

**Egg incubation temperature affects the timing of the Atlantic salmon *Salmo salar*  
homing migration**

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**ABSTRACT**

Here, we show that adult Atlantic salmon *Salmo salar* returned about 2 weeks later from the feeding areas in the North Atlantic Ocean to the Norwegian coast, through a phenotypically plastic mechanism, when they developed as embryos in *c.* 3°C warmer water than the regular incubation temperature. This finding has relevance to changes in migration timing caused by climate change and for cultivation and release of *S. salar*.

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## KEYWORDS

climate change, embryogenesis, epigenetics, migration, phenotypic plasticity, River Imsa

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Life begins when the egg cell is fertilized; then, during embryogenesis, the cell develops into millions of cells that form tissues and organs that prepare the individual's responses to future experiences (Bateson *et al.*, 2004; Dowling *et al.*, 2007; Fox *et al.*, 2010). The development is governed by the genotype that is open for epigenetic modifications by the early environment and temperature, in particular, has epigenetic effects (Bizuayehu *et al.*, 2015; Burgerhout *et al.*, 2017). Phenotypically plastic modifications in ecologically relevant traits can be generated through a suite of epigenetic mechanisms at the molecular level, with growing interest in ecology and behavioural sciences (Bossdorf *et al.*, 2008; Crews, 2008; Verhoeven *et al.*, 2016).

Phenotypes emerge from complex interactions between genes and environment during development (Jonsson & Jonsson, 2014). Temperature has a pervasive effect on growth and developmental rate, and warmer temperature during embryogenesis shorten the egg incubation time. Without any apparent change in genetic structure, higher temperature during larval development can affect later growth of juvenile fish (Korwin-Kossakowski, 2008; Finstad & Jonsson, 2012; Scott & Johnston, 2012), as well as later reproductive allocations of adults (Jonsson & Jonsson, 2016; Jonsson *et al.*, 2014). Based on a study of the domestic chicken *Gallus gallus domesticus*, Bertin *et al.* (2018) reported that temperature during embryogenesis can influence later behaviours of these birds.

Anadromous Atlantic salmon *Salmo salar* L. 1759 is an ectothermic fish that in the wild migrate between fresh and salt waters. They spawn in rivers in the autumn, the embryos develop within the eggshell during winter and they hatch in the subsequent spring. The young grow and develop in fresh water until they transform (smolt) and move into the ocean for feeding. They may migrate 1000 km or more before they start the return-migration back to the home river for reproduction, 1–3 years after they left the natal stream. When migrating to sea, the smolts are between 12 and 25 cm long and 1–5 years old (Jonsson *et al.*, 2016).

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*Salmo salar* are also commercially produced in hatcheries and some of the young are released to the wild for conservation purposes or to increase fishing opportunities (Jonsson & Jonsson, 2011).

There are inherited differences among salmonid populations in the timing of the return migration from the ocean (Hansen & Jonsson, 1991; Kovach *et al.*, 2012), possibly genetically adapted to the local conditions influencing the fitness of the adults and their offspring. Climate change is directional and often rapid (Peters *et al.*, 2012). Thus, a phenotypically plastic response to the climate experienced by the young in the river may be an effective way to adjust the timing of the return migration in a changing climate. It is known that *S. salar* spawn later in rivers that are warm during winter than in those that are colder (Heggberget, 1988). Possibly, *S. salar* from winter warm rivers may feed longer in the ocean before they start the return migration for spawning in fresh water and may thus be pre-adapted to the thermal climate they experience during the embryogenesis.

Here, we investigated the effects on water temperature during the embryogenesis on the time of the return migration in *S. salar*. We hypothesized that *S. salar* reared in relatively warm water during the embryogenesis prolong the stay in the North Atlantic Ocean before migrating back for spawning. In the experiment, Norwegian *S. salar* reared at the Norwegian Institute for Nature Research (NINA) research station, Ims, near Stavanger, south-western Norway (59° N; 6° E), were used. The research station is situated at the mouth of the River Imsa. The fish originated from three different populations, the Rivers Alta (69° N, annual mean flow 101 m<sup>3</sup> s<sup>-1</sup>), Imsa (59° N, 5 m<sup>3</sup> s<sup>-1</sup>) and Lone (60° N, 1 m<sup>3</sup> s<sup>-1</sup>) and more than five individuals of each sex and strain were used as brood stock. The eggs were incubated in natural (cold) or heated (warm) River Imsa water (Table 1).

