


# Habitat overlap of juvenile and adult lake trout of Great Bear Lake: Evidence for lack of a predation gradient?

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## Abstract

A range of organisms, from plankton to fish, commonly shift their habitat distributions horizontally or vertically due to predation risk. Juvenile lake trout, *Salvelinus namaycush*, are generally viewed as occupying deep areas of lakes to decrease predation pressure from adults. In contrast, we found that juvenile lake trout from Great Bear Lake, NT, Canada, occupied a variety of habitats and from shallow to deep depths (0–150 m), overlapping with adult lake trout. No evidence occurred for a length depth-based segregation (e.g., ontogenetic shift). Genetic variation was also similar among juveniles in the different depth zones. However, isotopic niches and C:N ratios among juveniles showed some variability in niche widths and positions for individuals caught from the 51–150 m zone compared to juvenile individuals caught from 0–20 m and 21–50 m zones. The uniformly distributed adult lake trout in Great Bear Lake may evenly distribute predation pressure (including cannibalism) across shallow- and deep-water habitats more than in other lakes. As a result, juveniles may respond to differences in foraging opportunities rather than predation risks. Juvenile lake trout did not appear to conform to the general pattern of juveniles seeking a deep-water refuge to reduce predation risks. In contrast, juvenile lake trout of Great Bear Lake displayed broad resource use across all depths and habitats.

## KEYWORDS

Arctic ecology, genetic, life history, niches, predator avoidance, stable isotopes

## 1 | INTRODUCTION

Organisms must balance their need to find food, avoid predation and produce offspring, but these activities can have trade-offs (Bentley et al., 2014; Clark & Levy, 1988). For example, if habitats optimal for foraging or reproduction also have high levels of predation risk, individuals may select risky habitats in return for high foraging or

reproductive benefits (or vice versa; Candolin, 1998; Quinn, Wetzel, Bishop, Overberg, & Rogers, 2001). Thus, trade-offs between cost (e.g., predation) and benefits (e.g., foraging, reproduction) may involve shifts among habitats in space and time. In freshwater ecosystems, species often shift their distributions over time across horizontal and vertical habitats to avoid predation. Such distribution shifts have been observed for a range of organisms, from plankton to

fish (Ahrenstorff, Hrabik, Stockwell, Yule, & Sass, 2011; Armstrong et al., 2013; Hrabik, Jensen, Martell, Walters, & Kitchell, 2006).

Lake trout *Salvelinus namaycush* is a cold-water predator, with a thermal preference of 5–15°C (Plumb & Blanchfield, 2009). Lake trout display adaptive foraging behaviours by moving across spatially disparate habitats (Guzzo, Blanchfield, & Rennie, 2017). These behaviours include diel vertical migration (Henderson & Anderson, 2002; Plumb, Blanchfield, & Abrahams, 2014), diel bank migration (i.e., deep vs. shallow demersal habitats) (Gorman, Yule, & Stockwell, 2012a, 2012b) and shifts between littoral and pelagic food sources (Blanchfield, Tate, Plumb, Acolas, & Beaty, 2009; Dolson, McCann, Rooney, & Ridgway, 2009). By taking advantage of habitat heterogeneity over a variety of spatial and temporal scales (e.g., due to resource phenology, thermal metabolic cost), lake trout capitalise on benefits associated with disparate habitats (Blanchfield et al., 2009; Martin & Olver, 1980). For example, lake trout are considered flexible and adaptable foragers, showing combinations of piscivory, benthivory, and planktivory, resulting in a broad diet strongly influenced by seasonality (i.e., thermal constraint) and food availability (France & Steedman, 1996; Martin, 1952).

Lacustrine ecosystems are mosaics of habitats, and habitat profitability to juvenile lake trout will depend on a variety of biotic and abiotic variables, including the abundance of prey, vulnerability to predators and physical features such as temperature that modify the physiology and behaviour of juvenile lake trout, their prey and predators (Guzzo et al., 2017; Schindler, 2017). Whereas most generalisations about lake trout are based on studies of adults, typically >450 mm (e.g., see Chavarie et al. 2013; Zimmerman et al., 2006, 2007), fewer studies have focused on early life stages. It is generally accepted that juveniles primarily use deep areas of lakes (e.g., >~40–50 m) to limit encounters with piscivorous fishes using shallower habitats, including adult lake trout (Elrod & Schneider, 1987; Evans, 2007; Zimmerman, Schmidt, Krueger, Vander Zanden, & Eshenroder, 2009). Trade-offs between cost (e.g., predation) and benefits (e.g., foraging) may involve habitat shifts that sustain different foraging opportunities. For example, juvenile lake trout may feed more on invertebrates in deep-water; in contrast, they may feed more on small fish nearshore (Madenjian, DeSorcie, & Stedman, 1998; Ng, Fredericks, & Quist, 2016). Studies that report juvenile lake trout using deep-water habitats define juveniles as ages 0–3 (Deroche, 1969; Evans & Willox, 1991; Peck, 1982), or as individuals up to 350–450 mm (Hanson, Holey, Treska, Bronte, & Eggebraaten, 2013; Marsden, Kozel, & Chipman, 2018; Zimmerman et al., 2009). Overall, habitat use varies among lakes, depending on the distribution, abundance and gape limitations of predators, the size of juveniles, and the distribution and sizes of their food resources. Occasionally, studies report shallow-water habitat use by juveniles (beyond young-of-the-year stage) (France & Steedman, 1996; Madenjian et al., 1998; Miller & Kennedy, 1948), illustrating that distributions other than the general deep-water pattern are possible across the species range. From these studies, some questions arise about juvenile lake trout ecology: (a) How often do temporal and spatial variations occur in distribution patterns of juvenile lake trout? and (b) Do juvenile lake

trout avoid shallow-water habitat in all lakes or do variations in this behaviour exist when lake characteristics change (e.g., lakes without summer thermal constraints)?

