

## Osmotic and Adaptive Challenges: Physiological and Biochemical Responses of Fish to Increased Salinity

### Ozmotik ve Adaptasyon Zorlukları: Balıkların Artan Tuzluluğa Fizyolojik ve Biyokimyasal Tepkileri

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**Abstract:** Climate change is known to affect abiotic factors in coastal and marine ecosystems. The increase in salinity, caused by climate change-related factors that raise soluble salts above optimal levels, leads to acute stress. This condition can affect the tissues and organs of aquatic animals. In chronic stress conditions, organisms become entirely insensitive to stress factors or organisms may either develop tolerance, resulting in altered growth and reproduction rates. Fish can be examined as bioindicators to monitor salt fluctuations, which may cause osmotic stress at the cellular level, and molecular and biochemical changes that are induced via the production of reactive oxygen species (ROS). In addition, enzymatic activities are particularly affected in mitochondrial functions. Although increasing salinity presents a positive picture in some freshwater fish species by supporting embryonic and larval development and preventing some diseases, species with lower adaptability may be adversely affected by excessive salinity. When examining the effects of salinity stress, analysis of energy metabolism during its acute phase is a common preferred approach due to its rapid and measurable indicators. With the increase in salinity, differences occur at the cellular and hormonal levels (e.g., cortisol, prolactin), reproduction, growth, and development processes. Tolerance and adaptation abilities vary depending on whether they are euryhaline or stenohaline fish species. Advanced analytical methods such as omics techniques, metabolic profiling, and imaging techniques are needed to obtain more detailed results in this field.

#### Keywords

- Salinity
- Stress
- Osmoregulation
- Adaptation
- Climate change

**Özet:** İklim değişikliğinin kıyı ve deniz ekosistemlerindeki abiyotik faktörleri etkilediği bilinmektedir. Çözünbilir tuzları optimum seviyelerin üzerine çıkaran iklim değişikliğiyle ilişkili faktörlerin neden olduğu tuzlulukta artış, suda yaşayan hayvanların dokularını ve organlarını etkileyebilen akut strese yol açar. Kronik stres koşullarında, organizmalar stres faktörlerine karşı tamamen duyarsız hale gelir veya organizmalar tolerans geliştirebilir, bu da değişmiş büyüme ve üreme oranlarıyla sonuçlanabilir. Balıklar, hücresel düzeyde ozmotik strese ve reaktif oksijen türlerinin (ROS) üretimiyle indüklenen moleküler ve biyokimyasal değişikliklere neden olabilen tuz dalgalanmalarını izlemek için biyoindikatör olarak incelenebilir. Ek olarak, enzimatik aktiviteler özellikle mitokondriyal işlevlerde etkilenir. Tuzluluğun artması, embriyonik ve larval gelişimi destekleyerek ve bazı hastalıkları önleyerek bazı tatlı su balık türlerinde olumlu bir tablo sunmasına rağmen, daha düşük uyum yeteneğine sahip türler aşırı tuzluluktan olumsuz etkilenir. Tuzluluk stresinin etkilerini incelerken, hızlı ve ölçülebilir göstergeleri nedeniyle akut fazındaki enerji metabolizmasının analizi yaygın olarak tercih edilen bir yaklaşımdır. Tuzluluğun artmasıyla hücresel ve hormonal düzeylerde (örn. kortizol, prolaktin), üreme, büyüme ve gelişim süreçlerinde farklılıklar meydana gelir. Tolerans ve adaptasyon yetenekleri, örihalin veya stenohalin balık türlerine bağlı olarak değişir. Bu alanda daha ayrıntılı sonuçlar elde etmek için omik teknikleri, metabolik profilleme ve görüntüleme teknikleri gibi gelişmiş analitik yöntemlere ihtiyaç vardır.

