

Review



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Fish reproduction in a warming world: vulnerable points in hormone regulation from sex determination to spawning

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Reproduction in fishes is sensitive to temperature. Elevated temperatures and anomalous ‘heat waves’ associated with climate change have the potential to impact fish reproductive performance and, in some cases, even induce sex reversals. Here we examine how thermal sensitivity in the hormone pathways regulating reproduction provides a framework for understanding impacts of warmer conditions on fish reproduction. Such effects will differ depending on evolved variation in temperature sensitivity of endocrine pathways regulating reproductive processes of sex determination/differentiation, gametogenesis and spawning, as well as how developmental timing of those processes varies with reproductive ecology. For fish populations unable to shift geographical range, persistence under future climates may require changes in temperature responsiveness of the hormone pathways regulating reproductive processes. How thermal sensitivity in those hormone pathways varies among populations and species, how those pathways generate temperature maxima for reproduction, and how rapidly reproductive thermal tolerances can change via adaptation or trans-generational plasticity will shape which fishes are most at risk for impaired reproduction under rising temperatures.

This article is part of the theme issue ‘Endocrine responses to environmental variation: conceptual approaches and recent developments’.

1. Climate change and fish reproduction

Freshwater and marine systems worldwide are experiencing higher average temperatures [1,2] and more frequent and severe anomalous ‘heat wave’ events [3,4] with climate change. Many fishes are now being impacted by those warmer conditions [5], with some populations changing abundance, shifting geographical range or changing phenology [6–8]. However, not all fishes will be capable of moving to higher latitudes or thermal refuges (i.e. higher elevation, deeper water), whether owing to geographical isolation, an upper elevation limit of available habitat, or rates of warming that exceed the ability to shift range [7].

Populations cannot persist without successful reproduction. However, reproduction in fishes often occurs within a narrower set of temperatures than adult survival [9–12]. Exposure to temperatures above a species’ normative range impacts reproductive processes with consequences from impaired gamete quantity and quality to altered sex ratios [9,12–15]. That vulnerability

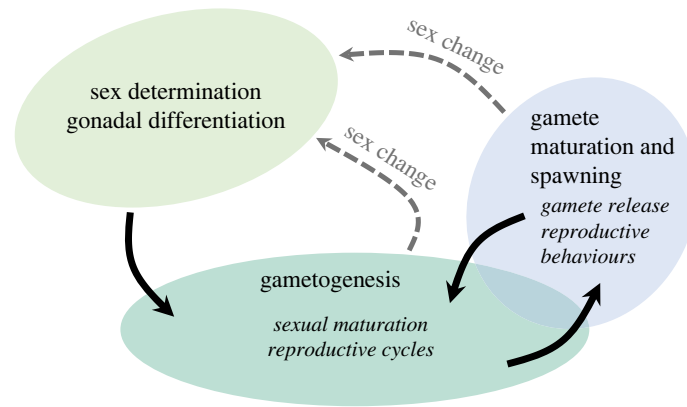


Figure 1. Temperature influences on fish reproduction occur during three developmental windows: (1) sex determination and gonadal differentiation, typically early in development, (2) gametogenesis (including initiation of sexual maturation), and (3) gamete maturation and spawning, which includes reproductive/mating behaviours. Solid arrows indicate developmental order. Dashed arrows reflect the ability of some hermaphroditic fishes to change sex. (Online version in colour.)

arises in part as a result of thermal sensitivity in the hormone pathways regulating reproductive processes from sex determination to spawning [14,16–18].

Successful reproduction depends on a sequential series of events occurring from early life through sexual maturation and spawning. Broadly, those events can be designated into ‘windows’ of development that all need to occur for effective reproduction: (1) sex determination and gonadal differentiation, (2) gametogenesis and (3) gamete maturation and spawning (figure 1). Each of those developmental processes is regulated by hormones, with earlier developmental outcomes providing definition to later processes. Each of those developmental periods, however, can be disrupted by elevated temperature, effectively making them vulnerable ‘windows’ for temperature to alter reproductive development and performance.

Together, those sensitive ‘windows’ of reproductive processes provide a framework for studying high-temperature impacts on fish reproduction. That framework points to the importance of understanding the hormonal basis for thermal sensitivities of each reproductive process and how high temperatures can alter each process. In this article, we outline that framework of hormonally mediated, thermally sensitive periods and examine how research focused on those periods can inform potential impacts of elevated temperatures on fish reproduction. While climate change increases temperature extremes and thus could lead to colder temperatures in some locations or at unexpected times of year, such effects of cooling are beyond the scope of this article.

2. Temperature effects on sex determination and differentiation

Sex determination in gonochoristic fishes (i.e. non-hermaphroditic species) ranges from strict genetic sex determination (GSD), with no documented environmental sensitivity or departures from an expected 1:1 sex ratio, to pure environmental sex determination (ESD), with no apparent underlying genetic basis [13,19]. Between those extremes, however, lie an array of sex determination mechanisms that combine genetic control by a master sex-determining gene with varying degrees of environmental sensitivity to particular conditions [15,20].

Among the environmental factors identified that may influence fish sex determination/differentiation, temperature is the best studied and leading factor associated with ESD (temperature-dependent sex determination; TSD). Temperature effects on phenotypic sex have been documented in over 70 fish species [20,21]. Some species exhibit a high level of TSD, whereas in others, TSD may represent an anomalous response occurring only when exposed to unnatural conditions in captivity, such as experimental exposure to temperatures beyond their normative range [22]. Still, should similar temperatures occur in the wild, they could have profound impacts on sex ratios and persistence of populations.

