Contents lists available at ScienceDirect

Journal of Great Lakes Research

journal homepage: www.elsevier.com/locate/jglr

Intraspecific variation in stable isotopes provides insight into adfluvial migrations and ecology of brook trout in Lake Superior tributaries

Troy G. Zorn [a,*], Kevin Pangle [b], Nick Peterson [c], Henry Quinlan [d], Brandon Gerig [e]

[a] *Michigan Department of Natural Resources Fisheries Division, Marquette Fisheries Research Station, 484 Cherry Creek Road, Marquette, MI 49855, USA*
[b] *Central Michigan University, Department of Biology, 1455 Calumet Court, Mount Pleasant, MI 48859, USA*
[c] *Minnesota Department of Natural Resources, Lake Superior Area Fisheries, 5351 North Shore Drive, Duluth, MN 55804, USA*
[d] *U.S. Fish and Wildlife Service, Ashland Fish and Wildlife Conservation Office, 2800 Lake Shore Drive East, Ashland, WI 54806, USA*
[e] *School of Freshwater Sciences, University of Wisconsin-Milwaukee, 600 E Greenfield Avenue, Milwaukee, WI 53204, USA*

ARTICLE INFO

Communicated by Joel Hoffman

Keywords:
Brook trout
Migration
Stable isotopes
Lake Superior
Stream
Life history

ABSTRACT

Identifying streams hosting salmonids with poorly understood adfluvial life histories, such as coaster brook trout, is challenging due to the lack of inexpensive, non-lethal techniques for confirming lake to stream movements for stream-captured fish. In this study, we used stable isotope data from 589 brook trout collected throughout the Lake Superior basin to characterize stream versus Lake Superior foraging. We observed strong isotopic separation in δ^{13}C between brook trout inhabiting Lake Superior and lake-inaccessible stream reaches (i.e., those lacking Lake Superior access). Using these data, we developed a linear discriminant function (LDF) which assigned brook trout to Lake Superior or stream habitats with over 97 % accuracy. LDF and Bayesian stable isotope mixing models were then used to estimate stream and lake energy use by brook trout collected from lake-accessible reaches. Brook trout caught in lake-accessible reaches had isotope signatures and sizes that were intermediate to fish from lake-inaccessible reaches and Lake Superior, potentially indicative of Lake Superior to stream migrations or possibly an energy subsidy from adfluvial migrants in streams. The LDF was used to estimate the probability that recently grown fin tissue from brook trout collected in lake-accessible reaches resulted from foraging in Lake Superior. We identified tributaries hosting "likely" coaster brook trout using a fish's length and LDF probability value. Our findings show the potential and limitations of this approach for confirming adfluvial migrations of brook trout.

1. Introduction

Protection of native salmonid stocks can be challenging due to the diversity of life history and migratory strategies of individual fishes, and the genetic discreteness and source-sink dynamics of populations. This diversity and discreteness are often associated with complex landscape patterns that shape habitat conditions and connectivity of stream reaches, which in turn influence migratory patterns and isolate populations (Rieman and Dunhamm 2000; Quinn, 2021). Diverse life histories are exemplified among trout and charr species throughout the world, and require careful and targeted conservation measures (Huckins et al., 2008; Muir et al., 2016; Muhlfeld et al., 2019). For example, brook trout *Salvelinus fontinalis* are native to many coldwater streams in eastern and northern portions of North America, with distinct life histories exhibited by anadromous stocks ("salters") on the northern Atlantic coast and lake-dwelling and adfluvial "coaster" life history forms within the Laurentian Great Lakes, most notably Lake Superior (Hudy et al., 2008; Mamoozadeh et al., 2023).

Coaster brook trout are defined as spending a portion of their lives in the Great Lakes (Becker, 1983), though a variety of life history patterns involving lake and stream habitat use have been described (Huckins et al., 2008). For example, coaster brook trout movement patterns involving Lake Superior may include adfluvial migrations (Huckins and Baker, 2008; Mucha and Mackereth, 2008), frequent movements between stream and lake habitats year-round (Kusnierz et al., 2009), or year-round lake residency (Boone et al., 2021). In addition, above-barrier brook trout stocks appear to contribute to some coaster populations (Miller et al., 2016; Mamoozadeh et al., 2023; Scribner et al., 2012).

Fishery agencies have identified 116 Lake Superior tributaries

---

* Corresponding author.
E-mail address: zornt@michigan.gov (T.G. Zorn).

https://doi.org/10.1016/j.jglr.2024.102487
Received 26 February 2024; Accepted 22 November 2024

Please cite this article as: Troy G. Zorn et al., *Journal of Great Lakes Research*, https://doi.org/10.1016/j.jglr.2024.102487

thought to historically support coasters (Newman et al., 2003), but stocks in many streams have declined due to factors including overfishing, habitat destruction and competition with non-native salmonids (Roosevelt, 1865, Newman et al., 2003; Zorn et al., 2020). Coasters presently occur in isolated areas, many having highly protective fishing regulations (Schreiner et al., 2008; Quinlan, 2021). Tagging projects and genetic analyses have confirmed nearly two dozen additional streams as supporting coasters (M. Chase, OMNR, pers. comm.; Miller et al., 2016; Mamoozadeh et al., 2023). Still, restoration of Lake Superior brook trout populations and the coaster life history form has been a long-standing priority of Great Lakes fisheries managers (Newman et al., 2003; Goldsworthy et al., 2017; Zorn et al., 2018; Quinlan 2021; Hanchin et al., 2024).

Identifying streams with remnant adfluvial brook trout for protection and rehabilitation is an important first step in conservation and rehabilitation of coasters. However, documenting an adfluvial life history from a single encounter of a large stream-captured brook trout (potentially a resident or adfluvial fish) is difficult due to a lack of techniques for confirming adfluvial migrations. Moreover, fish less than 200 mm have also been observed to make recurrent movement between lake and stream environments (Kusnierz et al., 2009), making classifications of resident or coaster based solely on body size questionable. Current approaches to documenting lake to stream movements of stream-caught brook trout involve tagging studies (e.g., Adams, 2020) which are costly and time-consuming (not feasible for an individual fish) or otolith microchemistry analyses (Pracheil et al., 2014) which are lethal. Both approaches are ill-suited for non-lethally and inexpensively confirming lake to stream movements of individual fish. Lack of simple non-lethal techniques for confirming occurrence of adfluvial brook trout in stream reaches hinders fishery managers' ability to justify and gain support from skeptical anglers, fishery administrators or funders for coaster rehabilitation activities (e.g., sportfishing regulation changes, habitat improvement).

Stable isotope analysis provides insight into energy pathways and is potentially useful for distinguishing lake- versus stream-based foraging of fishes, including brook trout. Stable isotope analysis is useful because the stable isotope of carbon δ^{13}C (delta C, ratio of δ^{13}C to δ^{12}C relative to a reference standard) shows considerable isotopic fractionation during carbon fixation by primary producers. Because of this, fish that rely on energy produced in a small stream or the nearshore zone of Lake Superior should be distinguishable (Robillard et al., 2011a; Sierszen et al., 2011). In addition, the stable isotope of nitrogen δ^{15}N shows consistent fractionation when assimilated, resulting in a predictable 3 %–4 % increase in the δ^{15}N (delta N, ratio of δ^{15}N to δ^{14}N relative to a standard) from prey to predator. While stable isotope analyses have been used to document fish movements elsewhere (e.g., McCarthy and Waldron, 2000; Trueman et al., 2012), limited application of such techniques has occurred for fishes captured in Lake Superior tributaries (Jones and Mackereth, 2016; Robillard et al., 2011a,b). However, Zorn et al. (2024) recently used stable isotope ratios of δ^{13}C and δ^{15}N from fin tissue to infer prior Lake Superior based foraging of stream-captured brook trout and coho salmon (*Oncorhynchus kisutch)*.

Our overall study objective was to use stable isotope analysis of δ^{13}C and δ^{15}N of fin tissue from brook trout captured in Lake Superior accessible tributaries to infer foraging habitats used (hence residency) prior to capture. If successful, this would provide a relatively simple, non-lethal tool for confirming adfluvial movements of brook trout from Lake Superior to spawning streams (i.e., a common coaster life history). We examined patterns in δ^{13}C and δ^{15}N from brook trout captured in Lake Superior, stream reaches accessible to Lake Superior (hereafter "lake-accessible"), and stream reaches without Lake Superior access (hereafter "lake-inaccessible") due to waterfalls or dams. Using brook trout from Lake Superior and lake-inaccessible reaches captured throughout the basin to provide isotopic signatures of these habitats, we hypothesized brook trout from lake-accessible reaches could have isotopic signatures indicative of prior foraging in stream, Lake Superior, or a combination of stream and Lake Superior habitats. Our specific objectives were to: 1) compare isotopic signatures of brook trout among three habitat types throughout the basin, specifically, Lake Superior, lake-inaccessible stream reaches, and lake-accessible stream reaches; 2) determine if stable isotope signatures of brook trout in lake-accessible reaches vary with brook trout total length, potentially indicative of a shift in foraging habitat use (i.e., from stream to Lake Superior); and 3) estimate the likelihood (probability) of foraging in Lake Superior for individual brook trout by length in individual rivers and identify streams having "likely" coaster brook trout (i.e., fish whose probability values suggest an adfluvial life history).

2. Methods

2.1. Sample collection

Tribal, State, Federal and Provincial agency crews voluntarily collected fin clip samples from brook trout during sampling of tributaries and nearshore areas of Lake Superior (Fig. 1; Table 1). Brook trout were primarily sampled in 2021via boat, backpack or tow-barge DC electrofishing, gill nets and angling. A clip of up to 1 cm^2 from the distal portion of the caudal fin was obtained from up to 10 brook trout that were 100–150 mm total length and all brook trout >=200 mm total length at each sampling location. The clip was placed in a scale envelope, noting information on the sampled fish (e.g., species, total length, location, date, and collector), and the sample was air-dried for later processing. Crews recorded length and width of the reach sampled, total number of brook trout observed and water temperature at each site.

