



The effects of egg incubation temperature and parental cross on the swimming activity of juvenile brown trout *Salmo trutta*

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Abstract

Personality varies among individuals and is influenced by the environment. Here, we tested the hypothesis that egg incubation temperature had carry-over effects on swimming activity of juvenile brown trout, *Salmo trutta*. Eggs from different crosses involving anadromous and lacustrine-adfluvial parents were incubated under two temperature regimes, unheated (cold) or heated c. 2.5 °C above ambient temperature (warm), until first exogenous feeding. In the laboratory, we used open-field tests to quantify swimming activity in a new environment, and mirror-image tests to measure time spent swimming and resting motionless near a mirror, measures often used as proxies for aggression. These tests were conducted for two cohorts, with one tested in June 2018 and the other in June and August 2019, enabling us to test for repeatability and if differences persisted over the summer. In June, when adjusting for differences in body size between cold- and warm-incubated trout, we found that juvenile trout incubated as embryos at cold temperatures showed more swimming activity and took less time to initiate swimming for their size than those incubated in warm water. There were also body size and year effects but no effects of parental cross. For August, none of the incubation temperature effects observed in June persisted, but cold-incubated trout spent a larger proportion of their time motionless near the mirror than warm-incubated trout and there was a general body size effect on time to initiate swimming. The lack of any persistent effects of incubation temperature between June and August suggests that the effect is ephemeral. Notwithstanding, these results support the hypothesis that incubation temperature has short-term effects on activity of juvenile of brown trout during their first summer.

Significance Statement

We studied the effect of embryonic temperature on juvenile fish behavior, focusing on swimming activity under different conditions. Brown trout eggs were incubated under two temperature regimes, cold and warm. We show that juvenile trout originating from cold conditions as embryos spent a greater proportion of time swimming and less time to initiate swimming than trout originating from warm conditions. These effects were present in June but not August, which suggests that the effect is short-lived, and occurs during the first summer when mortality of juveniles is high. The duration of the effects needs further study as our previous studies have shown persistent embryonic temperature effects on metabolism, body shape, reproductive potential and emigration of subsequent life stages of salmonids. These results also have bearing on ongoing climate change as even small differences in embryonic temperature may have ecological consequences for subsequent life stages.

Keywords Behavior · Brown trout phenotypes · Counter-gradient variation · Early life history effects · Locomotor activity · Personality

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Introduction

Globally, climate is gradually becoming warmer (McKenzie et al. 2021). Ectotherms, such as fish, are particularly vulnerable to temperature changes because their body temperature varies with the temperature of the surrounding water (Volkoff and Rønnestad 2020). A warmer future environment will alter an ectotherm's physiological reactions and

ecological rates (Schulte et al. 2011). Many of these changes, which include changes in growth rates and metabolism (Finstad and Jonsson 2012; Durtsche et al. 2021), are linked to life history and behavioral traits and may be set early in life, even during embryogenesis, with repercussions for later life stages (Jonsson et al. 2014, 2022).

Environmental conditions during embryogenesis play an important role in the development of phenotypic traits of animals, with temperature often being a critically important variable (Booth 2018; Perez et al. 2020; Jonsson et al. 2022). Most studies of vertebrates that examine the carry-over effects of early thermal conditions on later life stages have been performed on birds and reptiles (DuRant et al. 2013; Booth 2018; Andrieux et al. 2022), but there have also been studies on fish (Jonsson and Jonsson 2014, 2019; Massey and Hutchings 2020). Most studies of carry-over effects have focused on morphology (Anderson and Downie 2010; Sim et al. 2015; Greenberg et al. 2021), metabolism (Cook et al. 2018; Durtsche et al. 2021), growth (Finstad and Jonsson 2012; Siviter et al. 2019) and reproductive traits (Warner et al. 2010; DuRant et al. 2013; Jonsson et al. 2014). Fewer have studied effects of embryonic temperature on behavioral plasticity (Belnap et al. 2019), and thus there is a need to explore this further as it may provide new insights into understanding phenotypic plasticity within a life history context and in relation to global change.

Behavioral plasticity allows animals to respond quickly to environmental change, which can be especially important when animals have to adapt to anthropogenically-mediated changes to their habitats. In general, behavioral changes induced by anthropogenic habitat modifications are greater than those associated with natural environmental variation, and such human-induced changes typically signify phenotypic plasticity rather than genetic adaptation (Hendry et al. 2008). Behavioral flexibility is particularly important when environmental conditions change rapidly, as seen in climate warming or habitat fragmentation and destruction, where opportunities for emigration or dispersal are limited and genetic adaptation is too slow a process to cope with the changes (Wong and Candolin 2015).

Animal behavior is partly inherited (Brown et al. 2005; Krueger 2008; van Oers and Mueller 2010), but also environmentally influenced, and affected by experiences during early life (Frost et al. 2007; Li et al. 2021). There are two common, non-mutually exclusive explanations used to explain why early experiences are important. First, conditions experienced in early life may be a cue for the type of conditions that an animal will encounter later in life, and second, conditions experienced early in life may influence the somatic state of animals, with effects carried over to later stages (Nettle and Bateson 2015). Hence, studies on the mechanisms involved may help us understand how global change affects organisms in a future climate.

Risk taking is one behavioral trait that may be influenced by early experiences of animals. This notion is captured in the shyness–boldness continuum, i.e., the willingness to take risks in new situations (Biro and Stamps 2008), and temperature early in life may influence this trait (Malekpour 2007). Such temperature-dependent effects on behavior might be expected for ectothermic species because of temperature's influence on rates of physiological and biochemical reactions (Hochachka and Somero 1984). For instance, temperature during the egg stage has been shown to influence behavioral traits of larval striped marsh frogs *Limnodynastes perionii* (Seebacher and Grigaltchik, 2014) and young green sea turtles *Chelonia mydas* (Burgess et al. 2006). Yet another example is the bearded dragon lizard, *Pogona vitticeps*, which is faster and bolder when produced from warm-incubated eggs than from cold-incubated eggs (Siviter et al. 2017a, 2019). These findings highlight the potential generality of embryonic temperature effects on the behavior of juveniles, and warrant further testing with other ectotherm groups.

