The effect of thermal stress on fish development: a mini-review

L.M.Whitehouse PhD, Independent Researcher, France
ORCID: https://orcid.org/0000-0001-5385-7591
Scopus: https://www.scopus.com/authid/detail.uri?authorId=57195605595

DOI: https://doi.org/10.57098/SciRevs.Biology.3.4.3
Received October 18, 2024. Revised November 05, 2024. Accepted November 08, 2024.

Abstract: Projected temperature increases are predicted to significantly affect fish populations globally, impacting fish recruitment processes and altering population distribution. Fish embryos are perhaps at the most risk from temperature changes due to their sessile nature and overall sensitivity to temperature changes which could impact how well a fish population performs in a changing world. Research has shown that temperature can alter developmental trajectories, induce damage and abnormalities, increase development, and early hatching, and reduce survival. Other studies have shown that exposure to thermal stress can prime stress responses and result in changes in metabolic enzyme activity that persists post-hatch. Moreover, exposure to fluctuating temperature, which most closely mimics natural environments, can have a protective effect, increasing thermotolerance and survival while appearing to have no impact on developmental processes or hatching rate. Understanding how these early life stages respond to thermal stress and fluctuations is important for predicting how fish populations will respond to climate change.

Keywords: Fish, embryos, thermal stress, fluctuating temperatures, development, physiology

Introduction

Climate change is leading to an increase in global water temperatures which is having a significant impact on fish populations (Pörtner and Peck, 2010). As ectotherms, fish are particularly vulnerable to temperature changes; the ambient environmental temperature determines their body temperature (Jeyachandran et al., 2023). As a result, rising water temperatures are influencing the abundance and distribution of fish species globally, and having a significant impact on the aquaculture industry (Islam et al., 2022; Stuart-Smith, 2021).

Embryonic and larval stages are more sensitive to temperature changes than juveniles and adults (Rombough, 1997), since warming temperatures impact fish development by changing the timing of embryonic development and the formation and function of key tissues and structures (Koumoundouros et al., 1999). An increase in the temperature of the developmental environment accelerates developmental processes which can result in early hatching and mismatch with environmental conditions for feeding. Moreover, changes in developmental processes can result in abnormalities that negatively impact the fish's chance of survival (Pepin, 1991).

This short review will assess what we know about the impact of temperature on fish development. An understanding of how temperature impacts fish development is crucial to developing management practices and conservation efforts for fish species considering increasing global temperatures.

Embryological development

Fish embryonic development is complex and varies from species to species. Some species lay eggs on the bottom of a river, lake or close to shore, some make nests, and for some fish, their eggs are suspended in open water (Bessa et al., 2022; Prichard et al., 2017; Yohannan, 1998). Eggs that are produced by warm water fish often have a short developmental time, whereas eggs produced by fish that live in cool waters can take months to develop. These eggs laid in cool waters are often deposited under the cover of ice and then hatch in the spring (Karjalainen et al., 2015). These differences mean that warming temperatures are likely to impact fish development differently and could perhaps have more chance to impact cold-water-adapted fish that have traditionally taken longer to develop.

Studies to date have demonstrated that exposure to increased temperatures during development can result in damaged zygotes, cellular deformities, damaged yolk sac, and low hatching success (Ashaf-Ud-Dulah et al., 2021; Clarkson et al., 2020; Linares-Casenave et al., 2013; Wang and Tsai, 2000). Embryos are particularly sensitive to temperature fluctuations during the cleavage stages, which occur during the early developmental period following fertilization (Krone et al., 2003; Werner et al., 2003). For example, incubation of *Solea senegalensis* eggs at temperatures above 18 °C resulted in the appearance of deformities in the caudal vertebrae of the embryos compared to those incubated at 15 °C (Dionísio et al., 2012). Moreover, incubation of yellow croaker (*Larimichthys crocea*) at temperatures above and below (33 °C and 15°c, respectively) their optimum temperature (22 °C) resulted in a 100% deformity rate at hatch. These deformities included fin membrane decay, missing, bent, or decaying tails, and spinal deformity (Figure 1; Tian et al, 2022).

