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Stable isotopes indicate that zebra mussels (*Dreissena polymorpha*) increase dependence of lake food webs on littoral energy sources

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Abstract

- The influence of zebra mussels (*Dreissena polymorpha*) on phytoplankton abundance is well known, but their community-level impact on energy flow is less clear. Reduced phytoplankton abundance could increase reliance of fish and aquatic invertebrates on alternative energy sources such as epiphyton and benthic algae.
- 2. We assessed impacts of zebra mussels on energy flow by comparing food webs in two Minnesota, USA, lakes during summers of 2013 and 2014. Lake Carlos had a dense population of zebra mussels, while upstream Lake Ida was free of zebra mussels until this study began and maintained low densities during our study.
- 3. We used baseline-corrected (BC) δ^{13} C to test whether fish and littoral invertebrate primary and secondary consumers were more reliant on littoral carbon in Carlos compared to Ida. We also used BC δ^{15} N to determine if trophic position of fish species differed between lakes. Lastly, we compared isotopic niche space by estimating standard ellipse areas for fish species in Carlos and Ida lakes, and tested whether the community-level range of trophic levels, reliance on littoral carbon and standard ellipse area differed between lakes.
- 4. Results showed invertebrate secondary consumers had more enriched BC δ^{13} C in Carlos than in Ida, indicating greater reliance on littoral energy. Mixing models indicated that 10 of 11 fish species were more reliant on littoral carbon in Carlos, with littoral carbon use in the 10 species 1.5-fold higher in Carlos. Isotopic niche analysis also showed increased littoral reliance in Carlos fish, as the same 10 fish species in Carlos had statistically distinct ellipses that were enriched in δ^{13} C. Mixing models also indicated that seven of 11 fish species analysed had significantly higher trophic positions in Lake Carlos.
- 5. In contrast, community-scale metrics for fish showed no difference between lakes in the range of trophic levels, range of reliance on littoral energy, or size of standardised ellipse area of isotopic niche space. This indicates that, despite most individual fish species increasing their reliance on littoral energy and shifting upwards in trophic position, the overall size of the community isotopic niche area remained similar between lakes.

6. Our results indicate that zebra mussels have community-wide impacts on energy flow in lakes, with invertebrate predators and many species of fish increasing their reliance on littoral energy sources, and most species of fish shifting to higher trophic positions. A key question is whether increased water clarity associated with zebra mussels can increase littoral production sufficiently to compensate for higher demand. If not, it is plausible that invertebrate and fish production will decline due to increased intra- and inter-specific competition.

KEYWORDS

energy flow, niche space, trophic position, zebra mussel invasion

1 | INTRODUCTION

Since the first zebra mussel (Dreissena polymorpha) was sampled in Lake St. Clair in 1988 (Hebert, Muncaster, & Mackie, 1989), these highly invasive bivalve mussels have spread quickly to lakes and river systems across the eastern USA due to their prolific reproduction and multiple dispersal strategies, including natural as well as humantransport pathways (Griffiths, Schloesser, Leach, & Kovalak, 1991; Ludyanskiy, McDonald, & MacNeill, 1993). In Minnesota, zebra mussels were first found in the Duluth/Superior harbour of Lake Superior in 1989 and were subsequently detected and spread throughout the Mississippi River during 1992-1995, but introductions to inland lakes were delayed, beginning in 2006 (MN DNR 2017; http://www. dnr.state.mn.us/invasives/ais/infested.html, accessed 16 October 2017). As of October 2017, zebra mussels have been confirmed in 156 lakes, rivers and wetlands in Minnesota, a very small percentage of the state's 11,842 lakes >4.05 ha (MN DNR 2017; http://www. dnr.state.mn.us/fag/mnfacts/water.html; retrieved from 16 October 2017). However, the two most recent years have marked the highest rates of new infestations, with zebra mussels discovered in 32 and 34 water bodies in 2016 and 2017, respectively.

Fishing in Minnesota is an economic engine, generating \$2.4 billion/year in direct expenditures (US Department of the Interior, 2011) and features strongly as a component of Minnesota's cultural identity. The rapid expansion of zebra mussels highlights the need to understand the ecological and fishery impacts of this invasive species, which features among a group of the world's worst biological invaders (Lowe, Browne, Boudjelas, & De Poorter, 2000). Many studies have been conducted to document and synthesise ecological impacts of zebra mussels in freshwater ecosystems (Higgins & Vander Zanden, 2010), but very few assessments of impacts to fish communities of inland lakes have been conducted (but see Colvin, Pierce, & Stewart, 2015; Irwin, 2016).

Zebra mussels are ecosystem engineers, and through a process termed *benthification* alter abiotic and biotic physical habitat at both local and whole-lake scales, and generally increase the importance of littoral-benthic (hereafter littoral) relative to pelagic pathways in lakes (Higgins & Vander Zanden, 2010; Mayer, Zhu, & Cecala, 2016; Mayer et al., 2014). At local spatial scales, zebra mussels form dense aggregations, or druses, and by releasing faecal deposits, increase available nutrients, bacteria, and benthic algae (Armenio, Mayer, Heckathorn, Bridgeman, & Panek, 2016; Higgins & Vander Zanden, 2010). Habitat complexity resulting from druse architecture can boost certain invertebrate populations (Botts, Patterson, & Schloesser, 1996; Stewart, Miner, & Lowe, 1998), but Mayer et al. (2016) showed that increased benthic invertebrate production at the whole-lake scale was modest (4% increase). In a meta-analysis encompassing hundreds of studies, Higgins and Vander Zanden (2010) reported an average non-dreissenid zoobenthos biomass decrease of 45% in profundal habitats and a 210% increase in littoral habitats.

