Resource partitioning among top-level piscivores in a sub-Arctic lake during thermal stratification

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ABSTRACT

In systems with multiple piscivores, co-occurrence is dependent on resource partitioning. This is pronounced in oligotrophic northern lakes, which have simple food webs and short open-water seasons. We used acoustic telemetry and stable isotopes to quantify habitat and dietary partitioning during thermal stratification among three piscivores that commonly co-occur in Canadian sub-Arctic lakes—burbot (Lota lota), lake trout (Salvelinus namaycush), and northern pike (Esox lucius). Spatial core areas and core habitat niches (space and depth) did not significantly overlap among species. Although burbot and lake trout occupied similar mean daily depths (16.2 m and 13.4 m, respectively), and water temperatures (5.4 °C and 6.9 °C, respectively), they were spatially segregated. Burbot were closely associated with the lake bottom on steep drop-offs between the offshore and nearshore zone with moderate substrate complexity, whereas lake trout were located over deep offshore basins and suspended above the lake bottom. Northern pike occupied shallow depths (5.3 m) and warmer water (16.5 °C) within the nearshore region and were closely associated with bottom substrate of highest complexity. Some significant overlap among spatial home ranges and broad habitat niches indicated that these species interact. However, dietary niches did not significantly overlap at either the core or broad levels, suggesting that species were utilizing spatially diverse food sources. Our results highlight the importance of including depth and space when quantifying resource partitioning among fishes and provide insight into the mechanisms that promote piscivore co-occurrence in northern lakes.

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Introduction

Understanding patterns of resource partitioning among co-occurring species provides insights into processes that allow community co-existence. In aquatic ecosystems, segregation of food resources is often viewed as the principal mechanism of resource partitioning (Ross, 1986). However, in ectotherms such as fish, interactions between a species' physiology and the environment can also influence resource partitioning (Huey, 1991; Stevenson, 1985). Temperate freshwater fishes are classified into three thermal guilds, eurytherms (warm water), mesotherms (cool water), and stenotherms (cold water), which correspond to physiological optimal temperatures for growth (Magnuson et al., 1979). As a result, the distributions of fishes within aquatic ecosystems are often directed by thermal conditions of the water body they occupy (Magnuson et al., 1979). Habitat segregation of fishes differing in thermal niche is often observed in lakes that undergo thermal stratification. The existence of a metalimnion plays an important role as it forms a physical barrier to chemical exchange (e.g., renewal of hypolimnetic oxygen), as well as a biological barrier

to fish species that cannot tolerate warm water temperatures (Wetzel, 2001). In sub-Arctic regions, thermal stratification occurs during summer months, when lake production and fish growth is greatest (Hurst and Conover, 2003; Wetzel, 2001). Although summer in sub-Arctic regions is short, it represents a critical period for fishes to obtain energy for the development of gonads, somatic growth, and lipid storage to endure long, unproductive winters (Shuter et al., 2012).

Sub-Arctic regions are expected to undergo major physical and biological changes resulting from climate change and a rapidly expanding natural resource sector (Cott et al., 2015a; IPCC, 2013; Lemly, 1994; Prowse et al., 2006). Climate change is predicted to result in warmer annual air temperatures and extend the period of thermal stratification, and thereby potentially reduce preferred habitat for native cold water fishes (Reist et al., 2006). Consequently, warmer air temperatures will also develop suitable thermal habitat in northern lakes to support warm water fishes, such as smallmouth bass (Micropterus dolomieu), which can alter the habitat use and prey community of native fish populations (Sharma et al., 2007; Vander Zanden et al., 1999). Additionally, habitat alteration from natural resource extraction may lower the quality of nearshore habitat, and indirectly increase exploitation by providing access to pristine lakes (Cott et al., 2015a; Lemly, 1994; Schindler and Lee, 2010). Consequently, these potential changes to sub-Arctic

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lakes could alter interspecific interactions and lead to shifts in community dynamics.

Top-level piscivores are often highly mobile, allowing them to feed on a wide range of prey in disparate habitat types (e.g., nearshore–offshore regions; McCann et al., 2005; Schindler and Scheuerell, 2002). As such, piscivores have the potential for substantial habitat and dietary overlap with co-occurring species, including other piscivores. Quantifying the degree of resource partitioning among piscivores in sub-Arctic lakes can identify key bioenergetic pathways that enable the co-occurrence of otherwise trophically similar species (Cooke and Suski, 2008). Lake trout (*Salvelinus namaycush*), northern pike (*Esox lucius*), and burbot (*Lota lota*) are three piscivores that commonly co-occur in freshwater lakes of the Canadian sub-Arctic (Cott et al., 2011). Lake trout is stenothermic, but typically lives in pelagic habitats and is described as an opportunistic generalist predator, which as adults preferentially feed on pelagic forage fish (Martin and Olver, 1980; VanderZanden and Rasmussen, 1996). Northern pike is a mesotherm, and can be generally described as an opportunistic visual ambush predator associated with littoral habitat structure such as vegetation (Casselman and Lewis, 1996; Scott and Crossman, 1973). Burbot is also a stenotherm that is almost exclusively piscivorous and is associated with benthic habitats (Amundsen et al., 2003). Building on results of a previous study that found burbot, lake trout, and northern pike differ in mean food web position during the open-water season in sub-Arctic lakes (Cott et al., 2011), we sought to determine whether this dietary niche partitioning was a function of differences in habitat use, or differences in prey selection within common habitats. We predicted that habitat and dietary niches would follow a similar pattern, whereby each species would utilize spatially distinct food sources.

To address our research questions, we combined two commonly used methods to study resource partitioning in aquatic ecosystems: 1) high-resolution passive acoustic telemetry, used to quantify the horizontal (spatial) and vertical (depth) distributions of each piscivorous fish species and, 2) stable isotope ratios of carbon ($\delta^{13}C$) and nitrogen ($\delta^{15}N$), used to quantify dietary niche partitioning. This research will add to the limited studies (see Cunjak et al., 2005; Matich and Heithaus, 2014; Speed et al., 2011) that have corroborated multi-species results of telemetry and stable isotope analysis (SIA) in a similar framework to examine how habitat and dietary partitioning relate in aquatic ecosystems.

Methods

Study site

The study took place at Alexie Lake (62°40′36.59″ N, 114° 4′22.76″ W), a scientific research lake closed to the public, located approximately 30 km north east of Yellowknife, Northwest Territories (NT), Canada (Fig. 1). Alexie Lake is a medium-sized (402 ha, maximum depth 32 m), oligotrophic lake that undergoes thermal stratification during summer months (Healey and Woodall, 1973). In addition to the three top-level piscivores — burbot, lake trout, and northern pike — the fish community is composed of lake whitefish (*Coregonus clupeaformis*), cisco (*Coregonus artedi*), lake chub (*Couesius plumbeus*), ninespine stickleback (*Pungitius pungitius*), trout-perch (*Percopsis omiscomaycus*), slimy sculpin (*Cottus cognatus*), spoonhead sculpin (*Cottus ricie*), and deepwater sculpin (*Myoxocephalus thompsoni*) (Cott et al., 2011). The lake also contains the opossum shrimp, *Mysis diluvania*.

