Received: 13 October 2020 | Accepted: 2 January 2021

DOI: 10.1111/jfb.14693

REGULAR PAPER

JOURNAL OF FISH BIOLOGY

# Differences in growth between offspring of anadromous and freshwater brown trout *Salmo trutta*

**Bror Jonsson** | **Nina Jonsson**

Norwegian Institute for Nature Research,
Oslo, Norway

**Correspondence**
Bror Jonsson, Norwegian Institute for Nature Research, Sognsveien 68, 0855 Oslo, Norway.
Email: bror.jonsson@nina.no

## Abstract

In this study, individual growth of juvenile offspring of anadromous and freshwater resident brown trout *Salmo trutta* and crosses between the two from the River Imsa, Norway, was estimated. The juveniles were incubated until hatching at two temperatures (±S.D.), either 4.4 ± 1.5°C or 7.1 ± 0.6°C. Growth rate was estimated for 22 days in August–September when the fish on average were *c.* 8 g in wet mass, and the estimates were standardized to 1 g fish dry mass. Offspring of anadromous *S. trutta* grew better at both 15 and 18°C than offspring of freshwater resident *S. trutta* or offspring of crosses between the two *S. trutta* types. This difference appears not to result from a maternal effect because anadromous *S. trutta* grew better than the hybrids with anadromous mothers. Instead, this appears to be an inherited difference between the anadromous and the freshwater resident fish lending support to the hypothesis that anadromous and freshwater resident *S. trutta* in this river differ in genetic expression. Egg incubation temperature of *S. trutta* appeared not to influence the later growth as reported earlier from the studies of Atlantic salmon *Salmo salar*.

KEYWORDS

anadromous brown trout, daily growth, fish, freshwater resident, *Salmo trutta*, temperature

## 1 | INTRODUCTION

Somatic growth is a significant ecological character influencing competitive ability and reproductive success of animals (Laver *et al.*, 2012). It constructs the framework and metabolic machinery necessary to synthesize and protect the gametes until their release (Wootton, 1999). In ectotherms, temperature and consumption of adequate food are the main determinants of growth, and when fish are fed to satiation, growth increases with increasing temperature until constrained by the oxygen content in the water (Holt & Jørgensen, 2015; Pörtner, 2010). These animals may be compared with an engine using food as fuel, temperature as accelerator and oxygen as speed limiter (Jonsson *et al.*, 2013). Thus, there is good reason why growth is one of the most studied ecological traits of ectotherms (Zuo *et al.*, 2012) and is highly relevant during the present period of rapid climate change (Jonsson & Jonsson, 2009, 2019).

Many trouts (genera *Salmo*, *Salvelinus* and *Oncorhynchus*) are facultatively migratory species, and river resident and anadromous conspecifics are found in many of the same rivers (Jonsson *et al.*, 2019). Growth and size are important to determine whether offspring migrate or not, but little is known about whether this difference is phenotypically plastic and environmentally induced, or caused by genetic adaptation. On the one hand, Ferguson *et al.* (2019) reported that *c.* 50% of the variability in life-history traits between anadromous and nonanadromous trouts is because of genetic variance. They based this estimate on heritability studies from various trout species, such as examined changes in gene expression in offspring of anadromous and nonanadromous rainbow trout *Oncorhynchus mykiss* (McKinney *et al*., 2015). On the other hand, Cucherousset *et al*. (2005) reported that variation in life-history traits of brown trout *Salmo trutta* from the Oir River, France, was chiefly environmentally induced. Furthermore, Forseth *et al*. (1999) found that early migration of *S. trutta* was associated with high growth rate, if growth was later restricted because of high metabolic costs. The view that migration is initiated by growth restriction was supported by the studies on anadromous and nonanadromous brook trout *Salvelinus fontinalis* (Morinville & Rasmussen, 2003). Moreover, Olsson *et al*. (2006) and Wysujack *et al*. (2008) reported that food restrictions and poor growth induced migratory behaviour in *S. trutta*. Nonetheless, when the offspring of anadromous and nonanadromous *S. trutta* fed in the same habitat, Kallio-Nyberg *et al*. (2010) found no difference in growth or size up to catch size. But still, there can be quantitative migratory and genetic differences in the propensity to migrate between offspring of the two life-history types (Jonsson, 1982; Lemopoulos *et al*., 2019).

Temperature influences growth rate and other life-history traits of fishes (Elliott, 1994; Jonsson *et al*., 2013), and even temperature before hatching may have a knock-on effect on later growth (Jonsson *et al*., 2014). For instance, both Finstad and Jonsson (2012) and Burgerhout *et al*. (2017) reported that the eggs of Atlantic salmon *Salmo salar* incubated at 7°C gave better growing offspring than those incubated in 4°C cold water. Similarly, egg incubation temperatures modified growth performance of juveniles in Senegal sole *Solea senegalensis* (Carballo *et al*., 2018). Likewise, early environments of reptiles reflect later growth in turtles, lizards and crocodilians (Booth, 2006; Deeming, 2004). Nonetheless, the knock-on effect of early temperature may differ among species. In some cases, higher egg incubation temperature results in higher growth (Alberts *et al*., 1997; Hare *et al*., 2004), in others, growth is reduced (Kobayashi *et al*., 2018; Siviter *et al*., 2019), but in some species, it may not have any effect at all on later growth.

