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Accounting for Spatial Variation in Trophic Processes of Fishes in Large Lakes: An Ecoregion Approach

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ABSTRACT

1. For more than 50 years, Lake Ontario has experienced continuous ecological change. The causes and consequences of these changes are only partially understood. Existing monitoring and management programs collect lake-wide data and provide results and recommendations on perceived lake-wide processes, potentially overlooking regionally important dynamics.
2. We propose a framework that focuses on evaluating regional dynamics in food web structures by partitioning a large lake into six smaller ecological regions (i.e., ecoregions) based on multiple abiotic properties (bathymetry, thermal structure, tributary influence, trophic state, and anthropogenic influence). To evaluate this ecoregion approach, we investigated differences in trophic position ($\delta^{15}N$), carbon sources ($\delta^{13}C$), resource partitioning (isotopic niche size), and community metrics for round goby (*Neogobius melanostomus*), alewife (*Alosa pseudoharengus*), and lake trout (*Salvelinus namaycush*) in Lake Ontario sampled between 2009–2014 and 2018.
3. We observed that despite having different trophic roles and using different carbon pathways, the three species responded similarly to differences in bathymetry, nutrient levels, and thermal dynamics, resulting in greater variation among than within an ecoregion. Estimates of trophic position were low (3.2 ± 0.1) for round goby in ecoregions that had higher nutrient loading compared to those with lower (4.1 ± 0.2). While trophic position for alewife (3.1–3.7) and lake trout (4.4–5.2) followed similar patterns among ecoregions, indicating these species respond similar to abiotic variation within the lake. Macrohabitat use derived using $\delta^{13}C$ was either benthic ($\alpha < 0.70$) or pelagic ($\alpha > 0.30$) for all three species in ecoregions that had higher nutrient loading and less heterogeneous bathymetry. Fish from ecoregions with lower nutrient loading and more heterogeneous bathymetry used a mix of benthic and pelagic carbon sources, had higher trophic positions, and smaller isotopic niches that resulted in less trophic redundancy.
4. This study demonstrates that food webs in Lake Ontario operate in more discrete heterogenous spatial units (i.e., ecoregions) than as a single, large homogenous mixture. An ecoregion spatial framework, as our study developed and deploys, provides the specificity to support regional resource decision-making (i.e., watershed and fisheries) and reduces the biases created by a whole lake approach.

1 | Introduction

The Laurentian Great Lakes, *hereafter Great Lakes*, are the largest contiguous freshwater ecosystem in the world, influencing regional climates, supporting a USD$6 trillion regional economy including a USD$8 billion fishery, and providing extensive wildlife habitat and biodiversity conservation (Allan et al. 2013; Council of the Great Lakes Region 2017).

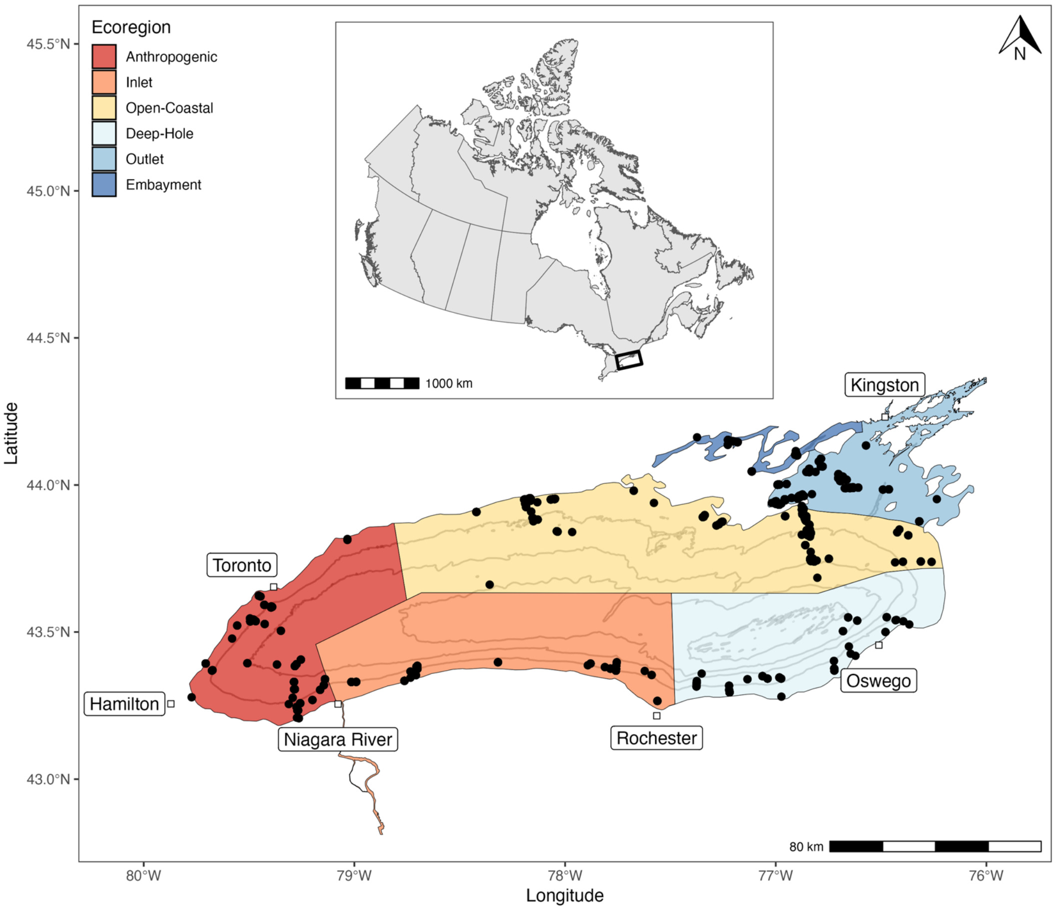
The lakes, however, are undergoing profound change related to a variety of existing and emerging threats (e.g., climate change, invasive species, nutrient loading, and habitat degradation) that are jeopardizing their stability and productivity (Lynch et al. 2010; Hecky and DePinto 2020; ECCC and US-EPA 2022). Efforts to track these changes and to report on progress toward remediation require an accurate description of the state of the lakes (Allan et al. 2013; ECCC and US-EPA 2022; Bowen et al. 2022). Current monitoring programs measure a myriad of physio-chemical and biological properties (e.g., Chlorophyll *a*, nutrient concentrations, fish abundance) that are designed to generate an understanding of whole lake (e.g., nutrient cycling, energy transfer, productivity) and component (e.g., fishery and water quality) health. These programs, however, are logistically complex and costly to implement, resulting in potentially limited data collection that can ultimately influence recommendations (Lynch et al. 2010, 2017, 2021; Carpenter et al. 2017). Therefore, tools and frameworks that can consistently and coherently report on the state of the Great Lake ecosystems and services they support are needed to objectively inform resource management planning.

