

1 **Seasonal variation of total mercury and condition indices of Arctic charr (*Salvelinus***
2 ***alpinus*) in Northern Québec, Canada**

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18 **Abstract**

19 The winter ecology of anadromous Arctic charr has remained poorly detailed in the literature
20 beyond descriptions of seasonal fasting and resulting declines in condition. However, prolonged periods
21 of reduced feeding can have significant consequences for other variables, such as tissue contaminant
22 levels. To more thoroughly detail seasonal changes, biological information (fork length, total weight, age,
23 sex, somatic condition), stable isotopes ($\delta^{13}\text{C}$, % carbon, $\delta^{15}\text{N}$, % nitrogen), dorsal muscle % lipid,
24 caloric densities, and total mercury (THg) concentrations were assessed in anadromous Arctic charr
25 collected from Deception Bay, Canada, during the summer and over-wintering periods. Significant
26 reductions in somatic condition, total weight, and % nitrogen, consistent with prolonged periods of
27 fasting, were found for post-winter captured Arctic charr, but % lipid and caloric densities were
28 significantly higher in these fish. THg also varied seasonally and was significantly higher in summer
29 collected tissue. When tested individually via linear regression, significant relationships were seasonally
30 dependent, but limited in number. All previously mentioned parameters were then incorporated into
31 multi-variable models which better explained variations in the data. While there was no clear best model
32 for explaining the % lipid values, caloric densities, and THg, season, condition, and stable isotope values
33 (% carbon and % nitrogen) were the best indicators of % lipid content and caloric densities. THg
34 concentrations were best explained by total weight, somatic condition, and $\delta^{13}\text{C}$. Seasonal variation in
35 fish condition measures and THg may be indicative of condition selective mortality that yields apparent
36 improvement through the disproportionate removal of poorer conditioned fish from the population during
37 the over-wintering period. This hypothesis was further supported by mortality estimates and the results of
38 the multi-predictor variable models. Collectively, this research highlights the importance of seasonal
39 dynamics for anadromous Arctic charr populations and suggests that future studies further consider
40 seasonality when evaluating this species.

41 **Keywords**

42 Arctic charr; total mercury; Nunavik; seasonal variation; condition; lipid content; caloric density

43 **1. Introduction**

44 Arctic charr (*Salvelinus alpinus*) are the most northerly distributed freshwater fish species on
45 Earth with populations ranging from southern temperate locations in eastern North America and the
46 European Alps to the northern extent of land masses in Eurasia and North America (Johnson 1980). These
47 fish are considered habitat generalists, occupying lakes, streams, rivers, and marine environments
48 depending on the time of year and life history form (Power et al. 2008). Arctic charr exhibit diverse life
49 history strategies (Jonsson et al. 1988) that include anadromous, lacustrine, and partial migratory types,
50 where anadromous and non-anadromous fish co-exist (Jonsson and Jonsson 1993), with the decision to
51 migrate dictated by environmental conditions, sex, genetics, and ontogenetic niche shifts (Jonsson and
52 Jonsson 1993; Jørgensen and Johnsen 2014; Klemetsen et al. 2003a). Both sexually mature and immature
53 fish perform migrations and first time migrants can be anywhere from 3 to 8 years of age (Johnson 1989;
54 Nordeng 1983).

55 Seaward migrations of anadromous Arctic charr begin after ice break up in the spring (Johnson
56 1983; Klemetsen et al. 2003a), with fish generally remaining in coastal areas for 1-2 months before
57 returning to freshwater environments (Klemetsen et al. 2003a; Mathisen and Berg 1968). The relative
58 abundance of anadromous individuals is variable within and among populations (Johnson 1980; Svenning
59 et al. 1992) and dependent on conditions, such as freshwater growth opportunities and differences in
60 productivity between freshwater and marine environments (Gross et al. 1988) and/or the physical
61 characteristics of the migratory route (Kristoffersen 1994; Moore et al. 2016). However, at the northern
62 extremes of their distribution lacustrine residency is favoured regardless of access to the marine
63 environment (Power et al. 2008).

64 For Arctic charr, the period of marine residency is characterized by rapid growth, with
65 anadromous fish growing faster than resident freshwater fish (Berg and Berg 1989; Johnson 1980; Moore
66 and Moore 1974). Fish may double their body weight and experience a five-fold increase in lipid content
67 while in the marine environment (Finstad and Heggberget 1993; Jørgensen et al. 1997; Mathisen and Berg

68 1968), with the carcass (head, skeleton, and skin) and muscle tissue accounting for 50% and 35-40%,
69 respectively, of the total body lipid content when fish re-enter freshwater from the sea (Jobling et al.
70 1998; Jørgensen et al. 1997; Jørgensen and Johnsen 2014). During the marine period fish feed
71 opportunistically on zooplankton, amphipods, pelagic and benthic fishes (Dempson et al. 2002; Grønvik
72 and Klemetsen 1987; Power et al. 2008).

73 Historically, studies of anadromous Arctic charr have focused on the period of marine residency
74 and its consequences for growth and maturation (Berg and Berg 1989; Jørgensen et al. 1997; Murdoch et
75 al. 2015), but have traditionally lacked winter data (Mulder et al. 2018b). The available over-wintering
76 data that does exist have focused on resident lacustrine Arctic charr condition, diet, and habitat during the
77 ice-covered months (Amundsen and Knudsen 2009; Eloranta et al. 2013; Klemetsen et al. 2003b). Thus
78 the ecology of over-wintering anadromous Arctic charr has remained poorly described in the literature
79 beyond the noted cessation of feeding and the resulting reduction of condition (e. g. (Boivin and Power
80 1990; Jørgensen et al. 1997; Rikardsen et al. 2003). More recently, telemetry studies of over-wintering
81 Arctic charr in southern Labrador have indicated reduced activity patterns (Mulder et al. 2018b) and
82 temperature-dependent diurnal movement patterns (Mulder et al. 2019) occurring within a narrow range
83 of temperatures (0.5–2 °C) that suggest a use of strategies to lower metabolic costs and minimize over-
84 winter energy expenditure (Mulder et al. 2018a).

85 During winter, whole body lipid body reserves have been reported to decline by up to 30% for
86 non-reproductive anadromous Arctic charr and between 35 – 46% for post-spawning individuals (Dutil
87 1986; Jørgensen et al. 1997). Lipids are depleted from all tissues, but mobilization of muscle and carcass
88 deposits has been determined to be the most significant during this period (Jobling et al. 1998; Jørgensen
89 et al. 1997). Additionally, emaciation is greatest in females with individuals on average losing
90 approximately 80% of their lipid stores during spawning and overwintering (Jobling et al. 1998;
91 Jørgensen et al. 1997). The documented declines in energy reserves, the minimization of movement, use
92 of colder water temperatures to reduce metabolism (Mulder et al. 2018b), lack of suitable prey (Boivin
93 and Power 1990), and the implications of light restrictions on prey capture efficiency (Mazur and

94 Beauchamp 2003; Turesson and Brönmark 2007) all suggest significantly reduced feeding during the
95 winter months. While in lacustrine populations of Arctic charr, winter feeding has been documented to
96 some extent in the literature (e.g., (Eloranta et al. 2013; Klemetsen et al. 2003b; Power et al. 2009)), it has
97 only been inferred for anadromous individuals based on activity and habitat use (Boivin 1987; Mulder et
98 al. 2018b).

99 In addition to losses in lipids and overall reductions in condition, prolonged periods of reduced
100 feeding can have other significant consequences for over-wintering fish. Critical among those effects are
101 the possible associated changes in tissue contaminant levels. Jørgensen et al. (2006) demonstrated that
102 winter fasting and subsequent emaciation of anadromous Arctic charr resulted in the redistribution of
103 lipophilic PCBs to sensitive organs (e.g., liver and brain). This was accompanied by significant increases
104 in hepatic biomarker activity and disruptions to endocrine mechanisms, immune function, and
105 smoltification processes. The results suggests that seasonal lipid dynamics may result in increased
106 sensitivity of Arctic animals to certain contaminants undergoing seasonal fasting (Jørgensen et al. 2002;
107 Jørgensen et al. 2006). Methylmercury (MeHg) is one contaminant of specific concern due to its
108 neurologically toxic health effects (Mergler et al. 2007) and its ability to bioaccumulate in aquatic food
109 webs to reach high concentrations in large-bodied predatory fish (Gantner et al. 2010; Kidd et al. 1995;
110 van der Velden et al. 2013a). In the muscle tissue of these fish, MeHg concentrations are typically greater
111 than 90% of total mercury, THg, (Eagles-Smith et al. 2016; Hall et al. 1997; Lockhart et al. 2005), and
112 generally increase with size and age (Lescord et al. 2018), making THg concentrations a suitable proxy
113 for MeHg levels and of particular concern to the Inuit people who consume large quantities of fish
114 (Lemire et al. 2015).

