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2 **Deciphering lifelong thermal niche using high-resolution otolith $\delta^{18}\text{O}$**
3 **thermometry exemplified within supplemented lake trout (*Salvelinus***
4 ***namaycush*) populations**

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16

17 ABSTRACT

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

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

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

36 **4.** This study reiterates that high-resolution otolith $\delta^{18}\text{O}$ thermometry is a uniquely well-suited
37 approach for unravelling the multiple factors that influence lifelong temperature selection in fish.

38 Our results illustrate that the realised thermal niche is influenced by a genetic-environment
39 interaction.

40 1 Introduction

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

57 Quantification of the realised thermal niche of fishes remains technically challenging in natural
58 environments. Over decades, the use of acoustic telemetry and internal archival tags have become
59 the gold standard for *in situ* assessment of thermal niches (Bergstedt *et al.*, 2003; Plumb &
60 Blanchfield, 2009). However, fish capture and the surgical implantation of such tags can be time
61 consuming and is generally unsuitable for small/young fish (Elrod, Ogorman & Schneider, 1996;
62 Lucas & Baras, 2000). This limitation is also accompanied with the risk of low recapture rate of

63 tagged fish. Oxygen isotope ratios ($\delta^{18}\text{O}$) in biogenic carbonates (i.e., molluscan shells,
64 foraminifera) can provide a reliable alternative method for *a posteriori* temperature estimations in
65 fish (Urey *et al.*, 1951), when applied to otoliths material (Devereux, 1967; Darnaude *et al.*, 2014;
66 Patterson, Smith & Lohmann, 1993). Otolith formation is the result of the progressive precipitation
67 of biogenic aragonite (or vaterite in a smaller proportion) under conditions where the oxygen
68 isotope ratio will be near equilibrium with ambient water via a temperature-dependent hydrolysis
69 reaction (Campana, 1999; Høie, Otterlei & Folkvord, 2004). Quantifying whole-otolith $\delta^{18}\text{O}$
70 values provides temperature information integrated across a fish's entire lifetime, although it does
71 not provide information regarding distinct periods of an individual fish's life (Kalish, 1991). High-
72 resolution transects of oxygen isotope ratios can be obtained by extraction of otolith material using
73 micromilling, giving access to the isotopic ratios recorded within the daily pattern of otolith
74 precipitation as well as their extension to individual bands that represent months to years (Campana
75 & Thorrold, 2001; Pannella, 1971), providing a record of the lifelong *in situ* thermal niche across
76 all life stages (Hanson, Wurster & Todd, 2010; Wurster, Patterson & Cheatham, 1999).

77 Subsampling otolith bands by micromilling is done using fine bit to drill into targeted regions of
78 the otolith. The material removed is subsequently collected and analyzed using isotopic ratio mass
79 spectrometry. However, micromilling is limited by the size of the otolith and annuli widths, which
80 can prevent study of particular species or life stages. More recently, technical advances in ion beam
81 sampling technologies coupled with high-precision, high-sensitivity isotope ratio mass
82 spectrometry have opened the opportunity to quantifying oxygen stable isotope ratios using
83 individual point-based analyses of otolith (Matta *et al.*, 2013). In particular, secondary-ion mass
84 spectrometry (SIMS) offers highly precise stable isotope quantification. Both micromilling and
85 SIMS provide comparable $\delta^{18}\text{O}$ results, whereby the latter offers a higher spatial resolution

86 (Hanson, Wurster & Todd, 2010). Previous research showed that otolith thermometry is uniquely
87 suited for assessing the role of temperature as an ecological resource subject to competitive
88 interactions and ontogenetic variations (Patterson, Smith & Lohmann, 1993; Kalish, 1991).
89 Despite growing access to these analytical techniques, otolith thermometry has been seldom used
90 for thermal niche assessment of exploited fish species, especially at or before their sub-adult life
91 stages (Shirai *et al.*, 2018).

92 Predatory cold-water fish occupying deep temperate lakes are likely to exhibit competitive
93 interactions for thermal habitats, as the volume of suitable habitat can be limited during the summer
94 season (Christie & Regier, 1988; Murdoch & Power, 2013) when these lakes undergo thermal
95 stratification (Wetzel, 2001). Lake trout (*Salvelinus namaycush*), a cold-water stenotherm living in
96 deep oligotrophic lakes across North America, represents a very relevant fish model for exploring
97 the importance of thermal resources (Martin & Olver, 1980). This species has a restricted optimal
98 temperature range (8 – 12 °C, Coutant, 1987; Mackenzie-Grieve & Post, 2006; Plumb &
99 Blanchfield, 2009) and a low tolerance for dissolved oxygen less than 6–7 mg/L (Evans, 2007;
100 Evans, Casselman & Wilcox, 1991). These environmental preferences are likely to promote
101 competition for thermal resources, which can be influenced by the ecological particularities of a
102 studied population. There is a growing body of evidence that boreal and arctic salmonids show
103 intraspecific variation in performance among ecotypes and strains in relation to temperature
104 (Bergstedt *et al.*, 2012; Bergstedt *et al.*, 2003; McDermid *et al.*, 2013). Accordingly, thermal niche
105 use (based on otolith $\delta^{18}\text{O}$ thermometry) was shown to differ between European whitefish
106 (*Coregonus lavaretus*) morphs (Kahilainen *et al.*, 2014; Kelly, Amundsen & Power, 2015), a
107 difference mostly attributed to trophic niche use (benthic/pelagic preys). McDermid *et al.* (2013)
108 demonstrated that small-bodied lake trout ecotypes usually seek out lower temperatures than large-

109 bodied ecotypes. Intra-specific variation of phenotypic traits influencing depth (and temperature)
110 has also been documented. For instance, the ecotypic differences in depth and thermal preference
111 have been linked to fat content (Eshenroder *et al.*, 1995) and swim bladder gas retention, both
112 determining the neutral buoyancy depth. Selective breeding of these ecotypes showed that both
113 traits were heritable, with inter-ecotype hybrids displaying fat content and gas retention
114 intermediate to parental values (Eschmeyer & Phillips, 1965; Ihssen & Tait, 1974). Those
115 observations suggest that depth and thermal niche use are, at least partially, genetically determined
116 and could be modified by inter-ecotype hybridization (Bergstedt *et al.*, 2003).

117 Although the thermal niche of adult lake trout has been studied extensively, thermal habitat use of
118 young-of-year (YOY) and juveniles is not well known. Temperature selection in lake trout is
119 believed to be correlated with age, with younger fish preferring higher temperatures than adults
120 (Bergstedt *et al.*, 2003). Peck (1982) observed that lake trout YOY in Presque Isle Harbor, Lake
121 Huron, exhibit a prolonged residence in relatively shallow waters (< 8 m) near spawning sites as
122 long as water temperature does not exceed 15°C over an extended period. Likewise, young lake
123 trout in Great Bear Lake, NWT, Canada concentrate in shallow shoreline waters from the ages of
124 0–3 years (Miller & Kennedy, 1948). Great Bear Lake juveniles and adults were largely
125 overlapping in term of depth and thermal niche, probably linked to the absence of thermocline
126 and/or predation gradient (Chavarie *et al.*, 2019). Arctic charr (*Salvelinus alpinus*) and European
127 whitefish were also shown by otolith $\delta^{18}\text{O}$ thermometry to use warmer thermal niche, linked to use
128 of shallower littoral zone in their first years of life, (Kahilainen *et al.*, 2014; Murdoch & Power,
129 2013; Godiksen *et al.*, 2012). Bronte *et al.* (1995) showed that lake trout fry in western Lake
130 Superior are most abundant in shallow waters (10–15 m) in July, after which they migrate to deeper
131 waters as they grow, being most abundant at 40–49 m depth in October. In contrast, other studies

132 have suggested that YOY lake trout seek deeper and colder habitats shortly after yolk-sac
133 absorption (Martin, 1951; Deroche, 1969; Royce, 1951). Precise factors influencing YOY and
134 juveniles thermal habitats remain to be identified.

135 Despite the majority of lake trout populations existing in small lakes (Gunn & Pitblado, 2004), data
136 on thermal habitat use is mostly coming from larger systems. Inter-population particularities,
137 exemplified by ecotypes identification, could have significant impacts on thermal niche. Two
138 common ecotypes (e.g., planktivorous and piscivorous) are recognized in small boreal lakes, their
139 expression reflecting the combined influence of environmental conditions, food availability (e.g.
140 access to pelagic prey fish) and genetics (Bernatchez *et al.*, 2016; McDermid, Shuter & Lester,
141 2010). The planktivorous ecotype is characterized by a low growth rate, early maturation (~ 6
142 years) and a shorter maximum length of fish (< 450 mm) and is associated with lakes where large
143 pelagic preys (cold-water pelagic fish) are absent. Piscivorous ecotype, which is feeding on large
144 pelagic preys, exhibit high growth rates, late maturation (> 9 years) and a larger (> 600 mm)
145 maximum length (Bernatchez *et al.*, 2016; Houde & Scrosati, 2003). Few lakes host both ecotypes
146 in sympatry, the vast majority only hosting a single allopatric ecotype.

