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Review Article

Unraveling the Impact of Climate Change on Fish Physiology: A Focus on Temperature and Salinity Dynamics

Deepak Agarwal,[1] **Seerappalli Aran Shanmugam**,[1] **Ayyathurai Kathirvelpandian**,[2] **Suresh Eswaran**,[3] **Mohd Ashraf Rather**,[4] **and Gowrimanohari Rakkannan**[1]

[1]*Department of Fish Biotechnology, Tamil Nadu Dr. J. Jayalalithaa Fisheries University, Institute of Fisheries Post Graduate Studies, OMR Campus, Chennai 603103, India*
[2]*Peninsular and Marine Fish Genetic Resources Division, National Bureau of Fish Genetic Resources, Kochi 682018, Kerala, India*
[3]*Department of Fish Genetics and Breeding, Tamil Nadu Dr. J. Jayalalithaa Fisheries University, Institute of Fisheries Post Graduate Studies, OMR Campus, Chennai 603103, India*
[4]*Division of Fish Genetics and Biotechnology, Faculty of Fisheries Ganderbal, Sher-e-Kashmir University of Agricultural Science and Technology, Wadoora, Jammu and Kashmir, India*

Correspondence should be addressed to Deepak Agarwal; deepakbfsc@gmail.com

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In recent decades, climate change has significantly altered the environmental dynamics of aquatic ecosystems, profoundly impacting the intricate balance of life within them. This review paper delves into the multifaceted impacts of climate change on the physiology of aquatic life, emphasizing temperature and salinity as pivotal ecological factors unique to aquatic environments. The intricate relationship between rising global temperatures and their repercussions on freshwater and seawater habitats forms the cornerstone of this exploration. Elevated temperatures and escalating frequency of extreme heatwave events have reshaped the paradigm for fish survival, pushing them beyond optimal temperature thresholds. Furthermore, the study delves into the interconnection of seemingly disparate abiotic factors, where heightened greenhouse gas concentrations amplify coastal winds, precipitating coastal upwelling. The consequence—nutrient-rich yet oxygen-deprived waters—fuels a cascade of challenges, inducing hypoxic conditions that significantly impact aquatic organisms. The plight of fish, as ectotherms finely tuned to environmental fluctuations, is underscored, illuminating their susceptibility to temperature variations. The direct correlation between external and internal temperatures, exacerbated by climate-induced fluctuations, accentuates the urgency of addressing climate change's impact on aquatic habitats. This review disentangles the complex web of interconnected environmental shifts, illuminating their far-reaching repercussions on the physiology of aquatic life. It emphasizes the imperative for collective endeavors aimed at understanding and addressing the challenges imposed by our evolving climate on these indispensable ecosystems.

Keywords: climate change; fish physiology; global warming; salinity and aquatic modifications; temperature

1. Introduction

Aquaculture plays a critical role in meeting the growing global demand for aquatic products, but its sustainability is increasingly threatened by climate change [1]. Climate change affects organismal biology by altering physiological, biochemical, and genetic traits, thereby compromising the health and survival of aquaculture species [2].

Aquaculture strives to provide a conducive environment for rapid fish growth. Fish, unlike other vertebrates, have thin respiratory epithelia that allow direct contact between their body fluids and the surrounding water. At different salinity levels, fish can theoretically maintain body fluid balance through food uptake and the functions of osmoregulatory organs. These processes, which include some from the brain, are regulated and integrated by hormones

[3]. The capability to control body fluids independently of the external environment is critical for fish survival in both freshwater and saltwater. Most stenohaline species are restricted to one of the two media, whereas euryhaline species have extraordinary osmoregulatory plasticity and can move between both types of habitats [3].

Temperature significantly influences organism distribution, life cycle traits, and biological activities. Elevated temperatures due to global warming disrupt homeostasis in fish, causing metabolic imbalances and increasing their vulnerability to stress and disease [4]. Research has investigated the effects of temperature on ion-regulatory mechanisms and various physiological processes in several fish species [5]. While some fish species exhibit resilience to wide temperature ranges [6], others endure temperature fluctuations in their habitat but are more susceptible to stress, detrimentally affecting their health [7].

Salinity fluctuations resulting from climate change can severely impact fish biology, affecting their health and homeostasis [8]. Many aquatic organisms have specific salinity ranges for optimal health, and deviations from these ranges can cause mortality, reduced growth, and impaired immune function [9, 10]. Euryhaline teleosts, which exhibit remarkable adaptability to a wide range of salinities, employ efficient osmoregulatory strategies to maintain homeostasis [11].

In aquaculture, handling, temperature variations, and salinity fluctuations are common stressors [12]. Handling stress disrupts fish internal equilibrium, affecting vital metabolic pathways essential for various biological functions, including immune responses against pathogens [13]. Maintaining effective immune responses is crucial in restoring cellular equilibrium after exposure to stressors [14].

Heat shock protein 70 (Hsp70) plays a significant role in the stress response, potentially offering cross-protection when upregulated by one stressor against subsequent stress exposures [15, 16]. Higher levels of Hsp70 could potentially act as an early sign of stress induced by elevated temperatures in fish [17]. Additionally, the duration of fish exposure to different water temperatures is a critical factor. The growth hormone (GH)–insulin-like growth factor (Igf)-1 axis may provide a comprehensive signal, influenced by environmental conditions, thereby affecting fish growth and development. Stressors have demonstrated a reduction in fish growth and metabolic alterations via the hypothalamus-pituitary interrenal (HPI) axis, regulated by the glucocorticoid mechanism [18].

Coping with thermal and osmotic stress involves various ion pumps, hormones, and genes. Key mechanisms include the upregulation of Hsp and the GH–insulin-like growth factor axis [15, 18]. As climate change continues to alter environmental conditions, understanding these biological responses is essential for developing strategies to mitigate its impact on aquaculture.

Temperature and salinity are crucial environmental factors influencing fish physiology, significantly impacting their metabolism and energy balance. Temperature governs energy acquisition through feeding behavior, regulation of food intake, digestion, absorption, and allocation of energy toward essential functions such as activity, growth (including larval and juvenile development), and reproduction. Each species generally operates within a specific temperature range that optimizes physiological processes. Variations from these optimal temperatures significantly impact fish health and survival, highlighting their vulnerability to temperature changes.

2. Effect of Salinity on Fish Physiology

Fish can tolerate different salinity levels in their environment. Euryhaline species can handle a wide range of salinity, while stenohaline species can only tolerate a narrow range. Euryhaline fish often move between oceans, estuaries, rivers, and lagoons, where salinity levels change subtly. To adapt, their ion and water regulation systems, including their gills, digestive systems, and kidneys, undergo significant structural and functional changes, enabling them to thrive in fluctuating salinity conditions [19].

