

# Embryo Temperature Has Knock-on Effects on Later Traits in Salmonid Fishes



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**Abstract** Through a phenotypic plastic response, early temperatures have knock-on effects on later appearing traits of organisms such as stream-spawning salmonids. Moderately warmer water during embryonic development has carry-over effects to later developing life history characters such as body shape, metabolic rate, growth rate, egg and gonad sizes. Also, adult size and time of the spawning migration may be affected by temperatures experienced at the embryo stage. These responses to early temperature may be regulated by epigenetic mechanisms, such as DNA methylation. The plasticity may be favourable for invasive organisms and for those living in changing habitats and climates. It has been hypothesized that over time, this plasticity may lead to speciation. Research on these early knock-on effects of early temperature is still in its youth, but is rapidly growing, and at the end of the review, issues for future research are suggested.

**Keywords** Body shape · Embryogenesis · Environmental influence · Epigenetic mechanisms · Life history · Metabolic rate · Migration · Phenotypic plasticity · Temperature effects

## 1 Introduction

Temperature during embryogenesis has pervasive effects on many later appearing, fitness-related, and ecological characters for a variety of organisms (Fusco and Minelli 2010; Jonsson and Jonsson 2019). These thermal effects are for instance related to morphological, population ecological and behavioural traits (Schmid and Guillaume 2017). In ectotherms, growth and metabolic rates increase with temperature, but still, many populations from cold environments exhibit similar or higher growth rates than conspecifics from warmer habitats (Conover and Present 1990).

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By use of common garden experiments, it has been demonstrated that such variation in genetic expressions can be a phenotypic knock-on effect of temperature experienced by the organisms during embryogenesis (Finstad and Jonsson 2012; Durtsche et al. 2021).

Through influences on the embryos prior to hatching, the incubation temperature may prepare organisms for thermal conditions that they may encounter later. A relatively high egg temperature may prepare organisms for life in a warm climate, and a lower egg temperature may prepare them for a colder environment. This mechanism may be particularly important for ectotherms having the same body temperature as their surroundings (Booth 2006, 2018; Taylor et al. 2021), and is known from a variety of animal and plant kingdoms (Nijhout et al. 2017; West-Eberhard 2003; Bateson et al. 2014).

As a phenomenon, phenotypic plasticity has been long known (Johannsen 1911), but the understanding that early environments may change reaction norms of organisms to function better under conditions that they may experience later, is more recent (e.g. Bateson et al. 2004; Lafuente and Beldade 2019). This mechanism does not influence the genetic population structure or composition, but may result from parental effects (Mousseau and Fox 1998), environmental quality provided by the parents (Booth 2018), or through epigenetic mechanisms (Singh et al. 2020), responds within generations, and may even have trans-generational effects (Salinas and Munch 2012; Jonsson and Jonsson 2016).

Epigenetic influences may result from DNA methylation, histone modifications that regulate gene expression at the level of chromatin structure and DNA, and micro RNAs (miRNAs), i.e. small non-coding RNAs that constitute a post-transcriptional mechanism regulating abundance and translation of mRNAs (Bollati and Baccarelli 2010). The understanding of these effects is rapidly growing although still in its infancy.

Here, I review how temperature during embryogenesis may influence later emerging ecological traits of river-spawning salmonids. Traits investigated are meristic characters of the skeleton, body shape, fin size, muscle development, growth and metabolic rates, egg size and age of the feeding migration to sea and timing of spawning migration. Although we report the various traits separately as they often are in the scientific literature, one should keep in mind that it is the entire phenotype that is influenced by the early temperature and that the various traits may be associated with each other. At the end, I briefly discuss mechanisms allowing the plasticity, its wider ecological significance and give topics for further research.

