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Evaluating the potential role of predation by native fish regulating the abundance of invasive spiny water flea

Benjamin E. Martin[a], Joseph T. Mrnak[a,b] and M. Jake Vander Zanden[a]

[a]Center for Limnology, University of Wisconsin- Madison, Madison, WI, USA; [b]Wisconsin Department of Natural Resources, Office of Applied Science, Escanaba Lake Research Station, Boulder Junction, WI, USA

ABSTRACT

Predation by native predators can hinder the success of an invasive species. *Bythotrephes, an invasive zooplankton species,* established in Trout Lake, Vilas County, Wisconsin, USA, in 2014. However, by 2020, *Bythotrephes* densities dropped to densities where they were barely detectable. Cisco (*Coregonus artedi*), a native zooplanktivore, is an abundant fish species in Trout Lake and has been shown to significantly prey on *Bythotrephes*. Given the decline in *Bythotrephes*, we asked whether Cisco predation could have played a role in the observed decline in *Bythotrephes* densities. We modeled Cisco consumption of *Bythotrephes* using bioenergetic modeling and *Bythotrephes* production from a production to biomass model. The model results suggested that Cisco consumption was lower than *Bythotrephes* production during the early years of the invasion, but since 2017 Cisco consumption exceeded *Bythotrephes* production and has likely played a role in the observed *Bythotrephes* density declines. Our study provides quantitative context for predation on *Bythotrephes*, and alongside other studies, suggests native predators can control *Bythotrephes* densities. Leveraging predation by native species could be an invasive species management tool, so it is important to synthesize and document cases in which predation may control or reduce impacts of invasive species.

KEY POLICY HIGHLIGHTS

1. Invasive species can have severe impacts on freshwater ecosystems and will continue to spread across the landscape. When species do invade, invasive species management tools are incredibly important as they can mitigate impacts. However, successful management of invasive species often goes undocumented.
2. Predation by native species can be an invasive species management tool to mitigate impacts of invasions. Leveraging native species to reduce the abundance of an invasive species can be difficult and requires thorough consideration of indirect impacts.

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CONTACT Benjamin E. Martin bemartin@wisc.edu Center for Limnology, University of Wisconsin- Madison, 680 North Park Street, Madison, WI, 53706, USA

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3. There have been some cases where predation by native species has been attributed to controlling the abundances of invasive species. In such cases, promoting native species abundances can reduce the abundance of invasive species. This can be highly advantageous for lake managers, however, natural resource management includes many different stakeholders and therefore decisions regarding invasive species management can be complex.

Introduction

The long-term persistence of an invasive species can depend on the characteristics of the recipient ecosystem (habitat suitability, prey availability, predation pressure, etc.). Of these characteristics, predation by native predators can have a strong impact on the establishment and long term persistence of an invasive species (Elton 1958; Abrams 1987; Mrnak et al. 2022). Many invasive species have or develop defense mechanisms to avoid predation. Further, those defense mechanisms can be strengthened by strong predation pressures (Freeman and Byers 2006). These defense mechanisms can contribute to a lag-time in native predators switching to consuming the novel prey (Carlsson et al. 2009). However, it can be advantageous for native predators to switch to consuming invasive prey, particularly when invasive prey are hyper-abundant. There are many cases where native predators consume invasive prey, and can regulate invasive species abundances (Byers 2002; DeRivera et al. 2005; Carlsson et al. 2011). This can minimize their impacts and such is the primary goal of invasive species management (Prior et al. 2018; Mrnak et al. 2022). Therefore, it is especially important to study cases of native predators regulating invasive species abundances. Yet, it is difficult to study these cases as it requires data collection from the early stages of the invasion.

Bythotrephes cederstoemi (spiny water flea; *Bythotrephes* hereafter) invaded the Great Lakes in the 1980s and have since spread to many inland lakes and reservoirs (Branstrator et al. 2006; Korovchinsky 2020; Karpowicz et al. 2021). *Bythotrephes* have a barb ridden caudal spine that can account for over half its total body length (Korovchinsky and Arnott 2019). As a large predatory zooplankton species, predation by *Bythotrephes* can have rapid and severe impacts on native zooplankton communities, especially cladoceran species (Yan et al. 2002), which in extreme cases has caused ecosystem level trophic cascades (Walsh et al. 2016a; Weidel et al. 2017). Further, by reducing native zooplankton abundances *Bythotrephes* can create a prey resource bottleneck for gape limited predators and slow the growth of juvenile fishes (Staples et al. 2017; Hansen et al. 2020). Although the defensive barbed caudal spine of *Bythotrephes* can reduce predation, it mostly guards against gape limited predators, particularly juveniles. Predation on *Bythotrephes* is size dependent where there is a gape threshold for predators to readily consume *Bythotrephes* (Barnhisel and Harvey 1995; Jarnagin et al. 2000; Compton and Kerfoot 2004). Studies investigating fish predation on *Bythotrephes* have found many species prey on *Bythotrephes* including but not limited to Cisco (*Coregonus artedi*), alewife (*Alosa pseudoharengus*), lake whitefish (*Coregonus clupeaformis*.), rainbow smelt (*Osmerus mordax*), and yellow perch (*Perca flavescens*) (Schneeberger 1991; Coulas et al. 1998; Storch et al. 2007; Isaac et al. 2012). The prevalence and diversity of native fish consuming *Bythotrephes* has further sparked interest into whether native predators could regulate *Bythotrephes* abundances, which has been supported in some cases (Branstrator et al. 2006; Young et al. 2009; Keeler et al. 2015).

