Received: 31 January 2024 | Revised: 13 May 2024 | Accepted: 29 June 2024

DOI: 10.1111/jfb.15874

REGULAR ARTICLE

JOURNAL OF FISH BIOLOGY fsbi

Stable isotopes reveal trophic ontogeny in Cisco (*Coregonus artedi*)

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Funding information
National Science Foundation, Grant/Award Number: DEB-1440297; Wisconsin Department of Natural Resources

Abstract

Cisco (*Coregonus artedi*) are a widespread, cold-water zooplanktivore native to North America. Although Cisco are generally referred to as an "obligate zooplanktivore," there is some evidence that the species exhibits considerable variability in trophic niche. Here, we assessed how Cisco body size relates to trophic position, that is, trophic ontogeny. We analysed ^{13}C and ^{15}N isotopes from Cisco ranging from 127 to 271 mm in body length ($n = 66$) from Trout Lake, Vilas County, Wisconsin, USA. ^{15}N isotopes showed smaller Cisco had a trophic position of ~3, which steadily increased to ~3.5 for larger Cisco. Further, ^{13}C isotope signatures showed Cisco transitioned to be more pelagically reliant (lower ^{13}C signatures). Using gillnet catch data, we found that larger Cisco were using deeper habitats than smaller Cisco. Our results support that Cisco have significant variability in trophic niche even though they are traditionally thought of as an obligate planktivore. Overall, we emphasize that researchers should be cautious when generalizing Cisco trophic function, particularly when considering the broader food web.

KEYWORDS
Cisco, *Coregonus artedi*, stable isotopes, trophic ontogeny, zooplanktivore

1 | INTRODUCTION

Cisco (*Coregonus artedi*) are a cold-water species that are highly studied throughout their range in North America (Page & Burr, 2011). In many inland lakes, Cisco are a highly populous species, and as a zooplanktivore, they can strongly structure zooplankton communities (Lampert & Sommer, 2007; Martin et al., 2022; Rudstam et al., 1993). Cisco are also an important prey resource for many piscivorous species of economic and ecological importance like lake trout (*Salvelinus namaycush*), muskellunge (*Esox masquinongy*), northern pike (*Esox lucius*), and walleye (*Sander vitreus*) (Kennedy et al., 2018; Mrnak et al., 2023; VanderBloemen et al., 2020). Cisco are often regarded as an "obligate zooplanktivore," yet there is growing evidence of Cisco feeding on higher trophic level prey, particularly when they increase in body size, that is, trophic ontogeny (Breaker et al., 2020; Muir et al., 2013; Mullins, 1991; Rosinski et al., 2020). However, there is a lack of consensus as to whether Cisco undergo trophic ontogeny.

Trophic ontogeny is common among fishes as gape size increases with body size, and thereby larger fish can consume larger, higher trophic level prey (Sánchez-Hernández et al., 2019). For Cisco and other zooplanktivorous fishes, gill raker morphology is an additional determinant of the size of prey items consumed (Gibson, 1988; Kahilainen et al., 2011; Langeland & Nøst, 1995). It was long thought that gill rakers act as a basic sieve filtering out prey items based on body size (i.e., dead-end sieve) (Hessen et al., 1988). However, more recent theory suggests that gill rakers function as a cross-flow filter (Sanderson et al., 2001; Smith & Sanderson, 2008). In a cross-flow filter, prey items move tangentially across the gill rakers rather than perpendicularly through the rakers like a dead-end filter. Here, the gill rakers filter prey items by size, and inter-gill raker spacing determines the minimum size of prey to be retained. Importantly, prey items that are retained by the gill rakers proceed to the oesophagus and are consumed. Inter-gill raker spacing increases with Cisco body size, and therefore the minimum retained prey item size also increases with body size (Langeland & Nøst, 1995; Link & Hoff, 1998; Mullins, 1991). Given this relationship between gill rakers and prey size selection, we expect Cisco trophic position to increase with body size, thereby establishing trophic ontogeny.

