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Rise of a native apex predator and an invasive zooplankton cause successive ecological regime shifts in a North Temperate Lake

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Abstract

Ecosystems can undergo abrupt regime shifts as a result of many factors. Shifts between turbid and clearwater states are well understood for human-impacted shallow lakes, but are not well understood in other types of lakes. Here we use long-term data to describe abrupt shifts in water clarity in Trout Lake, an oligotrophic lake with a largely undeveloped watershed. For several decades mean summer water clarity averaged 4.5 m, but then around 2007 water clarity sharply increased and the "clear water regime" persisted for nearly a decade. Nutrient availability did not explain these changes, but rather they were explained by a classic top-down trophic cascade. Around 2007, the population of the apex pelagic predator, Lake Trout, substantially increased. This was accompanied by a sharp decline in the lake's major pelagic prey fish, the zooplanktivorous Cisco. In turn, there was an increase in large-bodied zooplankton taxa (calanoids, *Daphnia*), which reduced algal biomass. This clear water regime was then disrupted in 2014 by the invasion of a predatory zooplankton, *Bythotrephes cederstroemi*. This invasion corresponded to strong impacts on lower trophic levels (decrease in large-bodied zooplankton and decreased water clarity), but more minor impacts on higher trophic levels (increased Cisco, decreased Lake Trout abundances)—in effect reversing the trophic cascade and shifting Trout Lake to a novel ecosystem state. Our study provides a long-term, empirically based example of successive ecological regime shifts that occurred from the rise of an apex predator and a mid-trophic level invasion in an undeveloped, oligotrophic lake.

The traditional concept of ecosystems is that they are relatively stable—there can be variability, but ecosystems tend to fluctuate around an equilibrium state. Yet there are cases in which ecosystems undergo abrupt regime shifts from one state to another (Scheffer et al. 2001; Scheffer and Carpenter 2003; Ratajczak et al. 2014). Such shifts can have dramatic consequences for environmental quality and the well-being of humans who rely on these ecosystems (Steele 1998; Nyström et al. 2000). The underlying theory of ecosystem regime shifts, especially relating to alternative stable states, is well-developed (Holling 1973; Scheffer et al. 2001; Scheffer and Carpenter 2003; Collie et al. 2004). Moreover, experimental manipulations of ecosystems have revealed insights into ecological thresholds, early warning indicators, as well as other aspects of regime shifts (Carpenter et al. 2011; Carpenter and Pace 2018). Yet aside from the handful of often-cited examples—coral reefs (Graham et al. 2015), shallow eutrophic lakes (Scheffer et al. 1993), and deserts (Foley et al. 2003), we have surprisingly little understanding of the phenomena of regime shifts in natural ecosystems, especially their drivers, and how commonly they occur. Extracting such insights requires long-term research, ideally spanning multiple trophic levels. Such long-term studies are rare.

Trophic cascades are a fundamental concept in ecology and can be a driver of regime shifts. In aquatic ecosystems, trophic cascade studies have largely focused on turbid and clear water states in human-impacted, shallow water lakes (Scheffer et al. 1993; Jeppesen et al. 1999; Scheffer and Jeppesen 2007). In many systems, trophic cascades have been used to promote a clear water state by removing zooplanktivorous fishes and/or stocking piscivorous fishes to reduce overall fish zooplanktivory (Carpenter and Kitchell 1996; Kasprzak et al. 2007; Potthoff et al. 2008; Ha et al. 2013). A classic example of this took place in Lake Mendota, Madison, Wisconsin, USA, where the stocking of piscivorous Walleye and Northern Pike (*Sander vitreus* and *Esox lucius*, respectively) in the late 1980s through the 1990s increased the lake's water clarity by decreasing the abundance of zooplanktivorous Yellow Perch (*Perca flavescens*), and increasing the abundance of large-bodied grazing zooplankton (*Daphnia*

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Additional Supporting Information may be found in the online version of this article.

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pulicaria) (Kitchell 1992). This biomanipulation was successful and longstanding, until the invasion of a predatory zooplankton, spiny water flea (*Bythotrephes cederstroemi; Bythotrephes* hereafter) (Korovchinsky and Arnott 2019) reversed the trophic cascade, and decreased water clarity by 1 m (Walsh et al. 2016, 2017). This highlights how ecosystems can experience rapid ecological regime shifts, especially in the wake of current ecosystem threats including invasive species, climate change, and pollution (Estes et al. 2011; Blois et al. 2013; Hintz et al. 2017).