By far the most observed type of TSD in fishes is gonadal masculinization at elevated temperatures [23]. Genetic females in many species are sensitive to high temperatures and can undergo a process known as ‘sex reversal’, whereby temperature overrides processes of sex determination and differentiation, inhibits the endogenous female programme, and drives testicular development (figure 2). Although the term sex reversal suggests a change of sex, this process actually reflects a decoupling of genetic (e.g. XX/XY) and phenotypic sex, creating a mismatch [33–35]. Interestingly, very few instances of masculinization in response to low temperatures or feminization to high temperatures have been reported in fishes. Thus, the possibility of strongly male-skewed sex ratios in fish populations experiencing warming waters is of significant concern under climate change scenarios [15,33–36] and hence will be the focus here.

Temperature effects on sex determination/differentiation in fishes usually occur during a discrete developmental period known as the sexually labile period. During that period, endogenous sex-determining processes driven by sex-determining genes may be active; however, in sensitive species, temperature can redirect gonadal sex differentiation. The sexually labile period typically occurs during early larval development and is completed by, or during, the juvenile stage. That period is thought to be influenced by body size; since higher water temperatures generally induce more rapid growth, the period may pass more quickly under warmer conditions. Given the early life stage when these effects occur, fish may not be able to relocate as they choose (e.g. during passive larval recruitment) to avoid exposure to warm, sex-reversing temperatures.

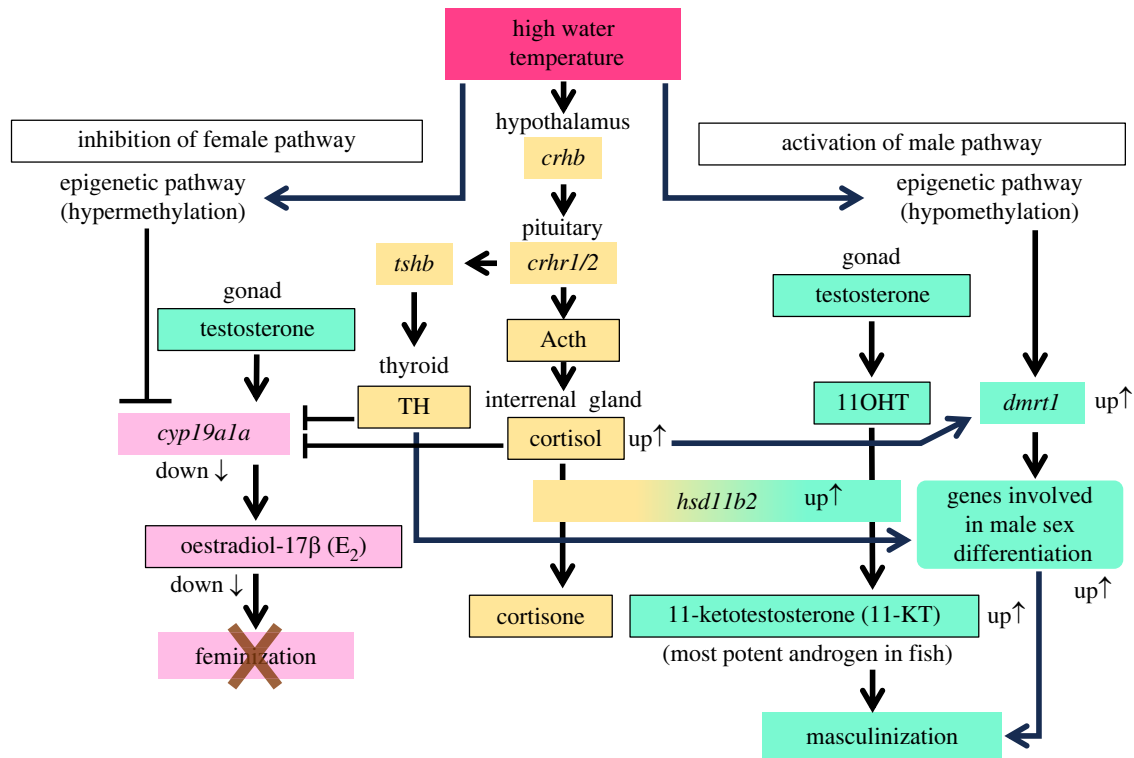


Figure 2. Potential molecular/endocrine changes associated with high water temperature-induced masculinization described in several fish species [24–32]. Green boxes indicate transcription factors, hormones and steroidogenic enzymes involved in the male pathway, while pink boxes indicate those involved in the female pathway. Yellow boxes indicate hormones and receptors involved in the stress and thyroid hormone pathways. High temperature induces masculinization via HPI/HPT-mediated and/or epigenetic-mediated pathways. Abbreviations: corticotropin-releasing hormone b gene (*crhb*); corticotropin-releasing hormone receptors 1 and 2 genes (*crhr1/2*); thyroid-stimulating hormone β -subunit gene (*tshb*); gonadal aromatase gene (*cyp19a1a*); thyroid hormone (TH); adrenocorticotropic hormone (Acth); hydroxysteroid dehydrogenase gene (*hsd11b2*); 11 β -hydroxytestosterone (11OHT); doublesex and mab-3 related transcription factor 1 gene (*dmrt1*). (Online version in colour.)

(a) Hormonal and molecular bases for temperature influences on sex differentiation

Mechanistically, gonadal sex differentiation is orchestrated by a relatively conserved suite of genes that drive testicular or ovarian differentiation [13]. To assess the impact of climate change on the sex ratios of wild fish populations, it is necessary to understand on a species-by-species basis when and how environmental temperature overrides genotypic sex. Here, we describe the hormonal and molecular mechanisms by which temperature cues override sex determination/differentiation systems in fishes, using several examples.

