j} - C_i) + z})$$

Where h is the cumulative percent hatched over time, x is the total percentage of the old egg bank expected to hatch over the course of year i, 67% (Brown and Branstrator 2011), y and z are fitted parameters specific to hatching at the 6°C treatment (in Lake Mendota, 6°C is typically reached within a month of C_i), and $t_{i,j}$ - C_i is the difference in days between the day at $t_{i,j}$ and the day of the onset of the hatching cue at the lake bottom, C_i (4°C at 24 m). We converted cumulative hatching percentage to daily hatching percentage for the model:

$$H_{old}(C_i, t_{i,j}) = h(C_i, t_{i,j}) - h(C_i, t_{i,j-1})$$

Here the daily hatching rate in percent of $E_{old}(t_{i,j=1})$ is the difference between cumulative hatching rate at $t_{i,j}$ and $t_{i,j-1}$.

Late season hatching from the "new" egg bank established during year i (Fig. S5) begins at a constant rate in proportion p of $E_{new}(t_{i,j-1})$ hatching at $t_{i,j}$ after a period of mandatory dormancy (114 days; Herzig 1985) after the first day of the hatching cue C_i and before the last day of the hatching cue C_i minus the duration of minimum observed dormancy (66 days; Herzig 1985):

$$\mathrm{H_{new}}\left(\mathrm{C_i}, \mathrm{t_{i,j}}\right) = \begin{cases} \text{if j} < \text{first day } \mathrm{C_i} + 114 \text{ or j} > \text{last day } \mathrm{C_i} - 66 & 0 \\ \text{if j} \geq \text{first day } \mathrm{C_i} + 114 \text{ and j} \leq \text{last day } \mathrm{C_i} - 66 & \mathrm{p} \end{cases}$$

Here, p is 3% d^{-1}, the peak hatching rate observed in Yurista 1992 at 10°C (Lake Mendota bottom temperatures typically reach 10°C by early June). However, within a reasonable range (1-10% d^{-1}) the value of p has little effect on the overall dynamics of the model assuming that p is offset with adjusting b (additional first instar stage mortality). Varying the duration of mandatory dormancy that lags the onset of hatching of newly laid eggs (from 114 days) and the minimum dormancy that terminates hatching of newly laid eggs (from 66 days) changes the timing of population dynamics, but not the observed year-to-year dynamics or prolonged lag dynamics. However, dramatically changing the onset of same-year hatching from the egg bank does change the early summer peak in population density and this is discussed further in the following section.

Results & Discussion

Investigating the Early Summer Peak in Modeled Population Density

Adjusting Early Summer Hatching - We lagged the hatching cue by adding a number of days to C (30, 60, and 90 days) and changing the thermal cue that defines C (8°C to 11°C). A large enough lag was able to limit and even remove the early season peak, producing the observed seasonal pattern in population density. No lag value eliminated the observed prolonged lag dynamic in 2009.

Adjusting Mortality - We manipulated seasonal mortality by altering the shape of the first instar stage mortality curve. To increase mortality at higher temperatures we increased B_0, B_1, and B_2 individually – all leading to population crashes. To reduce mortality at low temperatures and increase mortality at high temperatures we increased the value of B_2 and decreased the value of B_1, which lead to higher early summer peak densities, but did not alter the observed prolonged lag dynamic.

To increase mortality at low temperatures we increased B_0 and decreased B_1. This adjustment did not change the early summer peak nor did it change the prolonged lag dynamic. We also set B_1 to zero, switched the sign of B_2, and increased B_0 to force M_1 mortality into the shape we were looking for, that is higher mortality at low temperatures without creating too much negative mortality. This massive alteration led to huge, not sustained increases in 2009, and a *slight* reduction in the early summer peak. However, this is more likely due to pushing M_1 out of a realistic range than any potential mortality dynamics in Lake Mendota.

To increase early summer mortality, we added a constant mortality to all days before day 200. This decreased the duration of the early summer peak, but not the magnitude of the peak. This also did not change the prolonged lag dynamic.

Finally, we added a senescence term to third instar stage *Bythotrephes*. In the original model, we determined that mortality in the third instar stage was so large (sometimes as high as 200% d^{-1}, mortality >100% d^{-1} is offset by rapid development and reproduction) that it was unlikely that an individual would die of old age. The senescence term was temperature dependent following the general shape of the development curves (higher senescence at higher temperatures). The term did not impact the early summer peak or the prolonged lag dynamic.

Adjusting Asexual Reproduction – In the model, asexual reproduction (embryos produced per female per day) is a GAM-fitted function of temperature and day of the year. We adjusted the term to simply mean observed embryonic reproduction (constant through time), fit the function to temperature and day of the year separately, and we made the number of asexually reproducing adult females a function of the number of sexually reproducing adult females (1 – number of sexually reproducing adult females). No alteration of asexual reproduction reduced the magnitude of the early summer peak or eliminated the prolonged lag dynamic.

Effect of Same-Year Hatching from Resting Egg Bank

Eliminating the same-year hatching from the egg bank (setting p to 0) at the original fitted mortality value (b = 0.07) yielded a maximum active population density of just 30.0 ind m^{-3} on Day 161 of 2011 (Fig. S6A) and a maximum egg bank density of 99.0 eggs m^{-3} on Day 365 of 2012 (Fig. S6B). Additionally, there was a significantly smaller increase in the egg bank from pre-2009 egg bank density (7.75 eggs m^{-3}, s.d. = 8.78 eggs m^{-3}) to the mean post-2009 egg bank density of (30.8 eggs m^{-3}, s.d. = 32.7 eggs m^{-3}) with a proportional increase by a factor of 2.97 (compared to a factor of 13.2).

When we reduced mortality (b = 0.05), population growth was driven entirely by exponential growth in the early summer (Fig. S6C) that produced a large egg bank (Fig. S6D) before the population density declines with high summer temperatures, however the proportional increase from pre-2009 to post-2009 active and egg bank densities was much higher.

Effect of Secondary Peak in Resting Egg Production

Eliminating the mid-summer peak in resting egg production prior to the warmest surface water temperatures at the original fitted mortality value (b = 0.07) yielded a maximum active population density of just 3.40 ind m^{-3} on Day 172 of 1999 (Fig. S6E) and a maximum egg bank density of 3.62 eggs m^{-3} on Day 203 of 1999 (Fig. S6F) – with a rapid decline to near-zero population densities after 1999 and no recovery under favorable 2009 conditions.

When we greatly reduced mortality (b = 0.004), we observed a similar population collapse in the early years of the simulation with a recovery in 2009 and large increase in the population density of the active population (Fig. S6G) and resting egg bank in 2010 (Fig. S6H). These dynamics appear to be driven by rapid exponential growth in the early summer that fuels inefficient resting egg production and much slower population growth in the late season with more efficient resting egg production. While exponential growth in the water column yields high active population densities, the density of the egg bank is much lower than model simulations with the high temperature peak in resting egg production.

Appendix Table & Figure Legends

Table S1. Mathematical structure of the model and description *Bythotrephes*' life history through resting (E) and active (S) stages. Model components are described in more detail in Table 2 and Figure 1.

Figure S1. Stage-specific developmental rates (D; d^{-1}) are obtained from Lehman et al. 1997 (black over study temperature range 12°C - 22°C, grey outside of range) fitted to sigmoidal development curves (red) developed in Logan et al. 1985 and parameterized using values obtained in lab studies from Kim and Yan 2010. D_{xy} describes development of an individual from instar stage x to instar stage y and D_e is the embryonic development rate of embryos in maternal brood pouches. Maximum developmental rates occur near 25°C (highest development in Kim and Yan) and no development occurs near 30°C (100% mortality after 24 hrs. in Kim and Yan). These allow for more accurate estimates of development rates at high surface temperatures unique to Lake Mendota (22°C - 28°C).

Figure S2. Estimated values (solid) of asexual (P) and sexual (F) reproduction over inputted temperatures (T) and seasonality (Day of Year) +/- 1 s.e. (dashed). Asexual reproduction of embryos (embryos ind^{-1} d^{-1}) is fitted to both temperature (A; with day of year held constant at day 200) and day of year (B; with temperature held constant at 10°C) using generalized additive modeling (GAM). Sexual reproduction of resting eggs (eggs ind^{-1} d^{-1}) is fitted to temperature (C) using GAM. Note that *Bythotrephes* are rarely present in the water column prior to mid-June (day 166) and after ice cover.

Figure S3. Stage-specific mortality (S_1 = solid, S_2 = dashed, S_3 = dotted) is fitted to a polynomial function dependent on temperature ($M = B_0 + B_1 \times T + B_2 \times T^2$). A small value (b; here b = 0.07) is added to B_0 of M_1 (solid grey line) to adjust for negative mortality in first instar individuals and examine model dynamics over a range of mortality values.

Table S2. Parameter estimates and regression output data from polynomial regressions of mortality as a function of temperature.

Figure S4. The role of *b* in driving mortality in the modeled population (A), annual growth in the egg bank (B), and the relationship between annual mortality and annual egg bank growth (C) under temperature scenarios corresponding to average (black), cool (blue), and warm (red) years. Horizontal lines in B and C represent the initial seed size of the egg bank, therefore values much higher or lower than 10 resting eggs on day 365 yield rapid growth or decline in the egg bank, respectively (e.g., arrows in B). Decreasing temperatures increase annual growth in the egg bank (gold circles in C), but could be accomplished through a reduction in mortality without a change in temperature (orange circle in C).

Figure S5. Hatching rates from the previous year's egg bank (H_{old}) and the same-year egg bank (H_{new}). Hatching from the previous year's egg bank occurs as a function of time, t_j, as the number of days from the onset of the emergence cue in the lake bottom (C; bottom water temperature > 4°C; $t_j - C$). Hatching from the current year's egg bank occurs as a function of time as a constant rate 114 days after the population emerges from the egg bank ($C_{\text{first day}}$) and stops 114 days before the last day of egg emergence ($C_{\text{last day}}$; the last day of bottom water temperature > 4°C).

Figure S6. Without same-year hatching from the egg bank (A-D) or high temperature peaks in resting egg production (E-H), the *Bythotrephes* population would have either collapsed or persisted at low densities at modeled mortality levels (A, B, E, and F – upper panels). If mortality is reduced to unrealistic values (C, D, G, and H – lower panels), the population may have been able to grow exponentially prior to stressful summer peak temperature conditions, however this has never been observed in Lake Mendota.

Appendix Tables & Figures

Table S1.

Model Components	Component Description
$\mathbf{E_{old}}(t_{i,j}) = E_{old}(t_{i,j-1})$	• Old egg bank density from previous day
$- H_{old}(C_i, t_{i,j}) \times E_{old}(t_{i,j=1})$	• Hatching from the old egg bank
$\mathbf{S_1}(t_{i,j}) = S_1(t_{i,j-1})$	• First instar stage density from previous day
$+ P(T_{i,j}\ , t_{i,j}) \times D_e(T_{i,j}) \times S_3(t_{i,j-1})$	• Parthenogenetic reproduction from third instar stage
$+ H_{old}(C_i, t_{i,j}) \times E_{old}(t_{i,j=1})$	• Hatching from the old egg bank
$+ H_{new}(C_i, t_{i,j}) \times E_{new}(t_{i,j-1})$	• Hatching from the new egg bank
$- D_{12}(T_{i,j}) \times S_1(t_{i,j-1})$	• Development to second instar stage
$- M_1 (T_{i,j}) \times S_1(t_{i,j-1})$	• First instar stage mortality
$\mathbf{S_2}(t_{i,j}) = S_2(t_{i,j-1})$	• Second instar stage density from previous day
$+ D_{12}(T_{i,j}) \times S_1(t_{i,j-1})$	• Development from first instar stage
$- D_{23}(T_{i,j}) \times S_2(t_{i,j-1})$	• Development to third instar stage
$- M_2 (T_{i,j}) \times S_2(t_{i,j-1})$	• Second instar stage mortality
$\mathbf{S_3}(t_{i,j}) = S_3(t_{i,j-1})$	• Third instar stage density from previous day
$+ D_{23}(T_{i,j}) \times S_2(t_{i,j-1})$	• Development from second instar stage
$- M_3 (T_{i,j}) \times S_2(t_{i,j-1})$	• Third instar stage mortality
	•
$\mathbf{E_{new}}(t_{i,j}) = E_{new}(t_{i,j-1})$	• New egg bank density from previous day
$+ F(T_{i,j-1}) \times S_3 (t_{i,j-1})$	• Sexual production from third instar stage
$- H_{new}(C_i, t_{i,j}) \times E_{new}(t_{i,j-1})$	• Hatching from new egg bank

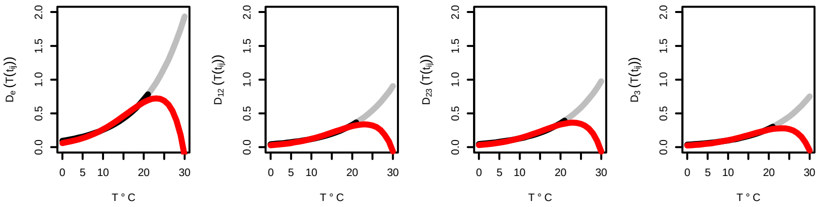

Figure S1.

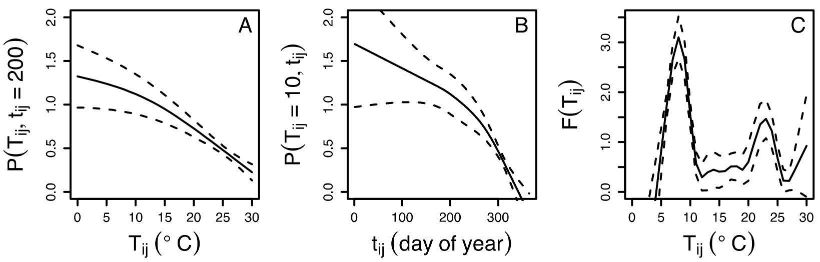
A
P(T_ij, t_ij = 200)
0.0
0.5
1.0
1.5
2.0
0
5
10
15
20
25
30
T_ij (° C)
B
P(T_ij = 10, t_ij)
0.0
0.5
1.0
1.5
2.0
0
100
200
300
t_ij (day of year)
C
F(T_ij)
0.0
1.0
2.0
3.0
0
5
10
15
20
25
30
T_ij (° C)

Figure S2.

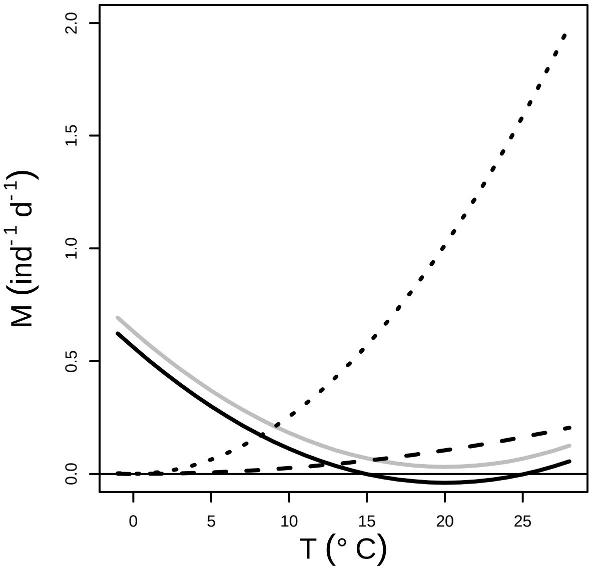

Figure S3.

Mortality$_{stage}$	B_0 (s.e.)	B_1 (s.e.)	B_2 (s.e.)	R^2	F	p
M_1	0.56 (0.096)	-0.059 (0.012)	0.0014 (0.00035)	0.44	17.33	<<0.0001
M_2	---	---	0.00026 (0.000061)	0.28	18.08	0.0001
M_3	---	---	0.0025 (0.00020)	0.78	157.8	<<0.0001

Table S2.

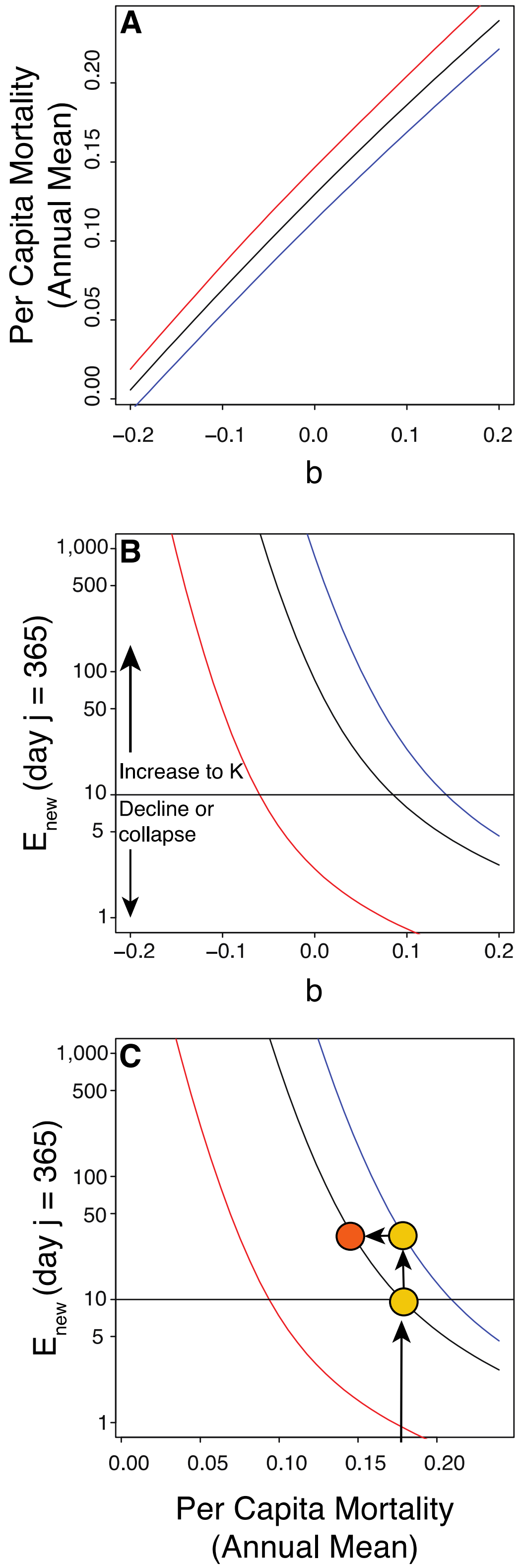
A
Per Capita Mortality
(Annual Mean)
0.00
0.05
0.10
0.15
0.20
−0.2
−0.1
0.0
0.1
0.2
b
B
E_{new} (day j = 365)
1,000
500
100
50
10
5
1
Increase to K
Decline or
collapse
−0.2
−0.1
0.0
0.1
0.2
b
C
E_{new} (day j = 365)
1,000
500
100
50
10
5
1
0.00
0.05
0.10
0.15
0.20
Per Capita Mortality
(Annual Mean)

Figure S4.