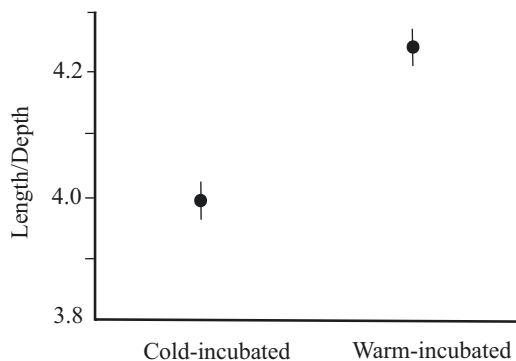
## 2 Characters Studied

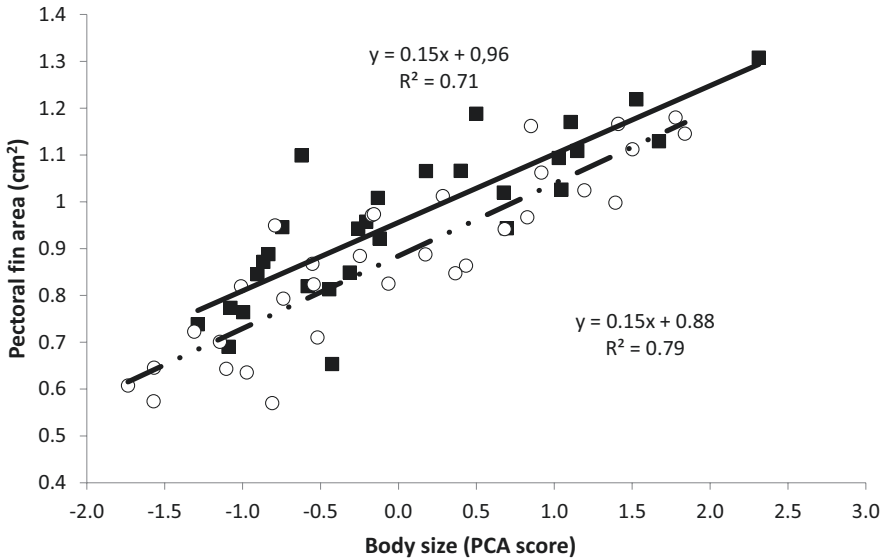
### 2.1 Anatomy and Morphology

Egg incubation temperature influences anatomic and morphologic characters of stream-living salmonids. For instance, it affects the number of vertebrae and fin rays developed in many fish species, amongst which brown trout *Salmo trutta* was the first species studied (Jonsson and Jonsson 2011). Tåning (1952) reported that this fish developed fewest vertebrae at 6 °C stable embryo temperature and more vertebrae at lower and higher temperatures. The vertebral numbers were determined during gastrulation, shortly before the so-called eyed-egg stage. Thus, the relationship between vertebral numbers and egg temperature is V-shaped, but there is still open whether the effect of temperatures above and below the minimum number of vertebrae is similar. Experiments with a model species, Mexican tetra *Astyanax mexicanus*, exhibited that fish incubated at low temperatures developed more precaudal vertebrae whilst conspecifics developed at higher temperatures developed more caudal vertebrae (Corral and Aquirre 2019), and possibly, this may also hold for other species.

Tåning (1952) also reported that maximum number of rays in the dorsal and pectoral fins occurred at 8–10 °C, and in the anal fin at 5–6 °C. The generality of these early knock-on effects of early temperature on meristic characters has been demonstrated for some other fishes, such as galaxids (McDowall 2003, 2008), ladyfish (Elopidea) (McBride and Horodysky 2004), Atlantic silversides *Menidia menidia* (Billerbeck et al. 1997), and three-spined sticklebacks *Gasterosteus aculeatus* (Ahn 1999). Skeletal variations may affect body shape and fin sizes (Aquirre et al. 2019; Corral and Aquirre 2019), and this thermal effect may explain why Atlantic salmon parr incubated as eggs at 5.6 °C, had more streamlined body shape than conspecifics incubated as eggs at 2.6 °C as demonstrated by Greenberg et al. (2021) (Fig. 1). Atlantic salmon also had smaller pectoral fins relative to body size if incubated at 5.6 °C relative to 2.6 °C (Fig. 2). Early temperature conditions may thus affect the maximum critical water velocity for juvenile fish (Sfakianakis et al.