147 This study aimed to document the relative of role of different biotic (e.g. life stage, genetic origin,
148 trophic position) factors driving thermal habitat use by lake trout. We assessed lifelong thermal
149 niche use through high spatial resolution SIMS otolith oxygen stable isotope ($\delta^{18}\text{O}$) thermometry.
150 The resulting high-resolution temporal estimations of experienced temperatures are used to
151 describe the thermal habitat of YOY and juvenile fish and shed light on the uncertainties
152 surrounding early life thermal habitats of lake trout. Our study targeted fish having distinct genetic
153 origins (i.e., local, stocked or hybrid, see method section) from two allopatric lake trout populations
154 of small-bodied planktivorous ecotype. Both lakes had been previously stocked for angling

155 supplementation with source populations of a large-bodied piscivorous ecotype (Morissette *et al.*,
156 2018). By combining genotype-by-sequencing technologies and SIMS stable isotope
157 measurements, we tested whether fish ontogeny and genetics were significant factors influencing
158 temperature selection by lake trout. We hypothesised that stocked and hybrid trout would tend to
159 use warmer habitats than local fish due to their genetic background (piscivorous ecotype), which
160 is shown to be more related to warmer thermal niche (McDermid *et al.*, 2013).

161 **2 Methods**

162 **2.1 Study systems and supplementation stocking history**

163 Stocking has been used for lake trout population supplementation for over a century (Kerr &
164 Lasenby, 2001). In Quebec, Canada, 46% of lakes hosting lake trout angling-exploited population
165 have been stocked at least once since 1928 (Ministère du Développement Durable de
166 l'Environnement de la Faune et des Parcs, 2013). In most cases, captive-reared first-generation
167 progeny of wild breeders captured from allopatric lake trout populations of the piscivorous ecotype
168 were stocked, no matter the ecotype of recipient populations. Breeders were captured from known
169 spawning sites in source lakes for eggs and milt collection. Eggs were artificially fertilized in
170 hatcheries and progeny reared in captivity until stocking. Neither domesticated strains nor adult
171 fish have ever been used for the stocking of these lakes (Morissette *et al.*, 2018).

172 **2.2 Fish sampling and processing**

173 We sampled two lakes, one in 2012 (Lake Louisa; 45.769°N, 74.419°W) and 2013 (Lake McFee;
174 45.714°N, 75.623°W) using the same experimental fishing protocol. Both lakes are small (<
175 500 ha) and deep ($Z_{\max} > 56$ m), located in southern Quebec, Canada, and both display similar
176 summer thermal stratification (Figure 1). Both lakes host an allopatric population of a

177 planktivorous ecotype (small-bodied) lake trout and both lack large pelagic prey, such as pelagic
178 forage fish (i.e. *Coregonus spp.* or *Osmerus mordax*) or large invertebrates (*Mysids spp.*). These
179 two fish communities are comprised mostly of white sucker (*Catostomus commersonii*), yellow
180 perch (*Perca flavescens*), pumpkinseed (*Lepomis gibbosus*), rock bass (*Ambloplites rupestris*) and
181 small cyprinids (Figure 1). Both lakes were stocked multiple times from the same source population
182 (Blue Sea Lake, Quebec). The most recent stocking event in both lakes took place no more than 12
183 years before our sampling. These lakes were characterised previously as displaying a relatively
184 balanced proportion of purely local and stocked fish as well as their hybrids (Valiquette *et al.*,
185 2014; Morissette *et al.*, 2018).

186 We collected 75 fish per lake using the gill net method from a normalised lake trout sampling
187 protocol, in collaboration with the Québec *Ministère des Forêts, de la Faune et des Parcs* (Service
188 de la faune aquatique, 2011). For each fish, we measured total length (TL, mm) and mass (g) in the
189 field. The adipose fin was sectioned and stored in 95% ethanol in individual plastic vials
190 (Eppendorf, Mississauga, Ontario). For both lakes at their deepest point, we collected temperature
191 profiles at each 1-meter depth up to 20 meters and surface and thermocline water samples using
192 clean Niskin bottles. Water samples were transferred in the field to airtight, nitric acid-washed
193 (HNO_3 , trace metal grade) Nalgene bottles and conserved at room temperature prior to $\delta^{18}\text{O}$
194 analyses. In the laboratory both of the sagittal otoliths were extracted from the lake trout using
195 nitric acid-washed plastic forceps. Otoliths were washed with ultrapure water, dried and stored in
196 Eppendorf plastic vials before further processing.

197 **2.3 Genetic assignment of individual fish**

198 Each fish was assigned a genetic origin (i.e., local, stocked or hybrid) based on their single
199 nucleotide polymorphism (SNP) genotype using next-generation sequencing (genotype-by-
200 sequencing; GBS) and the software ADMIXTURE (Alexander, Novembre & Lange, 2009). Our
201 methodology is presented in detail in Morissette et al. (2018). Briefly, to assign the fish genotype
202 we used the individual admixture proportions (Q), defined as the proportion of subsample parts of
203 the genome most likely to be related to the stocking source (Blue Sea Lake) compared to the local
204 (wild) genotype. We classified fish as being stocked when $Q_{\text{stocking source}} + SE \geq 90\%$, local fish
205 when $Q_{\text{stocking source}} + SE \leq 10\%$, and hybrid when Q values fell between 10 and 90%. No further
206 distinction was attempted between hybrid classes because the number of fish analyzed here would
207 have been too small (5 hybrids per lake, see below) in each category to draw any rigorous
208 interpretations.

209 **2.4 Preparation of otoliths and ageing of fish**

210 The right sagittal otolith was embedded in a two-component epoxy resin (Miapoxy 100, Freeman,
211 OH, USA) and cut into 1-mm-thick traversal sections using a slow-speed diamond-bladed saw
212 (IsoMet saw; Buehler, IL, USA). After sectioning, we amplified the annuli contrasts by progressive
213 grinding and polishing with sandpaper (2000 grit Wetordry™, 3M™) and aluminium oxide lapping
214 film (1- and 5- μm lapping film, 3M™). Periodical observations of the grinding stage were realised
215 during polishing, which guided the grinding/polishing procedure. Digital images of each otolith
216 were captured using a digital camera (Leica DMC) coupled to a dissection microscope (Leica
217 MZ12) at a 30 – 60x magnification. Age counts and increment measurements (μm) were done from
218 the nucleus to the maximum ventral radius of the otolith (longest axis) following established
219 methods and criteria (Casselman & Gunn, 1992; Simard & Magnin, 1972) using ImageJ v 10.2

220 software (Abramoff, Magalhaes & Ram, 2004). Two independent readings (two readers) were done
221 and a third additional count/measurement if the first counts were not in agreement (~ 25% of
222 otoliths). Using estimated age of the fish and length at capture, we back-calculated length-at-age
223 (for complete method, see Morissette *et al.*, 2018), using the body-proportional hypothesis
224 (Francis, 1990). We selected a subset of 30 fish of age >10 years (mean = 13.7 ± 2.4 years) based
225 on the lake and genetic origin (2 lakes \times 3 genetic origin [local, hybrid or stocked] \times 5 fish = 30
226 total).

227 **2.5 SIMS otolith $\delta^{18}\text{O}$ values analytical methods**

228 Two SIMS mounts were required to accommodate all 30 otolith samples while ensuring that all
229 areas to be measured remained within an 8-mm radius from the center of the circular, 25.4-mm
230 diameter mount. Each mount contained 20 crystals of IAEA-603 and three (3) sub-millimetre
231 pieces of UWC-3 calcite reference materials (IAEA, 2016; Kozdon *et al.*, 2009). To minimise the
232 amount of epoxy in each block—thereby minimising the amount of sample outgassing within the
233 SIMS ultra-high vacuum system—polycarbonate discs were milled to provide individual wells for
234 each otolith as well as a separate well for receiving the two calcite reference materials. We verified
235 surface topography using white light interferometry, and we found the topography to be <5 microns
236 for all regions of interest.

237 The samples were cleaned in an ultrasonic bath of high-purity ethanol before being carbon sputter-
238 coated for subsequent scanning electron microscopy (SEM) imaging. We produced both secondary
239 electron and backscattered electron images for each otolith to obtain information regarding the
240 locations of cracks within the material and also to provide clear identification of the main growth
241 axis of a given otolith. After completing the initial SEM imaging, an additional 35-nm thick, high-

242 purity gold film was sputter-deposited directly on top of the carbon coating. Both mounts were
243 then imaged fully using the stitching software of a Nikon Eclipse motorised optical microscope.
244 These images were then loaded into the SIMS point logger software.