#### Anahtar kelimeler

- Tuzluluk
- Stres
- Osmoregülasyon
- Adaptasyon
- İklim değişikliği



## 1. INTRODUCTION

Climate change is known to alter salinity and temperature patterns, which significantly stress aquatic biota (Elhakeem & Elshorbagy, 2013). Increased salinity, known as salinization, is the natural increase of soluble salts above the optimum level. Situations such as glacial/interglacial cycles, weather conditions of the basin, salt content in the rain, and extreme natural events can significantly alter salinity regimes, both spatially and temporally. Anthropogenic factors such as agricultural irrigation, land clearing, river regulation, and mining, along with global trends like sea level rise and increased drought, are key contributors to salinity shifts in aquatic systems. Collectively, these factors contribute to salinity increases that threaten biodiversity and disrupt ecological homeostasis (Herbert et al., 2015). While there has been an increase in saltwater inflow due to sea level rise with global warming, there has been a decrease in freshwater inflow due to the decline in snowfall (Cloern & Jassby, 2012).

Water bodies can be classified depending on their salinity. The salinity of different water bodies worldwide ranges from 0.5 to 400 ppt. According to salinity requirements, aquatic organisms are classified as freshwater (salinity: <0.5 ppt), brackish water (0.5-29 ppt), and marine organisms (>29 ppt) (Paul & Rashid, 2017).

As a result of global warming, the water salinity distribution in coastal areas increases with the increase in sea levels (OECD, 2012). The main impact on the coastline is caused by the increase in salinity and the effect on freshwater resources in the region. This situation can affect the reproductive readiness such as gametogenesis, maturation, and subsequent gonad development of fish, especially during the breeding period. As this process continues with high salinity levels, it may reveal differences in the physiological development of fish, the distribution of sex ratios, reproductive abilities, and may alter migration timing, sex differentiation, and reproductive success. It may promote the proliferation of invasive species and facilitate harmful algal blooms, affecting the survival of species in freshwater and marine ecosystems. It poses risks such as loss of flora and fauna in the terrestrial environment, damage to the living environments of living things, and affects the chemical structure of the land (Cloern & Jassby, 2012). In short, it is necessary to have

an integrated ecological framework for the change in salinity levels.

Studies on rising salinity trends must be carried out at regional and global levels. It should be considered that aquatic species with lower adaptability will be more affected by these processes. It is known that acute stress conditions can influence behavior, biochemical parameters, and various tissues and organs. Under chronic exposure, organisms may develop tolerance, often at the cost of growth and reproductive efficiency. Species-specific responses may be given depending on the species, such as developing resistance or becoming sensitive to diseases (Barton, 2002).

Since biochemical parameters, especially enzymes, are highly sensitive stress indicators and are thus preferred as biomarkers, they are also biomarkers in salinity stress (Agrahari & Gopal, 2009). These values are used to determine the physiological responses and survival rates caused by salinity stress on living things.

Changes in salinity can cause oxidative stress in vertebrates and invertebrates. Advanced techniques such as genomic, proteomic, transcriptomic, and metabolomic tools may also be preferred to observe changes. Thus, it can be clarified with biotechnological approaches which pathways stress factors affect at the molecular level (Hawkins & Storey, 2020).

There is a robust body of literature focusing on stress biology in fish, which is the preferred group for determining the changes occurring in the aquatic environment. These studies look at physical, chemical, and biological effects within the framework. In more detail, these studies examined the cellular, physiological, behavioral, and adaptive responses (Loro et al., 2012; Akbulut et al., 2014; Vargas-Chacoff et al., 2019; Chowdhury & Saikia, 2020). For this purpose, our study will evaluate the relationship of salinity with other factors, such as climate-induced stressors, temperature, ammonia levels as well as the osmoregulation process, the cellular and hormonal response processes and their effects on reproduction growth, tolerance and adaptation development processes.

### 1.1. Synergistic Effects of Salinity with Other Factors

Salinity alters thermodynamic properties such as density and solubility, which in turn influence water stratification, oxygen levels, and overall habitat suitability for aquatic organisms. Climate change scenarios project significant changes in

abiotic parameters such as temperature and salinity, especially in coastal ecosystems. These changes may disrupt physiological and genomic integrity, cause oxidative stress, compromise reproduction, and interfere with nutrient uptake in aquatic organisms. Notably, rising temperatures and sea level, key consequences of climate change, are expected to intensify salinity changes in coastal areas. As a result of the changes, oxidative stress will be triggered in aquatic aerobic organisms, and fish welfare will be affected (Loro et al., 2012).

