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ARTICLE

Temporal variation in the niche partitioning of Lake Michigan salmonines as it relates to alewife abundance and size structure

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Abstract: Stable isotope analyses offer a useful means for quantifying ecological niche dimensions, though few studies have examined isotopic response of an ecological community with respect to resource gradients such as fluctuations in prey availability. Stable carbon and nitrogen isotopes were measured for Lake Michigan salmonines and their prey collected from 2014 to 2016. Bayesian ellipse and mixing model analyses were used to quantify isotopic niche characteristics and diets, respectively, among species and years. During the 3-year study period, abundance and size structure of preferred alewife (*Alosa pseudoharengus*) prey changed substantially and offered an opportunity to explore predator isotopic niche response and diet shifts along a prey resource gradient. Results suggested increased reliance on alewives, especially small alewives, over the study period and were consistent with greater availability of this prey. However, differential use of alewife size classes and alternative prey sources by salmonine predators was apparent, which suggested possible resource partitioning. Characterization of ecological niche overlap using stable isotopes likely requires consideration of shared resource availability as well as specific prey and habitat preferences.

Résumé : Si les analyses d'isotopes stables constituent une approche utile pour quantifier les dimensions de niches écologiques, peu d'études se sont penchées sur la réaction isotopique d'une communauté écologique en fonction de gradients de ressources tels que les fluctuations de la disponibilité de proies. Des isotopes stables du carbone et de l'azote ont été mesurés pour des salmoninés du lac Michigan et leurs proies, prélevés de 2014 à 2016. Des analyses d'ellipses bayésiennes et de modèles de mélange ont été utilisées pour quantifier les caractéristiques des niches isotopiques et les régimes alimentaires, respectivement, des différentes espèces et d'une année à l'autre. Durant la période de trois ans qu'a duré l'étude, l'abondance et la structure de tailles de la proie de prédilection, le gaspareau (*Alosa pseudoharengus*), ont considérablement changé, ce qui offre l'occasion d'examiner la réaction des niches isotopiques et les changements des régimes alimentaires des prédateurs le long d'un gradient de ressources de proies. Les résultats indiqueraient l'augmentation du recours aux gaspareaux, particulièrement les petits gaspareaux, durant la période d'étude et concordent avec une disponibilité accrue de ces proies. Des variations de l'utilisation de gaspareaux de différentes classes de tailles et d'autres sources de proies par les prédateurs salmoninés ressortent toutefois, qui indiqueraient un possible partage différentiel des ressources. La caractérisation du chevauchement des niches écologiques à l'aide d'isotopes stables nécessite probablement la prise en considération de la disponibilité des ressources partagées, ainsi que des préférences en matière de proies et d'habitats des différentes espèces. [Traduit par la Rédaction]

Introduction

A growing number of studies have attempted to use stable isotope analyses to quantify multiple dimensions of an organism's ecological niche (e.g., Kornis et al. 2020; Layman et al. 2007; Schmidt et al. 2011; Yuille et al. 2015). Stable isotope ratios (e.g., $\delta^{13}C$, $\delta^{15}N$, $\delta^{34}S$, or δD) of an organism's tissue vary because of differential mixing and fractionation of heavy and light isotopes associated with environmental gradients and physiological processes (e.g., primary production, geology, temperature, hydrology, diet, trophic level, growth, and metabolic activity; Peterson and Fry 1987). Therefore, biotic resource use as well as the abiotic

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environment experienced by an organism affect mixing and fractionation processes, with resultant variation in isotopic signature. Quantifying an organism's position along various stable isotope gradients provides a continuous measure of that organism's environment and resource use (Vander Zanden and Vadeboncoeur 2002; Bowen et al. 2010; Turschak et al. 2019). In this way, the isotopic range that an organism occupies along various isotopic axes, referred to as its "isotopic niche", is somewhat analogous to the multidimensional ecological niche of that organism (Layman et al. 2007; Newsome et al. 2007; Jackson et al. 2011; Swanson et al. 2015). Examining intra- and interspecific species variation in isotopic niche facilitates bivariate or multivariate comparisons of multiple resource overlaps. However, isotopic niche area and position (and realized ecological niche) are likely to vary across multiple environmental or resource gradients. Therefore, quantifying potential for ecological niche overlap or resource switching among a community of organisms likely requires examination of isotopic niche parameters along these various resource gradients (Liem 1980; Robinson and Wilson 1998; Yuille et al. 2015).

Stable carbon and nitrogen (hereinafter C and N, respectively) isotopes are among the mostly commonly used isotopes in ecological studies. Stable C isotope ratios (expressed as δ^{13}C) vary broadly among primary producers but are relatively conserved (<1‰) during trophic transfer (Bootsma et al. 1996; France 1995; Hecky and Hesslein 1995). At the base of a food web, stable nitrogen isotope ratios (expressed as δ^{15}N) can vary according to the form of nitrogen assimilated. Above that base, δ^{15}N increases incrementally by 3‰–4‰ with each trophic transfer (Minagawa and Wada 1984; Vander Zanden et al. 1997). Enrichment of δ^{15}N also occurs in profundal organisms in the Great Lakes and oceans due to ^{15}N enrichment in settling phytoplankton (Altabet 1988; Ostrom et al. 1998; Sierszen et al. 2006). Thus, in aquatic systems δ^{13}C and δ^{15}N are used to determine primary energetic pathway (i.e., benthic or pelagic) and trophic level and (or) depth distribution of consumers, respectively (Vander Zanden et al. 1997; Vander Zanden and Vadeboncoeur 2002; Sierszen et al. 2006, 2014).

We sought to examine δ^{13}C and δ^{15}N isotopic niche overlap as it relates to the diets of the Lake Michigan salmonines. Lake Michigan, a Laurentian Great Lake, has a salmonine community comprised of native lake trout (*Salvelinus namaycush*), as well as introduced Pacific salmonines (*Oncorhynchus* spp.: Chinook salmon (*O. tshawytscha*), coho salmon (*O. kisutch*), pink salmon (*O. gorbuscha*), and steelhead (*O. mykiss*)), and Atlantic–European salmonines (*Salmo* spp.: brown trout (*S. trutta*) and Atlantic salmon (*S. salar*)). Pink salmon and Atlantic salmon are rarely encountered, and little is known about their feeding ecologies in Lake Michigan. In Lake Huron, these species seem to be exhibit strong reliance on various fish (rainbow smelt (*Osmerus mordax*) and sticklebacks (*Gasterosteus aculeatus* and *Pungitius pungitius*)) and invertebrates (*Bythotrephes longimanus* and terrestrial invertebrates; Roseman et al. 2014). However, numerous diet studies of the five common Lake Michigan salmonines, spanning decades, have yielded unequivocal evidence that the invasive pelagic planktivore alewife (*Alosa pseudoharengus*) is the primary salmonine prey species in Lake Michigan (Jude et al. 1987; Stewart and Ibarra 1991; Rand et al. 1993; Warner et al. 2008; Savitz 2009; Jacobs et al. 2010, 2013; Happel et al. 2018; Leonhardt et al. 2020). The extent of alternate prey use is lower than observed in systems without alewife prey (e.g., Roseman et al. 2014) but still varies among species. For instance, Chinook salmon appear almost exclusively reliant on alewives, whereas steelhead and coho salmon diets have varied to include larger proportions of invertebrate prey (Jacobs et al. 2013; Leonhardt et al. 2020). Lake trout and brown trout, while still highly dependent on alewives, also obtain large proportions of their diets from round goby (*Neogobius melanostomus*), an invasive benthivorous prey species (Kornis et al. 2017; Happel et al. 2018; Leonhardt et al. 2020).

The degree of dependence on alewife prey and hence potential for dietary niche overlap likely also varies spatiotemporally for Lake Michigan salmonines (Happel et al. 2018, 2020; Leonhardt et al. 2020). Early diet studies of Lake Michigan salmonines suggested very high degrees of dietary overlap corresponding to an abundant alewife population with multiple ages well represented in the diet (Jude et al. 1987; Stewart and Ibarra 1991; Jacobs et al. 2013). However, alewife and other pelagic forage fish have declined substantially, corresponding with sustained high consumptive demand by salmonine predators, which may have been further exacerbated by major declines in the abundance of the native amphipod *Diporeia* (Madenjian et al. 2002, 2006, 2015; Tsehaye et al. 2014*a*, 2014*b*). The age structure of the current alewife population is highly truncated, with relatively few old fish in any given year. Recruitment has also been variable and observed to be low in most years since 2013 (Vidal et al. 2019; Bunnell et al. 2020). With major long-term declines in pelagic prey fish biomass, some salmonine predators have been able to use alternative nearshore benthic or terrestrial energy pathways, which are decoupled from pelagic energy pathways (Johnson et al. 2005; Dietrich et al. 2006; Rennie et al. 2009; He et al. 2015; Fera et al. 2017). Here and throughout, major energetic pathways in Lake Michigan are defined by the location of carbon fixation. For instance, "nearshore benthic" energetic pathway refers to C fixed in the nearshore benthos (i.e., periphyton), which is subsequently available to higher trophic levels. The degree of species-specific dependence on these alternative pathways seems to correspond to long-term, lake-wide declines in pelagic alewife, as well as the size structure of locally available alewives among seasons (Roseman et al. 2014; He et al. 2015; Happel et al. 2018; Leonhardt et al. 2020).