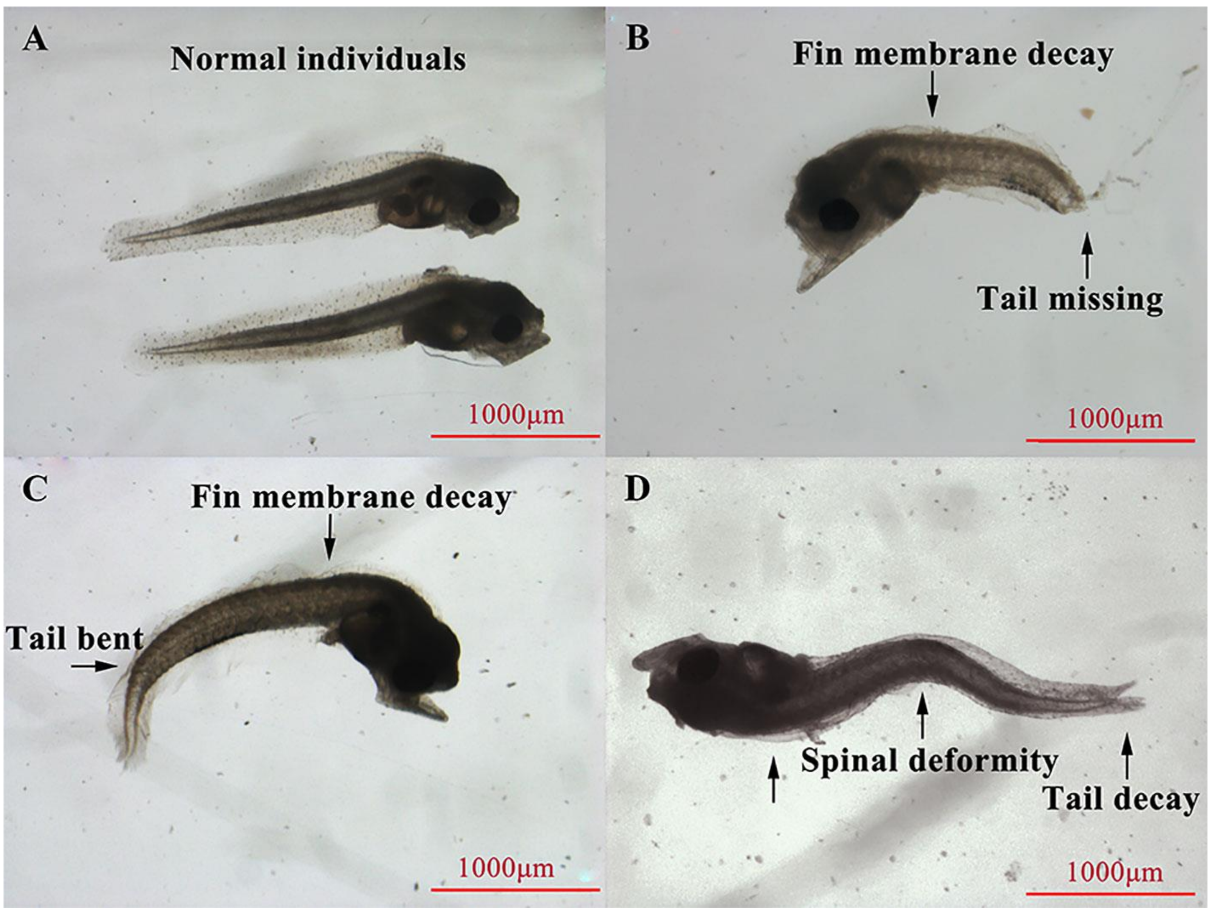

Figure 1: *Morphology of normal (A) and deformed (B – D) Yellow croaker (Larimichthys crocea) larvae taken from Tian et al (2022).* Embryos were exposed to seven different temperatures (15°C, 18°C, 21°C, 24°C, 27°C, 30°C, and 33°C) and observed until hatch. Embryos incubated at temperatures close to the optimal temperature of 22 °C (21 °C and 24 °C, respectively) had the highest hatching success rate and lowest deformity. Embryos incubated at 15 °C and 33 °C had the lowest hatching success rate and the highest rate of deformity, demonstrating the impacts of extreme temperatures on development and survival.

Higher temperatures are also known to accelerate embryonic development, resulting in premature hatching and smaller fish (Hansen and Falk-Petersen, 2001). Premature hatching could potentially impact overall hatching success as the hatching time may not align with the availability of external resources such as food (Viader-Guerrero et al., 2021). However, studies suggest that fish that hatch prematurely may survive longer without the presence of food, which is likely due to the increased size of their yolk sacs when compared with fish that hatched later (Laurel et al., 2008).

Physiological and cellular responses to thermal stress

Elevated temperatures can also disrupt gene expression and essential biochemical processes in embryonic development (Podrabsky and Somero, 2004.) Research has shown that embryonic fish can activate stress responses that could in theory be directing energy away from other important processes, resulting in the development of heightened stress responses and increased chances of developmental deformities that could impact later survival (Van de pol et al., 2021).

