

1 The effect of temperature on growth performance and aerobic metabolic scope of juvenile Arctic charr, *Salvelinus alpinus* (L.).

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## 24 Abstract

25 In recent years, Arctic charr populations in Iceland have declined and the objective of this experiment was to elucidate these changes by  
26 examining the effect of temperature (5, 9, 13, 17 and 21 °C) on the survival, growth rate, metabolism, and physiological indices of juvenile Arctic  
27 charr (initial mean body mass  $4.02 \pm 0.8$  g). During the 100-day study, mortality was 60% in fish reared at 21 °C, while at lower temperatures it  
28 was below 5%. However, Arctic charr populations in Iceland are declining in locations where the ambient temperature is lower, suggesting that  
29 other factors may be more important in determining the abundance of the species. The  $T_{opt}$  for growth was near at 14 °C. Growth rate was  
30 progressively reduced at supra-optimum temperatures with almost no growth at 21 °C. Indicators of energy reserves: condition factor, relative  
31 intestinal mass and hepatosomatic index are all consistent with reduced feed intake at supra-optimum temperatures. The standard and maximum  
32 metabolic rate (SMR; MMR), as well as the aerobic scope for activity (AS), were at maximum at 13 °C. The routine metabolic rate (RMR) increased  
33 exponentially with temperature and, at T21, it was equal to the MMR suggesting, that the RMR was limited by the MMR. Moreover, increased  
34 heart- and gill mass at 21 °C are consistent with increased stress on the cardiovascular system. These findings are in keeping with the OCLTT  
35 hypothesis that the thermal tolerance of fish is limited by the capacity of the cardiovascular system to deliver oxygen and support metabolism.  
36 Taken together, the results of this experiment suggest that growth rate is reduced at supra-optimum temperatures because of reduced energy  
37 intake, increased metabolic demand, and limitations in the capacity of the cardiovascular system to support metabolic rate at high temperatures.  
38 At lower temperatures, growth does not appear to be limited by the AS.

39

## 40 Introduction

41 Arctic charr has the northernmost distribution of all anadromous and freshwater fishes (Klemetsen et al., 2003). It is found in the Arctic, subarctic,  
42 boreal, and temperate regions, with natural populations as far south as the British Isles and in the Alps (Klemetsen et al., 2003). There is evidence  
43 that the distribution of the species is shifting due to climate change. Models predicting the future distribution of Arctic charr suggest that the  
44 southern distribution of Arctic charr will be pushed further north with global warming (Chu et al., 2005; Hein et al., 2012; Svenning et al., 2016).  
45 Moreover, at least 11% of Arctic charr populations in Britain and Ireland are now extirpated (Maitland et al., 2007). The decline in Arctic charr  
46 populations appears to be occurring simultaneously in different parts of the distribution range and under different physical and ecological  
47 conditions since parallel decreases in the catches of Arctic charr have been observed in the UK (Winfield et al., 2010), Norway (Svenning et al.,  
48 2012) and Iceland (Winfield et al., 2010; Svenning et al., 2012) over the last 20 to 30 years. The reasons for this decline in Arctic charr and other  
49 salmonid populations are not entirely clear although they are likely linked to a progressive increase in ambient temperature (Elliott and Elliott,  
50 2010; Jonsson and Jonsson, 2009), although it is difficult to establish causative links (Winfield et al., 2010).

51 The hypothesis of oxygen- and capacity-limited thermal tolerance (OCLTT) (Clarke and Pörtner, 2010; Pörtner and Farrell, 2008; Pörtner and  
52 Knust, 2007) was proposed to explain the effects of climate on the distribution of fish. It suggests that the upper thermal tolerance of fish is  
53 limited by oxygen supply, primarily due to the failure of the cardiovascular system to deliver oxygen from gills to tissues (Eliason et al., 2013;  
54 Farrell, 2009). The OCLTT draws on Fry's paradigm (Fry, 1971; Fry, 1947), which suggests that temperature limits processes or activities, such as  
55 growth, through its effect on metabolic rate. The metabolic scope for activity or aerobic scope (AS) is the difference between the maximum

56 aerobic metabolic rate (MMR) and standard metabolic rate (SMR: The metabolic rate of resting unfed animals) (Fry, 1971) and reflects the  
57 capacity of the animal to sustain aerobic metabolic activity over and above the SMR. The AS increases up to a maximum (or a plateau) at the  
58 temperature optimum ( $T_{opt}$ ) for aerobic scope and then decreases at supra-optimal temperatures in much the same way as the growth rate does  
59 (Brett and Groves, 1979; Clark et al., 2008; Eliason and Farrell, 2015; Farrell, 2009; Lee et al., 2003; MacNutt et al., 2006). The OCLTT suggests  
60 that reduced survival of fish at increased temperature is linked to reduced capacity to support the AS and, as a result, necessary metabolic  
61 functions (Pörtner and Farrell, 2008). However, the concept has been widely debated (Clark et al., 2013; Norin et al., 2014; Lefevre, 2016; Jutfelt  
62 et al., 2018).

63 The heat increment or the specific dynamic action (SDA) is the metabolic cost of digestion, absorption, and assimilation of nutrients and results  
64 in a near doubling of the SMR at peak levels (Beamish and Trippel, 1990; Jobling, 1981; Thorarensen and Farrell, 2006) following a meal. The  
65 metabolic cost of the SDA may limit the capacity of fish to perform other activities such as swimming (Alsop and Wood, 1997; Thorarensen and  
66 Farrell, 2006b). However, for long-term survival and growth, the AS must be large enough to accommodate the metabolic demands of the SDA.  
67 There appears to be a good correlation between the AS and growth rate of Atlantic cod at different oxygen levels (Claireaux et al., 2000) and in  
68 sea bass (*Dicentrarchus labrax*) at different temperatures (Claireaux and Lefrançois, 2007). Moreover, in many fish species, the  $T_{opt}$  for AS  
69 coincides with the  $T_{opt}$  for growth (Brett, 1976; Khan et al., 2014; Lefrançois and Claireaux, 2003) or feed intake (Brett, 1976; Khan et al., 2014;  
70 Mallekh and Lagardere, 2002). These results are consistent with Fry's paradigm and may suggest that the growth rate of fish at different

71 temperatures may be limited through effects on the AS. However, correlations do not necessarily suggest causation and the shape of the curve  
72 for AS at different temperatures may resemble the effect of temperature on growth without any causative link.

73 Several studies have been conducted on the effect temperature on the growth and survival of Arctic charr. The  $T_{opt}$  for growth of Arctic charr  
74 appears to lie between 12 and 17 °C (Imsland, Gunnarsson and Thorarensen, 2020; Elliott and Elliott, 2010; Gunnarsson et al., 2011; Jobling,  
75 1983; Larsson and Berglund, 1998, 2005; Larsson et al., 2005; Lyytikäinen and Jobling, 1998; Swift, 1964) depending, in part, on the size of the  
76 fish (M. Jobling, 1983; Joblin et al., 1993). Projections from a study of juvenile fish from 11 populations of Arctic charr acclimatized to 5-20 °C  
77 (Larsson et al., 2005) suggest that there is no growth at or above 21-22 °C and this is consistent with the finding of Thyrel et al., 1999) that Arctic  
78 charr juveniles acclimatized to 20-23 °C will cease feeding above 21-22 °C. The upper incipient temperature (the temperature at which 50% of  
79 fish can survive for extended periods) for juveniles is 22-24°C and the lethal temperature is 24-26 °C (Baroudy and Elliott, 1994; Elliott and  
80 Klemetsen, 2002; Lyytikäinen et al., 1997b). Arctic charr is more tolerant to low temperatures than other salmonids (Elliott and Elliott, 2010) and  
81 the lower incipient temperature for Arctic charr is less than 1°C (Siikavuopio et al., 2010). Arctic charr will grow at temperatures even as low as 0.3  
82 °C (Brännäs and Linnér, 2000; Brännäs and Wiklund, 1992; Siikavuopio et al., 2010; Wandsvik and Jobling, 1982).

83 The relationship between temperature and metabolism has been studied in many fish species (e.g Claireaux *et al.*, 2000; Lefrançois & Claireaux,  
84 2003; Tirsgaard, Behrens & Steffensen, 2015a) including salmonids (Brett and Glass, 1973; Brett, 1976; Atkins and Benfey, 2008; Hvas et al.,  
85 2017). However, there is limited information available about the relationship between metabolic rate and temperature in Arctic charr. Huuskonen

86 et al. (2003) studied the effect of temperature on SMR at 2°C and 7°C in newly hatched Arctic charr. The metabolic rate and heart rate of Arctic  
87 charr have been measured in acute thermal challenge tests where the temperature is increased at a rate of about 2 °C·hour<sup>-1</sup> (Gilbert et al., 2020;  
88 Penney et al., 2014) The results of Gilbert et al. (2020) suggest that the aerobic scope of Arctic charr is constant between 4°C and 16°C although  
89 MMR increases linearly and the minimum metabolic rate increases exponentially in this temperature range. Furthermore, heart rate during  
90 thermal challenge peaks near 20 °C and, at higher temperatures, heart rate is reduced (Gilbert et al., 2020; Penney et al., 2014). This suggests  
91 that the cardiovascular system of Arctic charr may have problems coping with temperatures above 20 °C, at least when acutely increased.  
92 Lyytikäinen and Jobling (1999) estimated the metabolic budget of juvenile Arctic charr at three constant temperatures (11°C, 14.4°C, and 17.7°C)  
93 and their results suggest that in this range the RMR of Arctic charr increases exponentially with increasing temperature. However, at the highest  
94 temperature, feed intake was reduced while the metabolic rate was increased and, as a result, the growth rate was reduced. Lyytikäinen and  
95 Jobling (1999) did not estimate the AS. The present study was undertaken to examine the effect of temperature on the relationship between  
96 survival, growth, and AS in Arctic charr and specifically to test the hypothesis that the growth performance of Arctic charr at different  
97 temperatures may be a function of aerobic scope.