Here, we asked whether predation on *Bythotrephes* by a native zooplanktivore, Cisco, exceeded *Bythotrephes* production in a lake where the *Bythotrephes* population fell to a threshold of very low detection. We used long-term data to inform a Cisco bioenergetics model and *Bythotrephes* production to biomass (P/B) model to examine the ratio of Cisco consumption to *Bythotrephes* production. We found that Cisco consumption was lower than *Bythotrephes* production during the early years of the invasion, but since 2017 Cisco consumption exceeded *Bythotrephes* production and likely played a role in the major *Bythotrephes* decline.

Study system

Trout Lake is a 1,608 hectare oligotrophic, drainage lake in Vilas County, Wisconsin, USA that is largely undeveloped and reaches a maximum depth of 35 m (Benson et al. 2006). Cisco dominate pelagic zooplanktivory, and their population dynamics in Trout Lake are mediated from the top down by Lake Trout (Parks and Rypel 2018; Martin et al. 2022). The lake's native zooplankton community is comprised of large-bodied grazers (*Daphnia* and calanoids), and smaller-bodied taxa (cyclopoid, rotifer and copepod nauplii) (Martin et al. 2022). The pelagic food web also has predatory invertebrate taxa including *Chaoborus*, *Mysis*, *Leptodora*, and invasive *Bythotrephes* (established 2014) (Martin et al. 2022). The Trout Lake food web has undergone multiple ecological regime shifts over the last 40 years, with the most recent occurring from the *Bythotrephes* invasion (Martin et al. 2022). In Trout Lake, the *Bythotrephes* invasion coincided with a decline in (1) water clarity, (2) large bodied grazing zooplankton and (3) native predatory invertebrate taxa (*Chaoborus*, *Mysis*, and *Leptodora*) (Martin et al. 2022). However, in 2020 the *Bythotrephes* densities declined to a very low abundance (almost undetectable), even though frequent monitoring continued as it has since *Bythotrephes* were first detected. For context, a single zooplankton tow yielded tens to even thousands of *Bythotrephes* from 2014 to 2019, but in 2020 and 2021, there were only a total of four and one individuals, respectively, captured across monitoring throughout the year.

Materials and methods

Field collected data

Trout Lake has been routinely sampled through the North Temperate Lakes Long Term Ecological Research (NTL-LTER) program since 1981. All sampling methods and data are freely available on their website https://lter.limnology.wisc.edu. For this study, we used the following datasets: pelagic fish density estimates from hydroacoustics, annual predatory zooplankton densities, fish length/weight from vertical gill nets, and daily water temperatures (Magnuson et al. 2020a; 2020b, 2021, 2022a, 2022b).

Cisco pelagic abundance was estimated annually in July or August with hydroacoustic surveys, typically within a week of gill net sampling. Hydroacoustic data were collected at night with a BioSonics DTX echosounder and downward facing 70-kHz split-beam transducer mounted 1 m below the water surface. Thresholds for data collection excluded raw echoes below −100 decibel (dB) for S_v data and -70dB for target strength data. Transmitted pulse duration was set at 0.4 ms. All hydroacoustic surveys were conducted at least 30 min after nautical twilight and followed a standardized-replicable transect on the south basin of Trout Lake. All acoustic data were analyzed in Echoview software (v5.4) following Mrnak et al. (2021). *Post-hoc* data analysis followed the Great Lakes

Standard Operating Procedures (Parker-Stetter et al. 2009; Mrnak et al. 2021); target strength threshold of −55 dB, 6-dB pulse length determination level, 0.5 minimum and 1.5 maximum normalized pulse length, 6-dB maximum beam compensation, and minor- and major-axis angles at 1°.

However, 48-hr vertical gillnet sets were used to (1) inform species composition from the hydroacoustic surveys and (2) to inform Cisco size-specific inputs into the bioenergetics model (detailed below). For each set, seven monofilament nets were deployed in the deep hole of Trout Lake from the surface to the bottom (~30 m). Vertical gillnets were 3 × 30 m with stretched meshes of 19, 25, 32, 38, 51, 64, or 89 mm. After a 24-hr period, all nets were processed and fish were measured for total length (TL; mm) and weight (g). Species-specific mean total length was then transformed into a target strength (dB) following Love (1971). Species classes were then designated using mean target strength and then assigned a proportion of total biomass (Mrnak et al. 2021). In 2019, a subsample of collected Cisco was further assessed for stomach content composition. Whole stomachs were removed from fish and the contents were emptied into a petri dish and visually assessed to estimate percent by volume of different prey types, with a focus on *Bythotrephes*. Prey categories included *Bythotrephes*, unidentifiable zooplankton, macroinvertebrates, *Mysis*, and plant matter. When *Bythotrephes* were found in stomach contents, the total number of *Bythotrephes* individuals was counted, and the life stage of *Bythotrephes* (instar) was noted.

