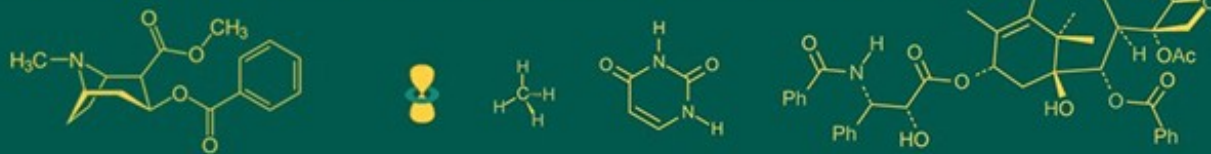


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Climate change impacts on fish reproduction and early life stages: A review

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ABSTRACT

This review examines the effects of climate change on fish reproduction and early life stages. It begins with an overview of the natural and anthropogenic drivers of climate change and their broad environmental consequences, followed by a summary of the natural, semi-natural and artificial methods used in fish propagation. The environmental, nutritional and physiological determinants of reproductive success in fish are then considered, together with the neuroendocrine pathway, centred on the hypothalamo-pituitary-gonadal axis, that integrates these determinants and underlies spawning migration and reproductive timing. The review then examines how rising temperature, ocean acidification, altered salinity and deoxygenation act on this pathway to affect the timing, quality and success of reproduction, before considering the consequences of the same stressors for egg incubation and larval growth and survival. The evidence reviewed indicates that climate-related change is already measurable in fish reproductive performance and early-life-history outcomes, with implications for wild fish populations, aquaculture production and the fisheries-dependent communities that rely on them.

Keywords: Climate change, Fish reproduction, Ocean acidification, Spawning migration

1. Introduction

Climate change is now regarded as one of the defining environmental challenges of the present century, expressing itself through erratic temperature swings, irregular rainfall and a rising incidence of extreme weather (Siddique *et al.*, 2022) [1]. The steady build-up of carbon dioxide (CO₂) and other greenhouse gases (GHGs) from human activity has altered the composition of the atmosphere and, in turn, produced far-reaching changes in aquatic environments. Acting as the planet's principal heat sink, the world's oceans exchange heat and gases with the atmosphere continuously; since the 1970s they are estimated to have absorbed close to 93% of the additional heat trapped within the Earth system. This uptake has slowed the pace of atmospheric warming even as it has raised sea-surface temperature and, through the melting of polar ice, contributed to rising sea levels. The ocean has additionally taken up roughly 28% of all CO₂ emitted by human activity since 1750, a process that has lowered surface pH and produced the phenomenon now known as ocean acidification (Servili *et al.*, 2020) [2].

These changes are not confined to the open ocean. Rising atmospheric CO₂ is altering the physio-chemical character of both marine and inland waters, producing shifts in temperature, salinity, pH, dissolved CO₂ and oxygen content, circulation, stratification and nutrient supply, all of which bear directly on physiological processes in fish, including reproduction (Doney *et al.*, 2012; Servili *et al.*, 2020) [3, 2]. Because capture fisheries and aquaculture depend on stable ecosystems and reliable breeding, the anticipated consequences of a changing climate extend beyond ecology to threaten productivity and the socio-economic security of communities that rely on these sectors (Klinger *et al.*, 2017; Siddique *et al.*, 2022) [4, 1]. Reproduction in fish is an energetically costly process governed by precise environmental cues that trigger and pace maturation and spawning and the conditions prevailing during early development are equally decisive for the survival of offspring (Servili *et al.*, 2020) [2].

Fish are, in general, more tightly coupled to their physical surroundings than terrestrial animals and aquatic habitats are comparatively more sensitive to environmental perturbation (Siddique *et al.*, 2022) [1]. Fish populations can therefore be expected to register the effects of a changing climate earlier and more acutely, than many land-based species. Beyond the purely ecological toll, the decline of fish stocks carries serious consequences for the millions of people whose livelihoods and food security depend on fisheries and aquaculture (Klinger *et al.*, 2017) [4]. This review draws together current evidence on how climate-related environmental change is affecting fish reproduction and early development, from the hormonal control of spawning through to the survival of eggs and larvae.

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2. Climate change: Concept and definition

Climate change is defined as a long-term shift in the average state of temperature and weather patterns, together with an increase in the frequency of extreme events, measured over periods of decades or longer, whether such a shift arises from natural variability internal to the climate system or from external forcing, including human activity (IPCC, 2021). It is conceptually distinct from ordinary weather variability: whereas weather describes the state of the atmosphere over hours to days, climate is the statistical description of weather conditions, typically its mean and variability, over a period of thirty years or more (National Academy of Sciences and Royal Society, 2020) [5]. Climate change reflects an alteration in this longer-term statistical baseline, arising from shifts in the atmosphere's radiative balance and its interaction with geological, oceanic, biological and geographic processes operating across the planet.