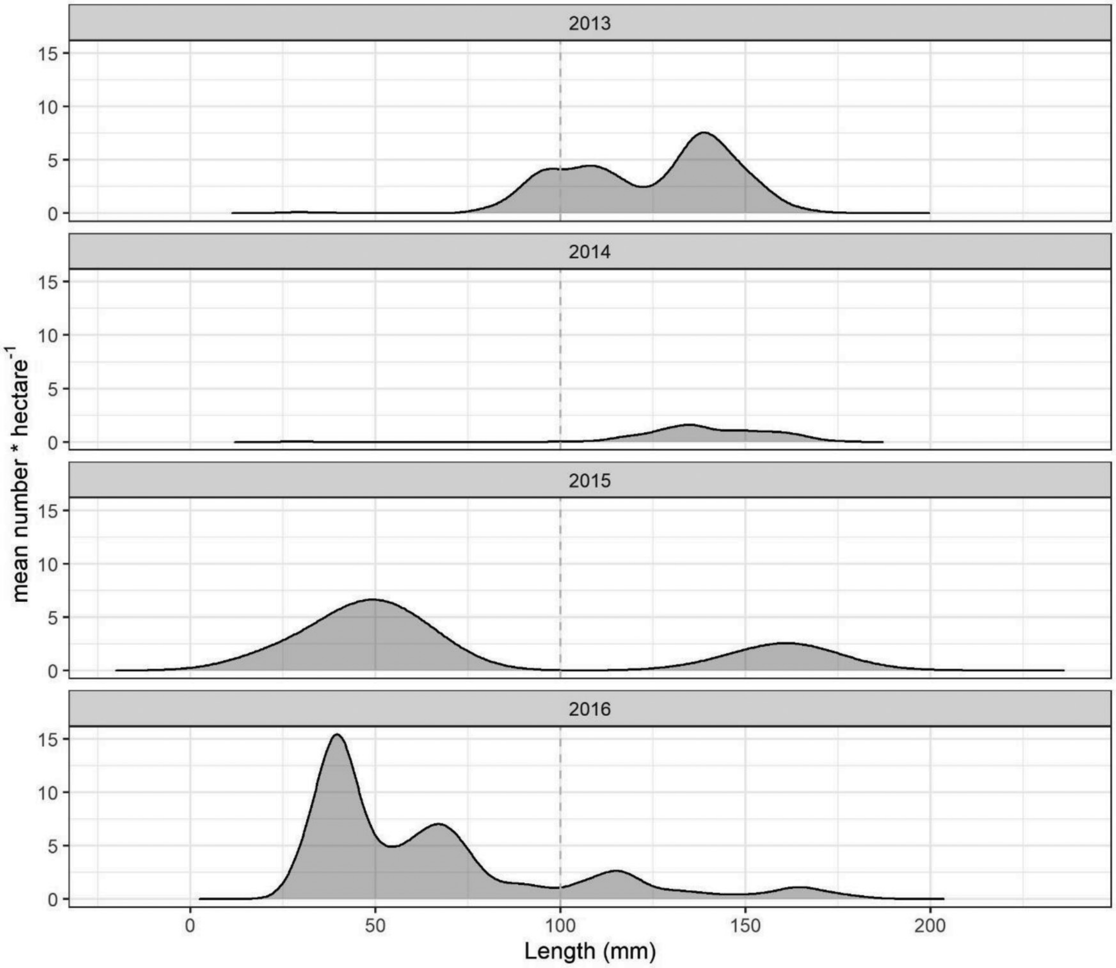
Stable C and N isotope data for Lake Michigan salmonines were available for the 3-year period from 2014 to 2016, during which time lake-wide alewife density increased markedly, and size structure shifted from larger to smaller individuals (Fig. 1; D. Warner, personal communication; Bunnell et al. 2020; Legler et al. 2017). Estimates of numeric and biomass density increased substantially from a record low density of primarily larger individuals in 2014 to numerically more abundant but smaller individuals in 2015 and 2016. This transition corresponds to the recruitment of age-0 fish (approximately <100 mm) in both 2015 and 2016 detected by the August lake-wide hydroacoustic survey (Fig. 1; Bunnell et al. 2020). During this same period, we collected muscle tissue from Lake Michigan salmonines and analyzed them for stable isotopes. This provided the opportunity to (1) characterize salmonine isotopic niche areas and positions as well as intra- and interspecies overlaps across a temporal resource gradient and (2) use stable isotope mixing models to evaluate temporal and regional diet differences, as they might relate to alewife density and size structure. Our objectives were to determine whether stable C and N isotopes were able to resolve changes in realized dietary niche area among species and, if so, the degree of niche partitioning and diet flexibility among these species along a dietary resource gradient.

Materials and methods

Sample collection

Stable isotope samples and biometric data were collected from the five most prevalent species of Lake Michigan salmonines (n = 2057) in 2014–2016. Most salmonine samples were collected from recreationally harvested fish as part of the US Fish and Wildlife Service Great Lakes Mass Marking Program (Bronte et al. 2012). Detailed stable isotope sampling strategy and methodology from the Mass Marking Program are given by Kornis et al. (2020), where tissue samples were collected from angler catches at fish cleaning stations and at recreational fishing tournaments at 28 port cities around Lake Michigan. In 2014, samples were collected from June–September, and in 2015 and 2016 samples were collected from April–September. Supplemental lake trout samples were also collected in 2016 as part of several independent gill net (38–152 mm stretch mesh) sampling efforts led by the Michigan Department of Natural Resources (Eastern Lake Michigan), Wisconsin Department of Natural Resources (Southwestern Lake Michigan), and Little Traverse Bay Band of Odawa Indians

Fig. 1. Lake Michigan alewife length density distribution scaled by average lake-wide areal density of alewives from 2013 to 2016 (D. Warner, personal communication; data source: Lake Michigan Hydroacoustic Survey). Cutoff for discrete alewife size classes used in this study are indicated by the vertical dashed lines: small alewives <100 mm and large alewives ≥100 mm, or ≈age 0 and ≈age 1+, respectively, during the August hydroacoustic survey.



(Northeastern Lake Michigan). In addition to biometric data (e.g., total length and weight), small (<10 g) skin-free dorsal muscle tissue plugs for stable isotope analysis and stomachs were removed from all salmonines sampled and were stored at −20 °C until they could be processed in the laboratory.

Forage fishes and invertebrate prey samples (n = 581) were collected in 2014–2016 using a variety of methods. In 2014 and 2015, forage fishes and invertebrates were captured in September bottom trawl surveys conducted by the US Geological Survey at their seven index sites around Lake Michigan (Bunnell et al. 2020). Dorsal muscle tissue plugs were collected from forage fish and stored frozen until samples could be processed in the laboratory. Aquatic invertebrates *Mysis relicta* and *Bythotrephes longimanus* were collected using vertical plankton net (500 μm) tows, and individuals were pooled according to taxa after each tow and stored frozen. In 2016, forage fish samples were collected from May to October using a combination of bottom trawls and micromesh gillnets (6–12 mm stretch mesh). Forage fish sampling was performed by the University of Wisconsin-Milwaukee, Purdue University, Illinois Natural History Survey, NOAA Great Lakes Environmental Research Laboratory, and Little Traverse Bay Band of Odawa Indians in 2016. Prey fishes collected in 2016 were frozen whole prior to laboratory analyses. Terrestrial invertebrates, which were an important component of steelhead observed diets in 2016 (Leonhardt et al. 2020), were removed from diets during gut content analyses, subset, and then set aside in desiccators for subsequent stable isotope analysis.

Protocols for sample collection and euthanasia were reviewed and approved by the University of Wisconsin-Milwaukee Institutional Animal Care and Use Committee following guidelines from the American Association for Laboratory Animal Science.

Sample processing and analysis

Laboratory processing and stable isotope analysis were done independently in each year of the study period. Forage fish homogenates, salmonine dorsal muscle plugs, and whole invertebrates were dried in 1.5 mL polypropylene microcentrifuge tubes using a drying oven at 60 °C for 48 h (2014) or were lyophilized (2015–2016) in polystyrene weighing boats. Dried samples were homogenized by grinding with a mortar and pestle (2014) or by chopping into a fine powder using surgical scissors or razor blades (2015–2016). Subsamples of dried tissue homogenate (0.8–1.2 mg) were then packed into a tin capsule for subsequent stable isotope analyses. In 2014, samples were analyzed for $\delta^{13}C$ and $\delta^{15}N$ at the UC-Davis Stable Isotope Facility using a PDZ Europa ANCA-GSL elemental analyzer (EA) front end coupled with a PDZ Europa 20–20 isotope ratio mass spectrometer (IRMS). In 2015, samples were analyzed at the Center for Environmental Science and Technology, University of Notre Dame, using an EA (Costech, Valencia, California) coupled to a

Delta Plus IRMS (Thermo Scientific, Waltham, Massachusetts). In 2016, samples were analyzed at the School of Freshwater Sciences, University of Wisconsin-Milwaukee, using an EA front end (ECS 4010, Costech Instruments, Valencia, California) coupled with a Delta V Plus IRMS (Thermo Fisher, Bremen). For each sample year, isotope ratios were adjusted after each sample run using a 3-point standard curve and known NIST laboratory standards. During all sample runs, an acetanilide control sample was analyzed for ^{13}C:^{12}C and ^{15}N:^{14}N ratios after every 12th sample to ensure precision of IRMSs used for each sample year ($\delta^{13}C$ SD = 0.20 and $\delta^{15}N$ SD $\leq$ 0.20). All stable isotope results were expressed in per mil (‰) differences between the isotope ratio of the sample and that of the standard (Pee Dee Belemnite carbonate or atmospheric air for $\delta^{13}C$ and $\delta^{15}N$, respectively), using the formula: $\delta^{13}C$ or $\delta^{15}N = (R_{\text{sample}}/R_{\text{Standard}} - 1) \times 1000$, where $R = {}^{13}C/{}^{12}C$ for $\delta^{13}C$ and $R = {}^{15}N/{}^{14}N$ for $\delta^{15}N$.