Lake water temperature and dissolved oxygen

Lake water temperatures were recorded 5 July–12 September, 2012 using a string of data loggers (HOBO Pendant Temp/Light, 64 k model UA-002-64, Onset Computer Co., Cape Cod, MA) installed over the
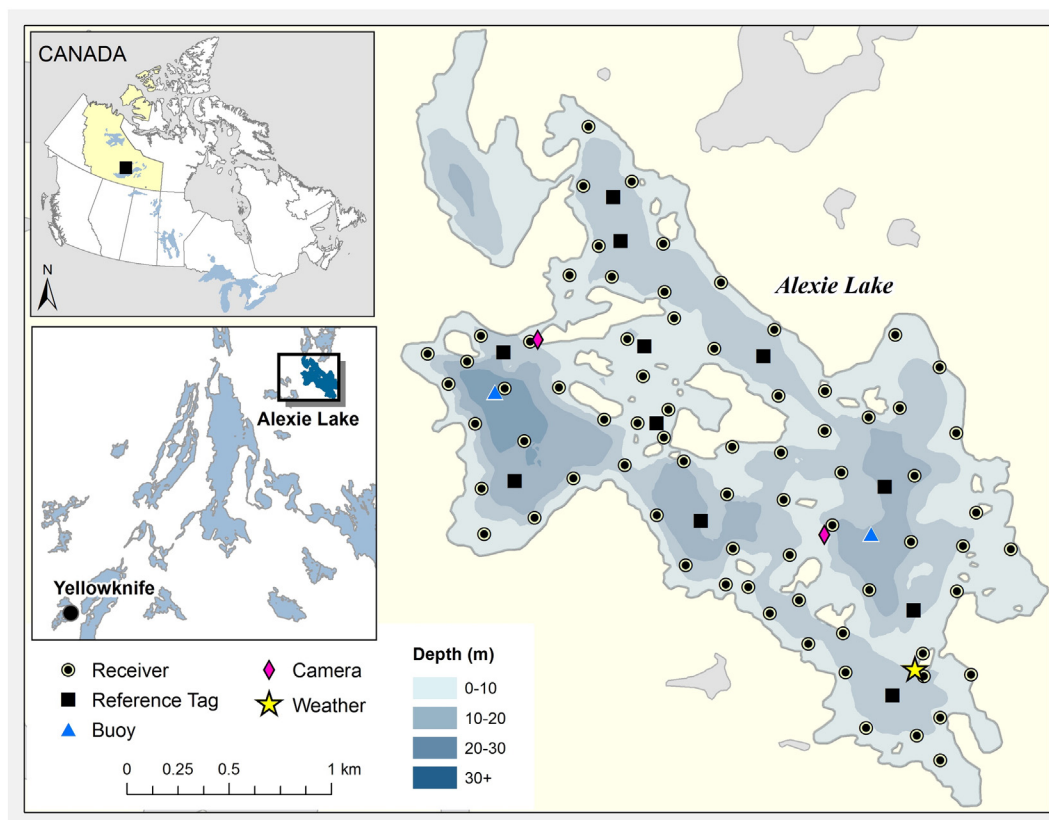

Fig. 1. Location of Alexie Lake, NWT, Canada (inset). The map of Alexie Lake, includes the locations of 72 telemetry receivers and corresponding co-located sync tags (circles), acoustic reference tags (squares), center buoys to which temperature and light loggers were attached (triangles), ice-monitoring cameras (diamonds), and the weather station used to monitor air temperature and wind direction and speed (star). Depth contours are every 10 m.

deepest point of Alexie Lake (Fig. 1). Data loggers were set at 0.5 m, at 1 m depth intervals from 1 m to 20 m, and at 25 m and 30 m below the surface of the water. Water temperatures were recorded hourly. We calculated a mean daily temperature for each depth followed by spline interpolation to obtain temperatures for every 0.1 m depth interval from the water surface to bottom. Interpolated daily thermal profiles were used to estimate the water temperature occupied by piscivorous fish implanted with pressure-sensing telemetry transmitters (see below and Plumb and Blanchfield, 2009). Dissolved oxygen measurements were not taken during the study period, but were measured in the two years following using an optical handheld dissolved oxygen and temperature meter (Pro ODO, YSI Inc., Yellow Springs, OH) at 1 m depth intervals over the deepest point of the lake. Therefore, we assumed deep water oxygen concentrations in 2012 were similar to those of 2013 and 2014.

Lake bathymetry and bottom habitat classification

We characterized the bathymetry and associated habitat characteristics of Alexie Lake in June 2012 using high-resolution hydroacoustic sensing (Milne Technologies, Keene, ON). Hydroacoustic data were collected using a 120 kHz Simrad EK60 $7.0° \times 7.0°$ split-beam echosounder system, and following a systematic parallel survey design with transects spaced 25 m apart. A bottom substrate complexity map was developed by calculating the total variance of distinct substrate classes within a 60 m search radius of each 3×3 m grid cell of Alexie Lake. Bottom substrate complexity in Alexie Lake averaged ~0.3 and ranged from <0.1 to 1.6, where a higher substrate complexity value indicated a greater number of distinct substrate types, relative to the entire dataset. Habitat classification was verified using video and Ekman dredge sampling (for details see Cott et al., 2015b).

Fish telemetry data

During the period 12–21 June 2012, lake trout (n = 30), northern pike (n = 4), and burbot (n = 4) (see Table 1 for biological information) were captured and implanted with acoustic transmitters. Discrepancy in sample size among species was because the main objectives of the study were focused on lake trout, and we opportunistically implanted acoustic transmitters within a small number of burbot and northern pike. Fish capture took place when the lakes surface waters were <15 °C. Lake trout and northern pike were captured together during daytime hours by trolling over shallow water (~3–10 m) around the perimeter and islands of the lake with barbless lures that targeted the top few meters of the water column. Burbot were captured at night using hook-less long-lines baited with cisco (bait was tied to the line using twine) from ~5 to 10 m of water to reduce the potential for barotrauma. Although burbot were captured at different times of the day than lake

trout and northern pike, all species were captured from similar areas, with respect to both depth and space, within the lake. Once captured, all fish were brought to shore in holding containers, lightly anesthetized in a solution of Tricaine Methanesulfonate (MS-222) (90 mg/L for lake trout and burbot and 180 mg/L for northern pike) buffered with sodium bicarbonate, and implanted with coded, acoustic, pressure-sensing (depth) transmitters (V13P-1 L; Vemco Ltd., Bedford, NS). See Blanchfield et al. (2005) for a detailed description of surgical procedures. Transmitters were 13 mm in diameter, 33 mm in length, and weighed 6 g in water. We ensured the weight of the transmitter did not account for more than 2% of a fish's body weight so that it did not affect swimming ability (Winter, 1983). Prior to implantation, each transmitter's depth sensor was individually calibrated at 4 m depth intervals from surface to bottom in Alexie Lake, and were accurate to ± 1.7 m with a resolution of 0.15 m. Transmitters randomly emitted an acoustic signal every 80–160 s.

The depth and spatial positions of individual acoustic-implanted fish were monitored using a Vemco Positioning System (VPS; Vemco Ltd.). The VPS array consisted of 72 underwater omni-directional acoustic receivers (VR2W, 69 kHz) with overlapping detection ranges (as determined by a range test performed prior to the study) that were anchored to the lake bottom, and allowed for near complete positioning coverage of transmitter-tagged fish throughout Alexie Lake (Fig. 1). Each receiver was outfitted with an acoustic transmitter ("sync tag"; V16-1 L, 69 kHz, code transmission every 1200 s ± 100 s), located 1–2 m above the receiver, to allow for internal clock synchronization during data processing. An additional 11 reference tags were distributed throughout the acoustic array to aid in system synchronization and positioning accuracy (Fig. 1). For a detailed description of VPS operation see Espinoza et al. (2011), Roy et al. (2014), and Smith (2013).

