

The Impact of Climate Change on Global Aquaculture: A Focus on Heat Stress

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Aquaculture is one of the fastest-growing sectors of global food production, contributing significantly to nutrition, livelihoods, and economic development, particularly in low- and middle-income countries. However, climate change poses a growing threat to the stability and sustainability of aquaculture systems, primarily due to rising water temperatures and the increasing frequency of extreme weather events. This review examines the diverse impacts of heat stress on aquaculture species and operations globally. It synthesises current knowledge of the physiological, immunological, behavioural, ecological, and socio-economic consequences. Particular emphasis is placed on metabolic disruptions, oxidative damage, immune suppression, changes in microbiota, and reduced growth and reproductive capacity under both acute and chronic thermal exposure. The regional vulnerability of aquaculture systems is discussed, highlighting disparities in adaptive capacity and resilience. The review further outlines adaptation and mitigation strategies, including thermal tolerance breeding, recirculating aquaculture systems (RAS), precision farming, and climate-smart management practices. It identifies critical research gaps regarding long-term adaptation, early-life exposure effects, and multi-stressor interactions under climate change scenarios. Strengthening science-policy integration and supporting small-scale producers through innovation and investment are key recommendations to enhance climate resilience in aquaculture.

Keywords: Climate change, aquaculture, heat stress, thermal tolerance, fish physiology, immune function, adaptation strategies, food security.

INTRODUCTION

Aquaculture is one of the most rapidly expanding sectors of the global agricultural economy, playing a critically important role in ensuring food security, employment, and a sustainable supply of animal-derived protein. However, climate change presents a significant threat to the stability of aquaculture production, which is particularly vulnerable to environmental stressors. Rising average temperatures and the increasing frequency of extreme weather events, including marine heatwaves, directly impact aquatic ecosystems and the physiological functioning of cultured aquatic organisms (Bricknell et al., 2020; Fernández et al., 2022; Fred-Ahmadu

et al., 2024). This review focuses on heat stress, defined as a rise in water temperature beyond the thermal tolerance limits of fish and other aquatic organisms. Heat stress may be acute (short-term thermal spikes) or chronic (prolonged exposure to elevated temperatures), and in both forms, it induces physiological, behavioural, and immunological disturbances in aquatic species. In the context of climate change, heat stress is one of the principal factors adversely affecting the profitability and resilience of aquaculture production systems (Mehrim & Refaey, 2023; Mitra et al., 2023; Neokye et al., 2024). The review covers several thematic areas: physiological and metabolic alterations in fish under heat stress; effects on immunity, reproductive functions and

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behavioural responses; consequences for aquaculture systems and aquatic ecosystems more broadly; regional variations and socio-economic implications; adaptation and mitigation strategies; and finally, research gaps and future priorities. Aquaculture supports food provision, livelihoods and income for more than 870 million people worldwide, particularly in developing countries. However, the impacts of climate change are exacerbating existing anthropogenic pressures on the sector. Current challenges include not only rising water temperatures but also declining aquatic productivity, disruption of ecosystem processes, and increasing social vulnerability in communities reliant on aquaculture (FAO, 2016). Overall, this review aims to synthesize current knowledge on heat stress in the context of global warming and to inform the development of practical solutions for enhancing the climate resilience of aquaculture systems.

Physiological consequences of heat stress in fish: Fish and other aquatic ectothermic organisms have body temperatures that are directly influenced by ambient water temperature. Therefore, increases in water temperature directly affect their metabolic processes, homeostasis, growth, and survival. Heat exposure activates a range of physiological responses aimed at maintaining internal equilibrium, although these responses are often energetically costly and can suppress other vital functions (Maulu et al., 2021; Mylostyva et al., 2022). Islam et al. (2021) provided a detailed description of the multifaceted response of fish to extreme thermal stress induced by climate change. They emphasized that temperature is the primary abiotic factor shaping all physiological functions in fish, including neuroendocrine responses, metabolism, immunity, growth, and reproduction. Both acute and chronic heat stress activate cascades of responses, such as the release of catecholamines and corticosteroids, followed by alterations in metabolism, cardiovascular function, osmoregulation, immunity, cortisol levels, and the expression of heat shock proteins (HSPs). Over time, these disruptions reduce growth performance, survival, and reproductive efficiency. Even short-term increases in temperature by 3 to 8 °C above optimal thresholds have been shown to cause mass mortality events in aquaculture across countries such as Norway, Vietnam, Australia, and Canada. Acclimation of rainbow trout to moderately elevated temperatures (20 °C), combined with dietary supplementation of antioxidants such as yeast selenium and chestnut-derived polyphenols, significantly improved their physiological resilience to heat waves. These measures resulted in higher survival under acute thermal stress, lower cortisol levels, increased erythrocyte counts, enhanced lysozyme activity, and greater expression of the pro-inflammatory cytokine IL-1 β . Interestingly, fish acclimated to heat showed reduced HSP70 and HSP90 expression during stress, indicating the development of improved thermotolerance mechanisms (Hosseinpour et al., 2024). In the Antarctic fish species *Harpagifer antarcticus*, the rate of temperature increase

played a critical role in shaping the physiological response. Fish subjected to gradual warming showed lower cortisol levels, reduced HSP70 expression, and more stable cardiovascular parameters compared to those exposed to rapid temperature increases. This suggests a stronger adaptive capacity to gradual environmental changes than to sudden thermal shifts (Saravia et al., 2021).

