Canadian Journal of
Fisheries and
Aquatic Sciences

Research Article

Potential effects of introduced salmonids on native lake trout *Salvelinus namaycush* in Lake Huron: evaluating niche overlap using stable isotopes

Jacob D. Lasci, Keith A. Hobson, and Bryan D. Neff

Department of Biology, University of Western Ontario, 1151 Richmond Street, London, Ontario, N6A 3K7, Canada

Corresponding author: **Jacob D. Lasci** (email: jlasci@uwo.ca)

Abstract

The Lake Huron fish community is comprised of many non-native species, including the piscivorous Pacific salmonids chinook salmon *Oncorhynchus tshawtscha*, coho salmon *Oncorhynchus kisutch*, and rainbow trout *Oncorhynchus mykiss*. The only abundant native piscivorous salmonid is the lake trout *Salvelinus namaycush*. Since 1980, there has been a steady decline in the biomass of the prey fishes these salmonids consume. Considering the collapse of alewife *Alosa pseudoharengus* in 2003, there has been growing concern that lake trout will be outcompeted by the non-native salmonids. Paramount to understanding this concern is determining the diet overlap between salmonids and how the overlap has shifted with changes in prey abundance. Here, stable isotope analyses (δ^{13}C, δ^{15}N) from lipid-extracted muscle tissues were compared among salmonids revealing large percentages of lake-wide isotopic niche overlap. Comparisons of these isotopes from salmonid scale samples taken before and after the alewife collapse revealed a shift in the diets of chinook salmon that now overlap with lake trout. Given the strong competitiveness of chinook salmon, this result is concerning for the management of the native lake trout.

Key words: Great Lakes, food web, competition, non-native species, restriction enzyme digestion, circular statistics

Introduction

In Lake Huron, the salmonids chinook salmon *Oncorhynchus tshawtscha*, coho salmon *O. kisutch*, lake trout *Salvelinus namaycush*, and rainbow trout *O. mykiss* represent commercially and recreationally valuable fisheries but recreational catches of salmonids have declined substantially since 1980 (Bunnel et al. 2014; Hudson and Ziegler 2014). Concurrent with these declines has been an 87% reduction in the overall biomass of prey fishes (Riley et al. 2008) and a reduction in the catch per unit of effort for chinook salmon and lake trout (Su and He 2013). The rising concerns regarding the imbalance between predator consumptive demand and prey fish abundance has been one of the most prevalent ecological questions across the Great Lakes (Johnson et al. 2010). Furthermore, in 2003, the population of the introduced prey fish, alewife *Alosa pseudoharengus* collapsed in Lake Huron and have failed to return to their prior status (O'Brien et al. 2021). This exotic planktivore was originally introduced to Lake Ontario in the late 1800s (Diana 1990) and by 1960 became widespread throughout the Great Lakes. Indeed, in Lake Huron, Diana (1990) found that by the late 1900s alewife contributed to diets of all of the salmonids and, using visual identification of stomach contents, determined that alewife contributed to 65% of chinook salmon diets, 5% of lake trout, and about 15% of both rainbow trout and coho salmon. The collapse of alewife has raised concerns that chinook salmon may now compete more strongly with the native lake trout for prey fishes.

Introduced species can have detrimental effects on native species, inducing not only changes in the community (Vilà et al. 2011), but also species interactions (Gallardo et al. 2016) and ecosystem function (Pejchar and Mooney 2009). Within ecology, conceptual models are used to describe the functions of species interactions with competition and predation being two important functions. Competition and predation can be conceptualized using food webs to draw connections between community members through qualitative trophic linkages (Scotti et al. 2009). However, competition is challenging to assess in freshwater ecosystems due to the constraints of what can be visualized across largely inaccessible habitats. By constructing food webs, ecologists can better understand the flow of food energy throughout an ecosystem, and in turn identify keystone species that indicate the overall health of the ecosystem (Libralato et al. 2006; Thompson et al. 2012; Valls et al. 2015). Moreover, food web depictions can provide insight into the dependencies that exist within a community, either through top-down or bottom-up species interactions within a food chain (Thompson et al. 2012; Lynam et al. 2017). In the context of conservation and ecosystem monitoring, food webs are irreplaceable conceptual tools used to identify sensitive, yet beneficial species interactions that inform

conservation authorities of vulnerabilities within the ecosystem that may need to be supplemented through targeted stocking efforts or localized habitat protection.

To determine the trophic interactions that define food webs, diet studies have conducted visual identifications on gut contents of tertiary consumers, genetically sequenced gut contents, or analyzed the stable isotopes or fatty acid profiles within tissues of species within a community (Nielsen et al. 2018; Hoenig et al. 2022). Since the 1980s stable isotope ratios of carbon (δ^{13}C) and nitrogen (δ^{15}N) have been used extensively in ecology to estimate the trophic positions and flow of food energy among organisms in a food web based on the assimilation of ingested diets by consumers (Hobson 1993). In freshwater ecosystems, δ^{13}C values in consumer tissues can indicate sources of primary production (i.e., inshore or offshore; Zanden and Rasmussen 1999). However, δ^{15}N values identify an organism's trophic level within the food web (Roth and Hobson 2000; Hoen et al. 2014).

Stable isotope analysis has been criticized for not directly quantifying the constituents of an organism's diet. MixSIAR is a mixing model that helps to address this concern by using Bayesian statistics to model proportions of isotopically distinct prey that make up the diets of the consumer (Stock et al. 2018). One limitation with MixSIAR analysis is that the model estimates proportions only for the prey items that are included in the analysis, which underscores the importance of the isotope analysis of potential prey items. Our analysis is timely because many of the previous studies that have characterized the diets of the salmonids in Lake Huron relied on the visual identifications of stomach contents, which reflects only a snapshot of the prey that were recently consumed. Determining long-term diet trends using stable isotopes can support conservation efforts across space and time.

Few food web isotope studies have been conducted in Lake Huron, and most studies cover only northern Lake Huron (e.g., Johnston and Wilson 2015; Gerig et al. 2019). To our knowledge, only three studies are relevant to piscivorous salmonid stable isotopes. Gerig et al. (2019) compared $\delta^{13}C$, δ^{15}N, and Hg accumulation in Atlantic salmon *Salmo salar*, lake trout, chinook salmon, and coho salmon in northern Lake Huron. They found that newly established Atlantic salmon occupied an isotopic niche more similar to chinook salmon and coho salmon than to the native lake trout due to their shared reliance on pelagic prey sources. Johnston and Wilson (2015) compared δ^{13}C and δ^{15}N of naturalized and domestic rainbow trout in the North Channel. Regardless of being naturalized or domestic, rainbow trout occupied an isotopic niche that was more depleted in ^{15}N and enriched in ^{13}C compared with lake trout in northern Lake Huron. A long-term study on the food-web changes in northern Lake Huron characterized the isotopic niches of lake trout from 1947 to 2017 (Trumpickas et al. 2022). Their findings highlight the small isotopic niche shifts of lake trout over the 70-year period since their collapse and eventual recovery in Lake Huron. Here, we used stable isotope analysis of δ^{13}C and δ^{15}N in salmonid and prey tissues to evaluate the diets of the salmonids throughout the Canadian side of Lake Huron. Muscle tissue and scales were collected from 2020 to 2021 and scales from pre-2003 (i.e., pre-collapse of alewife) were provided by the Ontario Ministry of Natural Resources. We used the analysis to (1) determine the diets of salmonids in Lake Huron for the years 2020–2021; and (2) determine how the diets of salmonids shifted in response to the collapse of alewife. Our analysis will help to guide conservation efforts of the salmonids in the lake.