**Fig. 1** Standard length on body depth of juvenile Atlantic salmon incubated from conception until first feeding fry in either cold (2.6 °C) or heated (5.6 °C) water, and then reared at natural water temperature until measured as 1-year-old juveniles. Error bars represent standard error (from Greenberg et al. 2021)





**Fig. 2** Relationship between pectoral fin area and body size of 1-year old, juvenile Atlantic salmon incubated from conception until first feeding in either cold (ca. 2.6 °C, open circles, dashed-dot-dot line) or warm (ca. 5.6 °C, solid squares, solid line), and then reared until measured at the same natural water temperature (from Greenberg et al. 2021)

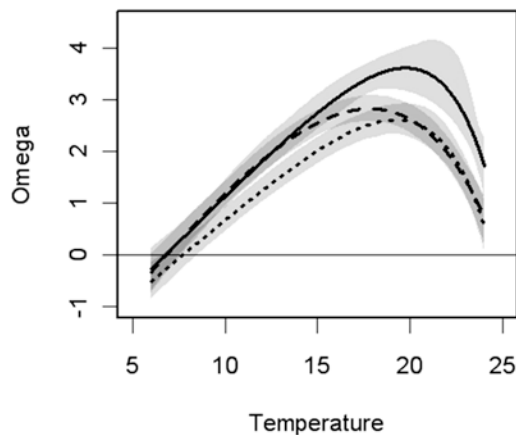
2011), with effects on feeding activity and predator defence (Nathanailides et al. 1995).

Body shape may be also influenced by muscular development, and early temperature may affect the rate of myogenesis, including composition of the functional structures within the cells, number, size and distribution of muscle fibres, fibre diameters and myofibril areas (Stickland et al. 1988; Johnston 2006; Scott and Johnston 2012). For instance, Stickland et al. (1988) reported that post-hatching embryos of Atlantic salmon develop larger but fewer muscle fibres at higher incubation temperatures. However, larvae developed from cold incubated eggs have higher muscle fibre hypertrophy so that the difference in muscle fibre size at hatching and later is small. Differences in hypertrophy between warm and cold incubated salmon may be due to a reduction in number of cell nuclei in the muscle fibres of warm incubated fish (Nathanailides et al. 1995). Also in other species, such as Senegal sole *Solea senegalensis*, incubation temperatures have both short- and long-term effects on muscle growth and cellularity (Carballo et al. 2018), suggesting a generality of the finding that embryo temperature influences muscle development of fish.

## 2.2 Growth, Size and Metabolic Rates

The effect of embryo temperature on later muscle growth is also reflected in how fast individuals grow in size later in life. For instance, juvenile Atlantic salmon produced from 3 °C warmer incubated eggs grew faster and became larger than those from eggs incubated in colder water when growth was tested 3 months after first feeding. The difference in growth rate was significant at the optimal temperature for growth, 18–20 °C (Fig. 3; Finstad and Jonsson 2012). The improved growth in fresh water results in increased size and reduced time until the juveniles are ready for seaward migration (Burgerhout et al. 2017). Moreover, the increased growth in fresh water increased size at maturity after 1 year at sea (Jonsson et al. 2014). However, a similar growth experiment with brown trout from the same Norwegian River Imsa, revealed no similar growth effect of temperature during the embryogenesis in this species (Jonsson and Jonsson 2021) suggesting that the effect of embryo temperature on later growth can vary even between very similar species.

Early temperature affects metabolic rates of trout. For instance, Cook et al. (2018) reported that incubation temperatures experienced by brook trout *Salvelinus fontinalis* embryos affected routine metabolic rates of free-swimming fry. Furthermore, Durtsche et al. (2021) reported that the standard metabolic rate (SMR), maximum metabolic rate (MMR), and aerobic scope (AS = MMR – SMR) of juvenile brown trout were higher for those incubated as embryos at 4 than 7 °C when tested for metabolic rates at 13 °C, i.e. at the optimal temperature for growth of this species (Elliott 1994; Forseth et al. 2009). All metabolic measures were lower in fish incubated as embryos in warm than colder water. The latter results are



