

1 **Bioenergetic consequences of warming rivers to adult Atlantic salmon *Salmo salar* during**
2 **their spawning migration**

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5 Running Head: Energy depletion of salmon in warming rivers
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24 **Summary**

25

26 1. Climate change poses a challenge to wild fishes, yet little is known about the behavioural use
27 and metabolic consequences of thermally heterogeneous water encountered by wild salmon
28 during their energetically demanding upstream spawning migration.

29 2. Temperature, body size, and activity levels were modelled to predict energy depletion of
30 salmon during their spawning migration in rivers. Archival temperature loggers revealed the
31 thermal habitat of adult migrating Atlantic salmon (*Salmo salar* Salmonidae), which we used
32 to apply bioenergetics models that estimated size-dependent temperature-driven metabolic
33 expenditures as part of the costs of the migration.

34 3. Between July 16 and August 19, the mean water temperature experienced by salmon (t_{FISH})
35 ranged from 11.5 – 18.0 °C (14.5 ± 1.2 SD °C) and closely followed the ambient surface water
36 temperature (t_{RIVER}) of the river (11.5 ° - 18.5 °C; 14.8 ± 1.4 °C) such that the regression
37 equation $t_{\text{FISH}} = 3.24 + 0.76(t_{\text{RIVER}})$ provided was highly correlated with observations ($R^2 =$
38 0.94).

39 4. Although temperature increases were predicted and confirmed to increase energetic costs,
40 rates of energy depletion were more sensitive to changes in swimming speed and body size
41 than to temperature increases in the range explored for this system.

42 5. We conclude that warming could contribute to changing life history phenotypes of salmon in
43 some rivers, e.g., delayed river entry or reduced probability of iteroparity, with potentially
44 more dire consequences for smaller individuals.

45

46 **Keywords:** iButton, telemetry, fisheries, iteroparity, bioenergetics

47 **Introduction**

48

49 Temperature constrains the distribution of species (Pörtner, 2002) and influences the
50 timing and expression of many life history events (Walther et al., 2002) such as breeding,
51 aestivation/hibernation, and migration (Lennox et al., 2016a). For ectotherms such as most
52 fishes, temperature directly influences and can ultimately limit the rates of enzymatic, metabolic,
53 and cardiac processes (Behrisch 1969; Fry, 1971; Farrell et al., 2009). At temperatures beyond
54 optimum, the tissue demands for oxygen continue to increase (Pörtner and Knust, 2007) but the
55 capacity to deliver that oxygen decreases (i.e. decline in aerobic scope; Priede, 1977) until
56 glycolytic ATP production replaces aerobic respiration (i.e. anaerobiosis; Pörtner 2002). Warm
57 water temperature can be energetically taxing (Rand et al., 2006; Katinic et al., 2015), accelerate
58 maturation (Morbey et al., 2005), and promote pathogen infection and development (Harvell et
59 al., 2002).

60 In many rivers, water temperature is increasing due to climate change (Webb, 1996; Mote
61 et al., 2003; Caissie, 2006). This is a particular concern in the Arctic where water temperatures
62 are projected to increase at a faster pace than at lower latitudes (O'Brien et al., 2004; Prowse et
63 al., 2006). As water temperatures rise, the costs of freshwater residence will be altered and
64 ectotherm biology will be affected (Crozier et al., 2008; Jonsson and Jonsson, 2009). There are
65 many freshwater animals in coastal zones that use both marine and freshwater environments to
66 complete their life history, with water temperatures generally much warmer in freshwater.
67 Migrants must negotiate the two environments and allocate energy such that their rate of energy
68 depletion does not exceed physiological limits or energetic reserves (Hodgson and Quinn, 2002;
69 Burnett et al., 2014). As temperatures increase, the physiology and behaviour of freshwater

70 animals is expected to reflect higher energetic costs of residence (Crozier and Hutchings, 2014).
71 Energetics models provide tools for ecologists to investigate energy allocation of animals; energy
72 acquisition must be balanced against depletion, which depends on the individual's size, activity,
73 and the water temperature (Brett, 1971; Fry, 1971; Kingsolver and Huey, 2008). Individuals
74 must allocate energy during the migration efficiently with a goal of successfully participating in
75 spawning and other life history events, which yields considerable diversity in physiological and
76 behavioural phenotypes to promote survival (Glebe and Leggett, 1981; Jonsson et al., 1997;
77 Standen et al., 2002).

78 Atlantic salmon (*Salmo salar* Salmonidae) have a Holarctic distribution and rely on
79 freshwater for spawning and nursery grounds. Adults return from the sea to spawn at various
80 sizes, often with an earlier timed river entry associated with southern latitudes (Heggberget,
81 1988; Klemetsen et al., 2003; Thorstad et al., 2011). Freshwater residence is also briefer for
82 many adult salmon at the northern edge of their range, although some individuals enter more
83 than a year before reproducing. Timing of entry is known to depend upon river characteristics as
84 well as individual size (Jonsson et al., 1991a) and salmon can exhibit a refuging behaviour
85 during the migration as a maintenance strategy (Richard et al., 2014; Frechette et al., In Press).
86 When salmon enter freshwater they cease feeding, such that stored energy must then suffice for
87 migration, completion of sexual maturation, and spawning (Moore, 1997). Consequently, an
88 iteroparous migrant, like the Atlantic salmon, must also preserve enough energy after spawning
89 for its return to the ocean where it can begin the reconditioning process for subsequent migration
90 and reproduction (Jonsson et al., 1991b, 1997; Halttunen et al., 2013). The Arctic is an area of
91 relatively sparse human habitation and impact; therefore, climate change may present one of the
92 most salient threats to salmon in the north. The phenotypic plasticity of salmon means that they

93 may adjust either their body size through changes in maturation schedules or their behaviour by
94 shifting run timing to adapt to changing demands associated with climate change (Clark et al.,
95 2012; Otero et al., 2014; Dempson et al., 2017). Models predicting the energetic costs of size,
96 activity, and water temperature therefore will yield a better understanding of Atlantic salmon
97 migration and potential responses to climate change.

98 Animal size, activity, and temperature contribute simultaneously to the metabolic rate
99 and the energy demands upon the individual. Warming temperatures portend bioenergetic failure
100 of some organisms (Farrell et al., 2008; Rummer et al., 2014) and the temperature-size rule
101 posits that smaller organisms should be favoured in warmer temperatures (Kingsolver and Huey,
102 2008). Given that thermal ecology of adult Atlantic salmon during their freshwater migration is
103 poorly understood (Bardonnnet and Baglinière, 2000), we designed a study to investigate the
104 contributions of water temperature and size, along with swimming activity, to energetic depletion
105 of this anadromous fish on its spawning migration in freshwater. We hypothesized that all three
106 variables (size, swimming activity, temperature) would influence energy demands on
107 individuals, which would imply that changes due to climate warming will the rate of accelerate
108 energy depletion of freshwater fish during their migration.

109

110 **Methods**

111

112 *Study Area*

113

114 We studied a population of Atlantic salmon in the Lakselva River in Finnmark, Norway.
115 These Atlantic salmon enter the river from May-September (E. Liberg, Personal

116 Communication), but based on quantitative catch records the majority begin their freshwater
117 migration in July and August (www.scanatura.no). The Lakselva River flows through two lakes,
118 Øvrevatnet and Nedrevatnet (Figure 1). River discharge is measured at Skoganvarre
119 (69°50'13.2"N 25°05'07.5"E), encompassing 61% of the watershed, which can be extrapolated to
120 estimate total discharge (T. Havn, unpublished). Estimated average yearly discharge from 2000-
121 2016 was $24 \pm 2.2 \text{ m}^3 \text{ s}^{-1}$ (range = 21-33 $\text{m}^3 \text{ s}^{-1}$). The river also has one major tributary, which
122 flows into Lake Nedrevatnet. Most salmon hold within the river just below the lakes (Lennox et
123 al., 2016b) until spawning begins in October (E. Liberg, Personal Communication). After
124 spawning, surviving Atlantic salmon typically overwinter in the river as kelts and then exit the
125 following spring to recondition at sea.

126 Lakselva has a catchment area of 1,536 km^2 and the mainstem of the river has 45 km
127 available to salmon for spawning habitat. Lakselva River drains into the Porsangerfjord within
128 the administrative district of the municipality of Lakselv (70°03'55.2" N 24°55'43.8" E). To
129 monitor ambient river water temperature, we deployed four HOBO temperature loggers (HOBO
130 Pendant Temperature/Light Data Logger 64K-UA-002-64, Onset, Massachusetts, USA) in the
131 river from 17 July to 24 October 2014 (see Supplementary Material for description of logger
132 calibration). One river temperature data logger was stationed in the lower section of the river,
133 one in Lake Nedrevatnet, and one in the upper section of the river; all were placed approximately
134 one meter below the surface (Figure 1). The river monitoring stations recorded water temperature
135 every 10 min. Previous monitoring by the Lakselva Landowners Association observed little
136 variability of the surface water temperatures among sites in the lower reach of the river (E.
137 Liberg, personal communication).