Bythotrephes is a notorious middle-trophic level invader that consistently disrupts food webs in both natural and impounded lakes and across eutrophic and oligotrophic environments (Straile and Hälbich 2000; Yan et al. 2011; Brown et al. 2012). *Bythotrephes* initially invaded the Laurentian Great Lakes in the early 1980s and have continued to spread to inland lakes (Yan et al. 2011). They prey heavily on large-bodied grazing zooplankton, especially Cladoceran species (Schulz and Yurista 1998; Yan et al. 2002; Boudreau and Yan 2003). By preying on grazing Cladocerans, *Bythotrephes* can relieve the grazing pressure on phytoplankton, which allows phytoplankton to increase in abundance and ultimately reduce water clarity (Straile and Hälbich 2000; Walsh et al. 2016). These effects can be severe by reversing trophic cascades and can be especially problematic for lakes where significant efforts have been made to manage the lake's water quality (Strecker and Arnott 2008; Walsh et al. 2017). Additionally, the barbed caudal spine of *Bythotrephes* makes it difficult for small planktivorous fishes to consume, although larger fish can readily prey on *Bythotrephes* (Barnhisel 1991; Coulas et al. 1998; Compton and Kerfoot 2004). Consequently, the growth rates of native fishes, particularly juveniles, have been reduced in lakes invaded by *Bythotrephes* (Staples et al. 2017; Hansen et al. 2020). Overall, *Bythotrephes* impacts can initially be seen through zooplankton community shifts, but in several cases *Bythotrephes* invasions have also had impacts on higher trophic levels.

Here, we synthesized 39 years (1981–2019) of ecological data to understand the history of a pelagic food web in a nonexperimental lake with relatively little human influence, with a special interest in ecological regime shifts. Our results show that the rise of a native apex predator, Lake Trout (*Salvelinus namaycush*), triggered a top-down trophic cascade around 2007, which shifted the food web from being zooplanktivore dominant (*Coregonus artedi*, Cisco hereafter) to piscivore dominant. Subsequently, the invasion of *Bythotrephes* in 2014 abruptly shifted the lake's lower trophic levels (zooplankton, water quality), yet the abundances of higher trophic levels were minimally impacted. Since *Bythotrephes* ecologically functions as a zooplanktivore, the invasion of *Bythotrephes* increased total zooplanktivory and shifted the lower food web to function similarly to the zooplanktivore dominant regime, but with several notable differences. Overall, our study shows how ecological regime shifts and associated cascading effects can occur from both a top-down trophic cascade by a native predator and a middle-trophic level invasion.

Methods

Study system

Trout Lake is a 1608 ha drainage, oligotrophic lake in Vilas County, Wisconsin, USA, that is largely undeveloped and reaches a maximum depth of 35 m (Benson et al. 2006). The native apex predator, Lake Trout, has been stocked for the last 70 years for sportfishing opportunities, and the lake's unique genetic strain of Lake Trout has been stocked since 1983 (Supplementary Fig. S4) (Piller et al. 2005; Ahrenstorff et al. 2013). Cisco dominate pelagic zooplanktivory and their population dynamics in Trout Lake are mediated from the top down by Lake Trout (Parks and Rypel 2018). The lake's zooplankton community is comprised of large-bodied grazers including *Daphnia* and calanoids taxa, and smaller-bodied cyclopoid, rotifer, and copepod nauplii (Supplementary Fig. S1). There are also several invertebrate predator taxa including *Chaoborus*, *Mysis*, *Leptodora*, and invasive *Bythotrephes* (2014). In addition, Rusty Crayfish (*Orconectes rusticus*) invaded Trout Lake in 1979 and has had considerable effects to the littoral zone, especially the macrophyte community (Wilson et al. 2004). A recent study suggested the rusty crayfish population in Trout Lake has not shown long-term decline like populations in several nearby lakes (Larson et al. 2019). Our study will focus on the pelagic food web (Lake Trout, Cisco, etc.) and given Rusty Crayfish are a littoral species they are unlikely to play a strong role in our pelagic food web synthesis.

Big Musky Lake is in close proximity to Trout Lake and are both part of the NTL-LTER program. Big Musky is the most similar lake to Trout Lake as it is the closest in size (396 ha), maximum depth (21 m), and pelagic food web (has a Cisco population) (Benson et al. 2006). These characteristics make Big Musky suitable for comparison to Trout Lake and serve as a reference lake in this study.

Data collection and handling

Trout Lake has been a study site of the North Temperate Lakes-Long-Term Ecological Research program (NTL-LTER) since 1981. The NTL-LTER sampling design aims to track the long-term dynamics of lake ecosystems and LTER specific methodological details can be found at https://lter.limnology.wisc.edu/data. The methods specific to this study have been summarized below.

Secchi depth, chlorophyll *a* (Chl *a*), dissolved organic carbon (DOC), dissolved reactive silica, nutrients (nitrogen and phosphorus), and zooplankton were sampled fortnightly during the ice-free season and monthly during the ice-on season. All samples were collected at Trout Lake's deep hole (35 m). Zooplankton were collected with both a 2-m long Schindler trap (53um mesh) at multiple depths and one vertical tow (from 1 m above the bottom) using a Wisconsin net (80 μm mesh). Zooplankton samples were integrated volumetrically, and species were identified and counted. A subset of individual zooplankton was measured digitally under a microscope, which allowed for dry mass calculations (McCauley 1984). Annually, a larger meshed vertical zooplankton tow (1 mm mesh and 1 m in diameter) was used to sample the predatory pelagic invertebrate community i.e., *Chaoborus*, *Leptodora*, *Mysis*, and *Bythotrephes*. Predatory zooplankton sampling was conducted at night. Pelagic fish were sampled annually with vertically hung gillnets (33 m long, mesh sizes 19, 25, 32, 38, 51, 64, and 89 mm) for two 24-h sets at the deep hole. Collected fish were identified and measured for length and a subset were weighed. Beginning in 2001, annual nighttime hydroacoustic surveys were conducted alongside gillnet sampling to better estimate pelagic fish densities following methods outlined in Parks and Rypel 2018.

