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# Impacts of zebra mussels (*Dreissena polymorpha*) on isotopic niche size and niche overlap among fish species in a mesotrophic lake

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**Abstract** Zebra mussels (*Dreissena polymorpha*) filter feed phytoplankton and reduce available pelagic energy, potentially driving fish to use littoral energy sources in lakes. However, changes in food webs and energy flow in complex fish communities after zebra mussel establishment are poorly known. We assessed impacts of zebra mussels on fish littoral carbon use, trophic position, isotopic niche size, and isotopic niche overlap among individual fish species using $\delta^{13}$C and $\delta^{15}$N data collected before (2014) and after (2019) zebra mussel establishment in Lake Ida, MN. Isotope data were collected from 11 fish species, and from zooplankton and littoral invertebrates to estimate baseline isotope values. Mixing models were used to convert fish $\delta^{13}$C and $\delta^{15}$N into estimates of littoral carbon and trophic position, respectively. We tested whether trophic position, littoral carbon use, isotopic niche size, and isotopic niche overlap changed from 2014 to 2019 for each fish species. We found few effects on fish trophic position, but 10 out of 11 fish species increased littoral carbon use after zebra mussel establishment, with mean littoral carbon increasing from 43% before to 67% after establishment. Average isotopic niche size of individual species increased significantly (2.1-fold) post zebra mussels, and pairwise-niche overlap between species increased significantly (1.2-fold). These results indicate zebra mussels increase littoral energy dependence in the fish community, resulting in larger individual isotopic niches and increased isotopic niche overlap. These effects may increase interspecific competition among fish species and could ultimately result in reduced abundance of species less able to utilize littoral energy sources.

**Keywords** Zebra mussels · Fish community · Littoral versus pelagic energy · Interspecific competition · Isotopic niche size · Isotopic niche overlap

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## Introduction

Zebra mussels (*Dreissena polymorpha*) originated from Eastern Europe and were first detected in North America in the 1980s (Ricciardi et al. 1998). Multiple studies have assessed impacts of zebra mussels on lake ecosystems, and one of the most consistent effects is increased water clarity due to filter feeding on seston (Higgins and Vander Zanden 2010). Increased abundance of submerged aquatic plants and periphyton is often a concomitant response due to increased water clarity and perhaps increased nutrient availability at the sediment interface due to zebra mussel biodeposits (Ozersky et al. 2012). The combined impacts of reduced phytoplankton and increased periphyton abundance represents a major shift in available energy from pelagic to littoral sources for invertebrate primary consumers (Higgins and Vander Zanden 2010). Several studies have examined impacts of this littoral shift on aquatic invertebrates, and have found increased reliance on littoral energy (Ozersky et al. 2012; Rennie et al. 2013; McEachran et al. 2018) and increased abundance of littoral invertebrates and decreased abundance of zooplankton (Higgins and Vander Zanden 2010; Ozersky et al. 2012; Rennie et al. 2013).

Given the overall restructuring of primary producers and primary consumers in aquatic ecosystems by zebra mussels, it follows that fish communities could also be impacted by zebra mussel colonization. Studies have shown that fish in north-temperate lakes fall along a continuum of relying mainly on pelagic energy to relying mainly on benthic and littoral sources (Vander Zanden and Vadeboncoeur 2002). However, a common finding is that once zebra mussels are introduced, multiple species of fish increase their reliance on littoral energy, shifting the continuum away from pelagic sources and towards littoral sources (Higgins and Vander Zanden 2010; Rennie et al. 2013; McEachran et al. 2018). Thus, increased availability of littoral energy at the expense of pelagic energy could have effects on competitive interactions among fish, and could shift competitive advantages to species better adapted to littoral habitats such as members of the Centrarchidae family (Higgins and Vander Zanden 2010; McEachran et al. 2018). Although studies have found that zebra mussels cause fish species to increase reliance on littoral energy, it is unknown whether this

shift increases niche overlap and the potential for stronger competitive interactions among fish species.

The impact on competitive interactions is an important question, especially given some gamefish such as walleye (*Sander vitreus*) rely less on littoral energy than members of the Centrarchidae family (Vander Zanden and Vadeboncoeur 2002). Walleye may be less suited for both foraging in high-light conditions and foraging in littoral habitats relative to centrarchids like largemouth bass (*Micropterus salmoides*) (Robillard and Fox 2006). The planktivore cisco (*Coregonus artedi*) may also be especially sensitive to effects of zebra mussels on energy flow given their pelagic habitat requirements and heavy reliance on zooplankton prey (Ahrenstorff et al. 2013). Cisco are important diet components of gamefish such as walleye (Kaufman et al. 2009) and northern pike (*Esox lucius*) (Kennedy et al. 2018), and likely serve as an important link to sources of pelagic energy for piscivorous fish. As a species with cold water and high oxygen requirements, cisco are already sentinels for effects of climate change on fish communities (Jacobson et al. 2012). Climate and eutrophication effects, combined with reduced pelagic energy due to zebra mussels, may reduce abundance of cisco in moderately productive lakes, with subsequent impacts on piscivores that feed on this species.

Stable isotopes ratios of carbon ($\delta^{13}C$) and nitrogen ($\delta^{15}N$) are a powerful tool for assessing impacts of zebra mussels on aquatic energy flow. Values of $\delta^{13}C$ can be used to determine the relative amounts of littoral versus pelagic energy (hereafter carbon) use due to littoral primary producers being more enriched in $\delta^{13}C$ relative to pelagic primary producers (France 1995; Hecky and Hesslein 1995). Moreover, $\delta^{15}N$ can estimate the trophic position of a consumer due to the average increase of 3.4‰ per trophic transfer (Post 2002). $\delta^{13}C$ and $\delta^{15}N$ can be used together in mixing models to obtain more precise estimates of littoral carbon use and trophic position than would otherwise be obtainable without mixing models (Post 2002), and the transformation from raw isotopic values to dietary proportions and trophic position facilitates a meaningful analysis of the isotopic niche of fish species (Newsome et al. 2007). Subsequent analyses can then test whether zebra mussels reduce the isotopic niche size of individual species or the community of sampled species (Jackson et al. 2011) and if zebra mussels increase isotopic niche overlap among fish

species in a lake (Swanson et al. 2015). We recognize that isotopic niches are not the same as trophic niches, though they should be highly correlated (Jackson et al. 2011). Isotopic niches are based on ecologically relevant data and can thus be used to estimate key characteristics of a species niche in the traditional sense of Hutchinson's hypervolume (Newsome et al. 2007; Jackson et al. 2011). Although several studies have documented increased use of littoral carbon in response to zebra mussels (Ozersky et al. 2012; Rennie et al. 2013), and some have found impacts on trophic position (McEachran et al. 2018), zebra mussel impacts on isotopic niche size of individual fish species and the fish community, as well isotopic niche overlap among species, is less understood. Moreover, many studies on zebra mussels have been conducted in large, deeper north temperate lakes with higher reliance on pelagic production (MacIsaac 1996; Ozersky et al. 2012; Rennie et al. 2013; Armenio et al. 2016). Fewer studies exist for smaller, shallower lakes with more balanced littoral and pelagic production where community shifts might be more subtle (Irwin et al. 2016; McEachran et al. 2018). Finally, logistics limit some studies to comparing lakes with zebra mussels to lakes without (McEachran et al. 2018), limiting their ability to fully capture zebra mussel impacts versus natural differences between lakes. In this study we use isotope data collected in a moderately sized mesotrophic lake before and after establishment of zebra mussels to assess impacts on (1) fish energy use and trophic position, (2) fish species and sampled community isotopic niche size, and (3) isotopic niche overlap among fish species.

## Methods and materials

We studied Lake Ida, a lake with 40% littoral area (water depth < 4.6 m) in Minnesota, USA (46.0002° N, 95.4082° W). Lake Ida was previously sampled for stable isotopes by McEachran et al. (2018) in 2013 and 2014, and zebra mussels were first detected in the lake in 2014 when two adults were found during extensive underwater surveying. By 2019, Ida was fully infested with zebra mussels ubiquitous throughout the entire lake. Lake-wide impacts on water clarity and phytoplankton abundance were pronounced, with citizen data (https://www.rmbel.info/data/) showing chlorophyll *a* declined from 4.4 µg L$^{-1}$ during 2010–2013

(mesotrophic status) to 2.1 µg L$^{-1}$ during 2016–2019 (oligotrophic status), while Secchi depth increased from 3.2 to 5.4 m during the same time periods. Thus, we used data collected by McEachran et al. (2018) in 2014 as "before zebra mussel establishment" (hereafter referred to as "Before") data, and data we collected in 2019 as the "after zebra mussel establishment" ("After") data. Methods described below for 2019 are identical to those used by McEachran et al. (2018), allowing us to test for significant changes in isotope characteristics between Before and After periods.