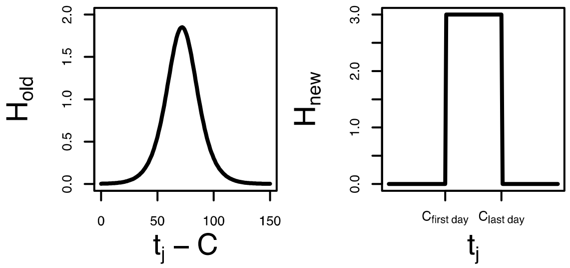
H_{old}
0.0
0.5
1.0
1.5
2.0
0
50
100
150
$t_j - C$
H_{new}
0.0
1.0
2.0
3.0
$C_{first\ day}$
$C_{last\ day}$
t_j

Figure S5.

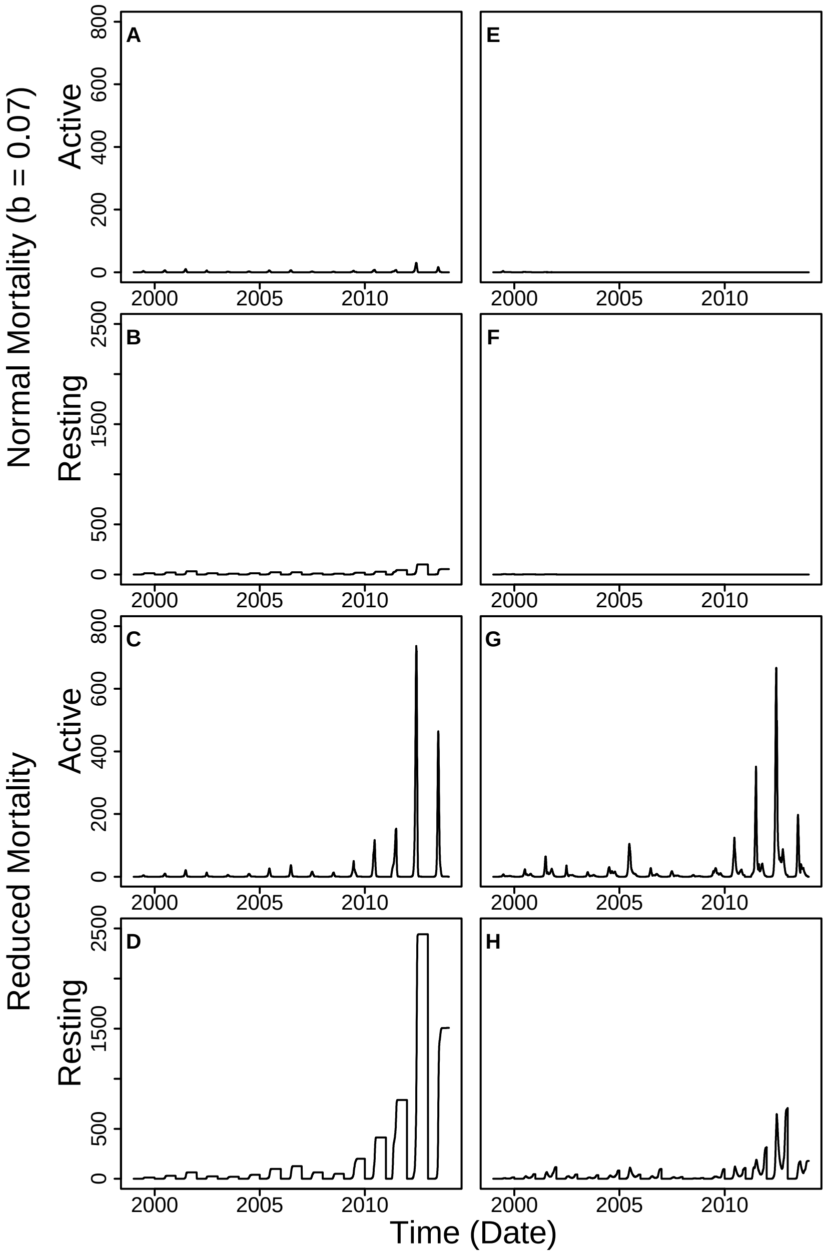
Normal Mortality (b = 0.07)
Reduced Mortality
Active
Resting
Active
Resting
A
B
C
D
E
F
G
H
0
200
400
600
800
0
500
1500
2500
2000
2005
2010
Time (Date)

Figure S6.

CHAPTER TWO: Invasion triggers a massive loss of ecosystem services through a trophic cascade

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Abstract

Despite growing recognition of the importance of ecosystem services and the economic and ecological harm caused by invasive species, linkages between invasions, changes in ecosystem functioning, and, in turn, the provisioning of ecosystem services remain poorly documented and poorly understood. We evaluate the economic impacts of an invasion that cascaded through a food web to cause substantial declines in water clarity, a valued ecosystem service. The predatory zooplankton, spiny water flea (*Bythotrephes longimanus*), invaded the Laurentian Great Lakes in the 1980s, and has subsequently undergone secondary spread to inland lakes, including Lake Mendota (WI, USA) in 2009. In Lake Mendota, *Bythotrephes* has reached unparalleled densities compared to other lakes, decreasing biomass of the grazer *Daphnia pulicaria*, and causing a decline in water clarity of nearly 1 m. MARSS time series modeling revealed that the loss in water clarity, valued at US$140M (US$640 per household), could be reversed by a 71% reduction in phosphorus (P) loading. A phosphorus reduction of this magnitude is estimated to cost between US$86.5 and US$163M (US$430 - US$810 per household). Estimates of the economic effects of Great Lakes invasive species may increase considerably if cases of secondary invasions into inland lakes such as Lake Mendota are included. Further, such extreme cases of economic damages call for increased investment in the prevention and control of invasive species to better maximize the economic benefits of such programs. Our results highlight the need to more fully incorporate ecosystem services into our analysis of invasive species' impacts, management, and public policy.

Significance

Invasive species represent a largely unquantified threat to ecosystem services. Though investment in the prevention of species invasions may sustain ecosystem services, these effects of invasions have rarely been measured in monetary terms useful to decision makers. We quantify the economic damages of the degradation of an important ecosystem service, water clarity, due to invasion by the spiny water flea. We find that the costs of restoring this service, US$86.5M - US$163M, are comparable to the willingness to pay for the service itself, US$140M. This highlights the severity of invasive species' impacts when their damages to ecosystem services are considered. These economic considerations emphasize the effects of invasive species' secondary spread that aggregate across many invasive species and ecosystem services.

Introduction

Despite growing recognition of the importance of ecosystem services (Guerry et al. 2015) and the harm caused to ecosystems by invasive species (Ehrenfeld 2010, Sidle et al. 2013), linkages between species invasions and ecosystem services are rarely made (Charles and Dukes 2007, Keller et al. 2009, Pejchar and Mooney 2009). Investments in the prevention of species invasions may sustain ecosystem services. However, the effects of invasions are rarely quantified in monetary terms that assess damages to services alongside the costs and ecological mechanisms of restoration options (Vander Zanden and Olden 2008, Keller et al. 2009). Invasive species are a major threat to freshwater ecosystems (Strayer 2010) and thereby endanger several ecosystem services that are essential for human well-being.

Freshwater ecosystems are a cornerstone of human society, providing drinking water, fisheries, pollution dilution, recreation, and other goods and services ("Millennium ecosystem assessment. Ecosystems and human well-being" 2005). Valuation of these services is critical for public policy (Keeler et al. 2012, Schaefer et al. 2015), but many of the services provided by freshwater ecosystems are not monetized (Wilson and Carpenter 1999, Polasky et al. 2015), leaving them overlooked and poorly integrated into decision frameworks (Sidle et al. 2013, Guerry et al. 2015). Water quality of lakes and reservoirs has been degraded by phosphorus pollution, leading to loss of recreation and aesthetic value, decreased lakeshore property values, beach closures, fish kills, harmful blooms of cyanobacteria, and loss of water clarity (Carpenter et al. 2011). *Daphnia*, a genus of freshwater zooplankton, improves water quality by consuming algae (Carpenter and Kitchell 1988, Hansson et al. 1998). Accordingly, lakes are sometimes managed to support large *Daphnia* populations by reducing the abundance of their predators (Carpenter et al. 1995, Hansson et al. 1998).

The spiny water flea, *Bythotrephes longimanus* (hereafter *Bythotrephes*), non-native in North America, is a voracious zooplanktivore that has the capacity to consume more zooplankton than do fish and other invertebrate planktivores combined (Bunnell et al. 2011). Despite this planktivory and large documented ecological impacts on zooplankton communities (Yan et al. 2002, 2011), *Bythotrephes* has not been found to have cascading effects on lake primary production and water clarity (Strecker and Arnott 2008). The lack of cascading effects of *Bythotrephes* invasion is perhaps because the productive lakes most vulnerable to impaired water clarity are thought to be relatively unsuitable for *Bythotrephes* establishment (Potapov et al. 2011).

Bythotrephes was detected in the well-studied eutrophic Lake Mendota in fall 2009 at some of the highest densities on record (> 150 m^{-3}; mean open-water density). The invasion was of immediate concern as a preferred prey of *Bythotrephes*, *Daphnia pulicaria*, has been the focal point of Lake Mendota's food web management, supporting the lake's fishery (Johnson and Kitchell 1996) and maintaining clear water through grazing algae (Lathrop et al. 2002) (Fig. 1). Lake Mendota is located within an agricultural watershed and receives large amounts of phosphorus from farm runoff, reducing water quality by stimulating algal growth (Lathrop and Carpenter 2014) (Fig. 1). This ecosystem service provided by *D. pulicaria* has delivered huge economic benefits, providing recreational value to citizens who have been estimated to be willing to pay US$140M (present day value) for 1 m of water clarity (1.6 m to 2.6 m change in summer clarity) (Lathrop et al. 1998, Stumborg et al. 2001).

Results & Discussion

Since the detection of *Bythotrephes* in 2009, average water clarity in Lake Mendota has declined by 0.9 m (Fig. 2F) alongside a 60% reduction in *D. pulicaria* biomass (Fig. 2B). In addition, there was a decrease in total phosphorus (TP) (Fig. 2D) despite no clear change in P loading (Fig. 2E), and an overall increase in total grazing zooplankton biomass (Fig. 2C; 17% overall, 56% increase in non-*D. pulicaria* grazers). These findings demonstrate a cascading impact of *Bythotrephes* that has not been previously documented in other lakes (Strecker and Arnott 2008) and is unusually large for an invertebrate predator (Terborgh and Estes 2010). Possibly, this effect is related to the feeding mode of *Bythotrephes* versus other invertebrate predators (Branstrator 2005, Yurista et al. 2010, Bunnell et al. 2011) and this topic could be addressed by further research.

The strongest effects of *Bythotrephes* on *D. pulicaria* are observed in the fall (Fig. 2B) when *Bythotrephes* is most abundant (Fig. 2A). These effects occur at a time critical to the overwintering success of *Daphnia*, which may explain declines that linger into the spring (Fig. 2B). Despite a compensatory increase in non-*D. pulicaria* zooplankton grazers (e.g., *Daphnia mendotae*), spring water clarity declined due to an overall decline in algae filtration rates by zooplankton. This decline further reveals the distinct advantage in filtration efficiency of *D. pulicaria* (Kasprzak et al. 1999). Notably, *Daphnia* of all species collapsed from fall 2014 to spring 2015, which included the less efficient but more predation-resistant *D. mendotae*. Prior to 2014, *D mendotae* increased with the *Bythotrephes* invasion in Lake Mendota (Fig. 2C) as reported in other lakes (Yan and Pawson 1997, Boudreau and Yan 2003). While not as efficient as a grazer as *D. pulicaria*, *D. mendotae* does provide better water clarity relative to smaller, more selective grazers like copepods (Lathrop et al. 2002). If *D. mendotae* declines in years with high *Bythotrephes* biomass as in fall 2014, water clarity could decline in the future.

Multivariate autoregressive state space modeling (MARSS) (Holmes et al. 2012) revealed that higher external phosphorus loading and seasonal surface temperatures accompany lower water clarity while *D. pulicaria* biomass is associated with higher water clarity over the past two decades (1995 – 2014) in Lake Mendota (Fig. 3). These results are consistent with previous evaluations of the lake's food web (Lathrop et al. 2002) and suggest that reducing external P loading into the lake can offset the negative impact of *Bythotrephes* on *D. pulicaria* and thus on water clarity.

To quantify the P loading reduction required to offset the impact of *Bythotrephes*, we predicted water clarity under high (pre-2009) and low (post-2009) *D. pulicaria* biomass under varying P loading scenarios (-99% to +100%) using the fitted MARSS model. External P load reduction of 71% is needed to offset the decline in *D. pulicaria* (i.e., obtain pre-2009 water clarity under post-2009 *D. pulicaria* biomass) (Fig. 4).

Recent estimates of the cost of phosphorus diversion from Lake Mendota indicate that a P load reduction of 71% will cost between US$86.5M and US$163M (US$430 - US$810 per household in Dane County) (*Yahara CLEAN engineering report* 2013). This conservative estimate is drawn from a detailed, itemized, and expert-elicited review investigating this very question in Lake Mendota. Investing in a 71% reduction would return the lake to pre-invasion clarity, and any further improvements to water clarity would have to be made on top of this investment. These costs illustrate the challenges associated with mitigating invasive species impacts.

An additional perspective on this economic impact is offered by the estimate that citizens in the region (Dane County, WI) are willing to pay US$140M present day value (US$640 per household) for 1 m of water clarity gained by managing the lake (Stumborg et al. 2001) - roughly equivalent in magnitude to the loss of 0.9 m caused by the *Bythotrephes* invasion. The similarly large costs of restoring clarity suggest that managers should consider new strategies to directly mitigate *Bythotrephes* effect on *D. pulicaria* (e.g., via managing the fishery, Fig. 1, or limiting the production and hatching of *Bythotrephes'* resting eggs). Direct control of populations is thought to be an inefficient use of management funds (Leung et al. 2002), however the high cost of *Bythotrephes*' impacts makes investment in research and development of control options more attractive. Additionally, *Bythotrephes* amplifies the effect of cultural eutrophication and its many negative implications for freshwater ecosystem services. Therefore, managers should focus on limiting further spread of this non-native species among agriculturally-impacted lakes.

While only representing a single aspect of *Bythotrephes*' impact on ecosystem services, these damage and cost estimates illustrate the potential harm due to a single invasive species in a single lake affecting a single ecosystem service. Additional impacts of *Bythotrephes*, such as fouling fishing lines and disrupting the base of lake food webs (Yan et al. 2011), were not considered here but could increase these costs. While we do not have the data to put a price tag on current and future economic damages of *Bythotrephes* or other invasive species at the landscape scale, our work highlights the importance of considering the aggregate impact of chains of secondary invasions as inland lakes in the region are colonized. We also note that in just the U.S. states bordering the Great Lakes, inland lakes have 36 times more shoreline than do the Great Lakes (Winslow et al. 2014). Since lake ecosystem services are often delivered at this critical ecotone, the importance of inland lakes cannot be ignored (Strayer and Findlay 2010).

Accounting for the many possible effects of secondary invasions on a diverse range of ecosystems and their services will require more research, yet this accounting is critical in accurately weighing the costs and benefits of invasive species management options. Further, this accounting must consider economic damages while taking into account potential positive effects of invasions. Our study demonstrates substantial economic damages from a secondary invasion, suggesting that investments in large-scale prevention or research on control and eradication tools may yield net economic benefits.

Furthermore, the economic damages quantified here have broader public policy implications regarding transatlantic shipping and the Laurentian Great Lakes St. Lawrence Seaway. While allowing transatlantic ships to enter the Great Lakes provides US$55M of annual savings relative to alternative transport options (Taylor and Roach 2009), these ships are also responsible for the majority of the non-native species that have established in the Great Lakes in recent decades. Damage estimates for these invasions have been confined to the Great Lakes only and have not considered costs of secondary invasions such as that of *Bythotrephes* in Lake Mendota (Rothlisberger et al. 2012). Benefit-cost assessments of transatlantic shipping in the Great Lakes may indicate significantly larger costs if secondary invasions are included in these assessments.

Linkages of ecological processes with economic or social benefits are needed to apply ecosystem service concepts in public policy development, implementation, and evaluation

(Guerry et al. 2015, Polasky et al. 2015, Schaefer et al. 2015). Understanding impacts of non-native species requires field measurements of ecosystem consequences in terms useful to managers (Strayer 2012). We have shown how an invasive species altered a lake food web, amplifying the harmful effects of cultural eutrophication and impairing water clarity, thereby reducing the benefits that humans derive from lakes. Water quality targets for the lake are more difficult and expensive to achieve as a result of the invasion. These economic damages followed a trophic cascade triggered by a voracious predator that originated in Eurasia, and invaded through the Great Lakes and overland to Lake Mendota. Ecological mechanisms, as well as economic ones, must be analyzed together to bring ecosystem services into decision processes regarding species invasion (Polasky et al. 2015).

Methods Summary

Lake Mendota (Lathrop and Carpenter 2014). Lake Mendota is a 39.6 km^2, dimictic (mixes in spring and fall), and culturally eutrophic lake located adjacent to Madison, WI, USA. Maximum and mean depths are 25.3 m and 12.7 m, respectively, and the lake has a mean water residence time of roughly 4 yrs. A large portion of the land use within total drainage area in the watershed (602 km^2) is agricultural and urban. Lake Mendota is the largest, deepest, and most upstream lake in the Madison Chain of Lakes connected by the Yahara River. Therefore phosphorus dynamics in Lake Mendota have important implications for waters downstream like the southern chain lakes - Lake Monona, Lake Waubesa, and Lake Kegonsa - as well as the Rock River, which flows into the Mississippi River.