Methods

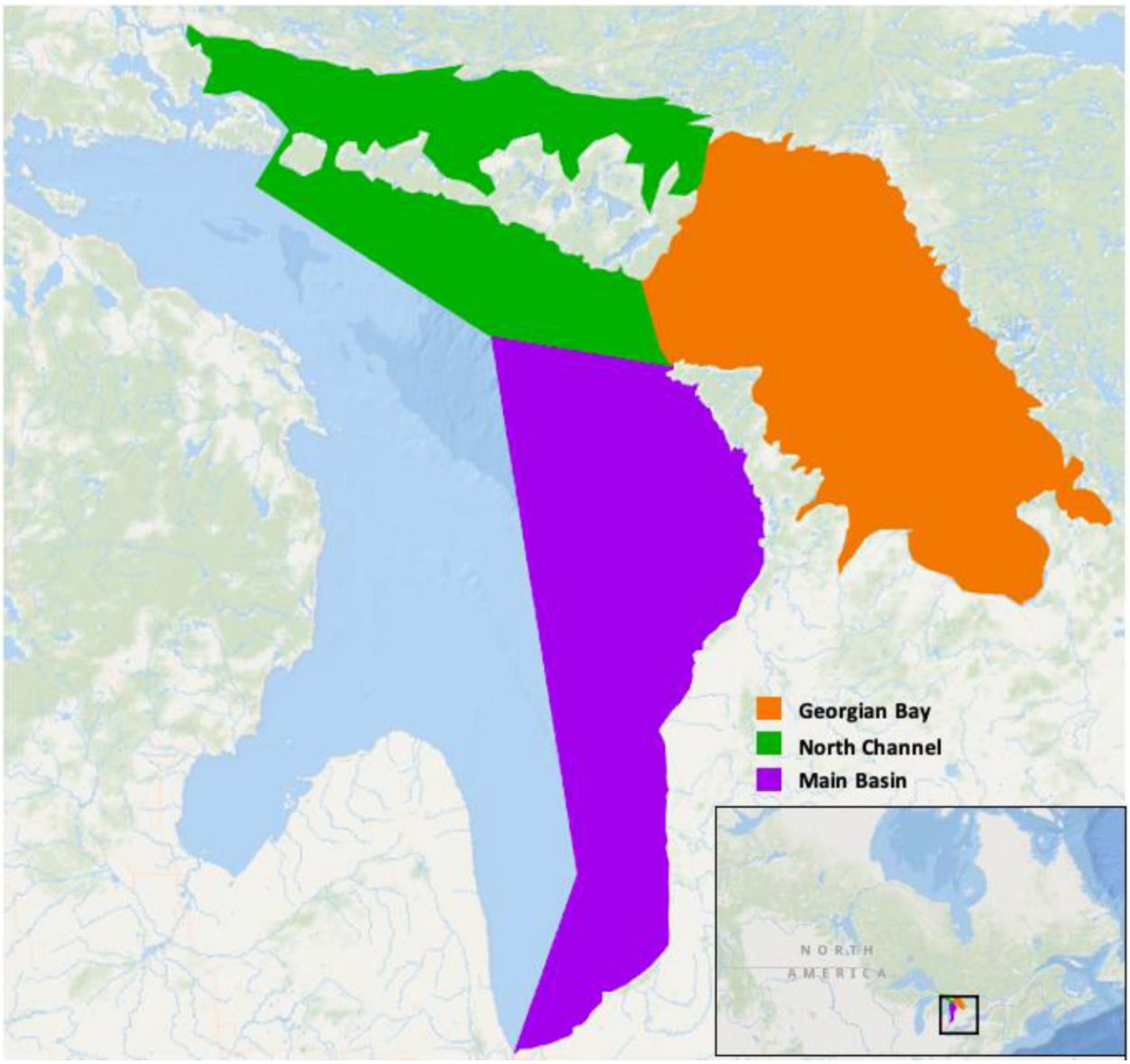
Sample collection

Salmonids were angled from three regions within Canadian Lake Huron: the Main Basin, North Channel, and Georgian Bay (Fig. 1) mapped using ArcGIS Pro (v3.4; ESRI 2011). Chinook salmon, coho salmon, rainbow trout, and lake trout of a minimum 30 cm in fork length were collected from June through October in both 2020 and 2021. Samples were obtained from lab angling, charter fishing, and through donations from recreational anglers taking part in salmon derbies. The derbies included the Owen Sound Salmon Spectacular, the Manitoulin Salmon Shootout, the Manitoulin Expositor Salmon Classic, and the Meaford Salmon and Trout Derby. Prey fish serving as the sources in isotope mixing models were subsampled fresh from the gut contents of the salmonids. These included rainbow smelt *Osmerus mordax*, bloater chub *Coregonus hoyi*, hereafter referred to as bloater, and round goby *Neogobius melanostomus*. Alewife were not found within the stomach contents of any salmonids in this study and were thus not included in the prey isotope analysis. In addition, a small sample of pink salmon *Oncorhynchus gorbuscha* and crayfish *Orconectes propinquus* was initially included in the stable isotopes analysis but were subsequently discarded due to the restricted sample size.

Donated salmonids that were sampled from derbies and charter fisheries were photographed for digital fork length measurement (ImageJ, University of Wisconsin). Scale samples of salmonids were removed from behind the pectoral fin on the left dorsal side of the salmonids using a scalpel. A muscle sample was taken from the dorsal region posterior to the dorsal fin. Muscle tissue, whole stomach, liver, and intestines were dissected, and sex was recorded. All tissue samples were stored on ice until returning to the lab where they were stored at −20 °C. Samples that were angled by the lab were euthanized via percussive stunning and neural pithing prior to sampling and photography as described above (Animal Ethics Committee Protocol Number: 2020-061).

Samples of salmonid scales from 2002 were obtained from an archive kept by the Ontario Ministry of Natural Resources and Forestry (OMNRF). These samples were collected through an offshore index monitoring program which covered the same three regions of the Canadian waters of Lake Huron. Scales were taken from the salmonids using the same methods as described above. The scale samples were rinsed, air dried, then archived in individually labelled envelopes. Samples from tributaries made up a majority of the archived scale samples available and were excluded from this study. Although the salmonids in the tributaries were likely not feeding (most were collected during the migration runs), we

Fig. 1. Sampling Sites for Canadian Lake Huron. The coloured regions correspond to the three sampling regions from which salmonids were angled: Main Basin (purple), Northern Channel (green), and Georgian Bay (orange). Custom map generated using ArcGIS, map projection Mercator, and datum NAD83.



excluded those scale samples to ensure we were only comparing lake-based salmonids.

Species identification

Potamodromous Pacific salmonids, chinook salmon, coho salmon, and rainbow trout, often share many morphometric characteristics including colouration, size, and shape, which can make it challenging to ensure correct taxonomic identification. To verify the taxonomic identifications of salmonids sampled in this study, we followed a PCR-RFLP protocol developed by Rasmussen et al. (2010). A subsample of muscle tissue was taken for DNA extraction. Using a Qiagen DNeasy Blood and Tissue Extraction Kit (Qiagen, Germany), DNA was extracted from the 1 g of muscle tissue. A 463–464 bp region of the *t*RNA^{Glu}/cytochrome b gene was amplified through PCR, see Rasmussen et al. (2010). As we were only interested in distinguishing between the Pacific salmonids, we used the NlaIII restriction enzyme purchased from New England BioLabs® (Ipswich, MA). The restriction digest included 4.5 μL of PCR-grade water, 1 μL of Buffer G, 4 μL of PCR product, and 0.5 μL of N1aIII (1 U/μL), which was then incubated in a 37 °C water bath for 1 h. After the restriction enzyme digest, all samples were visualized using agarose gel electrophoresis, with each gel containing a positive and negative blank and a DNA ladder. Samples that showed a single band were identified as chinook salmon; two bands at 150–300 bp were identified as coho salmon; and finally, the presence of two to three bands at 100, 180/210 were identified as rainbow trout (Rasmussen et al. 2010).

Sample preparation

Stable isotope analysis was performed on muscle tissue of prey fish and on the soft tissue of the dreissenids *Dreissena bugensis* and *Dreissena polymorpha*. Skin-free muscle and liver tissue samples from salmonids that were frozen at –20 °C were cut to uniform dimensions of 1 cm × 1 cm × 2 cm. Each sample was placed in an Eppendorf tube and lyophilized for 48 h. The freeze-dried muscle samples were then transferred to individually separate 25 mL scintillation vials for the manual extraction of lipids. Then, 20 mL of 2:1 chloroform:methanol was added to each of the vials (modified from Bligh and Dyer 1959) and the capped vials were left to soak in the solvent for 48 h at room temperature in a fumehood. The solvent was then decanted, and the tissues were rinsed with distilled water. After air-drying for 24 h, each sample was homogenized to a fine powder using mortar and pestle.

At least 20 individual scales from each salmonid were placed in 1.7 mL Eppendorf tubes and soaked in distilled water to remove excess mucous. Once decanted, the scales underwent 48 h of lyophilization followed by the same chloroform:methanol soak as above. After air drying, the scales were manually lacerated, within their respective Eppendorf tubes, to a coarse grit using Eppendorf scissors.

Isotope analysis

Samples were weighed out to between 0.9 and 1.0 mg and placed into 5 × 9 mm tin capsules with a high precision balance (Mettler Toledo® XP6 Excellence Plus XP Micro Balance, Greifensee, CHE). Each capsule was rolled and compressed, then placed into numbered wells in a sample tray. Muscle tissue, liver tissue, and scales were analyzed for δ^{13}C and δ^{15}N at the Cornell University Stable Isotope Laboratory in Ithaca, NY. All samples were combusted into N_2 and CO_2 gases using a NC2500 elemental analyser (Thermo, Bremen, Germany) interfaced with a Thermo Delta V isotope ratio mass spectrometer (IRMS). The in-house standards were routinely calibrated against international reference materials provided by the International Atomic Energy Association (IAEA). To ensure the accuracy and precision of the instrument, an in-house standard of deer muscle tissue was analyzed after every 10 samples (6.3‰ ± 0.1‰ for δ^{15}N and −20.1‰ ± 0.1‰ for δ^{13}C). Stable isotope corrections were performed using a two-point linear regression of all δ^{15}N and δ^{13}C data using two additional in-house standards: (1) "KCRN"—corn (1.3‰ ± 0.2‰ for δ^{15}N and −13.0‰ ± 0.1‰ for δ^{13}C) and (2) "CBT"—brown trout muscle tissue (17.5‰ ± 0.03‰ for δ^{15}N and −25.6‰ ± 0.1‰ for δ^{13}C). To determine instrument linearity a chemical standard of methionine was used (−0.3‰ ± 0.3‰ for δ^{15}N and −26.8‰ ± 0.3‰ for δ^{13}C).