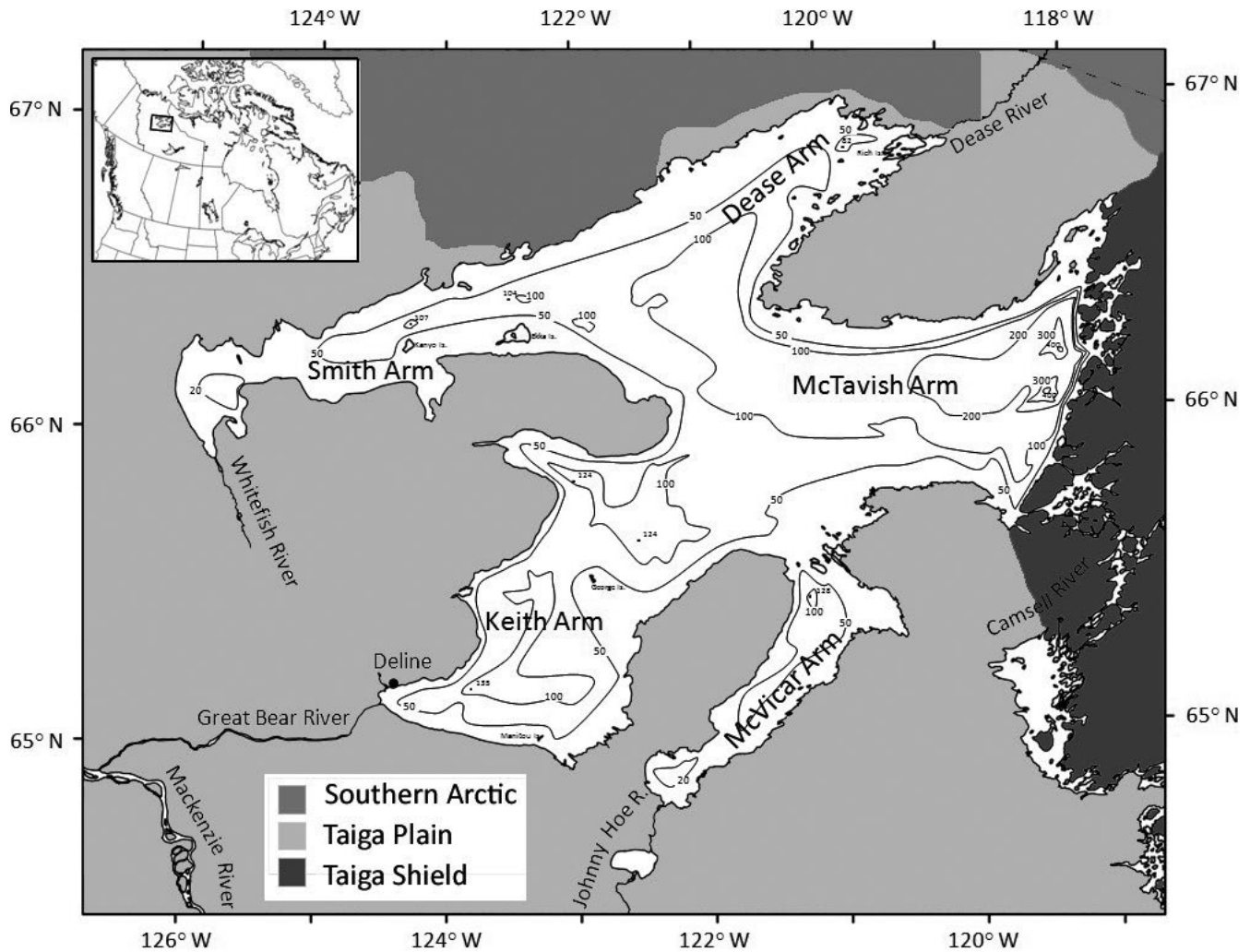
Historical studies of Great Bear Lake in Canada's Northwest Territory (N66°06'W120°35') include anecdotes of juvenile lake trout using shallow-water habitat (Miller & Kennedy, 1948). Great Bear Lake provides abundant cold habitat throughout the entire lake, including surface waters during the summer (Johnson, 1975a, 1975b). Thus, the influence of thermal habitat on the distribution of lake trout in this lake is minimal, especially in comparison with lakes in the southern portion of the species range. Lake trout of Great Bear Lake are highly polymorphic as adults, with three of the four morphs known to be generalists that use both benthic and pelagic habitats, across shallow- and deep-water zones (Chavarie, Harford et al., 2016; Chavarie et al., 2018; Chavarie, Howland, & Tonn, 2013). Lake trout morphs have diet overlaps that encompassed a large range of prey, from terrestrial invertebrates to fish, but also displayed high levels of cannibalism on both juveniles and adults (Chavarie, Harford et al., 2016; Chavarie, Howland, Gallagher, & Tonn, 2016). Given that lake trout have the highest relative abundance among fish species in Great Bear Lake (K. Howland, unpublished data; Johnson, 1975a), the level of cannibalism on juvenile lake trout could be considerable and therefore influence juvenile lake trout distribution.

The objective of this study was to investigate juvenile lake trout ecology and habitat preferences over horizontal and vertical gradients in Great Bear Lake. Our first aim was to determine whether juvenile lake trout were restricted to a deep-water benthic zone within Great Bear Lake. Based on our previous studies, we assumed high and uniform levels of predation risk across depth habitats, and hypothesised juveniles would be distributed throughout the water column and habitats. Second, we sought to determine whether the juvenile distribution was associated with a depth-based variation in genetic characteristics, trophic ecology or life history traits.

## 2 | MATERIAL AND METHODS

### 2.1 | Study area and data collection

Great Bear Lake is an oligotrophic Arctic freshwater system designated as an UNESCO (United Nation Educational, Scientific and Cultural Organization) biosphere reserve, in north-eastern Northwest Territories, 250 km south of the Arctic Ocean (Johnson, 1975a). The lake has five semi-isolated "arms" (Figure 1). For this study, Dease Arm, within the southern Arctic ecozone along the northern shore of Great Bear Lake, was sampled 16 July to 2 August 2015. Monofilament multi-mesh gill nets (11 panels, 3.8 to 14.0 cm stretch mesh, 275 m long and 1.8 m wide) were set with a typical soak time of 24 hr. Three habitat depth zones (a) littoral (0–20 m depth), (b) offshore (21–50 m depth) and (c) profundal zone (51–150 m depth) were established based on productivity levels reported previously (Johnson, 1975b). Within each zone, nets were set on the bottom (0–20 m, 21–50 m and 51–150 m zones), in mid-water (21–50 m and 51–150 m) and just below the surface (0–20 m



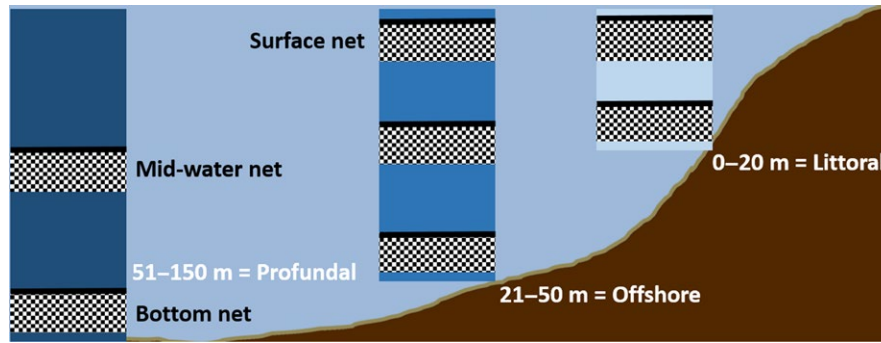
**FIGURE 1** Map of Great Bear Lake, Northwest Territories, Canada, adapted from Johnson (1975b), indicating general bathymetry, the adjacent terrestrial ecozones (i.e., geographical region having a distinct biodiversity of flora and fauna), and major inflowing and outflowing rivers. For this study, Dease Arm, within the southern Arctic ecozone along the northern shore of Great Bear Lake, was sampled mid-July to mid-August 2015. Insert: location of study area within Canada

and 21–50 m; surface nets of the 51–150 m zone were excluded to target deep-water habitat only) (see Figure 2 for more details). To increase sample size for genetic, isotope and life history analyses, catches from different depths within a habitat zone were combined. Thus, we focused on lake trout variation expressed through a variety of habitats (i.e., shallow- vs. deep-water and littoral vs. open water).

