

Review

The Hidden Fitness Costs of Aquatic Heatwaves with Lasting Demographic and Ecosystem Impacts

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Abstract: The frequency, intensity and duration of aquatic heatwaves are increasing due to climate change globally. However, the ecological consequences of heatwaves are still mainly assessed by acute mass mortality events. This emphasis overlooks the less visible but more pervasive fitness costs that persist after acute exposure. Here, we review the cryptic costs of heatwaves and show how sublethal, delayed and transgenerational effects can possibly depress population fitness and destabilize ecosystems even if the immediate mortality observed is limited. We synthesize evidence that aquatic heatwaves impose cryptic costs through four major pathways. First, heatwaves impair physiology by driving overload of bioenergy, oxidative damage, immune dysfunction and imbalance of host-microbiome interactions. These reactions force organisms to prioritize short-term survival and sacrifice self-maintenance and repair. Second, these physiological costs could alter the trajectories of growth, reduction of reproductive investment and trade-offs in stage-specific life-history. Third, behavioral responses caused by thermal stress often create new ecological liabilities by impairing cognition and locomotion, compressing usable habitat and increasing exposure risks to predators, pollutants and human activities. Fourth, parental heatwave exposure can modify offspring performance through altering provision behavior, disrupting microbiomes and causing epigenetic effects. Thus, these adverse effects extend across generations. In this review, we point out the priorities for future research should particularly focus on integrative frameworks that link multi-stressor environments with multigenerational processes. Therefore, assessments of aquatic heatwave impacts should extend beyond immediate resistance during exposure to include post-event recovery, recruitment and future population dynamics. Instead, aquatic heatwaves should be understood as disturbances that can leave lasting demographic and ecosystem legacies even in the absence of obvious die-offs. Therefore, integrating cryptic fitness costs into demographic models, multi-stressor experiments and ecosystem forecasting will be essential for predicting the effect of heatwaves in reshaping aquatic biodiversity in a warming world.

Keywords: climate change; aquatic heatwaves; fitness costs; sublethal effects; life-history trade-offs; transgenerational effects

1. Introduction

Global warming is one of the most pervasive manifestations of anthropogenic climate change, reshaping the thermal regimes of marine and freshwater ecosystems worldwide [1]. These temperature changes fundamentally reshape the thermal landscape of global

aquatic ecosystems with unequivocal evidence [2]. This warming trend is accompanied by increasingly frequent and severe extreme weather events including storms, floods, and heatwaves which cause profound disruptions to ecological systems [3,4]. As a critical environmental factor, temperature controls physiology, behavior, and



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survival of organisms, thereby structuring the spatiotemporal patterns of species distribution and abundance [5–7]. For ectothermic taxa, in particular, the environmental temperature directly modulates their metabolic rates, growth, and reproductive success rate through thermodynamic constraints on biochemical processes [5,8]. While thermal regimes have fluctuated throughout Earth's history, contemporary aquatic species now face unprecedented rates of environmental change [9]. Global ocean surface temperatures have risen by approximately 0.88 °C since the pre-industrial era [10]. Likewise, global-mean lake surface temperatures in 2024 were 0.3 °C above the 2001–2023 average, with continued warming projected at 0.26 °C per decade [11]. Under a 2 °C warming scenario, 9% of freshwater species are projected to lose more than half of their geographic range [12]. These trends demonstrate the broad-scale warming of aquatic thermal environments and provide the background conditions under which extreme thermal events can occur more frequently and with greater ecological consequences. Beyond this gradual increase in mean temperature, changes in thermal extremes—particularly marine and freshwater heatwaves—represent an additional and more acute dimension of climate-driven risk to aquatic organisms and ecosystems. [13,14].

The World Meteorological Organization (WMO) broadly defines terrestrial heatwaves as periods of accumulated excess heat over consecutive unusually hot days and nights. However, standardizing cross-ecosystem research requires precise, quantitative definitions. Contemporary studies adopt a unified statistical framework that defines heatwaves in marine and freshwater systems relative to local historical baselines [14,15]. Therefore, a heatwave is characterized as a discrete period lasting five or more consecutive days, during which temperatures exceed the 90th percentile of a long-term climatological record for that time of year (Figure 1A). Observational data and predictive models indicate that marine heatwaves (MHWs) are increasingly exceeding acute thermal thresholds, and this trend is projected to fundamentally alter ocean climates by the end of the 21st century [13,15]. Under high-emission scenarios (RCP 8.5), MHW durations are expected to rise from 40–160 days (historical baselines) to nearly year-round conditions in over 90% of the ocean globally. Meanwhile, the peak intensities of MHW are substantially increasing (Figure 1B) which will trigger widespread ecological and socioeconomic impacts [16,17]. Freshwater heatwaves are similarly intensifying, with projected durations increasing from ~8 days (historical

baselines) to nearly 100 days under RCP 8.5 (Figure 1C), accompanied by marked increased peak intensities [14]. Such thermal extremes destabilize ecological communities from polar to tropical latitudes, often causing mass mortality or forcing migration of key species from habitats [16]. A recent synthesis of marine heatwave research also showed that current studies remain biased toward field-based observations of abundance, distribution and mortality, whereas repeated heatwaves, recovery periods, behaviour, reproduction and multi-stressor effects are still comparatively underrepresented [18]. This gap supports the need to examine delayed and sublethal fitness costs beyond immediate survival.

Historically, ecological assessments of HWs mainly focus on acute, lethal outcomes and large-scale mortality. Traditional ecophysiological approaches have largely quantified thermal risk through critical thermal maxima (CT_{max}) and absolute lethal limits by focusing on mortality thresholds [19]. This method provides key insights into upper thermal tolerance of species [20,21]. Moreover, it is evident that heatwaves lead to coral bleaching [22,23], the loss of habitat-forming kelp forests and benthic invertebrates [24], sudden population collapses of pelagic fishes Pacific cod [25], showing that aquatic heatwaves are distinct class of ecological disturbance rather than a mere extension of baseline warming. Yet these cases have also created bias. When ecological assessments focus mainly on mortality, bleaching or range shifts, they may overlook individuals that survive the thermal peak but subsequently experience metabolic dysregulation, reduced reproductive performance or behavioural impairment. This distinction is crucial because individual-level survival during the thermal peak reflects resistance to acute stress, whereas population-level resilience depends on post-event recovery, recruitment and future demographic performance. Individuals that remain alive through a heatwave may still emerge with metabolic dysregulation, oxidative damage, suppressed immunity, disrupted microbiomes, altered developmental trajectories and diminished reproductive performance [26,27]. Because these sublethal effects may be weak during the exposure period but become evident only during recovery, later life stages or subsequent generations, they can be missed by monitoring approaches that focus primarily on acute mortality or immediate abundance changes [26,28,29]. In that sense, the ecological footprint of a heatwave is often much larger than the mortality it causes during the event itself.

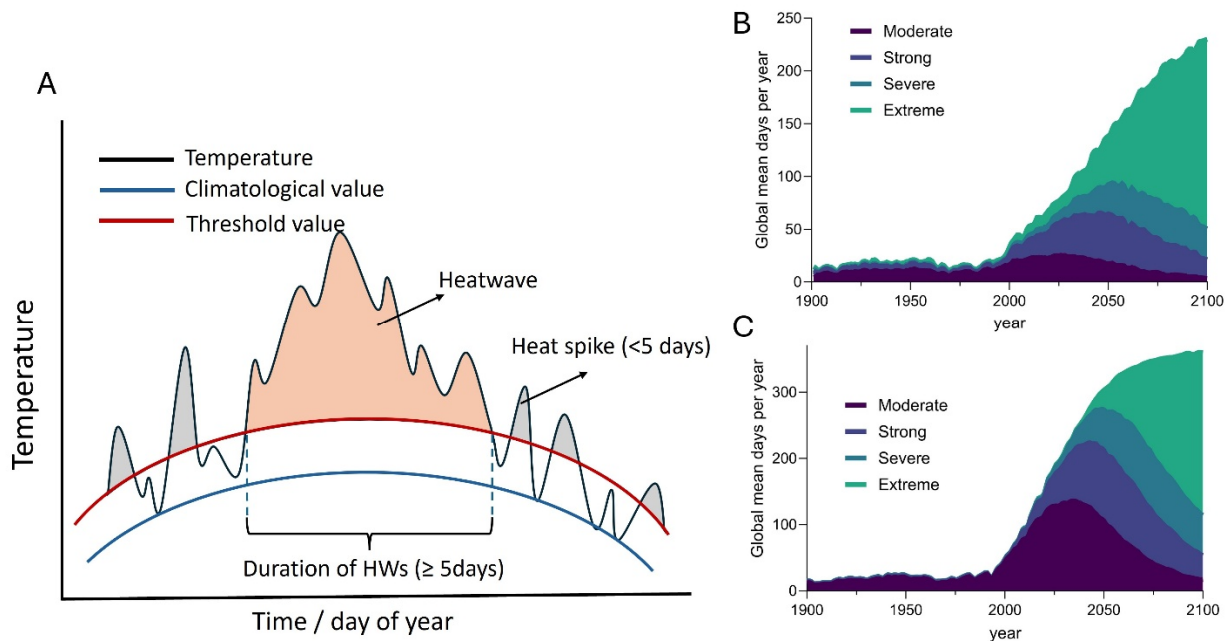


Figure 1. Definition and projected increase of aquatic heatwaves. **(A)** Schematic illustration of a heatwave, defined as a discrete period of at least 5 consecutive days during which temperature exceeds the seasonally varying 90th percentile threshold of a long-term climatological baseline. The blue line indicates the seasonal climatological mean temperature, and the red line indicates the heatwave threshold. Shorter thermal anomalies lasting fewer than 5 days are classified as heat spikes. **(B,C)** Simulated global annual mean number of moderate, strong, severe and extreme heatwave days in marine **(B)** and lake **(C)** ecosystems under historical and future climate forcing. Future projections are shown under the high-emissions scenario RCP8.5. Adapted from Refs. [14,17].