Perhaps the most consistent and dramatic effect of zebra mussels in lakes is the decrease in phytoplankton biomass and subsequent increase in water clarity (Heiskary, Hirsch, & Rantala, 2016; Higgins & Vander Zanden, 2010; Higgins, Vander Zanden, Joppa, & Vadeboncoeur, 2011; Idrisi, Mills, Rudstam, & Stewart, 2001; Mayer et al., 2016; Miller & Watzin, 2007). Two additional but somewhat inconsistent lower trophic level impacts are decreased zooplankton populations (Higgins & Vander Zanden, 2010) and increased growth of toxic cyanobacteria (Armenio et al., 2016; Fishman, Adlerstein, Vanderploeg, Fahnenstiel, & Scavia, 2009; Knoll et al., 2008). Relatively few studies have examined impacts of zebra mussels on fish communities, but the general response has been an increased reliance on littoral energy sources as evidenced by enriched δ^{13} C in fish following colonisation (Fera, Rennie, & Dunlop, 2017; Rennie, Evans, & Young, 2013).

Carbon (C) and nitrogen (N) stable isotopes are widely used biological tracers that record information on trophic ecology and spatial feeding patterns. In lakes, boundary-layer effects limit the amount of C fractionation by benthic and littoral sessile primary producers relative to free-floating pelagic phytoplankton (Hecky & Hesslein, 1995). This results in naturally-occurring differences in stable isotopes of C in pelagic versus littoral primary producers, and these differences persist as energy from those sources is transferred to consumers (France, 1995; Hecky & Hesslein, 1995; Post, 2002). Because trophic enrichment of δ^{13} C is known (0.4‰; Post, 2002), a consumer's δ^{13} C can be used to identify its energy source (Cole et al., 2011; Peterson & Fry, 1987; Post, 2002). Additionally, δ^{15} N shows a fractionation of 3.4‰ between trophic levels, making it useful for assessing trophic position in food webs (Post, 2002). Together, $\delta^{15}N$ and $\delta^{13}C$ isotope ratios can be used to estimate the proportion of energy derived from littoral sources (Post, 2002) as well as the isotopic niche space of individual species (Jackson, Inger, Parnell, & Bearhop, 2011).

In this study, we assess the impact of zebra mussels on energy use and trophic structure of fish and aquatic invertebrates by comparing a lake with a well-established zebra mussel population to a similar lake where zebra mussels were first detected during our study and populations remained very low. We measured δ^{13} C and δ^{15} N of littoral and pelagic primary and secondary consumers to estimate the importance of littoral resources for fish and aquatic invertebrates in each lake. We hypothesised that: (a) littoral support would be significantly more important for invertebrate secondary consumers and fish in the lake with zebra mussels; (b) the two pelagic fish in our study (yellow perch *Perca flavescens* and walleye *Sander vitreus* [Percidae]) would show the smallest shift towards littoral resources in the lake with zebra mussels; and (c) despite difference in the importance of littoral resources between lakes, trophic positions of fish would be similar for fish species.

2 | METHODS

Our study, conducted during summers 2013-2014, was focused on two lakes, Carlos and Ida, which are in a chain of interconnected lakes in the midst of zebra mussel colonisation. north of Alexandria. Minnesota, USA. Lake Carlos and Lake Ida are popular recreation lakes, with moderate water quality and a fish community supporting various warm-, cool- and cold-water fish species. At least 37 fish species have been documented in the two study lakes and fish communities in each lake are similar. A couple exceptions are that Carlos contains the cold-water species, burbot (Lota lota, Lotidae) while Ida does not, and vice versa for muskellunge (Esox masquinongy, Esocidae), where a low-density population exists in Lake Ida due to downstream movement from Lake Miltona. Lake Carlos is the smaller and deeper of the lakes, with a surface area of 1,055 ha and a maximum and mean depth of 50 m and 15.2 m, respectively, while Lake Ida encompasses 1,792 ha and has a maximum and mean depth of 32 m and 8.5 m, respectively. Percent littoral area is larger in Ida (40%) compared to Carlos (35%). Both lakes are classified as mesotrophic with a 10-year (2006-2015) mean summer epilimnetic total phosphorus concentrations of 13 μ g L⁻¹ and 16 μ g L⁻¹ in Carlos and Ida lakes, respectively (MPCA 2017: https://cf.pca.state.mn.us/ water/watershedweb/wdip/waterunit.cfm?wid=21-0123-00).

Zebra mussels were first detected in Lake Carlos in 2009 and were well established by 2013 (Heiskary et al., 2016). Over this period, Secchi depth transparency doubled to >6 m (Figure 1), while chlorophyll-*a* dropped over 50% to approximately 5 μ g L⁻¹ by 2013 (Engel, Valley, & Anderson, 2010; Heiskary et al., 2016). Zooplankton densities also declined over 57%, from >35 animals/L during 2008 and 2009 to <15 animals/L during 2013 and 2014 (Heiskary et al., 2016). In contrast, zebra mussels were first detected in extremely low densities in Lake Ida during the last year of this study (2014),



FIGURE 1 Mean Secchi depth transparency (m) using all available data for Lake Carlos (black line) and Lake Ida (grey line) lakes from 2001 to 2016. Arrows indicate the year zebra mussels were first detected in each of the study lakes

and changes in water clarity were not observed until the summer of 2015 (Figure 1). These patterns indicate that zebra mussels were well established in Lake Carlos and had impacted pelagic primary and secondary production in 2013–2014 compared to Lake Ida. Thus, we used Lake Carlos as an example lake heavily colonised with zebra mussels, while Ida served as a non-colonised contrast.

Preliminary sampling was done in Carlos in July of 2013 and Carlos and Ida were both sampled during June and July of 2014. Target fish species were collected using trap nets, vertical and horizontal gill nets, beach seines, and back-pack and boat-mounted electrofishing equipment (Table 1). The fish were sacrificed and a tissue sample was removed from the lateral muscle for medium and large-bodied fish, kept on ice, and frozen until analysis in the laboratory. For smaller fish such as young-of-year bluegill (Lepomis macrochirus, Centrarchidae) and bluntnose minnow (Pimephales notatus, Cyprinidae), the entire body (minus the digestive tract) was frozen until analysis in the laboratory. Zooplankton were collected by towing a 163-µm plankton net from 1 m above the bottom of the lake to the lake surface at three locations along the centre axis of each lake with repeated tows taken at each location to collect sufficient material. Collected animals were rinsed with lake water into plastic sample jars and placed on ice until processed in the laboratory. Each location was analysed separately unless insufficient material was collected, in which case two or more stations were combined into composite samples.