115 Measured concentrations of THg are often related to biological variables such as: fish size, age,
116 trophic position ($\delta^{15}\text{N}$), feeding strategies and habitat use ($\delta^{13}\text{C}$), growth, and somatic condition (Dittman
117 and Driscoll 2009; Power et al. 2002; Wiener et al. 2003), but also depend on lipid and protein contents
118 (Eisler 1987; Kahilainen et al. 2016; Swanson and Kidd 2010). THg in fish tissues is derived almost
119 exclusively from prey consumption (Hall et al. 1997) and after digestion THg is translocated to the liver

120 via blood and subsequently stored in muscle tissues (Oliveira Ribeiro et al. 1999; Wang and Wang 2015)
121 where it is almost exclusively bound within proteins (Amlund et al. 2007; Bury et al. 2003; Mason et al.
122 1995). Growth during the summer can lower THg concentrations during the growing season as
123 individuals accumulate tissue faster than THg (Karimi et al. 2007; Lepak et al. 2012; Olk et al. 2016),
124 while lipid losses prompted by a cessation of feeding during the winter months can result in a
125 phenomenon termed starvation – concentration (Cizdziel et al. 2003; Cizdziel et al. 2002) that increases
126 mercury in remaining protein-containing tissues (Kahilainen et al. 2016). The result is higher THg during
127 the ice-covered period (Keva et al. 2017; Olk et al. 2016). While seasonal variations in THg have been
128 reported in lacustrine resident Arctic charr and other fish species (Kahilainen et al. 2016; Keva et al.
129 2017; Olk et al. 2016), such variations are relatively understudied and have yet to be documented for
130 anadromous Arctic charr. Additionally, quantifying seasonal variations in THg concentrations in
131 anadromous Arctic charr may help determine differences in seasonal risks for capture and consumption
132 associated with the winter fishery for this species, which provides an important component of the year-
133 round diet of Inuit people, including those of the Nunavik region of northern Québec (e.g., (Boivin and
134 Power 1990)). Similar to other areas of Arctic Canada, anadromous Arctic charr in Deception Bay,
135 Nunavik, Québec, are of significant cultural and economic importance to the local Indigenous
136 communities (e.g., Salluit and Kangiqsujuaq). However, literature on Arctic charr populations in this
137 region remains scarce (e.g., (Boivin and Power 1990; Murdoch et al. 2013; Murdoch and Power 2013)),
138 with only one study having directly examined issues related to seasonality (Boivin and Power 1990).

139 Here samples collected from Deception Bay, Nunavik, where Arctic charr migrate and feed in
140 summer, and lakes Duquet and François-Malherbe, where Arctic charr spawn and over-winter, are used
141 to investigate patterns of seasonal change in fish condition measures and THg concentrations.
142 Specifically, it was hypothesized that (i) over-wintering anorexia and fasting (e.g., as represented by
143 reduced total weight and somatic condition (Fulton’s K) (Jobling 1981; Jørgensen et al. 1997) would
144 result in significant declines in percent lipid (% lipid) and caloric densities of anadromous Arctic charr
145 collected during post-winter sampling as stored energy reserves are mobilized to meet metabolic demands

146 during this period (Jobling et al. 1998; Jørgensen et al. 1997). Additionally, seasonal relationships with
147 co-measured biological information (fork length, total weight, age, sex, and somatic condition) and stable
148 isotopes used as proxies for feeding behaviour, habitat use, and trophic position ($\delta^{13}\text{C}$, % carbon (C),
149 $\delta^{15}\text{N}$, % nitrogen (N)) were evaluated.

150 Samples were also used to test a contamination hypothesis: (ii) that THg values would be higher
151 during the post-winter sampling period than in the late summer sampling period as a result of fasting-
152 induced emaciation and the subsequent increase of mercury in the remaining tissues (Kahilainen et al.
153 2016; Keva et al. 2017; Olk et al. 2016). Again, seasonal correlations with biological information and
154 stable isotope ratios were assessed, with specific relationships between measured THg concentrations %
155 lipid and caloric density values being evaluated. Finally, data were used to model dorsal muscle % lipid
156 content, caloric density, and THg concentrations as a function of multi-variable statistical models
157 inclusive of combinations of the above tested biological information, stable isotope values, and their
158 interactions. Specifically, we hypothesized that (iii) season and/or fish condition would best describe %
159 lipid values and caloric content (Dutil 1986; Thompson et al. 1991; Todd et al. 2008) and variables
160 associated with bioaccumulation (fork length, total weight and/or age and trophic position represented by
161 $\delta^{15}\text{N}$) (Cizdziel et al. 2002; Power et al. 2002; van der Velden et al. 2013a) and season (Kahilainen et al.
162 2016; Keva et al. 2017; Köck et al. 1996), would best describe THg concentrations as these variables are
163 known to significantly influence measured THg concentrations in fish tissue (Kahilainen et al. 2016;
164 Wiener et al. 2003).

165 **2. Methods**

166 *2.1 Study Area*

167 The Deception River and its tributaries (Fig. 1) are located east of Salluit, Québec ($62^{\circ}10'46\text{ N}$,
168 $75^{\circ}40'13\text{ W}$) with a watershed spanning an area of 3870 km^2 between latitudes $61^{\circ}31'26''\text{ N}$ and
169 $62^{\circ}11'01''\text{ N}$. The river flows into Deception Bay, which is associated with the Hudson Strait marine
170 ecosystem (Goldsmit et al. 2014), a deep and wide channel that connects Hudson Bay and the Foxe Basin

171 with the Labrador Sea and the Davis Strait. Average daily temperatures range from -25.6°C in February,
172 to 10.5°C in August (Environment Canada 2018a; Environment Canada 2018b), with a growing season of
173 less than 120 days per year. In addition to traditional hunting and fishing, the area is impacted by two
174 nickel and copper mining projects: Glencore - the Raglan Mine Project and Canadian Royalties Inc. – the
175 Nunavik Nickel Project, and is proximate to the now closed Asbestos Hill Mine (Purtiniq). A 95
176 kilometre road connects the main Raglan mining site with an additional camp and deep-water port in
177 Deception Bay. Mine personnel are present year-round and the road closely follows the Deception River
178 and its tributaries for most of its length. Some contaminant input is believed to result from the mining
179 facilities proximate to Deception Bay in addition to atmospheric deposition.

180 Arctic charr spawn and overwinter in headwater lakes Duquet (62°03'18 N, 74°31'51 W) and
181 François-Malherbe (62°00'06 N, 74°15'25 W) from October to June. Lake Duquet is less than half the
182 size of Lake François-Malherbe and the lakes are located 2.5 km and 15 km, respectively, upstream of
183 the river mouth. There is usually a commercial fishing permit active for Deception Bay and both lakes,
184 and a Raglan Mine sport fishing permit is active for Deception Bay. Lake Watts, a third lake in the
185 Deception River system upstream of Lake François-Malherbe, is assumed to have received some direct
186 input of mining waste prior to the 1984 closure of the Asbestos Hill Mine located 10 km from the lake.
187 Traditional knowledge suggests that Arctic charr are predominately non-migratory in Lake Watts and
188 access to this lake was not possible during the course of this study.

189 *2.2 Sample Collection*

190 Summer collection of anadromous Arctic charr was completed using multi-mesh experimental
191 gill nets (25 – 150 mm mesh panels with a length of 120 m and a hanging depth of 2 m) set coincident
192 with the returning upstream migration period. Arctic charr were caught at eight locations equally
193 distributed throughout Deception Bay and from the mouth of the Deception River in August of 2016. A
194 post-winter sample was obtained from lakes François-Malherbe (May 8th – 11th, 2017) and Duquet (May
195 12th – 13th, 2017), approximately a month prior to ice break-up (as reported for the area by the Canadian
196 Ice Service (2018) as June 26th, 2017). Post-winter dorsal muscle samples were collected from fish

197 captured throughout the lakes with jigging lines by Nunavik Research Centre (NRC) staff in collaboration
198 with Inuit elders during the Salluit community Elder's Spring Fishing Event hosted by Qaqqalik
199 Landholding Corporation and supported by Raglan Mine. All fish captured were sacrificed after capture
200 with a sharp blow to the head and all sample collection was performed in accordance with standards
201 dictated by the Ministère des Forêts, de la Faune, et des Parcs – Direction de la gestion de la faune du
202 Nord-du-Québec (permis de gestion de la faune #2016-02-199-152-10-G-P N/D : 9053_36).

203 Fish were sexed, weighed (± 1 g) and measured for fork length (± 1 mm). Measurements were
204 used to calculate Fulton's condition factor ($K = 10^5 * W/L^3$), which was only determined after performing
205 standardized weight-length regressions and ensuring that the slope of this regression did not significantly
206 deviate from a value of three (Ricker 1975). A sample of dorsal muscle tissue (mass ≈ 10 g wet weight)
207 was removed from above the lateral line and posterior to the dorsal fin on the left side of each Arctic charr
208 (van der Velden et al. 2013a) and frozen at -20°C for subsequent laboratory analyses. A random sample
209 of 50 fish from the summer sampling was selected for THg analysis. A sub-sample of 40 fish was used
210 for lipid analysis and a sub-sample of 30 fish was used for bomb calorimetry. From the winter sampling a
211 total of 55 fish dorsal muscle samples were provided by the Salluit community Elder's Spring Fishing
212 Event. To guard against inadvertent use of resident fish from the post-winter sampling, anadromy was
213 confirmed with $\delta^{34}\text{S}$ stable isotope analysis following methods described in Doucett et al. (1999). After
214 removal of resident fish, the remaining anadromous fish were used for THg analyses. Similar to the
215 summer sampling, a sub-sample was retained for lipid and bomb calorimetry analyses. Dorsal muscle
216 samples were generally used for all (lipid, bomb calorimetry and THg) analyses except where tissue was
217 limited.

218 To minimize accidental metal contamination, tissues for THg analysis were placed in Eppendorf
219 polypropylene tubes. These tubes had been acid washed in 15% HNO_3 for at least 24 hours before being
220 rinsed 5 times with distilled water, twice with ultrapure water, and then dried under a laminar-flow fume
221 hood before use. The upper gastrointestinal tracts (e.g., esophagus and stomach) of all post-winter
222 collected fish were examined for evidence of short-term winter feeding. Aging of all sampled fish was

223 completed by NRC staff, with fish ages determined by submersing the otolith in water and examining the
224 distal surface with reflected light under a dissecting microscope (Chilton and Beamish 1982). Ages were
225 used to estimate von Bertalanffy growth equations (Ricker 1975) for each seasonal sample from which
226 the von Bertalanffy growth coefficient (K) was used to estimate mortality following (Jensen 1996).