Statistical analysis

Isotopic niches of the Lake Huron community 2020–2021

All statistical analyses were done in R (R Core Team 2021), using R Studio (Version 1.2.5019; R Studio Team 2015). Stable Isotope Bayesian Ellipses in R (SIBER) was used to visualize the isotopic niches of salmonids (Jackson et al. 2011). The multivariate ellipses-based approach compares the core isotopic niche area of isotopically distinct groups within a food web in bivariate isotope space. Isotope-based estimates of trophic niches were based on the core isotopic niche area calculated at a p interval of 40%. Comparisons of niche overlap between species across regions of Lake Huron had fewer than 20 individuals in multiple pair-wise comparisons, so all SEAs were corrected to account for small sample sizes (SEAc) following Jackson et al. (2011). Isotopic niche overlap was evaluated within SIBER using the "*maxLikOverlap*" function, where each pairwise isotopic niche overlap between species was calculated for each region (Jackson et al. 2011).

The MixSIAR package in R (Stock et al. 2018) was used to quantify the dietary proportions of prey sources using consumer and prey tissue δ^{13}C and δ^{15}N for the lake-wide dataset, with region in Lake Huron assigned as a random effect, and fork length assigned as a continuous covariate. As part of the model, estimates of trophic enrichment needed to be incorporated. These factors represent the average per mil shift in tissue δ^{13}C and δ^{15}N resulting from the fractionation that occurs between trophic levels (Post 2002). Our study used trophic discrimination factors found in the literature that were experimentally derived for salmonids to inform the MixSIAR models. Specifically, trophic discrimination factors (mean + SD) of 1.3 + 0.4‰ for δ^{13}C and 3.5 + 1‰ for δ^{15}N were included as lab evaluated values of lipid-extracted muscle tissue for both chinook salmon (Lerner et al. 2021) and rainbow trout (Pinnegar and Polunin 1999). Due to the similarity of the trophic discrimination factors between these two species, the same values were used for coho salmon and lake trout.

For MixSIAR models, an uninformative generalist Bayesian prior was used with three Markov chain Monte Carlo (MCMC) simulations of 1 000 000 iterations. The burn-in period for each iteration chain was 500 000 and all subsequent values were reduced by a factor of 500. A Gelman-Rubin and Geweke diagnostic test was run at the end of each simulation to determine whether the model reached convergence. When the chains did not converge, a second model run was performed at the next longest MCMC iteration value (3 000 000 chains, 1 500 000 burn-in period). The results are reported using the mean and 95% Bayesian credibility intervals.

Effects of season, size, and location on isotopic niche

Variables influencing Lake Huron resource use for each predatory salmonid species were assessed using linear mixed models (LMMs) for tissue δ^{13}C and δ^{15}N values. Sampling date (as month), fork length, sex, and their interactions were used as fixed effects in the model, while sampling location (as general basin: Main Basin, Georgian Bay, or North Channel) was the random effect. Month was added to account for seasonal changes in diet that may affect the stable isotope ratios of the salmonid tissues, reflecting the weighted average of the integrated diet over multiple previous seasons. Fixed effects were removed one at a time in order of *t*-value magnitude to

Table 1. Summary statistics for all salmonids sampled from Canadian Lake Huron from 2020 to 2021.

	Female			Male		
Species	*n*	FL range (cm)	Mean FL ± SD (cm)	*n*	FL range (cm)	Mean FL ± SD (cm)
CHK	36	40–84	61 ± 11	42	40–86	60 ± 11
COH	17	41–61	54 ± 5	10	44–56	52 ± 4
LAK	24	34–76	58 ± 9	31	44–73	59 ± 9
BOW	30	40–72	62 ± 6	21	37–70	53 ± 11

Note: Species codes: CHK = chinook salmon, COH = coho salmon, LAK = lake trout. Fork length (FL) measured using ImageJ with photos taken immediately post-capture. Angler bias restricted the range of FL to reflect only adult salmonids.

Table 2. Isotopic data (δ^{13}C and δ^{15}N means ± SD) for baseline isotope references (*Dreissena* spp.) and for prey items of salmonids collected from three locations in Lake Huron between 2020 and 2021.

Species	Area	*n*	δ^{13}C (‰ ± SE)	δ^{15}N (‰ ± SE)
Dreissena spp. (Baseline isotopes)				
	Main Basin	6	−21.9 ± 0.5	3.7 ± 0.2
	Georgian Bay	2	−22.6 ± 0.3	2.5 ± 0.3
	North Channel	7	−24.4 ± 0.3	2.9 ± 0.2
Neogobius melanostomus				
	Main Basin	11	−20.0 ± 2.5	8.3 ± 1.7
	Georgian Bay	8	−21.4 ± 1.3	8.2 ± 0.7
	North Channel	3	−18.9 ± 0.5	8.4 ± 0.1
Osmerus mordax				
	Main Basin	6	−22.9 ± 1.5	7.2 ± 1.2
	Georgian Bay	15	−23.4 ± 0.8	9.6 ± 0.7
	North Channel	7	−23.1 ± 1.2	9.0 ± 1.4
Coregonus hoyi				
	Main Basin	9	−22.9 ± 2.1	7.4 ± 1.6
	Georgian Bay	24	−23.5 ± 0.9	10.4 ± 0.6
	North Channel	22	−21.7 ± 1.6	10.0 ± 0.5

generate representative candidate models. Each of the fixed effects were tested and sorted based on the results of likelihood ratio tests. The factors that did not produce a significant change in the model fit (at $P < 0.05$) were removed from the final model. We applied Gaussian and gamma error distributions with inverse or link functions based on visual inspections of the probability distributions for each isotope and each (Kokubun et al. 2015). Linear mixed-effects model selection was conducted using the lme4 and MASS (stepwise backwards regression) packages for R (Version 1.2.5019; Bates et al. 2015).

Species isotopic niche shift in response to the loss of alewife

To simplify the presentation of isotope niches, circular statistics were used to investigate lake-wide directional changes in tissue δ^{13}C and δ^{15}N combined between pre-alewife collapse and post-alewife collapse for chinook salmon, rainbow trout, and lake trout. Coho salmon was excluded from this analysis as there were too few archived samples to generate a mean for pre-2002. The average directional change in isotopic values at each temporal scale (mean vector) was calculated using the mean angle (μ) and length (r). Rayleigh's *Z*-tests ($\alpha = 0.0125$) were used to determine whether isotopic niche shifts deviated from the pre-2002 isotopic niches. The center of each plot was arbitrarily assigned to the isotopic niches pre-2002 when calculating differences in salmonid tissue δ^{13}C and δ^{15}N. To visualize the shift magnitude in a circular polar plot, the Plotly package in R was used (Version 4.9.3; Sievert, 2020).

Animal ethics approval and scientific collector's permit

This study was approved by a division of the Canadian Council on Animal Care (CCAC), the Animal Care Committee of the University of Western Ontario (Protocol Number: 2020-061). The angling for salmonids out of Lake Huron was carried out in accordance with the approved Scientific Collectors Permit provided by the OMNRF (License No. UGLMU2021-07).

Results

Isotopic niches of the Lake Huron community 2020–2021

A total of 207 salmonids, 104 forage fishes, and 15 dreissenids (Tables 1 and 2) from Lake Huron were analyzed for lipid-extracted tissues for δ^{13}C and δ^{15}N (Figs. S1–S3). Isotopic niche metrics generated from SIBER indicated that the

Table 3. Summary of Layman metrics for convex hulls generated using SIBER for all salmonid muscle tissue δ^{13}C and δ^{15}N across three regions of Lake Huron 2020–2021.

	Georgian Bay	Main Basin	North Channel	Lake Huron
δ^{15}N range (‰)	2.2	1.1	1.5	1.4
δ^{13}C range (‰)	0.9	0.7	1.4	0.7
Total area (‰^{2})	0.3	0.3	1.0	0.6
CD (‰)	0.9	0.4	0.8	0.6
MNND (‰)	1.1	0.5	0.8	0.6
SDNND (‰)	0.4	0.2	0.6	0.03

Note: CD = Distance to centroid, MNND = mean nearest neighbour distance, and SDMNND = standard deviation of nearest neighbour distance. All values were calculated using SIBER.

breadth of the food web (as measured by the δ^{13}C range) and the length of the food chain (as measured by the δ^{15}N range) varied across the regions for the predatory salmonids (Table 3). The North Channel (δ^{13}C range = 1.4‰) had a larger food web breadth than Georgian Bay (0.9‰), the Main Basin (0.7‰), and the lake wide range (0.7‰). In terms of food chain length based on tissue δ^{15}N, Georgian Bay (δ^{15}N range = 2.2‰) had a larger range than the Main Basin (1.1‰), North Channel (1.5‰), and the lake wide range (1.4‰, Table 3). Of all the regions, the North Channel occupied the largest total isotope area based on SIBER descriptive area niche metrics of salmonid muscle tissue.

All salmonids from 2020 to 2021 had similar mean muscle δ^{13}C values (−22.3 to −23.0‰) and δ^{15}N values (10.4 to 11.9‰) (Table S1, Fig. 2). As a result, there was extensive lake wide isotopic niche overlap between chinook salmon, coho salmon, lake trout, and rainbow trout (Table 4, Fig. 3). In Georgian Bay, however, there was minimal overlap between chinook salmon, lake trout, and rainbow trout. Specifically, proportional SEAc overlapped between chinook salmon and lake trout revealed that, in Georgian Bay, there was only a 41% chance that an individual Chinook Salmon would be found within the isotopic niche of lake trout and a 42% chance that an individual lake trout would be found in the isotopic niche of chinook salmon. In the other two regions of the lake, each salmonid species overlapped with each other to a greater degree. The highest probability of overlap was for lake trout to be found in the isotopic niche of chinook salmon in the North channel (80%) (see Table 4, Fig. 3).

