ORIGINAL ARTICLE

Freshwater Biology **WILEY**

Deciphering lifelong thermal niche using otolith $\delta^{18}O$ thermometry within supplemented lake trout (*Salvelinus namaycush*) populations

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Abstract

1. The selection of thermal habitat by fish is strongly regulated by physiology and behaviour. However, delineation of a species lifelong thermal niche remains technically challenging. Lake trout (*Salvelinus namaycush*) survival and productivity are recognised as being tightly linked to a somewhat restricted thermal habitat. The factors guiding temperature selection during each life stage remain poorly understood.

2. In this study, we tested the significant factors controlling the realised thermal niche of lake trout from two southern Quebec small boreal lakes that experienced supplementation stocking during the last 20 years. We used oxygen stable isotope ($\delta^{18}O$) thermometry of otolith calcium carbonates (aragonite) using secondary-ion mass spectrometry to estimate experienced lifelong temperatures. We investigated the thermal habitat of lake trout with known genotypes (local, hybrid, and stocked).

3. Ontogeny and genetic origin influenced temperature selection in both studied lake trout populations. Young-of-the-year consistently used warmer, shallower habitats (10.7 ± 2.6°C, 7.5 m depth) prior to a juvenile transition to colder and deeper waters (8.5 ± 3.3°C, 10 m depth). Stocked lake trout, originating from a genetically distinct ecotype, exhibited a more variable thermal niche, with some individuals consistently using warmer habitat (10.4 ± 1°C) than local fish. Their hybrid progeny also occupied a warmer thermal niche, intermediate to the parental strains. We propose that increased fat content and genetic origin are potential explanatory factors for warmer temperature use.

4. This study reiterates that high-resolution otolith $\delta^{18}O$ thermometry is a uniquely well-suited approach for unravelling the multiple factors that influence lifelong temperature selection in fish. Our results illustrate that the realised thermal niche is influenced by a genetic–environment interaction.

KEYWORDS
early life, ontogeny, oxygen stable isotopes, secondary-ion mass spectrometry, thermal boundaries

1 | INTRODUCTION

Water temperature is a critical property in aquatic environments as it defines suitable habitats for ectotherms, such as fishes and amphibians. Thermal conditions can have a strong impact on both physiological (e.g. growth rates, reproductive success) and ecological processes (e.g. prey and habitat selection) (Clarke, 2006). There is an apparent correlation between fish physiology and adapted behaviour, whereby temperature preference and performance of physiological functions co-vary for a given species or a specific life stage (Coutant, 1987). This suggests that fish actively seek a temperature that will maximise their fitness. Potential competition and partition of thermal habitats suggest that temperature should be envisioned as an ecological resource, comparable to trophic and reproductive resources (Magnuson, Crowder, & Medvick, 1979). Indeed, the range of temperatures selected could be considered as one of the n-dimensional niche axes according to Hutchinson's (1957) definition of an ecological niche. However, a distinction should be made between the *realised thermal niche* and the preferred temperature, the latter only applying to temperature ranges measured in laboratory, under conditions where all other parameters are controlled (Bergstedt, Argyle, Krueger, & Taylor, 2012). A gap may then exist between temperature preference and occupancy, owing to complex ecological constraints imposed by the natural environment.

Quantification of the realised thermal niche of fishes remains technically challenging in natural environments. Over decades, the uses of acoustic telemetry and internal archival tags have become the gold standard for in situ assessment of thermal niches (Bergstedt, Argyle, Seelye, Scribner, & Curtis, 2003; Plumb & Blanchfield, 2009). However, fish capture and the surgical implantation of such tags can be time-consuming and is generally unsuitable for small/young fish (Elrod, Ogorman, & Schneider, 1996). Oxygen isotope ratios (δ^{18}O) in biogenic carbonates can provide a reliable alternative method for a posteriori temperature estimations in fish, when applied to otolith material (Devereux, 1967; Patterson, Smith, & Lohmann, 1993). Otolith formation is the result of the progressive precipitation of biogenic aragonite under conditions where the oxygen isotope ratio will be near equilibrium with ambient water via a temperature-dependent hydrolysis reaction (Høie, Otterlei, & Folkvord, 2004). Quantifying otolith δ^{18}O values provides temperature information integrated during otolith precipitation. High-resolution transects of oxygen isotope ratios provide access to the isotopic ratios recorded within the daily pattern of otolith precipitation as well as their extension to individual bands that represent months to years (Campana & Thorrold, 2001; Pannella, 1971), and a record of the temperature experienced across all life stages (Dufour, Höök, Patterson, & Rutherford, 2008; Hanson, Wurster, & Todd, 2010). Technical advances in ion beam sampling technologies coupled with high-precision, high-sensitivity isotope ratio mass spectrometry have created the opportunity to quantify oxygen stable isotope ratios using individual point-based analyses of otoliths (Matta et al., 2013). In particular, secondary-ion mass spectrometry (SIMS) offers highly precise stable isotope quantification. Despite growing access to these analytical techniques, otolith thermometry has been seldom used for thermal niche assessment of exploited fish species, especially at or before their sub-adult life stages (Shirai et al., 2018).

Predatory cold-water fish occupying deep temperate lakes are likely to exhibit competitive interactions for thermal habitats, as the volume of suitable habitat can be limited during the summer season (Christie & Regier, 1988; Murdoch & Power, 2013) when these lakes undergo thermal stratification. Lake trout (*Salvelinus namaycush*), a cold-water salmonid stenotherm living in deep oligotrophic lakes across North America, represents a very relevant fish model for exploring the importance of thermal resources. This species has a restricted optimal temperature range (8–12°C, Coutant, 1987; Mackenzie-Grieve & Post, 2006; Plumb & Blanchfield, 2009) and a low tolerance for dissolved oxygen <6–7 mg/L (Evans, 2007). These environmental preferences are likely to promote competition for thermal resources, which can be influenced by the ecological particularities of a studied population. There is a growing body of evidence that boreal and arctic salmonids show intraspecific variation in performance among ecotypes and strains in relation to temperature (Bergstedt et al., 2012; McDermid, Wilson, Sloan, & Shuter, 2013). Accordingly, thermal niche use (based on otolith δ^{18}O thermometry) was shown to differ between European whitefish (*Coregonus lavaretus*, salmonid) morphs (Kahilainen, Patterson, Sonninen, Harrod, & Kiljunen, 2014; Kelly, Amundsen, & Power, 2015), a difference mostly attributed to trophic niche use (benthic/pelagic preys). McDermid et al. (2013) demonstrated that small-bodied lake trout ecotypes usually seek out lower temperatures than large-bodied ecotypes. Intraspecific variations of phenotypic traits influencing depth (and temperature) have also been documented. For instance, the ecotypic differences in depth and thermal preference have been linked to fat content (Eshenroder, Crossman, Meffe, Olver, & Pister, 1995) and swim bladder gas retention, both determining the neutral buoyancy depth. Selective breeding of these ecotypes showed that both traits were heritable, with inter-ecotype hybrids displaying fat content and gas retention intermediate to parental values (Eschmeyer & Phillips, 1965; Ihssen & Tait, 1974). Those observations suggest that depth and thermal niche use are, at least partially, genetically determined and could be modified by inter-ecotype hybridisation (Bergstedt et al., 2003).