## 98 **Material and methods**

### 99 **Experimental fish**

100 Juvenile Arctic charr (4.02±0.8g, mean body mass±S.D.) from an aquaculture strain were obtained from Holalax fish farm and brought to Verið  
101 research station in Sauðárkrókur, Iceland, where the experiments were performed. Fish were distributed at random among 25 circular tanks(17L),

102 40 - 46 fish in each tank. The water temperature in the tanks was 10 °C and the fish were given 15 days to acclimate to these conditions. After  
103 that, the temperature was changed to the target temperature of the treatments over three days. At the end of the experiment, fish were  
104 euthanized with an overdose of anesthesia (ethylenglycomophenylether, 0.3mL·L<sup>-1</sup>, Ásgeir Sigurðsson ehf., Iceland). The experiment was  
105 conducted in compliance with the regulations of the Icelandic commission for animal welfare.

#### 106 **Control of oxygen saturation, temperature, and feeding**

107 During the experiment, the fish were reared at five different temperatures for 96 days. The target temperatures were 5°C, 9°C, 13°C, 17°C and  
108 21°C (T5, T9, T13, T17, T21) covering a large part of the temperature range for Arctic charr (Elliott and Elliott, 2010). The mean temperatures  
109 during the experiment were (mean±SD) 5±0.3°C, 9.2±0.3°C, 13.1±0.5°C, 17.4±0.4°C, and 21.3±0.5°C. Each treatment was tested in five replicates.  
110 The fish were reared in freshwater, maintaining oxygen saturation close to 100%. The oxygen saturation was measured daily with a handheld  
111 oxygen meter (YSI 550A) in the tanks each morning before the fish were fed and adjusted by increasing the water flow rate if required. The total  
112 water flow into each tank was 1.5-3 L·min<sup>-1</sup>.

113 The fish were fed extruded feed (1.0mm, 1.2mm, and 1.5mm) from Biomar, Denmark, and 1.8mm and 2mm from LAXÁ feed mill, Iceland adjusting  
114 pellet size as the fish grew. The feed contained 52% crude protein, 19% crude fat, and 9% crude ash. Feed was presented with automatic feeders  
115 that delivered continuously feed in excess (as indicated by the presence of feed remains on the bottom of the tanks) except on Sundays when  
116 the fish were not fed.



117 **Growth**

118 Before measurements, the fish were netted out of the rearing tanks and anesthetized. All fish were individually weighed and measured (fork  
119 length) to the nearest 0.01 g and 0.1 cm at the beginning of the experiment and then at four-week intervals until the end of the experiment after  
120 96 days. The specific growth rate (SGR) was calculated as (%·day<sup>-1</sup>):

121 
$$SGR = 100 \times \frac{\ln w_2 - \ln w_1}{t_2 - t_1}$$

122 Where  $w_1$  and  $w_2$  are the body mass at the beginning ( $t_1$ ) and end ( $t_2$ ) of the growth period respectively.

123 The Fulton's condition factor (K) was calculated as:

124 
$$K = \frac{W \times 100}{L^3}$$

125 Where, W=body mass of fish (g), L=Length of fish (cm).

126 The body-mass length relationship was calculated according to the formula:

127 
$$W = a \times L^b$$

128 The hepatosomatic index (HSI) and relative intestinal mass (RIM) were calculated as indicators of the amount of energy reserves in the fish.

129 Furthermore, as indicators of stress on the cardiorespiratory system, the relative ventricular (RVM) and gill (RGM) masses were calculated as a  
130 percentage of the body mass from a sample of 20 fish at each temperature treatment:

131

$$\%BM = \left( \frac{\text{organweight}}{\text{bodymass}} \right) \times 100$$

132 Where organ and body mass are in g.

### 133 [Measurements of oxygen consumption](#)

134 All measurements of metabolic rate were performed during the last five weeks of the experiment alternating the measurements between  
135 treatments to reduce any potential effects of changes during time.

136 The standard metabolic rate (SMR) was measured in 9 fish with an automated intermittent flow respirometer (Svendsen et al., 2016). Food was  
137 withheld for 48h before the measurement. Three fish were netted at random out of the rearing tanks and placed in each of three horizontal  
138 chambers (ID 33-80 mm, Loligo System®) at their rearing temperature. The bacterial oxygen consumption was measured simultaneously in an  
139 identical chamber without any fish during the same period. The respirometers were cleaned after each measurement session. The oxygen  
140 consumption was measured by automatically closing the water inflow into the chambers for 30 minutes while simultaneously measuring oxygen  
141 concentration with OXY-4 mini oxygen meter probes (Loligo System). A side branch, continuously circulated water from the chambers over the  
142 probes, mixing the water in the tubes at the same time. During the time the water inflow was closed the oxygen saturation in the chambers was  
143 reduced from 100% down to 60-83% saturation. Such a decrease is harmless for Arctic charr (Beuvarid et al., in preparation). After each  
144 measurement, the inflow was opened again to restore the oxygen levels. The oxygen concentration was recorded automatically with  
145 OXY4v2\_11FB (Loligo Systems). Oxygen consumption was calculated from the slope of the curve of oxygen concentration ( $\text{mg}\cdot\text{L}^{-1}$ ) over time:

$$\dot{M}O_2 = \frac{\Delta[O_2]_T/\Delta t - \Delta[O_2]_B/\Delta t}{\text{body mass of fish}} \times V$$

146

147 Where  $V$  is the net volume of water in the chamber, hoses, and pump (1.7L) excluding the volume of fish. The  $\dot{M}O_2$  measurements were corrected  
148 by subtracting the background oxygen consumption  $\Delta[O_2]_B/\Delta t$  measured in the empty chamber from the  $\Delta[O_2]/\Delta t$  from the total oxygen  
149 consumption  $\Delta[O_2]_T/\Delta t$  in the chambers with fish.

150 When measuring SMR, the fish were placed in the chambers at 8 am before the measurements. The SMR was measured during the following  
151 night when the fish had settled in the chambers. The  $\dot{M}O_2$  was measured once every hour for seven hours starting at 10 pm (Fig. 1). The mean  
152  $\dot{M}O_2$  was stable during the time of measurements in groups T5, T9, and T21, while in T13 it decreased towards the end of the period and in T17  
153 it decreased progressively over the night (Fig. 1). For each fish, the three lowest values for  $\dot{M}O_2$  with the highest R-squared ( $R \geq 0.99$ ) were used  
154 to estimate the SMR. Routine Metabolic Rate (RMR) and Maximum Metabolic Rate (MMR) were measured on groups of fish in the rearing tanks  
155 to reflect as well a possible the  $\dot{M}O_2$  of undisturbed and fed continuously fish. Probes were placed in four tanks at each temperature. The  
156 measurements of RMR and MMR were performed one week before SMR measurements. The total number of fish measured was 195 fish for T5  
157 and T9, 191 for T13, 179 for T17, and 82 for T21. The  $\dot{M}O_2$  was measured by closing off the inflow into the tank and calculated from the drop in  
158 oxygen concentration as described above. This procedure was repeated three times for each tank with 24 hours intervals between  
159 measurements.

160 Since the tanks were not closed to air at the surface, tests were performed to estimate the amount of oxygen entering the water while  $\dot{M}O_2$  was  
161 measured. First, the oxygen saturation was reduced to near zero by bubbling nitrogen gas through the water. Then the rise in oxygen  
162 concentration was measured over six hours. The diffusion of gasses from air to water is determined by Fick's law:  $V'_{gas} = A \times D \times \Delta P / T$ , where  
163  $V'_{gas}$  is the rate of diffusion of gas across a permeable membrane,  $D$  is the diffusion coefficient for the gas,  $A$  is the surface area of the membrane,  
164 and  $T$  is the thickness of the membrane and  $\Delta P$  is the difference in partial pressure across the membrane. Other factors will also affect the  $\dot{M}O_2$   
165 measurements, such as the convective mixing of water in the tanks. The tests were performed under the same temperature conditions as the  
166 measurements of oxygen consumption and with the same placements of the probes. Therefore, all factors in the Fick's equation, apart from  $\Delta P$ ,  
167 were assumed to be equal during the tests and the actual measurements of  $\dot{M}O_2$ . The mean increase in  $[O_2]$  during the six hours while the tests  
168 were performed was  $0.25 \text{ mg} \cdot \text{L}^{-1}$  (4 mmHg). The mean  $\Delta P$  between air and water during the tests was 153 mmHg while the mean  $\Delta P$  during the  
169 measurements of oxygen consumption was 30 mmHg. These calculations suggest that oxygen entering from the air would change the  
170 measurements of oxygen consumption by less than 4%.

171 The maximum metabolic rate (MMR) was similarly measured in the rearing tanks with all fish present, fed, and active. The fish were chased to  
172 exhaustion with a pipe for 5 minutes and at this point, most or all of the fish ceased to respond to prodding. The metabolic rate was measured  
173 immediately after that.