All After data were collected during summer 2019, with fish sampled in August and aquatic invertebrates and zooplankton sampled during May and late July. Our goal for sample collection was to match the invertebrate and fish taxa collected and analyzed by McEachran et al. (2018). Therefore, we focused on black crappie (*Pomoxis nigromaculatus*), bluegill (*Lepomis macrochirus*), largemouth bass, northern pike, pumpkinseed (*Lepomis gibbosus*), rock bass (*Ambloplites rupestris*), smallmouth bass (*Micropterus dolomieu*), walleye, yellow bullhead (*Ameiurus natalis*), yellow perch (*Perca flavescens*), and cisco for fish taxa, and used the same littoral invertebrates as McEachran et al. (2018) (Trichoptera, Chironomidae, *Hyalella*, and Ephemeroptera) to characterize the littoral baseline. Fish were collected using trap nets, gill nets, beach seines, and boat-mounted electrofishing equipment. We collected and froze dorsal muscle tissue from larger fish in the field, and we froze the entire body of smaller fish and subsequently removed dorsal muscle tissue later in the lab. Littoral invertebrates were collected from multiple locations using dip nets and by rinsing submerged vegetation and rocks. Zooplankton were used as pelagic primary consumers and samples were collected in three locations on each date by towing a 153 µm Birge closing net through both the epilimnion (top of metalimnion to surface) and hypolimnion (1 m from lake bottom to bottom of metalimnion). Zooplankton and littoral invertebrates were kept separated and rinsed into 0.7 µm pre filtered lake water, where they were kept for at least two hours to allow them to clear gut contents. In the lab, littoral invertebrates were identified, rinsed with nanopure water, and frozen. Zooplankton were rinsed with nanopure water using a 250 µm mesh, filtered onto a precombusted GF/C filter, wetted with 1% HCL to remove

particulate inorganic carbon, rinsed with nanopure, and frozen.

All tissue and filter samples were dried to a constant weight at 60 °C, and fish and invertebrate samples were then ground into a homogenous sample. Samples were wrapped in tin and analyzed for $\delta^{13}C$ and $\delta^{15}N$ by the University of California Davis Stable Isotope Facility. Fish and invertebrate tissue were analyzed using a PDZ Europa ANCA-GSL elemental analyzer interfaced to a PDZ Europa 20–20 isotope ratio mass spectrometer, while zooplankton tissue was analyzed using an Elementar Vario EL Cube or Micro Cube elemental analyzer interfaced to a PDA Europa 20–20 isotope ratio mass spectrometer. Precision (1 SD) was $\pm 0.2‰$ ($\delta^{13}C$) and $\pm 0.3‰$ ($\delta^{15}N$) in 2014, and $\pm 0.04‰$ ($\delta^{13}C$) and $\pm 0.11‰$ ($\delta^{15}N$) in 2019.

$\delta^{13}C$ estimates can be biased by lipids naturally depleted in $\delta^{13}C$ relative to other tissue (Smyntek et al. 2007). We therefore applied lipid corrections using regression Eq. 3 from Post et al. (2007) to all samples with a C: N value greater than 3.25. Hereafter all $\delta^{13}C$ values are lipid corrected. We then used the average $\delta^{13}C$ and $\delta^{15}N$ values from all of our zooplankton samples as the baseline estimate for the pelagic food web, and the mean $\delta^{13}C$ and $\delta^{15}N$ from all littoral macroinvertebrates as the estimate of the littoral baseline. Baseline values for $\delta^{13}C$ in 2014 were slightly more enriched for both zooplankton and littoral invertebrates, while $\delta^{15}N$ values changed very little in both habitats (Table 1). We used zooplankton

for our pelagic baseline instead of longer-lived mussels given McEachran et al. (2018) also used zooplankton.

Equations described in Post (2002) and McCutchan et al. (2003) were then used to convert raw $\delta^{13}C$ and $\delta^{15}N$ values into proportional littoral carbon in diets and trophic position, respectively. Briefly, proportion littoral carbon ($\alpha$) is estimated as: $\alpha = (\delta^{13}C_{\text{pelagic base}} - \delta^{13}C_{\text{secondary consumer}} + \Delta t_{sc}) / (\delta^{13}C_{\text{pelagic base}} - \delta^{13}C_{\text{littoral base}})$. $\delta^{13}C_{\text{pelagic base}}$ represents the average $\delta^{13}C$ of zooplankton, $\delta^{13}C_{\text{secondary consumer}}$ represents the $\delta^{13}C$ of an individual fish, $\delta^{13}C_{\text{littoral base}}$ represents the average $\delta^{13}C$ of littoral invertebrate primary consumers, and $\Delta t_{sc}$ represents the trophic fractionation of $\delta^{13}C$ multiplied by the trophic position of individual fish. We used 0.4‰ as the trophic fractionation of $\delta^{13}C$ based on Post (2002). Trophic position was estimated as: trophic position $= \lambda + (\delta^{15}N_{\text{secondary consumer}} - [\delta^{15}N_{\text{littoral base}} * \alpha + \delta^{15}N_{\text{pelagic base}} * (1- \alpha)]) / \Delta_N$, and we set $\lambda = 1$ so that estimates are for trophic levels above primary consumers. $\delta^{15}N_{\text{secondary consumer}}$ represents the $\delta^{15}N$ of an individual fish, $\delta^{15}N_{\text{littoral base}}$ represents the average $\delta^{15}N$ of littoral aquatic invertebrate primary consumers, $\delta^{15}N_{\text{pelagic base}}$ represents the average $\delta^{15}N$ for zooplankton, $\Delta_N$ represents the trophic fractionation of $\delta^{15}N$, and $\alpha$ represents the proportion littoral carbon from the previous equation. We used 3.4‰ for the trophic fractionation of $\delta^{15}N$ (Post 2002). The equations share the terms trophic position and $\alpha$, and

Table 1 Average $\delta^{13}C$ and $\delta^{15}N$ in littoral baseline, pelagic baselines and in the 11 species of fish in both 2014 and 2019 ($\pm$ 1SD). Numbers following taxonomic group are sample sizes for 2014 and 2019

| Taxonomic group | 2014 | | 2019 | |
| --- | --- | --- | --- | --- |
| | $\delta^{15}N$ | $\delta^{13}C$ | $\delta^{15}N$ | $\delta^{13}C$ |
| Littoral primary consumers (23, 24) | 4.5 (2.2) | − 20.2 (2.7) | 4.8 (0.8) | − 22.2 (1.2) |
| Pelagic primary consumers (10,12) | 7.9 (0.9) | − 26.7 (0.8) | 7.7 (1.3) | − 27.9 (0.7) |
| Black crappie (7, 7) | 12.8 (0.5) | − 23.9 (0.2) | 12.2 (0.9) | − 23.9 (0.8) |
| Bluegill (6, 7) | 11.7 (1.0) | − 23.3 (0.3) | 9.9 (0.9) | − 22.2 (0.4) |
| Largemouth bass (7, 30) | 13.3 (0.8) | − 23.2 (0.8) | 12.8 (0.8) | − 22.6 (0.8) |
| Northern Pike (6, 30) | 12.9 (1.0) | − 22.8 (0.5) | 12.7 (0.5) | − 23.2 (0.7) |
| Pumpkinseed (7, 7) | 10.8 (1.3) | − 23.0 (0.9) | 9.9 (1.0) | − 23.3 (1.0) |
| Rock bass (7, 7) | 12.4 (0.6) | − 21.5 (1.2) | 11.6 (0.4) | − 22.6 (0.8) |
| Smallmouth bass (7, 15) | 12.5 (0.6) | − 22.1 (0.5) | 12.6 (0.7) | − 23.0 (0.9) |
| Cisco (7, 15) | 11.6 (0.4) | − 26.6 (0.2) | 11.4 (0.4) | − 27.2 (0.3) |
| Walleye (10, 30) | 14.2 (0.4) | − 23.3 (0.6) | 13.4 (0.6) | − 23.3 (0.6) |
| Yellow bullhead (7, 7) | 12.0 (1.2) | − 22.6 (0.6) | 12.0 (0.6) | − 23.0 (1.1) |
| Yellow perch (8, 20) | 11.2 (0.5) | − 24.0 (1.3) | 11.6 (0.6) | − 23.2 (1.3) |

the equations are fit in an iterative process until parameter estimates stabilize (Post 2002).

