Oecologia
https://doi.org/10.1007/s00442-020-04776-9

COMMUNITY ECOLOGY – ORIGINAL RESEARCH

Trophic structure of apex fish communities in closed versus leaky lakes of arctic Alaska

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Received: 22 April 2019 / Accepted: 3 October 2020

Abstract

Despite low species diversity and primary production, trophic structure (e.g., top predator species, predator size) is surprisingly variable among Arctic lakes. We investigated trophic structure in lakes of arctic Alaska containing arctic char *Salvelinus alpinus* using stomach contents and stable isotope ratios in two geographically-close but hydrologically-distinct lake clusters to investigate how these fish may interact and compete for limited food resources. Aside from different lake connectivity patterns ('leaky' versus 'closed'), differing fish communities (up to five versus only two species) between lake clusters allowed us to test trophic hypotheses including: (1) arctic char are more piscivorous, and thereby grow larger and obtain higher trophic positions, in the presence of other fish species; and, (2) between arctic char size classes, resource polymorphism is more prominent, and thereby trophic niches are narrower and overlap less, in the absence of other predators. Regardless of lake cluster, we observed little direct evidence of arctic char consuming other fishes, but char were larger (mean TL = 468 vs 264 mm) and trophic position was higher (mean TP = 4.0 vs 3.8 for large char) in lakes with other fishes. Further, char demonstrated less intraspecific overlap when other predators were present whereas niche overlap was up to 100% in closed, char only lakes. As hydrologic characteristics (e.g., lake connectivity, water temperatures) will change across the Arctic owing to climate change, our results provide insight regarding potential concomitant changes to fish interactions and increase our understanding of lake trophic structure to guide management and conservation goals.

Keywords Arctic char · Lake trout · Trophic ecology · Predator diets · Stable isotopes

Introduction

In fresh waters, the relative importance of abiotic factors in structuring community assemblages is largely influenced by ecosystem size and morphometry (Paszkowski and Tonn 2000; Jackson et al. 2001), whereas biotic factors (e.g., predation) also contribute to strong direct and indirect effects on fish communities (Robinson and Tonn 1989; He and Kitchell 1990; Gilliam and Fraser 2001). For many arctic lakes, species distribution and general trophic structure is largely determined by foundational abiotic filters such as geography, climate, and surface water connectivity (Hershey et al. 1999), and further, fishes must be adapted to cool temperatures and short growing seasons (e.g., Jeppesen et al. 2010). Multiple periods of glaciation and glacial retreats resulted in repeated expansion and contraction of species ranges and fish habitats (Power et al. 2008). These types of environmental extremes have been shown to affect predator distribution to a greater degree than lower trophic levels (Jackson et al. 2001). As such, overall fish species diversity is low (ranging from two to five) in many Arctic lakes (Kling 2009; Hobbie and Kling 2014). Fishes native to arctic lakes are well-adapted to extreme conditions and possess the ability to grow quickly during the brief growing season when lakes are ice-free (lasting approximately 100 days; Wrona et al. 2006). Other

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Communicated by Brian Shuter.

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adaptations in connected ecosystems include large-scale, seasonal movements (e.g., arctic grayling *Thymallus arcticus*), which can contribute to individual and population level fitness (Golden 2016; Heim et al. 2016). These movements between lake systems, or between lakes and streams, can represent important subsidies influencing overall lake trophic structure (e.g., Sierszen et al. 2003). Accordingly, lake morphometry, landscape position, and surface water connectivity often determines fish presence-absence, and, at a coarse scale, fish community composition (Hershey et al. 1999).

In arctic Alaska, lake connectivity, and thus fish community openness, ranges from completely isolated (hereafter 'closed') to varying degrees of connectedness (e.g., strings of lakes fully connected by perennial streams = hereafter 'open' and seasonally, moderately connected lakes = hereafter 'leaky'; Rastetter et al. 2016). These lake classifications are broadly a function of past glaciations and concordant geomorphic changes (Hershey et al. 1999, 2006). Fish community composition of closed lakes often consists of only arctic char (*Salvelinus alpinus*) and slimy sculpin (*Cottus cognatus*). The trophic structure of these isolated lakes is largely regulated by internal processes including density dependent size structures (Budy and Luecke 2014; Klobucar 2018; Klobucar et al. 2020). Alternatively, lakes open to more contemporary fish colonization and movement are characterized by different fish communities, trophic structures, and pathways of energy flow (Laske et al. 2016; Jones et al. 2017). Lake trout (*Salvelinus namaycush*) often function as the top predator in these leaky lakes and influence trophic structuring of prey fishes (e.g., Hanson et al. 1992; Goyke and Hershey 1992) through direct consumptive and competitive interactions (Zarnetske et al. 2020). In fact, in foothill lakes of arctic Alaska, it is theorized that lake trout generally exclude arctic char in lakes where theoretically both of these top predators could occur (open lakes), and arctic char generally persist in lakes where lake trout cannot invade (closed lakes; Hershey et al. 2006). However, a growing body of literature focused on surface water connectivity in arctic Alaska suggests fish communities are increasingly dependent on landscape connectivity, especially given climate-driven hydrologic shifts (e.g., Golden 2016; Heim et al. 2016; Laske et al. 2016). Accordingly, fish communities could be more heterogeneous across the landscape than previously expected and there is evidence that some lakes (e.g., leaky lakes) function in a way that allows coexistence of these large salmonid species.

Arctic char is a generalist predator with Holarctic distribution that exhibit a high degree of polymorphic variability among and within populations (e.g., Alekseyev et al. 2002; Klemetsen 2013). Feeding ecology of arctic char is often classified to distinct types of intraspecific niche partitioning (e.g., littoral, pelagic, profundal) and multiple general foraging patterns (e.g., planktivorous, piscivorous) can occur within the same lake (Jonsson and Jonsson 2001; Klemetsen 2010). The degree of habitat segregation and char polymorphism may be positively related to overall ecosystems size and lake morphometry including depth (e.g., maximum, mean), surface area, and volume (Recknagel et al. 2017). Alternatively, or in combination with lake physical characteristics, biotic interactions can affect overall resource use, size structure, and trophic position of arctic char (Eloranta et al. 2015a, b; Klobucar et al. 2020).

In this study, we investigated and quantified trophic structure in two contrasting clusters of lakes in arctic Alaska. While relatively close geographically (within 5 km), the lakes in one cluster of lakes are isolated with no surface water connectivity between the lakes (closed; $n = 4$) and contain arctic char as the only apex predator (e.g., Klobucar et al. 2017). The other cluster of lakes are leaky ($n = 3$) and defined by increased surface water connectivity (e.g., seasonal inlet and outlet steams). These lakes contain arctic char as well as lake trout as apex predators and arctic grayling (*Thymallus arcticus*) and burbot (*Lota lota*) as potential competitors as well as prey (e.g., juvenile fishes). Slimy sculpin are present in both lake clusters. Beyond the physical template structuring these clusters of lakes, we would expect particular biological interactions that allow the persistence of arctic char in each of the postglacial lake clusters. Thus, between and within these clusters of lakes, we used stomach contents and stable isotopes to test hypotheses related to trophic ecology of arctic char, including: (1) arctic char are more piscivorous, and thereby grow larger, in the presence of more prey fish species in leaky lakes; and, (2) between arctic char size classes, resource polymorphism is more prominent, and thereby trophic niches are narrower and overlap less, in the absence of other predators. Thus, to better understand trophic structure in leaky lakes, we also explored the potential for arctic char diet and niche overlap with other predators in the leaky lakes.