174

## 175 Statistical analyses

176 All statistical analyses were performed by using R version 3.2.0 (R Core Team, 2014). The initial and final mean body mass, length, and condition  
177 factor of the fish were compared with a nested one-way ANOVA (tanks nested as random factors within treatments) using the lme function of  
178 the nlme package in R (Pinheiro et al., 2017). The assumptions of normality and homoscedasticity of the data were confirmed with Q-Q-plots of  
179 residuals and by comparing the variances within treatments with Levene's tests. The data for body mass was square-root transformed to conform  
180 to the assumptions of normality. The  $T_{opt}$  for growth were estimated by fitting third order polynomials to the data for the mean increase in body-  
181 mass and length in different tanks. Third-order polynomials gave a significantly better fit ( $p < 0.0001$ ) than second-order polynomials (F-test) while  
182 fourth-order polynomials did not give a significant ( $p = 0.3$ ) better fit than the former. Furthermore, the third-order polynomial gave the lowest  
183 AIC values. The  $T_{opt}$  for growth and the 95% confidence intervals (95%CI) were determined with non-parametric bootstrap methods using the  
184 Boot package in R (Angelo and Ripley, 2016). The relative organ masses and  $\dot{M}O_2$  were compared using a one-way ANOVA and the SGR was  
185 compared with a one-way ANOVA on the mean values for each tank. A Tukey's HSD test was used for post hoc comparison of different treatments.  
186 Mortality was compared with a Kruskal-Wallis test and pairwise comparisons using Wilcoxon rank sum test with Benjamini and Hochberg  
187 adjustment for multiple comparisons.

## 188 Results

### 189 Mortality

190 The mortality was highest in the T21 group (Fig. 2) and from day 21, the mortality in this group was significantly higher than in other groups.  
191 (Kruskal-Wallis chi-squared = 14.2-16.5, df = 4, p-value = 0.002-0.005) (Fig. 2). At the end of the study, the mortality was 60% in T21 and less than  
192 5% in all other groups. Most of the mortality in T21 occurred between days 45 and 70 (Fig 2).

193

### 194 Growth

195 Temperature significantly ( $p=0.0003176$ ,  $F=13,072$ ) affected the growth of the fish (Fig 3). The final body-mass was highest in T13 and  
196 significantly higher than in all other groups (Table 1) similarly, the increase in body mass and SGR were highest in T13 and T17 (Table 1; Fig. 2a).  
197 The mean increases in body-mass in T5 and T21 were 70% and 96% lower respectively than in T13 (Fig. 3a). The growth in T9 was intermediate.  
198 The estimated optimum temperature for growth in body mass (Fig. 3a) was 14.3 °C (95%CI 13.7-14.9).  
199 The mean increase in length was also highest in T13 (Fig. 3b). The increase in length in T5 and T21 was 46% and 8% of T13 respectively (Fig 3b).  
200 The estimated optimum temperature for growth in length (Fig. 2b) was 13.8 °C (95%CI 13.2-14.4).  
201 The Fulton's condition factor (K) increased progressively, albeit not significantly ( $p=0.2551$ ,  $F=1.3623$ ), from 5 to 17 °C while the lowest  
202 condition factor was in T21 (Table 1). The allometric relationship between body mass and length was estimated for all groups during the entire  
203 experiment (Table 1) and was not significantly different among groups T5, T9, and T13. However, the higher exponents (b) at T17 and T21 than

204 at lower temperatures indicate that the growth in mass relative to length was comparatively higher at the higher temperatures. Furthermore,  
205 the constants (a) for T17 and T21 were significantly lower than in the other groups (Table 1).

206 Temperature affected both indicators of cardio-respiratory stress, RVM, and RGM. The RVM was significantly different at different  
207 temperatures ( $p < 0.0001$ ,  $F = 70.107$ ). The mean RVM was highest in T21 (0.204%) and 48% higher than at 13 °C (0.138%) (Fig 4a). Furthermore,  
208 there was a significant positive correlation ( $R: 0.33$ ;  $p = 0.003$ ) between temperature and RVM at temperatures between 5 to 17 °C although  
209 mean values were not significantly different (Fig. 4a). The RGM was also significantly affected by the temperature ( $p = 0.1179$ ,  $F = 2.4873$ ),  
210 decreasing progressively from 5 to 17 °C (by 20%) and then increasing by 24% from 17 to 21 °C (Fig. 4b).

211 The indicators of energy reserves, the hepatosomatic (HSI) index, and the relative intestinal mass (RIM) both suggested reduced energy  
212 reserves at higher temperatures. The HSI decreased significantly ( $p < 0.0001$ ,  $F = 72.937$ ) from 5 to 13 °C (Fig 4c), and similarly the RIM was  
213 reduced at elevated temperatures ( $p < 0.0001$ ,  $F = 10.475$ ), being significantly lower at either 17 or 21 °C than at 5, 9, and 13 °C (Fig 4d).

214 Table 1. The growth fish during the experiment, condition factor (K), and coefficients for the relationship  $\text{body-mass} = a \times \text{length}^b$  of Arctic  
215 charr. Values shown in parentheses are standard errors of the means. Values labeled with different superscripts are significantly different.

216

217

218

T°C	n	Initial body-mass	Final body-mass	Initial fork length	Final fork length	SGR	K	a	b
5	195	3.83(±0.04) <sup>b</sup>	9.87(±0.24) <sup>d</sup>	7.81(±0.03) <sup>b</sup>	10.15(±0.07) <sup>c</sup>	0.98(±0.05) <sup>c</sup>	0.886(±0.006) <sup>a</sup>	0.0035(±0.0002) <sup>a</sup>	3.42(±0.02) <sup>a</sup>
9	195	4.07(±0.05) <sup>a</sup>	17.06(±0.51) <sup>c</sup>	7.96(±0.03) <sup>a</sup>	11.86(±0.10) <sup>b</sup>	1.49(±0.03) <sup>b</sup>	0.908(±0.009) <sup>a</sup>	0.0035(±0.0002) <sup>a</sup>	3.42(±0.01) <sup>a</sup>
13	191	4.24(±0.06) <sup>a</sup>	23.95(±0.64) <sup>a</sup>	8.00(±0.03) <sup>a</sup>	13.12(±0.10) <sup>a</sup>	1.80(±0.03) <sup>a</sup>	0.94(±0.009) <sup>b</sup>	0.0033(±0.0002) <sup>a</sup>	3.45(±0.01) <sup>a</sup>
17	179	4.22(±0.06) <sup>a</sup>	20.71(±0.68) <sup>b</sup>	7.93(±0.04) <sup>ab</sup>	12.18(±0.13) <sup>b</sup>	1.66(±0.05) <sup>ab</sup>	0.963(±0.009) <sup>b</sup>	0.0027(±0.0002) <sup>b</sup>	3.55(±0.01) <sup>b</sup>
21	82	3.73(±0.05) <sup>b</sup>	4.69(±0.10) <sup>d</sup>	7.64(±0.03) <sup>c</sup>	7.96(±0.06) <sup>d</sup>	0.29(±0.06) <sup>d</sup>	0.837(±0.009) <sup>c</sup>	0.0017(±0.0002) <sup>c</sup>	3.78(±0.05) <sup>c</sup>

219

## 220 Oxygen consumption

221 Temperature significantly ( $p < 0.0001$ ) affected SMR ( $p = 0.004058$ ,  $F = 9.2191$ ), MMR ( $p = 0.03126$ ;  $F = 5.8267$ ) and RMR ( $p < 0.001$ ,  $F = 30.763$ ) (Fig. 5).

222 The SMR was highest at 13 °C and significantly higher than in either T5 or T9. The SMR in T17 and T21 was intermediate (Fig. 5). The MMR was

223 also highest at 13 °C and significantly higher than at all other temperatures (Fig. 5). The MMR was significantly lower in T5 than at all other

224 temperatures. The AS was also the largest in T13 and smallest in T5 (Fig. 5). The AS in T17 and T21 were not significantly different. The RMR

225 increased exponentially with increasing temperature and in T21, the RMR was equal to the MMR and consumed the entire AS.

## 226 Discussion

### 227 *Effect of temperature on mortality*



228 This is the first study to measure simultaneously survival, growth, metabolic rate, and scope for activity of juvenile Arctic charr at different  
229 temperatures and provides novel insights into the capacity of the species to tolerate higher temperatures. High mortality was found only at 21  
230 °C, where 60% of the fish died during the experiment while mortality at temperatures of 17 °C or lower was under 5% (Fig. 2). These results are  
231 consistent with the findings of other studies showing that the upper incipient lethal temperature for juvenile Arctic charr is 19-21 °C, depending  
232 on the life stage and acclimation temperature (Baroudy and Elliott, 1994; Elliott and Klemetsen, 2002; Thyrel et al., 1999a). A similar pattern of  
233 protracted mortality was observed in Atlantic salmon reared at 23°C (Hvas et al., 2017). The thermal tolerance of juvenile Arctic charr appears to  
234 be similar for populations at the southern distribution range of the species in Lake Windermere, England (54°22' N) (Baroudy and Elliott, 1994),  
235 at high latitudes (69–70° N) in Lake Inari, Finland (Lyytikäinen et al., 1997) and Fjellfrøsvatn, Norway (Elliott and Klemetsen, 2002) as well as in  
236 populations found between 63 and 68 °N in Sweden (Thyrel et al., 1999) and Iceland (present study). The population used in the present study  
237 comes from an aquaculture breeding program but still has similar thermal tolerance as other populations of Arctic charr throughout the  
238 distribution range. These findings suggest that populations from the entire distribution range of Arctic charr show little or no specific adaptations  
239 of the traits tested for temperature tolerance. The protracted mortality over time and the fact that some of the fish survived the experiment  
240 suggests that there is a significant individual variation in thermal tolerance of juveniles Arctic charr. However, the similarities in thermal tolerance  
241 of populations at the northern and southern borders of distribution suggest that the phenotypic plasticity of the Arctic charr allows them to

242 adequately cope with the range of temperatures to which it is exposed in its natural distribution range. In contrast, different populations of  
243 sockeye salmon (*Oncorhynchus nerka*) appear to show adaptations to their thermal environment (Eliason et al., 2011)

244 It is of interest to consider the decline in Arctic charr populations in Iceland and other Nordic countries (Malmquist et al., 2009; Reist et al., 2006;  
245 Svenning et al., 2016; Svenning et al., 2012) in light of these results. Detailed, long term temperature records exist from the shallow lake Elliðavatn  
246 (64°05'16"N 21°46'37"W), which has comparatively high summer temperatures for Iceland. These records show that while the lake temperature  
247 has increased over the past 30 years, it rarely reaches 18-21 °C and then only for few consecutive days each summer (Malmquist et al., 2009).