**Fig. 3** Temperature scaling (°C) of growth standardized to 1 g body mass ( $\Omega$ , %, Ostrovsky 1995) of juvenile Atlantic salmon incubated as embryos in natural water (dotted line), in natural water but kept in ca. 4 °C warmer water from hatching until first feeding (stippled line), or incubated in ca. 4 °C warmer water from conception until first feeding (solid line). Grey-shaded areas are 95% confidence intervals. Horizontal line indicates zero growth (From Finstad and Jonsson 2012)

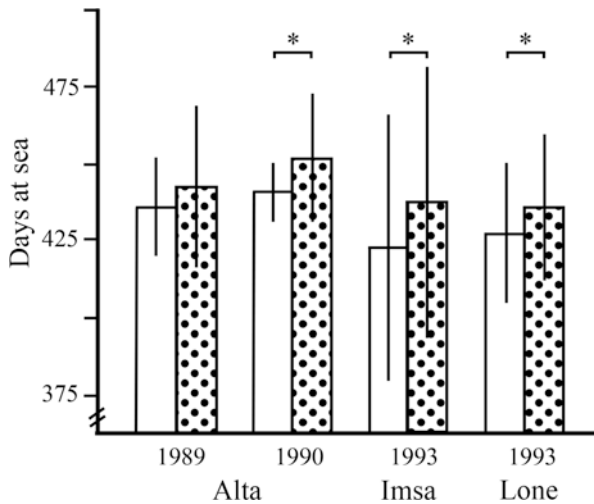
consistent with the countergradient variation (CGV) hypothesis saying that CGV occurs when an environmental gradient counteracts the phenotypic variation of a trait as influenced by genetics (Levins 1969; Conover and Schultz 1995). In this case, variation in metabolic rates are inversely related to the thermal conditions during egg incubation. Whilst previous studies have suggested that CGV is caused by genetic differences between conspecific populations (Álvarez et al. 2006), this study exhibits that thermal differences encountered at the embryonic stage can have a phenotypic effect consistent with the CGV hypothesis. A similar negative correlation between egg temperature and metabolic rate has been demonstrated for the snapping turtle *Chelydra serpentina* (O'Steen and Janzen 1999; Steyermark and Spotila 2000) showing that this relationship holds for more than brown trout.

### 2.3 Reproductive Traits

Atlantic salmon typically feed and gain most of its size in the ocean, whereas the adults spawn in rivers where the young (parr) grow up. Experimentally, Jonsson and Jonsson (2018) showed that egg incubation temperature influenced the timing of their return migration from the sea. Atlantic salmon incubated as eggs in either natural river temperature, which in this case was 2–5 °C from conception to first feeding, returned 2 weeks earlier for spawning than those incubated in ca. 3 °C warmer water (Fig. 4). From first feeding onwards, the juveniles were reared at the same natural river temperature until released at smolting (the physiological transition stage when they become ready for sea life), 1 or 2 years later. The fish fed at sea for more than 400 days before they returned to the river of release. Similar results were demonstrated for three populations, 2 year classes and in 3 different years. Thus, the temperature experienced at the embryo stage influenced the timing of the spawning migration through a phenotypically plastic reaction norm.

The expressions of reproductive traits such as egg and gonad size in Atlantic salmon, are also influenced by the temperature the fish experienced during the embryogenesis (Fig. 5). This was experimentally demonstrated when Atlantic salmon eggs were incubated under 3 embryonic thermal regimes: cold, mixed and warm treatments (Jonsson et al. 2014). The cold group received ambient river water (mean  $\pm$  SD: 2.6  $\pm$  0.4 °C) and the warm group received water at 4.6 °C above ambient temperature, from fertilization until first feeding. The mixed group received ambient river water until hatching, whereupon the larvae received heated water until the start of external feeding. Thereafter, all groups were reared under identical, natural thermal conditions. In adulthood, fish that developed from warm incubated eggs were the largest and had the highest mass–length relationship. The females developed larger eggs and both sexes had higher gonad mass relative to their own body size. There was no similar effect of increased temperature during larval development.

