



Swimming performance of brown trout and grayling show species-specific responses to changes in temperature

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1 **Swimming performance of brown trout and grayling show species-specific responses to**
2 **changes in temperature**

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10
11 **Running title:** Swimming performance of trout and grayling

12
13 **Abstract**

14 Fishways have historically been constructed to restore and preserve the ecological
15 connectivity for fish in fragmented rivers. . However, the fishways are often selective on
16 species due to different size and swimming capacity. As the proportion of dammed rivers are
17 still increasing, there is a growing need for more information on wild fish and their migration
18 potential. In this study, we compare the swimming capacity of wild caught brown trout and
19 grayling until the fish were exhausted in a critical swimming speed (U_{crit}) test, under three
20 different naturally occurring stream temperatures in Norway; 1.7, 5.5 and 10 °C. The results
21 indicate that trout swim better at the warmer temperatures than at colder temperatures.
22 The grayling showed consistent swimming patterns with little variation across all tested
23 temperatures. The results therefore signify the need to have operational fishways already
24 early in the spring when the grayling migration starts and highlight the need for more
25 studies on fish migration abilities across a wider range of species and seasons.

26
27 **Key words:** migration, fish, Norway, salmonids, *Salmo trutta*, *Thymallus thymallus*

28
29
30 **Introduction**

31 During the last century, many natural river systems have been subjected to fragmentation
32 due to human constructions, such as hydropower installations (Nilsson et al. 2005). The
33 reduced or non-existing connectivity that usually follows these artificial landscape
34 alterations can result in loss of populations and species of freshwater fish (Gehrke et al.
35 2002; Parrish et al. 1998; Penczak and Kruk 2000). Thus, with the aim to reduce the negative

36 effects, there has been an increased focus on facilitating up- and downstream migration
37 through the use of for example fishways (Silva et al. 2018). However, the successful function
38 of fishways depends on species, individual size, time of year, water flow and temperature,
39 individual motivation and condition for migration (Haugen et al. 2008; Roscoe and Hinch
40 2010). If fish fail to use assigned fishways, but instead remain in the river section
41 downstream the dams, this will likely result in unnatural crowding and thereby reduced
42 growth (Bærum et al. 2013; Van Leeuwen et al. 2016). Further, by imposing size-selective
43 fishways, there might be selection on certain phenotypes, by for instance introducing shifts
44 from natural directional selection on growing larger and thereby having a higher migratory
45 potential (Videler 1993; Videler and Wardle 1991), to stabilizing selection on a smaller body
46 size (Haugen et al. 2008) and lower overall migration potential. Designing fishways with high
47 functionality for a broad range of fish species is highly demanding (Mallen-Cooper and Brand
48 2007; Noonan et al. 2012), but important in order to maintain natural diversity and genetic
49 variability in river systems.

50

51 The ability to move efficiently through waterways is especially important for fish such as
52 salmonids that may migrate long distances to spawn (Jonsson and Jonsson 1993). Brown
53 trout (*Salmo trutta*, hereafter referred to as trout) and European grayling (*Thymallus*
54 *thymallus*, hereafter referred to as grayling), are cold water fishes that often use different
55 sections within a river/lake system for feeding (Godin and Rangeley 1989; McLaughlin and
56 Noakes 1998), overwintering and spawning, and seasonal movement between different
57 habitat types are important for growth, survival and reproduction (Hegggenes and Dokk 2001;
58 Jonsson and Jonsson 2009; Sempeski and Gaudin 1995b). Both trout and grayling are
59 salmonids, but have different spawning time. The trout typically move upstream at the end
60 of the summer to spawn at the onset of winter (Elliott 1994; Klemetsen et al. 2003), and the
61 grayling typically migrate upstream in spring to deposit eggs in the gravel at the onset of
62 summer (Nykänen et al. 2001; Sempeski and Gaudin 1995a). Radiotelemetry and genetic
63 data on trout and grayling from the Norwegian rivers Glomma and Gudbrandsdalslågen
64 illustrate that both species move considerably and directionally during early spring at low
65 water temperatures (Van Leeuwen et al. 2016), and that both species use large sections of
66 the river throughout the year (Junge et al. 2014; Van Leeuwen et al. 2016).

67

68 Both trout and grayling have relatively high swimming capacity compared to other
69 Scandinavian freshwater fishes, with indications of trout having higher swimming capacity
70 than grayling. Therefore, the objectives of our study were to 1) actually explore differences
71 in swimming capacity for trout and grayling. In addition, water temperature has profound
72 effects upon the physiology and performance of ectotherms (Angilletta et al. 2002, Beamish
73 1964, Jonsson and L'Abée-Lund 1993, Kavanagh et al. 2010). Temperature may also serve as
74 an ecological timer, initiating behavioral reactions such as migration from one habitat to
75 another (Jonsson and Jonsson 2009), and has been found to directly influence swimming
76 capacity (Keefer et al. 2008) We therefore also 2) tested the swimming capacity for both
77 species at three different temperatures, 1.7, 5.5 and 10°C. The overall goal was to compare
78 the species-specific swimming capacity and to contribute with better understanding of how
79 fishways should be constructed and operated.

80

81 **Materials and methods**

82

83 *Fish collection*

84 The fish used in this study was wild caught at Otta, Norway, using traditional angling gear,
85 see Figure 1a and 1b for the sampling location. The sampling river, Gudbrandsdalslågen,
86 typically varies in seasonal temperature from about 0 °C (December) to about 14°C (August).
87 In its lower parts, River Gudbrandsdalslågen is slow-running, with stretches of rapids with
88 broken surface and at some points also shorter sections of white-water-rapids. After
89 capture, the fish were transported to the Hunderfossen fish hatchery facility in an aerated
90 fish-tank. The fish were kept at the facility for a period of one to three weeks in concrete
91 tanks with continuously flowing, untreated, river water prior to experiments. The holding
92 tanks were approximately 1 x 3 meters, with water depth of 0.5 meter.

93

94 *Experimental setup and measurement of critical swimming speed, (U_{crit})*

95 The experiments were run at the Hunderfossen hydropower plant at three different periods
96 during late autumn and winter 2014; October 7th – 13th, November 3rd – 7th, and December
97 1st – 4th. The water used in the experimental setup was untreated river water, from the same
98 source as for the holding tanks, where the natural water temperatures averaged 9.67 ± 0.04

99 (referred to as 10°C), 5.39 ± 0.06 (referred to as 5.5°C) and 1.7 ± 0.02 (referred to as 1.7°C), at
100 the three experimental times, respectively, as the water cools from August to December.