248 The findings of the present and other studies (Baroudy and Elliott, 1994; Elliott and Klemetsen, 2002; Lyytikäinen et al., 1997b; Thyrel et al.,  
249 1999a) suggest that Arctic charr should be able to tolerate these temperatures for short periods without significant mortality. Nonetheless, the  
250 catches of Arctic charr in the lake and the abundance of juveniles have decreased by 70% since 1987 (Malmquist et al., 2009). The same trend is  
251 observed in several other anadromous and resident charr populations in Iceland (Guðbergsson, 2017; Thordardottir and Guðbergsson, 2017)  
252 living at even lower summer temperatures. This suggests that the temperature-dependent mortality observed in the present study is not  
253 contributing to the decline in Arctic charr populations in Iceland. However, thermal tolerance at other life stages may be important, such as the  
254 thermal limits for egg and embryonic development, which are lower than the limits for growth or survival of juvenile and adult fish (Gillet, 1991;  
255 Jobling, 1996; Van Der Kraak and Pankhurst, 2008; Olk et al., 2019). Egg survival of Arctic charr is negatively correlated with summer and autumn  
256 temperatures (Jeuthe et al., 2015; Jeuthe et al., 2013), and similarly, temperatures above 5-8 °C during the last weeks before spawning can reduce

257 egg quality (Gillet, 1991). Furthermore, the disease and parasite tolerance of Arctic charr at higher temperatures may also contribute to the  
258 decline in charr populations (Bruneaux et al., 2017; Karvonen et al., 2010). Interestingly, there is no evidence of food shortage causing the  
259 reduction in the Arctic charr population in Elliðaavatn since the k and stomach content of the Arctic charr have not changed in recent years  
260 (Malmquist et al., 2009).

### 261 ***Effect of temperature on growth***

262 The optimum temperatures for growth in body mass and length were both near 14°C (Fig. 3) and this is in accord with results from previous  
263 studies on the effect of temperature on Arctic charr that have reported optimum temperature for growth between 13°C and 17°C (Elliott and  
264 Elliott, 2010; Gunnarsson et al., 2011; Jobling, 1983; Jobling et al., 2010; Larsson and Berglund, 1998, 2005; Larsson et al., 2005; Lyytikäinen et  
265 al., 1997a; Siikavuopio et al., 2013; Swift, 1964; Thyrel et al., 1999b). As for the temperature tolerance discussed above, these findings suggest  
266 that few if any specific adaptations with regards to growth at different temperatures in Arctic charr populations from different latitudes. Results  
267 from a comprehensive study of the growth of 11 Arctic charr populations from watercourses between 54 and 70° N suggests no major differences  
268 in the shape of temperature growth curves of the populations and no evidence of significant counter gradient in growth potential depending on  
269 latitude (Larsson et al., 2005). The only indication found of adaptive variation in growth potential was related to life-history characteristics and  
270 diet (Larsson et al., 2005).

271 At supra-optimum temperatures, the growth rate fell precipitously with increasing temperature, and, at 21 °C, there was little or no growth (Fig.  
272 3). Feed intake could not be directly measured in the present experiment, however, results from other studies suggest that feed intake of Arctic  
273 charr decreases progressively as temperature increases above the optimum and near 21-22 °C they do not feed at all (Larsson and Berglund,  
274 2005; Lyytikäinen and Jobling, 1999; Lyytikäinen et al., 1997a; Thyrel et al., 1999a). The lack of growth in T21, as well as indications of lower  
275 energy reserves (k, RIM, and HIS; Table 1; Fig. 4c, d), are all consistent with feed intake being progressively reduced above  $T_{opt}$ .

### 276 ***Oxygen consumption***

277 The measurements of oxygen consumption provide an interesting insight into the energy budgets of the fish. Here, we first discuss the validity  
278 of the methods used. The SMR was measured using common techniques for respirometry (Chabot et al., 2016). However, the measurements of  
279 RMR and MMR were performed in open tanks and this method may be prone to errors due to the diffusion of oxygen from the air to water.  
280 However, the tests we performed under identical conditions without any fish present suggested that this error is minimal (<4%). A second factor  
281 that could have introduced an error is insufficient mixing of the water in the tanks while the inflow was turned off (Rodgers et al., 2016).  
282 Insufficient mixing can affect the outcome of the measurements by decreasing the apparent volume of the tanks if all the fish are aggregated in  
283 a certain area. As a result, the position of the probe and the distribution of the fish can cause errors in measurements that either increase or  
284 decrease the apparent RMR and MMR. If the fish were evenly distributed through all parts of the tanks, the error would have been minimal. The  
285 density of the fish in the tanks, when the metabolic rate was measured, was rather high (17-59 kg·m<sup>3</sup>) and observations of the tanks showed that

286 the fish were fairly evenly distributed. Besides, the spontaneous activity of the fish facilitates mixing (Rasmussen et al., 2005). Therefore, we  
287 suggest that any errors introduced into the measurements of RMR and MMR due to lack of mixing were minimal. The measurements of the MMR  
288 were performed by chasing all the fish and then measuring the MMR in the tanks after most or all of the fish had ceased to respond to prodding.  
289 A more common method to estimate MMR is to measure each fish individually either in a swim tunnel or in a chamber after chasing (Norin and  
290 Clark, 2016). Here we measured MMR in the tanks with spontaneously active fish without the added stress of removing them from the tanks or  
291 exposing them to an alien environment in a swim tunnel or metabolic chamber. In a separate study (Nelson and Thorarensen, 2018), conducted  
292 on similar size Arctic charr from the same source, the MMR was measured in swim tunnels following a constant acceleration test (CAT). The MMR  
293 ( $5.6 \text{ mg} \cdot \text{min}^{-1} \cdot \text{kg}^{-1}$ ) at  $5 \text{ }^{\circ}\text{C}$  was 28% higher than measured in the present study ( $4.36 \text{ mg} \cdot \text{min}^{-1} \cdot \text{kg}^{-1}$ ) while, at  $13 \text{ }^{\circ}\text{C}$ , the MMR was 48% lower ( $6.7$   
294  $\text{mg} \cdot \text{kg}^{-1} \cdot \text{L}^{-1}$ ) than estimated in the present study ( $12.6 \text{ mg} \cdot \text{min}^{-1} \cdot \text{kg}^{-1}$ ). This comparison suggests that the MMR estimated in the present study did  
295 not introduce a systematic error that either under- or overestimated the variables and we suggest that they provide a valid estimate of RMR and  
296 MMR. Moreover, the measurements of RMR and MMR at different temperatures are comparable since all were performed under identical  
297 conditions.

298 The values for metabolic rate obtained in this study correspond well with those of other studies on Arctic charr and salmonids. The SMR increased  
299 progressively with temperature although a small peak was evident at  $13 \text{ }^{\circ}\text{C}$  (Fig. 5). Similar increases in SMR with temperature have been observed  
300 in studies on other fish species (Brett, 1976; Brett, 1971; Claireaux and Lagardère, 1999; Khan et al., 2014; Lefrançois and Claireaux, 2003; Mallekh

301 and Lagardère, 2002; Tirsgaard et al., 2015; Hvas et al., 2017). Studying larger (747 g), seawater-acclimated Arctic charr in a swim tunnel at 10.5  
302 °C, Penney et al. (2014) found a lower SMR ( $1.4 \text{ mg} \cdot \text{min}^{-1} \cdot \text{kg}^{-1}$ ) than the present experiment ( $2.3 \text{ mg} \cdot \text{min}^{-1} \cdot \text{kg}^{-1}$  for 17 g fish), however, these  
303 differences are likely primarily due to scaling effects on metabolic rate and adjusting the values with a mass exponent of 0.8-0.85 (Clarke and  
304 Johnston, 1999; Killen et al., 2007) yields similar SMR. The rise in RMR with temperature was much more pronounced than the rise in SMR (Fig.  
305 5). Similar increases in RMR with temperature have previously been reported in other salmonid species (Brett, 1971, 1979; Hvas et al., 2017) and  
306 Arctic charr at higher temperatures (Lyytikäinen and Jobling, 1999). The RMR measured in the present experiment was similar to that reported  
307 in other studies on slightly larger (90-105 g) Arctic charr (Christiansen et al., 1991; Jorgensen et al., 1993; Lyytikäinen and Jobling, 1999) at similar  
308 temperatures when corrected with a mass exponent of 0.8-0.9 (Killen et al., 2010; Killen et al., 2007; Norin and Gamperl, 2018). Lyytikäinen and  
309 Jobling (1999) measured the RMR of Arctic charr of similar size at 11, 14.4, and 17.7 °C. At 11 and 14.4 °C, the RMR measured in the present  
310 study (extrapolating values between temperatures) was 27% and 36% higher than that reported by Lyytikäinen and Jobling (1999) while at 17 °C,  
311 the difference was less than 6%. Furthermore, the proportional increases in RMR between temperatures were similar in both studies. The  
312 similarities between the metabolic values reported in the present and other studies on Arctic charr lends further credence to the results of the  
313 present study.

