



Regional variability of resource use, trophic position and habitat coupling within Lake Superior

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ABSTRACT

Food web characterizations of large lakes have rarely considered spatial variation in resource use or trophic connections among species. This is also true of Lake Superior, the world's second largest freshwater lake. While instances of habitat coupling in Lake Superior have been documented, the extent to which coupling or resource specialization in this system varies spatially, particularly within a species, remains unknown. To address this, stable isotopes of common fish species and prey were collected and analyzed along a depth gradient at four geographically and bathymetrically distinct regions of Lake Superior; 1099 fish and 60 composite invertebrate samples (separately for zooplankton and benthos) were collected from both deeper regions (Keweenaw and Western Arm) and shallower regions (Nipigon Bay and Whitefish Bay). Benthic and pelagic species of fish and invertebrates were collected to characterize different energy pathways. Within regions and taxa, benthic reliance and trophic position differences across depth strata were large and comparable to those previously observed among species lake wide. Across regions, large within-taxa differences in resource use patterns and trophic position existed at similar depth strata, as well as among taxa. Generally, there was a high reliance on pelagic resources across all fish species with greater benthic resource use observed at medium and deep strata. As expected, higher trophic organisms tended to have greater evidence of benthic-pelagic coupling. Our findings reinforce the need to consider regional variation in resource use and trophic position in large lake systems over broad approaches that can overgeneralize patterns of energy flow.

1. Introduction

Habitat coupling is defined as the utilization and integration of nutrients and energy through different ecological processes linking otherwise discrete habitats (e.g., Gamble et al., 2011a; Schindler and Scheuerell, 2002; Sierszen et al., 2014). Processes that facilitate coupling through the movement of nutrients from one habitat to another include foraging (Dolson et al., 2009), migration (Jones and Mackereth, 2016), and sedimentation (Schindler and Scheuerell, 2002), and can be particularly important in large lake ecosystems (Stockwell et al., 2010). Habitat coupling can result in more stable food webs that are resilient to change (Haddad et al., 2011; McCann et al., 2005; Rooney et al., 2006; Rooney and McCann, 2012) and can also enhance production through

the transport and mobilization of excess nutrients between habitats (Cloern, 2007). Additionally, habitat coupling can be critical in bridging seasonal changes in food availability, allowing for the utilization of less abundant resources between periods of high resource abundance (Stockwell et al., 2014).

Benthic-pelagic coupling is a well-documented example of habitat coupling in lake ecosystems (Hecky and Hesslein, 1995). This process highlights how contributions of energy from both benthic and pelagic resources can be important to consumer species, and is commonly observed in apex predators in lakes (Vadeboncoeur et al., 2002). However, several abiotic factors may alter the degree of benthic-pelagic coupling in lakes; for example, bathymetric characteristics can create thermal limitations for cold-water mobile predators by limiting access to

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nearshore habitats for certain parts of the year (Dolson et al., 2009). Further, the degree of coupling has also been shown to depend on variation in ecosystem benthic production (Schindler and Scheuerell, 2002), ecosystem size (Post et al., 2000), or depth of occurrence of consumers (Sierszen et al., 2006; Vander Zanden and Rasmussen, 1999). In the Great Lakes, organisms such as *Diporeia* spp. at the base of the food web have been reported to rely heavily on nearshore benthic algae, with this reliance transitioning to sedimented pelagic-derived phytoplankton at depths greater than 40 m (Sierszen et al., 2006). Previous work examining a lake-wide assessment of diets has also shown distinct structure between nearshore and offshore habitats in Lake Superior (Gamble et al., 2011a,b), with the nearshore food web relying mostly on nearshore benthic primary production via the amphipod *Diporeia* spp., and the offshore fish community diet more dominated by pelagic production via the filter feeder *Mysis diluviana* (Gamble et al., 2011a; Sierszen et al., 2014). While variation in depth between habitats has been linked to the degree of benthic-pelagic coupling in Lake Superior (Sierszen et al., 2014), little is known about how this relationship varies spatially within taxa. Both zooplankton and fish communities show distinct patterns in abundance, size, and species composition not only with depth (Auer et al., 2013; Sierszen et al., 2014; Stockwell et al., 2014) but also across ecoregions in large lake ecosystems like Lake Superior (Gorman et al., 2012; Johnson et al., 2004; Sierszen et al., 2006). These existing patterns suggest that patterns of nearshore-offshore coupling with depth are also likely to vary spatially around the lake.

Relationships between trophic position and habitat coupling are also expected (Vander Zanden and Vadeboncoeur, 2002). Larger predators, which are higher in trophic position, tend to be more mobile. This mobility allows for greater movement and in turn couples resources more effectively, integrating energy from both benthic and pelagic habitats (Maitland et al., 2024; Svanbäck et al., 2015). Taxa that are lower in the food web may not have the ability to travel sufficient distances to utilize multiple resources and are expected to be more likely to specialize on a single resource pathway (McMeans et al., 2016; Vander Zanden and Vadeboncoeur, 2002).

Stable isotopes can provide insight into the sources of energy in ecosystems, as adjacent habitats can be isotopically dissimilar. Specifically, the range of carbon ($\delta^{13}\text{C}$) and nitrogen ($\delta^{15}\text{N}$) stable isotopes of consumers compared to baseline end members across habitats can be used to provide insights into degrees of habitat coupling and trophic position/complexity within habitats. Carbon stable isotopes are typically conserved between prey and predator, and in cases where alternative resources are isotopically distinct, can allow for the assessment of contributions from unique production sources in consumer species (DeNiro and Epstein, 1978; France, 1995; Vander Zanden and Rasmussen, 1999). Examples of source differentiation include terrestrial versus aquatic (Carpenter et al., 2005) or nearshore versus offshore (France, 1998; Rennie et al., 2013). This information is supplemented by $\delta^{15}\text{N}$, which tends to vary systematically with depth in lakes (Rennie et al., 2009; Sierszen et al., 2006; Vander Zanden and Rasmussen, 1999), but also characterizes trophic levels of a food web, typically fractionating by approximately 3.4‰ between prey and consumer (Post 2002; Vander Zanden and Rasmussen 2001).

Lake Superior is the world's second largest lake, and a valuable resource for commercial, recreational, and subsistence fisheries. Largely due to its size and location at the headwaters of the Laurentian Great Lakes, it is generally considered to be the least affected by invasive species and pollution (Anderson et al., 2017; Bronte et al., 2003; Pagnucco et al., 2015). As such, this lake provides a unique opportunity to evaluate within-species spatial variation in food web structure in a large lake system otherwise free of anthropogenic disturbance, particularly given previous efforts to document the strengths of food web connections lake-wide (Gamble et al., 2011a,b; Isaac et al., 2012), and lake-wide patterns in depth dependence of benthic-pelagic coupling across various species (Sierszen et al., 2014).

In this study, we compared variation in both trophic position and the

degree of habitat coupling with depth among different regions of Lake Superior to better understand regional variation in food web structure across a representative large lake ecosystem. More specifically, we report the degree of variation in benthic-pelagic habitat coupling and trophic position across depth gradients for several taxa of fish across four geographically and limnologically distinct regions of the lake. Along with fish samples, plankton and benthic invertebrates were collected from the same regions and depths to establish regional, depth-specific baselines. This effort of collection led to the isotopic analysis of 1099 individual fish and 60 composite invertebrate baseline samples overall to compare and contrast spatial differences in resource use and trophic position in a large lake ecosystem.

2. Methods

2.1. Study site

Data were collected across four regions in Lake Superior; Nipigon Bay, Whitefish Bay, the western side of the Keweenaw Peninsula, and the Western Arm of Lake Superior (Fig. 1). These sites are geographically separate, located generally at the cardinal directions of the compass rose around the lake, and represent common major ecotypes within Lake Superior. Nipigon Bay and Whitefish Bay represent regions with shallow bathymetry that are relatively closed off embayments, somewhat protected from the strong wind and wave action from the open lake. By contrast, the Western Arm and Keweenaw regions have greater maximum depths with steeper depth gradients and are more open to wind and wave action from the main lake than our shallow regions.