In this study, the authors tested if offspring of anadromous and freshwater resident *S. trutta* or crosses between the two of the River Imsa population grew differently. The eggs were incubated at two temperatures, *c*. 4°C and *c*. 7°C until hatching. Four degrees is the present winter temperature in the River Imsa, and 7°C is the expected winter temperature around the year 2080 (Durtsche *et al*., 2021). Then, they were reared at the same natural River Imsa temperature until the start of the growth experiment when groups were gradually acclimatized to either *c*. 15°C or *c*. 18°C. These are the temperatures experienced by *S. trutta* during summer and are not far from the optimal temperatures for growth, which for this population was found to be between 14°C and 16°C (Forseth *et al*., 2009; Forseth & Jonsson, 1994). In nature, anadromous *S. trutta* typically grow faster and become larger than freshwater resident *S. trutta*, because anadromous *S. trutta* feed in less energy constrained habitats (Ferguson *et al*., 2019; Nevoux *et al*., 2019), although exceptions occur where the resident *S. trutta* feed on fish (Hughes *et al*., 2019). The authors hypothesized that (a) offspring of anadromous *S. trutta* would grow better than freshwater resident *S. trutta* when reared under similar conditions and fed *ad libitum* in a hatchery, and (b) elevated embryo temperature would stimulate the growth rate of juveniles later in life.

## 2 | MATERIALS AND METHODS

The experiment was performed at the NINA Research Station Ims, southwestern Norway (59°N, 6°E) (Map, Figure 1). The fish used in the experiment were the offspring from crosses of anadromous *S. trutta*, collected in a fish trap 150 m upstream of the mouth of the River Imsa as they returned from the sea, and resident *S. trutta*, collected by electrofishing in the Fossbekk Brook, a tributary to the River Imsa 1 km upstream from the sea. The *S. trutta* in the Fossbekk Brook are freshwater resident, as there is an artificial waterfall build in the River Imsa in 1993 that prevents anadromous *S. trutta* from moving farther upstream and reaching this brook (Jonsson & Jonsson, 2017). It is unknown to what degree *S. trutta* spawning in this brook before the waterfall was built, but the brook could be accessed by anadromous fish. Furthermore, it is also unknown whether offspring of *S. trutta* spawning in the Fossbekk brook still emigrate to sea, but knowledge from another rivers indicates that the migratory trait is soon lost if migration no longer is profitable (Sandlund & Jonsson, 2016).

Four different crosses were created: anadromous male × anadromous female, anadromous male × resident female, resident male × resident female and resident male × anadromous female (Figure 2). Eggs were collected from 12 anadromous females (mean length ± 1 S.D.: 38.0 ± 3.5 cm, range: 31.4–44.2 cm; mean mass: 577.3 ± 185.9 g, range: 315–993 g) and 12 freshwater resident females (length: 27.9 ± 3.8 cm, range: 20.5–34.4 cm; mass: 220.5 ± 93.0 g, range 83–423 g), and crossed with sperm from 12 anadromous males (length: 40.4 ± 8.0 cm, range: 31.1–53.4 cm; mass: 771.3 ± 451.0 g, range 309–1539 g) and 12 freshwater resident males (length 26.0 ± 4.1 cm, range: 19.5–32.1 cm, mass: 167.0 ± 64.5 g, range: 76–271 g) on 9 November 2018. Each adult was used in two different crosses, one by partnering it with a resident *S. trutta* a nd the other with an anadromous *S. trutta*. The cross cohorts were raised separately in incubation trays with constant water flow until the start of exogenous feeding. Each family group was split into two groups, one incubated in ambient River Imsa water and the other in 2.7° warmer water (mean ± 1 S.D.: 4.4 ± 1.5 *vs*. 7.1 ± 0.6°C) to simulate the potential climate impact on embryogenesis in *c*. 2080 (Durtsche *et al*., 2080) (Figure 3).

The fertilized eggs were split from each crossing into four groups, two groups incubated at ambient River Imsa temperature and two groups incubated in warmer water until hatching. After hatching, the larvae were transferred to sixteen 60 l tanks (4 parental crossings × 2 embryonic temperatures × 2 replicates) and reared at ambient water conditions of the River Imsa and maintained at similar densities and fed on food pellets (Ewos, Cargill®, Norway) to satiation. On 22 February and 9 April 2018, the "warm" and "cold" *S. trutta* were moved into rearing tanks, respectively, and the next day, exogenous feeding was initiated. From 10 April 2018 onwards, all *S. trutta* were maintained at the ambient temperature conditions of the River Imsa.

By incubating eggs over winter at two temperatures, ambient River Imsa winter temperature and 2.7°C warmer than ambient temperature, the authors tested for the effects of embryonic temperature on the growth of juveniles. Growth was tested at two temperatures (±S.D.), 14.9 ± 2.2°C and 18.3 ± 1.5°C measured once every hour

