ORIGINAL ARTICLE

WILEY *Ecology of* FRESHWATER FISH

Generalist feeding strategies in Arctic freshwater fish: A mechanism for dealing with extreme environments

Sarah M. Laske[1,2] 🔘 | Amanda E. Rosenberger[3,4] | Mark S. Wipfli[5] |
Christian E. Zimmerman[2]

[1]Alaska Cooperative Fish and Wildlife Research Unit, College of Fisheries and Ocean Sciences, University of Alaska Fairbanks, Fairbanks, AK, USA

[2]U.S. Geological Survey, Alaska Science Center, Anchorage, AK, USA

[3]U.S. Geological Survey, Missouri Cooperative Fish and Wildlife Research Unit, School of Natural Resources, University of Missouri, Columbia, MO, USA

[4]U.S. Geological Survey, Tennessee Cooperative Fishery Research Unit, Tennessee Tech University, Cookeville, TN, USA

[5]U.S. Geological Survey, Alaska Cooperative Fish and Wildlife Research Unit, Institute of Arctic Biology, University of Alaska Fairbanks, Fairbanks, AK, USA

Correspondence
Sarah M. Laske, U.S. Geological Survey, Alaska Science Center, Anchorage, AK, USA.
Email: slaske@usgs.gov

Funding information
Changing Arctic Ecosystems Initiative of the U.S. Geological Survey Ecosystems Mission Area

Abstract

Generalist feeding strategies are favoured in stressful or variable environments where flexibility in ecological traits is beneficial. Species that feed across multiple habitat types and trophic levels may impart stability on food webs through the use of readily available, alternative energy pools. In lakes, generalist fish species may take advantage of spatially and temporally variable prey by consuming both benthic and pelagic prey to meet their energy demands. Using stomach content and stable isotope analyses, we examined the feeding habits of fish species in Alaska's Arctic Coastal Plain (ACP) lakes to determine the prevalence of generalist feeding strategies as a mechanism for persistence in extreme environments (e.g. low productivity, extreme cold and short growing season). Generalist and flexible feeding strategies were evident in five common fish species. Fish fed on benthic and pelagic (or nektonic) prey and across trophic levels. Three species were clearly omnivorous, feeding on fish and their shared invertebrate prey. Dietary differences based on stomach content analysis often exceeded 70%, and overlap in dietary niches based on shared isotopic space varied from zero to 40%. Metrics of community-wide trophic structure varied with the number and identity of species involved and on the dietary overlap and niche size of individual fishes. Accumulation of energy from shared carbon sources by Arctic fishes creates redundancy in food webs, increasing likely resistance to perturbations or stochastic events. Therefore, the generalist and omnivorous feeding strategies employed by ACP fish may maintain energy flow and food web stability in extreme environments.

KEYWORDS
dietary niche, food web, overlap, SIBER, stable isotopes, stomach contents

1 | INTRODUCTION

Adaptive foraging strategies not only allow fish to rapidly respond to changes in food abundance or availability, but insure food availability in fluctuating environments (Hayden, Harrod, & Kahilainen, 2014; Rooney, McCann, Gellner, & Moore, 2006). Food webs with generalist feeders will be more resilient to climatic variability and harshness (Beaudoin, Prepas, Tonn, Wassenaar, & Kotak, 2001). The use of alternative energy pathways and prey switching imparts stability on food webs by dampening oscillations in food resources brought about by environmental variability or predation (Beckerman, Petchey, & Warren, 2006; Rooney et al., 2006) and maintains energy flow when prey species are diminished (Dunne, Williams, & Martinez, 2002; Gravel, Canard, Guichard, & Mouquet, 2011). Also, generalist fishes couple food web compartments (e.g. benthic and pelagic) and transfer energy across habitat boundaries, which could profoundly affect community interactions, nutrient cycling and top-down regulation of the food web (Schindler & Scheuerell, 2002; Vander Zanden & Vadeboncoeur, 2002).

Fluctuating availability of food resources is common in cold-climate regions (Hayden, Harrod, & Kahilainen, 2013; Rautio, Sorvari, & Korhola, 2000), and seasonal variation in prey abundance can affect the trophic ecology of predators (Hayden et al., 2014). Fish often respond to food limitations with high rates of consumption when food becomes available in space or time (Craig, 1984; Prowse et al., 2006), incorporating prey from multiple trophic levels (e.g. macroinvertebrates and fish) or habitats (e.g. terrestrial and aquatic). They may even briefly specialise on abundant prey; however, the breadth of the overall diet remains broad (Amundsen, 1995; McFarland, Wipfli, & Whitman, 2017). Arctic charr (*Salvelinus alpinus*) shift from littoral to pelagic foods with increasing lake size (decreased littoral area) and in the presence of sympatric fish species (Eloranta et al., 2015), demonstrating potential for trophic niche plasticity. For example, if littoral resources are dominated by co-occurring brown trout (*Salmo trutta*), Arctic charr will shift away from littoral macroinvertebrates to pelagic zooplankton, which facilitates coexistence with sympatric species by reducing competitive interactions and consumer-resource oscillations (Eloranta, Knudsen, & Amundsen, 2013; Eloranta et al., 2015; Rooney et al., 2006).

The importance of generalist fishes in coupling energy sources may be prominent in oligotrophic, high-latitude lakes, where relatively simple communities persist (Christoffersen, Jeppesen, Moorhead, & Tranvik, 2008; Eloranta et al., 2013). Temporal and spatial variation in pelagic zooplankton and benthic macroinvertebrate abundance may require fish predators to adapt their feeding strategies or alter their trophic niche to access sufficient resources (Amundsen, 1995; Eloranta et al., 2013). European whitefish (*Coregonus lavaretus*) switch from benthic macroinvertebrates to zooplankton when zooplankton abundance peaks in late summer, a switch that coincides with increased body condition and somatic growth important for overwinter survival (Biro, Morton, Post, & Parkinson, 2004; Hayden et al., 2013, 2014). In response to adverse conditions, some species migrate to seasonal feeding sites to access food resources (Buzby & Deegan, 2000; Heim, Wipfli, Whitman, & Seitz, 2016). For example, Arctic grayling (*Thymallus arcticus*) take advantage of seasonally abundant food at summer feeding sites, which provide energy for rapid growth and accumulation of lipid reserves important for winter survival (Biro et al., 2004; Heim, Wipfli, Whitman, & Seitz, 2016; McFarland et al., 2017). These energy reserves are critical for species that reside in extreme environments like the Arctic (Rautio et al., 2011).

Fish must grow and accumulate sufficient energy stores over a contracted period of time due to the length and severity of an Arctic winter (Biro et al., 2004; McDonald, Hershey, & Miller, 1996). Freeze-up is early on Alaska's 50,000 km^2 Arctic Coastal Plain (ACP) and begins in September, with ice reaching depths of up to 1.8 m deep in lakes, persisting on large lakes until late June or early July (Martin et al., 2009). Because of the persistent cold, the region is underlain by thick permafrost, which is primarily responsible for the formation of related surface features, including ice wedges and associated thermokarst water bodies (Martin et al., 2009). Ice dynamics play an important part in the survival and success of fish by restricting access to viable habitat (Reist et al., 2006). The lakes and streams form a heterogeneous hydrologic network that fish use for migratory routes, feeding areas and seasonal refuge on an area of low relief tundra that spans from the foothills of the Brooks Range to the Arctic coast (Craig, 1984; Heim, Wipfli, Whitman, & Seitz, 2016; Hershey et al., 2006). Lakes are shallow and well-mixed due to strong winds (Grosse, Jones, & Arp, 2013; Laske et al., 2016), often suspending sediments in the water column and supporting greater benthic carbon production for nektonic consumers like zooplankton (Rautio & Vincent, 2006; Rautio et al., 2011). Benthic production may dominate shallow Arctic lakes because of the extreme seasonal photoperiod (24 hr in summer), and sunlight penetration to the bottom of clear, oligotrophic lakes (Rautio et al. 2011; Sierszen, McDonald, & Jensen, 2003).

The extreme seasonality and physiological challenges of the cold Alaskan Arctic limit biotic diversity in the region (Prowse et al., 2006). Only fifteen species of fish occupy lentic habitats on the ACP (Alaska Freshwater Fish Inventory, Alaska Department of Fish and Game, accessed October 2016), but little is known regarding their dietary habits, trophic niches, or associated food webs. A handful of studies offer information regarding individual species' diets, but fall short of cross-species comparisons or community analyses (e.g. Alaska blackfish [*Dallia pectoralis*] in Ostdiek & Nardone, 1959; ninespine stickleback [*Pungitius pungitius*] in Cameron, Kostoris, & Penhale, 1973; Arctic grayling and ninespine stickleback in McFarland et al., 2017). Additional studies in the neighbouring foothills region, near Toolik Lake, provide information regarding trophic ecology for several of these species (e.g. lake trout [*Salvelinus namaycush*], round whitefish [*Prosopium cylindraceum*] and Arctic grayling in Merrick, Hershey, & McDonald, 1992; slimy sculpin [*Cottus cognatus*] in Cuker, McDonald, & Mozley, 1992) that could than provide useful comparison across physiographic regions of the Arctic (Jorgenson & Grunblatt, 2013).

Determining the current trophic ecology of fishes in the ACP is important for understanding energy flow and mechanisms that face disruption from resource development and climate change (Schindler & Smol, 2006). The fish species in this region are important as a native subsistence resource, as prey for multiple species of water birds and, along with their habitats, as indicators or sentinels of environmental change (Adrian et al., 2009; Christiansen et al., 2013; Haynes et al., 2015; Reist et al., 2006). Human development associated with oil and gas extraction (e.g. roads and wells) on the National Petroleum Reserve Alaska—where this study is located—can affect hydrologic processes important for resident organisms (Schindler & Smol, 2006; Walker et al., 1987). Furthermore, the region's climate has warmed rapidly in recent decades, with temperature increases at twice the global average. Mean annual air temperature of −10.3°C and mean summer air temperature of 7.1°C were recorded between 2006 and 2012 on the central ACP (U.S. Geological Survey's Ikpikpuk meteorological station; Urban & Clow, 2013). Future climate projections for the region indicate an annual temperature increase of 7.3°C by the end of the century (Martin et al., 2009). These changes coincide with milder winters, warmer summers and longer ice free seasons that may provide more opportunities for human development (Schindler & Smol, 2006; Wrona et al., 2006). Climatic changes may also enhance planktonic primary production (Rautio et al., 2011) and increase fish

metabolic needs and their associated food requirements (Reist et al., 2006). The balance between available food and metabolic need will ultimately determine future fish production (Carey & Zimmerman, 2014; McDonald et al., 1996). Under changing conditions, a generalist feeding strategy will allow fish to shift to readily available resources, imparting food web resilience to new climatic patterns (Eloranta et al., 2015; Hayden et al., 2014).

We aim to describe the diets of fishes residing in lakes of the ACP, Alaska, where little information is currently available. We then describe the dietary strategies of these fishes by examining stomach contents and isotopic niches. Because generalist ecological traits are beneficial in variable or severe environments (Beaudoin et al., 2001), we anticipate that fishes of the ACP (at the level of species or size class) will exhibit generalist or flexible feeding patterns and trophic omnivory—either consuming prey across habitat boundaries (i.e. benthic and pelagic/nektonic) or on different trophic levels. At the community level, we anticipate trophic redundancy among fish species and overlapping trophic niches due to the use of shared prey resources, which may contribute to overall stability and resilience in food web structure as energy pathways are maintained in the presence of differing fish assemblages (Eloranta et al., 2015; Rooney et al., 2006).