Moderate heating stimulates metabolic activity in fish by increasing energy demand and oxygen consumption (Q_{10} effect). However, once critical thermal thresholds are exceeded, metabolism becomes destabilized, leading to appetite suppression, impaired growth, energy depletion, and cardiovascular stress. Warmer waters also contain less dissolved oxygen, thereby increasing the risk of hypoxia as an additional metabolic burden. High temperatures disrupt osmoregulation as well, decreasing salinity tolerance and causing dehydration or oedema in both marine and freshwater species (Assan et al., 2020; Liu et al., 2022; Mugwanya et al., 2022). In *Lateolabrax maculatus* (Japanese sea bass), hypoxia followed by reoxygenation resulted in increased hepatic oxidative stress. This was characterized by elevated malondialdehyde (MDA) levels and decreased activities of superoxide dismutase (SOD) and catalase (CAT). These oxygen fluctuations, often intensified by heat stress in warm waters, highlight the compounding effect of multiple stressors that weaken antioxidant defences and elevate toxicity risk in fish (Yan et al., 2021). While optimal water temperatures can improve growth and feed conversion efficiency, chronic overheating reduces body weight gain. Under excessive heat conditions, fish redirect energy from growth and anabolism to thermoregulation and physiological adjustments. Appetite and digestive enzyme activity are suppressed, leading to reduced nutrient absorption. Elevated temperatures lower the activity of enzymes such as pepsin, amylase, and lipase, disturb gut microbiota composition, and alter levels of appetite-regulating hormones (Mehrim & Refaey, 2023; Agarwal et al., 2024). Liu et al. (2023) showed that acute thermal stress induces notable metabolic changes in the muscle tissue of yellowfin tuna. Exposure to 34 °C reduced muscle energy reserves (Ea), while the activity of catabolic enzymes (ACP, LDH, ALT, AST) significantly increased, indicating intensified metabolic breakdown. After six hours, the cellular energy allocation (CEA) index dropped, reflecting a reduced ratio of stored to expended energy, likely due to lipid and carbohydrate mobilization. CEA values returned to more stable levels after 24 hours, suggesting some degree of adaptation to thermal exposure. In addition to muscle-related changes, yellowfin tuna demonstrated temperature-sensitive shifts in energy allocation. Acute heat stress led to reductions in triglyceride and glycogen levels in tissues, and increased LDH activity pointed to enhanced anaerobic glycolysis as a compensatory mechanism (Liu et al., 2023). In *Pinctada fucata* (pearl oyster), high-temperature stress triggered multiple compensatory mechanisms, including heightened



activities of antioxidant enzymes (CAT, SOD, GST), upregulation of HSP genes, and increased expression of genes associated with energy metabolism. Transcriptome analyses revealed complex regulatory networks supporting cellular homeostasis under thermal load, indicating the potential for partial molecular adaptation possibly applicable to fish as well (Zhang et al., 2022).

In rainbow trout, acute exposure to 22.5 °C for 24 hours caused pronounced increases in cortisol, catecholamines, oxidative stress markers (MDA), and HSPs (HSP-70, HSP-90). At the same time, the activities of antioxidant enzymes (GSH, SOD, T-AOC) and the anti-inflammatory cytokine IL-10 decreased, while IL-1 β , IL-6, TNF- α , and TGF- α levels rose. These biochemical changes coincided with physical damage to muscle fibres, including rupture and widened intercellular spaces, signaling systemic physiological destabilization (Li et al., 2024). Prolonged thermal exposure leads to severe morphological and physiological alterations in fish. In *Trachidermus fasciatus*, chronic exposure to 31 °C resulted in gill damage such as epithelial proliferation, filament thickening, and ulceration. HSP genes (hspb1, hspb7, hspb11) were highly upregulated during the first 6 to 9 days but subsequently declined, indicating initial activation followed by exhaustion of protective mechanisms. The species' lethal temperature was found to be 33 °C, with survival dropping to just 8 percent, underscoring the importance of recognizing thermal thresholds in aquaculture management (Liu et al., 2025).

Temperature increases associated with global warming directly affect the stress physiology of fish by disrupting the function of key neuroendocrine systems, namely the hypothalamic-pituitary-interrenal (HPI) and brain-sympathetic-chromaffin (BSC) axes. Chronic heat exposure raises basal cortisol levels, alters catecholamine, serotonin, and dopamine signaling, and diminishes the ability to respond to secondary stressors. While acute heat stress triggers temporary responses including cortisol release, elevated blood glucose, lactate accumulation, and HSP induction, repeated or prolonged exposure may overwhelm adaptive capacity. Elevated temperatures during early development can also result in lasting changes in HPI regulation and stress responses, which can ultimately impair the population's capacity to adjust to rapid environmental shifts (Alfonso et al., 2020).