245 We used the Cameca 1280-HR secondary-ion mass spectrometer of the German Research Centre
246 for Geosciences (Potsdam) to produce $\delta^{18}\text{O}$ profiles. SIMS $\delta^{18}\text{O}$ analyses employed a *ca.* 2 nA
247 mass filter $^{133}\text{Cs}^+$ beam having a Gaussian density distribution. The beam was focused to a *ca.*
248 5 μm diameter on the polished sample surface. The total impact energy of the Cs^+ ions was 20 keV.
249 Each analysis was preceded by $25 \times 25 \mu\text{m}$ rastered pre-sputter for 80 s. Charge compensation was
250 achieved using low-energy, normal incidence electron flooding. To suppress within-run drift of the
251 isotope ratio, a $15 \times 15 \mu\text{m}$ raster was used during data collection, thus ensuring a flat-bottom crater
252 geometry. The dynamic transfer option of the secondary column ion optics was used to compensate
253 for the rastering of the primary beam during data collection. Analyses were performed as point
254 profiles from the otolith core and following the longest axis with stepping distances of *ca.* 100 μm
255 with both reference materials being analysed (typically after every 10th acquisition); the sequence
256 of data acquisition was not randomised.

257 Secondary ions were accelerated by a -10 kV potential applied to the non-magnetic, stainless
258 sample holder. Before the start of data acquisition, the SIMS conducted automated centering
259 routines for the field aperture in both the X and Y directions and the contrast aperture in the X
260 direction only. The instrument had a field of view of $80 \times 80 \mu\text{m}$, in conjunction with a 40 V energy
261 band pass. The mass spectrometer was operated in a static multi-collection mode with the $^{16}\text{O}^-$
262 being collected in the L2' Faraday cup and the $^{18}\text{O}^-$ signal being collected in the H2' cup; the
263 amplifier system used thermally stabilised $10^{10} \Omega$ and $10^{11} \Omega$ amplifiers. Magnetic field drift of the
264 mass spectrometer was eliminated effectively by the use of an NMR-controlled feedback loop. The

265 mass resolution of the instrument was determined to be $M/dM \approx 1,800$, which is effectively the full
266 transmission of the 1280-HR and is fully sufficient to eliminate both the $^{16}\text{O}^1\text{H}_2$ and the $^{16}\text{O}^2\text{H}$
267 isobaric interferences from the ^{18}O mass station. A single analysis consisted of 20 integrations of
268 4 s each, resulting in a data collection time of 80 s per analysis (equivalent to a total of ~ 3 min per
269 point when including the sample moving, pre-sputtering and automatic centering routines). This
270 analytical design resulted in a count rate of *ca.* 2.8×10^9 ion/sec on the ^{16}O mass station. A total of
271 375 $\delta^{18}\text{O}$ analyses were conducted on the 30 otoliths, along with 46 determinations on both the
272 IAEA-603 and UWC-3 calcite reference materials. All analyses were conducted over three days
273 and required a total of 31 hours of data acquisition. A 3sd filter was applied to all data with respect
274 to the 20 individual integrations conducted during the given analytical run.

275 To quantify the instrumental mass fractionation and to monitor the possible occurrence of a time-
276 dependent drift during our runs over the hour-long period, we used two calibration materials. We
277 detected a drift equivalent to 0.098‰ per hour toward higher $^{18}\text{O}/^{16}\text{O}$ values as defined by $n = 9$
278 determinations of the UWCV-3 calcite. This drift occurred solely on the third day of data
279 acquisition. Therefore, we applied a corresponding linear drift correction to all data collected on
280 this specific day. To calibrate the instrumental mass fractionation of our SIMS instrument on each
281 separate day, we used the value of $\delta^{18}\text{O}_{\text{VPDB}} = -2.37$ for the IAEA-603 (IAEA, 2016), and we used
282 the $\delta^{18}\text{O}_{\text{VSMOW}} = 12.49$ for the UWC-3 (Kozdon *et al.*, 2009). For converting between the two
283 oxygen isotope scales, we used the equation on page 440 of Brand *et al.* (2014). All analytical
284 results are reported in standard δ notation (‰) relative to Vienna Standard Mean Ocean Water
285 (VSMOW).

286 2.6 Quantification of the water $\delta^{18}\text{O}$ isotopes

287 The $\delta^{18}\text{O}$ values of surface and thermocline water samples were analysed at the Ján Veizer Stable
288 Isotope Laboratory (University of Ottawa, Canada). The $\delta^{18}\text{O}_{\text{water}}$ values were determined using a
289 Finnigan MAT Delta plus XP + Gasbench,; a precise water volume (0.2 mL) was pipetted into an
290 Exetainer vial. The vials were flushed and filled off-line with a gas mixture of 2% CO_2 in helium.
291 The flushed vials were left at room temperature for a minimum of 24 h. The CO_2 gas was analysed
292 automatically under continuous flow during this period. The results were normalised to Vienna
293 Standard Mean Ocean Water (VSMOW) using three calibrated internal standards that spanned
294 most of the natural range. The routine precision (2s) of the analysis was $\pm 0.15\text{‰}$. Lake-specific
295 $\delta^{18}\text{O}_{\text{water}}$ values were assumed to represent the average of the surface and thermocline results.

296 2.7 Calculation of experienced temperatures

297 Interspecific difference in life history and physiological mechanisms could influence oxygen
298 isotope fractionation in otoliths (Høie, Otterlei & Folkvord, 2004; Weidman & Millner, 2000).
299 Hence, many authors advise caution on the use of universal (e.g., multi-specific) temperature-
300 mediated $\delta^{18}\text{O}$ fractionation equation (Hanson, Wurster & Todd, 2010; Rowell *et al.*, 2005).
301 Hence, species-specific fractionation equation (or developed for closely related species) should be
302 preferred (Murdoch & Power, 2013; Storm-Suke *et al.*, 2007). Accordingly, we estimated
303 temperatures derived from the otoliths $\delta^{18}\text{O}$ using an oxygen isotope fractionation equation
304 developed for *Salvelinus* species, in a similar geographic distribution that of our study (Storm-Suke
305 *et al.*, 2007); this equation has been shown to produce reliable temperature estimation for charr
306 species. Lake-specific $\delta^{18}\text{O}_{\text{water}}$ values were used to calculate experienced temperature ($T^\circ\text{C}$). The
307 equation is expressed as the difference between otolith ($\delta^{18}\text{O}_{\text{otolith}}$) and water ($\delta^{18}\text{O}_{\text{water}}$) values:

308
$$\delta^{18}\text{O}_{\text{otolith}} - \delta^{18}\text{O}_{\text{water}} = 32.90 - 0.23 * \text{T}^{\circ}\text{C}$$

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

316 **2.8 Statistical analyses**

317 We modelled the effects of age and genetic origins on the occupied thermal habitats (response
318 variable temperature) of lake trout YOY using a linear mixed-effect model. Linear mixed model
319 was fitted using the function *lme* in the R package *nlme* (Pinheiro *et al.*, 2019). The factors of the
320 model were genetic origin (fixed, two levels: local and hybrid) and age (fixed, two levels: hatching
321 and end of first growing season). Individual fish nested within a lake were treated in the model as
322 a random slope to allow for the experimental repeated-measure design and individual variability.
323 We did not include an estimated temperature of the two first growing seasons for stocked fish in
324 our evaluation. Stocked fish $\delta^{18}\text{O}_{\text{otolith}}$ values were representative of the hatchery habitat (mean =
325 $19.07 \pm 1.22\text{‰}_{\text{VSMOW}}$) rather than that of the sampled lakes (mean = $22.89 \pm 0.88\text{‰}_{\text{VSMOW}}$);
326 therefore, the estimated temperatures were not biologically relevant ($> 20^{\circ}\text{C}$, max = 38.4°C). This
327 difference was only observed in the first two growth seasons, which is in agreement with the age
328 at stocking of hatchery fish (1+).

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

336 To test for the biotic factors influencing the temperature used by adults, we modeled the effects of
337 ecological individual variables on temperature at capture (estimated temperature at the last annuli).
338 Biotic variables included in the model were total length (TL, mm), percentage of fish population
339 attributed to stocked genotype (Q_{stocked}), C:N ratio (a measure of fat content), trophic position (TP)
340 and Δ_{Pelagic} (contribution of pelagic prey to diet); C:N, TP and Δ_{Pelagic} were estimated from stable
341 isotope ($\delta^{13}\text{C}$ and $\delta^{15}\text{N}$) from white muscle collected on the same fish (see Morissette et al. (2019)
342 for complete methodology). We tested the effects of biotic variables (TL, Q_{stocked} , C:N, TP and
343 Δ_{Pelagic}) on temperature at capture using a similar linear mixed-effect model with lake as a random
344 factor.

345 **3 Results**

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

351 *al.*, 2018). These stocked fish had a body length more typical of lake trout of the piscivorous
352 ecotype (i.e., their genetic origin). Otolith radius (μm) were found to correlate linearly with fish
353 TL ($\text{oto}_{\text{radius}} = 2.4 * \text{TL} + 398.4$, $p < 0.05$, $R^2 = 0.76$), where the largest fish have an otolith radius
354 $\sim 500 \mu\text{m}$ longer than smaller fish.