#### 314 ***Metabolic rate and growth***

315 The results of this study shed an interesting light on the potential relationship between RMR, MMR, AS, and the growth of fish. Previous studies  
316 have indicated that the growth of Atlantic cod and seabass may be limited by the AS (Chabot and Claireaux, 2008; Claireaux and Lefrançois, 2007).  
317 Consistent with this proposition, the growth, MMR, and AS all peaked at 13 °C (Fig. 3a,5), and from 5 to 13 °C, the growth rate was positively  
318 correlated with AS ( $R: 0.93$ ). However, a significant correlation does of course not necessarily indicate that the growth was limited by the AS. For  
319 the AS to limit growth, it would have to limit and/or protract the maximum SDA in postprandial fish. Digestion and absorption are a process that  
320 may take hours after a meal and, in aquaculture fish, it may be nearly continuous. Therefore, the SDA may be limited by the ability to sustain  
321 high metabolic rates over long periods in contrast to the MMR which is a measure of short-term (minutes) capacity (Norin and Clark, 2016). The  
322 sustainable metabolic output of fish is lower than the MMR (Beamish, 1978). For example, Hvas and Oppedal (2017) found that while Atlantic  
323 salmon post-smolts could only maintain  $U_{crit}$  for less than 30 minutes, they were able to swim for over 4 hours at 80% of  $U_{crit}$ . This suggests that  
324 the MMR (and AS) could be reduced without limiting the sustainable energy output. For example, the results of Beuvar et al. (in prep.) show  
325 that at 9 °C, the AS of Arctic charr is reduced when oxygen saturation is reduced from 100% to 60% without any effect on growth. In the present  
326 study, we found that the metabolic demands of the RMR between 5 and 13 °C only consumed 8-50% of the AS suggesting that growth is unlikely  
327 limited by the AS at temperatures of 13 °C and below.

328 The growth of the charr was reduced by 93% when the temperature was increased from 17 to 21 °C (Fig. 3a) while the AS was unchanged (Fig.  
329 5). However, the RMR increased exponentially with temperature and more so than the SMR (Fig. 5). A similar increase in RMR or maintenance

330 ration with temperature has been observed in other studies on salmonids (Brett, 1976; Hvas et al. 2017). At 21 °C, the RMR consumed all the AS  
331 and was equal to the MMR. This may suggest that, at 21 °C, the RMR is limited by the MMR. Furthermore, this may also suggest that growth was  
332 limited by the MMR (or AS) at this temperature if the maximum SDA was reduced and/or protracted. It is not clear why the RMR increases  
333 proportionately more than the SMR, but Brett (1979, 1976) suggested that this could be due to reduced efficiency of metabolic processes or feed  
334 processing as temperature increases.

335 The concept of scope for growth “the difference between the energy of the food an animal consumes and all other energy utilization and losses”  
336 was originally coined by (Warren and Davis, 1967) and later elaborated by Brett (1976, 1979). It describes the energy available for anabolic  
337 processes as the difference in energy intake and energy consumption (and losses). Therefore, it is better suited to predict growth than the  
338 concept of scope for activity and Fry’s paradigm, which only addresses catabolic processes. It is interesting to consider the results of the present  
339 study in the context of scope for growth. They and results of other studies on Arctic charr (Lyytikäinen and Jobling, 1999) suggest that as  
340 temperature increases above  $T_{opt}$ , feed intake is reduced and this would reduce the scope for growth. At the same time, the RMR increased  
341 exponentially which would reduce the scope of growth even further as the energy consumption increases. Therefore, the reduced growth at  
342 supra-optimum temperatures is consistent with the concept of scope for growth. At 21 °C, there was no growth suggesting that the fish were  
343 eating no more than maintenance rations. One of the factors contributing to the high mortalities at 21 °C may have been that some of the fish  
344 were not even able to acquire enough energy through feed and/or sustain the metabolic rate required to support maintenance functions. In



345 summary, the results of the present study may identify three factors that all may contribute to the reduced growth at supra-optimum  
346 temperatures: (1) Increased metabolic demands of the fish (RMR), (2) Reduced feed (energy) intake (3) Inability of the cardio-respiratory system  
347 to support the increasing energy demands of the fish. Of course, these factors may be interrelated and are not mutually exclusive. For example,  
348 reduced feed intake may be important to limit the high RMR when the temperature increases.

349 As mentioned above, Arctic charr appears to require the full capacity of the MMR (or AS) to support aerobic metabolism at 21 °C. Results from  
350 thermal challenge tests on Arctic charr (Gilbert et al., 2020; Penney et al., 2014) show arrhythmias and reduced heart rate above 20 °C which is  
351 also consistent with the cardiovascular system being challenged to its maximum. The MMR of salmonids depends on the capacity of the  
352 cardiorespiratory system to deliver oxygen (Gallaughner et al., 2001; P. Gallaughner et al., 1995a) and the results of the present study suggest that  
353 there was added stress on the cardio-respiratory system at 21 °C. The increased RVM at 21 °C (82% larger than in T5) indicates physiological  
354 adaptations to increase oxygen delivery to allow higher maximum cardiac output (Gamperl and Farrell, 2004). The RVM was also positively  
355 correlated with temperature below 21 °C and this is consistent with our previous results on Arctic charr (Ruiz and Thorarensen, 2001). This is  
356 uncommon among salmonids where RVM tends to decrease as temperature increases (Gamperl and Farrell, 2004; Anttila et al., 2015). The  
357 difference between Arctic charr and other salmonid species may relate to the fact that it is adapted to survive and grow at lower temperatures  
358 than other salmonids and, therefore, the increased temperature may pose a comparatively greater challenge to the cardiovascular system of  
359 Arctic charr. The RGM was reduced as temperature increased from 5 to 17 °C. However, there was a significant increase in RGM from 17 to 21

360 °C (Fig. 4b). This suggests that the charr acclimated to a high temperature by increasing the gill area to facilitate trans-branchial diffusion.  
361 Therefore, both the changes in heart and gill mass may reflect physiological changes aimed at supporting the increased RMR at high  
362 temperatures. These findings are consistent with the prediction of the OCLTT hypothesis (Pörtner and Farrell, 2008) that the upper incipient  
363 temperature for charr is limited by the capacity of the cardiorespiratory system to deliver oxygen to tissues. However, as described above, this  
364 limitation does not appear to be a factor contributing to the decline of Arctic charr populations in Iceland which is occurring at lower  
365 temperatures.

## 366 Conclusion

367 The results of the present study provide an interesting insight into the effect of increased ambient temperatures on the survival and growth of  
368 juvenile Arctic charr. The results suggest that up to 17 °C, the temperature has a limited effect on the survival of Arctic charr juveniles. The  
369 optimum temperature for the growth of Arctic charr juveniles in body mass and length is near 14 °C. The results of the present and other studies  
370 suggest that temperature tolerance and the optimum temperature for the growth of Arctic charr throughout the distribution range of the species  
371 is similar. Arctic charr populations in Iceland, and other countries, have declined recently. However, current ambient temperatures in Icelandic  
372 freshwater systems are unlikely to cause mortalities in juvenile fish. As the temperature is increased above supra-optimum levels, the growth of  
373 Arctic charr is reduced. The results of this study suggest that three factors could contribute to the reduced growth as temperature increases: (1)  
374 Reduced feed intake, (2) increased metabolic rate, and (3) the capacity of the cardiorespiratory system to sustain metabolism.

375

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377

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380

## 381 4. References

- 382 Alsop, D., and Wood, C. (1997). The interactive effects of feeding and exercise on oxygen consumption, swimming performance and protein usage in  
383 juvenile rainbow trout (*Oncorhynchus mykiss*). *J. Exp. Biol.* 200, 2337–46. Available at: <http://www.ncbi.nlm.nih.gov/pubmed/9320259>.
- 384 Angelo, C., and Ripley, B. (2016). boot: Bootstrap R (S-Plus) Functions. *R Packag. version 1.3-18*.
- 385 Anttila, K., Lewis, M., Prokkola, J. M., Kanerva, M., Seppänen, E., Kolari, I., et al. (2015). Warm acclimation and oxygen depletion induce species-specific  
386 responses in salmonids. *J. Exp. Biol.* 218. doi:10.1242/jeb.119115.
- 387 Atkins, M. E., and Benfey, T. J. (2008). Effect of acclimation temperature on routine metabolic rate in triploid salmonids. *Comp. Biochem. Physiol. - A Mol.*  
388 *Integr. Physiol.* 149, 157–161. doi:10.1016/j.cbpa.2007.11.004.
- 389 Baroudy, E., and Elliott, J. M. (1994). The critical thermal limits for juvenile Arctic charr *Salvelinus alpinus*. *J. Fish Biol.* 45, 1041–1053. doi:10.1111/j.1095-  
390 8649.1994.tb01071.x.
- 391 Beamish, F. W. H. (1978). "Swimming Capacity," in *Fish Physiology*, eds. W. S. Hoar and D. J. Randall (New York: Academic Press), 101–187.  
392 doi:10.1016/S1546-5098(08)60164-8.
- 393 Beamish, F. W. H., and Trippel, E. A. (1990). Heat Increment: A Static or Dynamic Dimension in Bioenergetic Models? *Trans. Am. Fish. Soc.* 119, 416–430.  
394 doi:10.1577/1548-8659(1990)119<0649:HIASOD>2.3.CO;2.

395 Brännäs, E., and Linnér, J. (2000). Growth effects in Arctic charr reared in cold water: Feed frequency, access to bottom feeding and stocking density. *Aquac.*  
396 *Int.* 8, 381–389. doi:10.1023/A:1009235130015.