Stable isotope data

Sampling of fish for SIA occurred from 19 to 23 August 2008. Lake trout and northern pike were captured using gillnets stratified at various depths, and burbot were captured using over-night sets of baited long lines. For a detailed description of fish sampling methods see Cott et al. (2011). Following fish collection, biological data, including fork length (FL), total length (TL), and wet weight (g), of each fish were recorded (Table 1); and a skinless dorsal muscle sample was removed and frozen at −20 °C. Dorsal muscle samples were later freeze–dried and pulverized for analysis. Stable isotope ratios of carbon (C) and nitrogen (N) were determined at the Stable Isotopes in Nature Laboratory, University of New Brunswick, NB, Canada. Stable isotope values were conveyed in δ notation (units ‰), where $\delta^{13}C$ or $\delta^{15}N = [(R_{sample} / R_{standard}) - 1] \times 1000$, where R is $^{13}C/^{12}C$ or $^{15}N/^{14}N$. The standard reference material was Vienna Pee Dee Belemnite carbonate for C, and atmospheric nitrogen for N. Analytical error (based on standard deviation) from the repeated analysis of internal and international standards was 0.16 and 0.15 for $\delta^{13}C$ and $\delta^{15}N$, respectively. Because all SIA samples had C:N ratios <3.5, and species did not differ in C:N ratio (data not shown), we did not apply lipid corrections on the data prior to analyses (Post et al., 2007).

Statistical analyses

All data processing, statistical analyses, and figures were completed using the R statistical computing package (hereafter "R"; Version 3.1.1, R Development Core Team, 2014).

Fish telemetry data processing

Telemetry data used in this study included only spatial positions (and corresponding depth measurements) that were estimated by the VPS. Prior to statistical analyses we filtered telemetry positions using the following methods. First, to reduce the possibility that fish behavior was altered by surgical procedures, we did not include data collected

Table 1
Comparison of biological data, including the mean (± 1 SD), and range of fork lengths (FL) and wet weights (WW), for burbot (BB), lake trout (LT), and northern pike (NP) included in acoustic telemetry and stable isotope analyses, Alexie Lake, NT, Canada. Fishes for acoustic telemetry were tagged 12–21 June, 2012. Fishes for stable isotope analysis were collected 19–23 August, 2008 (Cott et al., 2011).

Data Type	Species	n	Mean FL (mm)	FL range (mm)	Mean WW (g)	WW range (g)
Acoustic telemetry	BB[a]	3	578 ± 42	504–637	1433 ± 456	937–1823
	LT[a]	29	502 ± 44	427–651	1347 ± 349	870–2570
	NP[b]	4	714 ± 42	667–768	2065 ± 463	1682–2684
Stable isotopes	BB	9	552 ± 50	474–631	1147 ± 291	720–1660
	LT	8	465 ± 110	312–606	1144 ± 702	300–2220
	NP[b]	8	521 ± 98	354–662	944 ± 484	295–1820

[a] Data from 1 BB and 1 LT that died and were excluded from acoustic telemetry analyses and are not included in the table.
[b] Note that size of NP used in acoustic telemetry and stable isotope analysis do not overlap.

within 14 d of the final transmitter implantation in our analyses (Rogers and White, 2007). Second, we excluded data from fish that had died, shed their transmitter, or had transmitter malfunctions (n = 1 lake trout, n = 1 burbot removed; Table 1). Third, we removed positions that fell outside the spatial extent and depth range of Alexie Lake. Lastly, we calculated the twice the distance root mean squared (2DRMS) for each estimated sync tag position, relative to their known location to develop a relationship between measured error and hyperbolic positioning error (HPE), a unitless estimate of positioning error provided for each spatial position estimated by the VPS (Meckley et al., 2014). Using the relationship between 2DRMS and HPE for sync tag data, we determined that removing all data with an HPE >20 would result in an average spatial positioning error less than 5 m (our goal). The actual positioning error based on sync tag positions over the course of the study following filtering out all positions with HPE > 20 was 4.21 ± 0.04 m (mean ± se). We then used the HPE > 20 filter on our fish positions to eliminate positions with high error from the dataset. Our final filtered dataset contained a total of 699,669 positions (lake trout: n = 604,933; northern pike: n = 57,703; burbot: n = 37,033).

Depth and temperature occupancy

We produced frequency histograms of the depth distribution of each species throughout the study period by calculating the number of telemetry positions located within one meter depth increment. To test for differences in mean daily depth (MDEP) occupation among species, we used linear mixed effects models (LMM: *R* package: nlme). The use of mixed effects models allowed for unequal sample size among species, and enabled partitioning of random effects; individual fish (IND) were treated as random intercepts nested within species, so that the main effects of species (SPP) and the daily mean temperature of the lake at 1 m depth (TMP) could be analyzed (Zuur et al., 2009).

Assumptions of normality and heteroscedasticity were tested graphically using Q–Q plots, boxplots, and histograms of standardized residuals (Zuur et al., 2009). Multicollinearity was tested for using variance inflation factors. Temporal autocorrelation was evaluated using autocorrelation function (ACF) and partial autocorrelation function (PACF) plots of residuals. We determined MDEP observations to follow a first order autoregressive correlation structure (AR1; Pinheiro and Bates, 2000), which was accounted for in our LMM analysis (*R* function: corAR1).

Model selection for the LMM analysis was performed using AICc (*R* package: MuMIn). Model selection started with the fully parameterized model, which included the fixed factors SPP, TMP, the interaction SPP*TMP, and the random intercept individual fish nested within species (IND:SPP; Eq. 1).

$$MDEP = SPP + TMP + SPP * TMP + 1|IND : SPP + \varepsilon. \qquad (1)$$

We sequentially culled fixed factors from the fully parameterized model (Eq.1) to obtain models containing all possible combinations of fixed factors, ending with the random intercept model and ranked them using AICc (Electronic Supplementary Material (ESM) Table S1; Anderson et al., 2001). A marginal F test and Tukey multiple comparison post hoc test (*R* package: lsmeans) were performed on the top ranked AICc model to test for significance of fixed factors and to determine differences in MDEP among the SPP. Further, to identify the proportion of variance in MDEP attributed by the random effect (individual fish), we calculated the intraclass correlation coefficients (ICC) of the top ranked AICc model (Raudenbush and Bryk, 2002). Coefficients of determinations (conditional R^2) were estimated using the methods of Nakagawa and Schielzeth (2010) (R package: MuMIn). We used $P < 0.05$ to indicate statistical significance for all datasets.

Spatial habitat occupancy

We produced frequency histograms of the spatial distribution of each species by calculating the number of telemetry positions located within each 1 m bathymetric depth contour of the lake (0–32 m). To quantify bottom substrate complexity occupancy for each species, we matched each individual spatial position estimated by the VPS to the bottom substrate complexity raster map and grouped them according to species.

We assessed overlap in spatial habitat use among our study species using kernel estimated utilization distributions (UD; Worton, 1989). Briefly, individual spatial positions estimated by the VPS were used to estimate a UD, which was used to estimate the size (ha) and shape (coordinates) of spatial UDs using 50% ("spatial core areas") and 95% ("spatial home ranges") of data for each species (*R* package adehabitat HR; Calenge, 2006). Spatial core areas are representative of habitat used often by a species (e.g., foraging grounds), while spatial home ranges area represent the breadth of habitats used by a species. To account for unequal sample sizes, we used a bootstrapping technique to quantify the size and overlap of spatial core and home range areas among species. For each iteration of the bootstrap analysis we chose a random sample ($n = 3$) of individual lake trout and northern pike equal to the sample size of the burbot, which had the lowest number of individual fish tagged (Table 1). We then estimated the spatial core areas and home ranges for each species and conducted paired comparisons to estimate the probability that a randomly selected spatial position of one species would be found in the core or home range area of a second species, and vice versa (e.g., A on B and B on A). For overlap comparisons containing lake trout, this analysis was repeated up to 100 times to obtain a mean ± SD overlap value for each potential pairwise comparison with burbot and northern pike. For overlap comparisons between burbot and northern pike, the analysis was only repeated four times (total number of unique combinations of northern pike) to produce a mean core ± SD overlap. Burbot core and home range sizes were based on the three burbot tagged and those of northern pike were based on the four unique combinations of three individuals. Lake trout spatial habitat sizes were estimated as the mean ± SD from the 100 iterations used for overlap comparisons. We considered an ecologically significant spatial overlap probability to be >60%, the same criteria used in the Schoener diet overlap index (Schoener, 1968), here and in all subsequent analyses. We did not statistically test differences in size of core and home range areas because burbot only had a single estimate.