The overriding effects of high temperature on sex differentiation are exerted, in part, through the stress–endocrine (or hypothalamic–pituitary–interrenal gland; HPI) axis, in at least some fishes (figure 2). Broadly, the primary reaction to the perception of a stressor involves a neuroendocrine cascade involving the secretion and synthesis of catecholamines and glucocorticoids. In recent years, cortisol in particular has been identified as a key mediator between temperature and sexual development. The first response of the neuroendocrine system to environmental stress is an increase in hypothalamic corticotropin-releasing hormone (Crh). Crh then stimulates the secretion of adrenocorticotropic hormone (Acth) from the pituitary gland, which in turn regulates cortisol levels from the interrenal glands [37,38] (figure 2).

In medaka (*Oryzias latipes*) and a strong TSD species, pejerrey (*Odontesthes bonariensis*), transcripts of *crh* and its receptor *crhr* were upregulated at high water temperature during the sexually labile period and associated with elevated whole-body cortisol [38,39]. Interestingly, in pejerrey,

but not in medaka, heat-stress triggered elevated expression of *crh* and *crhr* in XX larvae relative to XY larvae, leading to a stronger stress response in the former, including higher cortisol during the labile period [39]. Such genotype-specific differential expression of *crh* and *crhr* may account for the higher thermal sensitivity of sex determination in XX-genotype in pejerrey compared with other species. Moreover, pejerrey larvae treated with cortisol showed elevated testosterone (T) and 11-ketotestosterone (11-KT) concentrations [24]. Those masculinizing effects are thought to be mediated by cortisol-induced upregulation of hydroxysteroid dehydrogenase (Hsd11b2), which catalyses 11-KT synthesis and promotes masculinization (figure 2).

Cortisol also affects transcript levels for other key genes associated with sex differentiation [24,25,38]. In medaka, a recent study showed that direct activation of autosomal *dmrt1* (*dmrt1a*) by cortisol during early development in XX embryos enabled this autosomal gene to take the place of *dmy/dmrt1bY*, the male sex-determining gene in this species, and induced masculinization at high temperatures [25]. Similarly in pejerrey, cortisol-induced elevation of the autosomal anti-Müllerian hormone (Amh) a gene (*amha*) in XX larvae may usurp Y-chromosome-linked anti-Müllerian hormone (*amhy*), thought to be the genotypic male sex determinant in this species [24,40]. Thus, expression of ancestral paralogous genes located on an autosome can function like a sex-determining gene and induce masculinization even in individuals lacking a sex-determining gene.

Recently, interaction between the HPI and hypothalamic–pituitary–thyroid (HPT) axes during high temperature-induced masculinization has been reported [26]. In medaka, high

temperature-induced elevations in Crh upregulate thyroid-stimulating hormone β -subunit (*tshb*) and elevate 3,5,3'-L-triiodothyronine (T_3), which in turn induces masculinization of XX individuals by concomitant up- and downregulation of gonadal soma-derived factor (*gsdf*; gene influencing testicular differentiation) and *cyp19a1a* (gonadal aromatase gene), respectively [26]. Thus, high temperature-induced masculinization in medaka is orchestrated by changes in HPI and HPT, as well as hypothalamic–pituitary–gonadal HPG axis signalling.

High temperature-induced masculinization typically involves inhibition of oestrogen synthesis (figure 2). Gonadal oestrogen synthesis is essential to ovarian differentiation and maintenance in fishes and regulated by the rate-limiting steroidogenic enzyme, Cyp19a1a, which converts T to oestradiol-17 β (E_2). When thermally sensitive fish are exposed to elevated temperature, *cyp19a1a* gene expression and plasma E_2 levels are strongly inhibited [23,41]. Lower E_2 downregulates cell signalling pathways driving ovarian differentiation and, in turn, pathways for testis differentiation are activated (figure 2). In olive flounder (*Paralichthys olivaceus*), cortisol activates a cAMP-responsive element on the *cyp19a1a* promoter to repress its expression [27]. The resulting reduction in E_2 production impairs ovarian differentiation in XX fish and induces masculinization.

Interestingly, in pejerrey, the level of transcripts of *amhy* declines during the sexually labile period, independent of temperature [42]. However, *cyp19a1a* is maintained at relatively high levels during this period, regardless of genotypic sex (XX/XY) or temperature [42]. These observations suggest that *cyp19a1a*-driven, ontogenetically programmed ovarian development is a default state that becomes self-sustaining in the absence of a timely and potent masculinizing stimulus (sex-determining gene and/or high temperature). Thus, the sexually labile period in pejerrey could be defined as the window of time between the decline in *amhy* expression and the attainment of a self-sustaining and sex-specific endocrine profile, at which point sexual commitment occurs [43].

Finally, epigenetics—specifically DNA methylation—also appears to underlie TSD in several fishes [28]. For example, in European seabass (*Dicentrarchus labrax*), high temperature can increase *cyp19a1* promoter methylation, inactivating its expression and leading to testicular development in genotypic females [29]. Similar epigenetic regulation was observed in olive flounder [30] and Nile tilapia (*Oreochromis niloticus*) [31]. By contrast, in half-smooth tongue sole (*Cynoglossus semilaevis*), exposure to elevated temperatures reduced methylation of the *dmrt1* promoter (hypomethylation), causing masculinization of chromosomal ZW females [32]. Of note, hypomethylation in those ZW males was heritable to ZW-genotype progeny, which later developed as phenotypic males without high temperature exposure [32]. Hence, high temperature-induced sex reversal in the parental line can give rise to a less stable GSD system in offspring [44].

