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COMPERVE
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ATENÇÃO! As respostas às questões deverão ser redigidas em PORTUGUÊS.

Questions 01 to 05 refer to the text below.

PHENOTYPIC PLASTICITY AND EPIGENETICS OF FISH: EMBRYO TEMPERATURE AFFECTS LATER-DEVELOPING LIFE-HISTORY TRAITS

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INTRODUCTION

Early temperature influences phenotypic plasticity, i.e. the ability of individual genotypes to produce altered phenotypes when exposed to different conditions. This includes the ability of organisms to change developmental trajectories, activities and resource allocation in response to variation in environmental conditions. Research suggests that early temperature plays a critical role in brain development and flexibility influencing cognition, behavior, social skills, stress responsiveness and personality development of mammals such as humans and mice. Furthermore, ecological traits expressed by juveniles and adults can be affected by the temperature during embryo development through epigenetic modifications, where genes can be activated or silenced by molecular mechanisms that can heritably alter gene expression without changing the DNA sequence. Although poorly investigated, it is reasonable that similar relationships hold for many other vertebrates.

Genotypes govern, and environment modifies, phenotypes. According to Lindström (1999), the earlier the environmental effect, the stronger its long-term impact can be. Environmental temperatures affect aquatic poikilotherms during embryogenesis within the eggshell and can have long-term phenotypic effects recognizable in the ecology of the species. Tåning (1952) observed that temperature during embryonic development affects the number of vertebrae in brown trout Salmo trutta. More recently, it was revealed that embryonic temperature affects muscle fiber recruitment in different fishes. However, less is known about how early temperature can modify ecological characters such as growth rate of juveniles, adult body size and other fitness-related traits. This was the background for the present review on phenotypic plasticity and epigenetic effects in fishes.

Here, we focus on how temperature during early ontogeny affects ecological traits. We show how early temperature affects the physiology of species and how these changes can be influenced by epigenetic modifications, i.e. changes in genetic expression, without changing the genetic structure of populations. At the end, we discuss the wider significance of phenotypic variation caused by variation in temperature during embryogenesis and suggest further research tasks. We are aware that early temperature level is one of several environmental variables that can have lasting impacts on phenotypic expression. Other stressors that affect embryos include hypoxia and chemical contamination. Temperature also has pervasive, controlling effects on the ecology and physiology of poikilotherms later in life, but it is beyond the scope of this paper to discuss thermal influences occurring at later life stages and environmental stressors other than embryo temperature.

Several ecological traits appearing at a later life stage may be influenced by the temperature affecting the embryo within the eggshell, including developmental rate, growth and reproductive allocation. Thermal effects of embryo temperature on growth were experimentally tested on Atlantic salmon *Salmo salar* by Finstad & Jonsson (2012). Eggs and alevins were incubated until the onset of external feeding at either heated or natural (= cold) temperatures of the River Imsa, Norway, or transferred from ambient to heated water at the time of hatching (= mixed temperature). This created 3 different embryonic temperature treatments. The cold group received natural river water (mean ± SD: 2.6 ± 0.4°C) and the warm group received water at on average 4.6°C above ambient temperature, which is an expected winter temperature in the river towards the end of this century. Thus, the warm treatment lasted from fertilization until exogenous feeding started. The mixed group received natural cold river water until hatching, whereupon the larvae received heated water until the commencement of exogenous feeding. From the start of exogenous feeding onwards, all 3 groups were reared under identical, natural thermal conditions. Somatic growth of the groups was tested at 8 different temperatures between 6° and 24°C. Maximum growth of juvenile *S. salar* was higher in the heated water than at the other 2 incubation temperatures. Growth was similar at cold and mixed temperatures. There was no significant difference in the thermal scaling of growth among groups or in upper (25°C) or lower (6°C) thermal limits for growth. Also, the optimal temperature for growth (19°C) was similar between treatments. The experiment revealed, however, that juvenile *S. salar* incubated in heated water

grew better than the others at the optimal temperature (Finstad & Jonsson 2012). Mortality prior to the growth experiment was low and similar in all groups, thus excluding selection as an explanation of the results. This finding was later supported by Burgerhout et al. (2017), who reported that embryos of *S. salar* incubated at 8°C grew better than those from eggs incubated at 4°C. Thus, temperature during embryo development can influence later expressed fitness-related ecological, behavioral and physiological traits of fishes. It influences competitive ability, social status, reproductive success and ability to evade predators. To what extent plasticity in this trait varies among populations of the species is unknown.