We used three analytical approaches to test whether the following variables showed significant change from the Before to After establishment periods: (1) littoral carbon and trophic position of individual species and the sampled fish community, (2) isotopic niche size of the sampled fish community and individual fish species, and (3) isotopic niche overlap among individual species. First we tested for significant effects of zebra mussels on trophic position and littoral carbon use in individual fish species using ANCOVA with year (Before versus After), fish length, and year*length interaction as possible explanatory variables. If the interaction was not significant we dropped the term and tested for year and length effects only. Fish length is an important factor to consider since fish $\delta^{13}C$ and $\delta^{15}N$ can change as they grow and increase length due to ontogenetic habitat and diet shifts. We tested for a community-wide change in littoral carbon use and trophic position using a linear mixed-effects model with fish species as random effect and year as a fixed effect. Length, littoral carbon, and trophic position were log transformed to equalize variance and normalize residuals. All analyses, including those described above, were conducted using JMP version 15 (SAS 2019), unless noted otherwise.

We secondly tested for significant change from Before to After in the size of isotopic niche space for individual species based on their standard ellipse area ($SEA_B$ method in Jackson et al. 2011) and also tested for change in the size of the entire sampled community isotopic niche space based on convex hulls (Jackson et al. 2011). Standard ellipse areas and convex hulls were estimated from littoral carbon use and trophic position using the R program SIBER (Jackson et al. 2011). We graphically evaluated changes in isotopic niche size of individual species by estimating standard ellipse area in both years and assessing overlap of 85% credible intervals for each year-size estimate. Credible intervals are based on the posterior distributions of estimates, which can be directly transformed to the distribution of the difference between 2 parameters. As such, non-overlapping 85% credible intervals infer an approximate 97% probability that the absolute difference between the 2 parameters is $> 0$ (large imbalances in posterior variances can have a small effect). We also tested whether average individual

species isotopic niche size changed from the Before to After period by testing whether the average difference between time periods (After-Before) differed from zero across the 11 species. For our community scale test, the After data set had more samples of walleye, northern pike, and largemouth bass compared to the Before period, potentially confounding sample composition with zebra mussel effects on isotopic niche size at the community scale. Thus, we modified our SIBER analysis at the community scale with a boot strapping procedure where 10 individuals were randomly drawn with replacement from each species in each year to estimate the convex hull using SIBER, and this procedure was repeated 1000-fold to develop credible intervals not influenced by sample composition. We then used 85% credible intervals of Before and After community isotopic niche size to test whether the community isotopic niche space changed after zebra mussel establishment. Cisco are the only exclusively pelagic species in our analysis, and they may be an important link to pelagic energy for piscivorous fish. Their pelagic reliance may also cause cisco to have a disproportionately large influence on the overall isotopic niche space of a fish community. Thus, we assessed the relative importance of cisco on the isotopic niche size of the fish community by estimating the convex hull in the Before and After periods both with and without cisco in the analysis.

Finally, we assessed the change in potential interspecific competition from Before to After among fish species by estimating the amount of overlap in isotopic niche space between species in both Before and After years using the R program NicheRover (Swanson et al. 2015). This analysis estimates both directions of overlap between each species pair (A on B, B on A), and the two estimates can be asymmetrical. We used the estimated overlap and 85% credible interval for each pairwise-species estimate in Before and After years to infer if isotopic niche overlap changed from before to after zebra mussels. We also tested whether isotopic niche overlap increased on average across the fish community by finding the difference in median percent isotopic niche overlap between years (After-Before) for each species pair, and then used a mixed model with species as a random effect to test whether the intercept (median percent change) differed from zero. Cisco showed virtually no overlap with other fish species in our analysis (discussed below), and so they

were not used in our test for significant change in isotopic niche overlap across species.

## Results

### Objective 1: Littoral carbon use and trophic position

Results showed 10 of 11 species increased reliance on littoral carbon in the After period, with smallmouth bass as the only species showing no length, year, or interaction effect (Fig. 1, 2; Supplementary Table S1). Black crappie, bluegill, pumpkinseed, yellow perch, yellow bullhead, northern pike, and cisco all showed significant year effects with higher littoral carbon reliance after establishment, but no length or interaction effect (Fig. 1, 2). Rock bass, largemouth bass, and walleye all had significant length and year effects, with all three species consuming more littoral carbon after establishment and in larger fish (Fig. 2). None of the 11 species showed a length*year interaction (Table S1). Effect size of zebra mussels on littoral carbon was large for both piscivorous and non-piscivorous fish species, as on average walleye increased littoral carbon use from 38 to 66%, while bluegills increased from 43 to 91%. The exception to the pattern of large increase in littoral carbon reliance was with cisco, where despite a statistically significant increase in the After period, littoral carbon use increased from 0% to just 4%, perhaps due to cisco's oxythermal and behavioral constraints that prevent them from increasing consumption of littoral carbon. Our mixed-model analysis with species as a random effect indicated littoral carbon use averaged across species increased in the After period ($P < 0.001$) (Table S2), shifting from 43 to 67% littoral carbon in the Before to After period, respectively.

Results for trophic position were far less pronounced, as only 2 of 11 species increased trophic position in the After period. Smallmouth bass and yellow perch had year and length effects, with both species showing an increase in trophic position in the After period and with increasing fish length but no interaction (Fig. 3, Table S3). Black crappie and bluegill both showed length*year interactions, but in both cases results appear to be driven by a single data point in the 2014 data (Fig. 3, Table S3). Rock bass also showed a significant year effect with no length or

interaction effect, but the pattern was a decrease in trophic position in the After period, while cisco showed no year, length, or interaction effect (Fig. 3, Table S3). Pumpkinseed, largemouth bass, northern pike, walleye, and yellow bullhead all showed significant length effects where each species' trophic position increased with fish size, but none showed a year or interaction effect (Fig. 4, Table S3). Results for the mixed model with species as a random effect showed an increase in trophic position averaged across species ($P = 0.013$) (Table S2), but the effect size was much smaller than that observed for littoral carbon, as trophic position increased from 1.73 to just 1.80 trophic levels above primary consumers from the Before to After periods.