101

102 We used a critical swimming speed (U_{crit}) test to measure prolonged swimming performance
103 (Brett 1964). In this test, the water speed is increased in a stepwise manner until a fish no
104 longer can maintain its position in the current. U_{crit} is predicted to be an ecologically relevant
105 measure of prolonged swimming capacity for fish (Plaut 2001; Lee et al. 2003).

106

107 The U_{crit} –tests were carried out using a tube-within-tube-design respirometer (see e.g.
108 (Thorstad et al. 1997; Tierney 2011) for description of respirometer and Figure 1c for an
109 illustration. The cross-sectional diameter of the inner tube is 24 cm and the outer tube 34
110 cm. A propeller connected to an engine pulls water past the fish in the inner tube. The water
111 is then returned to the front via the space between the two tubes. Plastic mesh structures in
112 the front and back prevents the fish from escaping from the inner tube or getting in contact
113 with the propeller. The velocity of the water passing the fish is adjustable within the range
114 0.3 – 2 m/s.

115

116 Prior to the U_{crit} -test, we placed a fish in the tunnel and let it acclimate for 30 minutes at 0.3
117 m/s. The test was then carried out by increasing the water speed with 0.2 m/s for every 2
118 minutes. A pilot study revealed that grayling was likely to lose motivation for swimming
119 entirely if the velocity was adjusted too fast. Adjustment of velocity between steps was
120 therefore consistently carried out over 30 seconds in the experimental set-up. The end-point
121 of the experiment was set to the time at which the fish collapsed on the rear plastic mesh-
122 structure or the point at which the fish would no longer swim but “lean on” the rear mesh.
123 When the fish leaned on the mesh, motivation was initiated after five seconds. Action taken
124 to motivate the fish for swimming included rapidly altering the water-velocity from last set-
125 point to zero and back to set-point. This routine was repeated up to three times in quick
126 successions. If the fish did not respond by re-entering swimming-mode, end-point was set to
127 the time five seconds prior to motivation. After the U_{crit} -test, the length and weight of the
128 fish was recorded before the fish was released back into the river. Each fish was only used in
129 one experiment. A plot of length and mass for the fish tested at different temperatures are
130 given in Supplementary information 1.

131

132 A total of 44 trout (28.2 cm \pm 0.7) and 48 grayling (33.8 cm \pm 0.5) were tested for swimming
133 capacity (mean \pm standard errors), Figure 2. Across temperatures, 13, 15 and 16 trout and
134 15, 17 and 16 grayling were tested in the three different water temperatures, 1.7, 5.5 and
135 10°C, respectively.

136

137 *Statistical analysis*

138 We analyzed the variation in U_{crit} utilizing linear models with species, temperature (included
139 as a factor variable), and fish length as predictor variables. We then constructed a global
140 model containing all three independent variables and their interactions. To compare and
141 weight all the nested models under the global model, we used the dredge-function in the
142 MuMIn-package (Bartoń 2017) and ranked the model based on AICc-values. We checked for
143 homogeneity of the variance and normality of the distribution of the residuals for the most
144 supported model. We also assessed the Cook distance (with a cut off value of 4/n) for each
145 point to check for particular influential individuals. Two fish were pinpointed from the
146 Cook's distance, two rather large grayling individuals that had relatively low U_{crit} compared
147 to other graylings. As they were high-leverage individuals, we choose to show predictions
148 from the models developed from a subset of the data excluding the two grayling individuals.
149 To obtain the final coefficient estimates used in our predictions, we used the model.avg-
150 function from the MuMIn-package (Bartoń 2017), which was set to model average all
151 parameter estimates included within an AICc-weight of 90%. Predictions were obtained
152 using the "full" averaged model, which then includes a type of shrinkage estimator for
153 variables with a weak relationship to the response. All statistical analysis were performed in
154 R (R 2017).

155

156 **Results**

157 In general, we found relatively large variations in the predicted U_{crit} values for the fish in the
158 experiment (Figure 3). This variation seemed to be rather stable across temperatures and
159 species. Further, the model predicted a general positive trend of fish length on U_{crit} (see
160 parameter estimates in Supplementary Table 1), however the slope of this trend varied
161 slightly between species. In general, our model predicted higher U_{crit} for trout compared to
162 grayling, although less obvious at the lowest temperature (1.7° C, Figure 3). Trout displayed

163 an overall increasing U_{crit} with temperature, but with comparable U_{crit} at 5.5° C and 10° C
164 (Figure 3). For grayling, the model predicted a much less pronounced increase in U_{crit} with
165 temperature from 1.7° C to 5.5° C than for trout, while there was no increase between 5.5° C
166 and 10° C (Figure 3). Specifically, our model predicted mean U_{crit} values of 1.42 (SD 0.26),
167 1.57 (SD 0.21) and 1.58 (SD 0.19) for trout, and 1.38 (SD 0.26), 1.43 (SD 0.26) and 1.42 (SD
168 0.20) for grayling at 1.7° C, 5.5° C and 10° C, respectively.

169

170 Discussion

171 To partially or completely re-establish free migration in fragmented waterways, it is
172 important to restore the habitat or build fishways in such a way that the natural fish
173 population can actually make use of up- and downstream habitats efficiently. Fish passage
174 success at an obstacle depends on many factors, such as the hydraulic conditions at the site,
175 on the swimming and leaping capacity for each given species (Ovidio and Philippart 2002),
176 that again are related to temperature, motivation and type of species. In this study, we
177 found that grayling and trout had comparable swimming capacity at the lower temperature
178 (1.7° C), while trout showed higher swimming capacity at the two higher temperatures, at
179 5.5 and 10° C. The swimming capacity for grayling was relatively stable across all
180 temperatures whereas the variation in swimming capacity within each test-group (i.e.,
181 temperature and species) was relatively high for both species, indicating a high level of
182 individual variation.

183

184 The result that trout performed best at the higher temperatures closer to their actual
185 spawning time in the river was expected. Previous studies have found temperatures around
186 15-16°C to be optimal for the swimming performance of other trout populations (Ojanguren
187 and Brana 2000). The swimming performance of grayling was less affected by temperature
188 and was lower compared to the trout at the two higher testing temperatures. The grayling
189 might prefer the colder part of the water-body in winter, as an acoustic telemetric study
190 found all tracked grayling through the period of ice cover to remain within two meters of the
191 surface and often at temperatures approaching 0°C (Bass et al. 2014) instead of mostly
192 residing in the thermocline as is common for other salmonids in the early winter months
193 (Levy et al. 1991). Another fish capable of enduring cold, such as the carp, was found to
194 plastically change the isoforms of their myosin heavy chain proteins following temperature

195 acclimation, suggesting a correlation between producing alternate myosin heavy chain-
196 proteins with improved swimming performance at low and high acclimation temperatures
197 (Fry and Hart 1948). It could be that grayling also has some kind of plastic “switch” in
198 relation to temperature and seasons as they were found to suddenly increase movement
199 during early spring at low temperatures (Heggenes et al. 2006; Van Leeuwen et al. 2016).