Since 2014, *Bythotrephes* density was estimated approximately every two weeks throughout the ice-free season. Each sampling day included two 30 m vertical tows that were taken with a zooplankton net (400 µm mesh and 0.5 m diameter). Entire samples were counted for *Bythotrephes* individuals to calculate species density. These samples were collected during the daytime. In addition, the broader predatory zooplankton community, i.e. *Chaoborus*, *Leptodora*, *Mysis*, and *Bythotrephes,* were sampled annually from several depths (10, 15, 20, 25, 32 m) using a zooplankton net (1 mm mesh and 1 m in diameter) since 1983. Three tows were taken at each depth except for at 32 m where five tows were collected. Predatory zooplankton sampling was conducted at night approximately on the same sampling date each year (July/August). Hereafter we will refer to the higher frequency daytime sampling as the "daytime" *Bythotrephes* sampling and the annual broader predatory zooplankton community sampling as the "nighttime" sampling. Water temperature was measured with a thermistor chain equipped to a buoy that is deployed throughout the ice-free season at the deep hole. Temperature data were collected at 1 m depth intervals and 1 min time intervals.

Cisco bioenergetics modeling

Cisco consumption

To examine the consumptive effect on *Bythotrephes* in Trout Lake, we estimated daily consumption rates (g consumed) of Cisco using Fish Bioenergetics 4.0 (Deslauriers et al. 2017) with physiological parameters developed for *Coregonus* spp. (Rudstam et al. 1994; Table 1). Model inputs included annual size-class specific Cisco starting weights (based on average weight from NTL-LTER vertical gillnet catches), diet composition (Keeler et al. 2015; Gatch et al. 2021), and prey item energy density (Dumont et al. 1975; Garton and Berg 1990). Diet composition was modeled at 10% *Bythotrephes* and 90% other with energy density values of 1,674 J/g wet weight (Stewart and Binkowski 1986; Bunnell et al. 2011; Walsh et al. 2017) and 3,000 J/g wet weight (Deslauriers et al. 2017), respectively. We estimated the daily thermal experience of Cisco as the daily mean whole water column temperature of Trout Lake's deep hole (~30 m) acquired *via* a long-term NTL-LTER buoy that records temperature every hour from the surface to bottom at 1 m intervals. Cisco consumption was estimated

Table 1. Parameter descriptions and values for the *Coregonus* species bioenergetics model from Rudstam et al. 1994.

Parameter	Value
Consumption equation used	$F(T) = VX \cdot e(X \cdot (1-V))$ (Kitchell et al. 1977)
CA; intercept fpr the consumption allometric mass function	1.61
CB; slope for the consumption allometric mass function	−0.32
CQ; water temperature-dependent coefficient of consumtion	3.53
CTO; optimal temperature for consumption (C)	16.8
CTM; maximum water temperature above which consumption ceases (C)	26.0
Respiration equation used	$F(T) = e(RQ \cdot T)$ (Stewart et al. 1983)
RA; intercept of the allometric mass function for standard metabolism	0.0018
RB; slope of the allometric mass function for standard metabolism	−0.12
RQ; rate at which the function increases over relatively low temperatures	0.047
SDA; specific dynamic action	0.17
Egestion equation used	$F = FA \cdot C$(Kitchell et al. 1997)
FA; egestion	0.25
Excretion equation used	$U = UA \cdot (C - F)$ (Kitchell et al. 1997)
UA; excretion	0.1

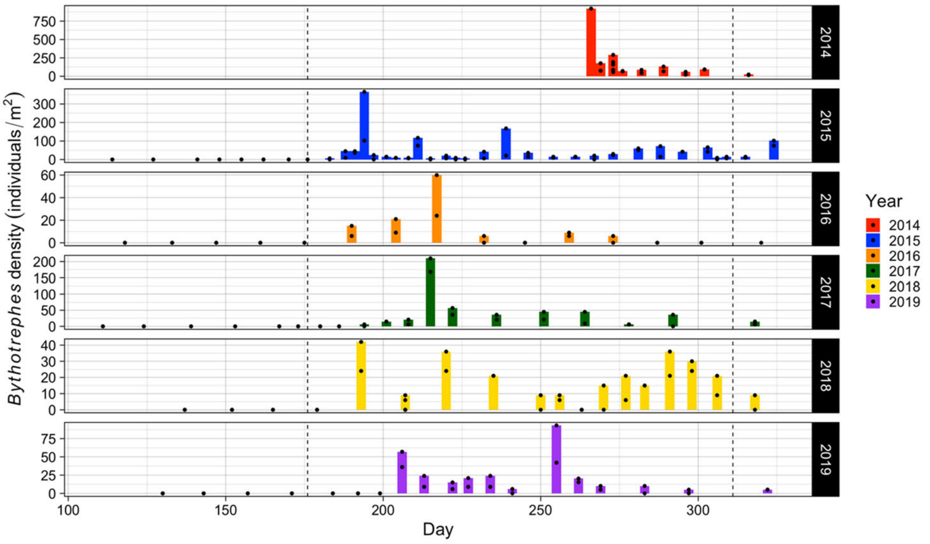

Figure 1. Daily *Bythotrephes* density (individuals/m^2) estimates from vertical zooplankton tows in Trout Lake, Vilas County, Wisconsin, USA, from 2014–2019. Each point represents an individual net tow estimate, with the bars showing the maximum estimate for each day. Dashed vertical lines at day 176 and 311 show the start and end of period modeled in subsequent graphs. Note the y-axis scales are adjusted for each year.