Data analysis

Time series plots were generated (mean ± CI) from raw data for Secchi depth, Chl *a*, DOC, silica, nitrogen, and phosphorus. We used generalized additive modeling (GAM) to assess annual shifts in the grazing zooplankton community, which we grouped by broad taxonomic groups (calanoids, cyclopoids, *Daphnia*, copepod nauplii, and rotifers). We further used GAM to deseasonalize Secchi depth measures that we used in change point analysis to test for a break point in the time series (Killick and Eckley 2014). In change point analysis, we first visually assessed the Secchi GAM coefficients for normality and tested using a Shapiro–Wilk test. The Secchi coefficients were left-skewed and not normally distributed. We tested Secchi coefficients for a Gamma distribution and it did not fail that test and therefore we used Gamma as the test statistics in change point analysis. We used the "PELT" method of change point analysis, which allows for the detection of multiple breakpoints in a time series. We evaluated the sensitivity in breakpoint detection by testing multiple models where we changed the minimum number of segments (years) required for a significant breakpoint. We additionally evaluated the sensitivity of breakpoint detection by changing the penalty value. We then compared models to determine if and where there were breakpoints in our timeseries. Data analysis and visualization were completed in R Studio (R Core Team 2019).

Results

Regime shifts and food web states

In the change point analysis, both methods we used to vary the strictness of the models indicated the strongest breakpoint in Secchi depth was 2007. Our models that had less strict penalty parameters indicated up to six breakpoints; however, many of these were short in length (2–3 years long). As we increased the strictness of the model penalties and minimum number of segments, the model converged on 2007 as the single strongest break (Supplementary Fig. S7). A modest model (penalty value of $p = 0.04$ and minimum segment length of 4) yielded an additional breakpoint at 2013. This second break point is within 1 yr of the invasion of *Bythotrephes*. Overall, the change point analysis was in agreeance with our visual assessment of the time series and justifies the breakpoints we use in the time series (2007 and 2014). The shift in water clarity did not coincide with a shift in nutrients or DOC, suggesting water clarity shifts were biologically driven (Supplementary Fig. S2). The 2006–2007 time period also corresponded to a drastic increase in Lake Trout density and decrease in Cisco density, which alongside the water clarity

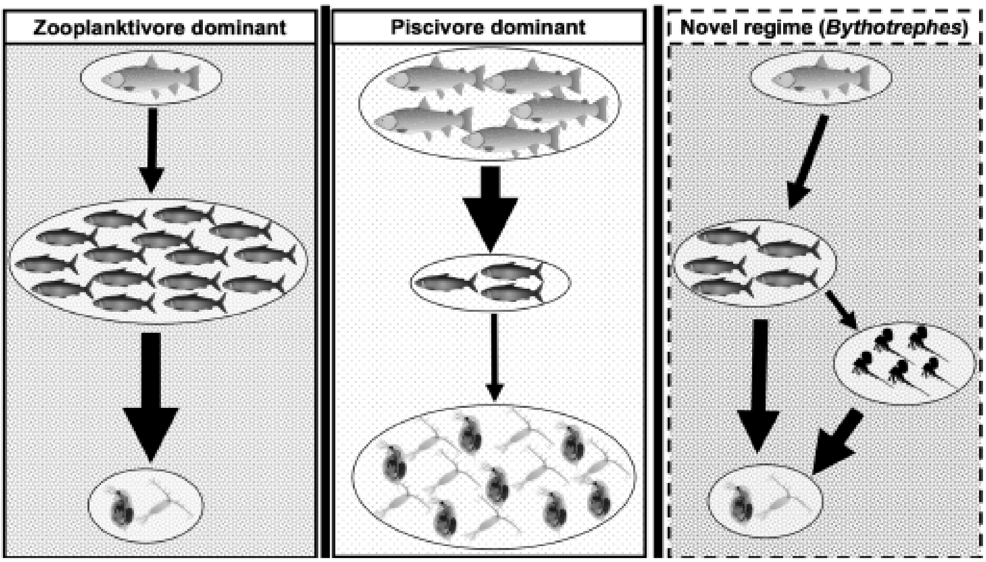

Fig. 1. Food web diagram of the (1) zooplanktivore dominant regime (1981–2006), (2) piscivore dominant regime (2007–2014), and (3) novel regime (*Bythotrephes*) (2015–2019) for Trout Lake, Vilas County, Wisconsin, USA.

results indicates an ecological regime shift. Further, in comparison to Big Musky Lake, we found that there were not any concurrent shifts in water clarity, Chl *a*, nitrogen, phosphorus, or DOC. Given this lack of concurrent shifts in Big Musky Lake, our results suggest the shifts in Trout Lake were not significantly driven by landscape level effects (Supplementary Figs. S5 and S6).

