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ARTICLE
Freshwater Ecology

Long-term analysis of body condition reveals species coupling and the impacts of an invasion

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Abstract

Predator–prey coupling can result in oscillations of predator–prey densities. These oscillations in predator–prey densities correspond to oscillations in intraspecific competition where a high population density causes high intraspecific competition. Strong coupling of native species can however be disrupted by the introduction of invasive species into food webs. Here, we investigated how the body condition (body mass relative to body length) of a predator, lake trout, and its primary prey, cisco, changed as their respective population densities shifted. We found that the body condition of lake trout and cisco was strongly influenced by their respective population densities, that is, density dependence. The body conditions of lake trout and cisco were also inversely related, which highlights strong predator–prey coupling. Further, we were able to detect the impacts of a recent invasive species, *Bythotrephes*, as we saw size-specific shifts in the body condition of prey following the invasion. Overall, this study highlights how the long-term study of a simple measure, body condition, can reveal predator–prey coupling and yield new insights into the impacts of an invasive species.

KEYWORDS
body condition, *Bythotrephes*, food webs, invasive species, predator–prey coupling, trophic ontogeny

INTRODUCTION

Food webs in nature tend to be highly complex and dominated by weak interactions, thus dampening predator–prey coupling and stabilizing food webs (McCann et al., 2005). Yet, there are specific situations where pairs of species exhibit tight predator–prey coupling, such that the population dynamics of predator and prey are closely linked, that is, Lotka–Volterra dynamics (Elton, 1924; Elton & Nicholson, 1942; Holmengen et al., 2009). In such situations, the species pairs can oscillate between periods of high predator–low prey abundance and low predator–high prey abundance. Theory indicates that the highly abundant species in the species pair experiences high intraspecific competition, while the low-abundance species has reduced intraspecific competition and would be expected to be freed from resource limitation (Casini et al., 2016; Osenberg & Mittelbach, 1996). It is argued that these simple chains of strongly interacting species tend to produce trophic cascades—referred to by Strong (1992) as "runaway consumption." This implies that oscillating species pairs are not only oscillating in population densities but also in the degree of intraspecific competition.

An approach to evaluating the role of resource and predation limitation is to examine indicators of physiological state in a coupled species pair. Body condition, which is simply body mass relative to body length/size, is a meaningful indicator of organismal status (Froese, 2006; Nash et al., 2006), and has been used for a large diversity of taxa (Brown, 1996; Choquenot, 1991; Zipkin et al., 2020). Fisheries science, from stock assessment to aquaculture, has long used body condition to assess the overall well-being of individuals and populations (Lloret et al., 2014). While body condition has many drivers, it reflects energetic reserves, which impacts important life history traits (growth, reproduction, etc.) (Feiner et al., 2019; Lloret et al., 2014). Studies have found population density to affect body condition, where higher population density corresponds to lower body condition due to prey limitation (Feiner et al., 2019; Gaidet & Gaillard, 2008; Schindler et al., 1997). Conversely, populations with low density experience reduced competition for prey and thus are higher in body condition. This suggests that body condition may be an effective indicator of relative population density, particularly in coupled predator–prey where population densities oscillate in tandem.

In this study, we examined long-term changes in body condition of a coupled predator and prey: lake trout (*Salvelinus namaycush*; predator) and cisco (*Coregonus artedi*; prey) respectively, from Trout Lake, Vilas County, Wisconsin, USA. In the mid-2000s, the lake trout population increased substantially, which caused a trophic cascade around 2007 (Figure 1) (Martin et al., 2022; Parks & Rypel, 2018). This shifted the lake from having low lake trout–high cisco densities to high lake trout–low cisco density (Figure 1). The lake experienced a second shift in 2014 when the invasive zooplankton, *Bythotrephes cederstroemi* (spiny water flea; *Bythotrephes* hereafter), established (Figure 1). *Bythotrephes* preys on native zooplankton, competing for food resources with cisco. However, when cisco grow large enough, they are capable of preying upon *Bythotrephes* (Barnhisel & Harvey, 1995; Isaac et al., 2012; Keeler et al., 2015). Therefore, the rise of *Bythotrephes* complicated the previously simple relationship between lake trout and cisco densities as *Bythotrephes* introduced a new source of zooplanktivory (Martin et al., 2022). Given the links between population density and body condition, we hypothesized that body condition could be an indicator of intraspecific density dependence, as well as predator–prey coupling, whereby body condition oscillates with species densities. We hypothesize that body condition of a strongly coupled predator–prey will oscillate out of phase from one another. Therefore, we expect there to be a negative relationship between predator and prey body condition. We further hypothesized that an analysis of