Similarly, salinity affects osmoregulatory processes essential for maintaining ionic and water balance. Deviations from optimal salinity ranges can lead to osmotic stress, which impacts growth, reproduction, and immune function. The combined effects of temperature and salinity fluctuations can pose substantial challenges to fish health, underscoring the need for adaptive management strategies in aquaculture [12].

Adapting to varying salinity levels requires changes in the activity and prevalence of ion transporters like GLUT1 and the Na+/K + ATPase pump [20]. This energy-intensive acclimation process involves altering protein expression at the cellular level and takes time [21]. Rapid salinity changes can negatively affect euryhaline fish, increasing susceptibility to stress and disease [22]. Salinity changes also impact neurochemical parameters, as seen in silver catfish brains, where higher salt concentrations reduce acetylcholinesterase (AChE) activity and increase NTPDase and 5′-nucleotidase activities [23]. This reflects the dynamic adjustments fish make to cope with increased salt exposure. This intricate interplay reflects the dynamic adjustments occurring in response by fish to increased salt exposure.

The fish gill, a versatile organ, participates in respiration, ion regulation, acid-base balance maintenance, and nitrogen excretion. Its crucial role contributes to overall body stability across diverse environments [11]. Fish gills experience noticeable changes in structure in response to shifts in temperature and salinity, along with alterations in the density and distribution of ionocytes [24].

While the intestine and kidney contribute to the intricate process of osmoregulation in fish, it is the gill that assumes a pivotal role as the chief orchestrator in regulating the ion flow equilibrium between acquisition and loss [25].

Ion transport and the role of ion pumps are critical in osmoregulation, as they help maintain the balance of salts and water in fish, essential for their survival in varying environmental conditions. The activity of these ion pumps, particularly under stress, ensures that fish can adapt to changes in salinity and temperature, underscoring their importance in maintaining cellular homeostasis [26].

The orchestration of this intricate process involves specialized ion pumps, such as branchial Na+/K + -ATPase (NKA) and V-H + -ATPase (VHA), which work together to establish and maintain an electrochemical gradient. This gradient enables active ion transport across both the basolateral and apical membranes of the gills [27]. Moyes and Ballantyne [28] noted that active ion transporters are more temperature-sensitive than carrier-mediated diffusive transporters, potentially causing imbalances. Changes in gill membrane integrity and fluidity can affect ion transport by altering transport protein function. Marine fish maintain a body fluid composition of 300–400 mOsm/kg, slightly higher than freshwater species. Seawater contains 60 of 92 basic chemical elements, with chloride and sodium as major components [29]. Freshwater composition is more diverse and not deionized [30]. Some fish can adapt to high salinity levels (> 100), while others show abnormal growth when acclimatized [31]. Marine fish are hypotonic compared to seawater (700–1000 mOsm/kg), leading to continuous water loss. They drink more seawater to compensate, resulting in a high salt load. Mitochondria-rich cells (MRCs) in their skin and gills actively expel excess Na+ and Cl- ions using key ion transporters: Na+/K + ATPase, Na+/K+/2Cl- co-transporter (NKCC), and CFTR Cl channel [31]. Osmoregulation, which can consume 10%–50% of their energy budget [30, 32], is crucial for maintaining osmotic pressure.

Additionally, the Na+/H+ exchanger and Na+/K+/2Cl- co-transporters also plays an important role in facilitating ion balance in fish [11]. For instance, a study by Marshall, Lynch, and Cozzi [33] on the European eel (*Anguilla anguilla*) demonstrated that the Na+/H+ exchanger plays a crucial role in acid-base regulation and ionic balance when the eels were transferred from freshwater to seawater. Whereas, the Na+/K+/2Cl- co-transporter is pivotal for ion uptake in freshwater and ion excretion in seawater, showcasing its importance in osmoregulation during the smoltification process of *Salmo salar* [34].

Partridge and Jenkins [35] found that juvenile black bream (*Acanthopagrus butcheri*) can thrive in a wide salinity range from freshwater to 48%. Fish reared at 24% showed the best growth, food consumption, and Food Conversion Ratio (FCR). High osmoregulatory demands affect reproduction and larval development, impacting growth and metabolism rates. Freshwater fish face significant osmoregulatory challenges, constantly gaining water from their dilute environment and losing essential ions like Na+ and Cl- through diffusion [36]. They expel excess water via glomerular filtration and tubular ion reabsorption, producing large volumes of diluted urine to minimize ion loss. The teleost fish urinary bladder reabsorbs ions, and dietary intake aids ion balance, though this is less explored and challenging during food scarcity [11]. It is hypothesized that H+-ATPase, which is specifically active in freshwater conditions, plays a crucial role in acid-base regulation and ion uptake in freshwater fish. In contrast, Na+/K + -ATPase is involved in maintaining ionic balance in both freshwater and saline environments through its activity in the gills [11]. Therefore, while H + -ATPase facilitates active ion absorption under freshwater conditions, Na+/K + -ATPase supports ion balance across a range of salinities.

For optimal growth in some freshwater fish larvae, a slightly elevated salinity (around 2 ppt) is recommended, enhancing the persistence of Artemia nauplii and boosting growth rates [37]. Higher salinity promotes growth in *Piaractus brachypomus* larvae, while *Cyprinus carpio* fingerlings show slower growth at salinity levels up to 10.5 ppt [38]. Most freshwater teleosts grow best at salinity levels lower than their blood's isotonic concentration, around 9 ppt [39]. Optimal salinity ranges vary: 0.5–3 ppt for catfish, 5 ppt for red drum *Sciaenops ocellatus*, and 9 ppt for *Pangasianodon hypophthalmus* [40].

Leopard grouper (*Mycteroperca rosacea*) eggs have the highest hatching rates at 32% salinity [41]. Fish adapt to different environmental conditions through their neuroendocrine system, which links external environments to physiological osmoregulatory responses [42].