While arctic char is an intriguing and well-studied Holarctic species, it is relatively understudied in Alaska compared to Scandinavia and Canada. We present important findings for arctic char populations and trophic ecology of fish communities in pristine and unexploited systems that may act as sentinels of climate change across the Arctic. As a whole, our study contributes valuable insight regarding surface water connectivity and trophic structure of lakes in arctic Alaska and sets the stage for subsistence management and conservation decisions for culturally- and ecologically-important fish species.

Methods

Study area

Our research was conducted in lakes near Toolik Field Station (68° 37.796′ N, 149° 35.834′ W), home of the Arctic Long-Term Ecological Research project (https://arc-lter.ecosystems.mbl.edu/), in the northern foothills of the Brooks Mountain Range, Alaska. We chose two isolated, closed lakes (Lakes Fog1 and Fog2) that have been monitored as part of other studies since the 2000s (e.g., Budy and Luecke 2014), and to increase sample size and inference, we initiated sampling in 2013 and 2014 on two additional lakes in the closed lake cluster (Lakes Fog3 and Fog5, respectively). We chose a nearby, more connected leaky lake cluster, the LTER lakes (Lakes LTER345, LTER347, and LTER348), to test our hypotheses and sampled these lakes, and the closed lakes, from 2014 – 2016 (Table 1). Generally, lakes in the area are shallow (maximum depths of 3–30 m) and oligo- to ultra-oligotrophic (chlorophyll-*a* concentrations < 5 µg L^{-1}; Kling et al. 1992). Typically, the lakes are ice covered from early October to early June and thermally stratified during summer (June–August).

Fish sampling

In each year, we sampled fish using hook-and-line through the ice beginning in May, and throughout the open water via hook-and-line and experimental gill nets (usually 3–4 sampling events lake^{-1} year^{-1}). We used experimental benthic gill nets (Lester et al. 2009) set perpendicular to shore on the lake bottom, which extended from the littoral zone to pelagic areas, and checked nets every half hour to minimize mortalities. We weighed and measured all fish captured, and clipped the adipose fin for stable isotope analyses. For many captures, we obtained diet information via gastric lavage, and additionally we collected diets (whole stomach) from incidental mortalities.

Diet and stable isotope analyses

In the field, we stored whole stomachs, or contents obtained via gastric lavage, in 95% ethanol until analysis in the lab, where we identified diet items to the lowest taxonomic group possible. We weighed prey fish individually, and for zooplankton and invertebrate prey, obtained blot-dry wet weight en masse to the nearest 0.01 g for each taxonomic group (e.g., chironomids, mollusks, trichoptera, zooplankton, terrestrial invertebrates, and organic material). To determine potential intra- and interspecific competition within lakes, as well as compare fish diets across and with lake clusters, we calculated diet overlap using Schoener's index (Schoener 1970; Eq. 1),

$$\alpha = 1 - 0.5 \cdot \left(\sum_{i=1}^{n} \left| p_{xi} - p_{yi} \right| \right),$$

where *i* is a given prey item, *p* is the mean biomass proportion of *i*, and *x* and *y* are the specified group of predators being compared by size class and lake cluster. The single value α is diet overlap from 0 (no overlap) to 1 (complete overlap), and values greater than 0.6 are indicative of significant diet overlap (Schoener 1970). To better compare between lake clusters, as well as life-stages of arctic char, we separated arctic char into 'small', 'medium', and 'large' size classes based on our other work of char morphology and allometry (Klobucar 2018; Klobucar et al. 2020). We determined these size classes for each lake cluster using model-based clustering based on morphological measurements related to feeding and swimming such that potential trophic morphs could be compared (Klobucar 2018). In the closed lakes, small char were generally < 200 mm, medium char were approximately 200–400 mm, and large char were general > 400 m. In the leaky lakes, small char were not present, medium char were generally 250–500 mm and large char were generally > 500 mm.

We used carbon ($\delta^{13}C$) and nitrogen ($\delta^{15}N$) stable isotopes to further explore a time-integrated representation of predator diets and assess potential intra- and interspecific competition

Table 1 Physical and chemical conditions of study lakes near Toolik Field Station, Alaska

Cluster	Lake	Latitude (°N)	Longitude (°W)	Surface area (ha)	Max. depth (m)	Mean depth (m)	Secchi depth (m)	Chl-α (µg L^{-1})
Closed lakes								
	Fog1	68.684	149.082	3.5	19.7	8.4	4.9	4.3
	Fog2	68.679	149.091	5.9	19.8	7.8	7.1	2.6
	Fog3	68.673	149.088	3.9	21.0	7.6	6.0	3.3
	Fog5	68.678	149.065	0.7	9.9	3.5	5.0	5.2
Leaky lakes								
	LTER345	68.623	149.151	30.7	28.6	12.3	1.5	1.4
	LTER347	68.625	149.139	13.5	17.6	5.6	1.8	4.0
	LTER348	68.641	149.127	5.7	9.6	3.2	3.7	-

Secchi depth and chlorophyll concentrations are average measurements ($n = 4$ for closed lakes, $n = 2$ for leaky lakes) from late July 2016 and mid-summer is usually the most productive period (Kling et al. 1992) within lakes and lake clusters. For stable isotope analyses, we used adipose fin clips for arctic char, arctic grayling, and lake trout, and a dorsal fin clip for burbot (e.g., Vinson and Budy 2011; Graham et al. 2013). Samples were dried for 48 h at 70 °C, ground into a homogenized powder, and placed into pre-weighed tin capsules. Fish tissues samples were processed at the Washington State University Stable Isotope Core laboratory (prior to 2016) and the Utah State University Stable Isotope Lab (2016) for analysis of $\delta^{13}C$ and $\delta^{15}N$, and percent composition of both carbon and nitrogen. Standard quality control protocols, including multiple blind quality control samples of similar, known composition, were used at both laboratories. Isotopic signatures are reported in δ-notation (Vander Zanden and Rasmussen 1999; Eq. 2):

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

where R_{sample} is the ratio of $^{13}C/^{12}C$ or $^{15}N/^{14}N$ found in the tissue or filter sample, and R_{standard} is the ratio of $^{13}C/^{12}C$ or $^{15}N/^{14}N$ found in the standard sample. The standard for $\delta^{13}C$ is PeeDee belemnite and the standard for $\delta^{15}N$ is atmospheric nitrogen and these standards insure a precision of ± 0.3‰.

To calculate trophic position of fishes we used (Vander Zanden and Rasmussen 1999; Eq. 3):

$$\mathrm{TP}_i = \left(\frac{\delta^{15}\mathrm{N}_i - \delta^{15}\mathrm{N}_{\mathrm{baseline}}}{3.4}\right) + 2,$$

where TP_i is the trophic position of species i, N_i is the nitrogen signature of species i, and N_{baseline} is the nitrogen signature for primary consumers (i.e. Vander Zanden and Rasmussen 1999). We assumed primary consumers have a trophic position of 2 and a $\delta^{15}N$ trophic fractionation value of 3.4 ± 1.1‰ (Minagawa and Wada 1984). We used a two-source baseline correction with mean $\delta^{15}N$ value of pelagic zooplankton (*Daphnia* spp.) and snails (*Lymnaea elodes*) from the littoral zone to represent primary consumers in each lake cluster ($\delta^{15}N_{\mathrm{closed}} = 3.07‰$; $\delta^{15}N_{\mathrm{leaky}} = 3.10‰$).