There is a critical distinction in concept of continuous baseline warming and acute aquatic heatwaves. Gradual warming can, at least in some cases, trigger compensatory responses such as acclimation, phenological adjustments, range shifts or transgenerational buffering [30–32]. In contrast, heatwaves are pulse disturbances which are fundamentally different from gradual warming trends. Although short-term sublethal heat exposure can induce heat hardening or rapid acclimation and increase subsequent heat tolerance, the degree of protection is highly species-, trait- and context-dependent [33–35]. Thus, heatwaves should not be viewed as events that universally preclude acclimation, but as disturbances in which the benefits of short-term thermal plasticity may be limited by event intensity, duration, recurrence, recovery time and co-occurring stressors. Biological responses to extreme temperatures during heatwaves are complex and frequently nonlinear, being mediated by both the ecological and geographic context of the affected species as well as the physical characteristics of the events themselves [36]. This helps explain why a species can evolve heat tolerance under long-term warming exposure yet still struggle to develop lasting heatwave tolerance [37]. It also means that the ecological consequences of heatwaves are strongly contingent on timing, background conditions and the presence of co-occurring stressors such as hypoxia, acidification, pathogens or pollutants

[38–40]. With climate models projecting a continued, exponential increase in heatwave frequency and intensity over the coming decades [41], a comprehensive understanding of their biological impacts is essential for conservation and fisheries management.

Here, we argue that the ecological burden of aquatic heatwaves may be underestimated because many impacts are expressed through sublethal, delayed and transgenerational pathways. This review focuses primarily on aquatic ectotherms, for which body temperature, metabolic rate and performance are tightly linked to external thermal conditions. We recognize that not all marine and freshwater organisms are ectothermic; aquatic endotherms may also be affected by heatwaves, but often through different physiological, behavioural and food-web pathways. We use the term cryptic fitness costs to describe effects that do not necessarily produce immediate mortality, but that nonetheless lower survival prospects, reproductive output, competitive performance or offspring quality. However, heatwave legacies are not universally negative. Short-term or prior thermal exposure can sometimes induce heat hardening, thermal priming or transgenerational plasticity that improves subsequent heat tolerance or stress responses [32,33,35,42]. The outcome of these responses is likely to be context dependent, varying with heatwave intensity, duration, recurrence, recovery interval, life stage and the match between parental and offspring environments. Our

focus is therefore not to argue that all heatwave legacies are detrimental, but to highlight the hidden costs that may be missed when assessments focus only on acute mortality or immediate resistance. This framing is closely aligned with the concept of ecological debts induced by heat extremes, in which biological responses that buffer immediate stress can generate delayed costs that become evident only during recovery or in subsequent population and community dynamics [29].

We first examine how heatwave survival is mediated by bioenergetic reallocation, cellular stress responses, immune dysfunction and destabilization of the holobiont (Section 2). We then consider how these mechanisms scale up into altered growth, impaired reproduction and delayed demographic responses (Section 3). Next, we discuss behavioral and ecological trade-offs, emphasizing that behavioral compensation can itself create new risks under multi-stressor environments (Section 4). Finally, we review parental and transgenerational effects and the possible epigenetic mechanisms involved (Section 5), and outline priorities for integrating cryptic costs into the forecasting and management of aquatic heatwave impacts (Section 6).

2. Physiological Mechanisms of Survival Under Heatwaves

2.1. Bioenergetic Constraints and Metabolic Reallocation

For aquatic ectotherms, which are the primary focus of this mechanistic section, the immediate physiological challenge during heatwaves is often bioenergetic. Acute warming thermodynamically accelerates standard metabolic rate (SMR) [8], thereby sharply increasing the energetic cost of maintaining basic cellular and organismal function [43] (Figure 2A). Under the Oxygen- and Capacity-Limited Thermal Tolerance (OCLTT) framework, this increase in oxygen and ATP demand is not always matched by a proportional increase in oxygen supply [44]. As temperatures approach or exceed the upper thermal range, cardiovascular and respiratory systems may reach functional limits, constraining maximum oxygen uptake and reducing the energy available above maintenance. The result is a contraction of aerobic scope (AS; Figure 2B), leaving progressively less surplus energy for growth, movement, immune defence and reproduction. Evidence from reef fishes shows that this oxygen-delivery limitation can become especially severe when heatwaves co-occur with secondary stressors. For example, under combined heatwave and hypoxia exposure, maximal oxygen uptake is constrained while routine metabolic demand remains elevated, intensifying the mismatch between oxygen supply and demand [45]. Thus, the physiological cost of heatwaves lies not only in approaching lethal thermal limits, but also in the rapid loss of aerobic capacity needed to sustain performance above maintenance. In addition to reducing aerobic scope, acute increases in maintenance

metabolism can accelerate the use of endogenous reserves that would otherwise support survival, recovery and reproduction. Some organisms can partially preserve aerobic scope across seasonal temperature cycles, indicating that acclimatory buffering is possible [46]. However, such buffering is not always sufficient under rapid, intense or recurrent heatwave exposure, particularly when recovery intervals are short or when heatwaves co-occur with other stressors [47]. In these cases, the metabolic adjustments that support short-term persistence may still generate energetic debt during recovery.

This organismal oxygen-delivery constraint is further intensified by changes in the external environment. Warm water holds less dissolved oxygen, and acute warming can also elevate critical oxygen tension, meaning that organisms require higher ambient oxygen concentrations to sustain aerobic metabolism [48,49]. Heatwaves can therefore generate a compounded oxygen-energy mismatch: metabolic demand rises rapidly while environmental oxygen availability declines [50]. In this situation, organisms may temporarily buffer the mismatch through physiological or behavioural adjustments. For example, native mussels (*Mytilus galloprovincialis*) may alter gaping behaviour and reduce cardiac activity to lower metabolic demand under heatwave stress [51]. However, these compensatory responses impose substantial costs. If metabolic depression persists, organisms may enter a state of negative scope for growth (SFG), in which energy is diverted to maintenance rather than somatic growth and other anabolic processes [52]. Repeated heatwaves may further exceed the capacity for physiological compensation. In pearl oysters, two consecutive marine heatwaves caused broad transcriptomic changes, including downregulation of genes associated with energy metabolism, body defence, cell proliferation and biomineralization, indicating impaired physiological performance after recurrent thermal stress [53].

Studies using the scope for growth (SFG) framework further show that apparent short-term heatwave tolerance may still involve substantial energetic trade-offs. For example, in the fouling mussel *Mytella strigata*, severe heatwave exposure did not immediately cause energetic collapse because clearance rate and absorption efficiency were partly maintained, allowing energy intake to continue under thermal stress [54]. However, this response was accompanied by reduced respiration, shifts toward the use of endogenous reserves and reallocation of energy away from growth and reproduction. Such metabolic depression can impose cryptic costs, including reduced reproductive performance and weakened structural functions such as byssus production [55,56]. The usage of endogenous reserves may enhance immediate persistence while leaving survivors more vulnerable to subsequent stressors and less able to sustain long-term population performance.

