



Spatially and temporally variable production pathways support the Lake Erie central basin food web

Joshua M. Tellier^{a,*}, Tomas O. Höök^{a,b}, Richard T. Kraus^c, Paris D. Collingsworth^{a,b}

^a Purdue University, Department of Forestry and Natural Resources, 715 W. State Street, West Lafayette, IN 47907, USA

^b Illinois-Indiana Sea Grant, 195 Marsteller Street, West Lafayette, IN 47907, USA

^c U.S. Geological Survey, Great Lakes Science Center, Lake Erie Biological Station, 6100 Columbus Avenue, Sandusky, OH 44870, USA

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ABSTRACT

In large freshwater systems, the dominant production pathways supporting food webs are often spatiotemporally variable. We used stable isotope analysis and analysis of covariance (ANCOVA) models to investigate spatial and interannual variation in the dominant production pathways supporting fish consumers within the central basin of Lake Erie. We examined C and N stable isotope ratios of zooplankton, benthic invertebrates, and four species of fish common to nearshore areas of the central basin (yellow perch, *Perca flavescens*; white perch, *Morone americana*; rainbow smelt, *Osmerus mordax*; and round goby, *Neogobius melanostomus*) using tissue samples collected in 2017 and 2019. $\delta^{13}\text{C}$ values varied by location consistent with expected baseline differences in nutrient loading (^{13}C was more enriched in the southern region) in two of six ANCOVA models. Furthermore, $\delta^{15}\text{N}$ values varied with individual fish size and by location in a manner consistent with spatial patterns of nutrient loading from surrounding agricultural landscapes (^{15}N was more enriched in the northern region) and a longitudinal gradient of eutrophication, decreasing from west to east. These patterns were not exhibited by all species and did not necessarily persist across years, suggesting that additional factors (e.g., regional diet differences, river plume dynamics) also contributed to observed $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ variation. We suggest that spatiotemporal variation of stable isotope ratios should be accounted for in studies of trophic basis of production and food web structure in Lake Erie.

Introduction

Food webs have traditionally been conceptualized as static in space and time. However, it is now widely recognized that food webs are dynamic and vary in response to phenomena such as changes in ambient environmental conditions (e.g., Schindler, 2001; Shimoda et al., 2011), species invasions (e.g., Pothoven and Madenjian, 2008; Strayer, 2010; Turschak et al., 2014), and anthropogenic modifications to habitat quality (e.g., Kalcounis-Rueppell et al., 2007; Potthoff et al., 2008). The Laurentian Great Lakes have extensively characterized food webs and a long historical record of alterations to food web structure (e.g., Blanke et al., 2018; Bunnell et al., 2014; Mills et al., 2003). The Great Lakes exhibit seasonal and inter-annual variability in food web dynamics concomitant with changes in resource availability (Hryciuk et al., 2018; Stewart et al., 2017; Zhang et al., 2012). Moreover, intraspecific spatial variation in resource utilization has been detected in several Great Lakes among lower trophic organisms (Camilleri and Ozersky, 2019; Heuvel

et al., 2023; Ives et al., 2013) and fishes (Foley et al., 2017; Happel et al., 2018; Happel et al., 2015a; Hryciuk et al., 2018; Senegal et al., 2021). Apparent spatial variation in resource utilization has been correlated with eutrophication (Camilleri and Ozersky, 2019), habitat heterogeneity (Sierszen et al., 2014), and niche availability (Ives et al., 2013), suggesting a connection between food web dynamics and external environmental factors.

Lake Erie, particularly its central basin, has strong potential for spatial and temporal variation in food web patterns and dominant energy pathways. Lake Erie has been substantially altered by human activities, including through excessive nutrient loading that has resulted in eutrophication and nearly annual hypoxia in offshore regions of the central basin (Kane et al., 2014; Scavia et al., 2014; Smith et al., 2015; Williams and King, 2020). However, land use, agricultural practices (e.g., fertilizer use), and prevailing climate differ between the northern and southern shorelines (Macrae et al., 2021), potentially producing spatial differences in the characteristics of nutrients available for biological

* Corresponding author.

E-mail address: TellierJ@michigan.gov (J.M. Tellier).

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uptake (Prater et al., 2017). Lake Erie contains three distinct basins that transition from eutrophic to mesotrophic, and gain increasing depth, along a west to east gradient. Eutrophication in Lake Erie is related to high riverine loading of nutrients from three large rivers that flow into the western basin (e.g., Maumee River, Sandusky River, and Detroit River). Discharge from these rivers results in large river plumes that generally flow from west to east along the lake, influencing the hydrological and ecological conditions of affected nearshore habitats, with the Detroit River strongly influencing the northern shore of the western and central basins and the Maumee and Sandusky Rivers influencing the southern shore (Jarrin et al., 2015; Jiang et al., 2015; Niu et al., 2018). Wind- and current-driven upwelling events also occur regularly in nearshore regions of Lake Erie (Valipour et al., 2019), particularly along the broad northern and southern coastlines within the central basin. These upwellings transport autochthonous offshore benthic organisms into nearshore regions, substantially altering water quality, primary production potential and dominant primary production sources in localized areas (Dunstall et al., 1990; Rowe et al., 2019). Upwellings in the central basin seemingly occur more frequently along the northern shoreline than the southern shoreline (Rowe et al., 2019). In total, there is evidence that spatiotemporal differences in both river input and wind-driven hydrological processes contribute to habitat heterogeneity (Jiang et al., 2015) and such factors may lead to differentially structured food webs.

Nutrient loading and lower trophic level taxonomic patterns often vary in space and time across freshwater systems. However, higher trophic level consumers may integrate such variation through diverse diets and broad movements and may thereby not reflect the spatio-temporal patterns of lower trophic levels (McMeans et al., 2016). Some fish undertake seasonal migrations in Lake Erie (e.g., walleye, *Sander vitreus*: Ruby et al., 2018; Wang et al., 2007) and may thereby integrate trophic variability, while others seemingly consistently feed more locally (e.g., round goby, *Neogobius melanostomus*: Ray and Corkum, 2001). To capture the diversity of foraging and habitat preferences found among the Lake Erie central basin fish fauna, four species were chosen for isotopic analysis. Rainbow smelt (*Osmerus mordax*) are introduced pelagic planktivores that experience seasonal conditions of sub-optimal habitat quality in central Lake Erie due to thermal stress and hypoxia (Arend et al., 2011). Central basin hypoxia has altered trophic interactions for rainbow smelt, limiting access to benthic resources and forcing increased reliance on zooplankton (Pothoven et al., 2012; Stone et al., 2020). Round goby are introduced obligate benthic generalists which have become a crucial component of the Lake Erie food web since their introduction into the system. Round gobies are now a critical forage species in the diets of many piscivorous fishes (Campbell et al., 2009; Johnson et al., 2005; Madenjian et al., 2011; Steinhart et al., 2004). Round goby is one of the few species within the lake that will principally feed upon dreissenid mussels (zebra and quagga mussels, *Dreissena polymorpha* and *D. rostriformis*), with measurable impacts on nutrient cycling and trophic energy transfer (Andraso et al., 2011; Barton et al., 2005; Bunnell et al., 2005). Yellow perch (*Perca flavescens*) are benthic-pelagic mesopredators that predate on a wide variety of organisms within Lake Erie and serve as a dominant component of the food web (Hryciuk et al., 2018; Parrish and Margraf, 1994; Roberts et al., 2009). White perch (*Morone americana*) are introduced pelagic generalists that overlap with yellow perch for similar prey (Schaeffer and Margraf, 1986) but display greater pelagic resource utilization (Parrish and Margraf, 1994).

