

Effects of Climate Change on Fish Reproduction and Early Life History Stages

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ABSTRACT

The fluctuation in temperature during different seasons exerts a significant impact on the reproductive patterns of fish. Elevated temperatures serve as a stimulus for the initiation of reproductive processes in species that spawn during the spring season, whereas declining temperatures act as a trigger for reproductive activities in species that spawn during the autumn season.

High temperatures shorten the duration of spring spawning and postpone the occurrence of fall spawning. The impact of temperature rises on reproduction is contingent upon the duration and magnitude of the increase. These impacts can range from altering the timing of spawning to completely preventing reproduction. The aforementioned impact will be more pronounced in species that face limitations in their ability to adjust their geographic distribution. Numerous studies conducted across various taxa, habitats, and temperature ranges consistently demonstrate the inhibitory consequences of increased temperature, albeit with variations in the specific environmental thresholds. The effects are produced via the endocrine system, specifically by suppressing the production of ovarian oestrogen. Larval fish typically exhibit greater susceptibility to environmental variations in comparison to their adult counterparts, rendering them potentially more susceptible to the impacts of climate change. Temperature has been found to have an impact not only on the duration of embryonic development and the survival of eggs, but also on the size of organisms at the time of hatching, the rate at which they develop, the duration of their larval stage in the open ocean, and their overall survival. Ocean acidification, a consequential outcome of climate change in marine environments, has the potential to pose a substantial risk by modifying the behaviour of larvae and compromising their sensory abilities. Consequently, this phenomenon has implications for the replenishment of populations and the patterns of connectedness among marine fish species.

I. INTRODUCTION

Fish rely heavily on temperature to control a wide range of physiological processes, especially those related to reproduction. The development, maturation, ovulation, spermiation, spawning, embryogenesis, hatching, and following phases of larval and juvenile development and survival are all under this sort of strong regulatory effect. When it comes to controlling the reproductive cycle of adults, temperature is typically considered to have a secondary role to photoperiod. However, as highlighted in the review by Pankhurst and Porter (2003), it plays an important function in synchronising the final phases of reproductive maturity and in shortening reproductive episodes. When in the annual thermal cycle spawning occurs can affect how strongly temperature effects are felt. Previous research suggests that spring and early summer spawners need warmer spring temperatures to begin maturation (Stacey 1984; Scott and Pankhurst 1992; Shimizu 2003). High temperatures, on the other hand, have been shown to postpone the commencement of maturation and ovulation in autumn-spawning species (Pankhurst & King, 2010). Embryogenesis and hatching (Pauly and Pullin 1988), larval development (Howell et al. 1998), growth (Jobling 1997), and survival (Sponaugle and Cowen 1996) are only some of the post-fertilization processes that temperature profoundly affects.

Atlantic salmon is the subject of this article. Barton (1996) reports that the highest temperature *Salmo salar* can tolerate is between 22 and 24.8 degrees Celsius. Reddin et al. (2000) note that in the ocean, the preferred temperature range for *Salmo salar* is between 4 and 10.8 degrees Celsius. As mentioned in the review by Pankhurst and King (2010), similar patterns have been identified in other salmonid species. This suggests that even temperatures that don't trigger reactions associated to tolerance in laboratory settings may have significant effects on preferences in the wild. The potential for temperature to interact with other physical and biotic variables in a synergistic manner is typically disregarded in the context of single-domain temperature research. It has been suggested that different photoperiod regimes lead to different manifestations of temperature impacts on reproduction (Pankhurst and Porter, 2003). Nutritional status appears to moderate the effect of temperature on reproduction in tropical damselfish, according to recent research (Donelson et al., 2010).

Several variables, including latitude, habitat type, water column properties, and flow patterns in riverine systems, influence how aquatic species will be affected by climate change. However, there are a few

widely held beliefs about what climate change might bring, such as a shift in seasonal temperature patterns, an increase in seasonal extremes, and an accompanying acidification of the oceans due to rising CO₂ levels in the atmosphere. Temperature increases are predicted for riverine ecosystems as a result of decreased flow rates and an increase in the prevalence of hypoxic conditions. It's worth keeping in mind, though, that these shifts' effects could vary widely according to location.