Data processing and analysis

All $\delta^{13}C$ values of salmonine predators and prey were corrected for lipid content, and $\delta^{13}C$ values presented hereinafter reflect lipid-corrected values. Lipid-correction for most species was done using Lake Michigan species-specific equations and coefficients developed and described in Appendix B of Turschak et al. (2014) and Turschak (2013). Correction coefficients were updated for salmonines and some prey by Kornis et al. (2020), and these updated coefficients were used for all applicable species. However, species-specific correction equations were not developed for several taxa, including bloater (*Coregonus hoyi*), *Bythotrephes*, and terrestrial invertebrates. For these taxa, the generic correction equations of Post et al. (2007) were used in place of species-specific corrections.

For analysis purposes, salmonine stable isotope samples from each of the various ports were grouped into four major quadrants of the lake (i.e., northwest (NW), southwest (SW), southeast (SE), and northeast (NE)) as described in Turschak et al. (2019). Analysis regions were selected a priori based on expected spatial variability observed in previous Lake Michigan stable isotope studies (Happel et al. 2015; Foley et al. 2017; Turschak et al. 2019). However, regional trophic baseline corrections were not made for salmonine predators. Given broad horizontal and (or) vertical (profundal–pelagic) movements of salmonine predators in the Laurentian Great Lakes, most are unlikely to reach isotopic equilibrium with regional or depth specific isotopic values (Adlerstein et al. 2008, 2007*a*, 2007*b*; Bronte et al. 2007; Clark et al. 2017; Haynes et al. 1986; Schmalz et al. 2002; and Michigan Department of Natural Resources, unpublished data). Therefore, imposing regional differences in baseline isotope signatures on predators caught within each region is likely to result in artificial regional differences that obscure true differences in predator isotopic niche (Vander Zanden and Rasmussen 1999; Post 2002; Foley et al. 2014; Turschak et al. 2019).

Sample sizes of prey taxa and size classes of interest (prey sources, hereinafter) were variable among years, so these data were pooled together to produce lake-wide, 3-year (2014–2016) mean and variance estimates of $\delta^{13}C$ and $\delta^{15}N$. For forage fishes, size structure and sample size collected for analyses during opportunistic sampling reflected natural lake-wide size structure and abundance (Appendix A, Fig. A1). Therefore, this study was unable to collect all possible prey sources for all years and required data pooling. Given known ontogenetic variation in stable isotope signatures (Turschak and Bootsma 2015; Mumby et al. 2018*a*) and changes in size structure for certain prey species (e.g., alewife) over the study period (Bunnell et al. 2020), interannual variation among prey source $\delta^{13}C$ and $\delta^{15}N$ were evaluated. Interannual variation among prey source $\delta^{13}C$ and $\delta^{15}N$ was very low for most species, especially those of high dietary importance such as alewife; therefore, data aggregation was justifiable. Small interannual differences probably reflected the variable size structure and regional variation among prey sources during various collections (Appendix A, Fig. A1; Mumby et al. 2018*a*; Turschak et al. 2019). To provide equal weight to annual $\delta^{13}C$ and $\delta^{15}N$ mean and variance estimates despite unbalanced annual collections, we used a bootstrap resampling procedure when prey source data was available for multiple years. Prey $\delta^{13}C$ and $\delta^{15}N$ values were resampled with replacement (n = 1000) to produce source-specific annual sampling distributions. Bootstrapped annual $\delta^{13}C$ and $\delta^{15}N$ distributions for each species were combined and the mean and SD was calculated to produce a 3-year pooled value wherein mean and variance for each year was given equal weight (Appendix A, Fig. A1). This procedure incorporated prey source variance observed across all study years and regions and allowed us to minimize biases associated with unbalanced sampling of prey source isotopic data.

Quantitative statistical analyses of stable isotope data were performed in R version 3.5.1 (The R Foundation for Statistical Computing). Diet proportions of salmonines were determined using the MixSIAR package (Stock et al. 2018) stable isotope mixing models. MixSIAR models were modified from the standard rjags package to operate using the runjags package in R, which better facilitated parallel processing (i.e., 4 cores) and extension of MCMC (Markov chain Monte Carlo) chain length without having to restart model runs. These modified MixSIAR models were structured with collection year as a random factor, region as a nested random factor, and consumer total length as a continuous covariate. Informative prior Dirichlet distributions were used based on wet weight diet proportions observed in salmonine diets in 2015 and 2016 (Leonhardt et al. 2020). Prior distributions varied with species but were held constant among years and regions included in this study. Apart from round goby, which were included as a nearshore benthic endmember in all models, predator-specific prey sources that made up less than 2% by weight in 2015–2016 observed annual lake-wide diet proportions were not included as potential sources in mixing models (Leonhardt et al. 2020). Trophic enrichment factors (mean ± SD) of 0.4 ± 1.3 and 3.4 ± 1.0 for $\delta^{13}C$ and $\delta^{15}N$, respectively, were also provided as model inputs (Post 2002). Models were run with 4 parallel MCMC chains of length 50 000. Burn-in length was 20 000 and chains were thinned by 10. Model convergence was evaluated visually using trace plots and quantitatively using the Gelman–Rubin diagnostic. If the Gelman–Rubin diagnostic exceed 1.05 for more than 5% of parameter estimates, the model was extended by an additional 50 000 iterations with the same burn-in length and thinning. The model was revaluated using the Gelman–Rubin diagnostic and iteratively extended as described above until this diagnostic indicated fewer than 5% of parameter estimates exceeded 1.05.

Isotopic niche area expressed as Bayesian standard ellipse area (SEA_B) and overlap were assessed using the SIBER (Jackson et al. 2011) and nicheROVER (Swanson et al. 2015) packages in R, respectively, by fitting 95% Bayesian ellipses to $\delta^{13}C$ and $\delta^{15}N$ biplot data. Ellipses were fit to each year–species combination to assess interannual variation in isotopic niche area within a salmonine species among years (e.g., Species A Year 1 × Species A Year 2 × Species A Year 3) and among salmonine species within years (e.g., Species A Year 1 × Species B Year 1 × Species C Year 1). Isotopic niche overlap was also evaluated among species on an interannual basis to better understand potential for ecological interactions from one year to the next (e.g., Species A $\cap$ Species B Year 1 × Species A $\cap$ Species B Year 2 × Species A $\cap$ Species B Year 3).

Results

Isotopic niche size and overlap

Lake Michigan salmonines occupied a broad range in the stable C and N isotope biplot ($\delta^{13}C$: –26‰ to –20‰; $\delta^{15}N$: 8‰ to 15‰) with niche area and interspecific overlap variable among species (Fig. 2 lower left panel; Fig. 3). When all data years were combined, non-Pacific salmonines, brown trout, and lake trout occupied the largest isotopic niche areas (Fig. 2 lower left panel). The

Fig. 2. Median 95% $\delta^{13}C$ and $\delta^{15}N$ isotopic niche for Lake Michigan salmonines from 2014–2016. Left panels (upper five) depict interannual differences in isotopic niche position and size for individual salmonine species. Lower panels (right three) depict interspecific isotopic niche area and niche overlap among salmonine species within individual study years. Lower-left-most panel depicts interspecific isotopic niche area and niche overlap for all study years combined, with individual data points shown to illustrate ellipse fitting. Block of panels in the upper right depict individual species–year combinations with trophic-adjusted prey position and standard deviation ($\delta^{13}C$: +0.8 ± 1.3; $\delta^{15}N$: +3.4 ± 1.0) overlaid as coloured cross bars. Dashed lines indicate the upper and lower 95% credible intervals around the shaded median ellipse, and the text indicates median ellipse area (95% credible interval).