Profundal and littoral habitats were sampled for representative groups of aquatic macroinvertebrates. Chironomids were collected from profundal habitats with a ponar grab and placed in lake water on ice until analysis in the laboratory. Littoral macroinvertebrates were collected from various habitats in each lake using dip nets and by hand, then placed in lake water until they could be sorted into taxonomic groups in the laboratory. Littoral macroinvertebrates collected in both lakes and analysed for stable isotopes included both primary consumers (snails [Planorbidae, Physidae], caddisflies [Trichoptera],

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	Lake Carlos		Lake Ida	
Common name	$\overline{x} \delta^{13}$ C (1 SD, n)	x̄ δ ¹⁵ N (1 SD)	$\bar{x} \delta^{13}$ C (1 SD, n)	x̄ δ ¹⁵ N (1 <i>SD</i>)
Black crappie	-24.5 (0.4, 10)	13.2 (0.5)	-23.9 (0.2, 7)	12.8 (0.5)
Bluegill	-24.2 (0.8, 8)	10.7 (0.8)	-23.3 (0.3, 6)	11.7 (1.0)
Bluntnose minnow	-22.7 (0.3, 15)	9.7 (0.4)	-22.7 (1.1, 7)	10.3 (1.3)
Largemouth bass	-23.8 (0.8, 15)	14.1 (0.7)	-23.2 (0.8, 7)	13.3 (0.8)
Northern pike	-23.8 (0.7, 10)	12.8 (1.2)	-22.8 (0.5, 6)	12.9 (1.0)
Pumpkinseed	-23.6 (0.8. 11)	10.1 (0.5)	-23.0 (0.9, 7)	10.8 (1.3)
Rock bass	-24.5 (1.2, 10)	11.3 (2.5)	-21.5 (1.2, 7)	12.4 (0.6)
Smallmouth bass	-22.8 (0.6, 6)	13.3 (0.7)	-22.1 (0.5, 7)	12.5 (0.6)
Walleye	-23.8 (0.6, 15)	14.1 (1.3)	-23.3 (0.6, 10)	14.2 (0.4)
Yellow bullhead	-24.0 (0.7, 8)	12.5 (0.9)	-22.6 (0.6, 7)	12.0 (1.2)
Yellow perch	-23.4 (0.7, 13)	12.9 (0.4)	-24.0 (1.3, 7)	11.2 (0.5)
Caddisfly	-21.6 (1.9, 5)	5.8 (0.7)	-18.1 (2.8, 4)	3.2 (1.7)
Profundal midge	-28.6 (1.1, 5)	7.8 (0.6)	-26.3 (0.5, 7)	5.4 (0.4)
Littoral midge	-22.7 (1.3, 3)	6.2 (2.3)	-23.4 (3.7, 3)	7.5 (4.8)
Damselfly	-23.5 (0.3, 6)	7.0 (0.5)	-22.7 (0.7, 4)	6.9 (0.5)
Dragonfly	-23.3 (1.3, 6)	5.8 (1.0)	-23.5 (1.4, 7)	4.5 (0.5)
Hyalella	-20.5 (1.4, 5)	4.8 (0.7)	-18.4 (2.2, 7)	3.4 (0.7)
Mayfly	-25.4 (1.2, 6)	3.9 (0.2)	-22.9 (1.0, 4)	3.3 (0.2)
Snail	-25.9 (1.9, 4)	4.6 (0.9)	-20.9 (0.8, 6)	6.4 (1.4)
Mussels	-29.0 (1.3, 14)	7.4 (0.3)	-25.1 (1.0, 8)	6.3 (0.7)
Water scorpion	-21.8 (0.4, 5)	5.6 (0.1)	-22.4 (0.4, 3)	5.9 (0.6)
Zooplankton	-29.1 (1.5, 7)	7.6 (1.6)	-26.7 (0.8, 10)	7.9 (0.9)

TABLE 1 Mean. standard deviation (SD) and sample size of lipid corrected $\delta^{13}C$ and $\delta^{15}N$ of fish and aquatic invertebrate taxonomic groups used in this study from Lake Ida and Lake Carlos. Sample sizes for δ^{13} C and δ^{15} N were the same for each taxonomic group in each lake

Note. Taxonomic names are as follows: black crappie, Pomoxis nigromaculatus; bluegill, Lepomis macrochrius; bluntnose minnow, Pimephales notatus; largemouth bass, Micropterus salmoides; northern pike, Esox lucius; pumpkinseed, Lepomis gibbosus; rock bass, Ambloplites rupestris; smallmouth bass, Micropterus dolomieu; walleye, Sander vitreus; yellow bullhead, Ameiurus natalis; yellow perch, Perca flavescens; caddisfly, Trichoptera; littoral and profundal midges Chironomidae; damselfly, Zygoptera; dragonfly, Anisoptera; mayfly, Ephemeroptera; snail, Physidae and Planorbidae; mussel, Lampsilis siliquoidea; water scorpion, Nepidae; zooplankton, primarily Cladocera.

Hyalella azteca, mayflies [Ephemeroptera], midges [Chironomidae]) and secondary consumers (damselfly larvae [Zygoptera], dragonfly larvae [Anisoptera], water scorpions [Nepidae]). We failed to find any native mussels in Lake Carlos, probably due to extirpation caused by zebra mussels. Thus, we collected zebra mussels in Lake Carlos and both zebra mussels and native mussels in Lake Ida. Similar to other studies (Post, 2002), we found no significant difference in δ^{13} C between zebra mussels and native mussels in Ida ($T_{1.6}$ = 1.20, p = .274) or $\delta^{15}N$ ($T_{1.6}$ = 1.18, p = .282). Thus, we used zebra mussels in Carlos and both native and zebra mussels in Ida.