It is reasonable to assume that temperature changes will have more far-reaching effects on reproductive processes in marine ecosystems than in riverine ecosystems. Lake inflows, water column structure, and the geography of lake basins are just a few of the variables that will determine the extent of the influence on lacustrine ecosystems (Wahl and Löffler, 2009). Ocean acidification is another way in which the increase in atmospheric carbon dioxide (CO₂) levels will affect marine ecosystems. As pointed out by Ishimatsu et al. (2008), this phenomena has the potential to have an immediate impact on the reproductive processes and early life stages of a wide range of marine species. Ocean acidification, it should be noted, can also combine with the effects of temperature, as explained by Portner and Farrell (2008).

II. REPRODUCTION

Endocrine control of reproduction

The hypothalamic-pituitary-gonadal (HPG) axis mediates the effects of environmental changes on reproductive processes. The hypothalamus produces peptide gonadotropin-releasing hormones (GnRH), which are then secreted into synapses in the pituitary gland that are directed at the gonadotropic cells there. Two protein hormones, follicle-stimulating hormone (FSH) and luteinizing hormone (LH), are produced and secreted in response to this interaction. Several authors, including Planas and Swanson (2008), Levavi-Sivan et al. (2010), and Zohar et al. (2010), have discussed these findings at length. The release of follicle-stimulating hormone (FSH) and luteinizing hormone (LH) is dependent upon the equilibrium between gonadotropin-releasing hormone (GnRH) stimulation and dopamine inhibition (as discussed in the review by Dufour et al., 2010). This is because the presence of dopamine (DA)-secreting neurons also contributes to inhibitory regulation. Pineal gland, which is sensitive to light, produces melatonin, which affects the interaction between GnRH and pituitary gland. According to the review by Migaud et al. (2010), it is still unclear how exactly melatonin influences this interaction. In addition, as detailed in Akazome et al.'s (2010) review, the kisspeptin system has direct effects on the activity of GnRH-producing neurons. Pankhurst (2008) reviews the literature and finds that gonadal steroid feedback effects also play a role in modifying this relationship.

TEMPERATURE AND THE HPG AXIS

Changes in temperature can affect the HPG axis in a variety of ways, including the rate of hormone synthesis and activity and the structure of hormones. Multiple endocrine processes have a base temperature below which they will not function, as detailed by Pankhurst and King (2010). Within the physiologically acceptable range, crossing this threshold increases hormone synthesis, activity, and metabolism. At the top end of this range, however, it causes activity to decrease. Proteins like FSH, LH, their receptors, and steroid-synthesizing enzymes undergo structural changes at elevated temperatures, which can have an inhibiting effect. Steroid hormones also play a role because of their tendency to generate water-soluble conjugates at elevated temperatures (Van Der Kraak & Pankhurst, 1997). When steroids are conjugated to sulphates or glucuronides, they lose both their solubility and their ability to cross cell membranes, reducing their capacity to interact with intracellular receptors. They are also much less stable in the plasma because they are more easily filtered out by the kidneys and eliminated in the urine.

Reproduction suppression due to temperature is reported across taxa, habitats, and temperature ranges, regardless of the mechanisms involved. When it comes to suppressive effects, different species have different thresholds, as seen in Table 1 (Pankhurst & Munday, 2016). However, temperatures of 30°C and above have a suppressive effect on tropical species (Table 1). This finding lends credence to the idea that similar responses to rising temperatures are common among all species, with differences in the sensitivity of species to heat. It has also been hypothesised that cool-water and temperate species may have a greater range of normal function compared to tropical species (Nilsson et al., 2009; Donelson et al., 2010).

Research on temperate species, with the majority of evidence coming from studies focusing on salmonids, has improved our understanding of the mechanisms behind the heat suppression of reproductive behaviours. Arctic charr (*Salvelinus alpinus*) kept at 10°C, which is known to inhibit regular ovulation, showed increased responsiveness in terms of LH secretion and subsequent ovulation when exposed to synthetic analogues of gonadotropin-releasing hormone (GnRH_a) in combination with the dopamine antagonist pimozide, as compared to GnRH_a alone, according to research by Gillet and Breton (2009). Based on these results, it appears that an increase in dopamine inhibition in the pituitary gland may play a role in the inhibitory mechanism that suppresses ovulation in Arctic charr. When temperatures rise in the summer and fall, they suppress the steroid-converting enzyme P450 aromatase (arom) in Atlantic salmon, *Salmo salar*, preventing the

ovary from producing E2 from androgen precursors. As a result, the liver produces less vitellogenin (Vtg), leading to smaller eggs overall, lower fertility, and worse rates of survival. The decreased binding strength of hepatic E2-receptors is another consequence of increased temperature during the vitellogenesis process. In late autumn, when vitellogenesis is complete, higher temperatures limit the production of the maturational steroid 17,20bP and, in turn, the progression of acolytes through final ovarian maturation and ovulation (Pankhurst & King, 2010).