In fish, cortisol has traditionally been considered the hormone for seawater adaptation, while prolactin is associated with freshwater adaptation. However, recent evidence suggests that the GH/insulin-like growth factor I axis also plays a crucial role in seawater adaptation across various teleost species with diverse evolutionary backgrounds [43]. Cortisol regulates physiological and behavioral stress responses in fish. Elevated cortisol levels, triggered by stressors, impact fish health and fitness, affecting growth, condition, and immunity [44]. According to McCormick [42], cortisol plays a significant role in enhancing the transcription and availability of crucial transport proteins responsible for secretion of salt in the gills, such as NKA, NKCC, and the CFTR. The impact of cortisol usually takes a few days to reach its maximum effects, suggesting that complete efficacy requires cell proliferation and differentiation. Cortisol has a discernible effect on NKA activity, as well as ion and water absorption, which aids in adaptation to increased ambient salinity. After being transferred to seawater, some salmonids treated with cortisol showed an increased drinking response [43].

Prolactin plays an important role in fish osmoregulation, particularly in freshwater adaptation. It prevents ion loss and water uptake, while regulating ion permeability in osmoregulatory tissues [45]. Prolactin has been observed to impact chloride cells by suppressing the formation of seawater chloride cells while enhancing the structure of ion uptake cells [42]. Prolactin not only inhibits the formation of seawater chloride cells but also increases the number and size of gill mitochondrion-rich cells, also known as ionocytes. Additionally, it enhances the abundance of sodium-potassium ATPase (NKA) and sodium-potassium-chloride cotransporter (NKCC) [42]. In teleost, Insulin like Growth Factors regulates myogenic cell processes, including proliferation, differentiation, and protein synthesis, while also influencing protein degradation and atrophy. Additionally, Insulin like Growth Factor-1 (IGF-1) in the gills plays a role in plasma osmolality regulation [46, 47]. The GH has been found to elevate circulating and local tissue production of IGF-1, increasing salinity tolerance in rainbow trout, Atlantic salmon, and killifish by enhancing gill NKA activity [42]. Sea bass exhibit remarkable control over ion concentrations like Na+, K+, and Cl- in their blood, skin, gills, and kidney. Consequently, their metabolism is minimally affected by the water's salinity, allowing sea bass to thrive in both saltwater and freshwater environments based on salt concentration [48].

Neuropeptides, including arginine vasotocin (AVT) and isotocin, are also crucial in the osmoregulatory processes of fish. AVT, an analog of arginine vasopressin found in mammals, plays a significant role in regulating water balance and blood pressure. In fish, AVT influences the permeability of the gill and renal tubules, thereby affecting ion and water balance [49]. Isotocin, analogous to oxytocin in mammals, is involved in the modulation of social behaviors and osmoregulatory functions. These neuropeptides, through their action on specific receptors in osmoregulatory tissues, help fish maintain homeostasis in varying salinities by modulating ion transport mechanisms and water permeability.

The gills, particularly through the regulation of chloride cells, play a pivotal role in salinity control. The cotransporter NKCC in chloride cells regulates ion concentrations in the blood, while the subunits of NKA work to maintain homeostasis. The expression of NKA is controlled by subunits of the protein Phospholemman (FXYD), enabling sea bass to adapt to changes in salinity for survival [48].

2.1. Salinity and Its Influence on Growth and Survival. The impact of salinity on the growth and survival of marine fish species has been widely studied [50–52]. While changes in salinity can delay hatching in *Oplegnathus fasciatus* [53], most research indicates no effect on the developmental rate [54]. In the case of *Inimicus japonicus* (Devil stinger), hatching is unaffected within a salinity range of 21–37 ppt. Lower salinity levels reduce egg buoyancy and hatching rates [55], with the highest hatching rate of 88.3% observed at 37 ppt, although this is similar to rates at 29 and 33 ppt. Optimal salinity for embryogenesis in *I. japonicus* is 30.5–37.3 ppt [56]. This species has a higher salinity tolerance compared to others like *Clupea harengus* and *Oplegnathus fasciatus* [57], partly due to the absence of oil globules which affects osmoregulation [58]. The ideal incubation salinity is 27–31 ppt, aided by the parents' ability to regulate egg osmotic balance through blood circulation before spawning [59]. Based on these case studies, it can be inferred that salinity has a significant influence on the hatching rate of marine fish eggs. Generally, there is an optimal salinity range that maximizes hatching success, and deviations from this range, either lower or higher, can negatively impact buoyancy, hatching rate, and embryogenesis. While many species demonstrate a degree of tolerance to varying salinities, the precise optimal range may vary among species. Therefore, understanding and maintaining the ideal salinity conditions are crucial for ensuring high hatching rates and successful development of marine fish embryos.

Holliday [60] observed that the gametes of teleost fish, prior to spawning, maintain an osmotic balance that is either equal to or lower than the body fluids of the parent fish. Furthermore, Shi et al. [61] found that as a fish progresses through its early stages of life, from embryo to yolk-sac larva, its ability to tolerate various salinity levels reduces. This pattern is also evident in *I. japonicus*, where salinity tolerance appears to be stage-dependent. Due to differences in body compositions, the eggs and larvae within a species have distinct isosmotic points. The osmotic relationships among osmoregulators are influenced by plasma osmolality, and variation in salinity tolerance from one developmental phase to another is linked to variations in osmotic concentrations [62].

In marine pelagic fish like *I. japonicus*, survival rates tend to decrease in environments with higher salinity [63]. This is often due to the increased energy demands associated with osmoregulation. When the external salinity is high, fish must expend more energy to prevent dehydration and maintain their internal osmotic concentration. Conversely, at lower salinity levels that are closer to the fish's internal osmotic concentration, less energy is required for osmoregulation [64], which can lead to improved survival rates [57]. This balance is crucial for the early developmental stages of marine organisms [56].

High or low salinity conditions severely disrupt the normal functioning of larval organs, like gills, leading to a higher occurrence of deformities [65]. Additionally, Shi et al. [66] observed that the eggs of *Pampus punctatissimus* shrink in size after a 30 min exposure to different salinity levels, with the size reducing progressively with increasing salinity. Salinity also influences the growth rate of larvae in various marine fish, including *C. harengus*, *P. major*, *Perca fluviatilis* L., and *O. fasciatus* [67]. Boeuf and Payan [30] suggested that under hyper- or hypo-osmotic conditions, larvae must expend huge energy to maintain osmotic balance, reducing the energy available for growth. Conversely, in an environment where the osmotic pressure of the water closely matches that of the body fluids, the energy demand for osmoregulation is reduced. This conservation of energy can then be redirected toward growth, resulting in better overall development of the larvae.

2.2. Effect of Temperature on Fish Physiology. Temperature is a crucial environmental factor influencing fish physiology, significantly impacting their metabolism and energy balance [4, 8]. Temperature governs energy acquisition through feeding behavior, regulation of food intake, digestion, absorption, and allocation of energy toward essential functions such as activity, growth (including larval and juvenile development), and reproduction [4]. Each species generally operates within a specific temperature range that optimizes physiological processes [6]. Variations from these optimal temperatures significantly impact fish health and survival, highlighting their vulnerability to temperature changes [7].