(b) Identifying skewed sex ratios in wild populations

Because of the difficulty in demonstrating causal relationships between temperature and sex imbalances in wild fish, only a few studies have clearly demonstrated TSD in wild populations. One such example is the southern flounder (*Paralichthys lethostigma*), which has an XX/XY sex determination system in which the female (XX) genotype is

temperature-sensitive [41,45]. In this species, both high and low temperatures induce masculinization during early development, whereas more balanced sex ratios are obtained at intermediate temperatures (approx. 23°C) [45]. The effect of high temperature on wild populations of southern flounder was recently assessed [36]. While flounder from northern nursery habitats close to 23°C showed balanced sex ratios, southern habitats with warmer temperatures (greater than 27°C) consistently produced male-skewed sex ratios. Laboratory-rearing experiments mimicking those temperatures provided further evidence that higher temperatures were a key factor creating male-biased sex ratios in warmer nursery habitats [36].

Another recent observation of temperature and sex ratio variation in the wild comes from studies of cobaltcap silverside (*Hypoatherina tsurugae*), which has an XX/XY system and strong TSD. In this species, high temperatures induce masculinization, and low temperatures induce feminization [46]. Notably, a potential sex-determining gene, *amhy*, was discovered in this species [47]. This gene makes it possible to assess mismatches between genotypic and phenotypic sex. One recent study of wild cobaltcap silverside from Tokyo Bay, Japan, revealed both female and male sex reversals (i.e. XX males and XY females) [46]. Temperature effects on sex determination were assessed across year-classes of wild silverside by looking at hatching date and ambient temperature experienced during early development. Over the three-year experimental study period (2014–2016), sex ratios became increasingly male-biased as sex-reversed males (XX males) in the population increased. That increase was associated with a delay in spawning season by approximately one month, resulting in larvae experiencing higher temperatures during the period of sex determination [46].

These examples demonstrate that warmer temperatures are already inducing male-skewed sex ratios in some fish populations via XX-male mismatches. Importantly, XX males can only pass on X chromosomes to their offspring (i.e. they do not have Y chromosomes), so when mated with normal females, offspring would be 100% genetically female. This begs several questions: What risk does that pose to these populations? Will the risk to these populations increase as temperatures rise? And, could more strict GSD fish species also begin to exhibit sex reversals in the wild as average temperatures and the frequency of heat wave events increase?

If a fish population with ESD experiences extreme temperature conditions, highly unbalanced sex ratios can occur [15]. Theoretically, frequency-dependent selection would increase the minority sex and decrease the sensitivity of ESD in subsequent generations. For example, repeated breeding of Atlantic silverside (*Menidia menidia*) with pronounced TSD at extreme temperatures in the laboratory initially resulted in highly skewed sex ratios, but the effects gradually disappeared, with the minority sex increasing proportionally each generation until balanced sex ratios were achieved in 8–10 generations [48]; thus, a transition from TSD to GSD was observed over several generations. However, another plausible scenario is that the Y chromosome could be lost entirely as the proportion of XX males increases, shifting a population's sex determination mechanism from GSD to a purer TSD system [15]. In either case, warming may disrupt sex ratios to contribute to population declines, as was recently proposed for southern flounder [49].

3. Temperature effects on gametogenesis

Gametogenesis in fishes is influenced by environmental conditions, including photoperiod, lunar cycle, tides, water flow rate and temperature, with the importance of different factors varying among taxa (e.g. [50,51]). For species in temperate and polar latitudes, changes in photoperiod may be the primary cue entraining gametogenesis, with temperature acting secondarily [52]. In such species, however, warming temperatures can promote gametogenesis if temperatures remain within a normative range. In tropical species, lunar cycles or water flow changes across wet and dry seasons of precipitation may be foremost factors synchronizing gametogenesis and spawning [50,52]. Even so, temperature still affects reproduction in many tropical fishes, and some tropical species may actually live closer to their upper thermal limits for reproduction, given the narrower temperature ranges these species typically experience [53,54].

(a) Elevated temperatures and the endocrine regulation of gametogenesis

Several recent articles have reviewed evidence that higher-than-optimal temperatures can alter HPG axis regulation of gametogenesis in fishes [14,16–18,54], so only an abbreviated summary is provided here. For sexually mature females, high temperatures inhibit oogenesis via endocrine changes across multiple tissues: the brain/pituitary gland, the ovary and the liver. Exposure to abnormally high temperatures commonly results in lower production of hypothalamic gonadotropin-releasing hormone (Gnrh) and the pituitary gonadotropins follicle-stimulating hormone (Fsh) and luteinizing hormone (Lh) [14,16–18]. Females at higher temperatures also may show lower ovarian sensitivity to gonadotropin action (i.e. lower ovarian gonadotropin receptor expression) as well as reduced expression of steroidogenic enzymes, including Cyp19a1a [14,16–18,54–56]. Elevated temperature downregulation of steroidogenesis leads to lower circulating E₂ (similar to high temperature-induced masculinization; see §2a), which diminishes vitellogenin and choriogenin synthesis by the liver [55,56], impairs secondary/vitellogenic oocyte growth and chorion formation, and, ultimately, results in fewer or smaller eggs and lower egg viability [14].

Adult male fish have also been observed in some species to exhibit changes in HPG axis function at high temperatures [14,56–58], although effects for males vary more across species than for females. Reductions in brain *gnrh1* mRNA levels, pituitary Fsh β -subunit (*fshb*) and Lh β -subunit (*lhb*) mRNA levels, testicular gonadotropin receptor and steroidogenic enzyme expression, and circulating T and 11-KT have been reported in males of some fishes at elevated temperature [14,16,17,56,58]. Those changes in HPG axis signalling are likely responsible, in part, for the delayed sperm maturation, lower semen volumes, or reduced sperm motility observed in some fishes subjected to elevated temperature (e.g. [14,57]). Interestingly, male rainbow trout (*Oncorhynchus mykiss*) exposed to high temperature during the juvenile parr stage had lower sperm volumes and impaired sperm motility later in life, but also higher rates of survival and growth for offspring when their progeny were exposed to warmer conditions [57]. Differences in DNA methylation were recently observed in spermatozoa from male rainbow trout experiencing 12 and 16°C during spermatogenesis [59], indicating

chromatin remodelling of spermatozoa by temperature. Changes in DNA methylation/hydroxymethylation of both the testis organ and spermatozoa were also observed in three-spined stickleback (*Gasterosteus aculeatus*) exposed to +1.5 or +4°C conditions during gametogenesis [60]. The sperm and resulting embryos produced by those males also showed temperature-mediated epigenetic reprogramming of gene expression [60], suggesting epigenetic modifications to sperm DNA could contribute to phenotypic and fitness variation for the offspring of males experiencing differing temperatures during spermatogenesis.