Here, we asked whether Cisco undergo trophic ontogeny in an inland lake and to examine whether ontogenetic shifts play a role in the ecology of the species? We used stable isotope analysis of ^{13}C and ^{15}N to detail the trophic niche of Cisco across a range of body sizes. Further, we investigated the relationship between Cisco body size and habitat occupancy to understand ontogenetic shifts in habitat occupancy.

2 | STUDY SYSTEM

Trout Lake is a 1608-hectare oligotrophic lake in Vilas County, Wisconsin, USA. The lake 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 past 70 years for sportfishing opportunities (Ahrenstorff et al., 2013; Piller et al., 2005). In Trout Lake, Cisco dominate pelagic zooplanktivory, and their population dynamics are mediated from the top down by lake trout (Martin et al., 2022; Parks & Rypel, 2018). The zooplankton community comprises large-bodied grazers, including *Daphnia* and *Calanoida* taxa, and smaller-bodied cyclopoid, rotifer, and copepod nauplii (Martin et al., 2022). There are also several predatory zooplankton species, including *Chaoborus*, *Mysis*, *Leptodora*, and, recently invasive *Bythotrephes* (Martin et al., 2022). Shifts in the pelagic food web occurred when lake trout abundances rose between 2007 and 2014 and when *Bythotrephes* invaded in 2014 (Martin et al., 2022). The increase in lake trout abundance between 2007 and 2014 coincided with a major decline in Cisco abundances. During this time, Cisco abundance was the lowest observed in several decades (Martin et al., 2022). By 2020, *Bythotrephes* abundance had declined, and the species was barely detectable even with frequent monitoring (Martin et al., 2023). Since 2020, only a few *Bythotrephes* individuals have been collected, so it is believed that their population crashed likely due to high predation by Cisco (Martin et al., 2023).

3 | MATERIALS AND METHODS

Zooplankton and benthic macroinvertebrates were sampled to establish baseline stable isotope reference points (Vander Zanden & Rasmussen, 1999). Zooplankton were sampled with a vertical tow using a Wisconsin net from the deepest depth of the lake (32 m). Zooplankton samples were sorted to remove predatory taxa, that is, *Mysis*, *Chaoborus*, *Leptodora*, and *Bythotrephes*. Benthic macroinvertebrate samples were collected using an Eckman dredge and a D-frame net. Profundal benthic macroinvertebrate samples were collected from the deepest depth of the lake within a few days of the fish sampling. Littoral benthic macroinvertebrate samples were collected using a D-frame net in ~1 m of water. All benthic macroinvertebrate samples were grouped and analysed by functional feeding groups.

Pelagic fishes were captured using a 24-h vertical gillnet survey following standardized North Temperate Lakes-Long Term Ecological Research (NTL-LTER) protocols (Magnuson et al., 2022; Mrnak et al., 2021). On July 27 and August 20, 2020, seven monofilament nets were set in the deepest part of the lake for 24 h. Nets extended from surface to bottom (~30 m). Vertical gillnets were 3 × 30 m with stretched mesh-sizes of 19, 25, 32, 38, 51, 64, or 89 mm. After 24-h, vertical gillnets were picked, and fish species were enumerated, measured to the nearest millimeter (total length [TL]), and weighed to the nearest gram.

3.1 | Ethics statement

The care and use of experimental animals complied with U.S. Fish and Wildlife welfare laws and animal care and use guidelines outlined by the University of Wisconsin, Madison (protocol number: A006182).