Samples were collected from 1356 brook trout in streams and Lake Superior nearshore areas in Minnesota, Ontario, Michigan and Wisconsin in 2021, nearly three times our capacity for analysis. Numbers of samples obtained varied throughout the Lake Superior basin likely due to uneven sampling effort and the voluntary sampling approach. We used stratified random subsampling to ensure brook trout analyzed represented all jurisdictions (state or province), habitat types (i.e., Lake Superior and lake-accessible and lake-inaccessible reaches), sampling locations, and the range of total lengths of brook trout at each location (subsampling from six length bins with cut points at <100, <175, < 250, <325, <400, >=400 mm). We optimized sample analysis to provide coverage of brook trout from all length bins and habitat types, with additional emphasis on lake-accessible streams and larger brook trout suspected of being coasters. For each site in Lake Superior, we analyzed up to five brook trout per size bin for all length bins. Because lake-inaccessible streams could not have coasters, for each we analyzed up to three brook trout per bin for the three smallest length bins and five fish per bin for the larger bins. To provide additional focus on identifying the scarce adfluvial life history, in each lake-accessible stream we analyzed up to five brook trout per bin for the two smallest length bins and up to 20 fish per bin for the four length largest bins. Brook trout selected for analysis were also required to have fin clip and maxilla samples available to allow future comparison between fin clip stable isotope ratio and maxilla microchemistry approaches to documenting brook trout migrations.

We selected 465 brook trout samples from 2021 for analysis (Fig. 1; Table 1). These included: 54 fish collected from Lake Superior via gill nets and electrofishing in June through August (except one October caught fish); 109 fish captured from lake-inaccessible stream reaches with wadeable electrofishing during July-October; and 312 fish caught from lake-accessible stream reaches in July-November, 287 by wadeable electrofishing and 25 by angling. Over 90% of stream brook trout analyzed from 2021 were collected during late-September to November. Additional isotope data for 124 brook trout, collected from Michigan waters of Lake Superior in August and lake-accessible or lake-inaccessible tributary reaches in October, were obtained from Zorn et al. (2024), to bring the total sample size for analysis to 589 brook trout.

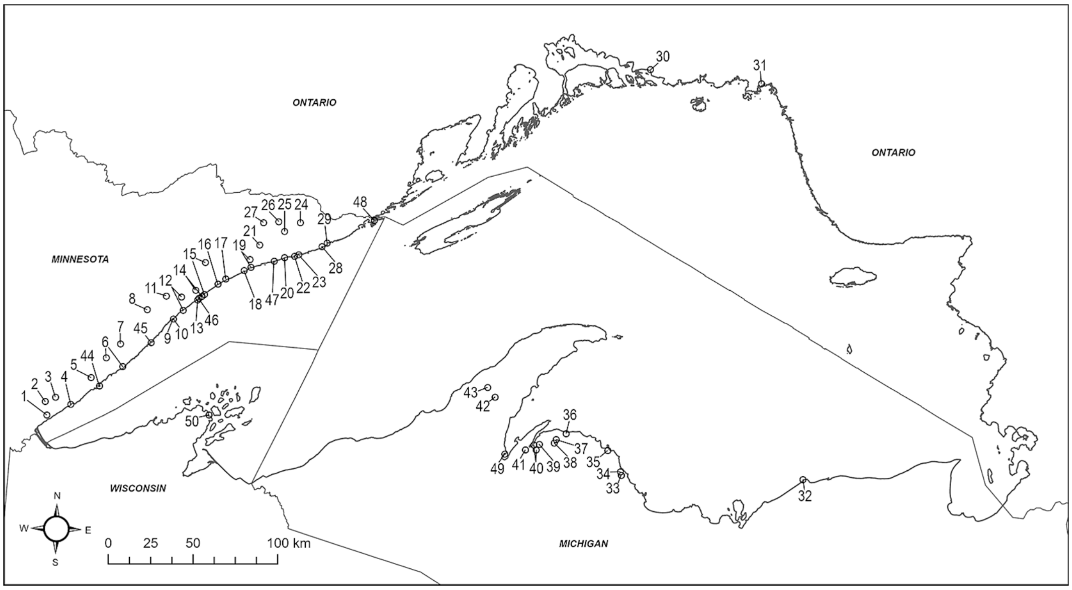

Fig. 1. Map of sampling sites with numbers corresponding to sites listed in Table 1.

Brook trout chosen for analysis represented an array of waters in the Lake Superior basin, with streams along the Minnesota's North Shore of Lake Superior and the western Upper Peninsula of Michigan most well-represented (Fig. 1; Table 1). Numbers of streams represented in our analysis by jurisdiction were Minnesota (29), Ontario (2), Michigan (12) and Wisconsin (0). Numbers of brook trout samples analyzed by jurisdiction were Minnesota (379), Ontario (17), Michigan (187) and Wisconsin (6). Numbers of brook trout analyzed by habitat type were Lake-accessible (382), Lake-inaccessible (150) and Lake Superior (57).

2.2. Sample processing

Fin clips were processed for analysis of stable isotope ratios following Zorn et al. (2024). Fin clips were oven-dried at 60 °C, homogenized into a fine powder using a mortar and pestle, encapsulated into a tin cup, weighed to the nearest 0.001 of a gram, and stored in a 96-well tray in a desiccator. All stable isotope samples were run on a Thermo Delta V isotope ratio mass spectrometer interfaced to an NC2500 Elemental Analyzer (Thermo Fisher Scientific, Waltham, MA) at the Cornell University Stable Isotope Laboratory (COIL).

Stable isotope ratios of N ($\delta^{15}N$) and C ($\delta^{13}C$) are expressed as:

$$\delta^{15}N \text{ or } \delta^{13}C = [(Rsample/Rstandard) - 1] \times 1000 \qquad (1)$$

where, R is the ratio of $\delta^{15}N$ to $\delta^{14}N$ or $\delta^{13}C$ to $\delta^{12}C$ for an unknown sample relative to a known isotope standard. Internationally approved standards for determining stable isotope ratios of carbon and nitrogen are Vienna Pee-Dee Belemnite and atmospheric N_2, respectively. To ensure the accuracy and precision, an in-house standard (*Odocoileus virginianus*) was analyzed after every 10 samples. For our brook trout samples, the overall standard deviation for the internal standard was 0.14 ‰ for $\delta^{15}N$ and 0.13 ‰ for $\delta^{13}C$. Isotope corrections were performed using a two-point normalization using in-house standards that are calibrated against international reference materials provided by the International Atomic Energy Association (IAEA). The ratio of carbon to nitrogen (C:N) was also determined from the Elemental Analyzer. $\delta^{13}C$ ratios were not mathematically corrected using the ratio of carbon to nitrogen because no fin clip samples had C:N ratios exceeding 4 (Hoffman et al., 2015). Samples from brook trout in the Pilgrim River were excluded for study objectives 1 and 2. Brook trout in the Pilgrim River exhibit adfluvial movements between the river and Portage Lake, which connects to Lake Superior (Adams 2020), but their isotopic values were enriched in $\delta^{15}N$, likely a result of treated wastewater effluent in Portage Lake (Zorn et al., 2024).

2.3. Objective 1. Brook trout sample comparisons and isotopic niche overlap

We compared brook trout total length, $\delta^{13}C$, and $\delta^{15}N$ among habitat types (i.e., Lake Superior, lake-inaccessible, lake-accessible) using a one-way analysis of variance. Model assumptions were assessed based upon visual examination of residuals and Q-Q plots. We used the NicheRover package in R to describe niche size and differences in isotopic niche overlap (Swanson et al., 2015) among brook trout from Lake Superior, lake-accessible, and lake-inaccessible habitats. Using NicheRover, we estimated the probability of overlap ±95 % credible interval for each comparison (Swanson et al., 2015). Overlap was interpreted as the probability that an individual from group A will be found in the niche of group B. Group A is listed in table rows while Group B are table columns (Swanson et al., 2015).

2.4. Objective 2. Stable isotope mixing model

Bayesian stable isotope mixing models were used to estimate the use of stream and lake energy sources for Brook Trout collected from lake-accessible stream reaches using the MixSIAR package in R (Stock et al., 2018). Prey sources were split into two categories reflecting the mean $\delta^{15}N$ and $\delta^{13}C$ (±standard deviation, SD), lake- accessible streams and the nearshore zone (depth < 15 m) of Lake Superior. Prey sources were collected by agency personnel. For lake-accessible streams, we averaged the isotopic signature of Heptagenidae mayflies ($n = 24$) from seven sampling sites ($\delta^{15}N = 4.2 \pm 1.5$, $\delta^{13}C = -29.2 \pm 1.1$). For the nearshore zone, we averaged the isotope ratios of nearshore prey fish across five Lake Superior sites. Species included were common shiner (*Luxilus cornutus*; $n = 9$), johnny darter (*Etheostoma nigrum*; $n = 10$), ninespine stickleback (*Pungitius pungitius*; $n = 15$), rainbow smelt (*Osmerus mordax*; $n = 18$), spottail shiner (*Notropis hudsonius*, $n = 12$), threespine stickleback (*Gasterosteus aculeatus*; $n = 20$), and trout-perch (*Percopsis omiscomaycus*; $n = 15$). For nearshore prey, the mean $\delta^{15}N$ was 6.1 ± 1.1 and $\delta^{13}C$ was -22.2 ± 2.8. For the mixing models, we applied trophic discrimination factors of 0.4 ‰ (SD = 1.2 ‰) for $\delta^{13}C$ and 3.4 ‰ (SD = 1.0 ‰) for $\delta^{15}N$. Mixing model estimates of dietary proportion were calculated as the mean and 95 % Bayesian credible interval of the posterior. Lake-accessible brook trout isotope ratios and

Table 1

Mean, standard deviation (SD) and sample size (n) of total length, $\delta^{13}C$ and $\delta^{15}N$ for brook trout in Lake Superior and tributaries. Sites are numbered clockwise starting from Duluth. Accessibility of tributary reaches to Lake Superior fishes is indicated by "Y" (yes, lake-accessible) or "N" (no, lake-inaccessible) under LS access field. Locations having small sample sizes (e.g., n < 5) were included to maximize geographic scope.