Time Series. We obtained time series data of Lake Mendota's water clarity (Secchi depth), zooplankton community (species abundance and mean length), total phosphorus concentrations in the surface waters, and surface temperature from the North Temperate Lakes Long-Term Ecological Research program database (lter.limnology.wisc.edu). Samples are taken on a monthly basis in the early spring and late fall, at least once during ice cover (all variables are sampled or observed through the ice), and fortnightly during the open season (roughly May - October). Data are available from 1995 through 2014 (2013 in the case of TP in Fig. 2D). Zooplankton abundance was converted to biomass using mean lengths and length to dry weight formulas (McCauley 1984). Daily P loading measurements are available through the United States Geological Survey (usgs.gov). Rather than calculate the total phosphorus load into the lake directly, we use the Yahara at Windsor Site as a proxy for loading into the lake (Total Load = 4.5*Yahara at Windsor Load; $R^2 = 0.97$). We summed daily P loading over fortnightly time steps. Clarity, zooplankton biomass, and P loading were log-transformed and all variables were converted to fortnightly means, and then z-scored. To visualize seasonal dynamics of pre- and post-*Bythotrephes* invasion time series, we fit cyclic cubic regression splines of day of the year to the log-transformed data for time periods both before (1995 – 2007) and after (2010 – 2014) the year of *Bythotrephes* detection (2009) using generalized additive models (GAM) with the package mgcv in R (Wood 2015). We exclude 2008 and 2009 as transition years. All statistical analyses were conducted in R (R Core Team 2014).

Statistical Analysis: MARSS – Model Fitting. We used a multivariate autoregressive state-space model (MARSS) to analyze the dynamics of water clarity in Lake Mendota using the MARSS package in R (Holmes et al. 2014). The model takes the following form:

$$\begin{bmatrix} x_s \\ x_c \end{bmatrix}_t = \begin{bmatrix} B_s & C \\ 0 & B_c \end{bmatrix} \begin{bmatrix} x_s \\ x_c \end{bmatrix}_{t-1} + w_t, w \sim MVN\left(0, \begin{bmatrix} Q_s & 0 \\ 0 & Q_v \end{bmatrix}\right)$$

$$\begin{bmatrix} y_s \\ y_c \end{bmatrix}_t = \begin{bmatrix} x_s \\ x_c \end{bmatrix}_t + v_t, v \sim MVN\left(0, \begin{bmatrix} R_s & 0 \\ 0 & R_v \end{bmatrix}\right)$$

Observations (lower equation) comprise interacting system variables such as Secchi depth*, D. pulicaria* biomass, and biomass of other (non-*D. pulicaria*) grazers in vector y_s and covariates such as P loading and surface temperature in vector y_c (observations from 1995 – 2014). All observations are transformed to z-scores. The observation vector estimates a partitioned vector of true values of system variables x_s and covariates x_c with errors v having covariances given by R_s and R_v respectively. System dynamics (upper equation) involve a square transition matrix with partitions for system interactions B_s, covariate effects on system variables C, and covariate changes over time B_c. System errors w have covariances given by Q_s and Q_c corresponding to system variates and covariates respectively. MARSS models are fit with maximum likelihood using a combination of the Kalman filter and an Expectation-Maximization algorithm.

Model fits estimated all elements of Bs and Qs (interactions among system variables and their variances and covariances) and diagonal elements of Bc and Qc (autoregressive coefficients of covariates and their variances). We allowed the model to estimate terms along the **R** matrix diagonal (observation variances). The final model structure was selected using AIC and previously published ecological interactions among variables. Here we allow interactions between zooplankton grazers and known drivers of water clarity like P loading, zooplankton, and surface temperature (i.e., arrows in Fig. 3). Temperature was allowed to affect all variates. Model selection (Table S1) and residual analysis (Figure S1 – S2) can be found in the Supporting Information.

Estimating Economic Costs. To estimate the effect of phosphorus loading on water clarity, we made predictions using our MARSS model under varying grazing (pre- and post-*Bythotrephes*, i.e., high and low grazing from *D. pulicaria*) and P loading (-99% to +100%) scenarios under post-2009 surface temperature conditions and long-term average P loading conditions. We chose to investigate improving water clarity through P loading reduction as opposed to other methods (e.g., chemical treatment or biological control) because of existing efforts to reduce P loading into Lake Mendota (Lathrop et al. 1998, Stumborg et al. 2001) and additional benefits to water quality of lakes downstream of Lake Mendota (Lathrop and Carpenter 2014).

The costs of P load reductions are estimated using a report conducted by Strand Associates in 2013 (*Yahara CLEAN engineering report* 2013) (PDF available via madsewer.org - url included in citation). The goal of the Yahara CLEAN Engineering Report was to develop a list of action items that would result in a 50% P load reduction into the Lake Mendota in addition to the costs of those items. The report not only takes into account the efficiency of each action item (in US$ per lb P reduced) but also non-monetary factors that will influence the prioritization of action items like implementability, social acceptance, benefits visible to the public, water management, maintaining functional farmland and farming culture, nutrient distribution, reliability of the action item or technology, and ancillary benefits. P loading reduction costs are estimated as present day value over a 20-year project period. The CLEAN Report also details the necessary investment for a maximum implementation plan or 86% reduction (97% reduction of direct drainage sources) in P loading. The cost of a 50% reduction was estimated to be US$70M over a 20-year period and the cost of an 86% reduction was estimated to be US$177M over a 20-year period. We estimated the economic costs of offsetting SWF's impact using Table 4.01-2 in the report which details the costs, efficiency, and P load reduction of each action item. To bound the estimate, we sum the least and most expensive (in US$ per lb P reduced) items that would achieve a 71% P load reduction.

Updating Willingness-to-Pay Estimates from Stumborg et al. 2001 (Stumborg et al. 2001). Stumborg and others estimate Madison's willingness-to-pay for 1m of water clarity in Lake Mendota at US$353.53 per household. We adjust this number to present value or buying power, US$645.49, using the Consumer Price Index Inflation Calculator (data.bls.gov). We also updated the number of households in Dane County from the 1990 census of 155,200 households to the 2014 estimate by the U.S. Census Bureau of 217,100 households (census.gov).

Acknowledgements

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Author Contributions

JW and JVZ conceived the study, JW analyzed the data with guidance from JVZ and SRC, and all three authors wrote the manuscript.

Figure Legends

Figure 1. Arrows represent connections among major components of the socio-ecological system, Lake Mendota. The introduction of *Bythotrephes* (red arrows) is presented here in the context of existing pathways affecting water clarity (orange arrow), a key ecosystem service in the lake, such as agricultural runoff (yellow arrows) and top-down control of the food web (black arrows). *Increasing phytoplankton biomass resulting from increased nutrient input or decreased grazing decreases water clarity. There are no direct options for the control or eradication of *Bythotrephes*.

Figure 2. Seasonal dynamics pre- (blue dashed; 1995 - 2007) and post-*Bythotrephes* (red solid; 2009 - 2014) of *Bythotrephes* (A; µg m^{-3}), zooplankton grazers (B-C; mg m^{-3}), phosphorus dynamics (D-E; µg TP l^{-1}, kg P d^{-1}), and water clarity (F; Secchi depth in m) are plotted as a smoothed GAM function of day of the year. Shaded areas represent 1 standard error. Note that all y-axes are log-scaled.

Figure 3. MARSS estimates of ecological interactions are shown with arrows and the strength of the interaction - estimate (s.e.). Red arrows are significant negative effects, black arrows are significant positive effects, and grey arrows are non-significant effects.

Figure 4. The cost of offsetting *Bythotrephes'* impact through P loading reductions is revealed through predicting water clarity under high (dashed blue; pre-2009) and low (solid red; post-

2009) grazing under a range of P loading conditions. This restoration cost is calculated as the cost of the P load reduction necessary to return the lake to pre-2009 clarity (blue filled circle) under post-2009 grazing (red filled circle). Here, cost is the estimated total present-day cost over a 20-year project.

Figures

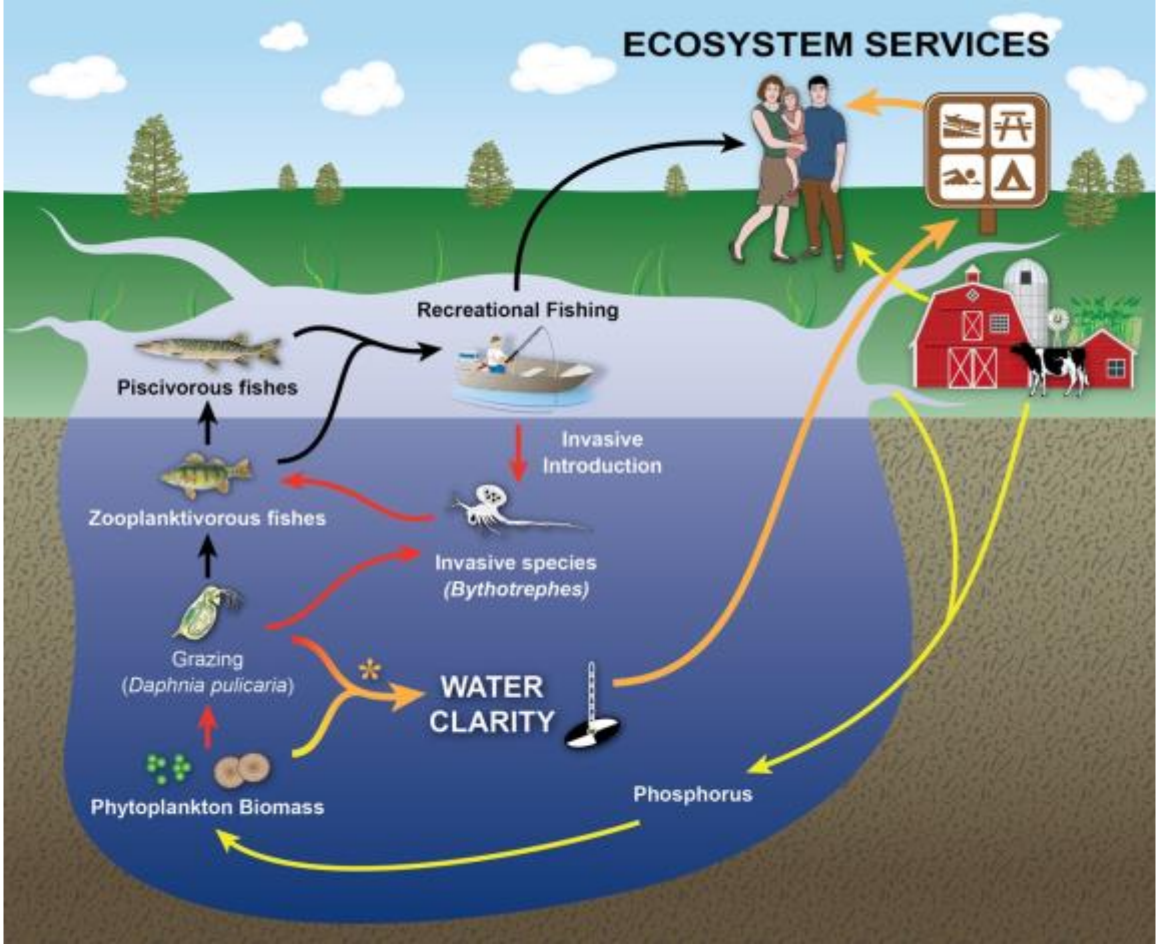


Figure 1

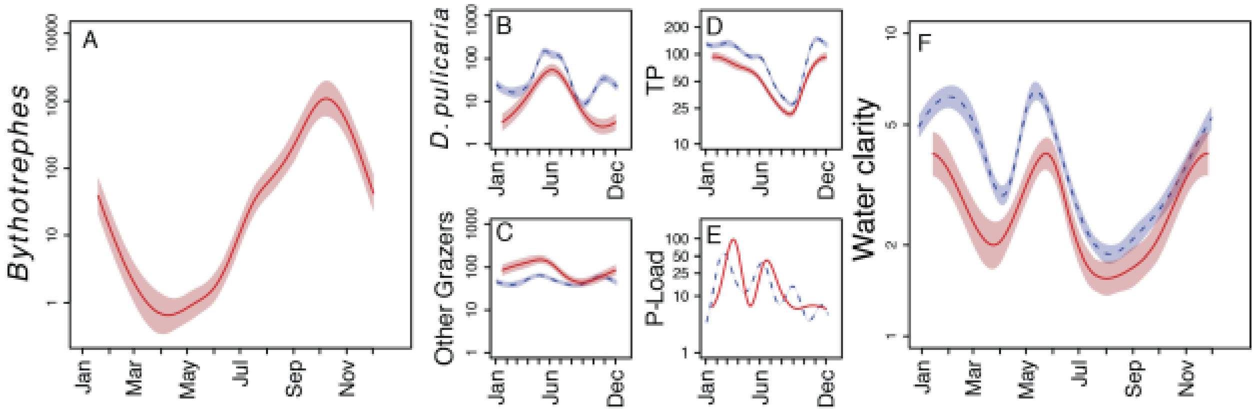

A
Bythotrephes
10000
1000
100
10
1
Jan
Mar
May
Jul
Sep
Nov
B
D. pulicaria
1000
100
10
1
C
Other Grazers
1000
100
10
1
D
TP
200
100
50
25
10
E
P-Load
100
50
25
10
1
Jan
Jun
Dec
F
Water clarity
10
5
2
1
Jan
Mar
May
Jul
Sep
Nov

Figure 2

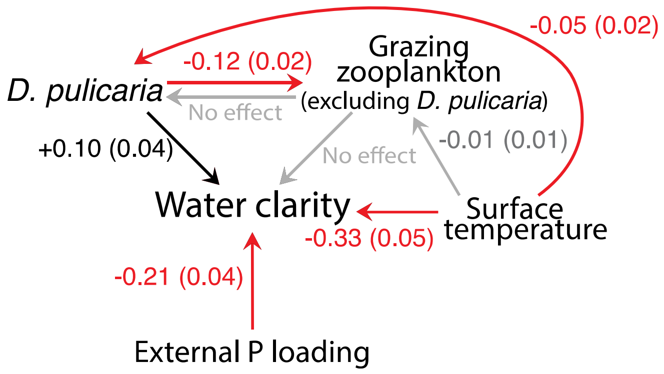

-0.05 (0.02)
-0.12 (0.02)
D. pulicaria
Grazing zooplankton (excluding D. pulicaria)
No effect
+0.10 (0.04)
No effect
-0.01 (0.01)
Water clarity
Surface temperature
-0.33 (0.05)
-0.21 (0.04)
External P loading

Figure 3

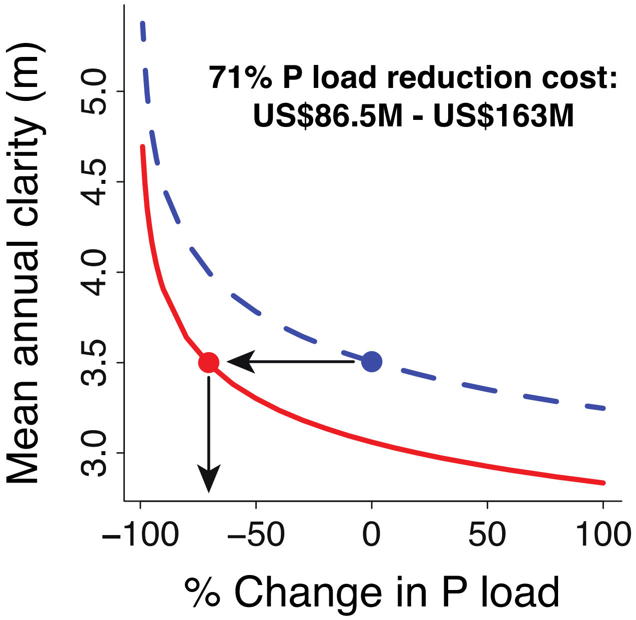

71% P load reduction cost:
US$86.5M - US$163M
Mean annual clarity (m)
3.0
3.5
4.0
4.5
5.0
–100
–50
0
50
100
% Change in P load

Figure 4

Appendices

Supporting Information

Massive ecosystem services impact by an invasive species

Jake R. Walsh, Stephen R. Carpenter, and M. Jake Vander Zanden

MARSS: Model Performance & Selection

MARSS: Residual Analysis of Clarity Predictions

MARSS: Model Performance & Selection

Base model formations were based on expected ecological interactions in order to help constrain the many possible **B**-matrix compositions for a matrix of five interacting variables. We selected the best model that included all five variables of interest using AIC (selected model AIC in Table S1).

Here we limit comparisons of different model configurations to observing performance without each variable's effect on water clarity. This assumes that the **B**-matrix described in Materials and Methods above creates a model that is both parsimonious and ecologically sound. It should be noted that adding ecologically reasonable effects (e.g., other zooplankton effect on *D. pulicaria*) does not significantly change the **B**-matrix interactions or AIC of the model, unless the number of interactions that the model is forced to estimate becomes so high that it can no longer converge on an estimate for all model parameters.

By removing each variable effect on water clarity, we see that temperature is the most important variable (AIC increases the most with its removal), followed by P loading, *D. pulicaria*, and other grazing zooplankton (Table S1; note *adding* the other grazing zooplankton effect made model fit worse). Each variable is highly seasonal. Therefore, including surface temperature as a seasonal surrogate should be a very important component of the model. Interestingly, P loading was more important to the model than *D. pulicaria* biomass. The important role of external P loading in driving water clarity may have implications for the efficiency of P load reductions in the new low-*D. pulicaria* grazing regime.

Table S1. Model selection for varying MARSS combinations as described in **MARSS: Model Performance & Selection.** Models are selected using Akaike Information Criterion and previously published ecological interactions.

MARSS Model Formation	Log-likelihood	AIC	Convergence (Iterations)
Selected Model	-1733	3515	Yes (35)
Remove temperature effect on clarity	-1762	3571	No
Remove P load effect on clarity	-1742	3530	Yes (41)
Remove *D. pulicaria* effect on clarity	-1736	3518	Yes (35)
Add other grazing zooplankton effect on clarity	-1733	3517	Yes (35)

MARSS: Residual Analysis of Clarity Predictions

We plotted the residuals of water clarity in our best-fit model through time (Fig. S1) and against z-scored model variates (Fig. S2). We found that the model fit the data well with a small seasonal signal possibly linked to surface temperature as a seasonal surrogate capturing indirectly related seasonal variation (e.g., low temperatures driving an overestimate of water clarity in spring months in Fig. S1) or possibly to a non-linear response in clarity to *D. pulicaria* biomass (e.g., slight bell shape of clarity residuals plotted against z-scored *D. pulicaria* biomass in Fig. S2 which may describe seasonal discrepancies in Fig. S1). However, with little to no shift in model residuals with the detection of *Bythotrephes* in 2009 (Fig. S1), it is unlikely that these affect the overall conclusions of the restoration cost estimate (i.e., obtaining pre-invasion clarity under post-invasion grazing).