3.2 | Stable isotopes

An ~1-mg piece of muscle tissue was sampled from individual Cisco at the caudal peduncle above the lateral line. Invertebrate samples were homogenized from whole-body samples of several individuals of the same taxa. Fish and invertebrate samples were dried in an oven for 24–48 h. Dried tissue was ground using a mortar and pestle, and ~1 mg was packed into a tin. Prepared tissue samples were sent to the UC-Davis Stable Isotope Facility for analysis of ^{13}C and ^{15}N (https://stableisotopefacility.ucdavis.edu/13cand15n.html). ^{15}N was corrected for baselines following methods outlined by Vander Zanden and Rasmussen (1999). In short, baselines from both the pelagic and littoral habitats were used to establish a lake-specific residual value, and the ^{13}C values were then used to calculate corrected ^{15}N values. The corrected ^{15}N values were then used to calculate trophic position that accounts for habitat differences in baseline isotope values. We included an older collection of stable isotope samples (2003) that focused more on littoral invertebrates, as the current collection was limited in the number of littoral taxa represented. Although these are unlikely to be prey resources for Cisco, they can be helpful to contextualize the entire range of stable isotope values within the food web. We visualized the trend in body size and isotope values with a loess smooth line. All statistical analysis and plots were generated using R Studio (R Core Team, 2019).

3.3 | Habitat use

We used NTL-LTER data from gillnet surveys to investigate if Cisco body size relates to vertical habitat use. The depth at which individual Cisco are captured was recorded, as well as body length. We statistically tested the relationship between depth of capture and Cisco body

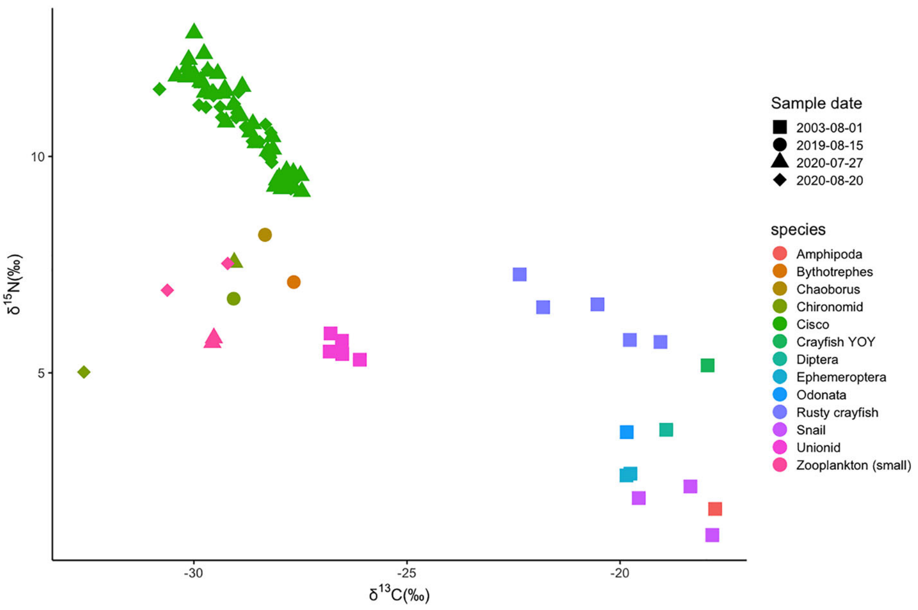

FIGURE 1 ^{15}N and ^{13}C biplot of Cisco (*Coregonus artedi*), zooplankton, and benthic macroinvertebrate taxa from Trout Lake, Wisconsin, USA. Sampling dates ($n = 4$) are shown as different shapes, and taxa ($n = 13$) are shown in different colors.