ID	WATERBODY	LS			Length (mm)			$\delta^{13}C$		$\delta^{15}N$	
		Access	Latitude	Longitude	Mean	SD	n	Mean	SD	Mean	SD
1	Amity Cr	N	46.86	−92.03	153	20	4	−27.4	0.5	9.2	0.3
2	Lester R	N	46.93	−92.05	194	57	8	−28.2	1.2	10.3	0.9
3	French R	N	46.95	−91.97	174	24	8	−28.8	1.1	9.5	0.5
4	Sucker R	Y	46.92	−91.85	218	49	5	−25.0	1.6	8.2	0.7
5	Stewart R	N	47.07	−91.71	244	26	6	−28.0	0.6	9.2	0.4
6	Gooseberry R	Y	47.14	−91.47	239	43	5	−25.2	0.7	9.6	0.9
6	Gooseberry R	N	47.18	−91.60	195	51	7	−26.4	0.6	9.0	0.6
7	W Br Split Rock R	N	47.26	−91.50	178	52	6	−27.0	0.6	9.7	1.6
8	Crown Cr	N	47.45	−91.31	146	52	9	−26.3	1.1	8.1	1.4
9	Little Marais Cr	Y	47.41	−91.10	155	32	4	−24.5	0.4	7.7	0.8
10	Dragon Cr	Y	47.41	−91.10	205	66	2	−25.9	1.1	8.3	0.1
11	Manitou R	N	47.53	−91.17	161	40	7	−26.4	2.2	8.4	0.4
12	Caribou R	Y	47.46	−91.03	186	36	12	−24.4	0.6	8.1	1.5
12	Caribou R	N	47.53	−91.05	177	60	6	−28.5	1.3	9.4	1.4
13	Two Island R	Y	47.52	−90.92	290		1	−18.8		7.5	
13	Two Island R	N	47.52	−90.92	153	30	4	−23.2	0.3	7.1	1.2
14	Cross R	Y	47.54	−90.89	237	60	40	−23.3	1.1	8.7	1.0
14	Cross R	N	47.57	−90.94	162	36	6	−24.7	0.1	8.8	0.6
15	Temperance R	Y	47.55	−90.87	263	48	4	−21.7	2.4	8.6	0.7
15	Temperance R	N	47.72	−90.88	170	34	6	−26.1	0.6	9.4	0.9
16	Onion R	Y	47.61	−90.77	189	40	15	−23.2	1.9	8.0	1.4
17	Poplar R	Y	47.64	−90.71	263	58	31	−22.6	1.7	10.0	1.6
18	Spruce (Deeryard) Cr	Y	47.69	−90.57	206	64	15	−23.9	1.3	8.4	1.6
19	Cascade R	Y	47.71	−90.52	227	50	16	−23.8	1.1	8.2	1.6
19	Cascade R	N	47.75	−90.53	169	22	6	−25.4	0.6	9.0	0.7
20	Devil Track R	Y	47.77	−90.26	243	87	45	−22.5	2.0	9.4	1.4
21	Junco Cr	N	47.83	−90.46	185	43	7	−27.1	1.1	8.6	0.5
22	Kimball Cr	Y	47.78	−90.18	172	37	12	−24.7	0.4	9.1	1.4
23	Kadunce R	Y	47.79	−90.15	178	65	15	−23.4	1.6	9.5	1.2
24	Greenwood R	N	47.96	−90.15	145	22	3	−26.7	0.4	9.4	0.5
25	Timber Cr	N	47.91	−90.27	215	5	2	−27.4	2.4	6.1	0.4
26	North Brule R	N	47.96	−90.32	194	43	5	−28.9	1.9	8.8	0.4
27	Fiddle Cr	N	47.95	−90.44	166	35	6	−27.9	1.2	9.0	0.5
28	Flute Reed R	Y	47.84	−89.97	281		1	−19.8		7.2	
29	Carlson Cr	Y	47.86	−89.93	193	34	2	−23.7	1.0	7.4	1.5
30	Hewitson R	Y	48.84	−87.40	168	37	11	−25.3	1.5	8.6	0.7
31	Mink Cr	Y	48.77	−86.51	131	12	5	−26.3	0.8	7.1	1.0
31	Mink Cr	N	48.77	−86.51	120		1	−24.8		6.9	
32	Hurricane R	Y	46.67	−86.17	155	11	2	−25.2	1.3	7.6	0.5
33	Big Garlic R	N	46.68	−87.57	144	17	22	−26.2	1.1	7.4	0.6
34	Wilson Cr	Y	46.70	−87.58	199	43	7	−26.8	1.1	8.3	1.7
35	Iron R	Y	46.81	−87.68	290	26	7	−27.6	0.9	8.9	1.2
36	Little Huron R	Y	46.90	−88.01	211	18	2	−25.2	1.0	8.0	1.2
37	Big Huron R	Y	46.86	−88.08	210	9	3	−25.0	0.9	9.8	1.0
38	W Br Huron R	Y	46.85	−88.10	216	36	2	−24.4	0.4	7.9	1.0
39	Ravine R	Y	46.84	−88.21	243	38	2	−22.4	3.6	10.3	1.7
40	Slate R	Y	46.83	−88.25	235	44	9	−21.0	1.0	9.2	0.9
40	Slate R	N	46.81	−88.23	229	27	21	−25.5	0.9	7.3	0.8
41	Silver R	Y	46.80	−88.32	194	15	3	−23.4	1.2	8.3	1.4
42	Pilgrim R	Y	47.08	−88.57	251	69	95	−26.3	0.9	11.2	1.1
43	Cole Cr	Y	47.13	−88.63	259	62	9	−24.1	1.2	9.9	1.6
44	LS-Two Harbors		47.03	−91.64	295		1	−22.6		8.7	
45	LS-Silver Bay		47.28	−91.26	290	71	7	−21.7	1.9	9.1	1.1
46	LS-Taconite Harbor		47.53	−90.91	273	85	18	−22.1	0.9	8.4	1.6
47	LS-Grand Marais		47.75	−90.34	307	82	18	−19.7	1.0	7.6	1.0
48	LS-Grand Portage		47.99	−89.57	441	139	4	−20.8	1.1	8.1	0.9
49	LS-Keweenaw Bay		46.78	−88.48	386	22	3	−19.3	1.6	8.7	0.8
50	LS-Apostle Islands		46.91	−90.78	415	77	6	−19.0	2.2	8.2	1.0

prey sources (mean ± SD) are displayed in Electronic Supplementary material (ESM) Fig. S1.

We used MixSIAR to fit six mixing models with different covariate structures. Covariates included individual stream, state or province of capture (Michigan, Minnesota, Ontario), and the continuous variable brook trout total length. Because each model was fit to the same data ($\delta^{13}C$ and $\delta^{15}N$ values for each of 287 brook trout), we compared the models against one another using information criteria. Following, Stock et al. (2018) we used the widely applicable information criterion (WAIC) and approximate leave-one-out cross-validation (LOO), both of which are more robust to the concerns associated with deviance information criterion (Stock et al., 2018). Each model was fit with the same mixture data and the relative support of different model parameterizations was compared using LOO and WAIC weights. WAIC and LOO weights are the probability each model will make the best predictions on new data (Anderson and Burnham, 2002; McElreath, 2018). Models were run with 3 parallel MCMC chains of length 100,000. Burn-in length was 50,000 and chains were thinned by 50. Model convergence was evaluated using the Gelman-Rubin diagnostic. Less than 5 % of parameter estimates should exceed the 1.05 Gelman-Rubin diagnostic. For our models, no parameter estimates exceeded the 1.05 cut-off.

2.5. *Objective 3. Linear discriminant function*

We also employed a classification-based approach in which stable isotope measurements were used to estimate the probability that a brook trout from a lake-accessible stream reach would have been foraging in Lake Superior. Specifically, we fit linear discriminant functions (LDF) using $\delta^{13}C$ values from brook trout from Lake Superior and lake-inaccessible reaches. We assumed a known history of habitat use (i.e., Lake Superior or stream) for these fish and that each habitat had the same prior probability of being assigned. Preliminary analyses also included $\delta^{15}N$ measurements in the LDFs, but its inclusion provided no additional discriminatory power, so the variable was removed from the final analysis. We performed jackknifed cross-validations to test the ability of LDFs to accurately classify between lake and stream origin.

After fitting the models using fish of known habitat history, we applied the LDFs to brook trout sampled from lake-accessible reaches to estimate their probability of having foraged in Lake Superior. We used this probability as an indication that a fish had a “coaster” life history. These probability estimates assume that data are normally distributed around their respective group means. This assumption was tested and found to be met using a Shapiro-Wilk test (Shapiro-Wilk test statistic = 0.99, $p = 0.69$). As for objective 2, we tested the effect of the length of a fish, its stream of capture (i.e., individual stream), and the interaction of these two factors on the probability of having foraged in Lake Superior using logistic regression. Statistical significance of these factors was evaluated using Wald chi-squared test (alpha = 0.05).

3. Results

3.1. *Objective 1. Brook trout sample comparisons and isotopic niche overlap*

Lengths and stable isotope ratios of brook trout examined varied among habitat types. We found that brook trout length differed ($F_{2,586} = 93.8$, $p < 0.001$; Fig. 2a) among Lake Superior, lake-accessible, and lake-inaccessible streams with fish captured in lake-inaccessible reaches being smallest (mean = 179 mm, SD = 65), brook trout captured in Lake Superior being largest (mean = 319 mm, SD = 97, Fig. 2a.), and brook trout from lake-accessible reaches having intermediate lengths (mean = 222 mm, SD = 66, Fig. 2a). For $\delta^{13}C$, we observed differences in $\delta^{13}C$ among habitat types ($F_{2,586} = 197.8$, $p < 0.001$; Fig. 2b). Brook trout in lake-inaccessible reaches were depleted in $\delta^{13}C$ (mean = -27.5, SD = 1.15) while Lake Superior captured brook trout were enriched in $\delta^{13}C$ (mean = −23.4, SD = 1.23, Fig. 2b). This strong separation is consistent with known differences in energy sources between stream and lake environments. Like length, brook trout sampled from lake-accessible reaches had intermediate $\delta^{13}C$ ratios (mean = -25.4, SD = 1.36). For $\delta^{15}N$, we observed differences among habitat types ($F_{2,586} = 32.2$, $p < 0.001$; Fig. 2c) with lake-inaccessible and Lake Superior samples having lower $\delta^{15}N$ than lake-accessible samples. Compared to total length or $\delta^{13}C$, the magnitude of differences among habitat types was small for $\delta^{15}N$ (Fig. 2c.).