### Objective 2: Isotopic niche size

Mean trophic position and littoral carbon use across species showed consistent increased use of littoral carbon across species (Fig. 5a). Analysis of community isotopic niche size with cisco included showed no difference in isotopic niche size between time periods based on credible intervals, while excluding pelagic cisco resulted in much smaller community isotopic niche size that also did not differ between time periods (Fig. 5b). However, this analysis illustrates the importance of cisco for tapping pelagic energy for the fish community and increasing the size of the isotopic community niche, as non-overlapping credible intervals indicated community isotopic niche size with cisco included was significantly larger in both the Before (1.8-fold larger) and After (2.5-fold larger) periods compared to the same time period with cisco excluded (Fig. 5b). Cisco drove the larger isotopic niche in both time periods because most other species relied more heavily on littoral carbon, while cisco remained almost exclusively pelagic during both time periods (Fig. 5a). This caused the estimated convex hull area to "stretch" across a wider range of littoral carbon use when cisco were included (Fig. 5c) compared to when they were excluded (Fig. 5d), causing a larger estimate of community isotopic niche size with cisco. When cisco are removed from the analysis, neither Before nor After periods are stretched along the littoral carbon axis, resulting in smaller but similar isotopic niche sizes between periods (Fig. 5d). With cisco excluded, the primary difference between time periods is the After community isotopic niche shifted
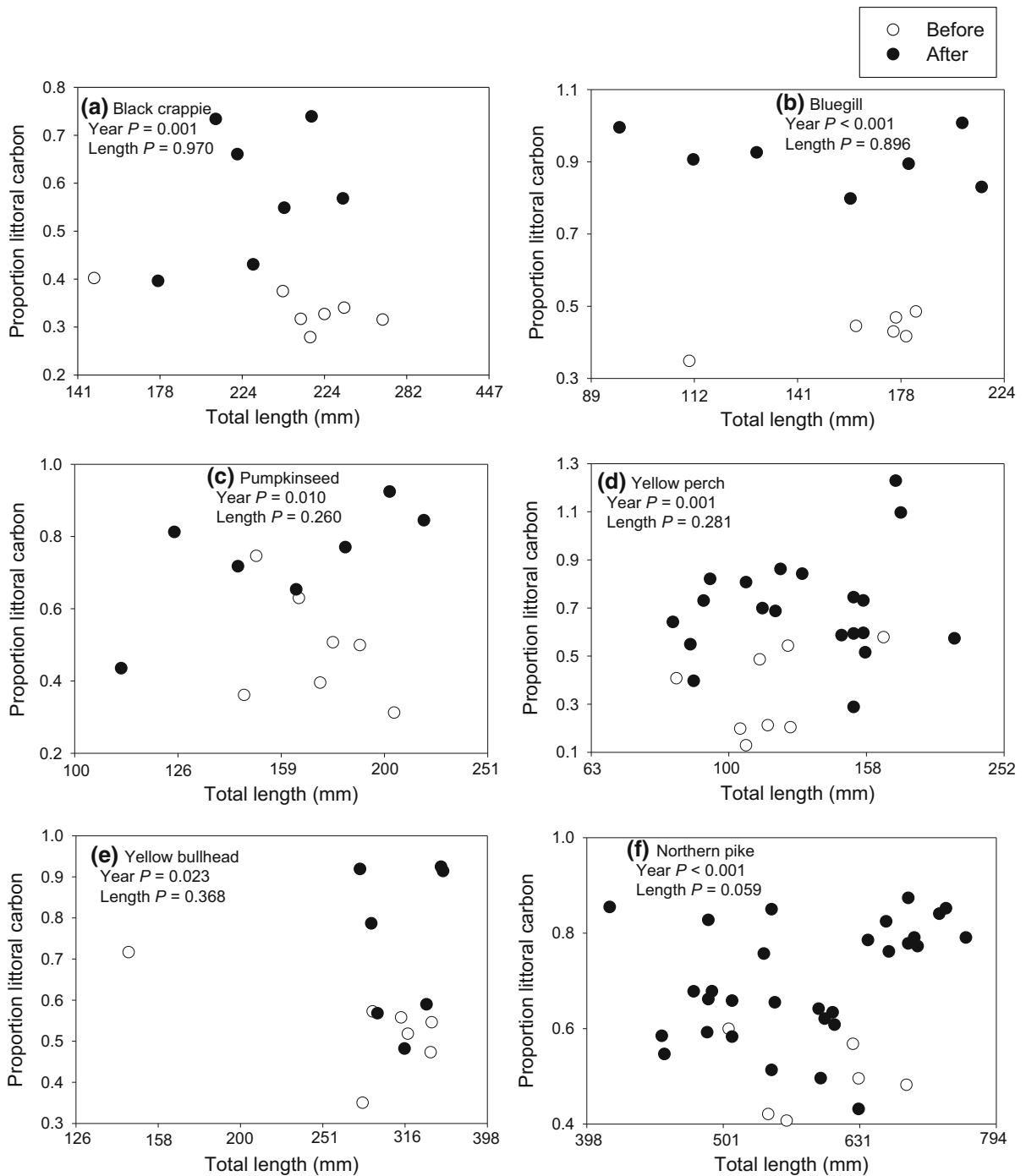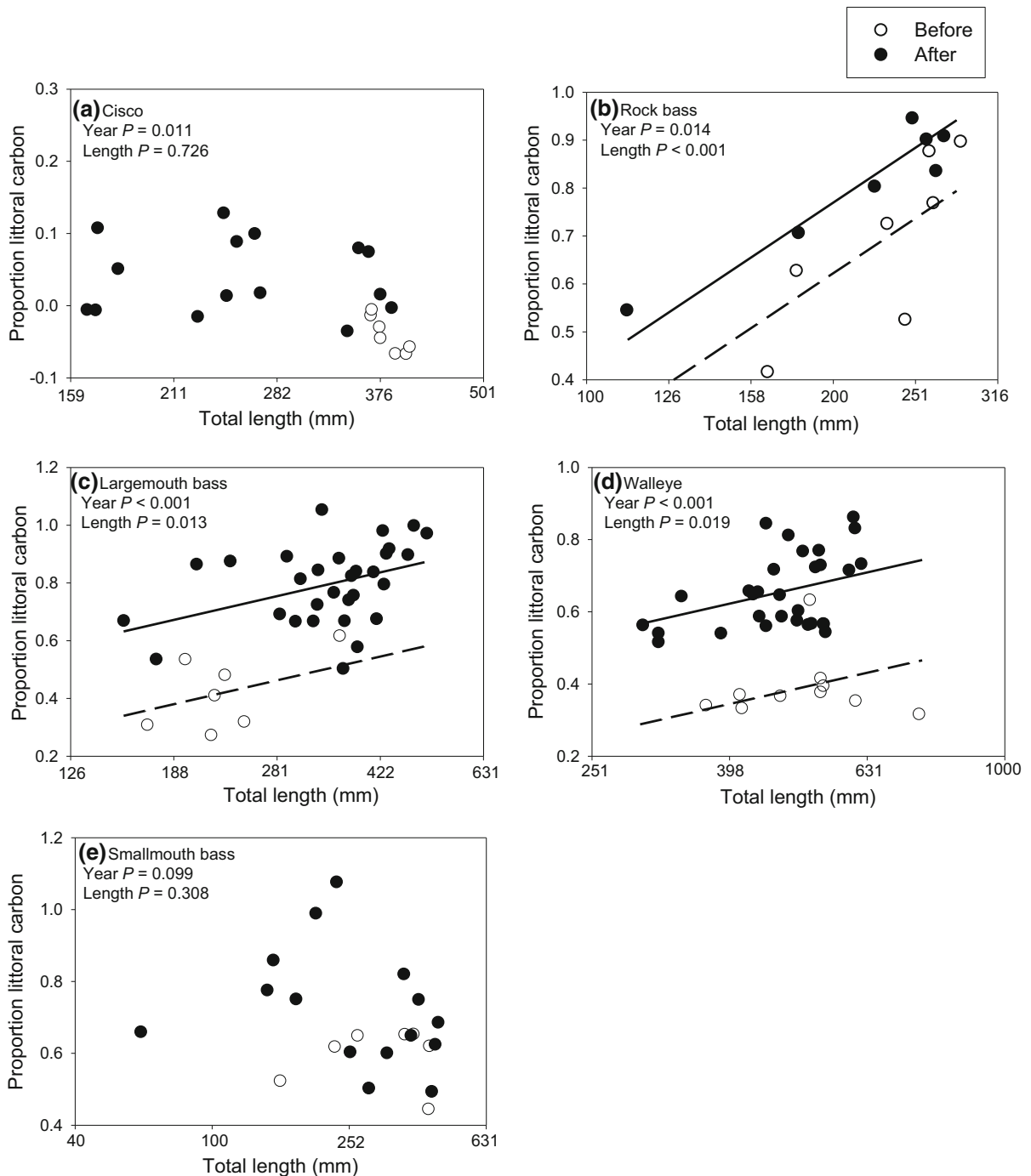
**Fig. 1** Proportion littoral carbon in diets of six fish species in Lake Ida before and after zebra mussel establishment and as a function of fish length. None of these species showed a significant length*year interaction (all $P > 0.05$)

to higher overall use of littoral carbon. Results for isotopic niche size of individual species showed that just one species changed their isotopic niche size

between time periods, with black crappie larger in the After period based on credible intervals (Fig. 6). However, using species as replicates, mean isotopic

Fig. 2 Proportion littoral carbon in diets of five fish species in Lake Ida before and after zebra mussel establishment and as a function of fish length. None of these species showed a significant length*year interaction (all $P > 0.05$)