Effects of incubation temperature on behavior have also been explored for fishes, such as salmonids. In particular, experiments using Atlantic salmon *Salmo salar* and brown trout *Salmo trutta* have shown that elevated egg temperature influences migratory behavior later in life (Jonsson and Jonsson 2018; Jonsson and Greenberg 2022). In addition, growth, metabolic rates and aerobic scope have been shown to be higher in juvenile salmonids that have experienced cold egg incubation temperatures than juveniles subjected to warm incubation temperatures (Finstad and Jonsson 2012; Durtsche et al. 2021). Thus, linkages between behavior, growth and metabolism are likely to exist.

As a partial migratory species, a single population of brown trout can consist of both freshwater resident and anadromous or lake-migrating individuals (Jonsson 1985; Nevoux et al. 2019), making this species a particularly interesting subject for behavioral studies. Behavioral differences would be expected, given that migratory brown trout have been shown to have higher growth rates, food consumption and energy budgets than residents (Forseth et al. 1999; Jonsson and Jonsson 2021). It is not known, however, whether embryonic temperature influences the behavior of brown trout, and if behavior differs between offspring of anadromous, lake-resident or crosses between the two.

Herein, we used offspring of anadromous and resident (lacustrine-adfluvial) brown trout and crosses between the two from a single river and tested whether egg incubation temperature had carry-over effects on behavioral traits, swimming activity and aggression in juveniles, and if the parental phenotype influenced these behavioral traits. We hypothesized that offspring incubated in cold water would be more active and aggressive than those incubated in warm water, based on Durtsche et al. (2021), who showed that

metabolic rates were higher in cold-incubated than in warm-incubated trout, and on the fact that metabolic rate has been shown to be positively related to dominance (aggression) and boldness (Metcalf et al. 1995; Huntingford et al. 2010). We also hypothesized that offspring of anadromous brown trout would have a higher swimming activity (be “bolder”) and level of aggression than offspring of freshwater resident parents, based on previous studies linking migration with growth and metabolism (Forseth et al. 1999; Jonsson and Jonsson 2021) and metabolism with aggression and boldness (Metcalf et al. 1995; Huntingford et al. 2010). The results of this study have bearing on future scenarios of global warming, as even small differences in embryonic temperature may have ecological consequences for subsequent life stages.

Material and Methods

Rearing of fish

We conducted an experiment at the Norwegian Institute for Nature (NINA) Research Station Ims in southwestern Norway (59° N, 6° E) in 2017–2018 and in 2018–2019 to test our hypotheses regarding behavior in relation to incubation temperature and parental crossing. The fish used in the

experiment were the offspring from crosses of anadromous brown trout spawning in the main stem of the River Imsa and resident brown trout spawning in the geographically isolated Fossbekk Stream, a tributary to the River Imsa. The anadromous spawners were collected in a box trap, situated 150 m upstream of the mouth of the River Imsa as the fish returned from the sea to spawn. These trout were previously captured and Carlin-tagged as outmigrating smolts, thereby enabling us to identify the returning spawners as anadromous trout of the River Imsa (Jonsson and Jonsson 2009). All trout in the Fossbekk Stream are freshwater resident as an artificial waterfall, constructed in 1993–95, prevents anadromous trout from reaching this stream (Jonsson and Jonsson 2017).

To assess our hypothesis regarding parental crossings, we created four different offspring crosses: (1) anadromous male x anadromous female (AA), (2) anadromous male x resident female (AR), (3) resident male x resident female (RR), and (4) resident male x anadromous female (RA) (Fig. 1). In 2017, we collected eggs from four anadromous and four resident females and fertilized them with milt collected from four anadromous and four resident males on 10 November 2017 (Table 1). Similarly, in 2018, we collected eggs from 12 anadromous and 12 freshwater resident females and crossed them with sperm from 12 anadromous males and 12 freshwater resident males on 9 November 2018 (Table 1). In both 2017 and 2018, each adult was used in

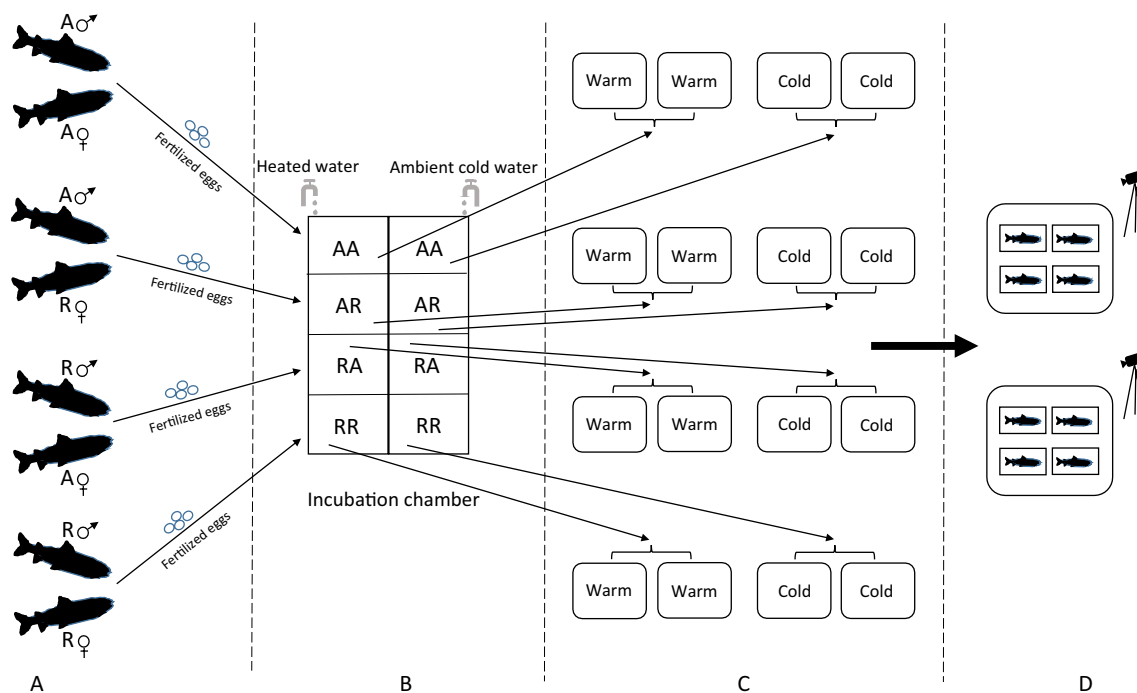


Fig. 1 Schematic drawing of the experimental protocol. **A** Gametes were removed from anadromous (A) and resident (R) adults and fertilized to create AxA, AxR, RxA, and RxR offspring. **B** Fertilized eggs were incubated, subjected to cold (ambient) water or warm (heated) water. **C** After trout began feeding exogenously, they were moved to