200

201 Previous studies have illustrated a positive effect of training and swimming performance in
202 lab-reared brown trout (Anttila et al. 2008). The fish used in this study were wild caught
203 from a river and kept in an aquarium with calm conditions for less than one (for the
204 experimental groups tested at 10 and 5.5°C) or up to three weeks (for experimental group
205 tested at 1.7 °C). There could therefore be that the fish tested at 1.7°C in this study
206 performed less well compared to the two higher temperatures as the levels of receptor
207 densities important for swimming performance likely declined over the period the fish were
208 held in aquaria, leading to earlier fatigue at the low temperatures later in the season (Anttila
209 et al. 2008). At the same time, seasonal changes also have complex interactive effects on
210 swimming activity of fishes and can affect motivation and capacity. Following the decrease in
211 temperature with time in the present study, the trout life history cues also changed from
212 “late migratory” to “refuge”. This is itself a factor that also could have contributed to lower
213 swimming performance in trout at lower temperatures, as it has been shown that trout in
214 the wild exploit more slow running water in winter compared to summer, and that this
215 switch from summer to winter activity appears when the temperature drops below 8°C
216 (Heggenes and Dokk 2001). As the timing of spawning, and hence probably motivation for
217 migration is different for the two species, it would be interesting to follow up this study also
218 in spring to get a better idea of the effects of temperature and motivation for swimming.

219

220 The interaction between temperature and swimming performance is complex and depends
221 on many factors (Videler 1993), and we found much variation in the swimming performance
222 for both species in the present study. Individual experience, motivation and genetic
223 background will likely play a part in overall swimming performance (Laporte et al. 2016;
224 Plaut and Gordon 1994), and repeatable individual variation has been found for several fish
225 species (Bass et al. 2014; Nelson et al. 2002). It could be that some of the variation is due to
226 individuals being partially migratory and likely more fit than individuals having a more

227 stationary lifestyle (Jonsson and Jonsson 2009). Further, this experiment was conducted in a
228 laboratory environment with constant water flow. The heterogeneities in physical structure
229 and water flow characterizing natural environments can influence swimming behavior and
230 performance (McLaughlin and Noakes 1998; Webb 1993). More propulsive movements have
231 been observed under field conditions relative to laboratory conditions in brook trout
232 (McLaughlin and Noakes 1998), imposing that fish probably work harder in the field to
233 maintain a given speed, indicating that the results in the present study should be viewed as
234 being higher than the swimming capacity would likely be in a natural context.

235

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245

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 368
 369

370 **Figure legends:**

371
 372 **Figure 1. a)** Map of a) the location of the study area in Norway and b) the river
 373 Gudbrandsdalslågen, where the capture sites (Otta) and experimental facilities
 374 (Hunderfossen) are shown. **c)** Illustration of the respirometer. A propeller connected to an
 375 engine pulls water past the fish in the inner tube before the water returns to the front via
 376 the outer walls. Plastic mesh structures in the front and back of the inner tubes prevents the
 377 fish both from escaping and potential injuries with the propeller. The measurements for
 378 each side are also given in the figure (in cm).
 379

380 **Figure 2.** The overall length distribution (in cm) for grayling (light gray) and trout (dark gray)
 381 in the three experimental temperature groups, showing the 25%-75% quantiles (boxes),
 382 median (black horizontal line), 95% limits (bars), and outliers (open circles) for the three
 383 experimental temperatures.
 384
 385

386 **Figure 3.** Predicted U_{crit} (y-axis) as a function of temperature ($^{\circ}\text{C}$, x-axis) for grayling (solid
 387 line) and trout (stippled line). The predictions are derived from a linear model with species,
 388 temperature (included as a factor variable), and length as predictor variables. Dots show the
 389 mean predicted value across the full range of the lengths in the data, and error bars show
 390 the standard error.
 391

392 **Supplementary Figure 1.** Length and weight for grayling (light gray) and trout (dark gray) for
 393 the three experimental temperatures, plotted in triangles (1.7°), squares (5.5° C) and circles
 394 (10° C) and their regression lines.

395

396 **Supplementary Table 1.** Model averaged parameter estimates, used to predict U_{crit} for trout
397 and grayling.