For each fish caught, measurements related to life history variables were recorded, including fork length, wet weight and stage of maturity (juvenile or mature). A dorsal muscle sample was removed and frozen at  $-20^{\circ}\text{C}$  for stable isotope analysis, and a fin clip was stored in 95% nondenatured EtOH for genetic analysis. For this study, juvenile lake trout were defined as individuals with undeveloped gonads (i.e., immature). Mature individuals were distinguished as having gonads that were fully developed and enlarged. Although the smallest mature individual in Great Bear Lake was 450 mm (Chavarie et al., 2013; Chavarie, Howland, Venturelli et al., 2015), large immature individuals (i.e., up to 580 mm in fork length) were included as juveniles for consistency with our definition.

## 2.2 | Distribution of catch

Adult lake trout distributions in Great Bear Lake have been reported previously (Chavarie et al., 2018) and were used for this study to compare against juvenile distributions. G-tests (Zar, 1999) were used to determine whether the proportions of juveniles and adults, based on our net catches, differed among the three depth zones (0–20 m, 21–50 m and 51–150 m). G-tests were also used to assess whether the proportion of juveniles and adults differed among vertical locations (bottom, mid-water and surface) within a depth zone. Juvenile and adult catch distributions were compared among the three depth zones (0–20 m, 21–50 m and 51–150 m) using a contingency table test (Zar, 1999). A contingency table test also compared juvenile and adult vertical distributions (bottom, mid-water and surface) within a depth zone. Catch-per-unit-effort (CPUE) was calculated as the number of fish caught per 100 m of gill net per 24 hr. For these comparisons, catch data were used from seven nets set within the 0–20 m depth zone, nine nets within the 21–50 m depth zone,



**FIGURE 2** Catches from all meshes and nets were defined in following zones: (a) littoral (0–20 m), (b) offshore (21–50 m) and (c) profundal zone (51–150 m) based on productivity levels (Johnson, 1975b). Sampling locations were distributed among horizontal (i.e., littoral vs. open water) and vertical (i.e., shallow- vs. deep-water) axes. At each sampling station, nets were set on the bottom (0–20, 21–50 and 51–150 m zones), in mid-water (21–50 and 51–150 m) and just below the surface (0–20 and 21–50 m)

and 10 nets set within the 51–150 m depth zone. CPUE data were log-transformed to conform to normality, and an analysis of variance (ANOVA) was performed to determine whether CPUE differed among the three depth zones.

### 2.3 | Genetic variation

Genomic DNA was extracted from fin tissue using Qiagen DNeasy Extraction Kits (Qiagen, Inc., Valencia, California) following the manufacturer's protocols. Variation at 23 microsatellite loci was assessed as previously described by Harris et al. (2015). PCR products were run on an ABI 3130xl Genetic Analyzer (Applied Biosystems, Foster City, CA) using the LIZ 600 size standard, and all allelic data were edited and scored by eye using GeneMapper (version 4.0, Applied Biosystems).

To determine whether juvenile lake trout differed genetically within Great Bear Lake, genetic variation was compared among depth zones (0–20, 21–50, 51–150 m) combining all catches within a zone. The program Microchecker v.2.2.3 (Van Oosterhout, Hutchinson, Wills, & Shipley, 2004) was first used to test each locus for the presence of genotyping errors due to null alleles and allelic dropout. We compiled descriptive statistics of genetic variation (number of alleles [ $N_A$ ], expected heterozygosity [ $H_E$ ; Nei's unbiased gene diversity], observed heterozygosity [ $H_O$ ] and the fixation index [ $F_{IS}$ ]) within each zone using the "diveRsity" package (Keenan, McGinnity, Cross, Crozier, & Prodöhl, 2013) in R (R Core Team, 2017). Allelic richness ( $A_R$ ) and private allelic richness ( $PA_R$ ) were calculated using HP-RARE (Kalinowski, 2004). Departures from Hardy-Weinberg equilibrium and linkage equilibrium were evaluated using the program GENEPOP v. 4.0 (Rousset, 2008). We evaluated tests involving simultaneous comparisons with a nominal  $\alpha$  of 0.05 and then with an adjusted  $\alpha$  obtained via the false discovery rate procedure (Benjamini & Yekutieli, 2001), as suggested by Narum (2006).

Genetic structure among lake trout was examined in the three depth zones (0–20, 21–50 and 51–150 m) using several different parameter estimates. A global estimate of  $F_{ST}$  (i.e., theta [ $\theta$ ]) (Weir & Cockerham, 1984) was generated in FSTAT, and 95% confidence

intervals (CIs) of the estimate were calculated after 10,000 permutations. Pairwise estimates of  $F_{ST}$  between each zone were calculated in ARLEQUIN v. 3.1 (Excoffier, Laval, & Schneider, 2005), with significance tested after 10,000 permutations. We used the hierarchical Bayesian clustering program STRUCTURE v. 2.3 (Pritchard, Stephens, & Donnelly, 2000) to identify potentially distinct genetic clusters ( $K$ ). Simulations were performed varying  $K$  from 1 to 10, with 20 iterations per value of  $K$ . Each run incorporated a burn-in of 500,000 iterations followed by 500,000 Markov chain Monte Carlo (MCMC) iterations. We assumed an admixture model, correlated allelic frequencies and, given a low amount of genetic differentiation, then ran STRUCTURE analyses, including a priori assumptions based on zone (Hubisz, Falush, Stephens, & Pritchard, 2009). STRUCTURE HARVESTER v. 0.6.91 (Earl & vonHoldt, 2012), which combines the results of independent runs and compiles the results based on  $\ln P(D)$  and the post hoc  $\Delta K$  statistic of Evanno, Regnaut, and Goudet (2005), was used to infer the most likely number of clusters. We used CLUMPP v. 1.1 (Jakobsson & Rosenberg, 2007) (under the LargeKGreedy algorithm) to determine alignment of replicate runs. Admixture plots were visualised using DISTRUCT v.1.1 (Rosenberg, 2004). Next, we used GenAlEx v. 6.5 (Peakall & Smouse, 2012) to perform a principal coordinate analysis (PCoA) using genetic distance matrices generated from our microsatellite data to further resolve potential genetic structuring among juvenile lake trout. Finally, discriminant analysis of principal components (DAPC) (Jombart, Devillard, & Balloux, 2010), implemented in the R package Adegenet (Jombart, 2008), was used to describe population structure within each grouping scenario. First, the "find.clusters" algorithm was used to identify the putative number of genetic clusters ( $K$ ), varying  $K$  from 1 to 10. The most likely number of genetic clusters within each grouping scenario was identified based on the lowest Bayesian information criterion (BIC). We then used the "compoplot" function to calculate the proportion of membership of each individual within each grouping scenario to the genetic clusters identified. For DAPC analyses, the stratified cross-validation method (carried out with the function `xvalDapc`) determined the optimal number of PCs (principal components) to retain in the analysis.