Fish, invertebrate and zooplankton samples were collected from each region based on a nearshore-offshore gradient ranging from shallow (5–30 m) to medium (30–100 m) and deep (>100 m). In previous studies, the 'nearshore' zone of Lake Superior has been defined to extend to depths as great as 80 m (Gorman et al., 2012; Stockwell et al., 2014) to as far as 100 m (Sierszen et al., 2014). The depth gradients chosen for this study followed a recommended stratification by Sierszen et al. (2006) in an effort to capture ecologically relevant characteristics across depth gradients known to generate variation in isotopic values (e.g., Rennie et al., 2009; Sierszen et al., 2006). The shallow littoral zone of the lake (0–30 m) receives significant light penetration, as the photic depth of Lake Superior is typically estimated to be between 20 and 40 m (Reinl et al., 2020; Schertzer et al., 1978; Yousef et al., 2017); the medium depth zone, which is transitional between littoral and pelagic is suggested to be the site of significant benthic-pelagic coupling (31–100 m; Sierszen et al., 2006); and the deepest profundal zone is characterized by the absence of light at bottom depths (>100 m).

2.2. Sample collection

Food web components across all sites and depth gradients were collected from June to September of 2016 and 2017, with the majority of samples being collected during the 2016 Cooperative Sampling and Monitoring Initiative (CSMI) sampling year on Lake Superior. Ten common fish species were targeted for collection: lake trout (*Salvelinus namaycush*), lake whitefish (*Coregonus clupeaformis*), cisco (*Coregonus artedii*), bloater (*Coregonus hoyi*), kiyi (*Coregonus kiyi*), rainbow smelt (*Osmerus mordax*), longnose sucker (*Catostomus catostomus*), slimy sculpin (*Cottus cognatus*), spoonhead sculpin (*Cottus ricei*), and deep-water sculpin (*Myoxocephalus thompsonii*). Although multiple morphs of lake trout exist in Lake Superior, individuals were chosen among sampling sites in an effort to represent only the 'lean' morphotype in this study (Hansen et al., 2016). These species are abundant in all four regions and represent the main feeding guilds and energy pathways among Lake Superior fishes (Gamble et al., 2011a; Table 1). Multiple government agencies collected samples through various gill and trawl netting protocols, and fish were selectively chosen to obtain as wide a range of sizes at each location as possible. This provided both fish and

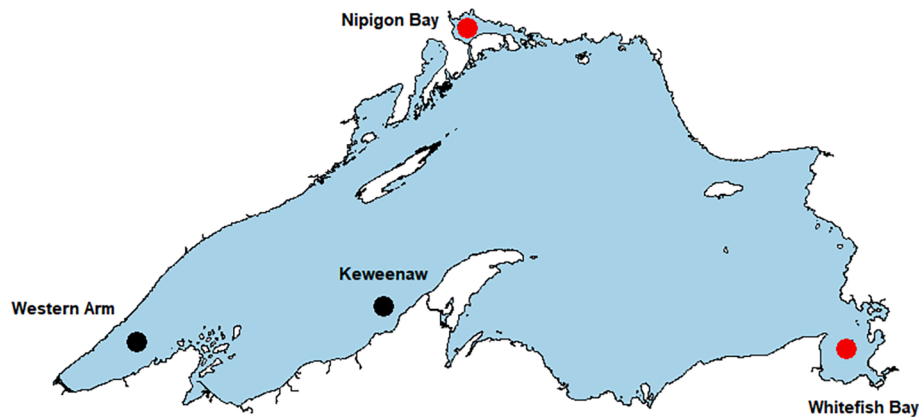


Fig. 1. Map of Lake Superior, labelled with the four study regions. Black dots denote the sites with a steeper depth gradient, and red dots denote the shallower closed off embayments in the study. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

Table 1

Species sampled for $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$, organized by feeding group from four regions and three depth strata of Lake Superior. Shallow (S) = 0–30 m, medium (M) = 30–100 m, deep (D) = 100+ m. – denote no samples collected at that depth strata.

Group	Species		Keweenaw	Western Arm	Nipigon Bay	Whitefish Bay	Total samples
Piscivore	Lake trout	<i>S</i>	15	23	18	1	137
		<i>M</i>	1	22	23	9	
		<i>D</i>	–	8	17	–	
Benthivore	Lake whitefish	<i>S</i>	25	25	28	20	162
		<i>M</i>	–	8	23	20	
		<i>D</i>	–	–	12	1	
	Slimy sculpin	<i>S</i>	20	5	9	2	57
		<i>M</i>	2	5	–	5	
		<i>D</i>	1	3	1	4	
	Spoonhead Sculpin	<i>S</i>	4	1	19	–	27
		<i>M</i>	–	–	–	1	
		<i>D</i>	–	1	1	–	
	Deepwater sculpin	<i>S</i>	–	1	–	–	31
		<i>M</i>	–	4	–	–	
		<i>D</i>	12	14	–	–	
	Longnose sucker	<i>S</i>	6	24	24	20	119
		<i>M</i>	–	15	21	9	
		<i>D</i>	–	–	–	–	
Planktivore	Cisco	<i>S</i>	15	20	29	20	167
		<i>M</i>	7	11	19	9	
		<i>D</i>	–	22	15	–	
	Bloater	<i>S</i>	20	25	1	2	128
		<i>M</i>	–	19	5	19	
		<i>D</i>	1	17	10	9	
	Kiyi	<i>S</i>	–	–	–	–	73
		<i>M</i>	1	–	–	–	
		<i>D</i>	29	37	6	–	
	Rainbow smelt	<i>S</i>	15	30	31	15	198
		<i>M</i>	19	15	–	31	
		<i>D</i>	1	9	14	18	
Totals			194	364	326	215	1099

invertebrate samples from a multitude of sites lake-wide where work was already being conducted. An effort was made to collect 20 individuals of each fish species from the 3 distinct depth strata at all 4 regions. Due to the large quantity of samples needed, all individuals collected were processed without discriminating between sexes. Agencies participating in sample collection were instructed to freeze fish whole and keep frozen until they could be transported to Lakehead University. Some agencies provided only the liver, muscle and stomach tissues with written length and weight metrics, which were also frozen upon collection. Once transported to Lakehead University whole fish were thawed and further processed to collect age structures, lengths,

weights, and tissue samples for stable isotope analyses.

Lower trophic prey species were collected from the same regions and depth gradients as fish samples. Zooplankton was collected to represent pelagic food sources, and benthic invertebrates were collected to represent benthic food sources. These samples provided a benthic and pelagic baseline across a nearshore-offshore gradient. Benthic invertebrates were collected with Ekman or Ponar dredges and sieved to remove sediment using a 500- μm wash bucket or metal sieve. Multiple government agencies aided in the collection and several grabs per site were taken depending on the various protocols of partner agencies. Individual benthic taxa were then separated into containers and frozen.

Zooplankton samples of the whole water column were collected at each depth strata within each region with triplicate vertical night-time net tows (153 μ m) between sunset and sunrise to account for diel vertical migration, and dried bulk for stable isotope analysis. All invertebrate and fish samples were immediately frozen upon collection for transport to Lakehead University.