2 | METHODS

We sampled fish from 16 lakes (mean surface area 0.7 km², mean depth 2 m) at two locations (eight lakes at each) on the Arctic Coastal Plain of Alaska (Figure 1). Over three summer seasons (2011–2013), we collected fishes using unbaited minnow traps (6-mm steel mesh, 23 cm diameter and 44.5 cm length with two 2.5 cm openings), fyke nets (0.6 cm mesh, 15.2 × 1.2 m wings and a 1.1 m square opening; or 0.6 cm mesh, 9 × 1 m wings and a 1 m diameter opening) and gill nets (24.8 × 1.8 m, eight panels with mesh size from 19 to 64 mm [North American standard, Lester, Bailey, & Hubert, 2009]). Each lake was sampled a minimum of four days over the span of the study, with a minimum of 6 hr of fishing per sampling event. In 2011, fyke nets were deployed overnight (up to 16 hr). During the 2012–2013, we deployed gear over short time intervals (3–4 hr) to reduce losses of prey items due to digestion and to limit the potential for net feeding. Additional overnight net sets were employed during 2013 to capture more fish for stable isotope samples.

At each lake, we sampled stomach contents from up to approximately 30 individuals of each species, depending on availability. All sample collections were performed under a University of Alaska Fairbanks Institutional Animal Care and Use Committee protocol (#233290), by sedating fish with a 20–30 mg/L clove oil solution (nonlethal sampling) or by severing the head from the spinal cord (lethal sampling). We sampled diets via nonlethal gastric lavage using a 60-ml syringe filled with filtered water and a 5 Fr catheter tube, or after euthanasia by direct collection of the stomach. We preserved contents from all stomachs with 95% ETOH. To determine feeding positions relative to one another and species dietary niches (Layman, Arrington, Montaña, & Post, 2007; Post, 2002), we collected muscle tissue for
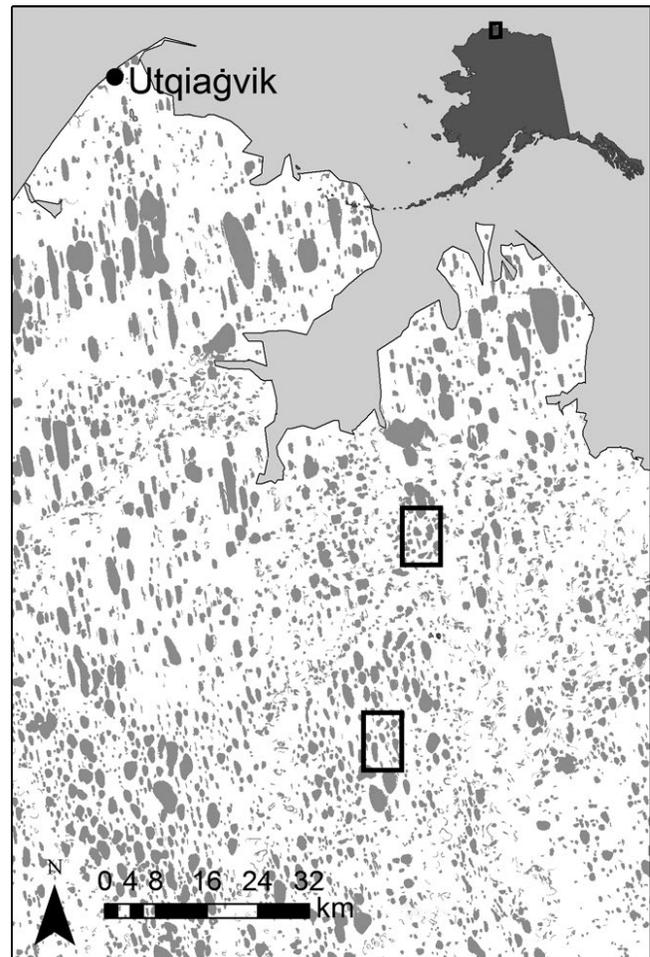
FIGURE 1 Study sites on the Arctic Coastal Plain of Alaska (inset) where common fish species were sampled for diet analysis. Stomach contents were collected at both sites and stable isotopes were collected at the northern most site

stable isotopes for each captured species at eight lakes (northern site only)—up to 11 individuals per available species per lake. With a scalpel, we extracted a small plug of dorsal muscle from the left side of the fish, anterior to the dorsal fin and preserved muscle plugs in 95% ETOH. Small fishes (<45 mm length) were preserved and ground whole for stable isotope analysis (Swanson, Kidd, & Reist, 2010). Further, we collected primary consumer stable isotopes from 10 snails (Gastropoda) from the same lakes at the northern site and preserved them in 95% ETOH.

We identified stomach contents to the lowest practical taxonomic level. For example, for items in good condition, we identified to the family level for macroinvertebrates and cladoceran zooplankton and to order for copepods. When digestion interfered with identification of prey, we identified organisms as low as possible, typically to the order level. Unidentifiable organic material was classified as well digested material. We also specified the life stage of prey (e.g. larva). Any invertebrate prey of terrestrial origin was identified to order when possible.

We placed fish muscle tissue and snail tissues (with shell removed) into individual 4 ml glass vials and freeze-dried at −50°C for 48 hr (LABONCO FreeZone 1 Liter Benchtop Freeze Dry Systems 77400

Series, Kansas City, MO). Once dry, we used petroleum-ether to extract any remaining lipids (Kelly & Martínez del Rio, 2010). Storing tissues in ETOH removed much of the tissue's lipid prior to formal extraction; therefore, only 48 hr of submersion in petroleum-ether was required. Tissues air-dried for 24 hr. We sent all samples to the Stable Isotope Facility at the University of Wyoming, Laramie, where they ground and analysed samples for of $\delta^{15}N$ and $\delta^{13}C$ with a continuous flow stable isotope ratio mass spectrometer (Costech 4010, Carlo Erba 1110, Thermo Flash Elemental Analyzer coupled to a Thermo Delta Plus XP and Delta V IRMS). Analytic precision was ±0.2‰, with standards L-glutamic acid and liver (36-UWSIF-Glutamic 1, $\delta^{15}N_{AIR}$ = −4.6‰, $\delta^{13}C_{VPDB}$ = −28.3‰; 39-UWSIF-Glutamic 2, $\delta^{15}N_{AIR}$ = 27.9‰, $\delta^{13}C_{VPDB}$ = 24.4‰; and UWSIF01 [Liver], $\delta^{15}N_{AIR}$ = −6.8‰, $\delta^{13}C_{VPDB}$ = −17.8‰).

2.1 | Data analysis

All analyses of stomach contents were performed at the order level or higher to establish consistency across samples and the degree of digestion, although at the expense of reducing taxonomic resolution. We did not include parasites within prey items (e.g. Nematomorpha or Cestoda) in the analyses because they were not directly consumed. Empty stomachs were not included in analyses. Nine individuals of three species (Arctic grayling, Alaska blackfish and least cisco) were included from the 2011 overnight samples to supply missing dietary information for two lakes. We examined the feeding strategy of each fish species, pooling individuals from all lakes, by plotting the prey-specific abundance against frequency of occurrence based on number of prey consumed. Prey-specific abundance is the proportion prey *i* constitutes of all prey items in predators that contain prey *i* (see Amundsen, Gabler, & Staldvik, 1996 and Chipps & Garvey, 2007 for more detail). Frequency of occurrence is defined as the proportion of fish with a given prey item in its stomach (Chipps & Garvey, 2007). The foraging plots show a generalised diet and high within-individual variation (i.e. high prey variety in individual stomachs) when points fall on the lower portion of the graph. Dietary specialisation is represented on the upper portion of the graph, with individuals showing specialisation of specific prey in the upper left and populations showing specialisation in the upper right. Flexible or mixed strategies show both individuals that are specialised and individuals are generalist (Amundsen et al., 1996; Chipps & Garvey, 2007). When all points are located along or below the diagonal from upper left to lower right, the species has a broad niche width (Amundsen et al., 1996).

Mean numeric proportion of each consumed taxa was calculated for individual fish species within each lake. We assume that the diets of all fish species captured in a lake represent the "snapshot" of diet for that species in space and time. Values were averaged across lakes, and 95% standard error calculated when fish occurred in more than one location (Chipps & Garvey, 2007). Differences were determined through a multivariate analysis of variance with function adonis in R (PERMANOVA; vegan, R package 2.4-1) on the Bray–Curtis distances of the mean numeric proportions, excluding unidentifiable, well digested material. We determined the contribution of potentially

influential diet items as those that contributed to at least 70% of the dissimilarity between species pairs (pairwise comparison of each fish species); the inclusion of one additional, unique species beyond those already included in all pairwise comparisons added little to the total amount of variation (≤6%). We also determined the overall per cent dissimilarity in diets between each fish species pair (SIMPER; vegan, R package version 2.4-1).

We analysed stable isotopes for the same fish species as those included in stomach content analyses. We examined data for correlations between fish length and $\delta^{15}N$ for each species. Also, fourteen fish between 55 and 60 mm length, from two genera (*Pungitius* and *Coregonus*), were used to test for differences in mean carbon and nitrogen signatures of whole body and muscle—to determine whether whole body samples could be compared to muscle samples when inadequate amounts of muscle tissue were available from small fish. To correct for variation in $\delta^{15}N$ at the base of the food web, we estimated species trophic positions (TP) using the following equation from Vander Zanden, Olden, Thorne, and Mandrak (2004) for individual fish:

$$TP_{consumer} = \frac{\delta^{15}N_{consumer} - \delta^{15}N_{baseline}}{3.4} + 2$$

where 3.4 is the trophic enrichment factor, and primary consumers are at level two. The nitrogen stable isotope signature of snails (Gastropoda) was averaged within each water body and used as the baseline in these shallow lakes. We then calculated the average trophic position for each species and determined whether differences in species trophic positions were biologically meaningful (i.e. equal to or greater than one trophic level). We could not correct for the differences in carbon baselines, and the calculation of niche area across an isotopically heterogeneous region would artificially inflate the breadth of species dietary niches. Therefore, we examined metrics of isotopic niche area, overlap and community-wide measures of trophic structure on an individual lake basis (Jackson, Inger, Parnell, & Bearhop, 2011; Layman et al., 2007; SIBER, R package version 2.1.3), but summarised findings for the region as a whole.

In each sampled lake, we determined the niche area (posterior standard ellipse area, SEA_B) of each occurring species using a Bayesian method, which is unbiased with respect to sample size (SEA_B contains *c.* 40% of the data regardless of sample size) and propagates uncertainty in the mean (Jackson et al., 2011). We then used species' posterior ellipses (from Markov chain Monte Carlo [MCMC] simulations in rjags, R Package version 4-6) from each lake to calculate the values of three community-wide measures of trophic structure to provide measures of trophic diversity (mean distance to centroid, CD), redundancy (mean nearest neighbour distance, MNND) and distribution of niches (standard deviation of nearest neighbour distance, SDNND; Layman et al., 2007). We visually assessed species dietary niche overlap by examining plots of species ellipses that encircled one standard deviation of the bivariate data. We also determined overlap as a proportion of nonoverlapping area, based on one standard deviation of the bivariate data, between each pair of species as an average across all lakes where that species pair occurred.