In the laboratory, zooplankton were condensed onto 80-µm mesh and detrital material and non-herbivorous zooplankton were removed by hand. The remaining sample was rinsed with nanopure water and filtered onto GF/F glass fibre filters and then frozen. We were unable to remove small secondary consumer zooplankton from our samples, but examination of sample content indicated mostly cladocerans Bosmina and Daphnia spp., and secondary consumers constituted a small fraction of sample contents and would have minimal influence on isotope values. Macroinvertebrates were sorted into the above taxonomic groups, rinsed with nanopure water, and frozen. The exceptions were snails and mussels, where we first manually removed the shells and only analysed soft tissue due to the shells being constructed largely from ambient dissolved inorganic C (reviewed by McConnaughey & Gillikin, 2008).

Fish and macroinvertebrate tissue and zooplankton filters were dried at 60°C until a constant weight was achieved. Fish and macroinvertebrate tissue were subsequently ground into a fine powder and weighed, and all samples were analysed by the University of California Davis Stable Isotope Facility. Samples (excluding zooplankton on filters) were analysed for $\delta^{13}C$ and $\delta^{15}N$ using a PDZ Europa ANCA-GSL elemental analyser interfaced to a PDZ Europa 20-20 isotope ratio mass spectrometer (Sercon Ltd., Cheshire, UK). Zooplankton filters were analysed for $\delta^{13}C$ and $\delta^{15}N$ using an Elementar Vario EL Cube or Micro Cube elemental analyser (Elementar Analysensysteme GmbH, Hanau, Germany) interfaced to a PDZ Europa 20-20 isotope ratio mass spectrometer (Sercon Ltd., Cheshire, UK). Analytical precision (standard deviation) was ±0.2‰ for ¹³C and ±0.3‰ for ¹⁵N, respectively. Standard deviations for duplicate samples were 0.2% for δ^{15} N and 0.1% for δ^{13} C. Final delta

(δ) values were reported as ratios of ¹³C:¹²C and ¹⁵N:¹⁴N relative to international standards Vienna PeeDee Belemnite and Air for C and N, respectively (Peterson & Fry, 1987).

Previous research has shown that lipids have depleted δ^{13} C values relative to other types of tissues, causing problems in food web studies as differences in δ^{13} C for a given species could be due to differences in lipid content instead of differences in C source (Smyntek, Teece, Schulz, & Thackeray, 2007). Thus, we used equation 3 in Post et al. (2007) to lipid correct all δ^{13} C values in samples with C:N > 3.25. Hereafter all reference to δ^{13} C values represent lipid-corrected values. Representative baselines of pelagic and littoral energy sources are also necessary for application of mixing models to estimate reliance on littoral versus pelagic C, and to compare δ^{13} C values between lake ecosystems (Post, 2002). Recommendations often focus on using mussels for the pelagic baseline and snails for the littoral baseline as both are relatively long-lived and their diets comprise the respective carbon pools (Post, 2002). However, we failed to find adequate numbers of snails in Lake Carlos, perhaps due to heavy infestation by zebra mussels. Thus, we used the mean value of all littoral primary consumers analysed in each lake for the littoral C source in mixing models and baseline corrections (Table 1). Using mussels as the baseline for pelagic energy sources also proved problematic as δ^{13} C in mussels in Ida were more enriched than a number of individual fish samples, and 1.6‰ more enriched relative to zooplankton (mussel and zooplankton δ^{13} C were similar in Lake Carlos; Table 1). This indicates that mussels did not fully capture the isotopic signature of the pelagic food web in Lake Ida, perhaps due to zooplankton feeding in deeper pelagic water on δ^{13} C-depleted seston (Francis et al., 2011; Vander Zanden & Rasmussen, 1999). Mussel δ^{13} C more enriched than individual fish samples would confound our mixing model estimates of reliance on littoral C (described below). Thus, we used the mean value of δ^{15} N and δ^{13} C of zooplankton as our pelagic baseline model so that $\delta^{15}N$ and $\delta^{13}C$ of pelagic and littoral energy sources bracket fish and invertebrate consumers in both lakes.

We used a three-pronged approach to assess impacts of zebra mussels on lake food webs. First, we tested whether baselinecorrected (BC) δ^{13} C values of three taxa of invertebrate secondary consumers (dragonflies, damselflies and water scorpions) and six groups of primary consumers (snails, caddisflies, *Hyalella azteca*, may-flies, midges from littoral habitats and midges from profundal habitats) differed between Lake Ida and Lake Carlos. BC δ^{13} C values were determined by subtracting the mean δ^{13} C value of zooplankton in each lake (Table 1) from the δ^{13} C value of each invertebrate sample. Given the reliance of zooplankton on pelagic energy sources (Post, 2002), BC δ^{13} C significantly higher than zero for macroinvertebrates indicates greater reliance on littoral energy (hereafter littoral C) relative to zooplankton, with the degree of reliance on littoral C positively related to BC δ^{13} C. We then used t tests to determine whether BC δ^{13} C values differed between lakes for each taxonomic group.