For the Alta (1 year-old smolts in 1989) and Lone (1 year-old smolts in 1993) *S. salar*, the groups of fertilized eggs were divided in two similarly large parts and incubated at

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two different temperatures (Table 1). For the two other groups compared, Alta (smolts in 1990) and Imsa (smolts in 1993), brood stocks from two consecutive years were used giving 1 year-old and 2 year old smolts, respectively. Alta (1990) consisted of cold-incubated fish from the Alta (1989), smolting at age 2 years and compared with 1 year-old warm-incubated fish. For the Imsa (1993), the parental fish of the cold and warm-water incubated groups were caught in the river in the autumns 1990 and 1991, respectively. The heating started in the autumn, within two weeks of the egg fertilization, when the natural water temperature decreased to *c.* 5°C and the heating was terminated in spring when the natural temperature started to increase. The warm egg incubation temperatures were on average 2.5–3.6° C warmer than the natural, cold river temperatures (Table 1).

One month prior to release, the pre-smolts were anaesthetized with benzocaine (30 mg l<sup>-1</sup>), measured (total length,  $L_T$ ) and tagged with numbered Carlin tags (Carlin, 1955) more than 2 weeks before release. The different smolt groups were released on the same dates, 7 May in 1989 and 1990 and 4 May in 1993, below the Wolf and box traps in the River Imsa situated approximately 150 m above the outlet and they migrated to sea (illustrated in Jonsson & Jonsson, 2011, figure 6.5). The respective smolt groups consisted of between 1908 and 1998 individuals. The fish were recaptured as maturing adults in the sea-fishery on the coast as they returned, one year after being released (one-sea-winter, 1SW) and time of recapture was used as estimate of time of return (*cf.* Hansen & Jonsson, 1991). On their return, *S. salar* hesitate at the mouth of the River Imsa until the water flow increases with autumn rain (Jonsson, N. *et al.*, 1990; Jonsson *et al.*, 2007). These fish were not included in the analysis. Furthermore, 27 (7.7% of all 353 recaptures) came back as two-sea-winter (2SW) *S. salar*. These were not included in the analysis, because 2SW *S. salar* return earlier in the season than 1SW *S. salar* (*cf.* Jonsson, N. *et al.*, 1990) and the proportion of 2SW *S. salar* varied among groups. Differences in mean  $L_T$  time of return were tested by *t*-tests and the overall

differences were tested by ANOVA. Whether egg incubation temperature influenced recapture north or south-east of the River Imsa, was tested by a  $\chi^2$ -test. Furthermore, the difference in spatial distribution of the recaptures was tested by a R  $\times$  C-test (Snedecor & Cochran, 1973). The distance from the River Imsa to the recaptures were grouped in five consecutive 100 km long groups (up to 500 km from the river). *Salmo salar* recaptured farther away were grouped in a 6th distance category.

Smolts produced from eggs incubated in warm water were significantly longer than similar aged smolts from eggs incubated in cold water (Table 1). Two-year-olds incubated at the egg stage in cold water was longer at smolting than the corresponding 1 year-old warm-incubated smolts. In only two of the groups, did larger smolts give larger 1SW *S. salar* (Table 1).

Adult *S. salar* were recaptured along the Norwegian coast within 1500 km from the River Imsa. More of the recaptures of the warm incubated *S. salar* tended to be located south of the River Imsa than the cold incubated groups, but the difference was not significant ( $\chi^2 = 1.59$ , 1 d.f.,  $P > 0.05$ ). Furthermore, the distance from the River Imsa to the recaptured fish was similar ( $\chi^2 = 7.9$ , 5 d.f.,  $P > 0.05$ ).