138

139 *Sampling*

140

141 We cooperated with local anglers and captured Atlantic salmon for our experiment from
142 July 7 – August 29, 2014. Cooperation with local anglers encouraged engagement of locals and
143 other stakeholders in the work and was important for ensuring that logging tags from recaptured
144 salmon were returned. Only experienced salmon anglers participated and we did not tag any
145 salmon that was in poor condition because of angling (i.e. critical hooking, extreme bleeding;
146 Lennox et al., 2016b). Twenty-One Atlantic salmon (mean = 90 ± 16 cm SD TL, range: 62 – 121
147 cm) were double-tagged with radio-transmitting tags in the frequency range 142.114 – 142.213
148 (model F2120, Advanced Telemetry Systems [ATS], Minnesota USA) and archival temperature
149 loggers (iButton Thermochron© Temperature Data Loggers DS1921Z-F5, Maxim Integrated,
150 San Jose, California, USA). The tagging methods used sterile hypodermic needles and steel wire
151 to secure the tag through the dorsal musculature at the base of the dorsal fin (described in
152 Lennox et al., 2016b). Opposite the radio tag, an iButton archival temperature logger (set to
153 record temperature at 90 min intervals) was attached instead of the usual plastic backplate
154 (Figure 2; see Supplementary Material for calibration information). All handling and tagging was
155 conducted in accordance with the Carleton University Animal Care and Use Committee.

156

157 *Data Analysis*

158

159 A 500 NOK reward for returning tags was offered to anglers that captured tagged salmon.
160 Archival temperature loggers were recovered from 10 of the 21 salmon that were tagged (Table
161 1). Five were recovered from salmon that were removed from the river by harpoon on 25

162 September and the other five loggers were removed from salmon that were recaptured and
163 harvested by anglers (one was recaptured as a kelt the following summer, June 20, 2015). As a
164 result, the sampling intervals differed among individuals, with some temperature records
165 spanning several days whereas others covered much longer periods. Our modelling was
166 implemented to determine the relationship between fish habitat and river temperatures using
167 linear regression in R (R Core Team, 2017). In consideration of possible differences among fish
168 attributable to differences in fish size, fish position in the river, or other factors, we generated a
169 mixed effects linear model (*lme* function in R package nlme; Pinheiro et al., 2014) with fish ID
170 as a random intercept. To determine whether the mixed effects model fit better than the fixed
171 effects model, the mixed effects model was compared to a generalized least squares regression
172 (*gls* function in R package nlme) with restricted maximum likelihood estimation using Akaike
173 Information Criterion (Zuur et al. 2009). Examination of the autocorrelation function revealed
174 residual autocorrelation, so we generated models accounting for residual autocorrelation by fish
175 ID while accounting for time (i.e. form= \sim time|fishID). Comparison of AIC values among *gls*
176 models with different autocorrelation structures (corGaus, corExp, corLin, corSpher, corAR1,
177 corRatio) revealed a best fit of the exponential correlation structure. Model predictions were
178 extracted with the *predict* function and compared to actual values measured by the tags placed on
179 the fish using linear regression.

180

181 *Bioenergetics Modelling*

182

183 To determine the rates of oxygen uptake of fish swum at different speeds and
184 temperatures, hatchery-raised adult Atlantic salmon (body mass: 2.6 ± 0.4 kg; fork length: $60.6 \pm$

185 3.9 cm SE) were held in outdoor 4000 L circular fiberglass tanks under ambient seawater
186 conditions (7-11°C, dissolved oxygen > 90% saturation) and seasonal photoperiod at the Centre
187 for Aquaculture and Environmental Research (West Vancouver, BC, Canada). Food was
188 withheld for 24 h before experiments. A subset of fish (N = 22) was instrumented to measure
189 cardiovascular parameters (data not shown here) while other fish were not instrumented (N =
190 14). Surgical protocols followed those detailed in Eliason et al. (2013a). The fish were
191 anesthetized in buffered tricaine methane-sulfonate (0.1 g L⁻¹ MS-222 and 0.1 g L⁻¹ NaHCO₃,
192 Sigma-Aldrich, Oakville, Ontario, Canada), weighed and transferred to a surgical table where
193 they were maintained under a lower dose of buffered anesthetic (0.075 g L⁻¹ MS-222 and 0.05 g
194 L⁻¹ NaHCO₃). A 3 mm SB flow probe (Transonic Systems, Ithaca, NY, USA) was placed around
195 the ventral aorta, a PE-50 cannula was inserted into the dorsal aorta, and a PE-50 cannula or an
196 oxygen probe (custom-designed, Ocean Optics, Dunedin, FL, USA) was placed in the sinus
197 venosus (Eliason et al., 2013a). The flow probe and cannulae/oxygen probe leads were sutured
198 along the dorsal ridge of the fish's body using 2-0 silk sutures. Fish were placed in a Brett-type
199 swim tunnel (220 L or 400 L; described in Steinhausen et al., 2008) and allowed to recover
200 overnight at ambient water temperatures at low water velocity (0.3-0.4 body lengths per second
201 (bl s⁻¹). This water velocity was sufficient to orient the fish but did not induce swimming.
202 Similar surgeries did not impair swimming metabolism of Pacific salmon compared to controls
203 (Eliason et al. 2013b). The next day, resting oxygen uptake (MO₂) was measured at the ambient
204 water temperature (ranged from 7-12°C over the study) and then the fish underwent a standard
205 ramp U_{crit} critical swimming challenge (Eliason et al., 2013a). Water velocity was increased
206 every 5 min until ~50% of the critical swimming speed (U_{crit}; ~1 bl s⁻¹) was attained. Thereafter,
207 the water velocity was increased in smaller velocity increments (~0.15 bl s⁻¹) every 20 min until

208 fatigue was induced (defined as the fish resting at the back of the swim tunnel for > 30 s). MO_2
209 was measured during the second half of each 20 min interval. When the fish became fatigued, the
210 water velocity was immediately reduced back to the resting velocity ($\sim 0.3 \text{ bl s}^{-1}$) and the fish was
211 allowed to recover overnight. The next day, the water temperature was acutely increased by $2 \text{ }^\circ\text{C}$
212 h^{-1} to the warm test temperature ($10\text{-}22^\circ\text{C}$). Resting MO_2 was assessed and then the fish
213 underwent the same U_{crit} protocol described above.

214 To account for the allometric scaling of standard metabolic rate (Brett and Glass, 1973),
215 we standardized the resting oxygen uptake for three fish sizes in the river, small (total length =
216 63.5 cm, mass = 3.03 kg), medium (total length = 89.0 cm, mass = 8.34 kg), and large (total
217 length = 119.0 cm, mass = 20.18 kg); these lengths approximately spanned the minimum,
218 average, and maximum lengths encountered in Lakselva. Corresponding weights were derived
219 from an empirical table of length-to-weight conversions for fish from the study site
220 (www.lakselva.no; the table is based on fork lengths which required that we convert our total
221 lengths to fork length by dividing by 1.046). The measured resting values of MO_2 were scaled
222 using an equation from Steffensen et al. (1994), in which the $MO_2^{\text{corrected}} = MO_2^{\text{initial}} \times (\text{Mass}^{\text{initial}} /$
223 $\text{Mass}^{\text{corrected}})^{(1-\text{exp})}$, where the MO_2^{initial} is the oxygen uptake of fish of $\text{Mass}^{\text{initial}}$, corrected by
224 dividing that fish's mass by the mass of the fish of the desired size (cm; in this case we used the
225 three values above) and the exp is the scaling exponent 0.80 (Winberg 1956; Steffensen et al.,
226 1994; Clarke and Johnston, 1999; Rosewarne et al., 2016). The oxygen uptake data at
227 temperatures between 7 and $22 \text{ }^\circ\text{C}$ (above) were fit with an exponential curve for resting data and
228 a second order polynomial relationship for fish swimming at 1.0 bl s^{-1} . Although oxygen uptake
229 was not measured at an intermediate swim speed, we estimated oxygen uptake at 0.5 and 0.7 bl s^{-1}
230 by interpolating from the resting and 1.0 bl s^{-1} data and fit exponential curves through the data

231 to evaluate the internal sensitivity of our oxygen consumption equations. For these curves, values
232 were derived using only fish at temperatures measured for both resting and swimming velocities.