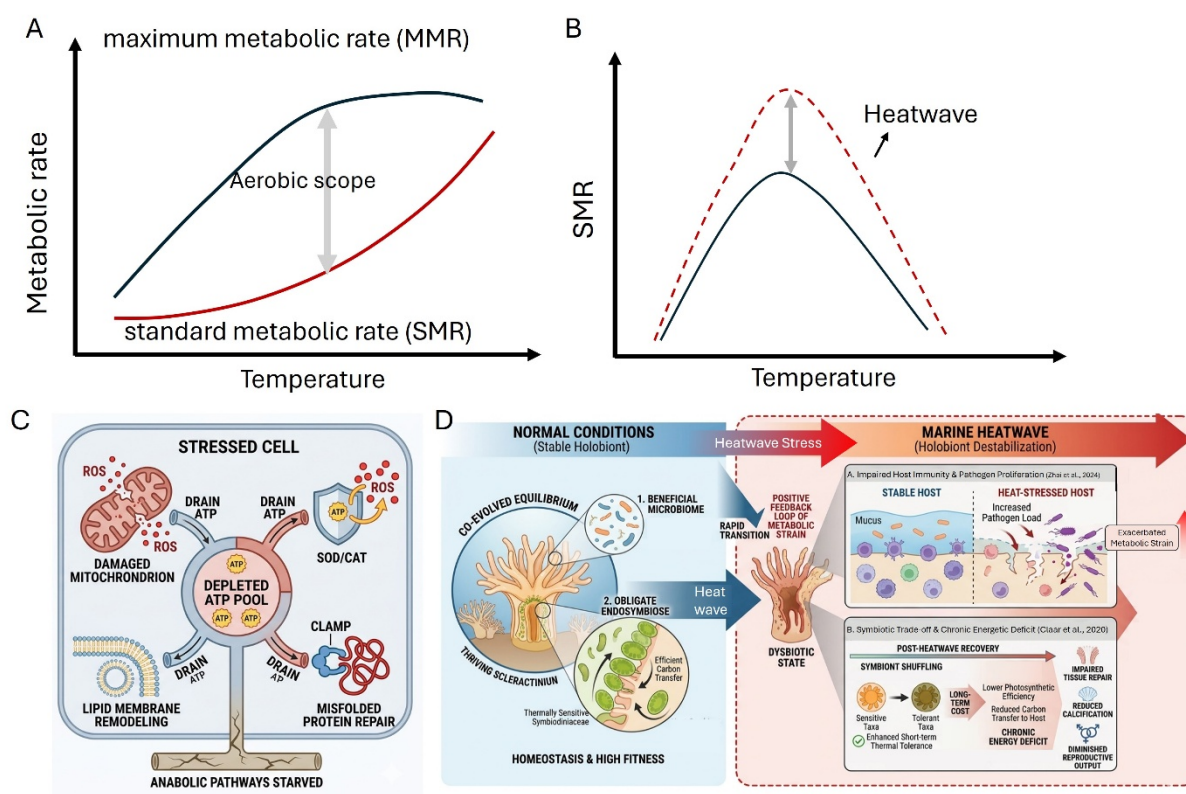


Figure 2. Physiological and cellular mechanisms underlying the cryptic fitness costs of aquatic heatwaves. **(A)** Temperature-dependent metabolic performance in aquatic ectotherms. The standard metabolic rate (SMR) increases exponentially with temperature, while maximum metabolic rate (MMR) is more steeply. This reaction results in a contraction of aerobic scope under warming conditions. **(B)** Heatwave-induced changes in metabolic demand. Acute warming elevates SMR (red dashed curve) relative to baseline conditions (blue curve), increasing basal energetic costs and narrowing the margin for performance. **(C)** Cellular consequences of thermal stress. Elevated metabolic demand and mitochondrial dysfunction increase reactive oxygen species (ROS) production, leading to oxidative damage, ATP depletion, lipid membrane remodeling and accumulation of misfolded proteins. These processes divert energy towards maintenance and repair, suppressing anabolic pathways. **(D)** Holobiont destabilization under marine heatwaves. Under normal conditions, the interactions between host and microbiome maintain homeostasis and high fitness. Heatwave stress disrupts this equilibrium, promoting a shift from a stable mutualistic microbiome to a dysbiotic state characterized by increased pathogen load and metabolic strain. Although symbiont restructuring or physiological adjustment may buffer short-term stress, it often results in reduced energy transfer, chronic energetic deficits and impaired recovery.

Rapid acclimation and heat hardening are often proposed as potential buffers against heatwave stress, and these responses can include metabolic reallocation, altered enzyme activity and changes in cellular protection pathways. A broad meta-analysis of ectotherms found that acclimation capacity is limited and varies among species, with many organisms unable to fully compensate for the effects of acute thermal extremes [47]. Moreover, such plasticity is unlikely to be cost-free. When heatwaves are intense, prolonged or recurrent, the same metabolic reallocation that supports short-term survival may reduce energy available for growth, immune defence, reproduction and recovery. Thus, energetic debt may remain a hidden legacy of extreme warming, even when acclimatory responses increase immediate heat tolerance. Such physiological costs can also differ strongly among species occupying similar ecological niches. For example,

Staniek et al. showed that two intertidal bivalves exposed to comparable heatwave conditions displayed different survival, condition, filtration and metabolic responses, suggesting that heatwave vulnerability cannot be inferred from habitat or niche similarity alone [57].

2.2. Cellular Damage, Immune Dysfunction and Holobiont Instability

The damage of heatwaves reaches the cellular level as well. Acute warming destabilizes membranes, impairs mitochondrial efficiency and increases the leakage of reactive oxygen species (ROS), thereby elevating the risk of oxidative damage [58–60] (Figure 2C). To maintain cellular integrity, organisms will activate antioxidant enzymes, heat-shock proteins and other cytoprotective pathways. Transcriptomic evidence from mussels and other marine ectotherms shows strong upregulation of

oxidative-stress, apoptosis and chaperone-related pathways during marine heatwaves indicating intense cellular repair [61]. The activation of antioxidant systems and heat-shock proteins is essential for preventing protein denaturation and cell death, but these defence systems have high energetic costs at the same time [62]. Due to this reason, even this system could allow cells to remain functional long enough for the organism to survive the heatwave, but it causes metabolic scars simultaneously. Lipid remodeling, protein turnover and repair of oxidized biomolecules can exist for a long time after the heatwaves have ended which cause the energetic burden during recovery phase [63]. This is one reason why post-heatwave performance often remains impaired even when ambient temperature has returned to normal. The costs are not merely the direct effects of heat, but also the delayed effect caused by cellular rescue.

Immune function is particularly sensitive to the energetic reallocation imposed by heatwaves [26,64]. Under acute thermal stress, resources are diverted away from immune surveillance and towards cellular maintenance and protection processes, weakening the immune system [65,66]. However, the severity of this trade-off differs among taxa, traits and ecological contexts. Some species may partly buffer immune or metabolic disruption through physiological plasticity, but this capacity should not be assumed to be restricted to any particular trophic level. For example, simulated heatwaves led to coordinated metabolic and immune adjustments across multiple tissues of adult small-spotted catsharks (*Scyliorhinus canicula*), including elevated plasma glucose and tissue-specific modulation of immune-related genes [67]. These responses suggest short-term compensation rather than complete avoidance of heatwave-induced immune costs.

When compared with predators, many benthic ectotherms appear far less able to sustain their immune systems under heat stress. For example, severe warming markedly reduces hemocyte abundance in intertidal bivalves, thereby weakening the first line of innate immune defense [68]. At the same time, elevated temperatures often approach the growth optima of bacteria such as *Vibrio* spp., increasing pathogen load precisely when host immune capacity is compromised [69,70]. Although prior acclimation may partly buffer these effects by maintaining higher baseline immune performance, the immune system of non-acclimated populations may still be easy to collapse [68]. Consequently, mortality caused by heatwaves may arise not only from direct thermal injury, but also from heat-induced immune collapse and secondary infections afterwards. This interaction between energy limitation of host and expansion of pathogens further reduces the fitness of organisms. This interaction represents an important but often underestimated damage pathway from heatwaves.

The cryptic costs of heatwaves also extend beyond host intrinsic physiology to the level of the holobiont (Figure 2D). In many aquatic ectotherms, the associations between host and microbiome are integral to nutrient acquisition, immune defense and physiological homeostasis [71,72]. However, acute thermal stress can destabilize this co-evolved equilibrium, shifting the microbiome from a relatively stable mutualistic state to dysbiosis. For example, in coral *Turbinaria peltata*, marine heatwaves caused the simultaneous breakdown of physiological condition of host and homeostasis of microbiome. Such breakdown caused the declines in beneficial symbionts, degradation of protective mucus barriers and increased proliferation of opportunistic and pathogenic bacteria [73]. This coupled deterioration raises pathogen pressure while forcing the host to divert limited energy towards microbial regulation and tissue maintenance, thereby intensifying metabolic strain.