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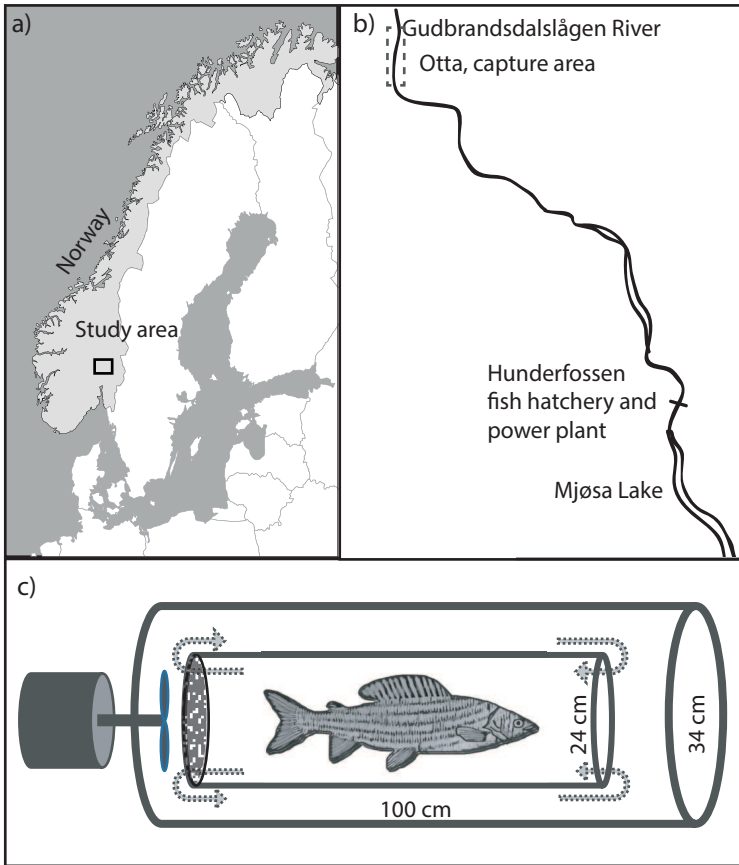
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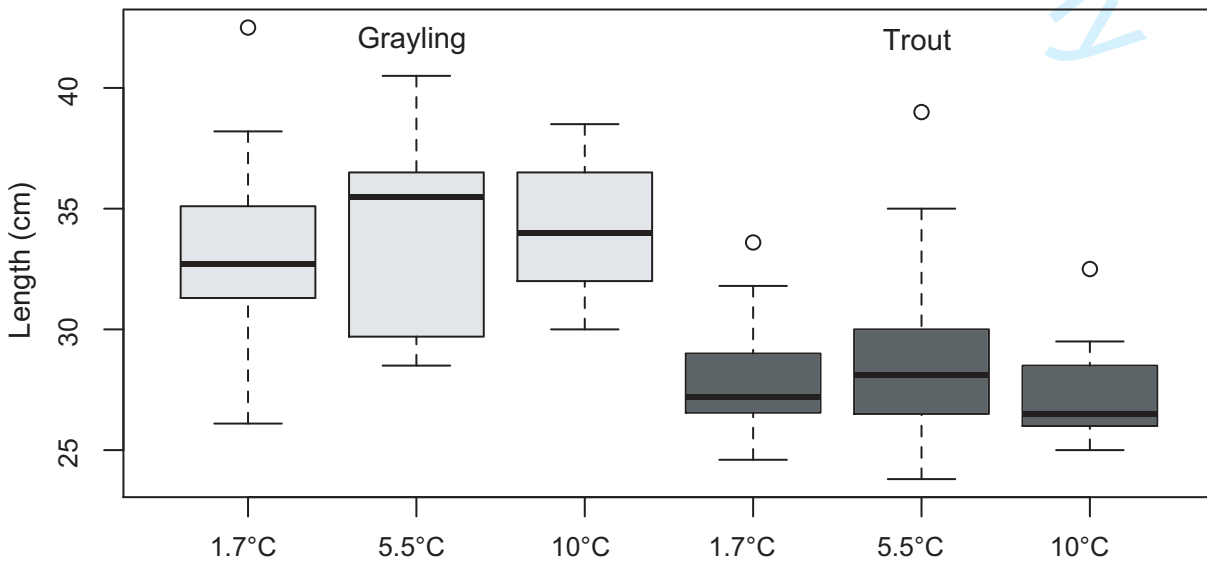
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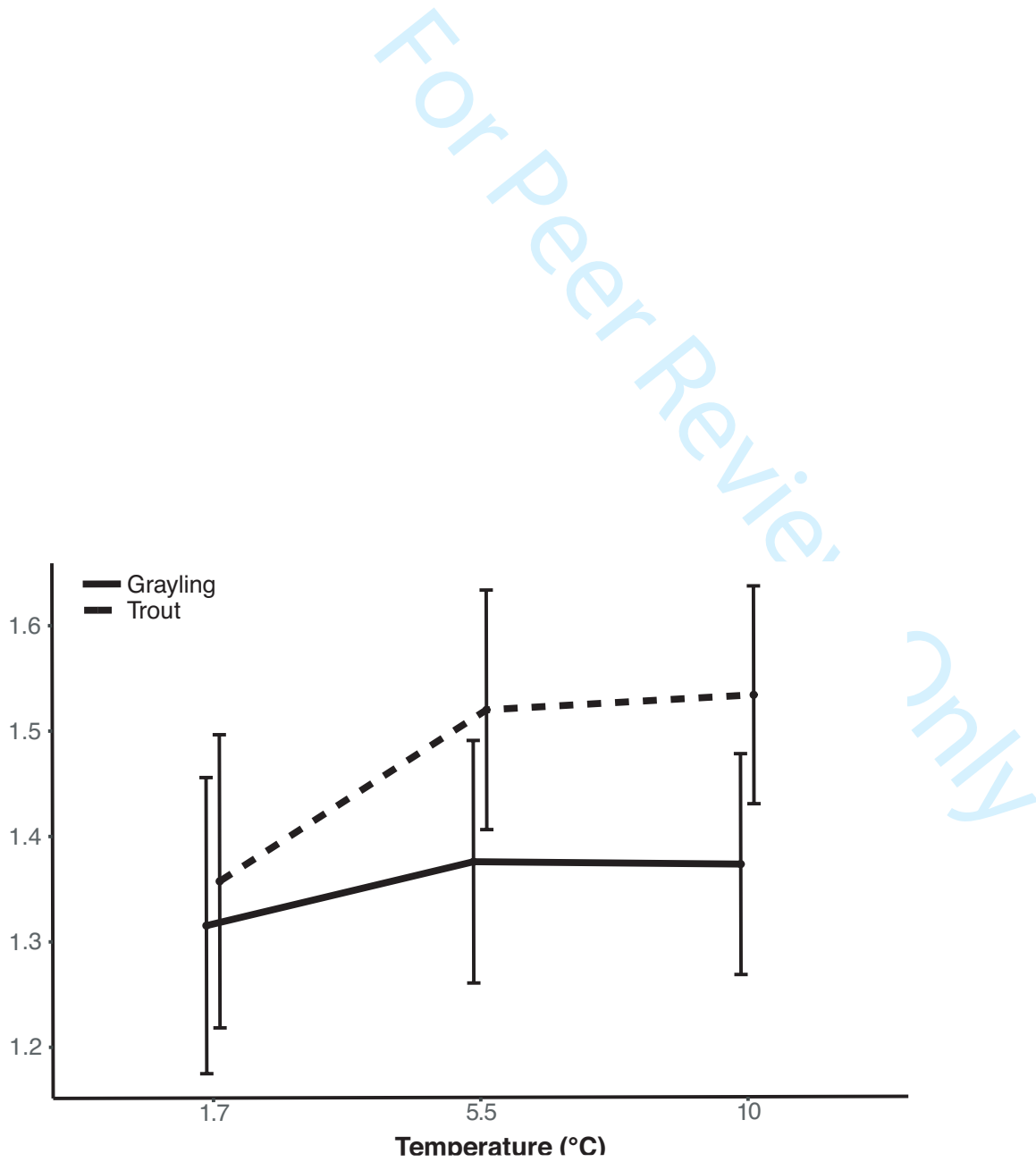
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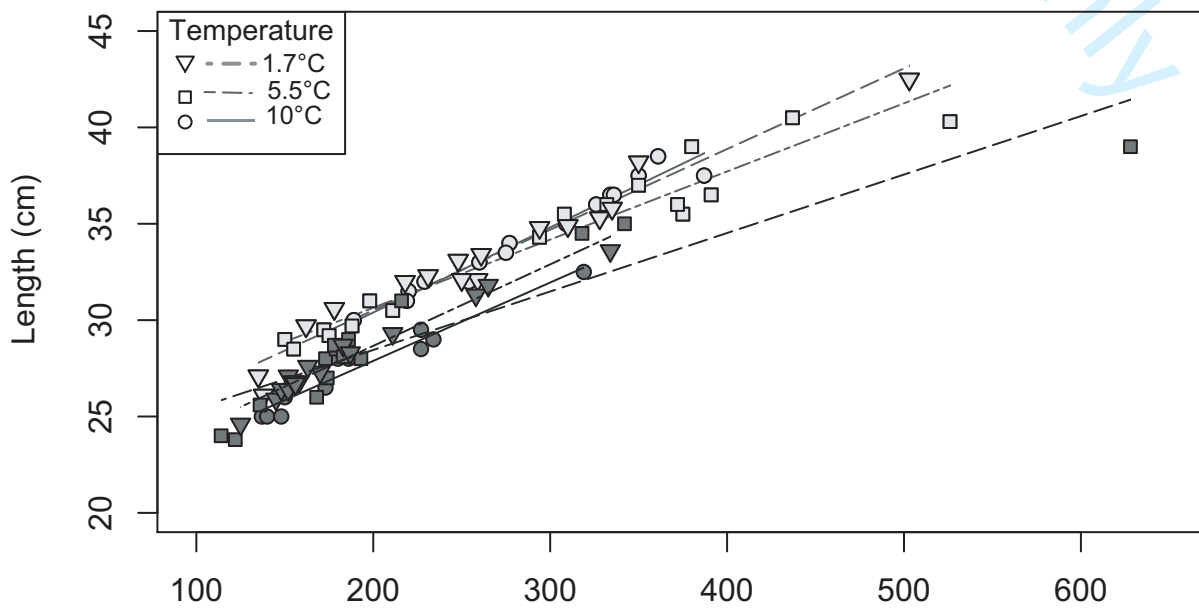
Supplementary Table 1.