The physical basis of anthropogenic climate change lies in the enhanced greenhouse effect: GHGs such as CO₂, methane (CH₄) and nitrous oxide (N₂O) absorb and re-emit outgoing longwave radiation, warming the lower atmosphere and surface. Since the pre-industrial era, atmospheric carbon dioxide concentration has risen from approximately 280 parts per million (ppm) to over 420 ppm today, driving a rise in global surface temperature of about 1.1 °C in the decade 2011–2020 relative to the 1850–1900 baseline, an increase the Intergovernmental Panel on Climate Change attributes unequivocally to human influence (IPCC, 2021).

3. Drivers of climate change

The factors that shape the Earth's climate are conventionally grouped into natural processes, which have operated over geological timescales and continue to modulate climate at regional and decadal scales and anthropogenic pressures, whose influence on the global energy balance has intensified markedly since the onset of industrialisation and now dominates the observed trend in global temperature (IPCC, 2021; NASRS, 2020) [6].

3.1 Natural drivers

Natural drivers have governed climate on timescales ranging from years to hundreds of millions of years and remain active today, modulating, though not reversing, the centennial warming trend attributable to human activity (NASRS, 2020).

3.1.1 Continental drift

Over tens to hundreds of millions of years, the slow movement of tectonic plates has repeatedly rearranged the continents, altering the configuration of ocean basins, the pathways of ocean currents and the position of mountain ranges that influence global wind and rainfall patterns. Plate tectonic activity also regulates the long-term carbon cycle through volcanic outgassing and the weathering of silicate rocks, a balance implicated in the unusually warm climate of the Cretaceous period, roughly 145 to 66 million years ago, when elevated volcanic and tectonic carbon dioxide outgassing coincided with high global sea level (NASRS, 2020).

3.1.2 Volcanic activity

Large explosive eruptions inject sulfur dioxide (SO₂) into the stratosphere, where it is converted to reflective sulfate (SO₄²⁻) aerosols that scatter incoming solar radiation and cool the surface for one to three years following the event, even as the aerosol layer itself warms the stratosphere (Robock, 2000) [7]. The 1991 eruption of Mount Pinatubo in the Philippines, for instance, is estimated to have lowered global mean surface temperature by roughly 0.5 °C for approximately two years. Because volcanic aerosols are removed from the atmosphere within a few years, such eruptions produce short-lived cooling rather than sustained climate change, in contrast to the centuries-long persistence of anthropogenic GHGs (Robock, 2000) [7].

3.1.3 Orbital variation and axial tilt

On timescales of tens to hundreds of thousands of years, cyclical variations in Earth's orbit around the Sun modulate the distribution and intensity of incoming solar radiation and are understood to have paced the advance and retreat of Pleistocene ice sheets. These Milankovitch cycles comprise the roughly 100,000-year eccentricity of Earth's orbit, the approximately 41,000-year cycle in axial obliquity, which varies between about 22.1 and 24.5 degrees and the roughly 23,000-year precession of the equinoxes; spectral analysis of deep-sea sediment cores has confirmed that these orbital periodicities are recorded in the geological climate record (Hays *et al.*, 1976) [8]. Independently of this long-term cycle, the present 23.4-degree tilt of Earth's rotational axis relative to its orbital plane is responsible for the ordinary annual cycle of seasons, as it causes each hemisphere to receive varying amounts of solar radiation over the course of a year.

3.1.4 Ocean currents

Covering more than two-thirds of the planet's surface, the ocean absorbs and redistributes vast quantities of solar heat through a global system of surface and deep-water currents driven by wind stress and by density differences arising from temperature and salinity. This thermohaline circulation, of which the Atlantic Meridional Overturning Circulation is a key component, transports heat between low and high latitudes and has been implicated in abrupt climate shifts of several degrees Celsius over centuries, evident in the palaeoclimate record of the last glacial cycle (Rahmstorf, 2002) [9]. Because the ocean's heat capacity is far greater than that of the atmosphere, shifts in the strength or pattern of these currents exert an outsized and comparatively slow-acting influence on regional and global climate.

3.2 Anthropogenic drivers

Since the mid-twentieth century, human activity has become the dominant driver of global climate change, chiefly through the combustion of fossil fuels, land-use change and industrial and agricultural emissions of greenhouse gases (IPCC, 2021).

3.2.1 Urbanisation

The replacement of vegetated, water-retentive land with impervious, built-up surfaces during urban expansion reduces evaporative cooling and increases the storage and re-radiation of absorbed heat, producing the well-documented urban heat island effect in which cities can remain several degrees warmer than their rural surroundings, particularly at night (Oke, 1982) [10]. At continental scale, the cumulative extent of urban and built-up land also modifies local wind patterns, cloud formation and precipitation, compounding broader climatic change.