Spatial variation in physical, chemical, and biological factors produces heterogeneity in underlying ecological processes (Bunnell et al. 2014; Ives et al. 2019). To better understand changes in ecosystem functionality to improve science, management, and conservation, we propose an approach to spatially partition large lakes into smaller ecological regions (i.e., ecoregions) based on multiple abiotic factors. Partitioning large, heterogenous landscapes into smaller units has been applied to terrestrial (Omernik 1995; Bailey 2014) and aquatic ecosystems (Oswood et al. 2000; Abell et al. 2008; Smith et al. 2018) to assist in developing and refining management strategies. Different spatial organizational frameworks have also been applied to Lake Ontario and other Great Lakes (Johnson et al. 2007; Riseng et al. 2018; Feiner et al. 2019; Ives et al. 2019) that broadly classify habitat types (e.g., nearshore vs. offshore) but do not consider the mechanisms that produce differences in ecosystem responses. Our proposed framework consists of six distinct ecoregions that differ in physico-chemical properties (bathymetry, thermal structure, tributary influence, water quality and clarity, trophic state, anthropogenic sources; Stewart and Robertson 1991; Rao et al. 2004; Makarewicz et al. 2012; Riseng et al. 2018; Turschak et al. 2019; Hill and Dove 2021) (Figure 1). Collectively, these properties (and others) can produce spatial differences in food web structure (e.g., energy source, trophic position, and niche dimensions) that form the basis of our ecoregion framework. Focusing on a single property, such as in- versus offshore dynamics, can provide insights on specific aspects of food webs (Sierszen et al. 2014) but can fail to capture the suite of complex processes influencing trophic dynamics, and thus limits the overall scope of observations and findings, especially in large lakes (Ives et al. 2019). Instead, recognition of persistent spatial features that represent different structural (e.g., biological communities, chemical concentrations) and relational (e.g., productivity, nutrient transfer) states, can inform sampling and reporting at appropriate scales reducing the likelihood that management and conservation outcomes are not compromised (Sterner et al. 2017). Thus, an ecoregional framework can capture prominent and influential properties of large heterogenous ecosystems and their responses to ongoing change.

Trophic dynamics refers to the network of interacting organisms and the transfer of energy among them that form the basis of a food web. Changes in trophic properties (e.g., trophic position, niche dimensions, carbon sources) can be associated with changes in structure and efficiency of a food web (Post 2002; Bearhop et al. 2004). Trophic dynamics integrate physiological, behavioural, and environmental responses of an organism. Evaluating trophic processes in higher level organisms such as fish, provides a more consolidated indicator of system processes than smaller, short-lived lower trophic level taxa more prone to short term and localized influences (Vander Zanden and Vadeboncoeur 2002). For example, recent work in Lake Superior has demonstrated regionally distinct resource use and trophic position among a number of fishes and cautioned against overgeneralising regional differences in energy flow (Wegher et al. 2024). Evaluating trophic processes at an ecoregional scale seeks to find balance between very intense (and expensive) lake wide sampling and spatially misaligned, discrete sampling that is meant to be interpreted as a representation of lake wide processes.

In freshwater ecosystems, values of δ^{13}C are used to describe macrohabitat use (e.g., benthic vs. pelagic) as the fixation of carbon by primary producers (e.g., phytoplankton) differs among these habitats with the ratio being relatively constant as trophic level increases (Rau 1978; France 1995). Conversely, values of δ^{15}N are not conserved by the consumer and increase through the food web allowing δ^{15}N to be used as a proxy for trophic position of a species or population (Post 2002). The isotopic niche represents the 2D distribution of δ^{13}C and δ^{15}N using the 95% ellipse and the area it covers (i.e., isotopic niche size) providing a metric for dietary niche (Bearhop et al. 2004; Jackson et al. 2011). Trophic position, carbon sources, and isotopic niches can be compared among species and/or within species among spatial units to evaluate similarities in trophic roles and macrohabitat use that can help describe aquatic ecosystems and the structure of their food webs (Jackson et al. 2011; Potapov et al. 2019). Differences among regional communities (e.g., ecoregions) can be compared using six metrics (i.e., Layman's metrics) that assess variability in carbon sources, trophic role diversity, and evenness in isotopic niches (Layman et al. 2007). These metrics are often used for a subset of species in an ecosystem and in the context of our study can provide additional information on whether spatially distinct regions trophically function as smaller interconnected ecosystems in large lakes.

Given the inherent problems of assessing food webs and trophic relationships for entire large lakes, we took an approach of quantifying the spatial variability in trophic position, carbon sources, isotopic niche sizes, and community metrics (e.g., trophic diversity) using a large, multiyear, δ^{13}C and δ^{15}N database (~2400 samples) for three fish species, round goby (*Neogobius melanostomus*), alewife (*Alosa pseudoharengus*), and lake trout (*Salvelinus namaycush*), among six ecoregions in Lake Ontario. We choose these three species because of their commonness among ecoregions, the frequency at which these species are collected and used in monitoring programs, and their different ecological roles reflecting benthic and pelagic near- and offshore processes that might vary among ecoregions. We hypothesized that ecoregion differences influence carbon sources, trophic position, isotopic niche sizes, and community metrics of fish species in a large lake. We had four predictions to support



Ecoregion Characteristics

	Anthropogenic	Inlet	Open-Coastal	Deep-Hole	Outlet	Embayment
Depth [mean (max); m]	79.3 (153)	122.9 (192)	71.2 (190)	125.8 (235)	20.6 (54)	15.0 (53)
Inflow[1]	~520 m^3/s/year	~7,500 m^3/s/year	~360 m^3/s/year	~240 m^3/s/year	~150 m^3/s/year	~315m^3/s/year
Trophic State[2]	Eutrophic	Mesotrophic	Mesotrophic	Mesotrophic	Eutrophic	Eutrophic
Nutrient Sources[3,4]	~ 650 mT P/ year	~5,700 mT P/ year	~30 mT P/ year	~ 330 mT P/ year	~ 135 mT P/ year	~ 360 mT P/ year
Thermal Dynamics[5,6]	Prone to upwelling events	Warmer water from Lake Erie	Stable water temperatures	Extensive hypolimnion	Variable temperatures	Warmer water from tributaries
Other	Higher industrial and municipal load	Nutrients from Lake Erie	Least disturbed ecoregion	Deepest region	Integrates all other ecoregions	Agricultural watershed
Expected Trophic Response	Lower trophic positions	Higher littoral carbon	Higher trophic diversity	Higher trophic position	Lower trophic diversity	Larger isotopic niches

FIGURE 1 | Lake Ontario segregated into six spatially unique ecoregions based on five criteria: Depth, inflow ([1]HYDAT—Canadian National Water Data Archive and USGS—National Water Information System), trophic state ([2]Riseng et al. 2018), nutrient source ([3,4]Makarewicz et al. 2012; Hill and Dove 2021), and thermal structure ([5,6]Stewart and Robertson 1991; Rao et al. 2004). The inset map is Canada with the square box representing the location of Lake Ontario. Black points represent the location that samples were collected for stable isotopes for three species, round goby (*Neogobius melanostomus*), alewife (*Alosa pseudoharengus*), and lake trout (*Salvelinus namaycush*) and two baselines (pelagic—dreissenids; benthic—chironomids, amphipods, and oligochaetes). Depth contours are every 50 m ranging from 0 to 250 m.

our hypothesis: (1) ecoregions with less nutrient loading (i.e., phosphorus [P] and nitrogen [N]) and heterogenous bathymetry will support more diverse carbon sources (Cole et al. 2006; Sierszen et al. 2014); (2) trophic position for all species will be lower in habitat disturbed ecoregions than less disturbed ecoregions caused by a simplification of the food web (Cabana and Rasmussen 1996; O'Gorman et al. 2012); (3) niche sizes will be smaller in ecoregions with less nutrient loading (i.e., P and N) and stable thermal dynamics due to the ability of the ecoregion to support specialization (Magnuson et al. 1979; Faillace et al. 2021; Merz et al. 2023); and (4) ecoregions with higher nutrient loading will have lower trophic diversity as increased nutrient loads often cause species to have similar trophic roles (O'Gorman et al. 2012; Alp and Cucherousset 2022). This approach and hypotheses centered on evaluating trophic processes using an ecoregion framework in Lake Ontario to provide ecologists, resource managers, and decision-makers improved knowledge of regionally specific patterns in food webs and how they differ based on distinct properties (e.g., bathymetry, nutrient load, and thermal dynamics) of the ecosystem.