Bayesian MixSIAR results based on 2020–2021 salmonid muscle tissue indicated that for all salmonids, the most common prey source was rainbow smelt. Overlapping posterior distributions with a left-skew described smaller contributions of the respective prey sources to the diets of these salmonids, whereas right-skews indicated higher proportions of prey (Fig. 4). Posterior distributions for each species indicated similarities in the lake-wide foraging strategies of salmonids as described in isotopic space. Chinook salmon and rainbow trout had the largest contributions of rainbow smelt to their diets (Table S2, Figs. 4*a* and 4*d*). The only native salmonid in the Great Lakes, lake trout, consumed similar proportions of the three forage fish species (Table S2, Fig. 4*c*). Similarly, coho salmon had low proportions of each of the forage fish species contributing to their diets (Fig. 4*b*). Interestingly, when mussels were included as a source in the MixSIAR model, rainbow trout incorporated a large proportion of dreissenid mussels into their diets (Table S2, Fig. S4). In the supplementary material we describe how this likely reflects a diet rich in invertebrates, a group that was otherwise unrepresented in the mixing models. Further regionally granular posterior plots are shown in the supplementary material (Figs. S5–S8). These MixSIAR results align with the SIBER lake-wide results and the measured niche overlap which identify a large overlap in SEAc among all salmonids, albeit lake trout have a unique ^{15}N enrichment (Fig. 5). This trophic enrichment is contextualized by the regional analysis showing that Georgian Bay has a unique isotopic niche distinction among the salmonids compared to the other two regions (see Fig. 3). These results highlight that regional trophic interactions may differ from lake-wide ones.

Effects of season, size, and location on isotopic niche

Generalized linear models revealed that multiple factors influence the stable isotope ratios of Lake Huron salmonid muscle (Table 5). Deviance explained for each species' most parsimonious model varied substantially. The deviance explained was greatest for the models of coho salmon δ^{15}N (65%) and lake trout δ^{15}N (40%). Whereas the deviance explained was lower for the models of δ^{13}C for coho salmon (34%) and lake trout (32%). Similarly, the deviance explained 12% (δ^{13}C) and 20.3% (δ^{15}N) for chinook salmon. For rainbow trout these values were 21% (δ^{13}C) and 8% (δ^{15}N). The month of the year fish were sampled was included in the most parsimonious models for all but rainbow trout. Fork length was included as a covariate in all the models apart from δ^{13}C for chinook salmon. Location was an effect in all δ^{15}N models except for coho salmon. Sex was included in almost all models as well (see Figs. S9–S11).

Species isotopic niche shift in response to the collapse of alewife

Salmonids occupied more distinct isotopic niche spaces before the collapse of alewife in Lake Huron in 2003 when compared to 2020–2021 (Table S3, Fig. 5). There was no overlap between chinook salmon, lake trout, and rainbow trout before 2003 based on mean scale δ^{13}C values (−18.4 to −20.8‰) and δ^{15}N values (7.9 to 12.9‰, Fig. 5*a*). However, there was considerable overlap among all salmonids from 2020 to 2021 and mean scale δ^{13}C values (−19.3 to −20.6‰) and δ^{15}N values (9.4 to 12.2‰, Fig. 5*b*).

Although not statistically significant, circular statistics revealed that chinook salmon had the largest shift in diet with a vector length magnitude of 0.04 compared to 0.02 for lake trout and 0.03 for rainbow trout (Table S4). These results revealed an enrichment in ^{15}N for chinook salmon and rainbow trout, and uniquely, an enrichment in ^{13}C for lake trout. Enrichment in ^{15}N suggests that chinook salmon and rainbow trout are now foraging on prey that are enriched in ^{15}N, whereas enrichment in ^{13}C for lake trout suggests they are

Fig. 2. Isotopic representation of the Lake Huron food web based on muscle tissue samples from 2020 to 2021. Region-wide mean (points) and S.D. (bars) for $\delta^{13}C$ and $\delta^{15}N$ (in ‰) of muscle tissue from prey sources: bloater, crayfish, quagga mussel, rainbow smelt, round goby, and zebra mussel as well as the salmonids: chinook Salmon, coho salmon, pink salmon, rainbow trout, and lake trout. Note that crayfish, quagga mussel, and pink salmon were excluded from further analysis for small sample sizes and regional distributions.

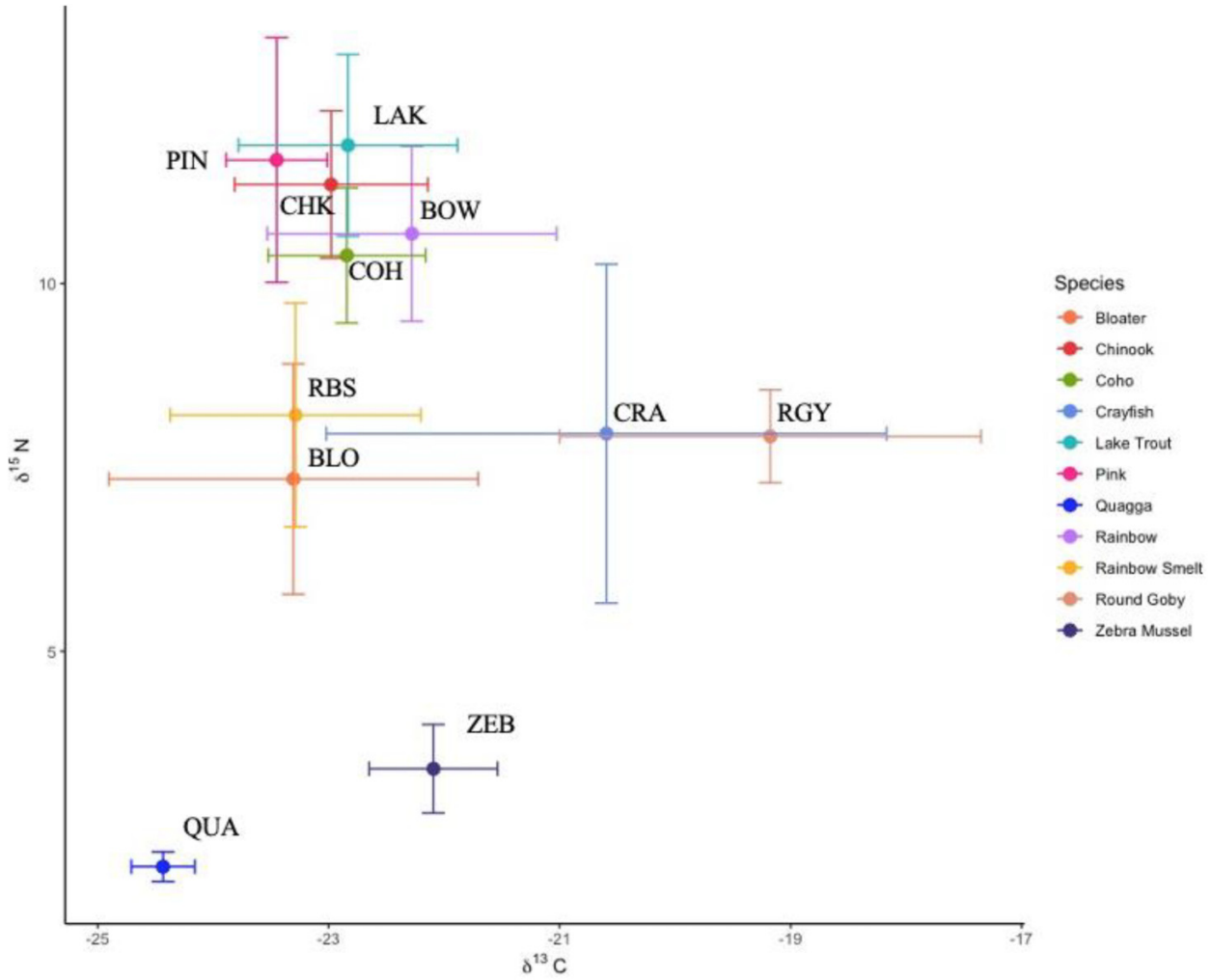


Table 4. Lake Huron (2020–2021) proportion of SEAc overlap between salmonid species based on posterior probability distributions of muscle tissue isotopic niche overlap (%).