Although the thermal niche of adult lake trout has been studied extensively, thermal habitat use of young-of-the-year (YOY) and juveniles is not well known. Temperature selection in lake trout is believed to be correlated with age, with younger fish preferring higher temperatures than adults (Bergstedt et al., 2003). Peck (1982) observed that lake trout YOY in Presque Isle Harbor, Lake Huron, exhibit a prolonged residence in relatively shallow waters (<8 m) near spawning sites as long as water temperature does not exceed 15°C over an extended period. Likewise, young lake trout in Great Bear Lake, NWT, Canada concentrate in shallow shoreline waters from the ages of 0–3 years (Miller & Kennedy, 1948), probably linked to the absence of thermocline and/or predation gradient (Chavarie et al., 2019). In contrast, other studies have suggested that YOY lake trout seek deeper and colder habitats

shortly after yolk sac absorption (Martin, 1951; Royce, 1951). Precise factors influencing YOY and juveniles thermal habitats remain to be identified.

Despite the fact that most lake trout populations are found in small lakes (Gunn & Pitblado, 2004), data on thermal habitat use mostly come from large systems, such as the Laurentian Great Lakes (Bergstedt et al., 2012). Inter-population particularities, exemplified by ecotypes identification, could have significant impacts on thermal niche. Two common ecotypes (e.g. planktivorous and piscivorous) are recognised in small boreal lakes, their expression reflecting the combined influence of environmental conditions, food availability (e.g. access to pelagic prey fish), and genetics (Bernatchez, Laporte, Perrier, Sirois, & Bernatchez, 2016; McDermid, Shuter, & Lester, 2010). The planktivorous ecotype is characterised by a low growth rate, early maturation (*c.* 6 years), and a shorter maximum length of fish (<450 mm) and is associated with lakes where large pelagic preys (mostly fish) are absent. Piscivorous ecotype, which is feeding on large pelagic preys, exhibits high growth rates, late maturation (>9 years), and a greater (>600 mm) maximum length (Bernatchez et al., 2016; Houde & Scrosati, 2003). Few lakes host both ecotypes in sympatry, the vast majority only hosting a single allopatric ecotype.

This study aimed to document the relative role of different biotic (e.g. life stage, genetic origin, trophic position) factors driving thermal habitat use by lake trout. We assessed lifelong thermal niche use through high spatial resolution SIMS otolith oxygen stable isotope ($\delta^{18}O$) thermometry. The resulting high-resolution estimates of temporal variability in temperature are used to describe the thermal habitat of YOY and juvenile fish and shed light on the uncertainties surrounding early life thermal habitats of lake trout. Our study targeted fish having distinct genetic origins (i.e. local, stocked or hybrid) from two allopatric lake trout populations of small-bodied planktivorous ecotype. Both lakes had been previously stocked for sport fishing supplementation with source populations of a large-bodied piscivorous ecotype (Morissette, Sirois, Lester, Wilson, & Bernatchez, 2018). By combining genotype-by-sequencing technologies and SIMS stable isotope measurements, we tested whether fish ontogeny and genetics were significant factors influencing temperature selection by lake trout. We hypothesised that stocked and hybrid trout would tend to use warmer habitats than local fish due to their genetic background (piscivorous ecotype), which is shown to be more related to warmer thermal niche (McDermid et al., 2013).

2 | METHODS

### 2.1 | Study systems and supplementation stocking history

Stocking has been used for lake trout populations supplementation for over a century. In Quebec, Canada, 46% of lakes hosting lake trout angling-exploited population have been stocked at least once since 1928 (Ministère du Développement Durable de l'Environnement de la Faune et des Parcs, 2013). Generally, stocked fish are progeny of wild breeders from allopatric lake trout populations of the piscivorous ecotype. Breeders are captured in autumn from known spawning sites for eggs and milt collection. Eggs are artificially fertilised in hatcheries and progeny is held in hatchery over winter months until stocking the next spring (age 0+). Precise information on rearing conditions (i.e. temperature, light daily regimen) experienced by stocked fish from both studied lakes are not known nor accessible, preventing us from testing any influence of this parameters on thermal niche. Neither domesticated strains nor adult fish have ever been used for the stocking of these lakes (Morissette et al., 2018).

2.2 | Fish sampling and processing

We sampled two lakes, one in 2012 (Lake Louisa; 45.769°N, 74.419°W) and 2013 (Lake McFee; 45.714°N, 75.623°W) using the same experimental fishing protocol. Both lakes are small (<500 ha) and deep (Z_{max} > 56 m), located in southern Quebec, Canada, and both display similar summer thermal stratification (Figure 1). Both lakes host an allopatric population of a planktivorous ecotype (small-bodied) lake trout and both lack large pelagic prey, such as pelagic salmonid forage fish (i.e. *Coregonus* spp. or *Osmerus mordax*) or large invertebrates such as the freshwater mysid shrimp (*Mysids* spp.). These two fish communities are comprised mostly of catostomid white sucker (*Catostomus commersonii*), yellow perch (*Perca flavescens*, percid), the centrachid pumpkinseed (*Lepomis gibbosus*), rock bass (*Ambloplites rupestris*), and small cyprinids (Figure 1). Both lakes were stocked multiple times from the same source population, Blue Sea Lake, a large (1,400 ha) and deep (Z_{mean} = 60 m) lake in the same region, hosting a similar fish community. The most recent stocking event in both lakes took place no more than 12 years before our sampling. These lakes were characterised previously as displaying a relatively balanced proportion of purely local and stocked fish as well as their hybrids (Valiquette, Perrier, Thibault, & Bernatchez, 2014).

We collected 75 fish per lake using the gill net method from a normalised lake trout sampling protocol, in collaboration with the Québec *Ministère des Forêts, de la Faune et des Parcs*. For each fish, we measured total length (TL, mm) and mass (g) in the field. The adipose fin was sectioned and stored in 95% ethanol in individual plastic vials (Eppendorf, Mississauga, Ontario). For both lakes at their deepest point, we collected temperature profiles at each 1-m depth up to 20 m and surface and thermocline water samples using clean Niskin bottles. Water samples were transferred in the field to airtight, nitric acid–washed (HNO_3, trace metal grade) Nalgene bottles and conserved at room temperature prior to $\delta^{18}O$ analyses. In the laboratory, both sagittal otoliths were extracted from the lake trout using nitric acid-washed plastic forceps. Otoliths were washed with ultrapure water, dried, and stored in Eppendorf plastic vials before further processing.
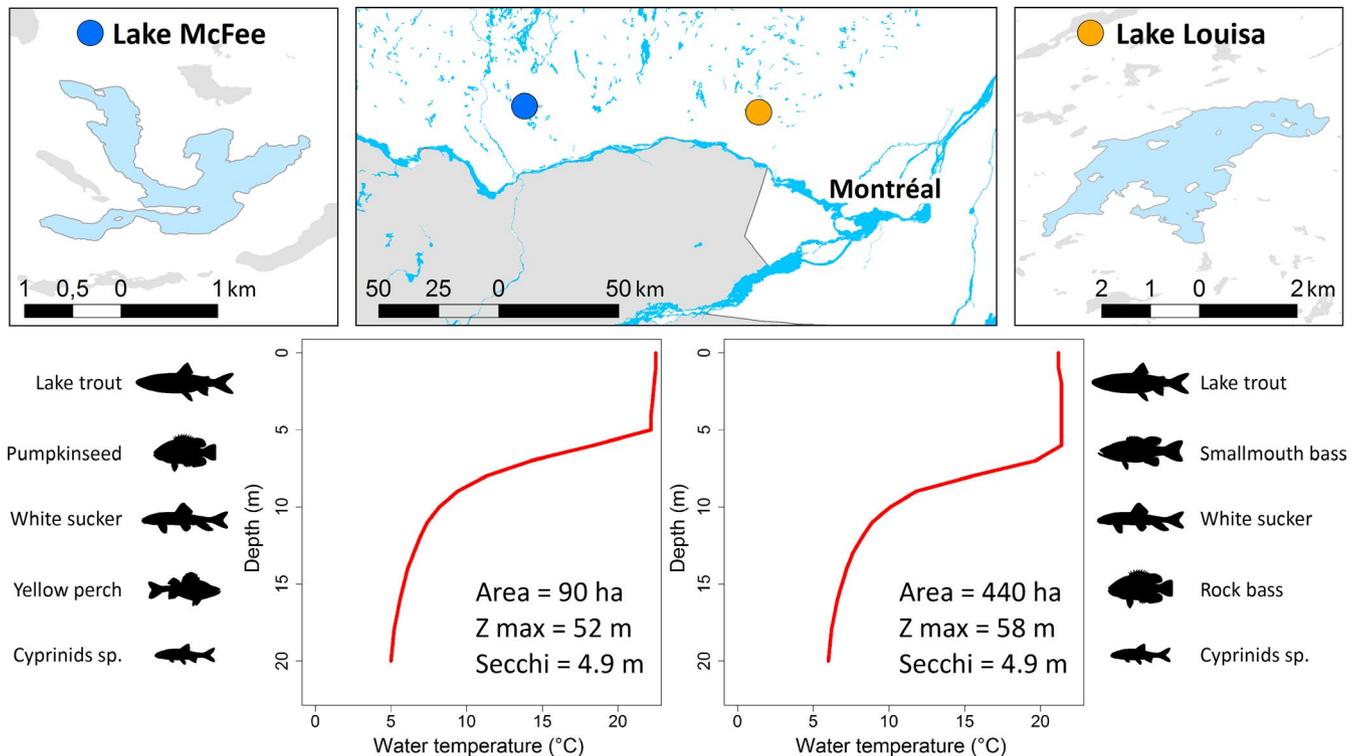
FIGURE 1 Ecological synopsis of studied lakes, maps are showing geographical position and morphology of both lakes. Fish communities of both lakes are depicted as fish silhouette (credit: Phylopic website) and common names (see text for scientific names) under each map. Temperatures by depth profiles of each lake are provided with lake area (ha), maximum depth (Z_{max}) and Secchi depth [Colour figure can be viewed at wileyonlinelibrary.com]