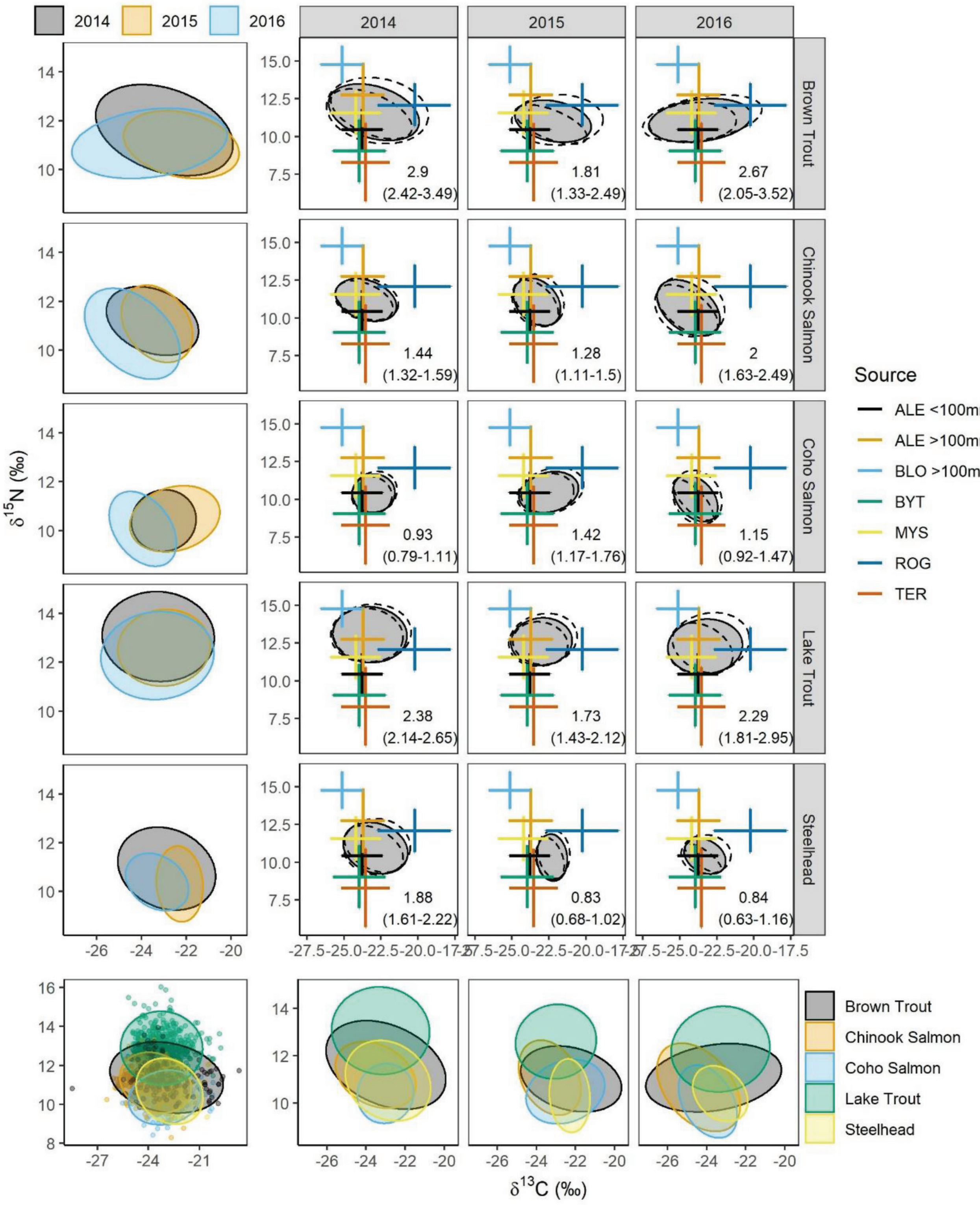
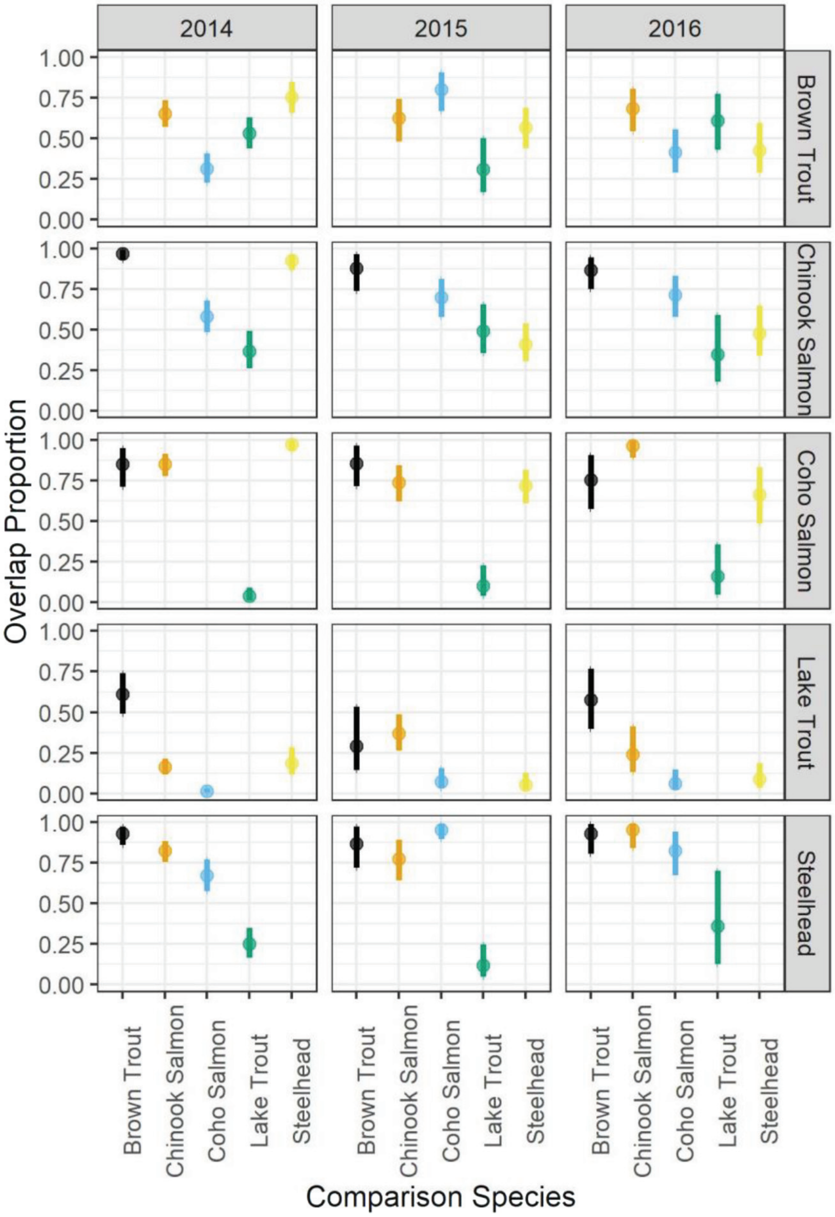


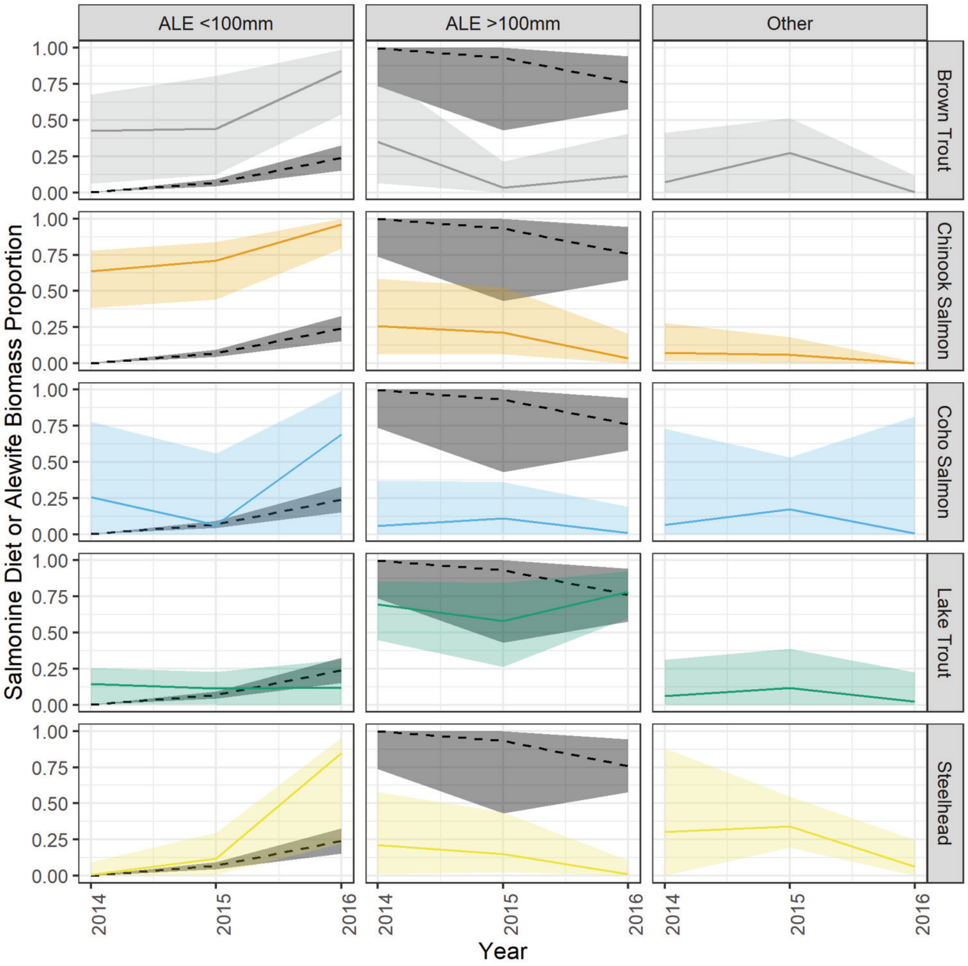
Fig. 3. Pairwise median (95% credible interval) $\delta^{13}C$ and $\delta^{15}N$ isotopic niche overlap among species expressed as a percentage of overlap in species-specific 95% isotopic niche region shown in Fig. 2. Horizontal panels (2014–2016) indicate the year for which the pairwise comparisons are being made, and vertical panels indicate the reference species. Pairwise comparisons are directional and are expressed relative to the reference species. For example, an individual from comparison species A (*x* axis) has X% probability of occurring within reference species B's (vertical panels) isotopic niche region.



large isotopic niche of brown trout encompassed much of the area occupied by other salmonines and resulted in a high degree of apparent isotopic niche overlap (60%–97%; Fig. 2 lower panels; Fig. 3). While lake trout also occupied a large isotopic niche area, they occupied the most unique area, with enriched $\delta^{15}N$ relative to other salmonines (Fig. 2 lower panels). As a result, lake trout had the least overlap with other salmonines (11%–55%; Fig. 2 lower panels; Fig. 3). Pacific salmonines occupied smaller isotopic niche areas, and there was greater niche overlap among these congeners (Fig. 2 lower panels; Fig. 3). Chinook salmon had the largest niche area of Pacific salmonines, with the smaller niche areas of steelhead and coho salmon mostly contained within the Chinook salmon niche area (coho: 87%; steelhead: 89% overlap with Chinook salmon; Fig. 2 lower panels; Fig. 3). Coho salmon and steelhead occupied the smallest niche areas of all salmonines, which resulted in a very low degree of overlap with lake trout and brown trout, although overlap between coho salmon and steelhead was large (88%–90%; Fig. 2 lower panels; Fig. 3).