## 2.4 | Stable isotopes

Samples analysed for stable isotope ratios were freeze-dried, ground to a fine powder and weighed in tin cups. We analysed a subset of 84 juvenile lake trout using a continuous flow isotope ratio mass spectrometer (Thermo-Delta 5 Plus) equipped with a Costech elemental analyser at the Fisheries and Oceans Canada Freshwater Institute in Winnipeg. Combustion and reduction columns were operated at 1,020 and 650°C respectively. Stable isotope results were expressed in delta ( $\delta$ ) notation, defined as the deviation from a standard reference material in parts per thousand (‰);  $\delta^{13}\text{C}$  results were relative to Vienna Pee Dee Belemnite (VPDB), whereas  $\delta^{15}\text{N}$  results were relative to atmospheric nitrogen. Results were calculated using the equation:

$$\delta X = [(R_{\text{sample}}/R_{\text{standard}}) - 1] \times 1,000$$

where  $X$  is  $^{13}\text{C}$  or  $^{15}\text{N}$ , and  $R_{\text{sample}}$  is the ratio ( $^{13}\text{C}/^{12}\text{C}$  or  $^{15}\text{N}/^{14}\text{N}$ ) in the sample, while  $R_{\text{standard}}$  is the same ratio in the standard. Standard deviations of repeated measurements of certified reference materials (USGS 40 and 41) were  $<0.1\text{‰}$  for  $\delta^{13}\text{C}$  and  $<0.16\text{‰}$  for  $\delta^{15}\text{N}$ . The standard deviation of repeated measurements of an in-house standard was  $<0.1\text{‰}$  for  $\delta^{13}\text{C}$  and  $\delta^{15}\text{N}$ . Data were normalised using Laboratory Information Management System for Light Stable Isotopes (LIMS-LSI) (Coplen, 2000).

Because lipids are relatively depleted in the heavier isotope of carbon (Post et al., 2007), a significant negative linear relationship of  $\delta^{13}\text{C}$  and C:N ratios ( $p < 0.01$ ) indicated variation in lipid content may confound analyses of  $\delta^{13}\text{C}$ . Thus, we lipid-corrected  $\delta^{13}\text{C}$  values for fish following Post et al. (2007). To investigate an indirect representation of lipid content (index of buoyancy; C:N ratios as a proxy) and depth (Bone, 1972; Corner, Denton, & Forster, 1969; Eastman, 1988), C:N ratios and  $\delta^{13}\text{C}$  (‰) were compared among depth zones (0–20, 21–50 and 51–150 m) with an ANCOVA (analysis of covariance). Pairwise *post hoc* comparisons followed to test differences among groups.

Niche region dimensions and pairwise niche overlap of lake trout were determined by depth zones (0–20, 21–50, 51–150 m) using the probabilistic method of Swanson et al. (2015), which is available in the nicheROVER R library. Their approach estimates parameters of the multivariate normal distribution, allowing isotopic niche dimensions to be defined as probability regions in multivariate space. Uncertainty in niche regions is accounted for using a Bayesian inference framework (Swanson et al., 2015). Ellipses representing 95% probability niche regions were generated using the posterior expectation of the bivariate normal distribution estimated using the Bayesian approach in nicheROVER.

## 2.5 | Life history parameters

Life history parameters were compared among juvenile lake trout caught among depth zones (i.e., 0–20, 21–50 and 51–150 m), combining all catches within a zone. Morphological characteristics, such as length (FL, mm), weight ( $W$ , g) and relative body condition, are

characteristics that can be interrelated, but may not differ consistently among groups. Thus, we compared characteristic among depth zones using a single-factor analysis of variance (ANOVA), with depth zone as a main effect (Zar, 1999). Relative body condition is defined as residuals from the power relationship between  $\log_{10}(W)$  and  $\log_{10}(FL)$  to correct for size-related trends (see Hansen, Nate, Muir et al., 2016).

A sub-sample of sagittal otoliths was used because they have been validated for age estimation of lake trout to an age of at least 50 years (Campana, Casselman, & Jones, 2008). To inform measurement of growth increments, two independent readers counted annuli on 400- $\mu\text{m}$  transverse sections of epoxy-embedded otoliths using criteria described by Casselman and Gunn (1992). To overcome a lack of small (young) fish in the age-growth sub-sample (otoliths were not processed for fish  $<300$  mm FL), incremental measurements from the nucleus to the maximum ventral radius of the otolith were used for back-calculating length at age using the biological intercept back-calculation model (Campana, 1990).

Growth in length with age was modelled using two versions of the von Bertalanffy length-age model (Mooij, Rooij, & Wijnhoven, 1999; Quinn & Deriso, 1999):

$$L_t = L_{\infty}(1 - e^{-K(t-t_0)}) + \epsilon$$

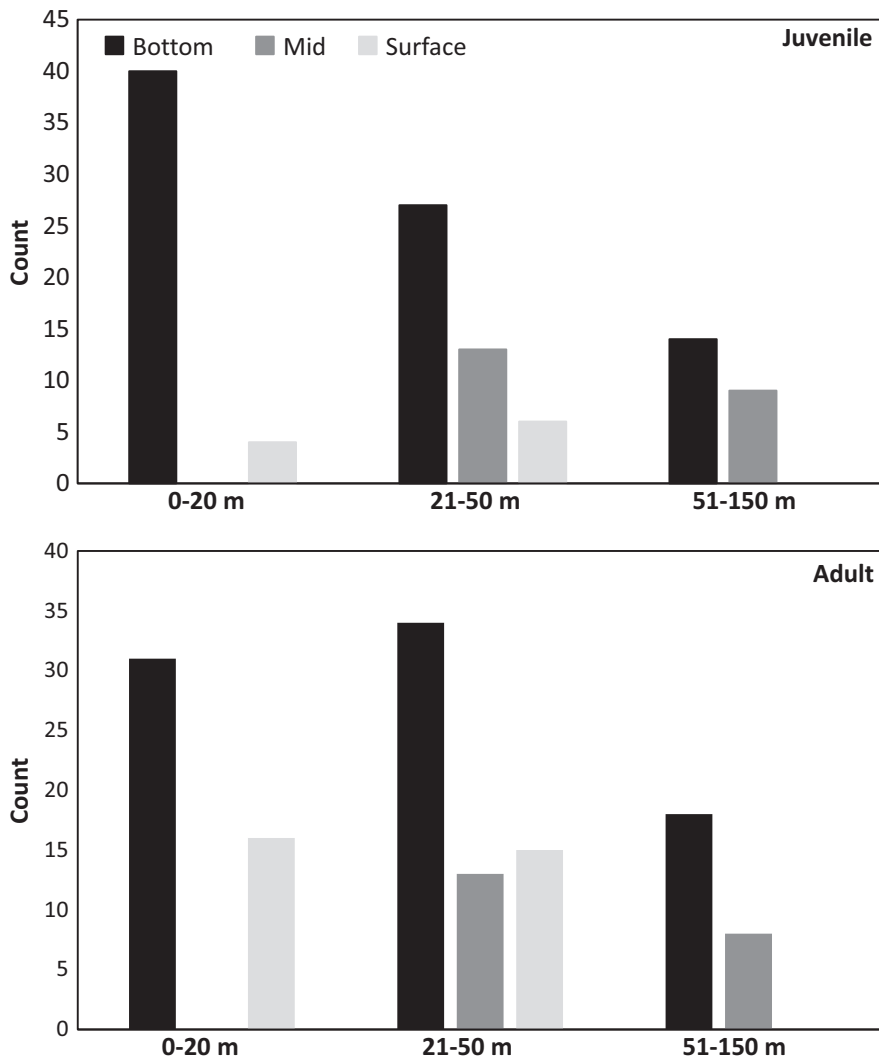
$$L_t = L_{\infty} - (L_{\infty} - L_0)(1 - e^{-(\omega/L_{\infty}) \times t}) + \epsilon$$