397 Brännäs, E., and Wiklund, B.-S. (1992). Low temperature growth potential of Arctic charr and Rainbow trout. *Nord. J. Freshw. Res.* 67, 77–81.

398 Brett, J. R. (1976). Scope for Metabolism and Growth of Sockeye Salmon, *Oncorhynchus nerka*, and Some Related Energetics. *J. Fish. Res. Board Canada* 33,  
399 307–313. doi:10.1139/f76-046.

400 Brett, J. R. (1979). “Environmental factors and growth,” in *Fish Physiology*, eds. W. S. Hoar, D. J. Randall, and J. R. Brett (London: Academic Press), 599–675.

401 Brett, J. R., and Glass, N. R. (1973). Metabolic Rates and Critical Swimming Speeds of Sockeye Salmon (*Oncorhynchus nerka*) in Relation to Size and  
402 Temperature. *J. Fish. Res. Board Canada* 30, 379–387.

403 Brett, J. R., and Groves, T. (1979). “Physiological Energetics,” in *Fish Physiology*, eds. W. S. Hoar, D. J. Randall, and J. R. Brett (London: Academic Press), 279–  
404 352. doi:10.1016/S1546-5098(08)60029-1.

405 Brett, R. (1971). Energetic Responses of Salmon to Temperature . A Study of Some Thermal Relations in the Physiology and Freshwater Ecology of Sockeye  
406 Salmon (*Oncorhynchus nerka*) Author ( s ): John R . Brett Published by : Oxford University Press Your use of the JSTOR ar. *Am. Zool.* 11, 99–113.

407 Bruneaux, M., Visse, M., Gross, R., Pukk, L., Saks, L., and Vasemägi, A. (2017). Parasite infection and decreased thermal tolerance: impact of proliferative  
408 kidney disease on a wild salmonid fish in the context of climate change. *Funct. Ecol.* 31, 216–226. doi:10.1111/1365-2435.12701.

409 Chabot, D., and Claireaux, G. (2008). Environmental hypoxia as a metabolic constraint on fish: the case of Atlantic cod, *Gadus morhua*. *Mar. Pollut. Bull.* 57,  
410 287–94. doi:10.1016/j.marpolbul.2008.04.001.

411 Chabot, D., Steffensen, J. F., and Farrell, A. P. (2016). The determination of standard metabolic rate in fishes. *J. Fish Biol.* 88, 81–121. doi:10.1111/jfb.12845.

412 Christiansen, J. S., Jorgensen, E. H., and Jobling, M. (1991). Oxygen-Consumption in Relation to Sustained Exercise and Social Stress in Arctic Charr  
413 (*Salvelinus-Alpinus* L). *J. Exp. Zool.* 260, 149–156. doi:10.1002/jez.1402600203.

414 Chu, C., Mandrak, N. E., and Minns, C. K. (2005). Potential impacts of climate change on the distributions of several common and rare freshwater fishes in  
415 Canada. *Divers. Distrib.* 11, 299–310. doi:10.1111/j.1366-9516.2005.00153.x.

416 Claireaux, G., and Lagardere, J.-P. (1999). Influence of temperature, oxygen and salinity on the metabolism of the European sea bass. *J. Sea Res.* 42, 157–

417 168. doi:10.1016/S1385-1101(99)00019-2.

418 Claireaux, G., Lagardere, J.-P., Webber, D., Kerr, S., Boutilier, R., Packer, L., et al. (2007). Influence of temperature, oxygen and salinity on the metabolism of  
419 the European sea bass. *J. Exp. Biol.* 362, 157–168. doi:10.1016/S1385-1101(99)00019-2.

420 Claireaux, G., and Lefrançois, C. (2007a). Linking environmental variability and fish performance : integration through the concept of scope for activity Rapid  
421 response Email alerting service Linking environmental variability and fish performance : integration through the concept of scope for acti. *Phil. Trans.*  
422 *R. Soc. B* 362, 2031–2041. doi:10.1098/rstb.2007.2099.

423 Claireaux, G., and Lefrançois, C. (2007b). Linking environmental variability and fish performance: integration through the concept of scope for activity.  
424 *Philos. Trans. R. Soc. Lond. B. Biol. Sci.* 362, 2031–2041. doi:10.1098/rstb.2007.2099.

425 Claireaux, G., Webber, D. M., Lagardère, J. P., and Kerr, S. R. (2000). Influence of water temperature and oxygenation on the aerobic metabolic scope of  
426 Atlantic cod (*Gadus morhua*). *J. Sea Res.* 44, 257–265. doi:10.1016/S1385-1101(00)00053-8.

427 Clark, T. D., Sandblom, E., Cox, G. K., Hinch, S. G., and Farrell, A. P. (2008). Circulatory limits to oxygen supply during an acute temperature increase in the  
428 Chinook salmon (*Oncorhynchus tshawytscha*). *Am. J. Physiol. Regul. Integr. Comp. Physiol.* 295, R1631–R1639. doi:10.1152/ajpregu.90461.2008.

429 Clark, T. D., Sandblom, E., and Jutfelt, F. (2013). Aerobic scope measurements of fishes in an era of climate change: respirometry, relevance and  
430 recommendations. *J. Exp. Biol.* 216, 2771–82. doi:10.1242/jeb.084251.

431 Clarke, A., and Johnston, N. M. (1999). Scaling of metabolic rate with body mass and temperature in teleost<sup>®</sup> sh. *J. Anim. Ecol.*, 893–905.

432 Clarke, A., and Pörtner, H.-O. (2010). Temperature , metabolic power and the evolution of endothermy. *Biol. Rev.* doi:10.1111/j.1469-185X.2010.00122.x.

433 Eliason, E. J., Clark, T. D., Hague, M. J., Hanson, L. M., Gallagher, Z. S., Jeffries, K. M., et al. (2011). Differences in thermal tolerance among sockeye salmon  
434 populations. *Science (80- )*. 332, 109–112. doi:10.1126/science.1199158.

435 Eliason, E. J., Clark, T. D., Hinch, S. G., and Farrell, A. P. (2013). Cardiorespiratory collapse at high temperature in swimming adult sockeye salmon. 1, 1–19.  
436 doi:10.1093/conphys/cot008.

437 Eliason, E. J., and Farrell, A. P. (2015). Oxygen uptake in Pacific salmon *Oncorhynchus* spp.: when ecology and physiology meet. *J. Fish Biol.*, 359–388.  
438 doi:10.1111/jfb.12790.

439 Elliott, J. M., and Elliott, J. A. (2010). Temperature requirements of Atlantic salmon *Salmo salar*, brown trout *Salmo trutta* and Arctic charr *Salvelinus alpinus*:  
440 predicting the effects of climate change. *J. Fish Biol.* 77, 1793–1817. doi:10.1111/j.1095-8649.2010.02762.x.

441 Elliott, J. M., and Klemetsen, a (2002). The upper critical thermal limits for alevins of Arctic charr from a Norwegian lake north of the Arctic circle. *J. Fish Biol.*  
442 60, 1338–1341. doi:10.1006/jfbi.2002.1934.

443 Farrell, A. P. (2009). Environment, antecedents and climate change: lessons from the study of temperature physiology and river migration of salmonids. *J.*  
444 *Exp. Biol.* 212, 3771–3780. doi:10.1242/jeb.023671.

445 Fry, F. E. J. (1947). Effects of the environment on animal activity. *Publ. Ontario Fish. Res. Lab.* 55, 1–62. Available at:  
446 <http://scholar.google.com/scholar?hl=en&btnG=Search&q=intitle:Effects+of+the+environment+on+animal+activity#0>.

447 Fry, F. E. J. (1971a). Effect of environmental factors on the physiology of fishes. *Yale J. Biol. Med.* 30, 152–153. doi:10.1016/S0044-8486(97)82982-1.

448 Fry, F. E. J. (1971b). “The Effect of Environmental Factors on the Physiology of Fish,” in *Fish Physiology* Fish Physiology., eds. W. S. Hoar and D. J. Randall  
449 (New York: Academic Press), 1–98. doi:10.1016/S1546-5098(08)60146-6.

450 Gallagher, P. E., Thorarensen, H., Kiessling, a, and Farrell, a P. (2001). Effects of high intensity exercise training on cardiovascular function, oxygen uptake,  
451 internal oxygen transport and osmotic balance in chinook salmon (*Oncorhynchus tshawytscha*) during critical speed swimming. *J. Exp. Biol.* 204, 2861–  
452 2872. Available at: <http://www.ncbi.nlm.nih.gov/pubmed/11683441>.

453 Gallagher, P., Thorarensen, H., and Farrell, a P. (1995). Hematocrit in oxygen transport and swimming in rainbow trout (*Oncorhynchus mykiss*). *Respir.*  
454 *Physiol.* 102, 279–292.

455 Gamperl, A. K., and Farrell, A. P. (2004). Commentary Cardiac plasticity in fishes : environmental influences and intraspecific differences. *J. Exp. Biol.* 207,  
456 2539–2550. doi:10.1242/jeb.01057.

457 Gilbert, M. J. H., Harris, L. N., Malley, B. K., Schimnowski, A., Moore, J.-S., and Farrell, A. P. (2020). The thermal limits of cardiorespiratory performance in  
458 anadromous Arctic char (*Salvelinus alpinus*): a field-based investigation using a remote mobile laboratory. *Conserv. Physiol.* 8, 1–12.  
459 doi:10.1093/conphys/coaa036.

460 Gillet, C. (1991). Egg production in an Arctic charr (*Salvelinus alpinus* L.) brood stock: effects of temperature on the timing of spawning and the quality of

461 eggs. *Aquar. Living Resour* 4, 109–116. doi:10.1051/alr:1991010.