niche size of individual species increased significantly from the Before to After time period ($P = 0.035$, Table S4), with isotopic niche size on average 2.1-fold larger in the After period.
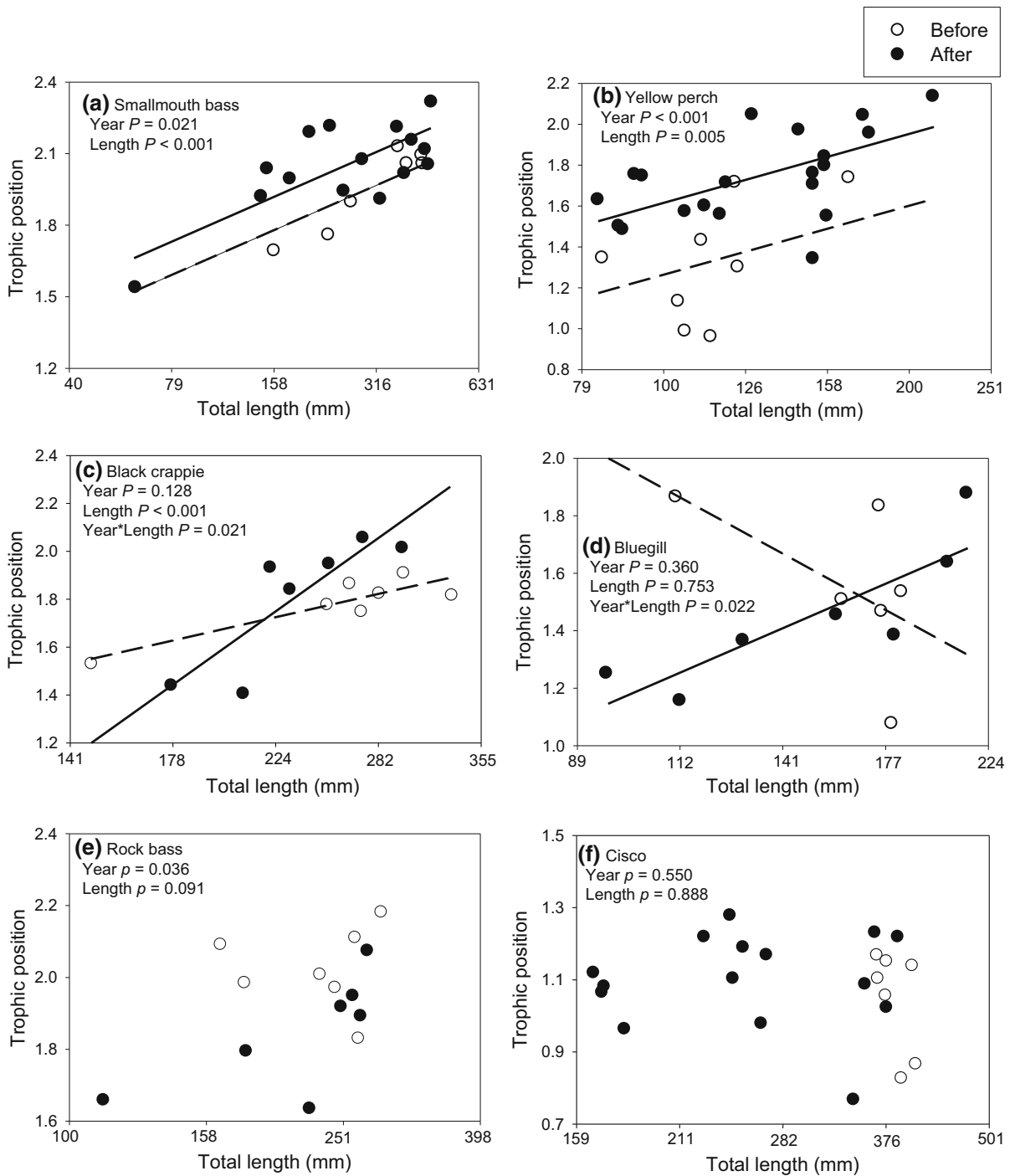
**Fig. 3** Trophic position above primary consumers for six fish species in Lake Ida before and after zebra mussel establishment and as a function of fish length. Black crappie and bluegill were the only species to show a significant length*year interaction
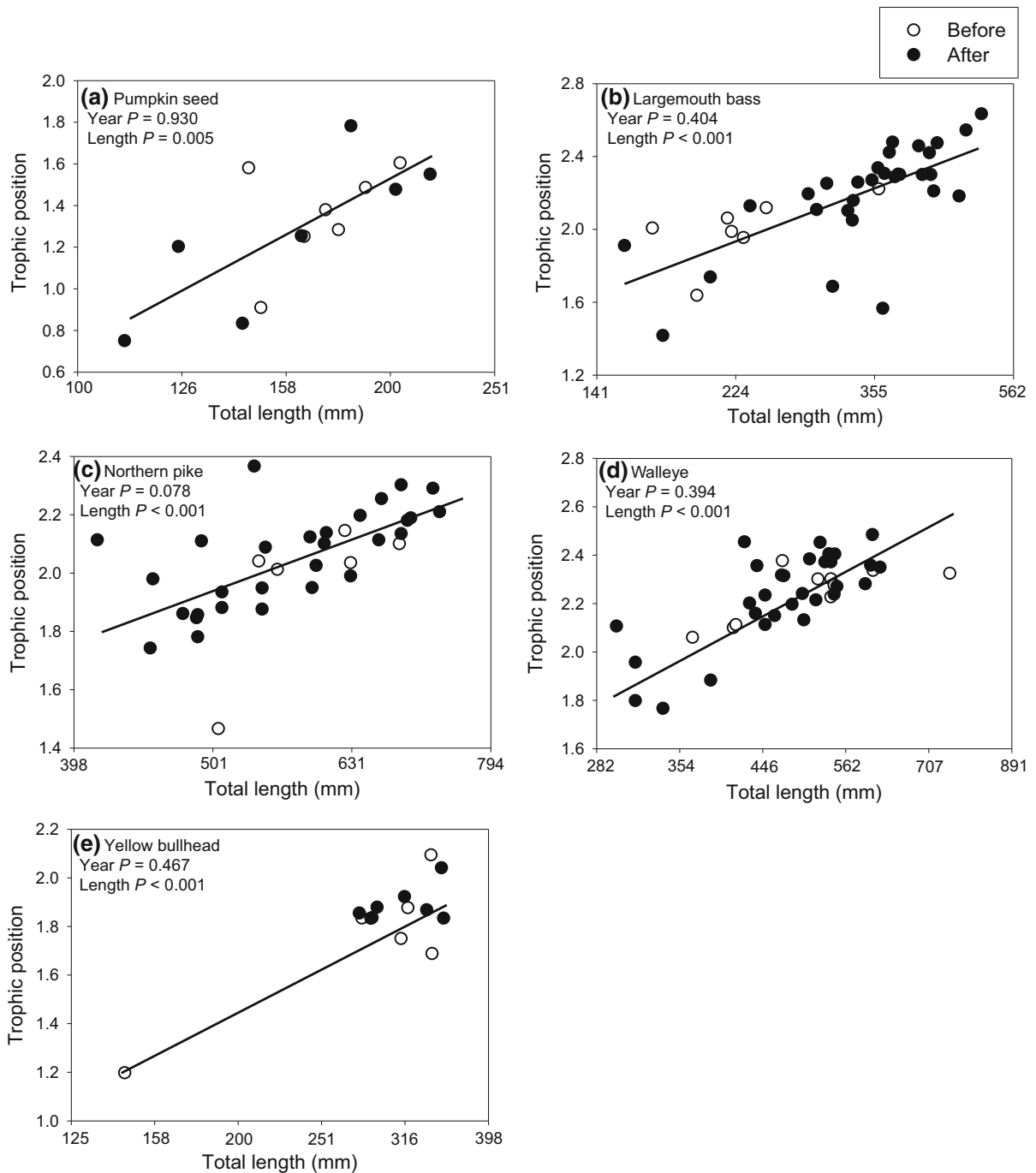
**Fig. 4** Trophic position above primary consumers for five fish species in Lake Ida before and after zebra mussel establishment. None of these species showed a significant length*year interaction (all $P > 0.05$)

Objective 3: Isotopic niche overlap

Estimates of pairwise isotopic niche overlap showed a general pattern of increased overlap for most species

