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

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Running title: Swimming performance of trout and grayling

Abstract

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

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

Introduction

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

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

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

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

Materials and methods

Fish collection

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

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

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

(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 the three experimental times, respectively, as the water cools from August to December.

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

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

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

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

Statistical analysis

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

Results

In general, we found relatively large variations in the predicted U_{crit} values for the fish in the experiment (Figure 3). This variation seemed to be rather stable across temperatures and species. Further, the model predicted a general positive trend of fish length on U_{crit} (see parameter estimates in Supplementary Table 1), however the slope of this trend varied slightly between species. In general, our model predicted higher U_{crit} for trout compared to grayling, although less obvious at the lowest temperature (1.7° C, Figure 3). Trout displayed an overall increasing U_{crit} with temperature, but with comparable U_{crit} at 5.5° C and 10° C (Figure 3). For grayling, the model predicted a much less pronounced increase in U_{crit} with temperature from 1.7° C to 5.5° C than for trout, while there was no increase between 5.5° C and 10° C (Figure 3). Specifically, our model 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 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, respectively.

Discussion

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

The result that trout performed best at the higher temperatures closer to their actual spawning time in the river was expected. Previous studies have found temperatures around 15-16°C to be optimal for the swimming performance of other trout populations (Ojanguren and Brana 2000). The swimming performance of grayling was less affected by temperature and was lower compared to the trout at the two higher testing temperatures. The grayling might prefer the colder part of the water-body in winter, as an acoustic telemetric study found all tracked grayling through the period of ice cover to remain within two meters of the surface and often at temperatures approaching 0°C (Bass et al. 2014) instead of mostly residing in the thermocline as is common for other salmonids in the early winter months (Levy et al. 1991). Another fish capable of enduring cold, such as the carp, was found to plastically change the isoforms of their myosin heavy chain proteins following temperature acclimation, suggesting a correlation between producing alternate myosin heavy chain-proteins with improved swimming performance at low and high acclimation temperatures (Fry and Hart 1948). It could be that grayling also has some kind of plastic “switch” in relation to temperature and seasons as they were found to suddenly increase movement during early spring at low temperatures (Heggenes et al. 2006; Van Leeuwen et al. 2016).

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

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

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Figure legends:

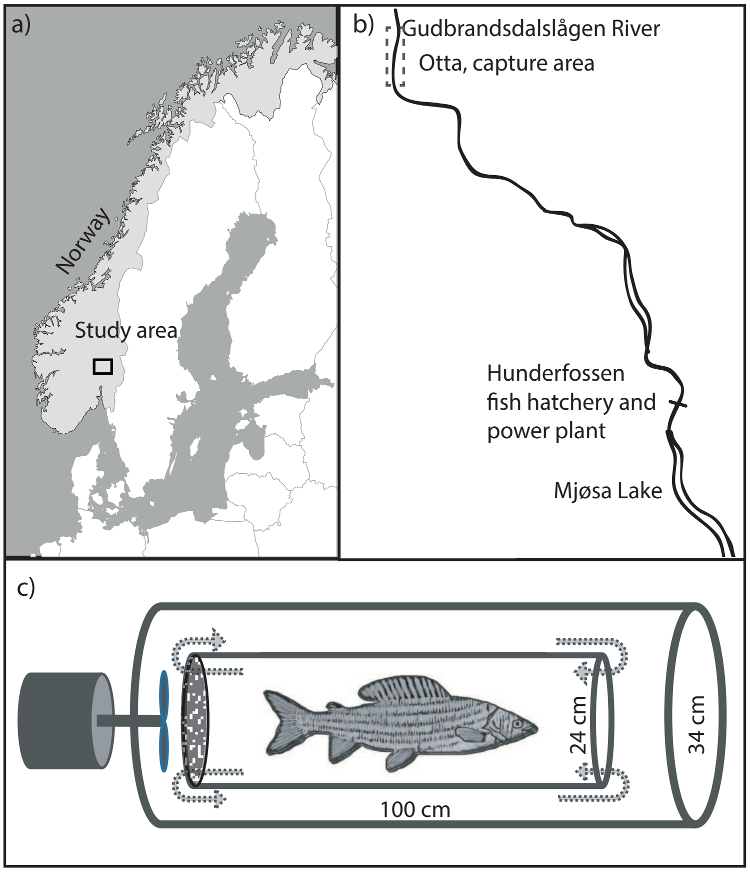
Figure 1. a) Map of a) the location of the study area in Norway and b) the river Gudbrandsdalslågen, where the capture sites (Otta) and experimental facilities (Hunderfossen) are shown. **c)** Illustration of the respirometer. A propeller connected to an engine pulls water past the fish in the inner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