To assess niche partitioning, we also determined whether each species was closely associated to bottom substrates (benthic) or was suspended within the water column (pelagic). We estimated the depth off bottom for each VPS position by calculating the difference between the bathymetric contour and the depth of the fish, as measured by the acoustic transmitter, and calculated a mean ± SD for each species. Values close to zero indicated fish were situated close to the lake bottom, and increasing values indicated fish were suspended above the lake bottom.

Dietary niches

To test for differences in mean δ^{13}C and δ^{15}N values among the three piscivorous species we used ANOVA with Tukey's post hoc tests. Dietary niche partitioning was quantified using population metrics of stable isotope data (Layman et al., 2007; Jackson et al., 2011, 2012). We used the methods of Swanson et al. (2014) to calculate the position, size, and overlap of dietary niches and corresponding carbon and nitrogen ranges, using 50% ("core dietary niches") and 95% ("broad dietary niches") of the data for each species (*R* package: nicheROVER). Briefly, two-dimensional Bayesian elliptical niche regions were estimated for each species by randomly selecting pairs of δ^{13}C and δ^{15}N with a Normal-Inverse-Wishart (NIW) prior (Swanson et al., 2014). A Monte Carlo estimation of overlap among species was used to estimate the probability that a randomly drawn individual from a given species would be found in the niche region of another, and vice versa. We calculated a mean ± SD overlap probability for each combination of two species (Swanson et al., 2014). We also calculated the mean ± SD size (‰^{2}) and shape of niche regions. The carbon range (*CR*) and nitrogen (*NR*) for

each species was estimated from the mean core and broad ellipse regions for each species and were expressed in ‰. Kruskal–Wallis tests with non-parametric Nemenyi post hoc tests were used to test for differences in the size of dietary niches among species. The nitrogen and carbon ranges of the core (NR_{50}, CR_{50}) and broad (NR_{95}, CR_{95}) dietary niches for each species represent the range of $\delta^{15}N$ and $\delta^{13}C$, respectively. CR describes the breadth (i.e., littoral–pelagic) of food sources consumed, whereas NR provides insight into the range of trophic levels occupied by each piscivore species.

Habitat niches

Core (50%) and broad (95%) habitat niche size, overlap, and spatial (SR) and depth ranges (DR) were estimated with the same statistical approach used to estimate dietary niches (explained above), where individual pairs of telemetry data, depth and bathymetric depth contour replaced $\delta^{15}N$ and $\delta^{13}C$ pairs. Habitat niches for each species are expressed in m^2 and SR and DR are expressed in m. Kruskal–Wallis tests with non-parametric Nemenyi post hoc tests were used to test for differences in the size of habitat niches among species using values derived from individual iterations of our habitat niche estimation.

Results

Lake thermal conditions

Alexie Lake was thermally stratified for the entire duration of the study (5 July–12 September, 2012; Fig. 2a). During this time, surface water temperatures (1 m from surface) averaged 18.6 °C, and ranged from 14.4 to 21.7 °C. The depth of the thermocline was shallowest on 5 July 2012 (6.5 m) and reached its deepest on 10 September, 2012
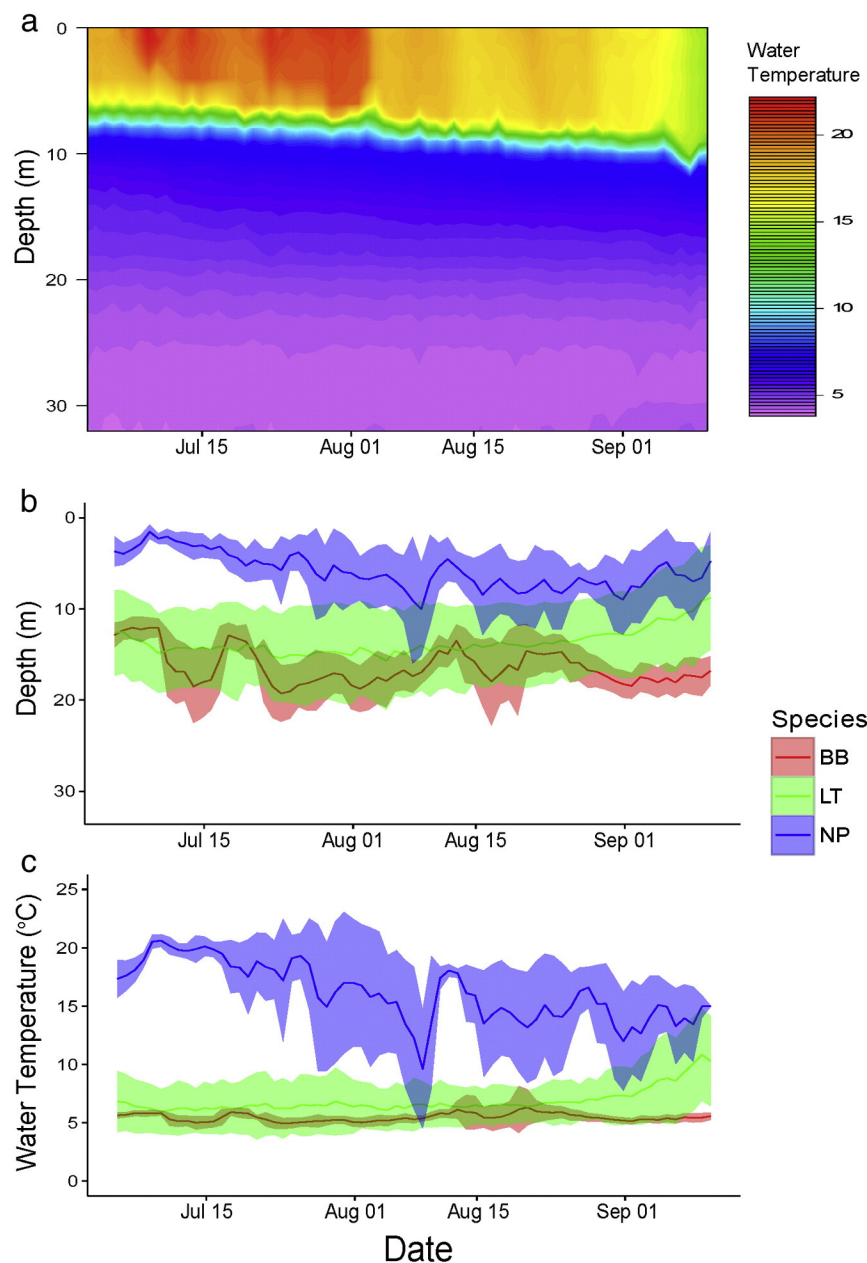

Fig. 2. a) Thermal structure (°C) of Alexie Lake, NT, Canada, during the summer stratified period (5 July 2012–12 September, 2012), and the corresponding mean (±SD) daily (b) depths (m), and (c) water temperatures (°C) occupied by acoustic-tagged burbot (BB), lake trout (LT), and northern pike (NP). In c) the dark lines represent the daily mean and shaded areas represent the SD.