The interaction between temperature, salinity, and ammonia levels plays a central role in defining water quality thresholds critical to aquatic species. Thermal and osmotic stress may occur if temperature and salinity deviate from optimal values. This affects normal physiological functions and can change the direction of energy consumption (Portz et al., 2006). Stress conditions during early life stages have been shown to impair larval growth and survival, thereby reducing overall aquaculture productivity (Rosemore & Welsh, 2012).

It is known that ammonia concentration may change with changes in temperature, salinity, and pH. Studies have determined that fish growth is affected by the acute elevation of ammonia levels, which is marine species' last main product of nitrogen metabolism (Randazzo et al., 2017)—involving the gene expressions of insulin-like growth factors (igf1 and igf2) and myostatin (mstn) as a stress response may also cause a decrease in growth (Davis & Peterson, 2006).

Salinity tolerance limits may vary in fish species living in freshwater. Environmental parameters, including salinity, are among the most critical drivers influencing fish growth and developmental processes (Kang'ombe & Brown, 2008). The effects of salinity, among environmental factors, have been examined in various fish species in different environments, such as ponds, tanks, and canals (Watanabe et al., 1990). These studies concluded that salinity fluctuations in tropical pond systems are more pronounced, especially during seasonal transitions (Boyd & Tucker, 2012).

In a study, the salinity of farm ponds in Western Australia remained below 0.5‰ during the rainy season; It has been reported that it can exceed 3‰ in dry seasons (Boyd & Tucker, 2012). Therefore, it is vital to determine the salinity tolerance of freshwater fish species in

environments where seawater enters or the evaporation rate is high. Aquatic organisms are affected by salinity both at cellular and extracellular levels, primarily through changes in ionic strength resulting from dissolved salts. The severity and frequency of stress caused by climate variability or climate-induced stressors, habitat degradation, anthropogenic effects, and salinity affect many species. It should be remembered that anthropogenic activities accelerate the entire process.

While some ocean regions may experience freshening due to ice melt, others, especially estuarine systems, are prone to salinity increase through sea level rise and saltwater intrusion. In addition to climate-induced gradual salinity changes, severe natural events (hurricanes, tsunamis, glacier melts) that are predicted to increase in frequency may also trigger salinity-related stresses (Nielsen et al., 2012).

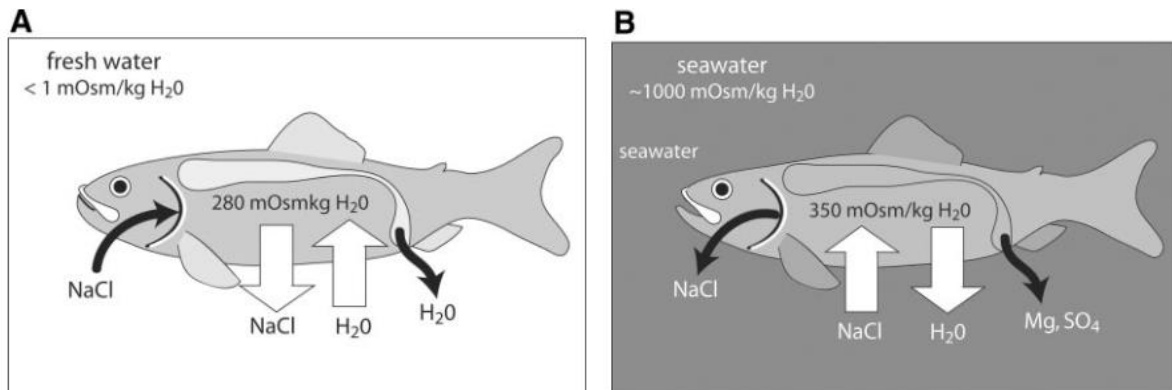
The synergistic effects of both salinity and temperature potentially impact altered osmoregulatory physiology. These effects may exert protective or degenerating roles (Stewart et al., 2016). In a study conducted in 2019, the neuroendocrine responses of *Harpagifer antarcticus* fish to hyposaline and hyperthermal exposure were examined. Changes in temperature and salinity affected tissue-specific neurotransmitter levels in the brain, intestine, and stomach. Serotonergic activity (brain tissue serotonin and 5-hydroxyindole-3-acetic acid levels), dopamine, and noradrenaline were significantly increased, especially under high temperature (11°C) and low salinity (23 psu) conditions. This species demonstrates physiological plasticity to environmental changes, suggesting that changes in serotonin levels may serve as signals in the early stages of the stress response. These findings suggest that *Harpagifer antarcticus* may serve as a suitable bioindicator species for monitoring combined hyposaline and thermal stress in polar regions (Vargas-Chacoff et al., 2019).