	Main Basin				North Channel				Georgian Bay				Lake Wide			
	CHK	COH	LAK	BOW	CHK	COH	LAK	BOW	CHK	COH	LAK	BOW	CHK	COH	LAK	BOW
CHK	-	70	26	51	-	15	46	69	-	-	42	1	-	38	71	70
COH	52	-	14	52	47	-	15	7	-	-	-	-	44	-	14	36
LAK	10	28	-	60	80	28	-	15	41	-	-	1	47	24	-	35
BOW	29	53	40	-	31	67	57	-	1	-	1	-	34	36	47	-

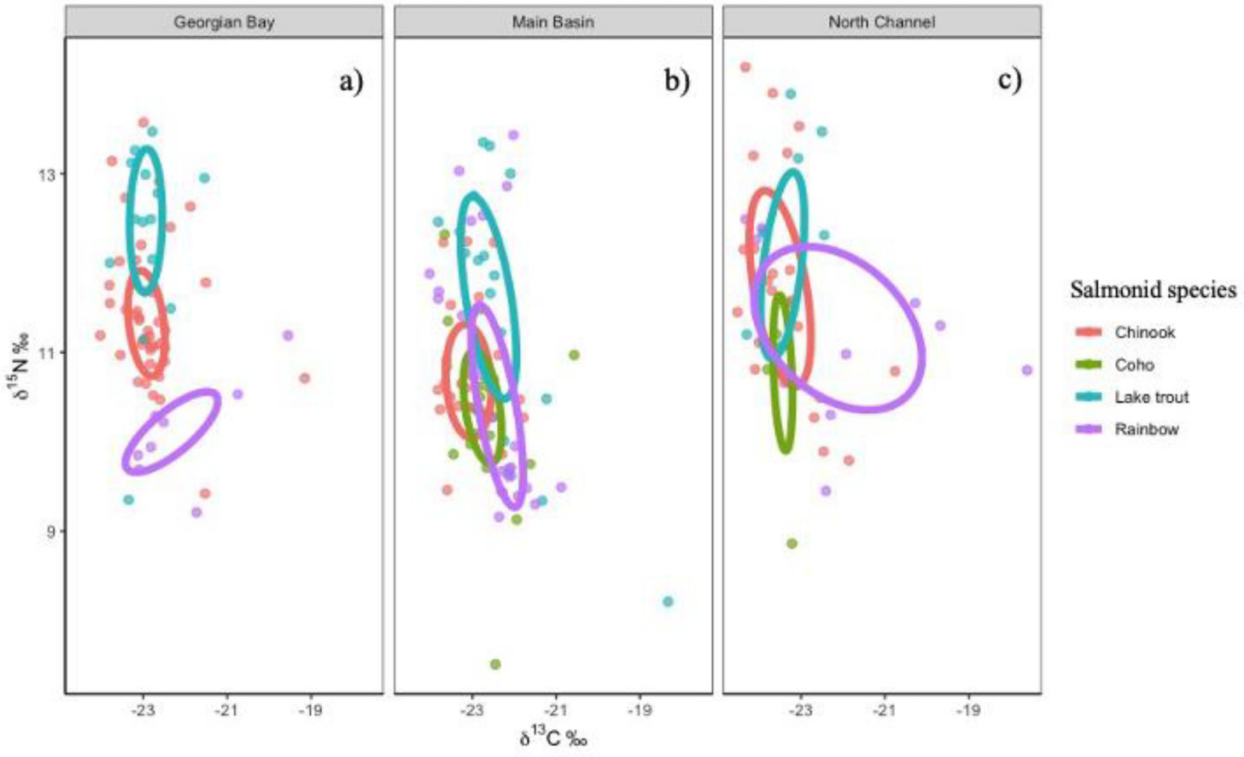
Note: Species codes: CHK = chinook salmon, COH = coho salmon, LAK = lake trout. Data displayed are mean isotopic overlap between each species combination. These SEAs are illustrated in Fig. 3. There are two numbers for each species because the values are relative to the species in the row. Dropped species resulting from low sample size and overlaps between identical species indicated with a dash symbol (-).

foraging more in the littoral zone. The directional shifts in isotopic niches reflect the changes between Figs. 5*a* and 5*b*. Nevertheless, the high variability of the isotopic values for individuals resulted in low mean vector lengths (r) for all salmonids (Fig. 5*c*).

Discussion

Stable isotope analysis of carbon and nitrogen has become a fundamental tool for understanding food webs and inferring levels of competition between species in aquatic and terrestrial ecosystems (Martínez Del Rio et al. 2009). We used

Fig. 3. Bayesian standard ellipses representing core (40%) isotopic niches (δ^{15}N and δ^{13}C in ‰) of muscle tissue samples from the four main salmonids (chinook salmon, coho salmon, rainbow trout, and lake trout) across the three subdivided sampling sites in Lake Huron from 2020 to 2021 (Georgian Bay, Main Basin, and North Channel). Overlapping core ellipses indicate similar resource use.

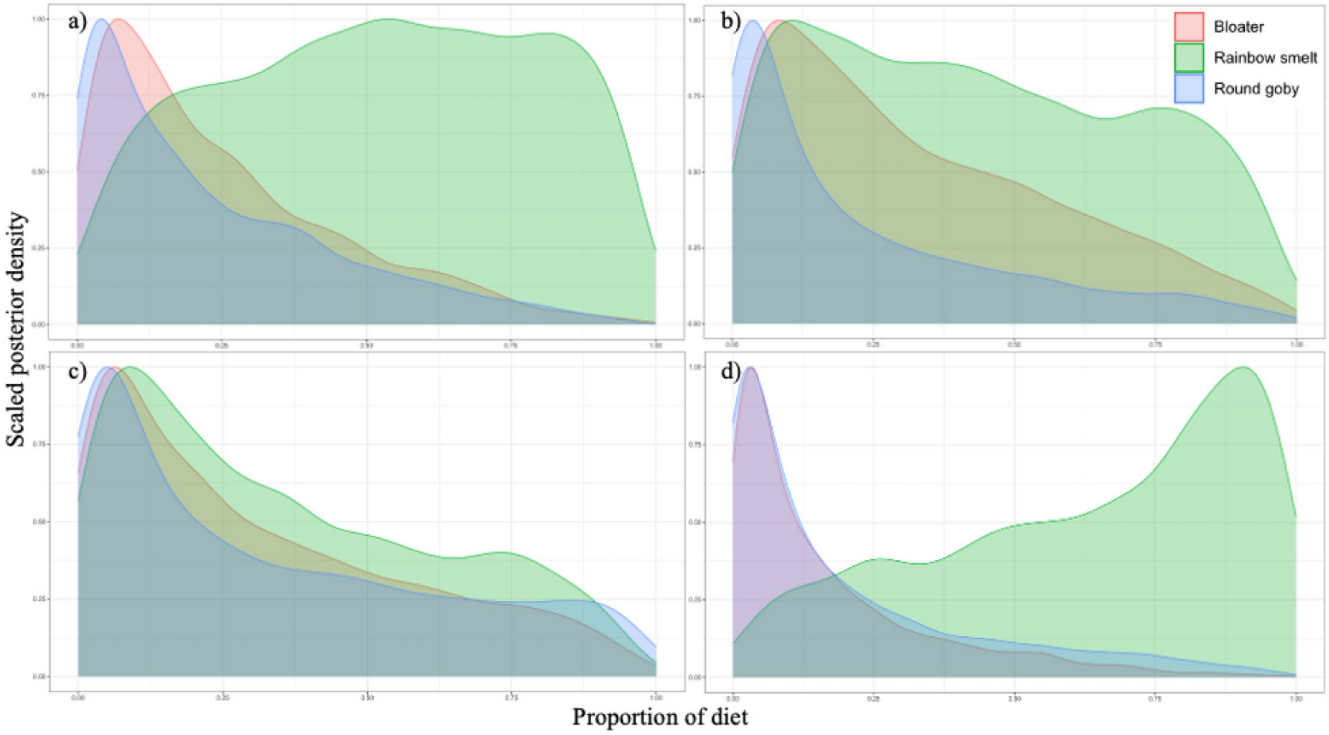


LMMs, SIBER, MixSIAR, and circular statistics to evaluate the isotopic niches of four salmonids in Canadian Lake Huron. The lake-wide salmonid isotopic niches displayed large percentages of overlap based on muscle tissue δ^{13}C and δ^{15}N values. Comparing our results to previous studies, Gerig et al. (2019) found that chinook salmon and coho salmon in the Northern Channel exhibited considerable isotopic niche overlap whereas there was little overlap between lake trout and its conspecifics. This differs from our results from 2020 to 2021 where we found that lake trout in the Northern Channel exhibited considerable isotopic niche overlap with both chinook salmon and coho salmon. Previous work on rainbow trout in northern Lake Huron has shown that they occupy an isotopic niche closer to the littoral piscivore walleye *Sander virtreus* than to lake trout (Johnston and Wilson 2015). Our results are similar insomuch as we found a large isotopic breadth for rainbow trout from the North Channel that would overlap with the isotopic niche of walleye. However, unlike these previous results, our data show isotopic niche overlaps between rainbow trout and the other three pelagic salmonids.