| | β-Estimate | Std. Error | Adjusted SE | Z value | Pr(> z) |
|--------------------|------------------------------------|-------------------|--------------------|----------------|--------------------|
| Intercept | -0.0474489 | 0.5850780 | 0.5896430 | 0.080 | 0.9359 |
| Trout | 0.0558839 | 0.2622062 | 0.2655798 | 0.210 | 0.8333 |
| Length | 0.0435308 | 0.0179703 | 0.0181130 | 2.403 | 0.0162 * |
| Temp 5.5 | 0.3066232 | 0.5934888 | 0.5961470 | 0.514 | 0.6070 |
| Temp 10 | 0.4036908 | 0.7672810 | 0.7697541 | 0.524 | 0.6000 |
| Trout:temp_cat5.5 | 0.1020385 | 0.1793856 | 0.1801159 | 0.567 | 0.5710 |
| Trout:temp_cat10 | 0.1185561 | 0.2037363 | 0.2044613 | 0.580 | 0.5620 |
| Length:temp_cat5.5 | -0.0078787 | 0.0177567 | 0.0178441 | 0.442 | 0.6588 |
| Length:temp_cat10 | -0.0110711 | 0.0232645 | 0.0233458 | 0.474 | 0.6353 |
| Trout:length | -0.0004426 | 0.0075712 | 0.0076807 | 0.058 | 0.9540 |

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Supplementary Figure 1.



1 **Swimming performance of brown trout and grayling show species-specific responses to**
 2 **changes in temperature**

3
4

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6

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10

11 **Running title:** Swimming performance of trout and grayling

12

13 **Abstract**

14

15 ~~Artificial landscape fragmentation are often may hindering fish migrations between~~
 16 ~~habitats, leading to unnatural altered genetic structuring and reduced lower habitat qualities~~
 17 ~~for the specific life events for different fish species, as the optimal environment may no~~

18

19 ~~longer be accessible. As an attempt to compensate for this, a variety of fishways have~~
 20 ~~historically been constructed to improve-restore and preserve the ecological connectivity for~~

21

22 fish in fragmented ~~rivers. -environments~~. However, the fishways are often selective on

23

24 species ~~due to different~~, size and swimming capacity, ~~and as~~ the proportions of dammed

25

26 rivers are still increasing, there is a growing need for more information on wild fish and their

27

28 migration potential. In this study, we compare the swimming capacity of wild caught brown

29

30 trout and grayling until ~~exhaustion the fish were exhausted~~ in a critical swimming speed

31

32 (U_{crit}) test, under three different naturally occurring stream temperatures in Norway; 1.7, 5.5

33

34 and 10 °C. The results indicate that ~~trout swim better at the warmer temperatures than at~~

35

36 ~~colder temperatures brown trout have a higher swimming capacity at all temperatures when~~

37

38 ~~compared to grayling, and that the trout swim better at the warmer temperatures~~. The

39

40 grayling showed consistent swimming patterns ~~with little variation~~ across all tested

41

42 temperatures. The results therefore signify the need to have operational fishways already

43

44 early in the spring when the grayling ~~runs migration starts and~~. ~~Further, the results~~ highlight

45

46 the need for more studies on fish migration abilities across a wider range of species and

47

48 seasons, ~~as this knowledge can help management to improve future constructions and~~

49

50 ~~operations of fishways, and hence allow for more natural migrations, despite artificial~~

51

52 ~~barriers, for wild fish populations in the future.~~

53

54

55

Comment [JM1]: Kan godt slettes og abstract can starte med Fishways have historically.....

36 **Key words:** migration, fish, Norway, salmonids, *Salmo trutta*, *Thymallus thymallus*

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41 Introduction

42 During the last century, many natural river systems have ~~been subjects to~~ been subjected to

43 fragmentation due to human constructions, such as hydropower installations (Nilsson et al.

44 2005). The reduced or non-existing connectivity that usually follows these artificial

45 landscape alterations ~~can have resulted~~ in loss of populations and species of freshwater fish

46 (Gehrke et al. 2002; Parrish et al. 1998; Penczak and Kruk 2000). Thus, with the aim to

47 reduce the negative effects, there has been an increased focus on facilitating up- and

48 downstream migration through the use of for example fishways (Silva et al. 2018). However,

49 the successful functionality function of fishways ~~are~~ depends ~~ent~~ on species, individual size,

50 time of year, water flow and temperature, individual motivation and condition for migration

51 (Haugen et al. 2008; Roscoe and Hinch 2010). If fish fail to use assigned fishways, but instead

52 remain in the river section downstream the dams, at the entrances, this will likely result in

53 unnatural crowding and thereby reduced growth (Bærum et al. 2013; Van Leeuwen et al.