2 | Methods

2.1 | Sample Collection

The tissue database represented 41 fish species sampled from Lake Ontario between 2008 and 2022. Supplementary data (available at 10.5281/zenodo.14051351) describes trends in the entire database, but this analysis focuses on skinless, boneless dorsal white muscle samples collected from three fish species, round goby, alewife, and lake trout from multiple locations in each ecoregion in Lake Ontario (Figure 1; Table 1) for each of the following years 2009–2014, and 2018. Samples were obtained using gillnets and bottom trawls described in OMNRF (2023) and Weidel et al. (2023). Bottom-set (19- to 152-mm monofilament mesh) or vertical (surface to 30 m depth, 19- to 39-mm monofilament mesh) gillnets were set along contours between 7.5 and 140 m. The bottom trawls (12–14 m head rope, all with 13 mm cod end liner) varied by location and included Western, Yankee, and 3n1 designs.

Dreissenid mussels were used as the pelagic baseline because they filter feed plankton (Uzarski et al. 2024; Heuvel et al. 2024) and a combination of chironomids, amphipods, and oligochaetes as the benthic baseline. Taxa for both baseline sources were sampled throughout each ecoregion in 2009, 2010, 2012, 2013, and 2018 using ponars and bottom trawls (OMNRF 2023; Weidel et al. 2023).

2.2 | Stable Isotope Analysis

Freeze-dried muscle samples (~2 g) were ground into a fine powder using a mortar and pestle or surgical scissors. Bulk (non-lipid extracted) powdered muscle samples were weighed into 5 mm × 9 mm tin capsules on a microbalance with masses between 400 and 600 μg. Muscle samples collected from higher trophic level species (i.e., piscivores) were lipid extracted using the chloroform/methanol lipid extraction method (Bligh and Dyer 1959). Carbon in lipids are isotopically lighter than in muscle tissue, thus lipid extraction or isotopic correction using C:N ratios is required before comparing $\delta^{13}C$ of individuals and/or species (DeNiro and Epstein 1977; Focken and Becker 1998; Post et al. 2007). Samples that were not lipid extracted and had C:N ratios ≥ 3.4 (i.e., salmonids) had $\delta^{15}N$ values corrected using lipid normalization models (Larocque et al. 2021), while $\delta^{13}C$ values were mathematically corrected using equations and values found in McConnaughey and McRoy (1979) and Hoffman et al. (2015). Lipid extraction was not performed on species that had low C:N ratios (≤ 3.4) (Post 2002). Combustion of the muscle sample into N_2 and CO_2 gases was done using an elemental analyzer (Costech, Valencia, CA, USA), and a Thermo Finnigan Delta V mass spectrometer (Thermo Finnigan, San Jose, CA, USA) to measure the relative abundances of carbon ($^{13}C/^{12}C$) and nitrogen ($^{15}N/^{14}N$) within each sample. Standard delta notation (δ) was used to express stable carbon ($\delta^{13}C$) and nitrogen ($\delta^{15}N$) isotope ratios in parts per thousand (‰) differences from a standard reference material as the following equation:

$$\delta^{13}\mathrm{C} \text{ or } \delta^{15}\mathrm{N} = \left(\frac{R_{\text{sample}}}{R_{\text{standard}}} - 1\right) \times 1000$$

where $R = {}^{13}C/{}^{12}C$ or ${}^{15}N/{}^{14}N$, respectively (Fry 1991; Hobson and Clark 1992). Instrument accuracy during the period of sample analysis was based on NIST standards (NIST 8573, NIST 8547, and NIST 8574 for $\delta^{15}N$ and NIST 8543, NIST 8573, NIST 8574 for $\delta^{13}C$; $n = 50$ for all). The mean difference from the certified values was −0.02‰, 0.10‰, and −0.20‰ for $\delta^{15}N$ and 0.20‰, −0.16‰, and −0.06‰ for $\delta^{13}C$, respectively. Precision of $\delta^{13}C$ and $\delta^{15}N$ was determined by running a set of four lab standards (bovine liver (NIST 1577c), internal lab tilapia muscle, USGS 40, and Urea IVA 33802174) every 16 samples and measured ≤0.20‰ for $\delta^{13}C$ and ≤0.18‰ for $\delta^{15}N$ for all standards. Accuracy, based on certified values of USGS 40 ($n = 50$ for $\delta^{13}C$, $n = 50$ for $\delta^{15}N$), analysed throughout runs and not used to normalize samples showed a difference of 0.16‰ for $\delta^{13}C$ and 0.03‰ for $\delta^{15}N$ from the certified value.

2.3 | Data and Statistical Analysis

Data cleaning, visualization, mapping, and statistical analyses were conducted in R v4.4.0. Data are reported as the mean ± the standard error of the mean (SEM), with $p > 0.05$ indicating statistical significance for all statistical tests. For posterior distributions, the median ± the 95% equal-tailed intervals (ETI) are reported. We set a minimum sample size of 10 for each species in each ecoregion.

To compare carbon sources of round goby, alewife, and lake trout among ecoregions, we first calculated α by using the following equation from Post (2002):

$$\alpha = \frac{\left(\delta^{13}\mathrm{C}_c - \delta^{13}\mathrm{C}_p\right)}{\left(\delta^{13}\mathrm{C}_b - \delta^{13}\mathrm{C}_p\right)}$$

where $\delta^{13}C_c$ is the carbon isotope for the consumer, in this case $\delta^{13}C_c$ is from round goby, alewife, and lake trout, $\delta^{13}C_b$ is the ecoregion-specific mean $\delta^{13}C$ of benthic baselines described above, and $^{13}C_p$ is the ecoregion-specific mean $\delta^{13}C$ for dreissenid (Post 2002). The ecoregion-specific mean of $\delta^{13}C_p$ was calculated by retaining samples collected between 5 and 80 m and the 10th and 90th percentile because values are known to vary with depth (Pettitt-Wade et al. 2018; Uzarski et al. 2024). Values of α that are closer to 0 indicate greater reliance on pelagic resources and values closer to 1 indicate greater reliance on benthic resources. Heuvel et al. (2024) developed a method to constrain values between 0 and 1, as values can fall outside these limits if all basal resources have not been sampled. Corrected α (α_r) can be calculated using the following equation.

$$\alpha_r = \frac{\left(\alpha - \alpha_{\min}\right)}{\left(\alpha_{\max} - \alpha_{\min}\right)}$$

where α derived from above, $\alpha_{\min}$ is the minimum α value for that group, and $\alpha_{\max}$ is the maximum value for that group. To estimate α_r we used a Bayesian framework that used an uninformed beta distribution as a prior for $\alpha_{r.}$ Our Bayesian model used two chains in parallel with burn-in set to 1000 samples, adaptive iterations set to 5000 samples, the number of posterior samples set to 4000 with a thinning of 1 to result in 8000 posterior samples. The model was created using package {trps} and {brms} (Bürkner 2017; Hlina 2025). This model used posterior estimates of α_r to estimate trophic position for round goby, alewife, and lake trout, using the following a two-source trophic position model based on the following equation (Post 2002):

$$\mathrm{TP} = \left[\left(\lambda_b \times \alpha_r\right) + \left(\lambda_p \times \left(1 - \alpha_r\right)\right)\right] + \frac{\delta^{15}\mathrm{N}_c - \left[\left(\delta^{15}\mathrm{N}_b \times \alpha_r\right) + \left(\delta^{15}\mathrm{N}_p \times \left(1 - \alpha_r\right)\right)\right]}{\Delta_{\mathrm{N}}}$$

TABLE 1 | Values of sample size, length, weight, δ^{13}C, δ^{15}N (mean ± 1 SEM) median α_r and trophic position (±ETI) for three fish species and two baseline species in Lake Ontario collected between 2008 and 2018.