Within individual years, niche area and degree of overlap among species varied relative to the more general patterns that were observed when all study years were combined (Fig. 2 and Fig. 3). Isotopic niche area for all salmonines except coho salmon declined from 2014 to 2015 and then increased again in 2016 with magnitude of interannual shifts variable among species (Fig. 2 left panels). Coho salmon — the only species to deviate from this pattern — also exhibited the least interannual variation in niche area from 2014–2016 (95% CI: 0.824‰^{2}–1.672‰^{2}). Conversely, brown trout and steelhead exhibited the largest change in niche area over the study period (95% CI: 1.44‰^{2}–3.49‰^{2} and 0.67‰^{2}–2.13‰^{2}, respectively; Fig. 2 left panels). Species-specific niche

Fig. 4. Estimates (median and 95% credible interval) of small alewife (left panels), large alewife (middle panels), and all other potential prey (right panels) to the lake-wide diets of salmonine predators over the study period (solid lines and light gray or coloured shading). Lake-wide biomass (mean and standard error) of alewife size classes as a proportion of total lake-wide alewife biomass measured by the August hydroacoustic survey are overlayed for comparison (dashed lines and dark gray shading; D. Warner, personal communication; see methods in Adams 2018 and Warner et al. 2019).



areas also shifted downward (lower $\delta^{15}N$) from 2014 to 2016. This was especially apparent for brown trout, lake trout, and Chinook salmon and less pronounced for coho salmon and steelhead (Fig. 2 left panels). All species were ^{13}C-enriched in 2015 relative to 2014 and 2016 (Fig. 2 left panels). Magnitude and direction of interannual shifts in both niche area and position were different among Lake Michigan salmonines (Fig. 2 left panels). Interannual changes in niche area and position were also asymmetric among salmonine species and resulted in interannual differences in interspecific niche overlap (Fig. 2 lower panels). These changes are depicted in detail in Fig. 3.

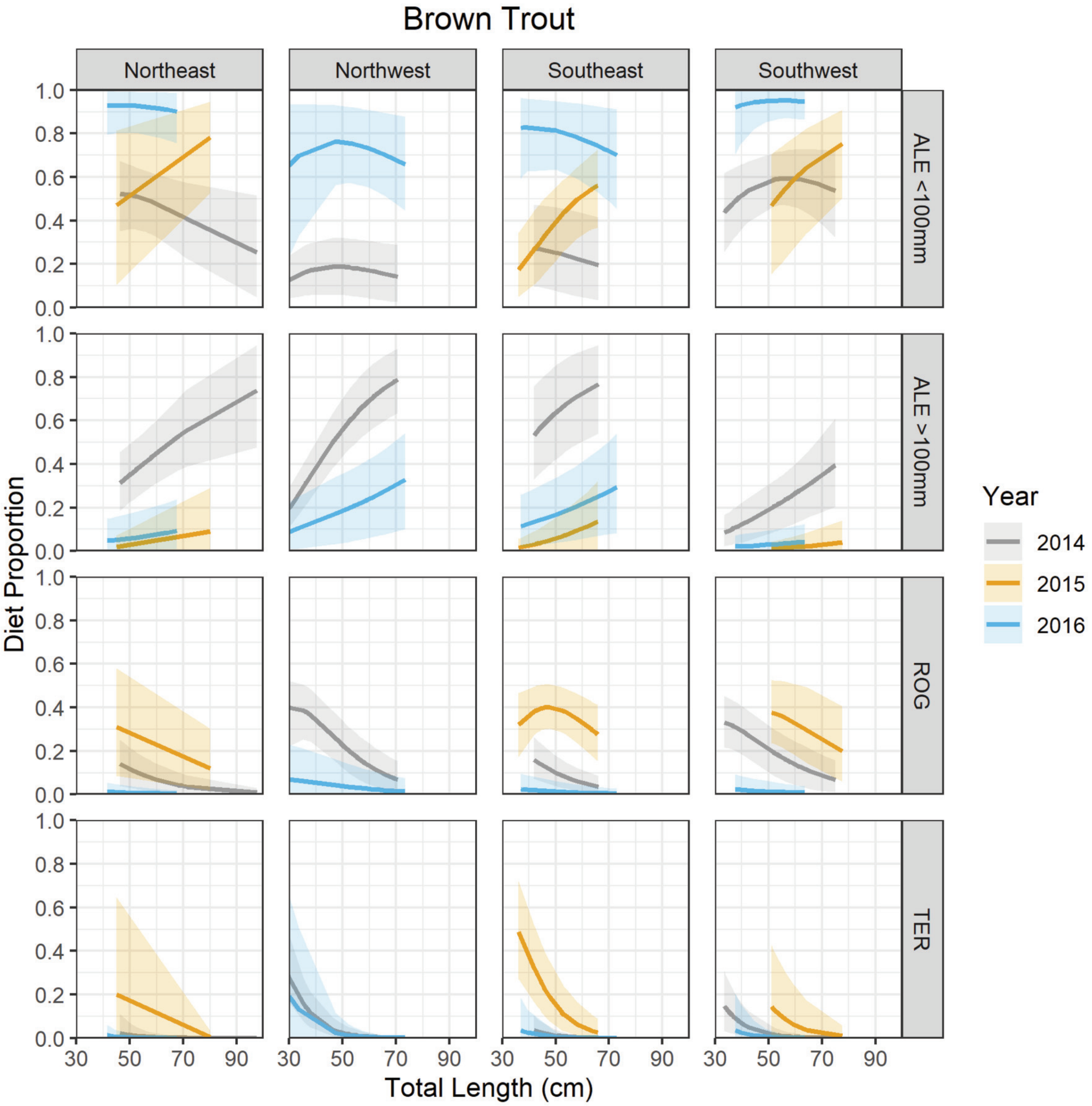
Isotope diet mixing models

Estimated brown trout diets shifted with increased total length as well as among study years (Fig. 4 and Fig. 5). Differences in brown trout diet among years were greater than relatively moderate regional differences within years. Among all years, large alewife ≥100 mm increased in dietary importance with increasing brown trout total length. However, large alewives were a larger overall proportion of brown trout diets in 2014 than they were in 2015 and 2016. Small alewives <100 mm, by comparison, increased in dietary importance from 2014 to 2016 despite variable ontogenetic diet patterns among years and regions for this prey item. Large and small alewives were the most important diet component for brown trout in all years, with substantial contributions of round goby and terrestrial invertebrates to diets at small sizes, particularly in 2015.

Estimated lake trout diets had the greatest regional diet differences of any Lake Michigan salmonine and also varied ontogenetically and interannually (Fig. 4 and Fig. 6). Among all years, large alewives dominated lake trout diets, except for lake trout from northwest Lake Michigan in 2015, which were apparently more reliant on round goby over the relatively smaller range of sizes that were available in that region. With increases in total length, lake trout appeared to transition to greater reliance on profundal prey fish like bloater and became less reliant on large alewife. Small alewives contributed less than other prey types to lake trout diets (<20%) among years and regions, and their contribution to lake trout diets varied little with changes in lake trout total length. Reliance on round goby varied little with length of lake trout but varied both interannually and regionally. For example, in 2015 round goby contributed more to regional diets than in other years. Round goby were apparently also of relatively high importance to lake trout diets in the northwest region, intermediate in the eastern regions, and least important in the southwest region.

Estimated Chinook salmon diets shifted from relatively high reliance on small alewives to large alewives with increasing total

Fig. 5. $\delta^{13}C$ and $\delta^{15}N$ mixing model predictions of dietary proportions as a function of total length (mm) for brown trout. Panels separate unique region (NE, NW, SE, and SW study) by prey source (ALE <100 mm: small alewives; ALE >100 mm: large alewives; ROG: round goby; and TER: terrestrial invertebrates) combinations. Lines represent the median of the posterior probability distribution, and the shaded areas represent the bounds of the 95% credible interval of the predicted diet proportion. Line colours correspond to specific study years (2014–2016).