A summary of physiological changes associated with heat stress in fish is provided in Table 1. In the study by Taenzer et al. (2024), it was demonstrated that the macroalgae *Ulva fenestrata* and *Palmaria palmata* exhibit a significant increase in hydrogen peroxide (H₂O₂) concentrations in response to heat stress and grazing pressure from molluscs. This oxidative surge represents a typical stress response, analogous to mechanisms observed in higher plants and animals, and may serve as a potential biomarker of health status in mariculture systems. Specifically, during a nine-hour

incubation at 20 °C, H₂O₂ concentrations in the surrounding medium increased more than 50-fold compared to standard conditions, indicating the activation of a robust antioxidant response. These findings highlight the relevance of H₂O₂ as a universal stress signal in aquatic organisms, including fish, and support the use of such biochemical indicators to assess immune function under thermal challenge. In rainbow trout, genetic variability in response to prolonged heat stress was confirmed to be of considerable importance, particularly in relation to growth and survival. Among 119 trout families, high heritability estimates were found for final body mass under chronic heating ($h^2 = 0.41$) and moderate heritability for survival ($h^2 = 0.13$ using a linear model), suggesting potential for selective improvement of these traits. The authors also noted that a sustained exposure to temperatures of 18-22 °C over 62 days did not suppress appetite but led to increased mortality beyond 20 °C, especially among more sensitive families (Gallardo-Hidalgo et al., 2021). In a study on starry flounder (*Platichthys stellatus*), thermal tolerance was found to vary significantly with age. Juvenile fish exhibited lower resilience to heat stress than adults, as evidenced by elevated cortisol levels, enhanced expression of HSP70 and HSP90, and reduced antioxidant enzyme activity in younger individuals. These differences underscore the need to account for age stratification when evaluating thermal tolerance in breeding programmes or adaptive strategies (Lee et al., 2021). In brook trout (*Salvelinus fontinalis*), molecular and physiological responses were shown to act as indicators of thermal acclimation thresholds. Exposure to 22 °C induced HSP70 expression, elevated cortisol, and reduced haematocrit and lactate levels. However, the ability to maintain these adaptive responses over time was limited, pointing to a narrow "thermal acclimation window" for this species (Mackey et al., 2021).

The same study also revealed marked morphological changes in muscle tissue following thermal stress. These included disrupted muscle fibre integrity, intercellular oedema, and vacuolization, indicative of structural destabilization. These alterations were likely caused by oxidative stress and metabolic disorganization, confirming the multisystemic nature of heat-induced damage in fish (Liu et al., 2023). Further research has demonstrated the critical role of heat stress in disrupting oxidative balance. Elevated water temperatures increase malondialdehyde (MDA) levels, a marker of lipid peroxidation, while reducing antioxidant enzymes such as superoxide dismutase (SOD) and catalase (CAT), reflecting the depletion of protective antioxidant mechanisms. This oxidative damage is a key factor in tissue injury under thermal stress (Liu et al., 2023). A study conducted on Atlantic salmon in commercial farm conditions revealed physiological and behavioural differences depending on heat stress duration. Short-term heat exposure (STHE) resulted in elevated heart rate (from 59 to 69 bpm) and increased activity, indicative of a typical secondary stress



response. In contrast, long-term heat exposure (LTHE) led to reduced activity and sometimes even a decrease in heart rate, reflecting a tertiary stress phase associated with energy depletion and general suppression of vital functions (Korus et al., 2024). In juvenile greater amberjack (*Seriola dumerili*), elevated temperatures negatively affected antioxidant defence, energy metabolism, and immune function, providing a useful model for examining heat stress in marine species. Early heat stress stages induced higher SOD, CAT, GSH, and immune markers (ACP, ALP, LYZ), indicating activation of protective responses. However, prolonged exposure reduced these indicators and increased MDA and glucose (GLU) levels, signifying oxidative damage and metabolic exhaustion. Thus, although an initial adaptive response occurs, chronic thermal stress leads to energy system fatigue and diminished immune competence (Hao et al., 2024). High temperatures disrupt hormonal balance and the function of the hypothalamic-pituitary-gonadal (HPG) axis, impairing gamete quality, delaying maturation, reducing fertility, or even halting the reproductive cycle. For instance, ovulation is inhibited in common carp at temperatures above 28 °C, while sperm motility in trout decreases at just 12 °C. Early life stages (eggs, larvae) are particularly vulnerable to thermal stress, which induces developmental abnormalities, reduced survival, altered morphology, and diminished offspring fitness (Servili et al., 2020; Marenkov et al., 2021; Maulu et al., 2021). Climate change affects the physiological traits of fish by altering growth rates, survival, and reproductive cycles. Elevated temperatures disrupt thermal regimes in aquatic habitats, potentially shifting spawning periods, reducing biomass, or causing population declines in heat-sensitive regions. Conversely, some species may experience compensatory growth in temperate zones where warming conditions become more metabolically favourable (FAO, 2016).

Immune function and health of fish under heat stress: Prolonged heat stress activates the hypothalamic-pituitary-interrenal (HPI) axis in fish, leading to elevated cortisol levels - the principal stress hormone. This hormonal response suppresses immune function, resulting in reduced leukocyte counts, diminished antibody production, and decreased phagocytic activity. Consequently, fish become more susceptible to infections, particularly when heat stress is combined with additional environmental stressors such as overcrowding, hypoxia, or water pollution (Maulu et al., 2021; Fernández et al., 2022). Authors also highlight that the fish immune system is highly sensitive to temperature fluctuations. Heat stress alters cytokine expression, impairs phagocyte activity, and disrupts the barrier function of the skin and gills. A decline in immunoglobulin levels, suppression of lysozyme production, and reduced neutrophil activity have been reported in fish exposed to elevated temperatures. Furthermore, thermal exposure increases the risk of secondary infections, a major concern in high-density

farming systems. Such immune dysfunction has been documented in several commercially farmed species, including tilapia, trout, and sea bass (Islam et al., 2021). In intensive aquaculture systems, prolonged thermal loads are often accompanied by reduced feeding frequency and diminished locomotor activity. These feeding restrictions can further compromise physiological resilience and immune competence, contributing to stress under conditions of metabolic exhaustion. One study proposed integrating heart rate and behavioural monitoring as part of precision aquaculture, enabling real-time optimization of environmental conditions (Korus et al., 2024).