To evaluate trophic overlap of arctic char with other apex predators (leaky lakes), and among size classes of arctic char (closed and leaky lakes), we used SIBER (Stable Isotope Bayesian Ellipses; Jackson et al. 2011) in *R* to estimate pairwise overlap of bivariate ($\delta^{13}C$ and $\delta^{15}N$) niche regions between species or size class. The SIBER model produces ellipses around the centroid that include ± 1 SD. We calculated the percent species overlap at the intersection of ellipse areas. Additionally, as a measure of carbon source use within lakes, we calculated percent littoral contribution using a two-source mixing model (Vander Zanden and Vadeboncoeur 2002; Eq. 4):

$$\text{Percentage contribution of littoral} = \left(\delta^{13}\mathrm{C_c} - \delta^{13}\mathrm{C_p}\right) / \left(\delta^{13}\mathrm{C_i} - \delta^{13}\mathrm{C_p}\right),$$

where $\delta^{13}C_c$, $\delta^{13}C_i$, $\delta^{13}C_p$ are the mean $\delta^{13}C$ of the consumer, littoral prey, and pelagic prey for each lake cluster. For trophic position comparisons between paired size classes and lake clusters we used Welch's *t* test of $\delta^{15}N$ values in *R* because this test does not assume equal variances among our variable sample sizes, and when applicable to compare across all size classes in the closed lakes ($n = 3$), we used a one-way ANOVA (see also Table 2). For this analysis, we confirmed homogeneity of variance and normal residuals, used $\alpha \leq 0.05$ to determine significance, and Tukey's test to determine pairwise differences.

Results

In total, we sampled 583 individual arctic char across all seven study lakes ($n = 360$ in closed lakes; $n = 223$ in leaky lakes; Table 2). We quantified diets using stomach content data from 171 arctic char ($n = 116$ for closed lakes; $n = 55$ for leaky lakes), as well as 10 arctic grayling and 11 lake trout from the leaky lakes. To further quantify diet overlap and niche partitioning, we analyzed stable isotopes from 236 arctic char ($n = 121$ for closed lakes; $n = 115$ for leaky lakes), and we also analyzed stable isotopes from 27 arctic grayling, 36 lake trout, and 8 burbot (Table 3).

Overall, char were significantly larger in the leaky lakes (mean TL ± SE = 468.1 ± 6.37 mm; range = 187–670 mm) relative to the closed lakes (mean TL ± SE = 264.2 ± 3.86; range = 113–486 mm; $t = 27.39$, df = 383, $P < 0.001$; Fig. 1). In both lake clusters, arctic char trophic position increased with size (Table 3). Large char in the closed lakes demonstrated generally, but not significantly, higher trophic positions than medium char in the closed lakes (mean TP ± SE = 3.77 ± 0.09 vs 3.57 ± 0.09; $t = 1.86$, $df = 9.73$, $P = 0.09$) and significantly higher trophic positions than small char (mean TP ± SE = 3.49 ± 0.05; $t = 2.52$, $df = 10.12$, $P = 0.03$; Fig. 2, Table 3). In the leaky lakes, large char demonstrated significantly higher trophic positions than medium char (mean TP ± SE = 4.00 ± 0.04 vs 3.85 ± 0.04; $t = 2.43$, $df = 111.76$, $P = 0.02$; Table 3). Accordingly, large char in the leaky lakes exhibited significantly higher trophic positions than large char in the closed lakes ($t = 2.23$, $df = 8.74$, $P = 0.05$), and medium char in the leaky lakes had significantly higher trophic positions than medium char in the closed lakes ($t = 4.28$, $df = 146$, $P < 0.01$; Table 3). Thus, our isotope data were generally consistent with our first hypothesis that arctic char are more piscivorous, and thereby grow larger, in the presence of more prey fish species.

Table 2 Catch summary for arctic char in study lakes near Toolik Field Station, Alaska

	Fog 'closed' lakes	Fog1	Fog2	Fog3	Fog5	LTER 'leaky' lakes	LTER345	LTER347	LTER348
Arctic char (n)	**360**	71	14	224	51	**223**	94	38	120
Mean TL ± SE (mm)	**264.2 ± 3.9**	275.3 ± 7.7	330.1 ± 19.3	243.2 ± 4.6	323.1 ± 7.9	**468.1 ± 6.4**	509.7 ± 5.2	460.7 ± 13.3	444.6 ± 10.1
Range (mm)	**113–486**	168- 454	230–460	113–435	197–486	**187–670**	362–580	223–595	187–670
Abundance		448 (290–693)	163 (105–288)	666 (477–1073)	75 (55–119)		277 (177–540)	73 (40–196)	331 (227–563)
Density by area		127 (82–197)	29 (19–51)	171 (123–276)	104 (76–164)		7 (6–17)	5 (3–14)	58 (39–98)
Arctic grayling (n)	–	–	–	–	–	**50**	16	34	–
Mean TL ± SE (mm)	–	–	–	–	–	**330.6 ± 6.7**	304.8 ± 14.6	342.8 ± 35.5	–
Range (mm)	–	–	–	–	–	**204–430**	232–430	204–407	–
Burbot (n)	–	–	–	–	–	**8**	–	–	8
Mean TL ± SE (mm)	–	–	–	–	–	**410.8 ± 23.1**	–	–	410.8 ± 23.1
Range (mm)	–	–	–	–	–	**272–490**	–	–	272–490
Lake trout (n)	–	–	–	–	–	**54**	44	10	–
Mean TL ± SE (mm)	–	–	–	–	–	**412.6 ± 7.1**	414.8 ± 8.3	402.7 ± 13.0	–
Range (mm)	–	–	–	–	–	**244–625**	244–625	345–454	–

Bold numbers reflect the statistics of all fish captured for each lake cluster

Considering all available stomach content data, arctic char diets were similar for medium and large char, but relatively dissimilar for each of those size classes relative to small char (Schoener's α between small and medium = 0.55, between medium and large = 0.81, between small and large = 0.40; Table 4). In general, the proportion of chironomids, trichoptera, and zooplankton in char diets decreased with size, while diet proportions of mollusks increased with fish size (Table 4). While we did not obtain any diet information for small arctic char (< 200 mm) in the leaky lakes, diets of medium char in the leaky lakes were similar to small char in the closed lakes (Table 4; Fig. 3). Overall, diets of large arctic char were relatively similar between lake clusters (Schoener's $\alpha = 0.64$). We only observed fish in char diets for medium char in the closed lakes and instances of piscivory (including cannibalism) were rare. Conversely, in the leaky lakes, lake trout did consume fish (Table 4; Fig. 4); all of prey fish we observed were slimy sculpin. Across all predators in the leaky lakes, there was a fair amount of diet overlap (Fig. 4), especially between medium arctic char and arctic grayling (Schoener's $\alpha = 0.68$), and medium arctic char and large arctic char (Schoener's $\alpha = 0.69$).