We found evidence of isotopic overlap and differentiation in brook trout captured among Lake Superior, lake-accessible, and lake-inaccessible reaches with patterns largely driven by $\delta^{13}C$ (Fig. 3). Lake Superior captured brook trout had an isotopically distinct niche, having only 5 % probability of overlap, when compared to lake-inaccessible brook trout (Fig. 3a, Table 2). In contrast, brook trout sampled from Lake Superior had a 74 % overlap probability with brook trout captured in lake-accessible streams (Fig. 3b, Table 2). Lake-inaccessible brook trout exhibited a 6 % overlap with Lake Superior brook trout and an 84 % overlap with lake-accessible brook trout. Brook trout in lake-accessible stream reaches exhibited moderate overlap with Lake Superior brook trout (57 %) and lake-inaccessible brook trout (46 %). This pattern of overlap appeared to be driven by fish size with smaller individuals appearing more closely associated with lake-inaccessible brook trout and larger individuals with Lake Superior brook trout (Fig. 3b). We observed differences in niche size among brook trout habitat types. Niche area was 50 % larger for brook trout captured in lake-accessible stream reaches compared to brook trout sampled from lake-inaccessible stream reaches or Lake Superior (Fig. 3b).

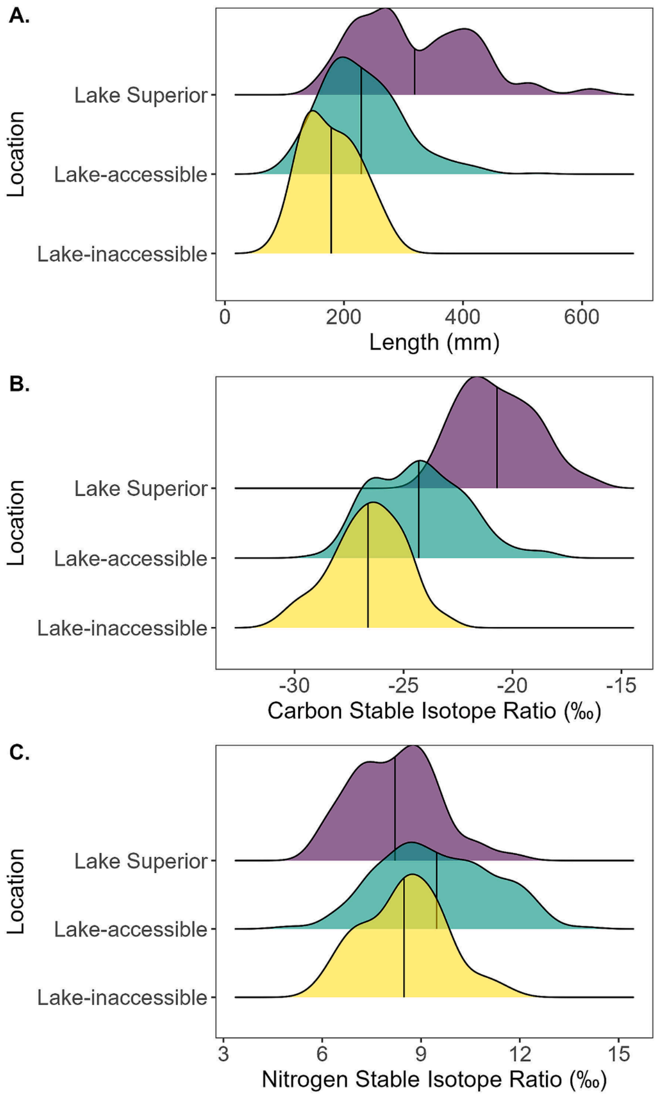

Fig. 2. Density distributions of total length (mm; Panel A), $\delta^{13}C$ (Panel B), and $\delta^{15}N$ (Panel C) for brook trout captured in Lake Superior, lake-accessible streams (streams with no movement barrier to Lake Superior), and lake-inaccessible streams (streams with a movement barrier to Lake Superior. Vertical line represents the median value for the respective variables.

3.2. *Objective 2. Stable isotope mixing model*

For brook trout in lake-accessible streams, we found that the best MixSIAR model included brook trout total length as a continuous fixed effect and individual stream as a categorical effect. The top model had the lowest leave-one-out cross validation value (LOO) and received all the model weight (Table 3). There was no support for any of the other models fit which included brook trout total length (mm), state/province of capture (Michigan, Minnesota, Ontario), or individual stream (Table 3). Based upon the posterior distributions from the top model, we found that the proportion of nearshore prey increased as a function of length (Fig. 4). Because there were only two isotope sources in the

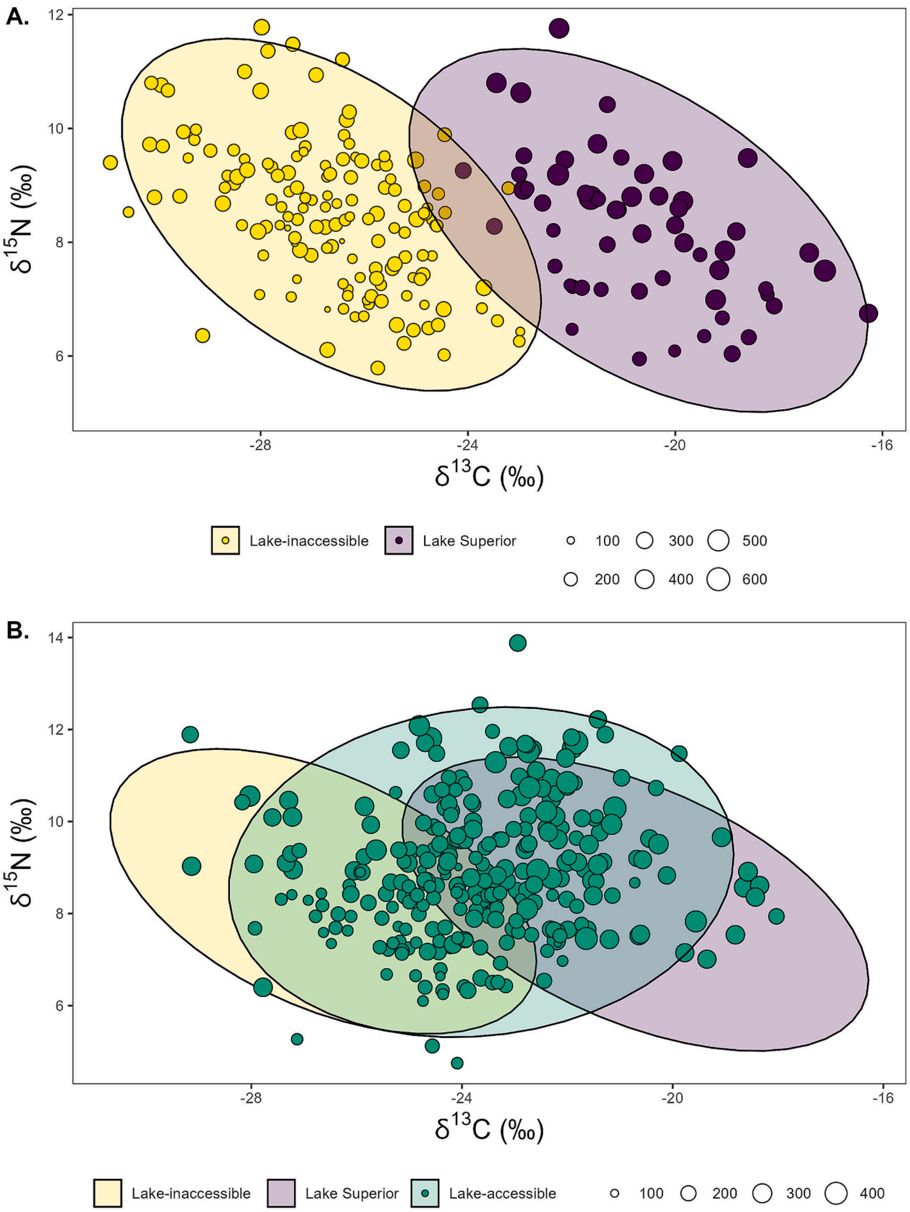

Fig. 3. Panel A. Stable isotope ratios and ellipses for brook trout captured in Lake Superior and lake-inaccessible stream reaches (streams with a movement barrier to Lake Superior). Panel B. Stable isotope ratios of brook trout captured in lake-accessible stream reaches (streams with no movement barrier to Lake Superior) and niche area of brook trout captured in Lake Superior, lake-accessible stream reaches, and lake-inaccessible stream reaches. See Table 2 for pairwise overlap probabilities (±95 % credible intervals). For both panels, size of each point is proportional to the length of an individual brook trout in 100 mm groups.

Table 2

Isotopic niche area (±SE) and isotopic niche overlap (±95 % credible interval) for brook trout captured in Lake Superior, stream reaches accessible to Lake Superior (lake-accessible), and stream reaches without Lake Superior access (lake-inaccessible) shown in Fig. 3b. Interpreted as the probability that an individual from a particular location (Location B) is found in the isotopic niche of another location (Location A).