Stable isotope analysis is a well-established approach for quantifying and comparing aquatic food web structure and function. Isotopic ratios of nitrogen are often used to estimate the relative trophic positioning of organisms within a food web. The lighter isotope of nitrogen (^{14}N) is preferentially eliminated by organisms during protein catabolism and excretion of nitrogenous waste, leading to a pattern of bioaccumulation of the heavier nitrogen isotope (^{15}N) at higher trophic levels. However, it should be noted that baseline values of $\delta^{15}\text{N}$ can vary among and

within systems based on the source of nitrogenous compounds entering the ecosystem (Cabana and Rasmussen, 1996; Richards et al., 2020), complicating any analysis of trophic structure across broad spatial scales and potentially over time. Isotopic ratios of carbon do not vary substantially along trophic gradients (Perkins et al., 2014; Post, 2002). Instead, differences in carbon sources at lower trophic levels are often conserved and remain evident in higher trophic level consumers (Doi et al., 2019; Finlay et al., 2002). $\delta^{13}\text{C}$ values generally indicate the source of organic compounds utilized by producers or the relative contribution of distinct production pathways to the diets of consumers (because distinct producers differentially incorporate C isotopes during photosynthesis). In aquatic systems, carbon isotopic ratios are often used to measure the relative contribution of various benthic and pelagic production pathways supporting the system. Dominant carbon sources supporting aquatic food webs can vary across broad spatial scales (i.e., 10 to 100 km; Arantes et al., 2019), and such differences may fluctuate over time, e.g., with seasonal patterns of riverine discharge and system productivity (Finlay, 2004; Gu et al., 2011; Hunt et al., 2012).

Together, isotopic ratios of carbon and nitrogen can help elucidate spatial and temporal differences in dominant production pathways supporting consumers. This is especially true of aquatic systems, wherein the individual species that make up the food web can be difficult to observe, and assessments of resource utilization are often bounded by a high degree of uncertainty. We employed stable isotope analysis to investigate the possibility of spatially and temporally distinct differences in dominant production pathways and food web dynamics within the Lake Erie central basin. Specifically, the primary objectives of the study were to evaluate intraspecific spatial differences of $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ among fishes of the Lake Erie central basin and secondly to evaluate if any such patterns were consistent across two study years.

Materials and methods

Sample collection

Fishes were collected from August to October during 2017 and 2019 within two broad regions of the central basin of Lake Erie: northern and southern (Fig. 1). The northern region covered an area from approximately 82.376° W and 41.787° N to 81.205° W and 42.530° N. The southern region covered an area from approximately 82.142° W and 41.548° N to 81.011° W and 42.082° N. The two regions are approximately parallel along the northern and southern shorelines of the central basin and are separated by the deeper offshore region that experiences seasonal benthic hypoxia. Moreover, these two regions represent potentially distinct hydrologic zones with unique water chemistry and nutrient loading patterns. Samples from within the southern region were collected by the U.S. Geological Survey (USGS) and Ohio Department of Natural Resources (ODNR). Samples from within the northern region were collected by the USGS and the Ontario Ministry of Natural Resources and Forestry (OMNRF). All fishes were collected using benthic trawls as part of long-term monitoring programs conducted by the respective agencies. Trawls were deployed and lowered to the lakebed for sampling in areas where the maximum depth of the lake ranged from 10 to 21 m. Exact specifications for tow duration, net size, trawl speed, and number of replicate samples per site varied slightly among agencies and full descriptions of trawling procedures can be found within the status reports associated with each monitoring effort (ODNR, 2019; OMNRF, 2019; USGS, 2018). Importantly, our aim was to collect organisms for analyses and not compare catch rates; thus, an adaptive sampling approach relying on slightly different sampling methods seemed appropriate. Invertebrate prey samples (benthic invertebrates and zooplankton) were collected during the 2019 season in the same regions previously described. Benthic invertebrates were collected using a 500 μm mesh PONAR grab sampler with an open-jaw area of 0.023 m^2 , and samples were rinsed and concentrated over a 500 μm mesh strainer. Zooplankton were collected by performing vertical daytime tows of the

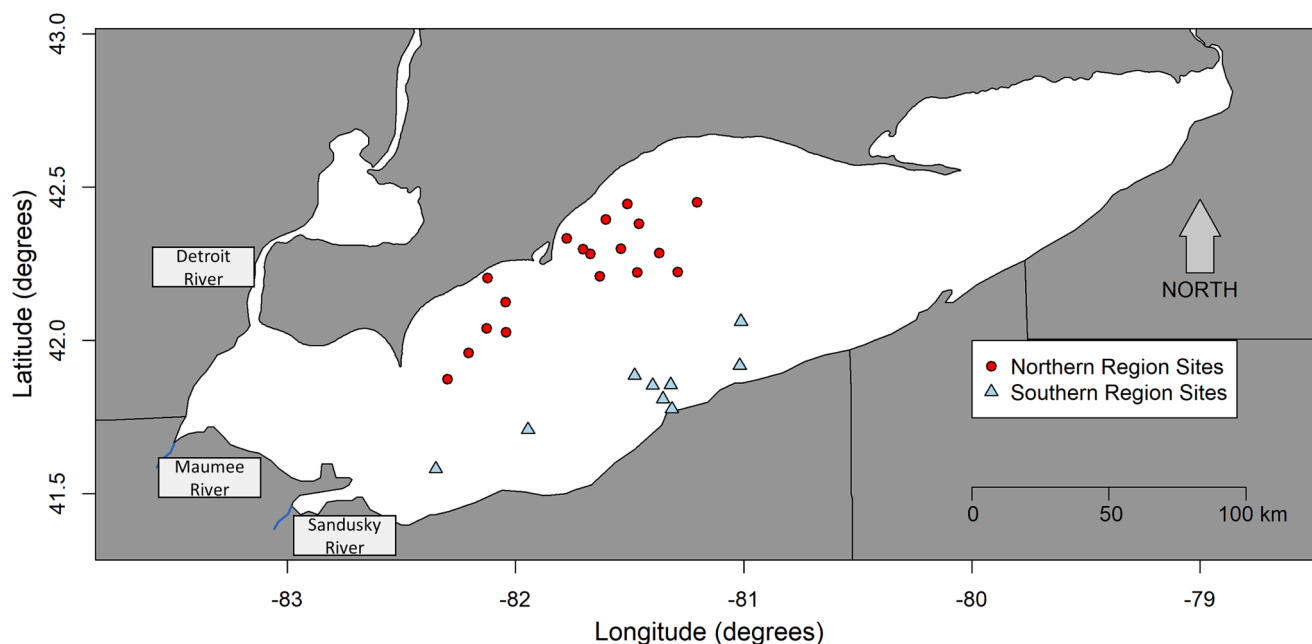


Fig. 1. Sampling locations from which fishes, zooplankton, and benthic invertebrates were collected as part of long-term monitoring programs. Red circles indicate sites that were considered within the northern region. Blue triangles indicate sites that were considered within the southern region. Sampling at northern sites was conducted by the Ontario Ministry of Natural Resources and Forestry and the U.S. Geological Survey. Sampling at southern sites was conducted by the Ohio Department of Natural Resources and the U.S. Geological Survey.

whole water column with a 150 μm , 0.3-m diameter zooplankton net. When performed during the same sampling excursion, PONAR grabs and zooplankton tows occurred before benthic trawls. All invertebrate samples were frozen immediately upon collection and transported to Purdue University (West Lafayette, Indiana) for later processing.