## 1.2. Osmoregulation of Salinity Stress in Fish

Fish have evolved diverse strategies to cope with osmotic challenges. Fish possess osmosensory signaling pathways that detect deviations in extracellular osmolality and initiate adaptive molecular responses (Kültz, 2015). As shown in Fig. 1, fish living in freshwater and seawater have differences regarding osmoregulation. Salinity can cause osmotic stress

at the cellular level. Osmotic stress alters the activity of excretory organs, such as increased ion transport and urine production, to re-establish homeostasis (Lamalakshmi Devi et al., 2017). Changes in plasma/serum ion concentrations can lead to changes in metabolic rates and gene

expressions (Zhou et al., 2021). The shift in osmoregulation can also be seen at high and low salinity levels; in waters with hypohalinity, the number, size, mitochondrial content, and  $\text{Na}^+/\text{K}^+$ -ATPase activity of ionocytes increase (Kültz, 2015).



**Figure 1.** Osmotic and ionic regulation in freshwater and marine water fish. A: Regulation in freshwater B: Regulation in seawater (Beyenbach, 2004).

$\text{Na}^+/\text{K}^+$ -ATPase is the most critical membrane protein in osmoregulation in ion control. It is significantly affected by sudden changes in salinity levels. The balance of osmotic pressure can be evaluated by monitoring the changes in its activity. While it plays a role in the uptake of  $\text{Na}^+$  and  $\text{Cl}^-$  in freshwater, it plays a role in their excretion in hypertonic water (Wang et al., 2016). Marine teleosts regulate internal salt concentrations at levels well below seawater. It tends to lose water across the large surface area of the gills. They also drink seawater to absorb water from the intestinal epithelium and maintain osmotic balance. The swallowed liquid is essential for the secretion of bicarbonate ions into the intestinal lumen (Wilson et al., 2002). These salts must be removed from the body to ensure intra-body osmoregulation. While  $\text{Mg}^{2+}$  and  $\text{SO}_4^{2-}$  are excreted in low volume from the kidneys,  $\text{Na}^+$  and  $\text{Cl}^-$  are excreted branchially (Genz et al., 2011). When the salinity level exceeds 35ppt, both water absorption and salt excretion from the body become difficult. At extreme salinity levels (e.g., 70 ppt, Mozambique tilapia), ionoregulatory mechanisms are severely impaired, leading to pronounced gill disruption and loss of osmotic balance (Gonzalez, 2012).

Upregulation of transcripts and proteins indicative of DNA damage is observed in fish as part of the response to hyperosmotic stress. This suggests that DNA strands may be affected after salinity changes (Whitehead et al., 2013). In

previous studies, it was thought that common DNA strand breaks in marine organisms may be related to this situation (Dmitrieva et al., 2006).

In tilapia, the salinity threshold of adaptive change in the osmoregulation strategy is approximately twice that of seawater ( $60 \text{ g kg}^{-1}$ ) (Kültz, 2015). It has been determined that water retention takes priority over paracellular  $\text{Na}^+$  secretion (transfer of  $\text{Na}^+$  across an epithelium by passing through the intercellular space) in extreme hypersaline conditions. Therefore, it is conceivable that in hypersaline environments, the  $\text{Na}^+$  secretion mechanism is downregulated to minimize ion loss in an environment with reduced osmotic permeability. Studies on hypersalinity-accustomed teleosts support the views regarding osmotic permeability and water balance (Lavery & Skadhauge, 2012). Migratory anadromous fish generally have high osmotic plasticity. Thus, they can survive in a wide range of salinity changes. For example, it has been revealed that when salmon migrate to salt water, genes such as ion binding and ion transport are expressed more, thus regulating osmoregulation (Lee et al., 2020). However, it has been shown in a study that salinity increases can induce behavioral disturbances, antioxidant defense activation, and, in extreme cases, mortality in *Poecilia latipinna* (Tietze & Gerald, 2016).