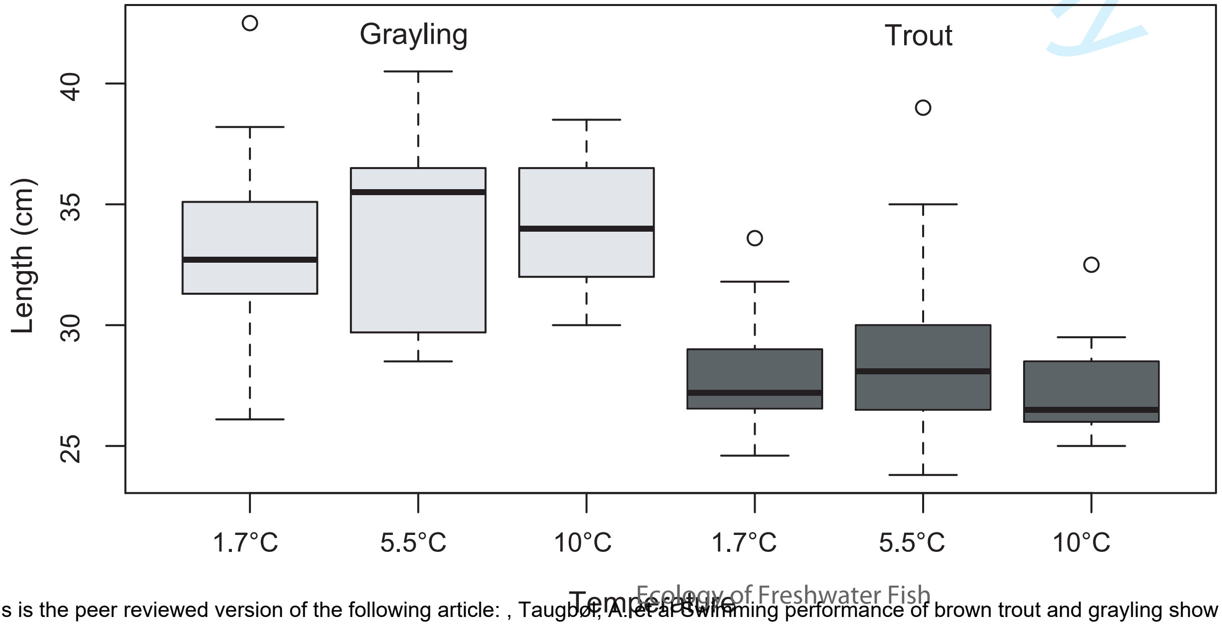
Figure 2. The overall length distribution (in cm) for grayling (light gray) and trout (dark gray) in the three experimental temperature groups, showing the 25%-75% quantiles (boxes), median (black horizontal line), 95% limits (bars), and outliers (open circles) for the three experimental temperatures.