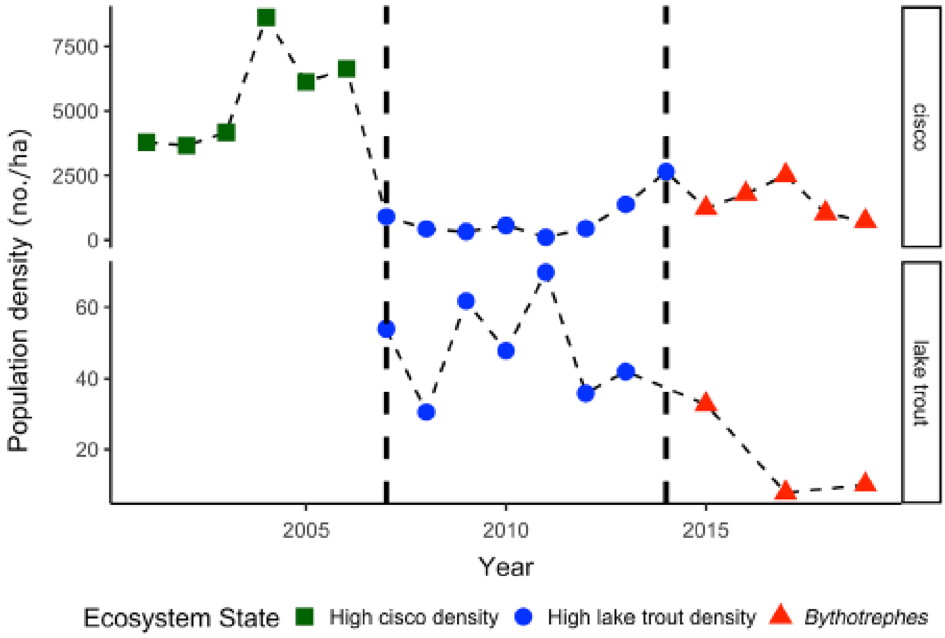

FIGURE 1 Population density estimates from hydroacoustic sampling for cisco and lake trout from 2001 to 2019 for Trout Lake, Vilas County, Wisconsin, USA. Dashed vertical lines in the years 2007 and 2014 represent transitions between ecosystem states. Ecosystem state 1981–2006 is characterized as "high cisco density," 2007–2014 as "high lake trout density," and 2015–2020 as *Bythotrephes* invasion. During the years 2001–2006, 2014, 2016, and 2018, the captured sample size for lake trout was too low for a population estimate to be calculated. Figure adapted from Martin et al. (2022).

long-term body condition in this coupled species could provide insights into the food web impacts of *Bythotrephes* by testing whether the relation between body condition and population density changed after invasion.

METHODS

Trout Lake is a 1608-ha oligotrophic lake with a largely forested watershed (Benson et al., 2006). Lake trout and cisco dominate the relatively simple pelagic food chain of Trout Lake and have been shown to exhibit strong predator–prey coupling (Martin et al., 2022; Parks & Rypel, 2018). All data were collected as part of the North Temperate Lakes Long-term Ecological Research (NTL-LTER), which has continuously collected ecological data from Trout Lake since 1981. All data are freely available at the NTL-LTER website (https://lter.limnology.wisc.edu/data). The data used in this study include lake trout and cisco lengths and masses collected from 1981 to 2019 and hydroacoustic population density estimates from 2001 to 2019 (Magnuson et al., 2020, 2022). Both datasets were collected annually during the summer within approximately the same week each year. All length–mass data were taken from fish captured by deep water trammel or vertical gill nets deployed annually for two nights each year. Yearly population density estimates were made from hydroacoustics surveys that were calibrated from the size and abundance of fish captured from gill nets each year (Mrnak et al., 2021; Parks & Rypel, 2018).