Regardless of size class, across and within the closed lakes, arctic char occupied similar trophic niches with considerable overlap (Fig. 5, Table 4). Lake Fog5 was the only lake with a sample size sufficient to estimate trophic niche space for large arctic char, but this space was very narrow (niche area = 1.24). In Lakes Fog1 and Fog3, trophic niche space of small char was smaller relative to medium char (e.g., niche area = 26.3 vs 62.9 in Fog3) and was almost completely overlapped by medium char trophic niche space (100% and 98.9% overlap, respectively). Accordingly, in the closed lakes, δ^{13}C isotopic signatures were similar across arctic char size classes ($F_{[2, 118]} = 1.20$, $P = 0.31$; Table 3). In contrast, there was more differentiation between δ^{13}C signatures for medium and large arctic char across the leaky lakes (e.g., % littoral = 76.9 vs 97.2 for medium and large arctic char; $t = 6.61$, $df = 77.97$, $p < 0.001$; Table 3). Estimates of trophic niche space demonstrated only 37.2, 65.7, and 53.2% of medium char trophic niche space was overlapped by large

Table 3 Summary of fish sampled for diets and isotopes by lake cluster and species, and average diet proportion for each size of char or other species (pooled), in study lakes near Toolik Field Station, Alaska, 2014–2016

	Arctic char (Fog 'closed' lakes)			Arctic char (LTER 'leaky' lakes)			Arctic grayling	Lake trout	Burbot
	Small	Medium	Large	Small	Medium	Large			
Number of diets	11	100	5	0	24	31	10	11	0
Mean TL ± SE (mm)	177.5 ± 4.2	312.1 ± 5.4	455.2 ± 7.8	–	420.3 ± 15.6	540.9 ± 3.3	327.3 ± 19.7	410.3 ± 15.5	–
Proportion of prey by weight									
Chironomidae	0.25	0.19	0.20	–	0.03	0.05	0.01	0.16	–
Fish	0.00	0.04	0.00	–	0.00	0.00	0.00	0.14	–
Mollusca	0.03	0.40	0.70	–	0.26	0.50	0.03	0.07	–
Trichoptera	0.58	0.23	0.00	–	0.60	0.34	0.76	0.35	–
Zooplankton	0.09	0.03	0.00	–	0.06	0.01	0.00	0.00	–
Terrestrial invertebrates	0.00	0.02	0.00	–	0.00	0.00	0.03	0.04	–
Aquatic invertebrates	0.00	0.07	0.10	–	0.04	0.10	0.17	0.24	–
Organic matter	0.05	0.02	0.00	–	0.01	0.00	0.00	0.00	–
Number of isotopes	29	85	7	0	63	52	27	36	8
Mean TL ± SE (mm)	163.6 ± 4.1	302.3 ± 6.1	457.4 ± 5.8	–	390.3 ± 9.4	559.2 ± 9.9	330.3 ± 10.4	422.4 ± 12.4	410.8 ± 23.1
Mean δ15N	8.1 ± 0.2	8.4 ± 0.2	9.1 ± 0.3	–	9.4 ± 0.2	9.9 ± 0.1	7.9 ± 0.2	11.6 ± 0.1	11.1 ± 0.4
Mean δ13C	−28.8 ± 0.3	−28.2 ± 0.2	−28.1 ± 1.1	–	−27.7 ± 0.2	−25.3 ± 0.2	−27.2 ± 0.2	−24.6 ± 0.2	−26.9 ± 0.2
Mean TP	3.49 ± 0.05	3.57 ± 0.05	3.77 ± 0.09	–	3.85 ± 0.04	4.00 ± 0.04	3.40 ± 0.06	4.51 ± 0.03	4.37 ± 0.12
Mean % Littoral	69.22 ± 0.03	76.61 ± 0.02	74.68 ± 0.12	–	76.91 ± 0.03	97.25 ± 0.01	89.20 ± 0.02	100 ± 0	95.82 ± 0.03

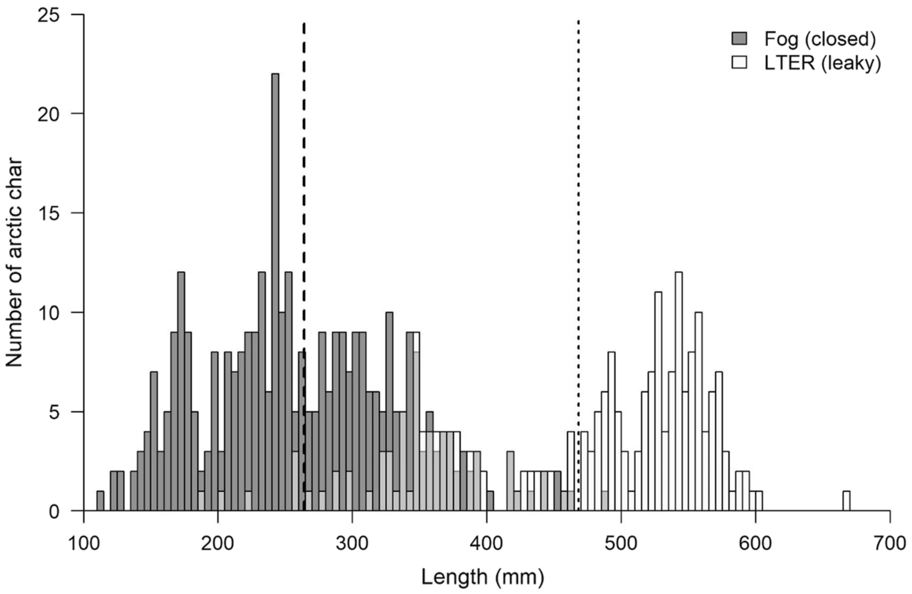

Fig. 1 Length-frequency of all arctic char (*Salvelinus alpinus*) sampled in 'closed' lakes (gray; $n = 360$) and 'leaky' lakes (white; $n = 223$) near Toolik Field Station, Alaska, 2014–2015. Dashed line is the mean length of 'closed' lakes arctic char (264 mm) and dotted line is the mean length of 'leaky' lakes arctic char (468 mm)

char niche space in leaky Lakes LTER345, LTER347, and LTER348, respectively. Thus, our data were generally not consistent with our second hypothesis that, across arctic char size classes, resource polymorphism is more prominent, and thereby trophic niches are narrower and overlap less, in the absence of other predators. Trophic niche spaces were variable across lakes and size classes (Figs. 5, 6); however, there was more overlap between size classes of arctic char in the closed lakes relative to the leaky lakes where other predators were present.

Across the leaky lakes, trophic positions of apex predators differed significantly (e.g., mean TP for large arctic char = 4.00; mean TP for lake trout = 4.51; $t = df = 9.42$, $df = 85.13$, $p < 0.001$; Table 3). Lake trout maintained the

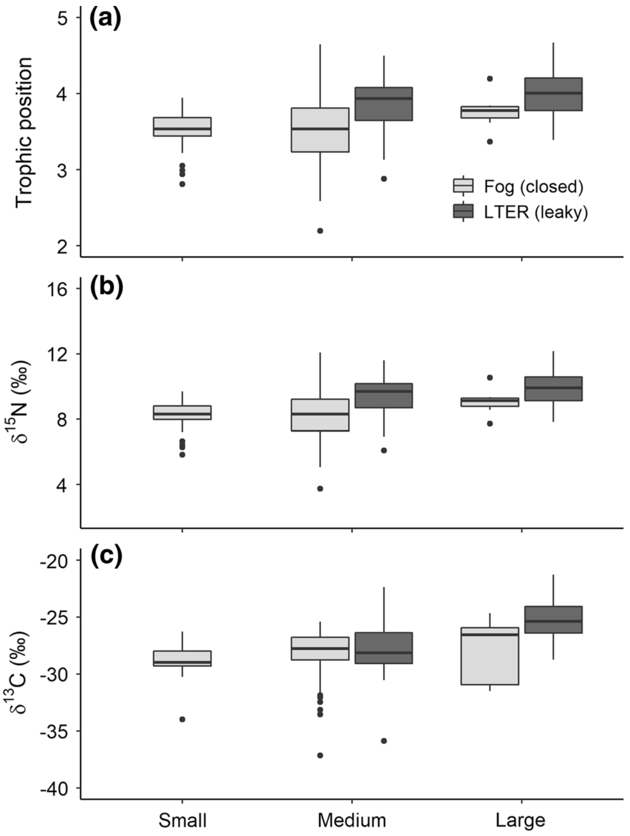

Fig. 2 Mean **a** trophic position, **b** δ^{15}N, and **c** δ^{13}C isotopic signatures for small, medium, and large arctic char size classes in the 'closed' and 'leaky' lakes near Toolik Field Station, Alaska