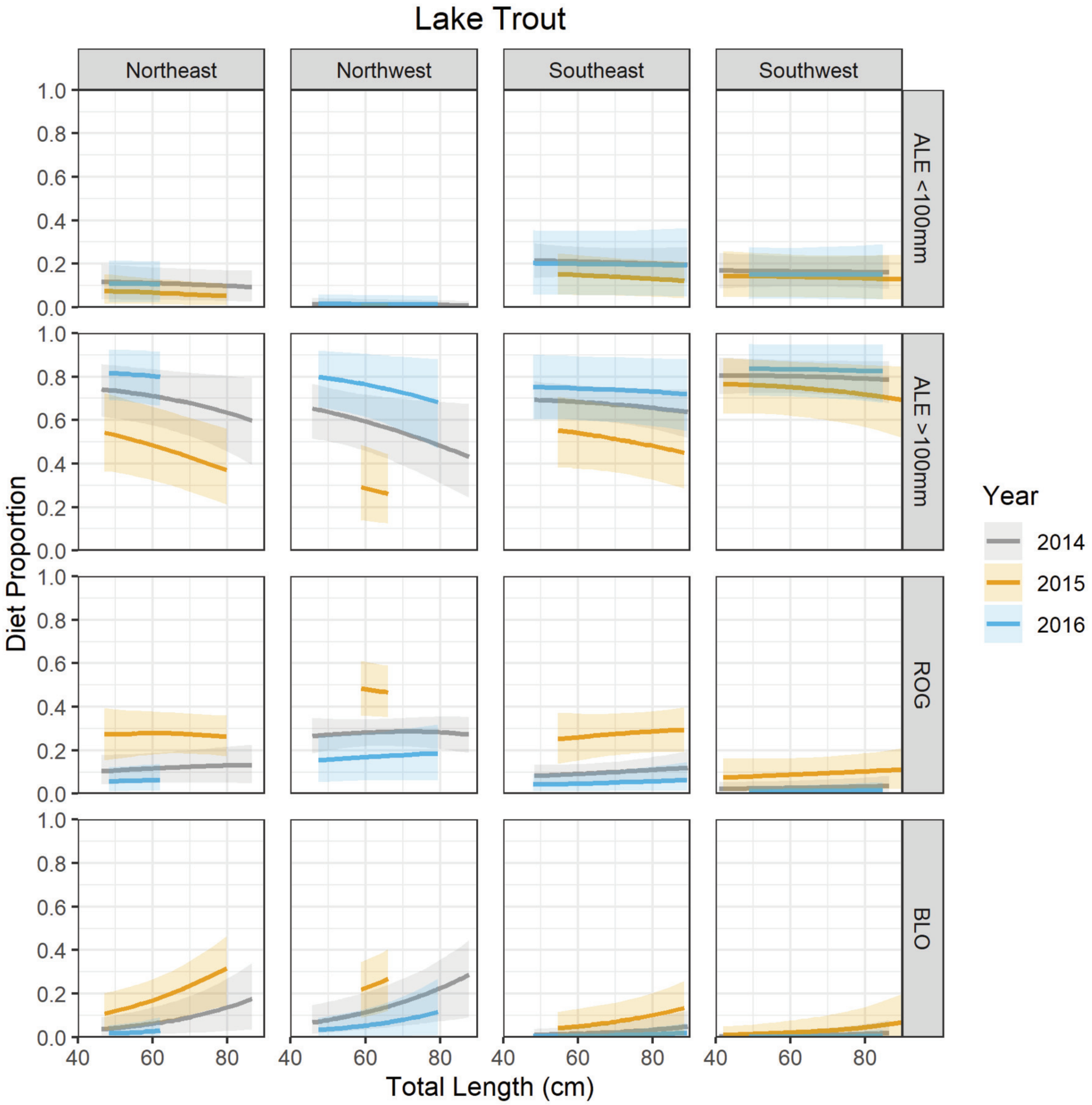


length (Fig. 4 and Fig. 7). The relative importance of small and large alewives remained similar regionally within a given year, but interannual differences were apparent. Greater importance of small alewives across all Chinook salmon sizes was observed in 2016, while all sizes of Chinook salmon were relatively more reliant on large alewives in 2014 and 2015. Round goby contributed relatively little to Chinook salmon diets, with greatest reliance on this prey occurring for small Chinook salmon in 2014.

Like Chinook salmon, estimated coho salmon diets varied little regionally, but ontogenetic and interannual differences were apparent (Fig. 4 and Fig. 8). At total lengths <500 mm, terrestrial invertebrates and *Bythotrephes* were the dominate prey sources for coho salmon but were largely replaced by small alewives as total length increased. Dietary importance of small alewives was high among years, with strongest reliance on this prey source occurring in 2016. In contrast, coho salmon had the lowest reliance on small alewives in 2015 and were relatively more reliant on alternate prey, including round goby and *Mysis*. Across the range of coho salmon total length and among years, large alewives and *Mysis* generally comprised a relatively small proportion of diets. Much greater uncertainty in mixing model diet proportions was observed for coho salmon than other salmonines.

Like the other Pacific salmonines, estimated steelhead diets were very similar regionally despite strong ontogenetic and interannual variation (Fig. 4 and Fig. 9). In 2014 and 2015, terrestrial invertebrates comprised a major component of steelhead diets, particularly at small total lengths. As steelhead total length increased, diets transitioned from terrestrial invertebrates to strong reliance on large alewives. Unlike 2014 and 2015, steelhead diets in 2016 were almost entirely dominated by small alewives, with very little reliance on other prey. From 2014–2016, there was a substantial increase in contributions of small alewives to steelhead diets and a subsequent decrease in terrestrial invertebrates and large alewives. Round goby also contributed relatively more to steelhead diets in 2015, as was observed for other salmonines.

Fig. 6. δ^{13}C and δ^{15}N mixing model predictions of dietary proportions as a function of total length (mm) for lake trout. Panels separate unique region (NE, NW, SE, and SW study) by prey source (ALE <100 mm: small alewives; ALE >100 mm: large alewives; ROG: round goby; and BLO: bloater) combinations. Lines represent the median of the posterior probability distribution, and the shaded areas represent the bounds of the 95% credible interval of the predicted diet proportion. Line colours correspond to specific study years (2014–2016).

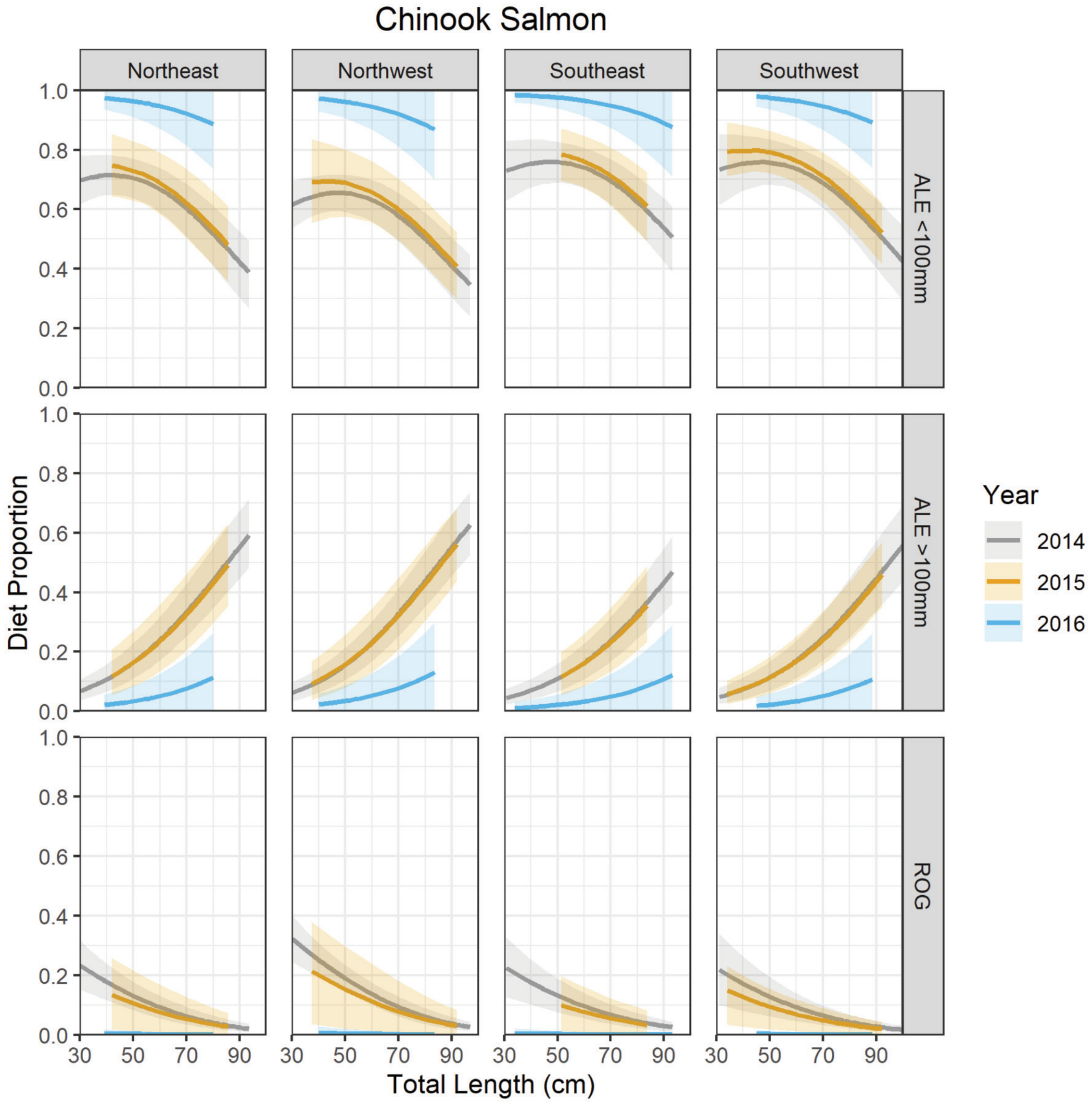


Discussion

The magnitude and direction of species-specific interannual changes in isotopic niche area and position, as well as trophic overlap among salmonine species, were consistent with shifts in abundance and size structure of the Lake Michigan alewife population and resulting consumption of potential alternative prey items. This study focused on the effects of changes in alewife density and size structure because this prey is highly preferred by Lake Michigan salmonines and dynamics of alternate prey, such as round goby, are largely unknown at this time (Happel et al. 2020; Leonhardt et al. 2020). However, when preferred alewife prey density is low, it appears that Lake Michigan salmonines, like other species (Robinson and Wilson 1998; Hayden et al. 2014; McMeans et al. 2015), switch from preferential feeding on alewives to alternative prey (e.g., terrestrial invertebrates and round goby). The threshold for prey switching varied among salmonines, with Chinook salmon apparently tolerating very low alewife abundance, whereas lake trout may use alternate prey even at relatively higher alewife abundance. Use of alternate prey by Lake Michigan salmonines may offer some evidence for how this community of predators partitions available prey by means of species-specific foraging locations or behaviors (e.g., nearshore benthos, surface, or profundal) when preferred pelagic prey are scarce. However, this also means that consideration must be given to resource gradients when examining potential for competition using stable isotopes.