holding tanks, two tanks per cross and incubation temperature. Trout were fed daily with pellets administered by pre-programmed feeders. **D** Trout were removed from the holding tanks and released individually into tubs, which were situated in two experimental tanks, and filmed. Behavior of the fish was scored from the films

Table 1 Mass (g), mean (± 1 SD) and range of the brown trout parents used in the different crosses in 2017 and 2018. The number of individuals is also shown

Year	Parents	Male			Female		
		Mean \pm SD (g)	Range (g)	N	Mean \pm SD (g)	Range (g)	N
2017	Anadromous	423 \pm 253	167–659	4	754 \pm 642	257–1443	4
	Resident	156 \pm 70	64–233	4	170 \pm 18	133–171	4
2018	Anadromous	771 \pm 451	309–1539	12	577 \pm 186	315–993	12
	Resident	167 \pm 64	76–271	12	220 \pm 93	83–423	12

two different crosses, one with a freshwater resident and the other with an anadromous trout (see Durtsche et al. (2021) and Jonsson and Greenberg (2022) for more details).

For both years, eggs from the four crossings were incubated using water piped in from the River Imsa to the NINA Research Station at either ambient (cold) temperature conditions or at temperatures elevated approximately $+2.5$ °C above ambient (warm) conditions (4 crossings \times 2 incubation temperatures \times 2 replicates). The elevated temperature was attained using a heat exchanger. There were daily variations in temperature, but heated water was always warmest (Fig. 1). The mean temperature during the incubation regimes was 4.1 ± 1.5 °C (± 1 SD) for cold conditions and 6.4 ± 1.3 °C for warm conditions (a difference of 2.4 °C) for 2017–18 and 4.3 ± 1.5 for cold conditions and 7.1 ± 0.6 °C for warm conditions (a difference of 2.7 °C) for 2018–19 (Fig. 2). The rearing tanks had a water level of 30 cm, a water flow of 2 L min^{-1} , and a surface light intensity of approximately 70 lx during daytime (12 h light: 12 h dark cycle).

The different crosses were raised in separate incubation trays with constant water flow until the start of exogenous feeding. Mortality was negligible. On 6 March and 17 April 2018 and on 22 February and 9 April 2019, the warm- and cold-incubated trout were moved into sixteen 60 L holding tanks, respectively (2 tanks for each cross \times incubation temperature) (Fig. 2). The following day, exogenous feeding was initiated, using commercial pellets (Ewos Opal food pellets with 29–31.5% lipids, 42–45% proteins and a digestible energy density of 21 kJ g^{-1} , Cargill®, Norway). In 2019, when fish were also studied in August, the fish were subsequently moved to 500 L holding tanks due to their large size. From 18 April 2018 and 10 April 2019 onwards, all trout in each respective year were maintained using unheated River Imsa water.

Behavioral experiments

We studied the individual behavior of each trout using open-field and mirror-image tests, conducted in a laboratory environment. These laboratory tests have been previously used for salmonids to quantify swimming activity in new environments (sometimes referred to as shy-boldness) and aggression level (Norton and Gutierrez 2019). Previous research on brown trout shows high inter-individual variation in these behaviors (Sundström et al. 2004; Höjesjö

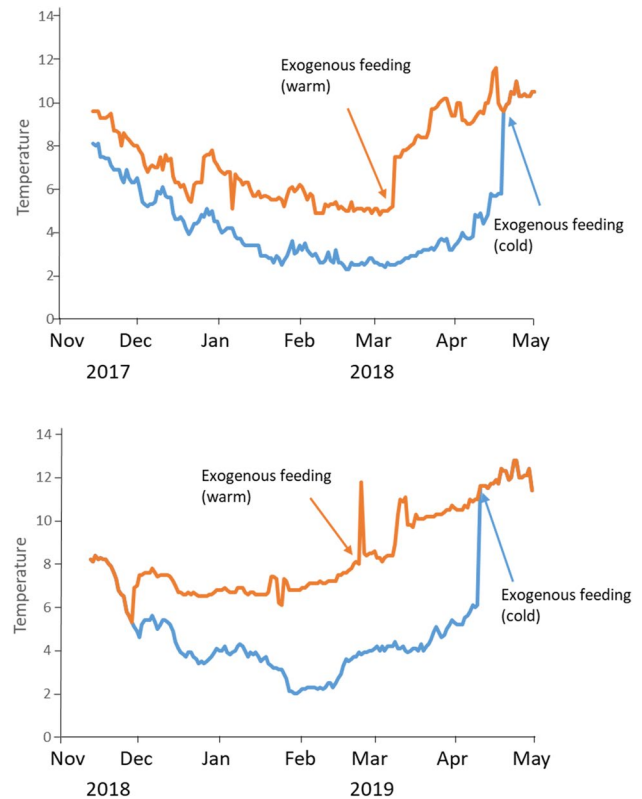


Fig. 2 Temperature (°C) during incubation and post-hatching of brown trout in 2017–18 (upper panel) and 2018–19 (lower panel). Blue line shows cold conditions and the orange line, warm conditions. The point at which exogenous feeding was initiated is also depicted. After exogenous feeding was initiated by the ambient group, temperature conditions were the same for the two groups, following conditions in the Imsa River

et al. 2011; Adriaenssens and Johnsson 2013; Závorka et al. 2015), which make them suitable parameters for studies of behavioral variation.