Data analysis

We used three approaches to evaluate changes in body condition of the coupled predator and prey species in Trout Lake across three distinct food web states we observed over time in the lake: high cisco density (1981–2006), high lake trout density (2007–2014), and *Bythotrephes* invaded (2015–2019) (Martin et al., 2022) (Figure 1). First, we tested for differences in the relationship between length and mass for each species across the three food web states. Both length and mass were log10-transformed to yield a linear relationship for analysis. We used analysis of covariance (ANCOVA) to test for differences in slope and intercept in length and mass among the three food web states. A post hoc test (Tukey honestly significant difference) was used to compare slopes and intercepts of length–mass relationships for each of the three food web states for both lake trout and cisco.

For the second approach, we used linear regression to calculate a universal log(length)–log(mass) relationship for each of the two species. The residual values from the universal relationship represent the body condition for each individual fish. Body condition was regressed against individual body length to test for length bias in the calculated body condition. For each year where at least three individuals of cisco or lake trout were captured per vertical gillnet sampling, we calculated the median body condition for each species. SD in annual body condition was calculated to be used as mass in linear regression. Weighted linear regression was used to test for a relationship between annual median body condition and population density for cisco and lake trout, where weighting was calculated as 1/annual SD in body condition. Finally, linear regression was used to test the relationship between mean annual body condition of cisco and lake trout in order to test their species coupling. For all analysis, minimum body lengths of 100 and 350 mm were used for cisco and lake trout, respectively, to reduce the influence of juvenile fish and gear selectivity (Zale et al., 2012). Sample sizes for cisco and lake trout used throughout analyses are displayed in Table 1. All data analysis was conducted using R-Studio (R Core Team, 2019).

RESULTS

Both analyses indicated a strong relationship between population density and body conditions of lake trout and cisco. Length–mass ANCOVA showed that both lake trout and cisco had significantly different intercepts, but not slopes between the high cisco and high lake trout density states (Table 1, Figure 2; Appendix S1: Table S1). For both species, the intercepts were lower when the respective species was in the highest density state. For cisco, the *Bythotrephes* invasion state had a significantly higher slope and lower intercept compared with the high cisco and high lake trout density states. For lake trout, the *Bythotrephes* period only had a significantly different intercept compared with the high lake trout density state, but the length–mass relationship did not differ between the *Bythotrephes* period and high cisco density state (Table 1, Figure 2; Appendix S1: Table S1).

The length–mass residuals analysis showed that body length was not significantly related to calculated body condition (cisco, $r^2 = -0.0005$, $F_{1,1866} = 0.097$, $p = 0.76$; lake trout, $r^2 = -0.005$, $F_{1,194} = 0.0001$, $p = 0.99$) (Appendix S1: Figure S1), and therefore, body lengths were pooled together for further analysis. Year-specific body condition for both cisco and lake trout was significantly negatively related to their respective densities (cisco, $r^2 = 0.298$, $F_{1,16} = 8.21$, $p = 0.011$; lake trout, $r^2 = 0.692$, $F_{1,8} = 21.2$, $p = 0.0017$) (Figure 3). Yearly

TABLE 1 Linear model results of cisco and lake trout log10 body mass and log10 body length during each ecosystem state.

Species	Ecosystem states	Slope	Intercept	n
Cisco	High cisco density	3.027 (0.02)^{a}	−5.19 (0.04)^{c}	1179
	High lake trout density	3.048 (0.02)^{a}	−5.194 (0.05)^{d}	343
	Bythotrephes invasion	3.151 (0.03)^{b}	−5.454 (0.07)^{e}	346
Lake trout	High cisco density	3.165 (0.096)^{f}	−5.546 (0.27)^{g}	81
	High lake trout density	3.081 (0.10)^{f}	−5.364 (0.28)^{h}	96
	Bythotrephes invasion	3.075 (0.18)^{f}	−5.302 (0.50)^{g}	19

Note: SE for slope and intercept coefficients are in parentheses. Sample sizes (n) for both species by ecosystem state are shown. Different superscripts in slope and intercept columns signify a statistically significant pairwise difference ($p < 0.05$) tested by analysis of covariance (ANCOVA). Detailed test statistics for pairwise ANCOVA are shown in Appendix S1: Table S1.