Similar analyses have also been conducted in the connected Lake Michigan revealing a high percentage of isotopic niche overlap for the Pacific salmonids, but low overlap between those conspecifics and lake trout (Kornis et al. 2020). Lake Michigan salmonids have also been shown to occupy a large isotopic niche (δ^{13}C: −26‰ to −20‰; δ^{15}N: 8‰ to 15‰: Turschak et al. 2022). The opposite was true for Lake Huron (from our data: δ^{13}C: −23‰ to −22.3‰; δ^{15}N: 10.4‰ to 11.9‰). Another isotope study in Lake Ontario similarly found that Pacific salmonids shared moderate to high percentages of isotopic niche overlap but not with lake trout (Mumby et al. 2018). In both lakes Michigan and Ontario, the native lake trout occupied an isotopic niche that was enriched in ^{15}N relative to the Pacific salmonids. One caveat that must be considered when comparing isotopic niches across distinct lakes is the differing baseline isotope values, which affect the isotope ratios throughout the food web. However, considering the similarity in prey isotope values between lakes Michigan and Huron (Kornis et al. 2020), direct comparisons should represent differences in diet and not differences in isotopic baselines. Lake Huron and Lake Michigan are connected by the Straits of Mackinac and could technically be considered one lake, although Lake Huron is unique for having suffered an alewife population crash in 2003 that has yet to recover. Thus, the loss of alewife may be contributing to the high percentages of isotopic niche overlap among all salmonids in this lake. Indeed, niche comparisons of scale tissues from pre-2003 and scales from 2020 to 2021 indicate shifts in diet, especially for chinook salmon, which are characterized as alewife specialists in Lakes Ontario and Michigan, where alewife remain abundant.

The main drivers of interspecific competition are resource partitioning of habitat and food. Chinook salmon are known

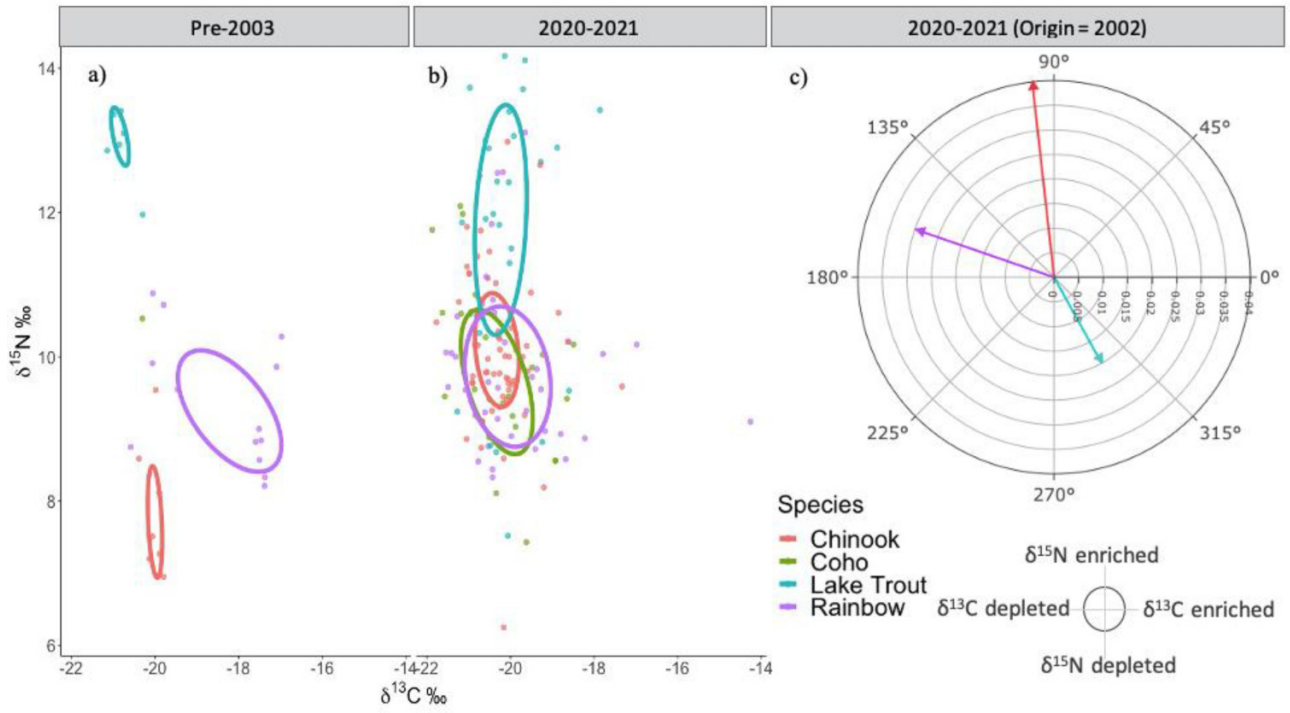
Fig. 4. Muscle tissue $\delta^{13}C$ and $\delta^{15}N$ mixing model predictions of isotopic diet proportions as a function of fork length (mm). chinook salmon (*a*), lake trout (*b*), rainbow trout (*c*), and coho salmon (*d*). Lines represent the mean of the posterior probability distribution and the shaded area represent the bounds of the 95% credible interval of the predicted diet proportion. Line and fill colours correspond to distinct prey species (bloater, round goby, and rainbow smelt).



throughout the Great Lakes to be strong competitors for prey, maintaining a specialist diet of alewife, despite the near universal consumption of this non-native prey fish by the other piscivorous salmonids in the Great Lakes (Leonhardt et al. 2020). High percentages of isotopic niche overlap can pose a major threat to weaker competitors like lake trout. Chinook salmon, coho salmon, and rainbow trout have shared isotopic niche space and have presumably competed across their native ranges as well as throughout the Great Lakes since their introduction. On the other hand, lake trout appear to have maintained a distinct isotopic niche in the other Great Lakes. In Lake Huron, the near collapse of alewife has diminished the selection of prey for all piscivorous salmonids, resulting in a dependence on two pelagic planktivores: bloater and rainbow smelt. A subsequent shift from chinook salmon's previous consumption of alewife to either bloater or rainbow smelt could pose a threat to the native lake trout, whose small isotopic breadth (limited range in $\delta^{13}C$) seen across all regions of Lake Huron is indicative of a less adaptable foraging strategy. These results align with the long-term study of food web changes in northern Lake Huron, where lake trout displayed relatively small isotopic niche shifts (also see Trumpickas et al. 2022; Sinnatamby et al. 2008).

Although isotopic niche overlaps were large for all four salmonids lake wide, they were predominately driven by two regions: the Main Basin and North Channel. In the third sampling region, Georgian Bay, there was almost no overlap between chinook salmon, lake trout, and rainbow trout. In accordance with the near absence of overlap for the posterior densities, SEAc plots illustrated the isotopic niche distinctions of these salmonids in Georgian Bay. The spatial differences were also supported by the LMMs that incorporated location as a main effect for all salmonids apart from coho salmon, which likely resulted from a low sample size from Georgian Bay. The interspecific isotopic niche distinctions in Georgian Bay may owe to multiple explanations. First, the absence of coho salmon from Georgian Bay samples may reflect their low density in Georgian Bay, thereby reducing interspecific competition among the remaining salmonids, and allowing chinook salmon, lake trout, and rainbow trout to specialize on distinct prey resources. Coho salmon were last stocked from the Canadian shores in Lake Huron in 1989. Since then, a naturally reproducing population has supported recreational fisheries across the lake, but fewer numbers of coho salmon are being entered in salmon fishing derbies in Georgian Bay (Bence et al. 2008). This explanation is further evidenced by the smaller isotopic niches of each of the other three salmonids in Georgian Bay compared to both the Main Basin and the North Channel. Second, the bottom-up effect of prey resource availability in Georgian Bay may differ from the Main Basin and the North Channel. Reduced abundance of prey typically leads to increased interspecific competition resulting in resource partitioning and the subsequent segregation of isotopic niches (Sánchez-Hernández et al. 2017; Larocque et al. 2021). A recent acoustic survey found that bloater biomass was considerably lower in Georgian Bay

Fig. 5. Bayesian standard ellipses representing the core (40%) isotopic niches (δ^{15}N and δ^{13}C) salmonid scale tissue samples from two distinct temporal sampling periods. The historical sample from 2002 (*a*) represents isotopic niches of chinook salmon, lake trout, and rainbow trout from prior to the alewife population crash. The later sampling period (*b*) describes the isotope niches of Lake Huron's four key predatory salmonids 18 years after the collapse of alewife. Panel (*c*) is the circular polar plot with arrow vectors depicting the angle (θ) and shift magnitude for three of the four salmonid species studied in Lake Huron between 2002 and 2020–2021. Each point represents mean directional isotopic change in each salmonid species in 2020–2021 relative to 2002.



than the North Channel and the Main Basin (O'Brien et al. 2021). Conversely, Georgian Bay held the heaviest biomass of rainbow smelt among the three basins (O'Brien et al. 2021), thereby providing a forage base that is abundant enough to support a large population of chinook salmon. This then leaves the remaining prey, including bloater, round goby, and invertebrates, to be shared between lake trout and rainbow trout.