From a molecular perspective, the physiological mechanisms of osmoregulation have mainly remained mysterious for fish that

exhibit osmoregulatory patterns. A complex system is used in estuarine fish to regulate cell volume in response to changing salinities, such as aquaporins and polyamine synthesis. This process includes MAPK cascades, cytokine-mediated transcription factors, and calcium signaling pathways. It has been observed that the number of fish decreases in high-salinity situations where regulation cannot be regulated (Komoroske et al., 2016). While the problem of osmotic water loss occurs in addition to excessive ion entry in increasing salinity rates, in cases of exposure to low salinity, issues such as increased water entry and ion depletion occur in the regulation of osmoregulation. Since preserving water and ionic homeostasis is critical for the continuation of life, balance is tried to be achieved in both cases. Cortisol, growth hormone, and IGF-I participate in the endocrine system, which works as one of the protection systems to ensure osmoregulation and adaptation (Sakamoto & McCormick, 2006).

In freshwater fish, this balance is achieved by the uptake of ions such as  $\text{Na}^+$ ,  $\text{Cl}^-$ , and  $\text{Ca}^{2+}$ , facilitated by combinations of ATPase pumps and ion channels in accessory cells. At the same time, freshwater fish balance the osmotic uptake of water and ion balance by excreting urine from the kidneys. In saltwater fish, this is compensated by branchial excretion of ingested ions and by reducing osmotic water loss through drinking (Evans et al., 2005). If the difference between the salinity of the fish's environment and its body fluid is too high or too low, the fish spend more energy to maintain osmotic balance. Therefore, this leads to an increased metabolic cost for osmoregulation and a subsequent reduction in growth efficiency. A study stated that fish use 10-50% of their energy to regulate osmoregulation (Bœuf & Payan, 2001). In isoosmotic salinity environments, the oxygen uptake rate is observed to be at its lowest level, and it has been observed that osmoregulation costs are also at their lowest level (Scott et al., 2007).

### 1.3. Cellular Control of Salinity Stress in Fish

Cellular stress responses in fish encompass a range of molecular mechanisms, including the upregulation of heat shock proteins (HSPs), a family of highly conserved molecular chaperones. These proteins are expressed ubiquitously in all domains of life. The expression of heat shock proteins in fish can change not only after exposure to thermal shock measured in the liver and heart tissues of

but also after osmotic shock and ammonia stress (Randazzo et al., 2017). In examining the cellular response in fish to salinity in the environment, sensitive species (stenohaline) and more tolerant species (euryhaline) should be considered separately. To understand the physiological basis, large-scale changes in environmental conditions can disrupt the structure of proteins, lipids, and DNA. It should be regarded as leading to a loss of homeostasis. In a constant ionic environment, in a state of osmotic balance, cellular function and physiological processes should be determined, and the resulting differences should be evaluated from this perspective (Gonzalez, 2012).

Aquatic organisms respond to salinity stress through biochemical pathways activated by the accumulation of reactive oxygen species (ROS), including superoxide, hydroxyl radicals and hydrogen peroxide. Enzymatic activities in mitochondrial functions are especially affected by the change in salinity (Paital & Chainy, 2014). When the salinity level of the environment increases, biochemical processes such as the electron transport chain, glycolysis, and fatty acid metabolism are affected in freshwater fish (Nguyen et al., 2016).