TABLE 1 Sample sizes (SCA—stomach content analysis, SIA—stable isotope analysis) and fish species' trophic position (TP) and standard ellipse area (SEA$_B$) for the common fishes of the central Arctic Coastal Plain, Alaska

Species	Length (SD)	n SCA	n SIA	TP (SD)	n Lakes	SEA$_B$ Mode	95% L CI	95% U CI
Alaska blackfish	63 (34)	24	21	3.3 (0.3)	5	0.29	0.05	3.65
Ninespine stickleback	47 (11)	429	81	3.5 (0.5)	8	2.22	0.86	5.27
Least cisco (small)	50 (23)	40	22	3.2 (0.3)	4	0.14	0.04	1.07
Least cisco (large)	229 (58)	49	24	3.7 (0.6)	3	0.95	0.26	5.22
Whitefish spp.	65 (18)	38	12	3.3 (0.2)	1	0.80	0.42	1.56
Broad whitefish	400 (147)	15	18	3.7 (0.5)	2	1.17	0.46	11.03
Arctic grayling	173 (58)	20	13	3.5 (0.6)	2	0.57	0.15	6.65

Mean total length (SD) for Alaska blackfish and ninespine stickleback and mean fork length (SD) for all other species were determined from all fish (n SCA). Mean trophic position (SD) was determined from fish sampled in SIA, and the SEA$_B$ mode and upper and lower 95% credible intervals was estimated from SIA samples in lakes (n Lakes) where species occurred. Ellipse areas used in the estimation of SEA$_B$ contain c. 40% of the data.

3 | RESULTS

We collected stomach contents and muscle tissues from 10 fish species: Alaska blackfish, ninespine stickleback, least cisco (*Coregonus sardinella*), broad whitefish (*Coregonus nasus*), Arctic grayling, slimy sculpin, humpback whitefish (*Coregonus pidschian*), Arctic charr, pike (*Esox lucius*) and rainbow smelt (*Osmerus mordax*). Five species provided limited dietary information (<10 individuals from ≤2 lakes) and were not included in the analysis: slimy sculpin, humpback whitefish, Arctic charr, pike and rainbow smelt. Detailed information on their diets and the diets of the fishes used in the analysis (Table 1) can be found in Appendix A (stomach contents) and Appendix B (stable isotopes). Least cisco was the only species among the five that increased in δ^{15}N over the range of sampled lengths (r = .81). Further, given the distribution of data, we were able to partition least cisco into two groups that allowed us to examine their diets according to size class and to account for potential ontogenetic shifts, small least cisco ≤100 mm FL and large least cisco >100 mm FL (see Table 1 for mean length). Small whitefish, <130 mm FL, either broad whitefish or humpback whitefish, could not be distinguished to the species level in the field and were considered as one group, whitefish spp.

Feeding strategy plots indicated that fishes had either a generalist or flexible feeding strategy (Figure 2). Alaska blackfish, ninespine stickleback and large least cisco had broad niche widths (Figure 2a, b, d); each point on the feeding strategy plots fell below the diagonal from upper left to lower right. Ninespine stickleback, as a species, consumed the greatest variety of prey; however, few individual fish consumed as great a variety, indicating that feeding may have been habitat or location specific. High prey-specific abundance of Gastropoda in broad whitefish diets (Figure 2f) and Diptera larva in Arctic grayling diets (Figure 2g) indicated greater use of those prey in conjunction with a broader prey base. Prey-specific abundance of Cladocera, Diptera larva and harpacticoid copepods in small least cisco diets (Figure 2c) and Trichoptera larva and Cladocera in whitefish spp. diets (Figure 2e) suggested that several prey, especially small zooplankton, were

important. However, all feeding strategy plots showed prey above and below the diagonal from lower left to upper right, indicating all fish species demonstrated some mixed foraging, with both high between-individual and high within-individual variation in feeding strategies. Most prey of broad whitefish and large least cisco fell below this line, indicating that variation within-individual diets were more typical for the species (Figure 2d, f).

Mean numeric proportion of stomach contents differed by species (PERMANOVA of 1,000 permutations; R^2 = .29, p < .001). Further examination of pairwise differences in diets through SIMPER provided estimates of average per cent dissimilarity between species. Dietary differences often exceeded 70%, with 19 of 21 pairwise comparisons showing little similarity in overall stomach content composition. Ninespine stickleback and Arctic grayling differed by an average of 67%, and ninespine stickleback and small least cisco differed by an average of 57%. Further, we identified prey items that cumulatively explained 70% of the variation in pairwise difference between fish species stomach contents. This amount of variation was described with three to six prey items per fish species pair, and a total of 12 prey items accounted for all of the differences: Notostraca, Gastropoda, Ostracoda, Hydrachnidia, Nematoda, Diptera larvae, Trichoptera larvae, Calanoida, Cladocera, Diptera pupae, aquatic Diptera adults and fish (Figure 3).

Alaska blackfish (n = 26, 7.7% empty) regularly consumed (frequency of occurrence ≥50% and/or mean numeric proportion ≥0.1) benthic invertebrate taxa of Diptera larvae, Gastropoda and Ostracoda, and fish (93% identified as ninespine stickleback; Figures 2a and 3a). Stomachs of ninespine stickleback (n = 468, 8.3% empty) contained 30 different taxa—more than any other fish species—but cladoceran zooplankton and Diptera larvae and pupae made up the largest numeric proportion with the greatest frequency of occurrence (Figures 2b and 3b). Small least cisco (n = 43, 7.0% empty) also consumed cladoceran zooplankton and Diptera larva and pupa (Figure 3c), but had reduced frequency of occurrence and a narrower selection of diet items, 13, than ninespine stickleback (Figure 2b,c). The ontogenetic shift in large
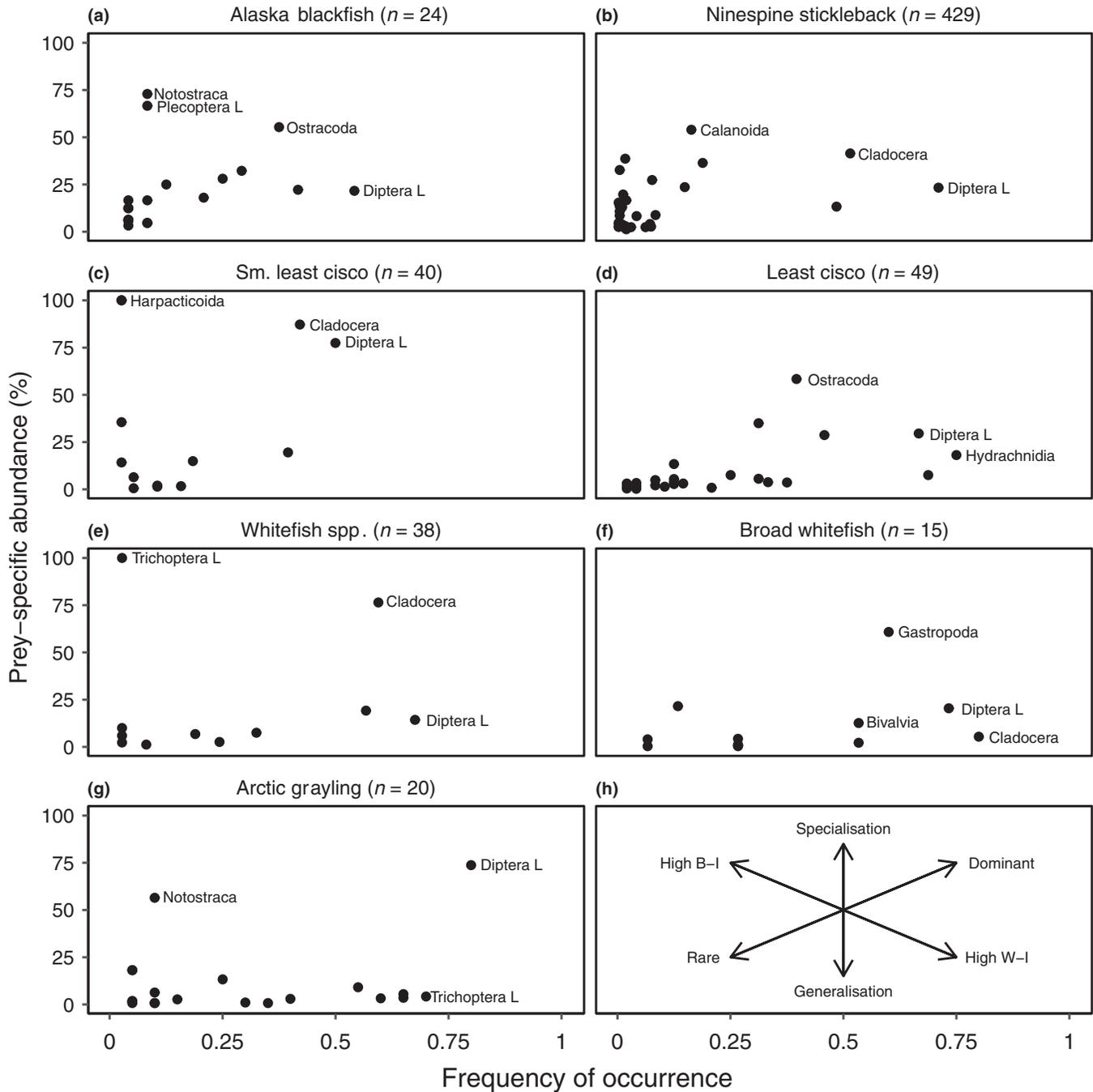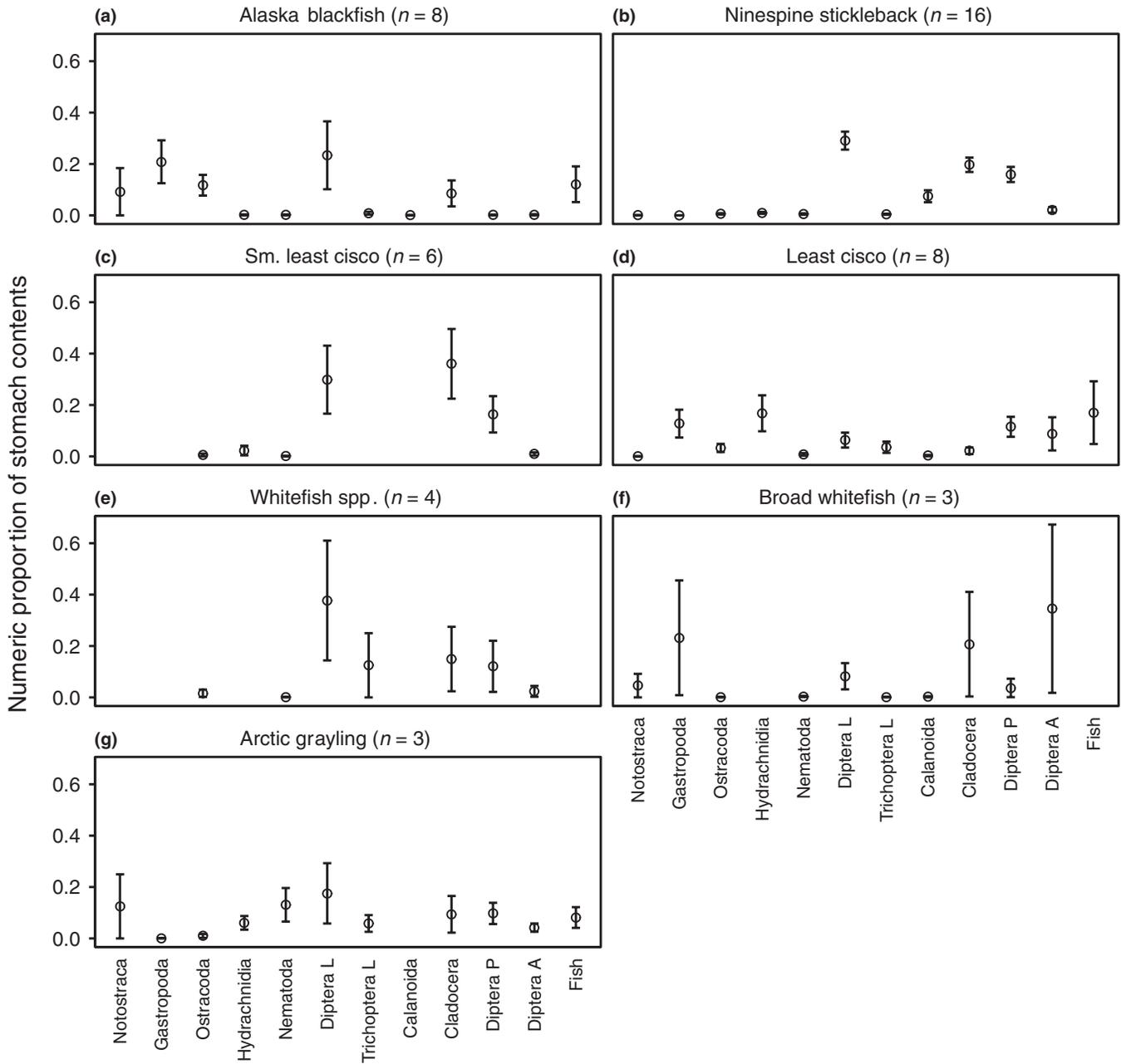
FIGURE 2 Feeding strategy plots for (a) Alaska blackfish, (b) ninespine stickleback, (c) small least cisco, (d) least cisco, (e) whitefish spp., (f) broad whitefish and (g) Arctic grayling in lakes on the Arctic Coastal Plain. Points represent individual prey taxa; taxa with high prey-specific abundance or high frequency of occurrence are labelled. The lower right plot (h) offers an explanatory diagram for point distribution (adapted from Amundsen, 1995). Above each plot, the names of the species and the number of stomachs included in the analysis are given. Small least cisco (sm. least cisco) are those ≤100 mm FL, and least cisco are >100 mm FL. L = larva.