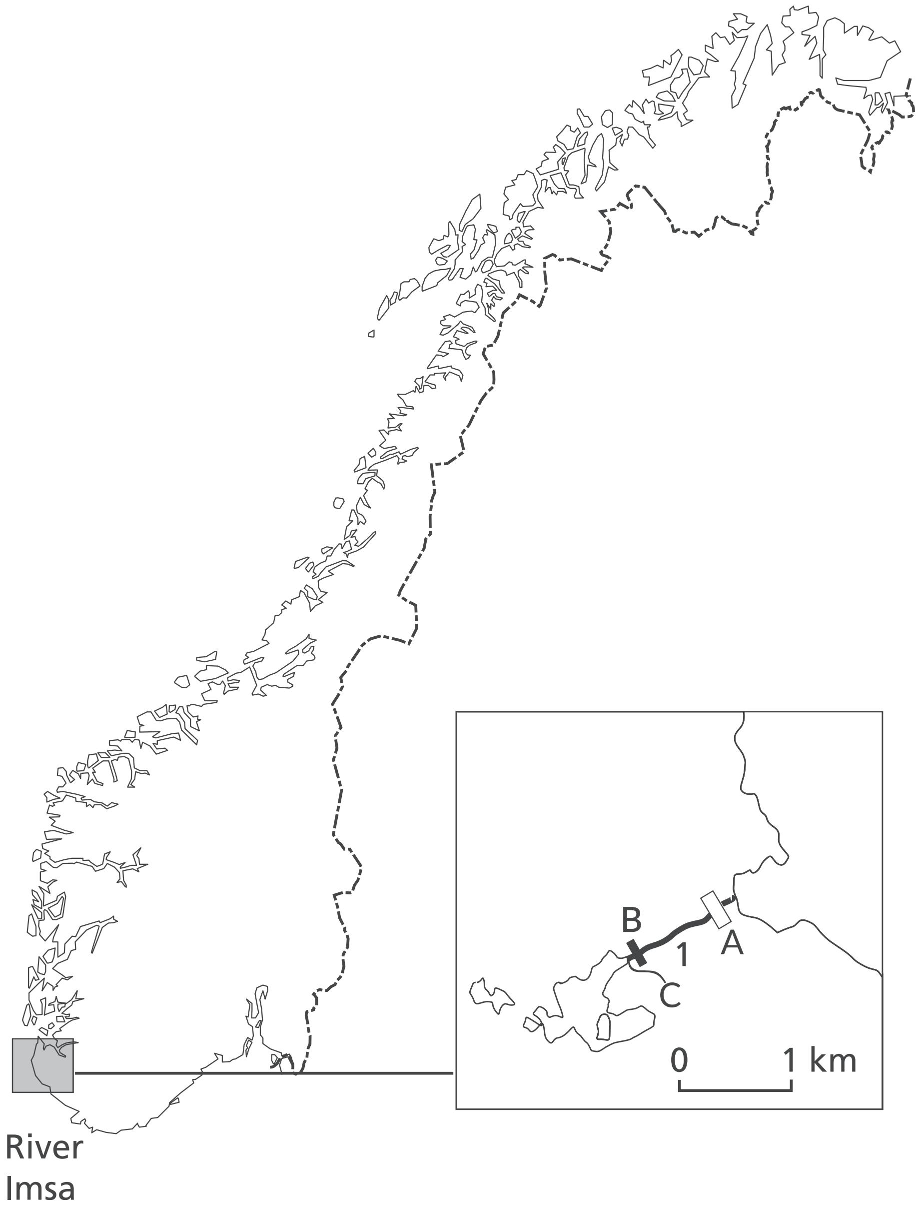

**FIGURE 1** The River Imsa (1) in southwestern Norway where the anadromous *Salmo trutta* spawned. (A) The location of the fish trap where the anadromous fish were sampled. (B) The location of the upstream impassable waterfall, built between 1993 and 1995. (C) The brook, Fossbekk, where the resident fish spawned

(here called 15°C and 18°C), and replicated. The authors used 10 fish in each replicate (4 parental crossings × 2 embryonic temperatures × 2 temperatures × 2 replicates × 10 fish per trial = 320 fish in total). All fish were individually colour marked with Alcian blue, and replaced fish was not used in the growth calculations. Somatic growth was measured for 22 days from 27 August, when the fish were *c*. 8 g, to 17 September 2019.

After the start of exogenous feeding and until the start of the growth performance measurements, the fish were reared at the natural River Imsa temperatures (range 6.5–20.0°C). The fish were kept in tanks that were 45 × 45 cm and 60 cm deep. The tanks had a water level of 30 cm, water flow of 2 l min$^{-1}$ and surface light intensity of *c*. 70 lx during daytime (12 h light:12 h dark cycle). No fish was used more than once. The setup was designed so that two replicates of each incubation temperature were run simultaneously for each experimental temperature. Ten individually marked fish were used in each tank. Experimental units were randomly distributed within each temperature regime to avoid systematic tank effects. Oxygen saturation was always close to 100% during the experiment. The fish were fed *ad libitum* with granulated fish food administered from automatic feeders. Each fish was weighted (precision: ±0.01 g) at the beginning and at the end of the experiment after the fish had been starved for *c*. 24 h. Fish that died during the experiment (46 of 320) were replaced with similar-sized fish to maintain densities at 10 fish per tank, but the replacement fish were not included in the results. The setup of the growth performance experiments followed a well-documented and standardized protocol (Finstad & Jonsson, 2012; Forseth *et al*., 2009; Jonsson *et al*., 2001; Larsson *et al*., 2005). After the growth experiment was finished, the fish were killed and dry masses were determined. The fish were dried for 48 h at 55°C and weighed to the nearest 0.0001 g. The authors tested for the effects of parental type and incubation temperature treatment on growth rate using standardized growth ($\Omega$) for 1 g fish (Ostrovsky, 1995):