462 Guðbergsson, G. (2017). Silungurinn í Mývatni - Yfirlit yfir rannsóknir og veiðitölur. Reykjavík Available at:  
463 <https://www.hafogvatn.is/static/research/files/hv2017-042pdf>.

464 Gunnarsson, S., Imsland, A. K., Árnason, J., Gústavsson, A., Arnarson, I., Jónsson, J. K., et al. (2011). Effect of rearing temperatures on the growth and  
465 maturation of Arctic charr (*Salvelinus alpinus*) during juvenile and on-growing periods. *Aquac. Res.* 42, 221–229. doi:10.1111/j.1365-  
466 2109.2010.02615.x.

467 Hein, C. L., Öhlund, G., and Englund, G. (2012). Future distribution of arctic char *Salvelinus alpinus* in Sweden under climate change: Effects of temperature,  
468 lake size and species interactions. *Ambio* 41, 303–312. doi:10.1007/s13280-012-0308-z.

469 Huuskonen, H., Penttinen, O.-P., and Piironen, J. (2003). Effects of temperature and parental background on the embryonic survival and metabolic rate of  
470 newly hatched Arctic charr. *Big Fish Bang. Proc. 26th Annu. Larval Fish Conf. 22-26 July 2002; Bergen*.

471 Hvas, M., Folkedal, O., Imsland, A., and Oppedal, F. (2017). The effect of thermal acclimation on aerobic scope & critical swimming speed in Atlantic salmon,  
472 *Salmo salar*. *J. Exp. Biol.* 220, 2757–2764. doi:10.1242/jeb.154021.

473 Hvas, M., and Oppedal, F. (2017). Hvas and Oppedal. 2017 Sustained swimming capacity of Atlantic salmon. 9, 361–369.

474 Jeuthe, H., Brännäs, E., and Nilsson, J. (2013). Effects of egg size, maternal age and temperature on egg, viability of farmed Arctic charr. *Aquaculture* 408–  
475 409, 70–77. doi:10.1016/j.aquaculture.2013.05.034.

476 Jeuthe, H., Brännäs, E., and Nilsson, J. (2015). Thermal stress in Arctic charr *Salvelinus alpinus* broodstock: A 28 year case study. *J. Fish Biol.* 86, 1139–1152.  
477 doi:10.1111/jfb.12634.

478 Jobling, M. (1981). The influences of feeding on the metabolic rate of fishes : a short review. *J. Fish Biol.* 18, 385–400.

479 Jobling, M. (1983). Influence of body weight and temperature on growth rates of Arctic charr, *Salvelinus alpinus* (L.). *J. Fish Biol.* 22, 471–475.  
480 doi:10.1111/j.1095-8649.1983.tb04767.x.

481 Jobling, M. (1996). *Temperature and growth: modulation of growth rate via temperature change*. doi:10.1017/CBO9781107415324.004.

482 Jobling, M., Arnesen, A. M., Benfey, T., Carter, C., Hardy, R., Le Francois, N. R., et al. (2010). “The salmonids (Family: Salmonidae).,” in *Finfish Aquaculture*

483 *Diversification*, eds. N. Le Francois, M. Jobling, C. Carter, and P. Blier (Oxfordshire: CAB International), 241–248.

484 Jobling, M., Jørgensen, E. H., Arnesen, A. M., and Ringø, E. (1993). Feeding, growth and environmental requirements of Arctic charr: a review of aquaculture  
485 potential. *Aquac. Int.* 1, 20–46. doi:10.1007/BF00692662.

486 Jonsson, B., and Jonsson, N. (2009). A review of the likely effects of climate change on anadromous Atlantic salmon *Salmo salar* and brown trout *Salmo*  
487 *trutta*, with particular reference to water temperature and flow. *J. Fish Biol.* 75, 2381–2447. doi:10.1111/j.1095-8649.2009.02380.x.

488 Jørgensen, E. H., Christiansen, J. S., and Jobling, M. (1993). Effects of stocking density on food intake, growth performance and oxygen consumption in Arctic  
489 charr (*Salvelinus alpinus*). *Aquaculture* 110, 191–204. doi:10.1016/0044-8486(93)90272-z.

490 Jutfelt, F., Norin, T., Ern, R., Overgaard, J., Wang, T., McKenzie, D. J., et al. (2018). Oxygen- and capacity-limited thermal tolerance: blurring ecology and  
491 physiology. *J. Exp. Biol.* 221, 1–2. doi:10.1242/jeb.169615.

492 Karvonen, A., Rintamäki, P., Jokela, J., and Valtonen, E. T. (2010). Increasing water temperature and disease risks in aquatic systems: Climate change  
493 increases the risk of some, but not all, diseases. *Int. J. Parasitol.* 40, 1483–1488. doi:10.1016/j.ijpara.2010.04.015.

494 Khan, J. R., Pether, S., Bruce, M., Walker, S. P., and Herbert, N. A. (2014). Optimum temperatures for growth and feed conversion in cultured hapuku (  
495 *Polyprion oxygeneios*) — Is there a link to aerobic metabolic scope and final temperature preference? *Aquaculture* 430, 107–113.  
496 doi:10.1016/j.aquaculture.2014.03.046.

497 Killen, S. S., Atkinson, D., and Glazier, D. S. (2010). The intraspecific scaling of metabolic rate with body mass in fishes depends on lifestyle and temperature.  
498 *Ecol. Lett.* 13, 184–193. doi:10.1111/j.1461-0248.2009.01415.x.

499 Killen, S. S., Costa, I., Brown, J. A., and Gamperl, A. K. (2007a). Little left in the tank : metabolic scaling in marine teleosts and its implications for aerobic  
500 scope. *Proc. R. Soc. B Biol. Sci.* 274, 431–438. doi:10.1098/rspb.2006.3741.

501 Killen, S. S., Costa, I., Brown, J. a, and Gamperl, a K. (2007b). Little left in the tank: metabolic scaling in marine teleosts and its implications for aerobic scope.  
502 *Proc. Biol. Sci.* 274, 431–438. doi:10.1098/rspb.2006.3741.

503 Klemetsen, A., Amundsen, P.-A., Dempson, J. B., Jonsson, B., Jonsson, N., O’Connell, M. F., et al. (2003). Atlantic salmon *Salmo salar* L., brown trout *Salmo*  
504 *trutta* L. and Arctic charr *Salvelinus alpinus* (L.): a review of aspects of their life histories. *Ecol. Freshw. Fish* 12, 1–59. doi:10.1034/j.1600-



505 0633.2003.00010.x.

506 Larsson, S., and Berglund, I. (1998). Growth and Food Consumption of 0+ Arctic Charr Fed Pelleted or Natural Food at Six Different Temperatures. *J. Fish Biol.*  
507 52, 230–242. doi:10.1111/j.1095-8649.1998.tb00795.x.

508 Larsson, S., and Berglund, I. (2005). The effect of temperature on the energetic growth efficiency of Arctic charr (*Salvelinus alpinus* L.) from four Swedish  
509 populations. *J. Therm. Biol.* 30, 29–36. doi:10.1016/j.jtherbio.2004.06.001.

510 Larsson, S., Forseth, T., Berglund, I., Jensen, a. J., Näslund, I., Elliott, J. M., et al. (2005). Thermal adaptation of Arctic charr: Experimental studies of growth  
511 in eleven charr populations from Sweden, Norway and Britain. *Freshw. Biol.* 50, 353–368. doi:10.1111/j.1365-2427.2004.01326.x.

512 Lee, C. G., Farrell, A. P., Lotto, A., MacNutt, M. J., Hinch, S. G., and Healey, M. C. (2003). The effect of temperature on swimming performance and oxygen  
513 consumption in adult sockeye (*Oncorhynchus nerka*) and coho (*O. kisutch*) salmon stocks. *J. Exp. Biol.* 206, 3239–3251. doi:10.1242/jeb.00547.

514 Lefevre, S. (2016). Are global warming and ocean acidification conspiring against marine ectotherms? A meta-analysis of the respiratory effects of elevated  
515 temperature, high CO<sub>2</sub> and their interaction. *Conserv. Physiol.* 4, cow009. doi:10.1093/conphys/cow009.

516 Lefrançois, C., and Claireaux, G. (2003). Influence of ambient oxygenation and temperature on metabolic scope and scope for heart rate in the common sole  
517 *Solea solea*. *Mar. Ecol. Prog. Ser.* 259, 273–284. doi:10.3354/meps259273.

518 Lyytikäinen, T., and Jobling, M. (1998). The effect of temperature fluctuations on oxygen consumption and ammonia excretion of underyearling Lake Inari  
519 Arctic charr. *Environmental Biol. Fishes* 54, 219–227.

520 Lyytikäinen, T., and Jobling, M. (1999). Lyytikäinen & Jobling 1999.pdf. *Environmental Biol. Fishes* 54, 219–227.

521 Lyytikäinen, T., Koskela, J., and Rissanen, I. (1997a). The influence of temperature on growth and proximate body composition of under yearling Lake Inari  
522 arctic char (*Salvelinus alpinus* (L.)). *J. Appl. Ichthyol.* 13, 191–194. doi:10.1111/j.1439-0426.1997.tb00120.x.

523 Lyytikäinen, T., Koskela, J., and Rissanen, I. (1997b). Thermal resistance and upper lethal temperatures of underyearling Lake Inari Arctic charr. *J. Fish Biol.*  
524 51, 515–525. doi:10.1111/j.1095-8649.1997.tb01509.x.

525 MacNutt, M. J., Hinch, S. G., Lee, C. G., Phibbs, J. R., Lotto, A. G., Healey, M. C., et al. (2006). Temperature effects on swimming performance, energetics, and  
526 aerobic capacities of mature adult pink salmon (*Oncorhynchus gorbuscha*) compared with those of sockeye salmon (*Oncorhynchus nerka*). *Can. J. Zool.*

527 84, 88–97. doi:10.1139/z05-181.