227 *2.3 Stable Isotope Analysis*

228 For stable isotope analyses, dorsal muscle tissue was dried at 50°C for 48 h and pulverized into a
229 homogenate powder with a mortar and pestle. After being weighed to 0.275 – 0.300 mg (UMX2, Mettler-
230 Toledo GmbH, Greifensee, Switzerland), each tissue sample was simultaneously analyzed for carbon and
231 nitrogen stable isotope ratios ($\delta^{13}\text{C}$, $\delta^{15}\text{N}$) at the Environmental Isotope Laboratory, University of
232 Waterloo, Ontario, Canada with a Delta Plus Continuous Flow Stable Isotope Ratio Mass Spectrometer
233 (Thermo Finnigan, Bremen, Germany) coupled to a Carlo Erba Elemental Analyzer (CHNS-O EA1108,
234 Carlo Erba, Milan, Italy) following methods described in van der Velden et al. (2013a). Elemental
235 compositions were expressed in percentage terms based on pre-analysis weights. All stable isotope
236 measurements were expressed using standard delta notation (δ) as parts per thousand differences (‰)
237 with respect to the international reference standards of Vienna Peedee Belemnite carbonate rock for $\delta^{13}\text{C}$
238 (Craig 1957) and nitrogen gas in the atmosphere for $\delta^{15}\text{N}$ (Mariotti 1983):

$$239 \quad \delta R = \left[\frac{R_{\text{sample}} - R_{\text{standard}}}{R_{\text{standard}}} \right] \times 1000$$

240 where δR is the measured carbon ($^{13}\text{C}/^{12}\text{C}$) or nitrogen ($^{15}\text{N}/^{14}\text{N}$) isotope ratio expressed with respect to
241 the appropriate international standard. Machine analytical precision was determined to be $\pm 0.2\text{‰}$ for $\delta^{13}\text{C}$
242 and $\pm 0.3\text{‰}$ for $\delta^{15}\text{N}$ and was established via repeat analysis of internal laboratory working standards
243 (IAEA-N₁ + N₂, IAEA-CH₃ + CH₆) cross calibrated to International Atomic Energy Agency (IAEA)
244 standards: CH₆ for $\delta^{13}\text{C}$ and N₁ and N₂ for $\delta^{15}\text{N}$. Internal standards were placed at the beginning, middle
245 and end of every run of samples and repeatability was assessed by repeat analysis of 1 in 10 samples. As
246 C:N ratios were consistently below the 4.0 threshold above which lipid extraction is required (Jardine et

247 al. 2011; Logan et al. 2008; Sanderson et al. 2009), $\delta^{13}\text{C}$ values were not lipid extracted or mathematically
248 normalized for lipid content.

249 *2.4 Lipid Analysis and Bomb Calorimetry*

250 Lipid analysis and bomb calorimetry were performed at the University of Waterloo, Waterloo,
251 Ontario, Canada. A modified version of the procedure outlined in Folch (1957) was used for lipid
252 extraction as this method provides accurate estimates of lipid content when lipids comprise greater than
253 2% of tissue (Iverson et al. 2001). After freeze drying (Freezone Plus 2.5 Liter Cascade Benchtop Freeze
254 Dry Systems, Labconco, Kansas City, USA), Arctic charr dorsal muscle tissue was ground with a mortar
255 and pestle and weighed to approximately 30.0 mg \pm 0.1 mg (XS205DU Analytical Balance, Mettler
256 Toledo, Mississauga, Canada). 2 mL of a 2:1 chloroform-methanol solution and 1.6 mL of a 0.9% KCl
257 solution were then added to the ground tissue. The resulting solution was homogenized with a vortex
258 (Fisherbrand Analog Vortex Mixer, Fisher Scientific, Hampton, USA) and centrifuged
259 (Fisherbrand™ Centrif Model 225A Benchtop Centrifuge, Fisher Scientific, Hampton, USA) at 2000
260 RPM for 5 minutes until the KCl, tissue, and chloroform-methanol layers were completely separated. The
261 lipid containing solution was extracted via Pasteur pipette through the KCl and residual biomass layers.
262 Three iterations of the procedure were performed until a final lipid solution of 8 mL was obtained. The
263 lipid-containing solution was then evaporated to dryness. Once dry, an additional 2 mL of 2:1
264 chloroform-methanol solution were added to the dried material and two, 100 μL aliquots were then
265 transferred to pre-weighed tin cups. The solution was evaporated at room temperature overnight until only
266 dry lipids remained. Remains were weighed on a micro-balance (UMX2, Mettler-Toledo GmbH,
267 Greifensee, Switzerland) to determine the percentage of lipid in the dorsal muscle tissue expressed as:

$$268 \quad \% \text{ Lipid} = \left(\left(\left(\frac{\text{Mass}_{\text{Dry}} (\text{g})}{\text{Mass}_{\text{Ground}} (\text{g})} \right) \right) * (1 - P_{\text{Water}}) * 100\% * 20 \right);$$

269 where Mass_{Dry} is the weight of the dried lipid following the extraction procedure, $\text{Mass}_{\text{Ground}}$ is the initial
270 ground mass of the tissue preceding extraction, P_{Water} is the proportion of water in the analyzed dorsal
271 muscle tissue (wet tissue mass (g) – dry tissue mass (g)), and 20 represents a correction as a result of

272 using only a subset of the final extraction solution volume for establishing the final dried mass (Folch
273 1957).

274 For bomb calorimetry, Arctic charr dorsal muscle tissue was dried at 50°C for 48 hours and
275 ground to obtain a homogenized sample using a mortar and pestle. Pellets were formed (Parr Pellet Press,
276 Parr Instrument Company, Moline, USA) with weights not exceeding 50.0 mg \pm 0.1 mg (XS205DU
277 Analytical Balance, Mettler Toledo, Mississauga, Canada) before ignition in a Parr Semi-micro
278 Calorimeter 6725 (Parr Instrument Company, Moline, USA) to measure caloric density (cal·g⁻¹ dry mass).
279 The wet mass caloric density was determined by multiplying the dry mass caloric density by the
280 proportion of final dry mass to original wet mass (Glover et al. 2010). Results were reported as wet
281 weight (ww) caloric density means \pm standard deviation. Benzoic acid pellets with a caloric density of
282 6318.4 cal·g⁻¹ dry weight (dw) were used to standardize the calorimeter and assess recovery every 10th
283 sample. Percent recovery \pm standard deviation of benzoic acid pellets ($n = 11$) was determined to be
284 100.35% \pm 1.07%.

285 *2.5 THg Analysis*

286 Mercury analysis was performed at the Institut National de la Recherche Scientifique (INRS) in
287 Québec City, Québec, Canada and at the University of Waterloo in Waterloo, Ontario, Canada. After
288 freeze-drying (FTS Systems TMM, Kinetics Thermal Systems, Longueil, QC, Canada; Freezone Plus 2.5
289 Liter Cascade Benchtop Freeze Dry Systems, Labconco, Kansas City, USA), tissue was weighed to
290 approximately 50.0 – 100.0 mg \pm 0.1 mg (Series 321 LT 220A Balance, Precisa Gravimetrics AG,
291 Dietikon, Switzerland; Mettler Toledo, Mississauga, Canada). Analysis was then performed with a direct
292 mercury analyzer (DMA-80, Milestone Inc., Shelton, USA) which enables assessment of THg through
293 thermal decomposition followed by atomic absorption spectroscopy as described in U.S. EPA method
294 7473 (United States Environmental Protection Agency 1998). Results were converted from dry weight to
295 wet weight using percent moisture calculations determined from weights (\pm 0.1 mg) taken before and
296 after lyophilisation (Eikenberry et al. 2015).

297 Past studies have indicated that age (van der Velden et al. 2013b) and/or length (Rigét et al. 2000;
298 Swanson et al. 2011) are often strongly correlated with THg concentrations such that THg concentrations
299 require age or length adjustment to permit comparisons among individuals. Accordingly, data were
300 examined for evidence of significant length and/or age correlations using linear regression (\log_{10} THg vs.
301 \log_{10} fork length, fork length, or \log_{10} age, and age) (Tran et al. 2015). The effect of lipids on analytical
302 results was examined by comparing differences in relationships obtained using raw and lipid corrected
303 THg concentrations, with lipid corrected THg concentrations computed following methods described in
304 Kahilainen et al. (2016).

305 Method detection limits and percent recoveries are reported as mean percentage of certified
306 values \pm standard deviation. Tissues were evaluated in triplicate with certified reference materials from
307 the National Research Council of Canada (NRCC) (TORT-3, DOLT-4, and DOLT-5). Blanks were used
308 every fifth sample in the same analytical cycle to establish accuracy and recovery rates. The method
309 detection limit, determined as $3\times$ the standard deviation of blanks, was 2.91 ng Hg (approximately 0.003
310 ($\text{mg}\cdot\text{kg}^{-1}$)) and mean relative standard deviation of the triplicates was 5.53% ($n = 108$). Percent recoveries
311 were determined to be $99.32\% \pm 7.42\%$ ($n = 52$), $93.16\% \pm 9.04\%$ ($n = 47$), and $88.95\% \pm 3.88\%$ ($n = 16$)
312 for TORT-3, DOLT-4, and DOLT-5 respectively.