from the Before to After period, though few changes for individual species were significant based on credible intervals. Species showing the most frequent increase of overlap on other species were piscivorous
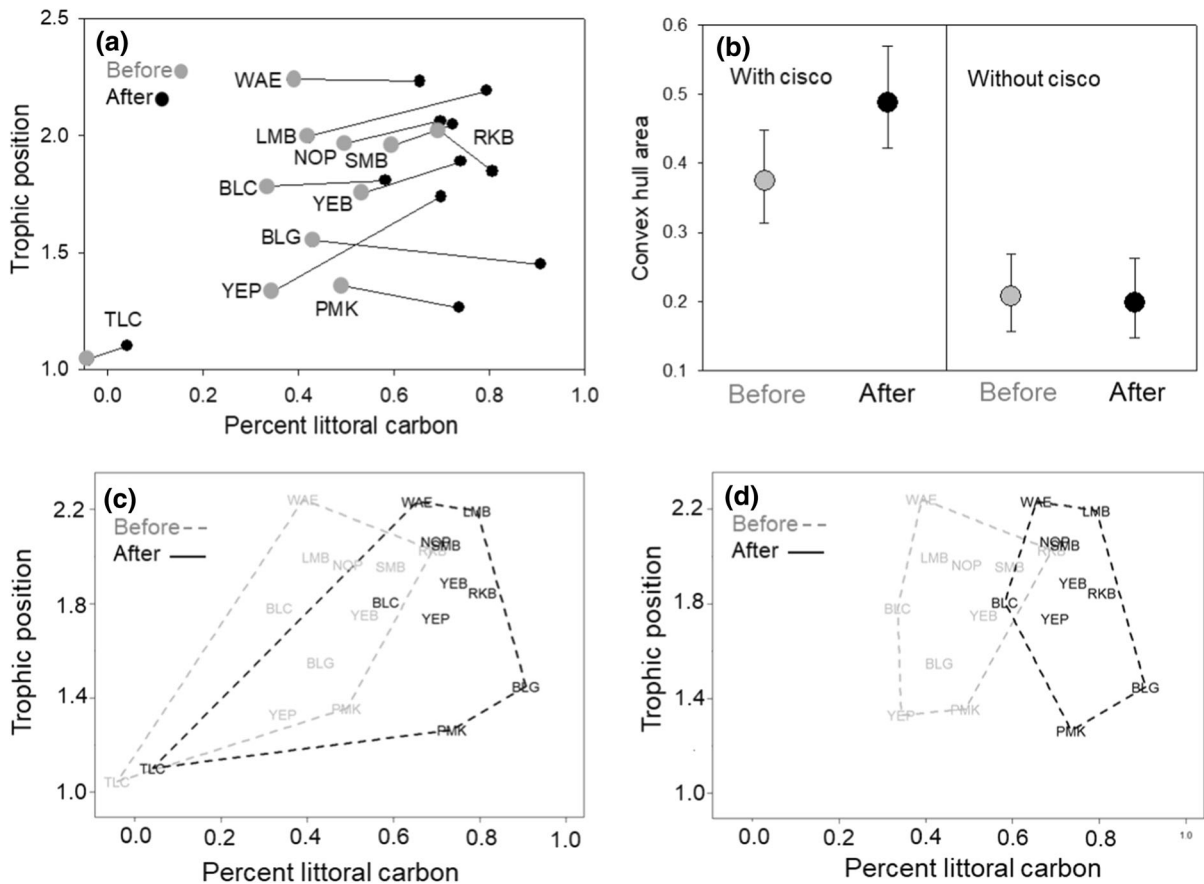
Fig. 5 Panel a shows average percent littoral carbon and trophic position for 11 species of fish in both the Before and After time periods and shows the overall increase in littoral carbon use among species. Panel b is the estimated median convex hull area and 85% credible intervals for both Before and After time periods for all 11 fish species including cisco and 10 fish species with cisco removed. Overlapping credible intervals indicate no significant difference in hull area at the 0.05 level for the analyses both with and without cisco, while non overlapping intervals show community isotopic niche size is significantly larger in the analysis with cisco compared to without cisco for

both Before and After time periods. Panel c shows the median convex hull (community isotopic niche size) for Before and After time periods based on the data for 11 species shown in panel a, while panel d shows median convex hull for Before and After time periods for 10 species of fish with cisco excluded. Species acronyms for this and subsequent figures are as follows: walleye (WAE), largemouth bass (LMB), smallmouth bass (SMB), northern pike (NOP), yellow perch (YEP), yellow bullhead (YEB), bluegill (BLG), pumpkinseed (PMK), rock bass (RKB), black crappie (BLC), cisco (TLC)

such as walleye and northern pike (Fig. 7), while non-piscivorous species such as pumpkinseeds and bluegills generally showed fewer cases of increased overlap in the After period (Fig. 8). Cisco were a notable exception to the overall pattern of isotopic niche overlap between species, as with the exception of yellow perch, they showed essentially zero overlap with other species in both time periods. A mixed-model analysis on 10 of the 11 species (cisco excluded) using species as a random factor showed a significant increase in percent isotopic niche overlap

(15%) in the After period (*P* = 0.007, Table S5). Of the 11 species, only bluegill (-8%) showed a sizeable decease in their average isotopic niche overlap on other species, while rock bass (37%), yellow perch (28%), and yellow bullhead (28%) increased their overlap on other species' isotopic niches the most. Bluegill reduced isotopic niche overlap on other species in the After period by having both sizable increases in use of littoral energy and by feeding at lower trophic levels relative to most other species (Fig. 5a). Species that had the greatest average
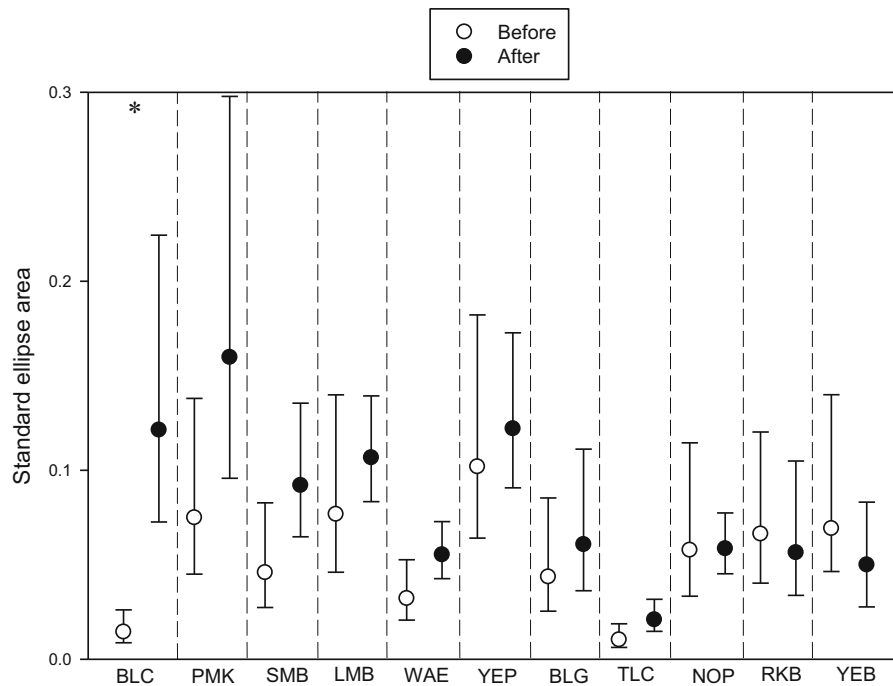
**Fig. 6** Estimated median standard ellipse area and 85% credible intervals in both Before and After time periods for 11 species of fish. Non-overlapping credible intervals indicate mean values are significantly different at the 0.05 level, and are indicated with an asterisk at the top of the panel. Species acronyms are given in Fig. 5

increase of other species overlapping on their isotopic niche included black crappie (50%), yellow perch (33%), and smallmouth bass (30%), while yellow bullhead ($-$ 15%), bluegill ($-$ 7%), and rock bass ($-$ 3%) showed the greatest decreases in being overlapped by other species.

## Discussion

Our results showed major shifts in food web dynamics following the establishment of zebra mussels in Lake Ida. We saw significant increases in use of littoral energy post zebra mussels for 10 of the 11 species, and this nearly ubiquitous littoral shift resulted in larger average isotopic niche space averaged across species. Larger isotopic niche size averaged across species, coupled with no change in size of community-level isotopic niche space, led to increased isotopic niche overlap averaged across species. Our results indicate zebra mussels have strong influences on energy pathways, and likely influence competitive interactions among species in the fish community. This may influence fish community composition through

impacts on relative abundance of fish species, with subsequent consequences for sport fisheries due to changes in abundance of both prey fish and gamefish.