2.3 | Genetic assignment of individual fish

Each fish was assigned a genetic origin (i.e. local, stocked, or hybrid) based on their single nucleotide polymorphism genotype using next-generation sequencing (genotype-by-sequencing) and the software ADMIXTURE (Alexander, November, & Lange, 2009). Our methodology is presented in detail in Morissette et al. (2018). Briefly, to assign the fish genotype we used the individual admixture proportions (Q), defined as the proportion of subsample parts of the genome most likely to be related to the stocking source (Blue Sea Lake) compared to the local (wild) genotype. We classified fish as being stocked when $Q_{stocking\ source}$ + SE ≥ 90%, local fish when $Q_{stocking\ source}$ + SE ≤ 10%, and hybrid when Q values fell between 10 and 90%. No further distinction was attempted between hybrid classes because the number of fish analysed here would have been too small (five hybrids per lake, see below) in each category to draw any rigorous interpretations.

2.4 | Preparation of otoliths and ageing of fish

The right sagittal otolith was embedded in a two-component epoxy resin (Miapoxy 100, Freeman) and cut into 1-mm-thick traversal sections using a slow-speed diamond-bladed saw (IsoMet saw; Buehler). After sectioning, we amplified the annuli contrasts by progressive grinding and polishing with sandpaper (2000 grit Wetordry[TM], 3M[TM]) and aluminium oxide lapping film (1- and 5-µm lapping film,

3M[TM]). Periodical observations of the grinding stage were realised during polishing, which guided the grinding/polishing procedure. Digital images of each otolith were captured using a digital camera (Leica DMC) coupled to a dissection microscope (Leica MZ12) at a 30–60× magnification. Age counts and increment measurements (µm) were done from the nucleus to the maximum ventral radius of the otolith (longest axis), following established methods and criteria (Casselman & Gunn, 1992; Simard & Magnin, 1972) using ImageJ v 10.2 software (Abramoff, Magalhaes, & Ram, 2004). Two independent readings (two readers) were completed and a third additional count/measurement if the first counts were not in agreement (c. 25% of otoliths). Using estimated age of the fish and length at capture, we back-calculated length-at-age (for complete method, see Morissette et al., 2018), using the body-proportional hypothesis (Francis, 1990). We selected a subset of 30 fish of age > 10 years (mean = 13.7 ± 2.4 years) based on the lake and genetic origin (2 lakes × 3 genetic origin [local, hybrid, or stocked] × 5 fish = 30 total).

2.5 | Secondary-ion mass spectrometry otolith $\delta^{18}O$ values analytical methods

Two SIMS mounts were required to accommodate all 30 otolith samples while ensuring that all areas to be measured remained within an 8-mm radius from the centre of the circular, 25.4-mm diameter mount. Each mount contained 20 crystals of IAEA-603 and three

sub-millimetre pieces of UWC-3 calcite reference materials (IAEA, 2016; Kozdon, Ushikubo, Kita, Spicuzza, & Valley, 2009). To minimise the amount of epoxy in each block—thereby minimising the amount of sample outgassing within the SIMS ultra-high vacuum system—polycarbonate discs were milled to provide individual wells for each otolith as well as a separate well for receiving the two calcite reference materials. We verified surface topography using white light interferometry, and we found the topography to be <5 μm for all regions of interest.

The samples were cleaned in an ultrasonic bath of high-purity ethanol before being carbon sputter-coated for subsequent scanning electron microscopy imaging. We produced both secondary electron and backscattered electron images for each otolith to obtain information regarding the locations of cracks within the material and also to provide clear identification of the main growth axis of a given otolith. After completing the initial scanning electron microscopy imaging, an additional 35-nm thick, high-purity gold film was sputter-deposited directly on top of the carbon coating. Both mounts were then imaged fully using the stitching software of a Nikon Eclipse motorised optical microscope. These images were then loaded into the SIMS point logger software.

We used the Cameca 1280-HR secondary-ion mass spectrometer of the German Research Centre for Geosciences (Potsdam) to produce $\delta^{18}O$ profiles (SIMS analysis analytical details are provided in Supporting information S1). Analyses were performed as point profiles from the otolith core and following the longest axis with stepping distances of c. 100 μm with both reference materials being analysed (typically after every 10th acquisition); the sequence of data acquisition was not randomised. To calibrate the instrumental mass fractionation of our SIMS instrument on each separate day of analysis, we used the value of $\delta^{18}O_{VPDB}$ = −2.37 for the IAEA-603 (IAEA, 2016), and we used the $\delta^{18}O_{VSMOW}$ = 12.49 for the UWC-3 (Kozdon et al., 2009). For converting between the two oxygen isotope scales, we used the equation on page 440 of Brand, Coplen, Vogl, Rosner, and Prohaska (2014). All analytical results are reported in standard δ notation (‰) relative to Vienna Standard Mean Ocean Water (VSMOW).

2.6 | Quantification of water $\delta^{18}O$ isotope values

The $\delta^{18}O$ values of surface and thermocline water samples were analysed at the Ján Veizer Stable Isotope Laboratory (University of Ottawa, Canada). The $\delta^{18}O_{water}$ values were determined using a Finnigan MAT Delta plus XP + Gasbench; a precise water volume (0.2 ml) was pipetted into an Exetainer vial. The vials were flushed and filled off-line with a gas mixture of 2% CO_2 in helium. The flushed vials were left at room temperature for a minimum of 24 hr. The CO_2 gas was analysed automatically under continuous flow during this period. The results were normalised to VSMOW using three calibrated internal standards that spanned most of the natural range. The routine precision (2-s) of the analysis was ± 0.15‰. Lake-specific $\delta^{18}O_{water}$ values were assumed to represent the average of the surface and thermocline results.