least cisco (n = 49, 0 empty) led to an increase in the variety of diet items (n = 24), including fish (90% identified as ninespine stickleback), Hydrachnidia, Gastropoda and Diptera pupae (Figure 3d).

Small whitefishes (n = 47, 19.1% empty) consumed Diptera and Trichoptera larvae, Diptera pupae and Cladocera (Figure 3e). However, they did not consume benthic organisms that adult broad whitefish (n = 16, 6.3% empty) consumed, such as snails (Gastropoda) and bivalves (Bivalvia; Figure 3f). Arctic grayling (n = 20, 0 empty) consumed

small proportions of prey items, and mean numeric proportion never exceeded 0.20 for any taxa; only Diptera larvae, Nematoda and Notostraca averaged >0.10 (Figure 3f). However, frequency of occurrence was high for six taxa, including fish (95% identified as ninespine stickleback) and Trichoptera larvae (Figure 2f).

For small fish, when comparing whole body signatures to muscle tissue only signatures, no biologically meaningful differences were found ($\delta C^{13}_{tissue} - \delta C^{13}_{body} = -0.21 \pm 0.07‰$ and

FIGURE 3 Mean numeric proportion (±1 *SE*) of important prey items found in the stomachs of (a) Alaska blackfish, (b) ninespine stickleback, (c) small least cisco, (d) least cisco, (e) whitefish spp., (f) broad whitefish and (g) Arctic grayling in lakes on the Arctic Coastal Plain. Prey shown here accounted for up to 70% of the variation in pairwise differences in fish diet and are arranged from left to right from benthic to nektonic. Above each plot, the species name and number of lakes where the species occurred is given. Small least cisco (sm. least cisco) are those ≤100 mm FL, and least cisco are >100 mm FL. A = adult, L = larva, P = pupa.

$\delta N^{15}_{tissue} - \delta N^{15}_{body} = 0.38 \pm 0.15‰$). Carbon values did not differ from analytical precision (0.2‰), and nitrogen difference was far less than 3.4‰ that constitutes a trophic level; therefore, whole fish were used for analyses when necessary. The overall mode of isotopic niche area (SEA_B) for each fish species ranged from 0.14‰^{2} for small least cisco to 2.22‰^{2} for ninespine stickleback (Table 1). Broad whitefish SEA_B exhibited the greatest variation, given their niche upper and lower bound of 0.46–11.03‰^{2}. Variation in SEA_B was lowest for small least cisco, (0.04–1.07‰^{2}) suggesting bivariate isotope signatures were consistently tightly clustered in lakes where they occurred

(n = 4). Yet SEA_B did not differ across species based on overlapping 95% credible intervals.

We examined niche overlap of species pairs in six of the eight lakes at the northern site, because isotopic data were available for only one species, ninespine stickleback, in two lakes. Overlap, as a proportion of nonoverlapping area, was found for 17 of 21 species pairs. Greatest overlap occurred between broad whitefish and least cisco niches at 41.6%; however, this was only documented in one lake (Table 2). Ninespine stickleback stable isotope niches overlapped with all species, with the exception of small whitefish spp. Small whitefish

Species pair		Overlap	SD	n Lakes
Broad whitefish	Least cisco	0.416		1
Arctic grayling	Ninespine stickleback	0.332	0.238	2
Broad whitefish	Ninespine stickleback	0.245	0.008	2
Arctic grayling	Broad whitefish	0.176		1
Least cisco	Ninespine stickleback	0.137	0.109	3
Arctic grayling	Least cisco	0.129		1
Alaska blackfish	Broad whitefish	0.105	0.127	2
Alaska blackfish	Ninespine stickleback	0.091	0.083	5
Alaska blackfish	Sm. least cisco	0.052	0.089	3
Alaska blackfish	Arctic grayling	0.040	0.047	2
Alaska blackfish	Least cisco	0.038	0.053	2
Alaska blackfish	Whitefish spp.	0.029		1
Arctic grayling	Sm. least cisco	0.025	0.022	2
Sm. least cisco	Ninespine stickleback	0.017	0.024	4
Sm. least cisco	Whitefish spp.	0.013		1
Broad whitefish	Sm. least cisco	0.010		1
Least cisco	Sm. least cisco	0	0	3
Arctic grayling	Whitefish spp.	0		1
Broad whitefish	Whitefish spp.	0		1
Least cisco	Whitefish spp.	0		1
Ninespine stickleback	Whitefish spp.	0		1

TABLE 2 The proportion of overlap in dietary niches based on one standard deviation of the bivariate (δ^{13}C and δ^{15}N) data for standard ellipse area

The proportion overlap is ranked from highest overlap to lowest overlap. When species pairs occurred in more than one lake the mean proportion overlap, standard deviation and number of lakes where each species pair occurred is given. Ellipse areas are corrected for small sample size. Small least cisco (sm. least cisco) are those ≤100 mm FL, and least cisco are >100 mm FL.

spp. niches seldom overlapped with other fishes. In only one instance, they overlapped by 1.3% with small least cisco (Table 2). Small least cisco niches also overlapped with Alaska blackfish (5.2%), Arctic grayling (4.0%), ninespine stickleback (1.7%) and broad whitefish (1.0%). However, niches of small least cisco did not overlap with those of large least cisco in any of the three lakes where they co-occurred. Most species displayed some amount of dietary niche overlap either in carbon signature, nitrogen signature or both (Figure 4). Nitrogen values varied across species, but, when corrected for a primary consumer baseline, we found no biological differences in trophic position (Table 1). In fact, mean trophic position spanned only half of one trophic level from 3.2 for small least cisco to 3.7 for large least cisco and broad whitefish. Carbon values of the fish assemblages centred near −28 to −27‰ δ^{13}C in each of the six lakes (Figure 4), with many of the species overlapping in carbon signatures—suggesting either averaging of disparate carbon resources (e.g. pelagic and benthic) or use of a single carbon resource (e.g. benthic only).

Lakes did not follow a prescribed pattern of community-wide trophic structure, rather, overlap in isotopic niche area and metrics of community-wide trophic structure varied with the number and identity of fish species present in a lake (Figure 4). The degree of trophic diversity, measured by CD, was greatest in lakes where species occupied discrete isotopic niches, with little to no overlap (Figure 4b, CD = 1.55) and was lowest in lakes where all of the sampled species' niches

overlapped (Figure 4c, CD = 0.48; and Figure 4d, CD = 0.99). The measure of density and clustering of species, MNND, which declines in webs with overlapping trophic ecology or increasing trophic redundancy, was reduced in lakes where species niches are tightly clustered (Figure 4a, MNND = 0.70; and Figure 4c, MNND = 0.61). The MNDD increased among fish assemblages with divergent trophic niches—or less overlap (Figure 4b, MNND = 2.04; and Figure 4d, MNND = 1.97). In agreement with the other two metrics, SDNND, which measures the evenness of species isotopic distributions, was highest also where species niches occupied discrete evenly spaced niches (Figure 4b, SDNND = 0.49). Lower SDNND values indicate even distribution of trophic niches—or similar use of bi-plot space by species (Figure 4f, SDNND = 0.17).

4 | DISCUSSION

Based on analysis of stomach contents and stable isotopes, Alaska blackfish, Arctic grayling, broad whitefish, least cisco and ninespine stickleback demonstrated use of generalist or flexible feeding strategies. All fish species foraged on benthic macroinvertebrate and zooplankton prey, and, therefore, across habitat boundaries. Fish feeding strategies that capitalise on a broad assortment of prey are common in stressful or variable environments where generalist ecological traits
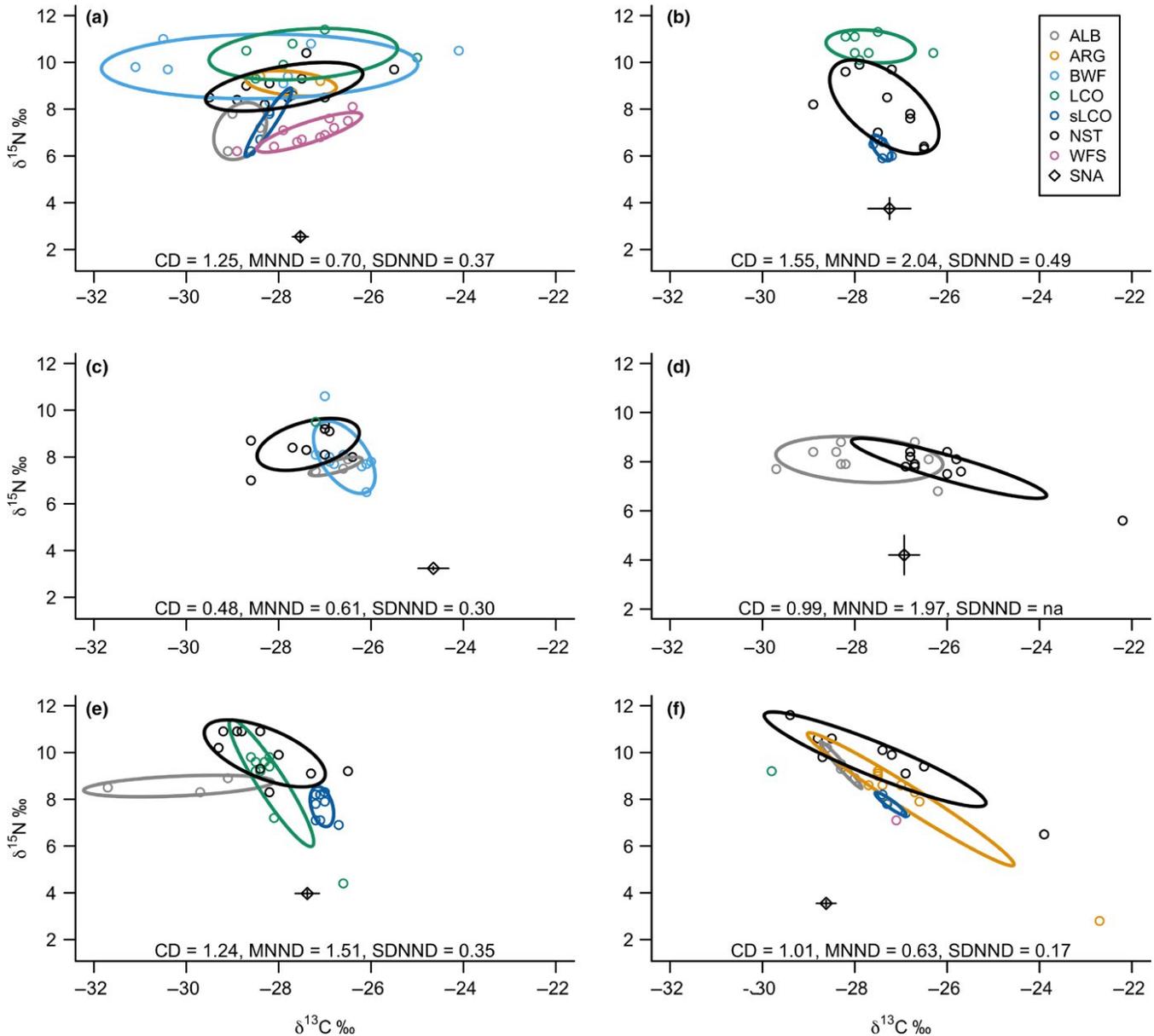
FIGURE 4 Stable isotope ellipses encircling one standard deviation of the bivariate data for fish species captured in six lakes on the Arctic Coastal Plain, Alaska. Points for individual fish and the carbon baseline (±1 *SE*) are shown. Layman metrics for each fish community are shown in the plots; CD, mean distance to centroid; MNND, mean nearest neighbour distance; SDNND, standard deviation of nearest neighbour distance. ALB, Alaska blackfish; ARG, Arctic grayling; BWF, broad whitefish; LCO, least cisco (>100 mm FL); sLCO, small least cisco (≤100 mm FL); NST, ninespine stickleback; WFS, whitefish spp. and SNA, snail (carbon baseline)