When considering the significance of the water temperature as a parameter, it is important to recognize that fish, being ectothermic or poikilothermic, regulate their body temperature based on the surrounding water. Fish species each have a specific temperature range for viability, defined by a minimum and maximum lethal temperature [68], which is determined by their evolutionary history and environmental adaptation. Within this range, there is an optimal temperature range where a fish species can thrive and grow efficiently. This optimal range is essentially the temperature a fish would prefer naturally [69]. Variations in ambient temperature have a significant impact on fish biology, influencing food consumption, feed conversion, growth rate, physiology, behavior, and other vital functions [70] (Figure 1). In their usual temperature range, most species tend to experience advantages with a slight rise in temperature, as it translates to increased energy and consequently faster growth reaction rates [71]. This phenomenon arises from the impact of temperature on the molecular structure of mitochondria. For every 10°C increase in ambient temperature within the tolerance range, the metabolic rate approximately doubles [72].

The developmental rate and feed conversion of freshwater fish, along with the metabolism of aquatic animals, are influenced by temperature [73]. Aquatic species have evolved to thrive within specific temperature ranges, with many tropical fishes exhibiting optimal performance between 25°C and 32°C [74]. Individual species responses to new temperature ranges, on the other hand, can vary.

Temperature can impact specific and nonspecific functions, including immune responses, as most fish species maintain a body temperature closely aligned with the surrounding water [75].

The correlation between temperature and has been examined in various aquatic species, including channel catfish, Asian catfish, juvenile turbot, and silversides [76]. Average temperature has shown a robust association with survival, metabolism and growth rate especially in the juvenile phase. The regulatory mechanisms governing the growth-temperature relationship are likely linked to enzymatic regulation in metabolic pathways [77]. In many temperate fish species, the growth rate increases as the temperature rises, reaching a point just below the upper lethal limit [78]. Ficke, Myrick, and Hansen [79] observed that in order to reach better growth each fish species has an optimal temperature range, generally ranging from 20°C to 32°C for temperate fish species.

Elevated rearing temperatures have been observed to increase hematocrit in European sturgeon [80] and uplift the hemoglobin levels and red blood cell count levels in the *Prochilodus scrofa* (Prochilodus fish) [81]. Temperature acts as a stressor by reducing the oxygen solubility in water [82], necessitating adjustments in the haematological parameters of fish to adapt.

In preacclimated sea bass, gill morphological parameters varied when exposed to temperatures of 24°C and 18°C, in seawater and freshwater environments. Notably, there was a reduced number of ionocytes in the gills when the fish were in warmer freshwater [83]. Additionally, Na+ levels in plasma were lower at 24°C than at 18°C under various salinities. Conversely, Cl- concentration in plasma was higher in tropical freshwater conditions compared to temperate environments, with no temperature effect in seawater. These observations might indicate the impact of higher temperatures on increased freshwater Cl- uptake and reduced Na+ uptake at the gill and kidney in sea bass [84].

Temperature acclimation and preference in sea bass have been studied using oxygen consumption, fish distribution, food intake, and swimming speed [85]. According to Person-Le Ruyet et al. [86], the optimal growth rate of *Dicentrarchus labrax* was at 25°C, which is considered relatively warm.

Recent research on European sea bass particularly on juveniles and adults revealed that the temperature at which they are acclimated can influence both their behavior and the neurochemical parameters in their Central Nervous System [87]. Specifically, the metabolic rate of fish is closely related to the ambient temperature: it decreases down in lower temperatures and elevated as the temperature increases, leading to an increased demand for oxygen and food [88]. In natural settings, fish instinctively react to changes in temperature by moving to different locations or depths to find the temperature that is optimal.

When fish are incapable find their optimal temperature, they adapt by producing proteins and enzymes variants that function effectively at varying temperatures, and by altering their cellular environment to lessen the effects of temperature fluctuations [89]. In laboratory settings, where fish are raised in tanks and incapable of selecting their preferred temperature, it is crucial to maintain the water temperature within the species-specific optimal range. Keeping the temperature stable is essential to prevent stress and promote the well-being of the fish. Additionally, any changes to the water temperature should be introduced slowly to avoid causing undue stress to the fish.

2.3. Temperature-Mediated Impacts on Fish Reproductive Physiology. Temperature also plays a pivotal role in reproductive responses, influencing physiological mechanisms related to gamete development, in addition to regulating metabolism and growth [90]. In female fish, the water temperature during oogenesis can shape egg size and biochemical composition, potentially impacting offspring ontogeny and fitness [91]. Spermatogenesis and sperm properties in males are also susceptible to temperature effects, thereby influencing overall reproduction ability. Elevated temperature has been demonstrated to hinder spermiation and alter sperm motility, both of which contribute to changes in fertilizing capacity [92].

The influence of temperature on various reproductive endocrine pathways is likely to mediate changes in offspring production and quality [93]. Higher temperatures can induce changes in reproductive hormone levels, impacting ovarian and testicular steroid production [94]. Disruption of steroid production and subsequent changes to vitellogenesis in the liver, may lead to decreased maternal investment and gamete viability [95]. Additionally, increased temperatures can disrupt the final stages of egg maturation and prevent ovulation, a phenomenon observed in various species, including Atlantic salmon [96].

In specific species such as the silver sea bream (*Sparus sarba*) and the greenback flounder (*Rhombosolea tapirina*), research has shown that both salinity and temperature play a crucial role in the growth and development of embryos and larvae. It has been noted that the ability of larvae to withstand higher salinity levels is limited when they are subjected to increased temperatures.