We conducted the experiment from 30 May to 4 June 2018, from 8 to 12 June 2019 and from 16 to 20 August 2019. The experimental set-up involved two sets of four white opaque plastic tubs. The tubs used in June 2018 and 2019 ($25 \times 35 \times 15$ cm) were smaller than those used in August 2019 ($37 \times 54 \times 21$ cm) to account for differences in fish size (June: 43 ± 5 mm (mean ± 1 SD) in 2018 and 49 ± 9 mm in 2019; August: 80 ± 11 mm) (Kuggis, IKEA,

Sweden). Four plastic tubs were placed in each of two large fiberglass tanks (110×110 cm; 150×150 cm), with a 2.5 cm deep continuous flow of circulating water in the tanks to keep the water in the tubs from warming (Fig. 2). Water depth in the tubs was 5 cm for the experiments conducted in June and 8 cm in August when the trout were larger. Water was supplied from the nearby River Imsa, and the water temperature was measured daily. Temperature during these trials was 14.3 ± 1.0 °C in 2018 and 10.6 ± 0.3 °C in June 2019 and 15.4 ± 0.1 °C in August 2019. Two cameras (Canon XA10; Canon Inc. Tokyo, Japan) were attached to tripods, and one camera was placed over each tank with its four tubs. The cameras were placed so they allowed observations of the fish from above. Simultaneous video recordings were carried out in the eight tubs (two tanks), with one trout in each tub. One fish per tub was used as this is standard practice when performing open field tests with this highly aggressive species. Thus, we conducted one replicate of each of the eight treatments (two incubation temperatures and four crossings) on each occasion. The tub in which each treatment was tested was altered between occasions, using a randomized block design. We replaced all water in each tub with fresh water between trials. In 2018, we performed 15–17 replicates (occasions) for each treatment, and 22–24 replicates for every treatment in both June and August 2019. A few trials were deleted due to camera malfunction and because we accidentally scared fish during filming, and in two cases, fish jumped out of their tubs into adjacent tubs.

Before each trial, trout were carefully netted from their holding tanks and placed in one of the experimental tubs, and were subsequently video recorded for at least 21 min to score the undisturbed swimming pattern of each trout (open field test). Upon completion of the open field test, we placed a mirror on one short side of each tub, alternating between replicates. Trout were subsequently video-recorded for an additional minimum of 21 min to assess their behavior in relation to their mirror image (Johnsson et al. 2003). Directly after each trial, the trout were removed from the experimental arenas and measured for total length (to the nearest mm). To minimize bias, the observer was unaware of the treatments assigned to each tub when behavior was quantified from the films.

Recorded behaviors and analyses

We measured behavior using the open field test and the mirror test. For the open field test, we quantified (1) the proportion of time the fish spent swimming, and (2) the time it took them to initiate swimming (swimming defined as when the fish moved at least half a body length per second). For the mirror test, we quantified (3) the proportion of time the fish spent motionless within 5 cm of the mirror, and (4) the proportion of time spent swimming within 5 cm of

the mirror. Many authors have used proximity to a mirror as a measure of aggression for young brown trout (Peterson and Järvi 2000; Johnsson et al. 2003; Adriaenssens and Johnsson 2013; McGlade et al. 2022), owing to the species' highly aggressive nature (Kalleberg 1958). For this study, the angle and height of the cameras in relation to the fish did not allow us to consistently identify aggressive behaviors, such as fin and opercular displays, typical behaviors associated with aggression in brown trout (Kalleberg 1958). We were able to observe fish swim rapidly towards the mirror, i.e., lunging, but this behavior did not occur often enough to use, based on a pilot study of 56 fish, in which only 11 fish (20%) made lunges, often only once during 5 min of observation. As the reason for a fish spending time near a mirror may also reflect activity of the fish as found for some other species of fish (Balzarini et al. 2014), we interpret any significant patterns with caution.

Three observers scored the films after training together, doing blind tests and comparing results until they were similar. To reduce the work involved, we did not analyze the entire period. Instead, we quantified behaviors during the following time intervals from the start of a trial: 0–1 min, 5–6 min, 10–11 min, 15–16 min and 20–21 min, to encompass and reflect behavior over the entire period of observation.

For the statistical analyses, we used the average for the five time periods for each individual trout and performed separate linear model analyses (using GLM in SPSS) for each behavioral variable. The data were analyzed using two approaches, which explored the effects of incubation temperature and cross on each behavior. The first tested for effects on juveniles to see if behavioral patterns were consistent for two different cohorts. For this analysis, we used data from June 2018 and June 2019. A model was constructed with three fixed factors: incubation temperature, cross and year (note that year is treated as a fixed factor and not a random factor as there are only 2 years studied). Body length was entered as a covariate. We also included the interactions, incubation temperature x cross and incubation temperature x year interactions, because the different crosses could be expected to have different responses to incubation temperature, and the temperature during the behavioral tests differed between years (mean of 14.3 °C in 2018 and 10.6 °C in 2019). The cross x year interaction and three-way interaction were not included as we expected crosses to have the same response between years. This analysis was done using all of the data and then re-run, including only fish from the two incubation temperature groups that overlapped in size (i.e., truncate the size range to eliminate the smallest cold-incubated and largest warm-incubated fish), as the results may be obfuscated when including non-overlapping size ranges. The size range was reduced from 30–58 mm to 33–49 mm and from 26–69 mm to 35–56 mm for the June 2018 and 2019 data, respectively, representing an overall reduction of 17% of the data points. The second approach

was designed to determine if the differences were still present later in the season, i.e., in August (2019). This model contained incubation temperature, cross and the interaction term as the main factors, and length as a covariate. Again, this analysis was done using all of the data and then re-run, including only fish from the two incubation temperature groups that overlapped in size. Thus, the size range was reduced from 54–106 mm to 66–86 mm, representing an overall reduction in the amount of data by 36%. Proportional data were arcsine square root transformed, and time was log-transformed ($x + 1$). Normality of the transformed variables' distributions was tested using a Kolmogorov–Smirnov test for the residuals, and homogeneity of variance was tested with Levene's test for homogeneity of variance. Variances were not significantly different from each other for 13 of the 16 analyses (four variables, two time periods, full size and truncated size distributions; Tables 2–3). In terms of normality, five of the 16 analyses showed distributions that

differed from normality, and these were for the proportion of time spent swimming (June: full and truncated data set; August: full) and the time to first swim (June: full and truncated). As ANOVA is robust against violations to normality and homoscedacity (Zar 2010; Kikvidze and Moya-Laraño 2008; Blanca et al. 2017), we elected to retain our analyses.