(b) Considering temperature influences in the context of reproductive ecology

Impacts of high temperatures for gametogenesis should be expected to vary depending on how the timing and magnitude of temperature exposure relate to gametogenesis. Some fishes are semelparous; they only have one reproductive cycle in their lifetime and have coordinated recruitment of oocytes in the ovary. Others are iteroparous and spawn over multiple seasonal reproductive cycles. Characteristics of those repeated spawnings, however, vary widely [61]. For instance, some iteroparous taxa spawn a single batch of eggs per reproductive season, while others are multiple-batch spawners. Multiple-batch spawners further vary in synchrony of oogenesis of those multiple batches: some perform multiple spawnings within a reproductive season via asynchronous oocyte recruitment (spawning of a few eggs at a time), while others have temporally coordinated secondary oocyte growth where a batch of oocytes develops synchronously to be spawned together.

Identifying when key gametogenic processes occur in a fish population will be critical to understanding effects of elevated temperatures on that population. For instance, secondary oocyte growth requires vitellogenesis, which is regulated by E₂ [62]. Elevated temperatures, however, affect gonadotropin stimulation of E₂ production [14,16–18]. Given that, secondary oocyte growth may be particularly vulnerable to disruption by high temperatures. The frequency and timing of secondary oocyte growth, however, varies with differences in reproductive ecology [61] (figure 3). For semelparous fishes, secondary oocyte growth may occur long before spawning. In coho salmon (*Oncorhynchus kisutch*), for instance, pituitary Fsh secretion increases and the ovary produces more E₂ to stimulate synchronous cortical alveoli (CA) development nearly 1 year prior to final oocyte maturation [63]. Since coho salmon are complete spawners, exposure to high temperatures during that CA development period—or during vitellogenesis nearly a year later—may permanently impact fecundity. For iteroparous fishes, the timing of primary and secondary oocyte growth can vary more throughout the year, as iteroparous fishes are more variable in their reproductive ecology (figure 3). Total spawner iteroparous fishes may only experience a single year of poor egg quantity or quality if they experience elevated temperatures in a given year. Alternatively, for iteroparous multiple-batch spawners, it may be that only oocytes in secondary growth at the time of high temperature exposure are affected, but that new oocytes can be subsequently recruited when temperatures decline. Notably, some iteroparous fish species also show significant population-level variation in reproductive seasonality (e.g. [64]), suggesting

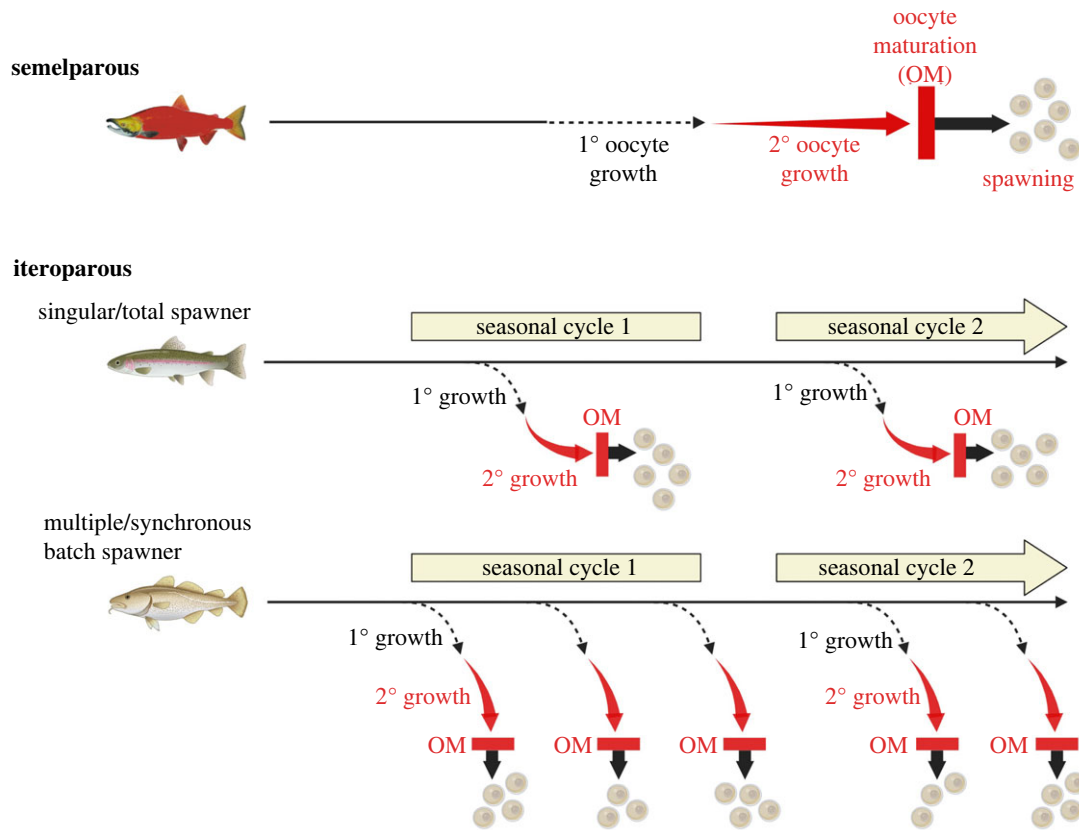


Figure 3. Frequency and timing of thermally sensitive periods for oogenesis vary with reproductive life history. Gametogenic phases when oocyte maturation is sensitive to high temperatures are illustrated in red. The developmental timing and duration of thermally sensitive periods for secondary (2°) oocyte growth and oocyte maturation (OM) vary with spawning frequency (semelparous, iteroparous) and synchrony of oocyte development (total spawner, batch spawner). Created with Biorender.com. (Online version in colour.)

potential for variation in the timing of gametogenic processes with local conditions.