Although *Bythotrephes* was first detected in 2014, their abundance was lower than other predatory zooplankton for the first year of the invasion. However, from 2015 to 2019 *Bythotrephes* was the most numerous predatory zooplankton. The *Bythotrephes* invasion also corresponded to a second shift in water clarity and suggests this as an ecological regime shift. Given these two points of interest, we broke Trout Lake's 39-year food web history into three time periods: (1) 1981–2006, (2) 2007–2014, and (3) 2015–2019 (Fig. 1).

Zooplanktivore dominant regime (1981–2006)

The 1981–2006 period is best summarized by a low piscivory, low water clarity regime: low density of Lake Trout (below hydroacoustic detection), high density of Cisco, low density of predatory zooplankton, a zooplankton community dominated by small-bodied taxa (Cyclopoids, Rotifers, and Copepod nauplii), high silica and Chl *a* concentrations, and low water clarity (4–4.5 m) (Figs. 2–7). The Cisco population size structure had a smaller average and range in body lengths compared to other time periods (mean = 182; IQR = 51 mm). The Cisco population had a low abundance of Cisco greater than or equal to 250 mm in total length (Fig. 8). Overall, this food web state was driven by high zooplanktivory by Cisco. For the sake of clarity, we will refer to this regime as "zooplanktivore dominant" hereafter (Carpenter and Kitchell 1996) (Fig. 1).

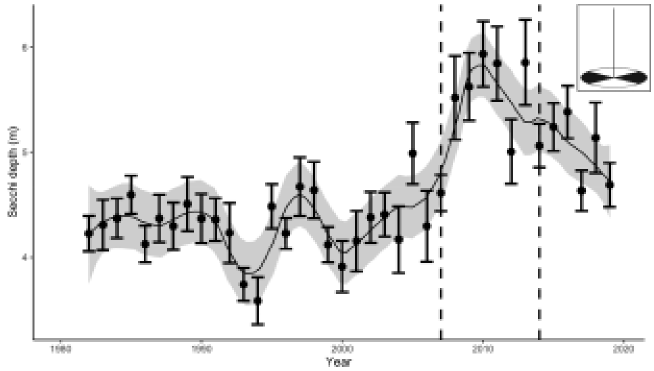

Fig. 2. Mean annual Secchi depth (m) (± 95% CI) from 1982 to 2019 for Trout Lake, Vilas County, Wisconsin, USA. A loess smooth line (span = 0.2) is used to aide visualization. Vertical lines at 2007 and 2014 represent regime shifts.

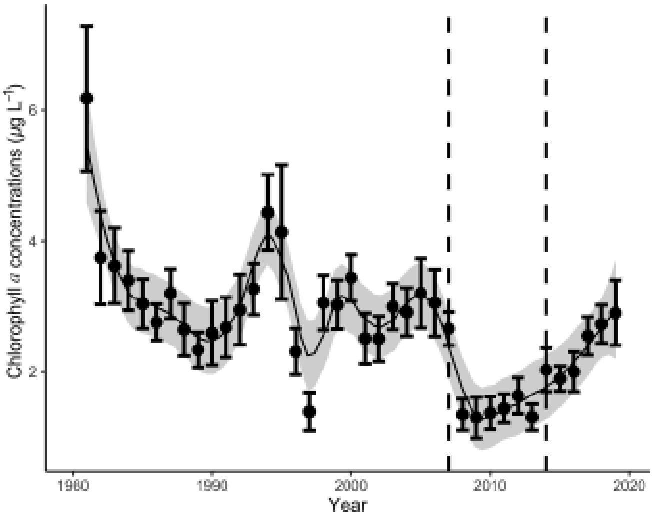

Fig. 3. Mean annual chlorophyll *a* concentrations (surface; μg L^{-1}) (± 95% CI) from 1981–2019 for trout Lake, Vilas County, Wisconsin, USA. A loess smooth line (span = 0.2) is used to aide visualization. Vertical lines at 2007 and 2014 represent regime shifts.

Piscivore dominant regime (2007–2014)

Increased Lake Trout density and water clarity around 2007 indicated a shift away from the previous zooplanktivore dominant regime. This time period had a relatively high density of Lake Trout, low Cisco density, high density of predatory zooplankton, a zooplankton community dominated by large-bodied taxa (*Daphnia* and calanoids), lower silica, and Chl *a* concentrations, and an ~ 1 m increase in water clarity to ~ 5.5 m (Figs. 2–7). Compared to historically collected water clarity data, the water clarity during this time period was higher than any other time across 79 years of data (Supplementary Fig. S3). Although Cisco were lower in abundance, Cisco in this time period had a larger average and range in total body lengths (mean = 209; IQR = 84 mm). Further, the Cisco population had higher abundances of individuals