Results

June 2018 and 2019

Overall, the trout spent an average of $64.2 \pm 6.5\%$ (mean \pm 1 SD, range of means from 49.3–73.1%) of their time swimming in the open field test. The trout spent a greater proportion of their time swimming in 2018, when the average temperature during the trials was 14.2 °C, than in 2019 when the temperature

Table 2 F-values, degrees of freedom and probability values for the linear models testing the effects of incubation temperature, cross, year (only for June experiments), incubation temperature x cross, incubation temperature x year and fish length on different behaviors measured in the open field test and mirror test in June. Separate tests were done on the whole data set and a truncated set that included only fish from the two incubation temperature groups that overlapped in size (i.e., truncate the size distribution to eliminate the smallest cold-incubated and the largest warm-incubated fish). The variables are

the proportion of time the fish spent swimming (Time swim, arcsine square root transformed), the time it took the fish to initiate swimming (First swim, $\log(x + 1)$ transformed), the proportion of time the fish rested motionless near the mirror (Motionless mirror, arcsine square root transformed) and the proportion of time the fish swam near the mirror (Swim mirror, arcsine square root transformed). Significant values depicted in boldface. Levene's test for homogeneity of variance is also presented

Variable	Data set	Stat	Levene's	Incub Temp	Cross	Year	Inc. x Cross	Inc. x Year	Length
Time swim	Full	df	15, 304	1, 309	3,309	1, 309	3, 309	1, 309	1, 309
		F	1.260	12.172	0.228	10.638	0.816	0.806	17.045
		P	0.226	0.002	0.877	0.001	0.486	0.370	< 0.001
	Truncated	df	15, 236	1, 241	3, 241	1, 241	3, 241	1, 241	1, 241
		F	1.431	12.358	0.475	7.906	0.495	0.611	16.477
		P	0.134	< 0.001	0.700	0.005	0.686	0.435	< 0.001
First swim	Full	df	15, 304	1, 309	3, 309	1, 309	3, 309	1, 309	1, 309
		F	0.685	3.360	0.860	0.136	0.729	0.014	22.164
		P	0.799	0.068	0.462	0.712	0.535	0.905	< 0.001
	Truncated	df	15, 236	1, 241	3, 241	1, 241	3, 241	1, 241	1, 241
		F	0.935	4.559	0.602	0.029	1.905	0.036	23.659
		P	0.526	0.034	0.615	0.866	0.129	0.850	< 0.001
Motionless mirror	Full	df	15, 295	1, 311	3, 311	1, 311	3, 311	1, 311	1, 311
		F	0.979	2.236	1.194	3.516	0.622	1.160	0.021
		P	0.478	0.136	0.312	0.062	0.601	0.282	0.884
	Truncated	df	15, 229	1, 234	3, 234	1, 234	3, 234	1, 234	1, 234
		F	1.064	0.381	0.459	68.437	1.290	2.626	0.693
		P	0.391	0.538	0.712	< 0.001	0.279	0.106	0.406
Swim mirror	Full	df	15, 295	1, 311	3, 311	1, 311	3, 311	1, 311	1, 311
		F	1.404	2.544	0.707	0.676	0.914	3.814	4.393
		P	0.144	0.112	0.548	0.412	0.435	0.052	0.037
	Truncated	df	15, 229	1, 234	3, 234	1, 234	3, 234	1, 234	1, 234
		F	1.705	1.843	0.442	0.313	0.413	3.391	5.441
		P	0.051	0.176	0.723	0.577	0.744	0.067	0.021

Table 3 F-values, degrees of freedom and probability values for the linear models testing the effects of incubation temperature, cross, incubation temperature x cross and fish length on different behaviors measured in the open field test and mirror test in August. Separate tests were done on the whole data set and a truncated set that included only fish from the two incubation temperature groups that overlapped in size (i.e., truncate the size distribution to eliminate the smallest cold-incubated and the largest warm-incubated fish). The

variables are the proportion of time the fish spent swimming (Time swim, arcsine square root transformed), the time it took the fish to initiate swimming (First swim, $\log(x+1)$ transformed), the proportion of time the fish rested motionless near the mirror (Motionless mirror, arcsine square root transformed) and the proportion of time the fish swam near the mirror (Swim mirror, arcsine square root transformed). Significant values depicted in boldface. Levene's test for homogeneity of variance is also presented

Variable	Data set	Stat	Levene's	Incub. Temp	Cross	Incub. x Cross	Length
Time swim	Full	df	7, 172	1,171	3, 171	3, 171	1, 171
		F	1.088	0.148	1.295	1.851	2.314
		P	0.373	0.701	0.278	0.140	2.314
	Truncated	df	7, 109	1, 108	3, 108	3, 108	1, 108
		F	0.970	0.023	0.317	2.038	0.423
		P	0.457	0.880	0.813	0.113	0.517
First swim	Full	df	7, 172	1,171	3, 171	3, 171	1, 171
		F	2.292	1.543	1.276	1.211	7.543
		P	0.029	0.216	0.284	0.307	0.007
	Truncated	df	7, 109	1, 108	3, 108	3, 108	1, 108
		F	2.737	1.511	1.095	1.020	5.789
		P	0.012	0.222	0.355	0.387	0.018
Motionless mirror	Full	df	7, 173	1,171	3, 171	3, 171	1, 171
		F	0.356	2.693	0.686	0.879	1.441
		P	0.926	0.103	0.562	0.453	0.232
	Truncated	df	7, 109	1, 108	3, 108	3, 108	1, 108
		F	0.238	5.277	0.469	0.551	1.362
		P	0.975	0.024	0.704	0.648	0.246
Swim mirror	Full	df	7, 176	1,171	3, 171	3, 171	1, 171
		F	2.575	0.102	0.282	0.391	0.262
		P	0.015	0.750	0.838	0.760	0.610
	Truncated	df	7, 110	1, 108	3, 108	3, 108	1, 108
		F	2.005	0.173	0.190	0.730	0.020
		P	0.061	0.678	0.903	0.536	0.888