3.2.2 Industrialisation

Fossil-fuel combustion for energy and manufacturing releases CO₂, CH₄, N₂O and short-lived pollutants such as SO₂ and black carbon; these GHGs persist in the atmosphere for years to centuries and are the principal cause of the observed rise in global temperature since the industrial revolution, a conclusion the IPCC now states with very high confidence (IPCC, 2021).

3.2.3 Agrochemical use and agricultural expansion

The intensification of agriculture to meet the demands of a growing and wealthier global population has driven substantial increases in nitrogen fertiliser application and pesticide use, with associated N₂O emissions and is projected to convert further natural ecosystems to cropland over coming decades, compounding both greenhouse gas emissions and biodiversity loss (Tilman *et al.*, 2001) [11].

3.2.4 Deforestation

Forest clearance for timber, agriculture and settlement reduces the terrestrial carbon sink and alters surface albedo, evapotranspiration and the hydrological cycle; because these biogeophysical and biogeochemical effects can either amplify or dampen warming depending on latitude and forest type, deforestation represents one of the more com-

plex, but consistently climate-relevant, anthropogenic land-use pressures (Bonan, 2008) [12].

4. Broad consequences of climate change

The consequences of climate change documented by the IPCC's Sixth Assessment Report include a sustained rise in global mean surface temperature, now roughly 1.1 °C above the 1850–1900 baseline; an accelerating rate of sea level rise, from about 1.3 mm per year in the first half of the twentieth century to 3.7 mm per year between 2006 and 2018, driven by thermal expansion and the melting of glaciers and ice sheets; increasingly variable rainfall and monsoon patterns; and a growing frequency and intensity of extreme weather events such as heatwaves, droughts and heavy precipitation (IPCC, 2021). These physical changes are compounded by progressive land degradation and habitat loss and by measurable declines in wildlife populations and biodiversity across terrestrial and aquatic ecosystems alike (NASRS, 2020).

These consequences are not independent of one another: warming and precipitation anomalies together drive habitat loss and degradation, which in turn accelerates biodiversity decline, so that the cumulative effect on aquatic ecosystems is generally greater than any single driver considered in isolation.

5. Fish propagation and its methods

Fish propagation refers to the natural or induced process of reproduction and improving the survival of fish, whether in open water bodies such as rivers, lakes and seas or in controlled environments such as ponds and hatcheries. The method chosen for a given operation depends on the reproductive biology of the species concerned, the environmental conditions of the site and the facilities available and propagation techniques are conventionally grouped into three broad categories: natural, semi-natural and induced breeding (Woynarovich *et al.*, 1980; Jhingran *et al.*, 1985) [14, 13].

5.1 Natural breeding

In natural breeding, mature males and females are simply kept together in a suitable breeding enclosure, such as a small pond, where spawning proceeds without further intervention. Certain species require additional environmental cues to spawn successfully, such as a sudden inflow of fresh water for African catfish or the presence of vegetation to serve as an egg-collection substrate for common carp (Woynarovich *et al.*, 1980) [14].

5.2 Semi-natural breeding

Semi-natural breeding begins with a single hormonal injection, typically a pituitary gland extract (PGE), administered to the female to trigger the onset of spawning. The treated fish are then placed together with hormone administered males in a prepared enclosure where spawning occurs naturally, after which the fertilised eggs are collected and reared under improved and either natural or artificial conditions (Woynarovich *et al.*, 1980) [14].

5.3 Artificial breeding

Artificial breeding advances reproduction ahead of a species' natural cycle or induces spawning outside the normal season. Females receive one or more hormonal injections to bring dormant eggs to final maturity; once ripe, the eggs are stripped by hand, fertilised with milt obtained from injected males and the resulting embryos are reared entirely under controlled hatchery conditions (Woynarovich *et al.*, 1980; Jhingran *et al.*, 1985) [14, 13].

6. Determinants of reproductive success in fish

Reproductive performance in fish is governed by an interacting set of environmental, nutritional and physiological determinants.

6.1 Environmental determinants

6.1.1 Temperature

Temperature is among the most decisive factors shaping the geographic distribution of fish species, since maturation and spawning in most marine and freshwater fish proceed only within a comparatively narrow thermal window. At higher latitudes in particular, the minimum and maximum temperatures compatible with spawning effectively set the geographic limits of a species and determine whether it can be successfully introduced into a new habitat. Indian major carps; *Catla* (*Labeo catla*), Rohu (*Labeo rohita*) and Mrigal (*Cirrhinus mrigala*), for example, spawn within a range of roughly 28–32 °C and fail to do so outside it, while Chinese silver carp (*Hypophthalmichthys molitrix*) and grass carp (*Ctenopharyngodon idella*) have been bred successfully at temperatures between about 28 °C and 34 °C (Jhingran *et al.*, 1985) [13]. By contrast, Pacific halibut (*Hippoglossus stenolepis*) spawn in far colder water, generally between 3 °C and 8 °C.