Common name	Ecoregion	n	Length (mm)	Weight (g)	δ^{13}C (‰)	δ^{15}N (‰)	α_r	Trophic position
Round Goby	Anthropogenic	67	107 ± 2 (80–141)	21 ± 1 (2–55)	−22.3 ± 0.2	14.2 ± 0.2	0.41 ± 0.05	3.8 ± 0.2
	Inlet	31	105 ± 4 (80–150)	17 ± 2 (6–44)	−22.2 ± 0.2	14.0 ± 0.2	0.30 ± 0.09	4.2 ± 0.8
	Open-Coastal	177	119 ± 2 (80–190)	28 ± 1 (6–104)	−21.2 ± 0.1	12.8 ± 0.1	0.52 ± 0.04	3.3 ± 0.1
	Deep-Hole	21	101 ± 3 (81–130)	17 ± 2 (7–35)	−23.0 ± 0.2	15.5 ± 0.2	0.24 ± 0.11	4.1 ± 0.2
	Outlet	192	97 ± 1 (80–182)	15 ± 1 (6–106)	−20.3 ± 0.1	12.5 ± 0.1	0.45 ± 0.04	3.2 ± 0.1
	Embayment	31	101 ± 2 (81–126)	15 ± 1 (8–29)	−24.3 ± 0.4	11.1 ± 0.1	0.46 ± 0.12	3.2 ± 0.2
Alewife	Anthropogenic	219	158 ± 2 (110–203)	32 ± 1 (6–60)	−23.4 ± 0.0	12.4 ± 0.1	0.44 ± 0.01	3.3 ± 0.2
	Inlet	88	150 ± 2 (114–191)	30 ± 1 (11–60)	−23.1 ± 0.1	12.5 ± 0.1	0.64 ± 0.04	3.8 ± 0.6
	Open-Coastal	381	164 ± 1 (110–204)	33 ± 1 (1–61)	−23.2 ± 0.0	12.9 ± 0.1	0.55 ± 0.01	3.4 ± 0.1
	Deep-Hole	53	153 ± 3 (114–196)	30 ± 1 (12–60)	−23.3 ± 0.1	12.4 ± 0.1	0.74 ± 0.05	3.2 ± 0.2
	Outlet	237	159 ± 1 (110–197)	31 ± 1 (10–58)	−23.0 ± 0.1	12.7 ± 0.1	0.27 ± 0.02	3.4 ± 0.1
	Embayment	87	166 ± 1 (130–194)	36 ± 1 (18–62)	−23.5 ± 0.3	12.2 ± 0.1	0.51 ± 0.06	3.5 ± 0.2
Lake Trout	Anthropogenic	87	569 ± 15 (311–895)	2736 ± 197 (243–8840)	−21.9 ± 0.1	17.6 ± 0.1	0.45 ± 0.05	4.8 ± 0.3
	Inlet	75	626 ± 18 (346–886)	3257 ± 240 (387–7675)	−22.2 ± 0.1	17.4 ± 0.1	0.56 ± 0.06	5.4 ± 1.0
	Open-Coastal	309	680 ± 5 (327–925)	3905 ± 88 (308–9516)	−21.9 ± 0.0	17.6 ± 0.0	0.32 ± 0.01	4.8 ± 0.2
	Deep-Hole	87	694 ± 10 (336–848)	4089 ± 175 (339–7501)	−22.4 ± 0.1	17.4 ± 0.1	0.24 ± 0.03	4.7 ± 0.2
	Outlet	221	641 ± 8 (302–843)	3212 ± 109 (234–6825)	−22.0 ± 0.0	17.2 ± 0.0	0.44 ± 0.02	4.6 ± 0.2
	Embayment	30	515 ± 35 (350–934)	1904 ± 463 (308–8880)	−22.3 ± 0.1	16.8 ± 0.1	0.57 ± 0.09	4.9 ± 0.3
Dreissenids	Anthropogenic	24	—	—	−25.3 ± 0.2	9.8 ± 0.3	—	—
	Inlet	5	—	—	−23.2 ± 1.0	8.8 ± 0.4	—	—
	Open-Coastal	102	—	—	−25.4 ± 1.1	9.5 ± 0.1	—	—
	Deep-Hole	48	—	—	−25.4 ± 0.2	9.9 ± 0.2	—	—
	Outlet	121	—	—	−25.6 ± 0.1	9.2 ± 0.1	—	—
	Embayment	12	—	—	−23.4 ± 0.3	7.8 ± 0.2	—	—

(Continues)

TABLE 1 | (Continued)

Common name	Ecoregion	n	Length (mm)	Weight (g)	δ^{13}C (‰)	δ^{15}N (‰)	α_r	Trophic position
Benthic Baseline	Anthropogenic	22	—	—	−21.3 ± 0.5	8.1 ± 0.4	—	—
	Inlet	2	—	—	−20.2 ± 3.9	4.2 ± 0.1	—	—
	Open-Coastal	209	—	—	−21.4 ± 0.2	9.0 ± 0.2	—	—
	Deep-Hole	8	—	—	−16.27 ± 0.48	8.64 ± 0.23	—	—
	Outlet	185	—	—	−20.62 ± 0.25	9.44 ± 0.14	—	—
	Embayment	14	—	—	−24.56 ± 0.48	8.28 ± 0.47	—	—

where λ_b is the trophic position of the benthic baseline organism (i.e., 2), λ_p is the trophic position of the pelagic baseline organism (i.e., 2.5; Uzarski et al. 2024), α_r is the corrected alpha, $\delta^{15}N_c$ is the isotopic value for the consumer, $\delta^{15}N_b$ is the isotopic value for the benthic baseline organisms (i.e., chironomids, amphipods, and oligochaetes,; informed prior assumed a normal distribution with a mean of 9‰ and variance of 1‰), $\delta^{15}N_p$ is the isotopic value for the pelagic baseline organisms (i.e., dreissenids; informed priors assumed a normal distribution with a mean of 10.5‰ and variance of 1‰), and Δ_n is trophic enrichment factor (informed prior assumed 3‰ and 4‰ with a mean of 3.4‰ and variance of 0.25‰). The results presented below are posterior estimates produced using a Bayesian approach that estimated trophic position.