In our second approach, we used mixing models to test whether the reliance on littoral C differed between fish species in Lake Carlos versus Lake Ida. We estimated the trophic position of each fish and the proportion of C ultimately derived from littoral Freshwater Biology -WILEY

aquatic invertebrates based on mixing models from Post (2002). Proportion of littoral C (a) was estimated by: $\alpha = (\delta^{13}C_{\text{pelagic base}} \delta^{13}C_{\text{secondary consumer}} + \Delta t_{\text{sc}})/(\delta^{13}C_{\text{pelagic base}} - \delta^{13}C_{\text{littoral base}})$, where $\delta^{13}C_{\text{pelagic base}}$ is the average $\delta^{13}C$ of zooplankton, $\delta^{13}C_{\text{secondary consumer}}$ is the δ^{13} C of each individual fish, Δ is the trophic fractionation of δ^{13} C (set to 0.39‰; Post, 2002), t_{sc} is trophic position of each individual fish, and $\delta^{13}C_{iittoral hase}$ is the $\delta^{13}C$ of littoral invertebrate primary consumers. Trophic position of each fish was estimated as: trophic position = λ + ($\delta^{15}N_{secondary consumer} - [\delta^{15}N_{littoral base} \times \alpha + \delta^{15}N_{pelagic base}$ × $(1 - \alpha)$])/ Δ_N , where λ is the trophic position of littoral aquatic invertebrate primary consumers, $\delta^{15}N_{secondary\ consumer}$ is the $\delta^{15}N$ of individual fish, $\delta^{15} N_{\text{littoral base}}$ is the average $\delta^{15} N$ of littoral aquatic invertebrates primary consumers, $\delta^{15}N_{\text{pelagic base}}$ is the mean $\delta^{15}N$ for zooplankton and Δ_N is the trophic fractionation of δ^{15} N (set to 3.4 %; Post, 2002). We set λ equal to one so results for fish are expressed as trophic position above invertebrate primary consumers. Trophic position and α appear in both equations, so the two equations are fit iteratively until estimates stabilise (Post, 2002). Proportion littoral C and trophic position were estimated for each individual fish using the above mixing models, and we then used ANCOVA to test for significant effects of fish length and lake on proportion littoral C and trophic position of each species of fish.

Our third approach was focused on community-level analyses of fish. First, we estimated the isotopic niche space of each fish species in each lake using sample size-corrected standard ellipse area (SEAc) proposed by Jackson et al. (2011). The SEAc is a descriptive measure of a bivariate distribution, analogous to the standard deviation of a univariate distribution (Batschelet, 1981). In this analysis the y axis of niche space consisted of the trophic position of each fish and the x axis the proportion littoral C in diets for each fish as estimated by the mixing models described above. Thus, larger scores on the y axis reflect higher trophic positions, while larger scores on the x axis indicate greater reliance on littoral energy. We assessed differences in community niche structure between lakes by comparing species' SEAc ellipse sizes and locations on the trophic position and littoral C axes between lakes. We also estimated the trophic range, range of littoral C reliance and SEAc for the entire fish community in both lakes using the Bayesian framework described by Jackson et al. (2011). Similar to the SEAc described above for individual species, these metrics estimate the range of littoral C use (x axis), range of trophic positions (y axis), and size of the SEAc (using both axes) for the entire fish community. We used the resulting credible intervals to assess whether these three community metrics differed between lakes. Finally, McMeans et al. (2016) proposed that fish in higher trophic positions feed across multiple trophic levels and in both pelagic and littoral habitats, and that anthropogenic disturbances can reduce integration by forcing fish to feed at higher trophic levels and specialise on either pelagic or littoral energy sources. We tested this prediction by assessing whether littoral C in diets was positively related to trophic position of fish, and whether presence of zebra mussels increased reliance on littoral C. This analysis tested for significant effects of fish species, trophic position, lake and trophic position-lake interaction on littoral C in diets of individual fish.



FIGURE 2 Mean baseline corrected δ^{13} C for nine taxonomic groups of aquatic invertebrates in Lake Ida and Lake Carlos (±95% confidence intervals). Baseline corrected δ^{13} C are the difference between average zooplankton δ^{13} C and each littoral macroinvertebrate (macroinvertebrate δ^{13} C – \bar{x} zooplankton δ^{13} C). Thus, a baseline corrected δ^{13} C of zero indicates similar reliance on pelagic C as zooplankton, while higher positive numbers indicate increasing higher reliance on littoral C

Though fish species was included in our analysis, we focus on the effects of lake and trophic position on littoral C given our interest in community-scale patterns.

3 | RESULTS

-2

In both lakes, confidence intervals showed that BC δ^{13} C for caddisflies, mayflies, *Hyalella* and littoral midges were significantly higher than zero, indicating greater reliance on littoral C compared to zooplankton (Figure 2a–d). No differences were detected between lakes, indicating similar reliance on littoral C between systems for these taxa. Confidence intervals for profundal midges did not differ significantly from zero, indicating a reliance on pelagic C similar to zooplankton, and no differences were detected between lakes (Figure 2e). In contrast, all three groups of secondary invertebrate consumers (damselflies, dragonflies and water scorpions) had higher reliance on littoral energy relative to zooplankton, and in each group the reliance on littoral energy was significantly higher in Lake Carlos compared to Lake Ida (Fig 2f-h). Finally, snails also relied more heavily on littoral C compared to zooplankton, and reliance was higher in Ida compared to Carlos, the reverse of the pattern observed in secondary consumers (Figure 2i).

Mixing model estimates of proportion of littoral C in fish diets were similar to results for BC δ^{13} C in invertebrate secondary consumers in that 10 of 11 species of fish had a higher reliance on littoral C in Lake Carlos compared to Lake Ida. Black crappie (*Pomoxis*)

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Lake Ida



FIGURE 3 Mean proportion littoral carbon in tissue of nine species of fish in Lake Carlos and Lake Ida as estimated from isotope mixing models (±95% confidence intervals). A value of 0.50 indicates equal amounts of pelagic and littoral carbon in fish tissue



FIGURE 4 Proportion littoral carbon in dorsal muscle tissue of two species of fish in Lake Carlos and Lake Ida as a function of fish length. Values were estimated via isotope mixing models, and a value of 0.50 indicates equal amounts of pelagic and littoral carbon in fish tissue