For organisms that depend on obligate endosymbioses, heatwaves also impose an additional trade-off between immediate tolerance and long-term performance. For example, the reef-building corals could restructure their *Symbiodiniaceae* communities with replacing sensitive symbionts with more heat-tolerant taxa under prolonged warming [74,75]. Although this symbiont shuffling can reduce the risk of acute bleaching and mortality, it is often accompanied by lower photosynthetic efficiency and reduced transfer of fixed carbon to the host [75,76]. This replacement will result in a chronic energetic deficit that can last longer than the heatwave itself, constraining tissue repair, calcification and reproductive output. Overall, such holobiont destabilization may represent a critical but often overlooked pathway through which heatwaves generate lasting impacts on host fitness and ecosystem functioning due to microbial dysbiosis.

3. Life History and Demographic Costs

3.1. Growth Trajectories under Acute Heatwave Stress

When aquatic ectotherms exhaust their finite energetic reserves in coping with the physiological challenges imposed by HWs (Section 2), these constraints inevitably manifest as substantial costs at the life-history level. Somatic growth is highly sensitive to acute thermal perturbations because it depends on surplus energy after maintenance [77] (Figure 3A). The classic Temperature-Size Rule (TSR) predicts that warming often accelerates development while producing smaller adult body size [78,79]. Heatwave studies can be broadly consistent with this expectation, but the magnitude and direction of growth responses may depend on event duration, timing, recovery interval and food availability [80]. Under acute warming, maintenance costs increase, leaving less surplus energy for somatic growth [81]. In some cases, short heat exposure may transiently increase feeding, activity or

early growth, whereas longer or repeated exposure can reduce final body size or alter the timing of maturation [82,83]. Thus, heatwaves do not necessarily contradict the TSR; rather, they can reveal how pulse-like warming interacts with energy allocation and life-stage-specific constraints to shape growth trajectories. However this compensation will substantially increasing the metabolic energy expense of routine processes such as digestion and locomotion, thereby constraining growth [84]. For example, Spinks et al. found that heatwave exposure could enhance early performance in juvenile reef fishes, while chronic exposure could lead to substantial reductions in body size [82]. Moreover, heatwaves can decouple growth

from reproductive maturation. Rosemond et al. reported that rockfishes under severe marine heatwaves were found with accelerated growth in juvenile stage but delayed sexual maturation. This also reduced the reproductive contribution of younger cohorts and weakening population resilience [83]. In longer or repeated heatwaves, such compensation can shift developmental trajectories, reduce size at maturation or delay the transition to reproduction [83]. Thus, growth responses to heatwaves should be interpreted not as simple performance outcomes but as evidence of altered allocation across the life cycle.

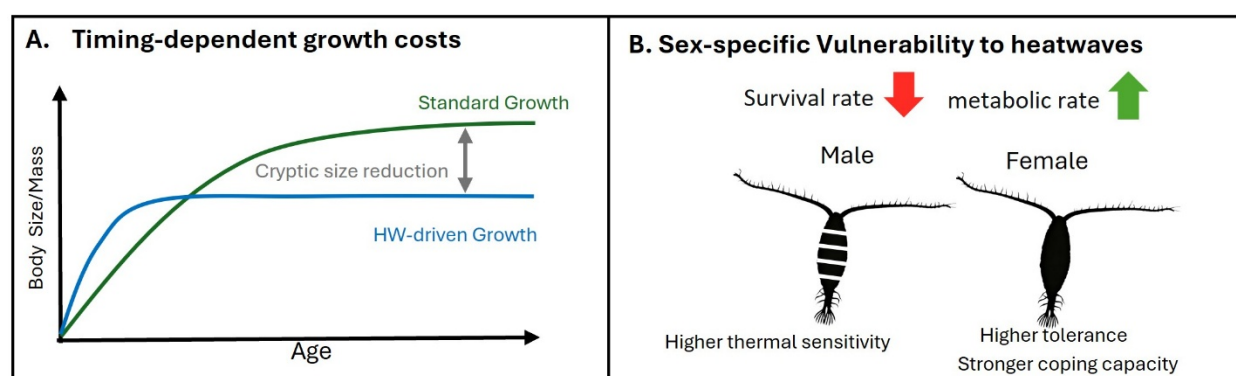


Figure 3. Life-history and demographic costs of aquatic heatwaves. **(A)** Heatwaves can reshape growth trajectories and development speed, generating cryptic size reduction even the early growth is maintained. **(B)** Responses to heatwaves may differ between sexes which could affect the physiological sensitivity, tolerance and subsequent mating dynamics.

The demographic implications of altered growth are substantial. Body size influences fecundity, competitive ability, predator avoidance and age at maturity across many aquatic taxa [85–87]. Therefore, a small reduction in size or condition at settlement, metamorphosis or first reproduction can propagate into lower cohort contribution. In fishes, heatwave-associated changes in juvenile growth can alter the timing of maturation and reduce the reproductive value of younger age classes. In invertebrates and habitat-forming species, depressed growth also slows tissue repair and structural recovery, which can lengthen ecosystem-level recovery after the event itself has passed.

3.2. Reproductive Investment and Timing-Dependent Vulnerability

Reproduction is one of the clearest pathways through which sublethal heatwave stress is translated into demographic change. When heatwaves occur with gametogenesis, spawning, embryogenesis or early larval development, organisms are forced to reallocate finite energy from reproduction to immediate survival. This reallocation of energy will lead to reduced gamete quality, impaired fertilization, disrupted developmental progression or lower offspring viability [88,89]. The severity of these effects is highly dependent on life stage.

A heatwave that is physiologically tolerable outside the breeding season may become disproportionately damaging when it occurs during the narrow reproductive window [89].

A key point is that reproductive costs do not always appear as immediate failure in reproduction. Heatwaves may not cause the death of adults, and even maintain apparently stable short-term fecundity in some cases, while heatwaves are still eroding population performance through hidden reductions in condition, offspring quality or later recruitment. This distinction is important because population vital rates can be altered even if the adult mortality is not observed. Individuals adapted to recurrent thermal exposure, such as those from high-intertidal habitats, may survive extreme events, yet still incur sublethal physiological costs that reduce subsequent reproductive performance or demographic contribution [88]. In this sense, the cryptic reproductive burden of heatwaves lies not only in failed spawning, but also in the decoupling of apparent adult persistence from actual reproductive value.

Recent evidence also indicates that reproductive responses depend not only on peak temperature, but on the internal structure of the heatwave itself. Xiao and Wang showed that fluctuating thermal regimes can generate complex reproductive outcomes on *Daphnia magna*, with the cooling phase itself imposing substantial

physiological and reproductive stress [37]. Repeated exposure did not produce clear acclimation in *Daphnia magna*. In contrast, reproductive costs accumulated across events, implying that duration, recurrence, recovery interval and rate of temperature change may be as important as maximum temperature in shaping reproductive outcome [37]. Thus, a single metric of thermal intensity is often insufficient to capture reproductive risk.

The short-term stability of a reproductive trait should not be interpreted as evidence that reproduction is unaffected. The marine copepod *Acartia tonsa*, showed lower survival and higher metabolic demand under a 5-day exposure to marine heatwave and hypoxia conditions. Sex-specific physiological differences were found, with females showing lower metabolic thermal sensitivity than males, yet egg production rates remained statistically unchanged across treatments [90] (Figure 3B). This result suggests that short-term fecundity can appear buffered even while other traits that ultimately determine reproductive success and population dynamics are already compromised. In other words, the absence of an immediate decline in egg production does not necessarily indicate the absence of reproductive cost. In contrast it may reflect temporal lag, compensation, or the insensitivity of short-term fecundity metrics to broader demographic damage.

At the population level, these hidden impairments can scale up into prolonged recruitment failure. For example, Chandrapavan et al. showed that an extreme marine heatwave caused reproductive collapse in blue swimmer crab populations, generating multiple years of reduced recruitment and extended fishery closures before partial recovery occurred [91]. Such cases showed that the demographic legacy of heatwaves often emerges with a delay. The most severe consequences can be observed only in the next cohort or breeding season after the heatwave exposure. Reproductive disruption is therefore one of the principal routes by which heatwaves impose cryptic fitness costs, linking sublethal physiological stress to long-term population decline.

3.3. Latent Within-Generation Effects and Delayed Demographic Responses

Another reason why cryptic costs are underestimated is that their demographic expression is often delayed within the same generation. Individuals exposed to thermal extremes may survive the event, but they can carry reduced energetic condition, impaired immune capacity or altered developmental trajectories into later life stages or subsequent seasons. These latent effects may become apparent only during settlement, overwinter survival, migration, maturation or later reproductive events. In this sense, heatwaves can produce a “live fast, die young” phenotype, in which early survival or

development is maintained at the expense of later performance. Viewed demographically, heatwaves act not only as acute stress events but also as delayed population filters. They remove some individuals immediately, while reducing the future contribution of many survivors through hidden deficits in growth, condition, immune function or reproductive value. Detecting this fragility requires moving beyond event-based monitoring towards life-cycle and cohort-based assessment.