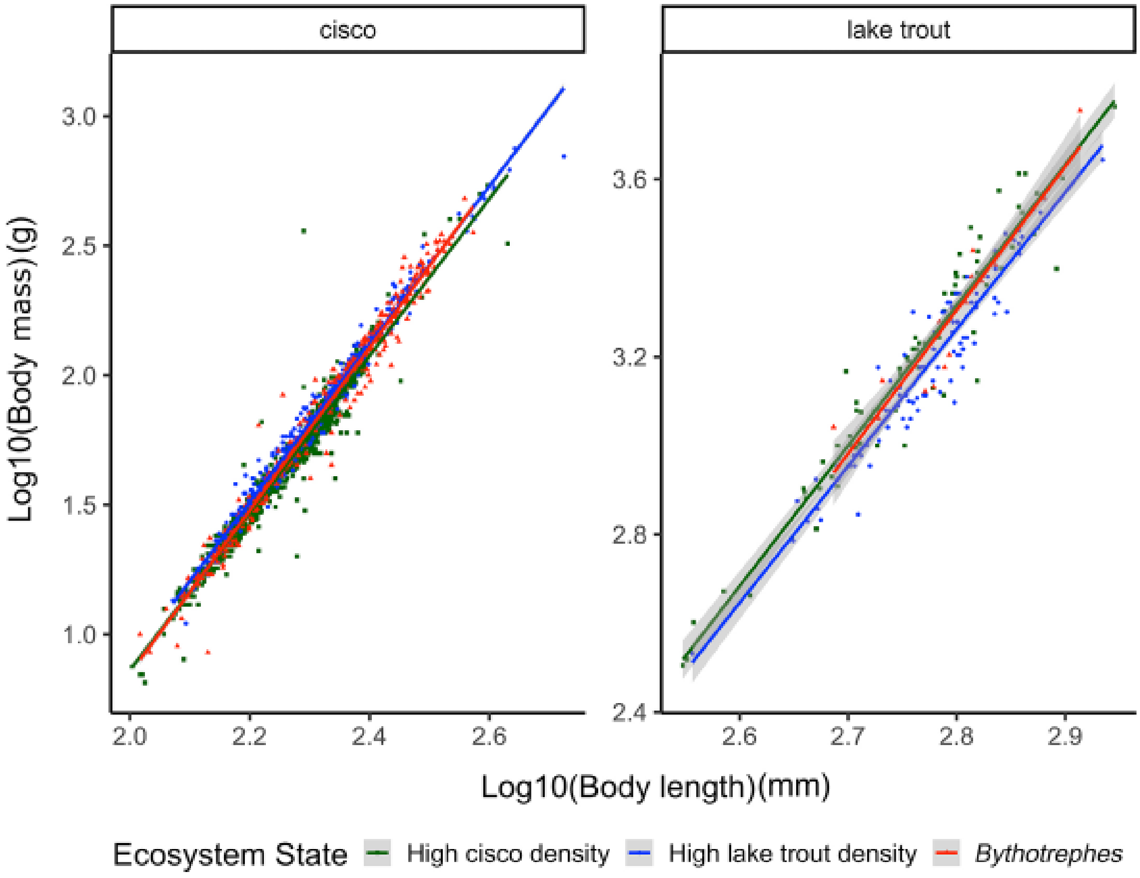

FIGURE 2 Linear models of log10 body mass and body length of cisco (n = 1884) and lake trout (n = 196) colored by ecosystem state. Linear models were tested for differences in slope and intercept using analysis of covariance, and the results are detailed in Table 1 and Appendix S1: Table S1. Colors signify the three ecosystem states: high cisco density (green), high lake trout density (blue), and *Bythotrephes* invasion (red) from Trout Lake, Vilas County, Wisconsin, USA, from 1981 to 2019.

median lake trout and cisco body conditions were significantly negatively related to each other ($r^2 = 0.197$, $F_{1,17} = 5.43$, $p = 0.032$) (Figure 4). However, there appeared to be an outlier year for lake trout, 1992, and without the 1992 data point, the relationship between lake trout and cisco body condition was strengthened ($r^2 = 0.315$, $F_{1,16} = 8.81$, $p = 0.0091$) (Figure 4).