Sample processing

Samples were stored at $-20\text{ }^{\circ}\text{C}$ until thawed for processing. Zooplankton samples were separated into 1/8th sample fractions using a splitter, then fraction contents were identified to one of four major taxonomic groupings (calanoid copepods, cyclopoid copepods, herbivorous cladocerans, predatory cladocerans) and separated, according to standard protocol (EPA, 2003). Benthic invertebrates were hand-picked from PONAR grabs, identified, and separated to the lowest practical taxonomic grouping. Invertebrate field collections resulted in fewer viable organisms for analyses than anticipated. Therefore, to increase sample sizes, gut contents were removed from all fish samples and five zooplankton and ten benthic invertebrate samples were extracted from the diet contents of fishes and included in invertebrate sample processing.

For fishes, individual fish wet mass (to 0.1 mg) and total length (to 1 mm) were recorded prior to processing. Fish ≤ 120 mm total length were dried whole following the removal of the cranium, caudal fin, and gut contents, according to standard practice (e.g., Keough et al., 1996; O'Reilly et al., 2002). Fish > 120 mm total length had a section of dorsal white muscle tissue removed and dried for stable isotope analysis. Lower trophic samples were dried whole. In the case of small taxa (e.g., calanoid copepods), multiple individuals from the same sample (i.e., zooplankton tow or PONAR grab) were pooled to produce sufficient dry mass for analysis. All samples were dried at $40\text{ }^{\circ}\text{C}$ for at least 72 h.

Dry samples were ground into a fine homogenous powder. For each sample, ~ 1 mg of dry material was sealed into a 3.5×5 mm tin capsule. Individual tin capsules were placed into labeled 96-well plates and shipped to the Cornell University Stable Isotope Laboratory (COIL; Ithaca, New York) for isotopic analysis of values of $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ (measured using a Thermo Scientific Delta V Advantage Isotope Ratio

Mass Spectrometer (IRMS)). Percent carbon and nitrogen were measured by combustion analysis within an elemental analyzer (Carlo Erba NC2500). For quality control and measuring precision of sample values, COIL uses in-house standards that are routinely calibrated against the international reference materials provided by the International Atomic Energy Association (IAEA) for carbon (Vienna Pee Dee Belemnite, $\delta^{13}\text{C}_{\text{VPDB}}$) and nitrogen (atmospheric air, $\delta^{15}\text{N}_{\text{AIR}}$). The in-house standard used for animal samples ('Deer') was analyzed after every ten samples to ensure accuracy and precision, and to measure error. Our samples were measured over three separate runs between April and December of 2020. Among these three runs, the in-house standard indicated a sample standard deviation ranging from $\pm 0.07\text{--}0.11\text{ }_{\text{‰}}$ for $\delta^{13}\text{C}$ and $\pm 0.03\text{--}0.04\text{ }_{\text{‰}}$ for $\delta^{15}\text{N}$. Following raw isotopic analysis, preliminary isotope corrections were performed by COIL via a two-point normalization of all $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ data using two additional in-house standards ('KCRN' – corn, and 'CBT' – trout). Final delta values were calculated as:

$$\delta^{13}\text{C} = \left(\frac{^{13}\text{C}_{\text{sample}}}{^{12}\text{C}_{\text{sample}}} \right) \left(\frac{^{12}\text{C}_{\text{VPDB}}}{^{13}\text{C}_{\text{VPDB}}} \right) - 1 \quad \text{and} \quad \delta^{15}\text{N} = \left(\frac{^{15}\text{N}_{\text{sample}}}{^{14}\text{N}_{\text{sample}}} \right) \left(\frac{^{14}\text{N}_{\text{AIR}}}{^{15}\text{N}_{\text{AIR}}} \right) - 1$$

Ratios of carbon stable isotopes, especially those constituted from whole-body samples, are affected by the presence of lipids within tissues (Cloyd et al., 2020; Logan et al., 2008; Mateo et al., 2008). To account for lipid compositional effects, quantitative lipid correction is typically preferred over lipid extraction with chemical solvents when analyzing broad taxonomic groups because chemical extraction carries the risk of introducing bias to $\delta^{15}\text{N}$ values (Carabel et al., 2006; Murray et al., 2006). Post-hoc lipid corrections using mass-balance equations based on proportional carbon composition were conducted for the $\delta^{13}\text{C}$ values of all samples. Separate equations were used for fishes (Hoffman et al., 2015; Equations 2 and 5), zooplankton (Smyntek et al., 2007; Equations 1 and 2), and benthic invertebrates (Logan et al., 2008; Equation 1).

Data analysis

Sampling occurred over two separate years (2017 and 2019) with

potentially different physiochemical conditions and differences in species-specific sample sizes by year. Thus, data were initially separately analyzed by year, in part to evaluate if any observed patterns were temporally consistent. Isotopic values were initially visualized using $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ biplots. Chironomids (all collected in 2019) were the only lower trophic taxa with a large enough sample size to statistically compare isotopic ratios between regions. Welch's two-sample t-tests were conducted to test for significant difference between the northern and southern groups, both with and without the inclusion of individual chironomids retrieved and processed from stomach contents (see Electronic Supplementary Material (ESM) Figure S1).

To consider intraspecific spatial variation in fish stable isotope ratios, a series of analysis of covariance (ANCOVA) models were evaluated. Isotopic ratios of fishes often vary with individual size and ontogeny due to shifts in prey selection (e.g., Dixon et al., 2012; Heuvel et al., 2019; Johnson et al., 2004; Pennock et al., 2019). To account for such effects, first, the interquartile range rule was used to identify sample outliers for total length in each species and year dataset, so that only samples of comparable size ranges were included. Second, individual length was included as a covariate in ANCOVA models to compare isotopic ratios between the northern and southern regions. Longitude of sample collection site was also included as a covariate in the ANCOVA models to potentially capture any variation in stable isotope ratios along the east–west gradient of the central basin. Separate ANCOVA models to describe spatial variation in $\delta^{13}\text{C}$ or $\delta^{15}\text{N}$ were produced for each of the four study species (yellow perch, white perch, rainbow smelt, round goby) and for each year, i.e., 12 total ANCOVA models were produced (data were insufficient for yellow perch in 2019 and white perch in 2017). Region of origin (northern or southern), total length, longitude of collection site, and all two-way interactions were considered as explanatory variables. Non-significant ($\alpha = 0.05$) interaction terms were not included in the final models.

Sufficient sample numbers were collected for two of the four fish species (round goby and rainbow smelt) to consider interannual variation in isotopic ratios. To consider temporal variation, year-effects were evaluated using ANCOVA's similarly to those developed to examine spatial patterns. However, these ANCOVA's also included year of collection (either 2017 or 2019) as a potential explanatory variable. The models initially considered region, year, longitude, total length, and all 2-way interactive effects. Non-significant ($\alpha = 0.05$) interaction terms were not included in the final models. All graphical and statistical analyses were conducted in R Version 3.6.3 (R Core Team, 2020) using RStudio Version 1.1.456 (RStudio Team, 2016).

Results

Collection of isotopic samples

In total, isotopic ratios of carbon and nitrogen were measured for 310 individual fishes, 14 zooplankton samples (10 predatory cladocerans, specifically *Bythotrephes longimanus* and *Cercopagis pengoi*, and 4 calanoid copepods), and 43 benthic invertebrate samples (33 Chironomidae, three dreissenid soft tissue samples, five Oligochaeta, two Amphipoda) across both regions and years. Sample sizes were generally comparable between the northern and southern regions for all four fish species (Table 1). White perch and lower trophic samples were only collected in 2019 due to constraints related to sampling durations and equipment. In addition, insufficient numbers of yellow perch were collected in 2017 to allow for statistical comparisons between regions. Mean total lengths of all fishes (mm \pm SD) were 59.3 \pm 15.7, 48.6 \pm 11.3, 139.6 \pm 45.9, and 218.2 \pm 51.0 for rainbow smelt, round goby, yellow perch, and white perch, respectively.