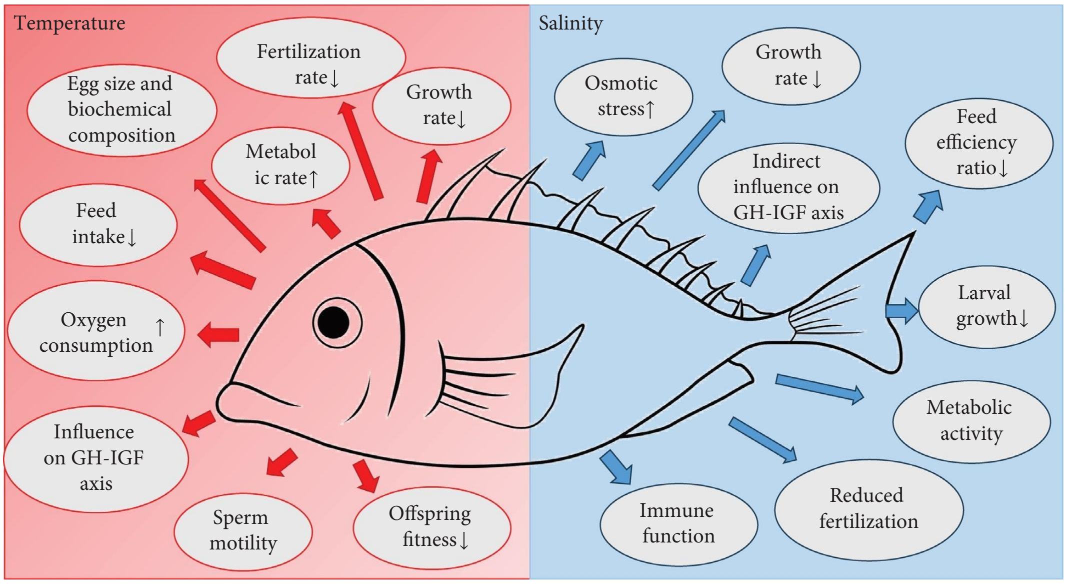

Figure 1: The impact of increased temperature and salinity on fish physiology.

2.4. Influence of Temperature and Salinity on Fish Breeding and Hatchery Management. Climate change, especially fluctuations in temperature and salinity impact broodstock development, breeding success, and larval survival, causing various physiological and reproductive challenges [97].

On a global scale, climate change has also been shown to affect hatchery productivity and fish breeding. For example, in the Pacific Northwest of the United States, rising temperatures and altered stream flows have been linked to decreased survival rates of salmon eggs and juveniles. Studies have found that higher water temperatures and changes in flow patterns disrupt the timing of salmon spawning migrations, reduce the availability of suitable spawning habitats, and increase the incidence of disease among eggs and larvae [98]. A study conducted on the Indian major carp in West Bengal reported that increased temperatures and erratic monsoon patterns led to significant disruptions in breeding cycles. The delayed onset of the monsoon resulted in reduced water levels in rivers and ponds, affecting broodstock migration and spawning success [99]. Additionally, high temperatures during the breeding season led to decreased fertilization rates and lower hatching success.

Similarly, optimal temperature and salinity ranges are essential for hatching rates and larval survival, with deviations from these conditions leading to reduced reproductive success and higher mortality rates [97]. Adjustments in hatchery practices to account for these climatic factors are crucial for enhancing breeding outcomes and ensuring the viability of aquaculture operations. In Centropyge species aquaculture, larval mortality poses a significant challenge, with marine fish eggs and larvae being highly sensitive to variations in salinity. Research on *Centropyge aurantonotus* [100] showed that salinity levels between 30% and 40% were optimal for egg and larval development, leading to improved buoyancy, hatching rates, and survival. Lower salinities, especially below 30‰, resulted in higher mortality rates and deformities.

2.5. Impact of Climate Change on Parental Influence on Progeny Development. Unlike adult fish, embryos and larvae have limited ability to actively respond to their environment and are thus more vulnerable to stressors like temperature changes. This susceptibility is reflected in well-established thermal optima and lethal incubation limits across numerous species, with extensive studies exploring the ramifications of temperature exposures during early developmental stages [101].

Temperature during these formative stages can affect a range of developmental factors, including, larval size, meristic counts, yolk utilization efficiency, muscle physiology, larval deformities, and progeny sex ratios [102]. Notably, investigations into influence of temperature during early development often neglect the potential effects of parental traits on offspring development in response to temperature.

Primarily, parental genetics plays a significant role in defining the traits of their progeny. In quantitative genetics methodologies, paternally derived offspring variation serves as a representation of the additive genetic variation for a trait within a population. Second source of offspring variation stems from the specific phenotypic traits of the female or male parents, respectively, contributing to phenotypic variation [103]. The maternal influence, in particular, is recognized as an influential factor in the diversity seen among a fish offspring population [104]. Commonly, larger mothers tend to produce larger eggs and offspring, but other maternal behaviors can also affect the survival rate of embryos, the size and composition of the yolk, growth speed, metabolic physiology, stress response, and swim ability [105]. While females typically have a major impact on fecundity, egg laying site choice, and nutrition provided in the yolk, recent findings highlight that male spawners can also have a substantial effect on the characteristics of their offspring [106]. Incubation temperature studies in fish predominantly focus on entire populations, overlooking potential variations in offspring responses due to their individual parentage.

Similarly, while the use of quantitative genetics to explore the heritability of traits in offspring is becoming more common, the quantification of genetic effects inherited through the parents under varying temperatures remains rare [107]. In situations where high mortality and selective pressures affect the early development of fish, understanding individual differences in offspring response patterns is crucial for predicting how populations might respond or adapt to environmental changes [108]. Ignoring the role of parental influences when evaluating the response of offspring to environmental factors can lead to misattributing variations that are actually due to parental traits in the treatment effect estimate. This oversight can result in less comprehensive insights into the ecology of juvenile and a misinterpretation on the impact of environmental conditions [109].

2.6. Interaction of Salinity and Temperature on Teleost Fish. The combined effects of salinity and temperature on fish survival, growth rate, and physiological parameters are well-documented. Research has shown that the synergistic impact of temperature and salinity can be more severe than the effects of each factor alone [110–113]. In a month-long rearing experiment, juvenile spotted wolfish exhibited a notably higher mean weight when nurtured at 10°C compared to 7°C across diverse salinity levels. Moreover, the specific growth rate (SGR) demonstrated superior performance at 10°C, particularly in treatments with salinities of 25 and 34 ppt, in contrast to 15 ppt and 7°C treatments [114].

Investigating the impact of different salinity (0, 6, and 12 ppt) and temperature (21, 27, and 31°C) combinations on goldfish growth, Imanpoor et al. [115] discovered adverse effects on individual weight gain, SGR, and final goldfish biomass at 12 ppt and 31°C. For juvenile turbot reared at temperatures varying from 10°C to 22°C and 15°C to 33.5°C, the insulin-like growth factor 1 (IGF-1) levels exhibited an increasing trend with rising temperature, peaking around 18°C. However, the daily feed intake, feed conversion efficiency, and overall growth were significantly influenced by the dynamic interplay of temperature, salinity, and their interactions [110].