Location A	Niche Area (‰^{2})	Location B		
		Lake Superior	Lake-inaccessible	Lake-accessible
Lake Superior	35.4 (4.7)	NA	5 (1–11)	74 (63–85)
Lake-inaccessible	52.9 (3.3)	6 (1–15)	NA	84 (71–88)
Lake-accessible	33.3 (2.8)	57 (44–77)	46 (33–55)	NA

Table 3

Comparison of mixing models fit using MixSIAR on brook trout captured in lake-accessible reaches of streams. Covariates in models were stream of origin (Stream), brook trout total length (Length) and state or province (State). LOOic = leave-one-out cross-validation information criteria, SE LOOic = standard error of leave-one-out cross-validation, dLOOic = delta leave-one-out cross-validation, SE dLOOic = standard error of delta leave-one-out cross-validation. dLOOic is the difference in LOOic between each model and the model with lowest LOOic.

Model	LOOic	SE LOOic	dLOOic	se_dLOOic	Weight
Stream, Length	864.5	47.7	0	NA	1
Stream	924.3	44.2	59.8	13.8	0
State, Length	1017.1	39.4	152.6	29.5	0
Length	1026.7	38.8	162.2	30.7	0
State	1070.9	36	206.4	30.7	0
Null	1092.4	35.1	227.9	32.5	0

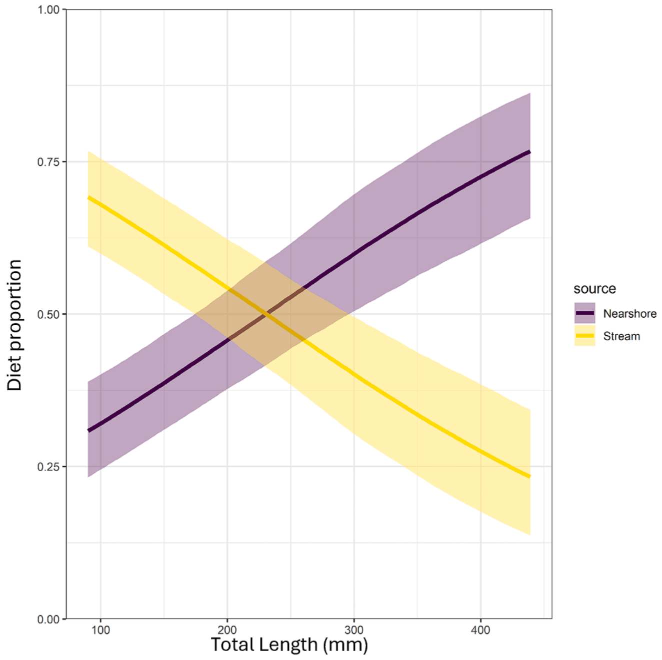

Fig. 4. MixSIAR model results of the mean estimated diet proportions for brook trout in lake-accessible stream reaches (streams with no movement barrier to Lake Superior). Solid lines indicate the median value and shading represents 95 % credible interval of each prey item.

mixing model, an increase in the proportion of nearshore prey corresponded with a reciprocal decline in the proportion of stream prey. Consideration of streams also yielded interesting results. Based upon the top mixing model, the estimated proportion of nearshore prey ranged from 0.065 (0.015–0.129) in the Iron River to 0.81 (0.56–0.96) for the Two Island River. Overall, we found the proportional contribution of nearshore items to brook trout diets was over 0.3 at 93 % of streams (27 out of 29) examined (Table 4). Moreover, brook trout in 41 % our study streams showed moderate use of nearshore resources ranging from 0.4 to 0.6, and nearshore resources made up over 75 % of brook trout diets in 14 % of streams (Table 4).

3.3. Objective 3. LDF-based Lake Superior assignment probabilities

The linear discriminant function (LDF), which was fit using δ^{13}C ratios, accurately distinguished brook trout from Lake Superior and lake-inaccessible reaches (Fig. 5). Based on the jack-knifing evaluation of the LDF, 97.3 % of brook trout from Lake Superior (n = 150) and 98.2 % of brook trout from lake-inaccessible reaches (n = 57) were correctly assigned back to their habitat type. The transition (i.e, cut-off) between the two habitat assignment was at a δ^{13}C ratio of −23.67 (Fig. 5), and, from the function, a solution for the probability of Lake Superior assignment (Pr(LS)) can be simplified as:

$$Pr(\mathrm{LS}) = \frac{e^{ax+\beta}}{e^{ax+\beta}+e^{-ax+\gamma}} \qquad (2)$$

where x is the δ^{13}C value and α, β, and γ are fitted parameters of values 1.060, 23.514, and −26.652, respectively.

When the LDF was applied to brook trout collected from lake-accessible reaches, the probability of lake assignment ranged from 0 to 100 % across individual fish (Fig. 6). Variation in the probability of lake assignment could be explained in part by a significant positive effect of fish length (chi sq = 9.60, df = 1, p = 0.002) as well as significant differences among individual streams (chi sq = 33.67, df = 16, p = 0.006), but not the interaction between these factors (chi sq = 4.80, df = 16, p = 0.997). The importance of fish length and individual stream as explanatory factors was evident in different patterns observed across lake-accessible streams (Fig. 6). For example, brook trout collected from the Cross River, Spruce Creek, and Cascade River showed a relatively gradual increase in the probability of lake assignment as total length increased. In contrast, fish from the Onion River and the Devil Track River had relatively high probabilities of lake assignment, even at small total lengths, and fish from Wilson Creek and the Iron River had

Table 4
MixSIAR model estimates of mean (±95 % credible interval) proportions of Lake Superior nearshore and stream prey in diets of brook trout captured in lake-accessible stream reaches (i.e., those accessible to Lake Superior). Sample size of brook trout by stream is indicated by “n”.

Stream	Mean (± 95 % credible interval)		n
	Nearshore	Stream	
Iron River	0.07 (0.02–0.13)	0.94 (0.87–0.99)	7
Wilson Creek	0.18 (0.07–0.30)	0.82 (0.70–0.93)	7
Dragon Creek	0.31 (0.13–0.51)	0.69 (0.49–0.87)	2
Mink Creek	0.32 (0.15–0.46)	0.68 (0.54–0.85)	5
Gooseberry River	0.35 (0.21–0.50)	0.65 (0.51–0.79)	5
Little Huron River	0.38 (0.20–0.60)	0.62 (0.40–0.8)	2
Sucker River	0.39 (0.27–0.51)	0.61 (0.49–0.73)	5
Hewitson River	0.43 (0.33–0.54)	0.57 (0.46–0.67)	11
Hurricane River	0.45 (0.23–0.67)	0.55 (0.33–0.77)	2
W. Br. Huron River	0.46 (0.28–0.69)	0.54 (0.31–0.73)	2
Cole Creek	0.47 (0.35–0.62)	0.53 (0.38–0.65)	9
Big Huron River	0.47 (0.36–0.60)	0.53 (0.40–0.64)	3
Caribou River	0.48 (0.39–0.58)	0.52 (0.43–0.61)	12
Kimball Creek	0.49 (0.39–0.59)	0.51 (0.41–0.61)	12
Cascade River	0.49 (0.41–0.58)	0.51 (0.42–0.59)	16
Spruce (Deeryard) Creek	0.50 (0.42–0.59)	0.50 (0.41–0.59)	15
Little Marais Creek	0.52 (0.38–0.67)	0.48 (0.33–0.62)	4
Carlson Creek	0.54 (0.36–0.77)	0.46 (0.23–0.64)	2
Cross River	0.54 (0.48–0.61)	0.46 (0.39–0.52)	40
Silver River	0.61 (0.45–0.81)	0.39 (0.20–0.55)	3
Onion River	0.65 (0.55–0.74)	0.36 (0.26–0.45)	15
Poplar River	0.65 (0.55–0.75)	0.35 (0.25–0.45)	31
Kadunce River	0.66 (0.56–0.76)	0.34 (0.24–0.44)	15
Temperance River	0.70 (0.53–0.90)	0.3 (0.10–0.47)	4
Devil Track River	0.71 (0.63–0.80)	0.29 (0.20–0.37)	45
Flute Reed River	0.77 (0.51–0.96)	0.23 (0.04–0.49)	1
Ravine River-Up	0.79 (0.59–0.96)	0.21 (0.04–0.42)	2
Slate River-Lo	0.79 (0.67–0.91)	0.21 (0.09–0.33)	9
Two Island River	0.80 (0.57–0.97)	0.20 (0.03–0.44)	1

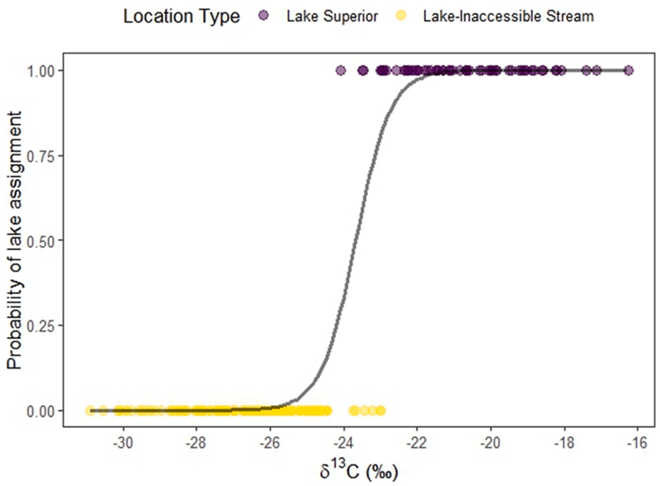

Fig. 5. Linear discriminant function-based probabilities of individual brook trout being classified as foraging in Lake Superior as a function of δ^{13}C values. δ^{13}C values used to fit the model were from brook trout collected from Lake Superior and lake-inaccessible reaches of streams (purple and yellow circles, respectively). (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