(10.6 m). As a result, the proportion of cold hypolimnetic water was greatest at the start of the study (64% of total volume) after which it steadily decreased to 46% of the total volume of Alexie Lake. The opposite trend was observed for warm water habitat, where the depth of the epilimnion increased steadily from the first day of the study. Profiles of early and late summer dissolved oxygen concentrations (DO) (from subsequent years, see Methods section) indicated changes throughout the stratified period. In early July, DO concentrations were >4 mg·L^{-1} to 30 m depth, but by mid-September suitable DO concentrations (i.e. >4 mg/L) were only found in water depths of 20 m or less. The proportion of Alexie Lake with depths >20 m is low, contributing only 12% and 5.2% of total lake area (402 ha) and volume (4.8×10^7 m^3), respectively (Fig. 1).

Depth and water temperature occupancy

Model selection using AICc selected the fully parameterized model (Eq. 1) to best describe the mean daily depths (MDEP) of acoustic-tagged fish in Alexie Lake during thermal stratification (ESM Table S1). Eq. 1 accounted for 100% of the Akaike weight and had a conditional R^2 of 52.7%. However, calculation of ICCs on the best model indicated that within a species, individual habitat selection accounts for 33.9% of the variation in mean daily depths.

The MDEP of acoustic-tagged lake trout, northern pike, and burbot differed over the course of the study (Fig. 2b). The significant interaction between the fixed factors species and lake surface water temperature (SPP*TMP: $F_{2, 2335} = 15.26$, $P < 0.001$) indicated that species were adjusting their daily depth and the corresponding water temperature they occupied according to the thermal conditions of the lake. Overall, burbot had the deepest MDEP occupancy, at 16.22 m ($\pm$SE; ± 0.24 m), but were not significantly different (Tukey test, $P = 0.34$) from lake trout (13.36 ± 0.10 m); however, northern pike (5.32 ± 0.21 m) occupied significantly shallower depths than both lake trout (Tukey test, $P < 0.001$) and burbot (Tukey test, $P < 0.001$; Fig. 2b, 3a). Differences in depths occupied by species were correlated with differences in mean water temperatures occupied (Fig. 2c). Over the duration of the study, tagged burbot and lake trout occupied cold average water temperatures of 5.41 ± 0.04 °C and 6.94 ± 0.05 °C, respectively. Tagged northern pike occupied warmer and more variable water temperatures 16.45 ± 0.24 °C, relative to burbot and lake trout (Fig. 2c).

Spatial habitat occupancy and overlap

Because bottom complexity is a measure of the number of distinct substrate types in an area, relative to the entire dataset, bottom substrate complexity was greatest in nearshore areas, where bottom substrates changed rapidly from rock/cobble to sand or clay bottom types. Areas of moderate complexity were associated with transitions zones, such as those between boulder-dominated nearshore and silt-dominated offshore zones. Low complexity areas tended to be in deep areas of the lake with homogenous bottoms of mud, silt, or clay (Fig. 4a).

The position of space-based core areas (50%) among the piscivores in Alexie Lake showed low probability of overlap with one another (Fig. 4a). Burbot core areas were (25.9 ha) located over steep drop-offs between nearshore and offshore zones (10–20 m), corresponding to occupancy of large rocky substrates with moderate habitat complexity (0.30 ± 0.24; Table 2, Fig. 3b, and 4a, b). Northern pike occupied shallow depths (<10 m), had relatively small core areas (25.5 ha), similar to burbot, but located close to shore, and were associated with the highest substrate bottom complexity (0.42 ± 0.22) among study species (Table 2, Figs. 3b, and 4a, b). Core areas for lake trout were the largest (57.1 ha), and were situated over deep offshore basins (>20 m depth), where bottom substrates in Alexie Lake had lowest bottom complexity occupancy (0.21 ± 0.21; Fig. 3b, 4a, b). Based on spatial telemetry data, these three piscivores showed little overlap of core areas; however, home range areas did overlap significantly. The home range of
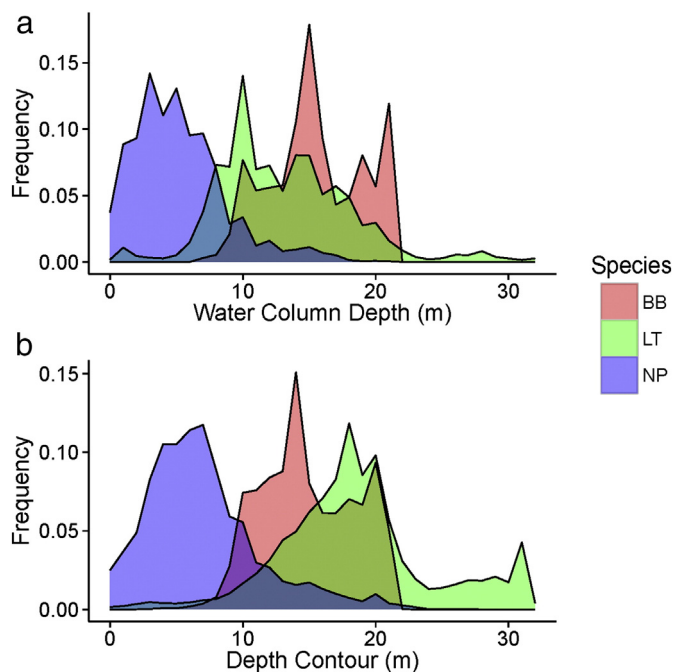

Fig. 3. Frequency histograms comparing (a) fish depth within the water column, and (b) lake bottom depth (within each 1 m bathymetric depth contour) over which telemetry-tagged burbot (BB), lake trout (LT), and northern pike (NP) were positioned during 5 July, 2012–12 September, 2012 in Alexie Lake, NT, Canada.
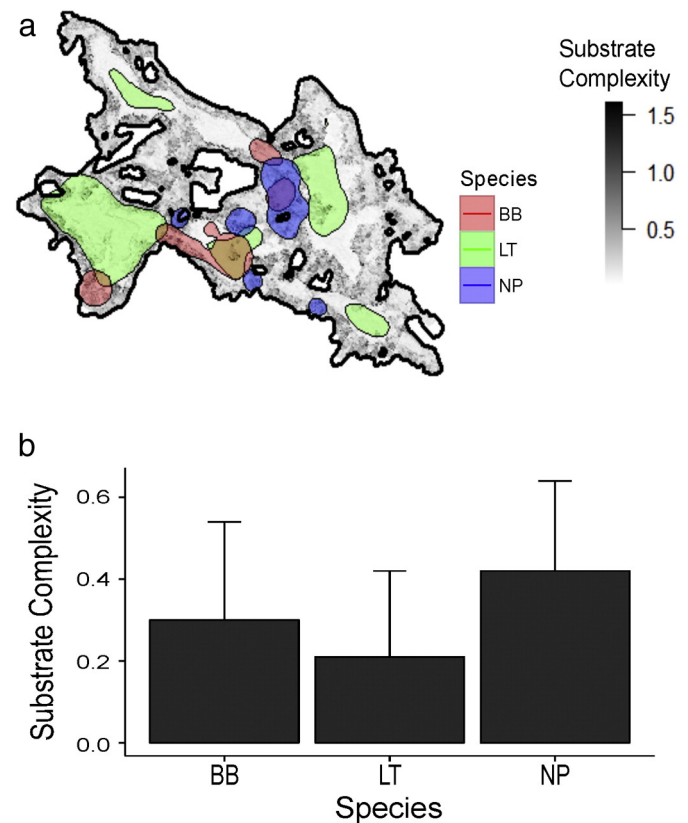

Fig. 4. Comparison of (a) spatial core areas (50% occupancy) relative to bottom substrate complexity occupancy and (b) mean $\pm$ SD substrate complexity occupancy scores of telemetry-tagged burbot (BB), lake trout (LT), and northern pike (NP) in Alexie Lake, NT, Canada, during 5 July–12 September, 2012. White represents lowest and black represents highest substrate complexity.