233 We estimated daily oxygen uptake for fish in the river between July 13 and December 16
234 based on the calculated daily average temperatures derived from the HOBO river temperature
235 logger. The HOBO river temperature logger was active in the river July 19 – August 19; beyond
236 these dates the water temperatures were estimated from the iButton archival temperature loggers
237 by back calculation using the regression equation (see Results). By fitting the regression
238 equations to the water temperature data, daily oxygen uptake ($\text{mg O}_2 \text{ kg}^{-1} \text{ min}^{-1}$) was estimated
239 for each day in the study period for three size classes of fish and at the four swimming speeds.
240 Daily energy consumption was then derived by multiplying by 1440 (minutes in a day) and by
241 the total mass of the fish converted from the three lengths we selected (2.67 kg, 7.00 kg, 17.69
242 kg) to calculate the $\text{mg O}_2 \text{ d}^{-1}$ consumed per fish of the three sizes. Values in $\text{mg O}_2 \text{ kg}^{-1} \text{ min}^{-1}$
243 were multiplied by 60 to get $\text{mg O}_2 \text{ kg}^{-1} \text{ h}^{-1}$ and then multiplied by 0.00325 to convert to kCal kg^{-1}
244 h^{-1} based on the caloric conversion for Pacific salmon (Brett, 1995). Daily kilocalories for fish
245 in each size class were then calculated by multiplying by the weight (kg) and by 24 (h).
246 Energetic scope of migrants was calculated based on equations in Jonsson et al. (1997). Energy
247 available for migration is a function of individual length (L_{TOTAL}); the initial energy in kilojoules
248 is described by the equation: $E = \exp(0.044 \times L_{\text{TOTAL}} + 6.99)$ and the post-spawn energy
249 described by the equation: $E = \exp(0.035 \times L_{\text{TOTAL}} + 6.51)$, and then converted from kJ to kCal
250 by multiplying by 0.239. Projected energy depletion was calculated based on the initial energy
251 available with a lower limit (i.e. threshold for life) considered to be the post-spawn energy.
252 Models of global temperature increase are available to project the rate of warming, but vary
253 based on latitude and have uncertainty associated with the emissions scenario, along with

254 concomitant changes in radiative forcing, precipitation, cloud cover, albedo, ecosystem structure,
255 etc. (Joos et al., 2001). Instead of using specific projections we calculated the expected energetic
256 use for the study period at the present water temperature and for warming scenarios of 1, 2, and 4
257 °C.

258

259 **Results**

260

261 Of the 21 salmon that were tagged, one salmon left the river prior to the spawning season
262 and one salmon died immediately after release (see Lennox et al., 2016b). Of the remaining 19
263 tagged salmon, archival temperature loggers were recovered from 10 salmon (Table 1). These
264 salmon were mostly tagged in the lower reaches of the river and none of them transited the lakes
265 to access upper reaches of the river or the tributary Vuolajohka. Therefore, no tagged salmon
266 was recorded by the fixed receiver stations and given that all tagged fish remained in this river
267 section (N = 39; Lennox et al., 2016b), only temperature readings from the lower section of the
268 river were used for modeling purposes (Figure 1).

269 We recorded a seasonal decline as well as daily oscillations in water temperature (range
270 in daily variation = 0.48 – 4.21 °C). Between July 16 and August 19, salmon were recorded at
271 temperatures between 11.5 °C and 18.0 °C (average: 14.5 ± 1.2 °C). By comparison, average
272 daily water temperatures during the same period ranged between 11.5 ° and 18.5 °C (average:
273 14.8 ± 1.4 °C). One salmon, which was caught by an angler in the river in the spring after its
274 release (fish ID 142.123-75; Table 1), provided a continuous 126 day temperature log through to
275 December 16, 2014 (Figure 3). This fish had experienced temperatures as low as -0.1 °C in
276 winter.

277 Comparison of the mixed effects and fixed effects models suggested a better fit of the
278 mixed effects model rather than the generalized least squares model ($\Delta AIC = 708$). There was a
279 significant relationship between river temperature and fish habitat temperature ($t = 260.82$, $p <$
280 0.01 ; Figure 4). Model-predicted values of fish habitat temperature had a strong (model adjusted
281 $R^2 = 0.94$) positive relationship to actual values. Predictions of fish habitat temperature could
282 therefore be accurately generated using river surface temperature data using a regression
283 equation: $t_{FISH} = 3.24 + 0.76(t_{RIVER})$.

284 Swim tunnel respirometry of hatchery Atlantic salmon was used to derive oxygen uptake
285 equations as a function of water temperature (Table 2; Figure 5). Based on published equations
286 for estimating energy content of Atlantic salmon, initial energy content of the wild salmon in
287 Lakselva were estimated based on their length to be 48,762, 13,026, and 4,242 kCal for salmon
288 measuring 119.0, 89.0, and 63.5 cm, respectively, with an expected depletion of 52, 39, and 21%
289 of somatic energy at present temperatures (Figure 6). During the 150-d modelled period (July 16
290 to Dec 16), large fish (119.0 cm) were projected to deplete the most gross energy, between
291 10,212 (at rest) and 47,610 kCal (swimming at 1.0 bl s^{-1} ; Figure 7). Small salmon had the most
292 extreme relative energy depletion; at rest, we estimated 52% energy depletion for small salmon
293 but only 21% for large salmon at ambient present temperatures (Figure 8). Projected increases in
294 temperature to $4 \text{ }^\circ\text{C}$ increased gross energy consumption to 65% and 26% for small and large
295 salmon, respectively. Faster swimming speeds depleted energy more rapidly than slower speeds,
296 demanding 169% of the somatic energy of small salmon compared to 98% from large salmon at
297 1.0 bl s^{-1} (present temperature regime). Warmer temperature ($+4 \text{ }^\circ\text{C}$) increased caloric
298 consumption for fish swimming at 1.0 bl s^{-1} by 9% for small individuals and 5% for large
299 individuals (Figure 7), with less drastic effects at slower swimming speeds. Overall, this

300 modelling revealed that an individual's activity accelerates energy depletion more drastically
301 than warming does, and the ability to moderate swimming can effectively conserve energy across
302 climate scenarios. Our estimates also suggest that large fish will be more resilient to temperature
303 increases than small fish provided they can hold using a slow swimming speed during the
304 migration.

305

306 **Discussion**

307

308 We derived a linear relationship between water temperature and fish habitat temperature
309 for an anadromous ectotherm during its spawning migration in freshwater. The ability to predict
310 the experienced temperature allowed us to estimate energetic expenditure in situ. In doing so, we
311 also provided the first equations approximating the relationship between water temperature and
312 oxygen uptake of Atlantic salmon at various swimming speeds, and the first estimates of the
313 energy metabolism of Atlantic salmon modelled to wild fish. Climate change is an ongoing
314 threat to all freshwater ecosystems including in the Arctic. Understanding how key parameters,
315 temperature, locomotion, and body size, contribute to energy depletion is relevant across species,
316 particularly as oncoming changes to the global climate will require physiological and
317 behavioural adaptations in order to cope. Our finding that activity is the most substantial
318 contributor to energy depletion suggests that animals will need to adapt their migration activity
319 and behaviours to adjust to the increased metabolic demands associated with warmer river
320 temperatures.

321 Compared to values published for pink (*Oncorhynchus gorbuscha* Salmonidae) and
322 sockeye (*Oncorhynchus nerka* Salmonidae) salmon, Atlantic salmon appear to have slower

323 metabolism (MacNutt et al., 2006; Eliason et al., 2011). Regression validated that ambient water
324 temperatures could predict fish habitat temperature in this river within the summer water
325 temperatures range of 11.5 - 18.5 °C, which is within the reported range of optimal temperatures
326 of this species (Mills, 1989; Booth, 1998; Anttila et al., 2014; Frechette et al., In Press). While
327 ongoing increases in summer temperature may portend an increasingly energetically demanding
328 freshwater migration, we found that the varying effects of body size and swimming speeds will
329 play a crucial role in energy management for the response of anadromous fish to warming.
330 Migrants that have stopped feeding necessarily economize energy during the migration in order
331 to ration their energy reserves for successfully spawning (Bernatchez and Dodson, 1987). This
332 strategy is true for today's thermal regime and also in future years when rivers are projected to
333 be warmer. Fleming (1998) provided a range of 52-65% energy depletion for Atlantic salmon
334 during the spawning migration, similar to that of migratory Arctic charr (*Salvelinus alpinus*) in
335 Canada (52%; Dutil, 1986). However, Jonsson et al. (1997) suggested a more extreme energy
336 depletion of 72% for salmon in the Norwegian River Drammen, similar to that of anadromous
337 American shad (70-80%; Glebe and Leggett, 1981) but less than long-distance migrating Pacific
338 salmon (males: 82%, females: 92%; Bowerman et al., 2017). The disparity within Atlantic
339 salmon is likely related in part to body size; applying our regression equation to the ambient
340 temperatures in the river provided a minimal (i.e. at rest) 20% depletion of somatic energy for
341 large salmon (119.0 cm length) and 51% for small salmon (63.5 cm length).