2.3. Stable isotope analysis

In total, 1099 individual fish and 60 composite invertebrate samples were analyzed for $\delta^{15}\text{N}$ and $\delta^{13}\text{C}$. For fish larger than 5 g, a small portion of white muscle was extracted (<1 g) from the posterior dorsal portion of the fish above the lateral line. For fish smaller than 5 g, a whole-body homogenate was used for analysis. For zooplankton and benthic invertebrates, whole body composites by taxonomic group were used. Appropriate mathematical lipid corrections were implemented after analysis as described below. Common benthic taxa used for isotopic analysis include amphipoda, chironomidae, mysidae, oligochaeta and gastropoda. An individual sample analyzed for stable isotopes consisted of numerous individuals from the same site combined to reach the necessary dried weight requirements for analysis. In a few instances there was not enough material to meet the required weight using only one taxon; in these cases, a combination of available amphipoda, chironomidae and oligochaetes were used and labelled as 'spc. homogenate'. All samples were dried at 60 °C over a 48-hour period or until weight was constant to remove water content. Dried samples were then homogenized with a mortar and pestle. All samples were then weighed into 8 mm $\times$ 5 mm tin capsules on a microbalance at specified amounts (0.4–0.6 mg for fish, 0.6–0.8 mg for invertebrates). Stable isotopes of all tissues were analysed by the Great Lakes Institute for Environmental Research (GLIER) at the University of Windsor using an Elemental Analyzer – Isotope Ratio Mass Spectrometer (EA-IRMS). Nitrogen ($^{15}\text{N}/^{14}\text{N}$) and carbon ($^{13}\text{C}/^{12}\text{C}$) stable isotope compositions were reported in standard delta notation (δ). Precision was assessed by the standard deviation of replicate analyses of four standards NIST1577c, internal lab standard (tilapia muscle), USGS 40, and urea. All standards measured $\leq 0.15\%$ for $\delta^{15}\text{N}$ and $\leq 0.14\%$ for $\delta^{13}\text{C}$ ($n = 15$ for each standard). Samples of USGS 40 ($n = 15$ for $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$) were analysed for accuracy throughout runs and not used to normalise samples, showed a mean difference of -0.20% for $\delta^{15}\text{N}$ and -0.06% for $\delta^{13}\text{C}$ from the certified value. Instrumentation accuracy was measured throughout sample runs based on NIST standards 8573, 8547 and 8574 for $\delta^{15}\text{N}$ and 8542, 8573, 8574 for $\delta^{13}\text{C}$ ($n = 20$ for all, except $n = 9$ for NIST 8574). The mean difference from the certified values were -0.04 , -0.07 , -0.05% for $\delta^{15}\text{N}$ and -0.23 , -0.10 and -0.07% for $\delta^{13}\text{C}$ respectively.

2.4. Lipid correction

Lipids were not extracted prior to analysis given impacts of extraction on $\delta^{15}\text{N}$ and $\delta^{13}\text{C}$ values (Logan et al., 2008). Instead, the carbon to nitrogen ratio (C:N), determined during stable isotope analysis, was used to evaluate the need for lipid correction among samples. Samples with a C:N ratio > 3.4 were considered to have high lipid content (Post, 2002; Skinner et al., 2016), and were corrected using a generalized model for tissue specific analysis across a range of aquatic species (Logan et al., 2008):

$$\delta^{13}\text{C}' = \frac{a \cdot \text{C} : \text{N} + b}{\text{C} : \text{N} + c} + \delta^{13}\text{C}, \quad (1)$$

where $a = 7.415$, $b = -22.732$, $c = 0.746$, $\delta^{13}\text{C}'$ is the lipid corrected carbon value, $\delta^{13}\text{C}$ is the original carbon value, and C:N is the carbon to nitrogen ratio of the sample. Just over 70 % (839/1186) of fish isotopic samples had C:N ratios above 3.4 and were lipid corrected using this formula.

A similar mass balance $\delta^{13}\text{C}$ correction model was used on invertebrate samples to eliminate bias in comparisons of zooplankton and fish stable isotope samples. The model used was created specifically for freshwater invertebrates (Smyntek et al., 2007):

$$\delta^{13}\text{C}_{\text{ex}} = \delta^{13}\text{C}_{\text{bulk}} + 6.3 \left(\frac{\text{C} : \text{N}_{\text{bulk}} - 4.2}{\text{C} : \text{N}_{\text{bulk}}} \right) \quad (2)$$

where $\delta^{13}\text{C}_{\text{ex}}$ is the lipid extracted carbon, $\delta^{13}\text{C}_{\text{bulk}}$ is the non-lipid extracted carbon, and C:N_{bulk} is the non-lipid extracted carbon to nitrogen ratio.

2.5. Isotopic baseline evaluation and mixing model selection

Benthic and pelagic habitats often have distinct isotopic signatures; algae in the littoral region generally exhibits more positive $\delta^{13}\text{C}$ values than in the pelagic zone (Vander Zanden and Rasmussen 1999). Stable isotopes of both carbon ($\delta^{13}\text{C}$) and nitrogen ($\delta^{15}\text{N}$) also vary between the pelagic and profundal zones in large lake ecosystems; $\delta^{13}\text{C}$ values decrease from pelagic to profundal sources and conversely $\delta^{15}\text{N}$ values increase over the same gradient (France, 1995; Hecky and Hesselin, 1995; Schindler and Scheuerell, 2002; Sierszen et al., 2006; Vander Zanden and Rasmussen, 2001). Benthic baseline organisms and zooplankton samples collected for this study were first plotted to determine if these same patterns were observed in our dataset. Multiple species were used to characterize the benthic pathway to obtain a baseline value for the entire benthic community available to consumers. To increase sample size of the benthic energy pathway baseline in the shallow and medium strata, longnose suckers were used in addition to benthic invertebrates. Longnose suckers are benthic specialists, relying on a diet of invertebrates, aquatic plants and benthic algae (Edwards, 1983); and although they are a generalist feeder within the benthic environment, the majority of their diet within the Great Lakes is dominated by amphipoda and isopoda (Senegal et al., 2023). This specialized benthic diet and the tendency for carbon isotopic values to be conserved up the food web (DeNiro and Epstein, 1978; Hecky and Hesselin, 1995) allow these carbon signatures to be indicative of the benthic energy pathway in each region from the depth in which they were captured.

The isotopic values of baseline samples from the benthic and pelagic communities were plotted by region and depth, and distinct differences were observed. Generally, $\delta^{13}\text{C}$ was more positive in the shallow depth strata compared with medium and deep depth strata which were more similar (Fig. 2). This pattern existed among all four regions driven primarily by the isotopic values of longnose sucker, which accentuates the distinct difference between benthic and pelagic $\delta^{13}\text{C}$ sources. By contrast, no consistent pattern of nitrogen with depth was observed in the baseline samples (Fig. 2). Because most variation in the isotopic baseline signatures with depth were associated with $\delta^{13}\text{C}$, a two-source mixing model was chosen to explain resource use along depth gradients and across regions of Lake Superior.

Depth-specific benthic reliance for each individual fish consumer was calculated using lipid-corrected carbon values from each region and depth strata where samples were available (Table 1). The benthic energy pathway was characterized using an average of all benthic invertebrate and longnose sucker samples from each depth strata, and an average of Mysis and zooplankton samples were used to characterize the pelagic energy pathway (Table 2). We were unable to obtain benthic end members for the deep region of Keweenaw and Western Arm, therefore percent benthic reliance was not calculated for those depths. The proportion benthic contribution (β) was estimated as:

$$\beta = \frac{(\delta^{13}\text{C}_c - \delta^{13}\text{C}_p)}{(\delta^{13}\text{C}_b - \delta^{13}\text{C}_p)} \quad (3)$$

where $\delta^{13}\text{C}_c$ is consumer carbon, $\delta^{13}\text{C}_p$ is pelagic prey, $\delta^{13}\text{C}_b$ is benthic prey (Vander Zanden and Vadeboncoeur, 2002). Values closer to 1 indicate a greater use of benthic carbon sources and values closer to 0 indicate a greater use of pelagic carbon sources.