Over the study period, niche area and position as well as diet mixing model results for brown trout, Chinook salmon, coho salmon, and steelhead suggested a shift to greater reliance on small alewives <100 mm and less reliance on large alewives ≥100 mm. One probable cause for this change is the increased availability of small alewives from improved recruitment in 2015 following very low recruitment in 2013 and 2014 (Fig. 1; Bunnell et al. 2020). That this event is not immediately reflected in the isotopic composition of predators is likely due to their preference for alewives larger than 50–125 mm (Leonhardt et al. 2020). It is

Fig. 7. $\delta^{13}C$ and $\delta^{15}N$ mixing model predictions of dietary proportions as a function of total length (mm) for Chinook salmon. Panels separate unique region (NE, NW, SE, and SW study) by prey source (ALE <100 mm: small alewives; ALE >100 mm: large alewives; and ROG: round goby) combinations. Lines represent the median of the posterior probability distribution, and the shaded areas represent the bounds of the 95% credible interval of the predicted diet proportion. Line colours correspond to specific study years (2014–2016).

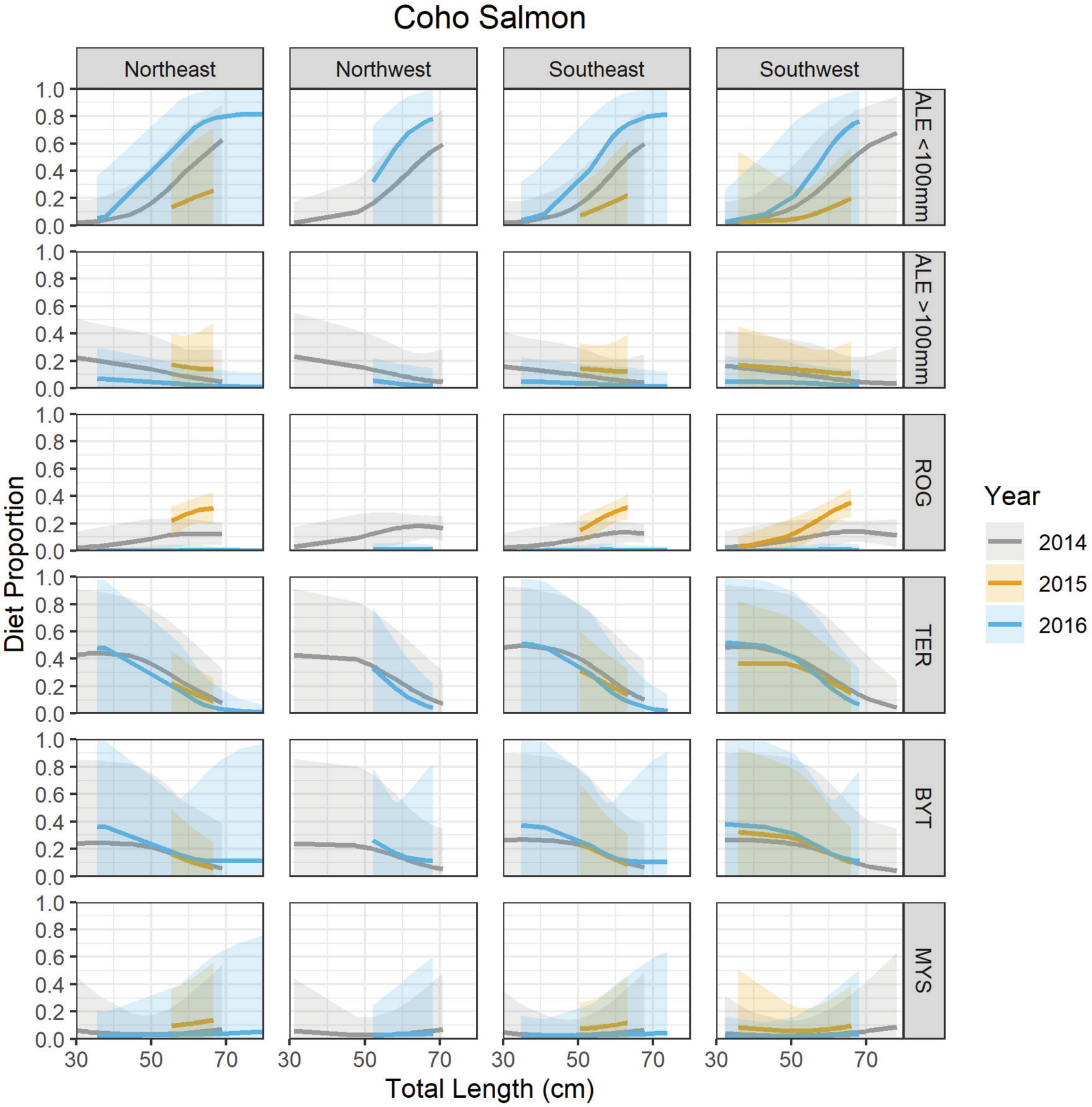


likely that young-of-year (YOY) alewives are poorly selected for by salmonines until late summer in Lake Michigan based on alewife growth rates and possible advection from nursery habitats (Höök et al. 2006, 2007; Höök and Pothoven 2009). Given the seasonally delayed availability of young alewife as potential prey and the relatively slow isotopic turnover rates of large adult salmonines (several months or more; Trueman et al. 2005; Vander Zanden et al. 2015), there may be a substantial temporal lag in the predator isotopic response to changes in small alewife availability. The rate of isotopic response will be dependent on the time or season that YOY alewife become selected for by a given predator and the rate of isotopic incorporation that varies as a function of predator catabolic turnover and growth (Weidel et al. 2011; Vander Zanden et al. 2015).

Lake trout consistently occupied some of the largest niche areas (surpassed only by brown trout) but were the least closely associated with small alewives in the isotope biplots. Enriched $\delta^{15}N$ of lake trout is likely the result of reliance on the enriched $\delta^{15}N$ profundal energy pathway and associated deeper dwelling prey such as bloater or sculpins (Turschak and Bootsma 2015; Kornis et al. 2020), as well as round goby and large alewife that were also enriched in $\delta^{15}N$ relative to small alewife. Small alewives also prefer warmer surface waters where lake trout, which prefer colder water, are unlikely to encounter them as prey (Wismer and Christie 1987; Bergstedt et al. 2012; Negus and Bergstedt 2012). Indeed, mixing model results suggest low importance of small alewife prey for lake trout. Nevertheless, niche area for lake trout did shift toward lower $\delta^{15}N$ from 2014 to 2016. Mixing model results suggest that this shift is the result of greater reliance on large alewives, which also increased in abundance in 2016 following 2015 recruitment (Bunnell et al. 2020), and a corresponding reduced reliance on bloater and round goby.

Except for Chinook salmon, which are nearly obligate alewife predators in Lake Michigan (Jacobs et al. 2013; Leonhardt et al. 2020), isotopic mixing models suggested that Lake Michigan salmonines shifted to greater reliance on round goby or isotopically

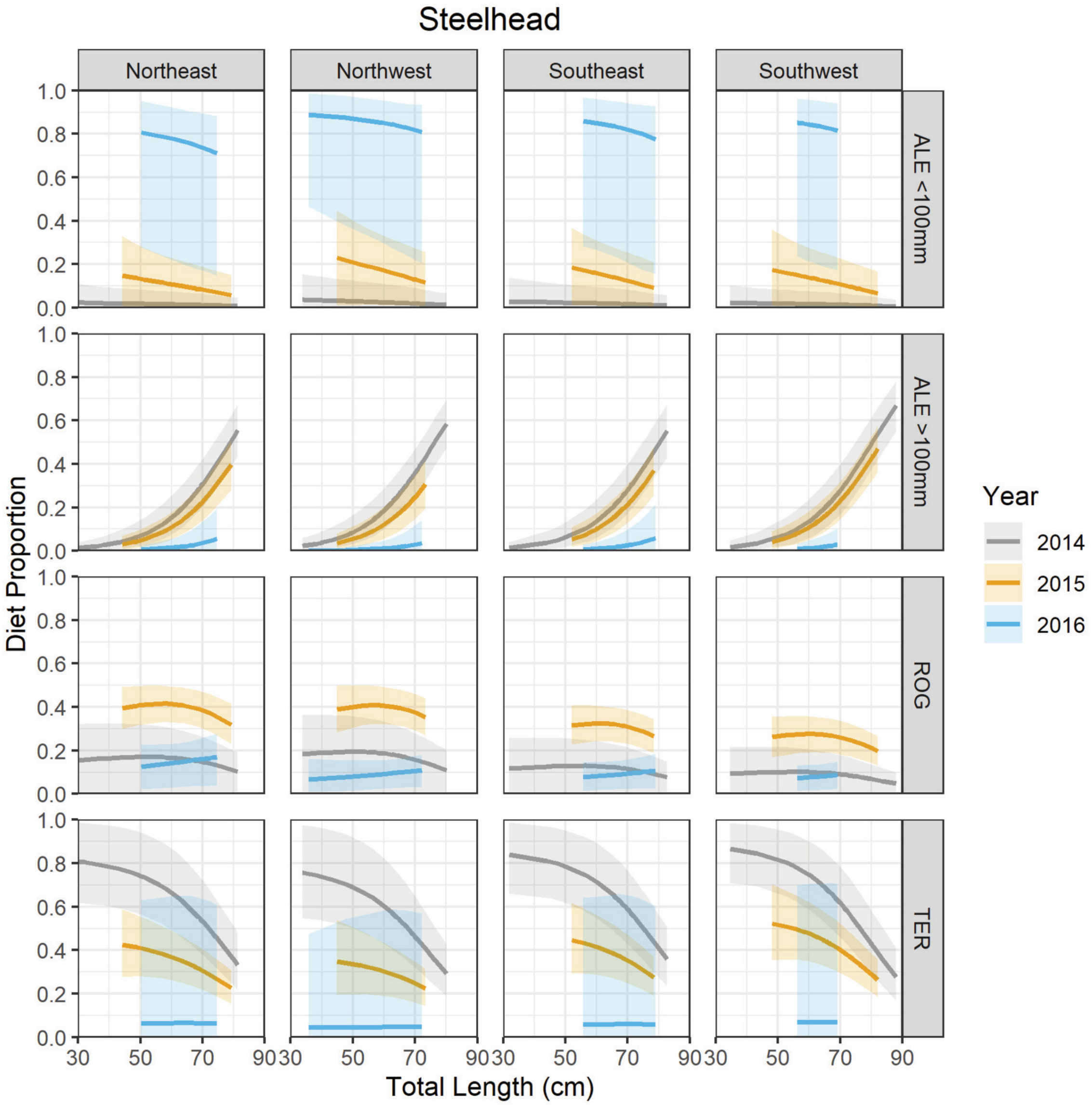
Fig. 8. δ^{13}C and δ^{15}N mixing model predictions of dietary proportions as a function of total length (mm) for coho salmon. Panels separate unique region (NE, NW, SE, and SW study) by prey source (ALE <100 mm: small alewives; ALE >100 mm: large alewives; ROG: round goby; TER: terrestrial invertebrates; BYT: *Bythotrephes*; and MYS; *Mysis*) combinations. Lines represent the median of the posterior probability distribution, and the shaded areas represent the bounds of the 95% credible interval of the predicted diet proportion. Line colours correspond to specific study years (2014–2016).