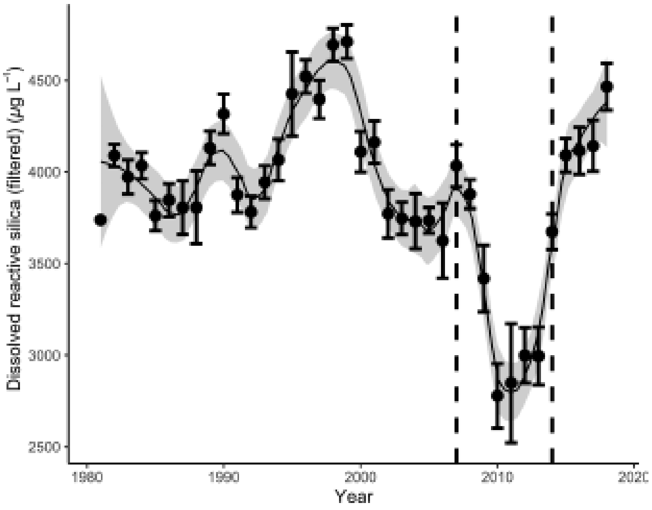

Fig. 4. Annual mean dissolved reactive silica (filtered; surface; μg L^{-1}) (± 95% CI) from 1981 to 2018 for Trout Lake, Vilas County, Wisconsin, USA. A loess smooth line (span = 0.2) is overlayed to aide visualization. Vertical lines at 2007 and 2014 represent regime shifts.

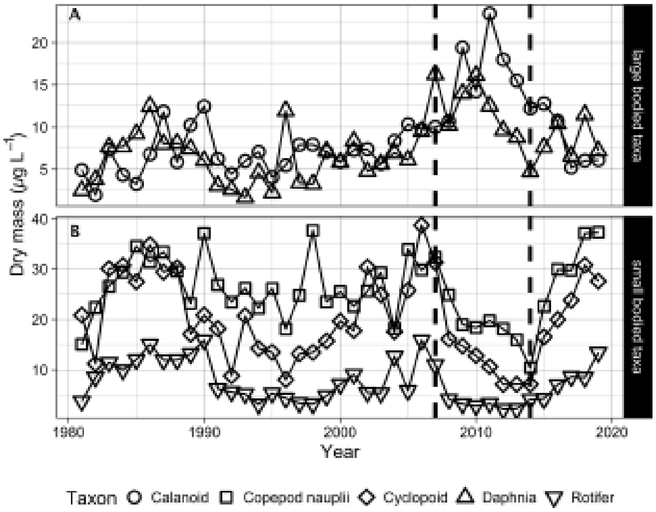

Fig. 5. Annual deseasoned GAM estimates of large-bodied zooplankton taxa (top; **A**) calanoids (circle) and *Daphnia* (triangle), and small bodied taxa (bottom; **B**) copepod nauplii (square), cyclopoid (diamond), and rotifer (triangle) from 1981 to 2019 in Trout Lake, Vilas County, Wisconsin, USA. Dashed vertical lines at 2007 and 2014 represent regime shifts.

greater than or equal to 250 mm (Fig. 8). Since top-down pressures from Lake Trout strongly influenced this regime, we will refer to this regime as "piscivore dominant" hereafter (Fig. 1).

A novel regime (2015–2019)

The *Bythotrephes* establishment in 2014 marked a second regime shift, and effects appeared to track with *Bythotrephes* density as it became the most populous predatory zooplankton species in 2015 (Fig. 5). *Bythotrephes* were also not established in the lake until the early fall of 2014 (September) and justifies the novel regime beginning in 2015. Densities of several native zooplankton taxa declined since the invasion of *Bythotrephes*, especially *Leptodora* and calanoids, which were at their historic highest abundances in the previous piscivore dominant regime (Figs. 5 and 6). Water clarity declined following *Bythotrephes* invasion and shifted back to levels similar to the planktivore dominant regime (Fig. 2). Silica and Chl *a* concentrations also shifted back to levels similar to the planktivore dominant regime (Figs. 3 and 4). After the *Bythotrephes* invasion, Lake Trout populations were intermittently detectable by hydroacoustic surveys (3/5 years), and Cisco abundances shifted to intermediate density between that of the planktivore and piscivore dominant regimes (Fig. 7). The Cisco size structure remained similar to the piscivore dominant regime, with relatively high proportions of Cisco > 250 mm (Fig. 8). Although some food web characteristics were similar to that of the planktivore dominant regime, others were more similar to the piscivore dominant regime, possibly representing a novel state resulting from food web shifts by *Bythotrephes* that we will be refer to as the "novel *Bythotrephes* regime" hereafter (Fig. 1).