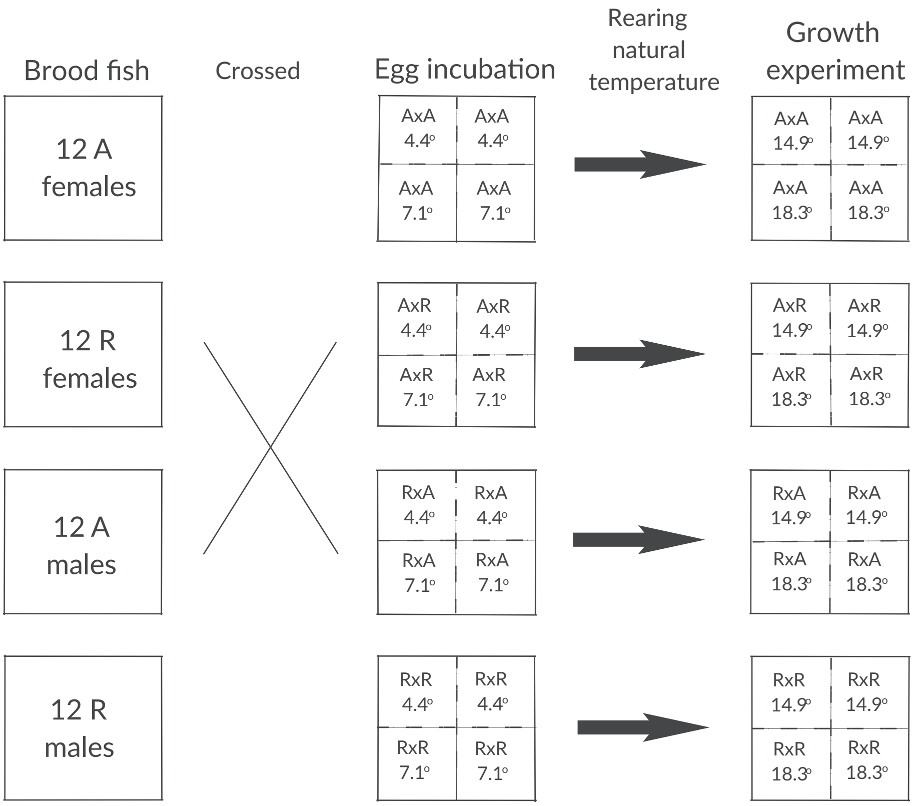

**FIGURE 2** The experimental design: 12 anadromous (A) and 12 freshwater resident (R) *Salmo trutta* of each sex were crossed. Parallel groups of the fertilized eggs from each cross were incubated at two temperatures (±S.D.), either 4.4 ± 1.5°C or 7.1 ± 0.6°C. After hatching, parallel groups were reared at natural River Imsa temperature until the commencement of the growth experiment when parallels of the 16 reared groups were tested at two temperatures (±S.D.), either 14.9 ± 2.2°C or 18.3 ± 1.5°C 14.9. Ten *S. trutta* were used in each group tested, 320 fish altogether

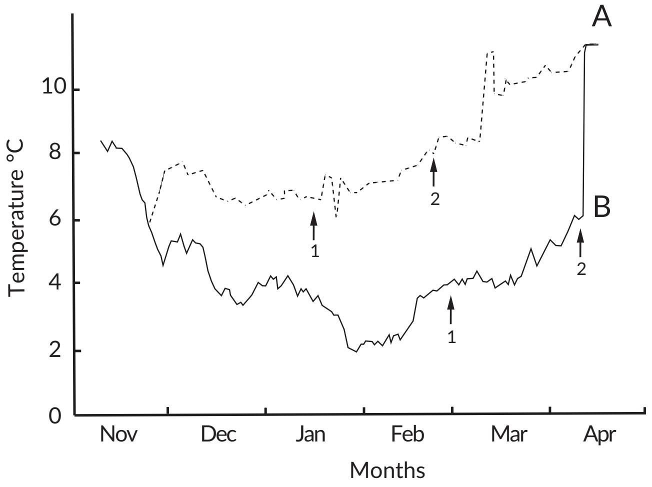

**FIGURE 3** Temperature from fertilization on 9 November 2018 to hatching (1) and start of feeding (2) of *Salmo trutta* eggs incubated in cold (solid line) and hot (broken line) water

$$\Omega = \left(M_t^{\,b} - M_0^{\,b}\right)(100/bt), \tag{1}$$

where $M_t$ and $M_0$ are the respective body masses (g) at the end and beginning of the experiment, $t$ is the duration of the experiment in days and $b$ is the allometric mass exponent for the relationship between specific growth rate and body mass, which was estimated at 0.308 (Elliott *et al*., 1995). $\Omega$ effectively eliminates the effects on growth rates of differences in initial body sizes (Finstad & Jonsson, 2012; Sigourney *et al*., 2008). At the start of the experiment, the respective mean lengths and wet masses (±S.D.) of the offspring crosses of anadromous males × anadrome females were 84.0 ± 14.7 mm and 7.6 ± 4.3 g, anadromous males × resident females were 83.7 ± 13.7 mm and 7.2 ± 3.4 g, resident males × anadromous females were 84.6 ± 16.9 mm and 7.9 ± 4.6 g, and resident males × resident females 84.2 ± 16.2 mm and 7.9 ± 3.1 g. Differences in growth were tested by ANOVA using IBM SPSS Statistics Version 27.

## 2.1 | Ethics statement

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.