2.7 | Calculation of temperatures experienced

Interspecific difference in life history and physiological mechanisms could influence oxygen isotope fractionation in otoliths (Høie et al., 2004; Weidman & Millner, 2000). Hence, many authors advise caution on the use of universal (e.g. multi-specific) temperature-mediated $\delta^{18}O$ fractionation equation (Hanson et al., 2010; Rowell, Flessa, Dettman, & Roman, 2005). Hence, species-specific fractionation equation (or developed for closely related species) should be preferred (Murdoch & Power, 2013; Storm-Suke, Dempson, Reist, & Power, 2007). To test this assertion, we estimated temperature using four different equations developed using different species; a multi-specific equation developed on freshwater fishes (Patterson et al., 1993), a specific cotid Atlantic cod (*Gadus morua*) equation (Høie & Folkvord, 2006), a specific Atlantic croaker (*Micropogonias undulutus*, sciaenid) equation (Thorrold, Campana, Jones, & Swart, 1997), and a genus-level equation using two salmonid species of the *Salvelinus* (*fontinalis* and *alpinus*) genus (Storm-Suke et al., 2007). The estimated temperatures derived from the oxygen isotope fractionation equation developed for *Salvelinus* species provide the results more closely related to species known thermal niche (Figure S1 and Table S1, see Supporting information S2) and subsequent analyses were based on those estimations. Lake-specific $\delta^{18}O_{water}$ values were used to calculate experienced temperature (T°C). As the Storm-Suke et al. (2007) equation was developed using a 350°C roasting procedure, which is not part of the preparation procedure for our samples, $\delta^{18}O_{otolith}$ values were transformed applying a global correction of + 1‰. Matta et al. (2013) have shown that 350°C roasting of otolith was having a + 1‰ effect, but preserved the inter-otoliths pattern of $\delta^{18}O_{otolith}$ values. The fractionation equation is expressed as the relationship between fractionation factor α ($\delta^{18}O_{otolith}$ + 1,000/ $\delta^{18}O_{water}$ + 1,000) and the inverse of estimated water temperature (T, Kelvin):

$$1000\ln\alpha = 20.69\left(10^3T^{-1}K\right) - 41.69$$

We transformed spot analyses positions (X, Y) along each otolith data acquisition axis of the SIMS analysis to fish age and length using the digitally measured position of each annulus along the data acquisition axis. We then used a non-linear regression of annuli position as a function of age to estimate the age of the specific fish at every point of analysis. Age estimates were then used for estimation of TL (mm) using an individual-specific von Bertalanffy growth model. Length–age and age–annulus models were fitted using the *FSA* package in the R statistical software (R Core Team, 2016). The growth model fitting is presented in detail in Morissette et al. (2018).

2.8 | Statistical analyses

We modelled the effects of age and genetic origins on the occupied thermal habitats (response variable temperature) of lake

trout YOY using a linear mixed-effect model. A linear mixed model was fitted using the function *lme* in the R package *nlme* (Pinheiro, Bates, Debroy, & Sarkar, 2019). The factors of the model were genetic origin (fixed, two levels: local and hybrid) and age (fixed, two levels: hatching and end of first growing season). Individual fish nested within a lake were treated in the model as a random slope to allow for the experimental repeated-measure design and individual variability. We did not include an estimated temperature of the two first growing seasons for stocked fish in our evaluation. Stocked fish $\delta^{18}O_{otolith}$ values were representative of the hatchery habitat (mean = −8.1 ± 1.2‰$_{VPDB}$) rather than that of the sampled lakes (mean = −6.9 ± 0.9‰$_{VPDB}$); therefore, the estimated temperatures were not biologically relevant (>20°C, max = 32.2°C). This difference was only observed in the first two growth seasons, which is in agreement with the age at stocking of hatchery fish (1+). Unfortunately, hatcheries that contributed to stocking of sampled lakes have been closed and no water samples could be tested to rigorously confirm that otolith core corresponded to hatchery waters.

We used a similar model to establish the thermal habitats used by sub-adult fish (<6 years) using a new factor for age (fixed, six levels: 1–6). We ran pairwise comparisons between age classes using the *lsmeans* function (*lsmeans* package) in R (Lenth, 2016). Since this analysis showed that the realised thermal habitat stabilised after the fourth growth season, we modelled the influence of genetic origin (fixed, three levels: local, hybrid and stocked) and age (continuous variable) on post-settlement thermal habitat (>fourth growth season) with individuals nested within the lake as a random slope.

To test for the biotic factors influencing the temperature used by adults, we modelled the effects of ecological individual variables on estimated temperature at the last annuli through linear model. Biotic variables included in the model were total length (TL, mm), percentage of fish population attributed to stocked genotype ($Q_{stocked}$), C:N ratio (a measure of fat content), trophic position (TP) and $\Delta_{Pelagic}$ (contribution of pelagic prey to diet), the last three factors were nested in factor lake. C:N, TP and $\Delta_{Pelagic}$ were estimated from white muscle $\delta^{13}C$ and $\delta^{15}N$ stable isotope values collected on the same fish (see Morissette, Sirois, Wilson, Laporte, and Bernatchez (2019) for complete methodology). Significance of contributions for every factor was assessed by analysis of variance.

3 | RESULTS

Fish selected from both lakes were similar in terms of age (mean = 13.7 ± 2.4 years) and total length (mean = 451 ± 82 mm TL). However, some stocked fish exhibited a larger size than observed for the local or hybrid fish (Table 1). Total observed length difference was consistent with our recent observation that *c.* 20% of stocked lake trout in allopatric populations of the planktivorous ecotype had a significantly larger size compared to local and hybrids (Morissette et al., 2018). These stocked fish had a body length more typical

of lake trout of the piscivorous ecotype (i.e. their genetic origin). Otolith radius (μm) were found to correlate linearly with fish TL (oto-radius = 2.4 * TL + 398.4, $p < 0.05$, $R^2 = 0.76$), where the largest fish have an otolith radius *c.* 500 μm longer than smaller fish.

3.1 | Secondary-ion mass spectrometry otolith $\delta^{18}O$ values

For the 3 days of data collection, we recorded 1-s repeatability for the IAEA-603 material of ± 0.30‰ ($n = 16$), ± 0.94‰ ($n = 22$), and ± 0.30‰ ($n = 8$), respectively. For the concurrent UWC-3 calcite, we recorded 1-s repeatability for the 3 days of data acquisition of ± 0.11‰ ($n = 15$), ± 0.16‰ ($n = 23$), and ± 0.17‰ ($n = 9$). We found that the IAEA-603 calcite contained significant isotopic heterogeneity at the sub-nanogram sample mass provided by our SIMS instrument. This is consistent with the results reported by Nishida and Ishimura (2017) who observed variations in the isotopic compositions of IAEA-603 at the single-grain scale.

On the second day of our SIMS analytical sequence, we observed a clear relationship between the measured $^{18}O^-/^{16}O^-$ ratio and the $^{16}O^-$ count rate with some 2.5‰ difference in the isotopic ratio detected between the two groups of the IAEA-603 grain types (opaque and translucent). It is noteworthy that Nishida and Ishimura (2017) found a $\delta^{18}O$ value difference of only 0.28‰ between the two subpopulations they observed for IAEA-603. However, these authors were working with test portion masses some four orders of magnitude larger than masses used in our SIMS determinations. As suggested by Nishida and Ishimura (2017), the isotope ratio for individual grains of IAEA-603 could be correlated with the optical clarity of a given grain.