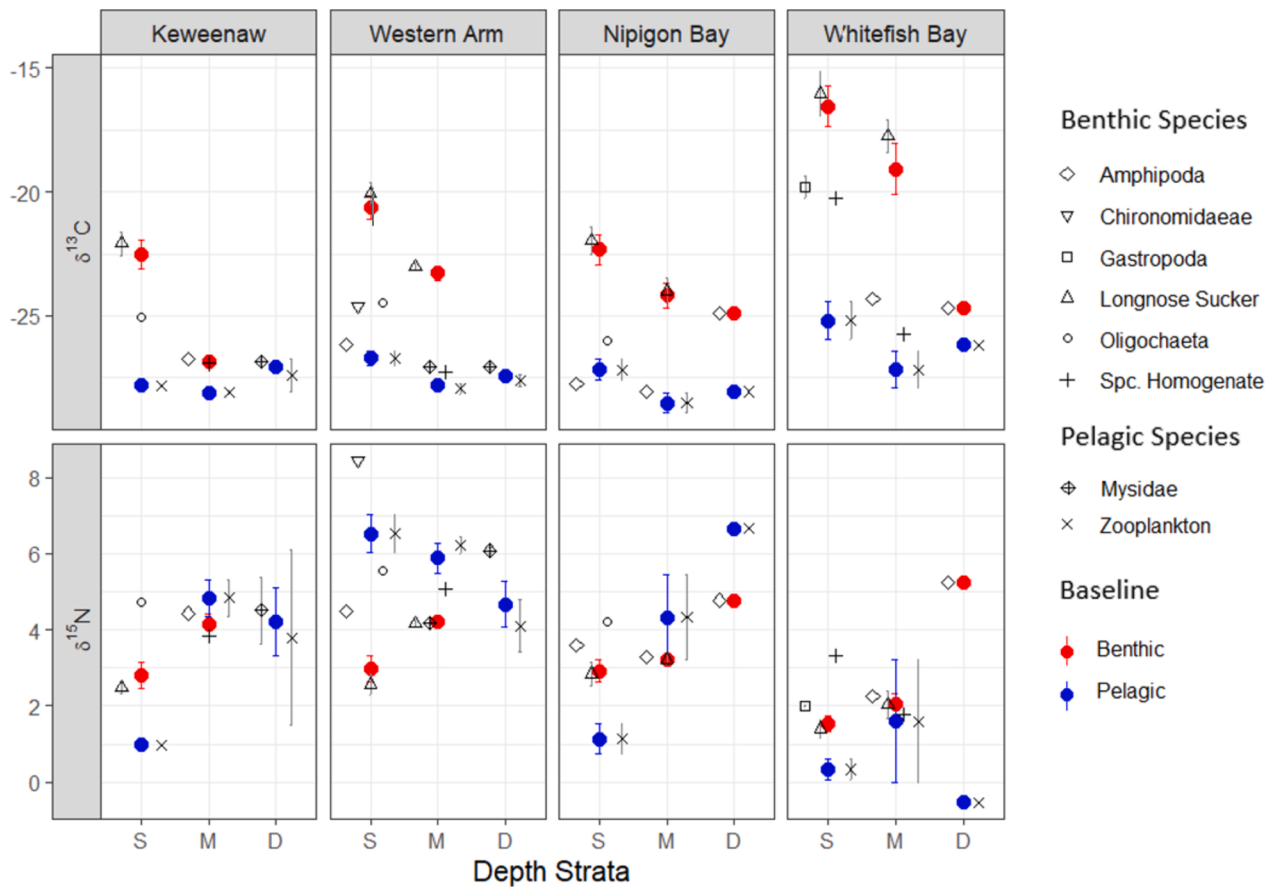


Fig. 2. Values of $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ (‰) of all benthic and pelagic taxa in Lake Superior organized by region and by depth strata, as well as the average of benthic and pelagic endmembers used as baseline values for calculations. $\delta^{13}\text{C}$ values have been mathematically lipid corrected. Shallow (S) = 0–30 m, medium (M) = 30–100 m, deep (D) = 100 + m. Error bars are $\pm$ one standard error where available. Values of $\delta^{15}\text{N}$ for longnose sucker are adjusted to reflect use in baseline values (e.g., observed value – 3.4‰; see text for details).

0 indicate a greater use of pelagic carbon sources. This model assumed there was no trophic enrichment (fractionation) in $\delta^{13}\text{C}$, as studies have found that carbon fractionation is usually $<1\text{‰}$ between trophic levels (Vander Zanden and Vadeboncoeur, 2002). If the benthic reliance of the consumer was estimated to be less than 0 or greater than 1 (occurred in 46 % of cases, 21 % were less than 0 and 25% were greater than 1), values were set to 0 or 1 respectively indicating all resource use was either benthic or pelagic.

2.6. Trophic position

Trophic position (TP) of each individual fish from each species of interest was calculated following Post (2002), and estimated as:

$$TP = \lambda + \left[\frac{\delta^{15}\text{N}_{\text{fish}} - \{(\delta^{15}\text{N}_{\text{pelagic}} * (1 - \beta)) + (\delta^{15}\text{N}_{\text{benthic}} * \beta)\}}{\Delta_n} \right] \quad (5)$$

$$\lambda = (TP_{\text{pelagic}} * (1 - \beta)) + (TP_{\text{benthic}} * \beta) \quad (6)$$

In this study, λ was modified to incorporate known trophic position values from the literature (rather than use the conventional value of 2) in comparative proportion to benthic resource use (Table 3). In cases where longnose suckers were used as benthic endmembers (which are one trophic level above the benthic organisms on which they feed), the trophic position was reduced by 1, and the $\delta^{15}\text{N}$ was reduced by 3.4‰ to reflect the $\delta^{15}\text{N}$ of sucker prey. $\delta^{15}\text{N}_{\text{benthic}}$ and $\delta^{15}\text{N}_{\text{pelagic}}$ are the benthic and pelagic baseline end members characterized by benthic invertebrates and zooplankton, Δ_n is the trophic fractionation of nitrogen (per mil), defined here as 3.4‰ (Minagawa and Wada, 1984), β is the

proportion of carbon in the target organism (fish) derived from benthic resources (Eq. (3)). All fish species were analysed for trophic position except for longnose sucker, given its use as an indicator of benthic baselines in our study. Because β values were estimated for individuals in our study, so too were estimates of λ .

2.7. Statistical analysis

Analyses were performed in R version 4.2.2 (R Core Team, 2022). Linear regressions were first conducted to assess relationships of both $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ with fish size (total length; Table 4) to ensure that patterns in benthic reliance were not an artefact of differences in size. Due to missing values in the data and an unbalanced design, non-parametric tests were conducted to evaluate differences in benthic resource use and trophic position among depths and regions using either Kruskal-Wallis tests or Mann-Whitney tests on the main effects (region and depth) to determine any trends or patterns within the data. To accommodate analysis using Kruskal-Wallis (KW) tests, each combination of depth and region was treated as a different level of a single factor. This was followed by a Dunn's test for post-hoc analysis (Zar, 2010). The critical α values for Kruskal-Wallis and Dunn's test results were adjusted to account for the number of tests that were being analyzed for each species, by applying a Benjamini-Hochberg procedure to account for the number of KW tests conducted (i.e. number of species). Due to small sample size, data for all sculpin species were combined into a single taxon, and kiyi were excluded from analysis.

The relationship between benthic reliance and trophic position was plotted to better understand relationships based on the regional

Table 2

Mean isotopic values of pelagic (zooplankton and *Mysis*) and benthic (benthic invertebrates and longnose sucker) baselines, across regions in Lake Superior. $\delta^{13}\text{C}$ reported with sample number and one standard error. Baselines were created to represent the pelagic, benthic-littoral (S) and benthic-profundal (M and D) regions. $\Delta \delta^{13}\text{C}$ describes the difference between the benthic and pelagic baselines for each region and depth strata in per mil.

Location	Depth	Group	N	SE	Average $\delta^{13}\text{C}$	$\Delta \delta^{13}\text{C}$
Keweenaw	S	Benthic	7	0.58	−22.5	5.3
		Pelagic	1	N/A	−27.8	
	M	Benthic	2	0.093	−26.8	1.3
		Pelagic	5	0.063	−28.1	
	D	Benthic	0	N/A	N/A	N/A*
		Pelagic	5	0.25	−27.1	
Western Arm	S	Benthic	27	0.49	−20.6	6.1
		Pelagic	6	0.30	−26.7	
	M	Benthic	16	0.29	−23.3	4.9
		Pelagic	6	0.24	−27.8	
	D	Benthic	0	N/A	N/A	N/A*
		Pelagic	7	0.20	−27.4	
Nipigon Bay	S	Benthic	26	0.58	−22.3	4.9
		Pelagic	5	0.42	−27.2	
	M	Benthic	22	0.52	−24.2	4.3
		Pelagic	4	0.40	−28.5	
	D	Benthic	1	N/A	−24.9	3.2
		Pelagic	1	N/A	−28.1	
Whitefish Bay	S	Benthic	23	0.83	−16.5	8.7
		Pelagic	3	0.76	−25.2	
	M	Benthic	11	1.04	−19.1	8.1
		Pelagic	3	0.73	−27.2	
	D	Benthic	1	N/A	−24.7	1.5
		Pelagic	1	N/A	−26.2	

Table 3

Trophic position of pelagic and benthic endmembers collected from Lake Superior derived from literature values. The trophic position for suckers was reduced by one trophic position to emulate the resources that suckers consume rather than the fish. Spc. Homogenate refers to baseline samples of combined Amphipoda, Chironomidae and Oligochaeta individuals.