342 Our estimates of energy depletion do not account for a heterogeneity in swim speeds that
343 would include increased activity during active migration, Bowerman et al. (2017) suggested
344 would contribute to the majority of the energy depletion for Pacific salmon. However, Pacific
345 salmon have a much more extensive spawning migration distance (920 km) compared to the

346 much shorter distance traveled by Lakselva salmon. Correspondingly, a large proportion of the
347 time in freshwater is spent holding because most Atlantic salmon enter rivers weeks or months in
348 advance of spawning (Økland et al., 2001). The precise costs of swimming activity are presently
349 not known because there are no long-term studies of migrating Atlantic salmon energetics;
350 therefore, we generated our model at several speeds. Speed is known to be closely linked to the
351 life history of fishes (Glebe and Leggett, 1981; Eliason and Farrell, 2016). Bernatchez and
352 Dodson (1987) calculated the average swimming speed of Atlantic salmon (rivermouth to
353 spawning grounds) to be 0.1 bl s^{-1} (using data from Belding, 1934), which is consistent with
354 observations from telemetry that Atlantic salmon hold for long periods in slow-moving pools
355 prior to spawning (Økland et al., 2001; Richard et al., 2014; Lennox et al., 2016b). Although fish
356 activity has been suggested to benefit energetically from burst-and-coast over steady-state
357 swimming (Weihs, 1974; Hinch and Rand, 2000), limitations in data availability require
358 simulations such as ours that assume continuous swimming (see McElroy et al., 2012). Our
359 model revealed energy depletion was sensitive to changes in the rate of continuous swimming;
360 individuals at slow swimming speeds will conserve energy across water temperature scenarios.
361 Higher resolution data of swimming behaviour during the migration and throughout the
362 migration (i.e. over the winter) will contribute to more complete models of the energy budget by
363 identifying actual movement rates during all phases of a spawning migration including
364 movement within pools.

365 Individual size was shown to be very important to depletion of energy stores, with larger
366 individuals depleting less energy and hence being more resilient than small to temperature
367 increases and activity demands. We found that large size conferred considerably greater scope
368 for activity, likely because of their higher energy reserves, whereas smaller individuals migrate

369 with less stored energy and are likely to have greater sensitivity to temperature increases that
370 accelerate energy depletion. Based on this, large salmon may be more resilient to climate
371 warming and have higher fitness; however, we did not account for larger fish having a lower
372 optimum temperature (Morita et al., 2010). Body size in Atlantic salmon is genetically and
373 phenotypically linked to environmental factors such as the difficulty of migration and the flow
374 regime of the natal river (Jonsson et al., 1991a). Larger salmon also have higher fecundity and
375 fitness (Fleming, 1996; de Gaudemar et al., 2000). Warming of environmental temperature
376 towards a species' optimum temperature accelerates growth and maturation, generally resulting
377 in smaller body size at the time of maturation (i.e. the temperature-size rule; Kingsolver and
378 Huey, 2008; Jonsson et al., 2014), which has been shown experimentally for semelparous salmon
379 (Clark et al., 2012) and reef fishes (Messmer et al., 2017). The temperature-size rule has received
380 attention in the context of climate change (e.g., Daufresne et al., 2009; Sheridan and Bickford,
381 2011; Cheung et al., 2013), although the validity of the underlying physiological mechanisms
382 requires further validation (Lefevre et al., 2017). Our data suggest that migratory fish such as
383 salmon could compensate for climate change with a larger size, but there are competing selective
384 pressures. Warm ocean temperatures favour earlier maturation and smaller body size of salmon
385 (Jonsson and Jonsson, 2004). Indeed, Atlantic salmon from warmer rivers at southern latitudes
386 tend to mature at smaller body size (Jonsson and Jonsson, 2004; Jonsson and Jonsson, 2009).

387 As a relatively cold river, warming of the Lakselva River will increase the cost of
388 freshwater residence by Atlantic salmon, with possible effects on life history such as reducing
389 pre-spawn and post-spawn survival (such impacts have been observed in other species, e.g.
390 American shad *Alosa sapidissima* Clupeidae; Glebe and Leggett, 1981; Castro-Santos and
391 Letcher, 2010). River temperatures and discharge are key factors moulding the life history of

392 Atlantic salmon populations including smolt ages, run timing, body sizes, and iteroparity (Power,
393 1981; Jonsson et al., 1991a). Rivers with less annual water discharge are generally characterized
394 by spawning runs of younger and smaller salmon (Jonsson et al., 1991a). Sea trout (*Salmo trutta*)
395 populations at high latitudes have less frequent iteroparity than do southern populations (Jonsson
396 and L'Abée-Lund, 1993), a trend that may also be true of the congeneric Atlantic salmon.
397 Phenological changes such as shifts to later run timing could also buffer energetic costs of
398 warming water, as has been observed for populations in Newfoundland and Labrador, Canada
399 (Dempson et al., 2017). Entering rivers later may decrease the accumulated thermal units during
400 migration and offset energetic costs of higher water temperatures (Katinic et al., 2015) and
401 entering earlier and swimming upriver to holding sites before temperatures become elevated will
402 avoid a collapse in aerobic scope (Farrell et al., 2008). Late entry is generally associated with
403 smaller Atlantic salmon with less somatic energy than larger individuals, and perhaps the
404 relationship can be explained by energy demands of migration (Shearer, 1990; Niemelä et al.,
405 2006). According to Power (1981), increased water temperature promoted the evolution of a
406 bimodal run timing distribution in Atlantic salmon to avoid movement in midsummer at high
407 temperature (i.e. an early run and a late run establish within the same river).

408 Physiological acclimation to warming thermal regimes is possible when fish rear in those
409 conditions. Anttila et al. (2014) identified significant thermal plasticity of Atlantic salmon
410 originating from the nearby Alta River (69°58'06.3" N 23°22'29.5" E) reared in warmer water,
411 suggesting that fish from these northern populations could adjust, to some extent, to warming
412 conditions in freshwater depending on early life experience. In the absence of species adaptation,
413 our estimates of energy depletion suggest that pre-spawn mortality of Atlantic salmon is liable to
414 increase in a warming world. For survivors of a first reproduction, it will probably result in

415 decreased survival and reduced iteroparity (Jonsson et al., 1991b; Halttunen et al., 2013). The
416 relationship among temperature, size, activity, and energy use are evidently complex and require
417 further investigation.

418 *Limitations*

419

420 Although bioenergetics modelling is well established as a field of ecological inquiry,
421 field metabolic data for fish including adult Atlantic salmon are scarce (Cooke et al., 2004). We
422 used hatchery Atlantic salmon for our bioenergetic equations, an approach that may be somewhat
423 limited; hatchery and wild salmon (and likely wild salmon of different origin) may have
424 somewhat different conversion of energy to locomotion and future research may address this.
425 Nonetheless, the use of surrogates is relatively common to physiological studies and surrogates
426 of the same species should provide the most reliable information (Cooke et al., 2017). Jonsson et
427 al. (1997) modeled somatic energy density of Atlantic salmon in the Drammen River (Jonsson et
428 al., 1997), which are generally smaller than those in Lakselva. Thus, our energy calculation for
429 the largest sized salmon lies beyond the data range derived for that population. Drammen is also
430 warmer and so the salmon there spawn several weeks later than salmon in Lakselva (Heggberget,
431 1988). The estimates would be improved by using oxygen uptake rates from wild Atlantic
432 salmon that have entered fresh water at temperatures ranging lower than ours (min = 7 °C)
433 instead of relying on extrapolations from hatchery fish oxygen uptake. Finer scale data on the
434 cost of swimming and the logged data on swimming effort would also improve the models
435 (Johnstone et al., 1992; Lucas et al., 1993; Hendry and Beall, 2004), but would still contain
436 inaccuracies because it is logistically difficult to perfectly estimate field metabolic rates based on
437 swim tunnel values. Such work would have to include the oxygen debt due to anaerobic exercise

438 (e.g., Lee et al., 2003a,b), especially because burst-and coast swimming behaviours are likely to
439 defer the immediate oxygen cost of swimming.