Table 2

Comparison of the mean ($\pm$SD) size of spatial core (50%) and home range (95%) areas, and core (50%) and broad (95%) habitat and dietary niches of burbot (BB), lake trout (LT), and northern pike (NP) monitored during the summer stratified period in Alexie Lake, NT, Canada. Spatial core and home range areas included spatial data from fish implanted with acoustic transmitters and monitored 5 July–12 September, 2012. Habitat niches utilized both spatial and depth telemetry data to evaluate habitat resource partitioning among species. Dietary niches utilized stable isotope data (δ^{15}N and δ^{13}C) collected 19–23 August, 2008 (see Cott et al., 2011). The size of spatial habitat and habitat niche estimates are not comparable. Spatial core and home range areal estimates are specific to the position of fish within Alexie Lake while habitat niches represent habitat use quantified on two dimensions (depth and bathymetric depth contour).

Species	Spatial habitat (ha)		Habitat niches (m^2)		Dietary niches (‰)	
	Core area	Home range	Core	Broad	Core	Broad
BB	25.9 ± 0.0	108.8 ± 0.0	19.2 ± 0.1	82.7 ± 0.4	1.6 ± 0.6	6.9 ± 2.4
LT	57.1 ± 18.2	270.3 ± 62.9	111.1 ± 0.1	480.1 ± 0.6	1.4 ± 0.5	6.0 ± 2.3
NP	25.5 ± 5.6	136.7 ± 18.9	49.4 ± 0.2	213.3 ± 0.9	4.2 ± 1.6	18.0 ± 6.8

lake trout overlapped those of both burbot and northern pike, and the home range of burbot overlapped that of northern pike (Table 3).

Burbot and northern pike were closely associated with benthic habitats, with each species positioned, on average, 0.1 ± 1.6 m and 1.7 ± 3.6 m (mean $\pm$ SD) above the bottom of the lake, respectively (Fig. 3), although northern pike occupied much shallower areas of Alexie Lake than did burbot (Fig. 2b). The proportion of positions within 0.5 m from the lake bottom was 96% for burbot and 60% for northern pike. Lake trout, had a more pelagic distribution than the other piscivores. Lake trout were positioned 5.5 ± 5.7 m above the lake bottom with only 27% of all positions ≤0.5 m from the bottom (Fig. 3).

Dietary niches

We detected significant differences in mean δ^{15}N ($F_{2,34} = 59.33$, $P < 0.001$) and δ^{13}C ($F_{2,34} = 50.42$, $P < 0.001$) among the three top-level piscivores in Alexie Lake. Tukey tests indicated that for δ^{15}N, lake trout (13.9 ± 0.9) and burbot (13.7 ± 0.6) did not differ from one another ($P = 0.85$), but were enriched in ^{15}N ($P < 0.001$) compared to northern pike (10.3 ± 1.2). There were also significant differences in δ^{13}C among species ($F_{2,34} = 50.42$, $P < 0.001$), where burbot, lake trout, and northern pike all differed from one another (all $P < 0.001$); lake trout (-26.7 ± 0.7) were least enriched in ^{13}C and northern pike (-22.9 ± 1.3) most enriched, with burbot (-25.1 ± 0.8) having an intermediate δ^{13}C value (Fig. 5). Note that the size ranges of lake trout and burbot used for SIA overlapped those for telemetry analysis; however, for northern pike size ranges did not overlap (Table 1). Northern pike used for SIA (FL range 354–662) were smaller than those used for telemetry (667–768 mm).

Core dietary niches differed in size among species (Kruskal–Wallis test: $H = 1.9 \times 10^4$, $P < 0.001$; Table 3; Fig. 5). Northern pike had a significantly larger core dietary niche than both burbot and lake trout (both $P < 0.001$), while lake trout and burbot did not differ in niche size ($P = 0.92$; Fig. 5). Significant differences in broad dietary niche sizes were also found among species (Kruskal–Wallis test: $H = 1.8 \times 10^4$, $P < 0.001$; Table 2). Similar to core dietary niches, northern pike had larger broad dietary niches than both burbot and lake trout

(both $P < 0.001$), and lake trout and burbot did not differ in niche size from one another ($P = 0.95$; Table 2). Northern pike foraged across a higher number of trophic levels ($NR_{50} = 2.1$‰, $NR_{95} = 4.3$‰) relative to lake trout ($NR_{50} = 1.6$‰, $NR_{95} = 3.2$‰) and burbot ($NR_{50} = 1.4$‰, $NR_{95} = 2.9$‰) at both core and broad dietary niche levels (Fig. 5). A similar pattern existed in the breadth of carbon used by each species, where northern pike had the largest carbon ranges ($CR_{50} = 3.0$‰, $CR_{95} = 6.2$‰) relative to lake trout ($CR_{50} = 1.8$‰, $CR_{95} = 3.7$‰) and burbot ($CR_{50} = 1.8$‰, $CR_{95} = 3.8$‰) at both core (Fig. 5) and broad dietary niche levels (not presented in figure).

The distribution of the core and broad dietary niches of lake trout, northern pike, and burbot showed a similar pattern as observed in the mean δ^{15}N and δ^{13}C values for each species. These piscivores did not exhibit significant overlap in either core or broad dietary niches (Table 3).

Habitat niches

The size of habitat niches differed among species at both the core (Kruskal–Wallis test: $H = 12.9 \times 10^4$, $P < 0.001$; Table 2; Fig. 5) and broad levels (Kruskal–Wallis test: $H = 12.7 \times 10^4$, $P < 0.001$; Table 2). Lake trout had significantly larger core and broad habitat niches than both burbot and northern pike (all $P = 0.001$; Table 2), while northern pike had larger core and broad habitat niches than burbot (both $P < 0.001$; Table 2). Lake trout utilized the greatest range of depths during the study ($DR_{50} = 11.5$ m, $DR_{95} = 23.8$ m) relative to northern pike ($DR_{50} = 8.3$, $DR_{95} = 17.3$) and burbot ($DR_{50} = 8.0$ m, $DR_{95} = 16.5$ m) at both core (Fig. 5) and broad (not presented in figure) habitat niche levels. A similar pattern existed in the extent of spatial habitat used by each species, where lake trout had greater space use ranges ($SR_{50} = 13.1$, $SR_{95} = 27.3$) relative to burbot ($SR_{50} = 8.0$, $SR_{95} = 16.6$) and northern pike ($SR_{50} = 10.0$, $SR_{95} = 20.8$) at both core (Fig. 5) and broad (not presented in figure) habitat niche levels.

The habitat niches of lake trout, northern pike, and burbot closely matched the pattern observed in their dietary niches (Fig. 5). There was no significant overlap of core habitat niches among species; however, for broad habitat niches, burbot overlapped that of lake trout (Table 3).