We estimated back-calculated length  $L_t$  (mm) at age  $t$  (years) as a function of age at length = 0 ( $t_0$  = years), length at age = 0 ( $L_0$  = mm), early annual growth rate ( $\omega = L_{\infty} \times K$  = mm/year; Gallucci & Quinn, 1979), instantaneous growth rate ( $K = 1/\text{year}$ ) at which  $L_t$  approaches the theoretical maximum length ( $L_{\infty}$  = mm) and residual error ( $\epsilon$ ). We estimated  $L_{\infty}$ ,  $K$ ,  $t_0$ ,  $L_0$  and  $\omega$  using nonlinear mixed-effect models (package “nlme” in R; R Core Team, 2015), with a fixed population effect (average growth for the population) and random individual effects (growth of individual fish sampled from the population; Vigliola & Meekan, 2009). Mixed-effects models are appropriate for modelling the within-group correlation of longitudinal, auto-correlated and unbalanced data, such as back-calculated growth histories (Pinheiro & Bates, 2000). We compared growth parameters among zones using single-factor ANOVA, with each parameter as a dependent variable and zone as the independent variable (Hansen, Nate, Chavarie et al., 2016; Hansen et al., 2012; Zar, 1999). To account for multiple comparisons from the same growth model, a Bonferroni correction was used to correct the overall  $\alpha$  downward to  $\alpha = 0.01$  ( $\alpha = 0.05/5$ ).

## 3 | RESULTS

### 3.1 | Distribution of catch

Juveniles ( $n = 113$  fish) and adults ( $n = 135$  fish) were regularly found within the same nets and similarly caught among the three depth zones. Overall, 42 juveniles were caught in the 0–20 m zone,



**FIGURE 3** Distribution of juvenile (above) and adult (below) lake trout captured among three depth zones (0–20, 21–50 and 51–150 m) in Great Bear Lake. At each sampling station, nets were set on the bottom (0–20, 21–50 and 51–150 m), in mid-water (21–50, 51–150 m) and just below the surface (0–20, 21–50 m)

48 in the 21–50 m zone and 23 juveniles in the 51–150 m zone (bottom, mid-water and surface sets combined). The distribution of juveniles ( $G = 3.2$ ,  $df = 2$ ,  $p > 0.05$ ) and adults ( $G = 2.6$ ,  $df = 2$ ,  $p > 0.05$ ) were not different among the three depth zones (Figure 3). Similarly, CPUE of juveniles did not differ among the three depth zones based on combined catches of surface, mid-water and bottom sets ( $F_{2,23} = 0.19$ ,  $p = 0.83$ ) (Supporting Information Figure S1). Juvenile catches differed within a depth zone ( $G = 9.3$ ,  $df = 2$ ,  $p < 0.01$ ), with fewer juveniles in surface nets relative to bottom or mid-water nets (Figure 3). In contrast, the distribution of adult lake trout was similar among bottom, mid-water and surface nets within a depth zone (Figure 3;  $G = 2.0$ ,  $df = 2$ ,  $p > 0.05$ ). The distribution of juveniles among three depth zones (0–20, 21–50 and 51–150 m) overlapped the adult lake trout distribution ( $G = 0.7$ ,  $df = 2$ ,  $p > 0.05$ ). Within a depth zone, fewer juveniles than adults were caught at the surface ( $G = 9.3$ ,  $df = 2$ ,  $p < 0.01$ ).

### 3.2 | Genetic variation

Genetic variation in juvenile lake trout at 21 microsatellite loci was low and the number of alleles among depth zones ranged from 12.05

to 15.67 (Table 1). The locus Smm21 was identified as having null alleles, and Sco218 was monomorphic. Both were removed from analyses. Deviations from Hardy–Weinberg equilibrium expectations were detected in five of 63 depth-locus comparisons after false discovery rate alpha adjustments. Linkage disequilibrium was detected in five of 630 tests.

Within juvenile lake trout, genetic variation did not differ but was similar among depth zones (Table 1). The global estimate of  $F_{ST}$  was 0.003 (95% CI = 0.000–0.006). Pairwise differences of  $F_{ST}$  among zones were also low, and no pairwise comparisons were significantly different from zero (adjusted alpha = 0.027, Table 2). Bayesian clustering analyses based on the post hoc  $\Delta K$  statistic of Evanno et al. (2005) identified eight genetic groups (Supporting Information Table S1), whereas the number of genetic groups inferred based on  $\ln P(D)$  was one. Genetic structure, based on admixture plots (for  $K = 8$ ), was weak for juveniles among depth zones (Figure 4). The 51–150 m zone appeared to be slightly differentiated from the other two depth zones (0–20 and 21–50 m) when visualising the admixture plot (Figure 4). However, the PCoA did not detect any genetic structuring among zones in juvenile lake trout (Supporting Information Figure S2).

**TABLE 1** Genetic variation at 21 microsatellite loci among groups of juvenile lake trout from three zones (0–20, 21–50, 51–150 m) in Great Bear Lake

Zone (m)	$N_A$	$H_O$	$H_E$	$A_R$	$PA_R$	$F_{IS}$
0–20	15.33	0.76	0.81	13.67	2.16	0.04
21–50	15.67	0.76	0.81	13.64	2.11	0.00
51–150	12.05	0.78	0.80	12.05	1.10	–0.01

Note. Columns indicate the number of alleles per locus ( $N_A$ ), observed ( $H_O$ ) and expected heterozygosity ( $H_E$ ), allelic richness ( $A_R$ ), private allelic richness ( $PA_R$ ) and the fixation index ( $F_{IS}$ ) all averaged across all loci.

### 3.3 | Stable isotopes

Juvenile lake trout  $\delta^{13}C$  values varied (all zones combined) from  $-21.4\text{‰}$  to  $-27.7\text{‰}$  and  $\delta^{15}N$  varied from  $10.6\text{‰}$  to  $14.9\text{‰}$ . The  $\delta^{13}C$  versus C:N ratios of juvenile lake trout varied among depth zones (ANCOVA,  $F_{2,80} = 16.4$ ,  $p < 0.01$ ). Pairwise comparisons indicated that the C:N ratio (and percentage of lipids) was higher for juveniles caught in the 51–150 m zone versus individuals caught in 0–20 m and 21–50 m zones ( $p < 0.01$ ), whereas no difference was found between the latter two zones ( $p < 0.05$ ). The slope of  $\delta^{13}C$  versus C:N ratios differed from zero for juveniles caught in the 51–150 m zone ( $R^2 = 0.63$ ,  $p < 0.01$ ) (Figure 5). The isospace plot from nicheROVER showed overlap in isotopic niches among depth zones, albeit with differences in niche widths and positions for some individuals from the 51–150 m zone (Figure 6).