highest trophic position in Lakes LTER345 and LTER347, with minimal trophic niche overlap with large arctic char (19.5% and 6.9%, respectively). Notably, lake trout and large arctic char in these lakes were also both nearly exclusively littoral (100 and 97.3%, respectively). Arctic grayling niche space fell between medium arctic char and large arctic char in both Lakes LTER345 and LTER347, while burbot overlapped with both size classes of arctic char in Lake LTER348, albeit it at a slightly increased trophic position (4.37 vs 4.00 (large AC) and 3.85 (medium AC); Table 4).

Discussion

Understanding the relative role of biotic interactions that contribute to structuring lake fish communities is important for ecological advancement as well as conservation of native fishes. Here, we explored the trophic ecology of fish communities in arctic lakes, in the absence of human alteration, with a focus on two very different lake clusters. One series of lakes is closed to other surface water connections and as such contains only arctic char as an apex predator ('closed lakes'). The second series of lakes are within 5 km of the closed lakes but are leaky with some inlet and outlet streams at least partially, and potentially only ephemerally, connected to other lakes across the landscape ('leaky lakes'). These leaky lakes surprisingly contain large arctic char in sympatry with lake trout, as well as arctic grayling and burbot as other potential predators. This natural dichotomy in lake structure provided a template to investigate our trophic hypotheses between lake clusters, which focused our analyses on intra- versus interspecific interactions.

Across all lakes and both lake clusters, arctic char trophic position increased with char length; however, between lake clusters, char size classes in the leaky lakes demonstrated higher trophic positions than those in the closed lakes. Accordingly, arctic char in the leaky lakes were significantly larger than arctic char in closed lakes. However, we did not observe direct evidence of increased piscivory based on diet data in these larger char. Diet data, however, represent only a snap shot of what a fish has consumed in the last 24–48 h, depending on temperature (e.g., Petersen and Kitchell 2001), and we have to limit the stress imposed on these arctic fish because population sizes are naturally very low (e.g., Strange et al. 1977; Power et al. 2008), resulting in relatively low sample size for our diets. In contrast, we did

Table 4 Schoener's α index for diet overlap between diets of arctic char (AC) in 'closed' lakes (by size class), compared with arctic char in 'leaky' lakes (by size class), arctic grayling (AG), lake trout (LT) for fish sampled in study lakes near Toolik Fields Station, Alaska, 2014–2015

	Closed lakes AC			Leaky lakes AC		
	Small	Medium	Large	Small	Medium	Large
Closed lakes AC						
Small	–	0.50	0.24	–	0.71	0.43
Medium	0.50	–	0.67	–	0.60	0.77
Large	0.24	0.67	–	–	0.34	0.64
Leaky lakes AC						
Small	–	–	–	–	–	–
Medium	0.71	0.60	0.34	–	–	0.69
Large	0.43	0.77	0.64	–	0.69	–
Leaky lakes AG	–	–	–	–	0.68	0.48
Leaky lakes LT	–	–	–	–	0.49	0.55

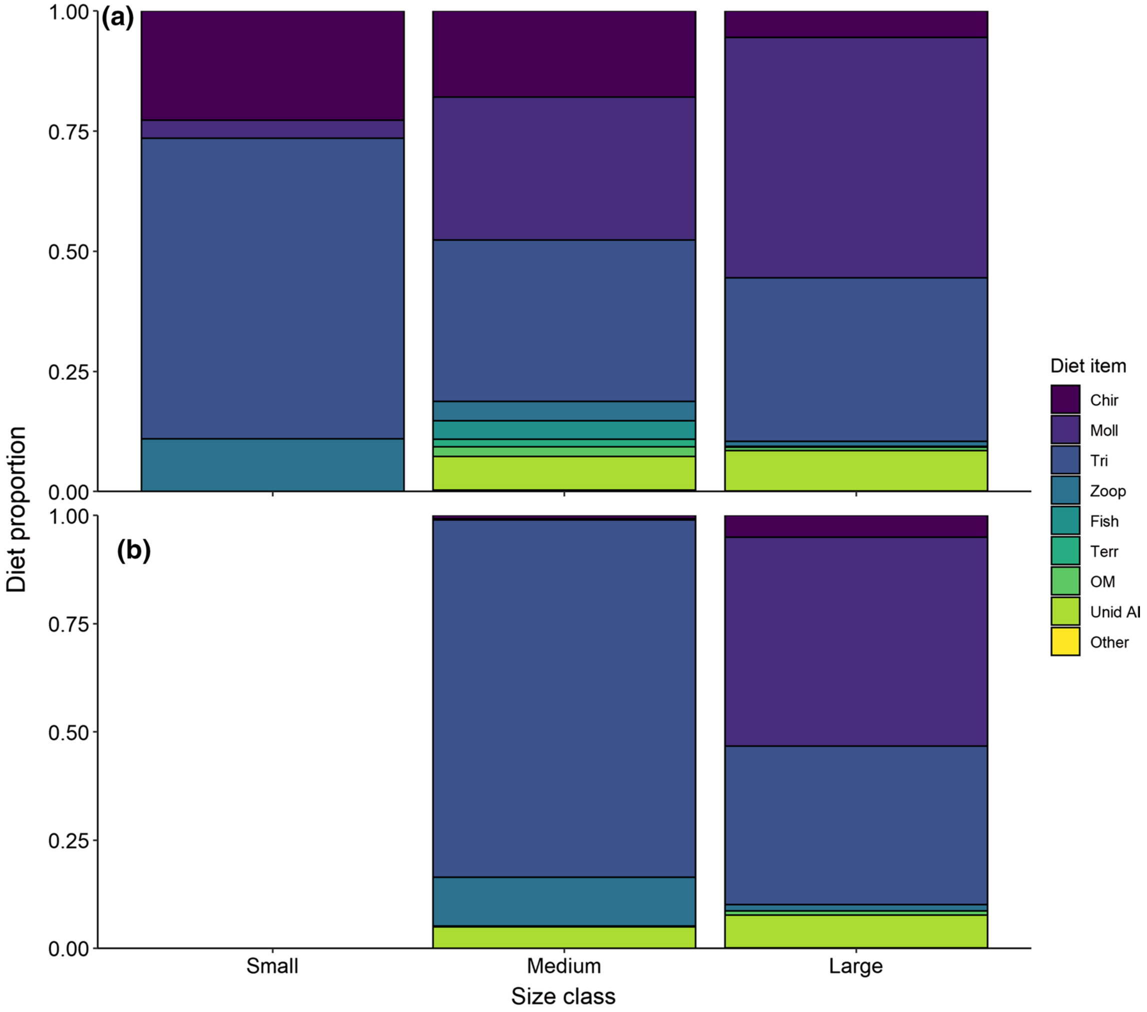

Fig. 3 Average diet proportion for arctic char in **a** 'closed' lakes and **b** 'leaky' lakes by size class: small, medium, and large, in study lakes near Toolik Field Station, AK, 2014–2015. Diet items include chironomids (Chir), mollusks (Moll), trichoptera (Tri), zooplankton (Zoop), fish, terrestrial invertebrates (Terr), organic material (OM), unidentified aquatic invertebrates (Unid AI) and other. Color figure is available online

observe potential evidence of low levels of piscivory occur based on our stable isotope data, a discrepancy that has been observed elsewhere (e.g., Clarke et al. 2005; McIntyre et al. 2006). We demonstrated that when co-occurring with other predators (e.g., lake trout), char are generally larger and feed at higher trophic positions relative to lakes where char are the only predator. However, in lakes with arctic char as the only apex predator, sample size for large char was relatively low. We did rarely observed piscivory (and cannibalism) in the closed lakes, but never in diets of any arctic char in any lake cluster greater than 400 mm.