There is also a trans-generational effect on the egg size of fish that were exposed to heated water during the egg maturation prior to spawning. Their offspring



**Fig. 4** Mean (SD) number of days at sea of one-sea-winter(1SW) adult Atlantic salmon 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 or in ca. 3 °C warmer water from conception to first feeding. *Asterisk*, mean significantly different ( $P < 0.05$ ) (From Jonsson and Jonsson 2018)

produced larger eggs than females that were kept in colder water during egg maturation (Jonsson and Jonsson 2018). Apparently, there was a maternal effect on the egg size of their offspring.

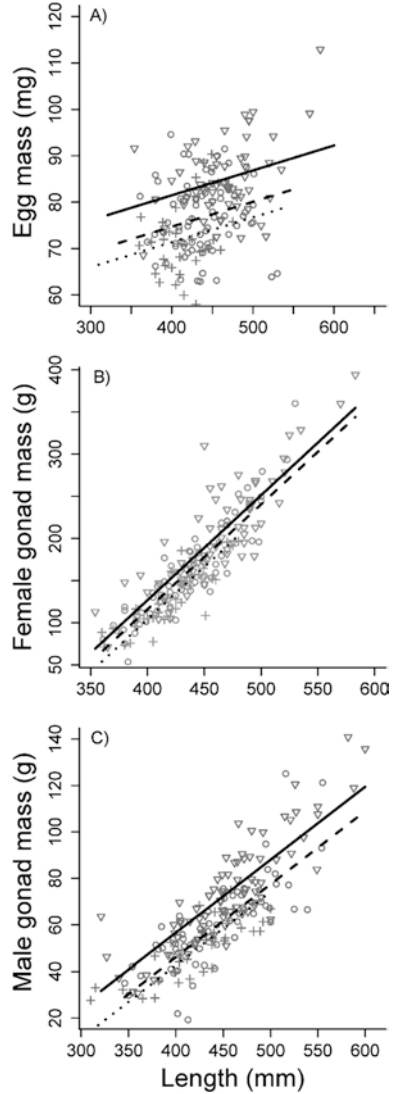
Thermal treatments during egg incubation had no effect on the age of maturity or fecundity of Atlantic salmon. However, Baum et al. (2005) reported that male Atlantic salmon parr exposed to heated water were larger than conspecifics living in colder water, and suggested that early temperature might increase the threshold size for maturation in male parr, i.e. maturation prior to smolting and seaward migration.

Thus, early thermal conditions affect expressions of adult life history traits of stream-spawning salmonids, a mechanism by which they may change the size of their propagules to the anticipated thermal offspring environment.

### 3 Discussion

Environments have pervasive roles in phenotypic plasticity. They determine the degree of variation and choose between possible phenotypes. This is not unique for ectothermic vertebrates, but can be found across the animal and plant kingdoms (Bateson et al. 2014). However, it may be particularly important for ectothermic organisms having the same temperatures as their surroundings. By being able to

**Fig. 5** Mean mass of (a) single eggs, (b) female gonads and (c) male gonads over total length (mm) for adult Atlantic salmon incubated in natural water during embryonic and larval development (+, dotted lines), natural water during embryogenesis and heated water during larval development (s, dashed lines), and heated water during embryonic and larval development (n, solid lines). Lines are predictions from the best-fit model with regression parameters given in Jonsson et al. (2014)



adjust their optimum performance temperature, plasticity may significantly increase their fitness (Salinas and Munch 2012).

Despite differences amongst species, the cited research suggests that embryonic temperature influences traits such as body shape, metabolic rates and aerobic scope, growth rate, smolt age, timing of spawning migration, size at maturation, gonadal and egg size of salmonid fish spawning in streams and rivers. Within temperatures naturally experienced by the fish, they may become more or less streamlined, grow faster or slower, return for spawning early or later in the season and produce larger or smaller gonads and eggs depending on the temperature during the



embryogenesis. The changes parallel those observed along climatic gradients where growth rate decreases and smolt age and egg size increase with increasing latitude in Atlantic salmon and brown trout (L'Abée-Lund et al. 1989; Metcalfe and Thorpe 1990; Jonsson et al. 1996; Jonsson and Jonsson 1999).