from one week before the earliest *Bythotrephes* seasonal detection to the latest that the majority of years had temperature data available (day of year 176–311, June 25–November 7, 135 d) (Figure 1). However, in instances of temperature data limitations, we estimated Cisco consumption during the *Bythotrephes* availability window only on the range of days where water temperature data existed. In 2016 there were issues with the data collection buoy that severely limited the available data and therefore we did not include 2016 in the models. Models were run by fitting to a specified p-value of 0.3 (Chipps and Wahl 2008; Deslauriers et al. 2017), where the p-value represents the proportion of maximum consumption with 0 representing no feeding and 1 indicating feeding at a maximum rate. To estimate

Table 2. Summary of studies that report Cisco (*Coregonus artedi)* diet proportions containing *Bythotrephes*.

Study	Study system	Sampling season	n	Cisco length	*Bythotrephes* proportion
Martin et al. (present study)	Trout Lake (WI, USA)	late Summer (August)	36	139–184	4%/ 22.5%*
Coulas et al. 1998	Harp Lake (Canada)	Summer- early Fall	57	214.5 (15.2)	15%
Gamble et al. 2011	Lake Superior	Summer	45	67–394	63%
		Fall	29	–	37%
Keeler et al. 2015	Lake Superior	Fall	101	<260	18%
			–	≥260	43%
Breaker et al. 2020	Lake Michigan	Spring-Fall	725	197–635	15%
Gatch et al. 2021	Lake Ontario	Summer (July)	10	200–250	6%
			32	250–300	27.8%
			65	>300	>99%

The sample size (n), and total length range (mm) are shown for Cisco from each study. *Bythotrephes* proportion is the average proportion across each study. A dash signifies the sample size or total length range applies to both size categories of Cisco reported. For Coulas et al. 1998, a size range was not reported so the average (standard deviation) is provided. A second diet proportion with an asterisk has been provided for the present study, which is calculated as the average *Bythotrephes* proportion from only fish that contained any *Bythotrephes*.

whole-lake *Bythotrephes* consumption, daily individual consumption rates of Cisco on *Bythotrephes* were multiplied by annual size-specific Cisco population estimates derived from hydroacoustic surveys (Magnuson et al. 2020a).

Bythotrephes biomass and production

To estimate *Bythotrephes* biomass, we first compared density estimates from the daytime and nighttime *Bythotrephes* sampling. *Bythotrephes* density estimates were generally higher from nighttime sampling than the daytime sampling, which is common for *Bythotrephes* and other zooplankton species (Supplementary Figures 1 and 2) (Keeler et al. 2015; Armenio et al. 2017; Doubek et al. 2020). However, as the nighttime surveys are only taken once a year, they are less likely to capture the seasonal peaks each year. Therefore, we used daytime sampling estimates to guide *Bythotrephes* biomass calculations. Given the primary goal of the model was to test if Cisco consumption could exceed *Bythotrephes* production, we erred on the side of overestimating *Bythotrephes* production when deciding how to model *Bythotrephes* production. Therefore, for each year, we applied the highest daytime *Bythotrephes* density in our biomass calculations to test if *Bythotrephes* densities could be regulated by Cisco predation. Although it is unlikely that average *Bythotrephes* densities were actually as high as the highest measured daytime density each year, by using such we are able to ensure we rigorously tested if Cisco consumption could exceed *Bythotrephes* production. The length-weight regression from Garton and Berg (1990) was used to calculate individual *Bythotrephes* weights. *Bythotrephes* biomass was converted from dry weight to wet weight by using a dry: wet weight ratio of 0.12 (Lehman and Cáceres 1993). Previously Keeler et al. 2015 multiplied daytime density estimates by 2.06 to account for day/night differences and therefore we did the same to allow for comparisons between our studies (Armenio et al. 2017). Ideally, we would have estimated our own value to account for day/-night differences, but the differences in our data were highly variable and limited to only five nighttime sampling events. To summarize, annual *Bythotrephes* biomass was calculated from the highest measured daytime density within each year, multiplied by 2.06 (Keeler et al. 2015). *Bythotrephes* biomass was modeled as a constant biomass each year, again to rigorously test if *Bythotrephes* densities could be regulated by Cisco predation. While *Bythotrephes* densities fluctuate throughout the season, our model is intended to test if Cisco predation could exceed production when *Bythotrephes* are at the highest densities we can reasonably expect. Daily thermal experience was modeled the same for *Bythotrephes* as

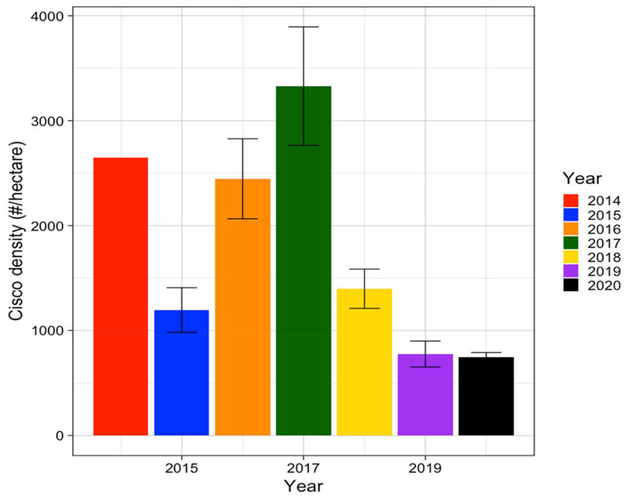

Figure 2. Cisco density estimates (# per hectare) from 2014–2020 for Trout Lake, Vilas County, Wisconsin, USA. Standard error is shown for each density estimate except for 2014 due to data limitations.