### 3.4 | Life history parameters

Overall, juvenile lake trout length ( $F_{2,110} = 1.01$ ,  $p = 0.37$ ), weight ( $F_{2,110} = 0.87$ ,  $p = 0.42$ ) and relative body condition ( $F_{2,110} = 0.13$ ,  $p = 0.88$ ) did not differ among depth zones in Great Bear Lake. Juvenile lengths were 120–541 mm at 0–20 m, 125–580 mm at 21–50 m and 192–445 mm at 51–150 m (Figure 7a). Juvenile weights were 17–3,175 g at 0–20 m, 17–2,100 g at 21–50 m and 69–977 g at 51–150 m (Figure 7b). Asymptotic length ( $L_\infty$ ) differed significantly among depth zones ( $p \leq 0.01$ ), whereas early growth rate ( $\omega$ ), instantaneous growth rate ( $K$ ), length at age 0 ( $L_0$ ) and age at length 0 ( $t_0$ ) did not after Bonferroni corrections ( $p \geq 0.01$ ; Table 3).

## 4 | DISCUSSION

Our study showed that juvenile lake trout in Great Bear Lake occupied a variety of habitats and depths in contrast to most studies that

**TABLE 2** Pairwise  $F_{ST}$  based on variation at 21 microsatellite loci among juvenile lake trout from three zones (0–20, 21–50, 51–150 m) in Great Bear Lake. Results do not differ significantly

	0–20 m	21–50 m	51–150 m
0–20 m			
21–50 m	0.001		
51–150 m	0.005	0.003	

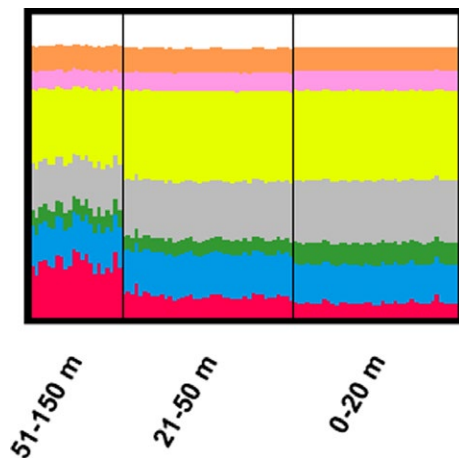
reported juvenile lake trout distributions were restricted to deep-water zones of lakes (Davis, Carl, & Evans, 1997; Elrod, 1983; Elrod & O'Gorman, 1991). Except for surface-water habitat, juveniles overlapped in their distribution with adult lake trout across and within depth zones. No evidence of segregation by length (i.e., ontogenetic shift) occurred because juveniles of all sizes were found in all depth zones. The profitability of any habitat to an individual fish depends on a variety of biotic and abiotic variables, and it is rare that a habitat satisfies all requirements (Guzzo et al., 2017; Schindler, 2017). The broad depth distribution of juvenile and adult lake trout observed in Great Bear Lake suggested that individuals at all sizes and life stages had the capacity to exploit a wide range of resources across a variety of habitats and depths (Chavarie, Harford et al., 2016; Chavarie, Howland, Harris, & Tonn, 2015).

An important variable affecting the distribution of fish, both spatially and temporally, is temperature (Blanchfield et al., 2009; Guzzo et al., 2017; Plumb & Blanchfield, 2009). Lake trout are generally restricted to deep habitats below the thermocline in southern lakes during summer stratification, whereas thermal gradients are typically weak in large northern lakes and have less effect on lake trout. Indeed, due to abundant suitable cold-water habitats found at all depths in Great Bear Lake, temperature is unlikely to be a variable driving lake trout distribution (Johnson, 1975a, 1975b). Although the lack of a strong thermocline should result in a minimal thermal influence on the distribution of lake trout, the broad juvenile distribution observed in Great Bear Lake did not appear to correspond to distributions observed elsewhere in comparable northern lakes (e.g., latitudinal trend) per se. For example, Great Slave Lake is a large northern lake with similar limnological characteristics to Great Bear Lake, where shallow thermoclines (~15 m) occur only briefly (mid-July to late August; Blanken, Rouse, & Schertzer, 2008). However, in Great Slave Lake, Zimmerman et al. (2009) found small individuals in habitats deeper than habitats used by large individuals of the shallow-water morph (i.e., piscivorous morph). Juvenile lake trout distribution in Great Slave Lake, based on Zimmerman et al. (2009), suggested that variables other than temperature may be important in affecting juvenile distribution. In Great Bear Lake, thermal gradients caused by thermoclines are similarly weak (Johnson, 1975a, 1975b); however, we found juvenile lake trout across all vertical and horizontal gradients. Thus, the difference between these two large northern lakes without strong thermoclines is that large adult trout were uniformly distributed in Great Bear Lake but not in Great Slave Lake (Chavarie et al., 2018; Zimmerman et al., 2009). The source of the difference in adult distribution may help explain differences in juvenile distribution between the lakes.

Distribution of juveniles may be related to gradients of predation risk across habitats (Edsall & Cleland, 2000; Evans, 2007; Evans & Willox, 1991). Usually, juvenile lake trout minimise overlap in habitat with adults due to higher predation risk in shallow-water habitats (Elrod & Schneider, 1987; Martin, 1952; Zimmerman et al., 2009). In Great Bear Lake, the predation pressure experienced by juvenile lake trout should be more equally distributed across depths than in other lakes due to the uniform adult lake trout distribution. Adults

commonly achieve remarkable sizes (>1,000 mm) in Great Bear Lake. Consequently, risk from cannibalism in Great Bear Lake is probably less restricted to a certain ages, sizes and habitats. With the exception of a slight surface-water avoidance, where predation might be more prevalent with the addition of other predation pressure (e.g., avian), juvenile lake trout in Great Bear Lake did not select specific habitats. Most juveniles, regardless of location, would be vulnerable to predation, and thus, these individuals seemed to not seek to find a predation refuge, as evidenced by their captures.

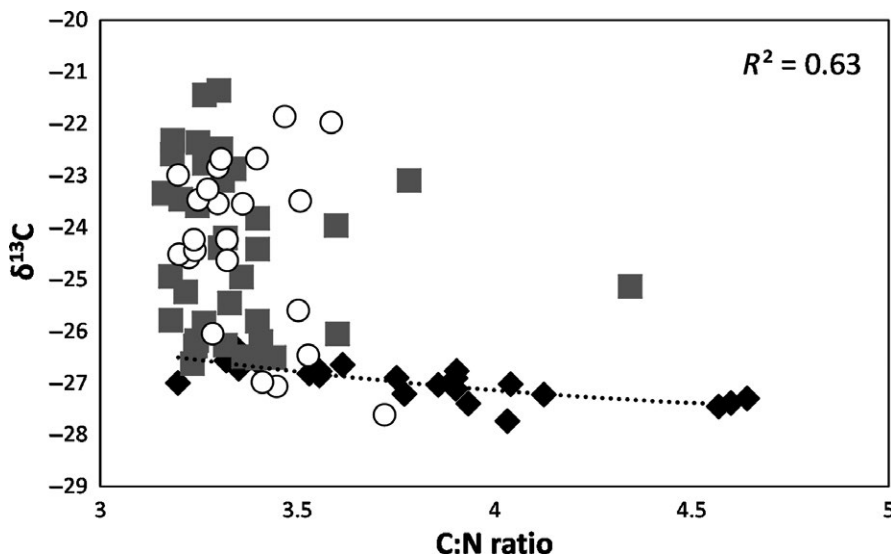
Lake trout ontogenetic shifts reflect the importance of entering the piscivore niche as early as possible (Andersson, Bystrom, Claessen, Persson, & Roos, 2007; Madenjian et al., 1998). The typical lake trout ontogenetic shift, from benthic/deep-water to pelagic/