440 Like Jonsson et al. (1997), we cannot predict the energy loss through the winter months.
441 Owing to the cold temperatures, the energy demands during this period are predicted to be small
442 (17.53 kCal d⁻¹ at 0 °C at rest) compared to during the summer (48.73 kCal d⁻¹ at 14.5 °C at rest),
443 as calculated for an average sized salmon (89.0 cm) for this site. Nevertheless, salmon kelts
444 clearly have exceedingly lower energetic reserves prior to outmigration (Moore 1997),
445 warranting the term ‘spent’. Consequently, warmer winter river temperatures will accelerate
446 energy depletion and could perhaps trigger an earlier outmigration, possibly resulting in a
447 mismatch of outmigration and peak ocean productivity that is believed to facilitate
448 reconditioning of spent Atlantic salmon, as it does for out-migrating smolts (Otero et al., 2014).

449 Intersexual differences were set aside from our analysis, yet Jonsson et al. (1991b) found
450 somatic energy loss to be much greater for males than females (this is different from Pacific
451 salmon; Bowerman et al., 2017). Correspondingly, more females survive spawning whereas
452 males are more prone to die (Hawkins and Smith, 1986; Jonsson et al., 1991b). The minimum
453 energy density at which salmon are capable of living and still spawning (i.e. threshold for life),
454 has been calculated for semelparous sockeye and pink salmon and ranged between 693 kCal kg⁻¹
455 (Hendry and Berg, 1999) to 956 kCal kg⁻¹ (Crossin et al., 2003, 2004). Bowerman et al. (2017)
456 calculated an energy density of 860 (female) and 980 (male) kCal kg⁻¹ in post-spawned chinook
457 salmon. Jonsson et al. (1997) provided an equation for estimating the somatic energy of a post-
458 spawn salmon based on length (see Methods), although their work did not identify an explicit
459 threshold for life.

460

461 *Conclusion*

462

463 As expected, energy depletion was accelerated at higher temperatures and under
464 scenarios of higher activity. However, activity had a more profound impact on the rate of energy
465 depletion than did increases in temperature within the modeled range. This disparity was more
466 evident among smaller salmon than for larger individuals given that larger individuals possess
467 greater energetic storage. Body size of Atlantic salmon is closely linked to reproductive success
468 (Fleming, 1996; de Gaudemar et al., 2000) and salmon exhibit considerable variation in life
469 history phenotypes across body sizes (Shearer, 1990; Niemelä et al., 2006). Our models should
470 inspire research into how physiological plasticity and behavioural adaptations, especially run
471 timing, could compensate for warming and should also be met with further research into
472 interacting effects of temperature and disease (Rand et al., 2006). Ultimately, a better
473 understanding of the behavioural and physiological mechanisms that facilitate successful
474 migration, associated life history events (i.e. run timing, spawning), and physiological processes
475 (i.e. cardiophysiology, biochemistry, and biomechanics; Anttila et al., 2014) is necessary to
476 understand and manage fish in a warming Arctic and advance efforts to focus conservation
477 initiatives on sensitive populations.

478

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480

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486

487 **Conflict of Interest**

488

489 The authors have no conflicts of interest to declare.

490 **References**

491

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787 **Tables**

788

789 Table 1. Summary of fish from which iButton archival temperature loggers were recovered. The table details the size of the salmon as
 790 well as the number of days the tags recorded data.

Fish ID	Tagging Date	Sampling Interval (days)	Total Length (cm)
142.144-8	July 13	73	73
142.123-14	July 14	18	97
142.213-14	July 15	4	98
142.203-12	July 16	12	91
142.123-9	July 16	70	90
142.144-11	July 17	11	80
142.213-9	July 19	67	95
142.114-8	July 30	30	111
142.123-75	August 12	126	94
142.144-112	August 28	27	66

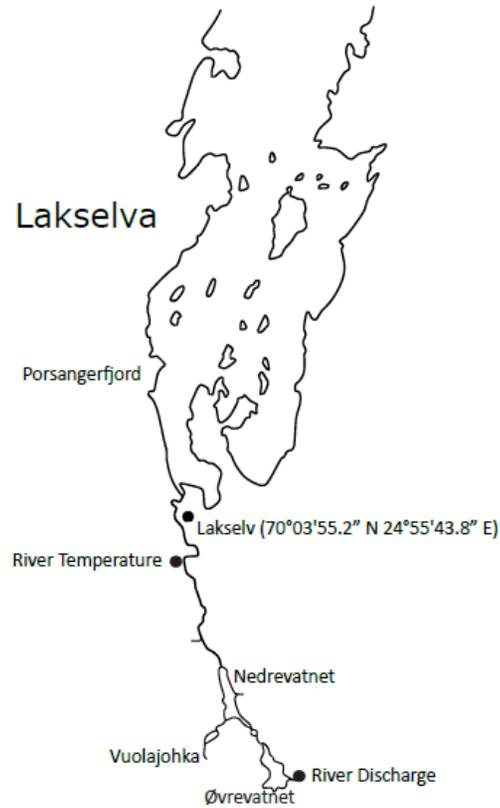
791

792

793 Table 2. Oxygen consumption equations derived from hatchery Atlantic salmon (*Salmo salar*) at rest and swimming at 1.0 bl s⁻¹. Data
 794 for 0.5 and 0.7 bl s⁻¹ were interpolated. T_w is the ambient water temperature. Oxygen consumption is returned in mg O₂ kg⁻¹ min⁻¹ and
 795 converted to mg O₂ d⁻¹ by multiplying by body size and 1440 (min d⁻¹).
 796

Swimming Speed	Fish Size	Oxygen Consumption Equation
Resting	Small (63.5 cm)	$MO_2 = 0.55 \times \exp(0.07 \times T_w)$
Resting	Medium (89.0 cm)	$MO_2 = 0.45 \times \exp(0.07 \times T_w)$
Resting	Large (119.0 cm)	$MO_2 = 0.38 \times \exp(0.07 \times T_w)$
0.5 bl s ⁻¹	All	$MO_2 = 1.32 \times \exp(0.03 \times T_w)$
0.7 bl s ⁻¹	All	$MO_2 = 1.85 \times \exp(0.03 \times T_w)$
1.0 bl s ⁻¹	All	$MO_2 = 2.90 + (0.02 \times T_w) + (0.0021 \times T_w^2)$

797



800 Figure 1. Lakselva in Porsanger, Finnmark, Norway. The watershed incorporates two major lakes, Øvrevatnet and Nedrevatnet. Atlantic
801 salmon return to Lakselva from the ocean via Porsangerfjord throughout the summer and migrate upriver to spawning grounds. The
802 location of the river temperature logger and river discharge metre are indicated on the map. For this study, all tagged salmon remained
803 in Lakselva below the lakes throughout their migration.