This plasticity appears adaptive rather than caused by some form of developmental stress, and seems to prepare the young for conditions they may experience later in life. For instance, when developed as embryos in warmer water, they exhibit characters later in life that is favourable in warmer environments. A more streamlined body shape may improve the swimming performance and reduce cruising and foraging costs (Webb 1984; Swain 1992; Ackerly and Ward 2016). Furthermore, as shown for brown trout, the juveniles exhibit reduced aerobic scope in warmer water, and a more streamlined body may reduce energetic costs (Durtsche et al. 2021). Predation pressure may also increase in warmer water, and if so, a more streamlined body shape may improve their ability to escape predators more than deeper bodies do. However, if fish incubated in warmer water experience a colder climate, they may be less well adapted because of less surplus energy with negative effects on movement activity, feeding and defence behaviour (Durtsche et al. 2021).

Atlantic salmon incubated as embryos in relatively warm water, grew better as juveniles and transform for sea life younger, than those incubated in colder water do (Finstad and Jonsson 2012; Burgerhout et al. 2017). This finding is consistent with field-based observations that cohorts of juvenile Atlantic salmon that undergo embryogenesis in warm winters tend to grow faster and move to sea at a younger age than cohorts developed from eggs incubated during colder winters (Jonsson et al. 2005). This may reflect an expectation of better feeding opportunities and willingness to feed more if developed in warmer water, as there is a close relation between growth rate and the amount of energy consumed (Jonsson et al. 2001).

In general, aquatic production increases with water temperature, and fishes that are incubated in a relatively warm habitat, may expect to encounter relatively rich feeding opportunities and keen competition as juveniles in the river. On the other hand, in a cold environment, a high appetite may be less advantageous not only because of poorer growth opportunities, but also because faster growth has increased costs in the form of higher mortality (Mangel 2003; Metcalfe and Monaghan 2003; Sundt-Hansen et al. 2009). In addition, fish are heterothermic, meaning reduced swimming speed and poorer ability to avoid homothermic predators in cold water. Thus, it may be advantageous to feed less and thereby be less exposed if the water is cold.

Larger, more yolk-rich eggs in warmer water may be advantageous because the efficiency of yolk conversion to body tissue is reduced in a warmer environment (Fleming and Gross 1990). Furthermore, the oxygen content in water decreases with increasing temperature, and larger eggs survive better than smaller ones do under poor oxygen conditions (Einum et al. 2002). Also, lower metabolic rates, as found for warm incubated brown trout (Durtsche et al. 2021), may be advantageous in warmer water in agreement with the CGV hypothesis. Also, a later return of Atlantic salmon from the ocean appears adaptive in warmer rivers as the fish should spawn later for the offspring to emerge at the proper time for first feeding in spring

because the duration of the egg incubation period is shorter in warmer water (Jonsson and Jonsson 2018).

Thus, temperature during embryogenesis is important for later emerging phenotypic expression. It may prepare offspring for environmental conditions that they may encounter later. This can contribute to adequate responses as it facilitates adaptive evolutionary reactions to directional change (Kingsolver and Buckley 2017). For instance, adaptive phenotypic plasticity may be important for how fish are able to cope with climate change (Merilä and Hendry 2014; Kingsolver and Buckley 2017). Climate warming does not only mean that the fish must cope with an increased mean temperature, but also respond adequately to increased thermal variability (IPCC 2013), and the experiments summarized above exhibit how salmonids change when the embryos develop under warmer conditions allowing them to produce larger eggs, grow faster, feed more, use less oxygen, swim faster and return later for spawning, adequate responses in both a warmer and a more variable climate.

Such a phenotypic plasticity may be also important for invasive species, such as trouts, facilitating colonization of thermally different habitats (Vogt 2017; Ardura et al. 2018). Offspring of strays to foreign rivers should adapt readily to the thermal conditions of their new home river. Invasive species typically exhibit higher phenotypic plasticity than non-invasive species, although the plasticity is not always associated with a fitness benefit, especially when resources are limited (Davidson et al. 2011; Wang and Althoff 2019).