Abiotic factors that determine the distribution of arctic fishes across the foothills of the Brooks Mountain Range, Alaska are predictable and generally well understood (Hershey et al. 1999, 2006); however, intra- and interspecific interactions likely vary at local scales and determine community structure (e.g., across and within lake clusters). Apex predators exhibiting strong prey preference have been shown to stabilize lake food webs by linking between littoral and pelagic food chains (Post et al. 2000). Arctic char often segregate between foraging arenas in lakes (e.g., benthic, littoral, pelagic) through resource polymorphism and morphological divergence (Hindar and Jonsson 1982). As such, char diets may be specialized for specific lake habitats without coupling of pelagic and littoral prey items or habitats (Riget et al. 1986). In Norway, when arctic char exist in sympatry with brown trout (*Salmo trutta*), coupling of littoral and pelagic food web compartments can be limited as a result of niche partitioning through competitive and consumptive interactions (Eloranta et al. 2013). On the other hand, arctic char, as well as the other predators in the leaky lakes, are often viewed as generalist consumers, which can also shift prey seasonally (Eloranta et al. 2010), and omnivory is much more likely in upper fish trophic levels (Thompson et al.

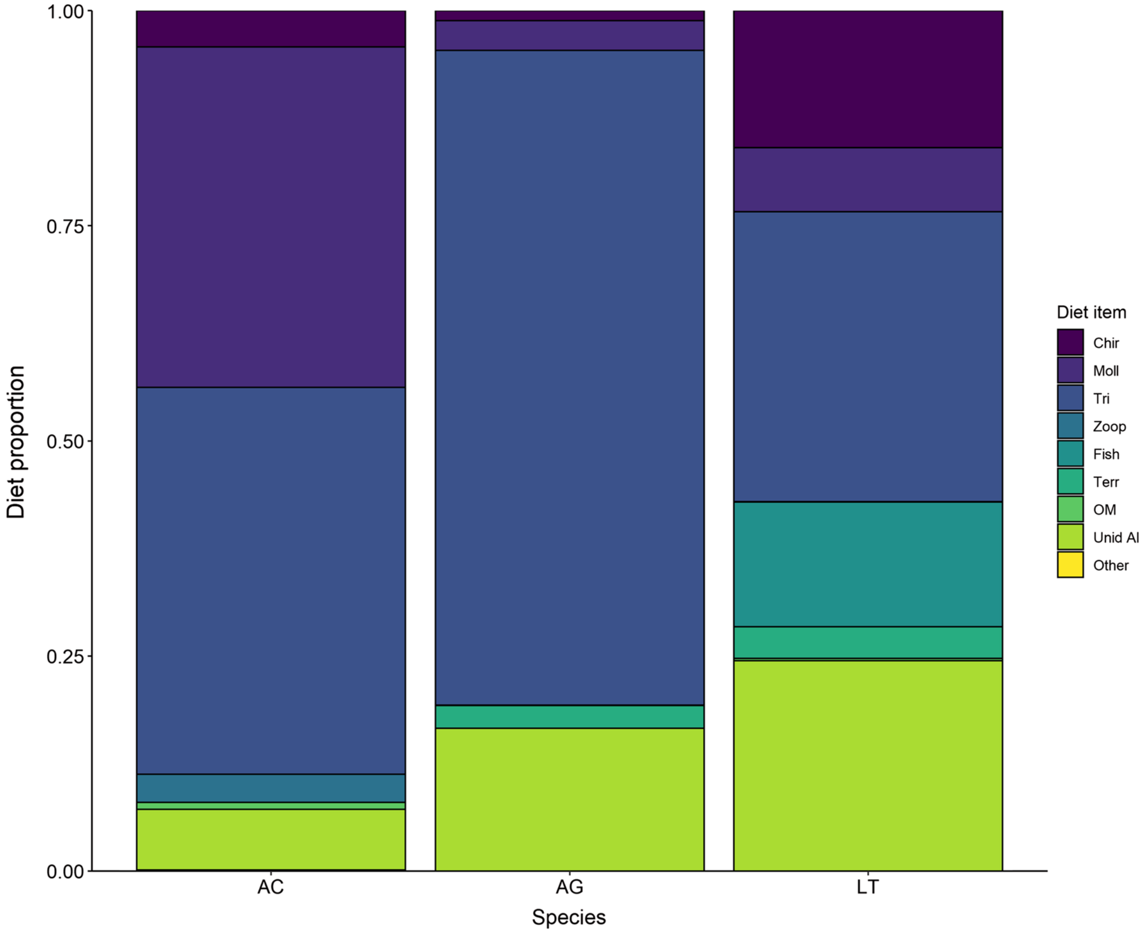

Fig. 4 Average diet proportion for arctic char (AC), arctic grayling (AG), and lake trout (LT) in 'leaky' lakes near Toolik Field Station, Alaska, 2014–2015. Diet items include chironomids (Chir), mollusks (Moll), trichoptera (Tri), zooplankton (Zoop), fish, terrestrial invertebrates (Terr), organic material (OM), unidentified aquatic invertebrates (Unid AI) and other. Color figure is available online

2007). In the closed lakes, we observed little diet preference and high overlap between char size classes. This was in opposition to our original hypothesis that resource polymorphism would be more prominent in the closed lakes as a result of increased intraspecific competition, as well as the absence of other apex predators. However, as the closed lakes are relatively small and homogenous, habitats may not be segregated enough to demonstrate strong habitat selection, and thus, prey preference. For example, the smallest lake (~ 25 ha) in a study of char in Norway showed similar diets across all char, while in larger lakes (> 1000 ha) char exhibited distinct trophic and habitat separation (Knudsen et al. 2006). Additionally, since our study lakes are oligotrophic, intraspecific competition for extremely limited resources may not allow for strong diet selection, and the most successful predators are likely those that feed opportunistically (e.g., Amundsen 1995; Jonsson and Jonsson 2001). In previous work, across all lakes regardless of lake cluster, we demonstrate primary production is a significant predictor of char size structure (Klobucar 2018; Klobucar et al. 2020). Accordingly, our isotopes results demonstrate mean littoral contribution to δ^{13}C was similar for all size classes of char in the closed lakes and was relatively low when compared to the leaky lakes.