355 **3.1 SIMS otolith $\delta^{18}\text{O}$**

356 For the three days of data collection, we recorded 1s repeatability for the IAEA-603 material of \pm
357 0.30‰ ($n = 16$), $\pm 0.94\text{‰}$ ($n = 22$), and $\pm 0.30\text{‰}$ ($n = 8$), respectively. For the concurrent UWC-3
358 calcite, we recorded 1s repeatability for the three days of data acquisition of $\pm 0.11\text{‰}$ ($n = 15$), \pm
359 0.16‰ ($n = 23$), and $\pm 0.17\text{‰}$ ($n = 9$). We found that the IAEA-603 calcite contained significant
360 isotopic heterogeneity at the sub-nanogram sample mass provided by our SIMS instrument. This
361 is consistent with the results reported by Nishida and Ishimura (2017) who observed variations in
362 the isotopic compositions of IAEA-603 at the single-grain scale.

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

371 Based on the above observations, we based our otolith data reduction solely on the results from the
372 UWC-3 calibration material. The observed repeatability of UWC-3 indicated that the overall

373 uncertainty on the individual otolith results was less than $\pm 0.2\%$ (1s). Calculating the mean ^{18}O
374 $/^{16}\text{O}$ ratios from the multiple grains analysed from IAEA-603, we obtained $\delta^{18}\text{O}_{\text{VPDB}}$ values of -
375 2.29‰, -2.86‰ and -2.36‰ for each of the three analytical sessions, respectively. These results
376 are in reasonable agreement with the assigned value for IAEA-603 of $\delta^{18}\text{O}_{\text{VPDB}} = -2.37 \pm 0.04\%$
377 (1s) (IAEA, 2016). We therefore believe that our absolute results are at least accurate to 0.5‰,
378 whereas the relative difference between any two analytical results is reliable at the 0.3‰ (1s) level
379 or better. Hence, these results highlight the need for caution regarding the possibility of calibration-
380 related issues when working at a high resolution and with such a small sample mass.

381 We measured an average of 12 SIMS analyses per otolith (stepping distance 99.6 $\mu\text{m}/\text{step}$)
382 distributed evenly over the entire length of a given otolith. No analysis failed to provide a result.
383 Two spots were systematically done within the first annuli (first growing season) for every fish.
384 Furthermore, a single point of analysis for the subsequent growing seasons was successful until the
385 sixth growing season, where points of analysis had an above-annual frequency since annuli were
386 narrower than our $\sim 100 \mu\text{m}$ step distance. As expected, the temporal resolution provided by this
387 methodology is significantly higher than that achieved by micromilling (e.g. 76 – 450 $\mu\text{m}/\text{spot}$;
388 Hanson, Wurster & Todd, 2010). The median observed otolith $\delta^{18}\text{O}_{\text{VPDB}}$ value was -7.60‰
389 ($\delta^{18}\text{O}_{\text{VSMOW}} = 23.08\%$) with values ranging from -13.45‰ to -5.76‰ ($\delta^{18}\text{O}_{\text{VSMOW}} = 16.74\%$ to
390 24.98‰). There was no significant difference between surface and thermocline water $\delta^{18}\text{O}_{\text{VSMOW}}$
391 values, but a significant difference was observed between our two lakes (Lake Louisa = $-8.05 \pm$
392 0.04% , Lake McFee = $-7.32 \pm 0.26\%$).

393 3.2 Thermal habitats of young-of-the-year and juvenile lake trout

394 Yearlings from both lakes occupied a wide spectrum of thermal habitats, ranging from 5.82°C (5th
395 percentile) to 15.52°C (95th percentile). The linear mixed-effects model revealed no significant
396 effect of age (hatching versus the end of the first growth season) or genetic origin (local and hybrid)
397 on the estimated used temperatures (Table 2) in the first year of life. The average estimated
398 temperature at hatching was $10.88 \pm 2.95^\circ\text{C}$ (standard error, SE) and yearlings lived in a relatively
399 constant thermal habitat during the entire first growing season. However, we observed pronounced
400 inter-individual variability in terms of thermal habitat being occupied. Temperature at hatching
401 was a significant predictor of the magnitude of temperature change during the first growing season
402 ($\Delta T = -0.87 * T_{\text{hatching}} + 9.45, p = 0.002, R^2_{\text{adj}} = 0.40$, Figure 2). Lake trout hatching at 10.9°C were
403 the least likely to initiate a change of temperature; other individuals born in warmer or colder waters
404 migrated to reach a thermal habitat closer to the observed temperature preference (10.9°C).

405 The temperature range occupied by juvenile lake trout was greater than that occupied by either
406 adult or YOY fish, ranging between 3.45°C and 18.60°C , which is within the range of observed
407 temperatures based on our determined depth-temperature profiles (Figure 1). The temperature
408 range occupied by juveniles was influenced significantly by age; there was a significant difference
409 between occupied temperatures after the third growing season (Table 3). Our model showed a
410 significant ontogenetic effect on thermal habitats with older (> 3 years old) lake trout inhabiting
411 colder temperatures (3°C colder) than younger juvenile and YOY (Figure 3). There was no
412 significant effect of genetic origin on the thermal habitat being used. Back-calculated length-at-age
413 from individual Von Bertalanffy models showed that movements to colder water was initiated at a
414 TL of 100 mm and completed at *ca.* 250 mm TL (Figure S1).

415 3.3 Adult thermal habitats

416 The estimated habitat temperatures for adult fish ranged from 2.61°C to 16.95°C (mean = 8.32 ±
417 2.90°C). These values are all within the assumed species' boundaries of thermal habitat (Plumb &
418 Blanchfield, 2009). Modelling of adults' thermal habitats showed a significant effect of genetic
419 origin; stocked fish were using significantly warmer waters than local and hybrid fish (Table 4).
420 However, lifelong experienced temperature at the adult life stage of stocked lake trout showed
421 important between- and within-individual variability (Figure 4). At some point during their lives
422 several fish occupied warmer habitats (average = 10.39°C) than the remainder of the stocked
423 (average = 8.33°C), local and hybrid lake trout (average = 7.76°C). Two stocked fish from Lake
424 McFee experienced a clear shift in their thermal niche at *ca.* 400 mm TL (Figure 4, Figure S2), a
425 consistent behaviour exhibited for subsequent years.

426 Model of temperature at capture showed that Q_{stocked} and C:N (fat content) both had a significant
427 positive relationship on temperature at capture (Table 5). According to this model, both fat content
428 and Q_{stocked} were factors promoting use of warmer temperature (Figure 5). Interestingly, hybrid fish
429 exhibited the use of thermal habitat intermediate to that of their parents, the hybrids more closely
430 related to stocked genetic origin (high Q_{stocked}) displaying use of warmer temperature,
431 comparatively to hybrid related to the local genotype (low Q_{stocked}), using colder water temperatures
432 at the time of capture (Figure 5, bottom panel).

433

434

435

436 **4 Discussion**

437 High-resolution analyses of oxygen stable isotopes provided life-long estimation of lake trout
438 thermal habitat. This study showed a marked difference between YOY/juvenile and adult thermal
439 habitat. Later in life, inter-individual difference in thermal habitat emerged, potentially linked to
440 genetic origin and related phenotypic traits. It has long been presumed that lake trout possess a
441 very narrow thermal optimum, a perception largely influenced by Christie and Regier (1988) who
442 showed a strong positive correlation between lake trout angling yield and the volume of lake that
443 encompassed the 8–12°C thermal habitat. Following this pioneering work, the assessment of lake
444 trout thermal habitat became of increasing interest for wildlife management and ecological theory.
445 Thus, a variety of techniques were deployed to quantify the temperature range of the species.
446 Notably, intensive gillnet sampling surveys (Elrod, Ogorman & Schneider, 1996; Elrod &
447 Schneider, 1987), bottom and otter trawls (Peck, 1982), archival tags (Bergstedt *et al.*, 2012;
448 Bergstedt *et al.*, 2016), acoustic and radio telemetry (Mackenzie-Grieve & Post, 2006; Plumb &
449 Blanchfield, 2009) and remotely operated vehicles (Davis, Carl & Evans, 1997) were used to
450 document trout habitat use in terms of depth and temperature. All of these methods proved to be
451 useful, but they remained time- and resource-intensive and were limited by the size of fish, biased
452 toward fish of larger size. From those studies, few studies reported on the thermal habitat of YOY
453 and juvenile lake trout in natural settings (Bronte *et al.*, 1995; Miller & Kennedy, 1948; Peck,
454 1982). However, Landsman *et al.* (2017) showed that otolith $\delta^{18}\text{O}$ thermometry could provide an
455 estimate of lake trout natal thermal habitat (lake Michigan) which were consistent with field
456 observations (Bronte *et al.*, 1995). Accordingly, our study is reiterating that $\delta^{18}\text{O}$ thermometry
457 based on the high-resolution SIMS analysis of otoliths is a powerful method for assessing the
458 thermal niche of any size class of fish.