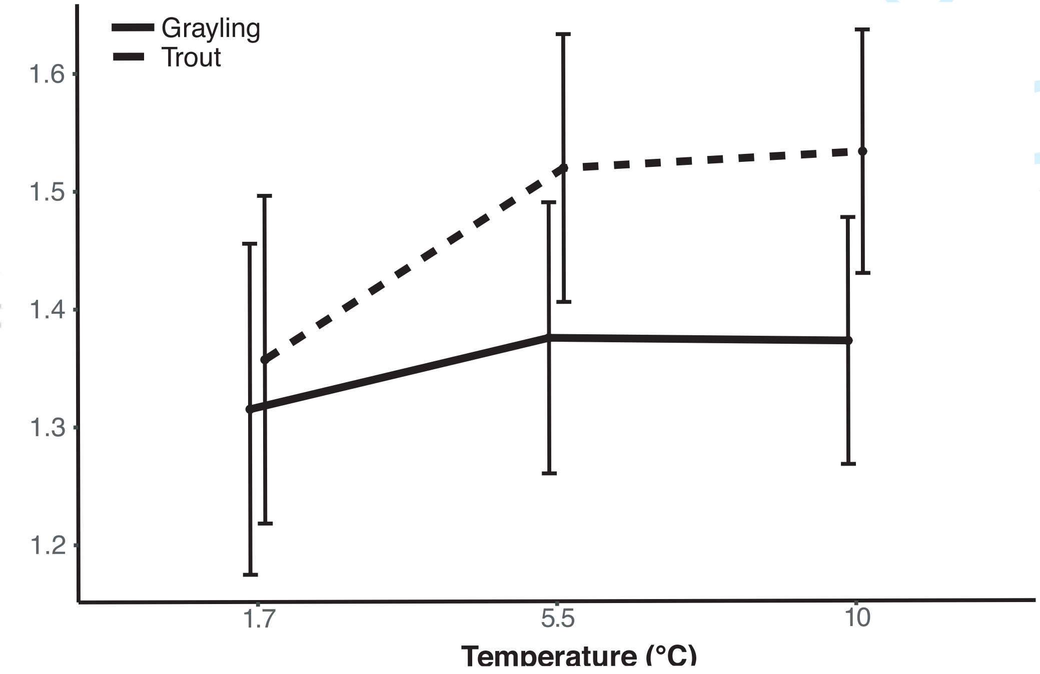
Figure 3. Predicted U_{crit} (y-axis) as a function of temperature (°C, x-axis) for grayling (solid line) and trout (stippled line). The predictions are derived from a linear model with species, temperature (included as a factor variable), and length as predictor variables. Dots show the mean predicted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

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

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


a)
Norway
Study area
b)
Gudbrandsdalslågen River
Otta, capture area
Hunderfossen
fish hatchery and
power plant
Mjøsa Lake
c)
24 cm
34 cm
100 cm

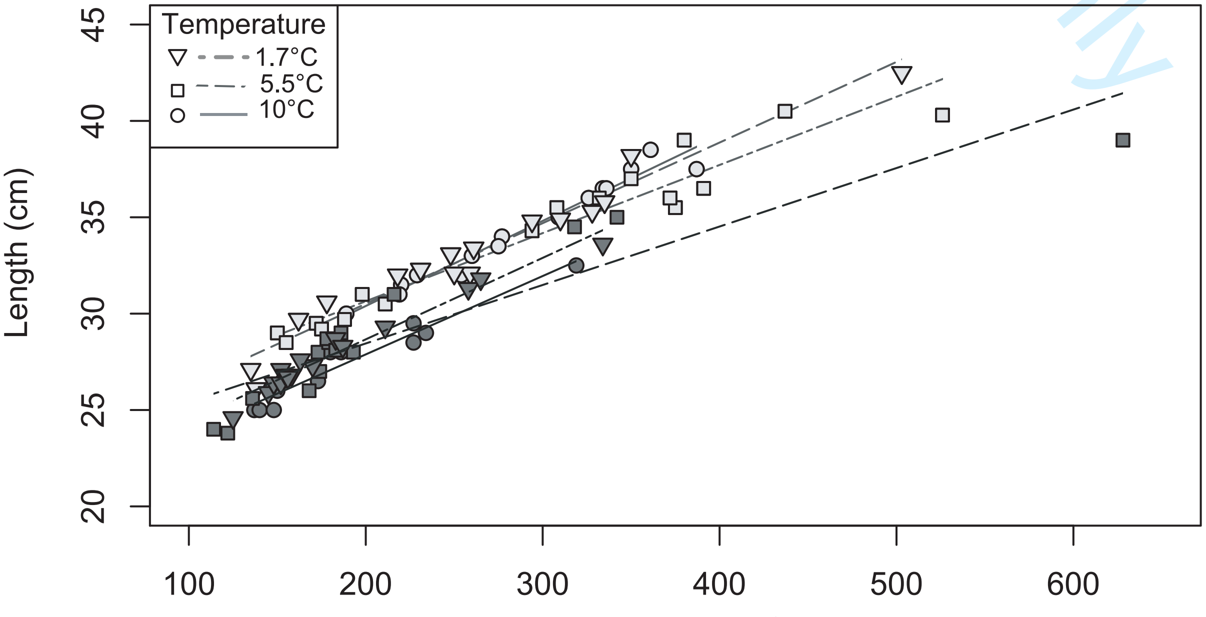

Grayling
Trout
Length (cm)
25
30
35
40
1.7°C
5.5°C
10°C
1.7°C
5.5°C
10°C
Temperature