**FIGURE 4** Admixture coefficient plots of the Bayesian clustering (STRUCTURE) analysis for juvenile lake trout from Great Bear Lake. Population structure was examined by depth zone (0–20, 21–50, 51–150 m). Each individual is represented as a vertical line partitioned into coloured segments representative of an individual's fractional membership in any given genetic cluster ( $K$ ). The most likely number of clusters based on the  $\Delta K$  statistic of Evanno et al. (2005) was eight, whereas the most likely number of clusters based on the traditional statistic mean  $\text{Ln}P(K)$  was  $K = 1$

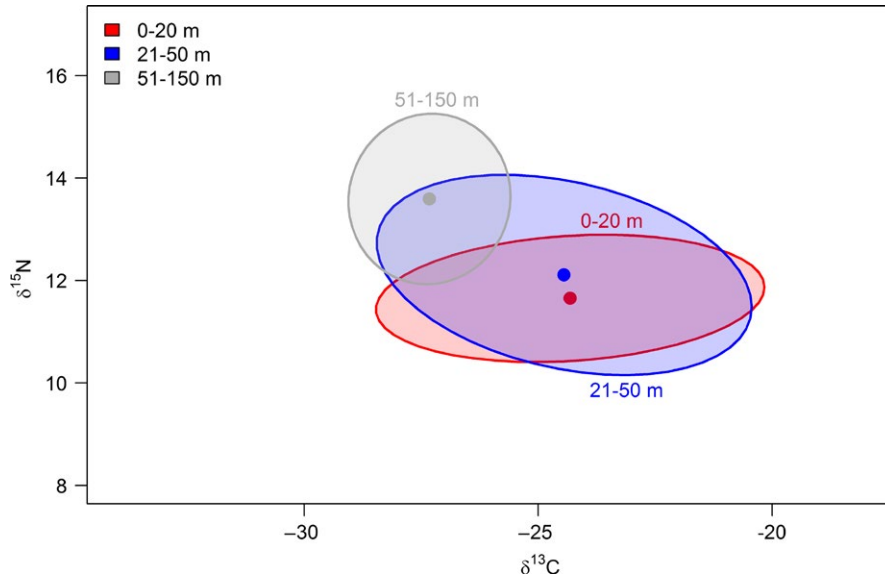
shallow-water habitat use, relates to body size, predation risk and foraging opportunities (Hjelm, Persson, & Christensen, 2000; Ward-Campbell & Beamish, 2005; Werner & Hall, 1988). These past observations were inconsistent with our observations of the distribution of juvenile lake trout in Great Bear Lake. Our study did not include young-of-the-year due to the lack of vulnerability to the nets used but did include a wide range of sizes (120–580 mm fork length), which provided a broad representation of juveniles. Great Bear Lake juvenile lake trout distribution may have been influenced more by foraging opportunities rather than predation pressure. Intraspecific competition may favour an expansion of the species niche (Svanbäck & Bolnick, 2007), producing a broad population-level niche as an overall outcome (Bolnick, Yang, Fordyce, Davis, & Svanbäck, 2002; Svanbäck & Bolnick, 2005).

Movement among depth zones may be limited in Great Bear Lake, based on the detection of a small genetic cline in profundal deep-water adults in comparison with their shallower counterparts (Chavarie et al., 2018), although this pattern was weaker for juveniles than for the adults. Another ecological depth-based trend, detected both in adults and juvenile, was related to lipid accumulation. C:N ratios were higher in profundal juveniles than individuals caught in other zones, a characteristic linked to higher lipid content that provides positive buoyancy (Bone, 1972; Corner et al., 1969; Eastman, 1988). Variation in buoyancy of lake trout caused by fat content has been associated with the capability to exploit trophic resources in deep- versus shallow-water habitats and has been observed across a number of North American lakes (Chavarie, Muir et al., 2016; Zimmerman, Krueger, & Eshenroder, 2006, 2007). Plasticity in lipid accumulation observed in Great Bear Lake could be an adaptive trait related to depth (Goetz et al., 2010), but could also be a physiological response to differing foraging opportunities across depths (Currens, Sharpe, Hjort, Schreck, & Li, 1989) or an interaction between genetics and environment (Siepielski, DiBattista, & Carlson, 2009; Snorrason & Skúlason, 2004). Outcomes depend, in part, on costs and developmental limitations to plasticity, influencing the expression of plasticity (i.e., lipid accumulation) as a response to particular

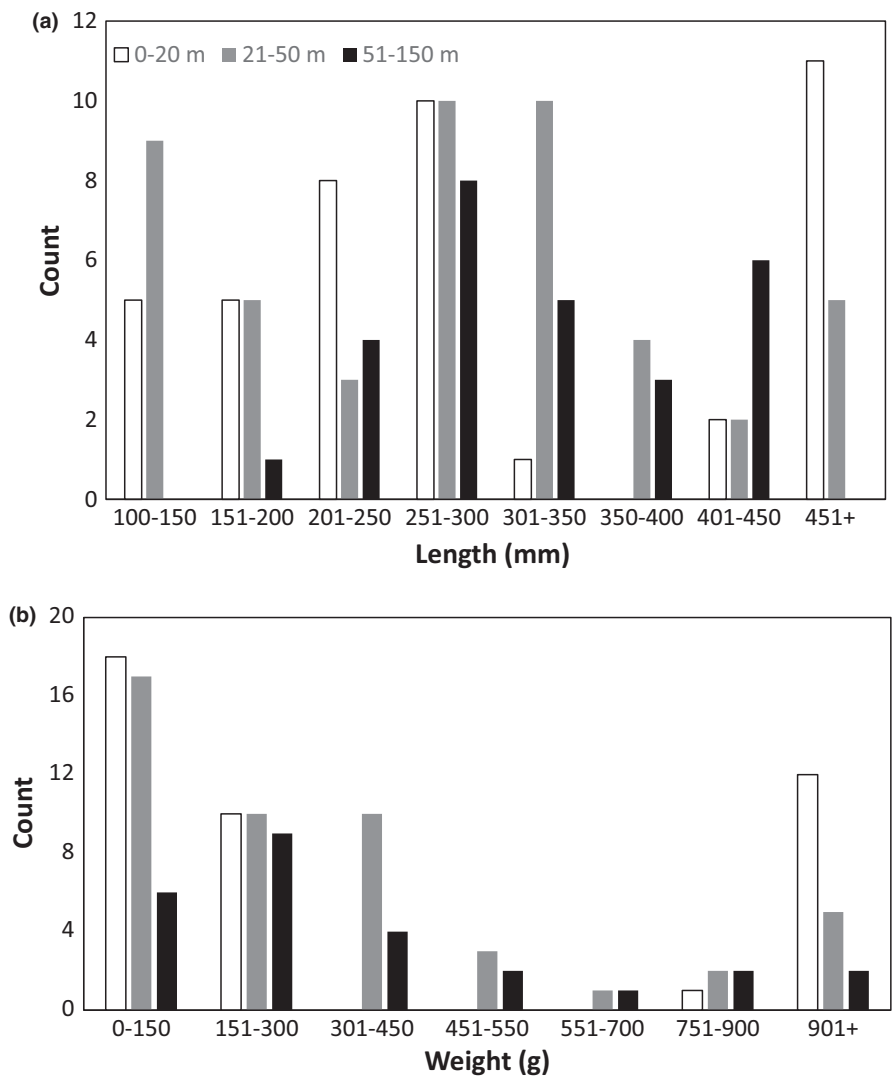


**FIGURE 5** Relationship between C:N ratio and  $\delta^{13}\text{C}$  (‰) in juvenile lake trout from Great Bear Lake caught within three depth zones, represented as follows: open circle = 0–20 m, light grey square = 21–50 m and black diamond = 51–150 m. A linear regression was fitted to individuals caught in 51–150 m depth zone, which differed from individuals caught in 0–20 m and 21–50 m zones, and trend differed from zero