Bivalves, especially at larval and juvenile stages, are highly vulnerable to heat stress, leading to mass mortalities and severe ecological and food security consequences. Elevated temperatures cause not only acute metabolic and osmoregulatory disturbances but also long-term structural damage, microbiome dysbiosis, reduced immune resistance, and impaired growth potential. Even deviations of 2-4 °C from optimal ranges can trigger physiological breakdown, particularly in stenothermal species. Mass die-offs of oysters, mussels, and scallops over the past decade have been directly linked to extreme marine heatwaves, which are projected to increase in frequency and intensity under climate change (Masanja et al., 2023). In a study by Ma et al. (2025) on largemouth bass (*Micropterus salmoides*), both acute increases and decreases in water temperature (± 8 °C) triggered pronounced shifts in metabolism, immunity, and gut microbiota. Antioxidant defences were activated (elevated T-AOC, SOD, CAT), alongside changes in serum glucose, cholesterol, and triglyceride levels, as well as immune enzyme activity (LZM, AKP, AST, ALT). Additionally, thermal stress induced intestinal mucosal damage and reduced goblet cell density, indicating impaired local immune protection. Microbiome analysis revealed a decline in Firmicutes and an increase in Fusobacteria and Proteobacteria, indicative of microbial dysbiosis. These findings confirm that even short-term thermal stress can substantially impact fish health via disruptions in physiology, immunity, and gut microbiota. Research by Ng et al. (2024) underscored the immunomodulatory potential of thermal conditioning in recirculating aquaculture systems. A brief rise in water temperature to 37-39 °C in barramundi triggered significant upregulation of Hsp70, IL1 β , and TNF α , indicating a protective immune response. However, excessive thermal stress induced skin microbiota dysbiosis and elevated levels of pathogenic bacteria (notably *Vibrio* and *Tenacibaculum*), ultimately leading to mortality. The authors proposed the Pseudomonadota:Bacteroidota (P:B) ratio as a potential non-invasive biomarker for early detection of microbial imbalance and fish health deterioration in intensive systems. Hence, thermal exposure can stimulate defence mechanisms and pose risks when tolerability thresholds are exceeded, underscoring the need for precise temperature



control. Recent studies show that heat stress in fish is accompanied by changes in microRNA (miRNA) expression involved in metabolic and immune regulation. A systematic review of 13 studies identified 214 differentially expressed miRNAs, with 15 consistently observed across multiple datasets. Notable miRNAs such as miR-1, miR-122, let-7a, let-7b-3p, miR-30b, and miR-301a-3p were associated with glucose homeostasis, oxidative stress response, and immune modulation. These miRNAs could serve as promising biomarkers for monitoring heat tolerance in fish and as targets for selective breeding or adaptation strategies in recirculating systems (Lin & Meegaskumbura, 2025). In Chinese mitten crab (*Eriocheir sinensis*), chronic heat stress significantly reduced survival, suppressed immune function (lower phenoloxidase, alkaline and acid phosphatase activities), and caused intestinal damage including outer membrane detachment and elevated histamine, LPS, and DAO levels. Supplementation with dietary yeast culture (3.2 g/kg) significantly improved immune indices, reduced oxidative stress (lower MDA, higher SOD and GSH-Px activity), maintained gut barrier integrity, and restored microbiota composition. These results demonstrate the potential of dietary interventions to enhance thermal tolerance in aquatic organisms under chronic overheating conditions (Wang et al., 2025). Heat stress not only weakens host defences but also facilitates the rapid development of pathogenic microorganisms and parasites. Elevated water temperatures enhance viral replication, bacterial proliferation (e.g., *Vibrio* spp., *Aeromonas* spp.), and accelerate the life cycles of ectoparasites such as *Ichthyophthirius multifiliis* and *Argulus* spp. Numerous disease outbreaks have been linked to warming, including increased prevalence of tilapia lake virus and streptococcosis during hot years. Rising temperatures are also associated with "summer mortalities" of molluscs, particularly oysters (Cascarano et al., 2021; Pepi & Focardi, 2021; Neokye et al., 2024). The combination of heightened infectious pressure and declining immune resistance increases the risk of epizootics and major economic losses in aquaculture. Heat-stressed fish exhibit reduced survival, slower growth, deteriorated fillet quality, and increased handling sensitivity. Since many farmers lack early disease detection systems or cooling infrastructure, even brief heatwaves can result in catastrophic losses, particularly in extensive farming systems (Mugwanya et al., 2022; Mehrim & Refaey, 2023).