Discussion

Our long-term food web synthesis showed that multiple ecological regime shifts occurred in an undeveloped, oligotrophic lake over the last ~ 40 years (summarized in Fig. 1). The first regime shift was a classic top-down trophic cascade. The substantial increase in the population density of the native apex predator, Lake Trout, had strong cascading effects throughout the food web and yielded a time period with higher water clarity and lower Chl *a* (Figs. 2 and 3). Further, the water clarity during the piscivore dominant regime was markedly higher than historical data from the early 1900s,

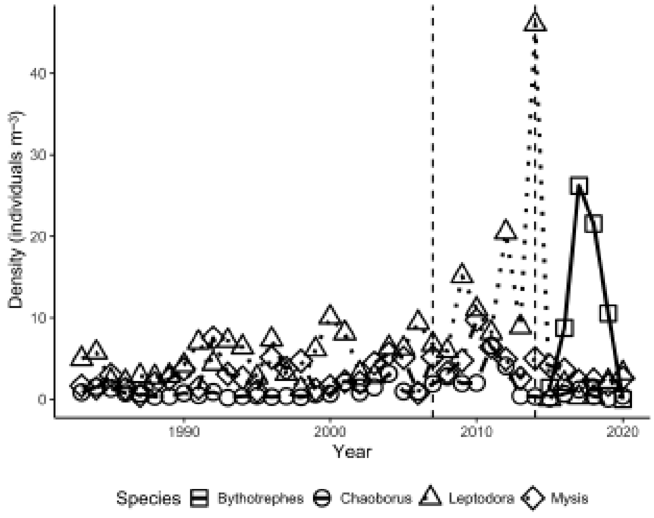

Fig. 6. Annual density estimates of predatory zooplankton species *Bythotrephes*, *Chaoborus*, *Leptodora*, and *Mysis* from 1984 to 2019 in Trout Lake, Vilas County, Wisconsin, USA. Dashed vertical lines at the years 2007 and 2014 represent regime shifts.

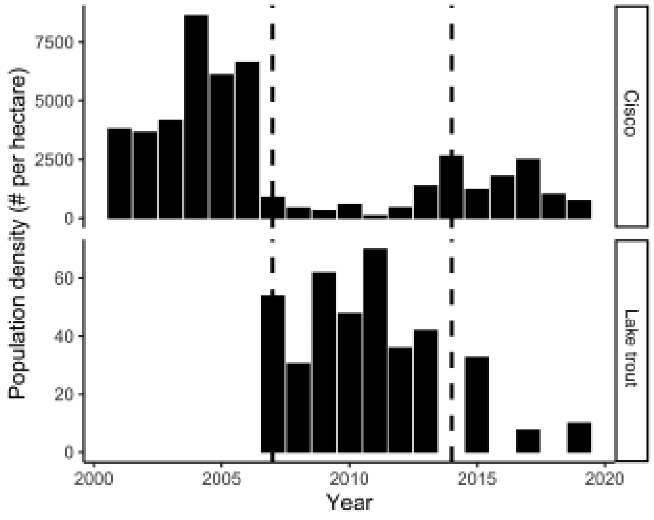

Fig. 7. Hydroacoustics density estimates (# per hectare) for Cisco (top) and Lake Trout (bottom) from 2001 to 2019 for Trout Lake, Vilas County, Wisconsin, USA. Dashed vertical lines at the years 2007 and 2014 represent regime shifts.

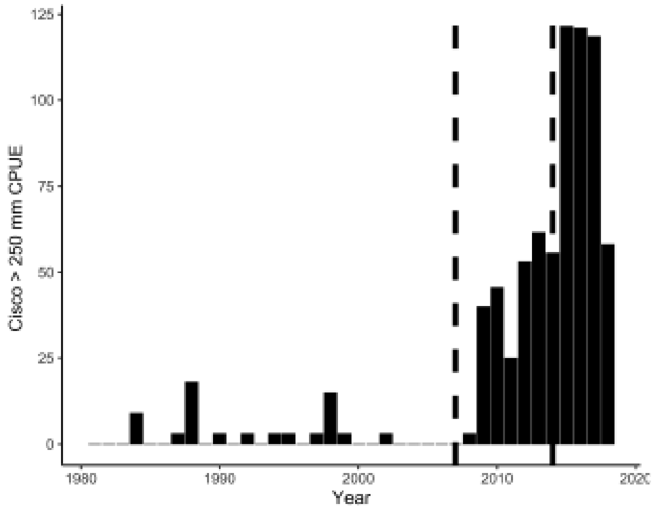

Fig. 8. Catch per unit effort (CPUE) of Cisco > 250 mm in total length from 1981 to 2019 for Trout Lake, Vilas County, Wisconsin, USA. Dashed vertical lines at the years 2007 and 2014 represent regime shifts.

further suggesting this was a unique regime for Trout Lake (Supplementary Fig. S3). Also, after the trophic cascade, there was a greater abundance of larger bodied grazing zooplankton taxa (calanoids and *Daphnia*), which more efficiently graze phytoplankton and therefore yielded clearer water (Gianuca et al. 2016) (Fig. 5). The shifts in the lower food web were triggered by an increased Lake Trout population that has previously been shown to regulate Cisco population dynamics in Trout Lake (Parks and Rypel 2018). While Lake Trout are stocked in Trout Lake, there was not a clear difference in the number, size, or strain of Lake Trout stocked that could explain their large increase in density around 2007 (Supplementary Fig. S4) (Piller et al. 2005). A pulse of natural reproduction in the mid-2000s is plausible but we do not have sufficient data to address that. The top-down trophic cascade triggered by increased Lake Trout densities was similar to several cases of Lake Trout introductions as a nonnative species where they had strong cascading impacts, especially in the western United States (Martinez et al. 2009; Tronstad et al. 2010; Ellis et al. 2011). More broadly, our results align with the foundational trophic cascade experiments that took place in close proximity to Trout Lake (Carpenter and Kitchell 1996). Overall, the regime shifts from zooplanktivore to piscivore dominant states demonstrated the lake's pelagic food web has strong trophic linkages that can yield rapid cascading interactions. Further, our study provides an example of long-term regime shifts occurring in a non-experimental ecosystem and in a habitat with little human influence.