Another reason why cryptic costs are underestimated is that their demographic expression is often delayed. Individuals exposed to thermal extremes may survive, grow and even reproduce. But these organisms still carry worse physical condition into later life stages or subsequent seasons. This condition is likely to happen when heatwaves deplete reserves energy required for settlement, overwinter survival, migration or future reproduction. Together, these pathways can generate a “live fast, die young” phenotype, in which early development or short-term survive is maintained at the expense of later survival, maturation or recruitment [92]. These examples show that heatwave effects can persist beyond direct exposure by embedding energetic and microbial liabilities into subsequent life stages. Recurring heatwaves can also generate complex life-history and transgenerational effects. In three-spine stickleback, single and recurring marine heatwave treatments altered growth and reproductive output across generations, with evidence for both fitness costs and partial heat-stress memory [42]. This suggests that repeated heatwave exposure can leave persistent demographic legacies even when some traits show priming.

Viewed demographically, heatwaves should therefore be considered not only as acute stress events, but also as drivers of delayed cohort-level demographic change. Here, we refer to differential outcomes among individuals within a population, rather than ecological filtering among species. Some individuals may die during exposure, whereas others may survive but carry reduced energetic condition, impaired immune function or lower reproductive value into later life stages. These latent effects can reduce settlement success, maturation, overwinter survival or recruitment after the heatwave has ended, creating delayed demographic costs that are not captured by immediate mortality estimates [29,88,91,92]. Detecting this fragility requires moving beyond event-based monitoring toward life-cycle and cohort-based assessment. In this way, heatwaves can reshape population dynamics and ecosystem stability through delayed fitness costs as well as direct mortality.

4. Behavioral and Ecological Trade-Offs

Behavioral responses are often among the earliest and most flexible ways by which aquatic organisms cope with thermal stress. Rather than acting only after

physiological compensation has failed, behavioral thermoregulation can precede severe internal stress by allowing individuals to avoid unfavorable temperatures, shift activity periods, alter habitat use, or move toward cooler refugia. In this sense, behavior and physiology should be viewed as interacting components of the heatwave response, with behavior often reducing the physiological burden of acute warming. However, under aquatic heatwaves, the effectiveness of behavioral buffering can become strongly constrained. Heatwaves may occur over broad spatial scales, compress usable thermal habitat, reduce the availability of refugia, and expose organisms to new ecological liabilities. In addition, extreme thermal stress can impair the cognitive and motor functions required to perform effective behavioral responses. Thus, the cryptic fitness costs of heatwaves arise

not because behavior is merely a fallback after physiology fails, but because behavioral thermoregulation itself can become limited, maladaptive, or associated with additional ecological risks under multi-stressor environments (Figure 4, Table 1). Recent multi-stressor ecology shows that such responses are frequently constrained by neurocognitive impairment, localized anthropogenic stressors and shifting trophic landscapes, thereby amplifying rather than alleviating vulnerability (Figure 4, Table 1). Behavioural effects may also persist beyond the heatwave itself. Spence-Jones et al. showed that marine heatwave exposure reduced exploratory behaviour long after exposure in threespine stickleback, indicating that behavioural impairment can act as a delayed carryover cost rather than only an immediate stress response [42].

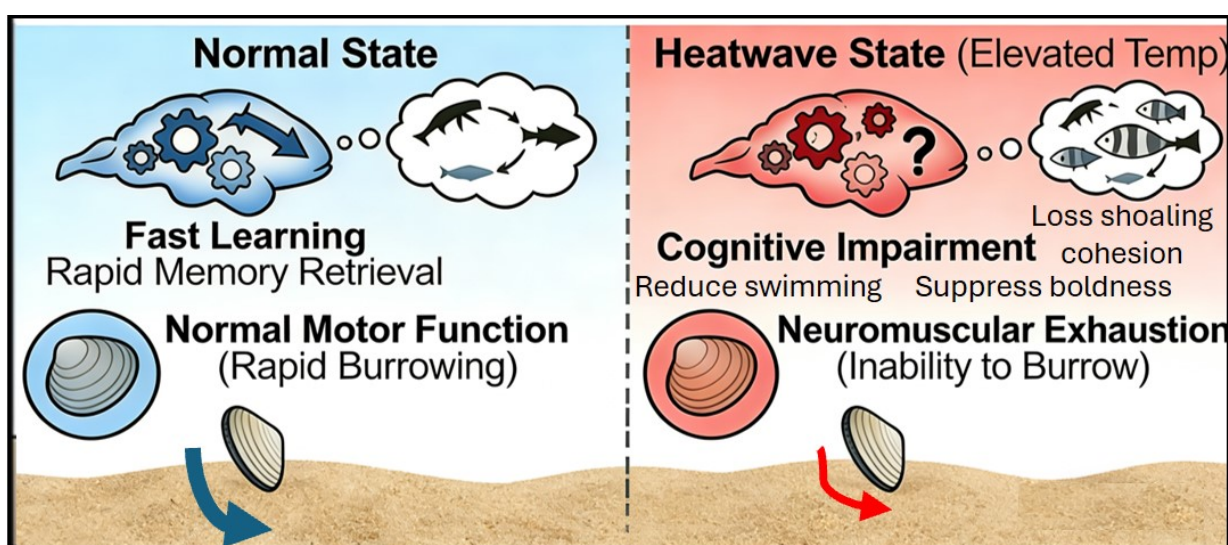


Figure 4. Behavioral impairment under heatwave conditions. Heatwave exposure can disrupt both cognition and motor performance in aquatic ectotherms. Relative to the normal state, heatwave conditions impair learning and memory-related processes, reduce swimming and boldness, weaken shoaling cohesion and compromise burrowing ability. These changes highlight how sublethal thermal stress can translate into hidden survival costs through behavioral failure.

Table 1. Representative evidence for behavioral, ecological and transgenerational fitness costs of aquatic heatwaves.

Species/System	Heatwave Treatment	Main response	Reference
Male guppies (<i>Poecilia reticulata</i>)	32 °C for 5 days (control 26 °C)	Heatwave exposure impaired cognitive performance, reducing learning and decision-making capacity.	[93]
Iberian barbel (<i>Luciobarbus bocagei</i>)	32 °C for 5 days (control 26 °C)	Heatwave exposure reduced swimming activity, suppressed boldness, and weakened shoaling cohesion.	[94]
White sturgeon	20 ± 1 °C for 20 days (control 13 °C)	Heatwave exposure altered global DNA methylation and induced lasting upregulation of stress-response genes.	[95]
Juvenile brown trout (<i>Salmo trutta</i>)	+3 °C for ~90 days	Parental thermal history exerted a stronger effect on offspring genome-wide DNA methylation than offspring developmental temperature itself.	[96]

Table 1. Cont.

Species/System	Heatwave Treatment	Main response	Reference
<i>Austrolebias nigripinnis</i> and <i>A. cyaneus</i>	18–30 °C for 6 h	Heatwaves disrupted embryonic diapause, causing complete cohort failure.	[97]
Guppies (<i>Poecilia reticulata</i>)	28 °C for 3–4 months (control 21 °C)	Maternal and paternal thermal histories asymmetrically shaped offspring morphology, metabolic enzyme activity, and swimming performance.	[98]
Zebrafish (<i>Danio rerio</i>)	34 °C for 2 weeks (control 28 °C)	Heatwave-induced sperm changes conferred little or no adaptive benefit to offspring survival.	[99]
Three-spined stickleback (<i>Gasterosteus aculeatus</i>)	23 °C for 5 days (control 18 °C)	Short-term heatwaves impaired paternal care, reduced offspring condition, and intensified cross-generational developmental costs.	[100]
Threespine stickleback (<i>Gasterosteus aculeatus</i>)	Single and recurring marine heatwaves across three generations	Altered reproductive output, offspring growth, exploratory behaviour and long-term survival, with trait-dependent evidence for heatwave costs and heat-stress memory across generations.	[42]
Soft-shell clam (<i>Mya arenaria</i>)	32 °C for 24–48 h (control 26 °C)	Heatwave-stressed bivalves failed to reburrow after disturbance, increasing exposure to predators.	[101]
Mussels (<i>Xenostrobus securis</i> and <i>Mytilus galloprovincialis</i>)	45 °C for 4 days (control 30 °C)	Heatwave exposure caused mortality of habitat-forming foundation species, reducing micro-scale refugia and altering competitive and predator–prey interactions.	[51]
Planktonic copepod (<i>Pseudodiaptomus incisus</i>)	8 days at 23.5 °C; 34 °C for 48 h (control 30 °C)	Parental heatwave exposure increased F1 vulnerability to micropollutants, indicating maladaptive cross-generational effects.	[102]
Hard clam (<i>Mercenaria mercenaria</i>)	30 °C for 20 days (control 25 °C)	Heatwaves reduced survival and threatened benthic–pelagic coupling in estuarine systems.	[103]
Intertidal bivalves (<i>Cerastoderma edule</i> and <i>Macoma balthica</i>)	15-day mild and strong heatwaves in near-natural mesocosms	Two species from similar intertidal settings showed different survival, condition, filtration and metabolic responses; strong heatwaves caused reduced post-exposure respiration.	[57]
Copepod assemblages (Calanoida, Cyclopoida, Harpacticoida)	+3 °C for 10 days	Marine heatwaves restructured zooplankton communities, altering size spectra and food-web nutritional quality.	[104]
Aquatic snail (<i>Lymnaea stagnalis</i>);	8 days at 23.5 °C; 34 °C for 48 h (control 30 °C)	Parental heatwave exposure increased F1 vulnerability to micropollutants, indicating maladaptive cross-generational effects.	[105]
Gastropods (<i>Lunella granulata</i>)	28, 30 or 32 °C for 5 days (control 26 °C)	Heatwave exposure impaired essential motor functions, including self-righting behaviour.	[106]
Freshwater microcosms	+4 °C offset for 8 days; 28 °C for 7 days (control 26.48 °C)	Heatwaves interacting with pesticides or herbicides triggered cascading, multi-trophic disruption in freshwater ecosystems.	[107,108]
Freshwater ectotherms	—	Heatwaves increased micropollutant uptake and reduced detoxification capacity, amplifying chemical stress.	[40]