Behavioural responses to heat stress: Elevated water temperatures directly influence fish appetite and feeding behaviour. Under excessive thermal loads, many species reduce or entirely cease feed intake to prevent metabolic overload. In aquaculture settings, shifts in feeding time are frequently observed, with fish showing a preference for early morning or evening hours when water temperatures are lower. This necessitates adjustment of feeding schedules to minimize feed loss and improve feed conversion ratios (Liu et al., 2022;

Mitra et al., 2023). In open or natural systems such as ponds and lakes, fish actively seek thermally favourable microhabitats, including deeper layers, shaded zones, or areas with flowing water. Behavioural adaptations commonly include increased gill ventilation, congregation near cooler water sources, and reduced activity during peak heat periods. In spatially restricted environments such as cages and tanks, where thermal avoidance is not possible, signs of distress emerge, including abnormal swimming, leaping attempts, and surfacing for air to compensate for hypoxia (Servili et al., 2020; Mugwanya et al., 2022). In response to elevated temperatures, fish typically exhibit specific behavioural changes such as avoidance of warm surface layers, migration to cooler zones, decreased physical activity, and suppressed appetite. In systems with limited volume or depth, the inability to escape heated waters leads to distress manifestations including rapid opercular movement, surface dwelling, escape attempts, or even self-harm. Studies indicate that most species alter their diel activity rhythms under heat stress, reducing both feeding and resting periods, which compromises growth performance and complicates husbandry operations (Islam et al., 2021).

Behavioural responses to heat stress also differ depending on its duration. Short-term heat exposure often results in increased locomotor activity, whereas prolonged overheating is associated with reduced overall movement, likely due to energy depletion or suppression of the central nervous system. Authors highlight the potential of using external acceleration patterns as proxies for activity level monitoring and early stress detection in aquaculture facilities (Korus et al., 2024). Behavioural thermoregulation is a widespread adaptive strategy among aquatic animals, involving movement to more favourable thermal environments. With ongoing climate warming, latitudinal and altitudinal shifts in fish distributions have been documented, as species migrate toward cooler polar or upland habitats. In the context of aquaculture, this implies potential for farming certain species in newly suitable regions. However, it also raises ecological concerns regarding escapees from aquaculture systems - such as the red drum (*Sciaenops ocellatus*) - establishing invasive populations in previously unsuitable areas (Fernández et al., 2022; Xiao et al., 2023).

Ecological context of heat stress in aquaculture: In Central Europe, traditional pond aquaculture, particularly carp farming in the Czech Republic, is increasingly affected by climate change. Long-term water body monitoring has revealed a substantial rise in the number of days when surface water temperatures exceed 28-29 °C, surpassing the thermal threshold for carp and reaching critical levels for the survival of salmonid and coregonid species. It is projected that by the mid-21st century, more than 25 such days will occur annually in the South Moravian region, with this number potentially exceeding 40 after 2050. Although high-altitude regions currently face a lower risk of heat stress, that risk is also



increasing. These changes pose serious threats to the resilience of pond ecosystems, particularly under conditions of eutrophication, water shortages, and limited capacity for cooling (Khromykh et al., 2023; Orság et al., 2023). The growing pace of aquaculture intensification under climate change conditions calls for the integration of ecologically sustainable management strategies. Efficient use of water resources, reduction of anthropogenic pressure, and regional adaptation of production systems can mitigate the risks associated with thermal stress in aquatic organisms (Ahmed et al., 2018). Rising water temperatures lead to reduced dissolved oxygen levels, which increases the risk of hypoxic conditions, especially in stratified or low-flow water bodies. This situation is common during summer, when surface layers warm while deeper layers remain cooler, forming a thermocline that inhibits vertical mixing. Such stratification facilitates the accumulation of ammonia, accelerates organic matter decomposition, and enhances the toxicity of nitrogenous compounds (Maulu et al., 2021; Mugwanya et al., 2022). Warming combined with eutrophication promotes the frequency and intensity of harmful algal blooms in both freshwater and marine aquaculture systems. These blooms, caused by cyanobacteria in freshwater ponds or dinoflagellates in coastal waters, produce toxins, deplete oxygen, and result in mass mortality events among fish and molluscs. Some farms are considered “sentinel sites” for climate change due to recurring outbreaks of such phenomena (Griffith & Gobler, 2020). High-resolution bioclimatic modelling, particularly using marine datasets such as Bio-ORACLE v2.0, enables spatial forecasting of heat stress risk and potential shifts in aquaculture species distributions under climate change (Assis et al., 2017). Warm water creates favourable conditions for the reproduction of pathogens and parasites by accelerating their life cycles and increasing infectivity. Simultaneously, heat stress weakens fish immune defences, resulting in a dual threat. For instance, the prevalence of vibriosis, streptococcosis, and fungal infections rises significantly under elevated temperature regimes. In molluscs, such as oysters, summer mortalities are often directly linked to anomalous marine heatwaves (Cascarano et al., 2021; Agarwal et al., 2024). Climate warming may alter interspecific interactions, with thermophilic, fast-growing, or invasive species gaining a competitive advantage. Tilapia, for example, is a resilient species capable of displacing other cultured fish into ponds. This disrupts ecosystem balance, alters trophic dynamics, intensifies pressure on feed resources, and undermines biodiversity (Xiao et al., 2023). It is important to emphasize that heat stress typically does not act in isolation. Instead, it interacts with other climate-related factors such as ocean acidification, salinity changes, extreme rainfall events, and droughts. The combination of multiple stressors may have a synergistic impact, leading to unforeseen system failures. Therefore, a holistic approach is essential for assessing the consequences of climate change (Fred-Ahmadu

et al., 2024). Significant geographical shifts in fish distributions and changes in aquatic ecosystem structure are anticipated due to alterations in temperature regimes. In tropical regions, primary productivity is expected to decline, negatively affecting biomass and feed availability. Conversely, in polar and temperate zones, short-term productivity gains may occur owing to extended growing seasons. These transformations necessitate adaptive responses by aquaculture operations to new environmental conditions (FAO, 2016).