SPC	TP	Reference	Location
Amphipoda	2.275	Kruger et al., 2016 (Diporeia)	Lake Superior
Chironomidae	2	Janjua et al., 2015 (other benthos)	Ecopath Model Great Bear Lake
Mysidae	2.5	Kruger et al., 2016	Lake Superior
Oligochaeta	2	Janjua et al., 2015 (other benthos)	Ecopath Model Great Bear Lake
Gastropoda	2	Vander Zanden et al., 1997	ON & QC inland lakes
Spc. homogenate	2	Janjua et al., 2015 (other benthos)	Ecopath Model Great Bear Lake
Zooplankton	2.11	Janjua et al., 2015	Ecopath Model Great Bear Lake
Longnose sucker	*3.5–1 = 2.5	Vander Zanden et al., 1997	ON & QC inland lakes
*food			

*Trophic position of 2.5 was used for longnose sucker instead of the literature value of 3.5 to reflect the resources that suckers are reliant upon.

distribution. Specifically, we were interested if higher trophic organisms showed a higher integration of benthic and pelagic sources. The average of benthic reliance and trophic position for each region and depth were treated as independent observations (i.e. n = 3; S, M, D).

Table 4

Range of $\delta^{13}\text{C}$ (‰) along with the corresponding total length (mm) in fish collected from Lake Superior. Regional abbreviations as follows KW = Keweenaw, WA = Western Arm, NB = Nipigon Bay, WF = Whitefish Bay. Where a significant relationship exists between $\delta^{13}\text{C}$ and total length values are bolded.

Species	Value	Range of values (min, max)			
		KW	WA	NB	WF
Lake trout	length	80, 653	232, 763	193, 785	355, 604
	$\delta^{13}\text{C}$	−28.7, −23.7	−30.7, −22.8	−31.8, −22.6	−28.3, −24.1
Lake whitefish	length	111, 441	183, 488	186, 957	176, 560
	$\delta^{13}\text{C}$	−28.7, −23.6	−31.3, −24.1	−29.4, −19.5	−28.7, −23.6
Sculpin spp.	length	30, 104	21, 114	36, 109	41, 90
	$\delta^{13}\text{C}$	−31.1, −21.6	−32.0, −24.3	−32.9, −25.8	−29.3, −20.1
Cisco	length	92, 417	118, 394	170, 425	183, 410
	$\delta^{13}\text{C}$	−28.8, −21.9	−30.5, −23.8	−29.3, −19.3	−29.7, −19.6
Bloater	length	81, 241	86, 261	156, 300	89, 310
	$\delta^{13}\text{C}$	−30.6, −24.5	−29.8, −24.4	−26.9, −23.7	−30.4, −24.2
Rainbow smelt	length	51, 163	35, 167	42, 220	45, 200
	$\delta^{13}\text{C}$	−30.4, −24.0	−28.3, −24.2	−30.2, −24.4	−28.1, −22.6

3. Results

3.1. Benthic reliance

Benthic reliance varied between regions and depths for all species (Table 5). Generally, considering all species across regions, benthic reliance was lowest in Whitefish Bay and highest in Nipigon Bay and Keweenaw (Fig. 3). Large among-species differences existed when looking at the same depth strata across the four regions. Across shallow depth strata, lake whitefish, cisco, bloater, and rainbow smelt showed higher benthic reliance in Nipigon Bay compared to any other region

Table 5

Results from Kruskal-Wallis analysis, where each combination of depth and region was treated as a different level of a single factor. The critical α values for each species is reported within the Species column as P_{crit} (Benjamini-Hochberg adjustment). Post-hoc analysis using Dunn's test allowed for observation of significant differences between and across region and depth strata, as reported in Tables A1 and A2 (Supplementary material).

Metric	Species	n	DF	X ²	P-value
Benthic Reliance	Lake Trout	129	8	16.3	0.039
	$P_{crit} = 0.05$				
	Lake Whitefish	162	8	79.1	<0.0001
	$P_{crit} = 0.0167$				
	Sculpin spp.	84	8	35.5	<0.0001
	$P_{crit} = 0.042$				
	Cisco	145	8	66.2	<0.0001
	$P_{crit} = 0.025$				
	Bloater	110	8	54.0	<0.0001
	$P_{crit} = 0.033$				
Trophic Position	Rainbow smelt	188	8	84.5	<0.0001
	$P_{crit} = 0.0083$				
	Lake Trout	129	8	81.6	<0.0001
	$P_{crit} = 0.042$				
	Lake Whitefish	162	8	117.8	<0.0001
	$P_{crit} = 0.0167$				
	Sculpin spp.	84	8	54.9	0.0001
	$P_{crit} = 0.05$				
	Cisco	145	8	89.3	<0.0001
	$P_{crit} = 0.025$				
	Bloater	110	8	93.3	<0.0001
	$P_{crit} = 0.033$				
	Rainbow smelt	188	8	148.9	<0.0001
	$P_{crit} = 0.0083$				

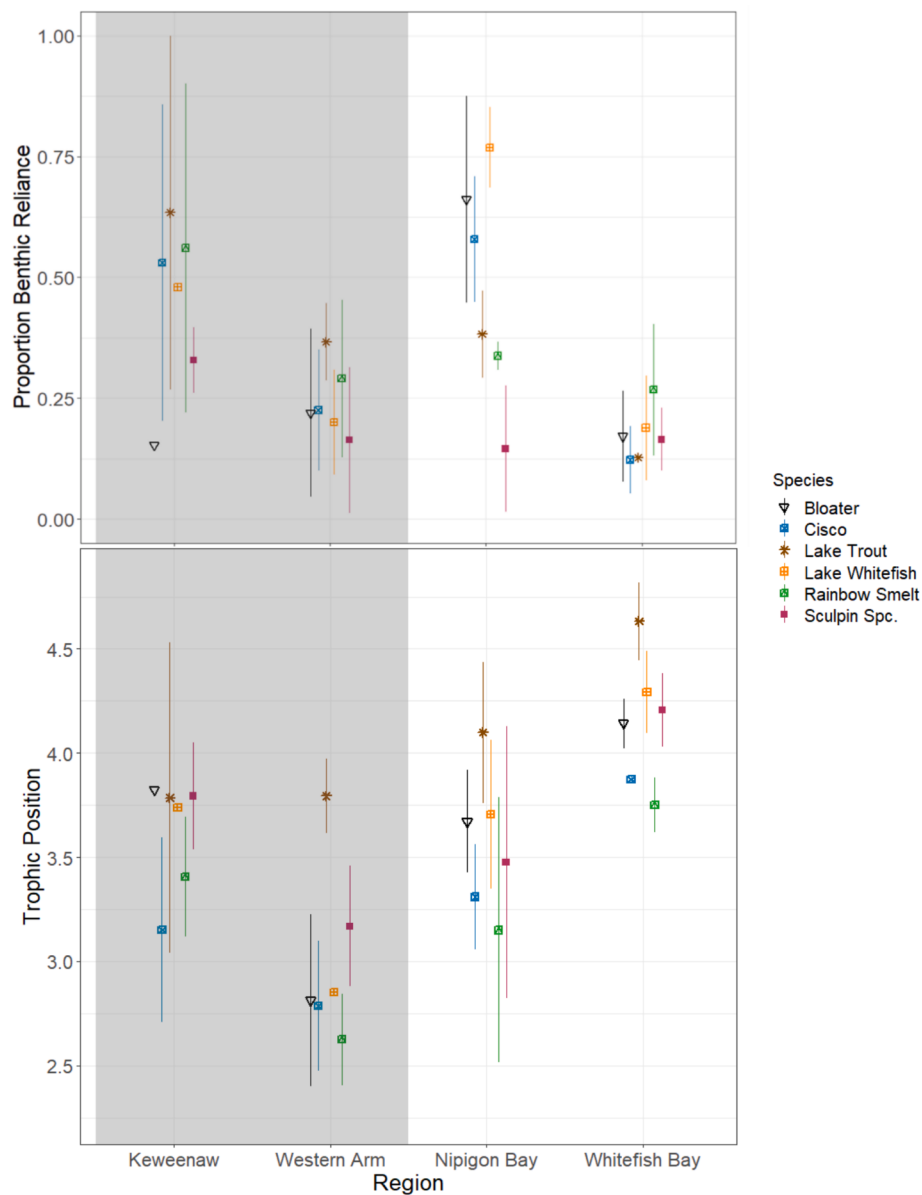


Fig. 3. Benthic reliance (top) and trophic position (bottom) of each species for each region averaged across depth strata (i.e. $n = 3$; S, M, D) to emphasize regional differences among communities. Regions are organized from deepest to shallowest with the two deeper sites being highlighted in grey. Error bars are $\pm$ one standard error; species listed without error bars are represented by only a single stratum.