313 *2.6 Statistical Analysis*

314 All statistical analyses were performed using JMP® statistical software (v. 13.0.0, SAS Institute,
315 CA) and Type I error was set to $\alpha = 0.05$. Data consistency with normality and homoscedasticity
316 assumptions were verified using residual diagnostic histograms, visual assessment of Q-Q plots, and the
317 Shapiro-Wilk W test (Shapiro and Wilk 1965). Data that did not meet parametric assumptions were \log_{10}
318 transformed (Zar 2007). Linear regressions were used to determine the relationship significance between
319 specific variables and outliers that may have unduly influenced regression results were assessed using
320 Cook's Distance statistic (Cook 1977) and subsequently removed. Un-paired, two-sample t-tests adjusted
321 for homogeneity of variance assumptions were used to determine significant differences among seasons
322 (Zar 2007) and the Wilcoxon approach was used when data did not conform to the required parametric

323 assumptions (Zar 2007). The Fisher exact test was used to test for significant differences among
324 proportions (Zar 2007) and incidental correlations were assessed using Pearson's correlation coefficient.

325 General linear models (GLM) inclusive of season, fork length, total weight, age, somatic
326 condition, $\delta^{13}\text{C}$, % C, $\delta^{15}\text{N}$ and % N were used to determine the best model to describe dorsal muscle %
327 lipid values, caloric densities, and THg concentrations. Pearson correlation analysis (Appendix A Tables
328 A.1 – A.3) and/or linear regression were used to establish the significance of variables expected to
329 correlate with dorsal muscle % lipid values, caloric densities, and THg concentrations, with only
330 significant variables being retained for use in GLM models. Significant two-way interactions among
331 variables were similarly assessed, with significant interactions retained for use in GLM models. To reduce
332 statistical issues associated with multicollinearity (Zar 2007), possible explanatory variables that were
333 highly correlated ($r^2 > 0.70$) or known to have biological redundancy (e.g., fork length and total weight)
334 were not included in the same model. To predict seasonal dorsal muscle % lipid values, caloric densities,
335 or THg concentrations models that included all possible combinations of the feasible set of significant
336 explanatory variables and two-way interactions, as determined above, were considered.

337 Model selection was performed using the Akaike Information Criteria adjusted for small sample
338 sizes (*AICc*). The model with the lowest *AICc* score was considered the most accurate, except in
339 circumstances where *AICc* values differed by less than two (Burnham and Anderson 2003). Detailed
340 description of the computation of the analytical metrics associated with the *AICc* methodology used here
341 can be found in Burnham and Anderson (2003).

342 **3. Results**

343 Of the 105 anadromous Arctic charr samples obtained, 100 were used in the comparison of
344 summer and post-winter levels of \log_{10} THg, \log_{10} % lipids, and \log_{10} caloric densities. A single sample
345 from the summer sampling was removed from use because of sample desiccation prior to shipment.
346 Testing with $\delta^{34}\text{S}$ stable isotope analyses indicated 4 Arctic charr from the post-winter collection were

347 non-anadromous and these fish were excluded from further consideration. This resulted in the loss of 4
348 Arctic charr samples from the lipid testing subset and 3 samples from the calorimetry testing subset.

349 *3.1 Seasonal Variation in Biological Variables and Stable Isotope Values*

350 Means \pm standard deviations and ranges for biological variables and stable isotope values for all
351 summer sampled and post-winter captured Arctic charr can be found in Table 1. Statistical testing of the
352 slope of the standardized weight-length regression (Deception Bay sampling – 3.12, post-winter sampling
353 – 3.03) confirmed isometric growth (Deception Bay t-test, $p = 0.457$, post-winter sampling t-test, $p =$
354 0.255), thereby allowing the use of Fulton's K. Estimated seasonal von Bertalanffy growth models yielded
355 von Bertalanffy growth coefficients from which differing mortality rates were estimated (summer
356 mortality: 22.3%; winter mortality: 24.5%). \log_{10} somatic condition significantly declined in post-winter
357 Arctic charr ($Z_{(1,98)} = 4.637$, $p < 0.001$) indicating possible over-wintering anorexia, as a result of a
358 significant decline in \log_{10} total weight during the over-wintering period ($Z_{(1,98)} = 2.444$, $p = 0.015$).
359 \log_{10} fork length ($t_{(1,98)} = 1.43$, $p = 0.156$), \log_{10} age ($t_{(1,95)} = 1.309$, $p = 0.194$), % carbon ($Z_{(1,98)} = -0.831$,
360 $p = 0.406$), and $\delta^{15}\text{N}$ values ($t_{(1,98)} = -1.258$, $p = 0.211$) of captured fish did not vary seasonally. $\delta^{13}\text{C}$ was
361 significantly more depleted in post-winter sampled Arctic charr ($Z_{(1,98)} = -5.754$, $p < 0.001$) as was % N
362 ($Z_{(1,98)} = 5.623$, $p < 0.001$). The sex ratio of summer and post-winter sampled fish did not vary between
363 seasons (Fisher's exact $\Pi_2 = 0.440$, $p < 0.657$) and sex was not significantly correlated with % lipids,
364 caloric density, or THg in any of the seasonal samples (all correlation $p > 0.466$). Furthermore, no
365 evidence of short-term winter feeding was determined via examination of the upper gastrointestinal tract.

366 *3.2 Lipid Content and Caloric Density*

367 Means \pm standard deviations and ranges for % lipid values and caloric densities are given in
368 Table 2. Significant seasonal variation existed for \log_{10} lipid content ($t_{(1,74)} = -6.49$, $p < 0.001$) and \log_{10}
369 caloric density ($t_{(1,55)} = -11.70$, $p < 0.001$) (Fig. 2). \log_{10} lipid content explained 28% of the variation in
370 \log_{10} caloric density of Arctic charr during the post-winter fishery ($r^2 = 0.28$, $p = 0.005$), but values were
371 not significantly correlated in Arctic charr captured returning from the marine environment ($r^2 = 0.09$, $p =$

0.118). Significant relationships between \log_{10} % lipid values and \log_{10} caloric densities and studied correlates are plotted in Fig. 3 and Fig. 4. A limited number of weak significant relationships were found and there was no consistent pattern of associations when comparing summer and post-winter samples. \log_{10} % lipids were not significantly correlated with any of the biological parameters (e.g., length, weight). However, \log_{10} % lipid values of late summer migrants significantly declined with increased offshore feeding ($r^2 = 0.12, p = 0.030$) and were generally related to % elemental composition, increasing with % C in post-winter sampled fish ($r^2 = 0.11, p = 0.048$) and decreasing with % N in both summer and post-winter sampled fish (summer ($r^2 = 0.14, p = 0.017$); post-winter ($r^2 = 0.12, p = 0.035$)) (Fig. 3). \log_{10} caloric density increased with fork length in summer sampled Arctic charr ($r^2 = 0.16, p = 0.031$) (Fig. 4) and in post-winter sampled fish was positively related to % C ($r^2 = 0.30, p = 0.003$) and negatively related to % N ($r^2 = 0.43, p < 0.001$) (Fig. 4).

3.3 THg

Mean THg concentrations \pm standard deviations are reported in Table 2 and all measured concentrations were determined to be below the regulatory $0.5 \text{ mg}\cdot\text{kg}^{-1}$ of mercury detailed in Health Canada's commercial guideline of maximum levels for chemical contaminants in foods (Government of Canada 2019; Health Canada 2018). Contrary to what was hypothesized, \log_{10} THg concentrations of summer captured Arctic charr were significantly higher than those obtained from post-winter fish ($t_{(1,98)} = 2.59, p = 0.011$) (Fig. 2). Significant relationships between \log_{10} THg concentrations and tested variables in both summer and post-winter sampled Arctic charr are plotted in Fig. 5. Regressions of fork length, weight and age against \log_{10} THg concentrations in summer or post-winter sampled fish were either non-significant or yielded regressions that poorly explained variation in \log_{10} THg concentrations (summer – \log_{10} THg vs. age ($r^2 = 0.20, p = 0.001$); post-winter – \log_{10} THg vs. fork length ($r^2 = 0.09, p = 0.034$); post-winter – \log_{10} THg vs. weight ($r^2 = 0.14, p = 0.006$)). Additionally, significant heteroscedasticity indicative of their statistical inadequacy was displayed, as such there was no compelling statistical evidence for length or age standardization of the \log_{10} THg concentrations data. Examination of differences in the relationships between tested variables and raw and altered \log_{10} THg values also

398 provided no compelling evidence for the correction of \log_{10} THg concentrations for lipids following
399 (Kahilainen et al. 2016), as relationships between the parameters did not significantly change after
400 transformation. Therefore, raw \log_{10} transformed results were used in all subsequent statistical analyses.
401 Weak and seasonally differentiated patterns of association between \log_{10} THg and stable isotope data
402 ($\delta^{13}\text{C}$, % C, $\delta^{15}\text{N}$) were found (Fig. 5). \log_{10} THg increased with $\delta^{13}\text{C}$ ($r^2 = 0.23$, $p < 0.0001$) in summer
403 and $\delta^{15}\text{N}$ in post-winter sampled fish ($r^2 = 0.09$, $p = 0.031$), and decreased with % C only in summer
404 sampled Arctic charr ($r^2 = 0.19$, $p = 0.002$). Significant relationships between \log_{10} THg concentrations
405 and \log_{10} % lipid values or \log_{10} caloric densities showed significant association (negative) only with \log_{10}
406 % lipids (Fig. 5) in late summer captured Arctic charr ($r^2 = 0.20$, $p = 0.018$).