Grayling
Trout
1.6
1.5
1.4
1.3
1.2
1.7
5.5
10
Temperature (°C)

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

Supplementary Figure 1.



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

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Running title: Swimming performance of trout and grayling

Abstract

~~Artificial landscape fRiver fragmentations are often may hindering fish migrations between habitats, leading to unnatural altered genetic structuring and reduced lower habitat qualities for the specific life events for different fish species, as the optimal environment may no longer be accessible. As an attempt to compensate for this, a variety of f~~Fishways have historically been constructed to ~~improve~~ restore and preserve the ecological connectivity for fish in fragmented rivers. ~~environments~~. However, the fishways are often selective on species due to different ~~,~~size and swimming capacity. ~~, and a~~As the proportion~~s~~ of dammed rivers are still increasing, there is a growing need for more information on wild fish and their migration potential. In this study, we compare the swimming capacity of wild caught brown trout and grayling until ~~exhaustion~~ the fish were exhausted in a critical swimming speed (U_{crit}) test, under three different naturally occurring stream temperatures in Norway; 1.7, 5.5 and 10 °C. The results indicate that trout swim better at the warmer temperatures than at colder temperatures~~brown trout have a higher swimming capacity at all temperatures when compared to grayling, and that the trout swim better at the warmer temperatures~~. The grayling showed consistent swimming patterns with little variation across all tested temperatures. The results therefore signify the need to have operational fishways already early in the spring when the grayling ~~runs~~migration starts and ~~. Further, the results~~ highlight the need for more studies on fish migration abilities across a wider range of species and seasons.~~, as this knowledge can help management to improve future constructions and operations of fishways, and hence allow for more natural migrations, despite artificial barriers, for wild fish populations in the future.~~

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

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

Introduction

During the last century, many natural river systems have ~~been subjects to~~been subjected to fragmentation due to human constructions, such as hydropower installations (Nilsson et al. 2005). The reduced or non-existing connectivity that usually follows these artificial landscape alterations can ~~have~~ result~~ed~~ in loss of populations and species of freshwater fish (Gehrke et al. 2002; Parrish et al. 1998; Penczak and Kruk 2000). Thus, with the aim to reduce the negative effects, there has been an increased focus on facilitating up- and downstream migration through the use of for example fishways (Silva et al. 2018). However, the successful ~~functionality~~ function of fishways ~~are~~ depends ~~ent~~ on species, individual size, time of year, water flow and temperature, individual motivation and condition for migration (Haugen et al. 2008; Roscoe and Hinch 2010). If fish fail to use assigned fishways, but instead remain in the river section downstream the dams, ~~at the entrances,~~ this will likely result in unnatural crowding and thereby reduced growth (Bærum et al. 2013; Van Leeuwen et al. 2016). Further, by imposing size-selective fishways, there might be selection on certain phenotypes, by for instance introducing shifts from natural directional selection on growing larger and thereby having a higher migratory potential (Videler 1993; Videler and Wardle 1991), to stabilizing selection on a smaller body size (Haugen et al. 2008) and lower overall migration potential. Designing fishways with ~~a~~ high ~~successfuleffective f~~functionality for ~~ality and a natural intake of~~ a broad range of ~~many~~ fish species is highly demanding (Mallen-Cooper and Brand 2007; Noonan et al. 2012), but important in order to maintain natural diversity and genetic variability in river systems. ~~Norway has implemented the EU Water Framework Directive, and is at the same time one of the largest producers of hydropower in Europe. Hence, it is of vital importance to restore connectivity in a vast number of regulated and fragmented rivers.~~

~~Water temperature has profound effects upon the physiology and performance of ectotherms (Angilletta et al. 2002), influencing respiration (Beamish 1964), growth (Jonsson~~