The warm-water incubated *S. salar* were recaptured significantly later than the respective cold-water-incubated groups, indicating that they fed longer at sea before they started the return migration (Figure 1). For all groups pooled, the difference was 12.3 days ( $F_{6,345} = 3.97$ ,  $P < 0.001$ ) and the differences in mean  $L_T$  of the sea-sojourn were also significant for all group pairs, except for the River Alta *S. salar* released in 1989 when the difference was not significant ( $P > 0.05$ ). The difference in duration of the sea-sojourn holds whether the cold-incubated fish were shorter or longer than the warm-incubated fish or released as 1 or 2 year-old smolts. Furthermore, there was no significant difference in time

from release to recapture between the two cold-incubated River Alta groups released in 1989 and 1990 and originating from the same parental crossing.

As hypothesized, our results indicate that maturing *S. salar*, kept as embryos in heated water, after release returned to the Norwegian coast later in the summer than corresponding *S. salar* incubated in colder water. This indication is strong, because the differences between the warm and cold groups hold independent of strain and whether the released smolts of the cold-water incubated groups were shorter or longer, similar aged or older than those from warmer-water incubated groups released the same year. On average, there was almost a two-week difference in duration of the sea-sojourn, which is significant when most of the fish return during a few weeks in summer.

It is well known that early experiences can affect salmonid behaviour. For instance, their homing ability requires that they learn the location of the home river when out-migrating to the ocean (Hasler & Wisby, 1951; Hansen *et al.*, 1993). It is also known that water temperature during the previous winter and early spring influences the time when the smolts leave the river in spring (Jonsson & Ruud-Hansen, 1985; Otero *et al.*, 2014). Similarly, the timing of the present return migration appears phenotypically plastic, depending on the temperature experienced by the embryos two or more years prior to the fish returned from the ocean. This plasticity appears general for *S. salar* and independent of population origin.

This appears to be the first record of such a variation in a behavioural decision of an adult ectotherm, caused by the ambient temperature during embryogenesis. However, effects of temperature during embryogenesis on later growth, life-history traits and locomotor behaviour have been reported (Shine & Olsson, 2003; Martell *et al.*, 2005; review in Jonsson & Jonsson, 2014). In these cases, temperature during early ontogeny drives the phenotypic plasticity and allows the organisms to cope better with conditions that they may experience

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later in life. In general, little is known about how temperature in early life may affect later behavioural decisions. This gap in knowledge is surprising, not the least because ectothermic animals are entirely dependent on their thermal climate.

Whether the different timing of the return migration of *S. salar* to the Norwegian coast is caused by the return of fish from different marine feeding-areas or by different innate responses to environmental cues, such as experienced temperature or photoperiod (*cf.* Mundy & Evenson, 2011), is unknown. From the distribution of the recaptures, it was not possible to conclude that the warm-incubated *S. salar* returned or fed farther south than the cold-incubated groups, as the slight difference in distribution of the recaptures was not significant.

The difference in timing of the recaptures may be associated with epigenetic modifications caused by the temperature that *S. salar* experience as developing embryos. It is known that the initiation of the homing migration in *S. salar* is linked to the onset of sexual maturation (Jonsson & Jonsson, 2011) and Morán and Pérez-Figueroa (2011) hypothesized that an environmentally induced methylation pattern of the genome, which alters its transcriptional capabilities (DNA-methylation), may cause early maturation. Furthermore, Morán *et al.* (2013) provided evidence that DNA-methylation was associated with seawater adaptation in brown trout *Salmo trutta* L. 1758. In addition, Baerwald *et al.* (2015) reported that DNA-methylation was associated with migration traits such as smolting in rainbow trout *Oncorhynchus mykiss* (Walbaum 1792) and recently, Saino *et al.* (2017) reported that migration phenology and breeding success are predicted by methylation of a photoperiodic gene in barn swallow *Hirundo rustica*. Thus, it appears reasonable to hypothesize that DNA-methylation or perhaps another epigenetic mechanism associated with the temperature during the embryogenesis, is responsible for the different timing of the return migration in *S. salar*, observed in the present study (*cf.* Roth, 2013).