Piscivore dominant to a novel regime

The second regime shift was triggered by a middle-trophic level invader, *Bythotrephes*, which yielded conditions similar to the zooplanktivore dominant regime, but with a few nuances. The *Bythotrephes* invasion quickly impacted lower trophic levels including water clarity, Chl *a*, silica, and the grazing and predatory zooplankton community. However, it is important to note that Cisco abundances increased slightly and likely contributed additional planktivory that in combination with *Bythotrephes* yielded these ecological shifts. *Leptodora* densities declined sharply after the invasion, as has been the case in other *Bythotrephes* invasions (Fig. 6) (Branstrator 1995, 2005; Hovius et al. 2007). Zooplankton community shifts have been noted as a consistent response in other *Bythotrephes* invasions, with larger ecosystem impacts like triggering a trophic cascade occurring in fewer, more extreme cases (Yan et al. 2002; Strecker et al. 2006; Walsh et al. 2016). The major shifts in the zooplankton community (decrease in large-bodied grazers) after the *Bythotrephes* invasion therefore had a cascading impact on Chl *a* and water clarity. Although lower trophic levels quickly responded to the invasion, impacts on the fish community were not as visible and will require continued monitoring. The Cisco population increased slightly in density and continued to be dominated by larger Cisco (>250 mm) (Figs. 7 and 8). Although Cisco densities stayed relatively low, the lower trophic levels during the novel regime were similar to the zooplanktivore regime configuration. Prior to *Bythotrephes*, the lower food web was largely controlled by zooplanktivory by Cisco, but since *Bythotrephes* are a zooplanktivore, the total zooplanktivory that controls the lower food web is the total zooplanktivory between *Bythotrephes* and Cisco (Schulz and Yurista 1995, 1998; Hoffman et al. 2001). The substitution of zooplanktivory by *Bythotrephes* has potential consequences that will be further discussed below. Overall, we found increased abundances of a predatory invertebrate, *Bythotrephes*, to have similar impacts as high abundances of a long-lived native zooplanktivorous fish.

Functional replacement by Bythotrephes

Not only has the invasion of *Bythotrephes* caused a novel regime, but it also has several potential consequences for the lake's future food web and fishery. Firstly, zooplanktivory by *Bythotrephes* is in direct competition with Cisco, which is a highly important prey-fish species and has been declining throughout the region. Loss of essential oxythermal habitat and species invasions have been attributed to regional Cisco decline, with recent state-wide surveys only confirming Cisco presence in 94 of 133 lakes (29% decline) that had historical Cisco populations (Krueger and Hrabik 2005; Magee et al. 2019; Renik et al. 2020). In the novel *Bythotrephes* regime, overall zooplanktivory is split between Cisco and *Bythotrephes*. As such, *Bythotrephes* invasion represents a functional replacement of a native species that is under multiple anthropogenic threats across the landscape. Not only do *Bythotrephes* consistently alternative zooplankton communities through direct predation, but in our case they may replace native zooplanktivores including Cisco as well as native predatory invertebrates i.e., *Leptodora*, *Chaoborus*, etc. (Weisz and Yan 2011). Therefore, our study supports *Bythotrephes* as a threat to pelagic biodiversity in temperate lakes throughout North America (Yan et al. 2002, 2011; Walsh et al. 2016). Overall, the functional replacement of zooplanktivory by *Bythotrephes* is a concern for native zooplanktivores, like Cisco, that directly compete for food resources with *Bythotrephes*.

Cisco and Bythotrephes interactions

In many invaded lakes, zooplanktivorous fishes, including Cisco, have integrated *Bythotrephes* into their diet; however, there is evidence that predation on *Bythotrephes* is size dependent (Barnhisel and Harvey 1995; Pothoven et al. 2007; Keeler et al. 2015). As is the case with many fish species, Cisco undergo trophic ontogeny where Cisco consume larger prey as they themselves grow larger (Muir et al. 2013). The specific body size at which Cisco transition to prey on greater proportions of *Bythotrephes* instead of alternative prey (calanoids, *Daphnia*, etc.) is not yet well established. However, an extensive diet study that focused on fish predation on *Bythotrephes* found higher proportions of *Bythotrephes* in the stomachs of Cisco ≥ 260 mm in Lake Superior (large = 0.43, small = 0.18) (Keeler et al. 2015). This is consistent with a subsample of smaller Cisco (n = 32; 139–184 mm) that we assessed from Trout Lake in the summer of 2019, where Cisco < 200 mm had larger proportions of *Daphnia* and calanoids (79.4%) in their stomachs rather than *Bythotrephes* (3.8%) (Martin & Vander Zanden, unpublished). Further this apparent omnivory of consuming both grazing zooplankton and an invasive zooplanktivore (*Bythotrephes*) is important to the broader food web configuration. The addition of *Bythotrephes* shifts the lake from previously functioning like a food chain to functioning like a food web when in the novel state (Fig. 1). Overall, the interactions between *Bythotrephes* and Cisco are complex and have not been deeply explored, particularly in inland lakes, but have important implications for understanding broader food web function and ecosystem response to perturbations.