Table 1. Cont.

Species/System	Heatwave Treatment	Main response	Reference
Foraging whales	—	Heatwave-driven coastal habitat compression concentrated prey nearshore, forcing whales into narrow foraging zones and increasing overlap with fisheries.	[109]
Purple sea urchin (<i>Strongylocentrotus purpuratus</i>)	20 °C for 28 days (control 14 °C)	Paternal heatwave exposure reduced sperm viability and fertilization success.	[110]
<i>Myriophyllum spicatum</i> ; <i>Ceratophyllum tomentosum</i>	+4 °C	Heatwaves altered reproductive strategies of submerged freshwater macrophytes and reduced nursery structural complexity.	[111]

During heatwaves, organisms may enter a state of behavioral triage, rapidly suppressing non-essential activities to prioritize immediate survival (for example, mating suppression in aquatic insect (*Xanthagrion erythronerum*) [112]. However, extreme hyperthermia can directly impair the neural and motor functions required to execute these compensatory behaviors. In aquatic ectotherms, Breedveld et al. showed that experimental heatwaves impair cognitive traits in male guppies (*Poecilia reticulata*), degrading learning and decision-making [93]. This cognitive impairment is often accompanied by broader behavioral changes. Mameri et al. found that freshwater fishes such as the *Iberian barbel* exhibit reduced swimming activity, suppressed boldness and weakened shoaling cohesion under heatwave exposure [94]. Similarly, Joyce et al. showed that extreme warming compromises essential motor responses such as self-righting in tropical gastropods [106]. In this context, behavioral failure becomes a hidden survival cost. Clements et al. observed that heatwave-stressed bivalves failed to reborrow after disturbance, leaving them exposed on the sediment surface to predators whose activity was simultaneously elevated by warming [101]. Behavior therefore functions as both a coping mechanism and a point of collapse.

For mobile species, the typical behavioral response to warming is to move towards cooler thermal refugia [113]. However, aquatic heatwaves often extend across broad spatial scales, compressing suitable habitat and shrinking the overlap between thermal refugia, prey availability and acceptable physiological conditions [114,115]. In heavily anthropized coastal and inland systems, these compressed refugia may become ecological traps rather than safe havens. Compressed thermal refugia may also intensify biotic interactions. As individuals aggregate in a shrinking number of cooler patches, local density can increase, strengthening competition for food, shelter and oxygenated microhabitats. At the same time, predators may track prey into the same refugia, increasing encounter rates and

predation risk. Crowding can also facilitate parasite and pathogen transmission, especially when heat stress has already weakened immune function or destabilized host-associated microbiomes. Thus, movement into cooler areas may reduce immediate thermal exposure but simultaneously increase competition, predation and disease-related risks [68–70,101,113]. Hermann et al. and Roth et al. showed that heatwaves can strongly amplify the toxicity of pesticides and herbicides, triggering cascading, multi-trophic effects in freshwater ecosystems [107,108]. Polazzo et al. further showed that warming can both increase contaminant uptake and depress detoxification capacity in aquatic ectotherms [40]. As a result, organisms attempting to behaviorally thermoregulate may be displaced into habitats where pollutant exposure, predation risk or resource limitation are intensified rather than reduced. Additionally, heatwaves not only directly affect the behavior of aquatic animals but also exacerbate the toxic effects of pollutants [116].

These trade-offs can be especially severe for benthic organisms, because the physical structure of refugia may itself be lost during marine heatwaves. Marine heatwaves can drive mass mortality of habitat-forming foundation species such as kelps and reef-building corals, eliminating the microhabitats on which smaller taxa depend [36,117]. This structural collapse renders behavioral thermoregulation ineffective and reorganizes local competitive and predator–prey interactions [51].

The profound cryptic costs also arise when these behavioral and distributional shifts intersect with human activities, generating broader ecological cascades. The 2014–2016 Northeast Pacific marine heatwaves showed severe coastal compression of upwelling habitat, which concentrated forage species into a narrow nearshore band [109,118]. Foraging whales tracked this shoreward prey distribution, but this shift also sharply increased their spatial overlap with the heavily capitalized Dungeness crab fishery, producing a record spike in whale entanglements. This example illustrates that heatwave-driven behavioral responses can extend beyond altered

individual performance to intensify indirect mortality, restructure trophic interactions and reduce resilience at ecosystem scale.

5. Maternal, Paternal, and Transgenerational Effects

The most prolonged cryptic fitness costs of aquatic heatwaves are not confined to the directly exposed parental generation (F0) but can be transmitted to subsequent cohorts via transgenerational plasticity (TGP) (Figure 5A, Table 1). As highlighted by Morosinotto et al., it is critical to evaluate cryptic reproductive costs by understanding the interaction between developmental plasticity and transgenerational effects [119]. These inherited physiological changes, which are mainly driven by epigenetic and transcriptional alterations, can impact the long-term resilience of aquatic populations, even months or years after a thermal anomaly has subsided. Some effects that may appear as delayed demographic responses are therefore more appropriately treated as transgenerational effects when they arise through parental exposure and are expressed in offspring. For example, parental heatwave exposure can alter offspring performance through reduced maternal provisioning, altered paternal thermal history, disrupted gamete quality or changes in vertically transmitted microbiomes. Minuti et al. showed that offspring of heatwave-exposed sea urchins developed rapidly during early larval stages but later experienced depleted energy reserves and elevated mortality during settlement [92]. Similarly, Strano et al. reported that parental exposure to marine heatwaves in temperate sponges disrupted vertically transmitted microbiomes and impaired offspring development, reducing settlement success and metamorphic performance. These examples show that heatwave effects can persist beyond direct exposure by embedding energetic and microbial liabilities into the next generation [28].

Due to heatwaves are short but intense and extreme thermal events, physiological acclimation within-generation often fails to keep pace with rapid thermal spikes [37]. By contrast, TGP driven by molecular reprogramming may partially buffer environmental challenges in subsequent generations and thereby contribute to longer-term persistence. Epigenetic responses to heatwaves can arise through both direct exposure and parental effects. Direct heatwave exposure can alter global DNA methylation and induce lasting changes in the transcription of stress-response genes in

exposed individuals [95]. Separately, studies that compare parental thermal history with offspring thermal experience show that offspring epigenetic profiles can also be shaped by parental exposure. For example, in juvenile brown trout (*Salmo trutta*), parental thermal history had a stronger effect on offspring genome-wide DNA methylation than the offspring's own developmental temperature [96]. These results suggest that heatwave legacies may reflect both direct thermal experience and parent-mediated epigenetic effects. Overall, these results indicate that transgenerational heatwave effects can be mediated primarily through inherited epigenetic change. Transgenerational effects of heatwaves can therefore be either adaptive or maladaptive. When parental exposure provides reliable information about the thermal environment that offspring will experience, parental effects may prime offspring physiology and improve heat tolerance. Such transgenerational buffering could contribute to population persistence under recurrent but predictable thermal extremes. However, this benefit is not guaranteed. If offspring encounter different stressors, repeated heatwaves, food limitation, pollutants, or hypoxia, the same priming responses may impose trade-offs by reducing growth, immune competence, reproductive investment, or tolerance to non-thermal stressors. Thus, thermal priming should be interpreted as a context-dependent response rather than as unequivocal evidence of resilience.