was 10.6 °C. In addition, incubation temperature and body size affected the proportion of time spent swimming, with cold-incubated and large trout spending a larger proportion of their time swimming than warm-incubated and small trout. Analysis of the time the fish spent swimming revealed significant effects of incubation temperature, year and body length, but no effects of cross or the interactions (Table 2). The analysis of the truncated data set produced a similar pattern (Table 2, Fig. 3).

Time to initiate swimming was also measured in the open field test, and this variable was inversely related to the proportion of time swimming ($r = -0.574$, $p < 0.001$, $N = 320$). Overall, the trout took an average of 153 ± 56 s (mean \pm 1 SD, range of means: 42–265 s) to initiate swimming. Linear model analysis of the time it took trout to initiate swimming revealed an effect of body length, with large trout initiating swimming sooner than small fish (Table 2). There were no other significant effects for this variable, but there was a non-significant tendency for an effect of incubation temperature

($p = 0.068$). The analysis of the truncated data also showed a significant effect of length, and the effect of incubation temperature was now significant ($p = 0.037$, Fig. 3). The cold-incubated trout initiated swimming earlier than the warm-incubated trout.

For the mirror test, the trout spent an average of $19 \pm 6\%$ (mean \pm 1 SD, range of means 8–31%) of their time resting motionless near the mirror and $26 \pm 5\%$ (range: 16–36%) of their time swimming near the mirror. There were no significant differences for the time the trout spent resting motionless near the mirror, although there was a non-significant effect of year ($P = 0.062$, Table 2). For the truncated data set, this effect was significant ($p < 0.001$), with fish spending more time resting near the mirror in 2018 than in 2019 (Fig. 3). For the time spent swimming near the mirror, the only significant effect for the mirror test was a positive one between body length and the proportion of time a trout spent swimming near the mirror (Table 2, Fig. 3).

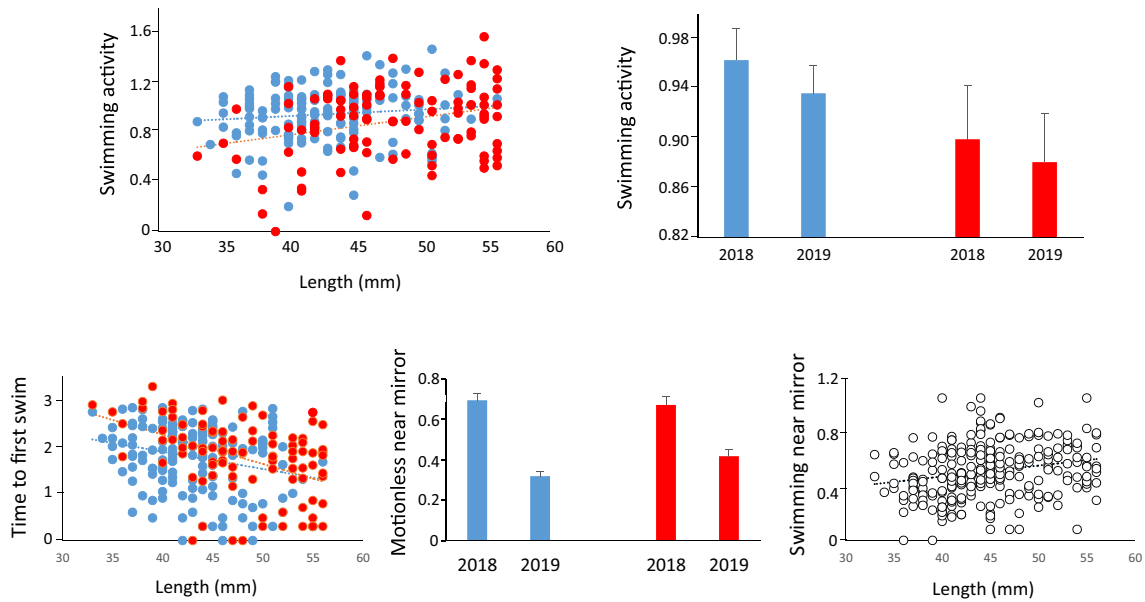


Fig. 3 Average swimming activity (arcsine square root transformed of proportion of time; upper left and right panels), time to first swim ($\log(x + 1)$ of times, lower left panel), time spent motionless near the mirror (arcsine square root transformed of proportion of time, lower middle panel) and time spent swimming near the mirror (arcsine square root transformed of proportion of time, lower right panel) of

brown trout (*Salmo trutta*) in relation to year or body length (mm) for the truncated data set from June 2018 and 2019. Trend lines are depicted for those variables with significant effects of length. Warm-incubated trout are represented by red and cold-incubated trout by blue. The error bars represent ± 1 standard error

August 2019

Overall, the trout spent an average of $50 \pm 6\%$ (mean ± 1 SD, range of means: 41–63%) of their time swimming in the open field test. None of the variables were significant when evaluated for the entire data set or the truncated one (Table 3).

The time to initiate swimming averaged 127 ± 46 s (mean ± 1 S.D., range of means: 48–178 s). For this analysis, there was a significant effect of length when evaluated

for both the entire data set and the truncated one (Table 3). Time to initiate swimming was inversely related to body size (Fig. 4).