DISCUSSION

In our case of strongly coupled predator–prey species, body condition was negatively related to population density within species, and the body conditions of predator and prey were inversely related to each other (Figures 3 and 4). These results indicate that body condition is

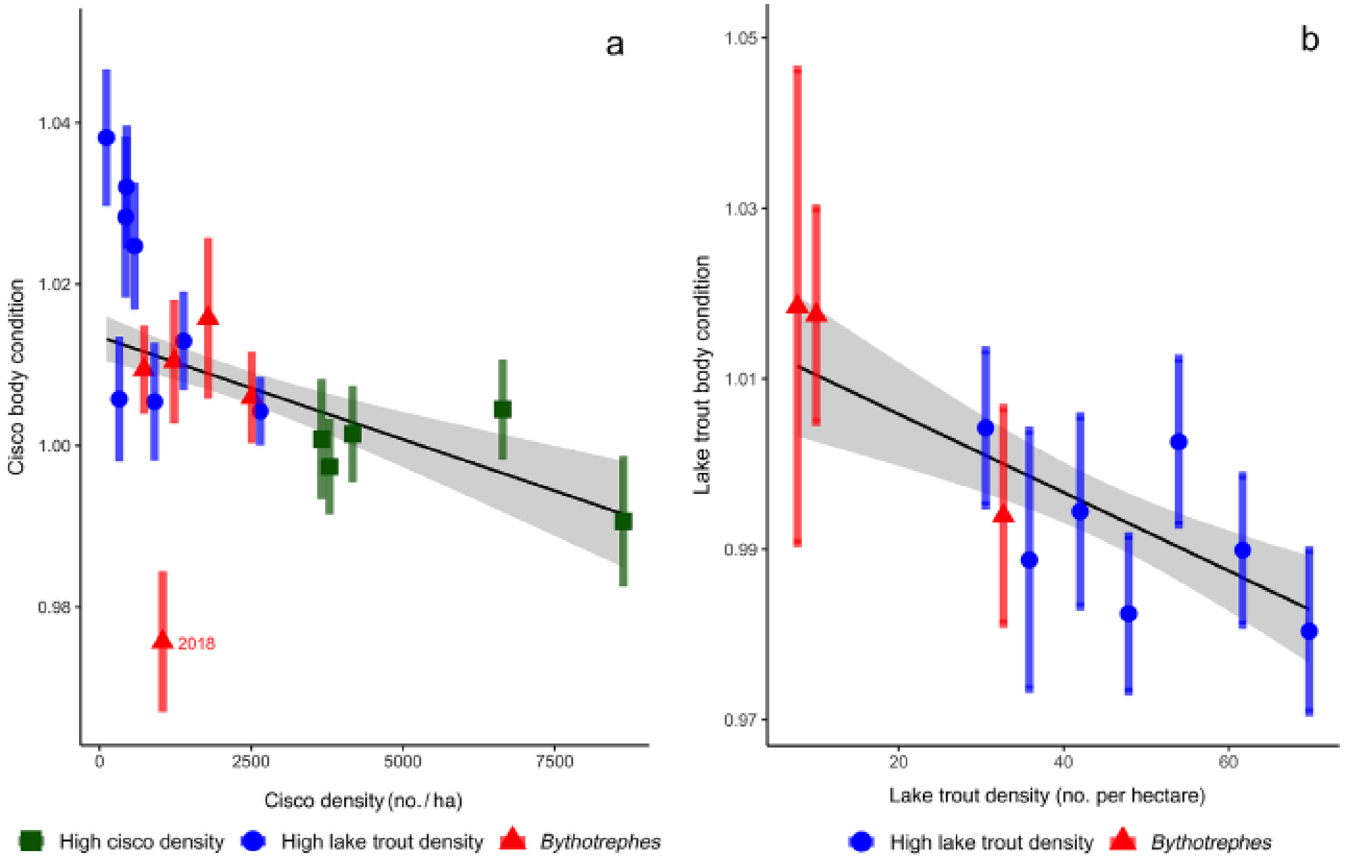

FIGURE 3 Annual mean body condition is negatively related to the density of both (a) cisco ($n = 17$) ($r^2 = 0.298$, $F_{1,16} = 8.21$, $p = 0.011$) and (b) lake trout ($n = 11$) ($r^2 = 0.692$, $F_{1,8} = 21.2$, $p = 0.0017$). Error bars represent 95% CIs. Colors signify the three ecosystem states: high cisco density (green), high lake trout density (blue), and *Bythotrephes* invasion (red) from Trout Lake, Vilas County, Wisconsin, USA, from 1981 to 2019.

reflective of oscillating predator and prey densities observed for coupled species pairs. The length–mass ANCOVA further supported that body condition was density-dependent as there was no change in slope, rather a change in intercept in the length–mass relationship in cisco and lake trout prior to *Bythotrephes* invasion (Table 1). While this is not the first example where population density strongly influenced individual body condition (Casini et al., 2016; Kamimura et al., 2021; Schindler et al., 1997), it is one of only a few cases where it was shown for coupled predator and prey. Classic theory suggests that a species undergoing high intraspecific competition would experience resource limitation and thereby have lower body condition (Laidre et al., 2006; Rennie & Verdon, 2008; Sass et al., 2004). Therefore, in the case of oscillating abundance of coupled predator and prey, we would expect to see similar but opposite oscillations in body condition for both species. Our results suggest this relationship could also occur in other classic examples of coupled predator and prey such as hare and lynx where we would see a strong inverse relationship in predator–prey body condition (Stenseth et al., 1997). Another example would be the foundational trophic cascade experiments in North Temperate Lakes that found predator (largemouth bass) population density to be strongly related to body condition; however, it is unknown whether this extended to zooplanktivorous fish (Schindler et al., 1997). In classic cases of strong predator–prey coupling, the oscillations in predator–prey densities are likely to be related to resource limitation, which perpetuate to the individual bioenergetic condition of an organism. Martin et al. (2022) showed the abundance of cisco prey resources, larger bodied zooplankton, was lower during the time of high cisco density, which supports the strong relationship between population density and body condition. Similarly, the increase in lake trout densities led to intraspecific competition for cisco as prey. It is worth considering that the ecological conditions for this strong relationship between density and body condition are rather specific to relatively simple food chains where resource limitation occurs. However, occurrences of these dynamics present an opportunity to empirically test classic ecological theory.