To assess resource partitioning and trophic niche sizes we used the package {SIBER} which uses a Bayesian multivariate ellipse-based approach to estimate niche size and six community metrics (Layman et al. 2007; Jackson et al. 2011). Prior to estimating niche size and Layman metrics described below, we used bootstrapping to ensure sample sizes were equal across each species in each ecoregion. This methodology resampled (n = 10 samples) 100 times with the mean of those samples (n = 100) used as the samples for estimating niche size and Layman metrics. The corrected standard ellipse areas (SEA$_c$; units of ‰^{2}) that contain 40% of the data were calculated to represent the core isotopic niche area (Jackson et al. 2011). A Bayesian iterative methodology was used to create posterior distributions of SEA$_c$ for each species by each ecoregion and was based on a subsample of stable isotope values extracted from each population to account for uncertainty in the data (Jackson et al. 2011). Posterior distributions were extracted using {nichetools} (Hlina 2024) and visualized using {ggplot2}.

To ascertain whether trophic communities varied among ecoregions, the following six community metrics were calculated: (1) δ^{13}C range indicates whether a food web supports multiple basal resources providing information on niche diversification at the base of a food web; (2) δ^{15}N range represents trophic level structure within a food web; (3) total convex hull area (TA) is a proxy for total extent of trophic diversity within a food web; however, the measure is easily influenced by outlying values; (4) distance to centroid (CD) is a metric that measures the average degree of trophic diversity within a food web and is not easily influenced by outlying values; (5) nearest neighbour distance (NND) is a measure of the overall density of species packing representing trophic redundancy indicating multiple species have similar trophic roles; and (6) standard deviation of the nearest neighbour (SDNND) is a measure of evenness in species packing and is a proxy for evenness in trophic niche distributions (Layman et al. 2007). A Bayesian iterative methodology was used to create posterior distributions of the six metrics using functions in the package {SIBER} (Jackson et al. 2011). While 41 species were represented in our dataset, there were large differences in their numerical representation among the six ecoregions, and thus using the entire dataset could produce extreme deviations in community metrics influenced by the simple presence of a given taxon. Therefore, we used the bootstrapped δ^{13}C and δ^{15}N of the three species described above for each ecoregion to estimate community metrics. Bootstrapped samples were used to ensure sample sizes did not influence the estimate for each metric. The posterior distribution for each metric allows comparisons of trophic structure and communities among ecoregions in Lake Ontario.

3 | Results

3.1 | Samples

Lake trout, alewife, and round goby samples were collected throughout Lake Ontario from depths that ranged between 1 and 133 m with a total of 2393 samples. The number of samples bootstrapped for each ecoregion for a given species or baseline, and the associated length, weight, δ^{13}C, δ^{15}N (mean ± SEM), the median α_r, and trophic position (± equal-tailed intervals [ETI]) are found in Table 1. Isotopic biplots (δ^{13}C and δ^{15}N) with the 95% median isotopic niche ellipse for round goby, alewife, lake trout, and both baselines among six distinct ecoregions in Lake Ontario are presented in Figure S1.

3.2 | Carbon Sources

Estimates of α_r for the inlet ecoregion were limited due to a small sample size (n = 2) for benthic baselines, thus this ecoregion has been presented but needs to be interpreted with caution. Round goby exhibited greatest variability in carbon source used among ecoregions and was more reliant on pelagic than benthic resources compared to alewife and lake trout (Figure 2). In open-coastal, round goby used more benthic carbon sources (0.52 ± 0.04) than lake trout (0.32 ± 0.01), but not alewife (0.55 ± 0.01). Carbon use in deep-hole and outlet were the most variable among the three species with round goby (0.24 ± 0.11)

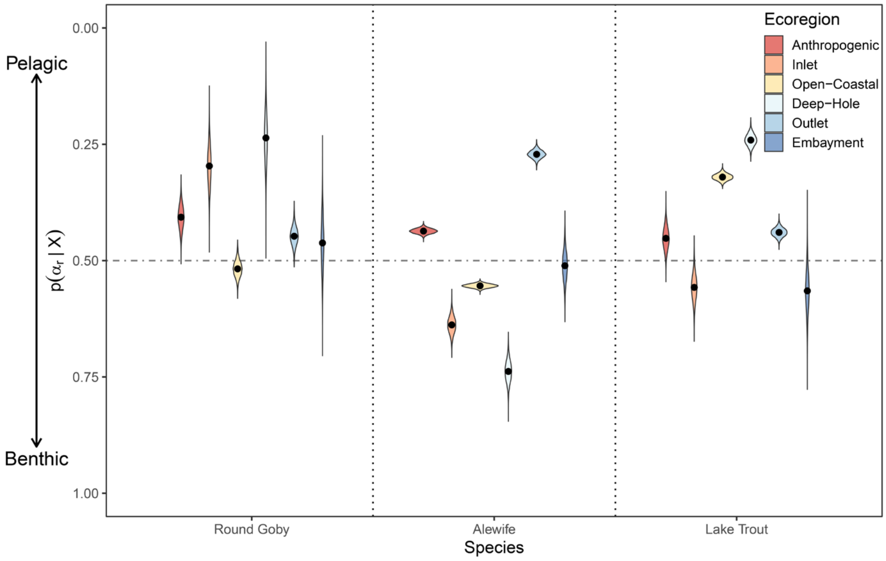


FIGURE 2 | Posterior distributions for α_r derived from equations from Post (2002) and Heuvel et al. (2024) for round goby (*Neogobius melanostomus*), alewife (*Alosa pseudoharengus*), and lake trout (*Salvelinus namaycush*), across six distinct ecoregions in Lake Ontario. α_r is proportion of benthic-pelagic carbon use with values closer to 1 representing greater benthic resource use and values closer to 0 representing greater pelagic resource use. Black points represent the median.

and lake trout (0.24 ± 0.03) using more pelagic sources than alewife for deep-hole (0.74 ± 0.05; Table 1; Figure 2) and the opposite occurring in outlet with round goby (0.45 ± 0.04) and lake trout (0.44 ± 0.02) having slightly less pelagic reliance than alewife (0.27 ± 0.01; Table 1; Figure 2). The variability in deep-hole and outlet could be a result of these ecoregion integrating carbon resources from other ecoregions. In anthropogenic (0.37–0.50) and embayment (0.34–0.66) ecoregions, carbon use among the three species appeared the most similar among species with fish tending to use a more pelagic source in the anthropogenic ecoregion and a mix of pelagic and benthic resources in the embayment ecoregion (Figure 2; Table 1).

3.3 | Trophic Position

Similarly to carbon sources, we were limited in estimates of trophic position for the inlet ecoregion due to a small sample size ($n = 2$) for benthic baselines, thus this ecoregion has been presented but needs to be interpreted with caution. Ecoregion differences in trophic position for all three species were relatively moderate for anthropogenic compared to other ecoregions with open-coastal having a similar trend for alewife and lake trout but not round goby (Figure 3). In eastern Lake Ontario ecoregions (i.e., outlet and embayment), trophic position for all three species followed similar patterns with trophic position being lower in outlet and increasing in embayment ecoregion (Table 1; Figure 3). Trophic position for round goby was the greatest in deep-hole (4.10 ± 0.23) compared to the other five ecoregions (Table 1; Figure 3). Overall, alewife exhibited similar estimates of trophic position in four ecoregions (i.e., anthropogenic, open-coastal, outlet, and embayment) with deep-hole being the lowest (3.15 ± 0.16). Lake trout had a similar trend; however, outlet was the lowest (4.56 ± 0.17) with deep-hole being slightly higher (4.66 ± 0.21).