459 **4.1 Assessment of the young-of-the-year thermal habitats**

460 Yearlings consistently occupy waters having an average temperature of $10.7 \pm 3.0^{\circ}\text{C}$. Our results
461 match the preferred temperatures of lake trout YOY observed under controlled laboratory settings:
462 11.7°C (McCauley & Tait, 1970) and $9.0\text{--}11.5^{\circ}\text{C}$ (Peterson, Sutterlin & Metcalfe, 1979). During
463 their first growth season, individual lake trout displayed a high variability in the occupied
464 temperature, but they tended to seek out a specific range of temperatures, initiating movements to
465 avoid temperatures $>14^{\circ}\text{C}$ and $<8^{\circ}\text{C}$, as suggested in the literature (Bronte *et al.*, 1995; Peck,
466 1982). This temperature range corresponded to the upper metalimnion (depth = 7.5 m) in the
467 sampled lakes during the period of summer thermal stratification (Figure 1). As such, our results
468 support the hypothesis of Peck (1982) of extended residency in shallow (<8 m) waters.

469 However, the inter-individual variability we observed provides insight into the lack of consensus
470 in the literature around thermal habitats during the early life stages of lake trout. Contrasting YOY
471 behaviour could be linked to the different thermal conditions prevailing in lakes inhabited by lake
472 trout, influencing early life tactics. Here, several individuals made marked migrations between
473 thermal habitats ($>6^{\circ}\text{C}$) during their first growing season. Yearlings tended to “escape” stressful
474 thermal situations, whereas those hatching in warmer sites modified their position to reach colder
475 habitats closer to their thermal optimum (and vice-versa). This is consistent with the results
476 observed for populations inhabiting lakes experiencing rapid warming in the spring (i.e., southern
477 or small lakes) in which YOY exhibit a rapid migration to lakes’ deepest parts (Martin, 1951;
478 Royce, 1951). Accordingly, littoral residency has been observed in northern (or large) lakes were
479 littoral zones, for most of the growing season, displayed water temperatures less than 16°C , such
480 as in Great Bear Lake which does not experience any summer stratification (Miller & Kennedy,
481 1948; Johnson, 1975) and Lake Superior (Bronte *et al.*, 1995; Peck, 1982).

482 Estimated temperatures from otolith cores show that local fish hatched under more variable
483 temperatures compared to hybrids, suggesting a broader use of spawning sites for local fish
484 compared to hybrids (Figure 2). Hence, while wild lake trout exhibit a certain degree of spawning
485 site fidelity (Binder *et al.*, 2015), hatchery-reared fish may not have the ability to recognize high-
486 quality spawning sites (Bronte *et al.*, 2007) or may even reproduce at a different time (Krueger,
487 Swanson & Selgeby, 1986). This hypothesis remains to be tested. Admittedly, our interpretation of
488 otolith core data should be taken with caution. Indeed, material accumulated in otolith core could
489 be linked to mother-specific isotopic values, biasing the estimated temperature. However, there are
490 still large uncertainties in maternally derived isotopes in otolith and no strong evidence exist in the
491 presence of mother's $\delta^{18}\text{O}$ signature (Elsdon *et al.*, 2008; Hegg, Kennedy & Chittaro, 2018).
492 Caution is also warranted as no otoliths roasting was done before SIMS analyses, which would
493 have suppressed organic matters present within the otolith structure. Intrinsic otolith organic
494 material has been shown to potentially affect oxygen isotopic ratios (Matta *et al.*, 2013), which
495 would impact temperature estimations. Otolith primordium has previously been identified as
496 organic fraction-rich zone (Jolivet *et al.*, 2008), which can introduce additional variability of
497 temperature estimation. However, observations of estimated temperature in the range of the
498 species' preference provide us confidence in our results.

499 Identifying a single thermal habitat in the same growing season may be obscured by seasonal
500 variability in lake temperature. However, it should be noted that both sampled lakes are deep
501 dimictic lakes that experience two turnover events (in spring and fall), and both have a relatively
502 stable thermal stratification during the summer. Hence, according to the assumed seasonal shifts in
503 thermal stratification, from the time of the eggs' hatching (April) to the end of the growing season
504 (October), the thermal zone with a temperature of *ca.* 10°C could be variable in term of its depth,

505 but would available throughout this period, (Wetzel, 2001). In August-September, this thermal
506 zone corresponds to a depth of 10 m (Lake Louisa) and 8.5 m (Lake McFee) (Figure 1). Our data
507 could not assess the YOY use of horizontal microhabitats during the first growth season. However,
508 they show clearly that these YOY used a relatively homogeneous thermal habitat, which was
509 consistently warmer than that used by juvenile and adult conspecifics.

510 **4.2 The onset of an ontogenetic thermal migration**

511 The first significant changes in thermal habitat use were observed beginning in the third growing
512 season, and this eventually stabilised within an “adult thermal habitat” during the fourth season.
513 Juvenile lake trout displayed an increasing use of colder habitats: $1.5 \pm 0.7^{\circ}\text{C}$ and $3.2 \pm 0.7^{\circ}\text{C}$
514 colder than the thermal habitats occupied at the time of hatching for the third and fourth seasons,
515 respectively. We suggest that predation pressure could be a factor contributing to this phenomenon.

516 As many other top-predator fish, lake trout seek larger prey as they get older and grow (Martin,
517 1970; Pazzia *et al.*, 2002; Sherwood *et al.*, 2002). This ontogenetic diet shift is hypothesised to
518 be the sum of the increasing capacity for eating larger prey (gape limit) and the need to achieve a
519 greater energetic input (Mittelbach & Persson, 1998; Pazzia *et al.*, 2002). Juvenile diet shifts in
520 lake trout initiate normally *ca.* 150–200 mm TL, a size covering the 1- to 4-year age group (Martin,
521 1951; Trippel & Beamish, 1989). Accordingly, our length-at-age back-calculations had an average
522 TL of 166.2 mm (± 20.6 SD) and 207.7 mm (± 23.9 SD), in their third and fourth growing seasons,
523 respectively. Adult planktivorous lake trout feed extensively on large zooplanktonic prey, benthic
524 macro-invertebrates and small littoral forage fish (Martin, 1966; Vander Zanden & Rasmussen,
525 1999).

526 The use of relatively warm, shallower habitats could be a juvenile life history tactic to avoid
527 potential predation by older and larger conspecifics. Large lake trout living in a habitat lacking
528 energy-rich pelagic prey items are prone to opportunistic feeding, including cannibalistic behaviour
529 on smaller conspecifics (Morissette *et al.*, 2018; Searle, Verde & Belk, 2018). As they grow,
530 juvenile lake trout will eventually exceed the upper gape limit of the majority of adult predator taxa
531 in the lake. Then, occupying the same thermal habitat as larger adult lake trout becomes less risky.
532 Accordingly, based on equations published by Keeley & Grant (2001), the average adult lake trout
533 in our study (mean = 451 mm TL) are not likely to feed on fish prey larger than 109 mm TL. This
534 observation is consistent with our results, whereby the first evidence of thermal transition occurred
535 *ca.* 100 mm TL. Therefore, when most of the juvenile fish settle into colder adult thermal habitat,
536 their average total length (207 ± 24 mm TL) exceeds the size at which they are generally preyed
537 upon—except for predation by lake trout that are > 800 mm TL. In summary, relatively warm,
538 shallow habitats offer reasonable protection from potential predation by adult conspecifics as most,
539 but not all (next section), adult fish rarely used thermal habitat $> 10^{\circ}\text{C}$ (Figure 4).

540 **4.3 Adult temperature use: evidence for genetic \times environment interactions?**

541 The obtained $\delta^{18}\text{O}$ values estimate a thermal niche for adult lake trout of $8.5 \pm 3.3^{\circ}\text{C}$. This is
542 consistent with the known adult lake trout thermal preference for 8°C (Bergstedt *et al.*, 2003;
543 Mackenzie-Grieve & Post, 2006). We observed that most fish rarely used thermal habitats $> 12^{\circ}\text{C}$,
544 the suggested upper limit of lake trout thermal preference (Plumb & Blanchfield, 2009), and lake
545 trout avoided temperatures $> 16^{\circ}\text{C}$ entirely (Guzzo, Blanchfield & Rennie, 2017), the assumed
546 upper threshold of lake trout's thermal habitat (Guzzo & Blanchfield, 2016; Cline, Bennington &
547 Kitchell, 2013; Plumb & Blanchfield, 2009). Lake trout from the stocked genetic group exhibited
548 a more variable thermal niche, with some of the individuals experiencing long-term use of warmer

549 water temperatures of 12–16°C. However, it is unlikely that genetics alone explain thermal habitat
550 use, as only a fraction of stocked fish exhibited this “warm water” behaviour. Our results tend to
551 suggest that individual variation of thermal habitat of adult lake trout can be linked to the combined
552 interaction of genetic and dietary elements.