Table 1.
Summary of inhibitory effects of elevated temperature on reproduction across a range of species, habitats and thermal ranges
Temperatures above which effects occur (where known)

Species	Habitat	Effects	Authors
Arctic charr <i>Salvelinus alpinus</i>	Cold temperate/sub-Arctic freshwater	Inhibition of LH secretion, ovulation (10–118C)	Gillet 1991; Jobling et al. 1995; Gillet and Breton 2009
Wolffish <i>Anarhichus lupus</i>	Cold temperate/sub-Arctic marine	Reduced steroid (T and E2) production, ovulation, fertility and survival (128C)	Tveiten and Johnsen 2001; Tveiten et al. 2001
Lake whitefish <i>Coregonus lavaretus</i>	Cold temperate lacustrine	Delayed ovulation and spawning	Wahl and Löffler 2009
Atlantic salmon <i>Salmo salar</i>	Cold temperate anadromous	Reduced Vtg and ZP gene expression, steroid (T, E2 and 17,20bP) production, aromatase activity, ovulatory frequency, fertility, egg survival (188C)	Pankhurst and King 2010
Rainbow trout <i>Oncorhynchus mykiss</i>	Temperate freshwater	Reduced steroid production (T, E2, 17,20bP), fertility and survival (18–218C)	Pankhurst et al. 1996; Pankhurst and Thomas 1998
Red seabream <i>Pagrus major</i>	Temperate marine	Aromatase and 11b-hydroxylase inhibition(248C)) Lim et al. 2003
Pejerrey <i>Odontesthes bonariensis</i>	Warm temperate freshwater	Reduced LH b-subunit and FSH-receptor gene expression, T and E2 levels, fertility (248C)	Soria et al. 2008
Spiny damselfish <i>Acanthochromis polyacanthus</i>	Tropical marine	Reduced reproductive output, aromatase activity, E2 production (308C)	Donelson et al. 2010; N. W. Pankhurst, P. M. Pankhurst and L. Gonzalez-Reynoso, unpubl. data
Humbug <i>Dascyllus dascyllus</i>	Tropical marine	Reduced E2 production (338C)	N. W. Pankhurst, P. M. Pankhurst and L. Gonzalez-Reynoso, unpubl. data

The impact of global warming on fish populations is at the heart of this debate. Marine and Freshwater Research shows that this effect is suppressive on the pituitary gland as well. It is important to emphasise that our understanding of how temperature affects reproductive physiology as a whole is still limited. The function of temperature in reproduction regulation, however, cannot be denied at any point in the reproductive process (see

Figure 1).