Stable isotope patterns by taxonomic groups

Among benthic invertebrates, chironomids exhibited the most

Table 1

Mean $\delta^{13}\text{C}$ values (± 1 SD) for samples collected in 2017 and 2019 and submitted for isotopic analysis from spatially distinct regions of the Lake Erie central basin. Empty cells (represented by dashes) indicate no data were collected for that year for that group.

Species/ Functional Group	Northern Region (2017)	Northern Region (2019)	Southern Region (2017)	Southern Region (2019)
Rainbow smelt (<i>Osmerus mordax</i>)	-23.6 \pm 0.2 ‰ (n = 32)	-23.6 \pm 0.3 ‰ (n = 30)	-23.2 \pm 0.2 ‰ (n = 30)	-23.4 \pm 0.4 ‰ (n = 29)
Round goby (<i>Neogobius melanostomus</i>)	-23.2 \pm 0.3 ‰ (n = 30)	-24.0 \pm 0.5 ‰ (n = 30)	-23.5 \pm 0.4 ‰ (n = 31)	-23.4 \pm 0.3 ‰ (n = 30)
Yellow perch (<i>Perca flavescens</i>)	-23.0 \pm 0.4 ‰ (n = 15)	-23.1 \pm 0.4 ‰ (n = 6)	-23.2 \pm 0.2 ‰ (n = 15)	-22.3 \pm 0.6 ‰ (n = 3)
White perch (<i>Morone americana</i>)	-	-23.2 \pm 0.4 ‰ (n = 15)	-	-22.8 \pm 0.7 ‰ (n = 14)
Zooplankton	-	-25.8 \pm 0.9 ‰ (n = 4)	-	-25.3 \pm 0.8 ‰ (n = 10)
Benthic invertebrates	-	-23.3 \pm 1.0 ‰ (n = 31)	-	-23.3 \pm 0.7 ‰ (n = 12)

enriched $\delta^{13}\text{C}$ values (-23.2 ± 0.9 ‰, n = 33; mean ± 1 SD), followed by oligochaetes (-23.2 ± 0.62 ‰, n = 5), amphipods (-24.0 ± 0.8 ‰, n = 2), and dreissenids (-24.4 ± 1.2 ‰, n = 3). Among zooplankton, ^{13}C was enriched in predatory cladocerans (-25.0 ± 0.5 ‰, n = 10) relative to calanoid copepods (-26.5 ± 0.2 ‰, n = 4). Among fish species, white perch exhibited the most enriched $\delta^{13}\text{C}$ values (-23.0 ± 0.6 ‰, n = 29), followed by yellow perch (-23.1 ± 0.4 ‰, n = 39), rainbow smelt (-23.5 ± 0.3 ‰, n = 121), and round goby (-23.5 ± 0.5 ‰, n = 121) (Fig. 2). When accounting for slight ^{13}C enrichment with increasing trophic position (Vander Zanden et al. 1999; Post 2002), isotopic ratios of carbon from invertebrate samples matched the range of relative isotopic ratios of carbon reported for fish species. ^{13}C was depleted in zooplankton samples (-25.4 ± 0.8 ‰, n = 14) relative to benthic invertebrates (-23.3 ± 0.9 ‰, n = 43). Among benthic invertebrates, chironomids exhibited the most enriched $\delta^{15}\text{N}$ values ($+12.9 \pm 0.7$ ‰, n = 33), followed by amphipods ($+11.6 \pm 1.5$ ‰, n = 2), oligochaetes ($+10.9 \pm 0.6$ ‰, n = 5), and dreissenids ($+9.5 \pm 0.9$ ‰, n = 3) (Fig. 3). Among zooplankton, ^{15}N was enriched in predatory cladocerans ($+14.6 \pm 0.8$ ‰, n = 10) relative to calanoid copepods ($+11.6 \pm 1.5$ ‰, n = 4). Among fish species, rainbow smelt exhibited the most enriched $\delta^{15}\text{N}$ values ($+15.8 \pm 0.8$ ‰, n = 121), followed by white perch ($+15.3 \pm 0.6$ ‰, n = 29), yellow perch ($+15.3 \pm 0.6$ ‰, n = 39), and round goby ($+14.4 \pm 0.7$ ‰, n = 121). Most zooplankton and benthic invertebrate samples were depleted in ^{15}N relative to fishes, and mean $\delta^{15}\text{N}$ values among lower trophic organisms ($+12.7 \pm 1.5$ ‰, n = 57) were, on average, 2.5 ‰ lower than those reported for fishes ($+15.2 \pm 1.0$ ‰, n = 310). Small sample sizes precluded the spatial analysis of most lower trophic taxa beyond simple baseline context for fish species. Mean stable isotope values for each taxonomic group, further separated by year and region, are summarized in Tables 1 and 2.

Stable isotope spatial patterns

Values of $\delta^{13}\text{C}$ for chironomids collected during 2019 did not significantly differ between the northern and southern regions when individuals collected from fish stomach contents were included ($t_{25.4} = 0.874$, $p = 0.3902$, north mean = -23.1 ‰, south mean = -23.4 ‰), but did significantly differ when stomach content individuals were excluded ($t_{18.6} = 3.274$, $p < 0.01$, north mean = -22.5 ‰, south mean = -23.4 ‰) (Figure S1). Values of $\delta^{15}\text{N}$ for chironomids collected during 2019 did not significantly differ between the northern and southern regions whether stomach content individuals were included ($t_{11.7} = -0.376$, $p = 0.714$, $t = -0.376$, north mean = 12.8 ‰, south mean = 12.9 ‰) or