6.1.2 Photoperiod

Light exposure is a second major determinant of reproductive timing. Prolonged daylength accelerates maturation and spawning in genera such as *Fundulus* and *Oryzias* and *Cirrhinus reba* matures earlier when exposed to artificially extended daylength even under otherwise cool conditions. Photoperiod is thought to influence the thyroid gland, which in turn affects migratory behaviour linked to gonadal development. At high latitudes, spawning is typically synchronised with a specific combination of photoperiod and temperature that times the seasonal surge of primary production on which larval survival depends; at lower latitudes, where daylength, temperature and food availability vary comparatively little across the year, other cues such as monsoon timing, competition for spawning sites or habitat and food availability assume greater importance.

6.1.3 Water flow and rainfall

Many fish display a well-documented rheotactic response to water current and fresh rainwater together with flooding are primary triggers of spawning in carps. The rapid dilution of dissolved electrolytes that accompanies heavy monsoon rain is understood to promote hydration in fish and stimulate the gonads and spawning has repeatedly been observed to intensify during and immediately after periods of heavy rainfall and cloud cover.

6.1.4 Salinity

Salinity gradients, which are often pronounced within estuaries, can prompt some species to shift their spawning grounds in response to local changes. Water mixing, precipitation and freshwater runoff all modulate salinity and, through it, exert a further influence on spawning patterns.

6.2 Nutritional determinants

Broodstock diet has long been recognised as a determinant of fecundity, fertilisation rate, egg quality and larval performance and inadequate or unbalanced nutrition remains a major constraint on seed production in aquaculture (Pandey, 2024) [15].

6.2.1 Protein

Dietary protein level influences the onset of puberty, oocyte development, spawning performance and egg quality and the optimal protein requirement differs across species and life stages; in several carp species, egg and larval performance improve up to a threshold protein level beyond which further increases yield little additional benefit (Pandey, 2024) [15].

6.2.2 Lipid

Lipids supply the principal source of metabolic energy for spawning and are the most extensively studied macronutrient in broodstock nutrition. Certain fatty acids (FAs) influence pituitary function in teleosts and thereby help regulate gonadal and sex-steroid hormone levels, while polyunsaturated fatty acids (PUFAs), notably the precursors of prostaglandins, contribute to steroidogenesis, ovulation and other reproductive processes. Supplementing broodstock diets with long-chain PUFAs has been shown to raise fertilisation rates and improve larval survival in several cultured species (Pandey, 2024) [15].

6.2.3 Carbohydrate

Carbohydrates play a comparatively minor role in fish nutrition relative to protein and lipid, since most fish have a limited capacity to digest them; consequently, carbohydrate content is generally considered less critical to reproductive outcomes than other dietary components.

6.2.4 Vitamins

Several vitamins support fish health and growth more broadly, but vitamins A, C and E in particular have been linked to spawning performance, with their dietary importance increasing as females age (Pandey, 2024) [15].

6.2.5 Minerals

Dietary minerals also contribute to successful spawning, although their overall influence is generally regarded as smaller than that of protein, lipid or the fat-soluble vitamins (Pandey, 2024) [15].

6.3 Physiological determinants

Physiological regulation of reproduction in fish is mediated principally through hormones, which govern migratory behaviour, the timing of reproduction, morphological changes associated with maturation, the mobilisation of energy reserves and the expression of courtship behaviour. These physiological processes do not act in isolation from the environmental and nutritional determinants discussed above; rather, environmental cues and nutritional status are transduced into the hormonal signals described in the following section, which together coordinate the reproductive cycle from initial gonadal recrudescence through to spawning.

7. Neuroendocrine regulation of fish reproduction

Reproduction in fish is coordinated by an intricate network of environmental, social, neural, hormonal and metabolic signals (Gabilondo *et al.*, 2021) [16]. Central to this network is the hypothalamo-pituitary-gonadal (HPG) axis, in which gonadotropin-releasing hormone (GnRH), secreted by the hypothalamus, stimulates the anterior pituitary to release the gonadotropins (GtH) luteinising hormone (LH) and follicle-stimulating hormone (FSH). These, in turn, drive the gonads to synthesise the sex steroids estrogen and testosterone, which govern gametogenesis, vitellogenesis and final oocyte maturation in females and spermatogenesis and spermiogenesis in males, while also shaping secondary sexual characteristics, mediating feedback to the hypothalamus and pituitary and influencing reproductive behaviour and the timing of spawning (Pankhurst and Munday, 2011; Levavi-Sivan, 2018; Gabilondo *et al.*, 2021; Santhakumar, 2023) [16, 17, 18].