are beneficial (Beaudoin et al., 2001; Eloranta et al., 2015; Sternberg, Balcombe, Marshall, Lobegeiger, & Arthington, 2012). Further, the variability in community-wide measures of food web structure (i.e. Layman metrics) across lakes was related to both the composition of species and their dietary niche, which may signify the importance niche plasticity for species that occur in lakes with different fish assemblages (Eloranta et al., 2015; Hayden et al., 2014). Species partitioned their short-term resource use (based on high dissimilarity in stomach contents); however, overlapping dietary niches (based on stable isotope niche breadth) indicated a shared use of basal resources. Therefore, energy pathways from the base of the food chain to the top may travel along different or redundant routes depending on the

richness and composition of the fish species assemblage (Eloranta et al., 2013; Swanson et al., 2010).

The observed overlap of isotopic ellipses indicated that adult fish species used similar carbon sources in ACP lakes (Sierszen et al., 2003; Vander Zanden & Vadeboncoeur, 2002), however, it is unclear whether similarities arose from averaged use of pelagic (lower $\delta^{13}C$ values) and benthic (higher $\delta^{13}C$ values) carbon or from one unique carbon source. The average snail $\delta^{13}C$ baseline for all of the northern site lakes was −27.2 ± 0.4‰, which is similar to the average carbon signatures of sampled fish assemblages. Research on the productivity of shallow Arctic lakes indicates that benthic carbon (in the form of periphyton) supplies much of the energy to the system (Hecky & Hesslein, 1995;

Sierszen et al., 2003). Clear water, constant summer sunlight and expansive littoral areas accommodate high benthic production in shallow lakes. Also, some species of cladoceran zooplankton may graze benthic mats directly or filter out benthic material suspended by wind-induced mixing, creating an alternative pathway for benthic algae to reach fishes (Rautio & Vincent, 2006). Therefore, it is plausible that generalist fishes, which consume a mixture of prey from the benthos and water column, may rely heavily on periphyton-derived carbon in these lake food webs (Sierszen et al., 2003).

Trophic redundancy, or fish with similar trophic ecologies, is likely in lakes with high fish species richness and multiple top predators, because more fish may exhibit overlapping dietary niches (Layman et al., 2007; Thomas et al., 2016). The integration of food web compartments, via omnivory, is also prominent in small, climatically variable lakes, where piscivores feed on a mixture of fish and abundant invertebrate resources at lower trophic levels (Beaudoin et al., 2001; Eloranta et al., 2015). Based on stomach contents and stable isotope signatures, Alaska blackfish, Arctic grayling and large least cisco could clearly be considered omnivorous—consuming both fish and invertebrate prey. Overwhelmingly, the fish prey most often consumed was ninespine stickleback; and Alaska blackfish, Arctic grayling and large least cisco that consumed ninespine stickleback also consumed their shared prey resources. Even in lakes where fish clearly separated in their niches and trophic diversity was high, piscivorous fish (e.g. large least cisco) were rarely enriched a full trophic level in $\delta^{15}N$ compared to fish prey, likely because of a generalist diet comprised of high and low trophic level foods (Eloranta et al., 2015). Interestingly, even species that did not consume fish exhibited signs of omnivory in their trophic position, as average trophic position fell between whole values at trophic levels 3 and 4 (Svanbäck, Quevedo, Olsson, & Eklöv, 2015). Variation in fish species trophic position often results from a combination of highly flexible or opportunistic feeding or from variation in the trophic position of prey (Vander Zanden, Cabana, & Rasmussen, 1997).

Our findings, and those from other studies at northern latitudes (boreal and Arctic regions), showed omnivory and the use of benthic and pelagic prey in adult fishes (Beaudoin et al., 2001; Hayden et al., 2014; Merrick et al., 1992). For example, Alaska blackfish sampled southeast of Utqiaġvik (formerly Barrow, Alaska), consumed high proportions of benthic Diptera larvae and Ostracoada, and free-swimming Cladocera (Ostdiek & Nardone, 1959); stomach contents similar to Alaska blackfish captured in this study. Ninespine stickleback also have flexible diets in other ACP lakes and streams (Cameron et al., 1973; McFarland et al., 2017). They consumed a combination of Chironomidae larvae, Copepoda and Cladocera in a small lake near Utqiaġvik (Cameron, Kostoris, & Penhale), and additional benthic macroinvertebrates, Ephemeroptera and Trichoptera, in a small beaded stream (McFarland et al., 2017). Ninespine stickleback track prey according to availability and shift their diets as necessary to maintain foraging (Delbeek & Williams, 1988; Laske, Rosenberger, Kane, Wipfli, & Zimmerman, 2017). These fish were found to mediate energy transfer from littoral habitats up the food chain to fish predators (Gallagher & Dick, 2011), providing another pathway for littoral benthic carbon to reach upper level consumers.

Arctic grayling foraged on a wide array of prey. This species consistently uses flexible strategies and seasonally shifts their diet in locations throughout their range in high latitude and elevation habitats (Cutting, Cross, Anderson, & Reese, 2016; McFarland et al., 2017). Commonly thought of as an insectivore (Morrow, 1980), Arctic grayling will also feed on small fish (McFarland et al., 2017; Miller, 1946; Stewart, Mochnacz, Reist, Carmichael, & Sawatzky, 2007). Up to 90% of the summer diet of ACP Arctic grayling (>150 mm FL) was comprised of ninespine stickleback (McFarland et al., 2017). By contrast, Arctic grayling from the Toolik Lake region, in the Brooks Range foothills, consumed only invertebrates—benthic macroinvertebrates, snails and pelagic zooplankton (Merrick et al., 1992). Presumably, this dietary difference was due to the high availability of small ninespine stickleback on the coastal plain (elevation <20 m) compared to the absence of ninespine stickleback in the foothills region (elevation ~730 m).

Piscivory could elevate the relative trophic position of omnivores like Arctic grayling; however, analysis of trophic position and stable isotope niches indicated that fish spanned a single trophic level, with species like Arctic grayling in intermediate positions. In fact, top predators—those that consume fish—in ACP lakes may have more omnivorous or generalist diets, due to combined reliance on macroinvertebrates, zooplankton and fish, compared with top predators in relatively more stable habitats (e.g. large, deep lakes [Eloranta et al., 2015] or reduced disturbance [Beaudoin, Prepas, Tonn, & Wassenaar, 1999]). The trophic position of adult least cisco was less than a half of a trophic level above their fish prey (ninespine stickleback). Interestingly, least cisco, Alaska blackfish and Arctic grayling overlapped in dietary niche with ninespine stickleback, which not only suggested reliance on the same invertebrate prey resources, but indicates an averaging of the predators' trophic position between lower trophic level invertebrates and higher trophic level fish prey (Vander Zanden et al., 1997). Limitations on forage fish availability may result in increased omnivorous foraging. For example, after a winterkill event reduces the number of fish prey, the piscivore may respond by consuming lower trophic level organisms (e.g. benthic macroinvertebrates) that are readily available (Beaudoin et al., 2001).

Least cisco may be one of the top-generalist predatory fish in ACP lakes. Their niche location represented a midrange of carbon values and relatively elevated trophic position, and their broad foraging pattern indicated that this species linked energy sources from across habitats and transferred that energy up trophic levels (Schindler & Scheuerell, 2002; Vander Zanden & Vadeboncoeur, 2002). Small least cisco had smaller trophic niches discrete from adults of the same species, arguably due to a combination of age and diet. Ontogenetic shifts in these fishes should expand and shift the dietary and isotopic niche to incorporate large crustaceans, snails, and fish as they grow (Hammerschlag-Peyer, Yeager, Araújo, & Layman, 2011). Similar to large least cisco in ACP lakes, mature least cisco (>250 mm FL) in Trout Lake, Yukon Territory consumed an omnivorous diet of benthic invertebrates, surface insects and fish (Mann & McCart, 1981). Trout lake, at 9 m maximum depth, would be considered deep when compared to lakes of the ACP, however, it shares several fish species (broad whitefish, Arctic grayling and ninespine stickleback) with ACP lake communities. Interestingly, least cisco in Trout Lake exist as either a normal or

dwarf form, with the dwarf consuming fewer benthic organisms (e.g. snails) in favour of zooplankton. Whitefish divergence commonly leads to separation between pelagic and littoral morphs with discrete habitat and prey use patterns, a process that is documented in European whitefish (e.g. Hayden et al., 2014; Siwertsson et al., 2010). The reason both forms exist in sympatry may be related to interspecific competition for food resources, where the planktivore dwarf is derived from a generalist ancestor (Mann & McCart, 1981; Siwertsson et al., 2010).

The mean trophic position of broad whitefish was the same as that of least cisco, however, the broad whitefish had high variability in trophic niche area. The range of carbon values may have resulted from variability in the basal resource pool or from the range of resources used over a longer time period (Hammerschlag-Peyer et al., 2011). Migratory broad whitefish may consume prey over a wide range of habitats; fish visiting one lake in summer may individually represent a different overwintering area or several feeding areas along a migratory route (Hecky & Hesslein, 1995; Hesslein, Capel, Fox, & Hallard, 1991). Alternatively, seasonal dietary shifts and individual diet specialisation, within a generalist population, could widen the isotopic niche (Eloranta et al., 2013; Hecky & Hesslein, 1995). However, for slow growing fish, as would be the case in the Arctic, isotopic differences should reflect food choices rather than temporal changes, because changes in diet over time would average out in the slow turnover of the tissue (Hesslein, Hallard, & Ramlal, 1993). We do not have data that support either argument, and more research regarding temporal or spatial diet differences would be needed to clarify this pattern. Small whitefish spp. exhibited narrower diets than adults, which may result from multiple factors, including prey limitations due to gape restrictions or limitations on the area of foraging where there is a distinct basal signature (Hecky & Hesslein, 1995).