The observation that temperature during embryogenesis influences growth of juveniles may explain the earlier field observation that specific growth rate of *S. salar* during the first year of life in the River Imsa correlated positively with water temperature during winter, when the embryos developed within the eggshell in the bottom substratum of the river. Among years, growth did not vary with ambient temperature in the subsequent summer season in the investigated system (Jonsson et al. 2005). Typically, *S. salar* of the River Imsa smolt and migrate to sea at 2 yr of age, although large 1 yr old individuals will also smolt and migrate. The proportions of 1 yr old smolts varied among years and increased with water temperature during embryogenesis but not with temperature in the subsequent summer (Jonsson et al. 2005). This exhibits another significant effect of temperature during the embryonic stage for the developmental rate of *S. salar*. Fast growth, stimulated by high temperature at the embryo stage, can shorten river life by 1 yr. Those that smolt at the regular age become larger than the early smelting fish, and with that, size after each year at sea later in life. In addition, younger smolts tend to stay and feed longer at sea before attaining maturity. In this way, high embryo temperature affects future growth and size of *S. salar*.

FUTURE RESEARCH

Research on how the early environment influences genotypes and forms phenotypes, and mechanisms involved, is still in its youth. There is little knowledge about the processes leading to variation in appearance, physiology, life history and behavior, i.e. phenotypic variation. Early temperature is one of many external variables that affects phenotypic development. Oxygen level, toxic contaminants, nutrition, social environment with competition, parasites and predation also influence genotypic expressions. Future research should focus on how signals from environmental stressors trigger molecular biological changes of brain cells, and how this is transmitted to phenotypic characters and ecological decisions. In this review, we focused on one factor, namely the effects of early temperature. Future global temperature is expected to increase (IPCC 2013). In this con-text, new research should focus on how this change will affect populations and investigate to what degree populations buffer changes through phenotypic plasticity. For instance, there is little knowledge about how early environment affects migration versus residency of partly migratory species, and how early climate affects the timing of migrations before and after spawning. The mechanisms allowing this plasticity are largely unknown, although epigenetic changes caused by increased embryonic temperature appear involved (Jonsson & Jonsson 2014, 2018, Baerwald et al. 2016). Although the environment appears to play a key role in the ecology of species, these and similar relationships are still understudied.

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Question 1

Explain phenotypic plasticity, according to the authors, and how temperature in the embryo environment is known to influence the development of mammals.

Espaço para Resposta

Question 2

Write about the gap that the authors point out in the fish research literature, and how they aim to address it in the present review.

Espaço para Resposta

Question 3

Discuss what the findings in Finstad and Jonsson (2012) and Burgerhout et al. (2017) have shown about the thermal effects of embryo temperature on salmon growth.

Espaço para Resposta

Question 4

Discuss the future directions research should take, according to the authors, in the investigation of the role of environmental stressors and, more specifically, temperature on phenotypic plasticity.

Espaço para Resposta

Question 5

- Translate the excerpt below in the space provided.
- The translated text should be clear and accurate in terms of structure and meaning.

This exhibits another significant effect of temperature during the embryonic stage for the developmental rate of S. salar. Fast growth, stimulated by high temperature at the embryo stage, can shorten river life by 1 yr. Those that smolt at the regular age become larger than the early smelting fish, and with that, size after each year at sea later in life. In addition, younger smolts tend to stay and feed longer at sea before attaining maturity.

ESPAÇO DESTINADO AO TEXTO DEFINITIVO