In many species, dopaminergic neurons exert an inhibitory influence on FSH and LH release, so that gonadotropin output reflects a balance between GnRH stimulation and dopaminergic suppression. FSH primarily drives the early stages of gamete development, whereas LH governs final maturation, both acting at the level of the gonad. Testosterone and its more potent derivative, 11-ketotestosterone, are the principal androgens in males, while in females testosterone is further converted to the estrogen 17 β -estradiol (Pankhurst *et al.*, 2011) [18].

8. Spawning migration in fishes

Migration describes the large-scale, purposeful movement of animal populations undertaken to meet essential life-history needs rather than simple, incidental displacement and in fish it typically serves the ob-

jectives of spawning, feeding or seeking refuge (Meixler *et al.*, 2009; Deng *et al.*, 2023) [20, 19]. Long-distance migration between distinct aquatic environments, as seen in salmonids, contrasts with the short daily movements many juvenile fish make between open-water and nearshore zones chiefly to feed and avoid predators (Bohl, 1979; Dodson, 1997; Eklöv, 1997; Deng *et al.*, 2023) [21, 22, 23, 19]. Because migration links feeding and breeding grounds, it has a marked influence on population dynamics and can reshape the species composition of the habitats concerned (Brönmark *et al.*, 2008; Deng *et al.*, 2023) [24, 19].

Spawning migration is strongly tied to temperature, particularly among species that spawn in spring and its success depends on the synchrony of movement across the migrating population. Spring spawning migration is well documented in freshwater species such as northern pike (*Esox lucius*), roach (*Rutilus rutilus*), perch (*Perca fluviatilis*), ruffe (*Gymnocephalus cernua*), common bream (*Abramis brama*) and bleak (*Alburnus alburnus*); temperature influences both the duration and intensity of these movements, while light becomes an additional trigger where thermal conditions fluctuate (Deng *et al.*, 2023) [19]. Migration undertaken specifically to reach spawning grounds requires a destination that offers favourable abiotic and biotic conditions to support the eggs, embryos, newly hatched larvae and juveniles that will follow.

8.1 Environmental factors influencing migration

The relative importance of individual environmental cues varies with habitat, but movement, resource availability, predation risk, water flow and temperature are consistently implicated and many species show a striking capacity to return to their natal site once sexually mature.

8.1.1 Photoperiod

Seasonal changes in daylength act as a programmed cue that initiates the physiological preparations for migration and extended movements such as those of Pacific salmon and lampreys appear to be driven primarily by this signal.

8.1.2 Water flow

Rising water levels, especially during spring snowmelt, can trigger migration by helping fish locate stream entrances, although excessively strong flows risk displacing eggs and larvae.

8.1.3 Water temperature

Temperature can itself act as a migratory trigger, prompting fish to seek habitats within their thermal tolerance or to move toward conditions better suited to a particular life-history stage, since the thermal optimum for growth often differs from that required for reproduction. In many species with comparatively short migrations, temperature additionally functions as a synchronising cue for spawning.

8.2 Climate change and fish migration

Fish migration, an ecological process essential to the survival of numerous species, is increasingly threatened by human activity and climate change; recent scholarship has identified climate change as the foremost of these threats, given its capacity to disrupt the environmental conditions on which migratory success depends (Tamario *et al.*, 2019) [25]. Hydrogeography, temperature, precipitation, ice cover, sea level and salinity gradients are all changing rapidly under global warming, producing novel, more variable and more extreme conditions that reshape migration patterns, depress reproductive success and generate socio-economic losses. Beyond migration itself, these shifts alter the strength and character of natural selection, genetic diversity, population dynamics, species ranges and overall ecosystem composition.

Human pressures on migratory fish long predate the current climate crisis and compound its effects, since the complex life histories of migratory species leave them vulnerable to both stressors at different life stages. Anthropogenic threats to freshwater ecosystems include physical barriers such as dams, weirs, road crossings and hydropower in

stallations; habitat degradation from changing land use, pollution and channelisation; flow alteration through abstraction and flood control; and pressure from overfishing and invasive species, which introduce additional risks of predation, competition, disease transmission and genetic exchange.

Dam construction is among the most severe threats, fragmenting and degrading habitat and disrupting the migratory routes of numerous species; the decline of the Hilsa fishery in India illustrates the scale of damage that damming can inflict on migratory river systems. Fishways and fish passes are increasingly used to mitigate these effects, though they remain only a partial remedy and raise separate concerns about loss of genetic diversity and phenotypic variation among migrating populations. Intensive fishing and habitat degradation likewise threaten diadromous species that pass through heavily exploited estuarine, coastal and marine waters. Changes in land use can further contaminate stream habitats: heavy metals damage the lateral line and olfactory organs that fish rely on for orientation, other contaminants disrupt metabolism and impair swimming performance by reducing oxygen uptake and chemical pollutants can mask the olfactory cues that guide fish back to their natal streams. Taken together, anthropogenic climate change is understood to disrupt the distribution and productivity of migratory fish by interfering with growth, survival, habitat availability and migration timing, with effects that differ across life stages, particularly among diadromous species.