FIGURE 5 Mean trophic position above primary consumer for five species of fish in Lake Carlos and Lake Ida (±95% confidence intervals). Values were estimated from isotope mixing models, and a value of 1.0 indicates fish feed only on primary consumers

nigromaculatus, Centrarchidae), bluegill, bluntnose minnow, largemouth bass (*Micropterus salmoides*, Centrarchidae), northern pike (*Esox lucius*, Esocidae), pumpkinseed (*Lepomis gibbosus*, Centrarchidae), smallmouth bass (*Micropterus dolomieu*, Centrarchidae), walleye and yellow bullhead (*Ameiurus natalus*, Ictaluridae) all had higher proportions of littoral C in their diets in Lake Carlos compared to Lake Ida, while fish length did not influence proportion of littoral C in any of these species (Figure 3a–i). Yellow perch showed higher reliance on littoral C as fish length increased, and also higher littoral C reliance in Lake Carlos compared to Lake Ida (Figure 4a). Lastly, rock bass (*Ambloplites rupestris*, Centrarchidae) showed a positive relationship between proportion of littoral C and fish length but was the only species that did not differ between lakes in reliance on littoral C (Figure 4b).

Analysis of trophic positions as estimated from mixing models showed that black crappie and largemouth bass had higher trophic positions in Lake Carlos relative to Lake Ida, but these species showed no relationship between fish length and trophic position (Figure 5a, b). Bluegill, bluntnose minnow and walleye trophic positions did not differ between lakes or show a relationship with fish length (Figure 5c-e). The most common result was higher trophic position of fish in Lake Carlos and trophic position increasing with fish length in both lakes, as was observed for northern pike, smallmouth bass, yellow bullhead and yellow perch (Fig 6a-d). Finally, pumpkinseed and rock bass trophic position did not differ between lakes but did increase with fish size for both species, although results for rock bass were influenced by two data points (Figure 6e, f).

Results for isotopic niche SEAc ellipses showed that all species of fish excluding rock bass had niches more reliant on littoral C in Lake Carlos compared to Lake Ida (Figure 7), as rock bass was the only species whose SEAc ellipses overlapped between lakes. Differences in trophic position were largely consistent with parametric tests of trophic position, with SEAc ellipses of some fish species showing no overlap on the y axis between the two lakes (e.g., yellow perch and smallmouth bass), while other species had considerable overlap indicating no difference in trophic position between lakes (e.g., rock bass and pumpkinseed). In contrast to species-level results, we found no differences between lakes in community-scale estimates of niche space. Estimates of trophic range, range of littoral C reliance and SEAc total niche space were similar between lakes and all had widely overlapping credible intervals (Figure 8). Finally, trophic position, lake, and species all showed significant relationships with proportion littoral C in fish diets (all p < .001), but we detected no lake-trophic position interaction (p = .352; Figure 9). The overall pattern was higher reliance on littoral C in Lake Carlos at a given trophic level, as well as a shift to trophic levels higher than those observed in Lake Ida. The net result was fish at the highest trophic levels integrated more diverse energy sources in Lake Ida than in Lake Carlos. For example, predicted values for proportion of littoral C in diet for smallmouth bass were 64% in Lake Ida compared to 98% in Lake Carlos.

4 | DISCUSSION

Our results indicate multiple differences in trophic structure and pathways of energy flow between a lake heavily colonised with zebra mussels and a reference lake lacking a high-density zebra mussel population. Relative to reference Lake Ida, all three sampled Lake Carlos invertebrate secondary consumers were more reliant



FIGURE 6 Trophic position above primary consumers for six species of fish in Lake Carlos and Lake Ida as a function of fish length. Values were estimated from isotope mixing models, and a value of 1.0 indicates fish feed only on primary consumers

on littoral C, 10 of 11 fish species were more reliant on littoral C, 7 of 11 fish species fed at higher trophic levels, and the overall fish community showed a significant shift in their isotopic niche towards higher reliance on littoral C and increased trophic position. Taken together, these results indicate that impacts of zebra mussels on energy flow in lakes are pervasive and influence both invertebrate and fish communities. Although impacts on aquatic invertebrates were limited to predators, effects on the fish community included species from all major functional guilds of planktivores, benthivores and piscivores. The fact that all impacted



species in Lake Carlos increased their reliance on littoral C suggests the potential for increased interspecific resource competition, which may result in shifts in community structure of both aquatic invertebrates and fish based on a species' ability to exploit littoral energy sources. The most likely cause for the differences between lakes is the documented reduction in abundance of phytoplankton and zooplankton following the increase in zebra mussel abundance in Lake Carlos. These impacts are well-described in many studies (Higgins & Vander Zanden, 2010; Noonburg, Shuter, & Abrams, 2003), and we believe they are likely to be the cause for the differences we detected between food webs in lakes Ida and Carlos.

Our results showed that all invertebrate secondary consumers we sampled had higher reliance on littoral C in Lake Carlos, while one primary consumer (snails) relied more heavily on littoral C in Lake Ida and five other primary consumers did not differ between lakes. We suspect that the differences between lakes in use of littoral C by secondary invertebrate consumers is driven by higher consumption of zooplankton in Lake Ida, as damselflies, dragonflies, and water scorpions are all known to consume zooplankton prey (Blois & Cloarec, 1983; Heads, 1986; Johansson, 1993). In Lake Carlos, lower zooplankton abundance forced these groups to rely more heavily on littoral prey such as midges and amphipods.