407 *3.4 General Linear Models*

408 Models best explaining variation in \log_{10} % lipid values, \log_{10} caloric densities and \log_{10} THg
409 concentrations are reported in Table 3. *AICc* model selection yielded multiple models with a Δ_i within 2
410 of the best model that were considered as essentially as good as the best model. For \log_{10} % lipid values
411 these included two models including subsets of the variables season, % C, and % N, although Akaike
412 weight (w_i) and evidence ratio (ER_i) measures were better for the model including all three variables. For
413 caloric density there were three equivalent models that included combinations of the variables: season,
414 age, condition, fork length, total weight, % C and % N. Akaike weight (w_i) and evidence ratio (ER_i)
415 measures suggested better support for the models including either age or fork length as variables, rather
416 than weight. Similarly for \log_{10} THg, three equivalent models inclusive of subsets of the variables season,
417 total weight, condition $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ were estimated, with the model including season having the lowest
418 likelihood of being the best approximating model for describing the \log_{10} THg concentration data.

419 **4. Discussion**

420 Somatic condition and weight declined in post-winter captured fish as hypothesized. Significant
421 seasonal differences in %N (decline) and $\delta^{13}\text{C}$ (increase) were also observed, whereas no significant
422 seasonal variation was evident for the other biological parameters. Significant seasonal variation existed

423 for lipid content and caloric density, but contrary to what was hypothesized, values determined from
424 Arctic charr collected during the post-winter sampling were significantly higher than those determined
425 from fish returning from the marine environment in late summer. Percent lipid values and caloric
426 densities were correlated in the tissue of post-winter sampled Arctic charr, but were not significantly
427 related in late summer migrants. Additionally, significant relationships between % lipid values and caloric
428 densities existed between some, but not all of the studied variables of interest. Seasonal variation existed
429 for THg concentrations and was contrary to what was expected, declining in post-winter sampled Arctic
430 charr. THg concentrations were significantly related to some, but not all, of the tested variables and were
431 unrelated to % lipid values and caloric densities, except in late summer sampled Arctic charr where
432 concentrations significantly declined with increasing lipid content. Models best supporting the data from
433 the previously stated analyses better explained variation in data when inclusive of multiple parameters.
434 While no single model was exclusively best, models generally included variables considered of traditional
435 importance (i.e., fish size, condition and feeding patterns) as well as season.

436 *4.1 Seasonal Variation in Biological Variables and Stable Isotope Values*

437 Condition, driven by decreases in mean weight rather changes in mean length, declined between
438 seasonal sampling periods, with mean K values of post-winter collected Arctic charr being significantly
439 less than those of returning marine migrants. Similar significant over-winter reductions in somatic
440 condition have been reported for Norwegian resident lacustrine Arctic charr despite winter feeding
441 (Amundsen and Knudsen 2009; Klemetsen et al. 2003b). However, end of winter condition for non-
442 reproductive individuals captured near Kangiqsualujjuaq, Nunavik, Québec, was reported to consistently
443 exceed 1.0 (Boivin and Power 1990). Thus, variation in the extent of post-winter declines in condition is
444 apparent among populations and likely among years.

445 Declines in condition appear linked to reduced seasonal feeding reflected in the seasonal
446 differences of % N in the muscle tissue, with declines in % N having been reported for resident lacustrine
447 Arctic charr after prolonged periods of fasting (Power et al. 2009). Reductions in % N have similarly been
448 demonstrated in other species (Elliott 1976; Guerin-Ancey 1976; Van Weerd et al. 1995) and are

449 associated with continuous losses of nitrogenous compounds via waste products during fasting (Elliott
450 1976; Hobson et al. 1993; Steele and Daniel 1978). These losses are substantive when compared to
451 continuously fed fish (Van Weerd et al. 1995). During prolonged periods of fasting, enrichment of $\delta^{15}\text{N}$
452 values is anticipated via similar catabolization processes associated with reductions in % N values
453 (Gannes et al. 1997; Hobson et al. 1993; McCutchan Jr et al. 2003). While here tests of differences in
454 $\delta^{15}\text{N}$ between periods showed no significant changes, the differences in mean size between periods may
455 have masked the extent of the overall increase in $\delta^{15}\text{N}$ occurring during the fasting period. For example,
456 the significant relationship between fork length and $\delta^{15}\text{N}$ often reported in the literature (e.g., (Gantner et
457 al. 2010; van der Velden et al. 2013a) and seen here ($r^2 = 0.501, p < 0.031$) yields a $\delta^{15}\text{N}$ prediction range
458 (12.51-13.04) for summer fish of a size equivalent to the observed mean size of post-winter fish that does
459 not include the mean reported $\delta^{15}\text{N}$ value (13.33) found for post-winter fish. Furthermore, the overall
460 absolute increase in $\delta^{15}\text{N}$ between periods (0.27) observed here fell within the 95% confidence limits
461 (0.26-0.74) of the mean effect size for starvation induced changes in $\delta^{15}\text{N}$ estimated from a meta-analysis
462 of fasting studies (Hertz et al. 2015). Overall, the evidence suggests a biologically significant increase in
463 $\delta^{15}\text{N}$ occurred as a result of fasting in over-wintering fish. Similarly, use of lipid reserves as an over-
464 winter energy source (e.g., (Dutil 1986; Jørgensen et al. 1997)), typically in the range of -24.91 to -28.51
465 for salmonids (Aursand et al. 2000), suggests observable declines in $\delta^{13}\text{C}$ would occur over the winter
466 period as tissues equilibrated over time with catabolized lipid reserves (e.g., (Herzka and Holt 2000)). The
467 observed absence of short term feeding by post-winter captured Arctic charr, established here through an
468 analysis of the upper gastrointestinal tract, in conjunction with noted declines in weight, somatic
469 condition, %N, and $\delta^{13}\text{C}$ and the directional shifts in $\delta^{15}\text{N}$ are all indicative of prolonged periods of
470 fasting exceeding several months consistent with the over-wintering period (Hesslein et al. 1993; Power
471 et al. 2009).

472 *4.2 Lipid Content and Caloric Density*

473 Somatic condition, weight loss and % N values indicative of prolonged periods of fasting are
474 consistent with previous literature detailing the over-winter period for Arctic charr (Amundsen and

475 Knudsen 2009; Jørgensen et al. 1997; Power et al. 2009). Over-winter changes in lipid content and caloric
476 densities ran contrary to what was hypothesized and were significantly higher in the dorsal muscle tissue
477 of post-wintering Arctic charr. Elevated post-winter % lipid values and caloric densities might be
478 indicative of winter feeding, as previously inferred through observations of foraging behaviour (Boivin
479 1987) and examination of winter movement activities (Mulder et al. 2018b). However, evidence for the
480 absence of short term feeding provided by empty stomachs and upper gastrointestinal tracts, reductions in
481 somatic condition, weight, and % N, is more consistent with prolonged periods of non-feeding (Hesslein
482 et al. 1993; Power et al. 2009). While previous literature (Jobling et al. 1998; Jørgensen et al. 1997) has
483 reported female anadromous Arctic charr exhibiting significantly greater depletion of lipid stores
484 compared to their male counterparts during the over-wintering months, sex was not correlated with %
485 lipid or caloric densities in this study. The lack of a significant relationship between sex and fish
486 condition indices measures has been observed with other species (Kitts et al. 2004; Usydus et al. 2012),
487 with differences among studies possibly related to the proportion of spawning ready adults (Henderson
488 and Tocher 1987; Jobling et al. 1998; Medford and Mackay 1978).

489 Considered together, the evidence of over-winter fasting, increased mortality, reduced weight and
490 condition, and paradoxical increases in % lipids and caloric densities suggest condition selective mortality
491 may be operating over the winter period. Condition selective mortality acts through a range of phenotypic
492 and genotypic variables to remove poorly conditioned individuals from a population with consequences
493 for evolution and population demographics (Chen and Maklakov 2012; Gagliano et al. 2007; Ronget et al.
494 2017). Sources of condition dependent mortality often include starvation, thermal stress, predation, failure
495 to transition between ontogenetic life stages, and the interactions between the multiple factors (Gagliano
496 et al. 2007; Miranda and Hubbard 1994; Ronget et al. 2017). For a species such as Arctic charr, over-
497 wintering in low productivity, oligotrophic environments, and given the evidence noted above, starvation
498 would appear to be the mechanism of most interest.

499 Starvation or reduced feeding is a consistent driver of over-wintering and selective mortality and
500 has been implicated as the cause of mortality for different life stages of several fish species, including

501 Arctic charr (Biro et al. 2004; Byström et al. 2006; Post and Evans 1989). Fish size often has considerable
502 influence, as smaller fish with higher metabolic demands and lower lipid and protein reserves relative to
503 larger conspecifics deplete critical energy reserves at an escalated rate, resulting in more rapid starvation
504 and higher subsequent mortality (Henderson et al. 1988; Smith and Griffith 1994; Thompson et al. 1991).
505 For example, studies of condition selective mortality among age-0 walleye Pollock (*Theragra*
506 *chalcogramma*) showed that while lipid stores and body condition for the test group as a whole were
507 rapidly reduced by starvation, survivors had significantly higher lipid content than mortalities, with values
508 often exceeding those of pre-starvation fish (Sogard and Olla 2000). Additionally, Searcy and Sponaugle
509 (2001) examined mortality as a function of early life history traits (size-at-age and growth rates) at critical
510 periods in the Bluehead wrasse (*Thalassoma bifasciatum*) and the Slippery dick (*Halichoeres bivittatus*)
511 and similarly noted that the better conditioned fish survived. The effect of condition selective mortality,
512 therefore, would be to shift the mean of the trait distribution in ways that would yield no apparent effect
513 of over-wintering on lipid and body reserves, or as here, apparent improvement as a result of the
514 systematic removal of poorer conditioned individuals. Further, condition selective mortality should
515 increase apparent mortality within the population as was also noted here.