similar nearshore benthic prey in 2015, as indicated by enriched δ^{13}C among many individual salmonines in 2015 relative to 2014 and 2016. Indeed, recent diet studies have shown substantial reliance on this prey by lake trout and brown trout as well as occasional reliance by some Pacific salmonines (Johnson et al. 2005; Dietrich et al. 2006; Roseman et al. 2014; Happel et al. 2020; Leonhardt et al. 2020). Furthermore, salmonine charter angling effort and harvest of some Lake Michigan salmonines has also shifted to nearshore waters following major food web changes (Simpson et al. 2016). The shift toward nearshore energy sources coincides with the lowest biomass of alewives since forage fish monitoring began in 1962 (predator–prey ratio model results from the Lake Michigan Salmonid Working Group; Bunnell et al. 2020). Given the late season recruitment of alewives in 2015, it is reasonable that salmonines would have been somewhat more reliant on alternate nearshore benthic prey sources for much of that year.

In addition to increased reliance on nearshore benthic prey sources in 2015, mixing model results for brown trout, steelhead, and coho salmon (particularly smaller individuals of these species) suggests some reliance on invertebrate prey coincident with low alewife abundance. Terrestrial invertebrates are commonly observed in Lake Michigan salmonine diets, especially steelhead (Rand et al. 1993; Leonhardt et al. 2020), and are often associated with surface feeding in thermal bars, which entrain large numbers of terrestrial invertebrates in the spring and early summer (Haynes et al. 1986; Aultman and Haynes 1993; Höök et al. 2004). Other invertebrates commonly found in salmonine diets include the large predatory cladoceran *Bythotrephes longimanus* and the larger glacial relict *Mysis relicta* (Leonhardt et al. 2020). Poor growth rates of steelhead and coho salmon during years of low small alewife abundance suggest that diet switching to a lower energy density prey, such as invertebrates, is likely among some small salmonines and offers further evidence that invertebrates

Fig. 9. δ^{13}C and δ^{15}N mixing model predictions of dietary proportions as a function of total length (mm) for steelhead. Panels separate unique region (NE, NW, SE, and SW study) by prey source (ALE <100 mm: small alewives; ALE >100 mm: large alewives; ROG: round goby; and TER: terrestrial invertebrates) combinations. Lines represent the median of the posterior probability distribution, and the shaded areas represent the bounds of the 95% credible interval of the predicted diet proportion. Line colours correspond to specific study years (2014–2016).



are more common prey at low alewife densities (O'Gorman et al. 1987; Michigan Department of Natural Resources, unpublished data).

Spatial patterns in reliance on alternate prey sources were also apparent for lake trout and, to a lesser extent, brown trout, whereas little regional variation was apparent among Pacific salmonines. Lake trout typically occupy smaller geographic ranges than Pacific salmonines and prey upon regionally distinct prey sources, such as round goby, thereby increasing regional isotopic variation (Schmalz et al. 2002; Adlerstein et al. 2007*a*; Bronte et al. 2007; Foley et al. 2017; Turschak et al. 2019). While less information is available regarding the movement patterns of brown trout in Lake Michigan, similarities in observed diets and stable isotope signatures suggest that a similar reliance on locally distinct prey sources may be driving brown trout regional variation (Leonhardt et al. 2020). Conversely, available research for Pacific salmonines in Lakes Michigan and Huron suggest much broader spatial movement patterns as well as moderately stronger reliance on regionally indistinguishable pelagic prey sources such as alewives (Haynes et al. 1986; Adlerstein et al. 2007*a*, 2008; Clark et al. 2017; Turschak et al. 2019).

Species-specific responses to changes in resource availability were dissimilar and subsequently result in changes in potential interspecific interactions as revealed by isotopic niche overlaps among those species. Differential use of alternate prey resource pools (i.e., pelagic, profundal, nearshore–benthic, and terrestrial) is likely to aid sympatry among the Lake Michigan salmonine community, particularly if dynamics of those resource pools are decoupled from one another (i.e., asymmetric; Rooney et al. 2006; Rooney and McCann 2012). However, use of alternate resources may also allow this community to sustain itself at levels that are detrimental to the preferred alewife prey population. Compensatory declines in predator abundance resulting from low alewife abundance may be offset by these alternate resource subsidies (Schindler et al. 1996; Polis et al. 1997; Vander Zanden and Vadeboncoeur 2002). For example, following the population collapse of alewives in Lake Huron in the early 2000s, high predation pressure by lake trout — facilitated by reliance on alternate round goby prey — has maintained suppression of the alewife population (He et al. 2015).

Assessing niche overlap and potential for competition using stable isotope analyses has become a common practice in ecological studies, particularly with the growing availability of analytical tools catering to these needs (see Gerig et al. 2019; Kornis et al. 2020; Mumby et al. 2018*b* as examples from the Laurentian Great Lakes). However, little work has been done to explore how intraspecific niche areas and positions vary along resources gradients such as prey availability (McMeans et al. 2015). The isotopic niche of an organism reflects the discrete set of resource conditions within the spatiotemporal domain of a study. While analyses of niche overlap offer valuable insight into shared or differential resource use within a community, they are probably limited with respect to quantifying the actual potential for competition without also considering availability of shared resources. By decomposing isotopic niche area and position into specific prey proportions along a shared resource gradient using mixing models, changes in resource use and alternate resource subsidies become more apparent. Future work may consider incorporating resource gradients or other environmental gradients as explanatory variables in mixing models. This would aid in understanding and predicting potential for competition among species under different scenarios. Given the relatively short temporal scope of this study (3 years) and covariation among variables (i.e., alewife abundance increased proportionately with decreasing size), it was not possible to develop a statistically robust mixing model that included these explanatory variables.

Understanding how ecological communities partition available resources along environmental gradients is important as ecosystems cope with continued changes resulting from species invasions, habitat degradation, climate change, and other anthropogenic stressors (McMeans et al. 2015). Findings of this study add to literature suggesting that stable isotopes offer a useful means of understanding both species-specific and community-level response to spatiotemporal environmental gradients (Schmidt et al. 2009, 2011; Turschak et al. 2014, 2019). This work is novel in that it helps to quantify asymmetric diet response of a predator community to changes in a preferred prey resource. Niche area and position as they relate to specific diet proportions can be examined in the context of specific prey resource gradients or other environmental gradients. We focused on resource gradients associated with a single preferred prey source; however, a similar approach might be used to explore multiple environmental gradients including density of other prey and predators. Future work incorporating multiple environmental gradients as explanatory variables into mixing models will aid in understanding how species are able to cope with continued ecological changes and may aid resource managers in making decisions to mitigate loss of ecological function or economic value associated with these changes.

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Appendix Fig. A1 appears on the following page.

Appendix A

Fig. A1. Isotope biplots depicting the δ^{13}C and δ^{15}N of potential prey sources for Lake Michigan salmonines from 2014–2016. Each panel corresponds to a specific prey source, including small alewife <100 mm (ALE <100 mm), large alewife >100 mm (ALE >100 mm); bloater >100 mm (BLO >100 mm), *Mysis* (MYS), round goby (ROG), and terrestrial invertebrates (TER). Coloured points depict the year of collection (2014: yellow circles; 2015: blue triangles; 2016: pink squares), and cross bars indicate the mean and standard deviation (SD) of interannual prey δ^{13}C and δ^{15}N values. Black cross bars indicate the mean and SD of the prey δ^{13}C and δ^{15}N pooled across years. Pooled prey means and SDs were estimated by resampling annual raw prey source data (n = 1000 samples per data year with replacement) such that each year was given equal weight in estimating pooled means and SDs.