The growth rates of Nile tilapia, specifically food conversion rate, were found to be distinctly influenced by salinity, temperature, and their interactions. Nile tilapia, a freshwater fish *Oreochromis niloticus*, demonstrated rapid growth in the temperature range of 28°C–32°C. Notably, this growth is particularly pronounced in an intermediate salinity environment, such as 6–12 ppt [116].

Temperature and salinity have been recognized as crucial factors altering the responses of various fish taxa when exposed to challenging environments [117]. Beyond salinity and temperature, other abiotic factors also contribute to modifying fish physiology, ultimately impacting growth and reproduction. Numerous studies have explored differential gene expression in teleost under varying environmental conditions (Table 1).

2.7. Effects of Temperature and Salinity on Fish Feeding. Temperature has been demonstrated to impact the sensitivity of sensory systems, including vision, olfaction/taste and hearing, subsequently influencing feeding behavior. Changes in temperature may alter taste preferences in certain fish by influencing perception. To consume food successfully, having access to appropriate food items, efficient sensory perception, and the ability to move are essential. Feeding behavior, encompassing food detection, capture, ingestion, and swallowing, is intimately linked to food intake [137]. Different cues, including visual (eyes), chemical (olfaction and taste), and mechanical (lateral line), play a role in detecting food. Temperature has the potential to influence and regulate several of these processes and factors independently. In most species, olfaction primarily detects distant stimuli, touch and gustation identify nearby cues, and vision plays a crucial role in detecting prey or food [138]. However, there exists variability among fish species.

Plaice *Pleuronectes platessa*, for example, feeds primarily through vision, whereas sole *Solea solea* feeds primarily through chemoreception and mechanoreception [139]. Disrupting olfaction, while leaving vision and the lateral line unaffected, reduces feeding behavior in the Chinese perch (*Siniperca chuatsi*). Even when goldfish experience vision impairment or encounter reduced visibility due to heightened water turbidity, their food consumption remains unaffected, even though they may need to move more and spend extra time finding their food. However, olfactory function impairment significantly reduces the feeding behavior [140]. Predation in red drum *Sciaenops ocellatus* is unaffected when either vision or olfaction is blocked alone, but blocking the lateral line system results in a decreased predation rate [141]. Some fish species rely on hearing to detect both prey and predators, especially in murky or dark environments where the visibility is poor [142]. Table 2 provides a summary on the influence of water temperature on the sensory physiology of various teleost species.

The delta smelt (*Hypomesus transpacificus*), an endangered fish species native to the Sacramento–San Joaquin Estuary in northern California, faces environmental stress from changing salinity levels. The result of the study found that salinity was a significant factor influencing the cellular stress response. Increased salinity levels led to changes in the transcription of sodium–potassium-ATPase (Na/K-ATPase), an enzyme crucial for osmoregulation, indicating stress. These findings suggest that while salinity may not directly impact feeding rates, it influences the physiological stress levels that can indirectly affect overall health and feeding efficiency [147]. Additionally, a 10-week study on white-leg shrimp (*Penaeus vannamei*) examined the impact of different salinities (5, 10, and 15 ppt) on growth, feed utilization, and physiological parameters [148] and found that shrimp reared at the highest salinity of 15 ppt demonstrated the best growth performance and feed efficiency. In contrast, shrimp at the lowest salinity of 5 ppt showed poor growth and lower feed utilization. Salinity significantly affected all physiological parameters, with the highest

Table 1: Differential expression of selected genes under different environmental conditions.

Species name	Expression level	Reference
Barramundi (*Lates calcarifer*)	The mRNA expression of Hsp70 exhibited an elevation following exposure to crowding stress	Newton, De Santis, and Jerry [118]
Pearl spot (*Etroplus suratensis*)	Identified the LC50 for salinity and reported the expression of major osmotic responsive genes (IGF, Na+/K+ -ATPase, osmotic stress transcription factor (OSTF), etc.) at various salinity levels. The pearl spot exhibited the highest performance at the molecular level in 15 ppt saline water	Marbade et al. [119]
European sea bass (*Dicentrarchus labrax*)	Fluctuations in water temperatures result in an upregulation of the heat shock protein 70 gene (inducible form) when exposed to transport stress	Poltronieri et al. [120]
Rainbow trout (*Oncorhynchus mykiss*)	The hepatic Hsp70 levels remained unchanged despite the handling stress	Vijayan et al. [121]
Yellow perch (*Perca flavescens*)	The mRNA levels in liver exhibited a significant increase at 26°C, decreased at 20°C, and declined further at 14°C. Additionally, there was a noteworthy downregulation of insulin-like growth factor 1 (Igf1) at a temperature of 26°C and 14°C, whereas a significant upregulation was observed at 20°C immediately after fish handling. Interestingly, a reciprocal correlation was noted between Igf1 and Hsp70, with Hsp70 showing downregulation and Igf1 displaying upregulation at 20°C	Eissa et al. [14]
Atlantic salmon (*Salmo salar*)	The results suggested that acute stressors lead to a decrease in the growth of parr, with a more pronounced and rapid effect observed as the frequency of stress increases	McCormick et al. [122]
Chinook salmon (*Oncorhynchus tshawytscha*)	The group exposed to warmer temperatures showed a more significant increase in Igf1 expression compared to those kept at ambient temperature	Beckman et al. [123]
Black sea bream (*Mylio macrocephalus*)	At increased salinities, there was an observed upregulation of hepatic Hsp70, whereas at isosmotic salinity, a downregulation was evident	Deane et al. [124]
Black porgy (*Acanthopagrus schlegeli*)	After being exposed to hypo-osmotic stress, the levels of expression for SOD1 (superoxide dismutase 1) and GPX (glutathione peroxidase) increased	An et al. [8]
Olive flounder (*Paralichthys olivaceus*)	Being exposed to a hypo-osmotic environment resulted in an increase in GPX mRNA expression	Choi, An, and An [125]
Nile tilapia (*Oreochromis niloticus*)	The expression of Na^+/K^+ ATPase α1-a mRNA decreased, whereas Na^+/K^+ ATPase α1-b mRNA increased in response to salinity exposure	El-Leithy et al. [126]
Tilapia, salmon, and medaka	Upon transferring fish from freshwater to seawater, Na+/K+ -ATPase α1-a expression decreased, while Na+/K+ -ATPase α1-b expression increased	Wong et al. [127]
Freshwater cichlid fish (*Mozambique tilapia*)	The transfer of fish for acclimatization to seawater, Na+/K ± ATPase α1-a expression decreased significantly within 24 h, followed by a substantial increase in Na+/K ± ATPase α1-b expression, reaching peak levels after 7 days of the transfer	Tipsmark et al. [128]
Juvenile *Oreochromis mossambicus*	There was an observed elevation in Igf-1 gene expression during the acclimation of fish to seawater	Magdeldin et al. [129]
Juvenile gilthead sea bream (*Sparus aurata* L.)	The group acclimated to 20 psu exhibited an elevated expression of Igf-1	Mohammed-Geba, Mancera, and Martínez-Rodríguez [130]
Mediterranean meager, *Argyrosomus regius*	Fish specimens acclimated to nearly iso-osmotic salinity (12 ppt) exhibited a significant two- to fourfold upregulation in Igf-1 expression across different rearing salinities	Mohammed-Geba et al. [131]
Black sea bream and Atlantic salmon	Exposure to seawater nearly iso-osmotic salinity resulted in an upregulation of hepatic Igf-1 expression	Deane and Woo [132], and Breves et al. [133]