54 2016). Further, by imposing size-selective fishways, there might be selection on certain

55 phenotypes, by for instance introducing shifts from natural directional selection on growing

56 larger and thereby having a higher migratory potential (Videler 1993; Videler and Wardle

57 1991), to stabilizing selection on a smaller body size (Haugen et al. 2008) and lower overall

58 migration potential. Designing fishways with ~~a high successful effective ff~~ functionality for ality

59 ~~and a natural intake of a broad range of many fish~~ species is highly demanding (Mallen-

60 Cooper and Brand 2007; Noonan et al. 2012), but important in order to maintain natural

61 diversity and genetic variability in river systems. ~~Norway has implemented the EU Water~~

62 ~~Framework Directive, and is at the same time one of the largest producers of hydropower in~~

63 ~~Europe. Hence, it is of vital importance to restore connectivity in a vast number of regulated~~

64 ~~and fragmented rivers.~~

65

66 ~~Water temperature has profound effects upon the physiology and performance of~~

67 ~~ectotherms (Angilletta et al. 2002), influencing respiration (Beamish 1964), growth (Jonsson~~

68 and L'Abée-Lund 1993), activity (Anttila et al. 2008) and reproductive output (Kavanagh et al.
69 2010). Water temperature can also serve as an ecological timer, initiating behavioral
70 reactions such as migration from one habitat to another (Jonsson and Jonsson 2009), and
71 temperature has been found to directly influence swimming capacity (Keefer et al. 2008).
72

73 The ability to move efficiently through waterways is especially important for fish such as
74 salmonids that ~~may~~ migrate long distances ~~up river~~ to spawn (Jonsson and Jonsson 1993).
75 Brown trout (*Salmo trutta*, hereafter referred to as trout) and European grayling (*Thymallus*
76 *thymallus*, hereafter referred to as grayling), are cold water fishes that often use different
77 sections within a river/lake system for feeding (Godin and Rangeley 1989; McLaughlin and
78 Noakes 1998), overwintering and spawning, and seasonal movement between ~~different~~
79 ~~habitat types these localities~~ are important for growth, survival and reproduction (Heggenes
80 and Dokk 2001; Jonsson and Jonsson 2009; Sempeski and Gaudin 1995b). Both trout and
81 grayling are salmonids, but have different ~~life history patterns in relation to seasonal timing~~
82 ~~of reproduction spawning time~~. The trout typically move upstream at the end of the summer
83 to spawn at the onset of winter (Elliott 1994; Klemetsen et al. 2003), and the grayling
84 typically migrate upstream in spring to deposit eggs in the gravel at the onset of summer
85 (Nykänen et al. 2001; Sempeski and Gaudin 1995a). Radiotelemetry and genetic data on
86 trout and grayling from the Norwegian rivers Glomma and Gudbrandsdalslågen illustrate
87 that both species move considerably and directionally during early spring at low ~~water~~
88 temperatures (Van Leeuwen et al. 2016), and that both species use large sections of the
89 river throughout the year (Junge et al. 2014; Van Leeuwen et al. 2016).
90

91 Both trout and grayling have relatively high swimming capacity compared to other
92 Scandinavian freshwater fishes, with indications of trout having ~~higher better ss~~ swimming
93 capacity ~~compared to than~~ grayling. ~~Therefore, the objectives of our study were to 1) actually~~
94 ~~explore differences in swimming capacity for Norwegian trout and grayling. In addition, as~~
95 ~~water temperature has profound effects upon the physiology and performance of~~
96 ~~ectotherms (Angilletta et al. 2002, influencing respirat Beamish 1964, Jonsson and~~
97 ~~L'Abée-Lund 1993, Kavanagh et al. 2010). activi in addition to Temperature may also - serve~~
98 ~~as an ecological timer, initiating behavioral reactions such as migration from one habitat to~~
99 ~~another (Jonsson and Jonsson 2009), and~~ has been found to ~~to~~ directly influence swimming

100 ~~capacity (Keefer et al. 2008) To partially or completely re-establish free migration in~~
101 ~~fragmented waterways, it is important to restore the habitat or build fishways in such a way~~
102 ~~that the natural fish population can actually make use of up- and downstream habitats~~
103 ~~efficiently. Fish passage success at an obstacle depends both the hydraulic conditions at the~~
104 ~~site, and the swimming and leaping capacity for each given species (Ovidio and Philippart~~
105 ~~2002). Therefore, the objectives of our study were to 1) explore differences in swimming~~
106 ~~capacity for the trout and grayling, two commonly found salmonids in the eastern part of~~
107 ~~Norway, and as swimming capacity often is temperature dependent and that both grayling~~
108 ~~and trout might migrate at low water temperatures, ~~w~~We therefore -also 2) tested the~~
109 ~~swimming capacity for both species at three different temperatures, 1.7, 5.5 and 10°C. The~~
110 ~~overall goal was to compare the species-specific swimming capacity ~~as to and to contribute~~~~
111 ~~with better understanding ~~for of~~ how fishways should be constructed and placed and~~
112 ~~operated. ~~in future artificial river installations. understand requirements for constructed~~~~
113 ~~fishways.~~

114
115

116 **Materials and methods**

117

118 *Fish collection*

119 The fish used in this study was wild caught ~~at Otta, Norway,~~ using traditional angling gear ~~at~~
120 ~~Otta, Norway,~~ see Figure 1a and 1b for ~~the~~ sampling location. The sampling river,
121 Gudbrandsdalslågen, typically varies in seasonal temperature ~~in a range~~ from about ~~0~~zero °C
122 (December) to about 14°C (August). In its lower parts, River Gudbrandsdalslågen is ~~in general~~
123 slow-running, with stretches of rapids with broken surface and at some points also shorter
124 sections of white-water-rapids. After capture, the fish were transported to the Hunderfossen
125 fish hatchery facility in an aerated fish-tank. The fish were kept at the facility for a period of
126 one to three weeks in concrete tanks with continuously flowing, untreated, river water prior
127 to experiments. The holding tanks were approximately 1 x 3 meters, with water depth of 0.5
128 meter.

129

130 *Experimental setup and measurement of critical swimming speed, (U_{crit})*

131 The experiments were run at the Hunderfossen hydropower plant at three different periods
132 during late autumn and winter 2014; October 7th – 13th, November 3rd – 7th, and December
133 1st – 4th. The water used in the experimental setup was untreated river water, from the same
134 source as for the holding tanks, where the natural water temperatures averaged 9.67 ± 0.04
135 (referred to as 10°C), 5.39 ± 0.06 (referred to as 5.5°C) and 1.7 ± 0.02 (referred to as 1.7°C), at
136 the three experimental times, respectively, as the water cools from August to December.