Based on the above observations, we based our otolith data reduction solely on the results from the UWC-3 calibration material. The observed repeatability of UWC-3 indicated that the overall uncertainty on the individual otolith results was less than ± 0.2‰ (1-s). Calculating the mean $^{18}O^-/^{16}O^-$ ratios from the multiple grains analysed from IAEA-603, we obtained $\delta^{18}O_{VPDB}$ values of −2.29, −2.86, and −2.36‰ for each of the three analytical sessions, respectively. These results are in reasonable agreement with the assigned value for IAEA-603 of $\delta^{18}O_{VPDB}$ = −2.37 ± 0.04‰ (1s) (IAEA, 2016). We therefore believe that our absolute results are at least accurate to 0.5‰, whereas the relative difference between any two analytical results is reliable at the 0.3‰ (1s) level or better.

We took an average of 12 SIMS measures per otolith (stepping distance 99.6 μm*step^{-1}) distributed evenly over the entire length of a given otolith. No analysis failed to provide a result. Two spots were systematically done within the first annuli (first growing season) for every fish. Furthermore, a single point of analysis for the subsequent growing seasons was successful until the sixth growing season, where points of analysis had an above-annual frequency since annuli were narrower than our *c.* 100 μm step distance. The median observed otolith $\delta^{18}O_{VDPB}$ value was −7.7 ‰ with values ranging from −13.45 to −5.76‰. Surface and thermocline water $\delta^{18}O_{VSMOW}$ values

Lake	Genetic origins	Sample (n)	Total length (mm)	SD	Age (year)	SD
Louisa	Local	5	425	50	11.0	1.4
	Hybrid	5	440	16	14.3	1.4
	Stocked	5	501	95	13.6	2.7
McFee	Local	5	412	30	13.6	2.1
	Hybrid	5	390	51	12.8	2.4
	Stocked	5	534	125	16.2	2.2

were highly similar (difference between 0.1 and 0.7‰) but a significant difference was observed between our two lakes (t-test, *p* = 0.009, Lake Louisa = −8.05 ± 0.04‰, Lake McFee = −7.32 ± 0.26‰).

3.2 | Thermal habitats of YOY and juvenile lake trout

Yearlings form both lakes occupied a wide spectrum of thermal habitats, ranging from 6.4°C (5th percentile) to 15.0°C (95th percentile). The linear mixed-effects model revealed no significant effect of age (hatching versus the end of the first growth season) or genetic origin (local and hybrid) on the estimated used temperatures (Table 2) in the first year of life. The average estimated temperature at hatching was 10.7 ± 2.9°C (*SE*) and yearlings lived in a relatively constant thermal habitat during the entire first growing season. However, we observed pronounced inter-individual variability in terms of thermal habitat being occupied. Temperature at hatching was a significant predictor of the magnitude of temperature change during the first growing season ($\Delta T = -0.87 * T_{hatching} + 9.41$, *p* = 0.002, R^2_{adj} = 0.41,

TABLE 2 Linear mixed-effect models of the response variables for the occupied temperature of the first growing season

	Response		
	Occupied temperature (°C) during the first growing season		
Coefficient	Estimate	SE	df	p-value
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Fixed parts				
Intercept	10.89	0.83	20	**<0.001**
Genetic origin (local)	−0.26	1.19	16	0.82
Age	0.15	1.69	20	0.93
Interaction (origin × age)	−0.22	2.31	20	0.92
Random parts				
Ngrp	15 fish in 2 lakes			
Observations	41			

Note: Columns present the estimated differences (positive or negative) of group response variables with the model intercept, *SE*, degrees of freedom (*df*), and *p*-values of the factor. The *p*-values in bold indicate significant differences (*p* < 0.05). The random parts show the number of tested groups and experimental units (*Ngrp*) and total observations.

Figure 2). Lake trout hatching at 10.9°C was the least likely to initiate a change of temperature; other individuals born in warmer or colder waters migrated to reach a thermal habitat closer to the observed temperature preference (10.9°C).

The temperature range occupied by juvenile lake trout was greater than that occupied by either adult or YOY fish, ranging between 5.6 and 14.8°C (5–95% quartiles). The temperature range occupied by juveniles was influenced significantly by age; there was a significant difference between occupied temperatures after the third growing season (Table 3). Our model showed a significant ontogenetic effect on thermal habitats with older (>3 years old) lake trout inhabiting colder temperatures (3°C colder) than younger juvenile and YOY (Figure 3). There was no significant effect of genetic origin on the thermal habitat being used. Back-calculated length-at-age from individual Von Bertalanffy models showed that movements to colder water were initiated at a TL of 100 mm and completed at *c*. 250 mm TL (Figure 3, bottom panel).

3.3 | Adult thermal habitats

The estimated habitat temperatures for adult fish ranged from 4.8 to 13.0°C (5–95% quartiles, mean = 8.7 ± 2.7°C). Modelling of adults' thermal habitats showed a significant effect of genetic origin; stocked fish were using significantly warmer waters than local and hybrid fish (Table 4). However, lifelong experienced temperature at the adult life stage of stocked lake trout showed important between- and within-individual variability (Figure 4). At some point during their lives, several fish occupied warmer habitats (average = 10.4°C) than the remainder of the stocked (average = 8.8°C), local and hybrid lake trout (average = 8.1°C). Two stocked fish from Lake McFee experienced a clear shift in their thermal niche at *c*. 400 mm TL (Figure 4, Figure S2), a consistent behaviour exhibited for subsequent years.

Model of temperature at last annuli showed that total length, $Q_{stocked}$ and C:N (fat content) had a significant positive relationship on temperature at capture (Table 5). According to this model, both fat content and $Q_{stocked}$ were factors promoting use of warmer temperature (Figure 5). Hybrid fish exhibited the use of thermal habitat intermediate to that of their parents, the hybrids more closely related to stocked genetic origin (high $Q_{stocked}$) displaying use of warmer temperature, comparatively to hybrid related to the local genotype (low $Q_{stocked}$), using colder water temperatures at the time of capture (Figure 5, bottom panel).
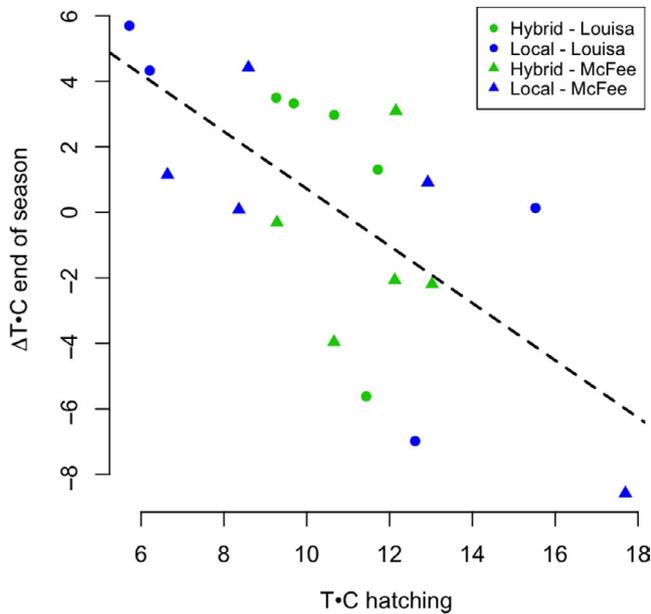
FIGURE 2 Difference between the occupied habitat temperature at the end of the first growing season and at the time of hatching (otolith core) of local (blue) and hybrid (green) young-of-the-year from lakes Louisa (circles) and McFee (triangles). The black dashed line is a linear regression ($\Delta T_{\text{end of season}} = -0.87 * T_{\text{hatching}} + 9.45$, $p = 0.002$, $R^2_{\text{adj}} = 0.40$) [Colour figure can be viewed at wileyonlinelibrary.com]

TABLE 3 Linear mixed-effect model of juvenile (<6 years) occupied temperature (response variable)

	Response			
	Juvenile occupied temperature (°C)			
Coefficient	Estimate	SE	df	p-value
Fixed parts				
Intercept	10.84	0.52	126	**<0.001**
Genetic origin (local)	−0.14	0.61	17	0.82
Growing season 2	0.57	0.56	126	0.31
Growing season 3	−1.28	0.59	126	**0.03**
Growing season 4	−2.80	0.63	126	**<0.001**
Growing season 5	−2.49	0.65	126	**<0.001**
Growing season 6	−2.83	0.64	126	**<0.001**
Random parts				
Ngrp	20 fish in 2 lakes			
Observations	151			

Note: Columns present the estimated differences (positive or negative) of factor response variables with the model intercept, *SE*, degrees of freedom (*df*), and *p*-values for the factor. The *p*-values in bold indicate significant differences ($p < 0.05$). The random parts show the number of tested groups and experimental units (*Ngrp*) and total observations.