9. Climate change and fish reproduction

The principal direct and indirect consequences of global climate change — temperature fluctuation, acidification, hypoxia and altered rainfall — are expected to substantially affect reproductive behaviour in fish. In polar and mountainous regions, melting ice is already altering the salinity and composition of local waters, while warming seas are prompting some species to shift toward higher latitudes, exposing them to a different photoperiod and light regime (Servili *et al.*, 2020) [2].

Reproduction in fish is entrained by cyclical environmental cues, chiefly photoperiod and temperature. In temperate latitudes, fish experience predictable daily and seasonal cycles of light and temperature and many species time reproduction to specific seasons, or even specific times of day, in response to these recurring signals (Falcon *et al.*, 2010; Servili *et al.*, 2020) [26, 2]. Most temperate and cold-water species are seasonal breeders whose reproductive cycle is set by cyclic temperature and photoperiod so as to align spawning with the period most favourable for offspring survival, whereas in tropical and subtropical regions reproduction is more often cued by temperature and prolonged rainfall. Unusual thermal patterns can shift the timing and duration of the breeding season and alter the quantity and quality of reproductive output (Servili *et al.*, 2020) [2].

Although photoperiod at a given location is unaffected by climate change, many marine fish have shifted poleward in response to warming and, in doing so, now experience a different photoperiod regime at their new latitude. This mismatch can delay reproduction and compress the breeding season (Vergés *et al.*, 2019; Servili *et al.*, 2020) [27, 2].

9.1 Temperature

Environmental influences on reproduction are transduced into physiological effects chiefly through the HPG axis and temperature can act at multiple points along this pathway by altering the rate of hormone-related reactions and even the structure of the hormones themselves.

At elevated temperature, inhibitory effects can arise from changes in the conformation of key proteins, including FSH, LH and their receptors and steroid-synthesising enzymes, as well as from an increased tendency for steroid hormones to form water-soluble conjugates (der Kraak, 1996). Once conjugated, typically as sulfates or glucuronides, these hormones lose the lipid solubility needed to cross cell membranes and reach intracellular receptors and become more readily fil-

tered by the kidney and excreted, sharply shortening their residence time in plasma.

Warmer water has been shown to alter GnRH secretion, gonadotropin clearance and gonadal steroidogenesis in salmonids and temperature shifts during critical developmental windows can even redirect gonadal sex determination (der Kraak, 1996; Servili *et al.*, 2020) [2]. Thermal thresholds for inhibition scale broadly with a species' thermal habitat: roughly 11–12 °C in cold-temperate and sub-Arctic species, around 18 °C in cold-temperate species more generally, below 24 °C in temperate species and 30 °C or higher in tropical species (Pankhurst *et al.*, 2011) [18].

Much of the mechanistic detail on thermal inhibition of reproduction comes from temperate species, particularly salmonids. In Arctic charr (*Salvelinus alpinus*), holding fish at 10 °C — a temperature that normally suppresses ovulation — but co-administering a synthetic GnRH analogue with the dopamine antagonist pimozide restored LH secretion and ovulation more effectively than the GnRH analogue alone, implying that part of the thermal inhibition operates through heightened dopaminergic suppression at the pituitary (Gillet and Breton, 2009). In Atlantic salmon, elevated summer and autumn temperatures suppress the steroid-converting enzyme aromatase, lowering ovarian estradiol synthesis and, in turn, hepatic vitellogenin production, with knock-on reductions in final egg size, fertility and survival. Heat exposure during vitellogenesis also lowers the affinity of hepatic estradiol receptors and, later in the cycle, impairs synthesis of the maturational steroid 17 α ,20 β -Dihydroxy-4-pregnen-3-one (17,20 β -P), disrupting the resumption of meiosis and ultimately preventing ovulation (Pankhurst *et al.*, 2010) [28].

Comparable effects have been reported in non-salmonids. Wolffish (*Anarhichas lupus*) show reduced plasma testosterone and estradiol, delayed ovulation and lower fertility and survival under warming; red seabream (*Pagrus major*) show suppressed expression of the genes encoding aromatase and 11 β -hydroxylase; and freshwater pejerrey (*Odontesthes bonariensis*) show reduced plasma estradiol in females and testosterone in males, alongside lowered expression of LH β and the FSH receptor in females exposed to moderately elevated temperature. There is also evidence that high temperature interferes with the transduction of photoperiod signals to the reproductive axis and that the amplitude of the nocturnal melatonin surge increases with temperature; if melatonin acts, as in some birds, by stimulating factors that inhibit GnRH synthesis, temperature-driven increases in melatonin secretion could constitute a further route of pituitary-level inhibition (Pankhurst *et al.*, 2011) [18].