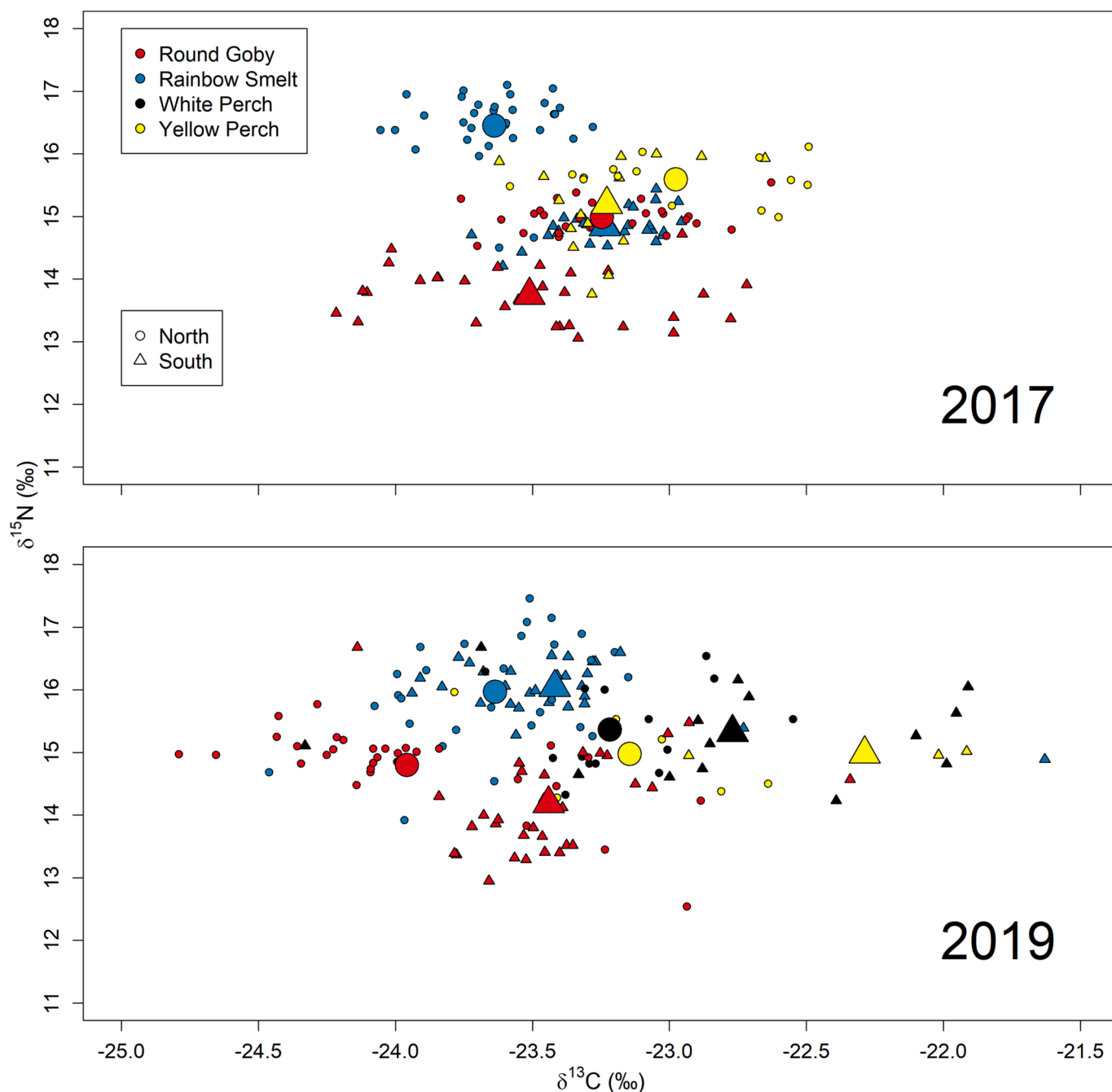


Fig. 2. Carbon-nitrogen biplot for round goby (*Neogobius melanostomus*), rainbow smelt (*Osmerus mordax*), white perch (*Morone americana*), and yellow perch (*Perca flavescens*) collected from spatially distinct regions of the central basin of Lake Erie during the summers of 2017 and 2019. Filled circles represent samples originating from the southern region. Filled triangles represent samples originating from the northern region. See Fig. 1 for locations of respective lake regions. Large shapes denote group means. (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

excluded ($t_{16,5} = -0.677, p = 0.508$, north mean = 12.7‰, south mean = 12.9‰) (Figure S1).

All six year-specific ANCOVA models significantly explained observed variation in fish $\delta^{13}\text{C}$ values (Fig. 4; ESM Table S1). The percentage variation explained varied from 10.3% (2019 rainbow smelt) to 49.6% (2017 rainbow smelt). Region of origin was a significant explanatory variable in two of the models (2017 rainbow smelt, 2019 round goby), and both of these models indicated that ^{13}C was significantly more enriched in the southern region relative to the northern region. Longitude was significant in two of the models (2017 and 2019 round goby), and both of these models indicated that ^{13}C became more depleted the further eastward that a goby was collected (ESM Figure S2).

Total length was a significant explanatory variable in two of the models (2019 rainbow smelt, 2017 yellow perch). The effect of total length on $\delta^{13}\text{C}$ was similar in both cases (<0.03 ‰ per mm). None of the final models for carbon contained any significant interaction terms among explanatory variables.

Five of six ANCOVA models significantly explained intraspecific $\delta^{15}\text{N}$ patterns, accounting for 17.7% (2019 round goby) to 86.2% (2017 rainbow smelt) of observed variation (Fig. 5; ESM Table S2). Of the five significant models, region of origin was a significant explanatory variable without any interactive effects in two of the models (2017 round goby and rainbow smelt), and both of these models indicated that ^{15}N was significantly more depleted for individuals in the southern region

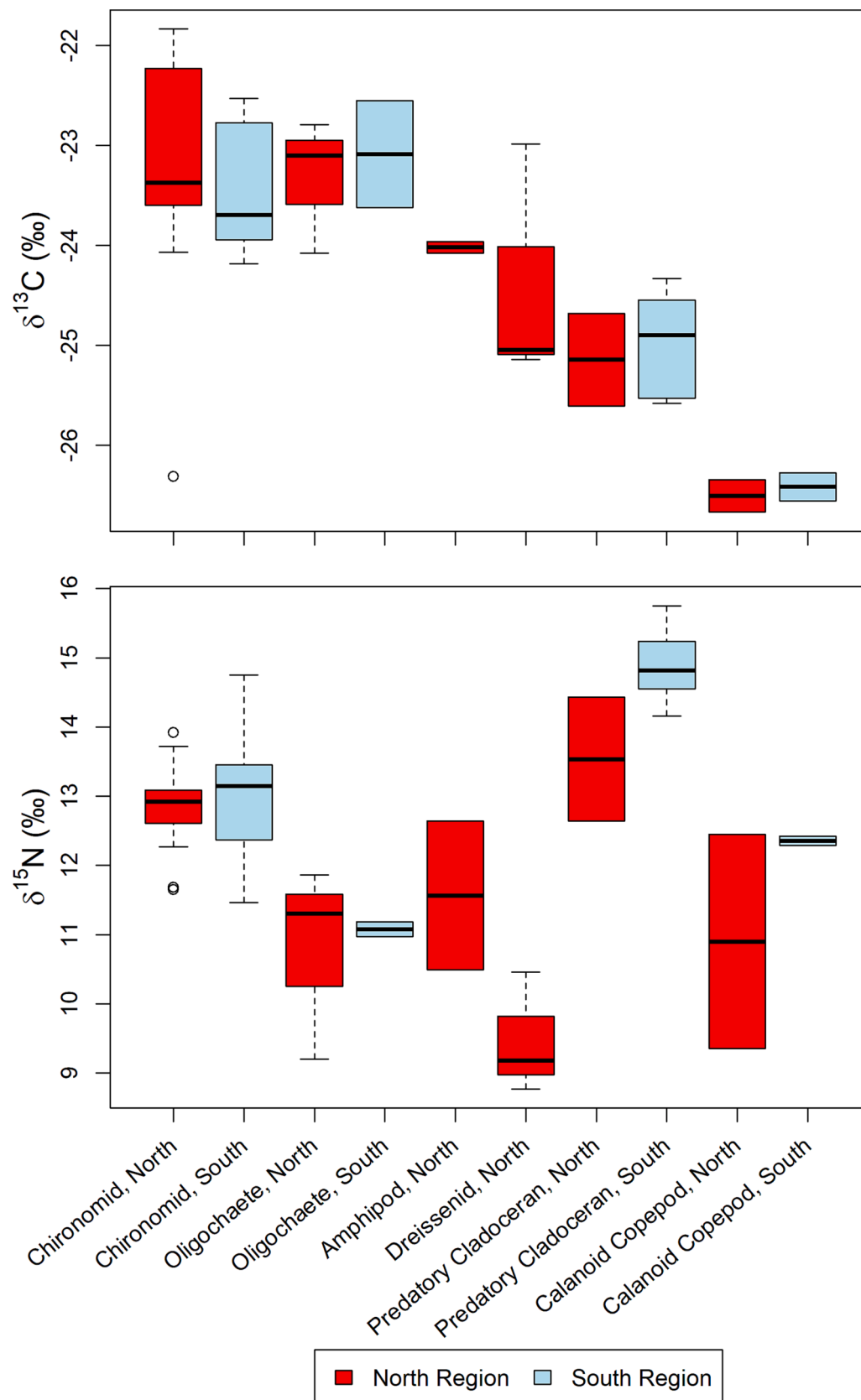


Fig. 3. Mean carbon and nitrogen stable isotope ratios for lower trophic (benthic invertebrate and zooplankton) samples collected in distinct regions of the Lake Erie central basin during the summer of 2019. Boxplot color indicates region of origin. See Fig. 1 for locations of respective lake regions. Note: All three dreissenid samples and both amphipod samples were collected in the northern region.