## 3 | RESULTS

Warming of eggs during incubation had no significant effect on later growth for any of the offspring groups when tested at either 14.9°C or 18.3°C (Figure 4). Furthermore, fish grew better at 14.9°C than 18.3°C ($F_{1,215)}$ = 7.86, $P$ = 0.006), but not for the individual crosses tested at each of the two temperatures (all $P > 0.05$). Nonetheless, offspring of anadromous *S. trutta* grew better than those of freshwater resident *S. trutta* when fish from the two incubation temperatures were pooled (14.9°C: $F_{1,56}$ = 5.16, $P$ = 0.03; 18.3°C: $F_{1,57}$ = 4.92,

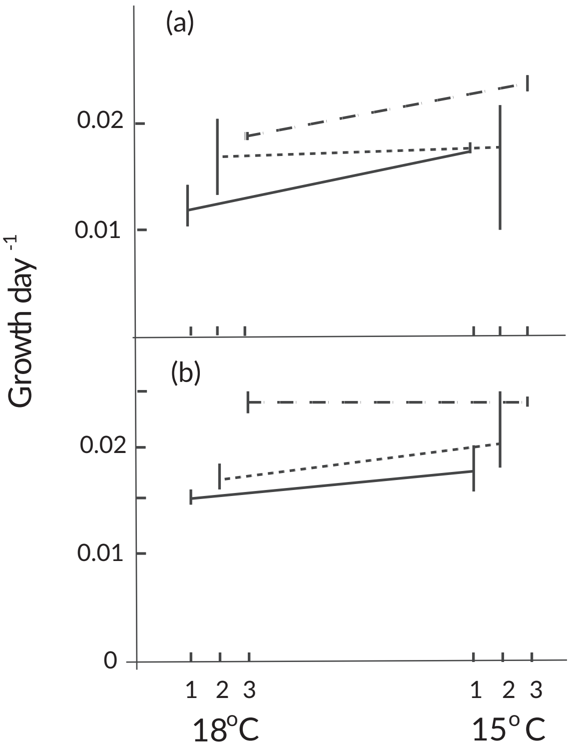

**FIGURE 4** Mean growth per day (Ω, Equation 1, ±S.D.) at 18.3°C and 14.9°C of juvenile age 0 offspring of (a) 7.1°C and (b) 4.4°C incubated freshwater resident *Salmo trutta* (1, solid line) and anadromous (3, broken line), and hybrids between freshwater resident and anadromous (2, dotted line) *S. trutta* of the River Imsa, Norway

$P$ = 0.03). Similarly, anadromous *S. trutta* offspring grew better than the hybrid groups ($F_{1,158}$ = 6.16, $P$ = 0.01), whereas offspring of freshwater resident and the hybrids grew at similar rates ($F_{2,158}$ = 0.8, $P$ = 0.5). In addition, the two hybrid groups grew similarly ($F_{1,101}$ = 0.18, $P$ = 0.7) and these were therefore treated together (Figure 4).

## 4 | DISCUSSION

The results of this study lend support to the authors' first hypothesis that juvenile offspring of anadromous *S. trutta* grew better than those of freshwater resident *S. trutta*. As there is a close relationship between feeding rate and growth rate (Jonsson *et al*., 2001), this result indicates that offspring of anadromous *S. trutta* fed at a highest rate when food was offered *ad libitum*, and therefore grew relatively fast.

Jonsson (1985) reported that the largest juvenile *S. trutta* at age 2 years in the River Voss, Norway, smolted and became anadromous, whereas smaller ones at the same age matured sexually and became freshwater resident or smolted 1 year later. A similar finding was reported for sockeye salmon *Oncorhynchus nerka* by Ricker (1938). Nonetheless, these earlier studies were performed under natural conditions, which meant that different habitat and feeding opportunities might influence the result (Jonsson, 1989). But in the present experiment, offspring of anadromous parents grew on average faster than offspring of freshwater resident parent from the same river when reared under similar experimental conditions. This might have been because the anadromous fish had largest eggs giving their offspring a size advantage early in life (Jonsson & Jonsson, 1999). Nonetheless, the size of the fish in the various groups was similar to the size they were at the commencement of the experiment, indicating no early growth advantage of anadromous offspring. Furthermore, anadromous offspring grew better than hybrid offspring from anadromous females indicating that the better growth of anadromous offspring was because of the differences in genetic expression between the test groups, and not being a maternal effect provided by nutrients or other matter in the eggs.

Is there any evidence that environmental growth-constraints initiate migration in *S. trutta*? According to Olsson *et al*. (2006) and Wysujack *et al*. (2008), low food availability and poor growth increase the proportion of migratory *S. trutta* in a population. Furthermore, experimentally Davidsen *et al*. (2014), Jones *et al*. (2015) and Archer *et al*. (2019) exhibited that restricted food rations induced smolting and migration in *S. trutta*, and the influence of low feeding appeared most effective in winter and spring. Apparently, these findings appear to contradict that of Forseth *et al*. (1999). These latter authors reported that the largest, most fast-growing individuals in a cohort migrated first. They claimed, nonetheless, that this probably was because future growth of these fish was more energy restricted than more slow growing individuals in the cohort. Fast-growing fish have high maintenance costs, and before migration, these authors showed that only a very small proportion of their energy was allotted to growth. Similarly, Morinville and Rasmussen (2003) exhibited that migrant *S. fontinalis* had lower growth efficiencies (ratio of growth to consumption) than residents, indicating that migrants have higher metabolic costs. Therefore, they concluded that their results agreed with the notion that there is a link between metabolic costs and the adopted life-history strategy. Thus, energy restrictions, especially in winter and spring, appear to induce smolting and migration in *S. trutta*, and that these restrictions are first experienced by the most fast-growing individuals in a food-restricted population (Jonsson & Jonsson, 1993).

There is also support for the fact that anadromy in *S. trutta* is partly genetic. Experimental evidence reported by Jonsson (1982) exhibited that offspring of anadromous *S. trutta* migrated to sea independent of place of release, and offspring of freshwater resident *S. trutta* from the same river tended to stay resident even when released in a lake supporting anadromous *S. trutta*. Furthermore, some earlier studies have shown genetic differences between the two life-history forms (Lemopoulos *et al*., 2018; Skaala & Nævdal, 1989). These findings support Ferguson *et al*. (2019) who, based on studies from various partly anadromous salmonids, estimated that *c*. 50% of the variability in life-history traits between anadromous and non-anadromous *S. trutta* is because of genetic variance.