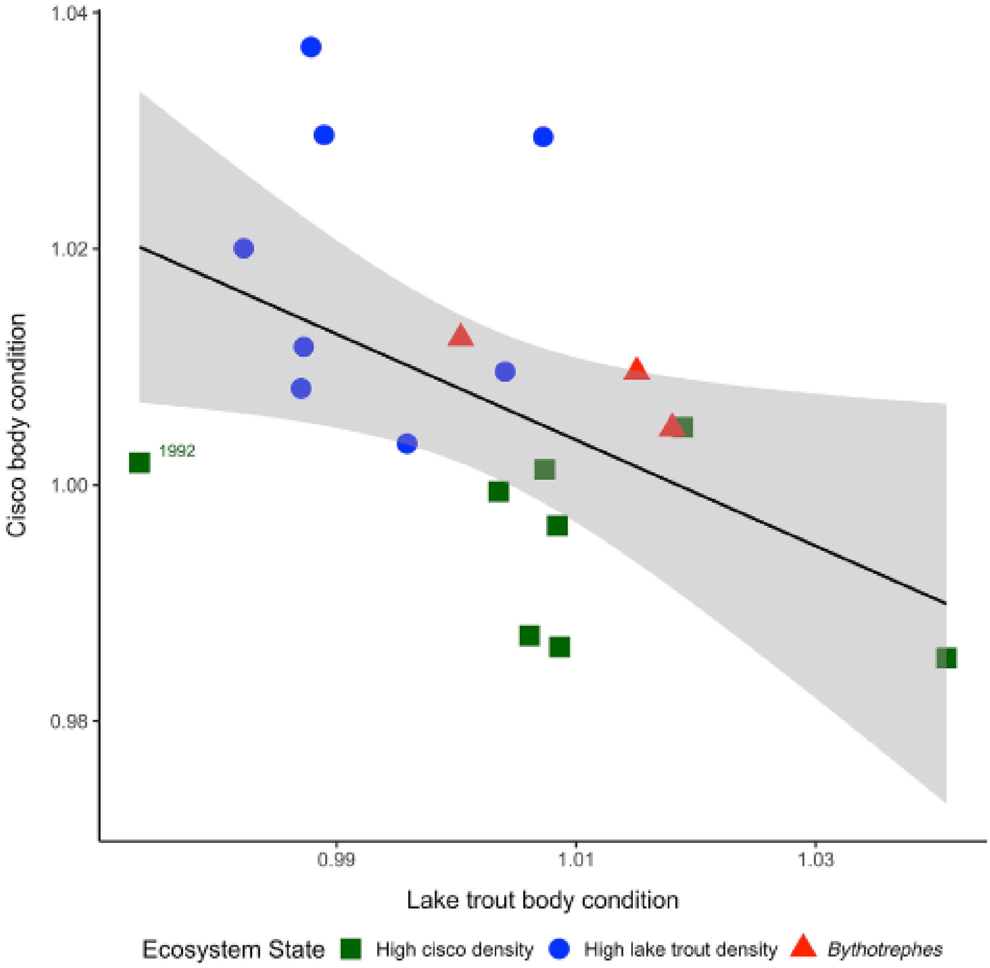

FIGURE 4 Yearly ($n = 19$) median body conditions for prey and predator are inversely related ($r^2 = 0.197$, $F_{1,17} = 5.43$, $p = 0.0324$). The linear model improves when removing 1992 as an outlier ($r^2 = 0.315$, $F_{1,16} = 8.81$, $p = 0.0091$). Colors signify the three ecosystem states—high cisco (green), high lake trout (blue), and *Bythotrephes* invasion (red) ecosystem states from Trout Lake, Vilas County, Wisconsin, USA, from 1981 to 2019.

Species invasion and body condition

In our study, the relationship between annual cisco body condition and population density was maintained through *Bythotrephes* invasion (red points in Figure 3a). This initial result could suggest that *Bythotrephes* invasion did not have an impact on the body condition of cisco body. However, the linear regression ANCOVA results showed the length–mass regression during invasion years had a higher slope and lower intercept than the other two ecosystem states. A higher slope reveals a size-dependent effect where smaller cisco were in lower body condition and larger cisco were in higher condition during invasion years relative to the pre-invasion states. For lake trout, the length–mass relationship during the *Bythotrephes* invasion did not differ in slope with either of the previous states but had a higher intercept with the high lake trout density state. The lack of change in the slope of the length–mass relationship for lake trout is not too surprising given the lake trout sample size is low during the invasion, and lake trout and *Bythotrephes* have a more indirect interaction than cisco and *Bythotrephes*.