Table 2

Mean $\delta^{15}\text{N}$ values (± 1 SD) for samples collected in 2017 and 2019 and submitted for isotopic analysis from spatially distinct regions of the Lake Erie central basin. Empty cells (represented by dashes) indicate no data were collected for that year for that group.

Species/ Functional Group	Northern Region (2017)	Northern Region (2019)	Southern Region (2017)	Southern Region (2019)
Rainbow smelt (<i>Osmerus mordax</i>)	16.4 \pm 0.6 ‰ (n = 32)	16.0 \pm 0.8 ‰ (n = 30)	14.8 \pm 0.3 ‰ (n = 30)	16.0 \pm 0.4 ‰ (n = 29)
Round goby (<i>Neogobius melanostomus</i>)	15.0 \pm 0.2 ‰ (n = 30)	14.8 \pm 0.6 ‰ (n = 30)	13.7 \pm 0.4 ‰ (n = 31)	14.2 \pm 0.8 ‰ (n = 30)
Yellow perch (<i>Perca flavescens</i>)	15.6 \pm 0.3 ‰ (n = 15)	15.0 \pm 0.7 ‰ (n = 6)	15.2 \pm 0.7 ‰ (n = 15)	15.0 \pm 0.1 ‰ (n = 3)
White perch (<i>Morone americana</i>)	–	15.4 \pm 0.7 ‰ (n = 15)	–	15.3 \pm 0.7 ‰ (n = 14)
Zooplankton	–	12.2 \pm 2.1 ‰ (n = 4)	–	14.4 \pm 1.2 ‰ (n = 10)
Benthic invertebrates	–	12.2 \pm 1.3 ‰ (n = 31)	–	12.6 \pm 1.1 ‰ (n = 12)

relative to the northern region. Two models included a significant effect of region with interactive effects with longitude (2019 rainbow smelt) and total length (2019 white perch). Longitude was a significant explanatory variable in three of the models (2017 and 2019 rainbow smelt, 2019 white perch). However, the directionality of the effect of longitude was not consistent among species or years (ESM Figure S3). Total length was a significant explanatory variable in three of the models (2017 round goby, 2019 rainbow smelt, 2019 white perch). For 2017 round goby, ^{15}N became more depleted as total length increased. For 2019 rainbow smelt and white perch, ^{15}N became more enriched as total length increased. The interaction between region and longitude was a significant explanatory variable for 2019 rainbow smelt. The interactions between total length and longitude, and between total length and region, were significant explanatory variables for 2019 white perch.

Stable isotope temporal patterns

For rainbow smelt and round goby, additional models were developed to examine the potential effect of sampling year on carbon and nitrogen isotopic ratios. These models included the same explanatory variables as described above, with the addition of ‘year of collection’ as an explanatory variable. There was no significant effect of year on $\delta^{13}\text{C}$ values of round goby, but $\delta^{13}\text{C}$ values of rainbow smelt were significantly lower in 2019 than in 2017. There was no significant effect of year on $\delta^{15}\text{N}$ values of either species. Interestingly, the inclusion of year as a potential explanatory variable did not substantially increase the overall explanatory power of the ANCOVA models in comparison to the spatial-only models for the same species. Furthermore, the statistical significance of other explanatory variables in the $\delta^{13}\text{C}$ models changed with the addition of a year effect compared to the spatial-only models (ESM Table S3). Region was no longer a significant explanatory variable for $\delta^{13}\text{C}$ values of round goby, while it remained significant for rainbow smelt. Models explaining variation in $\delta^{15}\text{N}$ for both species remained similar to their spatial-only counterparts (ESM Table S4), perhaps indicating that ^{15}N concentrations in consumer tissues are less temporally variable than ^{13}C concentrations. None of the final models that included year retained any significant interaction terms.

Discussion

Isotopic ratios for three of the four study species (rainbow smelt, round goby, and white perch) varied spatially by region (i.e., northern versus southern) and longitude (i.e., an east–west gradient). These

observed patterns suggest that these consumers remain and feed in these regions for a sufficient period to develop distinct isotopic profiles, and do not appear to move and forage broadly enough to integrate trophic pathways throughout the central basin of Lake Erie. Analyses indicated that ^{13}C was more enriched in the southern region relative to the northern region for round goby in 2017 and rainbow smelt in 2019, and that ^{15}N was significantly more depleted in the southern region relative to the northern region for three of the six groups. Round goby and rainbow smelt both displayed particularly strong regional differences in $\delta^{15}\text{N}$ during 2017, but this pattern was not evident in 2019. $\delta^{13}\text{C}$ values of round goby varied by longitude in both 2017 and 2019, however the directionality of this relationship was not consistent across years. Finally, in both 2017 and 2019 rainbow smelt became more depleted in ^{15}N as longitude increased (i.e., traveling eastward). Importantly, differences in $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ between regions and variation across longitudes and individual lengths far exceeded the quantified within-sample measurement variation (SD ± 0.07 for $\delta^{13}\text{C}$; $\pm 0.03 - 0.04$ for $\delta^{15}\text{N}$) reported by the laboratory that processed isotopic tissue samples.

All fish species overlapped heavily in reported values of $\delta^{13}\text{C}$, which may indicate niche overlap for preferred prey. Prior studies have indicated diet and trophic overlap between juvenile yellow perch and round goby (Duncan et al., 2011), and yellow perch and white perch (Guzzo et al., 2013; Parrish and Margraf, 1990; Schaeffer and Margraf, 1986) that are consistent with our findings. Moreover, mean isotopic ratios of carbon for zooplankton (-25.86 ‰), benthic invertebrates (-23.26 ‰), dreissenids (-24.39 ‰), and among all fish species (-23.41 ‰) suggest that studied consumers may be deriving more of their energy from benthic, rather than pelagic, pathways within the central basin. Further research is needed to explore the potential importance of benthic versus pelagic production pathways among consumers in Lake Erie, given the small sample size of invertebrates assessed during the present study. Most fishes generally rely on planktonic resources during early life stages, though exotic species invasions and increased water clarity due to *Dreissena* filtration have increased the importance of benthic production for the Lake Erie food web (e.g., Johannsson et al., 2000; Johnson et al., 2005; Munawar et al., 2005). Dreissenids redirect sestonic material to benthic production pathways (Garton et al., 2005; Ozersky et al., 2012) and thereby may lead higher trophic organisms to rely more heavily on benthic resources (Rennie et al., 2013). Moreover, offshore hypoxia may force fishes within the central basin to rely more on nearshore benthic production, which would be more accessible to primarily pelagic species in shallower waters.

Total length was related to $\delta^{15}\text{N}$ variation for some species and years. Specifically, ^{15}N became more enriched as total length increased for rainbow smelt and white perch in 2019. Most species experience an enrichment in ^{15}N with length, commonly considered to reflect feeding at higher trophic levels as fish grow and transition among life stages. However, round goby collected in 2017 showed the opposite pattern, with ^{15}N becoming more depleted as total length increased. This is likely reflective of an increased reliance on dreissenid mussels as gobies increase in size. Gape limitations prohibit round goby from feeding on dreissenids (which are characteristically depleted in ^{15}N) at very small sizes, but adult gobies begin feeding on dreissenids once they are large enough to consume the shells of the entire organisms (Andraso et al., 2011). Thus, as observed in other studies, round goby may unusually decrease in trophic level as they increase in size (e.g., Miano et al., 2021).