3.4 | Niche Size

Isotopic niche size for each ecoregion was highly variable for round goby compared to the other two species, although isotopic niche size for alewife from embayment ecoregion was also highly variable (Figure 4). Comparisons among ecoregions also resulted in high variability of isotopic niche for round goby (open-coastal = 8.2‰ ± 2.3‰^{2}; outlet = 5.4‰ ± 1.5‰^{2}) compared to alewife and lake trout, with lake trout having the least variation among ecoregions (outlet = 0.8‰ ± 0.2‰^{2}; anthropogenic = 1.0‰ ± 0.3‰^{2}; Figure 4). Observed patterns in isotopic niche size among ecoregions were similar regardless of species, with inlet and deep-hole producing smaller isotopic niches while the other four ecoregions produced larger isotopic niches. Furthermore, some neighbouring ecoregions (e.g., outlet-embayment and anthropogenic-inlet) exhibited similar niche size regardless of species (Figure 4).

3.5 | Community Metrics

Estimates for the range of δ^{13}C were greater in embayment (2.01 ± 0.52), outlet (1.89 ± 0.18), open-coastal (1.80 ± 0.40), and anthropogenic (1.73 ± 0.38) than inlet (0.99 ± 0.38), and deep-hole (0.88 ± 0.39; Figure 5a). The range for δ^{15}N was greatest in embayment (5.69 ± 0.52) compared to any other ecoregion with the rest of the ecoregions having comparable δ^{15}N ranges (4.55–5.13; Figure 5b). Isotopic area (i.e., trophic diversity) was highly variable among ecoregions, with the greatest total area (convex hull) observed in outlet (4.41 ± 0.96) followed by open-coastal (3.98 ± 1.00), then anthropogenic, (2.01 ± 1.08), inlet (1.50 ± 1.1), deep-hole (1.12 ± 1.07), and embayment (0.91 ± 0.88; Figure 5c). Conversely, estimates of distance to centroid (i.e., trophic diversity) were invariable (median range = 1.84–2.38 ± 0.17–0.20; Figure 5d). The

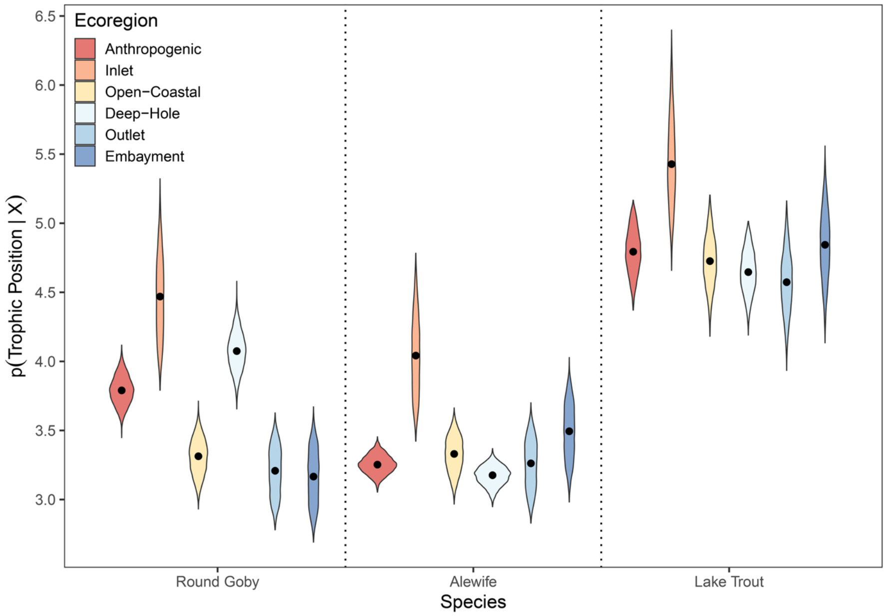


FIGURE 3 | Posterior distributions for two-source trophic position model based on Post (2002) for three species, round goby (*Neogobius melanostomus*), alewife (*Alosa pseudoharengus*), and lake trout (*Salvelinus namaycush*), across six distinct ecoregions in Lake Ontario. Black points represent the median.

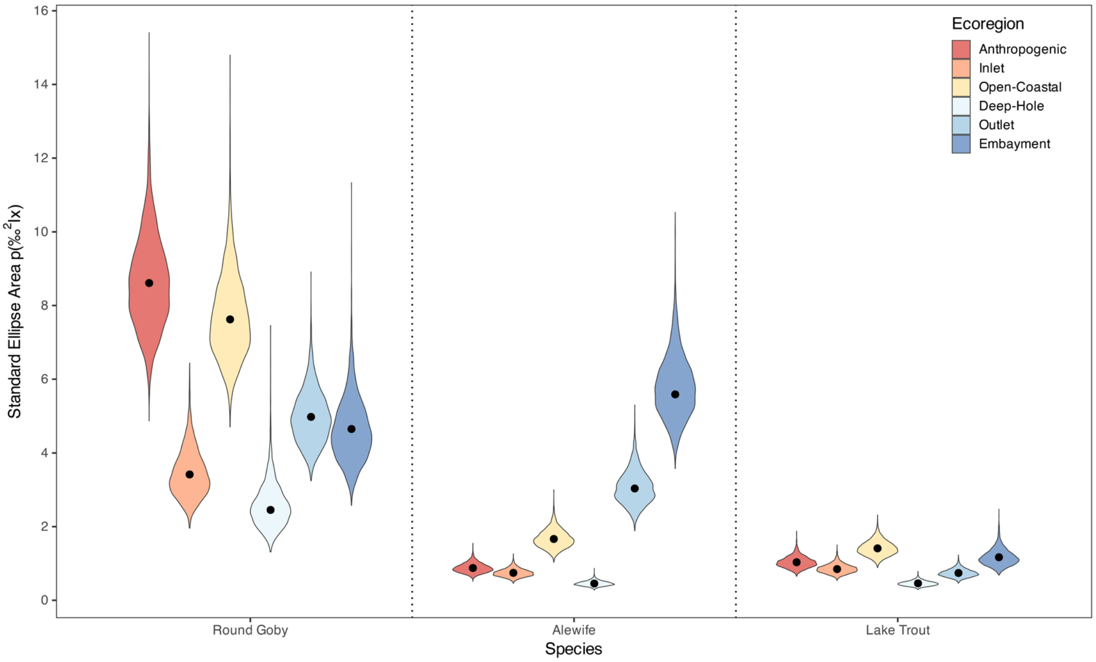


FIGURE 4 | Posterior distributions of standard ellipse area (i.e., proxy for niche size) for round goby (*Neogobius melanostomus*), alewife (*Alosa pseudoharengus*), and lake trout (*Salvelinus namaycush*) among six ecoregions in Lake Ontario. Black points represent the median posterior estimate with dotted lines separating each species.

nearest neighbour is a proxy for measuring trophic redundancy of an ecoregion and was greatest in outlet (2.82 ± 0.29), anthropogenic (2.79 ± 0.25), open-coastal (2.68 ± 0.32) while the other three ecoregions had median estimates that were comparable to each other (2.28–2.50; Figure 5e). Lastly, the standard deviation of the nearest neighbour is a proxy for evenness in trophic niches within an ecoregion and was greatest in embayment (1.88 ± 0.38), outlet (1.58 ± 0.29), open-coastal (1.49 ± 0.26) compared to the other three ecoregions (0.54–0.94; Figure 5f).