For the mirror test, the trout spent an average of $19 \pm 3\%$ (mean ± 1 SD, range of means: 15–24%) of their time resting motionless near the mirror and $20 \pm 2\%$ (mean ± 1 SD, range of means: 17–22%) of their time swimming near the mirror. The only significant effect for the mirror test was for the time spent resting motionless near the mirror, and only for the truncated data set (Table 3). Here, there was an

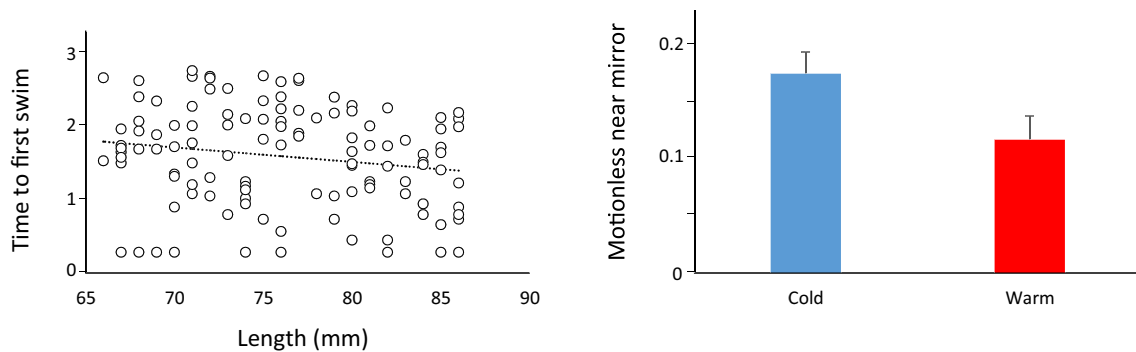


Fig. 4 Time to first swim ($\log(x + 1)$ transformed of proportion of time) in relation to body length (mm) and time spent motionless near the mirror (arcsine square root transformed of proportion of time) for the truncated data set from August 2019. A trend line is shown for

time to first swim, and warm-incubated trout are represented by red and cold-incubated trout by blue. Error bars represent ± 1 standard error

effect of incubation temperature, where the cold-incubated trout spent more time motionless near the mirror than the warm-incubated trout (Fig. 4).

Discussion

Cold incubated brown trout had higher swimming activity and initiated swimming earlier than warm-incubated conspecifics in June in the open field experiment. The higher activity lends support to our first hypothesis that cold-incubated juveniles are more active than warm-incubated conspecifics. The higher activity may be linked to differences in metabolic rates as low embryonic temperature has been shown to produce juvenile brown trout with high metabolic rates and aerobic scope (Durtsche et al. 2021), which should promote swimming (locomotor) activity. A high swimming activity in cold environments may be profitable, increasing feeding opportunities and make the fish less vulnerable to endothermic predators, as young life stages of brown trout depend on finding food within a limited amount of time to minimize exposure to predators (Elliott 1994). Low temperature has a dampening effect on swimming by ectotherms, and food production is lower in cold than in warm rivers, which might make high swimming activity at low temperatures profitable. This contention is consistent with the countergradient variation hypothesis, stating that in ectotherms, cold environments stimulate metabolic rates to compensate for negative effects of low temperatures and thus make conspecific phenotypes developed in warm and cold environments more similar (Levin 1968; Conover and Schultz 1995).

There are different views as to whether this countergradient effect is inherited or a phenotypically plastic, thermal carry-over response (review in Conover et al. 2009). Countergradient variation is expected to evolve when stabilizing selection favors similar phenotypes in different environments, and it may reflect adaptation to latitudinal or altitudinal gradients (Berven et al. 1979). For instance, Alvarez et al. (2006) suggested that local adaptation in warm environments selects for low standard metabolic rates of brown trout when compared to those adapted to colder streams. However, Durtsche et al. (2021) demonstrated in a common garden experiment that metabolic rates can be a phenotypically plastic carry-over effect caused by embryonic temperature. Alterations in metabolic rates may result from thermal effects on the cardiovascular system, changes in mitochondrial function, and/or changed activity of oxidative enzymes (Schnurr et al. 2014), and the effect may be a result of an epigenetic effect of embryonic temperature (Jonsson et al. 2022).

When tested in August, there was no significant difference in swimming activity between cold- and warm-incubated brown trout, suggesting that the behavioral effect of

incubation temperature observed in June may be short term. This parallels findings reported by Siviter et al. (2017b), who found a short-term response of egg incubation temperature for bearded dragon lizards. These authors suggested that incubation temperature only affected the rate of behavioral development and not the personality of the lizards per se. In contrast, an earlier study in the River Imsa, the source of our trout, showed that egg incubation temperature affected the rate of outmigration of brown trout juveniles when they were released as 6 or 12 month-old juveniles into the river (Jonsson and Greenberg 2022). Moreover, they showed that this effect was independent of body size. Thus, there are egg incubation temperature effects on the behavior of juveniles that persist after the first summer. Further research is needed on the persistence of carry-over effects of incubation temperature on the behavior of brown trout.

We know of only one previous study showing that embryonic temperature can affect later swimming performance of a fish species. Kourkouta et al. (2021) reported that metamorphosing larvae of gilthead seabream (*Sparus auratus*), incubated from the epiboly stage of the embryos to first external feeding, achieved higher critical swimming speeds when incubated at 17 °C than at 20 °C. It is also known that embryonic temperature can affect behavioral decisions by fish, associated with when and whether to migrate (Jonsson and Jonsson 2018; Jonsson and Greenberg 2022). From amphibians it is known that egg temperature can have carry-over effects on the behavior of tadpoles to perform better under prevailing thermal conditions (Van Buskirk and McCollum 2000). In reptiles, cold embryonic environments may in some cases stimulate later locomotor activity as reported from studies of jacky dragon lizards *Amphibolus muricatus* (Esquerré et al. 2014), wall lizards *Podarcis muralis* (Van Damme et al. 1992) and grass lizards *Takydromus wolteri* (Pan and Ji 2001). However, in other cases, high but not cold temperatures stimulate later activity as observed for green sea turtles *Chelonia mydas* (Burgess et al. 2006) and loggerhead sea turtles *Caretta caretta* (Kobayashi et al. 2018). The reason for species-specific differences in the response to embryonic temperatures is unclear and needs further research.