Importantly, our results showed a substantial shift in Cisco size structure that suggests predation on *Bythotrephes* was relatively high during the novel regime. We found that the abundance of large Cisco (> 250 mm) was low during the planktivore dominant regime and higher during both the piscivore and novel regimes (Fig. 8). The shift in cisco size structure between the planktivore to piscivore dominant regime is consistent with a similar trophic cascade study where the introduction of Lake Trout caused a decline in Cutthroat Trout (planktivore) abundance in Yellowstone Lake. In that case, Cutthroat Trout size structure also shifted to larger individuals (Tronstad et al. 2010). A potential explanation for size structure shifts after a trophic cascade is that when there is low zooplanktivore abundance, competition for prey resources is weakened, which allows for faster zooplanktivore growth rates and therefore larger individuals. Interestingly, the higher abundance of large Cisco persisted or potentially increased during the novel regime. For *Bythotrephes*, the shift in Cisco size structure likely increased predatory pressure, especially given Cisco at times will preferentially feed on *Bythotrephes* (Coulas et al. 1998). Further, since larger Cisco prey more readily on *Bythotrephes* the invasion could favor larger Cisco by providing a substantial prey base, while smaller Cisco that cannot readily prey on *Bythotrephes* compete for food resources with *Bythotrephes* (Coulas et al. 1998; Pothoven et al. 2007; Keeler et al. 2015). Again, while the trophic ontogeny of *Bythotrephes* consumption is not yet well understood, current studies suggest that there is a period where cisco cannot readily prey on *Bythotrephes* due to the large body size and predator defenses of *Bythotrephes*. Thus, cisco would be competing for alternative native zooplankton resources with *Bythotrephes* (Barnhisel and Harvey 1995; Compton and Kerfoot 2004). Our work suggests that the size structure shifts we found in the Cisco population are important to account for when considering interactions between Cisco and *Bythotrephes*.

Food web shifts and silica

We found dissolved silica concentrations shifted along the same timeline as the lake's major regime shifts, while also being asynchronous with our reference lake (Fig. 4 and Supplementary Fig. S6). Diatoms are especially influential to silica dynamics as diatoms uptake silica and then export it to the hypolimnion when they fall out of suspension (Kilham 1971). In the Laurentian Great Lakes, cultural eutrophication has increased diatom production and caused biologically mediated silica depletion (Schelske and Stoermer 1971; Conley et al. 1993). In our study, we saw reduced silica concentrations during the period of high water clarity, which is the opposite of what we would expect based on the Great Lakes studies. Also in contrast with Great Lakes studies, phosphorus did not co-vary with changes in silica. The shift in silica does however coincide with the major food web shifts and therefore it seems most likely that the shift in silica is related to the food web changes. Likely the depletion of silica during the clear water regime was in response to an increase in diatom production, but we cannot contribute the increased diatom production to eutrophication as we did not see any changes in nutrient levels. Further, the drought that occurred in this region from ~ 2005 to 2010 does not explain the drop in silica or other aspects of our results as there was no change in nitrogen, phosphorus, or DOC during the clear water era (Supplementary Fig. S2) (Perales et al. 2020). We can further see that drought is unlikely to have played a large role in our study as Big Musky Secchi, Chl *a*, and silica did not similarly respond to the drought period (Supplementary Figs. S5 and S6). Unfortunately, we do not have readily available data to investigate whether there was in a shift in the diatom community itself that may change their overall production levels. However, the needed samples have been archived on microscope slides and if analyzed they could provide a clearer explanation as to how these food web shifts may be related to the shift in silica concentrations.

Our study provides an empirical example of multiple regime shifts occurring in an undeveloped oligotrophic lake. This study is among only a few to show regime shifts occurring in a non-experimental setting. The regime shifts in this study included both a classic trophic cascade and a species invasion. The trophic cascade played out similarly to many other cascade studies where the ecosystem shifted between a three-tier and four-tier state and trophic interactions were linear. However, the species invasion was much more complex as it rewired the ecosystem and shifted it away from being a simple linear food chain. The novel food web had varying impacts on different trophic levels and highlights how disruptive *Bythotrephes* can be for aquatic food webs. There is still more we need to understand about the role of species invasions as a trigger for ecological regime shifts given that invasions continue to accelerate worldwide. Among the many questions that remain for species, invasions and regime shift include how the ecological impacts of species invasions will play out in the long term. To study this, we will need to continue to collect long term data, especially in ecosystems that have been invaded.

Data Availability Statement

All data used in this study can be accessed via the NTL-LTER website (https://lter.limnology.wisc.edu/data). Code can be made available upon request.

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Conflict of interest

None declared.

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