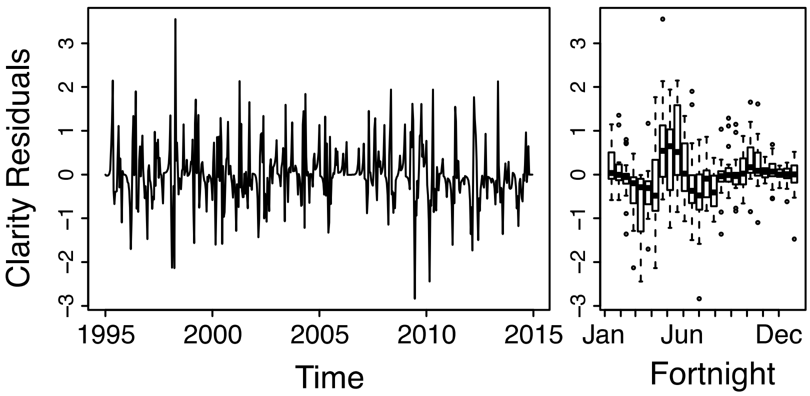


Figure S1. Clarity residuals plotted through time (long-term left and seasonal right).

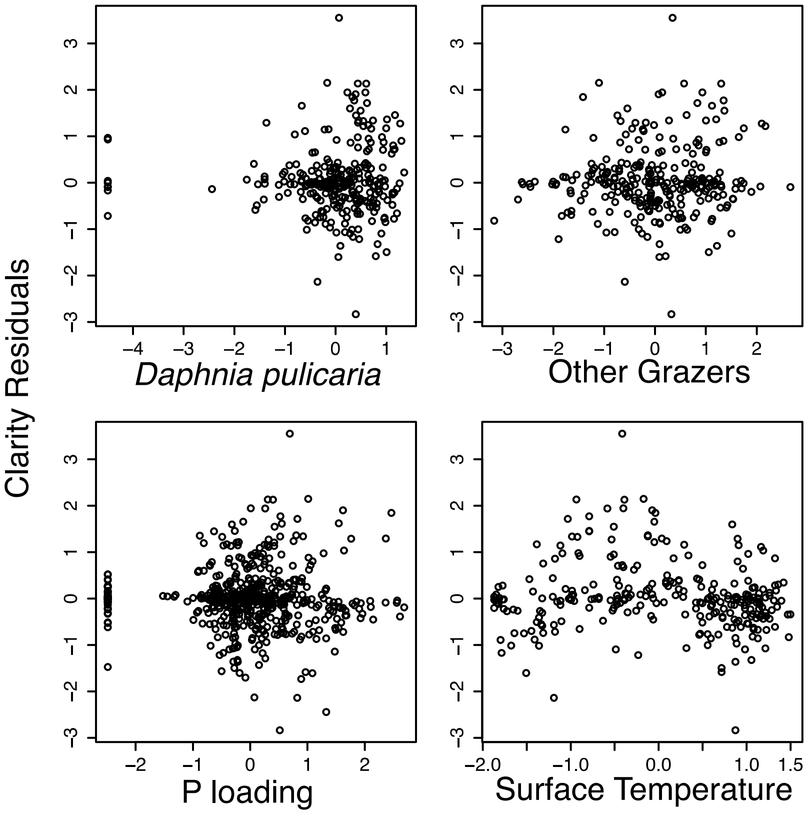


Figure S2. Clarity residuals plotted against z-scored model variates.

Chapter Three: Divergent responses in water quality to cascading impact of an invasive predatory zooplankton

In prep for submission to *Limnology & Oceanography*

Co-Author: M. Jake Vander Zanden

Manuscript

Abstract

Invasive species can profoundly change the biological make-up and functioning of ecosystems as a result of complex food web interactions. Outbreak of the invasive predatory zooplankton, spiny water flea (*Bythotrephes longimanus*) in Lake Mendota, WI (USA) led to a sharp decline in the keystone grazer *Daphnia pulicaria,* and in turn, water clarity. Yet lake pelagic systems are comprised of a complex web of species, with the potential for many direct and indirect food web interactions. Moreover, focus on water clarity masks important aspects of algal community composition that also influence water quality, such as the abundance of potentially harmful cyanobacteria. We use a 20-year dataset for Lakes Mendota and Monona to evaluate interactions among nutrients, zooplankton, and phytoplankton that manifested in an invasion-induced trophic cascade. We found that diatom biomass increased in both lakes, driving lower water clarity, but to a much larger extent in Lake Mendota. Cyanobacteria biomass did not change in either lake. Multivariate time series analysis (MARSS) revealed that diatoms are likely limited by *D. pulicaria* grazing while cyanobacteria are likely limited by nutrients in Lake Mendota. MARSS also revealed a strong negative effect of diatoms on cyanobacteria. Bioavailable phosphorus declined abruptly alongside the increase in diatom

biomass despite no change in phosphorus inputs into the lake. This change is consistent with expectations since diatoms are generally better at taking up phosphorus than cyanobacteria. Also, the number of beach closures in Lake Mendota due to cyanobacteria blooms declined over this period. Our results indicate that invasion of *Bythotrephes* simultaneously led to a decline in water clarity, largely due to increased diatoms, and a decline in cyanobacteria blooms. These two important components of water quality – clarity and fewer cyanobacteria blooms – can become uncoupled and show divergent responses under a food web shift. This has important implications for the water quality management in eutrophic lakes.

Introduction

Invasive species change the biological make-up and functioning of the planet's ecosystems (Clavero and García-Berthou 2005, Pejchar and Mooney 2009, Ehrenfeld 2010, Gallardo et al. 2015) and these changes can be responsible for degraded water quality in freshwater ecosystems (Carpenter et al. 2011). However, water quality refers to multiple characteristics that are mediated by many ecological interactions and, in turn, may be affected differentially through these various pathways of interactions. Here we focus on the facets of water quality that are degraded by eutrophication and the resulting increase in primary production – water clarity and the frequency and intensity of harmful cyanobacteria blooms. Each of these are primarily affected by phytoplankton community composition and interactions, which are structured by multiple environmental drivers as well as food web interactions.

These two examples of the many components of water quality represent different elements of phytoplankton community composition. Water clarity is a coarse measure of algal abundance in "green" freshwater ecosystems (i.e. lakes where clarity is most influenced by algal abundance rather than other organic matter). While water clarity is aesthetically valuable (Stumborg et al. 2001, Krysel et al. 2003), necessarily equating water clarity with water quality can be misleading due to complexity within the phytoplankton community. Water quality also refers to the frequency and intensity of harmful cyanobacteria blooms (Carpenter et al. 2011). While cyanobacteria blooms degrade water clarity, they are most damaging through the harmful toxins they produce that lead to recreational losses, beach closures, fish kills, and decreased property values. In this way, phytoplankton community composition determines whether water clarity and toxin-free water are coupled to the same ecological interactions. Understanding the ecological factors that drive each is critical for managing water quality and resulting human well-being (Kosenius 2010, Keeler et al. 2012).

Phytoplankton communities of lakes are thought to be driven primarily by food web composition and nutrients (Carpenter et al. 1987). Food webs that support abundant populations of large grazers, like *Daphnia*, have lower phytoplankton biomass and the communities are often dominated by large, grazing-resistant phytoplankton species (Hansson et al. 1998, Ekvall et al. 2014). For this reason, *Daphnia* are thought to improve water quality by reducing phytoplankton biomass and improving water clarity. However, this interaction is mediated by the availability of resources (e.g. phosphorus) to phytoplankton (Smith 2003). In highly eutrophic lakes, the ability of *Daphnia* to graze summer phytoplankton is limited (Gliwicz 1990, Elser and Goldman 1991). Therefore, water quality is more strongly influenced by nutrients in lakes with high external nutrient loading. Consequently, the frequency and intensity of toxic cyanobacteria blooms increases with external nutrient loading.

Species invasions provide natural experiments that generate new insights into the ecological factors governing different components of water quality. The invasive predatory zooplankton, spiny water flea (*Bythotrephes longimanus*) invaded eutrophic Lakes Mendota and Monona in 2009 and has degraded water clarity through predation on the grazer, *Daphnia pulicaria* (Walsh et al. 2016). This cascading impact has totaled US$140M in damages to water clarity, which is on par with the cost of restoring that clarity, estimated at $175M (Walsh et al. 2016). However, the largest decline in clarity was observed in the spring and fall, times when *D.*

pulicaria grazing on edible phytoplankton is strongest, but unlike summer, times when harmful cyanobacteria blooms are uncommon.

Here we investigate the changes in Lakes Mendota and Monona plankton communities that drove the decline in water clarity. We evaluate the role that phytoplankton community structure plays in water quality, specifically in how community composition, and its drivers, influence water clarity and cyanobacteria blooms. While a primary goal of this study is to better understand the mechanisms of an invasive species' impact, it will also serve to better understand how lake food webs influence water quality.

Methods

Study Systems

Lake Mendota (Lathrop and Carpenter 2014) is a 39.6 km^2, dimictic (mixes in spring and fall) and culturally eutrophic lake located adjacent to Madison, WI, USA. Maximum and mean depths are 25.3 m and 12.7 m, respectively, and the lake has a mean water residence time of roughly 4 yrs. A large portion of the land use within total drainage area in the watershed (602 km^2) is agricultural and urban. Lake Mendota is the largest, deepest, and most upstream lake in the Madison Chain of Lakes connected by the Yahara River. Therefore, phosphorus dynamics in Lake Mendota have important implications for waters downstream like the southern chain lakes - Lake Monona, Lake Waubesa, and Lake Kegonsa - as well as the Rock River, which flows into the Mississippi River. *Bythotrephes* was detected in 2009 at unprecedented high densities.

Lake Monona is a smaller (13.2 km^2) eutrophic lake forming the southern shoreline (with Lake Mendota to the north) of the Madison isthmus. While the majority of Lake Monona's watershed is urban, it receives a large portion of its phosphorus from Lake Mendota via the Yahara River. The ecology of the two lakes are similar, with key differences in their fisheries. Lake Mendota is managed to support large, piscivorous fishes to improve water clarity by suppressing small zooplanktivorous fish predation on *Daphnia* (Lathrop et al. 2002). Conversely, Lake Monona is managed to support zooplanktivorous fishes, like bluegill. This key difference sets up an interesting contrast in the two lakes food webs that will likely have implications for the planktivory-sensitive *Bythotrephes* (Wang and Jackson 2011).

Time Series

Phytoplankton (n = 391 taxonomic units), zooplankton (n = 24 taxonomic units), nutrient (soluble reactive phosphorus), and lake temperature time series data were obtained from the North Temperate Lakes Long Term Ecological Research (NTL-LTER) program database (lter.limnology.wisc.edu). NTL-LTER samples each lake monthly in the spring and fall, fortnightly in the summer, and at least once during ice cover. Plankton are identified to the lowest taxonomic level possible. All phytoplankton analyses are conducted by PhycoTech, Inc., a private lab specializing in phytoplankton analyses. Phytoplankton biomass is calculated prior to data entry using species counts from mounted slides, obtaining cell measurements to calculate the biovolume for geometric solids (e.g. spheres, cylinders, and cones), and cell density to convert biovolume to biomass. We calculate zooplankton biomass using zooplankton abundance, mean measured length, and published length-to-dry-weight relationships (McCauley 1984). We interpolate soluble reactive phosphorus linearly through sample depth and date. Finally, we take the average soluble reactive phosphorus from the lake surface to 4 m depth as a measure of resource availability to phytoplankton. Similarly, we average the top 5 m of lake surface temperature measurements.

Observing Change in Plankton Community

We observed change in seasonal plankton dynamics through fitting generalized additive models (GAM) of plankton biomass fitted to day of the year (Wood 2015) using package "mgcv" in R. Here, we fit a GAM for both pre- and post-invasion time periods to allow for seasonal trend comparisons over both time periods. We do this for the total biomass of the lakes' two dominant phytoplankton taxa: Bacillariophyta (diatoms) and Cyanophyta (cyanobacteria).

Observing Plankton Species Interactions

To investigate the ecological interactions driving the biomass of the two dominant phytoplankton divisions in Lake Mendota, diatoms (Bacillariophyta) and cyanobacteria (Cyanophyta), we constructed a multivariate autoregressive state-space model (Holmes et al. 2012) using package "MARSS" in R (Holmes et al. 2014). The model takes the following form:

$$\mathbf{x_t} = \mathbf{Bx_{t-1}} + \mathbf{u} + \mathbf{w_t}, \text{ where } \mathbf{w_t} \sim \text{MVN}(0, \mathbf{Q})$$

$$\mathbf{y_t} = \mathbf{Zx_{t-1}} + \mathbf{a} + \mathbf{v}_t, \text{ where } \mathbf{v_t} \sim \text{MVN}(0, \mathbf{R})$$

Where a vector of variable observations, $\mathbf{y_t}$, at time **t** are described by a vector of state values, $\mathbf{x_t}$. **B** is a matrix of potential interactions between state processes that allows us to estimate the direction and magnitude of state process interactions (e.g. drivers of water clarity and interactions among drivers). The matrix **Q** describes the correlation of the process deviations and the matrix **R** describes the correlation of the observation errors. MARSS models are fit with maximum likelihood using a combination of the Kalman filter and an Expectation-Maximization algorithm. All time series (*D. pulicaria* biomass, non-*D. pulicaria* grazer biomass, diatom biomass, cyanobacteria biomass, total phosphorus, and surface temperature) are log-transformed (except temperature) and z-scored.

Within the **B** matrix, we allowed competitive interactions between *D. pulicaria* and all other zooplankton grazers, top-down grazing interactions of each of these on diatom and cyanobacteria biomass, competition between diatoms and cyanobacteria, and nutrient availability to diatoms and cyanobacteria (i.e. arrows in Fig. 2). In all configurations the diagonal of the **B** matrix (first order autoregressive terms of each state variable) was allowed to vary between -1 and +1. Since our data is z-scored, we set **a** and **u** to 0. We allowed **Q** to remain unconstrained off the diagonal of the variates (clarity, zooplankton, and PP) and set **Q** terms to zero off the diagonal of the covariates (temperature and P loading). We allowed the model to estimate the **R** matrix diagonal. The best models were selected using AIC and previously published ecological interactions among variables. Insignificant interaction terms in the **B** matrix were dropped for parsimony in the final model estimates.

Results

We found that *Bythotrephes* was over a magnitude less abundant in Lake Monona (2.8 ind m^{-3}, annual geometric mean) relative to Lake Mendota (59 ind m^{-3}, annual geometric mean). Our GAM fitting algal abundance to day of the year revealed that in Lake Mendota, total algal biomass increased following Bythotrephes invasion in the spring and fall. This change was driven by increases in diatom biomass and no clear change in cyanobacteria biomass (Fig. 1a). These changes were less obvious in Lake Monona (Fig. 1b).

The **B** ("interactions") matrix of the best-fit MARSS model (AIC = 3810, log-likelihood = -1860, convergence in 269 iterations) for Lake Mendota reveals that these changes in the phytoplankton community may be due to three ecological interactions (Fig. 2). First, only diatom biomass appears to be associated with "top-down" influence from grazing with a strong negative "effect" of *D. pulicaria* on diatom biomass (-0.14, s.e. = 0.05). *D. pulicaria* have a negative effect on other grazer biomass (-0.12, s.e. = 0.02), which have no effect on phytoplankton biomass. Second, only cyanobacteria biomass appears to be associated with "bottom-up" influence from resource availability with a positive effect of total phosphorus on cyanobacteria biomass (0.11, s.e. = 0.05). Finally, diatoms have a strong negative effect on cyanobacteria (-0.16, s.e. = 0.09), which do not have a significant effect on diatoms. We did observe changes in resource availability to the two competing taxa - there was little long-term change in external phosphorus loading but a decline in the availability of phosphorus in the surface waters of the lake (Fig. 3). Temperature effects (here temperature acts as a seasonal surrogate) and first-order autoregressive effects were significant for all variables (Table 1).

Discussion

In this study we show that lake water quality is mediated through complex ecological interactions and we report a divergent response within the phytoplankton community to the *Bythotrephes* outbreak in Lake Mendota. An enormous increase in predation pressure on the zooplankton community affected a cascading change in Lake Mendota's phytoplankton community composition toward higher diatom biomass, specifically *Stephanodiscus* (see Appendix more more detailed analysis of community changes). It is likely that this increase in biomass makes up a large part of the change in phytoplankton biomass that drove the cascading effects of *Bythotrephes* on Lake Mendota water clarity. The distinction between diatoms and cyanobacteria is critical because 1) diatoms do not produce the same harmful toxins as cyanobacteria in the lake and 2) diatoms are less abundant at times when the lake is most heavily used by citizens for recreation (July and August). This study demonstrates that water clarity is unlikely to return unless *D. pulicaria* dominance is restored in the lake or heavy investment is made in phosphorus load reduction (-71%, US$86.5M - US$163M; Walsh et al. 2016). However, we also find that this loss in water clarity has not been accompanied by further loss in water quality due to harmful cyanobacteria blooms. Finally, these effects are larger in Lake Mendota which has over a magnitude more *Bythotrephes* than Lake Monona.

MARSS revealed that this divergent response in Lake Mendota's phytoplankton community is driven by three ecological interactions. First, diatom biomass is limited from the top down by *D. pulicaria* and increased with the release of grazing pressure due to *Bythotrephes* predation on *D. pulicaria*. Second, cyanobacteria biomass is limited by the availability of nutrients and a strong negative effect of diatom biomass. Interestingly, *Bythotrephes* may have indirectly restructured how Lake Mendota's food web processes phosphorus as evidenced by historically low surface soluble reactive phosphorus (i.e. bioavailable phosphorus) in the presence of *Bythotrephes*, despite relatively normal external phosphorus loading. This change may have intensified the strong negative effect of diatoms on cyanobacteria observed in the MARSS model. Alternatively, diatoms are thought to be better competitors for phosphorus than cyanobacteria, and this change may be a result of this competition. *D. pulicaria* and phytoplankton biomass are both critical components of the phosphorus cycle in Lake Mendota (Lathrop et al. 1996) and further investigation is required here. In this way, water quality may not only be differentially influenced by two distinct factors (grazing and nutrients), it may be divergently influenced by these two pathways as a loss in grazing may have influenced nutrient availability to cyanobacteria in the summer.