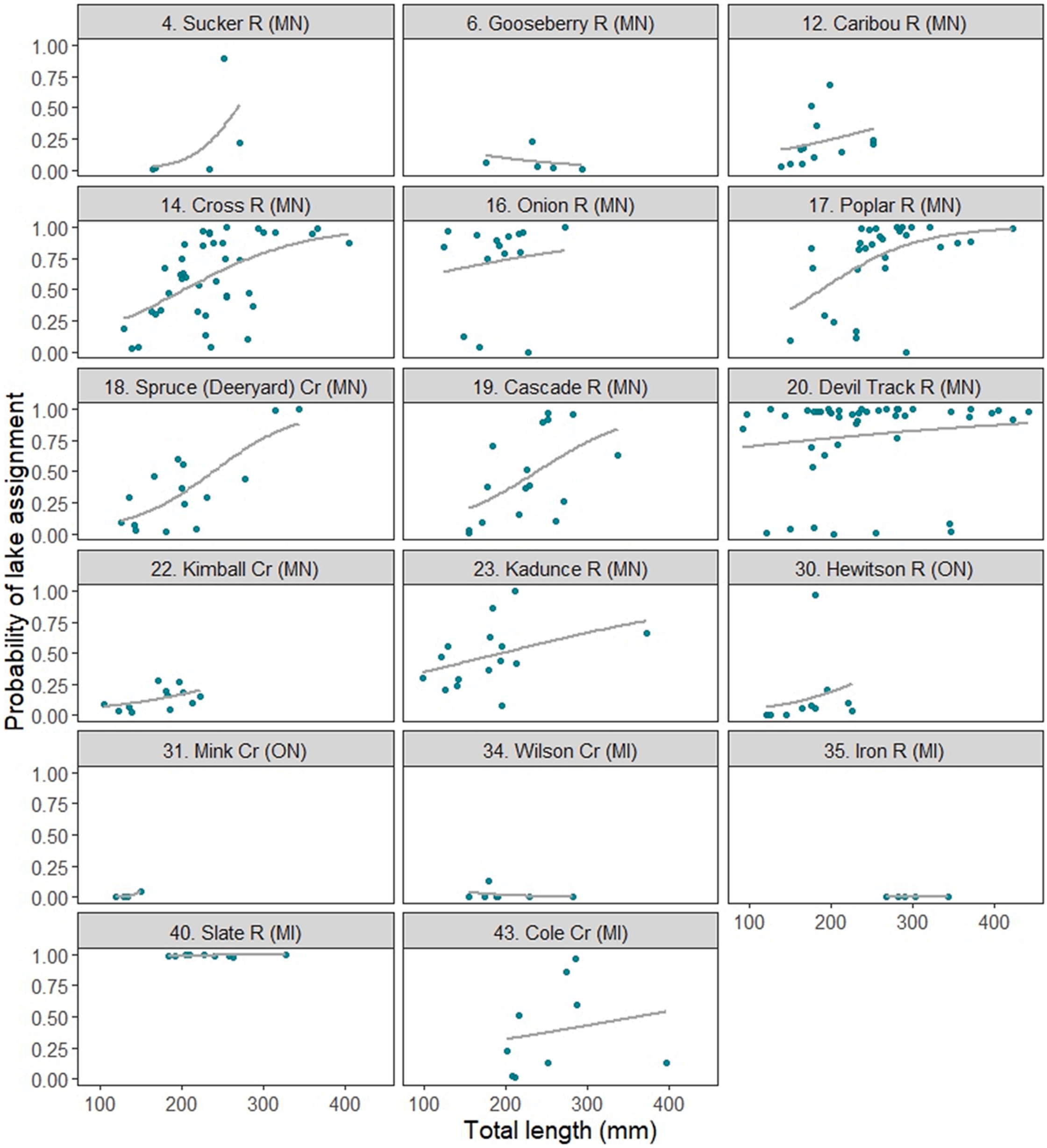

Fig. 6. Linear discriminant function-based probabilities of individual brook trout being classified as foraging in Lake Superior based on its δ^{13}C value for different streams plotted against fish length. Plots are for Lake Superior accessible (i.e., lake-accessible) stream reaches with 5 or more brook trout sampled, and streams are ordered based on their number in Table 1 and Fig. 1. Lines represent logistic regression models fitted to data for each stream.

relatively low probabilities of lake assignment, even at large total lengths.

4. Discussion

The ecology and life history of coaster brook trout populations are poorly understood (Huckins et al., 2008; Ridgway, 2008; Schreiner et al., 2008), but distinct adfluvial and resident life histories have been documented for brook trout in portions of Lake Superior and its tributaries (e.g., Huckins and Baker, 2008; Robillard et al., 2011b; Boone et al., 2021). Similar to previous work (Jones and Mackereth, 2016; Zorn et al., 2024), we found differences in the sizes and isotope ratios between brook trout captured in lake-accessible and lake-inaccessible stream reaches. Overall, coaster brook trout had greater lengths and were enriched in δ^{13}C, relative to brook trout located above impassable barriers. Prior research suggests that brook trout from Lake Superior and tributary stream habitats have different growth rates with Lake Superior captured fish having faster growth rates and achieving older ages (Robillard et al., 2011b).

Isotopic mixing and LDF models provided complementary approaches to test for prior foraging in Lake Superior by brook trout captured in lake-accessible stream reaches (Swanson et al., 2015). For both approaches, we found length an important predictor of the relative contribution of nearshore foraging and the probability of lake residency. The isotopic mixing model explicitly linked the fish's δ^{13}C and δ^{15}N ratios to stream and nearshore prey items. The LDF approach empirically fit a logistic model (Eq. (2)) to assign a fish's δ^{13}C value to Lake Superior or a tributary, doing it with high classification accuracy. Based on the mixing model estimates pooled across sites, the probability of feeding on nearshore prey in Lake Superior exceeded 50 % for brook trout greater than ~230 mm in total length (Fig. 4). These patterns varied by stream and were subject to both stream and individual variation (Table 4, Fig. 5). Similarly, for many streams (e.g., Cross, Caribou), the LDF often predicted increased probability of lake assignment with increased size, but this pattern was not universal.

Based upon our niche overlap and mixing model analyses, we found that brook trout caught in lake-accessible reaches had isotope signatures and sizes between those of fish from lake-inaccessible reaches and Lake Superior. Two plausible explanations exist for this. First, brook trout with Lake Superior access may regularly move between the stream and lake environment. Previous investigations have noted brook trout making repeated movements between lake and stream environments (Huckins and Baker, 2008; Kusnierz et al., 2009). Prior research suggests that resident salmonids move more than previously thought (Gowan et al., 1994). Moreover, the probability of movement between stream and lake environments may increase when the distance between the lake and an upstream barrier is small (Goldsworthy et al., 2017; Robillard et al., 2011a). Fisheries survey efforts indicated only 3 % of the total mainstem length in 29 rivers along the Minnesota North Shore was accessible to brook trout from Lake Superior (Goldsworthy et al., 2017). In addition, as fish increase in size they tend to be more mobile (McCann et al., 2005) allowing for greater habitat coupling (Vadeboncoeur et al., 2002). Increased movement may increase energy acquisition and growth. From an isotopic perspective this would lead to incorporation of both stream and lake derived carbon leading to an intermediate signature. Given the widespread phenotypic plasticity of brook trout this seems plausible (Huckins et al., 2008, Ridgeway, 2008).

Alternatively, the intermediate signature of brook trout in stream reaches with access to Lake Superior may reflect a subsidy effect from adfluvial migrants including suckers and introduced Pacific salmonids. Below-barrier reaches are often characterized by the presence of native suckers (Jones and Mackereth, 2016) and introduced salmonids (Gerig et al., 2018, Goldsworthy et al., 2017). Jones and Mackereth (2016) estimated that resident fish received between 25 and 58 % of their diet during the growing season from adfluvial sucker eggs in the Cypress River, a tributary emptying into eastern Lake Superior. Moreover, multiple studies have shown fish above barriers having lower δ^{13}C and δ^{15}N ratios than fish below barriers (Gerig et al., 2018; Robillard et al., 2011a,b; Jones and Mackereth, 2016) with fish occupying locations downstream of impassible barriers showing isotope ratios reflecting a mixed diet of adfluvial subsidies, primarily in the form of fish eggs and stream prey items.

Past studies have found that trout and charr isotopic turnover is dependent upon the isotope ratios of the diet item and growth rate of the individual (Vander Zanden et al., 2015) with fin clips turning over faster than muscle tissue (Heady and Moore, 2013). Both empirical (Xu et al., 2010) and modelling studies (Railsback and Rose, 1999) of trout suggest that growth accelerates in spring and slows during the summer due to increased metabolic costs (Hartman and Cox, 2008). Thus, despite sampling mostly during late September through November, it is plausible that the isotopic signature of brook trout captured in this study may still reflect consumption of adfluvial gametes (e.g. suckers, steelhead) from spring. Subsidy effects in the Great Lakes are context dependent with tributaries of Lake Superior exhibiting the strongest effect (Jones and McKenzie, 2024). Without either detailed movement data like Kusnierz et al. (2009) or Adams (2020), or microchemistry data (e.g., Daugherty et al., 2017), arbitrating between these competing hypotheses is difficult. However, given the widespread phenotypic variability observed in brook trout (Ridgeway, 2008), these explanations should not be viewed as mutually exclusive.

4.1. Management implications

Given the importance of protecting coaster brook trout to fishery managers and conservationists, knowledge of which streams still hold coasters (even if just one or a few fish) better equips managers and interest groups to target and justify actions to rehabilitate or restore remnant stocks. Our study provides an illustration of the broad geographic consistency of isotopic differences between brook trout that do or do not access Lake Superior and a LDF model to classify a stream captured brook trout as a coaster based on its length and isotopic signature. For example, data on total length and LDF-based estimate of probability of Lake Superior foraging of larger-bodied brook trout in this study suggested brook trout with an 80 % or higher likelihood of previously foraging in Lake Superior (and likely showing adfluvial migrations) occurred in 10 of 14 Minnesota rivers, 2 of 7 Michigan rivers and 0 of 1 Ontario rivers examined in this study (ESM Table S1).

Our findings support the use of this approach throughout the Lake Superior basin for identifying stream reaches likely supporting coaster brook trout for protection and rehabilitation efforts. As survey-based, non-lethal coaster brook trout identification techniques (e.g., genetics, stable isotopes, hard structure microchemistry) are refined and validated (and additional brook trout are sampled), future efforts should work to broadly apply them to screen for remnant individuals or populations of adfluvial brook trout in lake-accessible streams throughout the Lake Superior basin.