Some invertebrate groups did not show higher reliance on littoral C in Lake Carlos than in Lake Ida. The absence of differences in reliance on littoral C for caddisflies, mayflies, *Hyalella*, or littoral midges is probably due to these primary consumers being highly dependent on periphyton and benthic algae as an energy source regardless of phytoplankton abundance (reviewed in Thorp & Covich, 2009). Thus, their reliance on littoral C in Lake Carlos did not increase following zebra mussel colonisation as they were already feeding heavily on littoral C sources. We also found no difference in littoral C reliance between lakes for profundal midges. Profundal midges rely on rain of seston material from the pelagic habitat (Jónasson, 2004), and this is **FIGURE 7** Isotopic niche ellipses for 11 species of fish in Lake Carlos and Lake Ida. Ellipses constitute sample size-corrected standard ellipse area for each fish species in each lake. The y axis is trophic level above primary consumers and the x axis is the proportion of littoral C, with values for both axes estimated with mixing models. Species are defined as follows: BLC: black crappie; BNM: bluntnose minnow; LMB: largemouth bass; NOP: northern pike; PMK: pumpkinseed; WAE: walleye; YEP: yellow perch; BLG: bluegill; SMB: smallmouth bass; YEB: yellow bullhead; RKB: rock bass



FIGURE 8 Estimated community-scale metrics of isotopic niche size (±95% credible intervals). Trophic range is the estimated range of trophic levels, littoral proportion range is the estimated range of littoral C in diets, and SEAc is the standardised ellipse area based on trophic level and littoral C range of individual fish in each lake. Trophic level and littoral C in diets were estimated for each fish with mixing models

also indicated in our study by profundal midges in both lakes having BC δ^{13} C values similar to zooplankton (as indicated by BC δ^{13} C values not different from zero in either lake; Figure 2e). Chlorophyll-*a* values were much higher in Lake Ida (11.8 µg L⁻¹) than in Lake Carlos (3.4 µg L⁻¹) during this study, indicating much higher seston abundance in Lake Ida. No difference in reliance on littoral C between lakes for profundal midges, despite much less seston in Carlos, is



FIGURE 9 Effects of trophic position, lake and fish species on proportion littoral C in diets. Regression lines are not shown for individual fish in order to simplify the figure. Trophic position and littoral C were estimated for each fish using mixing models

probably driven by the inability of profundal midges to access nearshore benthic production enriched in δ^{13} C relative to seston (Hecky & Hesslein, 1995), as these animals remain confined to deep-water habitats and use existing depleted δ^{13} C sources. Less seston coupled with an inability to exploit near-shore benthic production may lead to reduced densities of profundal midges in Lake Carlos. Although anecdotal, it took approximately 10-fold more sampling effort to collect sufficient numbers of profundal midges in Carlos compared to Ida, suggesting a large difference in density. Finally, snails were the only taxonomic groups among all fish and invertebrates analysed to show higher reliance on littoral C in Lake Ida relative to Lake Carlos. This was a surprising result given the high reliance of snails on littoral C (Post, 2002). However, snails can be physically displaced by zebra mussels (Wisenden & Bailey, 1995), and so it is possible that altered habitat use in Lake Carlos forced snails to feed on resources more depleted in δ^{13} C.

Our results also showed reliance on littoral C was higher in Lake Carlos for almost all fish tested. We observed differences in a wide variety of fish types from the two lakes, as we found differences in planktivores, benthivores and piscivores, as well as littoral-oriented species (e.g., bluegill, pumpkinseed, smallmouth bass and largemouth bass) and pelagic-oriented species (e.g., black crappie, yellow perch and walleye). Moreover, the effect size for littoral C use was large; averaged across the 11 species that differed between lakes, littoral C use was 1.5-fold higher in Lake Carlos. The pervasive increase in littoral C in nearly all fish species tested was likely driven by increased consumption of littoral invertebrates by both invertebrate consumers (as discussed above) and fish at all trophic levels, but especially by fish in lower trophic levels with high rates of invertebrate consumption. For example, estimates of trophic position for the bluntnose minnow indicated that this species fed heavily on invertebrates in both lakes, but its reliance on littoral C increased from 54% in Lake Ida to nearly 100% in Lake Carlos. Higher reliance on littoral C in lower trophic levels was then subsequently passed to higher Freshwater Biology

trophic levels, resulting in the nearly ubiquitous increase in littoral C in the fish community. Even though many species had higher reliance on littoral C in zebra mussel-colonised Lake Carlos, the implications are probably greatest for yellow perch and walleye given their more pelagic nature (Irwin et al., 2016). It seems likely that these two species may be least suited to do well under a scenario of increased interspecific resource competition for littoral energy sources. The net result could be reduced abundance of walleye and perch (and other pelagic-orientated fish) coupled with increased abundance of littoral-associated species such as sunfish and smallmouth bass. Similar shifts from pelagic to littoral-associated fish have been observed in other lakes colonised by zebra mussels (Irwin et al., 2016) and in lakes with increased water clarity driven by reduced nutrient loading and zebra mussels (Robillard & Fox, 2006).

The isotopic niche analysis also indicated an increased reliance on littoral energy sources for the fish community impacted by zebra mussels, as all species excluding rock bass showed a higher reliance on littoral C in Lake Carlos relative to Lake Ida. This analysis also provides potential insight as to why we failed to detect differences in littoral C use between lakes for rock bass, as the SEAc ellipses in Lake Carlos for this species showed the greatest combined range on the x and y axes (Figure 7). This suggests C source and trophic position of rock bass in Lake Carlos were highly variable, making it more difficult to detect differences between lakes. The pattern of ellipses at the community scale also visually demonstrates the potential for increased interspecific competition for littoral resources in Lake Carlos, as the ellipses are clustered near to 80% reliance on littoral C in Carlos while clustering closer to 40% littoral C in Ida, reflecting a more balanced use of littoral and pelagic C across many species.