(Fig. 4; Electronic Supplementary material (ESM) Table A1). Lake trout and sculpin species did not follow this pattern, with the highest benthic reliance in Western Arm and Keweenaw respectively. The shallow depth strata showed a high reliance of pelagic resource use for all species compared to that observed in the medium and deep strata, except for lake whitefish in Nipigon Bay (Fig. 4). At medium depth strata, cisco, bloater, lake whitefish and rainbow smelt showed variation similar to patterns observed in the shallow strata (with the highest benthic reliance for cisco at Keweenaw and for bloater in the Western Arm; Fig. 4; ESM Table A1). Medium strata patterns in lake trout were unlike all other species, having the highest benthic reliance in Keweenaw, followed by lower, but similar, values in Western Arm and Nipigon Bay, and the lowest in Whitefish Bay. The deep strata were only represented in two regions, Nipigon Bay and Whitefish Bay (Fig. 4). Further, only lake whitefish, bloater, rainbow smelt, and sculpin species had samples in both of those regions. Of these 4 species, benthic reliance was higher in Nipigon Bay for all species except rainbow smelt.

When considering within region variability, the benthic reliance of

fishes varied significantly with depth for all species but not conclusively across all four regions (Fig. 4, ESM Table A1). Generally, within a region the benthic resource use in the shallow depth strata was lowest compared with that at medium or deep strata for all species except lake whitefish and sculpin species, rainbow smelt, cisco, lake trout and bloater all demonstrated consistent patterns across depth strata—more pelagic in shallow strata, more benthic in medium and deep strata. Whitefish Bay only showed a significant difference with depth in one species (rainbow smelt), followed by Keweenaw which demonstrated significant differences for both cisco and rainbow smelt. By contrast, Nipigon Bay showed significant differences with depth for three species (cisco, lake whitefish and lake trout) and in the Western Arm, four species differed significantly with depth (rainbow smelt, bloater, cisco, and sculpin species.). There was a general trend towards greater reliance on pelagic resource use overall, and the most surprising result was no distinct pattern based on feeding group.

While we found significant relationships between body size and isotopic values for several species (ESM Fig. A1), as well as variation in

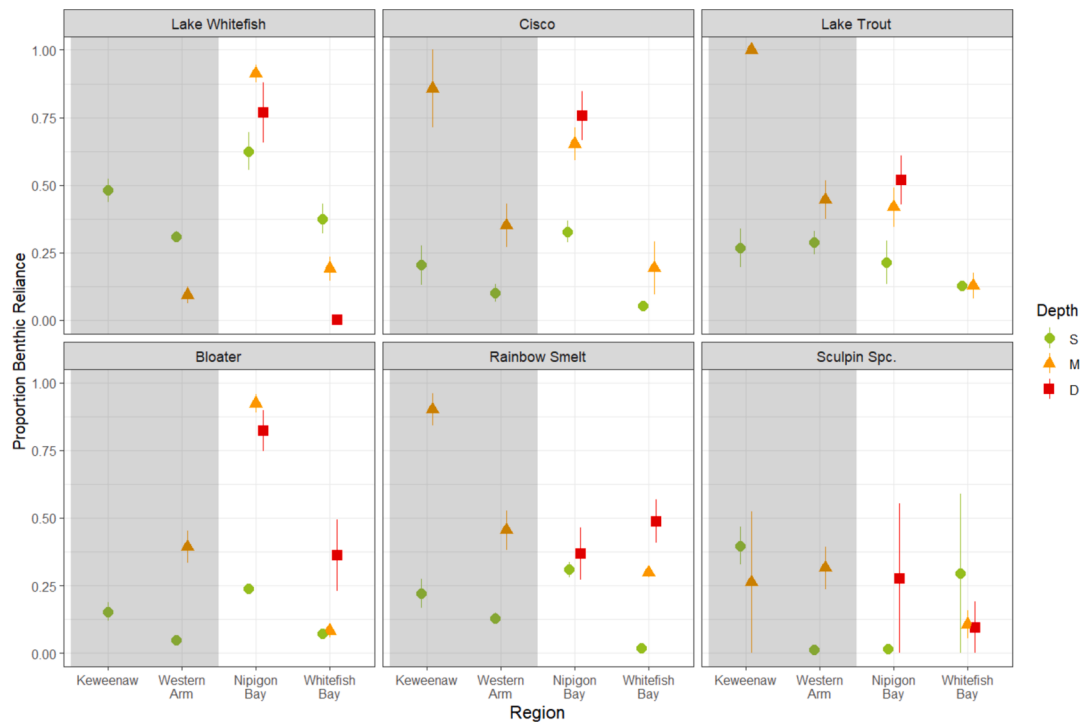


Fig. 4. Proportion benthic reliance, showing the proportion of pelagic resource use to the proportion of benthic-littoral (S) or benthic-profundal (M and D). Depth categories as defined in Fig. 2. Regions are organized from deepest to shallowest with the two deeper sites being highlighted in grey. Error bars are $\pm$ one standard error.

fish size among regions and across depth strata (ESM Fig. A2), patterns of differences in size were generally inconsistent with isotopic differences across regions and depths observed in our study with only a few exceptions. Values of $\delta^{13}\text{C}$ increased with body size in rainbow smelt, bloater and sculpin species, but declined with body size for lake trout and lake whitefish (ESM Fig. A1). In all species where there were

significant differences across regions in the shallow depth strata, body size was also significantly different, but not in a consistent pattern between the two metrics such that differences in body size would explain differences in benthic reliance (ESM Figs. A1 and A2). In the medium depth strata, significant differences in size were observed but again these patterns did not follow what was observed for benthic reliance

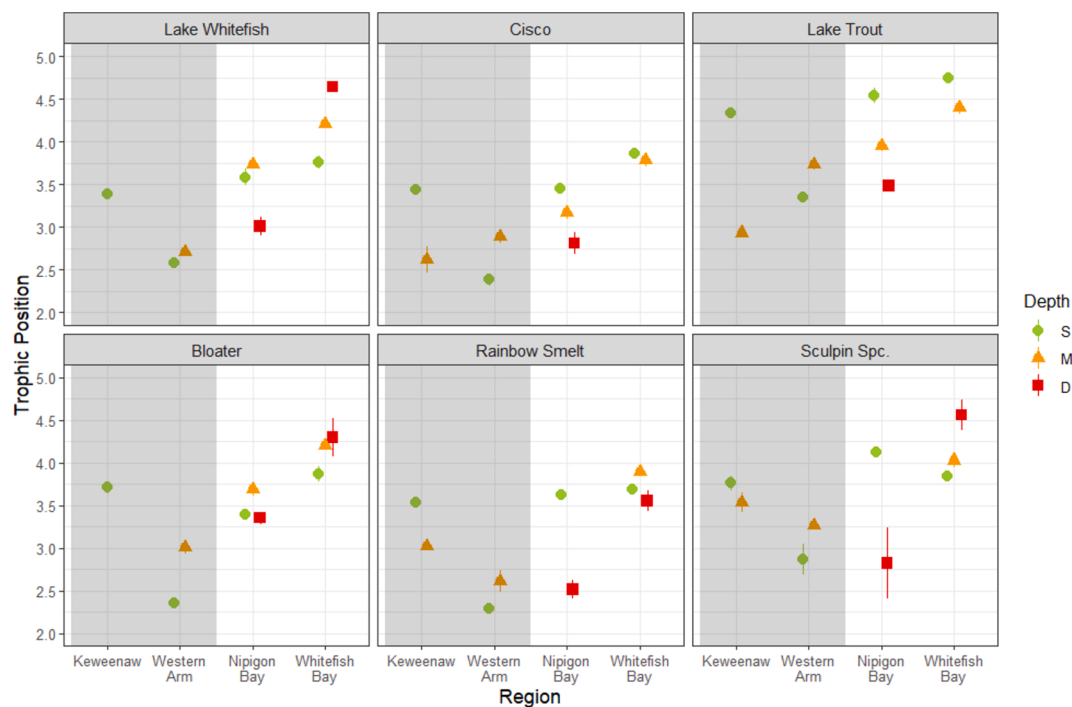


Fig. 5. Trophic position visualized by region and depth (benthic-littoral (S) or benthic-profundal (M & D). Depth categories as defined in Fig. 2. Regions are organized from deepest to shallowest with the two deeper sites being highlighted in grey. Error bars are $\pm$ one standard error.