553 In this study, those adult fish that consistently occupied a warmer thermal niche (12°C) were similar
554 in terms of three conditions; a large size (> 450 mm TL), high fat content (C:N ratio) and genotype
555 closely related to the source of stocking population (Figure 5). Exceptional growth within lakes
556 hosting planktivorous populations could be promoted by a cannibalistic diet, targeting juvenile
557 trout when other pelagic forage fish were absent, for which genetic origin (i.e. piscivorous ecotype)
558 is probably a predisposition factor (Morissette *et al.*, 2018). A realised thermal habitat of $10.3 \pm$
559 2.4°C for largest stocked fish is consistent with a thermal niche overlap with YOY lake trout (10.7
560 $\pm 2.9^\circ\text{C}$). The higher metabolic cost of long-term residency in warmer water could be mitigated by
561 access to readily available, high-fat content prey. Feeding-motivated thermal excursions to warmer
562 habitats are a common behaviour in some lake trout populations (Plumb & Blanchfield, 2009;
563 Sellers *et al.*, 1998; Guzzo, Blanchfield & Rennie, 2017; Morbey *et al.*, 2006). High lipid content
564 in lake trout, as well as being linked with high-fat content diet, may increase neutral buoyancy
565 which in turn may facilitate vertical migration and affect depth use (Eschmeyer & Phillips, 1965;
566 Eshenroder *et al.*, 1995). McDermid *et al.* (2013) showed that populations of large-bodied lake
567 trout ecotypes were more tolerant to warm water and exhibited higher within-population variability
568 in terms of thermal habitat. Tolerance of warmer environmental niches could therefore provide
569 additional opportunities for larger stocked fish (Pépin, Goyer & Magnan, 2015), giving access to
570 juvenile lake trout resources and other fish species present in the lake. Finally, the relationship
571 observed between thermal habitat and stocked origin admixture proportions (Q_{stocked}) in hybrid lake

572 trout (Figure 5) suggests that other factors, potentially genetically-determined, may influence
573 thermal habitat use. Assessment of those factors is, however, beyond the scope of this work.

574 To conclude, our study reiterates the value of otolith biogenic carbonate thermometry based on
575 $\delta^{18}\text{O}$ from high-resolution SIMS analyses as a tool for assessing lifelong temperature histories.
576 This methodology can greatly increase the resolution and number of spots analyses by otolith
577 compared to both whole-otolith analyses and micromilling. Estimated temperatures, for all life
578 stages, were consistent with published boundaries for this species' thermal habitat, providing high
579 confidence in the accuracy of this technique. Our results support the recent and growing realization
580 of a wider lake trout thermal niche than had been previously assumed (Challice, Milne & Ridgway,
581 2019; Plumb & Blanchfield, 2009). Many authors emphasised the importance of among-population
582 variability in strategies for using available thermal resources in salmonids (Elrod, Ogorman &
583 Schneider, 1996; McDermid *et al.*, 2013; Bergstedt *et al.*, 2012). Assuming a strict narrow thermal
584 habitat is probably a simplistic view of the life cycle for species, such as lake trout, that exhibit
585 high inter-population variability (Muir *et al.*, 2015). By being influenced by both heritable and
586 potentially adaptive phenotypic traits specific to local lake trout morphotype and ecotype
587 (Bergstedt *et al.*, 2003; Eshenroder *et al.*, 1995), we suggest that thermal habitat use (and/or its
588 associated traits) could be a component of the species' local adaptation (Mackenzie-Grieve & Post,
589 2006; McDermid, Shuter & Lester, 2010). Our results support this view; genetically and
590 phenotypically divergent fish (e.g. stocked from an exogenous population) exhibit an atypical use
591 of warmer, shallower water as compared to the indigenous population. A significant effect was also
592 observed on hybrid individuals, suggesting a genetically-based component. We stress that those
593 observations are not a rigorous test of local adaptation, which require explicit assessment of fitness.
594 Nevertheless, our observations are of particular interest given that small boreal lakes harbour the

595 vast majority of exploited and supplemented lake trout populations (Gunn & Pitblado, 2004).
596 Admittedly, it remains to be determined whether our observations can be generalised to other
597 populations. Improved understanding of the relationship between temperature use and intraspecific
598 interactions will assist wildlife managers in improving and refining management and conservation
599 practices.

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615 **Data availability**

616 All raw data and R scripts are available on an online Dryad repository (*link will be provided upon*
617 *acceptance*)

618

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896 TABLES

897 **Table 1.** Average total length (mm) and age (year) and standard deviation (SD) for sampled lake
 898 trout. Lake trout are classified according to their genetic origins within lakes Louisa and McFee

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

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900

901 **Table 2.** Linear mixed-effect models of the response variables for the occupied temperature of the
 902 first growing season. Columns present the estimated differences (positive or negative) of group
 903 response variables with the model intercept, standard error (SE), degrees of freedom (df) and *p*-
 904 values of the factor. *p*-values in bold indicate significant differences ($p < 0.05$). The random parts
 905 show the number of tested groups and experimental units (*N*grp) and total observations

Coefficient	Response			
	Occupied temperature (°C) during the first growing season			
	Estimate	SE	df	<i>p</i> -value
Fixed parts				
Intercept	10.95	0.95	20	<0.001
Genetic origin (local)	-0.36	1.36	16	0.80
Age	0.14	1.93	20	0.94
Interaction (origin × age)	-0.18	2.65	20	0.95
Random parts				
<i>N</i> grp	15 fish in 2 lakes			
Observations	41			

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908

909 **Table 3.** Linear mixed-effect model of juvenile (< 6 years) occupied temperature (response
 910 variable). Columns present the estimated differences (positive or negative) of factor response
 911 variables with the model intercept, standard error (SE), degrees of freedom (df) and *p*-values for
 912 the factor. *p*-values in bold indicate significant differences (*p* < 0.05). The random parts show the
 913 number of tested groups and experimental units (*N*grp) and total observations

Coefficient	Response			
	Juvenile occupied temperature (°C)			
	Estimate	SE	df	<i>p</i> -value
Fixed parts				
Intercept	10.88	0.60	126	< 0.001
Genetic origin (local)	-0.17	0.70	17	0.81
Growing season 2	0.64	0.64	126	0.32
Growing season 3	-1.47	0.67	126	0.03
Growing season 4	-3.22	0.72	126	< 0.001
Growing season 5	-2.86	0.74	126	< 0.001
Growing season 6	-3.25	0.73	126	< 0.001
Random parts				
<i>N</i> grp	20 fish in 2 lakes			
Observations	151			

914

915

916 **Table 4.** Linear mixed-effect model of temperature occupied by adults (response variable).
 917 Columns present the estimated differences (positive or negative) of factor response variables with
 918 the model intercept, standard error (SE), degrees of freedom (df) and *p*-values for the factor. *p*-
 919 values in bold indicate significant differences ($p < 0.05$). The random parts show the number of
 920 tested groups and experimental units (*N*grp) and total observations

Coefficient	Response			
	Adult occupied temperature			
	Estimate	SE	df	<i>p</i> -value
Fixed parts				
Intercept	10.39	1.02	163	< 0.001
Genetic origin (hybrid)	-1.54	0.61	26	0.02
Genetic origin (local)	-1.79	0.62	26	0.008
Ontogeny (age)	-0.11	0.07	163	0.14
Random parts				
<i>N</i> grp	30 fish in 2 lakes			
Observations	194			

921

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923

924 **Table 5.** Linear mixed-effect model of temperature at capture (last annuli) of adults lake trout
 925 (response variable). Columns present the estimated differences (positive or negative) of factor
 926 response variables with the model intercept, standard error (SE), degrees of freedom (df) and *p*-
 927 values for the factor. *p*-values in bold indicate significant differences ($p < 0.05$). The random parts
 928 show the number of tested groups and experimental units (*N*grp) and total observations

Coefficient	Response			
	Adult temperature at capture			
	Estimate	SE	df	<i>p</i> -value
Fixed parts				
Intercept	5.04	11.19	19	0.66
Total length	0.004	0.007	19	0.64
Qstocked	0.02	0.01	19	0.06
Trophic position	-3.31	2.28	19	0.16
ΔPelagic	-0.001	0.49	19	0.99
C:N	4.11	1.63	19	0.02
Random parts				
<i>N</i> grp	26 fish in 2 lakes			
Observations	26			

929

930

931 FIGURES CAPTIONS

932 Figure 1. Ecological synopsis of studied lakes, maps are showing geographical position and
933 morphology of both lakes. Fish communities of both lake are depicted as fish silhouette (credit:
934 Phylopic website) and common names (see text for scientific names) under each map.
935 Temperatures by depth profiles of each lake are provided with lake area (ha), maximum depth
936 (Z_{\max}) and Secchi depth.