137

138 We used a critical swimming speed (U_{crit}) test to measure prolonged swimming performance
139 (Brett 1964). In this test, the water speed is increased in a stepwise manner until a fish no
140 longer can maintain its position in the current. U_{crit} is predicted to be an ecologically relevant
141 measure of prolonged swimming capacity for fish (Plaut 2001; Lee et al. 2003). ~~that migrate,
142 live in the open ocean or in high flowing rivers (Plaut 2001), where the performance of
143 individual fish have been found to correlate with migratory difficulties among populations of
144 salmonids~~

145

146 The U_{crit} -tests were carried out using a tube-within-tube-design respirometer (see e.g.
147 (Thorstad et al. 1997; Tierney 2011) for description of respirometer and Figure 1c for an
148 illustration. The cross-sectional diameter of the inner tube is 24 cm and the outer tube 34
149 cm. A propeller connected to an engine pulls water past the fish in the inner tube. The water
150 is then returned to the front via the space between the two tubes. Plastic mesh structures in
151 the front and back prevents the fish from escaping from the inner tube or getting in contact
152 with the propeller. The velocity of the water passing the fish is adjustable within the range
153 0.3 – 2 m/s.

154

155 Prior to the U_{crit} -test, we placed a fish in the tunnel and let it acclimate for 30 minutes at 0.3
156 m/s. The test was then carried out by increasing the water speed with 0.2 m/s for every 2
157 minutes. A pilot study revealed that grayling was likely to lose motivation for swimming
158 entirely if the velocity was adjusted too fast. Adjustment of velocity between steps was
159 therefore consistently carried out over 30 seconds in the experimental set-up. The end-point
160 of the experiment was set to the time at which the fish collapsed on the rear plastic mesh-
161 structure or the point at which the fish would no longer swim but “lean on” the rear mesh.

162 When the fish leaned on the mesh~~In the previous case~~, motivation was initiated after five

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163 seconds. Action taken to motivate the fish for swimming included rapidly altering the water-
164 velocity from last set-point to zero and back to set-point. This routine was repeated up to
165 three times in quick successions. If the fish did not respond by re-entering swimming-mode,
166 end-point was set to the time five seconds prior to motivation. After the U_{crit} -test, the length
167 and weight of the fish was recorded before the fish was released back into the river. Each
168 fish was only used in one experiment. A plot of length and [weight-mass](#) for the fish tested at
169 different temperatures are given in Supplementary information 1.

170
171 A total of 44 trout (28.2 cm \pm 0.7) and 48 grayling (33.8 cm \pm 0.5) were tested for swimming
172 capacity (mean \pm standard errors), Figure 2. Across temperatures, 13, 15 and 16 trout and
173 15, 17 and 16 grayling were tested in the three different water temperatures, 1.7, 5.5 and
174 10°C, respectively.

175

176 [Data-analysis-and-Statistical analysis](#)

177 We analyzed the variation in U_{crit} utilizing linear models with species, temperature (included
178 as a factor variable), and fish length as predictor variables. We then constructed a global
179 model containing all three independent variables and their interactions. To compare and
180 weight all the nested models under the global model, we used the dredge-function in the
181 MuMIn-package (Bartoń 2017) and ranked the model based on AICc-values. We checked for
182 homogeneity of the variance and normality of the distribution of the residuals for the most
183 supported model. We also assessed the Cook distance (with a cut off value of 4/n) for each
184 point to check for particular influential individuals. Two [fish individuals](#) were pinpointed
185 from the Cook's distance, two [relatively rather](#) large grayling individuals that had relatively
186 low U_{crit} compared to other [graylings](#). As they were high-leverage individuals, we choose to
187 show predictions from the models developed from a subset of the data excluding the two
188 grayling individuals. To obtain the final coefficient estimates used in our predictions, we
189 used the model.avg-function from the MuMIn-package (Bartoń 2017), which was set to
190 model average all parameter estimates included within an AICc-weight of 90%. Predictions
191 were obtained using the "full" averaged model, which then includes a type of shrinkage
192 estimator for variables with a weak relationship to the response. All statistical analysis
193 [were as](#) performed in R (R 2017).

194

195 Results

196 ~~We found i~~ In general, ~~we found~~ relatively large variations in the predicted U_{crit} values for the
197 fish in the experiment (Figure 3). This variation seemed to be rather stable across
198 temperatures and species. Further, the model predicted a general positive trend of fish
199 length on U_{crit} (see parameter estimates in Supplementary Table 1), however the slope of
200 this trend varied slightly between species. In general, our model predicted higher U_{crit} for
201 trout compared to grayling, although less obvious at the lowest temperature (1.7° C, Figure
202 3). Trout ~~showed~~ ~~displayed an~~ overall increasing U_{crit} with temperature, but with comparable
203 U_{crit} at 5.5° C and 10° C (Figure 3). For grayling, the model predicted a much less pronounced
204 increase in U_{crit} with temperature from 1.7° C to 5.5° C ~~than fore~~ ~~compared to~~ trout, while
205 there ~~was~~ ~~ere~~ no increase between 5.5° C and 10° C (Figure 3). Specifically, our model
206 predicted mean U_{crit} values of 1.42 (SD 0.26), 1.57 (SD 0.21) and 1.58 (SD 0.19) for trout, and
207 1.38 (SD 0.26), 1.43 (SD 0.26) and 1.42 (SD 0.20) for grayling at 1.7° C, 5.5° C and 10° C,
208 respectively.

209

210 Discussion

211 To partially or completely re-establish free migration in fragmented waterways, it is
212 important to restore the habitat or build fishways in such a way that the natural fish
213 population can actually make use of up- and downstream habitats efficiently. Fish passage
214 success at an obstacle depends on many factors, such as the hydraulic conditions at the site,
215 on the swimming and leaping capacity for each given species (Ovidio and Philippart 2002),
216 that again are related to temperature, motivation and type of species. Freshwater habitats
217 are subjects to dramatic variability in various environmental factors, and the result of
218 environmental constrains of both natural and anthropogenic processes are becoming topics
219 of concern to both the scientific community and the public at large. There is a growing need
220 to explore how fish alter their swimming behavior in responses to physical structures and
221 how they alter their migratory potential throughout the season. In this study, we found that
222 grayling and trout had comparable swimming capacity at the lower temperature (1.7° C),
223 while trout showed higher swimming capacity at the two higher temperatures, at 5.5 and
224 10° C. The swimming capacity for grayling was relatively stable across all temperatures
225 ~~whereas t-~~ ~~Additionally,~~ the variation in swimming capacity within each test-group (i.e.,

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226 temperature and species) was relatively high for both species, indicating a high level of
227 individual variation.