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The present findings have implications for cultivation and management of *S. salar*. Increased temperature in hatcheries to accelerate the rate of embryogenesis, can influence several ecological traits including the timing of adult returns. It has been reported that hatchery salmon return later in the season than wild conspecifics and that their behaviours in the river differ (Jonsson, B. *et al.*, 1990; Økland *et al.*, 1995). Possibly, temperature during early development is responsible for at least some of these differences. This is at least partly supported by experiments with coho salmon *Oncorhynchus kisutch* (Walbaum 1792) (Le Luyer *et al.*, 2017). These authors compared genome-wide patterns of methylation and variation at the DNA level in hatchery-reared *O. kisutch* with those of their wild counterparts in two geographically distant rivers. They reported that the rearing environment explained a significant proportion of epigenetic variation. The differentially methylated regions showed enrichment for biological functions that may affect the capacity of hatchery-born smolts to migrate successfully in the ocean. Shared epigenetic variation between hatchery-reared *S. salar* provided evidence for parallel epigenetic modifications induced by hatchery rearing in the absence of genetic differentiation between hatchery and natural-origin fish for each river.

The present findings have implications relative to ongoing climate change. The temperature increase is expected to be strongest in winter when salmon eggs are incubated in the gravel bottoms of rivers and stimulate the fish to return later in the year. This adaptation improves the possibility of *S. salar* surviving in a warmer environment. Furthermore, for *S. salar* straying to another river, this phenotypic flexibility can adapt offspring quickly to new thermal environments. Fishery managers should be aware of this adaptation to the temperature experienced by the embryos in the river, as it affects when *S. salar* can be fished on the coast and in rivers.

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## REFERENCES

- Baerwald, M.R., Meek, M.H., Stephens, M.R., Nagarajan, R.P., Goodbla, A.M., Tomalty, K.M.H., Thorgaard, G.H., May, B. & Nichols, K.M. (2015). Migration-related phenotypic divergence is associated with epigenetic modifications in rainbow trout. *Molecular Ecology* **25**, 1785-1800. doi: 10.1111/mec.13231
- Bateson, P., Barker, D., Clutton-Brock, T., Deb, D., D'Udine, B., Foley, R.A., Gluckman, P., Godfrey, K., Kirkwood, T., Lahr, M.M., McNamara, J., Metcalfe, N.B., Monaghan, P., Spencer, H.G. & Sultan, S.E. (2004). Developmental plasticity and human health. *Nature* **430**, 419–421. doi:10.1038/nature02725
- Bertin, A., Calandreau, L., Meurisse, M., Georgelin, M., Palme, R., Lumineau, S., Houdelier, S., Darmaillacq, A.S., Dickel, L., Colson, V., Cornilleau, F., Rat, C., Delaveau, J. & Arnould, C. (2018). Incubation temperature affects the expression of young precocial birds' fear-related behaviours and neuroendocrine correlates. *Scientific Reports* **8**, Article number: 1857. doi:10.1038/s41598-018-20319-y
- Bizuayehu, T.T., Johansen, S.D., Puvanendran, V., Toften, H. & Babiak, I. (2015). Temperature during early development has long term effects on microRNA expression in Atlantic cod. *BMC Genomics* **16**, 305. Doi:10.1186/s12864-015-1503-7
- Bossdorf, O., Richards, C.L. & Pigliucci, M. (2008). Epigenetics for ecologists. *Ecology Letters* **11**, 106-115. doi:10.1111/j.1461-0248.2007.01130.x

This article is protected by copyright. All rights reserved.

Burgerhout, E., Mommens, M., Johnsen, 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(6): e0179918. doi: 10.1371/journal.pone.0179918

Carlin B. (1955). Tagging of salmon smolts in the River Lagan. *Report of the Institute of Freshwater Research Drottningholm* **36**, 57-74.