A further, non-exclusive explanation for heat-related reproductive inhibition is activation of the hormonally mediated stress response: an acute catecholamine surge that rapidly mobilises energy and oxygen delivery is followed by sustained activation of the hypothalamic-pituitary-interrenal axis and elevated plasma cortisol and prolonged elevation of cortisol is known to suppress reproduction, growth and immune function as well as circulating testosterone and estradiol.

Temperature also shapes the timing of spawning in species-specific ways. On Australia's Great Barrier Reef, the spring-and-early-summer-spawning spiny damselfish (*Acanthochromis polyacanthus*) shows inhibition of ovarian steroidogenesis above 30 °C, whereas the later-spawning humbug dascyllus (*Dascyllus aruanus*) tolerates temperatures up to 33 °C before steroidogenesis is affected, illustrating how rising temperature can truncate spawning in spring spawners while cueing its onset in summer spawners (Pankhurst *et al.*, 2011) [18].

Temperature-driven inhibition of gonadal aromatase activity also has consequences for sex differentiation and can drive sex reversal. Phenotypic sex is comparatively labile during the period of primary sex determination in fish: brain aromatase-dependent estrogen synthesis favours the female phenotype, while its absence favours the male phenotype (Devlin *et al.*, 2002) [29]. Because higher temperatures suppress aromatase activity, warming seas are predicted to skew sex ratios toward males even within the thermal range where reproductive performance otherwise remains viable and thermally suppressed and

matase activity may also force premature female-to-male transition in protogynous species and delay male-to-female transition in protandrous species regardless of social context. Larvae of pejerrey, medaka and Japanese flounder reared at high temperature have been observed

to masculinise and to show elevated whole-body cortisol (Servili *et al.*, 2020) [2].

Table 1 summarises reported inhibitory effects of elevated temperature on reproduction across a range of species, habitats and thermal ranges.

Table 1. Summary of thermal-inhibition effects on reproduction across selected species (adapted from Pankhurst *et al.*, 2011; Akash *et al.*, 2017) [30, 18].

Sr. No.	Species	Habitat	Reported thermal effect
1	Arctic charr (<i>Salvelinus alpinus</i>)	Cold-temperate / sub-Arctic freshwater	Suppression of LH secretion and ovulation near 10–11 °C
2	Wolffish (<i>Anarhichas lupus</i>)	Cold-temperate / sub-Arctic marine	Lowered testosterone and estradiol, delayed ovulation, reduced fertility and survival near 12 °C
3	Lake whitefish (<i>Coregonus lavaretus</i>)	Cold-temperate lacustrine	Delayed ovulation and spawning
4	Atlantic salmon (<i>Salmo salar</i>)	Cold-temperate anadromous	Reduced vitellogenin and zona pellucida gene expression, lowered aromatase activity and ovulatory frequency, reduced fertility and egg survival near 18 °C
5	Rainbow trout (<i>Oncorhynchus mykiss</i>)	Temperate freshwater	Reduced steroid output, ovulation, fertility and survival between 18–21 °C
6	Red seabream (<i>Pagrus major</i>)	Temperate marine	Inhibition of aromatase and 11 β -hydroxylase expression near 24 °C
7	Spiny damselfish (<i>Acanthochromis polyacanthus</i>)	Tropical marine	Reduced reproductive output and aromatase activity, lowered estradiol from about 30 °C

9.2 Ocean acidification

Continued uptake of atmospheric CO₂ at the ocean surface is lowering seawater pH and reducing the availability of carbonate ions in shallow waters, a process termed ocean acidification that poses a particular risk to calcifying organisms dependent on carbonate for shell and skeleton formation. Elevated partial pressure of CO₂ (pCO₂) can also act directly on fish physiology by disturbing acid-base balance and constraining oxygen availability (Pankhurst *et al.*, 2011) [18].

Experiments on red seabream indicate that larvae are more sensitive to CO₂-driven acidification than to an equivalent pH reduction achieved with mineral acids, suggesting that the physiological consequences of ocean acidification are not fully explained by pH alone (Kikkawa *et al.*, 2004; Akash *et al.*, 2017) [31, 30]. Elevated tissue pCO₂ produces acidosis — a fall in pH accompanied by bicarbonate (HCO₃) (accumulation — that can impair protein synthesis, enzyme activity and oxygen transport, with many of these effects linked to the additional branchial ion exchange fish undertake to compensate internal pH in acidified water (Servili *et al.*, 2020) [2].