Cisco (daily mean column temperature at the deep hole). Daily *Bythotrephes* production was modeled using P/B daily $=10^{*}$ $(\alpha+\beta \cdot T)$ where $P=$ production (g m^{-2} day^{-1}), $B=$ biomass (g), and $T=$ epilimnetic temperature (°C), $\alpha=-1.725$ and $\beta=0.044$ (Shuter and Ing 1997). *Bythotrephes* production estimates were calculated on an areal basis (g wet wt. m^{-2} day^{-1}) in order to allow for comparison with Cisco consumption, which was also calculated on an areal basis. Daily Cisco consumption of *Bythotrephes* was then divided by daily *Bythotrephes* production. Ratio values >1 indicate Cisco consumption of *Bythotrephes* exceeded *Bythotrephes* production, suggesting Cisco predation limitation on *Bythotrephes*. A ratio <1 indicates *Bythotrephes* production exceeds Cisco consumption of *Bythotrephes*.

Results

The subsample of Cisco that were assessed for stomach content analysis was made up of smaller sized Cisco as they all came from the gillnet panel with the smallest mesh size (139–184mm; average= 163.1 mm) (Table 2). *Bythotrephes* were present in 6/36 Cisco stomachs, which included all stages of *Bythotrephes* (1^{st} through 3^{rd} instar). Among the Cisco that had consumed *Bythotrephes*, *Bythotrephes* made up 22.5% by estimated volume of the stomach contents (Table 2). Unidentified zooplankton species was the most abundant prey item in the Cisco diets.

Daytime *Bythotrephes* densities estimates were highly variable within the same sampling day and estimates taken within weeks of sampling also varied (Figure 1). *Bythotrephes* densities were highest during 2014 and 2015, with a single density estimate in 2017 reaching similar densities to these years (Figure 1). *Bythotrephes* densities were relatively low for the rest of 2017 (Figure 1). Across all years, the peak densities were spread throughout the ice-free season, but were always captured in our modeled date range (days 176–311).

Cisco population density shifted considerably throughout the invasion (Figure 2). Cisco density peaked in 2016 and 2017, and was lowest during 2019 and 2020 (Figure 2). The estimated Cisco density in 2014 was relatively high, however, the limitations in data did not allow for error to be calculated for that year (Figure 2). Modeled individual Cisco consumption of *Bythotrephes* peaked in the early Fall (~270d) (Figure 3a). Comparing

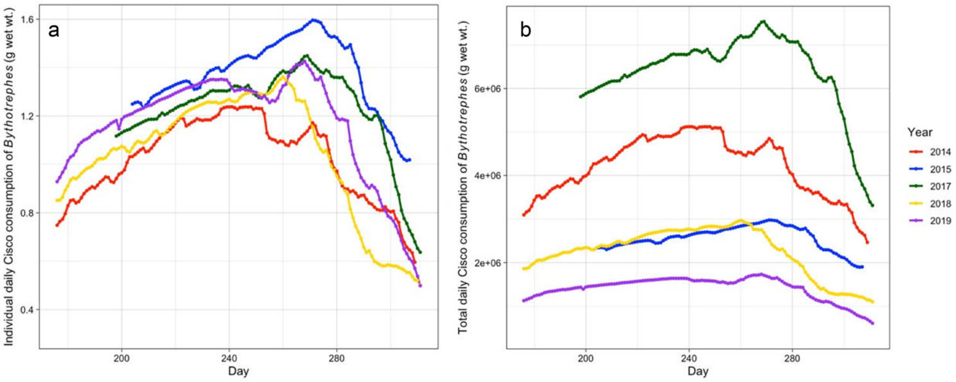

Figure 3. Modeled (a) individual and (b) total population daily Cisco consumption of *Bythotrephes* (g wet wt.) by day of year (176–311) in Trout Lake, Vilas County, WI, USA, from 2014–2019. Each year is displayed in a different color. 2016 is not shown because of insufficient temperature data for the model.

Table 3. Minimum, maximum, and average daily Cisco consumption (g wet weight) versus *Bythotrephes* production ratio from 2014–2019 for Trout Lake, Vilas County, WI, USA.