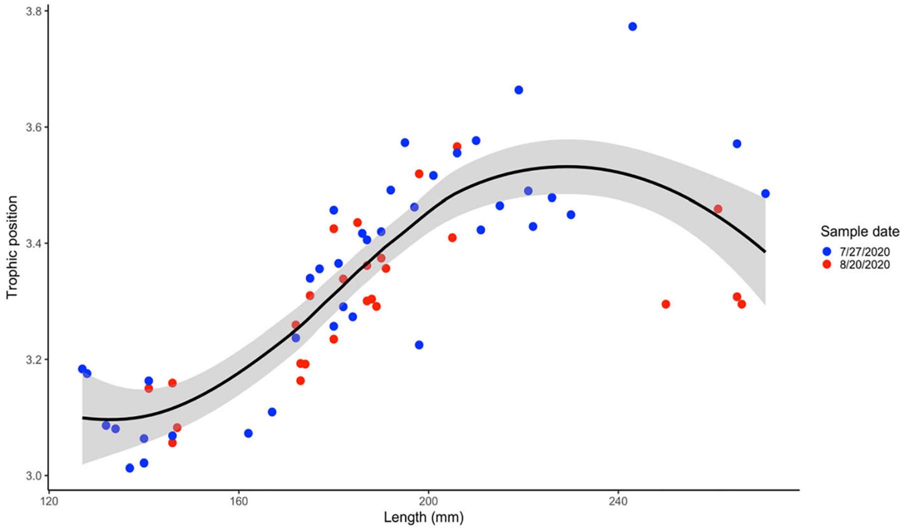

FIGURE 2 Trophic position and Cisco (*Coregonus artedi*) body length (in millimeters) from Trout Lake, Wisconsin, USA, in 2020. Points are colored by sample date. Trophic position was adjusted for baselines using methods detailed in Vander Zanden and Rasmussen (1999). A loess smooth line (span = 0.9) is displayed as a visual aide.

size using a linear regression and evaluated year as an interaction term. We limited the analysis to post-*Bythotrephes* invasion years as the relationship between *Bythotrephes* and Cisco has been noted to cause changes in diel vertical migration behavior (Young & Yan, 2008).

4 | RESULTS

Baseline stable isotope values from a suite of zooplankton and benthic macroinvertebrates followed general trends observed from freshwater lakes in North America (approximately −30 to −20 for ^{13}C) (Figure 1) (Fry, 1991). Baseline isotope values were relatively similar from recent sample dates. The species collected in the 2003 sample date had little overlap with the more recent collections. Stable isotopes of ^{15}N revealed that Cisco trophic position increased with body size (Figure 2) even after trophic position was adjusted from baseline data. Trophic level steadily increased with body size rather than incrementally. Stable isotopes of ^{13}C showed that Cisco shifted from moderate littoral reliance to rely more on pelagic resources (Figure 3). ^{13}C values decreased steadily with body size (Figure 3). The gillnet catch data indicated that larger Cisco were captured at deeper depths ($r^2 = 0.16$, $F_{2,3494} = 342.4$, $p < 0.001$) (Figure 4). We did not see a strong year effect as an interaction term ($t = -1.84$, $p < 0.001$ $p = 0.07$) (Figure 4). Although we saw evidence for trophic ontogeny, we were unable to point to the prey resource contributing to the increased Cisco trophic position because our sampling did not capture some profundal taxa as they rarely occurred in zooplankton samples (Martin et al., 2022).

5 | DISCUSSION

Stable isotope analysis confirmed that Cisco in Trout Lake undergo trophic ontogeny, as their trophic position increased by approximately