516 The life history of Arctic charr further argues for the influence of condition selective mortality.
517 Arctic charr are a long lived fish species (Johnson 1983; Johnson 1989; Power et al. 2008) and the
518 prevalence of condition dependent mortality has been theoretically linked with increased life spans (Chen
519 and Maklakov 2012). Arctic charr are also fall spawning and body lipids in fish generally decrease
520 coincident with maturation as individuals mobilize lipids into maturing gonads (Henderson and Tocher
521 1987). In Arctic charr, the overall change in body lipids maybe as high as 30 – 80% after spawning and
522 over-wintering (Dutil 1986; Jobling 1981; Jørgensen et al. 1997) with post-spawners being much more
523 depleted when compared to non-reproductive individuals (Dutil 1986). Spawning has also previously
524 been linked to increased over-winter mortality in Largemouth bass, *Micropterus salmoides* (Post et al.
525 1998). If condition-dependent mortality was influencing the Deception River population, it would be
526 expected to increase the mortality of spawned fish. Given the inverse relationship between body lipid

527 content and the gonadosomatic index (Henderson and Tocher 1987), fish preparing to spawn would have
528 lower muscle tissue reserves in comparison to non-spawning fish. Higher mortality among spawning fish
529 with lower muscle lipid reserves would, therefore, effectively act to remove a greater proportion of the
530 returning migrants at the lower end of % lipid spectrum. The net effect would be an increase in measured
531 mean % lipids among over-winter survivors, yielding the pattern of seasonal differences in % lipid and
532 caloric density values observed here. While we did not measure the proportion of spawning ready adults,
533 the seasonal effect can be expected to be particularly strong in years when there is a high proportion of
534 spawning ready fish among the marine re-entry migrants.

535 *4.3 THg*

536 Quantification of seasonal variation in THg concentrations determined all measured values were
537 below the regulatory $0.5 \text{ mg} \cdot \text{kg}^{-1}$ of mercury recommended in Health Canada's commercial guideline of
538 maximum levels for chemical contaminants in foods (Government of Canada 2019; Health Canada 2018).
539 Thus the seasonal risks for capture and consumption associated with the winter fishery for anadromous
540 Arctic charr in the Deception River system appear minimal. However, further evaluation of seasonal THg
541 consumption risks for the system's resident Arctic charr is recommended given previously documented
542 higher winter THg concentrations in other lacustrine resident Arctic charr populations (Kahilainen et al.
543 2016) and consistently higher THg concentrations in lake-dwelling life history forms for this species
544 (Swanson et al. 2011; Van der Velden et al. 2015; van der Velden et al. 2013b).

545 Hypothesized over-wintering anorexia, prompted by a cessation of feeding by anadromous Arctic
546 charr during the winter months, leading to seasonal energy reserve losses and increases in THg
547 concentrations (Cizdziel et al. 2002; Kahilainen et al. 2016; Keva et al. 2017) was not observed in the
548 Deception fish. Rather, THg concentrations were significantly higher in tissue collected from Arctic charr
549 sampled during the summer in the marine environment. Similar to seasonal % lipid and caloric density
550 data, seasonal differences in THg concentrations may have resulted from the consequences of condition
551 selective mortality, as suggested by estimated seasonal increases in mortality. The removal of poorly
552 conditioned, lower lipid content individuals via condition selective mortality would increase measured

553 mean lipid content, which itself is often negatively correlated with THg concentrations (Post et al. 2007;
554 Wiener et al. 2003). Thus, better conditioned post winter survivors with higher lipids would shift the
555 distribution of sampled THg concentrations, yielding a decrease in mean THg.

556 Differences in prey THg content in the seasonally occupied habitats and elimination of tissue
557 THg concentrations, can be reasonably excluded as potential drivers of the observed results. The absence
558 of short term prey intake, reduced somatic condition, weight, and % N point to a significant period of
559 fasting. Further, as elimination is a metabolically-dependent process correlated positively with
560 temperature (Trudel and Rasmussen 1997) it is unlikely to have played a major role in determining
561 seasonal differences because of the narrow range of cold (0.5-2°C) temperatures occupied by over-
562 wintering Arctic charr to reduce metabolism (Mulder et al. 2018a). The continued loss of proteins during
563 fasting via nitrogenous waste products (Elliott 1976; Hobson et al. 1993; Steele and Daniel 1978), e.g.,
564 reduced % N in post-winter fish, may have contributed to the declines in measured THg as THg in fish
565 tissues is almost exclusively bound within proteins (Amlund et al. 2007; Bury et al. 2003; Mason et al.
566 1995). The increase in caloric densities, which includes consideration of protein content, in post-winter
567 Arctic charr, however, suggests that protein loss during the over-wintering period did not substantially
568 influence seasonal variation in THg concentrations in Deception River anadromous Arctic charr. The
569 elimination and depuration of THg is remarkably slow (Amlund et al. 2007; Oliveira Ribeiro et al. 1999),
570 implying that physiological processes affecting protein content were not the main driver of the
571 significantly reduced THg concentrations observed in post-winter samples.

572 *4.4 General Linear Models*

573 While there were no clear best models for explaining the % lipid values, caloric densities, and
574 THg concentrations data, all dependent variable models were better supported when containing multiple
575 variables. The % lipids models all depended on season and % N, with the best model also including
576 consideration of % C. Key for % lipids then are variables associated with controlling food intake (season)
577 and/or the metabolic consequences of fasting (% N), with season and metabolism known to hold
578 implications for body energy reserves in fish (Dutil 1986; Jørgensen et al. 1997; Thompson et al. 1991)

579 and changes in % N being linked to continuous, non-replaced N losses via excretion during periods of
580 fasting (Post et al. 2007; Power et al. 2009). In contrast to % lipids, variation in caloric densities were
581 linked to a suite of biological and feeding variables, predominantly season, and variables reflective of
582 feeding status. Results here parallel previous research detailing seasonal feeding and its implications for
583 somatic condition and body reserve depletion in Arctic charr (Amundsen and Knudsen 2009; Rikardsen et
584 al. 2003; Sæther et al. 1996). Additionally, the inclusion of variables that have associations with both size
585 and reduced feeding were consistent with the hypothesis that condition selective mortality may be
586 exerting an influence on this population of Arctic charr, as size, starvation, and reduced feeding are
587 commonly associated with condition selective mortality (Biro et al. 2004; Byström et al. 2006; Sogard
588 and Olla 2000). Finally, models for describing variations in THg concentrations accorded with previous
589 research that has detailed relationships between metal concentrations and weight and condition (Dittman
590 and Driscoll 2009; Eastwood and Couture 2002; Swanson and Kidd 2010), season (Keva et al. 2017) and
591 indicators of diet and feeding habits (Goutte et al. 2015; Power et al. 2002; van der Velden et al. 2013a).
592 Collectively, the multivariate evidence for each of the studied variables suggests that single variable
593 correlations alone are likely insufficient for understanding variations in the environmental conditions
594 associated THg concentrations in anadromous Arctic charr.

595 *4.5 Conclusions*

596 In addition to addressing knowledge gaps associated with available regional and population
597 specific data, this research has increased the limited scientific data available on patterns of metal
598 contamination in the over-wintering anadromous Arctic charr. To our knowledge, the observed results are
599 the first detailing higher lipid content and caloric density in Arctic charr captured during the winter
600 months, a period that has previously been associated with significant reductions in body reserves.
601 Condition selective mortality is argued to be the most plausible explanation for the observed results,
602 particularly as concurrently measured variables (e.g., % N, condition, and weight loss) suggested
603 prolonged periods of fasting coincident with the known seasonal feeding behaviour of Arctic charr.
604 Relationships between THg and descriptive biological variables were consistent with the seasonally

605 dependent hypothesis, although season itself was not the single best predictor of THg concentrations.
606 Rather, multi-predictor models better described variation in the data for THg, % lipids and caloric
607 densities, with variables such as season, somatic condition, age, body size (length or weight) and feeding
608 tactics ($\delta^{13}\text{C}$, $\delta^{15}\text{N}$) being implicated in varying combinations for the best description of the data sets.
609 While there is large literature examining the associations between THg and biological or feeding
610 variables, much less is known about the effect of season. Quantification of seasonal variation in THg
611 concentrations has determined that winter consumption risks for anadromous Arctic charr in this region
612 are minimal. However, further work is necessary to elucidate global patterns of seasonal THg
613 accumulation, especially as seasonal trends may differ between life history forms for this species. Overall,
614 our corroboration of earlier studies that highlight the importance of season suggests further work is
615 required to understand seasonality in Arctic charr, especially in the face of climate change and the likely
616 effects it will have on Arctic aquatic environments.

617 **Acknowledgements**

618 We wish to acknowledge Makivik Corporation and the Nunavik Research Centre, the Raglan
619 Mine, Qaqqalik Landholding Corporation, the Ministère de la Forêt de la Faune et des Parcs, Société du
620 Plan Nord, and the Natural Sciences and Engineering Research Council (discovery grants awarded to M.
621 Power and P. Couture) for their financial assistance and logistical support. A Mitacs Accelerate Internship
622 award supported M. A. C. Martyniuk. We would also like to thank A. and S. Tayara, as well as the
623 participants in the Elder’s Spring Fishing Event, for their contributions to field work and sample
624 collection. Finally, we wish to extend our appreciation to individuals at the University of Waterloo and
625 Institut National de la Recherche Scientifique – Centre Eau Terre Environnement for help with sample
626 processing and laboratory analysis.