4 | DISCUSSION

High-resolution analyses of oxygen stable isotopes provided life-long estimation of lake trout thermal habitat. This study showed a
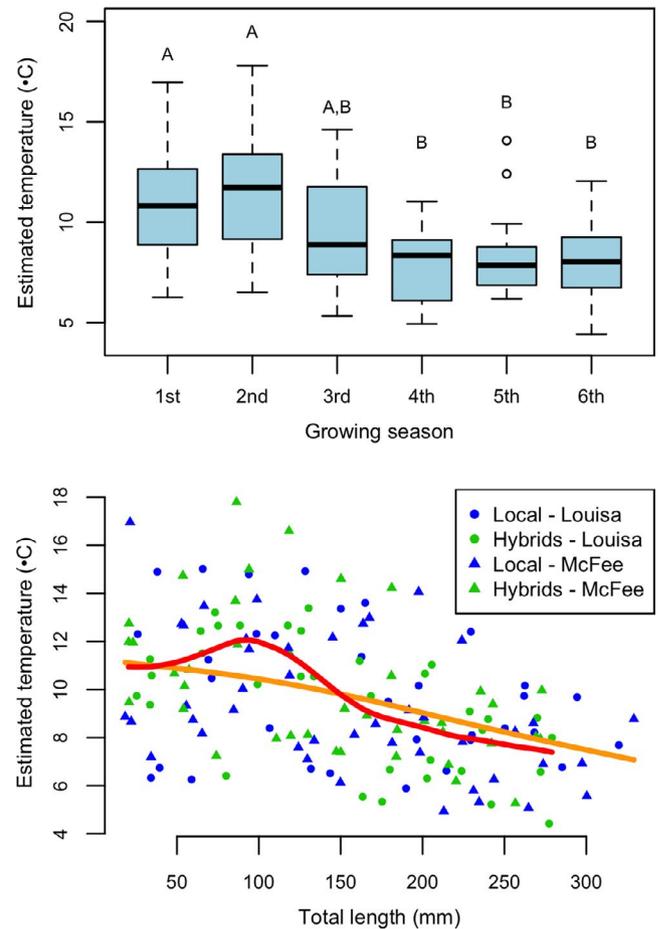
FIGURE 3 Estimated thermal habitat of juvenile lake trout for the first to the sixth growing season. Different letters indicate a significant difference in post hoc pairwise comparisons (top panel). Bottom panel: Occupied temperatures in function of back-calculated total length of local (blue symbols) and hybrid (green symbols) juvenile lake trout of lakes Louisa (circle symbols) and McFee (triangle symbols). Continuous lines are smoothed spline encompassing data from local (orange) and hybrid (red) fish [Colour figure can be viewed at wileyonlinelibrary.com]

marked difference between YOY/juvenile and adult thermal habitat. Later in life, inter-individual difference in thermal habitat emerged, potentially linked to genetic origin and related phenotypic traits. It has long been presumed that lake trout possess a very narrow thermal optimum, a perception largely influenced by Christie and Regier (1988), who showed a strong positive correlation between lake trout angling yield and the volume of lake that encompassed the 8–12°C thermal habitat. Following this pioneering work, the assessment of lake trout thermal habitat became of increasing interest for wildlife management and ecological theory. Thus, a variety of techniques was deployed to quantify the temperature range of the species. Notably, intensive gillnet sampling surveys (Elrod et al., 1996; Elrod & Schneider, 1987), bottom and otter trawls (Peck, 1982), archival tags (Bergstedt et al., 2012; Bergstedt, Argyle, Taylor, & Krueger, 2016), acoustic and radio telemetry (Mackenzie-Grieve & Post, 2006; Plumb & Blanchfield, 2009), and remotely operated vehicles (Davis, Carl, & Evans, 1997) were used to document trout habitat use in terms of

TABLE 4 Linear mixed-effect model of temperature occupied by adults (response variable)

Coefficient	Response			
	Adult occupied temperature			
	Estimate	SE	df	p-value
Fixed parts				
Intercept	10.51	0.82	177	**<0.001**
Genetic origin (hybrid)	−1.18	0.51	26	**0.029**
Genetic origin (local)	−1.49	0.54	26	**0.01**
Ontogeny (age)	−0.12	0.05	177	**0.023**
Random parts				
Ngrp	30 fish in 2 lakes			
Observations	194			

Note: Columns present the estimated differences (positive or negative) of factor response variables with the model intercept, *SE*, degrees of freedom (*df*), and *p*-values for the factor. The *p*-values in bold indicate significant differences (*p* < 0.05). The random parts show the number of tested groups and experimental units (*Ngrp*) and total observations.

depth and temperature. All of these methods proved to be useful, but they remained time- and resource-intensive and were limited by the size of fish, biased toward fish of larger size. From those studies, few studies reported on the thermal habitat of YOY and juvenile lake trout in natural settings (Bronte, Selgeby, Saylor, Miller, & Foster, 1995; Miller & Kennedy, 1948; Peck, 1982). However, Landsman, Stein, Whitledge, and Robillard (2017) showed that otolith δ^{18}O thermometry could provide an estimate of lake trout natal thermal habitat (Lake Michigan), which were consistent with field observations (Bronte et al., 1995). Accordingly, our study is reiterating that otolith δ^{18}O thermometry based on the high-resolution analysis is a powerful method for assessing the thermal niche of any size class of fish.

4.1 | Assessment of the YOY thermal habitats

Yearlings consistently occupy waters having an average temperature of 10.7 ± 2.9°C. Our results match the preferred temperatures of lake trout YOY observed under controlled laboratory settings: 11.7°C (McCauley & Tait, 1970) and 9.0–11.5°C (Peterson, Sutterlin, & Metcalfe, 1979). During their first growth season, individual lake trout displayed high variability in the occupied temperature, but they tended to seek out a specific range of temperatures, initiating movements to avoid temperatures >14°C and <8°C. This temperature range corresponded to the upper metalimnion (depth = 7.5 m) in the sampled lakes during the period of summer thermal stratification. As such, our results support the hypothesis of Peck (1982) of extended residency in shallow (<8 m) waters.