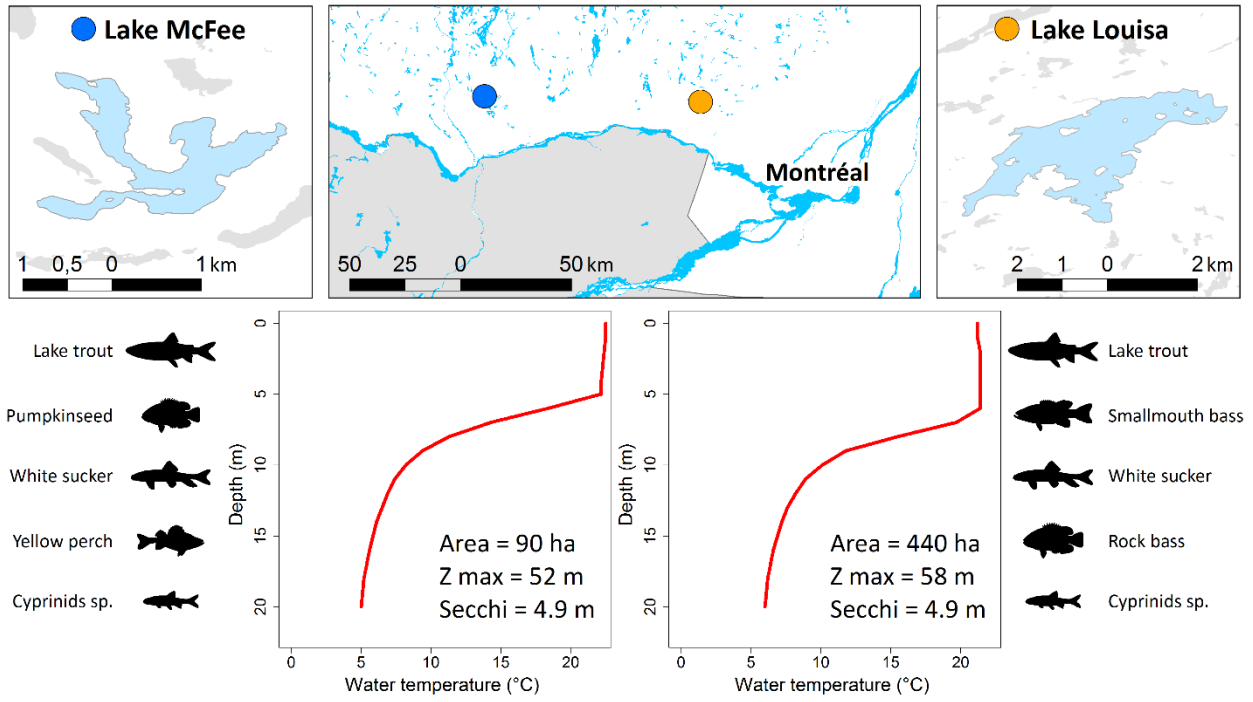
937 Figure 2. Difference between the occupied habitat temperature at the end of the first growing season
938 and at the time of hatching (otolith core) of local (blue) and hybrid (green) young-of-the-year from
939 lakes Louisa (circles) and McFee (triangles). The black dashed line is a linear regression ($\Delta T_{\text{end of}}$
940 $\text{season} = -0.87 * T_{\text{hatching}} + 9.45, p = 0.002, R^2_{\text{adj}} = 0.40$)

941 Figure 3. Estimated thermal habitat of juvenile lake trout for the first to the sixth growing season.
942 Different letters indicate a significant difference in post-hoc pairwise comparisons

943 Figure 4. Mean and standard deviation (error bars) of lake trout lifelong thermal by age class (4 to
944 18 years) in each genetic origin groups in lakes Louisa (left panel) and McFee (right panel).
945 Different colors in each graph represent a different genetic origin; local (green), hybrid (yellow)
946 and stocked (red). Only positive or negative error bars are shown to optimize visualization.

947 Figure 5. Estimated temperature ($^{\circ}\text{C}$) at time capture (last annuli) of adult lake trout in relation to
948 C:N ratio (top panel) and proportion of individual genotype related to source of stocking population
949 (Q_{stocked} , bottom panel). Different colors in each graph represent a different genetic origin; local
950 (green), hybrid (yellow) and stocked (red). In top panel, symbols are depicting lake of capture,
951 either Louisa (circle) or McFee (square).