Year	Minimum daily Cisco consumption v. *Bythotrephes* production	Maximum daily Cisco consumption v. *Bythotrephes* production	Average daily Cisco consumption v. Bythotrephes production
2014	0.37	0.63	0.53
2015	0.43	0.83	0.64
2016		Insufficient data available to model	
2017	2.1	3.76	6.28
2018	4.1	7.06	3
2019	1	1.96	1.2

Cisco consumption was modeled using bioenergetic modeling and *Bythotrephes* production was modeled using a production to biomass approach. If the ratio is greater than 1, there is over consumption of *Bythotrephes* by Cisco. Temperature data was insufficient for modeling in 2016.

across years, modeled individual Cisco consumption was relatively similar (Figure 3a). At the population level, total Cisco consumption of *Bythotrephes* peaked in 2017 and was lowest 2019 (Figure 3b). The changes in modeled total Cisco consumption are largely reflective of shifts in annual Cisco population densities (Figures 2 and 3b). The modeled ratio of Cisco consumption of *Bythotrephes* to *Bythotrephes* production showed Cisco consumption did not exceed *Bythotrephes* production during the first two years of the invasion, however, Cisco consumption exceeded *Bythotrephes* production from 2017–2019 (Table 3 and Figure 4). The ratio of Cisco consumption to *Bythotrephes* production was highest during 2017, where the ratio peaked at 7.06 (Table 3 and Figure 4). *Bythotrephes* production was higher than Cisco consumption for all of 2014 and 2015, with 2014 having a lowest average ratio of 0.53 (Table 3). The ratio of Cisco consumption to *Bythotrephes* production was either higher or lower than 1 for the entirety of all years- in no years did the ratio cross between over and under 1 (Table 3 and Figure 4).

Discussion

Our model results showed predation pressure by native Cisco was substantial and likely limited *Bythotrephes* densities in Trout Lake, especially given the observed decline in *Bythotrephes* densities. Predation did not exceed *Bythotrephes* production during the first two years of the invasion, which is what we would expect given *Bythotrephes* densities were

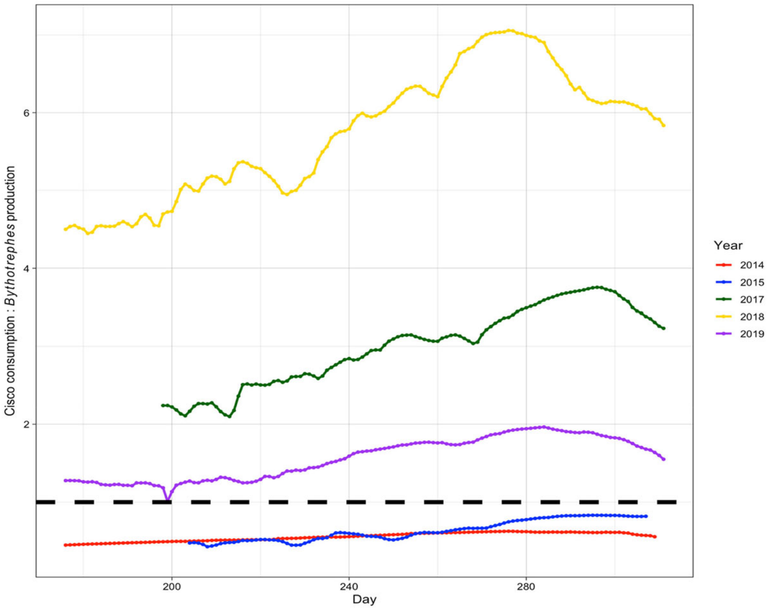

Figure 4. Ratio of modeled Cisco consumption of *Bythotrephes* to *Bythotrephes* production by day of year (176–311) in Trout Lake, Vilas County, WI, USA, from 2014–2019. The dashed horizontal line shows where Cisco consumption and *Bythotrephes* production are equal (1). Each year is displayed in a different color. 2016 is not shown because of insufficient temperature data for the model.

highest during these years (Table 3 and Figure 4). Importantly, Cisco population density increased early in the invasion and peaked during 2017, which was the year the model showed Cisco consumption to *Bythotrephes* production was highest (Figure 2). Excessive Cisco predation continued as our model showed Cisco predation exceeded *Bythotrephes* production during 2018 and 2019. The Cisco population estimate in 2020 was similar to that of 2019 (Figure 2), so we expect a similar level of Cisco zooplanktivory, however *Bythotrephes* densities fell to very low densities. In 2021, *Bythotrephes* densities remained at low densities. Given this invasion timeline, it is likely that Cisco predation was a limiting factor in the abundance of *Bythotrephes* in Trout Lake. Overall, our model was able to quantify and contextualize the predation pressure *Bythotrephes* experienced in Trout Lake.

In our study, we found that Cisco consumption of *Bythotrephes* exceeded *Bythotrephes* production at certain times, which corroborates several previous studies. A previous study in the nearshore of Lake Michigan showed Alewife (*Alosa pseudoharengus*), particularly those of larger body length, consumed *Bythotrephes* in large enough proportion that it exceeded *Bythotrephes* production (Pothoven et al. 2007). They further noted that *Bythotrephes* abundances were relatively low, especially in comparison to another invasive predatory zooplankton (*Cercopagis pengoi*) that was preyed upon less frequently by Alewife (Pothoven et al. 2007). Keeler et al. (2015) showed zooplanktivore consumption of *Bythotrephes* exceeded *Bythotrephes* production in Lakes Michigan and Superior. However, the habitats where zooplanktivore consumption of *Bythotrephes* exceeded *Bythotrephes* production were different for the two lakes, as were the individual zooplanktivore species. In Lake Michigan, they found that the nearshore habitat, where zooplanktivory was dominated by Alewife, had higher zooplanktivore consumption of *Bythotrephes* compared to *Bythotrephes* production, similar to Pothoven et al. (2007). In Lake Superior, the offshore habitat, where zooplanktivory was dominated by Cisco, had higher zooplanktivore consumption of *Bythotrephes* compared to *Bythotrephes* production (Keeler et al. 2015). Alongside these other studies, our study supports that *Bythotrephes* densities may be controlled by predation.