228

229 The result that trout performed best at the higher temperatures closer to their actual
230 spawning time in the river was expected. Previous studies have found temperatures around
231 15-16°C to be optimal for the swimming performance of other trout populations (Ojanguren
232 and Brana 2000) ~~and salmonids in general (Lee et al. 2003)~~. The swimming performance
233 ~~of results for~~ grayling ~~in this study~~ was less affected by temperature ~~and was lower compared~~
234 ~~to the trout at the two higher testing temperatures~~. The grayling might prefer ~~the colder~~
235 ~~part of their~~ water ~~body~~ in winter, as an acoustic telemetric study found all tracked grayling
236 through the period of ice cover to remain within two meters of the surface and often at
237 temperatures approaching 0°C (Bass et al. 2014) instead of ~~mostly~~ residing in the
238 thermocline as is common for other salmonids ~~in the early winter months~~ (Levy et al. 1991).

239 Another fish capable of enduring cold, such as the carp, was found to plastically change the
240 ~~surface loops isoforms~~ of their myosin heavy chain ~~proteins~~ following temperature
241 acclimation, suggesting a correlation ~~between producing alternate myosin heavy chain-~~
242 ~~proteins~~ with improved swimming performance at low and high acclimation temperatures
243 (Fry and Hart 1948). It could be that grayling also has some kind of plastic “switch” in
244 relation to temperature and seasons as they were found to suddenly increase movement
245 during early spring at low temperatures (Heggenes et al. 2006; Van Leeuwen et al. 2016).

246

247 Previous studies have illustrated a positive effect of training and swimming performance in
248 lab-reared brown trout (Anttila et al. 2008). The fish used in this study were wild caught
249 from a river and kept in an aquarium with calm conditions for less than one (for the
250 experimental groups tested at 10 and 5.5°C) or up to three weeks (for experimental group
251 ~~tested at~~ 1.7 °C). There could therefore be that the fish tested at 1.7°C in this study
252 performed less ~~well compared to the two warmer higher -temperatures~~ as the levels of
253 receptor densities important for swimming performance likely declined over the period the
254 fish were held in aquaria, leading to earlier fatigue at the low temperatures later in the
255 season (Anttila et al. 2008). At the same time, seasonal changes also have complex
256 interactive effects on swimming activity ~~of~~ fishes and can affect motivation and capacity.

257 Following the decrease in temperature with time in the present study, the trout life history

258 cues also changed from “late migratory” to “refuge”. This is itself a factor that also could
259 have contributed to lower swimming performance in trout at lower temperatures, as it has
260 been shown that trout in the wild exploit more slow running water in winter compared to
261 summer, and that this switch from summer to winter activity appears when the temperature
262 drops below 8°C (Heggenes and Dokk 2001). As the timing of spawning, and hence probably
263 motivation for migration is different for the two species, it would be interesting to follow up
264 this study also in spring to get a better idea of the effects of temperature and motivation for
265 swimming.

266

267 The interaction between Temperature and swimming performance is complex and depends
268 on many factors (Videler 1993), and we found much variation in the swimming performance
269 for both species in the present study. Individual experience, motivation and genetic
270 background will likely play a part in overall swimming performance (Laporte et al. 2016;
271 Plaut and Gordon 1994), and repeatable individual variation has been found for several fish
272 species (Bass et al. 2014; Nelson et al. 2002). It could be that some of the variation is due to
273 individuals being partially migratory and likely more fit than individuals having a more
274 stationary lifestyle (Jonsson and Jonsson 2009). Further, this experiment was conducted in a
275 laboratory environment with constant water flow. The heterogeneities in physical structure
276 and water flow characterizing natural environments can influence swimming behavior and
277 performance (McLaughlin and Noakes 1998; Webb 1993). More propulsive movements
278 have been observed under field conditions relative to laboratory conditions in brook trout
279 (McLaughlin and Noakes 1998), imposing that fish probably work harder in the field to
280 maintain a given speed, indicating that the results in the present study should be viewed as
281 being higher than the swimming capacity would likely be in a natural context.

282

283 ~~Artificially made dams create unnatural temperature shifts in the affected rivers. In Norway,~~
284 ~~the dam stores water during spring floods and autumn storms, and drains water during~~
285 ~~summer and winter, typically giving the river water under the dam a colder than natural~~
286 ~~temperature during the summer months, and a warmer than natural temperature during~~
287 ~~winter. This means that for a trout living in a regulated river below a dam, the temperature~~
288 ~~during late summer migration will be lowered by typically 5–10°C, depending on the depth of~~
289 ~~the river intake to the dam and the size of the dam. The grayling is likely also affected by~~

290 unnatural temperature variations during their spawning runs, but as the temperature
291 variation is less during winter, typically 1–3°C, the grayling is likely less affected by the
292 temperature changes. By increasing the knowledge on how swimming speed and endurance
293 differ between species, seasonal timing and temperature, the future fishways, fish passages
294 and guidance systems for fish can be improved, as can the building of dams, as for instance
295 to plan an intake of water where the temperature will be less affected downstream.

296

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306

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Figure legends:

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433 **Figure 1. a)** Map of a) the location of the study area in Norway and b) the river

434 Gudbrandsdalslågen, where the capture sites (Otta) and experimental facilities

435 (Hunderfossen) are shown. **c)** Illustration of the respirometer. A propeller connected to an

436 engine pulls water past the fish in the inner tube before the water returns to the front via

437 the outer walls. Plastic mesh structures in the front and back of the inner tubes prevents the

438 fish both from escaping and potential injuries with the propeller. The measurements for

439 each side are also given in the figure (in cm).

440

441 **Figure 2.** The overall length distribution (in cm) for grayling (light gray) and trout (dark gray)

442 in the three experimental temperature groups, showing the 25%-75% quantiles (boxes),

443 median (black horizontal line), 95% limits (bars), and outliers (open circles) for the three

444 experimental temperatures.

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447 **Figure 3.** Predicted U_{crit} (y-axis) as a function of temperature ($^{\circ}\text{C}$, x-axis) for grayling (solid

448 line) and trout (stippled line). The predictions are derived from a linear model with species,

449 temperature (included as a factor variable), and length as predictor variables. Dots show the

450 mean predicted value across the full range of the lengths in the data, and error bars show

451 the standard error.

452

453 **Supplementary Figure 1.** Length and weight for grayling (light gray) and trout (dark gray) for

454 the three experimental temperatures, plotted in triangles (1.7°), squares (5.5°C) and circles

455 (10°C) and their regression lines.

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457 **Supplementary Table 1.** Model averaged parameter estimates, used to predict U_{crit} for trout
458 and grayling.

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