Crews, D. (2008). Epigenetics and its implication for behavioral neuroendocrinology. *Front Neuroendocrinology* **29**, 344-357. doi:10.1016/j.yfrne.2008.01.003

Dowling, D.K., Friberg, U., Hailer, F. & Arnqvist, G. (2007). Intergenomic epistasis for fitness: within-population interactions between cytoplasmic and nuclear genes in *Drosophila melanogaster*. *Genetics* **175**, 235–244. Doi:10.1534/genetics.105.052050

Finstad, A.G. & Jonsson, B. (2012). Effect of incubation temperature on growth performance in Atlantic salmon. *Marine Ecology Progress Series* **454**, 75-82. doi:10.3354/meps09643

Fox, S.E., Levitt, P. & Nelson 3rd, C.A. (2010). How the timing and quality of early experiences influence the development of brain architecture. *Child Development* **81**, 28-40. doi: 10.1111/j.1467-8624.2009.01380.x

Hansen, L.P. & Jonsson, B. (1991). Evidence of a genetic component in seasonal return pattern of Atlantic salmon (*Salmo salar* L.). *Journal of Fish Biology* **38**, 251-258. doi:10.1111/j.1095-8649.1991.tb03111.x

Hansen, L.P., Jonsson, N. & Jonsson, B. (1993). Oceanic migration of homing Atlantic salmon. *Animal Behaviour* **45**, 927-941. doi:10.1006/anbe.1993.1112

Hasler, A.D. & Wisby, W.J. (1951). Discrimination of stream odors by fishes and its relation to the parent stream behavior. *The American Naturalist* **85**, 223-238. doi:10.1086/281672

This article is protected by copyright. All rights reserved.

- Heggberget, T.G. (1988). Timing of spawning in Norwegian Atlantic Salmon (*Salmo salar*). *Canadian Journal of Fisheries and Aquatic Sciences* **45**, 845–849. doi:10.1139/f88-102
- Jonsson, B. & Jonsson, N. (2011). *Ecology of Atlantic Salmon and Brown Trout: Habitat as a Template for Life Histories*. Fish and Fisheries Series 33, Springer, Dordrecht, the Netherlands.
- Jonsson, B. & Jonsson, N. (2014). Early environments affect later performances in fishes. *Journal of Fish Biology* **85**, 155-188. doi:10.1111/jfb.12432
- Jonsson, B. & Jonsson, N. (2016). Trans-generational maternal effect: temperature influences egg size of the offspring in Atlantic salmon *Salmo salar*. *Journal of Fish Biology* **89**, 1482-1489. doi:10.1111/jfb.13040
- Jonsson, B. & Ruud-Hansen, J. (1985). Water temperature as the primary influence on timing of seaward migrations of Atlantic salmon smolts. *Canadian Journal of Fisheries and Aquatic Sciences* **42**, 593-595. doi:10.1139/f85-076
- Jonsson, B., Jonsson, M. & Jonsson, N. (2016). Optimal size at seaward migration in an anadromous salmonid. *Marine Ecology Progress Series* **559**, 193-200. doi:10.3354/meps1189112
- Jonsson, B., Jonsson, N. & Finstad, A.G. (2014). Linking embryonic temperature with adult reproductive investment. *Marine Ecology Progress Series* **515**, 217-226. doi:10.3354/meps11006
- Jonsson, B., Jonsson, N. & Hansen, L.P. (1990). Does juvenile experience affect migration and spawning of adult Atlantic salmon. *Behavioral Ecology and Sociobiology* **26**, 225-230. doi:10.1007/BF00178315