In the River Imsa, anadromous and freshwater resident *S. trutta* probably originated from anadromous *S. trutta* entering the river after the last glaciation period when the sea level stood higher.

Nonetheless, the present anadromous and resident *S. trutta* have been geographically isolated for at least 25 years when an artificial waterfall was built in the River Imsa, stopping anadromous *S. trutta* from migrating more than 850 m upstream, whereas the resident fish spawn in a tributary *c*. 1000 m above the river outlet. This geographical isolation during at least five generations may have influenced the genetics of the test groups inducing a difference in genetic expression whether this is caused by allelic differences or epigenetically induced (*cf*. Baerwald *et al*., 2016; Jonsson & Sandlund, 1979; Sandlund & Jonsson, 2016). It is unknown to what extent anadromous trout spawned in the Fossbekk before the waterfall was built.

There was no support for the authors' second hypothesis that warm-incubated and cold-incubated *S. trutta* juveniles grew differently. This is further supported by the fact that the mass–length relationship between cold and warm incubated *S. trutta* is similar although the metabolic rates and aerobic scopes were different (Durtsche *et al*., 2021). This result differs from that of Finstad and Jonsson (2012) which investigated the growth of juvenile *S. salar* using a similar experimental protocol. There was no apparent reason for this difference between these two closely related species. Nonetheless, even populations of the same species may differ in developmental response to early environmental cues, as shown from the populations of the common frog *Rana temporaria*. Burraco *et al*. (2017) reported that the populations of *R. temporaria* from temporary pools had a higher degree of developmental plasticity than tadpoles of the same species from permanent pools. In contrast, juvenile *S. salar* incubated as eggs in warm water (7°C) were slimmer than conspecifics incubated in cold water (3°C) (Greenberg *et al*., 2021), showing another difference between *S. trutta* and *S. salar*.

The ecological significance of the present results is that offspring of anadromous *S. trutta* in a river grow differently from offspring of freshwater resident conspecifics, or crosses between the two. This may imply that offspring of anadromous *S. trutta* have increased probability to smolt and migrate to sea because of their greater size at the same age (Forseth *et al*., 1999; Jonsson, 1985). Given similar feeding opportunities, water temperature during egg incubation in winter should not have any effect on future growth of the juvenile *S. trutta*.

## ACKNOWLEDGEMENTS

The authors thank the staff at the NINA Research Station Ims for their support in preparing the crosses, housing and caring for the fish. The authors received financial support from the Norwegian Research Council, Klimaforsk, project no. 268005.

## AUTHOR CONTRIBUTIONS

Both the authors contributed to the planning, growth measurements, statistical testing and writing of the manuscript.

## ORCID

*Bror Jonsson* https://orcid.org/0000-0002-0614-6233

## REFERENCES

Alberts, A. C., Perry, A. M., Lemm, J. M., & Phillips, J. A. (1997). Effects of incubation temperature and water potential on growth and thermoregulatory behavior of hatching Cuban rock iguanas (*Cyclura nubile*). *Copeia*, *1997*, 766–776.

Archer, L. C., Hutton, S. A., Harman, L., O'Grady, M. N., Kerry, J. P., Poole, W. R., … Reid, T. E. (2019). The interplay between extrinsic and intrinsic factors in determining migration decisions in brown trout (*Salmo trutta*): An experimental study. *Frontiers in Ecology and Evolution*, *7*, 1–18. https://doi.org/10.3389/fevo2019.00222.

Baerwald, M. R., Meek, M. H., Stephens, M. R., Nagarajan, R. P., Goodbla, A. M., Tomalty, K. M. H., … Nichols, K. M. (2016). Migration-related phenotypic divergence is associated with epigenetic modifications in rainbow trout. *Molecular Ecology*, *25*, 1785–1800.

Booth, D. T. (2006). Influence of incubation temperature on hatchling phenotype in reptiles. *Physiological and Biochemical Zoology*, *79*, 274–281.

Burgerhout, E., Mommens, M., Johansen, H., Aunsmo, A., Santi, N., & Andersen, Ø. (2017). Genetic background and embryonic temperature affect DNA methylation and expression of *myogenin* and muscle development in Atlantic salmon (*Salmo salar*). *PLoS One*, *12*, e0179918.

Burraco, P., Valdés, A. E., Johansson, F., & Gomez-Mestre, I. (2017). Physiological mechanisms of adaptive developmental plasticity in *Rana temporaria* Island populations. *BMC Evolutionary Biology*, *17*(1), 164.

Carballo, C., Firmino, J., Anjos, L., Santos, S., Power, D. M., & Manchad, M. (2018). Short- and long-term effects on growth and expression patterns in response to incubation temperatures in Senegal sole. *Aquaculture*, *495*, 222–231.

Cucherousset, J., Ombredane, D., Charles, K., Marchand, F., & Baglinière, J.-L. (2005). A continuum of life history tactics in a brown trout (*Salmo trutta*) population. *Canadian Journal of Fisheries and Aquatic Sciences*, *62*, 1600–1610.

Davidsen, J. G., Daverdin, M., Sjursen, A. D., Rønning, L., Arnekleiv, J. V., & Koksik, J. I. (2014). Does reduced feeding prior to release improve the marine migration of hatchery brown trout *Salmo trutta* smolts? *Journal of Fish Biology*, *85*, 1992–2002.