4 | Discussion

Trophic structure of round goby, alewife, and lake trout varied among ecoregions in Lake Ontario, demonstrating that efforts to assess food webs in large lakes as a homogenous system could misrepresent trophic relationships and processes that differ at smaller, definable spatial scales. Differences among ecoregions showed persistent patterns across different trophic metrics, such as predominately pelagic resource use for all species

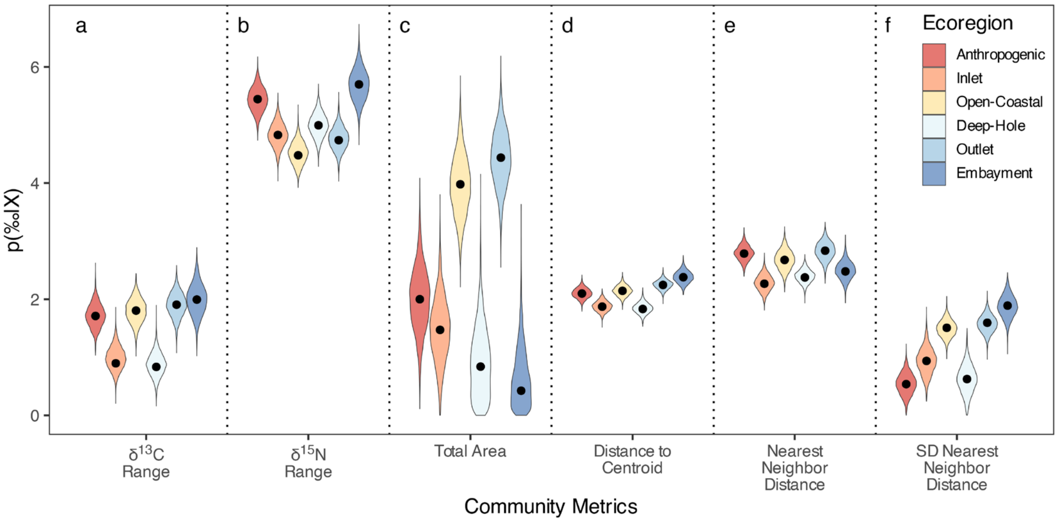


FIGURE 5 | Posterior distributions for six community metrics, δ^{13}C range (a), δ^{15}N range (b), isotopic total area (i.e., convex hull; c), distance to centroid (d), nearest neighbour distance (e), and the standard deviation (SD) to the nearest neighbour distance (f; Layman et al. 2007) for six ecoregions in Lake Ontario. Black points represent the median posterior estimate with dotted lines separating each metric. Dotted vertical lines are used to help visualize each grouping.

in anthropogenic ecoregion and a combination of benthic and pelagic resource use in embayment. Furthermore, comparisons among all six community metrics often resulted in the anthropogenic and inlet ecoregions having community metrics that were in the middle compared to other ecoregions, while embayment and deep-hole often produced extreme estimates when compared to the other four ecoregions. Outlet and embayment, which are a spatially adjacent ecoregion pairing, often produced estimates of community metrics that opposed each other, while another spatially adjacent ecoregion pairing, open-coastal and outlet, were synchronous regardless of whether estimates of community metrics were low or high. Therefore, assessing trophic structure using an ecoregion framework can provide a unique and more specific perspective that large freshwater lakes can function as smaller, interconnected but distinct ecosystems leading to more informed and evidence-based decisions.

The differences in trophic metrics across ecoregions supported most of our predictions on regional food webs. Ecoregions with greater nutrient loading, homogenous bathymetry and variable thermal dynamics (i.e., anthropogenic) supported more pelagic than benthic resources while ecoregions that had lower nutrient loading, heterogenous bathymetry, and stable thermal dynamics (i.e., open-coastal, deep-hole, and embayment) supported a mix of benthic and pelagic carbon use. Underlying variables, such as variability in carbon isotope biogeochemistry or water chemistry, could be contributing to differences we observed in community metrics among ecoregions (Focken and Becker 1998; Turschak et al. 2019). Differences in trophic redundancy (e.g., greater trophic redundancy in anthropogenic) could have negative effects on individual fitness metrics, (i.e., survival, growth, and reproduction), and more broadly impact population responses for species. Diversity in trophic roles was greater in ecoregions that had lower levels of nutrient loading and heterogenous bathymetry. These regions may support more variation in elemental sources (i.e., C, N, and P) for primary producers and consumers, allowing species to use different resources resulting in each species having a distinct trophic role, such as in eastern Lake Ontario (Busch and Lary 1996).

Trophic position for round goby and lake trout was lowest in the outlet ecoregion potentially because this ecoregion has more human disturbances (e.g., pollution and nutrient enrichment) resulting from water from multiple ecoregions mixing prior to draining through the St. Lawrence River. Increases in human-disturbances have been shown to cause simplification of aquatic food webs because, although there is often an increase in nutrients, this tends to increase the presence of generalists, resulting in lower trophic position for all species in the ecosystem (O'Gorman et al. 2012). Alewife and lake trout, showed similar trends in trophic position among ecoregions, suggesting these two species are likely responding similarly to regionally specific differences in lower trophic species (e.g., zooplankton and smaller fishes; Stewart et al. 2009; Colborne et al. 2016) potentially caused by changes in nutrients, bathymetry, and thermal dynamics (Holeck et al. 2008; Merz et al. 2023). These observations further support the use of our proposed ecoregion framework because these spatial differences can be aligned with physico-chemical properties (e.g., nutrient loading, water quality and clarity, development and land use, and industrial activities) and mechanistic outcomes that can assist in designing monitoring programs and evidence-based decision making (Feiner et al. 2019; Ives et al. 2019; Turschak et al. 2019).

Round goby had the greatest trophic plasticity among the three species across the six ecoregions of Lake Ontario. For instance, carbon sources (α_r) and niche sizes for round goby among ecoregions were highly variable, indicating the species is likely using pelagic or littoral/benthic resources depending on availability. Round goby habitat use has been described as ranging between littoral and deep-water benthic regions depending on season (Bunnell et al. 2005; Kornis et al. 2013). Furthermore, the species has been observed to exhibit small home ranges when occupying preferred habitats (e.g., rocky substrate; Charlebois et al. 1997; Ray and Corkum 2001; Walsh et al. 2007), with our observed variation in α_r and niche size being representative of the species using one habitat in an ecoregion (i.e., littoral or deep-water benthic) (Barton et al. 2005; Brush et al. 2012; Mumby et al. 2018).