(ESM Fig. A2). There were limited observations from deep strata with only lake whitefish, bloater, rainbow smelt and sculpin species having more than one data point. Of these species, bloater and rainbow smelt showed a consistent pattern between benthic reliance and size (i.e., larger fish with greater benthic reliance, where the relationship for $\delta^{13}\text{C}$ in these species with body size was positive), and only rainbow smelt showed a moderately significant difference of fish size across region (ESM Fig. A2).

3.2. Trophic position

Trophic position was found to vary both within regions and across depth strata for all species (Fig. 5; ESM Table A2); Generally, across regions, trophic position among all species was lowest in Western Arm and highest in Whitefish Bay (Fig. 3). Distinct differences occurred across depth strata, but not consistently among regions. Whitefish Bay was the only region that had no significant trophic position differences across depth strata within any of the study species.

Over shallow strata, all species showed the lowest trophic positions in Western Arm and generally highest in Whitefish Bay (all species except sculpin spp.), and these differences were significant for all species (Fig. 5; ESM Table A2). Although Western Arm obviously differed in trophic position, the other three regions showed less distinct differences. Patterns were very similar between the shallow and medium depth strata. In the medium strata, the Western Arm or Keweenaw had the lowest trophic position (depending on the species) and was the highest in Whitefish Bay (where data were available to estimate trophic position). The Western Arm and Whitefish Bay were significantly different in all species across the medium strata. Observations in the deep strata were limited, with only 4 of 6 species having more than one observation for comparison. All four of these species, lake whitefish, bloater, rainbow smelt, and sculpin spp. had significantly higher trophic positions in Whitefish Bay compared to Nipigon Bay.

Within a region, patterns across the three depth strata were less consistent (Fig. 5). The Western Arm had consistently lower trophic positions in the shallow than medium depth strata for all species. The opposite was true for Nipigon Bay where the shallow strata had higher trophic positions than medium (cisco and lake trout), and deep strata (lake whitefish, cisco, lake trout, rainbow smelt, and sculpin species). Within a single species in a single region, trophic position varied as much as 1.5 trophic positions, as observed in lake trout from the shallow (TP = 4.5) and deep (TP = 3.0) strata of Keweenaw. The second largest trophic position change across depths was observed in Nipigon Bay, where sculpin species from the shallow strata had a trophic position 1.3 higher than in the deep strata. Overall, lake trout generally had the highest trophic position within fish communities (Fig. 3), which was expected as the apex predator in Lake Superior. The lowest trophic position across regions was held by rainbow smelt in all regions except for Keweenaw where cisco was the lowest. Sculpin species were higher than expected overall, holding a position similar to lake trout in Keweenaw and second to lake trout in Western Arm. Where significant patterns were observed, $\delta^{15}\text{N}$ tended to scale positively with body size, apart from Nipigon Bay sculpin species where it was negative (ESM Fig. A3). Based on this, we would expect regions/individuals with higher trophic position to be associated with larger body sizes. However, mean body size trends were not consistent with patterns observed for trophic position in this depth strata (ESM Fig. A3), suggesting that trophic position patterns were independent of fish size.

Biplots of benthic reliance and trophic position for each region generally followed the pattern of increasing trophic position with greater integration of available benthic and pelagic resources, but the pattern was specific to each region. Although most regions tended to reflect higher pelagic reliance overall, top predators (i.e. lake trout) almost always tended to form the apex trophic position at a point between the available range of benthic reliance in each region (ESM Fig. A4).

4. Discussion

Our investigation revealed substantial within-taxa regional and depth-dependent differences in resource use patterns and trophic position across the Lake Superior fish community, of a similar magnitude to those previously reported among taxa of the same lake (Sierszen et al., 2014). Across regions, the same species from the same depth strata was observed to rely on contrasting energy pathways, from primarily benthic to primarily pelagic. For example, the proportion of cisco benthic reliance from medium depth strata ranged from 0.19 in the Whitefish Bay to 0.86 reliance in Keweenaw. Patterns of similar magnitude were observed for several other species and depth strata. Further, variation in the proportion of benthic energy use was observed not only across regions but also within a single region, as observed in rainbow smelt from Keweenaw, with the proportion of benthic resource use observed to be 0.22 in shallow strata, increasing to 0.90 at deep strata. The magnitude of these within-taxa differences in resource use reported here match or exceed among-species differences reported elsewhere from the same lake (Sierszen et al., 2014). Trophic positions were similarly variable within species, with individuals from the same species and region collected at different depths exhibiting differences of a full trophic position or greater. Importantly, we observed these patterns in benthic reliance and trophic position using both depth- and region-specific baselines, and thus control not only for depth dependence of stable isotopes as have been reported elsewhere (e.g., Rennie et al., 2009; Sierszen et al., 2006), but also regional patterns in isotopic variation known to exist in large lake ecosystems (e.g., Eberts et al., 2017; Nawrocki et al., 2023). The within-taxa disparities in both resource use (as reflected by benthic reliance) and trophic position reported here underscore the importance of regional and depth-specific considerations in food web connectivity and resource use when describing large lake food webs, versus more broad approaches which attempt to generalize across the entire lake (e.g., Schmidt et al., 2009) or even across broad habitat categories (e.g., Gamble et al., 2011a,b).

Based on our estimates of resource use, and despite observed within- and among-taxonomic variation, the fish consumer community in Lake Superior at all regions sampled was primarily reliant on pelagic energy pathways. This was expected, due to the high reliance on *Mysis* to the entire Lake Superior food web reported elsewhere based on diet studies (Gamble et al., 2011a,b), and has been shown to be the case for both nearshore and offshore communities in Lake Superior (Isaac et al., 2012). This high reliance on pelagic resources was also observed in species that are typically considered to be benthivorous, such as sculpin species (Gamble et al., 2011b; Sierszen et al., 2014). Since *Mysis* undergo diel vertical migration (Bowers, 1988; Jensen et al., 2006) and are important diet items for sculpin (Gamble et al., 2011b), it is possible that they may act to couple pelagic energy to benthic-oriented sculpin. Additionally, the majority of sculpin collected in our deepwater sites are deepwater sculpin, which have been previously reported to have benthic reliance estimates less than 0.5 in Lake Superior (Sierszen et al., 2014). Our findings also highlight the potential for energy coupling of pelagic with benthic littoral/profundal energy pathways regardless of the depth of the habitat occupied by a consumer (Sierszen et al., 2014). Nearly all species across all regions displayed some form of benthic-pelagic integration to varying degrees, with only a few instances of resource specialization (e.g., mid-strata Keweenaw lake trout, deep Whitefish Bay lake whitefish). While this pattern has been shown broadly across species from many different ecosystems (e.g., Vander Zanden and Vadeboncoeur, 2002), we demonstrate variation in this integration of benthic and pelagic energy pathways not just among species, but within species depending on both depth and location within a single ecosystem.