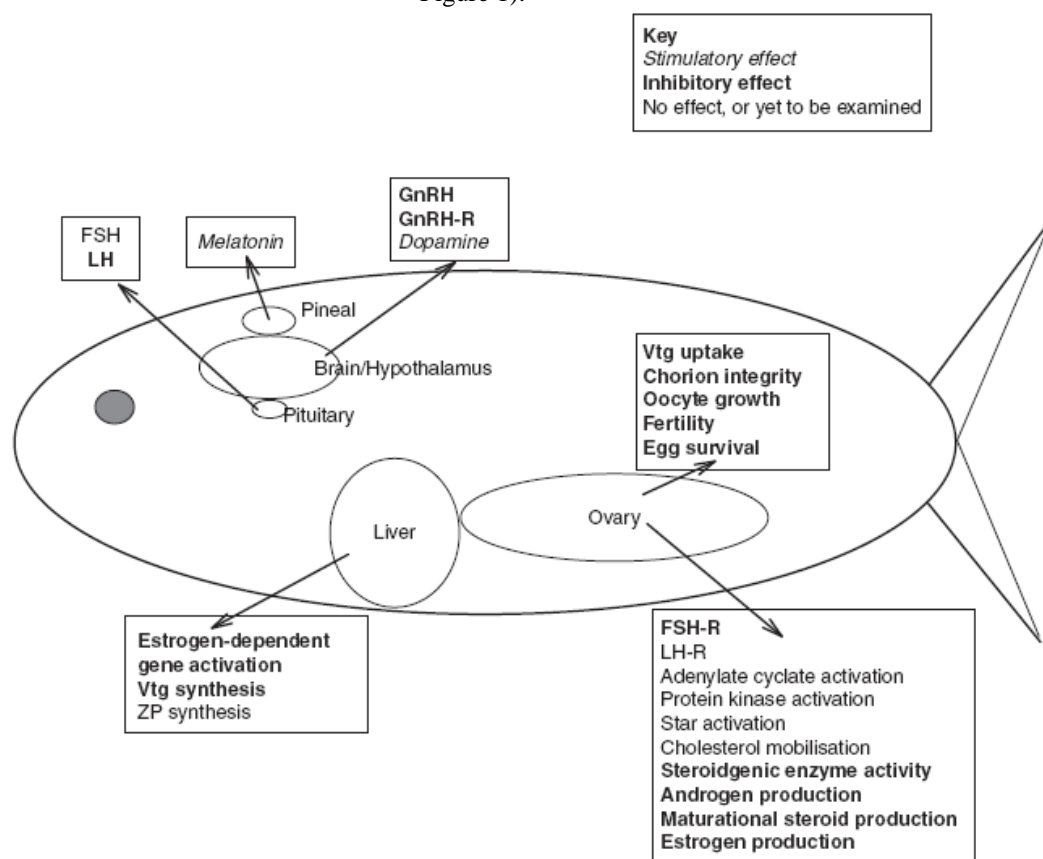


Fig. 1. Schematic summary of the effects of above-normal temperature on reproductive processes in teleost fish. Components in bold are inhibited by high temperature, items in italics are stimulated at high temperature, normal text means no measurable effect or yet to be investigated.

STRESS AND REPRODUCTION

The activation of a hormonally-mediated stress response as a mechanism of heat inhibition is one possible explanation, however it does not rule out alternative possibilities. Pankhurst and Van Der Kraak (1997), Leatherland et al. (2010), and Schreck (2010) all report that stress has a negative impact on fish reproductive. A fast response mediated by catecholamines is initiated in the presence of stress, leading to an instantaneous increase in energy availability and oxygen supply to the tissues. Following this, as mentioned in the review by Pankhurst (2011), the hypothalamic-pituitary-interrenal (HPI) axis is activated for a longer period of time, leading to increased levels of cortisol in teleosts and chondrosteans and 1 α hydroxycorticosterone in elasmobranchs. Pankhurst (2011) states that an increase in corticosteroids causes a temporary increase in the availability of certain energy substrates. Exposure to elevated cortisol levels, however, has inhibitory effects on various physiological processes, such as reproduction, growth, and immune function, if it lasts for an extended period of time.

Cortisol has a primarily catabolic function, which is responsible for the long-term repercussions. Also, after 15-30 minutes of stress, plasma levels of testosterone (T) and estradiol (E2) might drop significantly (Haddy and Pankhurst, 1999). The exact mechanism by which cortisol produces its rapid effect is unclear, however (Pankhurst et al., 1995).

Alterations in environmental temperature may limit reproductive processes, but it is important to consider whether or not stress plays a role in this suppression. Increasing temperatures have been shown to be a significant stressor in controlled laboratory environments (Pankhurst, 2011). Plasma cortisol levels do not significantly rise in broodstock Atlantic salmon when exposed to increased temperatures that impede reproduction (Pankhurst et al., 2011). This result clearly suggests that the hypothalamic-pituitary-interrenal (HPI) axis is not responsible for the substantial inhibitory effects seen in salmonids. There is also the issue of how commonplace it is for fish to experience stressful conditions in their natural environment. Evidence for the existence of stress reactions over a wide range of environmental conditions has been found to be weak (Schreck, 2010; Pankhurst, 2011). It is important to note that extreme weather is often the cause of stress reactions in

vertebrates of all kinds in the wild. Such occurrences are likely to coincide with storms and floods, which make it difficult to obtain samples from wild fish populations (Pankhurst, 2011).