MARSS revealed that cyanobacteria biomass in Lake Mendota is significantly bottom up limited. Therefore, phosphorus load reductions may still effectively control the frequency and intensity of harmful cyanobacteria blooms. However, reducing in-lake phosphorus concentrations has been a challenge and reductions to external phosphorus loads likely will not have immediate effects on in-lake phosphorus concentrations. For example, this “slow response” can be due to the persistence of internal loading or legacy phosphorus in soils that is mobilized due to increased precipitation with global climate change (Carpenter and Lathrop 2014). Despite the challenges associated with reducing phosphorus in the watershed and lake bottom, these results reveal that any investments made in reducing phosphorus loading should have nearly the same effects on reducing summer cyanobacteria biomass as before the *Bythotrephes* outbreak (Fig. 4).

This brings up an interesting socio-economic wrinkle in *Bythotrephes*’ impact. While water clarity is related to total phytoplankton biomass and declined with reduced grazing and increased diatom biomass, reduced water quality due to toxic phytoplankton blooms is singularly related to cyanobacteria (Fig. 5). Since we found that the frequency and intensity of harmful cyanobacteria blooms is driven primarily by nutrient availability, there should be little additional loss of recreation due to harmful cyanobacteria with the *Bythotrephes* invasion. In fact, it appears that the number of beach days lost to cyanobacteria blooms has declined (pre-2009 mean = 63 days, s.d. = 28 days; post-2009 mean = 17 days, s.d. = 16 days; Mann-Whitney U-test, W = 23, p-value = 0.02), despite lower water clarity (Fig. 6). If this decline is in fact due to fewer large cyanobacteria blooms, then the mechanism of the strong negative effect of diatoms on cyanobacteria (e.g. competition for phosphorus) will need to be investigated further.

This negative relationship may play a significant role in the differential provisioning of these two facets of water quality and, in turn, the economic value of water quality in Lake Mendota. For example, citizens were found to value water clarity in the Gulf of Finland more than fewer cyanobacteria blooms (Kosenius 2010). If there is similar differentiation in the value of the two components of water quality in Lake Mendota and the ecological pathways providing each component are different, then resources can and should be allocated more efficiently to manage for a particular water quality outcome. Similarly, the costs of managing agricultural run-off or directly managing the lake's food web (e.g. through the fishery) to ameliorate top-down pressure on *Daphnia* may differ. The ecological information here and the socio-economic information from a survey *sensu* Kosenius (2010) would help inform water quality management in the future.

However, a major caveat to this study is that resource-limited cyanobacteria biomass did not decline despite historically low availability of nutrients in the surface waters of the lake. If the decline in the availability of phosphorus is not due to a permanent shift in the food web, then a return to pre-2009 bioavailable phosphorus concentrations could be devastating for lake water quality and the frequency and intensity of toxic cyanobacteria blooms. This highlights the urgency to continue efforts to reduce phosphorus input from farm run-off in Lake Mendota's watershed.

The effects observed in Lake Mendota were larger than those in Lake Monona. Lake Monona is managed as a "planktivore" lake supporting its large bluegill fishery while Lake Mendota has been managed as a "piscivore" lake supporting its walleye fishery and *D. pulicaria* biomass through controlling yellow perch and other planktivorous fish biomass (Lathrop et al. 2002). This may describe why *Bythotrephes* is less abundant in Lake Monona and, in turn, why Lake Monona's food web did not change to the same degree as Lake Mendota. In both lakes, the dominant planktivorous fishes are known to consume *Bythotrephes* (Walsh, *unpublished data*), likely limiting its abundance in Lake Monona where these fishes are more abundant. In fact, in recent years (2014-205) both *D. pulicaria* and water clarity have been slightly better in Lake Monona than Lake Mendota (Walsh, *unpublished data*) – a phenomenon which has not occurred since before the Lake Mendota biomanipulation in 1988. Further investigation is required to determine the viability of manipulating Lake Mendota's fishery to control *Bythotrephes* and improve water clarity while mitigating the risk of further harm to the lake's *D. pulicaria* population.

Conclusion

Water quality is a complex of freshwater ecosystem characteristics that are governed by multiple ecological pathways. Here we show that a large and costly cascading effect by *Bythotrephes* on Lake Mendota's clarity was not accompanied by an increase in the frequency or intensity of harmful cyanobacteria blooms. Understanding the ecological pathways that yield specific outcomes in water quality will help inform water quality management. In any case, this study reveals preventing the spread of *Bythotrephes* and, likely, other harmful invasive species is a cost-effective water quality management strategy.

Table and Figure Legends

Table 1. MARSS model temperature effects on variables and first-order auto-regressive terms from the B-matrix. In this model, temperature acts as a seasonal surrogate and the first-order autoregressive terms are often thought of as analogous to density dependence (values closer to zero have stronger density dependence). All temperature effects are significantly different from zero and all autoregressive terms are significantly different from one.

Figure 1. Total phytoplankton biomass (A – Lake Mendota, B – Lake Monona; with the two dominant taxa inset in the plots of total phytoplankton biomass) increased after (GAM fitted to day of year; post-2009 = red, pre-2009 = blue; shaded = 1 s.e.) the spiny water flea invasion. Of the two dominant phytoplankton divisions in Lake Mendota, this is primarily driven by the diatoms (e.g. *Stephanodiscus*), with minimal change in the cyanobacteria (e.g *Microcystis* and *Aphanizomenon*). The increase in phytoplankton and diatom biomass in Lake Monona, though less clear, is interesting given no change in community composition.

Figure 2. Best-fit MARSS of Lake Mendota plankton dynamics. Arrows are weighted by effect size. Here cyanobacteria are bottom-up limited by resource availability and diatoms are top-down limited by *D. pulicaria* grazing. Note the large negative effect of diatoms on cyanobacteria. This may explain the observed trends in Lake Mendota. Temperature, a seasonal surrogate here, affects all model components significantly: strong negative effect on diatoms,

strong positive effect on cyanobacteria, strong negative effect on TP, and weak negative effects on *D. pulicaria* and other grazers.

Figure 3. Long-term moving average trend in phosphorus dynamics in Lake Mendota are plotted over time (external P-loading in blue and bioavailability of phosphorus in the surface waters in orange). There was an abrupt shift in surface soluble reactive phosphorus (SRP 0m – 4m) or bioavailable phosphorus the year after the spiny water flea was detected in Lake Mendota. However, this was following two very high P-loading years (2008 and 2009). Note the effects of the 2012 drought on P-loading.

Figure 4. MARSS model prediction from model developed in Walsh et al. (2016). *Bythotrephes*' predicted effect on clarity is plotted against day of the year. The decline in clarity due to loss in grazing was largest in winter, spring, and fall with minimal effects in the summer. Here, we show that this effect may be due to a differential impact on diatoms and cyanobacteria.

Figure 5. Conceptual diagram showing the different drivers (effects are shown as arrows and the sign of those effects is shown in red and blue) of the two components of water quality in Lake Mendota. This study revealed that the top-down effect of grazing has a stronger influence on diatom biomass than nutrient availability while the reverse was true for cyanobacteria biomass. This will have implications for water quality in Lake Mendota.

Figure 6. The number of beach days lost (total over all beaches) due to cyanobacteria blooms (vertical lines and solid circles) in Lake Mendota are plotted through time alongside the lake's water clarity (grey line; long-term moving average trend). Water clarity declined with the *Bythotrephes* invasion through an increase in diatom biomass (brown cells, red arrow), however this was not accompanied by an increase in the number of beach closures due to cyanobacteria blooms (green cells, grey arrow).

Tables & Figures

Variable	Temperature Effect (s.e.)	First-Order AR Term
Diatom biomass	-0.27 (0.06)	0.28 (0.09)
Cyanobacteria biomass	0.22 (0.06)	0.72 (0.07)
Total phosphorus	-0.10 (0.03)	0.75 (0.04)
D. pulicaria biomass	-0.07 (0.03)	0.77 (0.04)
Other zooplankton biomass	-0.05 (0.02)	0.90 (0.04)
Temperature	---	0.72 (0.04)

Table 1

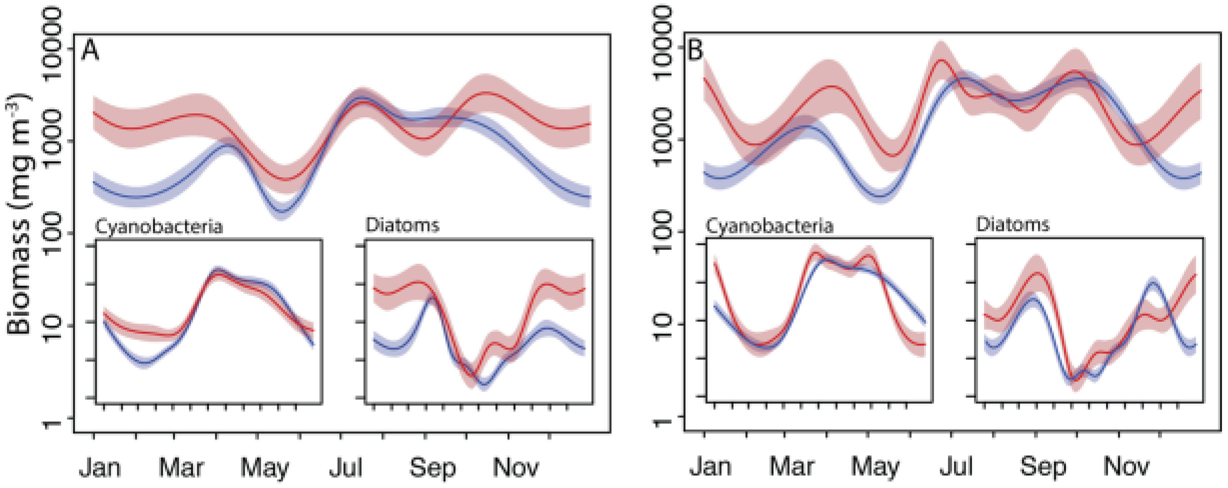

A
B
Biomass (mg m^{-3})
10000
1000
100
10
1
Cyanobacteria
Diatoms
Jan
Mar
May
Jul
Sep
Nov

Figure 1

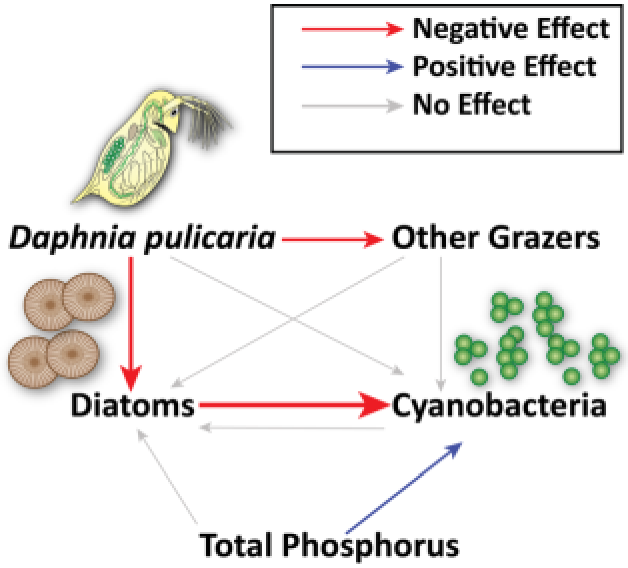

Negative Effect
Positive Effect
No Effect
Daphnia pulicaria
Other Grazers
Diatoms
Cyanobacteria
Total Phosphorus

Figure 2

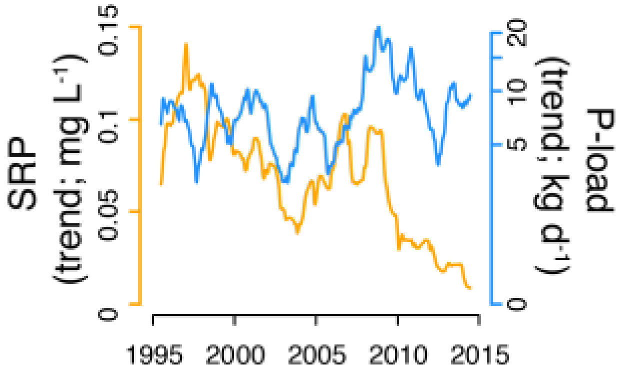

SRP
(trend; mg L^{-1})
0
0.05
0.1
0.15
P-load
(trend; kg d^{-1})
0
5
10
15
20
1995
2000
2005
2010
2015

Figure 3

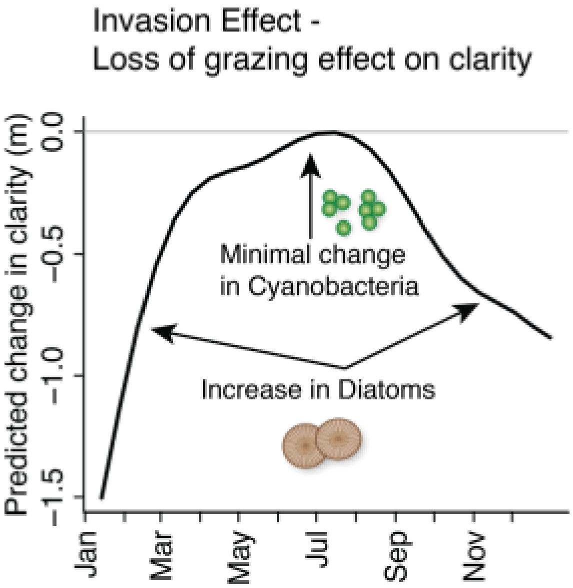

Invasion Effect -
Loss of grazing effect on clarity
Predicted change in clarity (m)
0.0
−0.5
−1.0
−1.5
Jan
Mar
May
Jul
Sep
Nov
Minimal change
in Cyanobacteria
Increase in Diatoms

Figure 4

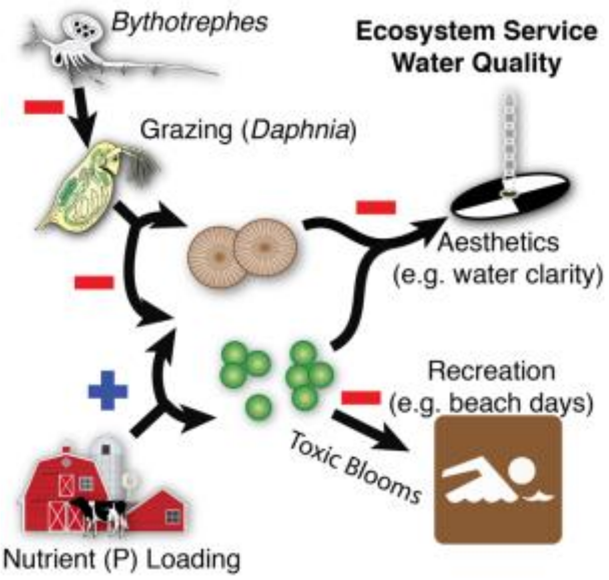

Bythotrephes
Ecosystem Service
Water Quality
Grazing (Daphnia)
Aesthetics
(e.g. water clarity)
Recreation
(e.g. beach days)
Toxic Blooms
Nutrient (P) Loading

Figure 5

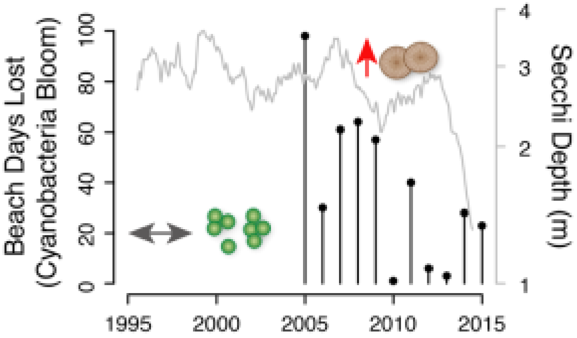

Beach Days Lost
(Cyanobacteria Bloom)
0
20
40
60
80
100
1995
2000
2005
2010
2015
Secchi Depth (m)
1
2
3
4

Figure 6

Appendix

Contents:

Statistical ordination of plankton community shifts in Lakes Mendota and Monona

Background

In Chapter 3, I show how *Bythotrephes* impact cascaded through the zooplankton community into the phytoplankton community through seasonal GAM models and MARSS multivariate time series models. This appendix provides a detailed analysis of plankton community changes through multivariate ordination, corroborating the coarser measures of diatom and cyanobacteria biomass.

Methods

We observed change in the composition of two plankton communities through principal component analysis using the package “vegan” in R (Oksanen et al. 2015). Phytoplankton were grouped by genus (n = 154 genera) and both groups were Hellinger transformed (Legendre and Gallagher 2001) prior to principal component analysis (PCA) for the zooplankton community and redundancy analysis (RDA) – which expands on PCA, allowing for the investigation of drivers of community composition - for the phytoplankton community using $\log_{10}$-transformed zooplankton grazer biomass (*Daphnia pulicaria, D. mendotae, D. retrocurva, Diacyclops, Mesocyclops,* and Diaptomid calanoids) as covariates. Phytoplankton community loadings onto grazer vectors were quantified using “envfit” in vegan which is a permutation test used to fit vectors onto ordinations. We conducted RDA for Lake Mendota and Lake Monona from 1995 – 2013 as well as separating each lake into pre- (1995 – 2008) and post- (2009 – 2013) *Bythotrephes* detection analyses (the latter results are described in more detail in the Appendix). In both phytoplankton and zooplankton ordinations, pre- and post-*Bythotrephes* detection time period centroids were mapped onto the ordination with 95% confidence interval ovals. In PCA space, points that are closer in space are thought to be more similar in community composition. Therefore, vectors that point in the direction of species' centroids or sample dates are more likely drivers of that species' dominance on a given sample date. Similarly, if centroids' 95% confidence intervals do not overlap in PCA space, then we assume that there was a significant shift in community composition. The length of vectors from the origin is reflective of the strength of the vector in describing community composition (e.g. long vectors are strong drivers of community composition).