Multiple studies have shown that zebra mussels reduce abundance of phytoplankton and zooplankton (Higgins and Vander Zanden 2010), and this reduction of pelagic primary producers and primary consumers likely played a key role in the shift towards increased reliance on littoral carbon in Lake Ida. Similar to other studies, chlorophyll *a* declined by 52% in the post zebra mussel period in Lake Ida. Additionally, the littoral shift in fish diets could also be driven by increased abundance of littoral prey. We have no data on abundance of littoral primary consumers for Lake Ida, but a meta-analysis by Higgins and Vander Zanden (2010) found zoobenthic biomass increased from 160 to 210% post zebra mussels. Thus, it seems likely the shift is due to both reduced prey in the pelagic area and increased littoral prey, with the relative importance of each change in prey varying among fish species. The overall impact of this shift in energy flow for each fish species will depend on its ability to respond to the changes in energy within the lake (Higgins and Vander Zanden 2010).
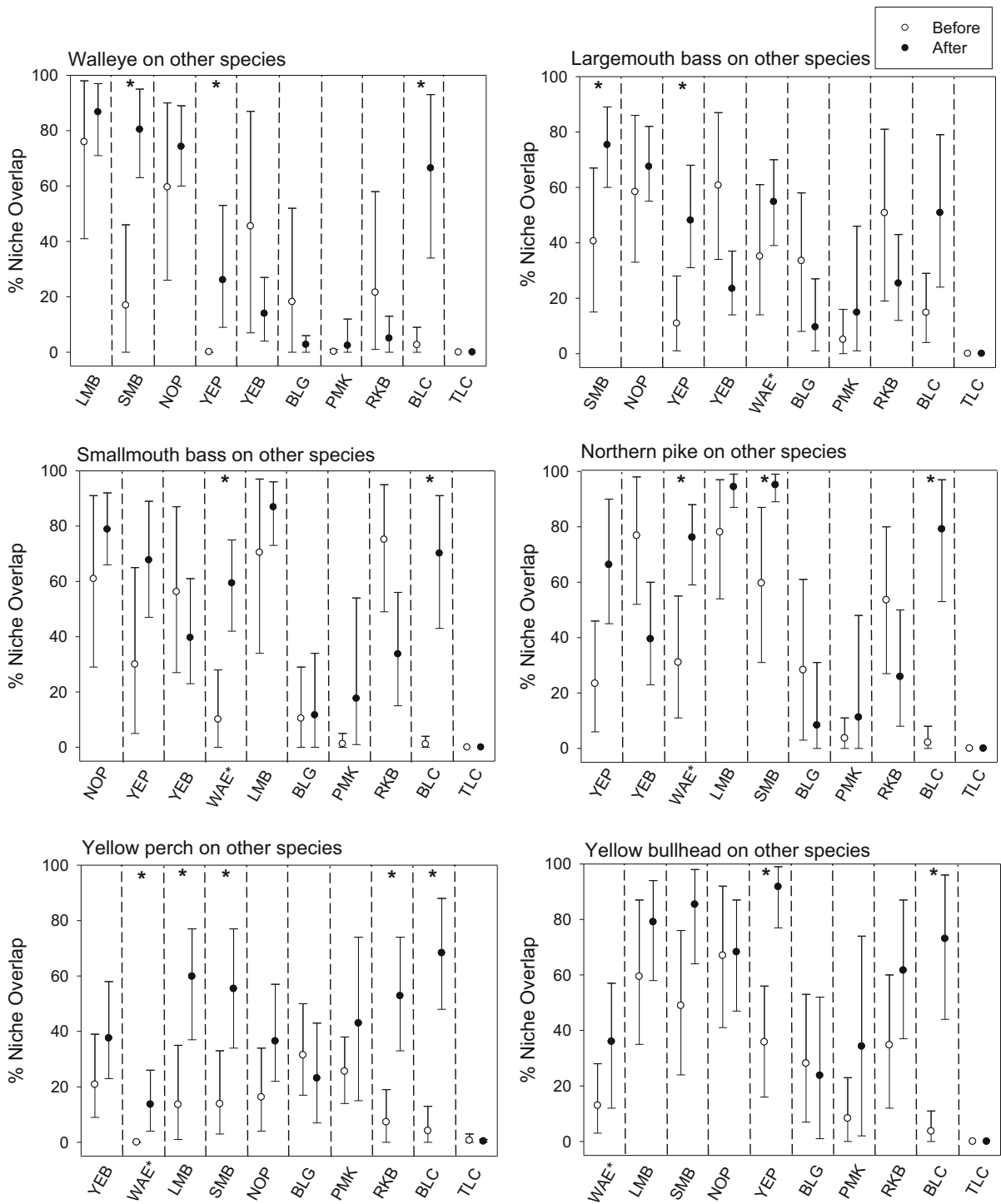
Our results showed no significant change in community-scale isotopic niche size, yet a significant 2.1-fold increase on average for individual species isotopic niche size. Within these broad patterns there was a large amount of variability for individual species, ranging from black crappie increasing 8.4-
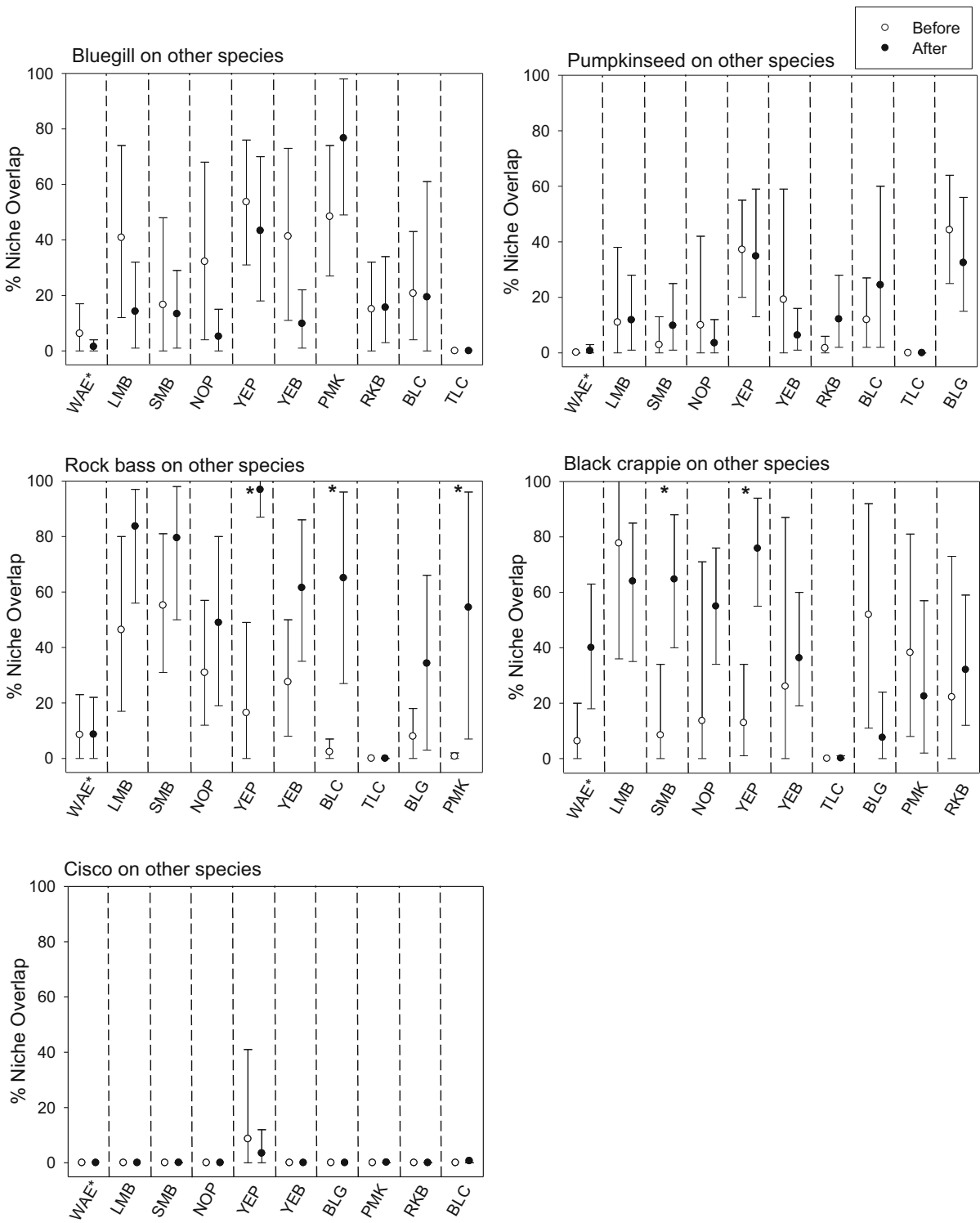
◄ **Fig. 7** Estimated median isotopic niche overlap and 85% credible intervals for 6 fish species on 10 other fish species in Lake Ida both before and after zebra mussel establishment. Non-overlapping credible intervals are significantly different at the 0.05 level and are indicated with an asterisk. Each of the six panels shows the overlap of that species on the isotopic niche of the 10 species listed on the x axis. The data also show the overlap of other fish species on an individual fish species. For example, the impacts of other species on WAE* can be seen by examining all five cases where WAE* is on the x axis, as well as the five case where it is on the x axis in Fig. 8. Species acronyms are given in Fig. 5

fold to yellow bullhead decreasing 0.7-fold in the After period. However, the change in isotopic niche size appears to be driven at least partially by a species reliance on littoral carbon in the Before period. The six species least reliant on littoral carbon in the Before period (mean littoral carbon = 31%) averaged a 2.7-fold increase in littoral carbon, while the five species most reliant on littoral carbon (mean = 56%) averaged just a 1.3-fold increase. This suggests species least reliant on littoral carbon may exhibit the largest change in isotopic niche size in response to zebra mussel colonization, driven by a wider range of littoral carbon use among individual fish after colonization.