804

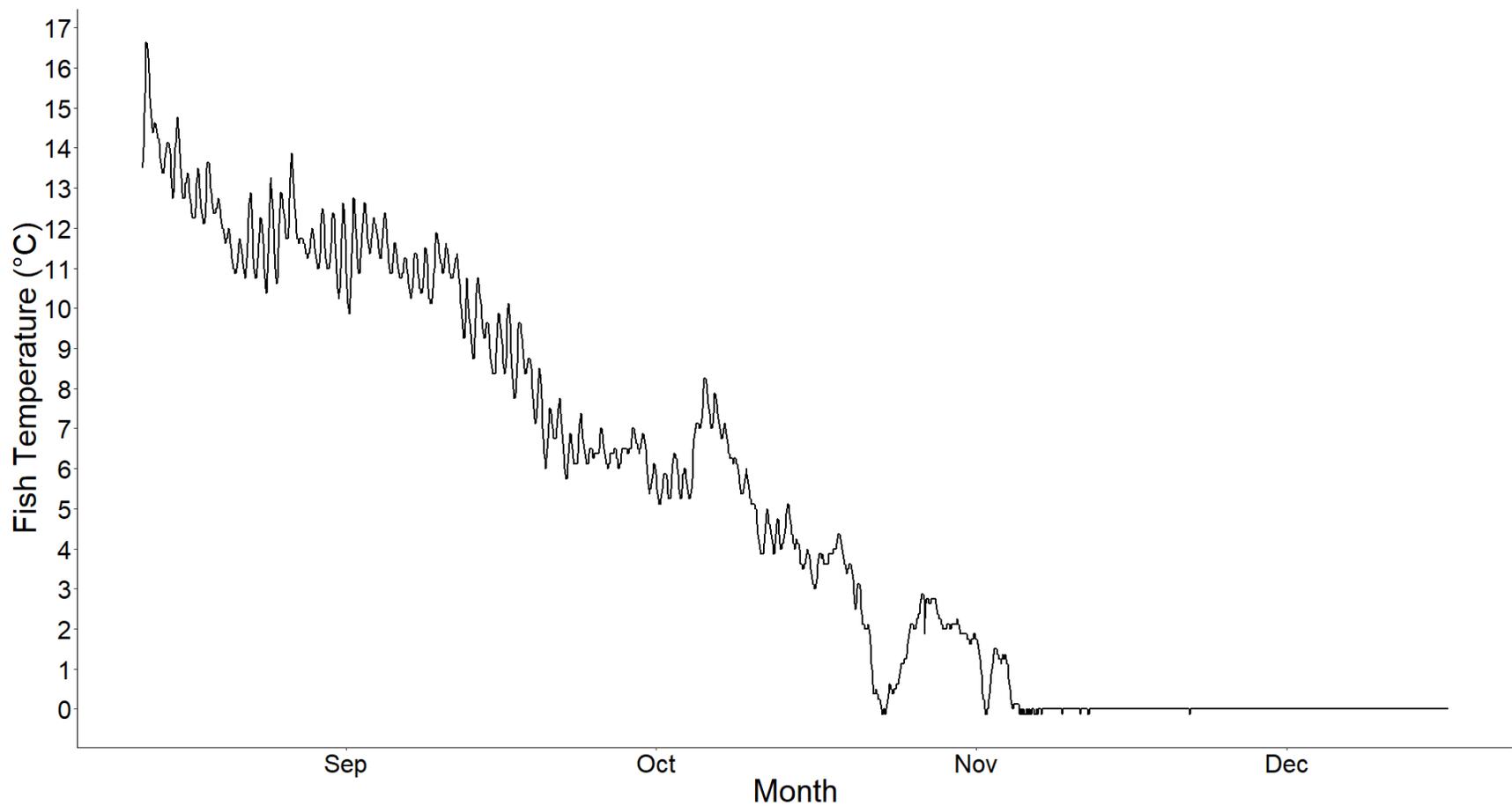


805

806 Figure 2. Double-tagging Atlantic salmon (*Salmo salar*) with coded radio transmitting tags (bottom) and archival temperature loggers

807 (top). Salmon were maintained submerged in water in a PVC tube during tagging and externally tagged prior to release. Colour image

808 available online only.



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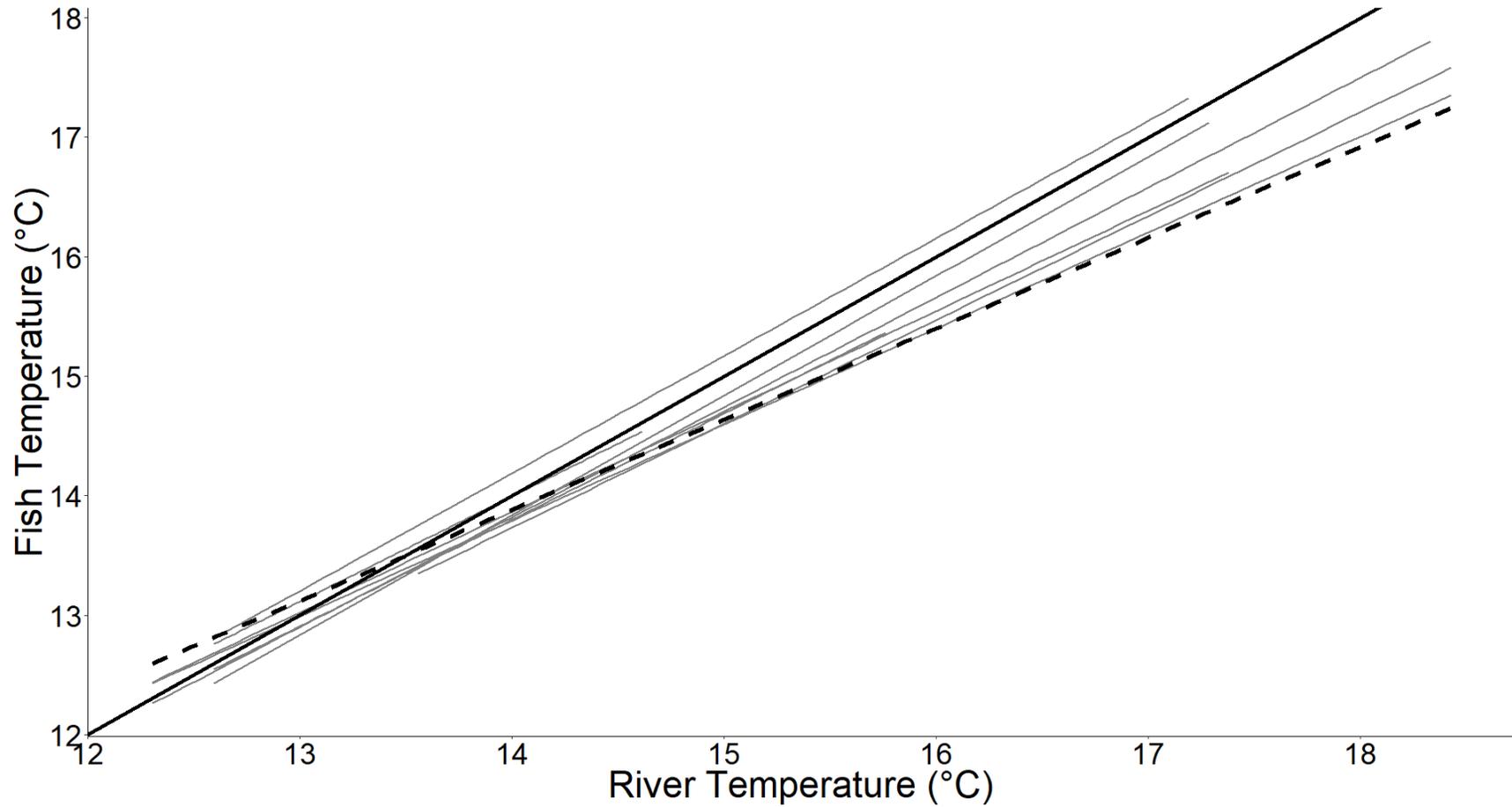
810

811 Figure 3. Fish thermal experience logged in Lakselva by salmon 142.123-75, whose logger remained active until December 16, 2014

812 (note that the values have been adjusted based on the regression analysis; see Supplementary Material).