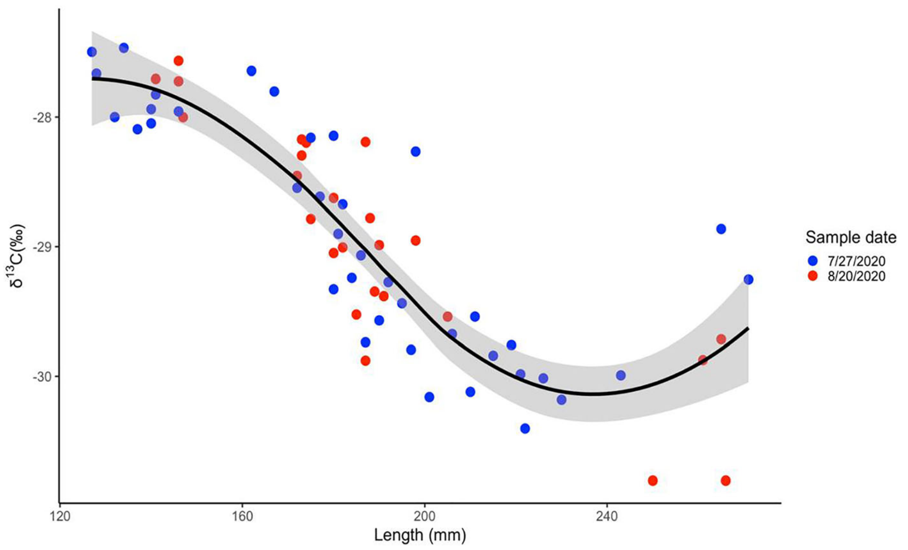

FIGURE 3 ^{13}C and body length (in millimeters) of Cisco (*Coregonus artedi*) from Trout Lake, Wisconsin, USA, in 2020. Points are colored by sample date. A loess smooth line (span = 0.9) is displayed as a visual aide.

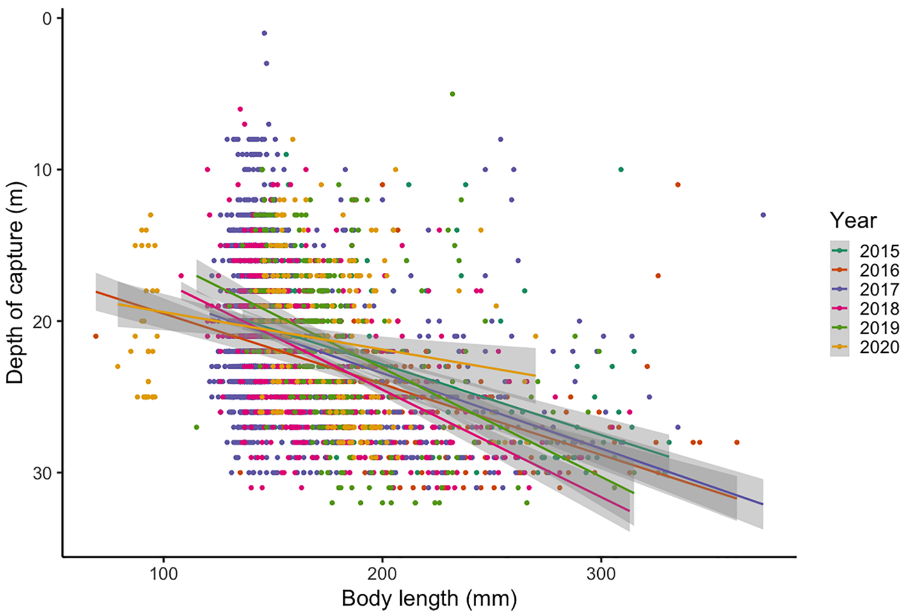

FIGURE 4 Cisco (*Coregonus artedi*) depth of capture (in meters) from vertical gillnets based on individual body length (in millimeters) from the years 2015 to 2020 (post- *Bythotrephes* invasion) from Trout Lake, Wisconsin, USA. Points are colored by the year. Body length was significantly related to depth of capture ($r^2 = 0.16$, $F_{2,3494} = 342.4$, $p < 0.001$). This relationship was mostly similar across years as year was tested as an interaction term in the linear model ($p = 0.07$).

half a trophic level in our study. Even after adjusting ^{15}N values from our baseline samples, we saw trophic position increased steadily as individuals were larger (Figure 2). Notably, our Cisco samples did not exceed 275 mm in body length, but Cisco can exceed 500 mm in length (Page & Burr, 2011). Cisco in Trout Lake grow well beyond the maximum size we analysed for isotopes here and, therefore, may continue to shift in trophic niche (Martin et al., 2022; Martin & Vander Zanden, 2023). Although our results show trophic ontogeny, an unfortunate shortcoming is that we were unable to pinpoint the higher trophic level prey resources that the larger cisco are consuming due to the rarity of capturing some taxa in zooplankton nets (Martin et al., 2022). From what we know about the food web in Trout Lake, larger Cisco are likely preying on predatory taxa such as *Mysis*, *Chaoborus*, *Leptodora*, or some *Calanoida* species (Martin et al., 2022). Given what we know about the invertebrate community of Trout Lake (Martin et al., 2022) and the trophic ecology of Cisco in other lakes (Grow et al., 2022; Ridgway et al., 2020; Rosinski et al., 2020), it is most likely that the observed increase in trophic position is due to larger Cisco consuming a combination of predatory invertebrate taxa, including those that were not readily captured in our study.