There was also wide variation among species in isotopic niche overlap despite a significant increase in the After period when averaged across species. Bluegill (− 8%), pumpkinseed (0%), and cisco (0%) showed the smallest mean increase in overlap on other species isotopic niches in the After period. The isotopic niche of bluegill and pumpkinseed remained distinct in the After period because they increased littoral carbon use even more than other species and remained at a lower trophic level. The cisco isotopic niche remained distinct by remaining very reliant on pelagic carbon in the After period despite other species shifting more littoral. Species with the largest increase in isotopic niche overlap on other species, indicating the largest potential for competition with other species, included rock bass (increased average overlap on other species 37%), yellow perch (+ 28%) and yellow bullhead (+ 28%). Going the other direction, the species that had the largest increase of other species overlapping their own isotopic niche included black crappie (+ 50%), yellow perch (+ 33%), and smallmouth bass (+ 30%). However, it is important to note that although a particular species could

experience increased isotopic niche overlap with other species, impacts to that species will be minimal if it is a better competitor for those resources or if resources are not limiting. For example, smallmouth bass are well adapted to feeding in littoral habitats (Irwin et al. 2016; McEachran et al. 2018), while black crappie are better suited for pelagic habitats (McEachran et al. 2018). Thus, increased overlap from other species will likely have a larger negative effect on black crappie in littoral habitats than it will smallmouth bass.

Cisco were unique among the fish we sampled in their near complete reliance on pelagic energy, and though their use of littoral energy increased from 0% Before to 4% After, their response was much more muted than all other species. We feel there are three possible interpretations to this pattern. First, cisco may be so specialized and efficient at consuming pelagic zooplankton that reduced zooplankton abundance post zebra-mussels does not affect their diets. This seems unlikely given the degree to which zooplankton decline post zebra mussel establishment. For example, Higgins and Vander Zanden (2010) conducted a meta-analysis and estimated zooplankton biomass declined 40% to 77% post zebra mussel infestation. The second interpretation is that cisco are so specialized on pelagic prey that they are unable to adjust their diets to littoral prey despite greatly reduced zooplankton abundance. We are unaware of any studies documenting cisco feeding on near-shore littoral prey, though they will feed on profundal invertebrates such as chironomid larva and benthic mayflies such as *Hexagenia* (Ahrenstorff et al. 2013; Jacobson et al. 2018). However, profundal invertebrates rely heavily on the "rain" of pelagic primary production for energy (Jónasson 2004), and so reduced phytoplankton abundance may also impact abundance of profundal prey for cisco. The third interpretation is that cisco, a cold-water species requiring high oxygen and cold water (Jacobson et al. 2012), are unable to shift to littoral feeding due to oxythermal constraints. Cisco are already threatened by climate change and eutrophication (Jacobson et al. 2012). Our results indicate they may also be unable to adjust to impacts of zebra mussels on energy flow in lakes, potentially making cisco populations even more vulnerable to effects of warmer and less oxygenated water. It is worth noting that the other fish species in our study are warm or cool-water species (Eaton and Scheller 1996) and had similar responses to zebra mussels, suggesting cold-

◀ **Fig. 8** Estimated isotopic niche overlap and 85% credible intervals for 5 fish species on 10 other fish species in Lake Ida both before and after zebra mussel establishment. Non-overlapping credible intervals are significantly different at the 0.05 level and are indicated with an asterisk. Each of the five panels shows the overlap of that species on the isotopic niche of the 10 species listed on the x axis. The data also show the overlap of other fish species on an individual fish species. For example, the impact of other species on WAE* can be seen by examining all five cases where WAE* is on the x axis, as well as the five case where it is on the x axis in Fig. 7. Species acronyms are given in Fig. 5

water, pelagic species such as cisco may be most impacted by zebra mussel establishment. Finally, warming waters from climate change can disrupt energy flow in lakes (Tunney et al. 2014) and "rewire" food webs (Bartley et al. 2019), suggesting the potential for synergistic effects of zebra mussels and climate change on trophic relationships in lake fish communities.

Our results also highlight the importance of cisco as a source of pelagic energy for fish communities, as isotopic niche space of the sampled fish community was 1.8-fold larger in the Before and 2.5-fold larger in the After period when cisco were included in the analysis. Cisco drove the sampled community isotopic niche size larger as they were the only species that remained nearly 100% reliant on pelagic carbon in both time periods, stretching the sampled community isotopic niche larger along the carbon source axis. Given their ability to exploit pelagic energy sources documented in this study, and their importance as prey for multiple species of gamefish such as walleye (Kaufman et al. 2009), northern pike (Kennedy et al. 2018), and muskellunge (*Esox masquinongy*) (VanderBloemen et al. 2020), loss of cisco from lake food webs will undoubtedly impact energy flow and trophic ecology of other fish species.

An important point regarding potential for interspecific competition among fish species is whether total primary and secondary production in Lake Ida stays relatively constant from the Before to After period. Deeper light penetration could result in greater littoral primary and secondary production (Higgins and Vander Zanden 2010), potentially offsetting decreased production in the pelagic habitat so that overall available energy remains constant and minimizes competition (Idrisi et al. 2001). Even if

enhanced littoral production is able to compensate for reduce pelagic production, changes in energy flow and changes to the physical environment in Lake Ida could shift the competitive advantage to certain species over others. Lie-and-wait predators with compressiform body shapes such as smallmouth bass and largemouth bass are more likely to benefit from increased abundance of littoral prey, higher abundance of submerged aquatic plants, and higher water clarity associated with zebra mussels relative to species with fusiform shapes better adapted to pelagic habitats such as walleye (Irwin et al. 2016). Robillard and Fox (2006) showed abundance of walleye decreased while abundance of smallmouth bass and largemouth bass increased following increased water clarity and macrophyte abundance in Ontario lakes, while Irwin et al. (2016) found that pelagic fish species declined while littoral species increased post zebra mussel infestation in Lake Oneida. Additional work is needed to see if similar shifts in community composition occur in Lake Ida and other lakes infested with zebra mussels, and whether shifts are driven primarily by increased interspecific competition or by physical changes in the habitat that favor some species over others.

An important caveat with this study is that isotopic niches are not the same as trophic niches, though isotopic niches are based on ecologically relevant data and can thus be used to estimate key characteristics of a species niche in the traditional sense of Hutchinson's hypervolume (Newsome et al. 2007; Jackson et al. 2011). Additionally, increased isotopic niche overlap indicates the potential for increased interspecific competition (Bellgraph et al. 2008), but demonstrating interspecific competition requires documenting two or more species competing for the same limiting resources with detrimental effects to the species involved (Crowder 1990). Experimental research provides the strongest evidence on the importance of interspecific competition (Crowder 1990), but is logistically impossible at a whole-lake scale with invasive zebra mussels and the number of fish species involved in this study. However, additional work examining abundance of specific prey both in fish diets and in the lake and testing for changes in abundance, growth rates, and reproduction rates of fish species would provide additional evidence that interspecific competition increased in the post zebra mussel period (Crowder 1990; Fayram et al. 2005). Despite these

limitations, our results do indicate that nearly all fish species increased their reliance on littoral carbon and that overlap of isotopic niches increased post zebra mussels, which taken together indicates increased potential for interspecific competition within the fish community.

McEachran et al. (2018) studied Lake Ida prior to zebra mussel infestation, using it as a reference lake to assess impacts of zebra mussels on nearby Lake Carlos. Their results were similar to this study in that both studies showed fish increase reliance on littoral carbon in response to zebra mussels. However, McEachran et al. (2018) found that multiple species increased trophic position, while this study did not, although averaged across species there was a significant trophic increase. The most likely reason for this discrepancy is that McEachran et al. (2018) compared two different lakes, and so any effects of zebra mussels are potentially confounded by natural differences between lakes. Our Before-After design controls for between lake differences, making results documented here more robust relative to comparative studies.

There has been considerable debate regarding the importance and impacts of invasive species on terrestrial and aquatic ecosystems (Boltovskoy et al. 2018). Our results indicate that zebra mussels cause pronounced shifts in energy flow in lake ecosystems where fish increase their reliance on littoral energy, which increases isotopic niche size of most fish species. The net result is increased isotopic niche overlap among species, which indicates enhanced potential for interspecific competition for resources. Enhanced competition, coupled with other known changes to physical characteristics of lakes after zebra mussel infestation, has high potential to shift species composition of the fish community. This has implications for recreational angling and fisheries management goals for infested lakes, making control of new infestations a priority for natural resource managers.

**Declarations**

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