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Tables

Table 1 Means \pm standard deviations and ranges are given for fork lengths, total weights, ages, somatic condition, $\delta^{13}\text{C}$, % carbon (C), $\delta^{15}\text{N}$, and % nitrogen (N) of Arctic charr used from the summer 2016 and post-winter 2017 sampling seasons. Sex ratios are also noted. Significant seasonal differences are denoted with * ($p < 0.05$), ** ($p < 0.001$), and *** ($p < 0.0001$)

Season of Capture	Sample Size	Fork length (mm)	Total weight (g)	Age (Years)	Sex	Condition (K)	$\delta^{13}\text{C}$ (‰)	% C	$\delta^{15}\text{N}$ (‰)	% N
Summer 2016	49	483.5 ± 107.1	$1380 \pm 819^*$	9.6 ± 2.4	67% Female	$1.06 \pm 0.28^{***}$	$-19.42 \pm 0.99^{***}$	47.36 ± 3.06	13.06 ± 1.11	$14.00 \pm 0.82^{***}$
		143.0; 689.0	20; 3300	5; 15	33% Male	0.57; 2.38	-22.97; -16.82	35.72; 52.19	8.12; 15.00	11.22; 15.73
Post-Winter 2017	51	449.4 ± 130.2	1031 ± 824	8.9 ± 2.9	73% Female	0.91 ± 0.11	-20.55 ± 1.00	48.30 ± 2.58	13.33 ± 1.01	12.92 ± 1.05
		221.0; 698.5	99.8; 3230	5; 20	27% Male	0.71; 1.46	-22.75; -16.89	44.03; 57.51	11.23; 15.22	8.60; 14.64

Table 2 Means \pm standard deviations and ranges of dorsal muscle % lipid values, caloric densities, and THg concentrations of anadromous Arctic charr captured in the summer 2016 and post-winter 2017 sampling periods. * ($p < 0.05$), ** ($p < 0.001$), and *** ($p < 0.0001$) indicate significant seasonal variation

Location of Capture	Sample Size	Lipids (%)	Sample Size	Caloric Density (cal·g ⁻¹)	Sample Size	THg (mg·kg ⁻¹)
Summer 2016	40	4.08 \pm 2.00 2.15; 11.76	30	1327.6 \pm 51.6 1180.8; 1409.8	49	0.12 \pm 0.05* 0.06; 0.26
Post-Winter 2017	36	8.34 \pm 4.85*** 2.66; 27.98	27	1545.8 \pm 88.5*** 1371.8; 1723.8	51	0.09 \pm 0.05 0.05; 0.35

Table 3 Sample size corrected Akaike information criterion (AICc) rankings of the models* that best described variation in \log_{10} % lipid values (top) \log_{10} caloric densities ($\text{cal} \cdot \text{g}^{-1}$) (middle) and \log_{10} THg concentrations ($\text{mg} \cdot \text{kg}^{-1}$) (bottom) from anadromous Deception River Arctic charr. Only models within $\Delta_i = 2$ are included in the table as these were considered equivalent to the best model. Also given are the number of model fitted parameters (k), residual sums of squares (RSS), delta values (Δ_i) defining model the difference between the estimated model AICc and the best model AICc, the Akaike weight (w_i) and evidence ratio (ER_i) for each model

Model	k	RSS	AICc	Δ_i	w_i	ER_i
Variations in \log_{10} % lipids						
Season, % C, % N	5	2.32	-38.78	0.00	0.26	1.00
Season, % N	4	2.42	-37.79	0.99	0.16	1.63
Variations in \log_{10} caloric density						
Season, Age, Condition, % C, % N	7	0.01	-296.32	0.00	0.28	1.00
Season, Fork length, Condition, % C, % N	7	0.01	-296.20	0.12	0.26	1.06
Season, Total weight, Condition, % C, % N	7	0.01	-294.69	1.64	0.12	2.27
Variations in \log_{10} THg						
Total weight, Condition, $\delta^{13}\text{C}$	5	2.40	-78.34	0.00	0.27	1.00
Total weight, Condition, $\delta^{13}\text{C}$, $\delta^{15}\text{N}$	6	2.37	-77.73	0.61	0.20	1.36
Season, Total weight, Condition, $\delta^{13}\text{C}$	6	2.39	-76.49	1.85	0.11	2.52

* General linear models were estimated using the following candidate variables: season (summer 2016 and post-winter 2017), fork length (mm), total weight (g), age (years), somatic condition (K), $\delta^{13}\text{C}$ (‰), % carbon (C), $\delta^{15}\text{N}$ (‰), % nitrogen (N), and significant two-way interactions. Explanatory variables that were highly correlated, or known to have biological redundancy (e.g., fork length and total weight) were not included in the same model

Figures

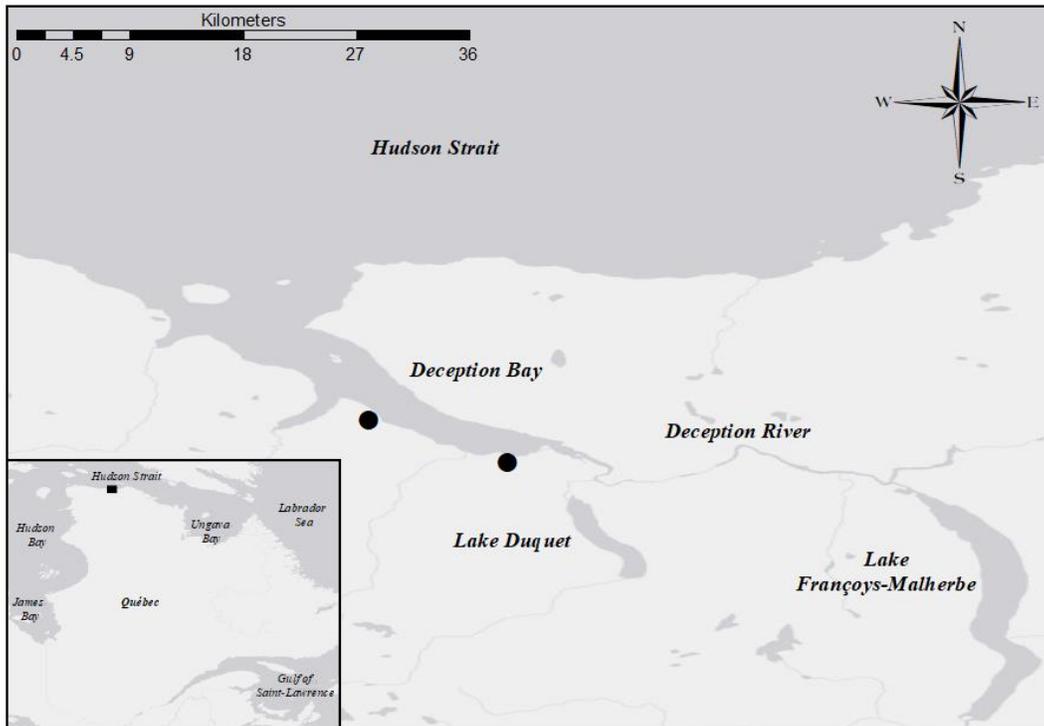


Fig. 1 Map of the Deception Bay, the Deception River, and the two over-wintering lakes, Lake Duquet and Lake François-Malherbe, from which Arctic charr were sampled for this study. Black circles represent mining operations present in the area, while the black square represents the sampling locations in relation to the province of Québec in eastern Canada

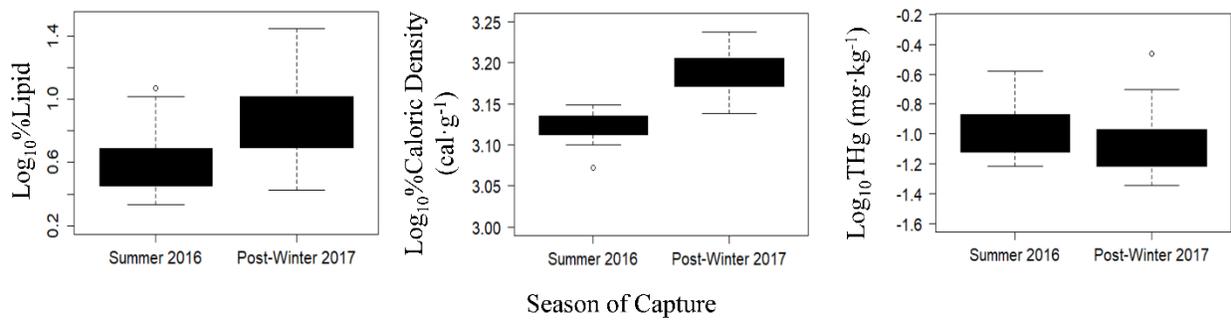


Fig. 2 Seasonal variation in dorsal muscle log₁₀ % lipid values, log₁₀ caloric densities, and log₁₀ THg concentrations from summer 2016 and post-winter 2017 sampled Deception River anadromous Arctic charr