Recognizing that, more studies need to characterize the timing of thermally sensitive gametogenic processes in wild populations to better understand how much and how rapidly the timing and sensitivity of those processes might vary across gradients of environmental variation. One recent study comparing two populations of Amargosa pupfish *Cyprinodon nevadensis amargosae*—one from a variable temperature river and the other from a stably warm marsh—observed differences in HPG axis sensitivity to temperature [55]; those populations were isolated for less than 50 years, implying differences in temperature regulation of hormonal pathways may arise relatively quickly under certain conditions.

4. Temperature effects on oocyte maturation and spawning

Depending on the species, post-vitellogenic oocytes may be latent for several days or months before being ovulated. Final oocyte maturation prior to spawning is regulated by Lh, which stimulates synthesis of a maturation-inducing hormone (MIH), such as $17\alpha,20\beta$ -dihydroxy-4-pregnen-3-one (DHP), from the oocyte's follicular layer [65]. MIHs trigger several changes resulting in egg maturation, including proteolysis of yolk proteins, hydration of the oocyte, and degradation of the follicular wall. Those final steps of egg emergence from the follicle are also regulated by prostaglandin $F2\alpha$, which stimulates follicular wall contraction for ovulation.

Elevated temperatures can shift the timing of spawning or cause partial or complete inhibition of ovulation [14]. Such inhibition of spawning at elevated temperatures results from a combination of impaired final oocyte maturation, oocyte atresia and resorption, or oocyte overripening [14,66]. Few studies to date have examined pathways underlying these temperature effects when gametogenesis is nearly complete. However, Atlantic salmon (*Salmo salar*) failed to show typical pre-ovulatory elevations of DHP when maintained at constant warm temperatures [67], and Arctic charr (*Salvelinus alpinus*) maintained at elevated temperature had lower DHP levels and diminished follicular DHP responsiveness [68].

Perhaps more common than complete ovulatory inhibition, shifts in the timing or locations of spawning owing to changes in temperature have been documented in wild fish populations [69,70]. Spawning at the right time and appropriate temperature and photoperiod can be crucial for offspring performance [71], as well as stable sex ratios (see §2 above). If the spawning season is shifted in response to higher temperatures or prolonged heat wave events, not only could the reproductive output of the parental generation be reduced, but the survival, growth and sex ratios of the next generation might be adversely affected [72].

(a) Using performance curves to assess temperature effects on gamete quality and quantity

Reproductive performance curves depict how reproductive measures vary across a range of temperatures and provide a tractable approach to study thermal limits in a comparative context (figure 4a). The y -axis on a thermal performance