813

814

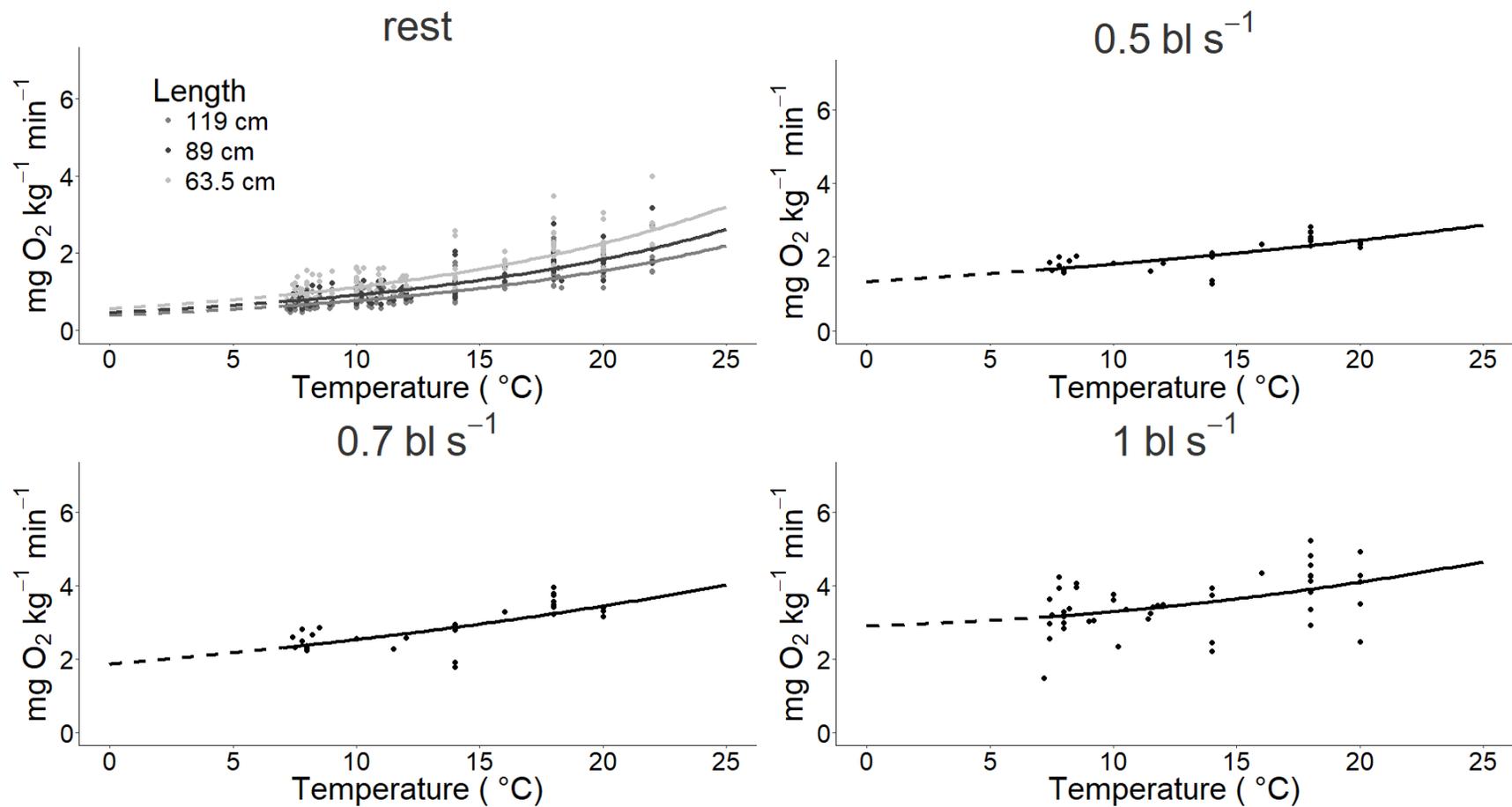


815

816

817 Figure 4. The relationship between fish temperature and the river temperature in Lakselva. Each grey line represents values from a
818 temperature logger of an individual salmon in the river. The solid black line is the line of identity at $y = x$. Linear mixed effects modelling

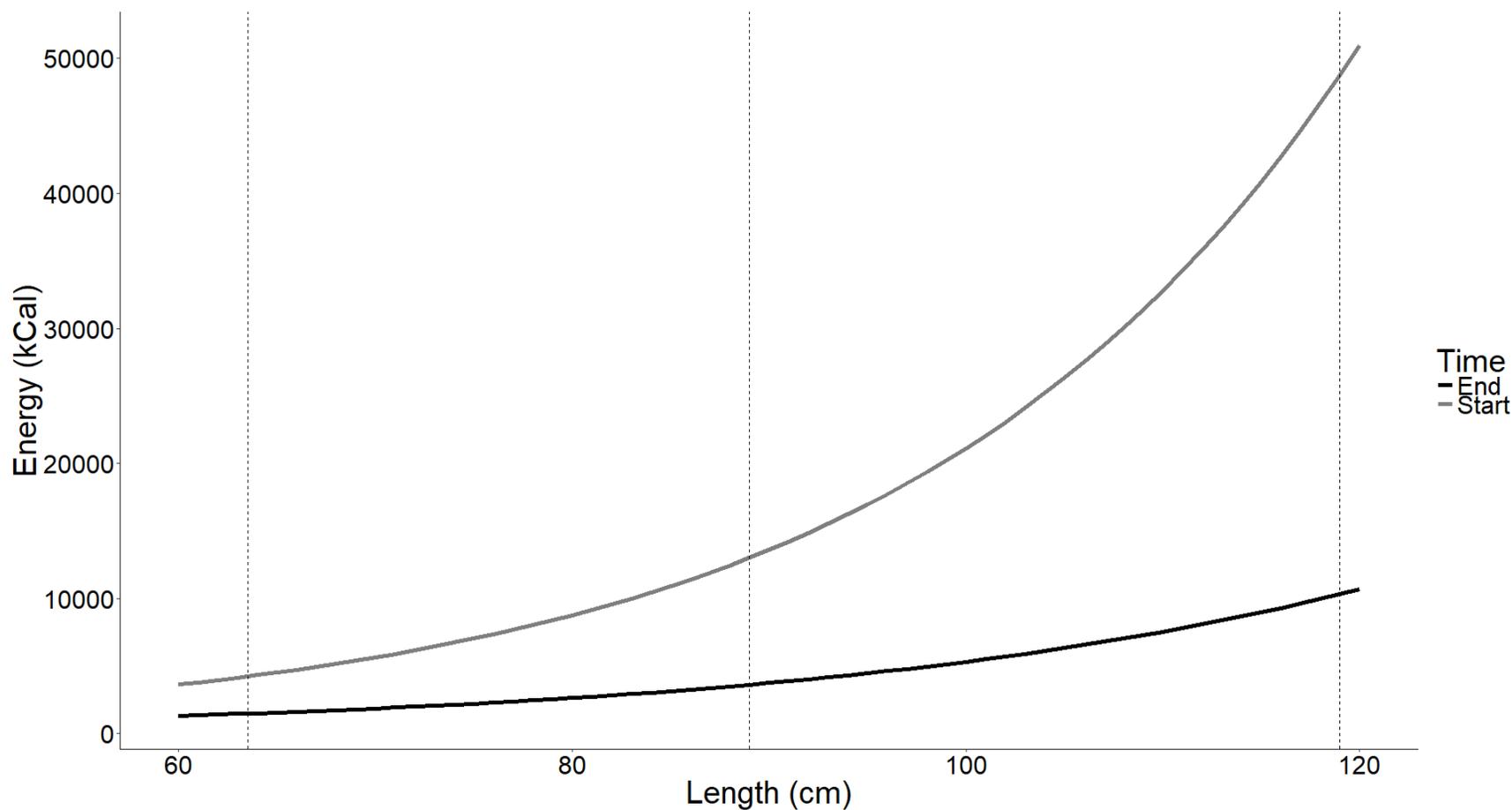
819 with an exponential temporal autocorrelation structure (see Methods) supported a linear relationship between river temperature and
820 habitat temperature of salmon during this period and the line of prediction is illustrated by the broken black line.
821



822

823 Figure 5. Atlantic salmon oxygen metabolism between 7 and 22 °C at four swimming speeds. Values for the resting fish were mass-
 824 corrected for three sizes using a scaling exponent of 0.80 (see Clarke and Johnston 1999). Curves are presented for three body lengths,
 825 near the minimum, mean, and maximum values we encountered in Lakselva. Values for resting and 1.0 bl s⁻¹ were derived from swim
 826 tunnel respirometry (see Table 2). Values for 0.5 and 0.7 bl s⁻¹ were interpolated from these data by averaging the oxygen uptake values.

827 Regression curves were fit to the plots using a polynomial (second order) equation fit to the 1.0 bl s^{-1} data and exponential curves fit at
828 other swimming speeds. Dashed portions of the curves are extrapolations made by the regression equations beyond the temperature
829 ranges at which oxygen uptake were measured (i.e. $0 - 7 \text{ }^{\circ}\text{C}$).
830