528 Maitland, P. S., Winfield, I. J., McCarthy, I. D., and Igoe, F. (2007). The status of Arctic charr *Salvelinus alpinus* in Britain and Ireland. *Ecol. Freshw. Fish* 16, 6–  
529 19. doi:10.1111/j.1600-0633.2006.00167.x.

530 Mallekh, R., and Lagardere, J.-P. (2002). Effect of temperature and dissolved oxygen concentration on the metabolic rate of the turbot and the relationship  
531 between metabolic scope and feeding demand. *J. Fish Biol.* 60, 1105–1115. doi:10.1006/jfbi.2002.1918.

532 Mallekh, R., and Lagardère, J. P. (2002). Effect of temperature and dissolved oxygen concentration on the metabolic rate of the turbot and the relationship  
533 between metabolic scope and feeding demand. *J. Fish Biol.* 60, 1105–1115. doi:10.1006/jfbi.2002.1918.

534 Malmquist, H. J., Antonsson, P., Ingvason, H. R., Ingimarsson, F., and Arnason, F. (2009). Salmonid fish and warming of shallow Lake Elliðavatn in Southwest  
535 Iceland. *Verhandlungen des Int. Verein Limnol.* 30, 1127–1132.

536 Nelson, J., and Thorarensen, H. (2018). Using extant fishes to predict the future of freshwater fishes facing climate disruption. *Integr. Comp. Biol.* 58, E163–  
537 E163.

538 Norin, T., and Clark, T. D. (2016). Measurement and relevance of maximum metabolic rate in fishes. *J. Fish Biol.*, 122–151. doi:10.1111/jfb.12796.

539 Norin, T., and Gamperl, A. K. (2018). Metabolic scaling of individuals vs . populations : Evidence for variation in scaling exponents at different hierarchical  
540 levels. 379–388. doi:10.1111/1365-2435.12996.

541 Norin, T., Malte, H., and Clark, T. D. (2014). Aerobic scope does not predict the performance of a tropical eurythermal fish at elevated temperatures. *J. Exp.*  
542 *Biol.* 217, 244–251. doi:10.1242/jeb.089755.

543 Olk, T. R., Jeuthe, H., Thorarensen, H., Wollebæk, J., and Lydersen, E. (2019). Brood-stock management and early hatchery rearing of Arctic charr (*Salvelinus*  
544 *alpinus* (Linnaeus)). *Rev. Aquac.*, 1–29. doi:10.1111/raq.12400.

545 Penney, C. M., Nash, G. W., and Gamperl, A. K. (2014a). Cardiorespiratory responses of seawater-acclimated adult Arctic char (*Salvelinus alpinus*) and  
546 Atlantic salmon (*Salmo salar*) to an acute temperature increase. *Can. J. Fish. Aquat. Sci.* 71, 1096–1105. doi:10.1139/cjfas-2013-0569.

547 Penney, C. M., Nash, G. W., Gamperl, A. K., and Tierney, K. (2014b). Cardiorespiratory responses of seawater-acclimated adult Arctic char ( *Salvelinus alpinus*  
548 ) and Atlantic salmon ( *Salmo salar* ) to an acute temperature increase. *Can. J. Fish. Aquat. Sci.* 71, 1096–1105. doi:10.1139/cjfas-2013-0569.

549 Pinheiro, J., Bates, D., DebRoy, S., Sarkar, D., and Team R Core (2017). nlme: Linear and Nonlinear Mixed Effects Models. *R Packag. version 3.1-131*,  
550 <https://CRAN.R-project.org/package=nlme>.

551 Pörtner, H.-O., and Farrell, A. P. (2008a). Physiology and climate change. *Science (80-. )*. 322, 690–692. doi:10.1126/science.1163156.

552 Pörtner, H. O., and Farrell, A. P. (2008b). Physiology and Climate change. *Science (80-. )*, 690–692.

553 Pörtner, H. O., and Knust, R. (2007). Climate change affects marine fishes through the oxygen limitation of thermal tolerance. *Science* 315, 95–97.  
554 doi:10.1126/science.1135471.

555 Rasmussen, M. R., Laursen, J., Craig, S. R., and McLean, E. (2005). Do fish enhance tank mixing? *Aquaculture* 250, 162–174.  
556 doi:10.1016/j.aquaculture.2005.02.041.

557 Reist, J. D., Wrona, F. J., Prowse, T. D., Power, M., Dempson, J. B., King, J. R., et al. (2006). An Overview of Effects of Climate Change on Selected Arctic  
558 Freshwater and Anadromous Fishes. *Ambio* 35, 381–387.

559 Rodgers, G. G., Tenzing, P., and Clark, T. D. (2016). Experimental methods in aquatic respirometry: the importance of mixing devices and accounting for  
560 background respiration. *J. Fish Biol.* 88, 65–80. doi:10.1111/jfb.12848.

561 Ruiz, M. A. M., and Thorarensen, H. (2001). Genetic and environmental effects on the size of the cardio-respiratory organs in Arctic charr (*Salvelinus*  
562 *alpinus*).

563 Siikavuopio, S. I., Foss, A., Sæther, B. S., Gunnarsson, S., and Imsland, A. K. (2013). Comparison of the growth performance of offspring from cultured versus  
564 wild populations of arctic charr, *Salvelinus alpinus* (L.), kept at three different temperatures. *Aquac. Res.* 44, 995–1001. doi:10.1111/j.1365-  
565 2109.2012.03112.x.

566 Siikavuopio, S. I., Knudsen, R., and Amundsen, P. A. (2010). Growth and mortality of Arctic charr and European whitefish reared at low temperatures.  
567 *Hydrobiologia* 650, 255–263. doi:10.1007/s10750-010-0192-0.

568 Svendsen, M. B. S., Bushnell, P. G., and Steffensen, J. F. (2016). Design and setup of intermittent-flow respirometry system for aquatic organisms. *J. Fish Biol.*  
569 88, 26–50. doi:10.1111/jfb.12797.

570 Svenning, M.-A., Sandem, K., Halvorsen, M., Kanstad-Hanssen, Ø., Falkegård, M., and Borgstrøm, R. (2016). Change in relative abundance of Atlantic salmon

571 and Arctic charr in Veidnes River, Northern Norway: a possible effect of climate change? *Hydrobiologia*, 1–14. doi:10.1007/s10750-016-2690-1.

572 Svenning, M. A., Falkegaard, M., and Hanssen, Ø. K. (2012). Anadromous Arctic Charr in North Norway—A Falling Queen? - NINA Report 780. Trondheim

573 Available at: <http://www.nina.no/archive/nina/pppbasepdf/rapport/2012/780.pdf>.

574 Swift D R (1964). The effect of temperature and oxygen on the growth rate of the Windermere char (*Salvelinus alpinus willughbii*). *Comp. Biochem. Physiol.*

575 12, 179–183.

576 Thorarensen, H., and Farrell, A. P. (2006a). Postprandial intestinal blood flow, metabolic rates, and exercise in Chinook salmon (*Oncorhynchus tshawytscha*).

577 *Physiol. Biochem. Zool.* 79, 688–94. doi:10.1086/505512.

578 Thorarensen, H., and Farrell, A. P. (2006b). Postprandial intestinal blood flow, metabolic rates, and exercise in Chinook salmon (*Oncorhynchus tshawytscha*).

579 *Physiol. Biochem. Zool.* 79, 688–94. doi:10.1086/505512.

580 Thordardottir, G., and Guðbergsson, G. (2017). Catch statistics for Atlantic salmon, Arctic charr and brown trout in Icelandic rivers and lakes 2016. Available

581 at: <https://www.hafogvatn.is/static/research/files/hv2017-030pdf>.

582 Thyrel, M., Berglund, I., Larsson, S., and Näslund, I. (1999a). Upper thermal limits for feeding and growth of 0+ Arctic charr. *J. Fish Biol.* 55, 199–210.

583 doi:10.1006/jfbi.1999.0986.

584 Thyrel, M., Berglund, I., Larsson, S., and Näslund, I. (1999b). Upper thermal limits for feeding and growth of 0 + Arctic charr. *J. Fish Biol.* 55, 199–210.

585 doi:10.1111/j.1095-8649.1999.tb00669.x.

586 Tirsgaard, B., Behrens, J. W., and Steffensen, J. F. (2015). The effect of temperature and body size on metabolic scope of activity in juvenile Atlantic cod

587 *Gadus morhua* L. *Comp. Biochem. Physiol. Part A Mol. Integr. Physiol.* 179, 89–94. doi:10.1016/j.cbpa.2014.09.033.

588 Van Der Kraak, G., and Pankhurst, N. W. (2008). Temperature effects on the reproductive performance of fish. *Glob. Warm. Implic. Freshw. Mar. Fish*, 159–?

589 Wandsvik, A., and Jobling, M. (1982). Observations on growth rates of Arctic charr, *Salvelinus alpinus* (L.), reared at low temperature. *J. Fish Biol.* 20, 689–

590 699.

591 Warren, C. E., and Davis, G. E. (1967). Laboratory studies on the feeding, bioenergetics, and growth of fish. Available at: <http://hdl.handle.net/1957/4348>.

592 Winfield, I. J., Hateley, J., Fletcher, J. M., James, J. B., Bean, C. W., and Clabburn, P. (2010). Population trends of Arctic charr (*Salvelinus alpinus*) in the UK :

593 assessing the evidence for a widespread decline in response to climate change. 650, 55–65. doi:10.1007/s10750-009-0078-1.

594