Additional considerations

Consistently elevated temperatures have been found to inhibit gonadal aromatase activity in fish, which has led researchers to notice that this suppression of aromatase will likely have two additional reproductive consequences related to the role of aromatase in sex determination and sex inversion. During the early stages of sex differentiation in fish, there is a wide range of phenotypic sex. Brain arom-dependent oestrogen production leads to the development of female phenotypes (Devlin and Nagahama, 2002), while arom inactivity leads to the development of male phenotypes. Guiguen et al. (2010) reviewed the effects of temperature on aromatase activity and found that it is suppressed at higher temperatures, which favours the male phenotype during sex determination. One theory suggests that within the temperature range that supports reproductive capability, a rise in sea temperatures may cause a greater preponderance of male fish. Potential population resilience impacts of this phenomena are still unknown.

Ocean acidification and reproduction

Surface oceans are absorbing more carbon dioxide (CO₂) as atmospheric CO₂ levels rise, lowering pH and lowering carbonate ion concentrations in the shallow ocean. The process of rising acidity in the ocean, or ocean acidification, is widely accepted as a serious threat to many marine organisms. Carbonate ions are essential for the production of shells and skeletons in calcifying organisms (Hoegh-Guldberg et al., 2007; Fabry et al., 2008; Smith, 2009). In addition to influencing acid-base balance and oxygen availability, a rise in carbon dioxide content (pCO₂) can have direct physiological effects on aquatic species (Po rtner et al., 2004; Po rtner and Farrell, 2008). Because gaseous CO₂ is so much more permeable to biological tissue than hydrogen ions are, the possible implications of rising pCO₂ levels in water are likely to be of greater significance than the direct fall in pH (Brauner, 2009). Larval fish, in particular the red seabream (*Pagrus major*), are more vulnerable to the effects of acidification due to CO₂ than they are to the same pH levels reached with mineral acids, according to research by Kikkawa et al. (2004). Tissue acidosis, typified by a reduction in pH and a buildup of bicarbonate, develops in response to elevated pCO₂ levels. Protein synthesis, enzyme function, and oxygen transport are just a few cellular processes that could be negatively impacted by this illness (Po rtner et al., 2004). Fish are able to neutralise acidosis by excreting ions that have an acidic or basic equivalent. The branchial epithelium is primarily responsible for this process, with the kidneys and intestines playing secondary roles (Claiborne et al., 2002). When compared to certain invertebrates, fishes are often more tolerant of high levels of ambient CO₂ (Ishimatsu et al., 2008; Widdicombe and Spicer, 2008). Fishes have sophisticated acid-base regulation mechanisms (Po rtner et al., 2004; Melzner et al., 2009), which may account for their increased tolerance. However, there is still a lack of knowledge about how long-term exposure to pCO₂ levels estimated to manifest in the next 50-100 years (reaching up to 1000 ppm CO₂) can affect fish reproduction. Initial research suggests the impacts may be minor because of the small sample size. When the flounder species *Limanda yokohamae* is exposed to even moderate increases in pCO₂, sperm motility stops moving, according to studies by Inaba et al. (2003). However, Inaba et al. (2003) stated that this effect was not seen in 10 other species from a variety of families. The Baltic cod species, *Gadus morhua*, was also found by Frommel et al. (2010) to not have any similar effects on sperm motility under the same conditions.

Species-specific differences exist in how fish eggs react to elevated CO₂ levels. However, current research indicates that the LC₅₀, or the concentration at which 50% of an organism's population dies within 24 hours, is typically greater than 10,000 ppm of CO₂ (Ishimatsu et al., 2008). In addition, the study by Munday et al. (2009a) found that exposing clownfish (*Amphiprion percula*) eggs to a concentration of 1000 parts per million of carbon dioxide (CO₂) had no detectable effect on the duration or viability of the eggs. Pelagic spawners' eggs may be more vulnerable to CO₂ stress than benthic spawners' eggs, such as clownfishes'. This could be because the environmental pCO₂ experienced by pelagic eggs is more stable than that experienced by benthic eggs. It should be noted, however, that this notion has not been thoroughly researched.