In the leaky lakes, which are also larger in surface area but relatively similar habitat proportions (e.g., littoral vs pelagic; Klobucar 2018), we did somewhat surprisingly, observe more separation between diets and habitat preference between medium and large char, as expressed by δ^{13}C signatures. In general, diet of smaller char in the leaky lakes suggested use of more pelagic habitats, while diets of the largest char were more littoral, consistent with other studies (e.g., Hindar and Jonsson 1982; Power et al. 2005). For larger char, increased reliance on littoral prey could be related to greater energy and larger sizes of primary consumers in the littoral zone relative to pelagic zone (Karlsson and Bystrom 2005). Accordingly, these largest char may exhibit phenotypic adaptations to increased foraging success in shallower, more productive habitats (Klobucar 2018; Klobucar et al. 2020); however, as the climate warms, the biomass and availability of prey may

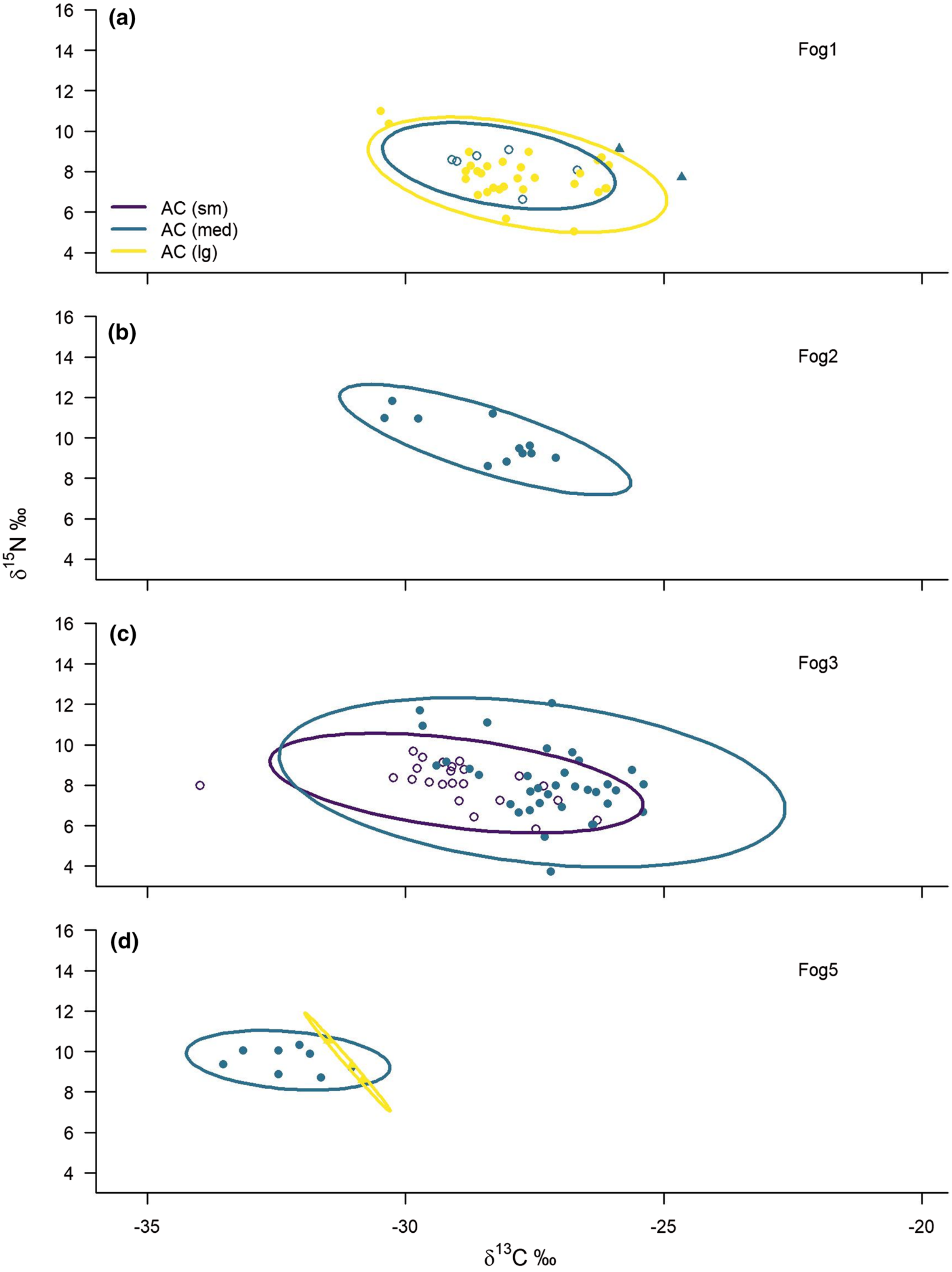

Fig. 5 Stable Isotope Bayesian Ellipses (SIBER) representing arctic char trophic niche space (by size class) for individual stable isotope measurements for 'closed' lakes **a** Fog1, **b** Fog2, **c** Fog3, and **d** Fog5 near Toolik Field Station, Alaska. Color figure is available online

also effect foraging success in different habitats (Budy and Luecke 2014; Klobucar et al. 2018).

As lake trout are widely believed to be the top predator across the landscape in arctic Alaska (as also indicated by our isotope analyses; Hershey et al. 1999, 2006), lake trout were thought to play an important role in structuring the populations of arctic char, with which they rarely coexist. However, our diet analyses did not indicate notable