Complex I and III of the mitochondrial electron transport chain are primary sites of ROS generation under salinity-induced mitochondrial dysfunction. Antioxidant enzymes such as superoxide dismutase (SOD), catalase (CAT), glutathione peroxidase (GPx), and antioxidants such as ascorbic acid, reduced glutathione, and vitamin A work to protect cells from this oxidation (Liu et al., 2018). Glutathione reductase and glutathione-S-transferase convert oxidized glutathione into reduced glutathione and play a role in removing xenobiotics. They are considered assistants of redox-regulating enzymes. If protection against oxidants fails, cells are subjected to oxidative stress (OS). Lipid peroxidation, protein carbonylation and peroxide accumulation are key biomarkers of oxidative stress. Oxidative stress and redox regulatory molecules may change in response to environmental factors, and their determination allows for analyzing harmful effects (Halliwell & Gutteridge, 2015). It can be explained by the disruption of free radical processes and the adaptability of antioxidants (Loro et al., 2012).

In a study supporting this situation, CAT, GSH, SOD activities and lipid peroxidation were sturgeon (*Acipenser naccarii*) during their

gradual transition from freshwater to seawater. It was determined that the fish had physiological adaptation to the new environment regarding plasma osmolarity and erythrocyte number at the end of 20 days spent in a 35‰ salinity environment. When the blood values were examined, it was evaluated that the cortisol level, antioxidant enzyme activities, lipid peroxidation, and protein levels did not return to the initial levels, and the osmoregulation process may cause physiological changes in the fish (Martinez-Alvarez et al., 2002). Changes in salinity levels can cause structural damage to macromolecules such as proteins, lipids and nucleic acids, affecting cellular integrity and function (e.g. *Anguilla anguilla*). Studies have shown that salinity levels can affect plasma pH in fish (Politis et al., 2018; Tresguerres et al., 2020). Proteins that are denatured due to changes in pH may cause instability. Like proteins, the structure of DNA and RNA can be affected by salinity stress. It has been shown that after acute salinity stress in the species *Oreochromis mossambicus*, the cell cycle can be arrested or apoptosis can occur as a cellular stress response (Kammerer et al., 2009).

ATPase pumps, co-transporters, and anion channels in mitochondria-rich chloride cells function to maintain salt balance in fish living in salty water (Evans et al., 2005). In adaptation to salt water, mRNA and protein expression of gill  $\text{Na}^+/\text{K}^+$ -ATPase increases (Zhu et al., 2018). As the water's salinity level increases, the plasma's osmotic pressure also increases. Energy production will increase to ensure this osmotic regulation in the gill tissue. When the tolerance limit is exceeded, the gill tissue suffers irreversible damage and becomes unable to maintain normal physiological function, resulting in compromised osmoregulatory capacity and ultimately death (Geng et al., 2016). A study examined the individual and combined effects of *Luciobarbus capito* on gill  $\text{Na}^+/\text{K}^+$ -ATPase enzyme activity, plasma ion concentration, and osmotic pressure against salinity. As salinity concentrations increased (5, 8, 11, and 14 g/L), it showed a biphasic response: an initial activation followed by a sustained elevation of  $\text{Na}^+/\text{K}^+$ -ATPase activity in *L. capito* gills occurred. Enzyme activity was affected by the difference between internal and external  $\text{Na}^+$  ion concentrations and osmotic pressure. Plasma ion concentration ( $\text{Na}^+$ ,  $\text{K}^+$ , and  $\text{Cl}^-$ ) and osmotic

pressure increased significantly ( $p < 0.05$ ) (Geng et al., 2016).

*Tilapia mossambicus* had been chosen as the species whose response to salinity was investigated in a study to define physiological differentiation. The study examined the effect of 3, 6, 9, 12, and 15 ppt salinity on the hematology of juvenile *Tilapia mossambicus* after 14 days of exposure. Complete mortality occurred at 15 ppt within two days, indicating a critical salinity threshold for the species. Fish exposed to 12 ppt salinity after 14 days of exposure showed a significant decrease in red blood cell count, hematocrit, hemoglobin, and mean corpuscular hemoglobin ( $p < 0.05$ ). The results of the study reveal that stress caused by salinity significantly affects *T. mossambicus* hematology (Rauf & Arain, 2014). In another study, the effect of salinity was evaluated in rainbow trout (*Oncorhynchus mykiss*). This study exposed fish to 7 and 11 ppt salinity for 0, 24, 48, 72 and 240 hours. It has been reported that there is a significant decrease in hematocrit and hemoglobin values. Hematocrit percentage values were found as 33, 27, 30, 30, 28 at 7 ppt salinity, respectively (0, 24, 48, 72 and 240 hours); and 33, 25, 29, 28, 26 at 11 ppt salinity, respectively (0, 24, 48, 72 and 240 hours) (Hosseini et al., 2011).