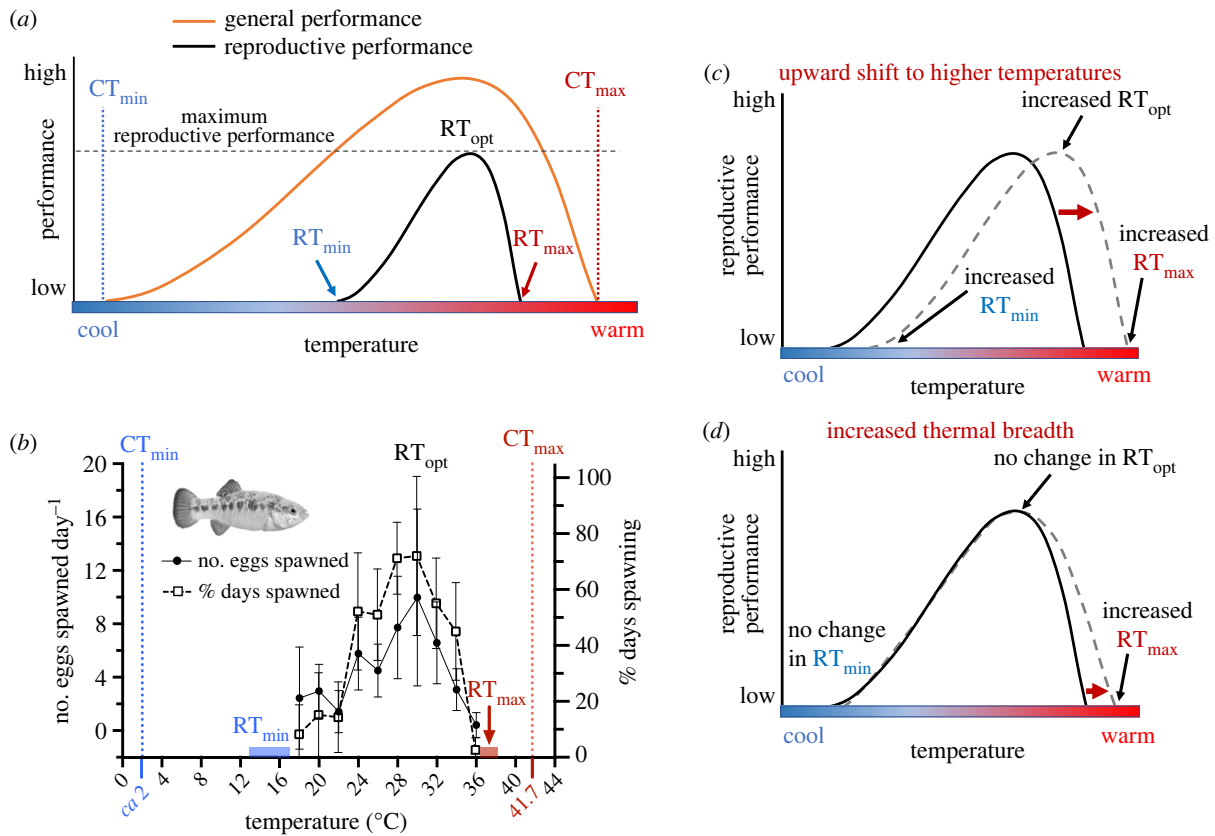


Figure 4. (a) Thermal reproductive performance curve (black line) nested within general performance (orange line) bound by critical thermal maximum (CT_{max}) and minimum (CT_{min}). Reproductive temperature minimum (RT_{min}), optimum (RT_{opt}), and maximum (RT_{max}) are indicated. (b) Reproductive performance curves for Amargosa pupfish *Cyprinodon nevadensis nevadensis* shown as eggs spawned and % days spawning. Approximate RT_{min} and RT_{max} denoted by blue and red bars, respectively. Data plotted as mean ± s.d. values. Data from [73–75]. (c,d) Developmental acclimation or evolutionary adaptation could shift reproductive performance curves as either an upward shift in the entire curve (c) or a broader thermal breadth via an increase in RT_{max} only (d). (Online version in colour.)

curve presents a measure of reproduction (e.g. number of days spawning, number of offspring produced), which is plotted against temperature on the *x*-axis. Performance curve shape can then be used to identify the optimum temperature for reproduction (RT_{opt}), and upper and lower thermal limits (RT_{max} and RT_{min}). Figure 4b presents the thermal performance curve for Amargosa pupfish *Cyprinodon nevadensis nevadensis* [73,76]. As expected, reproductive thermal limits for *C. n. nevadensis* were narrower than limits for survival (CT_{min} and CT_{max}) [74,75]. Reproductive activity was limited at 18°C, increased to a maximum level (RT_{opt}) at approximately 28–30°C, and then declined above 32°C. Subsequent studies with *C. nevadensis* and other pupfishes observed lower circulating E₂, ovarian steroidogenic enzyme gene expression, and liver vitellogenin and chorionin gene expression at temperatures greater than 34°C, suggesting impaired HPG axis function underlies the drop in reproductive performance at higher temperatures (figure 4b) [55,56].

Reproductive performance curve shapes should vary among taxa, populations and even individuals [77]. However, to date, performance curves have been generated for only a handful of fishes, and more studies are needed to classify how fish reproduction varies with not only temperature, but also other factors (i.e. photoperiod, food availability). Studying such variation can help us understand the ability of fishes to acclimate or evolve thermal tolerances for reproduction. Variation in fish reproductive performance with temperature will likely reflect differences in thermal sensitivity of endocrine pathways regulating gametogenesis,

noting that different hormone changes may be responsible for upper and lower limits (RT_{max} and RT_{min}). Since performance reflects physiological and/or behavioural processes, reproductive performance curves might be expected to change with developmental acclimation or evolutionary adaptation to warmer temperatures [77]. For instance, the entire thermal range could shift higher to increase RT_{max} but not thermal breadth (i.e. upward shift in RT_{max} and RT_{min}, RT_{opt}) (figure 4c). Alternatively, RT_{max} could increase without changes in RT_{min} or RT_{opt}, thereby increasing the overall temperature range for reproduction (figure 4d).

Few studies have tested whether fish reproductive thermal ranges can acclimate to warmer conditions. Based on available data, reproductive performance may show limited capacity for acclimation. In one study with *C. n. nevadensis* pupfish, parental exposure to higher temperatures did not lead to reproductive acclimation of offspring to warmer conditions in the next generation [78]. Pupfish bred from parents that were reared at 24, 28 or 32°C showed no differences in their own ability to reproduce at 32°C (figure 5a) [78], a temperature above RT_{opt} for the species (figure 4b) [76].

Studies of spiny chromis (*Acanthochromis polyacanthus*) likewise suggest limited reproductive acclimation. Adult spiny chromis collected from the wild and then maintained under a seasonally variable temperature regime that reached 31.5°C—a temperature +3.0°C higher than ambient condition (28.5°C) at the location of fish collection—produced smaller eggs and had lower reproductive output [80]. F₁-generation offspring from those wild-caught fish raised at +3.0°C continued to show reduced reproductive output [81]. Notably,