- Jonsson, B., Jonsson, N. & Hansen, L.P. (2007). Factors affecting river entry of adult Atlantic salmon in a small river. *Journal of Fish Biology* **71**, 943-956. doi:10.1111/j.1095-8649.2007.01555.x
- Jonsson, N., Jonsson, B. & Hansen, L.P. (1990). Partial segregation in the timing of migration of Atlantic salmon of different ages. *Animal Behaviour* **40**, 313-321. doi:10.1016/S0003-3472(05)80926-1
- Korwin-Kossakowski, M. (2008). The influence of temperature during the embryonic period on larval development and growth in carp, *Cyprinus carpio* L. and grass carp, *Ctenopharynx godonidella* (Val.): theoretical and practical aspects. *Archives of Polish Fisheries* **16**, 231–314. doi: 10.2478/s10086-008-0020-6
- Kovach, R.P., Gharrett, A.J. & Tallmon, D.H. (2012). Genetic change for earlier migration timing in a pink salmon population. *Proceedings of the Royal Society B* **279**, 1743. doi:10.1098/rspb.2012.1158
- Le Luyer, J., Laporte, M., Beacham, T.D., Kaukinen, K.H., Withler, R.E., Leong, J.S., Rondeau, E.B., Koop, B.F. & Bernatchez, L. (2017). Parallel epigenetic modifications induced by hatchery rearing in a Pacific salmon. *Proceedings of the National Academy of Sciences* **114**, 12964–12969. doi:10.1073/pnas.1711229114
- Martell, D. J., Kieffer, J. D. & Tripple, E. A. (2005). Effects of temperature during early life history on embryonic and larval development and growth in haddock. *Journal of Fish Biology* **66**, 1558–1575. doi: 10.1111/j.0022-1112.2005.00699.x
- Morán, P. & Pérez-Figueroa, A. (2011). Methylation changes associated with early maturation stages in the Atlantic salmon. *BMC Genetics* **12**, 86. doi: 10.1186/1471-2156-12-86

Morán, P., Marco-Rius, F., Meagías, M., Covelo-Soto, L. & Pérez-Figueroa, A. (2013).

Environmental induced methylation changes associated with seawater adaptation in brown trout. *Aquaculture* **392-395**, 77–83. doi:10.1016/j.aquaculture.2013.02.006

Mundy, P. R. & Evenson, D. F. (2011). Environmental controls of phenology of high-latitude Chinook salmon populations of the Yukon River, North America, with application to fishery management. *ICES Journal of Marine Science* **68**, 1155–1164. doi:10.1093/icesjms/fsr080

Økland, F., Heggberget, T.G. & Jonsson, B. (1995). Migratory behaviour of wild and farmed Atlantic salmon during spawning. *Journal Fish Biology* **46**, 1-7. doi:10.1111/j.1095-8649.1995.tb05942.x

Otero, J., L'Abée-Lund, J.H., Castro-Santos, T., Leonardsson, K., Storvik, G.O., Jonsson, B., Dempson, B., Russell, I.C., Jensen, A.J., Baglinière, J.L., Dionne, M., Armstrong, J.D., Romakkaniemi, A., Letcher, B.H., Kocik, J.F., Erkinaro, J., Poole, R., Rogan, G., Lundqvist, H., Maclean, J.C., Jokikokko, E., Arnekleiv, J.V., Kennedy, R.J., Niemelä, E., Caballero, P., Music, P.A., Antonsson, T., Gudjonsson, S., Veselov, A.E., Lamberg, A., Groom, S., Taylor, B.H., Taberner, M., Dillane, M., Arnason, F., Horton, G., Hvidsten, N.A., Jonsson, I.R., Jonsson, N., McKelvey, S., Naesje, T.F., Skaala, O., Smith, G.W., Sægrov, H., Stenseth, N.C. & Vøllestad, L.A. (2014). Basin-scale phenology and effects of climate variability on global timing of initial seaward migration of Atlantic salmon (*Salmo salar*). *Global Change Biology* **20**, 61-75. doi: 10.1111/gcb.12363

Peters, D.P.C., Yao, J., Sala, O.E. & Anderson, J.P. (2012). Directional climate change and potential reversal of desertification in arid and semiarid ecosystems. *Global Change Biology* **18**, 151-163. doi:10.1111/j.1365-2486.2011.02498.x

This article is protected by copyright. All rights reserved.