One potential problem is that adults' ability to engage in aerobic activity may be hindered by high pCO₂ levels (Po rtner and Farrell, 2008), which in turn may have an effect on their reproductive output. Two species of tropical cardinalfish, *Ostorhinchus doederleini* and *O. cyanosoma*, experienced a 33% and 47% loss in their aerobic capacity when exposed to a carbon dioxide concentration of 1000 ppm, respectively. The average summer temperature of the population under study was 29.8 degrees Celsius, therefore these people were also exposed to temperatures as high as 38 degrees Celsius above that. In 2009b, Munday et al. reported these data. It is reasonable to hypothesise that a loss in aerobic capacity may have an effect on reproductive function, albeit the exact nature of that relationship is yet unclear. Sockeye salmon, or *Oncorhynchus nerka* as they are called by their scientific name, fail to migrate and spawn because their aerobic scope collapses due to

extremely high water temperature (Farrell et al., 2008). There is still a lot of mystery about how elevated CO₂ levels might influence the endocrine pathways that control reproduction in fish.

Early life history stages

Effects on egg incubation

Eggs are a particularly temperature-sensitive stage in a fish's life cycle; several species show limited tolerance to temperatures 6 to 8 degrees Celsius above or below the spawning temperature (Rombough, 1997). Gagliano et al. (2007) found that in tropical species, even modest increases in temperature can have a major impact on the mortality rate of eggs. Unless species shift when they spawn to coincide with the optimal temperature conditions for the development of embryos, the chances of hatchling survival may fall as oceans and rivers warm. Due to the temperature sensitivity of gametogenesis in many fish species, it is expected that fish breeding patterns will change. It's possible that breeding efforts might stop before temperatures reached those essential for egg survival. For example, in brook trout (*Salvelinus fontinalis*), the temperature at which gametogenesis is triggered is 28 degrees Celsius lower than the temperature at which fertilised eggs will develop normally (Rombough, 1997). However, some species are known to engage in spawning behaviours at less-than-ideal temperatures, which can significantly reduce embryonic survival. Increased mortality during development owing to heat (Gillet et al., 1996; Pankhurst and Thomas, 1998; Janhunen et al., 2010) and the detrimental effect of heat on gamete viability during ovulation (Van Der Kraak and Pankhurst, 1997). Temperature has a major impact on the development time of an embryo. According to Rombough (1997), for many species, an increase of 10 degrees Celsius in temperature results in a Q₁₀ value of 3, meaning that the pace of embryonic growth more than triples. There appears to be a relationship between the average water temperature and the incubation period, with shorter times indicating faster development. Incubation times vary depending on egg size, with larger eggs taking more time to hatch than smaller ones (Pauly and Pullin, 1988). Therefore, higher temperatures can hasten the hatching process, cutting down the time required from minutes to hours for small eggs and from hours to days for large eggs. In cold water species with longer incubation times, this tendency is more pronounced (Rombough, 1997). Possible discrepancies between the timing of hatching and the presence of adequate conditions for the survival of larvae could mitigate the beneficial effects of shorter incubation periods on individual fitness. Nighttime is a common time for benthic eggs to hatch, as this is when the larvae are less likely to be preyed upon by predators that rely on sight (Robertson, 1991; Michael, 2008). In some species, environmental stimuli such as daily light cycles can have an effect on the hatching process. This system ensures that larvae hatch at the best possible time, even if they have the potential to do so.