We sampled the most common prey among the four salmonids to evaluate their niche overlap. However, the low abundance of alewife in Lake Huron resulted in a lack of those prey in our analysis. Nevertheless, Trumpickas et al. (2022) found that alewife occupied an isotopic niche similar to our measured isotopic niches for nearshore prey including round goby and crayfish. If chinook salmon are still able to forage on alewife, then we would have expected the results for the chinook to be quite different. In contrast, the MixSIAR model predicted contributions of the two most abundant pelagic planktivores, rainbow smelt and bloater, for all four salmonids. On a more granular level, MixSIAR model posterior plots (Figs. S8–S11) emphasize the relative importance of rainbow smelt across each of the basins in Lake Huron. Furthermore, our results align with past stomach content analyses (Yohannes et al. 2014), which showed that rainbow trout consume a large amount of invertebrate prey; here we found that rainbow trout were predicted to incorporate large proportions of dreissenid mussels which is a proxy for a diet rich in invertebrates (see Fig. S7). The incorporation of round goby is a more recent addition to the diets of salmonids in Lake Huron (Taylor et al. 2024). Interestingly, our model predicted similar, albeit low, contributions of round goby to chinook salmon, coho salmon, lake trout, and rainbow trout. Most prey species were predicted to contribute to less than 60% of the diets of any of the salmonids, which corroborates the high isotopic niche overlap across Lake Huron and suggests these salmonids aren't specializing on a single prey species. Most concerning, however, is the estimated shared reliance on rainbow smelt between chinook salmon and lake trout, which suggests increased competition for food between these two species. Indeed, analysis of lake trout diets from the American side of Lake Huron using fatty acids revealed that rainbow smelt comprised the largest proportions of lake trout stomach content biomass (Happel et al. 2018).

The diminishing diversity and abundance of prey fishes in Lake Huron poses a growing threat to the sustainability of the commercially and recreationally valuable fisheries of salmon and trout. Our study highlights the effects of the loss of a keystone prey species (alewife) to the diets of salmonids. Isotopic niche overlap of salmonids from 2020 to 2021 now emphasizes the shared reliance on a low diversity of prey within Lake Huron, which we suggest should be

Table 5. Formulation of the minimal adequate models for each salmonid–isotope combination.

Species	Isotope	Most Parsimonious model	Error	Link	Residual deviance	Residual df	Null deviance	Null df	Deviance explained
Chinook salmon	$\delta^{13}C$	~ Month + Sex + Month:Sex	Gaussian	Identity	51.7	77	59.0	84	12.4%
	$\delta^{15}N$	~ Sex + FL + Location + Sex:FL	Gamma	Inverse	47.5	79	59.6	84	20.3%
Coho salmon	$\delta^{13}C$	~ Month + Sex + FL + Month:Sex + Month:FL + Sex:FL	Gaussian	Identity	7.1	16	10.7	24	33.6%
	$\delta^{15}N$	~ Month + Sex + FL + Month:Sex + Month:FL	Gamma	Inverse	0.1	17	0.2	24	65%
Lake trout	$\delta^{13}C$	~ Month + Sex + FL + Sex:FL	Gaussian	Identity	25.2	33	37.0	40	31.9%
	$\delta^{15}N$	~ Month + Sex + FL + Location + Sex:FL	Gaussian	Identity	38.8	31	64.4	40	40%
Rainbow trout	$\delta^{13}C$	~ Sex + FL + Location + Sex:FL + Sex:Location + FL:Location	Gaussian	Identity	56	34	70.5	43	20.6%
	$\delta^{15}N$	~ FL	Gamma	Inverse	0.5	42	0.5	43	8%

Note: FL = fork length of the salmonid measure tip of snout to fork in tail fin.

supplemented through increased stocking efforts of native prey fish, such as bloater. Indeed, similar stocking enhancements have been ongoing since 2012 in Lake Ontario, although a naturally reproducing population has yet to establish (see Weidel et al. 2022). Our results also highlighted spatial distinctions in isotopic niche overlap between the basins of Lake Huron that may point to the establishment of a spatially segregated population of salmonids in Southern Georgian Bay. Future studies using acoustic telemetry to track salmonid movements throughout Lake Huron could help confirm spatially distinct populations of salmonids within the three basins of Canadian Lake Huron, allowing conservation authorities to geographically concentrate efforts of supplementing and restoring prey fish diversity and abundance. Further research should also look at the diets of earlier life stages of the salmonids to assess potential ontogenetic shifts in diet and varying competition among the salmonids for prey. In the face of Lake Huron's ongoing environmental changes, continued monitoring of its food web will help to better inform the management strategies that are crucial to the long-term health of the ecosystem.

Acknowledgements

This paper is dedicated to the memory of Dr. Keith Hobson, whose sudden passing during the preparation of this paper has left us in shock and sadness. Keith left an indelible mark in the fields of isotope ecology, migration, and conservation biology. His passion for teaching and unparalleled work ethic were testaments to his character. He was a fountain of isotopes knowledge and a kind-hearted teacher. He will be greatly missed.

We thank Xiomara Mora-Alvarez for training in tissue encapsulation and Shawn Garner for early project design. We also thank the Ontario Ministry of Natural Resources & Forestry for providing archived scale samples of salmonids collected from Lake Huron prior to 2003. We also thank the two anonymous reviewers and associate editor for their insightful comments and improvements to the manuscript.

Article information

History dates

Received: 19 July 2024
Accepted: 6 January 2025
Accepted manuscript online: 23 January 2025
Version of record online: 20 February 2025

Copyright

Data availability

Data generated or analyzed during this study are available within the Borealis Canadian Dataverse Repository https://doi.org/10.5683/SP3/CQWUVV.

Author information

Author ORCIDs

Jacob D. Lasci https://orcid.org/0009-0005-2221-8291

Author notes

Author Keith Hobson is deceased.

Author contributions

Conceptualization: JDL
Formal analysis: JDL
Investigation: JDL
Methodology: JDL, KAH, BDN
Resources: BDN
Supervision: BDN
Visualization: JDL
Writing – original draft: JDL
Writing – review & editing: JDL, KAH, BDN

Competing interests

The authors declare there are no competing interests.

Funding information

Funding for this project was provided in part by NSERC (Discovery and FishCAST CREATE Grants to BDN).

Supplementary material

Supplementary data are available with the article at https://doi.org/10.1139/cjfas-2024-0202.

References

Bates, D., Mächler, M., Bolker, B., and Walker, S. 2015. Fitting linear mixed-effects models using lme4. J. Stat. Softw. **67**(1): 1–48. doi:10.18637/jss.v067.i01.

Bence, J.R., Johnson, J.E., He, J., Schaeffer, J.S., Riley, S., Young, R.J., et al. 2008. Offshore predators and their fish community. The State of Lake Huron in 2004 08–01 (October 2014): 11–36.

Bligh, E.G., and Dyer, W.J. 1959. A rapid method of total lipid extraction and purification. Can. J. Biochem. Physiol. **37**(8). PMID: 13671378

Bunnell, D.B., Barbiero, R.P., Ludsin, S.A., Madenjian, C.P., Warren, G.J., Dolan, D.M., et al. 2014. Changing ecosystem dynamics in the Laurentian Great Lakes: bottom-up and top-down regulation. BioScience **64**(1): 26–39. doi:10.1093/biosci/bit001.

Diana, J.S. 1990. Food habits of angler-caught salmonines in western Lake Huron. J. Great Lakes Res. **16**. doi:10.1016/S0380-1330(90)71420-7.

ESRI. 2011. ArcGIS Desktop: release 10. Environmental Systems Research Institute, Redlands, CA.

Gallardo, B., Clavero, M., Sánchez, M.I., and Vilà, M. 2016. Global ecological impacts of invasive species in aquatic ecosystems. Global Change Biol. **22**(1): 151–163. doi:10.1111/gcb.13004.

Gerig, B.S., Chaloner, D.T., Cullen, S.A., Greil, R., Kapucinski, K., Moerke, A.H., and Lamberti, G.A. 2019. Trophic ecology of salmonine predators in northern Lake Huron with emphasis on Atlantic salmon (Salmo salar). J. Great Lakes Res. **45**(1): 160–166. doi:10.1016/j.jglr.2018.11.003.

Happel, A., Jonas, J.L., McKenna, P.R., Rinchard, J., He, J.X., and Czesny, S.J. 2018. Spatial variability of Lake trout diets in Lakes Huron and Michigan revealed by stomach content and fatty acid profiles. Can. J. Fish. Aquat. Sci. **75**. doi:10.1139/cjfas-2016-0202.

Hobson, K.A. 1993. Trophic relationships among high Arctic seabirds: insights from tissue-dependent stable-isotope models. Mar. Ecol. Prog. Ser. **95**(1–2): 7–18. doi:10.3354/meps095007.

Hoen, D.K., Kim, S.L., Hussey, N.E., Wallsgrove, N.J., Drazen, J.C., and Popp, B.N. 2014. Amino acid 15 N trophic enrichment factors of four large carnivorous fishes. J. Exp. Mar. Biol. Ecol. **453**: 76–83. doi:10.1016/j.jembe.2014.01.006.

Hoenig, B.D., Trevelline, B.K., Kautz., A, Latta, S.C., and Porter, B.A. 2022. Two is better than one: Coupling DNA metabarcoding and stable isotope analysis improves dietary characterizations for a riparian-obligate, migratory songbird. Mol. Ecol. **31**(21): 5635–5648. doi:10.1111/mec.16688.

Hudson, J.C., and Ziegler, S.S. 2014. Environment, culture, and the Great Lakes fisheries. Geogr. Rev. **104**. doi:10.1111/j.1931-0846.2014.12041.x.

Jackson, A.L., Inger, R., Parnell, A.C., and Bearhop, S. 2011. Comparing isotopic niche widths among and within communities: SIBER—stable isotope bayesian ellipses in R. J. Anim. Ecol. **80**(3): 595–602. doi:10.1111/j.1365-2656.2011.01806.x. PMID: 21401589

Johnson, J.E., DeWitt, S.P., and Gonder, D.J.A. 2010. Mass-marking reveals emerging self regulation of the Chinook salmon population in Lake Huron. North Am. J. Fish. Manage. **30**(2): 518–529. doi:10.1577/m09-094.1.