Table 1: Continued.

Species name	**Expression level**	**Reference**
Zebrafish (*wild-type*)	Temperature extremes (18°C and 34°C, with 26°C as the control) affects the energy metabolism but also result in the decreased expression of proteins related to synapses and neurotransmitter release	Toni et al. [134]
Goldfish	Higher temperatures lead to elevated orexin mRNA levels and reduced CART (Cocaine-Amphetamine regulated transcript) mRNA levels in the hypothalamus, while peptide YY and CCK (cholecystokinin) mRNA levels decrease in the intestine	Nadermann, Seward, and Volkoff [135]
Atlantic cod (*Gadus morhua*)	Reduced temperatures exert a suppressing effect on food intake, and this restraint is, to some extent, orchestrated by an augmentation in the expression of CART transcripts	Kehoe and Volkoff [136]

Table 2: Effects of water temperature on teleost's sensory physiology.

Species name	Effects of temperature	Reference
Rockfish (*Sebastes* sp.)	An increase of just 10°C in temperature results in the retina becoming ten times less sensitive to low-light conditions	Reilly and Thompson [143]
Channel catfish (*Ictalurus punctatus*)	Hearing sensitivity is at its minimum at 10°C and gradually improves as the temperature rises from 10°C to 26°C	Wysocki, Montey, and Popper [142]
Channel catfish (*Ictalurus punctatus*)	As temperatures rise, the lifespan of taste bud cells on the barbels decreases. At 14°C, the lifespan is approximately 40 days, while at 18°C, it is around 30 days. Further increases in temperature result in even shorter lifespans, with approximately 15 days at 22°C and only 12 days at 30°C	Raderman-Little [144]
Stellate sturgeon (*Acipenser stellatus*)	The palatability of specific amino acids, such as L-glutamic acid, L-tryptophan, L-alanine, L-valine, and L-leucine, is affected by temperature variations	Kasumyan [145]
Atlantic salmon (*Salmo salar*)	Changes in feeding behavior associated with temperature correlate with fluctuations in plasma concentrations of ghrelin and leptin	Vikesa, Nankervis, and Hevrøy [146]

salinity being optimal for shrimp health and performance. Thus, salinity at the optimum level has shown better feeding efficiency and growth in fish.

2.8. Effects of Temperature on Immune System and Metabolism. In fish, fluctuations in water temperature and salinity can impact their survival, physiological state, and immune responses. According to Faught and Schaaf [149], stress impacts metabolic pathways and immune responses in fish by activating the HPI axis, which releases stress hormones like cortisol. These hormones bind to glucocorticoid and mineralocorticoid receptors on immune cells, modulating inflammation by regulating pro-inflammatory and anti-inflammatory gene expression. This interaction can suppress or enhance immune function, highlighting the complex role of stress in immune regulation. Frequent extreme weather events, particularly severe temperature fluctuations, have significantly impaired the growth and health of fish, adversely impacting aquaculture production. Ma et al. [150] investigated the adaptive regulation of energy metabolism, immune function, and gut microbiota in largemouth bass (*Micropterus salmoides*) under acute warming (AW) and cooling (AC) conditions. Results indicated that extreme cold notably disrupted immune function and gut microbiota, highlighting the detrimental effects of dramatic weather changes on largemouth bass health.

Salinity, another major stressor affects the immune response and stress tolerance in striped catfish larvae [151]. The study found that lysozyme and peroxidase activities increased at higher salinities (15 and 20 ppt), indicating improved immune responses. However, these benefits were offset by significantly lower survival rates, with no survival observed at 15 ppt following heat shock. Consequently, while higher salinities can enhance immune functions, the optimal balance for survival and stress tolerance is at 5 ppt. Effects of salinity on the immune system of the tropical sea urchin *Echinometra lucunter* [152], showed no change in phagocytic activity at 25 or 45 ppt, but coelomocyte concentration increased at lower salinities.

In response to changes in salinity and temperature, fish experience a range of biochemical and physiological adjustments to cope with the resulting challenges [153]. For instance, the study conducted by Chen et al. [153] on *Triplophysa siluroides* under heat stress (28°C) identified upregulation of Hsps and significant impacts on the Phosphoinositide 3-kinase/protein kinase B (PI3K) and endoplasmic reticulum protein processing pathways. Metabolic analysis revealed that the pathways like ubiquitin-dependent proteolysis and purine metabolism were enhanced to help in fish adaptation to heat stress. Parallelly, a study on the amphidromous fish *Galaxias maculatus* (inanga) investigated the effects of varying salinities (freshwater to 43 ppt) on metabolism over 16 days [154]. The results showed minimal changes in plasma osmolality, metabolic rate, and energy expenditure, highlighting the fish's high salinity tolerance. While ammonia excretion decreased near the isosmotic point and oxygen to nitrogen ratios varied, suggesting shifts in fuel use, there was no significant trade-off between oxygen consumption and nitrogen excretion functions in the gills. Extra-branchial epithelia, such as skin and kidneys, contributed to gas exchange and ammonia excretion independently of salinity. This indicates that inanga can acclimate to a broad range of salinities with minimal physiological costs, but subtle advantages may exist at salinities close to their isosmotic point.