- Roth, T.L. (2013). Epigenetic mechanisms in the development of behavior: advances, challenges and future promises of a new field. *Development and Psychopathology* **25**, 1279-1291. doi:10.1017/S0954579413000618
- Saino, N., Ambrosini, R., Albetti, B., Caprioli, M., De Giorgio, B., Gatti, E., Liechti, F., Parolini, M., Romano, A., Romano, M., Scandolara, C., Gianfranceschi, L., Bollati, V. & Rubolini, D. (2017). Migration phenology and breeding success are predicted by methylation of a photoperiodic gene in the barn swallow. *Scientific Reports* **7**, 45412. doi:10.1038/srep45412
- Scott, G. R. & Johnston, I. A. (2012). Temperature during embryonic development has persistent effects on thermal acclimation capacity of zebrafish. *Proceedings of the National Academy of Sciences of the United States of America* **109**, 14247–14252. doi:10.1073/pnas.1205012109
- Shine, R. & Olsson, M. (2003). When to be born? Prolonged pregnancy or incubation enhances locomotor performance in neonatal lizards (Scincidae). *Journal of Evolutionary Biology* **16**, 823-832. doi:10.1046/j.1420-9101.2003.00600.x
- Snedecor, G.W. & Cochran, W.G. (1973). *Statistical Methods*, 6th edn. The Iowa State University Press, Ames, Iowa, USA.
- Verhoeven, K.J.F., Vonholdt, B.M. & Sork, V.L. (2016). Epigenetics in ecology and evolution: what we know and what we need to know. *Molecular Ecology* **25**, 1631–1638. doi:10.1111/mec.13617

### Legend to figure

FIG. 1. Mean ( $\pm$ SD) number of days at sea of one-sea-winter (1SW) adult *Salmo salar* of the strains from the Norwegian Rivers Alta, Imsa and Lone, released as smolts at the mouth of the River Imsa in 1989, 1990 and 1993 and recaptured on the Norwegian

coast as maturing adults. □, Produced from eggs incubated in natural, cold River Imsa

water; ■, eggs incubated in heated River Imsa water. \* Mean significantly different ( $P < 0.05$ ).