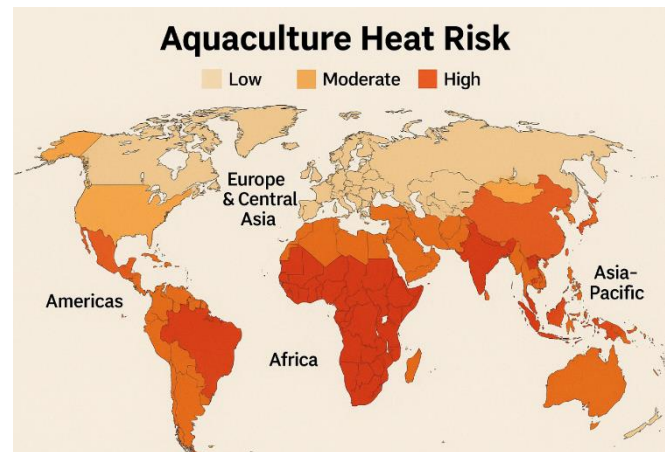


Figure 1. Global distribution of aquaculture risk regions associated with heat and water stress under climate change scenarios.

Socioeconomic implications of heat stress in aquaculture: Rising water temperatures do not affect all regions equally. Substantial differences exist in the species farmed, production systems used, and regional adaptive capacities. In particular, many tropical regions already operate near the upper thermal limits of aquaculture species, meaning that even modest warming can result in mass fish mortalities or outbreaks of disease (Cascarano et al., 2021). In Southeast Asia, Latin America, and Central Africa, water temperatures frequently exceed the optimal ranges for commercially important species. In tropical ponds, mass mortalities of tilapia, catfish, and shrimp have been recorded due to thermal peaks and hypoxia. In response, farmers have begun replacing more temperature-sensitive species with heat-tolerant ones. For instance, tilapia is being introduced in place of trout in highland areas. However, this transition is not always feasible, particularly in water-limited systems (Reverter et al., 2020; Maulu et al., 2021; Mugwanya et al., 2022). Sea-level rise, coastal erosion, habitat degradation, and more frequent extreme weather events increase the vulnerability of fishing communities, especially those reliant on small-scale fisheries and coastal aquaculture. The risk of material losses, infrastructure damage, and declining catches directly threatens livelihoods, food security, and social stability in



coastal regions (FAO, 2024). Of particular concern is the socioeconomic vulnerability of smallholder farmers. In many countries of the Global South, producers lack access to cooling technologies, insurance schemes, or credit for system upgrades. The loss of aquaculture products is not only an income issue but also a nutritional threat, as fish represents a primary protein source for millions of people (Abisha et al., 2022; Mehrim & Refaey, 2023). The rapid expansion of aquaculture, especially in Asian countries such as China, exerts additional pressure on natural resources, including wild fish stocks, and highlights the urgent need for climate-resilient and sustainable production models (Cao et al., 2015). Climate change presents major risks to food security, particularly in nations where aquaculture is a primary source of animal protein and household income. Small-scale producers remain the most vulnerable, lacking financial and technical resources to adapt to extreme weather events. The FAO projects increased economic pressures, displacement of communities, and worsening social inequality due to the loss of aquaculture-based livelihoods in both coastal and inland regions (FAO, 2016). In temperate regions such as Europe, North America, and East Asia, warming has a dual effect. On one hand, it extends the growing season and allows for the introduction of new warm-water species, such as tilapia in Italy or shrimp in China. On the other hand, cold-water aquaculture operations, including those farming salmon and trout, experience losses due to summer overheating of water bodies (Bricknell et al., 2020). Marine heatwaves in the North Atlantic have already led to reduced growth rates, elevated mortality, and parasite outbreaks in salmon sea cages (Neokye et al., 2024). Even northern regions like Norway and Chile are experiencing changes. Although the warming may be moderate, it still affects species with narrow thermal ranges, such as salmon and African catfish. The expansion of suitable zones for warm-water aquaculture could lead to economic competition from southern regions where these species are already established. One example is Egypt, a leading aquaculture producer in Africa, where rising temperatures are compounded by salinization, freshwater shortages, and pollution. These pressures contribute to fish mortalities, profit losses, and reduced production volumes (Mehrim & Refaey, 2023). In countries where aquaculture provides the main source of animal protein, thermal stress in production systems may have far-reaching consequences for food security. This is especially true in parts of Asia and Africa experiencing rapid population growth. Even if some regions benefit from extended growing periods, the global food system is becoming less stable and less equitable (Fred-Ahmadu et al., 2024).

Adaptation and mitigation strategies: In response to the growing threat of heat stress, a wide range of adaptation strategies have been developed, spanning from technological innovations to modifications in farming practices. One of the primary approaches is the regulation of water temperature in

aquaculture systems. To achieve this, farmers increase water exchange, utilize deep wells or spring water, install shading structures such as nets or vegetation over ponds, and employ aeration systems or even chillers in recirculating aquaculture systems (RAS) (Mugwanya et al., 2022). The implementation of innovative technologies including aquaponics, closed-loop systems (RAS), polyculture, selective breeding, alternative feed formulations, precision aquaculture, and genetic approaches is paving the way for climate-resilient aquaculture. Precision aquaculture, in particular, relies on sensors, data analytics, and artificial intelligence to optimize fish health, water quality, and feeding efficiency. Collectively, these innovations are transforming the sector into a more environmentally sound, efficient, and climate-resilient industry (Lal et al., 2024).