Results

Changes in Zooplankton Community Composition

PCA revealed large significant changes in the zooplankton communities of both lakes away from *D. pulicaria* (Appendix Fig. 1). In Lake Monona, the community also shifted away from the copepod *Mesocyclops* and toward *Diacyclops* (Appendix Fig. 1b), *Mesocyclops* was not a prominent component of the PCA in Lake Mendota (Appendix Fig. 1a), but declined substantially with the *Bythotrephes* eruption (84% decline in biomass).

Changes in Phytoplankton Community Composition & Influence of Grazers

Like PCA, RDA allowed for observing the structure of the lakes' phytoplankton communities and change in the lakes' phytoplankton communities. However, RDA also allows for observing the role of other drivers in structuring the phytoplankton community. The pre- and post-2009 ovals represent centroids of pre- and post-2009 phytoplankton community composition. Since zooplankton species vectors are plotted in the same space, they can be interpreted alongside the centroid ovals, but it should be noted that ovals do not describe changes in the zooplankton species vectors. With the invasion of the spiny water flea, there was a significant shift toward the diatom genus *Stephanodiscus* in the Lake Mendota phytoplankton community (Appendix Fig. 2a) and no significant shift in Lake Monona's phytoplankton community (Appendix Fig. 2b). Lake Mendota's phytoplankton community is characterized by *Stephanodiscus* as well as the cyanobacteria genera *Microcystis* and *Aphanizomenon*.

Lake Mendota's phytoplankton community structure is driven significantly by *Mesocyclops*, *D. pulicaria*, *D. mendotae*, and *Diacyclops* abundance (Appendix Fig. 2a, Table 1). Here, *Daphnia* species vectors oppose one another along the second principal component, driving changes from *Aphanizomenon* with *D. pulicaria* to *Microcystis* and *Stephanodiscus* with *D. mendotae*. Along the first principal component *Mesocyclops* is associated with the two cyanobacteria species while *Diacyclops* is associated with *Stephanodiscus* diatoms.

Similarly, Lake Monona's phytoplankton community is driven from the top down by *D. pulicaria*, *Diacyclops*, *Mesocyclops*, and *D. retrocurva* (Appendix Fig. 2b, Table 1). Interestingly in Lake Monona, the relatively uncommon *D. retrocurva* plays opposite to *D. pulicaria*, associated with *Stephanodiscus* while *D. pulicaria* is associated with *Aphanizomenon* along the second principal component.

The zooplankton drivers of the phytoplankton community do not change considerably with the spiny water flea invasion, with the exception of Lake Mendota where only *D. pulicaria* plays a significant role in structuring the phytoplankton community (Appendix Table 1).

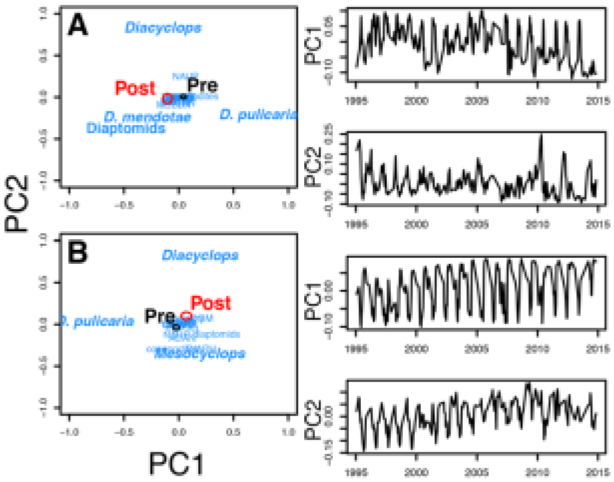
Change in phytoplankton community composition over two time periods

We find no significant changes in the structure or drivers of the Lake Monona phytoplankton community (Appendix Table 1; Appendix Figure 3C and 3D). In Lake Mendota, Microcystis and Cryptomonas became relatively less important in structuring the phytoplankton community (Appendix Figure 3A and 3B). Also, the only significant zooplankton driver of phytoplankton community composition in Lake Mendota post-2009 was *D. pulicaria* relative to four additional zooplankton species pre-2009 (Appendix Table 1).

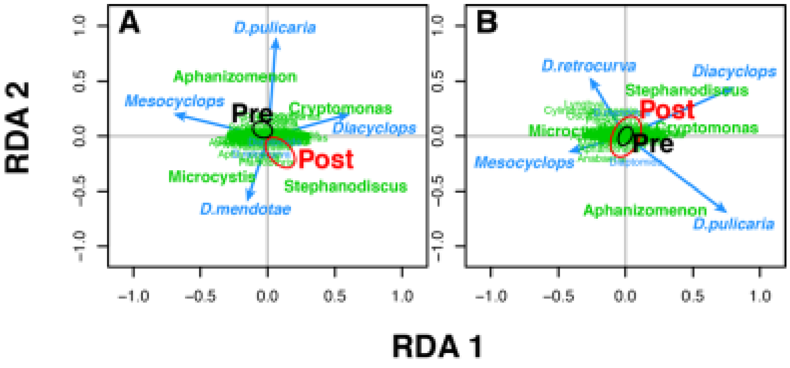
The significant changes with 2009 do not affect the general results of the manuscript as *D. pulicaria* remains a primary driver of phytoplankton community composition and diatoms and cyanobacteria remain the dominant phytoplankton groups.

Appendix Table 1. Phytoplankton community loadings onto grazer vectors – role of grazers in structuring phytoplankton community

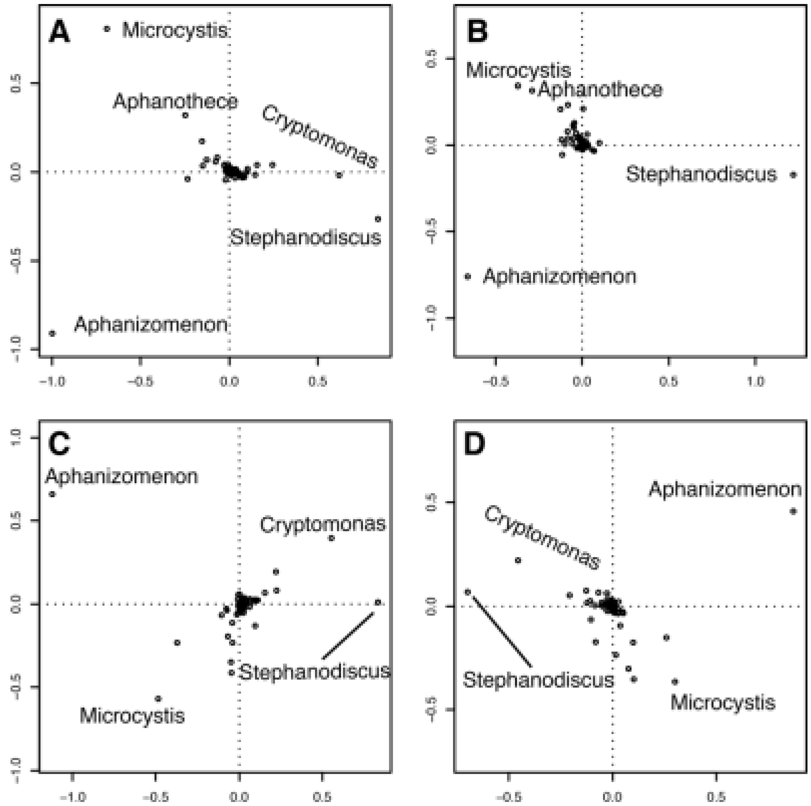
	Pre-2009				**Post-2009**			
	PC1	PC2	R^2	p	PC1	PC2	R^2	p
Mendota								
DGM	**-0.55**	**0.84**	**0.06**	**0.002**	-0.55	0.84	0.02	0.47
DPUL	**0.03**	**-0.99**	**0.15**	**0.001**	**-0.76**	**-0.65**	**0.10**	**0.03**
DRET	-0.76	0.65	0.02	0.23	-0.14	-0.99	0.02	0.58
DITHM	**0.86**	**-0.50**	**0.12**	**0.001**	0.73	-0.68	0.01	0.58
MEEDX	**-0.99**	**0.10**	**0.24**	**0.001**	-0.99	-0.14	0.01	0.72
DIAPT	**-0.18**	**-0.98**	**0.04**	**0.03**	-0.36	0.93	0.01	0.75
Monona								
DGM	0.09	-0.99	0.01	0.32	-0.98	0.16	0.06	0.26
DPUL	**-0.02**	**0.99**	**0.33**	**0.001**	**-0.15**	**0.99**	**0.49**	**0.001**
DRET	**0.13**	**-0.99**	**0.10**	**0.001**	**0.18**	**-0.99**	**0.55**	**0.001**
DITHM	**0.81**	**0.58**	**0.24**	**0.001**	**-0.62**	**0.78**	**0.18**	**0.01**
MEEDX	**-0.55**	**-0.83**	**0.16**	**0.001**	**0.83**	**-0.55**	**0.20**	**0.006**
DIAPT	-0.09	0.99	0.01	0.48	0.59	0.81	0.09	0.10



Appendix Figure 1. Principal component analyses for Lake Mendota (A) and Lake Monona (B) zooplankton communities are plotted in PCA space. Species centroids are plotted in blue text with significant drivers of zooplankton community composition identified with a larger font. Pre- (black text and oval) and post-2009 (red text and oval) community centroids are plotted as ovals representing 95% confidence intervals for the centroids. Each of the two first principal components are plotted through time to observe long-term change in each lakes' zooplankton community.



Appendix Figure 2. Plankton communities of Lake Mendota (A) and Lake Monona (B) ordination using redundancy analysis. The phytoplankton community (green) is plotted with effects of different algae grazing zooplankton (blue text; blue vectors and larger text represent significant drivers). Distance from the origin represent more important phytoplankton species or stronger effects in the case of vectors of zooplankton species. Pre- (black) and post-*Bythotrephes* (red) invasion centroids are plotted with 95% confidence intervals (ovals). Note that ovals overlap for Lake Monona (no significant invasion effect in the phytoplankton community) but do not for Lake Mendota (significant invasion effect).



Appendix Figure 3. Phytoplankton community PCA for pre-2009 Lake Mendota (A), post-2009 Lake Mendota (B), pre-2009 Lake Monona (C), and post-2009 Lake Monona (D). Species centroids are included as open circles and important genera are labeled.

Appendix 1 – Warming and *Bythotrephes* impact

Conclusion: *Bythotrephes* effect on *Daphnia* and water clarity may be mediated by lake surface temperature.

Background: In Chapter 2 we found that *Bythotrephes* drove a 60% decline in Lake Mendota's *Daphnia pulicaria* biomass which lead to a loss of nearly 1 m of water clarity in the lake. However, in Chapter 1 we found that *Bythotrephes* struggles through hot years (e.g. 2010 – 2012). Here, we investigate whether the population collapse of *Bythotrephes* due to summer surface temperatures exceeding its thermal optimum had any effect on *Daphnia pulicaria* biomass in the lake.

Approach: I plotted relationships among mean July air temperature, mean *Bythotrephes* abundance in the summer (e.g. during peak surface water temperatures), and mean *D. pulicaria* abundance in the following spring, when its grazing brings in the spring clear water phase. *D. pulicaria* abundance is likely to be low when *Bythotrephes* is abundant in the fall, but if *D. pulicaria* can maintain higher densities through the summer, it may have a better chance at successfully overwintering.

Results & Discussion: We find that summer *Bythotrephes* abundance is negatively correlated with mean July air temperature (Fig. 1A). Furthermore, high *Bythotrephes* abundance in the summer appears to drive low *D. pulicaria* abundance in the following spring (Fig. 1B). Because of this, *D. pulicaria* may be more successful in the spring following hot summers (Fig. 1C). Warm summers in 2011 and 2012 were particularly harsh on the *Bythotrephes* population, which may have driven higher *D. pulicaria* abundance in 2012 and 2013, respectively.

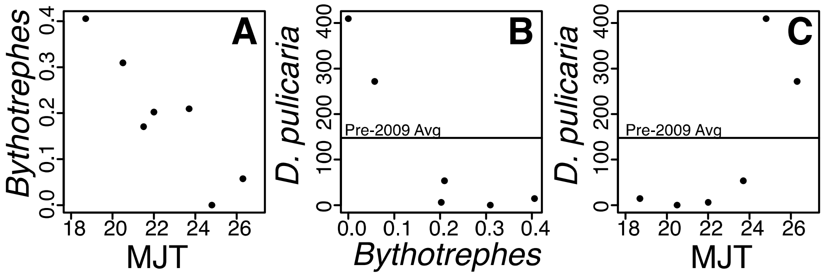


Figure 1. A – Summer *Bythotrephes* abundance is plotted against mean July air temperature (°C; MJT). B – *D. pulicaria* abundance the following spring is plotted against summer *Bythotrephes* abundance with the pre-2009 *D. pulicaria* abundance represented by a horizontal line. C – *D. pulicaria* abundance is plotted against mean July air temperature. The two points above pre-2009 *D. pulicaria* mean abundance were the springs of 2012 and 2013 following high MJT and low *Bythotrephes* abundance in the summer of 2011 and 2012.

Implications: Climate warming may mediate *Bythotrephes* impact on *D. pulicaria*. However, *D. pulicaria* is also a cool water zooplankton and though it was more successful under warm years that drove down *Bythotrephes* abundance, this may also have implications for the long-term persistence of *D. pulicaria* in Lake Mendota.

Appendix 2 – Mapping *Bythotrephes* sleeper cells onto North America

Conclusion: Generalizing and scaling up the population model from Ch. 1 could be a useful component of modeling *Bythotrephes*' ecological niche.

Background: In Ch. 1, I show how the population model can be used generally as a potential way to evaluate *Bythotrephes*' thermal niche. Here I provide more detail on that process.

Methods: I use mean July air temperature to model surface water temperatures (MJT) in lakes following the methods outlined in Sharma et al. (2007). Because MJT is widely available through WorldClim along with MJT under climate change scenarios, I can map *Bythotrephes* population dynamics onto theoretical lakes (coordinates with corresponding MJT) across North America using single-year simulations of my model. Specifically, I can use the model to predict where sleeper cells might occur in North America. A sleeper cell is any theoretical lake that would yield near-zero growth in the egg bank under mean climate conditions but large positive growth under cool year conditions (like Lake Mendota).

Results & Discussion: Doing this reveals a band of potential sleeper cells across North America that shifts northward under climate change scenarios (Fig. 1). The model accurately predicts sleeper cell dynamics in both Lake Mendota and Mille Lacs Lake, MN where *Bythotrephes* was detected in 2009 (Fig. 1 and Fig. 2). Note that, even under the mildest warming scenario (blue area), the modeled population of *Bythotrephes* is unlikely to persist in Lake Mendota (i.e. the southern edge of the band of sleeper cells delineates where annual egg bank growth is consistently negative rather than neutral).

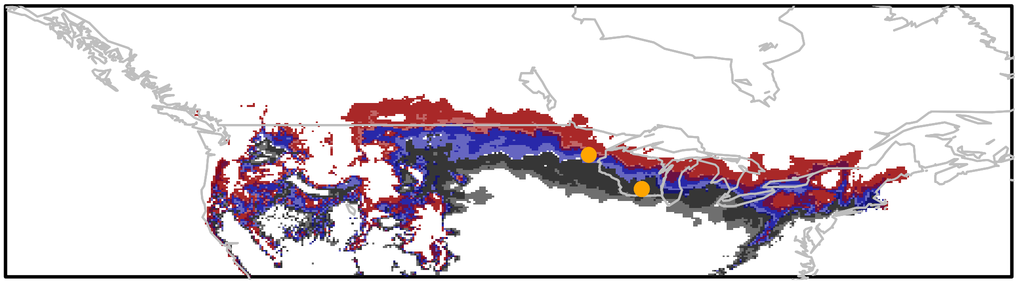


Figure 1. Current climate conditions that may produce sleeper cells in lakes are mapped in black. Note the location of the two 2009 detections (orange circles) Lake Mendota and Mille Lacs Lake, MN. This band of sleeper cells moves northward under mild (blue) and extreme (red) climate scenarios in 2050.

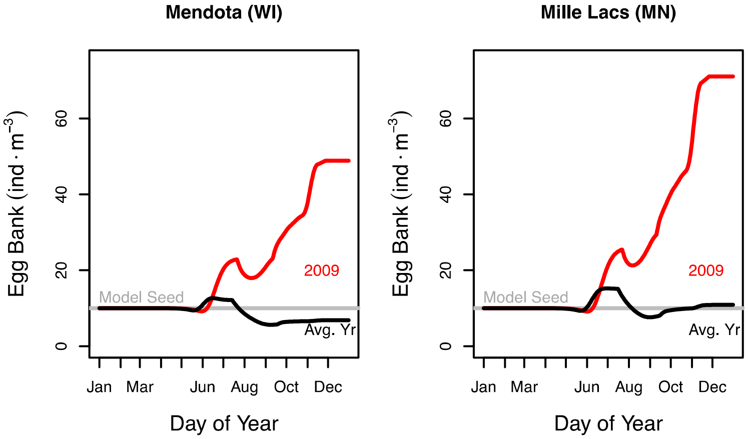


Figure 2. Within-year dynamics of modeled growth in the egg bank under mean (black line) and 2009 (red line) thermal conditions. Model seed of 10 eggs m^{-3} is presented in a horizontal grey line. In reality, the Mille Lacs Lake population is less abundant than the Lake Mendota

population highlighting the importance of biological factors in driving *Bythotrephes* carrying capacity after temperature is no longer limiting.

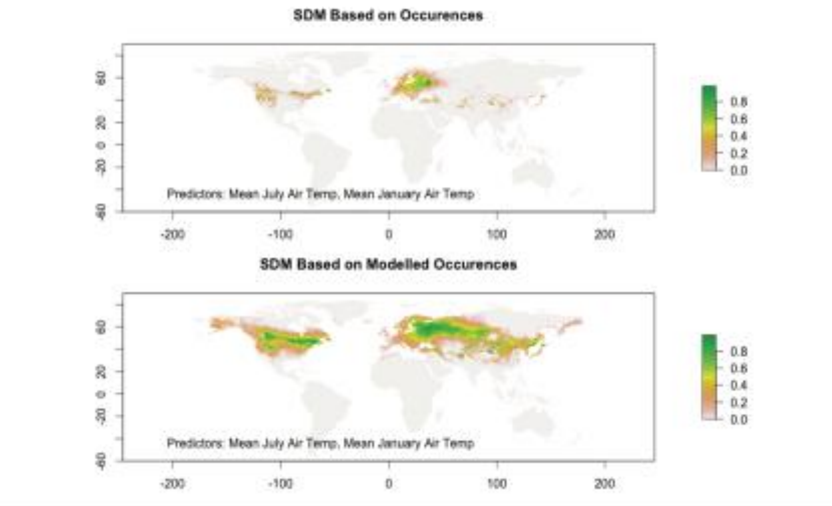


Figure 3. The population model reveals potential bias based on limited observations in a simple species distribution modeling exercise. In the top plot, *Bythotrephes* distribution is modeled from known native and invasive occurrences based on simple climate predictors. In the bottom plot, *Bythotrephes* distribution is modeled using the same climate predictors but instead using predicted occurrences from the population model. While neither model is practically useful, the surface area in the predictions based on potentially suitable thermal habitat (i.e. modeled occurrences) is significantly larger than the surface area in the predictions based on observed occurrences.