However, the efficacy of this transgenerational buffering is highly dependent on the environmental context. Recent studies reported by Sasaki et al. and Dinh underscore that transgenerational vulnerability is strongly shaped by seasonally variable thermal performance curves (TPCs). The parents acclimatized to summer conditions before a heatwave may shield offspring more effectively than winter-acclimatized cohorts [120,121] (Figure 5A). In contrast, TGP can act as a double-edged sword in multi-stressor environments. TGP may buffer offspring against an isolated thermal stressor, but it can also increase sensitivity to secondary anthropogenic stressors. For example, Salo et al. and Dinh et al. demonstrated that parental exposure to thermal extremes significantly amplifies the vulnerability of the F1 generation to subsequent micropollutants, including agricultural pesticides and copper. This phenomenon highlighted a cross-generational maladaptive cost in which thermal preparedness compromises broader ecotoxicological resilience [102,105].

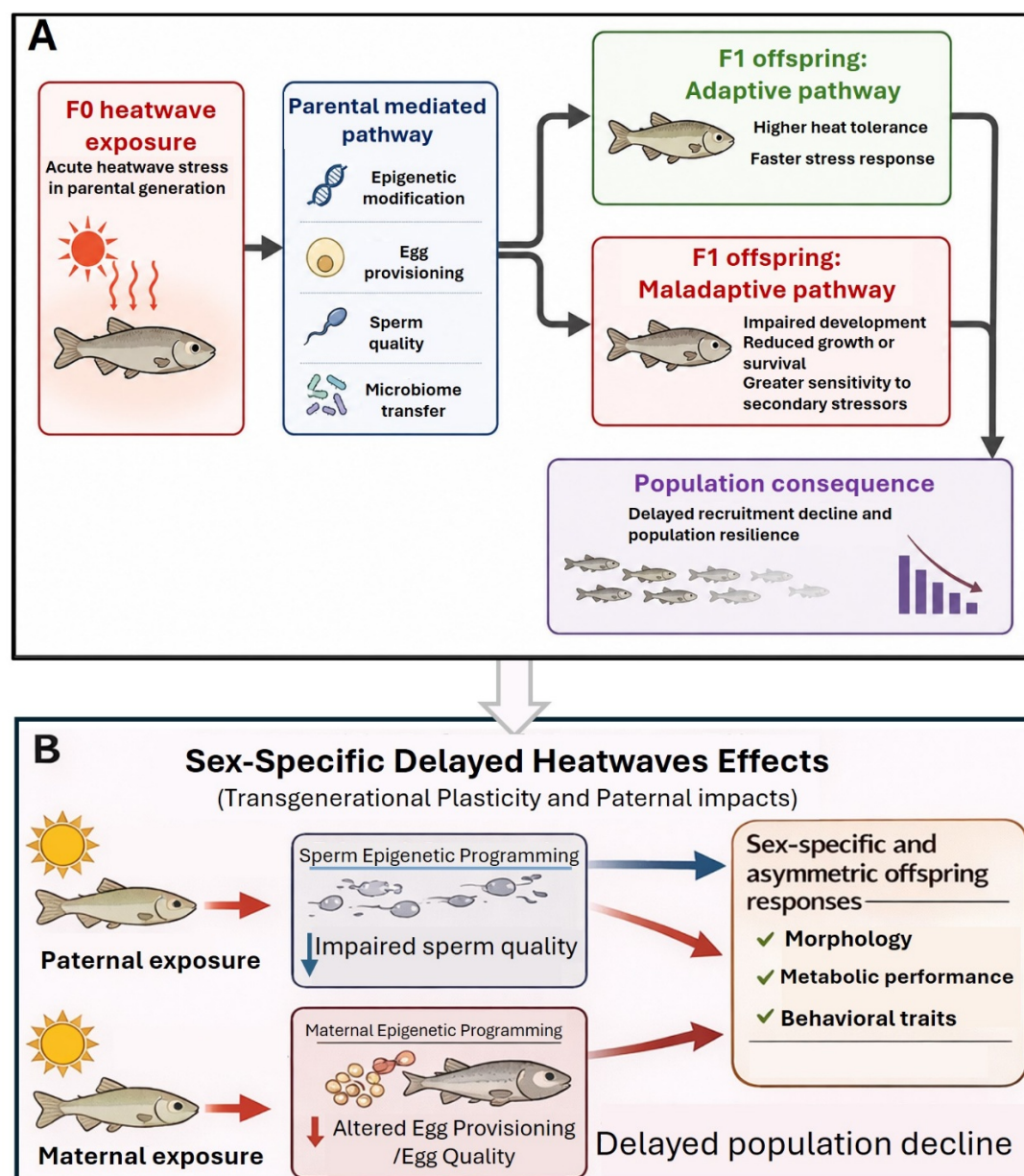


Figure 5. Transgenerational and sex-specific consequences of aquatic heatwaves. **(A)** F0 heatwave exposure may influence F1 offspring performance through parental or gamete-mediated pathways, including epigenetic modification, egg provisioning, sperm quality and microbiome transfer. These pathways may lead to adaptive priming when parental and offspring environments are matched, resulting in higher heat tolerance or faster stress responses in offspring. However, they may also generate maladaptive carryover effects, including impaired development, reduced growth or survival, and greater sensitivity to secondary stressors. These offspring-level effects can scale up to delayed recruitment decline or reduced population resilience. **(B)** Heatwave effects can also be sex specific. Paternal exposure may impair sperm quality, motility and epigenetic state, whereas maternal exposure may alter egg resource allocation, egg quality and maternal epigenetic or cytoplasmic programming of the egg. Post-fertilization parental care represents a separate, species-dependent pathway that may be maternal, paternal, biparental or absent. Together, these pathways can generate asymmetric offspring responses affecting morphology, metabolic performance and behavior, with delayed consequences for population persistence.

Research across multiple generations of guppies (*Poecilia reticulata*) further demonstrated that distinct maternal and paternal thermal histories can independently and asymmetrically shape offspring morphology, metabolic enzyme activity and swimming performance [98]. Similarly, Spence-Jones et al. showed in

a three-generation threespine stickleback experiment that single and recurring marine heatwaves altered reproductive output, offspring growth, exploratory behaviour and long-term survival, indicating that heatwave effects can persist beyond the directly exposed generation in a trait-dependent manner. These findings

show that transgenerational heatwave effects can be both trait specific and sex specific [42].

Maternal effects may operate through egg provisioning and egg quality. Heatwave-exposed females may alter the resources transferred to eggs, including egg size, lipid reserves, protein content, maternally derived transcripts or other cytoplasmic factors. However, the direction of these responses is likely to be species- and context-dependent. For example, in the purple sea urchin *Strongylocentrotus purpuratus*, females acclimated to marine heatwave temperatures during gametogenesis produced eggs with higher protein concentrations, whereas egg size and lipid content did not differ from controls [122]. Thus, maternal heatwave effects may alter offspring developmental potential through egg composition even when egg size does not change.

On the paternal side, the cryptic costs of heatwaves often emerge before fertilization or through post-fertilization behavioral impairment. Leach et al. demonstrated that the sperm viability and fertilization success of sea urchins were drastically reduced under exposure of marine heatwaves [110]. Furthermore, even when fertilization occurs, heatwave-induced changes in sperm appear to confer little adaptive benefit to offspring survival [99]. Likewise, short-term heatwaves can cause long-term degradation of paternal care behaviours in teleost fishes, directly reducing offspring condition [100]. Maternal and paternal thermal stress should therefore be viewed as distinct but interacting pathways that can jointly influence F1 developmental performance through egg provisioning, gamete quality, epigenetic state, microbiome transmission and, where present, sex- or species-specific parental care (Figure 5B). Aquatic heatwaves therefore act not only as acute parental stressors, but also as cross-generational stressors that may embed hidden fitness costs into offspring (Figure 5A). Consequently, when epigenetically and metabolically compromised offspring hatch into post-heatwave waters, they may encounter a functionally degraded environment that compounds inherited physiological damage with ecological food limitation [104]. Aquatic heatwaves therefore act not only as acute parental stressors, but as cross-generational selections that embed hidden fitness costs into both descendants and the ecosystems on which they depend.

6. Conclusions and Future Directions

Aquatic heatwaves are profoundly restructuring marine and freshwater ecosystems [1]. Current literature mainly focuses on high-profile mass mortality caused by heatwaves; however, this review shows that the ecological footprint of heatwaves is often hidden by pervasive, cryptic fitness costs that persist long after the acute thermal events (Figure 6). Even if organisms can

survive under the exposure of heatwaves, they may carry depleted energy reserves, impaired immune function, destabilized microbiomes, disrupted developmental trajectories and maladaptive behavioral responses that impact performance at subsequent life stages or generations. These hidden costs may constitute a long demographic shadow, propagating across generations through epigenetic modifications, altered parental effects and sex-specific effects, thereby reducing the long-term resilience of populations. Therefore, how to accurately predict the wide ecosystem consequences of heatwaves has become a central challenge for studying the biological response to global changes.