**FIGURE 6** Probabilistic (95%) niche regions based on stable carbon ( $\delta^{13}C$ ) and nitrogen ( $\delta^{15}N$ ) isotopes for juvenile lake trout grouped by depth zone (0-20, 21-50, 51-150 m) in Great Bear Lake. Each depth zone is represented by a coloured ellipse



**FIGURE 7** In (a), fork length (mm) and in (b) weight (g) distributions for juvenile lake trout from Great Bear Lake, caught within three depth zones: 0-20 m (white), 21-50 m (grey), 51-150 m (black)

ecological conditions (i.e., depth and foraging opportunities), which can lead to fitness benefits associated with trade-offs among individuals (DeWitt, 1998; Hendry, 2009; Svanbäck, Pineda-Krch, & Doebeli, 2009).

Environmental variation along a gradient can offer diverse ecological opportunities for fishes (Seehausen & Wagner, 2014; Snorrason & Skúlason, 2004; Svanbäck et al., 2009). Within lacustrine systems, resource use is generally constrained by variation in habitat and prey that occurs naturally along horizontal and vertical habitat gradients (Hooker et al., 2016; Kristjánsson, Skúlason, Snorrason, & Noakes, 2012; Siwertsson et al., 2013). Greater diversity and abundance of prey, such as small littoral fish, terrestrial insects and benthic invertebrates, is typically available in shallow-water regions of Arctic lakes because of higher littoral productivity than in deep waters (Eloranta et al., 2015; Johnson, 1975a, 1975b). Although isotopic niche overlap was evident among the three zones, juvenile lake trout caught in the profundal zone (51–150 m) of Great Bear Lake showed some differences in their isotopic niche compared to their shallow-water counterparts (especially with 0–20 m). Juvenile lake trout caught in the profundal zone of Great Bear Lake followed the same trend previously reported for adults, with a higher  $\delta^{15}\text{N}$  (trophic level) compared to their shallow-water counterparts (Chavarie et al., 2018). Differences in asymptotic length in relation to depth could support the assumption of different foraging opportunities encountered by individuals (Hansen, Nate, Chavarie et al., 2016; Hansen et al., 2012; Hansen, Nate, Muir et al., 2016). However, an isotopic enrichment signal linked with depth could also lead to the observed isotopic difference in juvenile individuals (Post, 2002; Sierszen et al., 2014; Stockwell, Yule, Hrabik, Sierszen, & Isaac, 2014). If isotopic enrichment is a result of different depth use in contrast with differential foraging opportunities encountered by individuals, this result still suggests limited movement between habitats. One way or another, limited movement among depths, would enforce an ecological cline, where tensions between homogenising and divergent evolutionary forces arise (Chavarie et al., 2018).

In highly polymorphic lake trout populations, such as in Great Bear Lake (Chavarie, Howland, Harris et al., 2015; Chavarie et al., 2013), the relatively uniform distribution of juveniles might have important consequences for how resource partitioning and habitat use contribute to the maintenance of diversity within a system. The juvenile distribution (if based on limited movement) could influence adult habitat preferences, promoting phenotypic variation through plastic responses best suited to the exploited environment (Arendt, 2015; Berner & Thibert-Plante, 2015; Camacho, Canal, & Potti, 2016), and could ultimately lead to genetic differentiation of phenotypes. Expression of phenotypic variation in lake trout generally occurs after an ontogenetic niche shift, at which point large fish display greater diversity in morphological characteristics than juveniles (Chavarie et al., 2013; Zimmerman et al., 2007, 2009). Thus, because morphological differentiation is low in juveniles from Great Bear Lake (Chavarie et al., 2013; Chavarie, Howland, Venturelli et al., 2015), classification of juveniles into morphs was not possible. Nonetheless, adult diversity and distribution in Great Bear Lake did not seem to be associated with a strong habitat selection (e.g., shallow- vs. deep-water and benthic vs. pelagic) (Chavarie, Harford et al., 2016; Chavarie et al., 2018), and juvenile distribution appears to also follow this pattern. Yet, how juvenile distribution and plasticity relate to adult phenotypic variation in Great Bear Lake remains unknown.

## 5 | CONCLUSION

A number of ecological parameters, such as predation, temperature and foraging opportunity, can influence differential distribution of juveniles within an aquatic ecosystem (Barth & Anderson, 2015; Richard, Cattaneo, & Rubin, 2015; Strakosh & Krueger, 2005). In this study, no evidence of length-based depth segregation (e.g., ontogenetic shift) occurred in the juvenile lake trout distribution in Great Bear Lake; juvenile lake trout occupied all depths and habitats (except for surface-water), similar to adults. If predation risk is

Parameter		Zone (m)			ANOVA	
		0–20	21–50	51–150	F	p
$L_{\infty}$	Estimate	1,00	915	843	7.25	0.003
	SE	32.7	29.3	25.7		
K	Estimate	0.071	0.057	0.065	1.54	0.23
	SE	0.006	0.0053	0.0047		
$\omega$	Estimate	69.8	52.4	55.0	4.71	0.017
	SE	4.52	4.04	3.54		
$L_0$	Estimate	46.9	58.5	57.0	2.11	0.14
	SE	4.53	4.05	3.55		
$t_0$	Estimate	-0.78	-1.27	-1.17	3.79	0.035
	SE	0.14	0.13	0.11		
	Number	8	10	13		

**TABLE 3** Growth parameter estimates for juvenile lake trout captured within three zones in Great Bear Lake (SE = standard error; F = F-ratio; p = p-value)

uniformly distributed across depths and habitats in Great Bear Lake, juvenile distribution could instead be more influenced by foraging opportunities rather than by a gradient of predation pressure. Lake trout display flexibility in the foraging behaviour (Guzzo et al., 2017), favouring a broad niche. Subsets of differently specialised individuals using spatially (i.e., depth) or temporally (i.e., season) separated resources may occur, producing a broad population-level niche as an overall outcome. In Great Bear Lake, all life stages of lake trout, juveniles to adults, displayed broad resource use across all depths and habitats.

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## AUTHORS' CONTRIBUTION

L.C., K.L.H., W.M.T., A.M.M. and C.C.K. conceived and designed the investigation. L.C., C.P.G., L.N.H. and M.J.H. performed field and/or laboratory work. L.C., C.P.G., L.N.H., W.J.H. and M.J.H. analysed the data. K.L.H. contributed materials, reagents and/or analysis tools. L.C. wrote the paper.

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## SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section at the end of the article.

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