Implications: This represents a highly useful tool. Also, *Bythotrephes* population dynamics are likely to change with changing climate within invaded systems. Though Figure 3 is based on an overly simplified analysis, it shows the potential of using the population model to better evaluate *Bythotrephes* niche and avoid biases of presence based modeling.

Appendix 3 – Invasive invertebrate predator, *Bythotrephes longimanus*, unravels a trophic cascade

In review at *Limnology & Oceanography Letters*

Co-Author: M. Jake Vander Zanden

Manuscript

Significance

Manipulating food webs to improve water quality is an important lake management tool. Our work reveals how lake biomanipulation may facilitate invasive invertebrate predators that can interfere with beneficial cascading effects on water quality; making lakes more vulnerable to the harmful effects of eutrophication. We find that the invasive spiny water flea unraveled the "textbook" Lake Mendota biomanipulation through predation on the herbivorous *Daphnia pulicaria*, uncovering a possible vulnerability of manipulated ecosystems to invasive predatory invertebrates. We highlight their importance in water quality management, and propose that biomanipulated ecosystems should be targets of invasion prevention efforts to protect water quality.

Abstract

In an era of global environmental change, freshwater ecosystems are subjected to a diverse set of stressors that complicate their management - chief among these are eutrophication and biological invasion. Manipulating lake food webs to improve water quality (i.e., biomanipulation) is well-studied but we must better understand the roles of eutrophication and invasion to ensure sustained improvements. We investigate the invasion of the spiny water flea (*Bythotrephes longimanus*) into Lake Mendota, WI (USA), the site of a textbook success story in biomanipulation. In 1987, piscivores were stocked to decrease zooplanktivore consumption of *Daphnia pulicaria*—an herbivorous zooplankton that supports clear water. Here, we estimate that *Bythotrephes* increased potential consumption of zooplankton fivefold. Further, *D. pulicaria* dominance and water clarity decreased with increasing zooplanktivory, highlighting *Bythotrephes* cascading impact. Our results reveal how a manipulated food web under stress of nutrient loading can be vulnerable to adverse impacts by invasive invertebrate predators.

Keywords: invasive species, trophic cascade, eutrophication, biomanipulation, *Daphnia*, *Bythotrephes*

Introduction

Efforts to manage aquatic ecosystems, and water quality in particular, must increasingly consider the broader context of ongoing habitat degradation and global environmental change (Strayer 2010, Carpenter et al. 2011). For example, anthropogenic disturbance is thought to increase the susceptibility of ecosystems to the establishment and impact of invasive species (MacDougall and Turkington 2005, Light and Marchetti 2007, Johnson et al. 2008, Vander Zanden et al. 2016), and invasive species can negatively influence water quality (e.g., Walsh et al. 2016). Understanding the interactions between our efforts to manage ecosystems, and factors such as changing climate and invasive species represents a key challenge for environmental management in the coming decades (Carpenter et al. 2011).

Water quality in eutrophic lakes is sometimes managed by manipulating cascading food web interactions, with the intent of controlling phytoplankton biomass (i.e., biomanipulation; Fig. 1). For example, herbivorous zooplankton may be released from predation by the removal of zooplanktivorous fishes or the addition of piscivorous fishes (Hansson et al. 1998, Bernes et al. 2015). Herbivorous zooplankton are then able to improve water quality from the top-down. In such cases, predatory invertebrates can interfere with the positive top-down effects of manipulation and dampen the strength of trophic cascades (MacKay and Elser 1998, Shurin et al. 2002). Despite this, relatively little attention has been paid to invasive invertebrate predators and their potential to interfere with cascading interactions in biomanipulated lakes (but see Ketelaars et al. 1999, Ellis et al. 2011).

To illustrate this concept, we present the case of the invasion of the predatory invertebrate, *Bythotrephes longimanus*, spiny water flea, into eutrophic Lake Mendota, WI

(USA). In the 1980s, piscivores were stocked in Lake Mendota in an effort to manipulate cascading food web interactions to ultimately increase water clarity. The project was a strong example of the use of biomanipulation as a water quality management tool (Kitchell 1992, Kalff 2002). Reduced zooplanktivory following piscivore stocking established *Daphnia pulicaria* as the lake's dominant grazer, improving water clarity by over 1 m (Lathrop et al. 2002). Despite decades of implementing best management practices to reduce agricultural runoff into the lake, the biomanipulation remains the single most effective tool to manage water clarity in Lake Mendota (Carpenter and Lathrop 2013).

The invasion of the predatory *Bythotrephes* into Lake Mendota in 2009 coincided with a 60% decline in *D. pulicaria*, and a nearly 1m decline in lake water clarity, incurring economic damages estimated at over US$100 million (Walsh et al. 2016). *Bythotrephes* is known as a voracious zooplanktivore (Bunnell et al. 2011), however this was the first report of such a strong cascading effect (first suggested in Strecker and Arnott 2008).

We examine how Lake Mendota's management history may have enhanced the cascading impact of the invasive *Bythotrephes* on the Lake Mendota food web. We evaluate the potential contribution of *Bythotrephes* to total zooplanktivory in Lake Mendota and demonstrate the mechanism by which *Bythotrephes* unraveled a trophic cascade that provided improved water quality for two decades. Our work also raises the possibility that eutrophic lakes that are managed through cascading trophic interactions may be uniquely vulnerable to invasive invertebrate predators such as *Bythotrephes*. Further, this reveals how ongoing habitat degradation, management efforts, and invasions, interact to yield novel management challenges.

Methods

Study Site and Species

Lake Mendota (39.6 km^2 area, 25.3 m max depth, and 12.7 m mean depth) is a culturally eutrophic lake adjacent to Madison, WI, USA. *D. pulicaria* and, in turn, water quality benefitted from the lake biomanipulation in the late 1980s whereby managers stocked the lake with piscivorous fishes and enacted strict regulation on their harvest. This, coupled with a massive die-off of zooplanktivorous cisco (*Coregonus artedi*; ~90% reduction in biomass in 1987), resulted in a 76% reduction in the biomass of zooplanktivorous fishes (Fig. 1A to Fig. 1B; Rudstam et al. 1993, Johnson and Kitchell 1996, Lathrop et al. 2002). Prior to *Bythotrephes* detection in 2009, the *Daphnia* community was dominated by *D. pulicaria* and, to a lesser extent, *D. galeata mendotae*, a smaller and less efficient grazer.

The lake's dominant zooplanktivorous fishes are yellow perch (*Perca flavescens*), white bass (*Morone chrysops*), and cisco, though cisco have been rare in the past three decades. The diets of adult yellow perch, white bass, and cisco are comprised of 77%, 74%, and 94% *Daphnia*, respectively, with no clear shifts to larger prey with age or size (Johnson and Kitchell 1996). Young-of-year cisco are large enough to consume primarily *Daphnia* by early summer, and white bass and yellow perch grow large enough to do so by late summer. The lake also has two predatory zooplankton, the invasive *Bythotrephes* and the native *Leptodora kindtii*. While the predatory invertebrate *Chaoborus* is present in the lake, they are exceedingly rare and unlikely to contribute to total zooplanktivory.

Long-term data

We obtained long-term (2005 – 2014) data of lake temperature profiles, fish abundance, lengths, and weights, zooplankton abundance and length, and phytoplankton biomass (available through 2013) from the North Temperate Lakes Long-Term Ecological Research program (NTL-LTER; link included in citation). Phytoplankton were divided into inedible (cyanobacteria) and edible (most diatoms, green algae, golden algae, and cryptomonads) taxa. We use re-transformed log-mean annual Secchi depth (NTL-LTER) as a measure of water clarity in Lake Mendota. Lakewide pelagic fish density is estimated in mid-summer by sonar runs using an HTI Model 241 echosounder with 120 kHz split beam configuration. Signals are interpreted using HTI sounder software v. 1.0, allowing for species-specific estimates of lakewide abundance and biomass (NTL-LTER).

Zooplanktivore consumption rates

To calculate an index of zooplanktivory in Lake Mendota, we estimate the maximum potential consumption of each zooplanktivorous fish and invertebrate taxa at daily time steps from 2005 to 2014. This approach contrasts with the typical use of consumption models in studies which estimate actual consumption rates by fitting the proportion of maximum potential consumption necessary to achieve observed growth rates. Notably, this proportion is often low (Armstrong and Schindler 2011). Therefore, the rates we report using maximum potential consumption rates alone are likely overestimated for each zooplanktivore. However, we were interested in the potential of each zooplanktivore to consume *Daphnia*, which, most importantly, allows us to directly compare predatory invertebrates and fishes. Thus, we did not require the extra information from estimates of actual consumption rates that might introduce additional sources of measurement error as well as additional model assumptions. We estimated daily potential consumption rates by zooplanktivorous fishes in Lake Mendota using the following general bioenergetics formula:

$$C_{max} = a \cdot W^{b} \cdot F(T) \cdot N$$

Where C_{max} is maximum potential daily consumption (hereafter, “zooplanktivory”, expressed as potential consumption of zooplankton biomass in g m^{-2} d^{-1}), a and b are a fitted intercept and coefficient (Table 1), respectively, W is the annual median weight (g), and N is abundance. We scale C_{max} to the entire population by multiplying mean individual C_{max} by N. $F(T)$ is a temperature-dependent function with the general shape involving a linear increase in consumption rate with temperature until an optimal temperature is reached, then a rapid decline as temperature increases further. Additional species-specific methods, equations, and parameters for estimating C_{max} are outlined in Table 1. Individual *Leptodora* were estimated to consume half their body weight per day (Table 1; Lunte and Luecke 1990). *Bythotrephes* consumption was estimated according to Bunnell et al. (2011) and Yurista et al. (2010) whereby instar stage consumption rates are fitted to second-order polynomial functions of temperature. We use the proportion of each instar stage present in net tows to estimate the contribution of each stage (P_i) to total consumption by *Bythotrephes*. For all zooplanktivores, daily zooplanktivory rates are summed across the entire year to obtain annual rates (lakewide tonnes yr^{-1}). All statistics and analyses are conducted in R (R Core Team 2014).

Results

Lakewide annual potential zooplanktivory in Lake Mendota increased from a pre-2009 average of 400 tonnes yr^{-1} to over 2,800 tonnes yr^{-1} with the *Bythotrephes* invasion. This was largely due to additional zooplanktivory by *Bythotrephes* (mean zooplanktivory of over 1,500 tonnes yr^{-1}), however mean zooplanktivory by fishes also increased to over 1,300 tonnes yr^{-1} after 2009 (Fig. 2A). The increase in fish zooplanktivory was due to a large population of white bass from 2010 – 2011 (62 kg ha^{-1} and 23 kg ha^{-1} biomass, respectively) and a large population of yellow perch in 2014 (74 kg ha^{-1} biomass) (Fig. 2A). Cisco and *Leptodora* contributed very little to total zooplanktivory in the lake (Fig. 2A). Annual zooplanktivory of *Bythotrephes* and fishes were weakly positively correlated over 2009 - 2014 (Fig. 3B; Pearson's r = 0.67, p = 0.14; slope = 1.2, s.e. = 0.65; intercept = -470, s.e. = 1000).

Potential daily consumption rates of zooplankton shifted from 0.014 g m^{-2} d^{-1} (re-transformed log-mean; 0.0014 – 0.12 g m^{-2} d^{-1} log-normal 95% CI) to 0.073 g m^{-2} d^{-1} (0.0035 – 0.95 g m^{-2} d^{-1} log-normal 95% CI) after 2009. Further, potential daily consumption rates never exceeded 0.15 g m^{-2} d^{-1} from 2005 to 2008, but exceed published thresholds for *Daphnia* tolerance (*Daphnia pulicaria* is rare at zooplanktivory rates higher than 0.9 g m^{-2} d^{-1}; Johnson and Kitchell 1996) on 3% of all days after *Bythotrephes* 2009 detection (Fig. 2B). Daily *Bythotrephes* consumption was often highest in the fall which is offset from zooplanktivory by native fishes, which peaks in the mid-summer, thus extending the season of high total zooplanktivory (Fig. 2B; Fig. 3A).

Annual and daily potential zooplanktivory rates were exceptionally high in 2014. Total annual zooplanktivory was nearly 6,000 tonnes, with daily zooplanktivory rates peaking at 1.7 g m^{-2} d^{-1} (1.5 g m^{-2} d^{-1} due to *Bythotrephes*). In fact, zooplanktivory exceeded 0.38 g m^{-2} d^{-1} from 3

June – 12 December for a total of 191 days. The entire *Daphnia* community collapsed below detection limits on 2 September 2014. The collapse persisted through 12 May 2015, when *Daphnia* densities rose back above detection limits (red shaded area Fig. 2B).

The percent of *D. pulicaria* in the *Daphnia* community decreased logistically with total zooplanktivory (*sensu* Johnson and Kitchell 1996; Fig. 4B; $y = a/(1+b*e^{cx})$; residual s.e. = 0.025, df = 7; a = 0.90, s.e. = 0.01; b = 7.0×10^{-8}, s.e. = 4.0×10^{-7}; c = 0.0056, s.e. = 0.0019). Using the fitted function, *D. pulicaria* comprise over half of the *Daphnia* community when zooplanktivory is less than 2,900 tonnes yr^{-1}. The %*D. pulicaria* in the whole zooplankton community of Lake Mendota decreased exponentially with increasing zooplanktivory (Fig. 4B; $y = a*e^{b}$; residual s.e. = 0.047, df = 8; a = 0.27, s.e. = 0.04; b = -0.00054, s.e. = 0.00015). The percent of edible to total phytoplankton biomass increased linearly with zooplanktivory (Fig. 4C; $R^2 = 0.84$, p = 0.0004, F = 37.85, df = 7; slope = 0.0067, s.e. = 0.001; intercept = 1.92, s.e. = 1.93) and, accordingly, re-transformed log-mean annual water clarity decreased linearly with increasing zooplanktivory (Fig. 4D; $R^2 = 0.61$, p = 0.0076, F = 12.54, df = 8; slope = -2.1×10^{-4}, s.e. = 6.0×10^{-5}; intercept = 3.2, s.e. = 1.5).

Discussion

The invasion of Lake Mendota by *Bythotrephes* corresponded with large declines in *D. pulicaria* and water clarity (Walsh et al. 2016) – unraveling many of the gains of the whole-lake biomanipulation of the 1980s (Lathrop et al. 2002). We found that *Bythotrephes* was the largest contributor to total zooplanktivory in the lake, combining with zooplanktivory by native fishes to match daily rates observed prior to the whole-lake biomanipulation (e.g., Johnson and

Kitchell 1996). We also found that elevated zooplanktivory had a cascading effect on herbivorous zooplankton, phytoplankton, and water clarity. Further, this cascade exacerbated the harmful effects of eutrophication, revealing multiple benefits of preventing such invasions in lakes like Mendota and of reducing nutrient loading into lakes. Finally, we report a management implication of this study: high annual zooplanktivory by fishes did not control *Bythotrephes* over the course of the study despite the fact that consumption by fishes includes *Bythotrephes*.

Bythotrephes dramatically elevated total zooplanktivory in Lake Mendota by extending the period of peak zooplanktivory into the fall. There was little seasonal overlap between zooplanktivory by *Bythotrephes* and zooplanktivory by the warm-water white bass and yellow perch that consume the most in the summer. This contrasts with the warm-water native predatory invertebrate *L. kindtii*; peak productivity of *L. kindtii* is more likely to overlap with peak zooplanktivory by native warm-water fishes as both occur in the summer (Lunte and Luecke 1990). Fall zooplanktivory by *Bythotrephes* offers *Daphnia* little to no reprieve after peak summer zooplanktivory by yellow perch and white bass. Zooplanktivory by *Bythotrephes* quickly succeeds peak zooplanktivory by fishes in years with high summer fish zooplanktivory (e.g., 2010, 2011, 2012, and 2014; Fig. 2B) while *Bythotrephes* makes up a significant portion of both summer and fall zooplanktivory in years with lower summer zooplanktivory by fishes (e.g., 2009 and 2013; Fig. 2B). In this way, *Bythotrephes* “fills the gaps” left by poor fish year classes and by the natural decline in warm-water fish zooplanktivory during the fall.

When total zooplanktivory was high (>2,900 tonnes yr^{-1}), *D. pulicaria* made up less than half of the *Daphnia* community by abundance (Fig. 4A) and relative *D. pulicaria* abundance drops precipitously with increased zooplanktivory. However, the relative contribution of *D. pulicaria* to the entire zooplankton community declined exponentially with total zooplanktivory (Fig. 4B). This effect on *D. pulicaria* appears to cascade to the phytoplankton, influencing both the biomass of edible phytoplankton relative to all phytoplankton (Fig. 4C) and water clarity (Fig. 4D). This cascade is consistent with the historical understanding of the role of zooplanktivory in governing lake plankton dynamics and water quality (Lathrop et al. 2002). Our findings build on this understanding and further demonstrate the importance of invertebrate predators in determining total zooplanktivory and, in turn, water quality (as in Ellis et al. 2011).

Zooplanktivorous fishes prey on both *Bythotrephes* and other zooplankton, like *Daphnia*. As a result, predation pressure on *Daphnia* from both *Bythotrephes* and zooplanktivorous fishes may not be completely additive. For example, *Bythotrephes* comprised 46% of yellow perch diets in Lake Mendota in July and August of 2011, 2012, and 2013 (*unpublished data*), and can comprise as much as 80% when *Bythotrephes* is even moderately abundant (34 individuals m^{-3} in July 2011 compared to 13 individuals m^{-3} in July and August log-average; *unpublished data*). However, we note that predation by zooplanktivorous fishes peaks in mid-summer and predation by *Bythotrephes* peaks in fall (Fig. 2B). Little overlap within years (Fig. 3A) likely limits zooplanktivorous fishes' capacity to ease *Bythotrephes* impact on *D. pulicaria* (e.g., no negative correlation in Fig. 3B).