Effective management of oxygen levels is critical. As water temperatures rise, oxygen solubility decreases, increasing the risk of hypoxia-induced mortality. In many countries, emergency aerators or low-cost sprinkler systems are installed to reduce water temperature. Adaptive strategies also include adjusting feeding schedules to cooler hours of the day and reducing feed quantities during periods of intense heat to avoid water quality deterioration. Stocking densities are lowered, and changes in stocking or harvesting periods are implemented to avoid peak summer heatwaves (Maulu et al., 2021; Mehrim & Refaey, 2023). Modern farms are investing in controlled-environment systems such as enclosed greenhouses, insulated tanks, and deep-water or submersible cages. Recirculating aquaculture systems with temperature regulation are regarded as among the most climate-resilient technologies, provided they have sufficient cooling capacity (Agarwal et al., 2024). Predictive temperature models and early warning systems, including mobile apps for pond temperature monitoring, are increasingly adopted in digitally advanced countries (Neokye et al., 2024). The FAO advocates for a holistic adaptation framework in aquaculture that includes the breeding of thermotolerant species, improved water management systems, diversification of income sources, and the development of insurance schemes and early warning networks. Special emphasis is placed on supporting small-scale producers through education, infrastructure upgrades, and access to innovation. These measures can significantly enhance the climate resilience of aquaculture systems across different regions (FAO, 2016). Selective breeding for heat-tolerant fish is among the most promising approaches. For example, ongoing breeding efforts with tilapia and trout have already yielded lines with elevated thermal maxima. Gene editing techniques are also being explored, although these remain constrained by ethical and regulatory considerations (Liu et al., 2022). Innovative closed-loop systems such as aquaponics represent a promising strategy for mitigating the impacts of climate change on aquaculture, especially for temperature-sensitive species like rainbow trout. Aquaponic systems allow precise control over



abiotic factors, reducing risks associated with thermal stress, oxygen fluctuations, and the accumulation of toxic compounds. Studies indicate that rainbow trout, despite their sensitivity to elevated temperatures, can be successfully cultured in aquaponic settings, making them strong candidates for such systems. Notably, their high-protein diets result in substantial nitrate production, which can serve as a nitrogen source for plants in a closed-loop growing system (Vasdravanidis et al., 2022). In regions where traditional species can no longer withstand the prevailing temperature conditions, producers are shifting species composition, for instance, replacing salmon with barramundi or implementing polyculture systems that include more thermotolerant species. Integrated systems combining fish, algae, and molluscs help stabilize the microenvironment and reduce stress on individual species (Cascarano et al., 2021; Fred-Ahmadu et al., 2024). Emerging solutions also include epigenetic programming (where parental environmental exposures influence offspring adaptation), use of probiotics and immunostimulants, and cryopreservation of genetic material from vulnerable species. In the long term, selective breeding must be accompanied by continuous monitoring of adaptive potential within populations (Servili et al., 2020). Government-led adaptation strategies are gaining momentum, including the zoning of aquaculture areas, integration of climate risk in licensing procedures, and updates to national regulations. Some countries have introduced aquaculture modernization programmes to increase climate resilience (Mitra et al., 2023). National adaptation strategies are being implemented in various regions, combining ecological, technological, and social elements. Belize, for example, has launched a ten-year climate adaptation plan for the fisheries sector incorporating geospatial data, stock monitoring, and climate-informed planning. In the Philippines, regional small pelagic fishery management plans are being developed based on ecosystem-based approaches, reforestation, and anti-poaching efforts. In Chile, support for small-scale aquaculture includes income diversification (e.g. ecotourism) and the promotion of voluntary eco-certification (FAO, 2024). Climate risk insurance models for aquaculture are being developed. While still in early stages in many countries, these instruments could substantially reduce risk and stimulate investment in adaptive measures. Training farmers in climate-smart practices, establishing information platforms, and deploying mobile applications for real-time monitoring and adaptation to thermal stress enable swift and effective responses even in remote communities (Abisha et al., 2022; Bondarev et al., 2022).

Aquaculture adaptation must be embedded in broader water management and climate mitigation strategies, such as integration into watershed conservation, shoreline protection, and rural development programmes (Maulu et al., 2021). Although aquaculture is not a major contributor to greenhouse gas emissions, the sector has the potential to play an important

role in global climate mitigation efforts. Reducing energy use in production, improving logistics, adopting renewable energy sources, and enhancing feed efficiency are all strategic steps to minimize the carbon footprint of aquaculture. Furthermore, the cultivation of algae and molluscs in multitrophic systems can promote carbon sequestration and improve water quality (FAO, 2016). To reduce carbon emissions from aquaculture operations, modern farms are adopting renewable energy technologies such as solar panels, biogas systems, and wind turbines. Temperature-regulated RAS systems are also advancing, enabling reductions in cooling-related energy demands and providing greater control over emissions. When combined with water reuse and reduced organic waste, these technologies significantly enhance the climate neutrality of production systems (Lal et al., 2024). The use of biologgers to monitor physiological parameters in real time, including heart rate and acceleration, has proven effective in detecting early signs of stress. These sensor-based technologies facilitate rapid responses to thermal fluctuations and can be integrated into predictive risk management systems. The combination of behavioural and physiological indicators within monitoring frameworks is essential for supporting climate adaptation in aquaculture (Korus et al., 2024).