Even though we included body size as a covariate in our analysis, body size effects might still be affecting our conclusions regarding the effects of incubation temperature on swimming activity. This is because the warm-incubated trout, which hatched first, had overlapping but larger body sizes than the smaller cold-incubated trout. To circumvent this potentially obfuscating effect, we re-analyzed our data by truncating size distributions, including only fish from the cold- and warm-incubated trout that overlapped in size. When doing so, we found that all the differences observed with a full data set still persisted in the truncated data set, suggesting this behavioral difference in activity was an effect

of incubation temperature and not body size per se. Moreover, two additional effects of incubation temperature were revealed. Cold-incubated trout initiated swimming earlier than warm-incubated (in June), as we predicted, and they also spent a greater proportion of their time motionless near the mirror than the warm-incubated trout (in August). If time in front of the mirror reflects differences in aggression, then this latter result would also support our hypothesis, namely that cold-incubated trout are more aggressive than warm-incubated ones.

One of the direct effects of incubation temperature is body size per se. Warmer incubation temperatures lead to earlier hatching dates, and thus, warm-incubated trout were on average larger than cold-incubated trout. Not surprisingly, there were many effects of body size, affecting swimming activity, both in the absence and presence of the mirror, as well as the time to first swim. Large brown trout juveniles swam more and initiated swimming sooner than smaller conspecifics of the same age. It is known that large fish swim faster (Fry and Cox 1970; Ojanguren and Braña 2003) and are less vulnerable to gape-limited predators than small fish (Miller et al. 1988; Persson et al. 1996). Thus, large size enables the trout to become more active and reduce predation risk. Furthermore, our study showed a positive relationship between body size and the proportion of time spent swimming in front of the mirror. This relationship may simply reflect large fish swimming more than small fish, but it likely also reflects a real relationship between body size and aggression. Earlier studies have demonstrated a positive correlation between growth rate and aggression (Nicieza and Metcalfe 1999; Lathi et al. 2001), and in common carp *Cyprinus carpio*, there is positive correlation between growth rate and boldness (Klefoth et al. 2017). This may explain why large individuals exposed themselves more in front of the mirror than smaller ones, as there is likely a correlation between boldness and aggressiveness (Ariyomo and Watt 2012; Barnett et al. 2012; Fu et al. 2021).

There was no significant difference in the time trout spent near the mirror among any of the crosses. This was unexpected, assuming time near the mirror reflects aggression, as Lathi et al. (2001) reported that anadromous brown trout were more aggressive than lacustrine-adfluvial and stream resident conspecifics. Furthermore, offspring of anadromous trout grew faster than offspring of freshwater resident trout and crosses between the two when reared under similar conditions, suggesting a genetic difference between trout forms from the same river (Jonsson and Jonsson 2021). Previously, Jonsson and Greenberg (2022) showed that similar sized anadromous and freshwater resident brown trout of the River Imsa differed in migratory behavior when released in a river, a difference that possibly resulted from adapted differences between the two.

The present experiment suggests that embryonic temperature has carry-over effects on the activity of juvenile brown trout. It may be that high winter temperature in rivers where the eggs are naturally incubated, acts as a cue indicating that the future juvenile environment will also be relatively warm. The fish respond by reducing metabolic rates and activity levels (Durtsche et al. 2021). As oxygen content of water decreases with temperature, lower activity and oxygen requirements of the trout should be advantageous in relatively warm habitats. Brown trout has a high oxygen demand, with an optimal temperature for growth of juveniles as low as 13 °C (Forseth et al. 2009; Elliott and Elliott 2010). At higher temperatures, growth is constrained by the oxygen content of the water (Jutfelt et al. 2021).

In this experiment, we tested if temperature during embryogenesis influenced behavior of young, juvenile brown trout. This does not mean that embryonic temperature can only carry-over to the young juvenile stage, but that early temperature may also affect later stages. For instance, egg incubation temperature has been shown to affect the timing of the spawning migration of adult Atlantic salmon *Salmo salar* years after thermal priming (Jonsson et al. 2014). Groothuis and Taborsky (2015) viewed development as a life-long interactive process of gathering information. This is understandable because the brain develops gradually during ontogeny and is especially sensitive to changes in genetic and environmental cues during early development. Thus, effects of early environments may not be manifested until quite late in an animal's life history, sometimes not until an organism reaches adulthood, as in the case of adult Atlantic salmon returning from the ocean (Jonsson and Jonsson 2018). Despite this possibility, we did not find long-term effects of incubation temperature on behavior in this study.

This research has relevance to the present situation with global warming. Higher incubation temperature in rivers will not only influence growth and breeding ecology of salmonid fishes (Finstad and Jonsson 2012; Jonsson et al. 2014), but has impacts on swimming activity and behavioral decisions (Jonsson and Jonsson 2018; Jonsson and Greenberg 2022). The activity level may be important for survival during the first summer, even if the effect is only present through early summer, as mortality of the young fish at that time is extremely high (Elliott 1994). However, it is difficult to predict the overall consequences in fitness of a warmer climate as warmer temperatures affect both salmonids and their food resources (Bærum et al. 2021). Nevertheless, the results from this study, combined with results regarding metabolic rates from our previous studies (Durtsche et al. 2021; Jonsson and Greenberg 2022), suggest that juvenile brown trout in a warmer climate will have lower metabolic rates and aerobic scopes and be less active, with similar consequences across migratory and non-migratory phenotypes.

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Author contributions LAG and BJ conceived and initiated the study. KF, LAG, EB set up the experiment and then filmed and measured the fish. KF and LAG quantified and analyzed the behaviors from the films. LAG and BJ wrote the first draft, and EB and KF read and commented on subsequent drafts. All authors approved the final version.

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Data Availability The datasets generated during and/or analyzed during the current study are available in the Figshare repository, <https://doi.org/10.6084/m9.figshare.20694676.v1>.

Declarations

Conflicts of interest The authors declare no competing interests.

Ethics approval The care and use of the experimental fish complied with the Norwegian animal welfare laws and policies as approved by the Norwegian Animal Research Experimentation Agency (NARA) with the Animal Care and Use ID: 15450.

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