The Cisco population in Trout Lake declined in population density in the years prior to the *Bythotrephes* invasion, which may have allowed for the initial population irruption of *Bythotrephes*. In 2007, Lake Trout populations increased substantially, which caused a major decline in Cisco densities (Parks and Rypel 2018; Martin et al. 2022). During this period of low Cisco density, the potential predation pressure on *Bythotrephes* would have been even lower than the year our model indicated the lowest total Cisco consumption of *Bythotrephes* (2019). In many *Bythotrephes* invasions, it has been found that *Bythotrephes* were present at very low abundances prior to their first detections (Walsh et al. 2016b; DeWeese et al. 2021). During this period, the *Bythotrephes* population density is where we are unable to detect their presence with typical zooplankton community monitoring efforts. Analyzing sediment cores for *Bythotrephes* caudal spines has proven to provide insights into early invasion dynamics and if done in Trout Lake we could test this hypothesis and would add to the continued debate on the colonization history of *Bythotrephes* in North America (DeWeese et al. 2021; Karpowicz et al. 2021). Overall, the historically low Cisco densities in the years prior to the invasion may have played a role in the initial population irruption of *Bythotrephes*, but then increased Cisco densities in 2016/2017 quickly limited their success.

In our model for Trout Lake, we assumed that Cisco would be preying on *Bythotrephes* during the first year of establishment, yet that is not often the case for predation on invasive species. There is often a lag time before native predators switch to consuming novel prey (Carlsson et al. 2009), especially when the prey has defense mechanisms like *Bythotrephes* (Barnhisel 1991a; Straile and Halbich 2000). This lag time in predators adjusting to prey on novel resources has been documented in several cases and has shown predation pressure can increase as predators adjust (Carlsson and Strayer 2009; Carlsson et al. 2009, 2011). The barbed caudal spine of *Bythotrephes* contributes to significant "handling time" for smaller predators (Barnhisel 1991b; Compton and Kerfoot 2004). However, larger predators are capable of handling *Bythotrephes,* and preferentially prey on *Bythotrephes* (Coulas et al. 1998). In many cases *Bythotrephes* can reach high densities, especially relative to alternative prey items, which promotes native predators switching to *Bythotrephes*, however given the defense mechanisms this adjustment likely takes time. In our model, we used a constant diet proportion of 10% *Bythotrephes*, but this likely varied throughout the invasion, as well as seasonally. Our limited diet data confirmed *Bythotrephes* were incorporated into the diets of even relatively small Cisco in 2019, which was also when *Bythotrephes* was at relatively low densities (Table 2). Unfortunately, that data is only a single snapshot and does not include larger Cisco that are present in Trout Lake. More diet analysis was completed in 2020, however, *Bythotrephes* densities had already declined dramatically so there were not any *Bythotrephes* in the Cisco diets. A diet proportion of 10% is lower than that of many other Cisco and *Bythotrephes* diet studies including Keeler et al. (2015), Coulas et al. (1998), Gamble et al. (2011), Breaker et al. (2020), and Gatch et al. (2021) (Table 2). Therefore, a 10% diet proportion is our best estimate when also aiming to conservatively test if Cisco could regulate *Bythotrephes* densities (Keeler et al. 2015; Gatch et al. 2021). If there was a lag time in Cisco incorporating *Bythotrephes* into their diets, then it would push *Bythotrephes* production to further exceed Cisco predation in the early years of the invasion, likely in 2014 and 2015. However, if *Bythotrephes* were present at low abundances prior to their irruption in summer of 2014, then it is likely Cisco had already encountered *Bythotrephes*, albeit at low abundances, and could have readily adapted to preying on *Bythotrephes*. Importantly, with a reasonable estimate of 10% diet *Bythotrephes*, our model shows overwhelming consumption by Cisco by 2017, which corresponds with when we begin to see a decline in *Bythotrephes* densities. Ideally, we would have diet data throughout the invasion, but with only data from one year and on a small size class of fish, we felt it was best to use a constant diet proportion that is relatively low. Therefore, while our model does not incorporate changes in Cisco diet proportions throughout the invasion, a lag time or shift in predation on *Bythotrephes* is not likely to change the main result from our model.