There is still little known about the mechanisms that enable such a phenotypic programming. Possibly, epigenetic mechanisms, activating or silencing genes, are involved. In ecology, epigenetics is a new, but fast-moving field with several recent advances (Flores et al. 2013; Venney et al. 2019). It is known that DNA methylation is sensitive to environmental changes (Anastasiadi et al. 2017), thermal climate (Varriale and Bernardi 2006), water quality, nutrition and environmental structure (Morán et al. 2013; Le Luyer et al. 2017). Furthermore, DNA methylation with silencing of genes, is most prevalent in cold habitats (Verrale 2014). It is known that both maternal food deprivation and temperature during maturation influence gene expression of offspring up to maturity (Jonsson and Jonsson 2016; Fan et al. 2019). These effects may be promoted by DNA methylation (Venney et al. 2019), but other epigenetic mechanisms such as histone modifications and micro RNA may be also involved, and it is important to intensify studies of the significance of these for phenotypic expressions.

Effects of environments on phenotypes vary by genotype, i.e. epigenetics may cause variation in phenotypic plasticity depending on the genetic makeup of the specific individuals at relevant loci (Banta and Richards 2018). It is hypothesized that epigenetic mechanisms may have the potential to develop into genetic variation and ultimately trigger speciation, although evidence is still meagre (Venney et al. 2019). One such proposed mechanism is “Plasticity First” (e.g. Levis and Pfennig 2016), where phenotypic plasticity leads to a range of phenotypes, some of which are favoured by selection. Over time, mutations can fix the favoured phenotypes, and ultimately the phenotypes initially resulting from plasticity will have a genetic

basis. Therefore, epigenetic variation might provide the first substrate for selection during evolutionary divergence.

## 4 Future Research

The understanding of how the thermal climate during embryogenesis influences later occurring ecological traits is limited. Only a few species and populations have been tested, and there is almost no knowledge about how the plasticity influences costs and benefits for organisms. Thus, the generality of the present findings should be tested across traits, populations and species. One should also work out the reaction norms for the various traits over a wide range of temperatures. Already now, however, it is evident that these knock-on effects are important for the ecology of many species.

The embryo temperature influences the body and fin shapes of Atlantic salmon, but no one has quantified what this means for their swimming performance. Furthermore, early temperature influences growth and metabolic rates of salmonids and thereby affects their aerobic scope (Álvarez et al. 2006; Finstad and Jonsson 2012; Durtsche et al. 2021). However, ecological consequences of these rates have not yet been investigated, but possibly, this will influence behavioural activities as it does for lizards (Siviter et al. 2019). In particular, this may influence the scope for activity at low temperatures when maximum power capacity is low (Pried 1985).

It is hypothesized that environmentally induced plasticity may facilitate and speed up the processes of adaptive evolution (Ghalambor et al. 2007; Levis and Pfennig 2016). There is, however, little evidence exhibiting the role of plasticity in facilitating the evolution of natural populations (Warner et al. 2010). Early temperature may play a critical role in the diversification of sympatric phenotypes in salmonid species as exhibited in experiments with European whitefish *Coregonus lavaretus* where co-occurring large and dwarf forms of the species developed at different water temperatures (Steinbacher et al. 2017). As much of the phenotypic difference disappeared when offspring of Arctic charr *Salvelinus alpinus* morphs were raised under similar thermal conditions (Hindar and Jonsson 1993), one may suspect that environmental differences play a role in the morph differentiation in this and possibly other salmonid species.

Much evidence show that cues experienced in early life can affect the development of phenotypes with consequences for life in environments encountered at a later stage. As yet, however, there are few examples that actually test if observed changes are adaptive and improve the fitness of organisms. Thus, such tests are needed. The capacity of salmonids to display adaptive plasticity in changing environments may determine their future success.

The understanding of how knock-on effects influence the development of phenotypes may in many cases involve epigenetic processes, although little is known about how these affect the development of ecological trait variation (Verhoeven et al. 2016). Investigations of how the environment influenced ecological traits

through epigenetic changes without influencing the genetic structure of populations is an urgent research need and may include also other mechanisms than DNA methylation, although this mechanism may be particularly important because of its temperature dependence.

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