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

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

Both trout and grayling have relatively high swimming capacity compared to other Scandinavian freshwater fishes, with indications of trout having higher ~~better s~~swimming capacity ~~compared to~~than grayling. Therefore, the objectives of our study were to 1) actually explore differences in swimming capacity for ~~Norwegian~~ trout and grayling. In addition, ~~as~~ water temperature has profound effects upon the physiology and performance of ectotherms (Angilletta et al. 2002, ~~, influencing respirat~~Beamish 1964, ~~, g~~Jonsson and L'Abée-Lund 1993, Kavanagh et al. 2010). ~~activi in addition to~~Temperature may also - serve as an ecological timer, initiating behavioral reactions such as migration from one habitat to another (Jonsson and Jonsson 2009), and has been found to ~~to~~ directly influence swimming capacity (Keefer et al. 2008)~~To partially or completely re-establish free migration in fragmented waterways, it is important to restore the habitat or build fishways in such a way that the natural fish population can actually make use of up- and downstream habitats efficiently. Fish passage success at an obstacle depends both the hydraulic conditions at the site, and the swimming and leaping capacity for each given species (Ovidio and Philippart 2002). Therefore, the objectives of our study were to 1) explore differences in swimming capacity for the trout and grayling, two commonly found salmonids in the eastern part of Norway, and as swimming capacity often is temperature dependent and that both grayling av trout might migrate at low water temperatures~~, ~~w~~We therefore ~~-~~also 2) tested the swimming capacity for both species at three different temperatures, 1.7, 5.5 and 10°C. The overall goal was to compare the species-specific swimming capacity ~~as to~~and ~~-~~to contribute with better understanding ~~for~~of how fishways should be constructed and ~~placed and~~ operated. ~~in future artificial river installations. understand requirements for constructed fishways. .~~

Materials and methods

Fish collection

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

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

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

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

Field Code Changed

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

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

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

~~Data analysis and~~ Statistical analysis~~s~~

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

Results

~~We found i~~In general, we found relatively large variations in the predicted U_{crit} values for the fish in the experiment (Figure 3). This variation seemed to be rather stable across temperatures and species. Further, the model predicted a general positive trend of fish length on U_{crit} (see parameter estimates in Supplementary Table 1), however the slope of this trend varied slightly between species. In general, our model predicted higher U_{crit} for trout compared to grayling, although less obvious at the lowest temperature (1.7° C, Figure 3). Trout ~~showed~~displayed an overall increasing U_{crit} with temperature, but with comparable U_{crit} at 5.5° C and 10° C (Figure 3). For grayling, the model predicted a much less pronounced increase in U_{crit} with temperature from 1.7° C to 5.5° C than for~~compared to~~ trout, while there was~~ere~~ no increase between 5.5° C and 10° C (Figure 3). Specifically, our model 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 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, respectively.

Discussion

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

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

The result that trout performed best at the higher temperatures closer to their actual spawning time in the river was expected. Previous studies have found temperatures around 15-16°C to be optimal for the swimming performance of other trout populations (Ojanguren and Brana 2000)~~ and salmonids in general (Lee et al. 2003)~~. The swimming performance of~~results for~~ grayling ~~in this study~~ was less affected by temperature and was lower compared to the trout at the two higher testing temperatures. The grayling might prefer the colder part of the~~er~~ water-body in winter, as an acoustic telemetric study found all tracked grayling through the period of ice cover to remain within two meters of the surface and often at temperatures approaching 0°C (Bass et al. 2014) instead of mostly residing in the thermocline as is common for other salmonids in the early winter months (Levy et al. 1991). Another fish capable of enduring cold, such as the carp, was found to plastically change the ~~surface loops~~isoforms of their myosin heavy chain proteins following temperature acclimation, suggesting a correlation between producing alternate myosin heavy chain-proteins with improved swimming performance at low and high acclimation temperatures (Fry and Hart 1948). It could be that grayling also has some kind of plastic "switch" in relation to temperature and seasons as they were found to suddenly increase movement during early spring at low temperatures (Heggenes et al. 2006; Van Leeuwen et al. 2016).

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

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

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

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

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Figure legends:

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

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

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

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

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