However, the inter-individual variability we observed provides insight into the lack of consensus in the literature around thermal habitats during the early life stages of lake trout. Contrasting YOY behaviour could be linked to the different thermal conditions prevailing in lakes inhabited by lake trout, influencing early life tactics. Here, several individuals made marked migrations between thermal habitats (>6°C) during their first growing season. Yearlings tended to *escape* stressful thermal situations, whereas those hatching in warmer sites modified their position to reach colder habitats closer to their thermal optimum (and *vice-versa*). This is consistent with the results observed for populations inhabiting lakes experiencing rapid warming in the spring (i.e. southern or small lakes) in which YOY exhibit a rapid migration to lakes' deepest parts (Martin, 1951; Royce, 1951). Accordingly, littoral
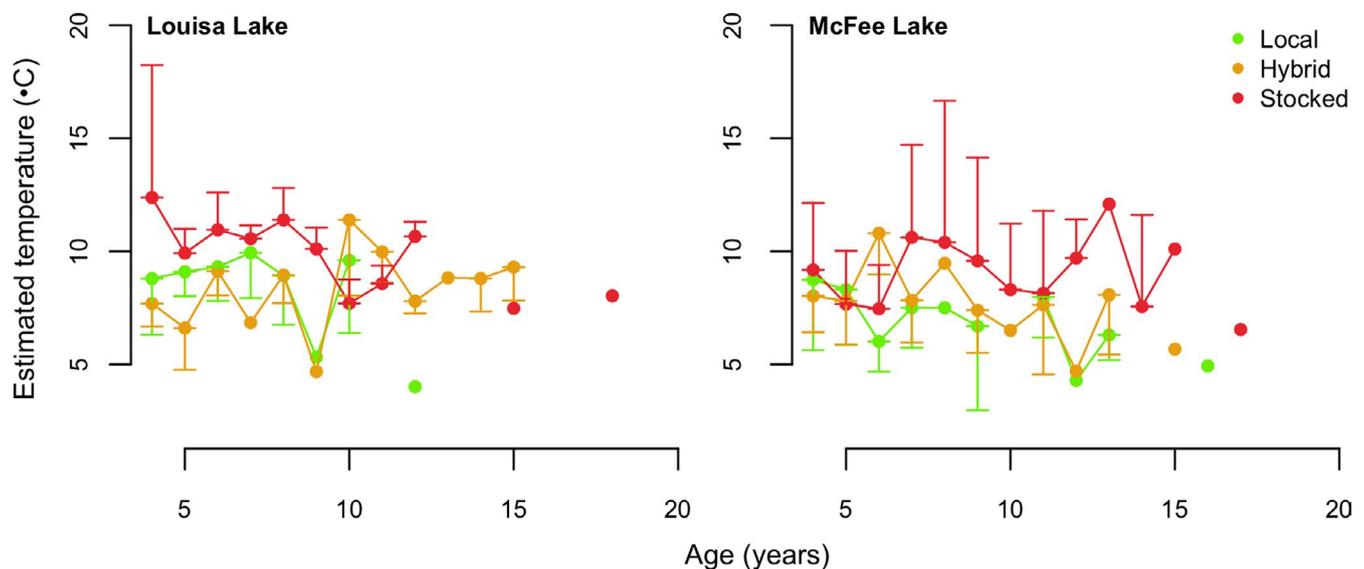
FIGURE 4 Mean and standard deviation (error bars) of lake trout lifelong thermal by age class (4–18 years) in each genetic origin groups in lakes Louisa (left panel) and McFee (right panel). Different colours in each graph represent a different genetic origin: local (green), hybrid (yellow), and stocked (red). Only positive or negative error bars are shown to optimise visualisation [Colour figure can be viewed at wileyonlinelibrary.com]

**TABLE 5** Analyses of variance of estimated temperature at last annuli of adult lake trout (response variable)

Coefficient	df	SS	MS	F value	p-value
	Response				
	Adult temperature at last annuli				
Total length	1	22.39	22.39	7.14	**0.02**
$Q_{stocked}$	1	14.0	14.01	4.47	**0.05**
Trophic position | lake	2	11.27	5.63	1.79	0.20
ΔPelagic | lake	2	4.88	2.44	0.78	0.47
C:N | lake	2	23.06	11.53	3.68	**0.05**
Residuals	17	53.27	3.13		

Note: Columns present the different coefficients (factors), degrees of freedom (*df*), sum of squares (SS), mean square (MS), *F* values, and *p*-values for each factor. The *p*-values in bold indicate significant differences (*p* < 0.05). Factors nested in lakes are represented by: | lake.

residency has been mostly reported in northern (or large) lakes where littoral zones displayed water temperatures <16°C, such as Great Bear Lake and Lake Superior (Bronte et al., 1995; Peck, 1982).

Estimated temperatures from otolith cores show that local fish hatched under more variable temperatures compared to hybrids, suggesting a broader use of spawning sites for local fish compared to hybrids. Hence, while wild lake trout exhibit a certain degree of spawning site fidelity (Binder et al., 2015), hatchery-reared fish may not have the ability to recognise high-quality spawning sites (Bronte et al., 2007). Admittedly, our interpretation of otolith core data should be taken with some caution. Otolith core isotopic values could have been influenced by maternally derived material, a vertical transmission known to operate during yolk sac absorption, biasing the estimated temperature. This phenomenon has been well described in anadromous salmonids (Hegg, Kennedy, & Chittaro, 2018; Zazzo, Smith, Patterson, & Dufour, 2006; Zimmerman & Reeves, 2002). However, there are still large uncertainties as to whether maternally derived δ18O in freshwater could be influenced by the mother's thermal niche. Caution is also warranted as no otolith roasting was done before SIMS analyses, which would have suppressed organic matters present within the otolith structure. Intrinsic otolith organic material has been shown to potentially affect oxygen isotopic ratios (Matta et al., 2013), which would impact temperature estimations. However, observations of estimated temperature in the range of the species' preference provide confidence in our results.

Identifying a single thermal habitat in the same growing season may be obscured by seasonal variability in lake temperature. However, it should be noted that both sampled lakes are deep dimictic lakes that experience two turnover events (in spring and autumn), and both have a relatively stable thermal stratification during the summer. Hence, according to the assumed seasonal shifts in thermal stratification, from the time of the eggs' hatching (April) to the end of the growing season (October), the thermal zone with a temperature of *c.* 10°C could be variable in terms of its depth, but would
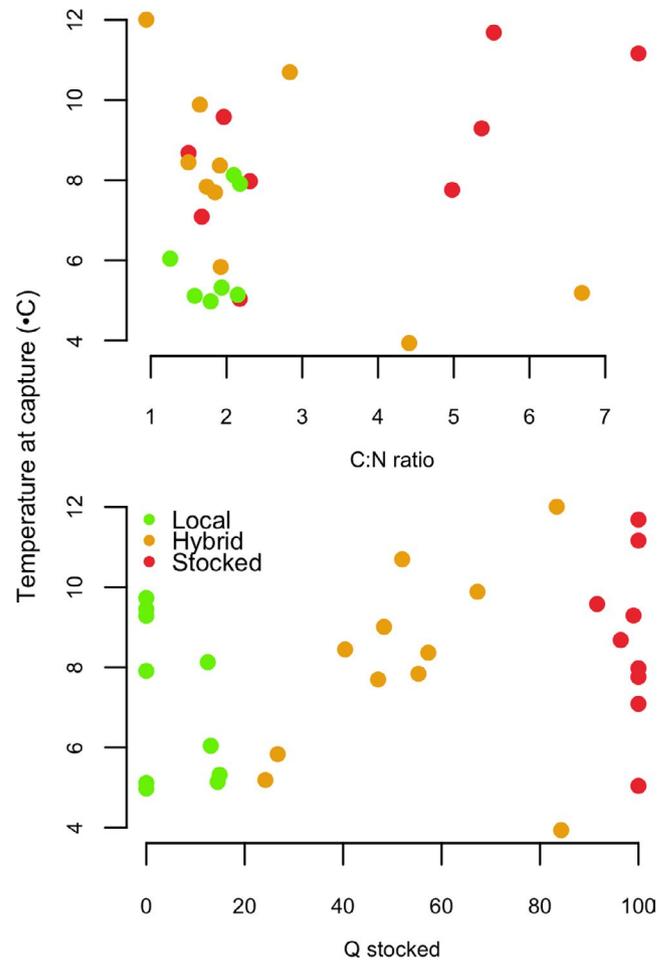
FIGURE 5 Estimated temperature (°C) at the last annuli of adult lake trout in relation to C:N ratio (top panel) and proportion of individual genotype related to source of stocking population ($Q_{stocked}$, bottom panel). Different colours in each graph represent a different genetic origin: local (green), hybrid (yellow), and stocked (red) [Colour figure can be viewed at wileyonlinelibrary.com]

be available throughout this period. In August–September, this thermal zone corresponds to a depth of 10 m (Lake Louisa) and 8 m (Lake McFee).