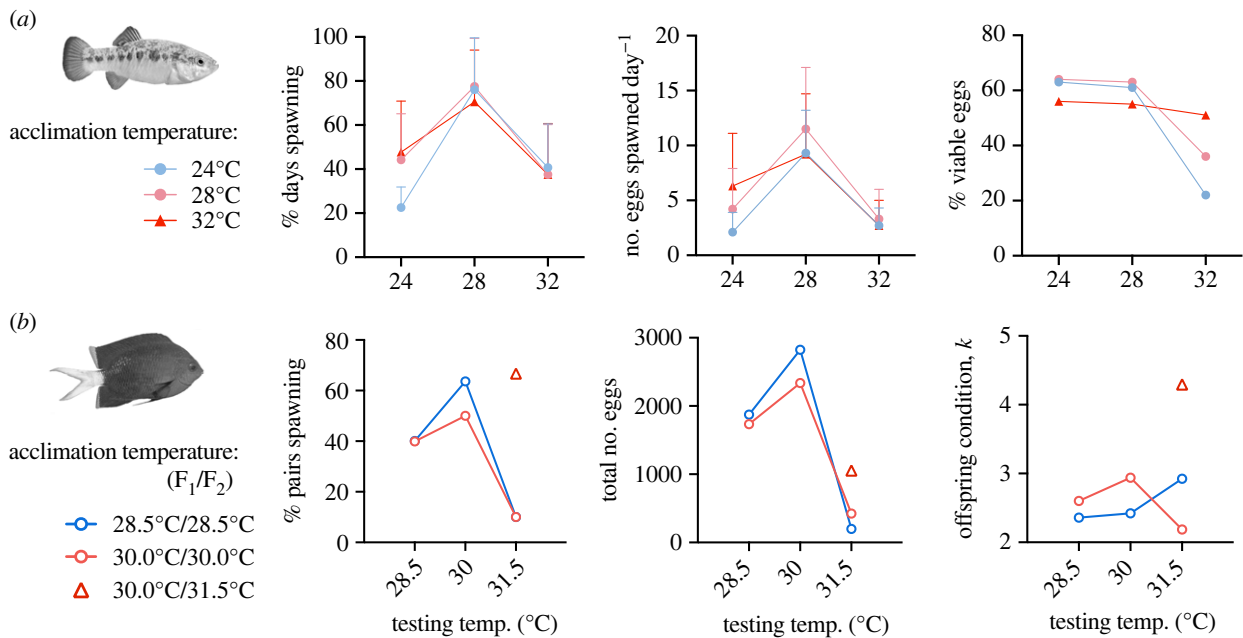


Figure 5. Tests for multi-generational acclimation of reproduction to temperature. (a) Amargosa pupfish *Cyprinodon nevadensis nevadensis* spawned from parents maintained at 24, 28 or 32°C and then tested as adults (F_1 generation) at those temperatures showed no evidence of reproductive acclimation. Data plotted as mean \pm s.d. values. (b) F_2 generation spiny chromis (*Acanthochromis polyacanthus*) derived from a wild-captured F_0 generation (held at 28.5°C) and F_1 generation parents maintained at 28.5, 30.0 or 31.5°C were themselves reared at 28.5, 30.0 or 31.5°C and assessed for reproductive performance. F_2 generation fish spawned from parents at 30.0°C (triangle) showed greater reproduction (% fish pairs spawning, no. eggs spawned) at 31.5°C and produced offspring with higher body condition (k , body condition factor). Data in (a) from [78] and (b) from [79]. (Online version in colour.)

however, F_2 -generation spiny chromis generated from an F_0 generation reared at 28.5°C and then an F_1 generation reared at 30.0°C (+1.5°C) showed improved reproductive performance at 31.5°C (+3.0°C) (figure 5b) [79]. That improvement appeared related to the ability of F_2 fish to maintain gonadotropin stimulation of spermatogenesis at 31.5°C [82], implying that reproductive acclimation may require transgenerational exposures [83]. Also important to note, the consequences of higher temperatures are different for female and male chromis depending on when exposure occurs during development [84]. Reproductive impacts of elevated temperatures thus appear to emerge via complex interactions that include transgenerational thermal history, sex and the developmental timing of temperature exposure.

5. Conclusion

Given the speed of temperature increase our planet is experiencing, knowledge of thermal sensitivity of reproductive processes may provide the best starting place to understand how fishes will reproductively respond. Studies to that end are already providing critical insights into how the sex determination/differentiation and reproductive performance of fishes can be impacted by higher temperatures. And yet, many questions remain unanswered. For instance, TSD has persisted in some poikilotherms (e.g. reptiles) for millennia and thus appears to be a resilient sex determination system. Yet, warming environments could lead to heightened selective pressure for GSD and reductions in TSD, perhaps through increased resilience of gonadal Cyp19a1a expression, which, as discussed above, can be extremely sensitive to temperature at multiple points in the reproductive life history of fishes.

Evidence at present suggests that fish may only have a limited capacity for plasticity in upper thermal limits for

gametogenesis and spawning [78,79,84]. However, temperature effects on reproduction have only been examined in a limited number of fishes to date, most of which are seasonally spawning temperate species. It is thus still largely unknown how reproduction in fishes from diverse evolutionary lineages and habitats will be affected by warmer conditions or more frequent 'heat wave' events. Even though several components of HPG axis signalling are thermally sensitive [14], it may be that reproductive acclimation requires more than just an individual experiencing warmer conditions earlier in life. Epigenetic regulation via DNA methylation, histone modification, and miRNAs has been documented for steroidogenic enzymes and hormone nuclear receptors [29,84]. Primordial germ cells may need to experience higher temperatures at very specific times during embryonic development for epigenetic modification [85]. Such a multi-generational requirement for plasticity could be adaptive for reproductive success if it reduces mismatches in reproductive timing among individuals of a population, even when individuals experience dissimilar temperatures during early development.

What is clear is that studies of fish reproductive endocrinology can provide critical information about how reproduction will be affected by the warmer, more thermally variable conditions predicted with climate change. And, given the indispensable role hormones play in regulating reproduction, acclimation or adaptation of reproductive processes via changes in endocrine regulation is likely to be crucial for the resilience of fishes in our warming world.

Ethics. This work did not require ethical approval from a human subject or animal welfare committee.

Data accessibility. This article has no additional data.

Declaration of AI use. We have not used AI-assisted technologies in creating this article.

Authors' contributions. S.C.L.: conceptualization, writing—original draft, writing—review and editing; J.A.L.: conceptualization, writing—original draft, writing—review and editing; Y.Y.: conceptualization, writing—original draft, writing—review and editing; M.J.H.: conceptualization, writing—original draft, writing—review and editing.

All authors gave final approval for publication and agreed to be held accountable for the work performed herein.

Conflict of interest declaration. We declare we have no competing interests.

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