This study highlights the overarching patterns in trophic dynamics among fish in ACP shallow lakes. Generalist and flexible feeding strategies couple energy pathways, reduce the amount of competitive interaction and reduce predation pressure on specific prey groups or energy channels, ultimately stabilising trophic dynamics and the food web (Eloranta et al., 2015; Rooney et al., 2006; Vander Zanden & Vadeboncoeur, 2002). For example, the use of zooplankton prey by whitefishes (*Coregonus spp.*) during the summer months coincides with seasonal availability in northern lakes (Hayden et al., 2013; Rautio et al., 2011). Zooplankton could provide fish with an additional energy pathway that brings stability to the food web (Rooney et al., 2006) and provides energy required during summer periods of rapid fish growth (Hayden et al., 2014). It is unclear whether adequate resources will be available to all fish species or age classes in the future Arctic, given potential climate induced changes in primary productivity and changes in timing or abundance of phytoplankton and zooplankton production (Carter & Schindler, 2012; Rautio et al., 2011). In a climate scenario study, young-of-year lake trout have difficulty acquiring adequate zooplankton resources to compensate for increased metabolic rates (McDonald et al., 1996). For pelagic-dependent species, like young lake trout, continued increases in summer water temperatures could prove lethal. In contrast, the effects of warming were less dire for least cisco, a species with generalist feeding behaviours; a bioenergetics model predicted increased growth among all age classes of fish provided they can maintain their current feeding rates (Carey & Zimmerman, 2014).

Additional information regarding the diets of spatially rare species, like pike, prevents a complete assessment of all trophic interactions. Certainly, pike, or other predators like burbot (*Lota lota*) or lake trout, have the potential to occupy higher trophic positions than the fishes included in this analysis and may have the ability to fundamentally change the food web structure and function (Beaudoin et al., 2001; Eloranta et al., 2015). However, even in boreal regions, pike tend to have diverse or omnivorous diets, rather than specialising on fish, because invertebrates are a more reliable source of food than fluctuating fish populations (Beaudoin et al., 2001; Danylchuk & Tonn, 2003). Understanding the roles of fishes in the region is critical to determining possible shifts in trophic dynamics of Arctic lakes due to future impacts. Changes in climate patterns (i.e. temperature and precipitation) and human development (i.e. oil wells, pipelines and roads) will affect hydrologic processes that are necessary for the movement and distribution of fishes (Heim, Wipfli, Whitman, Arp et al., 2016; Heim, Wipfli, Whitman & Seitz 2016; Laske et al., 2016). Further, the anticipation of warmer summers and longer ice free seasons brings with it potential to increase metabolic rates and provide a longer period of fish growth, which may indirectly alter the flow of energy through the food web (Reist et al., 2006; Wrona et al., 2006). Therefore, it is critical that we fully understand trophic ecologies of the species that will be affected by climate change.

ORCID

Sarah M. Laske 🆔 http://orcid.org/0000-0002-6096-0420

REFERENCES

Adrian, R., O'Reilly, C. M., Zagarese, H., Baines, S. B., Hessen, D. O., Keller, W., … Weyhenmeyer, G. A. (2009). Lakes as sentinels of climate change. *Limnology and Oceanography, 54*, 2283–2297. https://doi.org/10.4319/lo.2009.54.6_part_2.2283

Amundsen, P.-A. (1995). Feeding strategy of Arctic charr (*Salvelinus alpinus*): General opportunist, but individual specialist. *Nordic Journal of Freshwater Research*, 71, 150–156.

Amundsen, P.-A., Gabler, H.-M., & Staldvik, F. J. (1996). A new approach to graphical analysis of feeding strategy from stomach content data—modification of the Costello (1990) method. *Journal of Fish Biology*, 48, 607–614.

Beaudoin, C. P., Prepas, E. E., Tonn, W. M., & Wassenaar, L. I. (1999). Individual specialization and trophic adaptability of northern pike (*Esox lucius*): An isotope and dietary analysis. *Oecologia*, 120, 386–396. https://doi.org/10.1007/s004420050871

Beaudoin, C. P., Prepas, E. E., Tonn, W. M., Wassenaar, L. I., & Kotak, B. G. (2001). A stable carbon and nitrogen isotope study of lake food webs in Canada's Boreal Plain. *Freshwater Biology*, 46, 465–477. https://doi.org/10.1046/j.1365-2427.2001.00688.x

Beckerman, A. P., Petchey, O. L., & Warren, P. H. (2006). Foraging biology predicts food web complexity. *Proceedings of the National Academy of Sciences*, 103, 13745–13749. https://doi.org/10.1073/pnas.0603039103

Biro, P. A., Morton, A. E., Post, J. R., & Parkinson, E. A. (2004). Over-winter lipid depletion and mortality of age-0 rainbow trout (*Oncorhynchus mykiss*). *Canadian Journal of Fisheries and Aquatic Sciences*, 61, 1513–1519. https://doi.org/10.1139/f04-083

Buzby, K. M., & Deegan, L. A. (2000). Inter-annual fidelity to summer feeding sites in Arctic grayling. *Environmental Biology of Fishes*, 59, 319–327. https://doi.org/10.1023/A:1007626507936

Cameron, J. N., Kostoris, J., & Penhale, P. A. (1973). Preliminary energy budget of the Ninespine Stickleback (*Pungitius pungitius*) in an Arctic lake. *Journal of the Fisheries Research Board of Canada*, 30, 1179–1189. https://doi.org/10.1139/f73-188

Carey, M. P., & Zimmerman, C. E. (2014). Physiological and ecological effects of increasing temperature on fish production in lakes of Arctic Alaska. *Ecology and Evolution*, 4, 1981–1993. https://doi.org/10.1002/ece3.1080

Carter, J. L., & Schindler, D. E. (2012). Responses of zooplankton populations to four decades of climate warming in lakes of southwestern Alaska. *Ecosystems*, 15, 1010–1026. https://doi.org/10.1007/s10021-012-9560-0

Chipps, S. R., & Garvey, J. E. (2007). Assessment of diets and feeding patterns. In C. S. Guy, & M. L. Brown (Eds.), *Analysis and interpretation of freshwater fisheries data* (pp. 473–514). Bethesda, MD: American Fisheries Society.

Christiansen, J. S., Reist, J. D., Brown, R. J., Brykov, V. A., Christensen, G., Christoffersen, K., & Wrona, F. J. (2013). Fishes. In H. Meltofte (Ed.), *Arctic biodiversity assessment, status and trends in arctic biodiversity* (pp. 192–245). Akureyri, Iceland: Conservation of Arctic Flora and Fauna.

Christoffersen, K. S., Jeppesen, E., Moorhead, D. L., & Tranvik, L. J. (2008). Food-web relationships and community structures in high-latitude lakes. In W. F. Vincent, & J. Laybourn-Parry (Eds.), *Polar lakes and rivers: Limnology of arctic and antarctic aquatic ecosystems* (pp. 269–289). New York: Oxford University Press. https://doi.org/10.1093/acprof:oso/9780199213887.001.0001

Craig, P. C. (1984). Fish use coastal waters of the Alaskan Beaufort Sea: A review. *Transactions of the American Fisheries Society*, 113, 289–298.

Cuker, B. E., McDonald, M. E., & Mozley, S. C. (1992). Influences of slimy sculpin (*Cottus cognatus*) predation on the rocky littoral invertebrate community in an arctic lake. *Hydrobiologia*, 240, 83–90. https://doi.org/10.1007/BF00013454

Cutting, K. A., Cross, W. F., Anderson, M. L., & Reese, E. G. (2016). Seasonal change in trophic niche of adfluvial Arctic grayling (*Thymallus arcticus*) and coexisting fishes in a high-elevation lake system. *PLoS ONE*, 11, e0156187. https://doi.org/10.1371/journal.pone.0156187

Danylchuk, A. J., & Tonn, W. M. (2003). Natural disturbances and fish: Local and regional influences on winterkill of Fathead Minnows in boreal lakes. *Transactions of the American Fisheries Society*, 132, 289–298. https://doi.org/10.1577/1548-8659(2003)132<0289:NDAFLA>2.0.CO;2

Delbeek, J. C., & Williams, D. D. (1988). Feeding selectivity of four species of sympatric stickleback in brackish-water habitats in eastern Canada. *Journal of Fish Biology*, 32, 41–62. https://doi.org/10.1111/j.1095-8649.1988.tb05334.x

Dunne, J. A., Williams, R. J., & Martinez, N. D. (2002). Network structure and biodiversity loss in food webs: Robustness increases with connectance. *Ecology Letters*, 5, 558–567. https://doi.org/10.1046/j.1461-0248.2002.00354.x

Eloranta, A. P., Kahilainen, K. K., Amundsen, P.-A., Knudsen, R., Harrod, C., & Jones, R. I. (2015). Lake size and fish diversity determine resource use and trophic position of a top predator in high-latitude lakes. *Ecology and Evolution*, 5, 1664–1675. https://doi.org/10.1002/ece3.1464

Eloranta, A. P., Knudsen, R., & Amundsen, P.-A. (2013). Niche segregation of coexisting Arctic charr (*Salvelinus alpinus*) and brown trout (*Salmo trutta*) constrains food web coupling in subarctic lakes. *Freshwater Biology*, 58, 207–221. https://doi.org/10.1111/fwb.12052

Gallagher, C. P., & Dick, T. A. (2011). Ecological characteristics of ninespine stickleback (*Pungitius pungitius*) from southern Baffin Island, Canada. *Ecology of Freshwater Fish*, 20, 646–655. https://doi.org/10.1111/j.1600-0633.2011.00516.x

Gravel, D., Canard, E., Guichard, F., & Mouquet, N. (2011). Persistence increases with diversity and connectance in trophic metacommunities. *PLoS ONE*, 6, e19374. https://doi.org/10.1371/journal.pone.0019374

Grosse, G., Jones, B., & Arp, C. (2013). Thermokarst Lake, Drainage, and Drained Basins. In J. Shroder, R. Giardino, & J. Harbor (Eds.), *Treatise on geomorphology* (pp. 1–29). San Diego, CA: Academic Press.