Deeming, D. C. (2004). Post-hatching phenotypic effects of incubation in reptiles. In D. C. Deeming (Ed.), *Reptilian incubation environment, evolution and behaviour* (pp. 229–251). Nottingham, UK: Nottingham University Press.

Durtsche, R. D., Jonsson, B., & Greenberg, L. A. (2021). Thermal conditions during embryogenesis influence metabolic rates of juvenile brown trout (*Salmo trutta*). *Ecosphere*. *12*(2), e03374. https://doi.org/10.1002/ecs2.3374.

Elliott, J. M. (1994). *Quantitative ecology and the brown trout*. Oxford Series in Ecology and Evolution, (1st ed., pp. 1–286). Oxford, UK: Oxford University Press.

Elliott, J. M., Hurley, M. A., & Fryer, R. J. (1995). A new, improved growth model for brown trout, *Salmo trutta*. *Functional Ecology*, *9*, 290–298.

Ferguson, A., Reed, T., Cross, T., McGinnity, P., & Prodöhl, P. (2019). Anadromy, potadromy and residency in brown trout *Salmo trutta*: The role of genes and the environment. *Journal of Fish Biology*, *95*, 692–718.

Finstad, A. G., & Jonsson, B. (2012). Effect of incubation temperature on growth performance in Atlantic salmon. *Marine Ecology Progress Series*, *454*, 75–82.

Forseth, T., & Jonsson, B. (1994). The growth and food ration of piscivorous brown trout (*Salmo trutta*). *Functional Ecology*, *8*, 171–177.

Forseth, T., Larsson, S., Jensen, A. J., Jonsson, B., Näslund, I., & Berglund, I. (2009). Thermal performance of juvenile brown trout, *Salmo trutta* L.: No support for thermal adaptation hypotheses. *Journal of Fish Biology*, *74*, 133–149.

Forseth, T., Næsje, T. F., Jonsson, B., & Hårsaker, K. (1999). Juvenile migration in brown trout: A consequence of energetic state. *Journal of Animal Ecology*, *68*, 783–793.

Hare, K. M., Longson, C. G., Pledger, S., & Daugherty, C. H. (2004). Size, growth, and survival are reduced at cool incubation temperatures in the temperate lizard *Oligostoma suteri*. *Copeia*, *2004*, 383–390.

Holt, R. E., & Jørgensen, C. (2015). Climate change in fish: Effects of respiratory constraints on optimal life history and behaviour. *Biological Letters*, *11*, 20141032.

Hughes, M. R., Hooker, O. E., Van Leeuwen, T. E., Kettle-White, A., Thorne, A., Prodöhl, P., & Adams, C. E. (2019). Alternative routes to piscivory: Contrasting growth trajectories in brown trout (*Salmo trutta*) ecotypes exhibiting contrasting life history strategies. *Ecology of Freshwater Fish*, *28*, 4–10.

Greenberg, L. A., Jonsson, B., Norrgård, J., Erlandsson, A., & Bergman, E. (2021). Effects of temperature during embryogenesis on body and fin shape in juvenile Atlantic salmon, *Salmo salar*. *Canadian Journal of Zoology*.

Jones, D., Bergman, E., & Greenberg, L. (2015). Food availability in spring affects smolting in brown trout (*Salmo trutta*). *Canadian Journal of Fisheries and Aquatic Sciences*, *72*, 1694–1699.

Jonsson, B. (1982). Diadromous and resident trout *Salmo trutta*: Is their difference due to genetics? *Oikos*, *38*, 297–300.

Jonsson, B. (1985). Life history patterns of freshwater resident and sea-run migrant brown trout in Norway. *Transactions of the American Fisheries Society*, *114*, 182–194.

Jonsson, B. (1989). Life history and habitat use of Norwegian brown trout (*Salmo trutta*). *Freshwater Biology*, *21*, 71–86.

Jonsson, B., & Jonsson, N. (1993). Partial migration: Niche shift versus sexual maturation in fishes. *Reviews in Fish Biology and Fisheries*, *3*, 348–365.

Jonsson, B., & Jonsson, N. (2009). A review of the likely effects of climate change on anadromous Atlantic salmon *Salmo salar* and brown trout *Salmo trutta*, with particular reference to water temperature and flow. *Journal of Fish Biology*, *75*, 2381–2447.

Jonsson, B., & Jonsson, N. (2017). Fecundity and water flow influence the dynamics of Atlantic salmon. *Ecology of Freshwater Fish*, *26*, 497–502.

Jonsson, B., & Jonsson, N. (2019). Phenotypic plasticity and epigenetics of fish: Embryo temperature affects later developing traits. *Aquatic Biology*, *28*, 21–32.

Jonsson, B., & Sandlund, O. T. (1979). Environmental factors and life histories of river stocks of brown trout (*Salmo trutta* m. *fario*) in Søre Osa river system, Norway. *Environmental Biology of Fishes*, *4*, 43–54.

Jonsson, B., Forseth, T., Jensen, A. J., & Næsje, T. F. (2001). Thermal performance in juvenile Atlantic salmon, *Salmo salar* L. *Functional Ecology*, *15*, 701–711.

Jonsson, B., Jonsson, N., & Finstad, A. G. (2013). Effects of temperature and food quality on age at maturity of ectotherms: An experimental test of Atlantic salmon. *Journal of Animal Ecology*, *82*, 201–210.

Jonsson, B., Jonsson, N., & Finstad, A. G. (2014). Linking embryonic temperature with adult reproductive investment. *Marine Ecology Progress Series*, *515*, 217–226.