The gill rakers are a primary functional structure for Cisco (and other zooplanktivores) and influence the size of the prey that is retained for consumption. As inter-gill raker spacing increases with body size (Link & Hoff, 1998), the minimum size of retained prey increases with body size (Kahilainen et al., 2011; O'brien, 1987; Roesch et al., 2013). Our study found that trophic position increased steadily rather than in a step-like manner (Figure 2). Therefore, as Cisco body size increases, the change in inter-gill raker spacing steadily shifts the size of the prey that is retained. Therefore, some of the shift in trophic position could be caused by the lack of lower trophic position prey items included in Cisco diets. Therefore, although it is well acknowledged that larger Cisco integrate larger, omnivorous prey items, larger Cisco are also likely no longer retaining the smaller, lower trophic level prey species. This slow change in diet, based on prey size selection, is in agreement with the slow, steady increase in trophic position that we observed.

We additionally found that Cisco ^{13}C values decreased with body size and therefore shifted to be more pelagically reliant (Figure 3). This is likely reflective of the shift in diet where higher trophic level prey have lower ^{13}C values. Our invertebrate samples indicated that zooplankton, chironomids, and other pelagic taxa can exhibit ^{13}C values slightly lower than -30. Seeing large Cisco shift to have ^{13}C values down to -30 indicates that they shift to being more pelagically reliant. We often think of Cisco as a pelagic species, but our results show that at least the smaller Cisco are noticeably more reliant on littoral resources than we may typically expect. That shift for Cisco becoming more pelagically reliant is important for the transfer of energy between the pelagic and littoral habitats. Seeing that Cisco are reflecting diverse ^{13}C values, as a species they are providing greater integration of energy along the littoral–pelagic axis. The integration of energy between the littoral–pelagic axis is particularly important as Cisco are a populous prey fish in many inland lakes. In Trout Lake, lake trout are highly reliant on Cisco as a prey resource, but more littoral species will also prey on them, including muskellunge, walleye, smallmouth bass, and largemouth bass (Martin et al., 2022; Vanderbloemen et al., 2020).

Although trophic ontogeny is not overly surprising as it is common for many fish species, it has not yet been widely acknowledged for Cisco. Muir et al. (2013) detailed trophic and morphological ontogeny of Cisco in Great Slave Lake, Canada, but did not find nearly as strong an ontogenetic shift as our study. Importantly, Muir et al. (2013) included Cisco that spanned a wider range of body sizes (117–445 mm), which was almost twice the maximum body size that our study assessed. Although their results showed more subtle shifts in trophic ontogeny, the shift was in the same direction as we saw in Trout Lake; that is, larger Cisco were a higher trophic position and more pelagically reliant. As for prey resources in Great Slave Lake, the food web included a similarly diverse array of prey resources that would have allowed for shifts in trophic behavior. A more recent study from Great Slave Lake, Rohonczy et al. (2020), included stable isotope values for Cisco ($n = 13$) across a smaller range in body sizes (129–328 mm). In the study by Rohonczy et al. (2020), there was a trend of larger Cisco having higher ^{15}N and lower ^{13}C. The result was not a reported study as it was outside their project goals, but it can be seen in the archived data. Besides Muir et al. (2013), there have not been many studies detailing ontogeny in Cisco. Many studies have described stomach as indicators of trophic behavior of Cisco, and some have found diet differences based on body size (Breaker et al., 2020; Gatch et al., 2021; Keeler et al., 2015). Although our study found a stronger ontogenetic shift in Cisco trophic behavior than previous studies, the direction of change is consistent with findings from other lakes.