Hammerschlag-Peyer, C. M., Yeager, L. A., Araújo, M. S., & Layman, C. A. (2011). A hypothesis-testing framework for studies investigating ontogenetic niche shifts using stable isotope ratios. *PLoS ONE*, 6, e27104. https://doi.org/10.1371/journal.pone.0027104

Hayden, B., Harrod, C., & Kahilainen, K. K. (2013). The effects of winter ice cover on the trophic ecology of whitefish (*Coregonus lavaretus* L.) in subarctic lakes. *Ecology of Freshwater Fish*, 22, 192–201. https://doi.org/10.1111/eff.12014

Hayden, B., Harrod, C., & Kahilainen, K. K. (2014). Dual fuels: Intra-annual variation in the relative importance of benthic and pelagic resources to maintenance, growth and reproduction in a generalist salmonid fish. *Journal of Animal Ecology*, 83, 1501–1512. https://doi.org/10.1111/1365-2656.12233

Haynes, T. B., Schmutz, J. A., Bromaghin, J. F., Iverson, S. J., Padula, V. M., & Rosenberger, A. E. (2015). Diet of yellow-billed loons (*Gavia adamsii*) in Arctic lakes during the nesting season inferred from fatty acid analysis. *Polar Biology*, 38, 1239–1247. https://doi.org/10.1007/s00300-015-1690-3

Hecky, R. E., & Hesslein, R. H. (1995). Contributions of benthic algae to lake food webs as revealed by stable isotope analysis. *Journal of the North American Benthological Society*, 14, 631–653. https://doi.org/10.2307/1467546

Heim, K. C., Wipfli, M. S., Whitman, M. S., Arp, C. D., Adams, J., & Falke, J. A. (2016). Seasonal cues of Arctic grayling movement in a small Arctic stream: The importance of surface water connectivity. *Environmental Biology of Fishes*, 99, 49–65. https://doi.org/10.1007/s10641-015-0453-x

Heim, K. C., Wipfli, M. S., Whitman, M. S., & Seitz, A. C. (2016). Body size and condition influence migration timing of juvenile Arctic grayling. *Ecology of Freshwater Fish*, 25, 156–166. https://doi.org/10.1111/eff.12199

Hershey, A. E., Beaty, S., Fortino, K., Keyse, M., Mou, P. P., O'Brien, W. J., ... Whalen, S. C. (2006). Effect of landscape factors on fish distribution in arctic Alaskan lakes. *Freshwater Biology*, 51, 39–55. https://doi.org/10.1111/j.1365-2427.2005.01474.x

Hesslein, R. H., Capel, M. J., Fox, D. E., & Hallard, K. A. (1991). Stable isotopes of sulfur, carbon, and nitrogen as indicators of trophic level and fish migration in the lower Mackenzie River Basin, Canada. *Canadian Journal of Fisheries and Aquatic Sciences*, 48, 2258–2265. https://doi.org/10.1139/f91-265

Hesslein, R. H., Hallard, K. A., & Ramlal, P. (1993). Replacement of sulfur, carbon, and nitrogen in tissue of growing Broad Whitefish (*Coregonus nasus*) in response to a change in diet traced by δ^{34}S, δ^{13}C, and δ^{15}N. *Canadian Journal of Fisheries and Aquatic Sciences*, 50, 2071–2076. https://doi.org/10.1139/f93-230

Jackson, A. L., Inger, R., Parnell, A. C., & Bearhop, S. (2011). Comparing isotopic niche widths among and within communities: SIBER – Stable Isotope Bayesian Ellipses in R. *Journal of Animal Ecology*, 80, 595–602. https://doi.org/10.1111/j.1365-2656.2011.01806.x

Jorgenson, M. T., & Grunblatt, J. (2013). Landscape-level ecological mapping of northern Alaska and field site photography. Report for the Arctic Landscape Conservation Cooperative, Fairbanks.

Kelly, L. J., & Martínez del Rio, C. (2010). The fate of carbon in growing fish: An experimental study of isotopic routing. *Physiological and Biochemical Zoology*, 83, 473–480. https://doi.org/10.1086/649628

Laske, S. M., Haynes, T. B., Rosenberger, A. E., Koch, J. C., Wipfli, M. S., Whitman, M., & Zimmerman, C. E. (2016). Surface water connectivity drives richness and composition of Arctic lake fish assemblages. *Freshwater Biology*, 61, 1090–1104. https://doi.org/10.1111/fwb.12769

Laske, S. M., Rosenberger, A. E., Kane, W. J., Wipfli, M. S., & Zimmerman, C. E. (2017). Top-down control of invertebrates by ninespine stickleback in Arctic ponds. *Freshwater Science*, 36, 124–137. https://doi.org/10.1086/690675

Layman, C. A., Arrington, D. A., Montaña, C. G., & Post, D. M. (2007). Can stable isotope ratios provide for community-wide measures of trophic structure? *Ecology*, 88, 42–48. https://doi.org/10.1890/0012-9658(2007)88[42:CSIRPF]2.0.CO;2

Lester, N. P., Bailey, P. E., & Hubert, W. A. (2009). Coldwater fish in small standing waters. In S. A. Bonar, W. A. Hubert, & D. W. Willis (Eds.), *Standard methods for sampling North American freshwater fishes* (pp. 85–96). Bethesda, MA: American Fisheries Society.

Mann, G. J., & McCart, P. J. (1981). Comparison of sympatric dwarf and normal populations of least cisco (*Coregonus sardinella*) inhabiting Trout Lake, Yukon Territory. *Canadian Journal of Fisheries and Aquatic Sciences*, 38, 240–244. https://doi.org/10.1139/f81-032

Martin, P. D., Jenkins, J. L., Adams, F. J., Jorgenson, M. T., Matz, A. C., Payer, D. C., … Zelenak, J. R. (2009). Wildlife response to environmental Arctic change: predicting future habitats of Arctic Alaska. Report to the Wildlife Response to Environmental Arctic Change (WildREACH): Predicting Future Habitats of Arctic Alaska Workshop, 17–18 November 2008. Fairbanks, Alaska: U.S. Fish and Wildlife Service. 138 pages.

McDonald, M. E., Hershey, A. E., & Miller, M. C. (1996). Global warming impacts on lake trout in arctic lakes. *Limnology and Oceanography*, 41, 1102–1108. https://doi.org/10.4319/lo.1996.41.5.1102

McFarland, J. J., Wipfli, M. S., & Whitman, M. S. (2017). Trophic pathways supporting Arctic grayling in a small stream on the Arctic Coastal Plain, Alaska. *Ecology of Freshwater Fish*, 27, 184–197. https://doi.org/10.1111/eff.12336

Merrick, G. W., Hershey, A. E., & McDonald, M. E. (1992). Salmonid diet and the size, distribution, and density of invertebrates in an arctic lake. *Hydrobiologia*, 240, 225–233. https://doi.org/10.1007/BF00013464

Miller, R. B. (1946). Notes on the Arctic grayling, *Thymallus signifer* Richardson, from Great Bear Lake. *Copeia*, 1946, 227–236. https://doi.org/10.2307/1438109

Morrow, J. E. (1980). *The freshwater fishes of alaska*. Anchorage, AK: Alaska Northwest Publishing Company.

Ostdiek, J. L., & Nardone, R. M. (1959). Studies on the Alaskan Blackfish *Dallia pectoralis* I. Habitat, size and stomach analyses. *The American Midland Naturalist*, 61, 218–229. https://doi.org/10.2307/2422353

Post, D. M. (2002). Using stable isotopes to estimate trophic position: Models, methods, and assumptions. *Ecology*, 83, 703–718. https://doi.org/10.1890/0012-9658(2002)083[0703:USITET]2.0.CO;2

Prowse, T. D., Wrona, F. J., Reist, J. D., Hobbie, J. E., Lévesque, L. M. J., & Vincent, W. F. (2006). General features of the Arctic relevant to climate change in freshwater ecosystems. *Ambio*, 35, 330–338. https://doi.org/10.1579/0044-7447(2006)35[330:GFOTAR]2.0.CO;2

Rautio, M., Dufresne, F., Laurio, I., Bonilla, S., Vincent, W. F., & Christoffersen, K. S. (2011). Shallow freshwater ecosystems of the circumpolar Arctic. *Ecoscience*, 18, 204–222. https://doi.org/10.2980/18-3-3463

Rautio, M., Sorvari, S., & Korhola, A. (2000). Diatom and crustacean zooplankton communities, their seasonal variability and representation in the sediments of subarctic Lake Saanajärvi. *Journal of Limnology*, 59(Suppl. 1), 81–96.

Rautio, M., & Vincent, W. F. (2006). Benthic and pelagic food resources for zooplankton in shallow high-latitude lakes and ponds. *Freshwater Biology*, 51, 1038–1052. https://doi.org/10.1111/j.1365-2427.2006.01550.x

Reist, J. D., Wrona, F. J., Prowse, T. D., Power, M., Dempson, J. B., Beamish, R. J., … Sawatzky, C. D. (2006). General effects of climate change on Arctic fish and fish populations. *Ambio*, 35, 370–380. https://doi.org/10.1579/0044-7447(2006)35[370:GEOCCO]2.0.CO;2

Rooney, N., McCann, K., Gellner, G., & Moore, J. C. (2006). Structural asymmetry and the stability of diverse food webs. *Nature*, 442, 265–269. https://doi.org/10.1038/nature04887

Schindler, D. E., & Scheuerell, M. D. (2002). Habitat coupling in lake ecosystems. *Oikos*, 98, 177–189. https://doi.org/10.1034/j.1600-0706.2002.980201.x

Schindler, D. W., & Smol, J. P. (2006). Cumulative effects of climate warming and other human activities on freshwaters of Arctic and subarctic North America. *Ambio*, 35, 160–168. https://doi.org/10.1579/0044-7447(2006)35[160:CEOCWA]2.0.CO;2

Sierszen, M. E., McDonald, M. E., & Jensen, D. A. (2003). Benthos as the basis for arctic lake food webs. *Aquatic Ecology*, 37, 437–445. https://doi.org/10.1023/B:AECO.0000007042.09767.dd

Siwertsson, A., Knudsen, R., Kahilainen, K. K., Præbel, K., Primicerio, R., & Amundsen, P.-A. (2010). Sympatric diversification as influenced by ecological opportunity and historical contingency in a young species lineage of whitefish. *Evolutionary Ecology Research*, 12, 929–947.

Sternberg, D., Balcombe, S. R., Marshall, J. C., Lobegeiger, J. S., & Arthington, A. H. (2012). Subtle 'boom and bust' response of *Macquaria ambigua* to flooding in an Australian dryland river. *Environmental Biology of Fishes*, 93, 95–104. https://doi.org/10.1007/s10641-011-9895-y

Stewart, D. B., Mochnacz, N. J., Reist, J. D., Carmichael, T. J., & Sawatzky, C. D. (2007). Fish diets and food webs in the Northwest Territories: Arctic grayling (*Thymallus arcticus*). *Canadian Manuscript Report of Fisheries and Aquatic Sciences*, 2796, 21.

Svanbäck, R., Quevedo, M., Olsson, J., & Eklöv, P. (2015). Individuals in food webs: The relationships between trophic position, omnivory and among-individual diet variation. *Oecologia*, 178, 103–114. https://doi.org/10.1007/s00442-014-3203-4

Swanson, H. K., Kidd, K. A., & Reist, J. D. (2010). Effects of partially anadromous Arctic Charr (*Salvelinus alpinus*) populations on ecology of coastal Arctic lakes. *Ecosystems*, 13, 261–274. https://doi.org/10.1007/s10021-010-9316-7

Thomas, S. M., Kiljunen, M., Malinen, T., Eloranta, A. P., Amundsen, P.-A., Lodenius, M., & Kahilainen, K. K. (2016). Food-web structure and mercury dynamics in a large subarctic lake following multiple species introductions. *Freshwater Biology*, 61, 500–517. https://doi.org/10.1111/fwb.12723

Urban, F. E., & Clow, G. D. (2013). Air temperature, wind speed, and wind direction in the National Petroleum Reserve – Alaska and the Arctic National Wildlife Refuge, 1998-2011. U.S. Geological Survey Open-File Report 2013-1063.

Vander Zanden, M. J., Cabana, G., & Rasmussen, J. B. (1997). Comparing trophic position of freshwater fish calculated using stable nitrogen isotope

ratios (δ^{15}N) and literature dietary data. *Canadian Journal of Fisheries and Aquatic Sciences*, *54*, 1142–1158. https://doi.org/10.1139/f97-016

Vander Zanden, M. J., Olden, J. D., Thorne, J. H., & Mandrak, N. E. (2004). Predicting occurrences and impacts of smallmouth bass introductions in north temperate lakes. *Ecological Applications*, *14*, 132–148. https://doi.org/10.1890/02-5036

Vander Zanden, M. J., & Vadeboncoeur, Y. (2002). Fishes as integrators of benthic and pelagic food webs in lakes. *Ecology*, *83*, 2152–2161. https://doi.org/10.1890/0012-9658(2002)083[2152:FAIOBA]2.0.CO;2

Walker, D. A., Webber, P. J., Binnian, E. F., Everett, K. R., Lederer, N. D., Nordstrand, E. A., & Walker, M. D. (1987). Cumulative impacts of oil fields on Northern Alaskan Landscapes. *Science*, *238*, 757–761. https://doi.org/10.1126/science.238.4828.757

Wrona, F. J., Prowse, T. D., Reist, J. D., Hobbie, J. E., Lévesque, L. M. J., & Vincent, W. F. (2006). Climate change effects of aquatic biota, ecosystem structure and function. *Ambio*, *35*, 359–369. https://doi.org/10.1579/0044-7447(2006)35[359:CCEOAB]2.0.CO;2

APPENDIX A

Mean (*SE*) numeric proportions (as %) of prey for each of the fish species sampled from Arctic Coastal Plain lakes, the number of lakes used in the calculation of MN are provided below the common name of each fish species.