The niche analysis also visualises two groups of fish in terms of differences in trophic position between lakes. The first group is more planktivorous, and show no difference between lakes (e.g., bluegill, pumpkinseed and bluntnose minnow). The second group is more piscivorous and shows a shift upward in trophic position in Lake Carlos (e.g., yellow perch, largemouth bass, smallmouth bass etc.). These results are highly consistent with results of testing for significant differences in trophic position between lakes using mixing models. This raises the question of why trophic shifts upwards were more commonly seen in piscivorous fish than planktivorous in Lake Carlos, especially given that increased reliance on littoral C was nearly ubiquitous in both planktivorous and piscivorous fish in that system. It is possible that the trophic shift upwards in piscivores but not planktivores is driven by increased competition for littoral invertebrate prey in Lake Carlos. Piscivorous fish in Carlos may be responding to increased competition for littoral invertebrates by increasing consumption on prey fish, resulting in the observed trophic shifts upwards in that system. Planktivorous fish, in contrast, lack the morphological adaptations to feed effectively on fish prey, causing the trophic position of these species to be similar between lakes. Although we were unable to document specific mechanisms, the combined results of increased reliance on littoral energy and shifts upward in trophic position indicate that predator-prey relationships within the fish community and pathways of energy flow differ

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substantially between these two lakes. In contrast to our species-level analysis, we failed to find any differences in the size of isotopic niche space at the scale of the entire fish community. In general, the fish community in Lake Carlos shifted up and to the right in Figure 9 (and was perhaps slightly parabolic), but the overall size and range of energy use and trophic position remained unchanged. However, despite similar ranges of C use between lakes, interspecific competition for energy is likely to be higher in Lake Carlos given the much higher reliance on littoral C at the community scale. Although the general pattern was a shift up and to the right for Carlos fish in Figure 9, there also appears to be a more parabolic relationship in Carlos compared to Ida.

Recent work has shown that integration of energy sources increases with trophic position in food webs (McMeans et al., 2016; Rooney, McCann, Gellner, & Moore, 2006). Our results for Ida show the same pattern, as % littoral C in diets was 56% for fish in the highest trophic levels compared to 38% in the lowest trophic levels. In Lake Carlos, the upwards shift in both trophic level and reliance on littoral C caused fish in the lowest and highest trophic levels to increase reliance on littoral C to 67% and 89% respectively. Thus, it appears that zebra mussels reduced the ability of top predators to integrate energy flow between pelagic and littoral food webs, with integration shifting to lower levels of the food web. The implications of this shift in energy integration are unknown, but our results support the hypothesis that invasive species may reduce the ability of higher trophic levels to integrate sources of energy in food webs (Vander Zanden, Casselman, & Rasmussen, 1999; Vander Zanden, Olden, Thorne, & Mandrak, 2004). Reduced food web integration by large, mobile fish high in the food web may reduce the adaptive capacity of the ecosystem to respond to other stressors and environmental change (McMeans et al., 2016; Rooney et al., 2006).

Increased reliance on littoral energy and trophic shifts in piscivorous fish may result in shifts in the structure of both aquatic invertebrate and fish communities in Lake Carlos. Phytoplankton biomass decreased substantially in Lake Carlos following zebra mussel colonisation, but it is possible that primary production did not decrease due to a compensatory increase in mass-specific production rates of phytoplankton due to an improved light environment (Idrisi et al., 2001). If this were true, the ability of phytoplankton to support the lake food web may have remained largely unchanged. However, the consistent increase in reliance on littoral C among fish and invertebrate predators indicates that this is not the case, and the ability of phytoplankton to support the lake food web has decreased. It is also possible that overall lake primary production has remained relatively consistent despite reduced phytoplankton abundance due to increased abundance and production of littoral and benthic primary producers following the increase in water clarity (Higgins & Vander Zanden, 2010). If total primary production does stay consistent, and the food web can shift to increased reliance on littoral sources, it is plausible that lake-wide biomass of invertebrates and fish could also stay relatively consistent from pre- to post-zebra mussel infestation. Even though overall abundance could remain consistent, the species composition could shift towards invertebrate and fish species better suited to utilise littoral energy sources.

Despite weaknesses in our study design, including lack of replicate lakes and a lack of isotope data for Lake Carlos prior to colonisation by zebra mussels forcing us to use a space for time experimental design, we feel that several lines of evidence indicate that the observed differences are due to zebra mussels. First. littoral area was 5% larger in Lake Ida, vet the consistent pattern was higher reliance on littoral C by invertebrates and fish in Lake Carlos despite a smaller littoral area. Second, the lakes are in close proximity, they are in the same catchment and have similar physical characteristics and trophic status. Third, several other studies have documented δ^{13} C enrichment in lake food webs following zebra mussel infestation (Fera et al., 2017; Rennie et al., 2013; Turschak et al., 2014). Though previous studies have documented enriched δ^{13} C values in lake food webs post zebra mussels, our study builds on this past work by using mixing models to document the actual amount reliance on littoral C increases as well as significant effects on trophic positions in lake food webs. Another potential limitation in our study is the use of zooplankton for our pelagic baseline, given their potential seasonal variability (Post, 2002). We feel our results are robust, however, as using mussels for the pelagic baseline produced similar results, with the main differences being slightly higher estimates of pelagic C for fish and invertebrates in Lake Ida. Thus, relative to using mussels, our zooplankton baselines generated similar (though slightly conservative) estimates of the difference in pelagic versus littoral energy use between lakes Ida and Carlos.

In conclusion, our results indicate that zebra mussel infestation can cause large changes in pathways of energy flow in mesotrophic temperate lakes, with higher reliance on littoral C by both invertebrate secondary consumers and fish from multiple guilds, and can also result in piscivorous fish feeding at higher trophic levels. What is unknown is whether these changes will result in reduced abundance of fish or shifts in fish community structure. These patterns have implications for fisheries management and human recreation activities, as increased reliance on littoral energy could shift fish communities from balanced assemblages of pelagic- and littoral-orientated species to predominance of littoral-adapted species.

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ETHICS STATEMENT

The Minnesota Department of Natural Resources has the authority to regulate, manage, and undertake the scientific collection of fish in the waters of the state. Collection of fish for this study was completed under that authority and all guidelines and approved procedures were followed, including humane euthanasia and the release of unneeded live fish back into the lake. Live native mussels were collected under special permit number 20807 for the taking and possession of mussels.

CONFLICT OF INTEREST

The authors of this manuscript have no conflict of interest to declare.

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