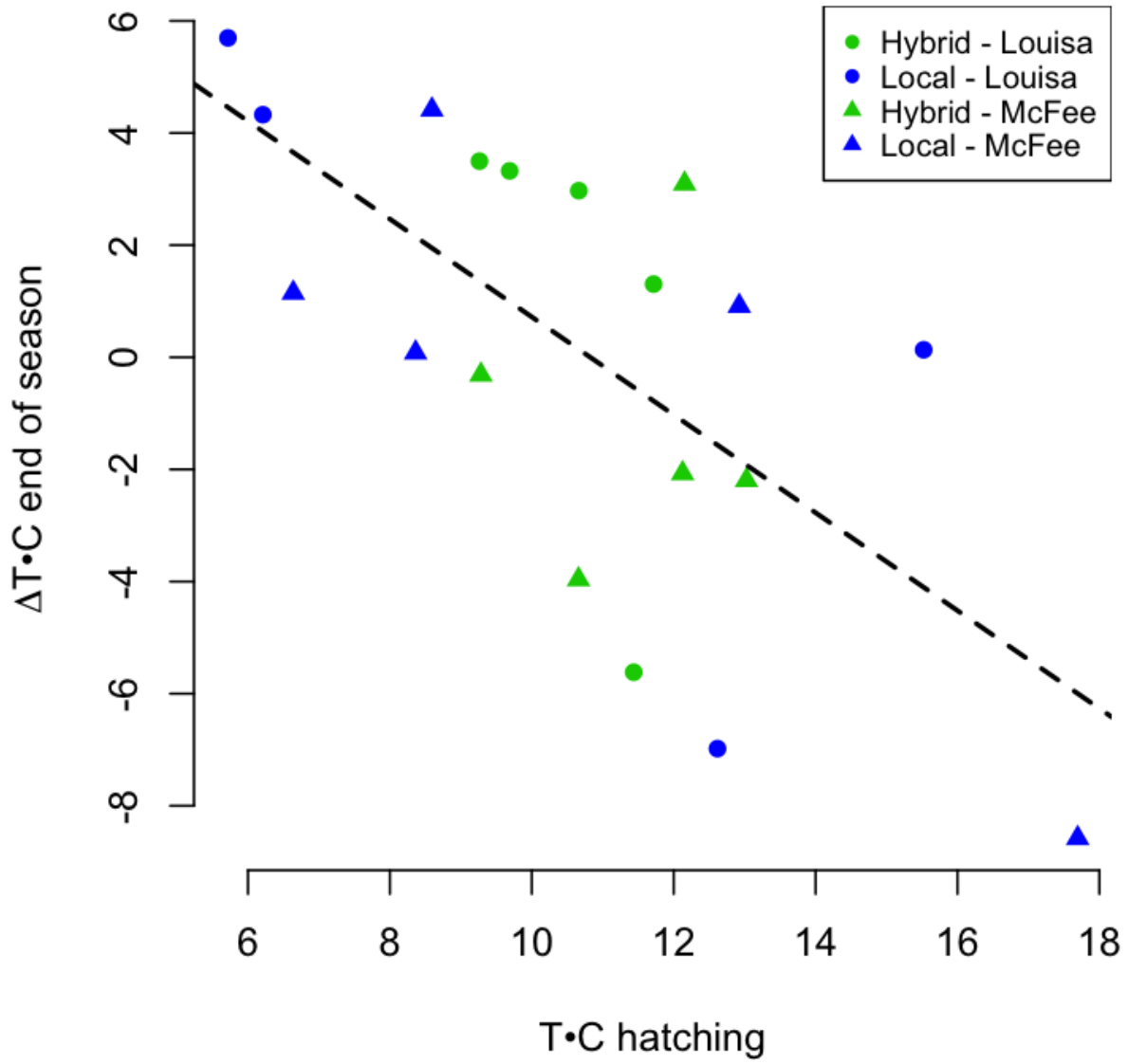
952 **Figure 1.**



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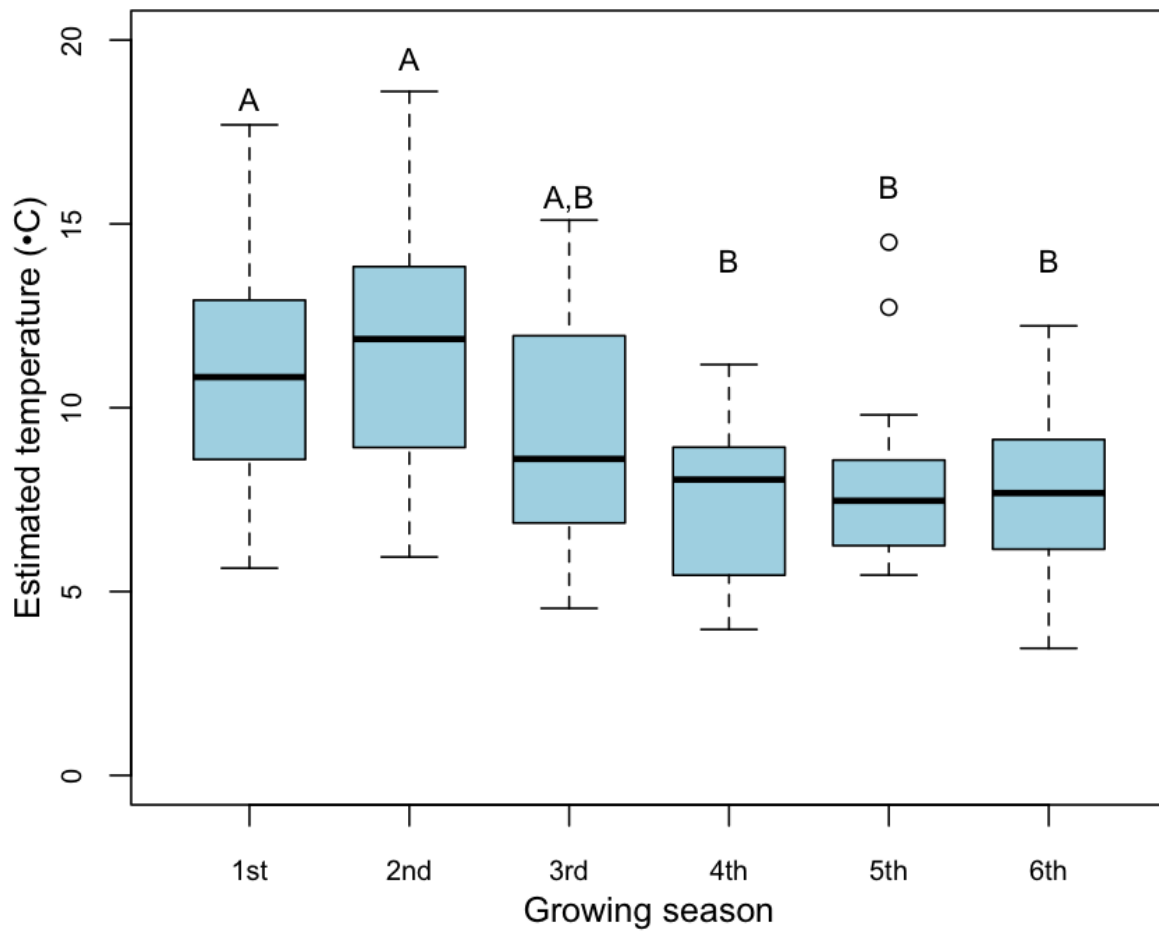
955 **Figure 2.**



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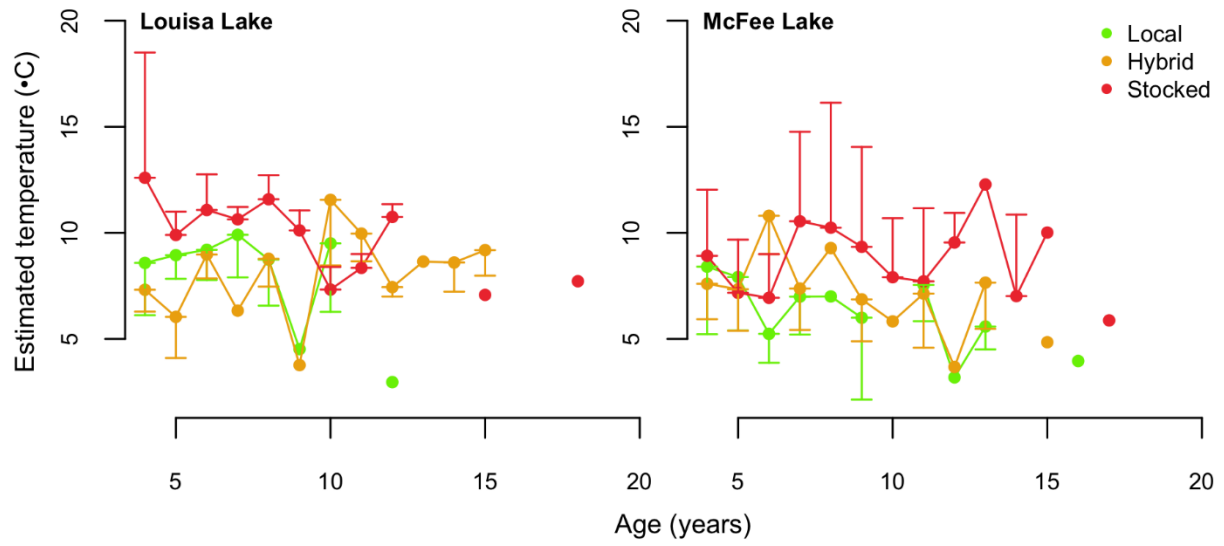
958 **Figure 3.**



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961 **Figure 4.**

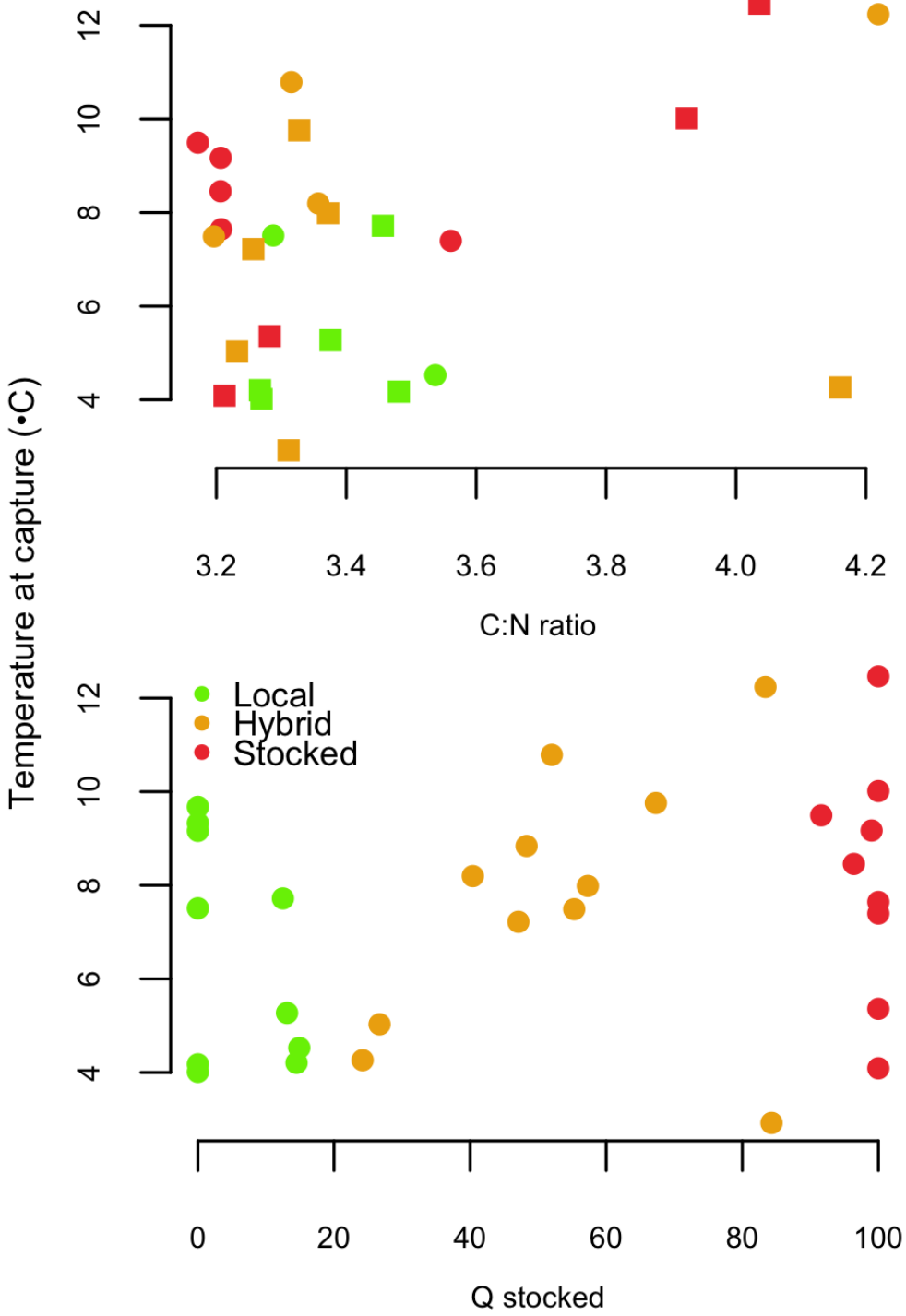


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965 **Figure 5.**



966