	Alaska blackfish n = 8		Ninespine stickleback n = 16		Least cisco n = 8	
Taxa	**MN**	**SE**	**MN**	**SE**	**MN**	**SE**
Notostraca	9.20	9.20	0.08	0.06	0.03	0.03
Gastropoda	20.84	8.35	0.01	0.01	12.74	5.42
Ostracoda	11.72	4.03	0.58	0.27	3.28	1.60
Nematoda	0.18	0.18	0.51	0.29	0.77	0.49
Diptera L	23.36	13.21	29.08	3.51	6.33	2.91
Trichoptera L	0.83	0.55	0.43	0.22	3.55	2.20
Hydrachnidia	0.18	0.18	0.95	0.38	16.76	7.00
Calanoida	0.09	0.09	7.44	2.33	0.28	0.26
Cladocera	8.54	5.06	19.67	2.81	2.15	1.28
Diptera Pupa	0.15	0.15	15.91	2.95	11.51	3.89
Diptera Adult	0.23	0.23	2.15	1.10	8.76	6.46
Fish	12.11	6.95	0		17.02	12.20
Amphipoda	0		2.84	2.31	0	
Annelida	0		0.06	0.04	0	
Anostraca	0		0.44	0.41	0	
Bivalvia	0.33	0.26	0.05	0.05	7.29	6.44
Coleoptera A	0		0.01	0.01	0.31	0.16
Coleoptera L	0.42	0.42	0.14	0.08	0	
Collembola	0		0.27	0.19	<0.01	<0.01
Copepoda (Unk)	0.09	0.09	4.79	1.53	0.19	0.19
Crustacea (Unk)	0		0.02	0.01	0	
Cyclopoida	4.68	3.33	4.73	1.47	1.36	1.24
Diptera E	0		0.04	0.03	0.13	0.12
Ephemeroptera L	0		0.01	0.01	0	
Fish Eggs	0		0.10	0.09	0	
Harpacticoida	1.24	1.24	1.70	0.77	0.20	0.14
Oligochaeta	0		0.07	0.07	0.03	0.03
Plecoptera L	5.00	3.62	0.15	0.08	0.11	0.11
Seed	0		0.53	0.27	0	

(Continues)

APPENDIX A (Continued)

Taxa	Alaska blackfish n = 8 MN	SE	Ninespine stickleback n = 16 MN	SE	Least cisco n = 8 MN	SE
Terrestrial	0.79	0.79	0.82	0.44	2.07	1.40
Trichoptera A	0		0		3.26	2.13
Trichoptera P	0		0.01	0.01	0.05	0.05

Taxa	Sm. least cisco n = 6 MN	SE	Whitefish spp. n = 4 MN	SE	Broad whitefish n = 3 MN	SE
Notostraca	0		0		4.58	4.57
Gastropoda	0		0		23.19	22.33
Ostracoda	0.54	0.54	1.59	1.42	0.08	0.04
Nematoda	0.09	0.06	0.10	0.10	0.36	0.23
Diptera L	29.85	13.24	37.71	23.31	8.23	5.10
Trichoptera L	0		12.50	12.50	0.12	0.12
Hydrachnidia	2.25	1.87	0		0	
Calanoida	0		0		0.23	0.23
Cladocera	36.02	13.57	14.92	12.55	20.71	20.36
Diptera Pupa	16.38	7.07	12.09	9.96	3.67	3.59
Diptera Adult	0.93	0.60	2.37	2.10	34.51	32.76
Fish	0		0		0	
Amphipoda	0		0		0	
Annelida	0		0		0.01	0.01
Anostraca	0		0		0	
Bivalvia	0		0		4.31	4.31
Coleoptera A	0		0		0	
Coleoptera L	0		0		0	
Collembola	0.40	0.40	0.03	0.03	0	
Copepoda (Unk)	4.93	3.45	0		0	
Crustacea (Unk)	0		0		0	
Cyclopoida	0.99	0.64	0.08	0.08	0	
Diptera E	1.52	1.52	0		0	
Ephemeroptera L	0		0		0	
Fish Eggs	0		0		0	
Harpacticoida	1.11	1.11	0		0	
Oligochaeta	0		0		0	
Plecoptera L	0		0		0	
Seed	0		0		0	
Terrestrial	2.36	2.00	5.93	5.81	0	
Trichoptera A	0		0.17	0.17	0	
Trichoptera P	0		0		0	

Taxa	Arctic grayling n = 3 MN	SE	Humpback whitefish n = 1 MN	SE	Pike n = 1 MN	SE
Notostraca	12.47	12.47	0.20		0	
Gastropoda	0.05	0.05	65.80		5.30	

APPENDIX A (Continued)

Taxa	Arctic grayling n = 3 MN	SE	Humpback whitefish n = 1 MN	SE	Pike n = 1 MN	SE
Ostracoda	0.97	0.77	0.40		1.20	
Nematoda	13.07	6.54	0		5.30	
Diptera L	17.53	11.74	0.40		5.30	
Trichoptera L	5.81	3.25	5.20		0	
Hydrachnidia	6.06	2.66	3.20		0	
Calanoida	0		0.40		0	
Cladocera	9.38	7.14	2.30		3.00	
Diptera Pupa	9.72	4.14	0		0	
Diptera Adult	4.20	1.60	0		0	
Fish	8.13	4.03	22.20		67.70	
Amphipoda	0		0		0	
Annelida	0		0		0	
Anostraca	0		0		0	
Bivalvia	0		0		12.30	
Coleoptera A	0.04	0.04	0		0	
Coleoptera L	1.29	0.88	0		0	
Collembola	0.09	0.09	0		0	
Copepoda (Unk)	0		0		0	
Crustacea (Unk)	0		0		0	
Cyclopoida	2.02	2.02	0		0	
Diptera E	0		0		0	
Ephemeroptera L	0.22	0.22	0		0	
Fish Eggs	2.02	2.02	0		0	
Harpacticoida	0.11	0.09	0		0	
Oligochaeta	0		0		0	
Plecoptera L	0		0		0	
Seed	0		0		0	
Terrestrial	5.39	4.45	0		0	
Trichoptera A	1.43	1.37	0		0	
Trichoptera P	0		0		0	

Taxa	Rainbow smelt n = 1 MN	SE	Slimy sculpin n = 2 MN	SE	Arctic charr n = 1 MN	SE
Notostraca	0		0		0	
Gastropoda	0		0		0	
Ostracoda	0		0		0	
Nematoda	0		0		0	
Diptera L	0		75.00	27.50	26.90	
Trichoptera L	0		11.10		1.10	
Hydrachnidia	0		0		0	
Calanoida	0		0		0	
Cladocera	62.30		5.50		0	
Diptera Pupa	37.70		0		25.40	

(Continues)

APPENDIX A (Continued)

Taxa	Rainbow smelt n = 1		Slimy sculpin n = 2		Arctic charr n = 1	
	MN	SE	MN	SE	MN	SE
Diptera Adult	0		0		13.30	
Fish	0		0		0	
Amphipoda	0		0		0	
Annelida	0		0		0	
Anostraca	0		0		0	
Bivalvia	0		0		0	
Coleoptera A	0		0		0	
Coleoptera L	0		0		0	
Collembola	0		0		0	
Copepoda (Unk)	0		0		0	
Crustacea (Unk)	0		0		0	
Cyclopoida	0		0		0	
Diptera E	0		0		0	
Ephemeroptera L	0		0		0	
Fish Eggs	0		0		0	
Harpacticoida	0		0		0	
Oligochaeta	0		0		0	
Plecoptera L	0		0		0	
Seed	0		0		0	
Terrestrial	0		0		0	
Trichoptera A	0		0		0	
Trichoptera P	0		0		0	

The first 12 taxa accounted for known variation in pairwise fish species comparisons. Small least cisco (Sm. least cisco) are those ≤100 mm FL, and least cisco are >100 mm FL. A = adult, L = larva, P = pupa, Unk = unknown.

APPENDIX B

Mean and standard deviation of stable carbon and nitrogen isotopes for fish and the primary consumer baseline (snails) in lakes on the Arctic Coastal Plain, Alaska.

Species	Lake	Num. Individuals	Mean $\delta^{15}N$	SD $\delta^{15}N$	Mean $\delta^{13}C$	SD $\delta^{13}C$
Alaska blackfish	1	3	7.07	0.81	−28.83	0.38
	4	3	7.60	0.26	−26.77	0.38
	5	9	8.09	0.62	−27.90	1.20
	6	3	8.57	0.31	−30.17	1.36
	7	3	9.47	0.67	−28.30	0.30
Arctic grayling	1	3	9.10	0.36	−27.73	0.65
	7	10	8.00	1.88	−26.79	1.48
Broad whitefish	1	8	9.83	0.91	−28.41	2.27
	4	10	7.99	1.02	−26.58	0.44
Least cisco	1	6	10.35	0.73	−27.47	1.35
	2	7	10.69	0.47	−27.66	0.64
	4	1	9.50		−27.20	
	6	9	8.69	1.79	−28.16	0.61
	7	1	9.20		−29.80	

(Continues)

APPENDIX B (Continued)

Species	Lake	Num. Individuals	Mean δ^{15}N	*SD* δ^{15}N	Mean δ^{13}C	*SD* δ^{13}C
Sm. least cisco	1	5	7.44	0.97	−28.22	0.33
	2	5	6.34	0.36	−27.42	0.15
	6	8	7.69	0.57	−27.06	0.17
	7	4	7.80	0.33	−27.23	0.22
Ninespine stickleback	1	10	8.96	0.69	−27.88	1.13
	2	10	8.10	1.33	−27.36	0.78
	3	11	9.95	2.27	−28.15	0.63
	4	10	8.54	0.74	−27.36	0.73
	5	10	7.73	0.81	−25.96	1.40
	6	10	9.96	0.95	−28.30	0.87
	7	10	9.71	1.34	−27.56	1.59
	8	10	7.85	0.67	−26.52	1.80
Whitefish spp.	1	11	7.01	0.56	−27.34	0.75
	7	1	7.10		−27.10	
Humpback whitefish	1	3	10.53	0.67	−27.10	0.61
Pike	1	2	10.30	1.41	−28.80	0.14
Slimy sculpin	3	4	8.30	0.29	−27.28	1.22
	6	3	8.57	0.51	−26.33	0.38
Rainbow smelt	1	2	8.10	2.26	−28.85	0.78
Snail	1	10	2.55	0.70	−27.53	0.55
	2	13	3.75	1.68	−27.25	1.68
	3	4	4.03	0.65	−24.45	3.11
	4	10	3.24	0.24	−24.65	1.03
	5	9	4.20	2.40	−26.93	0.98
	6	10	3.97	0.45	−27.38	0.84
	7	10	3.55	0.42	−28.62	0.67
	8	10	3.58	0.41	−28.92	0.68

A lake identification number is provided to compare species signatures across the table, as well as the number of individuals included in the mean. Small least cisco (Sm. least cisco) are those ≤100 mm FL, and least cisco are >100 mm FL. Whitefish spp. are <130 mm FL.