831

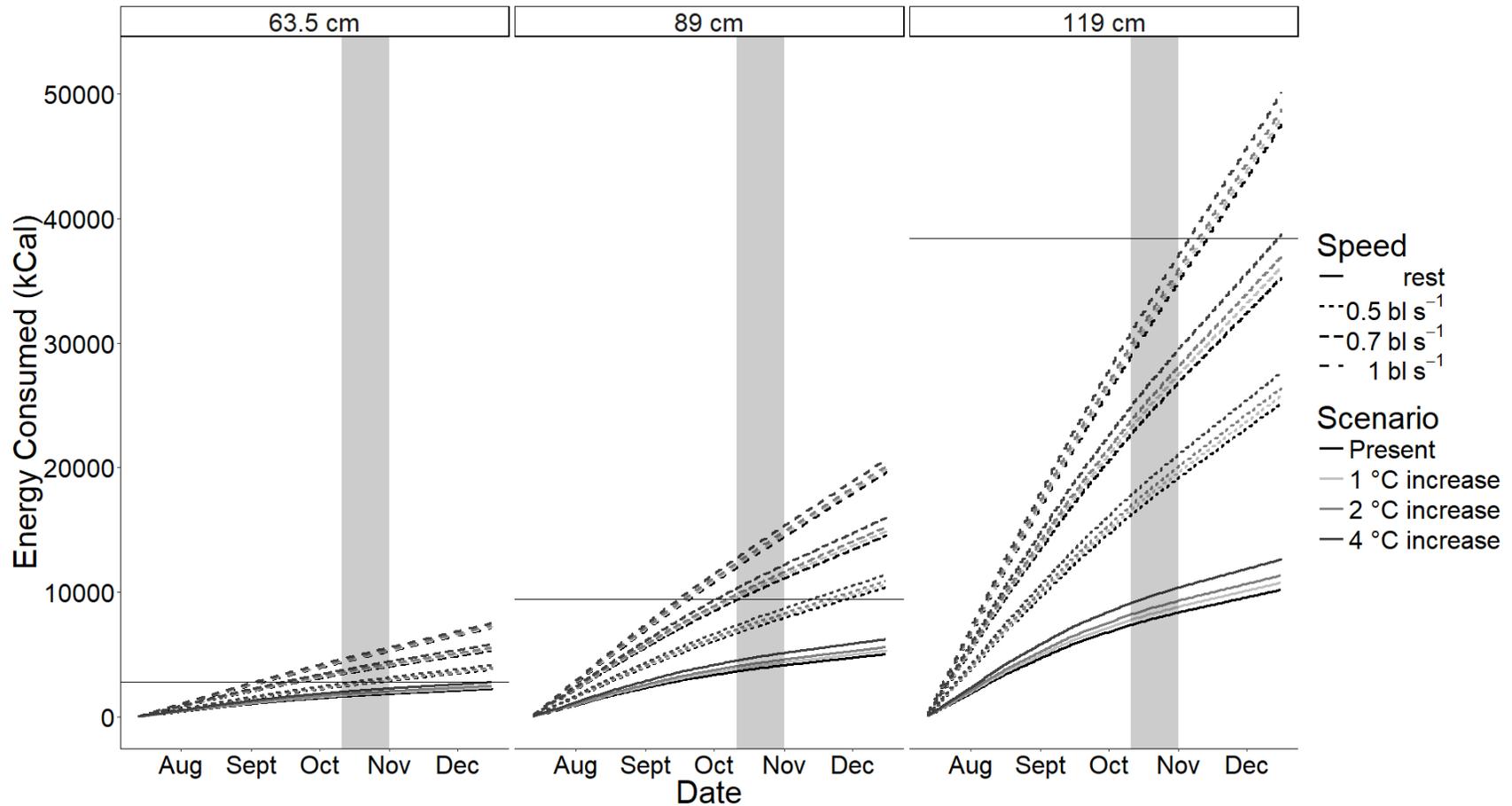
832 Figure 6. Predicted somatic energy density at length (cm) of Atlantic salmon (*Salmo salar*) based on equations derived by Jonsson and

833 Jonsson (1997) in the River Drammen, Norway. Both curves follow exponential equations and represent measurements made in July

834 ($E_{\text{initial}} = \exp(0.044 \times L_{\text{TOTAL}} + 6.99)$) and November, following spawning ($E_{\text{post-spawn}} = \exp(0.035 \times L_{\text{TOTAL}} + 6.51)$). Broken vertical lines

835 represent the lengths we selected for our bioenergetics modelling in this study, showing the energetic scope during the freshwater
836 migration.

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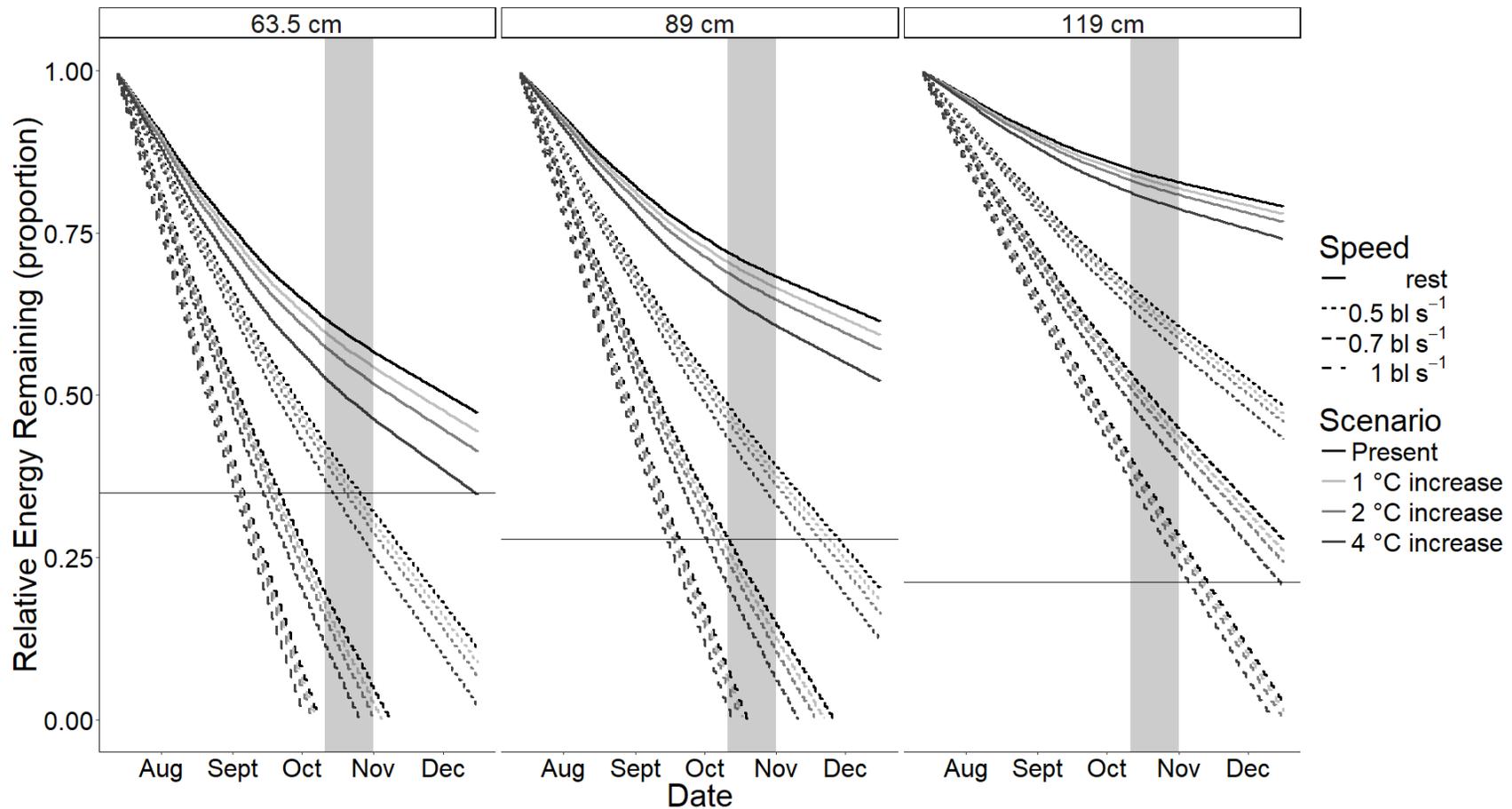


839

840 Figure 7. Predicted cumulative energetic expenditure (kCal) of Atlantic salmon measuring either 63.5, 89.0, or 119.0 cm, either resting
 841 or swimming at 0.5, 0.7, and 1.0 bl s⁻¹ from July 13 – December 16. Monthly ticks are the first day of the noted month. Daily
 842 temperatures experienced were converted from measured river values with the regression equation: $t_{\text{FISH}} = 3.24 + (0.76 \times t_{\text{RIVER}})$ at

843 present river temperatures or given increases of 1, 2, or 4 °C. The horizontal line indicates the scope for depletion (i.e. initial energy
844 minus post-spawn energy) for each size class based on regression equations in Jonsson et al. (1997). The shaded area signifies the
845 approximate spawning period in Lakselva, October 10-31. Energy depletion increased at higher temperatures, faster rates of movement,
846 and larger body size.

847



848

849 Figure 8. Predicted proportion of energy remaining to Atlantic salmon measuring either 63.5, 89.0, or 119.0 cm, either resting or
 850 swimming at 0.5, 0.7, and 1.0 bl s⁻¹ from July 13 – December 16. Monthly ticks are the first day of the noted month. Fish habitat
 851 temperatures were calculated from the regression equation: $t_{\text{FISH}} = 1.62 + 0.88(t_{\text{RIVER}})$ at present river temperatures or given increases of
 852 1, 2, or 4 °C. The horizontal line represents the expected proportion of energy remaining in a post-spawn salmon of each size based on

853 a regression equation in Jonsson et al. (1997). The shaded area signifies the approximate spawning period in Lakselva, October 10-31.

854 Relative energetic depletion increased at higher temperatures and for faster rates of movement but decreased with body size.

855