Guzzo et al. (2011) found that nutrient loading and discharge from the Detroit and Maumee River plumes directly influences the isotopic ratios of fish populations in the northern and southern regions of the western basin of Lake Erie, with ^{13}C depleted and ^{15}N enriched in the Maumee River plume (southern) relative to the Detroit River plume (northern). In contrast, our analyses indicated that a) ^{15}N was depleted in the southern relative to the northern central basin for round goby and rainbow smelt during 2017 and b) ^{13}C was relatively enriched in the southern region for round goby in 2019 and rainbow smelt in 2017. This

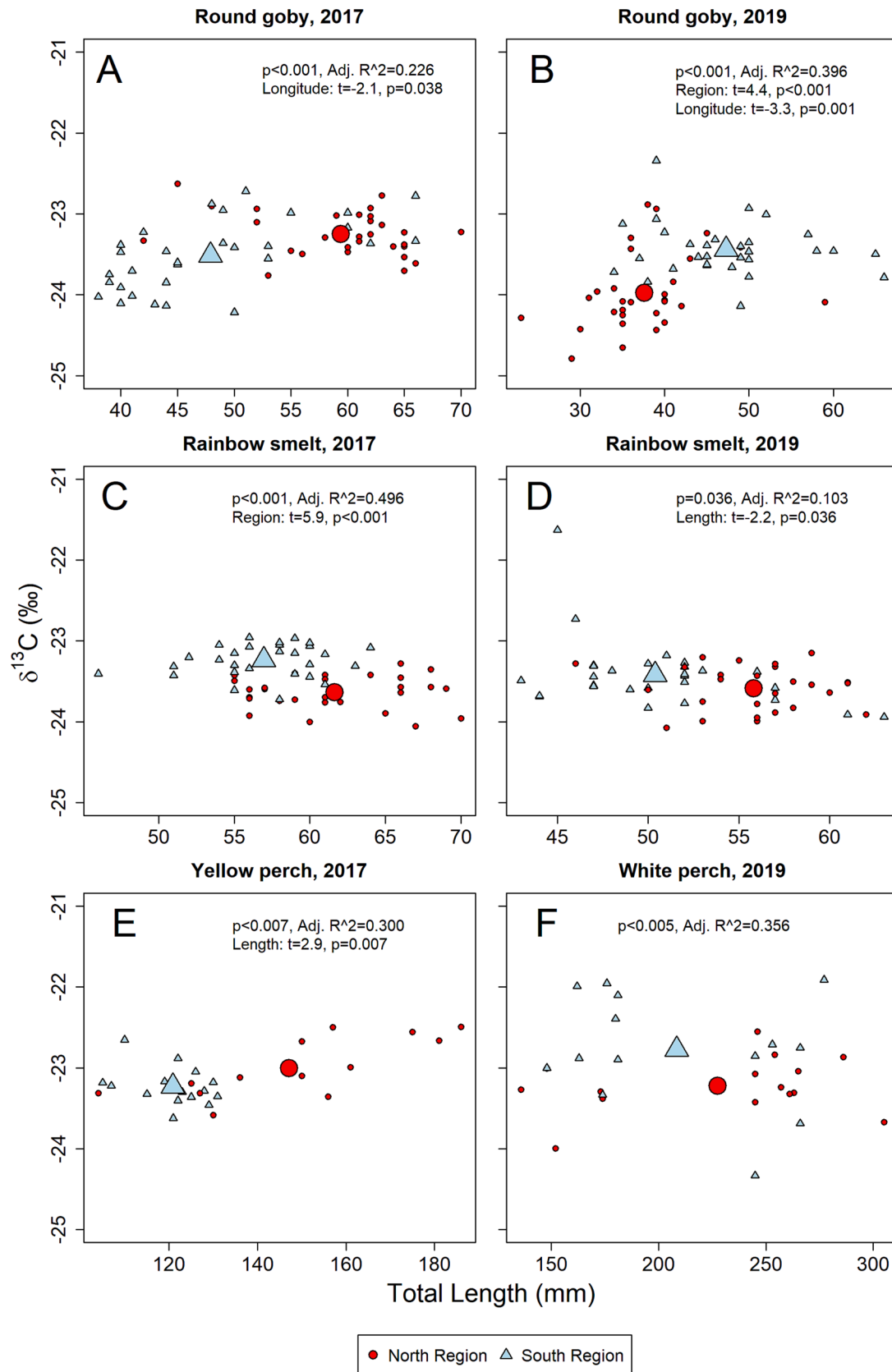


Fig. 4. $\delta^{13}\text{C}$ by total length for each of six groups that were subjected to analysis of covariance. Species included are round goby (*Neogobius melanostomus*), rainbow smelt (*Osmerus mordax*), white perch (*Morone americana*), and yellow perch (*Perca flavescens*). Red circles indicate samples from the northern region. Blue triangles indicate samples from the southern region. See Fig. 1 for locations of respective lake regions. Statistics displayed on each subplot describe overall model statistics (first line) and significant explanatory variables (any subsequent lines). Interaction term only included in final models if significant. Large symbols denote group means. (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