Fish generally tolerate rising ambient CO₂ better than many invertebrates, owing to comparatively well-developed acid-base regulatory mechanisms and lethal-concentration thresholds for fish eggs typically lie well above 10,000 ppm CO₂. Nonetheless, little is known about the consequences of chronic exposure to the pCO₂ levels projected for the next 50–100 years and sensitivity varies considerably between species (Pankhurst *et al.*, 2011) [18]. Ocean acidification also impairs olfactory performance in several fish species and in sharks, which could indirectly compromise reproduction given the importance of chemical cues and sex pheromones for mate location and courtship (Servili *et al.*, 2020) [2]. A further concern is that elevated pCO₂ may narrow the aerobic scope of adult fish and, through it, curtail reproductive output; a collapse of aerobic scope under anomalously warm water has, for example, been linked to failed spawning migration in sockeye salmon (*Oncorhynchus nerka*) (Pankhurst *et al.*, 2011) [18].

9.3 Other contributing factors

Salinity also shapes breeding success: sustained reductions in ambient salinity can disrupt reproductive and parental behaviour, interfere with spermatogenesis and testicular homeostasis and even alter male

nest-building behaviour, such as nest-entrance size, in some marine species (Servili *et al.*, 2020) [2].

Comparatively little is known about how water deoxygenation affects reproductive performance, though fish unable to escape hypoxic water are known to respond by improving oxygen delivery and uptake, reducing overall energy demand and, eventually, shifting toward anaerobic metabolism. Prolonged hypoxia depresses growth and feeding, which can indirectly compromise reproduction and has been shown to reduce reproductive output by impairing gonadal development and gamete production in both sexes (Servili *et al.*, 2020) [2].

10. Climate change and early life stages

10.1 Egg incubation

Eggs represent a particularly sensitive stage of fish development, with tolerance in most species confined to roughly ± 6 °C of the temperature at which spawning occurred. Even modest warming can substantially raise egg mortality, especially in tropical species, implying that survival to hatching may decline as oceans and rivers warm unless species are able to shift the timing of spawning to match the thermal optimum for embryo development. Species that spawn at sub-optimal temperatures risk reduced embryonic survival on two counts: elevated temperature during ovulation can compromise gamete viability and elevated temperature during embryogenesis directly raises mortality (Pankhurst *et al.*, 2011) [18].

10.2 Larval development

Temperature strongly influences metabolism, growth, developmental rate and stage duration in larval fish. Mass-specific oxygen consumption, a proxy for metabolic rate, rises sharply with temperature, though the magnitude of this response varies markedly between species and higher metabolic rates translate into greater baseline energy demand. Larval growth rates likewise increase with temperature in both temperate and tropical species, with temperature alone accounting for as much as 89 % of the variation in growth rate among cohorts in some species (Pankhurst *et al.*, 2011) [18].

In warmer water, faster development shortens the duration of each life stage: the time to yolk absorption, the onset of metamorphosis and pelagic larval duration are all negatively correlated with temperature, both within and across species and shorter pelagic larval duration is

closely linked to faster growth. Because mortality during the larval phase is typically very high, faster growth and reduced pelagic duration at higher temperature could, in principle, improve larval survivorship (Pankhurst *et al.*, 2011) [18].

At the same time, larvae require proportionally more food at higher temperature to sustain elevated metabolic demand, leaving them more vulnerable to starvation and contributing to the greater recruitment variability, including outright recruitment failure, observed during anomalously warm periods. Recruitment of most reef fish species failed in French Polynesia during a warm El Niño event, for instance, suggesting that either reproduction or larval survival was sharply reduced across a broad range of species under high summer temperature. Modest warming may favour recruitment in some species, particularly at higher latitudes, but larger increases are more likely to produce recruitment failure, especially at lower latitudes and wherever food supply is already limited (Pankhurst *et al.*, 2011) [18].

10.3 Ocean acidification and early life stages

Larvae are expected to be more sensitive to elevated pCO₂ than adults, owing to their larger surface-area-to-volume ratio and their comparatively less developed capacity for acid-base compensation. One particularly serious consequence of rising pCO₂ is impairment of the olfactory system in some marine fish, leaving larvae unable to distinguish ecologically important chemical cues; olfactory impairment has been documented in larval clownfish and damselfish (*Pomacentrus wardi*) at CO₂ concentrations of 700–850 ppm (Pankhurst *et al.*, 2011) [18].

Conclusion

Climate change affects fish reproduction and early life-history stages through changes in temperature, ocean acidification, salinity, dissolved oxygen, rainfall and water flow. These stressors can disrupt hormonal regulation, gonadal development, spawning migration, fertilisation, egg incubation, larval growth and recruitment. Eggs and larvae are particularly vulnerable because their tolerance to environmental changes is limited. The effects vary among species according to their habitat, reproductive strategy, thermal tolerance and ability to acclimatise or adapt.

Climate change also intensifies existing pressures such as overfishing, pollution, habitat degradation, dam construction and altered river flow. Protecting spawning and nursery habitats, maintaining migratory connectivity, improving broodstock nutrition, conserving genetic diversity and monitoring environmental conditions will be important for sustaining wild fish populations and aquaculture production. Further research should focus on the combined effects of multiple climate-related stressors across different fish species and life stages.

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