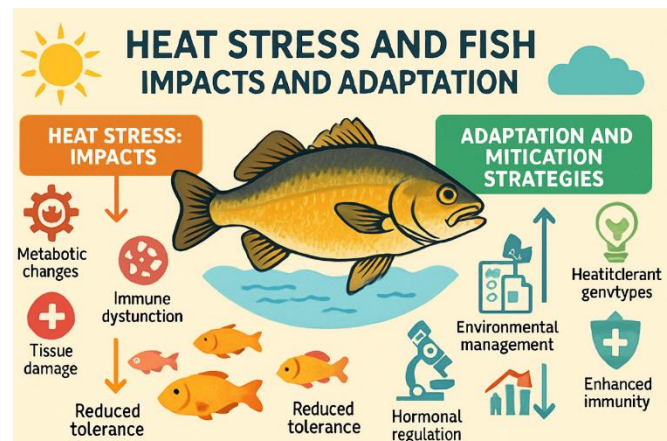


Figure 2. Heat stress in aquaculture: influencing factors, physiological consequences and adaptation strategies.

Future perspectives: Climate change, and particularly heat stress, represents a major threat to global aquaculture, affecting fish physiology, behavioural responses, farm productivity, water quality, and food security. Heat stress disrupts metabolic functions, reproduction, and immune responses, while increasing disease prevalence and the risk of mass mortality, especially in intensive or poorly managed systems (Maulu et al., 2021; Liu et al., 2022). At the same time, aquaculture possesses substantial adaptive capacity and the potential to contribute to climate change mitigation. The



implementation of climate-smart practices - including the selection of thermotolerant strains, water cooling technologies, integrated systems, early warning tools, and spatial farm zoning - significantly reduces climate-related risks (Fernández et al., 2022; Mehrim & Refaey, 2023). Integrated systems, such as IMTA and agro-aquaculture, can enhance system resilience while lowering greenhouse gas emissions (Abisha et al., 2022; Fred-Ahmadu et al., 2024). Despite the growing body of research, critical knowledge gaps remain concerning the long-term adaptive capacity of fish under sustained thermal stress. Islam et al. (2021) note that most studies are based on acute exposure models, which fail to accurately reflect real-world production conditions. Interspecific differences in thermal tolerance, particularly among larvae and juveniles, remain understudied. Similarly, the role of the microbiome, epigenetic regulation, and transgenerational effects in heat adaptation is not yet fully understood. There is a clear need for integrative approaches combining ecology, physiology, immunology, and genetics to develop robust climate adaptation strategies. Selective breeding of rainbow trout for enhanced growth and survival under warm conditions has revealed important trade-offs: families selected for fast growth did not always exhibit superior heat resistance. Genetic correlation analyses identified moderately negative relationships between survival at high temperatures and traits such as feed conversion ratio and haematocrit, highlighting the importance of balancing thermotolerance with overall productivity (Gallardo-Hidalgo et al., 2021). Experimental evidence also indicates partial adaptive responses in yellowfin tuna following short-term heat exposure. After 24 hours, some parameters - including the cellular energy allocation index (CEA) and glycogen content - began to recover, suggesting the activation of compensatory mechanisms. This supports the concept of a “thermal tolerance window,” within which fish can restore homeostasis after mild stress. However, extended exposure to elevated temperatures has consistently shown far more harmful effects (Liu et al., 2023). Well-documented field case studies, such as those focusing on farmed salmon, are essential for understanding the true impacts of heat stress in aquaculture. These observations highlight discrepancies between laboratory models and real production conditions, where additional factors such as feeding schedules, handling stress, and stocking density significantly influence outcomes. Integrating such practical insights into stress assessment frameworks is crucial for developing effective and realistic adaptation strategies (Korus et al., 2024). Nonetheless, successful adaptation requires supportive policies, increased investment in research, and robust training programmes for producers. Particular attention must be paid to developing countries, where aquaculture is a vital source of animal protein, income, and employment, but adaptive capacity remains limited (Mitra et al., 2023; Agarwal et al., 2024; Hapich et al., 2024). Future research should expand to include

a wider range of species and production systems, accounting for the multifactorial nature of climate stressors. There is an urgent need to explore long-term and intergenerational adaptation mechanisms and to invest in practical innovations that strengthen the climate resilience of aquaculture systems while minimizing their ecological footprint. The integration of scientific expertise, technological progress, adaptive management, and government support will enable aquaculture not only to endure but also to contribute meaningfully to sustainable development in the era of climate change.

Conclusion: In summary, heat stress poses a multifaceted challenge to aquaculture by compromising the physiological stability of aquatic organisms, intensifying pathogen pressure, and undermining system productivity. Despite these risks, aquaculture demonstrates considerable potential for adaptation through integrated approaches involving technological innovation, genetic improvement, and improved management practices. Strengthening climate resilience in aquaculture will require coordinated efforts at scientific, policy, and producer levels. Future strategies should prioritise preventive monitoring, resource-efficient production, and the development of inclusive adaptation frameworks that support small-scale operators and vulnerable regions. With appropriate investment and innovation, aquaculture can not only withstand climate challenges but also contribute to sustainable food systems and global climate mitigation goals.

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