Johnston, T.A., and Wilson, C.C. 2015. Comparative ecologies of domestic and naturalised rainbow trout in Northern Lake Huron. Ecol. Freshwater Fish, **24**(3): 338–354. doi:10.1111/eff.12147.

Kokubun, N., Choy, E.J., Kim, J.H., and Takahashi, A. 2015. Isotopic values of antarctic krill in relation to foraging habitat of penguins. Ornithol. Sci. **14**(1): 13–20. doi:10.2326/osj.14.13.

Kornis, M.S., Bunnell, D.B., Swanson, H.K., and Bronte, C.R. 2020. Spatiotemporal patterns in trophic niche overlap among five salmonines in Lake Michigan, USA. Can. J. Fish. Aquat. Sci. **77**. doi:10.1139/cjfas-2019-0288. PMID: 32461710.

Larocque, S.M., Johnson, T.B., and Fisk, A.T. 2021. Trophic niche overlap and abundance reveal potential impact of interspecific interactions on a reintroduced Fish1. Can. J. Fish. Aquat. Sci. **78**(6): 765–774. doi:10.1139/cjfas-2020-0204.

Leonhardt, B.S., Happel, A., Bootsma, H., Bronte, C.R., Czesny, S., Feiner, Z., et al. 2020. Diet complexity of Lake Michigan Salmonines: 2015–2016. J. Great Lakes Res. **46**(4): 1044–1057. doi:10.1016/j.jglr.2020.05.010.

Lerner, J.E., Forster, I., and Hunt, B.P.V. 2021. Experimentally derived trophic enrichment and discrimination factors for Chinook Salmon, Oncorhynchus Tshawytscha. Rapid Commun. Mass Spectrom. **35**(13): 1–11. doi:10.1002/rcm.9092.

Libralato, S., Christensen, V., and Pauly, D. 2006. A method for identifying keystone species in food web models. Ecol. Modell. **195**(3–4): 153–171. doi:10.1016/j.ecolmodel.2005.11.029.

Lynam, C., Philip, M., Llope, C., Möllmann, P., Helaouët, G., Bayliss-Brown, A., and Stenseth, N.C. 2017. Interaction between top-down and bottom-up control in marine food webs. Proc. Natl. Acad. Sci. **114**(8): 1952–1957. doi:10.1073/pnas.1621037114.

Martínez Del Rio, C., Wolf, N., Carleton, S.A., and Gannes, L.Z. 2009. Isotopic ecology ten years after a call for more laboratory experiments. Biol. Rev. **84**(1): 91–111. doi:10.1111/j.1469-185X.2008.00064.x.

Mumby, J.A., Larocque, S.M., Johnson, T.B., Stewart, T.J., Fitzsimons, J.D., Weidel, B.C., et al. 2018. Diet and trophic niche space and overlap of Lake Ontario salmonid species using stable isotopes and stomach contents. J. Great Lakes Res. **44**(6): 1383–1392. doi:10.1016/j.jglr.2018.08.009.

Nielsen, J.M., Clare, E.L., Hayden, B., Brett, M.T., and Kratina, P. 2018. Diet tracing in ecology: method comparison and selection. Methods Ecol. Evol. **9**(2): 278–291. doi:10.1111/2041-210X.12869.

O'Brien, T.P., Hondorp, D.W., Esselman, P.C., and Roseman, E.F. 2021. Status and Trends of the Lake Huron Prey Fish Community, 1976-2021 pp. 1–36.

Pejchar, L., and Mooney, H.A. 2009. Invasive species, ecosystem services and Human well-being. Trends Ecol. Evol. **24**(9): 497–504. doi:10.1016/j.tree.2009.03.016.

Pinnegar, J.K., and Polunin, N.V.C. 1999. Differential fractionation of Δ13C and Δ15N among fish tissues: implications for the study of trophic interactions. Funct. Ecol. **13**(2): 225–231. doi:10.1046/j.1365-2435.1999.00301.x.

Post, D.M. 2002. Using stable isotopes to estimate trophic position: models, methods, and assumptions. Ecology, **83**. doi:10.1890/0012-9658(2002)083[0703:USITET]2.0.CO;2.

R Core Team. 2021, R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. https://www.R-project.org/.

R Studio Team. 2015. RStudio: Integrated Development for R. RStudio. PBC, Boston, MA. http://www.rstudio.com/.

Rasmussen, R.S., Morrissey, M.T., and Walsh, J. 2010. Application of a PCR-RFLP method to identify salmon species in U.S. Commercial products. J. Aquat. Food Prod. Technol. **19**(1): 3–15. doi:10.1080/10498850903297576.

Riley, S.C., Edward, F., Roseman, S., Nichols, J., O'Brien, T.P., Kiley, C.S., and Schaeffer, J.S. 2008. Deepwater demersal fish community collapse in Lake Huron. Trans. Am. Fish. Soc. **137**. doi:10.1577/t07-141.1.

Roth, J.D, and Hobson, K.A. 2000. Stable carbon and nitrogen isotopic fractionation between diet and tissue of captive red fox: implications for dietary reconstruction Can. J. Zoology **78.5** 848–852.

Sánchez-Hernández, J., Gabler, H.M., and Amundsen, P.A. 2017. Prey diversity as a driver of resource partitioning between river-dwelling fish species. Ecol. Evol. **7**(7): 2058–2068. doi:10.1002/ece3.2793.

Scotti, M., Bondavalli, C., Bodini, A., and Allesina, S. 2009. Using trophic hierarchy to understand food web structure. Oikos, **118**(11): 1695–1702. doi:10.1111/j.1600-0706.2009.17073.x.

Sinnatamby, R.N., Dempson, J.B., and Power, M. 2008. A comparison of muscle-and scale-derived δ13C and δ15N across three life-history stages of Atlantic salmon, *Salmo salar*. Rapid Commun. Mass Spectrom. **22**(18): 2773–2778. doi:10.1002/rcm.3674.

Stock, B.C., Jackson, A.L., Ward, E.J., Parnell, A.C., Phillips, D.L., and Semmens, B.X. 2018. Analyzing mixing systems using a new generation of bayesian tracer mixing models. PeerJ, **6(** 6): 1–27. doi:10.7717/peerj.5096.

Su, Z., and He, J.X. 2013. Analysis of Lake Huron recreational fisheries data using models dealing with excessive zeros. Fish. Res. **148**: 81–89. doi:10.1016/j.fishres.2013.08.012.

Taylor, C.E., Lauzon, R., Davis, C., Lee, V., and Dunlop, E.S. 2024. Regional predatory fish diets following a regime shift in Lake Huron. J. Great Lakes Res. **50**(2): 102301. doi:10.1016/j.jglr.2024.102301.

Thompson, R.M., Brose, U., Dunne, J.A., Hall, R.O., Hladyz, S., Kitching, R.L., et al. 2012. Food webs: reconciling the structure and function of biodiversity. Trends Ecol. Evol. **27**(12): 689–697. doi:10.1016/j.tree.2012.08.005.

Trumpickas, J., Rennie, M.D., and Dunlop, E.S. 2022. Seventy years of food-web change in South Bay, Lake Huron. J. Great Lakes Res. **48**(5): 1248–1257. doi:10.1016/j.jglr.2022.06.003.

Turschak, B., Bronte, C.R., Czesny, S., Gerig, B., Happel, A., Höök, T.O., et al. 2022. Temporal variation in the niche partitioning of Lake Michigan salmonines as it relates to alewife abundance and size structure. Can. J. Fish. Aquat. Sci. **79**(3): 487–502. doi:10.1139/cjfas-2021-0027.

Valls, A., Coll, M., Christensen, V., and Ellison, A.M. 2015. Keystone species: toward an operational concept for marine biodiversity conservation. Ecol. Monogr. **85**(1): 29–47. doi:10.1890/14-0306.1.

Vilà, M., Espinar, J.L., Hejda, M., Hulme, P.E., Jarošík, V., Maron, J.L., et al. 2011. Ecological impacts of invasive alien plants: a meta-analysis of their effects on species, communities and ecosystems. Ecol. Lett. **14**(7): 702–708. doi:10.1111/j.1461-0248.2011.01628.x.

Weidel, B.C., Ackiss, A.S., Chalupnicki, M.A., Connerton, M.J., Davis, S., Dettmers, J.M., et al. 2022. Results of the Collaborative Lake Ontario Bloater Restoration Stocking and Assessment, 2012–2020. J. Great Lakes Res. **48**(2): 371–380. doi:10.1016/j.jglr.2021.11.014.

Yohannes, E., Franke, L., and Rothhaupt, K.O. 2014. Zebra mussel Δ13C and Δ15N as a proxy for depth-specific pelagic isotope profiles and lake temperature. Hydrobiologia, **731**(1): 191–198. doi:10.1007/s10750-013-1786-0.

Zanden, M.J.V., and Rasmussen, J.B. 1999. Primary consumer (Delta 13 C) and (Delta 15 N) and the trophic position of aq … Ecology, **80**. doi:10.1890/0012-9658(1999)080[1395:PCCANA]2.0.CO;2.