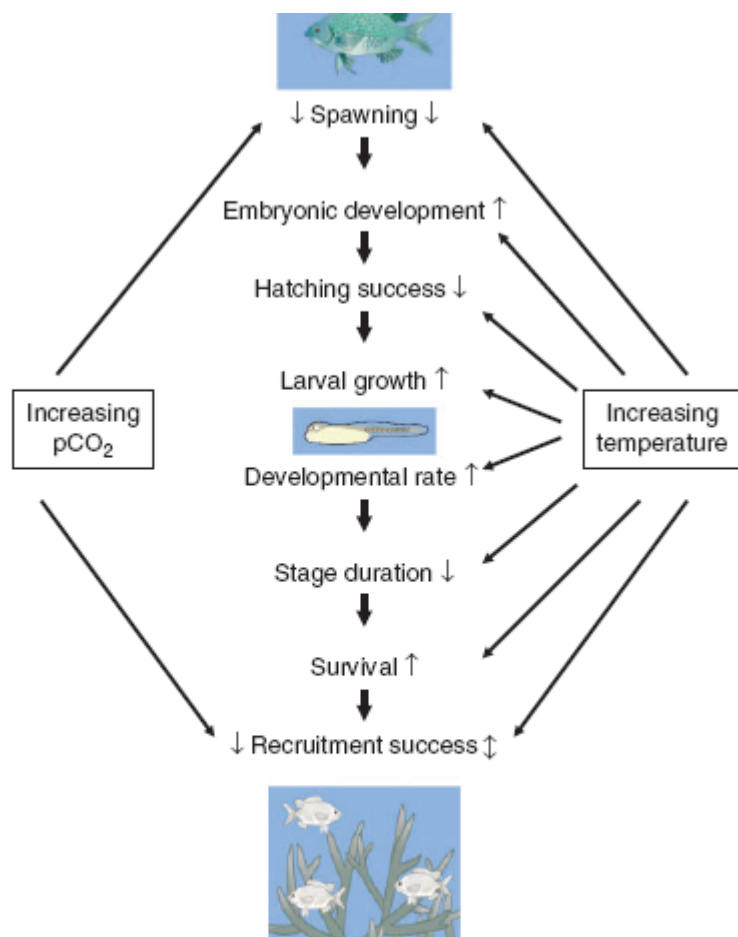


Fig. 2. Physiological and ecological responses to increased water temperature and elevated pCO₂ during the early life history of fishes. ↑ = increasing rate, ↓ = decreasing rate, ↕ = rate may increase or decrease depending on other environmental parameters.

Acclimation and adaptation

Numerous fish species are found in water at temperatures spanning the entire temperature spectrum, from mild to extremely cold. According to Munday et al. (2008a), this finding suggests that these species are able to modify or adapt to environmental temperature shifts. There is scientific evidence to support the idea that a person's previous exposure to heat may affect how they respond to high temperatures in the future. Bullhead populations, specifically *Cottus gobio*, originating from a stream system with a narrower annual thermal range (4.5-11.58C) were found to be less resilient to the detrimental impacts of elevated temperatures than those originating from a stream system with a wider thermal range (0.5-19.28C), according to research by Reyjol et al. (2009). Gardiner et al. (2010) found that under high temperature conditions, northern Great Barrier Reef (GBR) populations of four reef fish species belonging to the families Apogonidae and Pomacentridae performed worse than southern GBR populations of the same species. It's important to note that fish in the southern GBR are subjected to more extreme temperature swings. This finding indicates that the native populations of these species have acclimated or adapted to the climatic conditions of their native habitat. It also suggests that populations from more variable environments may be better equipped to deal with future heat stress.

Prolonged exposure to elevated temperatures, however, can result in some improvements due to acclimatisation mechanisms, even if acute thermal stress normally leads to a loss in reproductive potential. Spiny damselfish were studied in the lab, and it was found that animals kept at high temperatures from birth had a greater ability to sustain reproductive activities at temperatures exceeding 30.8°C compared to those individuals who only underwent a brief period of thermal acclimation lasting a few weeks (Donelson et al., 2011). The thermal history of the parent species is also very important to think about. When exposed to high temperatures, the offspring of parents who thrived in hotter environments show improved thermal tolerance or increased performance (Rombough 1997).

III. CONCLUSION

Most fish species can expect, or are currently experiencing, an effect on reproductive and early life history events due to climate change. This phenomenon is observable on various levels and is supported by a wide variety of systems, the complexity of which is growing in recognition as our understanding deepens. Fish react differently to thermal challenges depending on a number of factors, including the interaction between changes in physical variables and their habitat, the fish's energy status and reproductive age, the challenge's intensity in triggering a physiological stress response, the timing of spawning events, and the fish's specific stage in the reproductive cycle. There is also a general consensus that, with the exception of a select few species, our current understanding is insufficient to create reliable predictions of the probable consequences of different circumstances. This hinders our capacity to devise effective management methods. A fish's ability to survive temperature changes is profoundly affected by this factor. Unfortunately, our current knowledge of these repercussions is extremely restricted.

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