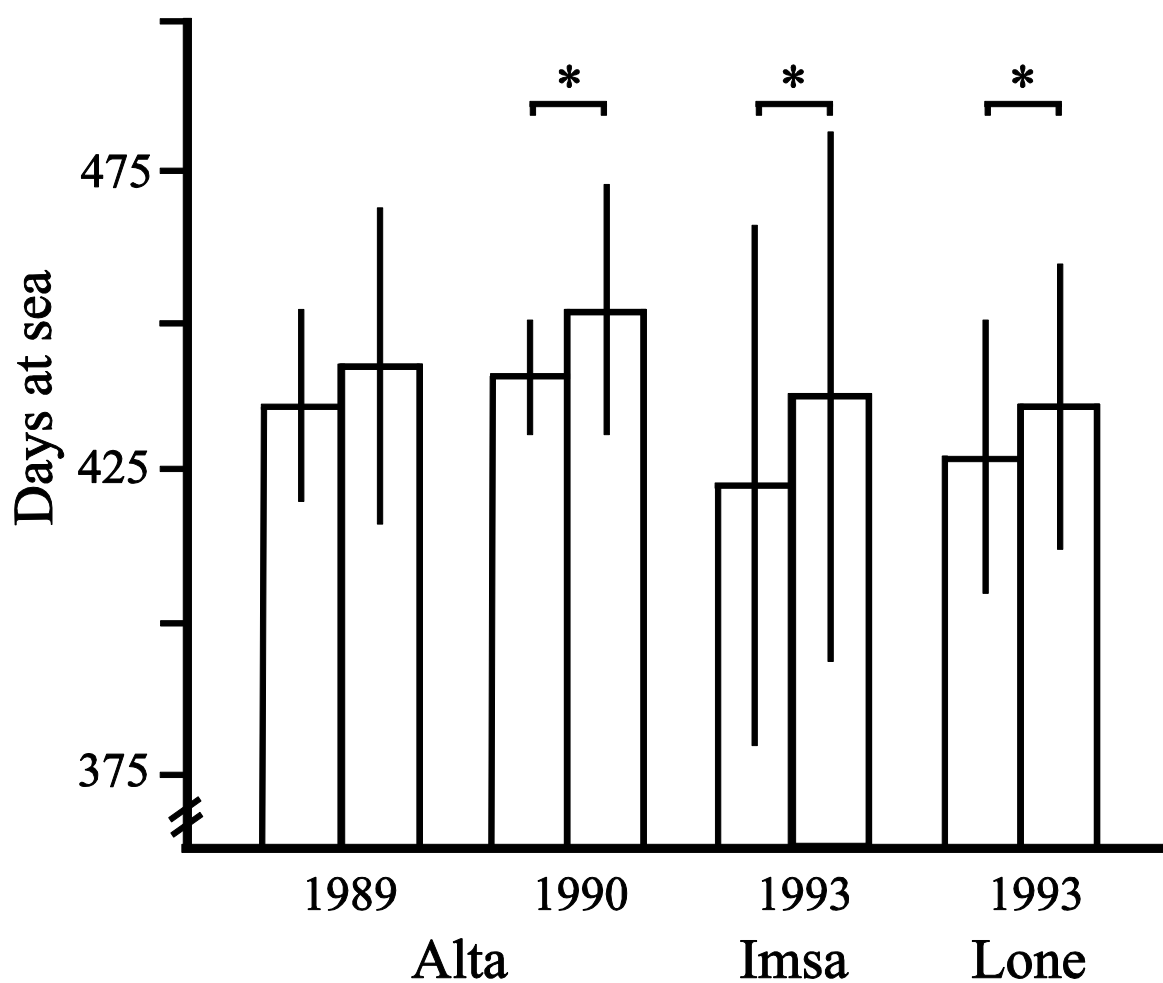




Table 1 Number and total length ( $L_T$ ) of recaptured, adult one-sea-winter (1SW) *Salmo salar* on the Norwegian coast when they returned from the feeding area in the North Atlantic Ocean. The fish were reared from eggs incubated in natural (cold) and heated (warm) water from the River Imsa and released as 1 year-old or 2 year-old smolts downstream of the fish trap in the River Imsa

Year released	River	Cold-water incubated ova						Warm-water incubated ova				
		Smolt age (years)	Mean $\pm$ SE (range) egg incubation temperature ( $^{\circ}$ C)	Recaptures (n)	Smolt $L_T$ (cm)	Adult $L_T$ (cm)		Smolt age (years)	Mean $\pm$ SE (range) egg incubation temperature ( $^{\circ}$ C)	Recaptures (n)	Smolt $L_T$ (cm)	Adult $L_T$ (cm)
1989	Alta	1	4.92 $\pm$ 1.52 (2.5–8.2)	36	16.5 $\pm$ 0.7	62.7 $\pm$ 2.8		1	7.69 $\pm$ 0.33 (6.5–8.2)	39	18.6 $\pm$ 1.9*	63.7 $\pm$ 4.2 <sup>s</sup>
1990	Alta	2	4.92 $\pm$ 1.52 (2.5–8.2)	8	33.9 $\pm$ 7.7*	67.4 $\pm$ 5.5*		1	7.46 $\pm$ 0.76 (4.8–8.4)	26	18.6 $\pm$ 1.2	59.5 $\pm$ 2.6
1993	Imsa	2	3.72 $\pm$ 0.97 (2.2–6.7)	49	25.2 $\pm$ 3.7*	62.6 $\pm$ 6.3*		1	7.33 $\pm$ 0.61 (4.6–8.0)	50	18.0 $\pm$ 1.7	57.2 $\pm$ 3.4
1993	Lon e	1	4.49 $\pm$ 0.91 (3.7–7.3)	63	15.9 $\pm$ 14.7	56.4 $\pm$ 4.2		1	7.11 $\pm$ 0.79 (4.6–8.0)	55	19.2 $\pm$ 2.0*	57.5 $\pm$ 4.3
All				156	19.9 $\pm$ 6.0*	60.3 $\pm$ 5.8				170	18.6 $\pm$ 1.8	59.3 $\pm$ 4.6

\*, Mean length significantly larger than the compared group ( $P < 0.05$ ).