In contrast, alewife, a pelagic planktivore, had lower levels of variation in α_r and isotopic niches that did not align with a previous study that identified distinct δ^{13}C and δ^{15}N values for the species in Lake Ontario (Mumby et al. 2018). Instead, we observed alewife exploiting similar benthic resources among open-coastal and deep-hole with the species having more of a reliance on pelagic resources in anthropogenic and outlet. In the embayment ecoregion they appear to be using a mix of benthic or pelagic resources. Diets of alewife in Lake Ontario previously shifted over ~25-year period as the species switched from preying on smaller zooplankton in the 1970s to preying heavily on *Mysis* and predatory cladocerans by the mid-1990s (Stewart et al. 2009). This shift in food sources is likely caused by the invasion of dreissenid mussels in the 1990s that has reduced densities of smaller zooplankton (O'Gorman et al. 2000, 2008). Our observations could be indicative of a more recent change in alewife trophic ecology as the species may be consume more zooplankton similarly to pre-dreissenid invasion (Johannsson et al. 1991; Metcalfe et al. 2025) and/or preying on nearshore larval fishes (e.g., lake trout and yellow perch (*Perca flavescens*)) (Krueger et al. 1995; Mason and Brandt 1996; Madenjian et al. 2008). Seasonal and/or spatial shifts in phyto- and zooplankton community composition have been observed in other Great Lakes and could be influencing trophic dynamics and our findings for alewife in Lake Ontario (Turschak et al. 2014; Driscoll et al. 2015; Uzarski et al. 2024). Our study design did not consider potential seasonal influence on trophic structure (most samples were collected in the summer), that may obscure the previously reported patterns (Mumby et al. 2018) and supports the need to assess trophic structure of ecoregions seasonally. Studies that emphasize the underlying mechanisms (e.g., seasonal differences, nutrients, and anthropogenic disturbances) need to be further pursued to solidify the causes of our observed regional differences in trophic structure in Lake Ontario.

Lake trout, a piscivorous predator in Lake Ontario (Colborne et al. 2016), often used similar resources among ecoregions, demonstrating the species regularly assumes the similar trophic role throughout Lake Ontario. The species has been documented to move among ecoregions, but rarely at a lake wide scale, as other salmonids do (e.g., Chinook salmon) (Ivanova, Johnson, and Fisk 2021; Ivanova, Johnson, Metcalfe, and Fisk 2021), thus trophic metrics were more similar in neighbouring ecoregions. These similarities could be due to movement and the ability to consume a wide variety prey from multiple habitats (i.e., pelagic, benthic, and littoral) in Lake Ontario (Dietrich et al. 2006; Chavarie et al. 2016; Nawrocki et al. 2022). Lake trout in Lake Ontario are often considered trophic integrators with diet consisting of alewife (~40%) and round goby (~40%), two species that occupy different habitats (Walsh et al. 2007; Colborne et al. 2016; Riha et al. 2017; Nawrocki et al. 2022). Our study further demonstrates that lake trout hold an important trophic role in Lake Ontario by consistently occupying similar trophic niches across the lake.

Ecosystem and habitat heterogeneity and/or anthropogenic disturbances often cause trophic roles to converge (Schindler and Scheuerell 2002; O'Gorman et al. 2012; Alp and Cucherousset 2022), which we observed in trophic metrics across Lake Ontario. Spatial variation in natural and anthropogenically derived nutrients (e.g., biogeochemical properties and nutrient loading) can disrupt trophic structure and dynamics in freshwater ecosystems (Holeck et al. 2008). Differences in regionally specific habitats can influence prey resources and species abundances resulting in potential consequences (e.g., reduced abundance, reproduction, and growth) for valuable Great Lakes fishes (Dove and Chapra 2015; Collingsworth et al. 2017). For example, in the Bay of Quinte on Lake Ontario (i.e., representing much of the embayment ecoregion), shifts in nutrients have altered habitats that have influenced the food web causing large changes in species composition for multiple valuable fish stocks (Hoyle et al. 2012; Shimoda et al. 2023). Our study provides a foundation and framework to build on with future investigations to reveal the mechanisms that drive regional changes in trophic structure in Lake Ontario. These studies could directly link trophic patterns we observed to changes in biomass, anthropogenic disturbances, and nutrient levels, and measure species diversity among ecoregions.

Trophic processes in Lake Ontario are complex and potentially difficult to understand. Our study, however, highlights two main patterns across ecoregions that help simplify these interactions. The first is, in general, species at different trophic levels responded similarly to distinct abiotic (e.g., nutrient loading) and biotic (e.g., changes in fish abundances) processes demonstrating that localized changes to trophic structure occur in Lake Ontario causing spatially distinguishable regions. The second pattern is common relative differences in trophic structure exist among ecoregions suggesting they function as smaller unique ecosystems within a large lake. These two patterns provide justification that ecoregions can capture differences in lake processes (e.g., nutrient cycling, productivity, and energy transfer) not evident with standardized sampling locations or other survey methodologies. As previously mentioned, current sampling regimes are costly and could be mitigated by using a systematic sampling design that strategically distributes effort among ecoregions to better characterize lake-wide spatial variability. Using information collected in one location or area that is extrapolated to the whole-lake could result in a misrepresentation of these regional food webs leading to poor decision-making. Therefore, we suggest monitoring and management programs potentially integrate an ecoregion framework into their sampling methodology and decision-making processes. This framework can be applied not just to trophic ecology and fisheries management in Lake Ontario (and other Great Lakes), but also, to efforts focused on water quality and clarity, land use, habitat restoration, and development planning. Further investigations are needed to understand the causal mechanisms producing these ecoregional differences.

Large lakes are complex and dynamic ecosystems that support high biodiversity and numerous ecosystem services (Steinman et al. 2017; Council of the Great Lakes Region 2017). Lake Ontario (surface area of 18,960 km^2) has considerable natural variation (e.g., depth, surrounding watershed, inflows and outflows) compounded by large differences in urban, agricultural, and industrial development producing heterogeneity in sources and stressors that affect trophic processes and ultimately ecosystem health and productivity (Mills et al. 2003; McMeans et al. 2016; Guthrie et al. 2019). Our results demonstrate that observable differences in trophic structure occur within definable ecoregions of Lake Ontario providing a definable approach for characterizing spatial heterogeneity and improving our understanding of regional food webs. Resource monitoring and the resulting management decision-making processes could benefit from adopting spatially distinct units (such as ecoregions) as we and others have proposed (Minns and Wichert 2005; Feiner et al. 2019; Ives et al. 2019; Budnik et al. 2024). For example, resource monitors and managers could develop and adopt ecoregion-specific management objectives and strategies. These could include fostering high abundances of nearshore fishes in nutrient rich ecoregions (e.g., anthropogenic and embayment) or promoting pelagic and benthic species (e.g., lake trout and lake whitefish [*Coregonus clupeaformis*]) in ecoregions that have high trophic diversity. These adopted strategies could design sampling programs to align with ecoregional differences, and/or understand the uncertainties in extrapolated results from one (or more) ecoregion to reflect whole lake (or other ecoregional) outcomes. Using such frameworks could ensure both data and decisions are conveyed at appropriate spatial scales and improve resource monitoring, thus ensuring the health and sustainability of the Lake Ontario ecosystem.

Author Contributions

Conceptualisation, development of methods: T.B.J., B.W.M., A.T.F.; data analysis, preparation of figures and tables: B.L.H.; writing: B.L.H.; Editing: all authors.

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Conflicts of Interest

The authors declare no conflicts of interest.

Data Availability Statement

Data and code related to this study are available at 10.5281/zenodo.14051351.

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Supporting Information

Additional supporting information can be found online in the Supporting Information section. **Figure S1:** Isotopic biplots (δ^{13}C and δ^{15}N) with the median 95% ellipse derived from posterior draws of the mean and covariance for round goby (*Neogobius melanostomus*), alewife (*Alosa pseudoharengus*), lake trout (*Salvelinus namaycush*), a benthic baseline comprised of chironomids, amphipods, oligochaetes, and sphaerids, and a pelagic baseline of Dreissenids among six ecoregions in Lake Ontario.