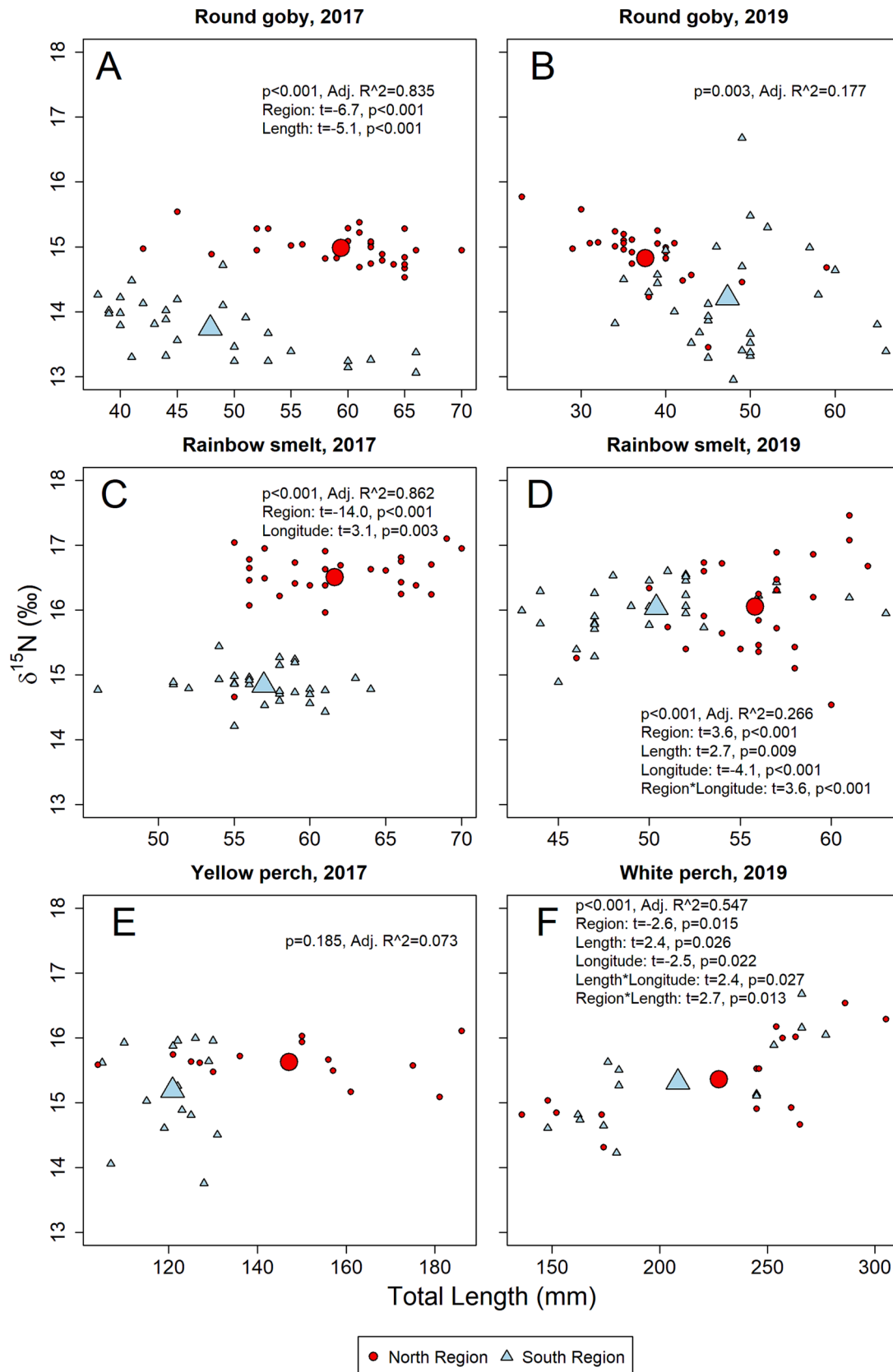


Fig. 5. $\delta^{15}\text{N}$ by total length for each of six groups that were subjected to analysis of covariance. Species included are round goby (*Neogobius melanostomus*), rainbow smelt (*Osmerus mordax*), white perch (*Morone americana*), and yellow perch (*Perca flavescens*). Red circles indicate samples from the northern region. Blue triangles indicate samples from the southern region. See Fig. 1 for locations of respective lake regions. Statistics displayed on each subplot describe overall model statistics (first line) and significant explanatory variables (any subsequent lines). Interaction term only included in final models if significant. Large symbols denote group means. (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

finding may indicate that the strong influence of the western basin river plumes on isotopic values of consumers may not extend into the central basin, or that river plume contributions are temporally variable and subject to rapid turnover. An inter-basin ridge separates the western basin from the central basin near Pelee Island (Holcombe et al., 1997), causing the river plumes to potentially mix before flowing eastward into the central basin and seemingly limiting congruent spatial isotopic patterns between basins. Furthermore, yellow perch and round goby exhibit regional diet preferences (Brush et al., 2012; Foley et al., 2017; Happel et al., 2015b) that may supersede or confound allochthonous drivers of isotopic variation.

Prior studies have found that land use and watershed characteristics may influence isotopic values of consumers. For example, natural fertilizer use (e.g., manure) in surrounding catchments decreases $\delta^{13}\text{C}$ and increases $\delta^{15}\text{N}$ relative to artificial chemical fertilizer use (Choi et al., 2017; Guiry, 2019). Widespread use of artificial fertilizers results in negative shifts in $\delta^{15}\text{N}$ because over-abundant dissolved inorganic nitrogen allows for greater discrimination against ^{15}N during assimilation by primary producers (Fogel and Cifuentes, 1993; Needoba et al., 2004). Our results align with these expectations given agricultural practices in the surrounding watersheds. ^{13}C was depleted and ^{15}N was elevated in the northern region (where manure is widely used as fertilizer on Canadian farms) relative to the southern region (where artificial fertilizer use is the dominant practice among US farms). The apparent differences between the US and Canada in nutrient supplementation for agricultural practices (Bertsos, 2017; Macrae et al., 2021) are detectable in the nitrogen isotopic ratios of aquatic organisms in Lake Erie. Furthermore, ^{15}N is often elevated in urban catchments or those with widespread industrial activity (e.g., Cole et al., 2006; Dillon and Chanton, 2008; Pierce et al., 2020). However, consumer ^{15}N was elevated in the northern region relative to the southern region despite the abundance of urban and industrial centers along the southern coastline of the central basin. It is possible that regional differences in resource utilization mask and overwhelm contributions of allochthonous urban nitrogen loading on consumer $\delta^{15}\text{N}$. Moreover, internal processes like anaerobic denitrification (common in benthic sediments during the hypoxic season) may confound isotopic patterns expected from baseline effects (Dähnke and Thamdrup, 2013).

Eutrophication is a widespread issue afflicting Lake Erie and is associated with elevated baseline levels of ^{15}N in aquatic systems (Camilleri and Ozersky, 2019; Wang et al., 2015; Zheng et al., 2019). Moreover, it has long been understood that a west to east trophic gradient exists in Lake Erie relative to the depths and nutrient loading experienced in each of the three distinct basins. Previously, the shallow western basin and central basin were both regarded as mesotrophic, while the deep eastern basin was oligotrophic (Dahl et al., 1995). However, with the present eutrophication issues afflicting the watershed (Scavia et al., 2014), the western basin is now regarded as eutrophic, the central basin on the verge of becoming eutrophic, while the eastern basin tenuously retains its oligotrophic status (e.g., Scofield et al., 2020). Longitudinal trends in rainbow smelt $\delta^{15}\text{N}$ during both 2017 and 2019 are consistent with the distinctive east–west trophic gradient that exists within the lake. Relative eutrophic intensity decreases from west to east, and smelt tissues experienced a significant decrease in $\delta^{15}\text{N}$ with increasing longitude, consistent with documented patterns relating system eutrophy status to isotopic ratios (Torres et al., 2012; Vander Zanden et al., 2005). However, longitudinal trends in fish $\delta^{13}\text{C}$ values were not as concordant with the established trophic gradient, despite evidence that lake productivity influences $\delta^{13}\text{C}$ of aquatic consumers (Gerdeaux and Perga, 2006). The lack of a consistent longitudinal pattern across both isotopes indicates that additional factors, beyond allochthonous input, likely also contribute to observed isotopic variation among the fish assemblage of Lake Erie. Heuvel et al. (2023) found that sestonic $\delta^{13}\text{C}$ varied temporally (i.e., monthly) in Lake Erie, potentially confounding expected spatial patterns of integration among consumers.

Recent studies have brought to light the importance of considering spatially explicit drivers of variation when drawing inference from the results of stable isotope analysis (Graham et al., 2010; Guiry, 2019; Kjeldgaard et al., 2021). Internal (i.e., microbial metabolism, regional prey abundance) and allochthonous factors (i.e., fertilizer use, excess nutrient input, urbanization, etc.) influence isotopic ratios by altering the relative availability and proportions of heavy and light isotopes in the ambient aquatic environment. These phenomena, in turn, set the baseline for the isotopic ratios that are assimilated by producers and consumers in a localized area. While several of our findings are generally consistent with known patterns of isotopic baseline variation, the present study did not assess isotopic ratios of primary consumers, so it is not possible to definitively determine whether the isotopic differences seen within the Lake Erie central basin are reflective of ambient baseline isotopic ratios being spatially conserved, or true spatial differences in resource utilization among consumers. Importantly, baselines are known to vary among (e.g., Belle et al., 2017; Cabana and Rasmussen, 1996) and within systems (e.g., Mbabazi et al., 2010; Smyntek et al., 2012; Syvaranta et al., 2006) at various spatial and temporal scales.

The present study reports the broad occurrence of spatiotemporal variation in isotopic signatures of consumers within the Lake Erie central basin. Such variation should ideally be accounted for in future isotope-based studies of Lake Erie's food web. The mechanisms contributing to spatiotemporal variation in isotope ratios were not explicitly evaluated but may be related to differential allochthonous inputs across regions or spatially distinct resource utilization among consumers. Given the complex chemistry of isotopic fractionation, more work is necessary to elucidate the drivers of this variation within and among species. Investigating the dynamic patterns of resource use present within aquatic food webs may help resource managers more accurately characterize aquatic food webs and predict the effects of internal and external drivers of isotopic variation.

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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.

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Appendix A. Supplementary data

Supplementary data to this article can be found online at <https://doi.org/10.1016/j.jglr.2023.07.006>.

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