Although our study found an ontogenetic shift in Cisco, it is important to consider if this shift is ecologically relevant. It has been acknowledged that the effects of trophic ontogeny go well beyond the individual (Nakazawa, 2011, 2015; Sánchez-Hernández et al., 2019). At a population level, trophic ontogeny lessens intraspecific competition for prey resources, which can increase growth rates and allow for more overall reproduction (Nakazawa, 2015; Sánchez-Hernández et al., 2019). More broadly, trophic ontogeny increases population-level niche breadth, couples pelagic and benthic food webs, and thereby adds to food web complexity and stability (Nakazawa, 2015; Sánchez-Hernández et al., 2019; Sánchez-Hernández & Cobo, 2016). With our findings of trophic ontogeny in Cisco, it is important to consider the size structure of a Cisco population as it can impact ecosystem function. Among inland lakes around Trout Lake, Cisco populations have been characterized as high-density, low maximum body size or low density, high maximum body size populations (Ahrenstorff et al., 2013). The Cisco population in Trout Lake has undergone large changes in density (Martin et al., 2022), but during the time of this study, it would be characterized as an intermediate density (Martin et al., 2023). However, Cisco greater than 300 mm in body size are extremely rare (2 individuals captured out of 2403 total Cisco sampled between 2020 and 2022), so our dataset covers current size structure of Cisco in Trout Lake. Even at this density and without analysing large Cisco, we found strong evidence of trophic ontogeny. Therefore, we may expect to see this relationship across many other Cisco populations in this area, which could be an important direction for future study.

Overall, our study detailed trophic ontogeny in Cisco that was unlike the lack of ontogeny others have previously found. As Cisco grew to larger sizes, they were found to be of higher trophic position and be more pelagically reliant. This followed the general trend among previous studies that have described the trophic behavior of Cisco. We further discussed how trophic ontogeny is important beyond the individual scale, as it can have effects across population and ecosystem level scales. Future work assessing trophic ontogeny in Cisco in other lakes would address potential drivers of the extent to which Cisco trophic behavior shifts.

AUTHOR CONTRIBUTIONS

Benjamin E. Martin and Joseph T. Mrnak contributed to conception and design of the work, as well as acquisition, analysis, and interpretation of the data. Benjamin E. Martin and Joseph T. Mrnak drafted and revised the manuscript.

ACKNOWLEDGMENTS

We want to acknowledge the staff at Trout Lake Station for their help in allowing us to conduct this study amid a global pandemic. It is important to acknowledge the many scientists who have contributed to the NTL-LTER database over the past 40 years, as it continues to shed light into the changes in the suite of study lakes. Our manuscript was improved from comments and discussions from Jake Vander Zanden, Andrew Muir, Greg Sass, and three anonymous reviewers.

FUNDING INFORMATION

This work was funded by the Wisconsin Department of Natural Resources, Tug Juday Memorial Fund, Juday/Lane Fellowship, Anna

Grant Birge Memorial Fund, United States Fish and Wildlife Service Federal Aid in Sportfish Restoration, and the National Science Foundation North Temperate Lakes Long-Term Ecological Research Program grant (DEB-1440297).

CONFLICT OF INTEREST STATEMENT

The authors have declared none.

DATA AVAILABILITY STATEMENT

All data used in this manuscript are publicly available on the North Temperate Lakes Long Term Ecological database (https://lter.limnology.wisc.edu/data).

CODE AVAILABILITY

Code is available upon request.

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How to cite this article: Martin, B. E., & Mrnak, J. T. (2024). Stable isotopes reveal trophic ontogeny in Cisco (*Coregonus artedi*). *Journal of Fish Biology*, *105*(6), 1555–1561. https://doi.org/10.1111/jfb.15874