A size-specific change in cisco body condition supports that the interaction between cisco and *Bythotrephes* shifts throughout the life of a cisco. As a functional zooplanktivore, *Bythotrephes* compete for food resources with cisco, a functional zooplanktivore itself. However, cisco are fairly long-lived and exhibit trophic ontogeny, where they consume larger prey items as their body size increases (Link & Hoff, 1998; Muir et al., 2013). This trophic ontogeny makes the predator–prey relationship between cisco and *Bythotrephes* complex. Smaller zooplanktivorous fish have been shown to consume low proportions of *Bythotrephes*, and therefore, the interaction between smaller zooplanktivores and *Bythotrephes* is described as one of the resource competition for native zooplankton (Barnhisel & Harvey, 1995; Compton & Kerfoot, 2004; Jarnagin et al., 2004). However, larger zooplanktivores have been shown to readily prey on *Bythotrephes* (Barnhisel & Harvey, 1995; Isaac et al., 2012; Keeler et al., 2015). Specifically for cisco, *Bythotrephes* can be a substantial and sometimes preferred prey resource (Coulas et al., 1998; Gamble et al., 2011; Keeler et al., 2015). This difference in cisco–*Bythotrephes* interaction aligns with our finding of smaller cisco in lower body condition and larger cisco in higher body condition after *Bythotrephes* invasion. Research studies continue to address the potential impacts of *Bythotrephes* on fisheries in North America but have generally lacked the required long-term data needed to more rigorously test for size-dependent interactions. While some studies have shown negative impacts of *Bythotrephes* on juvenile fish (Hansen et al., 2020; Rennie et al., 2010), our analysis provides empirical evidence that the impacts of *Bythotrephes* is size dependent and not necessarily bioenergetically harmful for larger fish. Overall, we found that synthesizing long-term trends in body condition was able to reveal key insights into an applied ecological issue that continues to be investigated by the field.

While we found that there were statistical differences in body condition between ecological regimes, there is still question of whether those differences are biologically meaningful. Using the length–mass relationships in our ANCOVA, we estimate that when cisco are at a lower population density, they are ~1 g heavier at 110 mm, ~6 g heavier at 200 mm, and ~60 g heavier at 415 mm. In other words, cisco body mass is ~10% greater during the high lake trout density period. Further, we can relate this change in body mass to change in fecundity by using the mass–fecundity relationship for cisco from Yule et al. (2006). For a 200-mm cisco, a 6 g increase in body mass equates to an increase in fecundity of ~300 eggs, and for a 415-mm cisco, there is an increase of ~2700 eggs (Yule et al., 2006). This increase in fecundity while cisco are at low densities is a positive feedback for the population and could allow them to recover from low densities. Therefore, while the differences in our ANCOVA seem rather small, when considering the physical differences in body mass and its relation to fecundity, the change in body condition is biologically relevant.

Sample size and error

Sample sizes and potential error are especially worth noting because while the relationships are significant and ecologically sound, annual lake trout sample sizes are low and there are a couple of suspect data points. Firstly, LTER sampling protocol is not specifically designed to target lake trout, and annually, there are usually between 3 and 10 lake trout captured across the two-day sampling period. Additionally, there is an associated error that comes from using a spring scale to weigh a fish on a rocking boat. The 2018 cisco condition data (annotated in Figure 3a) are suspected, and historical weather data show there were high winds. Further, the 2018 point is the lowest mean cisco body condition, which is highly unlikely considering in 2017 and 2019, cisco were in "moderate" body condition. For lake trout, 1992 has a suspect data point (annotated in Figure 4) as it was the historically lowest lake trout body condition, even though 1991 and 1993 were slightly above one. Again, this seems highly unlikely and is why we have included data analysis with and without the 1992 data point. Overall, human error is inevitable in a study like this due to 40 years of personnel turnover, weighing fish on a rocking boat, and low lake trout sample sizes. However, it is noteworthy that we can still significantly relate population density of both predator and prey from their length–mass relationships. This additionally highlights how strongly coupled these species are in our study system given the relationships were significant despite the associated sampling error.

In our case, the simplicity of this food web provided a unique opportunity to see strong relationships between population density and body condition that may not be evident in more complex systems. In addition, long-term data collection allowed us to evaluate the effect an invasive species can have on a strongly coupled predator–prey. Overall, we find this to be an intriguing example where synthesizing long-term changes in body condition yielded insights into both basic and applied ecology that continues to be investigated by the field.

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CONFLICT OF INTEREST STATEMENT

The authors declare no conflicts of interest.

DATA AVAILABILITY STATEMENT

The data (Magnuson et al., 2020, 2022) are available from the Environmental Data Initiative: https://doi.org/10.6073/pasta/7540b9201b1dbc7ab1074d40cf9da115 and https://doi.org/10.6073/pasta/5d81c463cc5be38f7dd96eae2715322f.

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SUPPORTING INFORMATION

Additional supporting information can be found online in the Supporting Information section at the end of this article.

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