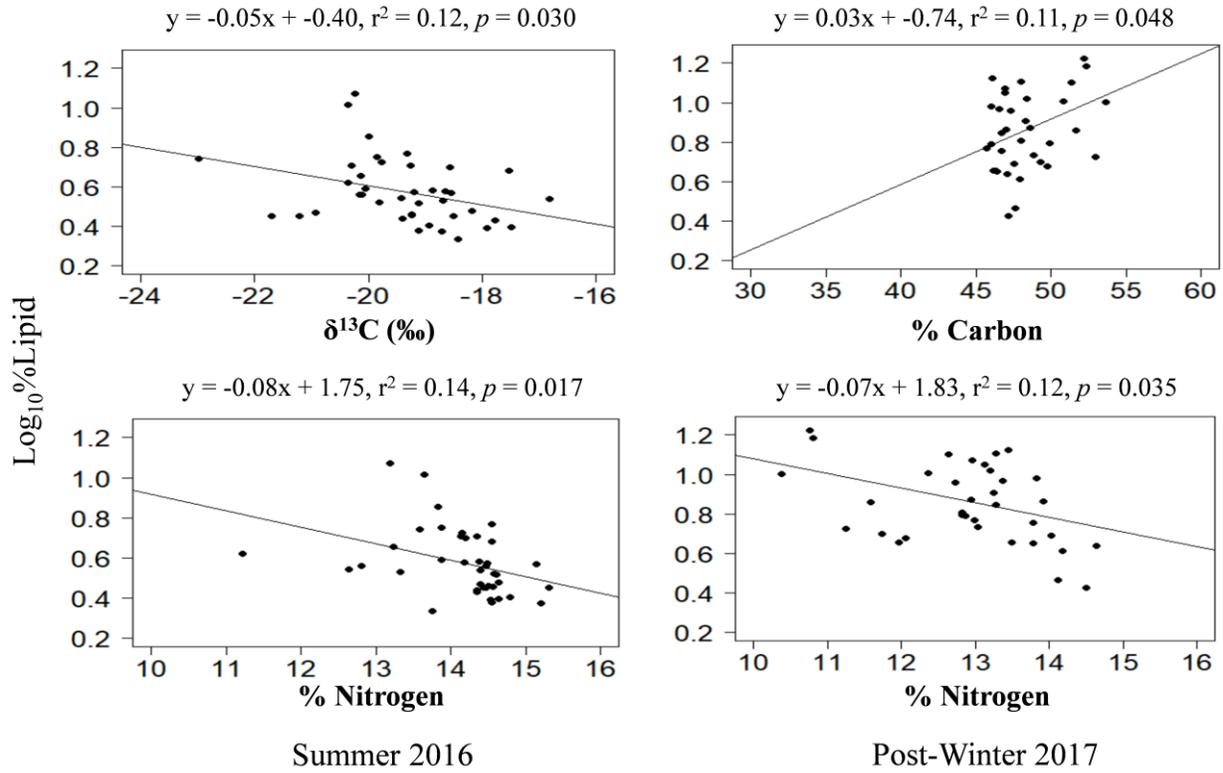


Fig. 3 Relationships between dorsal muscle log_{10} % lipid values and biological variables (fork length, total weight, fish age, and somatic condition), as well as stable isotopes ($\delta^{13}\text{C}$, % carbon, $\delta^{15}\text{N}$, and % nitrogen)

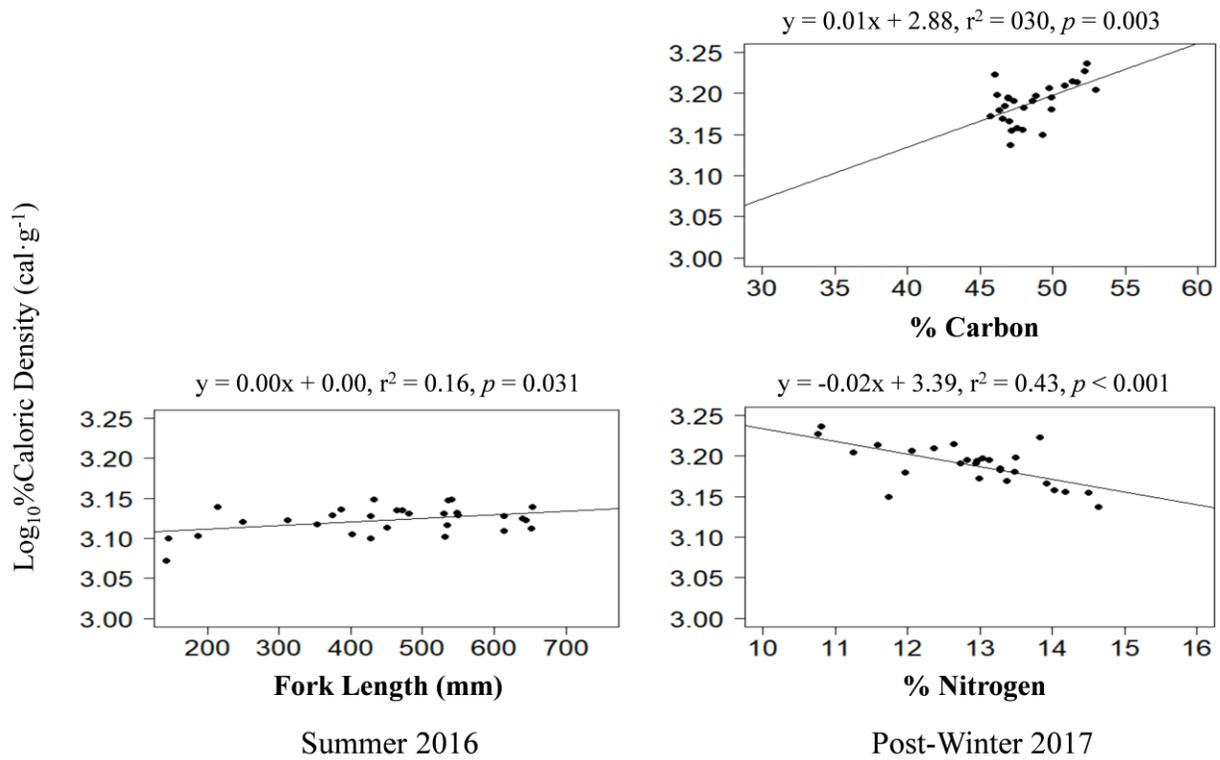
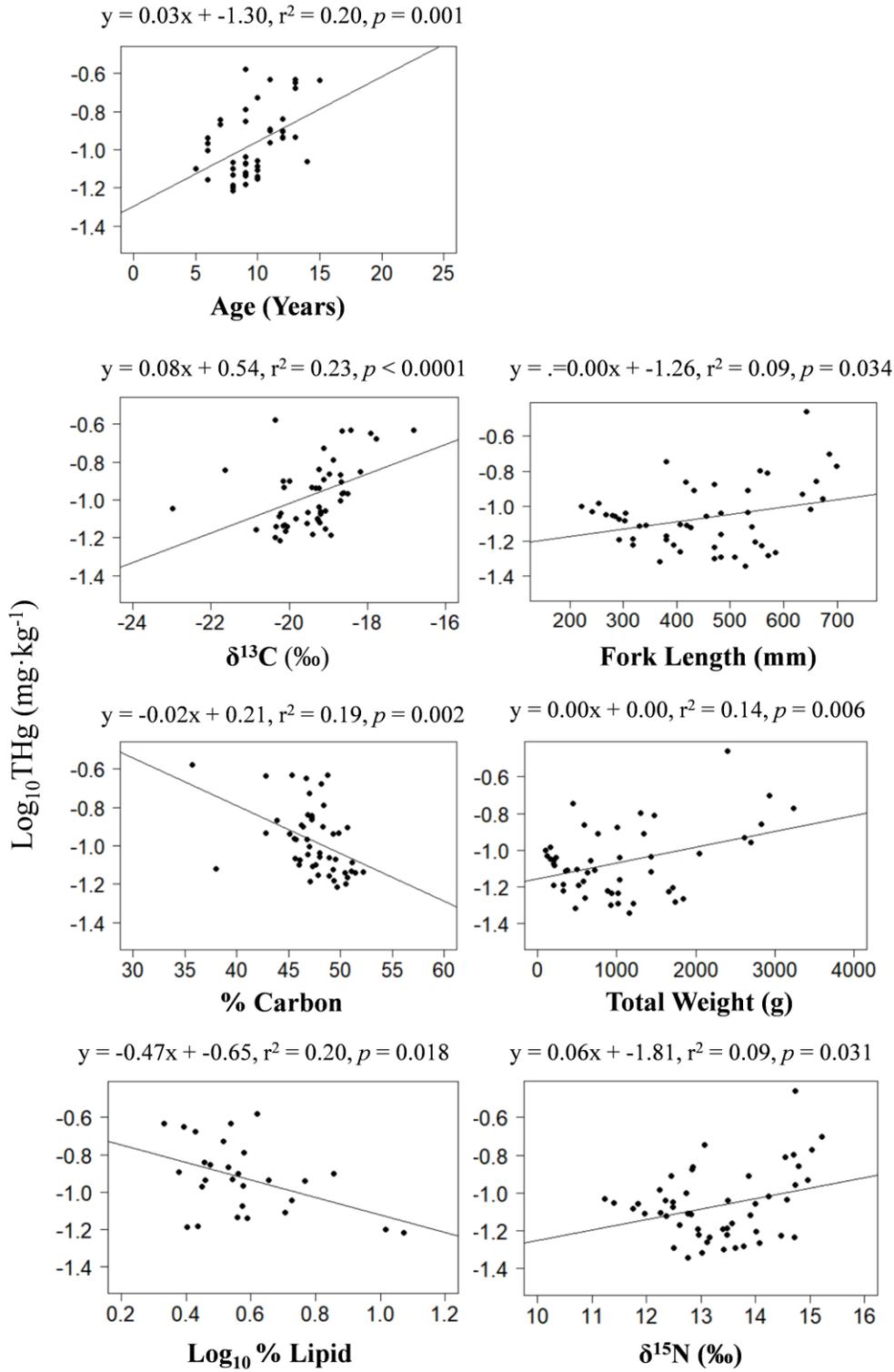


Fig. 4 Relationships between collected dorsal muscle log_{10} caloric densities and biological variables (fork length, total weight, fish age, and somatic condition), as well as stable isotopes ($\delta^{13}\text{C}$, $\% \text{ carbon}$, $\delta^{15}\text{N}$, and $\% \text{ nitrogen}$)



Summer 2016

Post-Winter 2017

Fig. 5 Relationships between sampled dorsal muscle \log_{10} THg concentrations and biological variables (fork length, total weight, age, and somatic condition), stable isotopes ($\delta^{13}\text{C}$, $\delta^{15}\text{N}$, and % carbon, and % nitrogen), and fish condition measures (\log_{10} % lipid values)