Examining patterns within species and regions, this study found that benthic reliance generally increased from shallow to mid- or deep strata. Other studies have reported higher pelagic contributions in species that tend to occupy deeper habitats relative to those that occupy more shallow habitats (Sierszen et al., 2014); however, ours is the first we

know of to evaluate resource use along depth gradients within taxa. Sierszen et al., (2014) reported cisco as having low benthic resource use (<0.4), which is supported by our observations in Western Arm. However, proportions of benthic contributions for this species generally exceeded 0.5 in the medium and deep strata from Keweenaw and Nipigon Bay; moreover, Nipigon Bay had the highest benthic reliance in shallow strata for four of six species in this study. This phenomenon could be due to the input from the Nipigon River, the largest contributing riverine source into Lake Superior, potentially reflecting higher terrestrial inputs of carbon being incorporated by baseline organisms being confounded with nearshore/ benthic production (e.g., France, 1998). While dreissenids have recently been found and reported in significant densities in Nipigon Bay and parts of the Western Arm (e.g. Apostle Islands; M. Wegher, pers. comm), the date of sampling in this study (2016–17) predates these reported increases in densities, suggesting that among-region differences in benthic reliance of consumer species in Lake Superior are not related to dreissenids. Higher rates of benthic resource use in the Keweenaw region (e.g., cisco, rainbow smelt, lake trout at mid-strata depths) could reflect significant benthic production at depth along steep shoreline gradients. Photosynthetically active radiation in Lake Superior can penetrate to 45 m (Reinl et al., 2020), permitting benthic production at depths we defined as mid-strata. This deep light penetration combined with nutrient delivery through upwelling events (e.g., high-amplitude internal seiches, Beletsky et al., 2021) could combine to support benthic production along these steep gradient locations.

It was expected that similar patterns would be observed across regions that were morphometrically similar, as resource use has been previously observed to differ based on habitat availability and lake morphometry (Dolson et al., 2009; Hayden et al., 2014). Contrary to these expectations, our results show that resource use by fishes at Keweenaw were more similar to Nipigon Bay, and Western Arm more similar to Whitefish Bay when comparing benthic reliance across regions. Several species from the mid-depth strata in Keweenaw (lake trout, cisco, and rainbow smelt) and Nipigon Bay (lake whitefish, cisco, and bloater) were observed to have high rates of benthic reliance. Similarities between Keweenaw and Nipigon Bay could be due to deep-water benthic production in the former and terrestrial inputs in the latter, as proposed above. However, further investigations are clearly needed to better understand the potential mechanisms behind these unexpected similarities. Trophic position organization among fish consumers remained relatively consistent across regions, with lake trout positioned as apex predators, and invertivorous cisco and rainbow smelt occupying the lowest trophic positions. Perhaps surprisingly, sculpin species trophic position was much higher than expected, comparable to the top predator lake trout in several regions and strata and occupying the second highest trophic position in Western Arm. Sculpin are well known to be egg predators of other species (Bunnell et al., 2014; Wasylenko et al., 2014), which could elevate their trophic position to levels similar to predatory lake trout, despite their small size.

We observed some of the lowest benthic reliance among fishes in Whitefish Bay, one of the shallower embayments. This is likely more a reflection of the flow direction of the lake; Whitefish Bay receives energy from the main portion of the lake as the outflow of Lake Superior. The increase in pelagic resource use compared to other regions could be due to high amounts pelagic material transported from the main basin of the lake on its path out of the lake through Whitefish Bay. Not only does Whitefish Bay have the most pelagic resource use compared with other regions examined here, but it also had the highest trophic position across the fish community. The flow of the lake may also have an effect on the pattern observed in trophic positions; generally lower in the west (Western Arm) and highest in the east (Whitefish Bay).

When considering resource use and trophic position across regions, our data provide evidence of increasing habitat coupling in higher trophic organisms, which is represented by the apex predator, lake trout. This pattern of integration of multiple resource pathways at higher

trophic position is comparable to previous studies which also show that larger, more mobile predators were better able to utilize multiple energy pathways (McMeans et al., 2016; Vander Zanden and Vadeboncoeur, 2002). However, this pattern was only obvious when considering species regionally, reinforcing the need to consider spatial variation in trophic structure in large lake ecosystems. Given that increased resource integration has been shown to create ecosystem stability in the face of changing environments (Rooney et al., 2006; Rooney and McCann, 2012), this is an important attribute of freshwater ecosystems generally.

Similar to Sierszen et al., (2014), our study used stable isotopes to investigate depth-based changes to resource use in Lake Superior. Both studies collected samples lake-wide and at different depths to find that species commonly rely on both benthic and pelagic energy pathways. However, our study differs by not generalizing species lake-wide, but instead considers both region and depth, focusing on differences at finer spatial scales. Based on patterns among species, Sierszen et al. (2014) inferred a decrease in benthic reliance with increasing depth, but our findings evaluating depth patterns in resource use within species highlight that offshore species such as rainbow smelt, cisco, and bloater may utilize benthic energy pathways to similar or greater extents compared to the shallow depths. Thus, despite broad lake-wide generalities in nearshore and offshore resource use in the fish community (e.g., Gamble et al., 2011a), regional variation in resource use and trophic structure should be considered in whole lake studies. Although some patterns we observed in benthic reliance and trophic position could be attributed to differences in consumer body size among regions or depth strata, these applied only to a few cases and cannot explain the overall range of variation reported here.

One potential criticism of baseline collections in this study is that though they were spatially explicit (across both regions and with depth), they were limited to a single collection point in time, and lower sample size/representation across all regions and depths than was originally desired. Isotopic values for both $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ are known to vary in freshwater lakes seasonally (e.g., Matthews and Mazumder, 2003). The faster growth rates of lower food web species commonly used as baselines have a high isotopic turnover rate, making them representative of a relatively short time period prior to when they were collected (e.g. days to weeks). By comparison, muscle or whole-body homogenate of fish turnover at a slower rate (e.g. weeks to months) which means the baselines collected may not directly correspond to the study species collected at the same time. This was partially addressed by our ability to use longnose sucker as a benthic endmember species, where fish muscle tissue has a much slower turnover rate than other benthic endmembers utilized. Previous considerations of depth-specific mixing models in Lake Superior have also suffered from similar sampling issues when considering isotopic baselines applied to fishes (e.g., Sierszen et al., 2011; Sierszen et al., 2014). This mismatch in baselines and study species contributes to the challenge of securing sufficient and appropriate samples across such a vast ecosystem as Lake Superior, with limited resources to support multiple within-season lake-wide expeditions. Despite these challenges faced by the above studies in characterizing isotopic baselines, significant within-taxa variation among regions in benthic reliance and trophic position, novel to the current study, further highlight the need to consider these aspects when evaluating food web connections and resource use in large lake systems such as the Laurentian Great Lakes. Future efforts focused on isotopic analysis of bony structures (e.g. scales, which integrate isotopic information over longer time periods) or the use of compound-specific stable isotopic analysis (alleviating the need for baseline collections, but at significantly greater cost per sample) could help address some of these potential shortcomings.

Given the considerable within-taxa variability in resource use and trophic position reported here, spatially explicit considerations regarding these variables may need to be accounted for in developing appropriate conservation actions. While generalizations of species can be useful for characterizing large lake ecosystems in some instances,

management actions are typically instituted at the provincial or state level and, as a consequence, are almost exclusively implemented at regional scales. Given that regional variation in resource use within taxa reported here can match or exceed both observed and previously reported between-taxa estimates is an important consideration in applying conservation actions at this regional scale. Although the offshore/deepwater food web tends to be less complex (i.e., less taxonomically diverse) compared with the nearshore (Gamble et al., 2011b), the regional variation in resource use among offshore fishes reported here indicates a more nuanced regional understanding of the Lake Superior ecosystem may be required.

CRedit authorship contribution statement

M.E. Wegher: Writing – review & editing, Visualization, Investigation, Formal analysis. **A.T. Fisk:** Writing – review & editing, Resources, Methodology, Funding acquisition, Formal analysis. **T.B. Johnson:** Writing – review & editing, Resources, Funding acquisition. **M.D. Rennie:** Writing – review & editing, Writing – original draft, Supervision, Resources, Methodology, Conceptualization.

Declaration of competing interest

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

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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.2024.102457>.

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