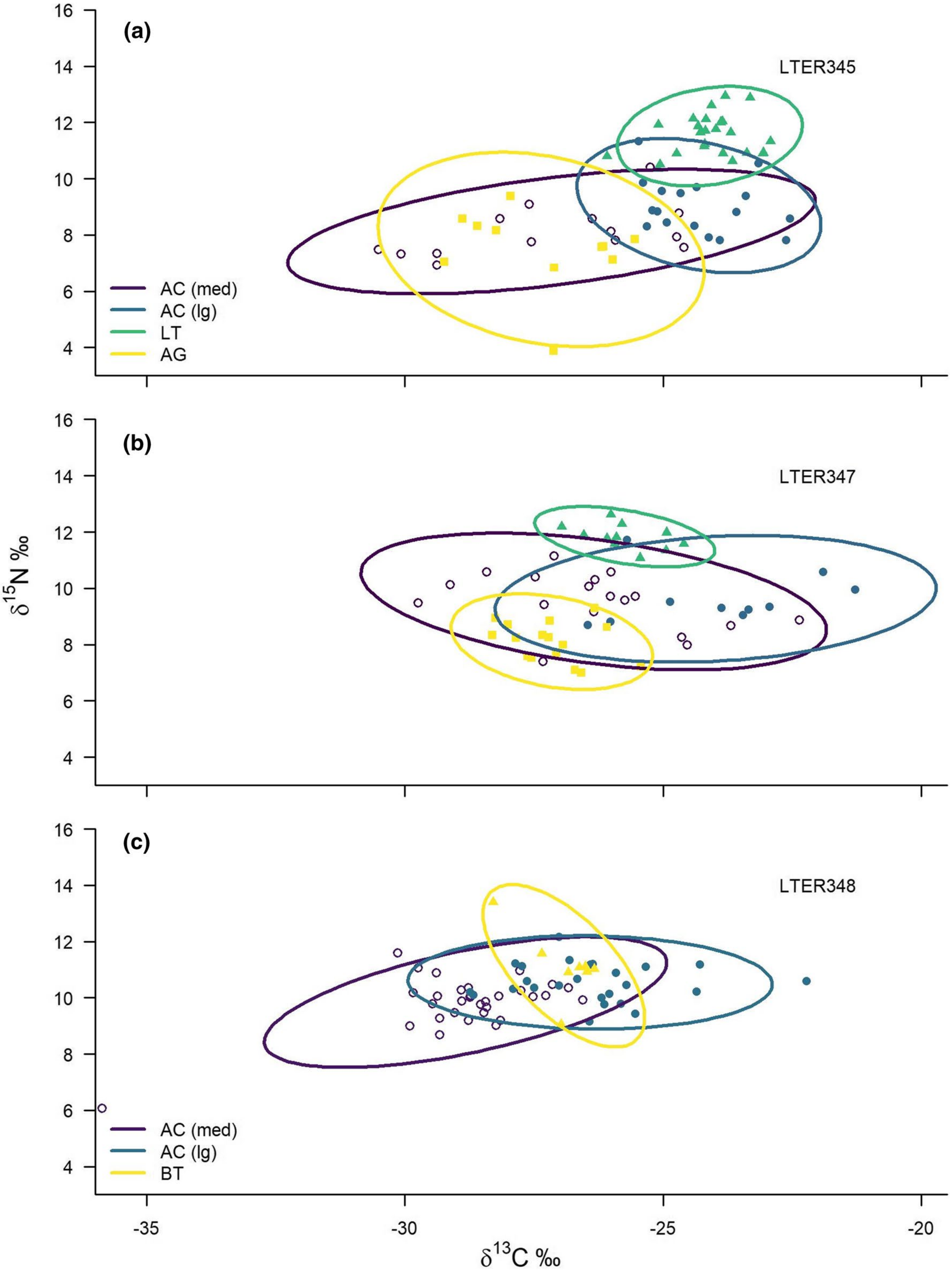

Fig. 6 Stable Isotope Bayesian Ellipses (SIBER) representing arctic char trophic niche space (by size class or species) for individual stable isotope measurements for 'leaky' Lake **a** LTER345, **b** LTER347, and **c** LTER348 near Toolik Field Station, Alaska. Color figure is available online

differences between arctic char diets in the closed lakes relative to the leaky lakes. Further, arctic char are larger and more numerous than lake trout in the leaky lakes (see Table 2). While relatively rare in Alaska, sympatric populations of arctic char and lake trout in northern Quebec, Canada, revealed similar results, arctic char were not piscivorous in lakes that also contained lake trout, but their growth rates were faster and their longevity was shorter (Fraser and Power 1989). Similarly, in northern Finland, introduced lake trout potentially impact native arctic char populations, and interestingly, lake trout are shown to be more generalist feeders relative to char (Eloranta et al. 2015a, b). In other work, we have noted higher growth rates for char in the leaky lakes than those of char in the closed lakes (Klobucar 2018; Klobucar et al. 2020). Competitive or consumptive pressure from lake trout may have selected for faster growing arctic char. Notably, however, in one leaky lake without lake trout (Lake LTER348), and where arctic char densities were the greatest of the leaky lakes (Klobucar 2018; Klobucar et al. 2020), we still caught large arctic char, and caught more small-medium arctic char as well. Other mechanisms by which these arctic char can grow large and coexist with lake trout should be further addressed. The population of burbot in this lake (which are extremely rare in other leaky lakes) could be large enough and piscivorous enough to influence arctic char size structure. Indeed, burbot trophic position is greater than arctic char in Lake LTER348.

At the onset of this study, we expected overall arctic char niche space would be reduced in the closed lakes relative to the leaky lakes, as a likely result of intraspecific competition. However, we observed generally larger and wider niche space of char in the leaky lakes. While we did observe a fair amount of diet overlap between arctic char, lake trout and arctic grayling (Schoener's $\alpha = 0.49–0.68$), less overlap of overall niche space was present in our isotopic analyses in the leaky lakes. For example, lake trout niche overlap with large arctic char was less than 20% in both leaky lakes where they co-occur. The leaky lakes may be large enough, and are slightly more productive, allowing multiple large predators to coexist, especially at the relatively low densities (Klobucar et al. 2020). In the leaky lakes, snails are the primary food item of large arctic char, whereas lake trout consume more chironomids. In comparison, in the absence of lake trout, arctic char across the closed lakes generally consume more chironomids relative to leaky lakes arctic char. Furthermore, in another nearby lake with lake trout but not arctic char, we observe lake trout selecting and consuming snails at proportions similar to arctic char in the leaky lakes (Klobucar and Budy, unpublished data). Collectively, these results suggest there could be species-specific tradeoffs regarding prey selection in the presence of interspecific competition, and overall, generalist characteristics may allow apex fish communities to succeed in different types of lakes and potentially persist in changing environments (e.g., Laske et al. 2018).

In addition to warmer temperatures in the arctic, surface water connectivity is likely to become more variable, with seasonal disconnection of currently connected lakes (Prowse et al. 2006). This climatic driver could have important population and community level effects regarding lake trophic dynamics as this study indicates. Accordingly, we have shown that biotic factors influence arctic char size structure in these lakes (Klobucar 2018), and thus, the trophic dynamics in this study could be driven by similar factors (e.g., primary production, density-dependence). If seasonal subsidies of arctic grayling, particularly important for lake trout growth, no longer reach the leaky lakes (e.g., Golden 2016), lake trout competition with arctic char may increase. In the closed lakes, which are already closed to species movements, internal processes are likely to regulate future char population dynamics (Budy and Luecke 2014), and the direction and magnitude of population abundances will ultimately depend on how prey resources respond (Klobucar et al. 2018).

In northern Alaska, where thousands of fish-bearing lakes are important subsistence resources, understanding the factors influencing trophic ecology of fish communities is critical for species management and conservation. Apex predators, such as arctic char and lake trout are important for local subsistence, but, fishes at the apex of these fish communities are also slow-growing and susceptible to over-harvest (Scanlon 2015). In fact, in contrast to much of Alaska, many subsistence fishers in the Alaskan Arctic prefer non-anadromous species such as char and lake trout (Carothers et al. 2013), and annual subsistence fish harvests by weight can exceed those of caribou and beluga whales (Magdanz et al. 2010). In Noatak, per capita subsistence harvest of fish exceeds 68 kg with as many as 98% of household using fish for food (Magdanz et al. 2010). Thus, many lakes of arctic Alaska provide important ecosystem services, while some unexploited lakes (this study) present a largely unaltered template to study lake trophic structure explicitly within a framework of inter- and intraspecific community dynamics, especially in a rapidly changing climate.

Acknowledgements We are indebted to G.P. Thiede for considerable logistics support throughout this project. We also thank the many technicians and volunteers that contributed to the field sampling and laboratory analyses of this work, including J. Goethlich, and L. Simmons. The staff of Toolik Field Station and Lounge One Science also greatly contributed to the success of this research. J.G., N.H., C.L., and S.N provided helpful comments on previous versions of this manuscript. This work was partially funded under the Arctic Long-Term Ecological Research program (National Science Foundation DEB 1026843 to P. Budy, co-PI). Additional support was provided by the US Geological Survey, Utah Cooperative Fish and Wildlife Research Unit (in-kind) and The Ecology Center at Utah State University. Any use of trade, firm or product names is for descriptive purposes only and does not imply endorsement by the U.S. government. All applicable institutional and/or national guidelines for the care and use of animals were followed.

Author contributions statement SK and PB designed and coordinated the study. Analyses and initial manuscript draft were completed by SK with support of PB. SK and PB wrote and edited the final manuscript.

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