2.9. Effect of Climate Change on Fish and Their Physiology. Understanding the effects of global warming on fish, one must acknowledge the physiological alterations occurring at molecular, cellular, and organismal levels (Figure 2). Prolonged exposure of higher temperature can lead to impaired reproductive function and sterile fish [155]. The continuous rise in temperatures in natural habitats may contribute to reduced natural reserves in certain species [156]. This cause-and-effect comprehension is crucial for accurately predicting global warming effects on economically significant fish species, differentiating them from the combined influence of fishing pressure. Aquatic temperature profoundly influences fish survival, distribution, and metabolic processes. Fish mortality due to temperature variations is often attributed to their physiological inability to respond adequately, leading to alterations in metabolic pathways. Temperature fluctuations involve intricate interactions among hormones, metabolic pathways, enzyme properties, and behavior, occurring at molecular, cellular, organismal, and population levels [157].

Temperature variations within the tolerance limits of ectotherms have a profound impact on metabolism, influencing various physiological processes, including growth, development, and overall performance, encompassing both physiological and behavioral capacities [158]. The impact of global warming on fish populations are already evident, leading to alterations in fish population abundance, extinctions, or migrations to colder regions [159]. The broader ramifications of global warming include indirect consequences, such as alterations in prey-predator dynamics and diminished oxygen availability [160]. These indirect impacts play a crucial role in shaping ecosystems and affecting the delicate balance of life within them.

However, the principal mechanism driving these population shifts appears to be the direct physiological effects of temperature [161]. Global warming typically drives fish toward, or even beyond, their upper thermal tolerance limits, reflecting a primary direct effect [162]. Moreover, stenothermal species in tropical or polar region may be more vulnerable to the warming trend, given their limited ability to tolerate temperature fluctuations [163]. This incapacity poses a potentially life-threatening challenge for these species [164]. While the complete comprehension of the physiological characteristics governing thermal tolerance remains elusive, cellular-level defense against heat involves the production of chaperone proteins, notably Hsps, which exhibit evolutionary conservation across various taxa [165]. HSPs play a pivotal role in averting protein aggregation, aiding in the restoration of stress-denatured proteins, and

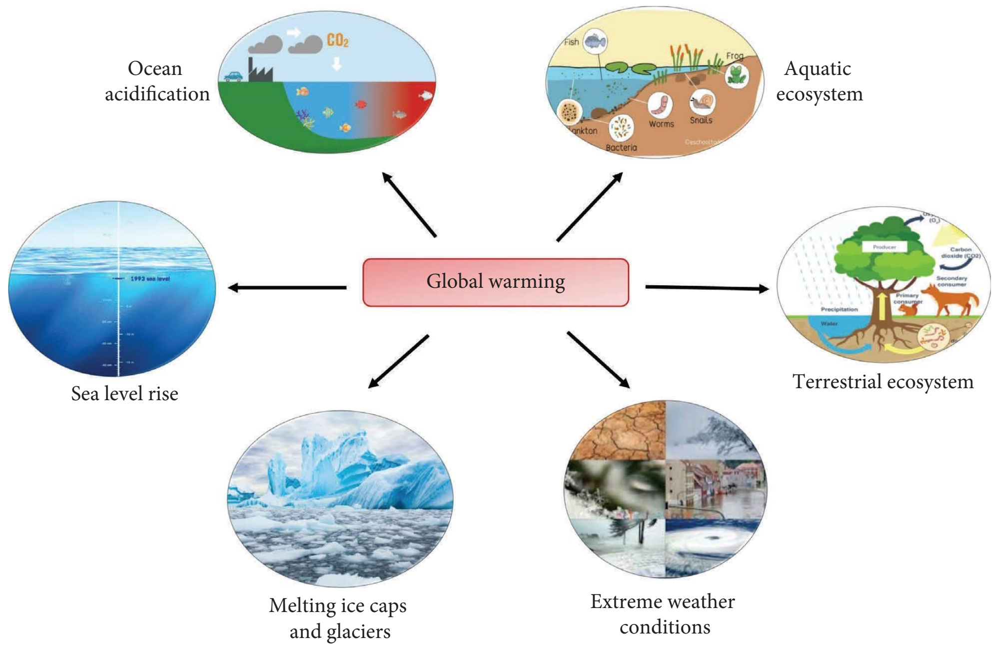

Figure 2: Impact of global warming.

forestalling apoptosis and cellular demise, as documented by Roberts et al. [166]. Multiple investigations suggest a correlation between the capacity to enhance HSP expression and thermal tolerance in aquatic organisms [167], thereby proposing that HSPs could bear ecological importance within the framework of global warming.

3. Conclusion

In conclusion, this review provides a comprehensive examination of how salinity, temperature, and their interactions intricately shape various aspects of fish physiology, including osmoregulation, growth, immunity, survival, and reproduction. It underscores the critical influence of these environmental factors on aquaculture dynamics, highlighting the adaptability of euryhaline species to fluctuating salinity levels and the nuanced impacts of temperature on metabolic rates, feeding behavior, and broader physiological functions. The review also emphasizes the overlooked roles of parental influences and genetic factors in early life responses to temperature fluctuations, promoting a holistic understanding. Future research should investigate the cumulative and synergistic effects of various environmental changes on marine organisms to better understand their adaptive responses. Specifically, studies should focus on elucidating species-specific responses in teleost fish to the complex interplay between salinity and temperature, offering insights crucial for navigating climate change impacts on aquatic ecosystems. This forward-looking perspective aims to advance aquaculture practices and enhance our ability to manage fish populations amid ongoing global environmental changes. Diving deep into molecular studies and integrating multiomics approaches will also help uncover the complex molecular pathways involved in these adaptive processes.

Nomenclature

AChE:	Acetylcholinesterase
ADP:	Adenosine diphosphate
CART:	Cocaine-amphetamine regulated transcript
CCK:	Cholecystokinin
CFTR:	Cystic fibrosis transmembrane conductance regulator
FCR:	Food conversion ratio
FW:	Fresh water
FXYD:	Phospholemman
GH:	Growth hormone
GLUT1:	Glucose transporter 1
GPX:	Glutathione peroxidase
HPI:	Hypothalamus-pituitary interrenal
HSP70:	Heat shock protein 70
IGF1:	Insulin-like growth factor 1
MRCs:	Mitochondria rich cells
NKA:	Na ++ K+ ATPase
NKCC:	Sodium potassium chloride cotransporter
NTPDase:	Nucleoside tri-phosphate di-phosphohydrolase
OSTF:	Osmotic stress transcription factor
PI3K:	Phosphoinositide 3-kinase/protein kinase B
SOD1:	Superoxide dismutase 1
SW:	Sea water
VHA:	V-H+ -type ATPase

Data Availability Statement

Data sharing is not applicable to this article as no new data were created or analyzed in this study.

Conflicts of Interest

The authors declare no conflicts of interest.

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