While brook trout in several rivers (e.g., Cross, Caribou) showed a pattern of increasing probability of Lake Superior assignment with fish length until a threshold length was achieved, in other rivers (e.g., Onion, Devil Track, Slate) even the smallest brook trout showed high probabilities of Lake Superior foraging (Fig. 6). This could relate to the proximity of individual fish to Lake Superior and associated movements of individuals into the lake for foraging, or increased access to Lake Superior based forage, or consumption of adfluvial gametes. If short lake-accessible stream reaches function as a continuum of coaster brook trout habitat rather than being distinct from Lake Superior (Huckins et al., 2008), fishery managers might consider extending Lake Superior's more protective brook trout sport fishing regulations to them rather than maintaining less protective inland stream regulations.

Management and research efforts to identify factors that favor a stream's production of coasters is complicated when river reaches where coaster brook trout originate differ from reaches where coasters are later observed. Brook trout in Minnesota waters of Lake Superior are largely sourced from individuals from stream-resident populations above barriers that swim over barrier waterfalls to below barrier stream habitats and Lake Superior (Mamoozadeh et al., 2023). Below barrier habitat in lake-accessible reaches of Minnesota coaster streams is often thermally unsuitable for year-round occupation or is frequently characterized by low quality spawning habitat and the presence of introduced salmonids (Mamoozadeh et al., 2023). In such cases, instream habitat characteristics of downstream lake-accessible reaches may seldom be associated with presence or density of adfluvial brook trout. These observations highlight the source-sink dynamics of coaster brook trout within an individual river and importance of above barrier populations of brook trout in maintaining populations of coaster brook trout along the Minnesota's North Shore (Mamoozadeh et al., 2023). Understanding sources of coaster production and factors influencing movement patterns is key to sustainable management of coaster brook trout populations.

4.2. Limitations and future research

Our findings suggest promise for using stable isotopes of fin clips as a non-lethal tool for inferring migrations of brook trout from Lake Superior into streams where they were captured in autumn, presumably before spawning. However, some aspects of the study limit our findings. A primary limitation and area for further research relates to our inability to distinguish foraging patterns associated with Lake Superior residency versus those due to in-stream foraging on adfluvial fishes and their offspring. Validation of isotope-based results for individual fishes against other methods (e.g., tagging studies, hard structure microchemistry) may provide insight on this. We are currently studying microchemistry of the maxilla bone as another potential non-lethal means for confirming Lake Superior to stream migrations. Comparison of results for individual brook trout between both approaches may prove insightful.

The LDF modeling approach provided a relatively simple, empirical means for estimating the likelihood of a stream captured brook trout's having recently foraged in Lake Superior. However, users should note that LDF modeled probabilities of Lake Superior usage were based on fish samples collected in an individual year and should not be used make definitive statements that coaster brook trout are not present because conditions that vary among years may periodically prevent fish movements between the tributary and Lake Superior. For example, a gravel bar at the river mouth of Kimball Creek during 2021 prevented any movement of brook trout between stream and Lake Superior habitats (Fig. 6), but the occurrence of the gravel bar varies among years and Kimball has been documented as a coaster producer (Mamoozadeh et al., 2023). Therefore, stable isotope-based results from an individual year, especially if they suggest migration does not occur, should not be considered representative of the permanent status of brook trout migration patterns for a river. This caution may apply to other isotope-based estimates of lake versus tributary use.

Our ability to make definitive conclusions about absence of adfluvial brook trout was limited by sample size in many systems. We analyzed all brook trout over 250 mm in length in lake-accessible streams, but in many streams there were relatively few fish of such size. While our findings highlight the overall utility of isotopic approaches, because of limited sampling and low densities of brook trout in many streams studied, our results for individual streams may be more definitive for confirming the presence of coaster brook trout in individual reaches than concluding adfluvial brook trout are absent. We attempted to provide good coverage of jurisdictions and habitat types, but our limited project budget resulted in fewer fin clip samples being analyzed than collected in some systems. Future efforts should seek to analyze these samples while collecting additional samples from brook trout in other water bodies.

Comprehensive isotopic characterization of basal resources in Lake Superior, lake-inaccessible and lake-accessible stream reaches was not possible due to project budget constraints. Understanding such differences for waters indirectly connected to Lake Superior may enable application of stable isotope approaches to identify coaster brook trout at additional locations. For example, the Pilgrim River hosts a partially migratory population of coaster brook trout (Adams, 2020; Zorn et al., 2024) but drains into Portage Lake and indirectly connects to Lake Superior via the Keweenaw Waterway. Our LDF identified none of the river's brook trout as likely coasters but isotopic characterization of the Keweenaw Waterway may have allowed for identification of coasters in the Pilgrim River and other streams draining into the Keweenaw waterway.

Uncertainties in mixing model results could have been addressed by more detailed baseline characterization of lake and stream primary consumers and a more diverse sample of potential prey including gametes of adfluvial migrants. Developing mixing-models which include adfluvial fish gametes may be useful in separating lake-based foraging from in-stream consumption of eggs (or other products) from adfluvial fishes. Evaluation of isotopic approaches from this study in other aquatic settings would aid in assessing their utility for documenting migrations of fish between habitats (e.g., inland lake and stream, ocean and tributary, etc.).

5. Conclusions

Our study represented the first attempt to use stable isotopes to characterize Lake Superior to stream movements of brook trout across multiple jurisdictions in the basin. We observed clear differences in δ^{13}C between brook trout captured from Lake Superior versus lake-inaccessible stream reaches. We developed a LDF (Eq. (2)) for predicting the probability of a brook trout's previously foraging in Lake Superior based on its δ^{13}C. This formula can be used to estimate probability of prior Lake Superior foraging for other stream captured brook trout when δ^{13}C data are available. Combining data on δ^{13}C, total length and individual stream of capture for each brook trout, the LDF enabled estimation of the proportion of "likely" coaster brook trout in lake-accessible stream reaches. Such an application of the LDF has utility for managers, providing insight on potential streams to target for coaster brook trout protection, conservation and rehabilitation. Adding δ^{15}N values to the aforementioned parameters for each brook trout enabled development of an isotope mixing model which provided insight on prey contribution percentages from stream and Lake Superior nearshore habitats to brook trout.

Given the importance of rehabilitating coaster brook trout to fishery managers and conservationists, knowledge of which streams still hold coasters (even if just one or a few fish) better equips managers and interest groups to target and justify actions to rehabilitate or restore remnant stocks. As survey-based, non-lethal coaster brook trout identification techniques (e.g., genetics, stable isotopes, hard structure microchemistry) are refined and validated, future efforts should work to broadly apply them to screen for remnant individuals or populations of migratory brook trout in lake-accessible streams throughout the Lake Superior basin (e.g., ESM Table S1).

CRediT authorship contribution statement

Troy G. Zorn: Writing – review & editing, Writing – original draft, Visualization, Validation, Supervision, Project administration, Methodology, Investigation, Funding acquisition, Formal analysis, Data curation, Conceptualization. **Kevin Pangle:** Writing – review & editing, Writing – original draft, Visualization, Validation, Project administration, Methodology, Investigation, Funding acquisition, Formal analysis, Data curation, Conceptualization, Supervision. **Nick Peterson:** Writing – review & editing, Writing – original draft, Supervision, Methodology, Investigation, Data curation. **Henry Quinlan:** Writing – review & editing, Writing – original draft, Supervision, Resources, Investigation, Funding acquisition. **Brandon Gerig:** Writing – review & editing, Writing – original draft, Visualization, Validation, Supervision, Project administration, Methodology, Investigation, Funding acquisition, Formal analysis, Data curation, Conceptualization.

Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

Acknowledgments

Funding was provided by the Environmental Protection Agency's Coordinated Science Monitoring Initiative (Grant number 00E02930), Michigan Department of Natural Resources Fish and Game Fund, Minnesota Department of Natural Resources Fish and Game Fund. Lake Superior Technical Committee and Great Lakes Fishery Commission collaborators led brook trout biosample collection, specifically: Ontario Ministry of Northern Development, Mines, Natural Resources and Forestry (F. Fischer, K. Stratton, A. Sarno, C. Lewis, D. Musko, J. Moore, Kok, P. Drombolis); Red Cliff Band of Lake Superior Chippewa (I. Harding); Grand Portage Bay Band of Lake Superior Chippewa (E.J. Isaacs); Wisconsin Department of Natural Resources (P. Piszczek); Minnesota Department of Natural Resources (N. Peterson, E. Torvinen); U. S. Fish and Wildlife Service (J. Schloesser, J. Mutchler. S. Schier) ; Michigan Department of Natural Resources (D. Traynor, L. Doerr, K. Rathbun), with assistance from Michigan Technological University (C. Adams, C. Huckins) on the Pilgrim River. L. Doerr performed data entry and biosample accession. A. Bartos prepared the map showing sampling locations. This manuscript was improved following reviews by several anonymous reviewers.

Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.jglr.2024.102487.

References

Adams, C.C., 2020. Life History Variation in Migratory Salmonid Populations (Doctoral dissertation). Michigan Technological University, Houghton.

Anderson, D.R., Burnham, K.P., 2002. Avoiding pitfalls when using information-theoretic methods. J. Wildl. Manage. 912–918.

Becker, G.C., 1983. Fishes of Wisconsin. University of Wisconsin Press, Madison, Wisconsin.

Boone, E.C., Brouder, M.J., Quinlan, H.R., 2021. Status and movement of adfluvial brook trout *Salvelinus fontinalis* at Isle Royale, Lake Superior. J. Great Lakes Res. 47, 1804–1813.

Daugherty, D.J., Pangle, K.L., Karel, W., Baker, F., Robertson, C.R., Buckmeier, D.L., Smith, N.G., Boyd, N., 2017. Population structure of alligator gar in a Gulf Coast river: insights from otolith microchemistry and genetic analyses. N. Am. J. Fish. Manag. 37, 337–348.

Gerig, B.S., Chaloner, D.T., Janetski, D.J., Moerke, A.H., Rediske, R.R., O'Keefe, J.P., de Alwis Pitts, D.A., Lamberti, G.A., 2018. Environmental context and contaminant biotransport by Pacific salmon interact to mediate the bioaccumulation of contaminants by stream-resident fish. J. Appl. Ecol. 55, 1846–1859.