Branstrator et al. (2006) noted two lakes in Minnesota where *Bythotrephes* were no longer observed, and they proposed the mechanism limiting *Bythotrephes* densities likely goes beyond simple zooplanktivore abundance. Beyond planktivore abundance, they suggested it is important to consider the presence of "predation refuge" (low-light, warm water, mid-depth) where *Bythotrephes* can minimize their risk of predation. The described predation refuge was hypothesized to be thermally incompatible for coldwater zooplanktivores (Cisco), while also being incompatible for low-light limited visual feeding warmwater fishes (Yellow Perch). They quantified light-refuge thickness using the following formula:

$$\text{Refuge thickness (m)} = \text{Maximum lake depth (m)} - (2.41 * \text{Secchi depth (m)})$$

In the cases where there is thicker light-refugia, it was suggested that zooplanktivore abundances would have a less direct control over *Bythotrephes* because *Bythotrephes* could better evade predators in the refuge habitat. For comparison, we have estimated refuge thickness for Trout Lake. Trout Lake's estimated refuge thickness since 2014 would be ∼24 m (Secchi depth ∼5 m; maximum depth = 35.7 m), which is much higher than the two Minnesota lakes where *Bythotrephes* were no longer observed (Boulder Lake = 0.9 m and Fish Lake = 7.9 m). Therefore, according to the predation refuge hypothesis, *Bythotrephes* in Trout Lake would have substantial habitat that minimizes predation risk. However the ample availability of proposed predation refuge was not enough for *Bythotrephes* in Trout Lake. The predation refuge hypothesis was not supported by a later study, where Cisco in Harp Lake, Canada occupied the proposed *Bythotrephes* refuge habitat (metalimnion) (Young et al. 2009). Cisco were also shown to selectively feed on *Bythotrephes* in Harp Lake (Coulas et al. 1998). Therefore, in addition to the work from Harp Lake, our study indicates predation refuge was not enough for *Bythotrephes* to overcome excessive predation pressure.

Bythotrephes life history traits make them problematic to model with a traditional modeling approach, which likely underestimates the predation necessary to mediate *Bythotrephes* densities. The main trait that makes *Bythotrephes* problematic for modeling is that *Bythotrephes* can successfully reproduce even after they are consumed by a predator (Jarnagin et al. 2000; Kerfoot et al. 2011). *Bythotrephes* diapausing eggs are still viable after passing through a predator's intestinal tract and subsequently excreted. The excreted eggs settle into lake sediment and then have the potential to successfully hatch. So, even though a predator removes an individual *Bythotrephes* from the population, there is still the potential for reproduction by the individual *Bythotrephes* that was preyed upon. This life history characteristic of *Bythotrephes* makes them unlike other prey species where an individual that is preyed upon is instantaneously removed from the population without reproductive potential. This predator-prey interaction can be likened to *endozoochory*, which is a common plant dispersal strategy where predators consume and disperse viable plant seeds. For *Bythotrephes*, a predator gains nutritional value by consuming *Bythotrephes*, but also the predator transports and excretes viable diapause eggs. While the diapause eggs do not hatch until the following season, this dynamic makes *Bythotrephes* complicated to model as a prey item because consumption does not exclude the possibility of successful reproduction from *Bythotrephes*. Overall, this life history characteristic of *Bythotrephes* causes traditional modeling to overestimate 'effective' predation rates because some *Bythotrephes* will successfully reproduce after being preyed upon. Development of a *Bythotrephes* specific predation model that would include this unique life history trait could greatly improve our ability to more accurately model their population dynamics.

While there may be more factors influencing the *Bythotrephes* dynamics in Trout Lake, our study highlights a key factor that can limit the abundance of a major invasive species. The shifts in *Bythotrephes* densities are unlikely to be simply driven by predation, or any other single factor, but our model results give us a sense for the potential impact of predation pressure on *Bythotrephes*. Boom-bust dynamics are common in species invasions and the invasion of *Bythotrephes* in Trout Lake is still relatively recent (<10 years) (Strayer et al. 2017). Long-term monitoring will continue for Trout Lake through NTL-LTER, and this will increasingly provide context for the dynamics at play in this invasion. So far, Trout Lake has provided an exceptional opportunity to understand the complex drivers of *Bythotrephes* population dynamics and impacts, as long-term study has given us 20 years of data prior to the invasion and increased monitoring since the invasion.

Conclusions

Here we have compared Cisco consumption of *Bythotrephes* and the population production of *Bythotrephes*. Our results indicate predatory pressure initially was low enough for the success of *Bythotrephes*, however, Cisco predation exceeded *Bythotrephes* production starting in 2017 and likely influenced the decline in *Bythotrephes* densities. The disappearance of *Bythotrephes* in invaded lakes has been observed in a few instances and our model results suggest that predation can limit *Bythotrephes* densities. Biological control of *Bythotrephes* and other invasive species is an important tool to minimize the impacts of invasive species, and this study provides as example of where a native predator may limit the population density of an invasive species. Long term data collection will continue on Trout Lake and we will have the opportunity to closely monitor the invasion and whether *Bythotrephes* densities will remain low or if they will rise again. The management of invasive species through predation is one of the few tools available for managers; therefore, it is important that cases where invasive species decline are documented and synthesized. These cases can help inform potential management actions like stocking or other food web alterations to mitigate the impacts of invasive species. As invasive species continue to colonize new systems, there will be more opportunities to test the role native predators have in managing invasive prey.

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Authors' contributions

BEM, JTM, and JVZ contributed to conception and design of the work, BEM, JTM, and JVZ contributed to the acquisition, analysis and interpretation of the data, BEM, JTM, and JVZ drafted and revised the manuscript.

Disclosure statement

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ORCID

Benjamin E. Martin http://orcid.org/0000-0001-7309-9871
Joseph T. Mrnak http://orcid.org/0000-0003-0909-7390
M. Jake Vander Zanden http://orcid.org/0000-0002-8122-1416

Code availability

Code will be made available upon request.

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