One of the most universal responses to thermal stress is the heat shock response (HSR; Hu et al., 2022). This cellular stress response involves increased production of heat shock proteins (hsps), which under normal conditions help maintain cellular proteostasis. Under stressful conditions, including thermal stress, these proteins protect cellular function by repairing proteins that have been degraded and preventing the build-up of non-native proteins. The HSR is present throughout the life history of fish, from embryogenesis to adulthood and may play an important role in the ability of fish to respond to increasing temperatures (Iwama et al., 1999). Several studies have shown that *hsp* levels increase in response to increased temperatures in embryonic fish (Sales et al., 2019; Stefanovic et al., 2016; Takle et al., 2005; Werner et al., 2001, Werner et al., 2007; Whitehouse et al., 2017), and the amount of HSPs present plays an important role in protecting embryos against damage induced by exposure to increased temperatures (Mirkes et al., 1999).

In addition to stress responses, increasing temperatures can also result in physiological adjustments in metabolism, respiration, and immune function (Little et al., 2020). Research has shown that the thermal conditions experienced during embryogenesis can influence energy metabolism, impacting oxygen consumption and leading to adjustments in metabolic pathways such as glycolysis and lipid metabolism. Additionally, temperature has been shown to have long-term impacts on the thermal optima of enzymes involved in these processes. For example, zebrafish (*Danio rerio*) embryos raised at higher temperatures had increased mitochondrial and glycolytic enzyme activity at hatch compared to enzymes raised at optimal temperatures. This difference persisted into adulthood demonstrating that developmental environments can have long-term impacts on metabolic mechanisms (Schnurr et al., 2014). This notion is further supported by research that revealed that developmental temperature affects resting oxygen consumption in larval zebrafish (Barrionuevo and Burggren,1999) and resting and maximal oxygen consumption in larval cyprinids (Wieser and Forstner, 1986; Kaufmann and Wieser, 1992).

Constant vs fluctuating temperatures

While most studies have focused on the effects of rearing fish at constant temperatures, there is a growing body of research that is examining the impact of heat shock events or diel cycles that expose developing fish to short bursts of increased temperatures. Fluctuating or cycling temperatures more closely mimic the natural environment as fish developing in the wild experience natural fluctuations because of seasonal variations. These fluctuations are expected to increase because of climate change. Moreover, anthropogenic activity such as the release of thermal plumes from nuclear power plants exposes embryos in their vicinity to frequent temperature spikes (Reutter and Herdendorf, 1976.).

Research has shown that regular exposure to temperatures above a fish's optimal range can aid in increasing thermotolerance and survival (Bilyk et al., 2012; Grinder et al., 2020; Morgan et al., 2018). For example, exposing juvenile Atlantic salmon (Salmo salar) to one diel cycle increased their Critical Thermal Maxima (CTMax; Corey et al., 2017), a measure used to assess thermotolerance in fish (Becker and Genoway, 1979). Moreover, Colorado Squawfish (*Ptychocheilus Lucius)* exposed to fluctuating temperatures during development had a 10 – 30% increased chance of survival post-hatch compared to those reared at control temperatures (Bestgen and Williams, 2011).

Lim et al (2019) demonstrated that exposure to temperature spikes had no impact on the development of lake whitefish (*Coregonus clupeaformis*). Exposing embryos to a + 3°C spike in temperature for 1 hour, three times a week had little impact on hatch timing, mortality, or yolk sac absorption. Moreover, exposure to fluctuations in temperature during development appeared to have no impact on developmental processes. In contrast, Artic charr

(*Salvelinus alpinus*) exposed to +5 °C heat shocks for 24 hours, a total of seven times during embryogenesis displayed smaller body size at hatch and were less social than their counterparts raised at constant temperatures. Additionally, the fish exposed to heat shocks during embryogenesis had an accelerated growth rate and higher body condition compared to the control group (Lubin et al., 2024). Together, these results highlight the importance of the duration of such fluctuations and the fact that any observed changes due to temperature, can be species-specific.

Conclusions

Climate change is predicted to increase global water temperatures and extreme weather events, resulting in temperature fluctuations that are outside optimal developmental temperatures for fish species globally. Temperature can impact fish development in several ways, increasing growth rates and reducing time to hatch, altering phenotypes, and activating stress responses. Moreover, temperature spikes that occur in areas where fish are already surviving at the edge of their thermal range could result in temperatures that the embryos are not able to withstand.

Changes in developmental trajectories and altered phenotypes could result in emerging fish that have developed abnormalities that impact their chances of long-term survival or could, on the other hand, result in phenotypes that are better suited to environments that are less stable than those the fish historically experienced. As temperature impacts a wide range of developmental, physiological, and cellular processes, it is difficult to predict how a fish species will respond, especially during those sensitive early life stages.

Understanding the impacts of temperature on developing fish is important for predicting how fish recruitment and population levels will be impacted by climate change. Moreover, this can help inform conservation plans for wild fish populations and management strategies of global fisheries and aquaculture.

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Conflict of Interest

The author declares that there is no conflict of interest.