4.2 | The onset of an ontogenetic thermal migration

The first significant changes in thermal habitat use were observed beginning in the third growing season, and this eventually stabilised within an *adult thermal habitat* during the fourth season. Juvenile lake trout displayed an increasing use of colder habitats: 1.3 ± 0.6°C and 2.8 ± 0.6°C colder than the thermal habitats occupied at the time of hatching for the second and third seasons, respectively. We suggest that predation pressure and predator avoidance could be factor contributing to this phenomenon.

As many other top-predator fish, lake trout seek larger prey as they get older and grow (Pazzia, Trudel, Ridgway, & Rasmussen, 2002). This ontogenetic diet shift is hypothesised to be the sum of the increasing capacity for eating larger prey (gape limit) and the

need to achieve a greater energetic input (Mittelbach & Persson, 1998). Juvenile diet shifts in lake trout initiate normally c. 150–200 mm TL, a size covering the 1- to 4-year age group (Martin, 1951; Trippel & Beamish, 1989). Accordingly, our length-at-age back-calculations had an average TL of 166.2 mm (± 20.6 SD) and 207.7 mm (± 23.9 SD), in their third and fourth growing seasons, respectively. Adult planktivorous lake trout feed extensively on large zooplanktonic prey, benthic macro-invertebrates, and small littoral forage fish (Martin, 1966; Vander Zanden & Rasmussen, 1999).

The use of relatively warm, shallower habitats could be a juvenile life history tactic to avoid potential predation by older and larger conspecifics. Large lake trout living in a habitat lacking energy-rich pelagic prey items are prone to opportunistic feeding, including cannibalistic behaviour on smaller conspecifics (Morissette et al., 2018; Searle, Verde, & Belk, 2018). As they grow, juvenile lake trout will eventually exceed the upper gape limit of the majority of adult predator taxa in the lake. Then, occupying the same thermal habitat as larger adult lake trout becomes less risky. Accordingly, based on equations published by Keeley and Grant (2001), the average adult lake trout in our study (mean = 451 mm TL) are not likely to feed on fish prey larger than 109 mm TL. This observation is consistent with our results, whereby the first evidence of thermal transition occurred c. 100 mm TL. Therefore, when most of the juvenile fish settle into colder adult thermal habitat, their average total length (207 ± 24 mm TL) exceeds the size at which they are generally preyed upon—except for predation by lake trout that are >800 mm TL. In summary, relatively warm, shallow habitats offer reasonable protection from potential predation by adult conspecifics as most, but not all (next section), adult fish rarely used thermal habitat >14°C.

4.3 | Adult temperature use: Evidence for genetic × environment interactions?

Delta^{18}O values estimate a thermal niche for adult lake trout of 8.7 ± 2.7°C. This is consistent with the known adult lake trout thermal preference for 8°C (Bergstedt et al., 2003; Mackenzie-Grieve & Post, 2006). We observed that most fish rarely used thermal habitats >12°C and lake trout avoided temperatures >16°C entirely (Guzzo, Blanchfield, & Rennie, 2017), the assumed upper threshold of lake trout's thermal habitat. Lake trout from the stocked genetic group exhibited a more variable thermal niche, with some of the individuals experiencing long-term use of warmer water temperatures of 12–16°C. However, it is unlikely that genetics alone explain thermal habitat use, as only a fraction of stocked fish exhibited this warm water behaviour. Our results tend to suggest that individual variation of thermal habitat of adult lake trout can be linked to the combined interaction of genetic and dietary elements.

In this study, adult fish that consistently occupied a warmer thermal niche were similar in terms of three conditions; large size (>450 mm TL), high-fat content and genotype closely related to the source of stocking population. Exceptional growth within lakes

hosting planktivorous populations could be promoted by a cannibalistic diet, targeting juvenile trout when other pelagic forage fish were absent, for which genetic origin (i.e. piscivorous ecotype) is probably a predisposition factor (Morissette et al., 2018). A realised thermal habitat of 10.4°C for largest stocked fish is consistent with a thermal niche overlap with YOY lake trout (10.7 ± 2.9°C). The higher metabolic cost of long-term residency in warmer water could be mitigated by access to readily available, high-fat content prey. Feeding-motivated thermal excursions to warmer habitats are a common behaviour in lake trout populations (Guzzo et al., 2017; Morbey, Addison, Shuter, & Vascotto, 2006; Plumb & Blanchfield, 2009). High lipid content in lake trout, as well as being linked with high-fat content diet, may increase neutral buoyancy, which in turn may facilitate vertical migration and affect depth use (Eschmeyer & Phillips, 1965; Eshenroder et al., 1995). Finally, the relationship observed between thermal habitat and stocked origin admixture proportions ($Q_{stocked}$) in hybrid lake trout suggests that other factors, potentially genetically determined, may influence thermal habitat use. Assessment of those factors is, however, beyond the scope of this work.

To conclude, our study reiterates the value of otolith biogenic carbonate thermometry based on δ^{18}O from high-resolution analyses as a tool for assessing lifelong temperature histories. Estimated temperatures, for all life stages, were consistent with published boundaries for this species' thermal habitat, providing high confidence in the accuracy of this technique. Our results support the recent and growing realisation of a wider lake trout thermal niche than had been previously assumed (Challice, Milne, & Ridgway, 2019; Plumb & Blanchfield, 2009). Many authors emphasised the importance of among-population variability in strategies for using available thermal resources in salmonids (Bergstedt et al., 2012; Elrod et al., 1996; McDermid et al., 2013). Assuming that a strict narrow thermal habitat is probably a simplistic view of the life cycle for species, such as lake trout, that exhibit high inter-population variability (Muir, Hansen, Bronte, & Krueger, 2015). By being influenced by both heritable and potentially adaptive phenotypic traits specific to local lake trout morphotype and ecotype (Bergstedt et al., 2003; Eshenroder et al., 1995), we suggest that thermal habitat use (and/or its associated traits) could be a component of the species' local adaptation (Mackenzie-Grieve & Post, 2006; McDermid et al., 2010). Our results support this view; genetically and phenotypically divergent fish (e.g. stocked from an exogenous population) exhibit an atypical use of warmer, shallower water as compared to the indigenous population. A significant effect was also observed on hybrid individuals, suggesting a genetically based component. We stress that those observations are not a rigorous test of local adaptation, which requires explicit assessment of fitness. Nevertheless, our observations are of particular interest given that small boreal lakes harbour the vast majority of exploited and supplemented lake trout populations (Gunn & Pitblado, 2004). Admittedly, it remains to be determined whether our observations can be generalised to other populations. Improved understanding of the relationship between temperature use and intraspecific interactions will assist

wildlife managers in improving and refining management and conservation practices.

DATA AVAILABILITY STATEMENT

All raw data and R scripts are available on Dryad repository doi:10.5061/dryad.xgxd254cp

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SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section.