Table 3

Comparison of mean ($\pm$SD) overlap probabilities of spatial core (50%) and home range (95%) areas, and core (50%) and broad (95%) habitat and dietary niches for burbot (BB), lake trout (LT), and northern pike (NP) implanted with acoustic transmitters for the summer period (28 June–12 September, 2012) and collected for SIA 19–23 August, 2008 (Cott et al., 2011) in Alexie Lake, NT, Canada. Overlap probability for spatial and niche methods ranged from 0–100% and represented the chance that a randomly selected position of one species would be found in the habitat/niche of a second species (e.g., A on B and B on A). **Bold** values represent a significant overlap probability >60%.

| Paired Comparisons	Overlap Probability (%)					
	Spatial habitat		Habitat niches		Dietary niches	
	Core area	Home range	Core	Broad	Core	Broad
BB on LT	8.3 ± 11.3	27.3 ± 10.6	42.8 ± 1.6	**99.6 ± 1.5**	5.6 ± 6.6	33.9 ± 20.3
LT on BB	16.7 ± 19.9	**77.8 ± 14.4**	6.3 ± 0.8	21.2 ± 1.3	6.7 ± 7.6	38.0 ± 21.6
BB on NP	3.7 ± 1.6	**63.6 ± 6.3**	3.0 ± 0.6	32.0 ± 1.5	0.2 ± 1.2	5.4 ± 12.4
NP on BB	2.5 ± 1.3	49.1 ± 6.6	1.0 ± 0.3	12.7 ± 1.1	0.1 ± 0.5	1.8 ± 4.2
LT on NP	6.8 ± 6.9	**69.7 ± 18.7**	3.8 ± 0.6	25.6 ± 1.4	0.0 ± 0.4	0.6 ± 3.8
NP on LT	2.7 ± 2.6	44.3 ± 12.2	8.0 ± 0.9	59.8 ± 1.4	0.0 ± 0.1	0.2 ± 1.5
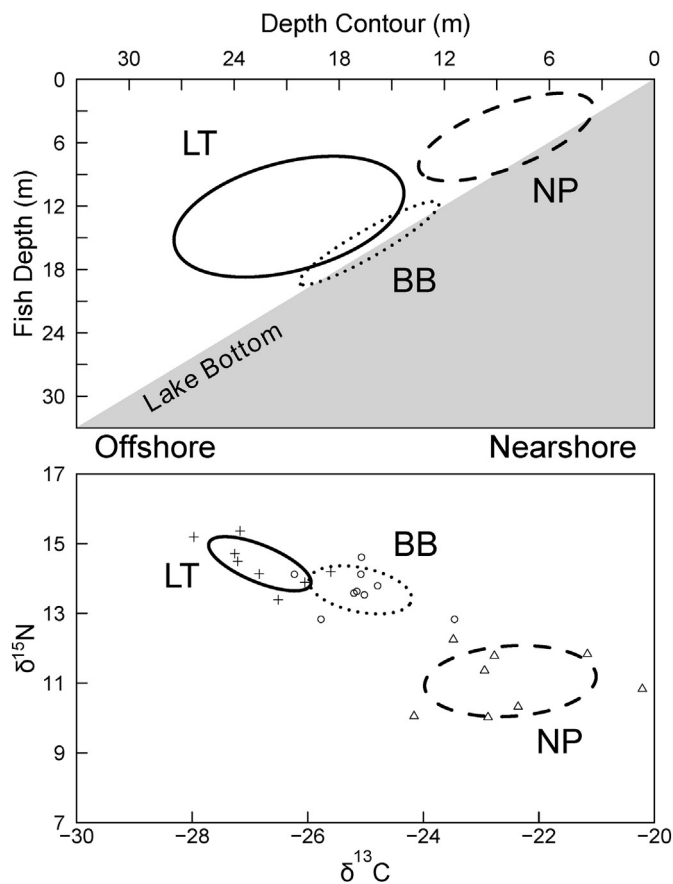
Fig. 5. Resource partitioning among burbot (BB), lake trout (LT), and northern pike (NP) in Alexie Lake, NT, Canada, during thermal stratification. Core (50%) (a) habitat based on depth and spatial relocation telemetry data and (b) dietary niche ellipses based on, stable isotope data.

Discussion

We found strong evidence for resource partitioning among three co-occurring piscivores in a sub-Arctic lake during the period of summer thermal stratification. Habitat partitioning, depicted by telemetry in combination with dietary niches inferred from SIA, clearly indicated that lake trout, northern pike, and burbot were utilizing different sources of energy obtained from different habitats within the lake. Spatial core areas and core habitat niches showed little to no habitat overlap among fish species. Moreover, observed patterns in habitat niches closely matched those of core dietary niches. Although telemetry and SIA showed almost complete exclusion in core habitat and dietary niches among species, significant overlap of spatial home ranges and broad habitat niches did exist between some species, suggesting interactions among top-levels piscivores do exist, albeit to a low degree. Together these results highlight the resolution that combined telemetry and SIA can provide toward a more quantitative understanding of resource partitioning of piscivores in lake ecosystems.

Resource partitioning in fish communities should be a function of optimizing the balance between resource segregation and metabolism among species involved. Our results indicate that the three piscivorous species in Alexie Lake effectively segregated core habitat and dietary niches while occupying water temperatures near or within their preferred thermal ranges. The mean temperature occupied by lake trout in the current study (6.9 °C) was toward the lower range of thermal preference observed for this species (5–15 °C; reviewed in Plumb and Blanchfield, 2009), but consistent with other studies of in situ thermal preferences of lake trout (Blanchfield et al., 2009; Mackenzie-Grieve and Post, 2006; Morbey et al., 2006). Northern pike occupied an average

temperature of 16.5 °C, below the range for optimal growth (19–21 °C) reported for this species (Casselman and Lewis, 1996). Average temperatures below optimal range occupied by northern pike could be due to water temperatures only exceeding 20 °C for a portion of the stratified season, and may be a common feature of sub-Arctic lakes relative to southern temperate lakes (Pierce et al., 2013). Water temperatures occupied by burbot in this study (mean: 5.4 °C) fell below laboratory-derived estimates of preferred temperatures for this species (14.2 °C; Hofmann and Fischer, 2002) and were also cooler than those recorded from telemetry studies in a British Columbia reservoir (8–10 °C Harrison et al., 2013), and in a southern Ontario boreal lake 10–12 °C (Carl, 1995). Our results are in agreement with underwater observations of Hofmann and Fischer (2002), who found burbot mainly occupying water temperatures of 5 °C in profundal zones. Together, the general agreement between water temperatures occupied by telemetry-tagged fish and known preferred temperatures suggests that water temperature is an important component of habitat partitioning in multi-predator lake ecosystems (Magnusson et al., 1979), including in northern regions where the period of stratification can be brief.

All top-level predatory fish species had distinct spatial core areas and core habitat niches within a thermally-stratified Alexie Lake, despite burbot and lake trout occupying similar depths and corresponding cold water temperatures. Habitat partitioning found in our study is in agreement with existing literature describing the habitat use of burbot, lake trout, and northern pike. Our results support those of a recent study that found burbot in Alexie Lake to be closely associated with bottom substrates and move along steep transition zones between nearshore-littoral and offshore-profundal zones in diel bank migration (Cott et al., 2015b). Transition zones occupied by burbot in Alexie Lake were moderately complex, characterized by large boulders, which may represent a key habitat feature used by this species to forage on small fish (Cott et al., 2015b; Fischer, 2000). Rocky transition zones inhabited by burbot may also provide this photophobic species (Beaty, 1969) protection from sunlight (Cott et al., 2015b).