High consumption rates by *Bythotrephes* and all fishes led to compounding negative impacts on *D. pulicaria*. *Bythotrephes'* effect was synergistic with zooplanktivorous fishes in years where zooplanktivory from both sources were high (e.g., 2010, 2011, and 2014), resulting in historically low levels of *D. pulicaria* (33%, 33%, and 6% in the *Daphnia*, respectively). In post-

2009 years where just zooplanktivory by *Bythotrephes* was high (e.g., 2009, 2012, and 2013), *D. pulicaria* dominance was largely unaffected by total zooplanktivory (88%, 90%, and 88% in the *Daphnia*, respectively). In fact, 2014 was the highest year of zooplanktivory for both *Bythotrephes* and yellow perch. Therefore, it is unsurprising that the entire *Daphnia* community collapsed for the first time in over 25 years (Lathrop et al. 2002) that fall. Further, water clarity was 0.5 m higher in low zooplanktivory years (2.8 m in 2009, 2012, and 2013 versus 2.3 m in 2010, 2011, and 2014, and 3.3 m from 1995 - 2008). Interestingly, both 2010 and 2011 are nearly identical in total zooplanktivory (just over 3,000 tonnes yr^{-1}) and *D. pulicaria* dominance (33%), but vary in the relative contributions of zooplanktivores to zooplanktivory (primarily white bass in 2010 and primarily *Bythotrephes* in 2011). Further research should investigate the role of zooplanktivore identity, as the seasonal timing and intensity of zooplanktivory is critical to *Daphnia* community dynamics (Johnson and Kitchell 1996).

The dominant zooplanktivorous fishes of Lake Mendota have not controlled *Bythotrephes*. Therefore, our findings suggest that simply increasing zooplanktivorous fish populations is not likely to control *Bythotrephes* and stabilize *D. pulicaria*. However, successful examples of such efforts have been reported (e.g., Wissel et al. 2000). Notably, cool-water zooplanktivorous fishes (e.g., cisco; Coulas et al. 1998) or fishes with more efficient feeding methods (e.g., pumpkinseed and bluegill; LeDuc et al. *Submitted*) may be more successful in controlling *Bythotrephes*. However, these fishes would likely also prey on *D. pulicaria* and potentially harm water quality, as in the case of cisco (Johnson and Kitchell 1996). Additional research should investigate whether additional zooplanktivory by fishes would mitigate or compound *Bythotrephes* effect on *D. pulicaria*.

Ecological degradation is thought to increase ecosystem vulnerability to nonnative species establishment and impact (MacDougall and Turkington 2005, Light and Marchetti 2007, Johnson et al. 2008, Vander Zanden et al. 2016). For example, cultural eutrophication in Lake Mendota was managed through biomanipulation (Lathrop et al. 2002). With the biomanipulation, the biomass of zooplanktivorous fishes declined and the biomass of large zooplankton like *D. pulicaria* increased (Johnson and Kitchell 1996). *Bythotrephes*' range expansion and establishment is limited by biological factors like predator abundance and prey availability (Young et al. 2011); as such the Lake Mendota biomanipulation may have changed the food web to favor *Bythotrephes*. *Bythotrephes* has reached higher densities in Lake Mendota than any other system in its native or invaded range (e.g., Jokela et al. 2011, Young et al. 2011). It is possible that the food web structure brought by biomanipulation of Lake Mendota contributed to the establishment and elevated abundance of *Bythotrephes*.

Furthermore, Lake Mendota is the first reported case of *Bythotrephes*' impact cascading through *Daphnia* decline into lake water clarity (Walsh et al. 2016). *Bythotrephes* invaded range has been limited to less productive lakes that are not subject to the same degree of cultural eutrophication as Lake Mendota (Strecker and Arnott 2008). As *Bythotrephes* expands into lakes in highly agricultural watersheds, additional research should investigate the interactions among eutrophication, *D. pulicaria* grazing, and *Bythotrephes* zooplanktivory. Further, if cultural eutrophication is a key factor driving *Bythotrephes*' impact, lakes like Mendota should be targets of invasion prevention efforts to avoid such drastic and expensive impacts in the future. Likewise, efforts to reduce nutrient loading into lakes should offset *Bythotrephes* impact on water quality (Walsh et al. 2016). The *Bythotrephes* invasion into eutrophic Lake Mendota highlights the need to research how food webs and nutrients interact to influence vulnerability to invasion and impacts.

Conclusion

Our work documenting the *Bythotrephes* invasion of Lake Mendota reveals the potential role of invasive invertebrate predators in interfering with trophic cascades in lakes. Furthermore, it demonstrates how a manipulated food web can be vulnerable to such impacts. The biomanipulation that favored *D. pulicaria* provided the only documented improvement to water quality in Lake Mendota and the predatory *Bythotrephes* was positioned to undo these improvements. We show that invasions can interfere with top-down cascading effects in food web management. This interference has costly implications for managed ecosystem services and such vulnerable ecosystems should be high-priority targets of invasion prevention efforts.

Acknowledgements

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Table & Figure Legends

Table 1. Bioenergetics modeling of **C_{max}** in zooplanktivore populations in Lake Mendota. **C_{max}** of each fish is modeled by equation 1 in the text where F(T) is a temperature dependent function outlined in the accompanying citations (relevant parameters included here). *Bythotrephes* and *Leptodora* consumption rates are modeled through different approaches outlined in the text here and in the accompanying citations. **C_{max}** of *Leptodora* is the only model that does not depend on temperature.

Figure 1. Panels depict the Lake Mendota food web before (A) and after (B) the whole-lake biomanipulation in 1987, as well as after the detection of *Bythtorephes* in 2009 (C). Arrows represent zooplanktivory on *Daphnia pulicaria* after *Bythotrephes* invasion as well as zooplanktivory of native fishes on *Bythotrephes*. Species boxes change in size in response to management (A to B) and invasion (B to C) to reflect changes in biomass.

Figure 2. A - Total annual zooplanktivory in Lake Mendota in the past decade (fishes in shades of blue and zooplankton in shades of red). B - Daily maximum consumption or zooplanktivory estimates for *Bythotrephes* (red) and native planktivorous fishes (blue) are stacked. The *D. pulicaria* population density time series is overlaid in grey and the 2014 *Daphnia spp.* collapse is denoted by the vertical light red shaded area (continues through May 2015).

Figure 3. The relationship between zooplanktivory by *Bythotrephes* and zooplanktivorous fishes at daily (A) and annual (B) time steps. 2014 is highlighted in red in both timescales.

Figure 4. Cascading relationships between annual zooplanktivory, *D. pulicaria* (dominance in the A - *Daphnia* and B – zooplankton), and the phytoplankton community (C - % edible phytoplankton biomass; D – water clarity). Solid dark grey circles represent pre-*Bythotrephes* years (2005 – 2008) and solid red diamonds represent post-*Bythotrephes* years (2009 – 2014). The black line represents a regression of variables fitted to annual zooplanktivory (A – three-parameter logistic curve *sensu* Johnson and Kitchell 1996, B – exponential decay curve, and C, D – linear). Note that 2010 and 2011 have nearly identical total zooplanktivory (just over 3,000 tonnes yr^{-1}) and % *D. pulicaria* (33%) and, as a result, overlap in (A). Also, 2014 data was not available for phytoplankton biomass in (C).

Tables & Figures

Table 1.

<table>
<tr><th>Species</th><th>Relevant Equations and Parameter Values</th><th>Citation</th></tr>
<tr><td>Yellow perch
(<i>Perca flavescens</i>)</td><td>$a = 0.25$, $b = -0.27$, $T_{opt} = 23°C$, $T_{max} = 28°C$, $Q = 2.3$</td><td>Kitchell et al. 1977,
Post 1990</td></tr>
<tr><td>White bass
(<i>Morone chrysops</i>)</td><td>$a = 0.60$, $b = -0.25$, $T_{opt} = 28°C$, $T_{max} = 31°C$, $Q = 2.9$</td><td>Johnson 1993</td></tr>
<tr><td>Cisco
(<i>Coregonus artedi</i>)</td><td>$a = 1.6$, $b = -0.54$, $T_{opt} = 17°C$, $T_{max} = 26°C$, $Q = 3.5$</td><td>Rudstam et al. 1994</td></tr>
<tr><td><i>Leptodora kindtii</i></td><td>$C_{max} = 0.5 * W * N$</td><td>Lunte and Luecke 1990</td></tr>
<tr><td><i>Bythotrephes longimanus</i></td><td>

$$C_{max} = \sum_{i=1}^{3} P_i \cdot N \cdot (a_i + b_i \cdot T + c_i \cdot T^2 + d_i \cdot W_i + e_i \cdot T \cdot W)$$

Where i = instar stage and P = proportion of population represented by instar stage, i.

<table>
<tr><th></th><th>P_i</th><th>a_i</th><th>b_i</th><th>c_i</th><th>d_i</th><th>e_i</th></tr>
<tr><td>Stage 1</td><td>0.26</td><td>22</td><td>-1.9</td><td>0.09</td><td>-0.18</td><td>0.07</td></tr>
<tr><td>Stage 2</td><td>0.26</td><td>70</td><td>-6.6</td><td>0.30</td><td>-0.20</td><td>0.07</td></tr>
<tr><td>Stage 3</td><td>0.48</td><td>74</td><td>-5.9</td><td>0.32</td><td>-0.14</td><td>0.05</td></tr>
</table>

</td><td>Yurista et al. 2010,
Bunnell et al. 2011</td></tr>
</table>

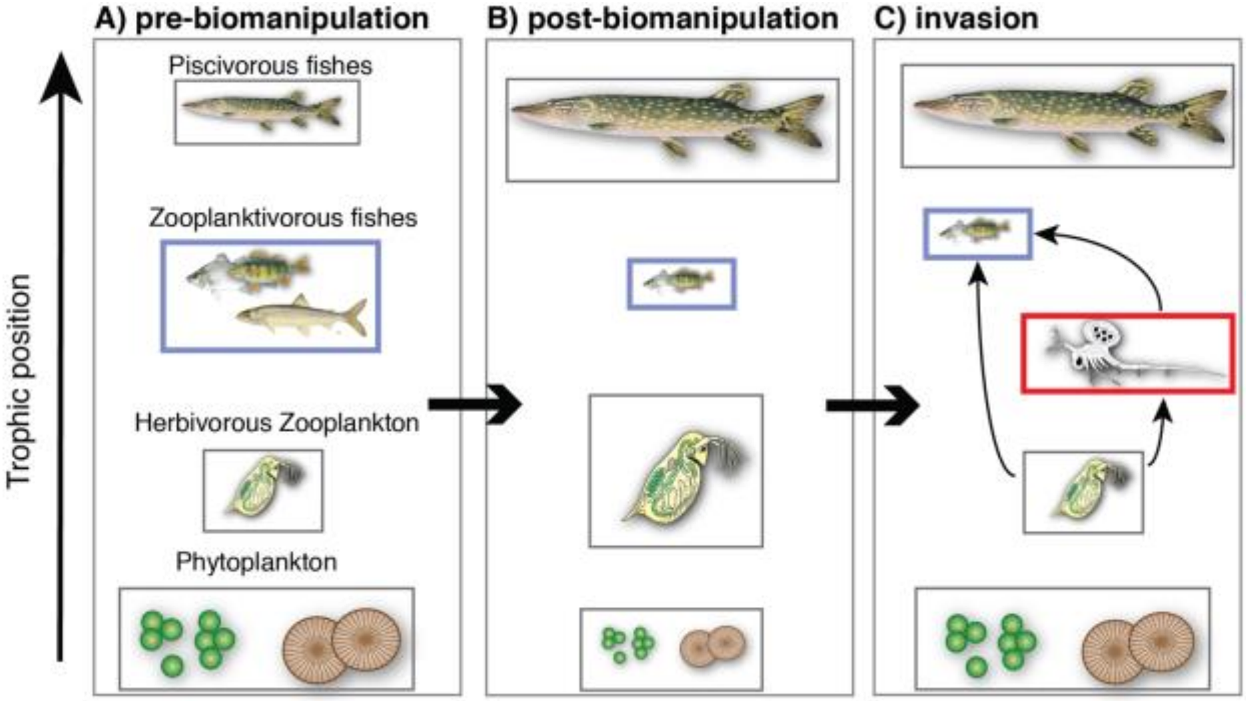
A) pre-biomanipulation
B) post-biomanipulation
C) invasion
Trophic position
Piscivorous fishes
Zooplanktivorous fishes
Herbivorous Zooplankton
Phytoplankton

Figure 1.

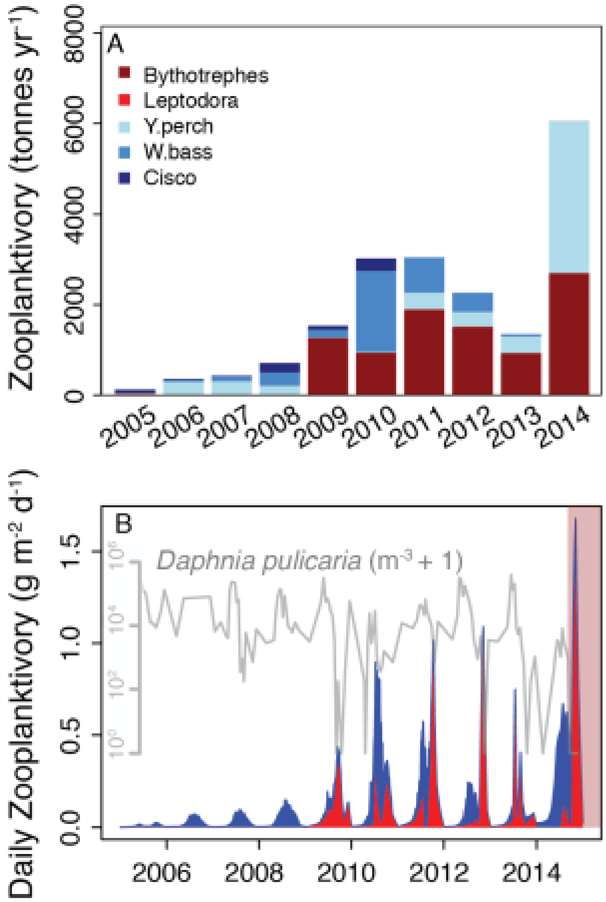
A
Bythotrephes
Leptodora
Y.perch
W.bass
Cisco
Zooplanktivory (tonnes yr^{-1})
0
2000
4000
6000
8000
2005
2006
2007
2008
2009
2010
2011
2012
2013
2014
B
Daphnia pulicaria (m^{-3} + 1)
10^0
10^2
10^4
10^6
Daily Zooplanktivory (g m^{-2} d^{-1})
0.0
0.5
1.0
1.5
2006
2008
2010
2012
2014

Figure 2.

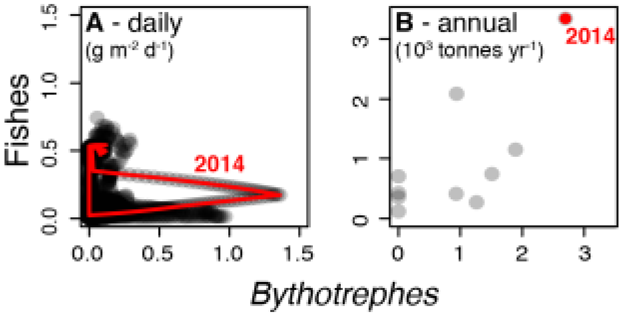
A - daily
(g m-2 d-1)
2014
Fishes
0.0
0.5
1.0
1.5
0.0
0.5
1.0
1.5
B - annual
(10³ tonnes yr-1)
2014
0
1
2
3
0
1
2
3
Bythotrephes

Figure 3.

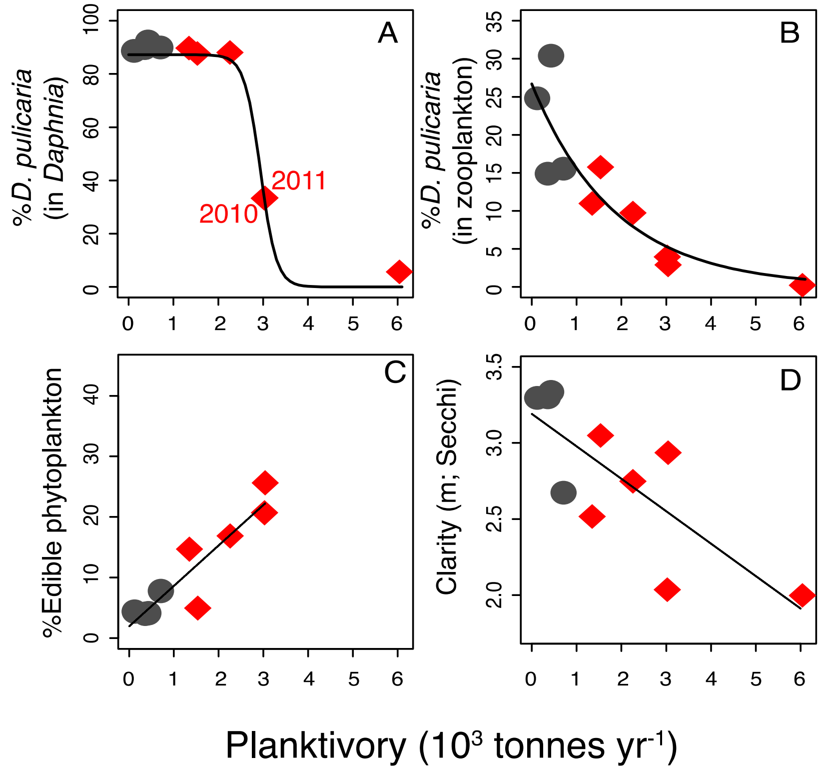
A
%D. pulicaria (in Daphnia)
0
20
40
60
80
100
2011
2010
B
%D. pulicaria (in zooplankton)
0
5
10
15
20
25
30
35
C
%Edible phytoplankton
0
10
20
30
40
D
Clarity (m; Secchi)
2.0
2.5
3.0
3.5
0
1
2
3
4
5
6
Planktivory (10^3 tonnes yr^{-1})

Figure 4.

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