A key challenge is to distinguish adaptive thermal priming from delayed ecological debt, because prior heat exposure that improves short-term tolerance may also carry energetic, reproductive or cross-generational costs under recurrent or multi-stressor conditions. From this perspective, cryptic fitness costs can be viewed as a form of ecological debt: apparent short-term persistence of individuals or populations may be followed by delayed declines in reproduction, recruitment, community stability or ecosystem function [29]. A caveat of this review is that much of the currently available mechanistic evidence comes from ectothermic aquatic taxa. This reflects both the strong thermal dependence of ectotherm physiology and the concentration of experimental heatwave studies on fishes, invertebrates, corals and planktonic organisms. The framework proposed here is therefore most directly applicable to aquatic ectotherms. Endothermic marine organisms may also experience lasting heatwave impacts, but these effects are likely to be mediated more strongly through prey redistribution, habitat compression, altered migration, reproductive disruption and increased overlap with human activities. Future work should explicitly compare ectothermic and endothermic pathways to determine which cryptic fitness costs are general across aquatic taxa and which are specific to thermoregulatory strategy.

A major limitation in current research is the gap between sub-cellular stress responses and population-level demographic outcomes. Currently, how transient molecular damage causes long-term declines in survival, recruitment and lifetime reproductive success of a population still need to be addressed. Thus, future research needs to employ integrative frameworks that connect molecular responses to life-history trade-offs and demographic change. Additionally, multi-omics approaches (transcriptomics, epigenomics and metabolomics) should be coupled with long-term demographic tracking. One possible approach is the dynamic energy budget (DEB) models [123] that incorporate the costs of energy with cellular repair, immune maintenance and recovery. This novel model could provide a mechanistic bridge from sub-cellular damage to organismal performance and population dynamics.

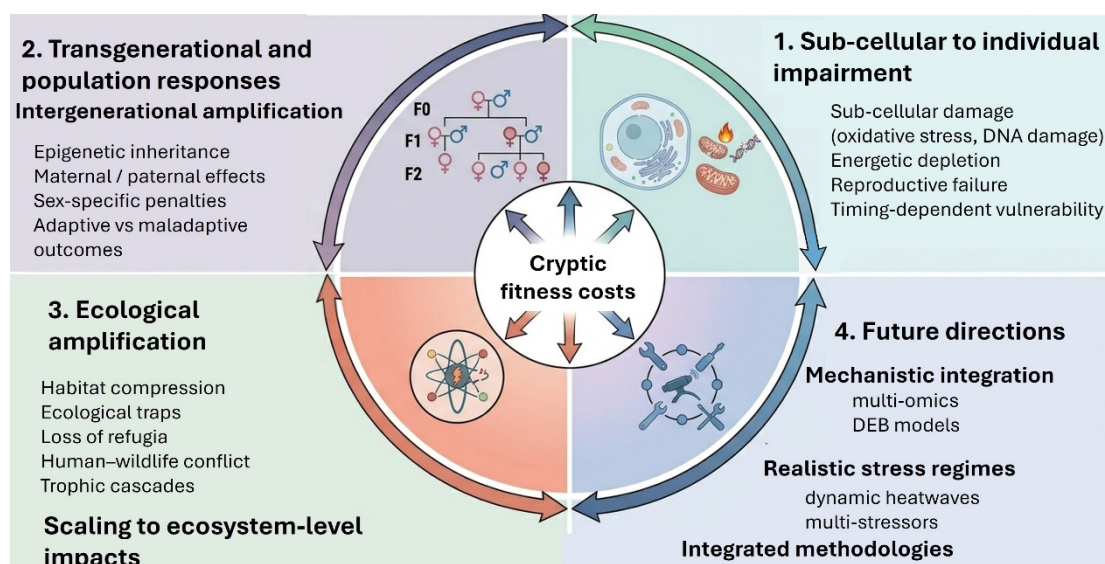


Figure 6. Cross-scale framework for cryptic fitness costs under aquatic heatwaves. Aquatic heatwaves induce hidden fitness costs that emerge from sub-cellular damage to ecosystem-level impacts. Heatwave stress first impairs cellular and organismal function through oxidative damage, energetic depletion and reproductive disruption. These effects can then extend across generations via epigenetic inheritance, parental effects and sex-specific impacts, while simultaneously scaling up through ecological amplification, including habitat compression, ecological traps, trophic cascades and human–wildlife conflict. Addressing these hidden costs will require integrative, multi-scale approaches that link mechanistic understanding with predictive ecological frameworks.

A second major challenge is that most experimental studies still treat heatwaves as isolated warming events, whereas they are dynamic in nature. Thus, experimental designs should shift from stable warming paradigms to fluctuating thermal regimes that capture the warming and cooling phases of natural heatwaves [37]. Meanwhile, heatwaves frequently co-occur with hypoxia, acidification and anthropogenic micropollutants such as pesticides [38]. These stressors often interact synergistically, while single-stressor experiments are likely to underestimate ecological risk of heatwaves. Especially large-scale in situ mesocosms will be important for testing how extreme temperature interacts with local pollutants under more realistic environmental conditions [124]. Additionally, predictive models need to move beyond additive assumptions to include synergistic interactions and altered toxicokinetics under hyperthermic conditions [125]. Future work should also place greater emphasis on ecosystem-level effects and species interactions. Most heatwave studies still focus on responses of single species or isolated physiological traits, yet heatwave impacts in natural systems are likely to emerge through interaction networks. Compressed refugia, altered phenology and differential thermal sensitivity can modify competition, predator–prey interactions, host–parasite dynamics, mutualisms and trophic energy flow. For example, a heatwave may not only reduce the performance of a focal species, but also change its predators, prey, competitors, pathogens or habitat-forming partners. Ecosystem-level mesocosms, long-term monitoring and food-web models

will therefore be essential for identifying when species-level heatwave responses scale up to community reorganization, altered ecosystem function or delayed ecological debt.

The transgenerational consequences of heatwaves need to be taken into consideration in future studies. Although heatwave-induced epigenetic signatures and altered parental provisioning can shape offspring performance, however, it still remains unclear whether these effects primarily act as adaptive buffers or maladaptive traps in repeated or sequential extreme events [126]. This uncertainty is especially important when maternal and paternal effects induce different responses or existence of sex-specific responses in the F1 generation. Thus, future studies can use a long-term, multi-generational experimental framework to explicitly separate the maternal and paternal effects and track the persistence, modification or erasure of DNA methylation across several generations. Importantly, integrating seasonal thermal performance curves (TPCs) into experimental designs would further clarify how previous thermal history determines whether transgenerational plasticity reduces or amplifies intergenerational costs [121].

Finally, although behavioral plasticity is a key defense against heat stress [127], the broader ecological consequences of these reactions remain poorly studied. Heatwaves can compress the habitat and alter interactions between predator and prey, intensify conflict between human and wildlife [128] and increase exposure to ecological traps. These behavioral responses may fail

entirely when heatwaves cause the death of foundation species such as kelps and corals [129], and high mortality could destroy the micro-refugia which many benthic organisms depend on [24]. Future ecological monitoring should therefore combine advanced biotelemetry, passive acoustics and high-resolution spatial mapping to track behavioral shifts in real time during heatwaves. These data should then be integrated into trait-based, end-to-end ecosystem models, such as Atlantis or Ecopath with Ecosim, to predict how behavioral trade-offs and nursery collapse propagate through food webs. Overall, incorporating these cryptic behavioral and structural costs into marine spatial planning and fisheries management will be essential for reducing human–wildlife conflict and limiting fisheries collapse.

Taken together, we here suggest that aquatic heatwaves should not be viewed solely as acute thermal disturbances, but as propagating drivers of hidden physiological, demographic and ecological change. Their most consequential effects are often delayed, context dependent and expressed across levels of biological organization. Revealing these hidden costs will require a shift from mortality-based descriptions of heatwave impacts towards integrative, mechanistic and multi-generational frameworks capable of linking sub-cellular damage to ecosystem decline.

Author Contributions

J.X. conceived and drafted the review, conducted the literature survey, and prepared the figures and tables. Y.X. contributed to the conceptual development of the review, critically revised the manuscript, and supervised the study. All authors have read and agreed to the published version of the manuscript.

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Conflicts of Interest

The authors declare no conflict of interest.

Use of AI and AI-Assisted Technologies

During the preparation of this work, the author used ChatGPT to go through the English. After using this tool, the author reviewed and edited the content as needed and took full responsibility for the content of the published article.

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