Habitat partitioning between burbot and lake trout was achieved by spatial segregation during the stratified period. Unlike burbot, lake trout were mainly suspended in the water column over the deepest areas of the lake. While these deep basins are related to low substrate complexity, the fact that lake trout were most often suspended well above bottom (mean: 5.5 m), indicates this species is not highly dependent on bottom habitat structure during summer months in Alexie Lake. Pelagic distribution of lake trout is a common feature of lakes where pelagic prey fishes, such as ciscoes and rainbow smelt (*Osmerus mordax*), are a primary diet item during summer (Trippel and Beamish, 1993; VanderZanden and Rasmussen, 1996). Lake trout may not have been able to utilize deep-water bottom substrate due to low dissolved oxygen concentrations (<4 mg·L^{-1}; Plumb and Blanchfield, 2009), which would have occurred at depths >20 m during the peak of stratification in Alexie Lake. However, because this habitat represents a small volume of the entire lake (5.2%), and because lake trout were regularly positioned at much shallower depths (mean: 13.3 m), it is doubtful that low oxygen concentrations had a large influence on the pelagic and spatial distribution of this species in Alexie Lake.

Burbot and lake trout did show significant overlap when considering a broad habitat niche, which suggests limited interactions exist among these top piscivores within Alexie Lake. About a quarter of the lake trout positions were in close proximity to the bottom, so it is possible that benthic species, such as sculpin and stickleback, may also be important prey in northern lakes. This use of benthic habitat by lake trout could explain the probability (albeit low) of lake trout overlapping the core habitat and dietary niches of burbot. Northern pike, mainly occupied the upper few meters of the water column and were spatially distributed in shallow, nearshore waters consistent with their with warm water preference (relative to burbot and lake trout). Nearshore habitat use of northern pike was also expressed by their having the most enriched δ^{13}C value, corresponding with the greatest littoral diet of

the three piscivores. As a visual predator that utilizes structure to ambush prey (Casselman and Lewis, 1996; Scott and Crossman, 1973), it is likely that northern pike are limited to nearshore-littoral areas of Alexie Lake to forage while remaining within their preferred thermal range. Nevertheless, northern pike did have the largest habitat niche and greatest variation in mean depth, suggesting that this species utilized habitats of variable depth in the nearshore areas.

Traditional methods of determining habitat partitioning (e.g., core areas and home ranges) use only two-dimensional spatial (i.e. horizontal area) data, providing areal estimates of overlap. However, in aquatic ecosystems are three-dimensional, making estimates of habitat partitioning based on areal data of limited use (Simpfendorfer et al., 2012). Differences in the degree of habitat overlap among piscivores were dependent on the type of data (e.g., depth, space, or both) used to quantify overlap. When species differed in depth, spatial home ranges overestimated the overlap of species occupying deeper water on shallow water species (e.g., overlap of burbot or lake trout on northern pike habitat) by 31–44% relative to broad habitat niches. For species that overlap in home ranges (e.g., burbot and lake trout), spatial-only methods overestimate habitat overlap of lake trout on burbot by 10.4–56.6%, but underestimate overlap of burbot on lake trout by 51.1–72.3%, relative to habitat niches. These inconsistencies in habitat overlap estimates based on only depth or space with those based on both depth and space highlight the importance of accounting for both vertical and spatial habitat partitioning in aquatic ecosystems. Thus, we suggest that habitat niches that include space and depth axes provide a more robust and ecologically relevant depiction of habitat use and niche separation.

The corroboration of telemetry and stable isotope data, and the fact that dietary niches did not overlap at either core or broad levels, suggested that lake trout, northern pike, and burbot, were indeed foraging in different habitats and assimilating different prey items. Lake trout and burbot occupied highest trophic positions (δ^{15}N) and differed in carbon sources (δ^{13}C), but both had more pelagic carbon sources than northern pike. Similar patterns in food web positions among these predatory species were found in three neighboring lakes with near-identical food webs (Cott et al., 2011). In a tundra lake with a similar fish community as Alexie Lake, but lacking northern pike, burbot and lake trout also occupied similar food web positions, as found in our study (Hulsman et al. this issue). Intermediate δ^{13}C, relatively small *CR* and *NR*, and low probability of dietary overlap with other piscivores are suggestive of highly specialized feeding by burbot within transition zones. The more pelagic δ^{13}C of lake trout relative to burbot and pike clearly matches its core habitat use and further supports a greater reliance on pelagic prey (e.g., cisco) in their summer diets (Trippel and Beamish, 1993; VanderZanden and Rasmussen, 1996). The higher δ^{15}N values of burbot and lake trout might suggest a greater contribution of fishes in their diets relative to northern pike. However, because northern pike utilized littoral habitat and prey items, where food chains are ^{15}N depleted relative to pelagic zones in Alexie Lake (Cott et al., 2011), the lower δ^{15}N may not represent lower contribution of fishes to this species diet.

Observations of large northern pike attacking smaller conspecifics, as well as lake trout with obvious scars (Cott et al., 2015b), and existence of juvenile burbot in the stomachs of northern pike (M. Guzzo *personal observation*), indicate that the largest northern pike prey on other piscivorous species in Alexie Lake. Our results do not suggest predation by northern pike on burbot or lake trout; however-er, because the size of northern pike used to estimate dietary niche overlap were not as large as those used in telemetry, we may have underestimated dietary overlap or predation among piscivores. Similarly, we acknowledge that the low numbers of telemetry-tagged northern pike and burbot could have reduced the extent of habitat used by these species and their potential for habitat overlap. Notwithstanding these limitations, predation is known to play a key role in how smaller species or individuals segregate food and habitat resources (e.g., Diehl and Eklov, 1995; He and Kitchell, 1990), and could play a role in the resource partitioning.

The corroboration of SIA and telemetry data suggested that piscivores fed on unique prey items obtained from different habitats within of Alexie Lake. Although, it is possible that because SIA samples were collected four years prior to acoustic telemetry data, in late August 2008, we may not have accurately estimated dietary niches during the 2012 stratified period, we feel that it is unlikely that these factors would affect the dietary patterns observed. First, the lake is remote and closed to public fishing, making it unlikely that any major changes in food web interactions or fish densities occurred between sampling years. Second, SIA values collected in late August likely represented a time-integrated diet over a period of several months (Perga and Gerdeaux, 2005), encompassing most of the period when Alexie Lake was thermally stratified. We are therefore, confident that our SIA data provide an accurate representation of the dietary niches of our study species during the study period.

This study focuses on the thermally stratified period during the brief sub-Arctic summer, a period when relatively distinct thermal habitats exist (Magnusson et al., 1979). While thermal stratification should aid in reducing interspecific interactions among fish from different thermal guilds, many sub-Arctic lakes are isothermal for most of the year. For example Alexie Lake is isothermal over most of the year with approximately seven months of ice-cover. During the non-stratified period, thermal habitat boundaries are removed, light is low, and consequently interspecific interactions among fishes of multiple thermal guilds could change (Amundsen and Knudsen, 2009; Blanchfield et al., 2009). In addition to changes in habitat use and interspecific interaction, isothermal conditions also coincide with critical periods for many fish species, including spawning (e.g. Callaghan et al., this issue) and overwintering. As a result, studies that evaluate resource partitioning among piscivores during isothermal conditions are needed.

We found that resource partitioning among top level predatory fish was an interaction of species thermal tolerances, available water temperatures and space, and accessibility of prey in disparate habitat types. However, other factors, such as food web structure and changes in thermal regime may also affect patterns of resource partitioning (Amundsen et al., 2003; Hulsman et al. this issue; Vander Zander et al., 1999). Although we demonstrate that co-occurring piscivores were able to clearly partition habitat and dietary niches during thermal stratification, potential habitat alterations caused by resource extraction and climate warming may alter patterns of resource partitioning and lead to shifts in community dynamics.

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