Jonsson, B., Jonsson, N., & Gresswell, R. E. (2019). Life history diversity. In J. L. Kershner, J. E. Williams, R. E. Gresswell, & J. Lobon-Cervia (Eds.), *Trout and char of the world* (pp. 141–191). The American Fisheries Society: Bethesda, MD.

Jonsson, N., & Jonsson, B. (1999). Trade-off between egg size and numbers in brown trout. *Journal of Fish Biology*, *55*, 767–783.

Kallio-Nyberg, I., Jutila, E., Koljonen, M. L., Koskiniemi, J., & Saloniemi, I. (2010). Can the lost migratory *Salmo trutta* stocks be compensated with resident trout stocks in coastal rivers. *Fisheries Research*, *102*, 69–79.

Kobayashi, S., Aokura, N., Fujimoto, R., Mori, K., Kumazawa, Y., Ando, Y., … Saito, T. (2018). Incubation and water temperature influence the performances of loggerhead sea turtle hatchlings during the dispersal phase. *Scientific Reports*, *8*, 11911.

Larsson, S., Forseth, T., Berglund, I., Jensen, A. J., Näslund, I., Elliott, J. M., & Jonsson, B. (2005). Thermal adaptation of Arctic charr: Experimental studies of growth in eleven charr populations from Sweden, Norway and Britain. *Freshwater Biology*, *50*, 353–368.

Laver, R. J., Purwandana, D., Ariefiandy, A., Imansyah, J., Forsyth, D., Ciofi, C., & Jessop, T. S. (2012). Life history and spatial determinants of somatic growth dynamics in komodo dragon populations. *PLoS One*, *7*, e45398.

Lemopoulos, A., Uusi-Heikkilä, S., Huusko, A., Vasemägi, A., & Vainikka, A. (2018). Comparison of migratory and resident populations of brown trout reveals candidate genes for migration tendency. *Genome Biology and Evolution*, *10*, 1493–1503.

Lemopoulos, A., Uusi-Heikkilä, S., Hyvärinen, P., Alioravainen, N., Prokkola, J. M., Elvidge, C. K., … Vainikka, A. (2019). Migration experiment reveals candidate genes for migration tendency in brown trout. *G3, Genes, Genomes, Genetics*, *9*, 2887–2896.

McKinney, G. J., Hale, M. C., Goetz, G., Gribskov, M., Thrower, F. P., & Nichols, K. M. (2015). Ontogenetic changes in embryonic and brain gene expression in progeny produced from migratory and resident *Oncorhynchus mykiss*. *Molecular Ecology*, *24*, 1792–1809.

Morinville, G. R., & Rasmussen, J. B. (2003). Early juvenile bioenergetic differences between anadromous and resident brook trout (*Salvelinus fontinalis*). *Canadian Journal of Fisheries and Aquatic Sciences*, *60*, 401–410.

Nevoux, M., Finstad, B., Davidsen, J. G., Finlay, R., Josset, Q., Poole, R., … Jonsson, B. (2019). Environmental influences of life history strategies in partial anadromous brown trout (*Salmo trutta*, Salmonidae). *Fish and Fisheries*, *20*, 1051–1082.

Olsson, I. C., Greenberg, L., Bergman, E., & Wysujack, K. (2006). Environmentally induced migration: Importance of food. *Ecology Letters*, *9*, 645–651.

Ostrovsky, I. (1995). The parabolic pattern of animal growth: Determination of equation parameters and their temperature dependencies. *Freshwater Biology*, *33*, 357–371.

Pörtner, H. O. (2010). Oxygen-and-capacity-limitation of thermal tolerance: A matrix for integrating climate-related stressor effects in marine ecosystems. *Journal of Experimental Biology*, *213*, 881–893.

Ricker, W. E. (1938). Residual and kokanee salmon in Cultus Lake. *Journal of Fisheries Research Board of Canada*, *4*, 192–218.

Sandlund, O. T., & Jonsson, B. (2016). Life history plasticity: Migration ceased in response to environmental change. *Ecology of Freshwater Fish*, *25*, 225–233.

Sigourney, D. B., Letcher, B. H., Obedzinski, M., & Cunjak, R. A. (2008). Size-independent growth in fishes: Patterns, models and metrics. *Journal of Fish Biology*, *72*, 2435–2455.

Siviter, H., Deeming, D. C., & Wilkinson, A. (2019). Egg incubation temperature influences the growth and foraging behaviour of juvenile lizards. *Behavioural Processes*, *165*, 9–13.

Skaala, Ø., & Nævdal, G. (1989). Genetic differentiation between freshwater resident and anadromous brown trout, *Salmo trutta*, within watercourses. *Journal of Fish Biology*, *34*, 597–605.

Wootton, R. J. (1999). *Ecology of teleost fishes*. Fish and Fisheries Series, (1, 2nd ed.). London, UK: Chapman and Hall.

Wysujack, K., Greenberg, L., Bergman, E., & Olsson, I. C. (2008). The role of the environment in partial migration: Food availability affects the adoption of a migratory tactic in brown trout. *Ecology of Freshwater Fish*, *18*, 52–59.

Zuo, W., Moses, M. E., West, G. B., Hou, C., & Brown, J. H. (2012). A general model for effects of temperature on ectotherm ontogenetic growth and development. *Proceedings of the Royal Society B*, *279*, 1840–1846.

**How to cite this article:** Jonsson B, Jonsson N. Differences in growth between offspring of anadromous and freshwater brown trout *Salmo trutta*. *J Fish Biol*. 2021;1–7. https://doi.org/10.1111/jfb.14693