Goldsworthy, C.A., Reeves, K.A, Blankenheim, J.E., Peterson, N.R., 2017. Fisheries management plan for the Minnesota waters of Lake Superior. Special Publication 181, Minnesota Department of Natural Resources, St. Paul, Minnesota.

Gowan, C., Young, M.K., Fausch, K.D., Riley, S.C., 1994. Restricted movement in resident stream salmonids: a paradigm lost? Can. J. Fish. Aquat. Sci. 51, 2626–2637.

Hanchin, P., Baker, E., Kovacs, C., Madison, G., Rook, B., Sitar, S., Zorn, T. 2024. Lake Superior Management Plan 2023–2033. Michigan Department of Natural Resources, Fisheries Report 38, Lansing.

Hartman, K.J., Cox, M.K., 2008. Refinement and testing of a brook trout bioenergetics model. Trans. Am. Fish. Soc. 137, 357–363.

Heady, W.N., Moore, J.W., 2013. Tissue turnover and stable isotope clocks to quantify resource shifts in anadromous rainbow trout. Oecologia 172, 21–34.

Hoffman, J.C., Sierszen, M.E., Cotter, A.M., 2015. Fish tissue lipid-C:N relationships for correcting δ^{13}C values and estimating lipid content in aquatic food-web studies. Rapid Commun. Mass Spectrom. 29, 2069–2077.

Huckins, C.J., Baker, E.A., Fausch, K.D., Leonard, J.B.K., 2008. Ecology and life history of coaster brook trout and potential bottlenecks in their rehabilitation. N. Am. J. Fish. Manag. 28, 1321–1342.

Huckins, C.J., Baker, E.A., 2008. Migrations and biological characteristics of adfluvial coaster brook trout in a south shore Lake Superior tributary. Trans. Am. Fish. Soc. 137, 1229–1243.

Hudy, M., Thieling, T.M., Gillespie, N., Smith, E.P., 2008. Distribution, status, and land use characteristics of subwatersheds within the native range of brook trout in the eastern United States. N. Am. J. Fish. Manag. 28, 1069–1085.

Jones, N.E., Mackereth, R.W., 2016. Resource subsidies from adfluvial fishes increase stream productivity. Freshw. Biol. 61, 991–1005.

Jones, N.E., McKenzie, M., 2024. Spatial patterns of resource subsidies in Great Lakes tributaries from migratory fishes. J. Great Lakes Res. 50 (1), 102272.

Kusnierz, P.C., Stimmell, S.P., Leonard, J.B.K., 2009. Movement and growth indicators in resident and adfluvial coaster brook trout (Salvelinus fontinalis) in the Hurricane River, Lake Superior, Michigan, USA. J. Great Lakes Res. 35, 385–391.

Mamoozadeh, N., Goldsworthy, C., Miller, L., Peterson, N., Meek, M., 2023. Sources of coaster brook trout (Salvelinus fontinalis) revealed by genomic analysis of brook trout populations along Minnesota's shoreline with Lake Superior. J. Great Lakes Res. 49, 901–917.

McCann, K.S., Rasmussen, J.B., Umbanhowar, J., 2005. The dynamics of spatially coupled food webs. Ecol. Lett. 8, 513–523.

McCarthy, I.D., Waldron, S., 2000. Identifying migratory *Salmo trutta* using carbon and nitrogen stable isotope ratios. Rapid Commun. Mass Spectrom. 14, 1325–1331.

McElreath, R., 2018. Statistical rethinking: A Bayesian course with examples in R and Stan. Chapman and Hall/CRC.

Miller, L.M., Schreiner, D.R., Blankenheim, J.E., Ward, M.C., Quinlan, H.R., Moore, S., 2016. Effects of restrictive harvest regulations on rehabilitation of coaster brook trout in Minnesota's portion of Lake Superior. J. Great Lakes Res. 42, 883–892.

Mucha, J.M., Mackereth, R.W., 2008. Habitat use and movement patterns of brook trout in Nipigon Bay, Lake Superior. Trans. Am. Fish. Soc. 137, 1203–1212.

Muhlfeld, C.C., Dauwalter, D.C., D'Angelo, V.S., Ferguson, A., Giersch, J.J., Impson, D., Koizumi, I., Kovach, R., McGinnity, P., Schöffmann, J., Vøllestad, L.A., 2019. Global status of trout and char: Conservation challenges in the twenty-first century. J. Lobón-Cerviá, J.L. Kershner, J.E. Williams, R.E. Gresswell (Eds.), Trout and char of the world. American Fisheries Society, Bethesda, 717–760.

Muir, A.M., Hansen, M.J., Bronte, C.R., Krueger, C.C., 2016. If Arctic charr Salvelinus alpinus is 'the most diverse vertebrate', what is the lake charr Salvelinus namaycush? Fish Fish 17, 1194–1207.

Newman, L.E., DuBois, R.B., Halpern, T.N., 2003. A brook trout rehabilitation plan for Lake Superior. Miscellaneous Publication 2003-03. Great Lakes Fishery Commission.

Pracheil, B.M., Hogan, J.D., Lyons, J., McIntyre, P.B., 2014. Using hard-part microchemistry to advance conservation and management of North American freshwater fishes. Fisheries 39, 451–465.

Quinlan, H.R., 2021. Status of brook trout rehabilitation in Lake Superior in 2017. In: The state of Lake Superior in 2017. *Edited by* M.P. Ebener and T.C. Pratt [online]. Available from http://www.glfc.org/pubs/SpecialPubs/Sp21_02.pdf [accessed 24 April 2021].

Quinn, T.P., 2021. Differential migration in Pacific salmon and trout: patterns and hypotheses. Anim. Migration 8 (1), 1–18. https://doi.org/10.1515/ami-2021-0001.

Railsback, S.F., Rose, K.A., 1999. Bioenergetics modeling of stream trout growth: temperature and food consumption effects. Trans. Am. Fish. Soc. 128, 241–256.

Ridgway, M.S., 2008. A roadmap for coasters: landscapes, life histories, and the conservation of brook trout. Trans. Am. Fish. Soc. 137, 1179–1191.

Rieman, B.E., Dunham, J.B., 2000. Metapopulations and salmonids: a synthesis of life history patterns and empirical observations. Ecol. Freshw. Fish 9 (1–2), 51–64. https://doi.org/10.1034/j.1600-0633.2000.90106.x.

Robillard, M.M., McLaughlin, R.L., Mackereth, R.W., 2011a. Diversity in habitat use and trophic ecology of brook trout in Lake Superior and tributary streams revealed through stable isotopes. Trans. Am. Fish. Soc. 140, 943–953.

Robillard, M.M., Casselman, J.M., Mclaughlin, R.L., Mackereth, R.W., 2011b. Alternative growth histories in populations of Lake Superior brook trout: critical support for partial migration. Biol. Cons. 144, 1931–1939.

Roosevelt, R.B., 1865. Superior Fishing—The Striped Bass, Trout, and Black Bass of the Northern States. G.W. Carleton, Minnesota Historical Society Press, St. Paul, Minnesota.

Schreiner, D.R., Cullis, K.I., Donofrio, M.C., Fischer, G.J., Hewitt, L., Mumford, K.G., Pratt, D.M., Quinlan, H.R., Scott, S.J., 2008. Management perspectives on coaster brook trout rehabilitation in the Lake Superior basin. N. Am. J. Fish Manag. 28, 1350–1364.

Scribner, K., Huckins, C., Baker, E., Kanefsky, J., 2012. Genetic relationships and gene flow between resident and migratory brook trout in the Salmon Trout River. J. Great Lakes Res. 38, 152–158.

Sierszen, M.E., Kelly, J.R., Corry, T.D., Scharold, J.V., Yurista, P.M., 2011. Benthic and pelagic contributions to Mysis nutrition across Lake Superior. Can. J. Fish. Aquat. Sci. 68, 1051–1106.

Stock, B.C., Jackson, A.L., Ward, E.J., Parnell, A.C., Phillips, D.L., Semmens, B.X., 2018. Analyzing mixing systems using a new generation of Bayesian tracer mixing models. PeerJ 6, e5096.

Swanson, H.K., Lysy, M., Power, M., Stasko, A.D., Johnson, J.D., Reist, J.D., 2015. A new probabilistic method for quantifying n-dimensional ecological niches and niche overlap. Ecology 96, 318–324.

Trueman, C.N., MacKenzie, K.M., Palmer, M.R., 2012. Identifying migrations in marine fishes through stable-isotope analysis. J. Fish Biol. 81, 826–847.

Vadeboncoeur, Y., Vander Zanden, M.J., Lodge, D.M., 2002. Putting the lake back together: reintegrating benthic pathways into lake food web models. Biosci. 52, 44.

Vander Zanden, M.J., Clayton, M.K., Moody, E.K., Solomon, C.T., Weidel, B.C., 2015. Stable isotope turnover and half-life in animal tissues: a literature synthesis. PloS One 10 (1), e0116182.

Xu, C., Letcher, B.H., Nislow, K.H., 2010. Context-specific influence of water temperature on brook trout growth rates in the field. Freshw. Biol. 55, 2253–2264.

Zorn, T.G., Cwalinski, T.A., Godby Jr., N.A., Gunderman, B.J., Tonello, M.A., 2018. Management Plan for Inland Trout in Michigan. Michigan Department of Natural Resources Fisheries Report 30, Lansing.

Zorn, T.G., Hessenauer, J., Wills, T.C., 2020. Increasing connectivity of Great Lakes tributaries: interspecific and intraspecific effects on resident brook trout and brown trout populations. Ecol. Freshw. Fish 29, 519–532.

Zorn, T.G., Rudh, B.C., Gerig, B.S., 2024. Use of stable isotopes to document lake to stream movements of brook charr *Salvelinus fontinalis*: a case study from southern Lake Superior. Ichthyol. Res. 71 (4), 529–539. https://doi.org/10.1007/s10228-024-00961-5.