In another study, the physiological responses of river pufferfish, *Takifugu obscurus*, tiger pufferfish, *Takifugu rubripes*, a hybrid of the two (river pufferfish × tiger pufferfish), and a hybrid triploid to acute salinity changes (from 0 psu to 30 psu / from 30 psu to 0 psu) were investigated. Blood and plasma factors (Hematocrit, hemoglobin, red blood cell,  $\text{Na}^+$ ,  $\text{K}^+$ ,  $\text{Cl}^-$ , aspartate aminotransferase, alanine aminotransferase) of the species increased for 48, 72, or 96 hours and then decreased due to hyper-osmoregulation and hypo-osmoregulation. While chloride cells in the gill filaments of the species increased with increasing salinity (from 0 psu to 30 psu), melano-macrophages in the kidney tissue increased with decreasing salinity (from 30 psu to 0 psu) (Park et al., 2019).

#### 1.4. Hormonal Control of Stress Factors in Fish

The stress response in fish is a coordinated set of behavioral, endocrine, and physiological reactions triggered by environmental perturbations, aimed at re-establishing homeostasis. The primary stress response in fish

involves releasing catecholamines and activating the hypothalamic-pituitary interrenal axis. Corticotropin-releasing factor from the hypothalamus acts on the pituitary to synthesize corticotrophic hormone. This stimulation results in the synthesis and release of glucocorticoids, primarily cortisol, from interrenal tissue (Romero, 2004). Cortisol acts as an agonist of the glucocorticoid receptor. It has a role in increasing ion uptake and adaptation to water salinity; in some cases, it acts with the prolactin hormone. Cortisol plays a pivotal role in mediating osmoregulatory and metabolic adjustments during salinity-induced stress (Pelis & McCormick, 2001).

Glucose is a primary energy substrate for neural tissue, and its availability is often disrupted under osmotic stress. As salinity increases, glucose flow to the brain decreases, which is thought to be a compensatory mechanism developed to combat stress. However, this decrease may have a seriously harmful effect on brain tissue. During stress, the demand for glucose in tissues increases to provide energy to osmoregulation mechanisms, resulting in increased gluconeogenesis (Sangiao-Alvarellos et al., 2003).

In a study conducted on *Oreochromis mossambicus*, it was determined that there was a significant increase in plasma glucose levels with the increase in salinity levels. They attributed this situation to the stress response and/or increased energy demand to maintain a water-electrolyte balance with higher salinity (Fiess et al., 2007). In a 2012 study on *Carassius auratus*, the fish were exposed to 10 ppt salt for 30 minutes. Serum cortisol and glucose levels were monitored at 0, 0.5, 3, and 24 hours after exposure. While there was a rapid increase in cortisol levels, they remained high until the 24th hour. While glucose levels increased at 0.5 and 3 hours, they returned to the initial value at 24 hours. The hyperglycemia that occurs here can be interpreted as a secondary stress response induced by primary stress responses (release of catecholamines and corticosteroids) (Tarkhani & Imanpoor, 2012).

If sudden environmental salinity increases, euryhaline fish stop active transport and ensure reverse system transport. In the acute phase, short-acting hormones such as angiotensins, natriuretic peptides, and neurohypophyseal hormones take part (Wood, 2011). There are high the *Siniperca chuatsi* species determined that

levels of prolactin receptors in gill ionocytes and enterocytes, especially cells involved in osmoregulation (Sandra et al., 2000). It has been determined that prolactin can directly or indirectly regulate cell proliferation and/or apoptosis in fish exposed to salinity stress (Sakamoto & McCormick, 2006).

### **1.5. Effect of Salinity on Growth and Reproduction in Fish**

Changes in seasons, fluctuations in temperature, sun duration, humidity, precipitation regimes, and salinity can affect the physiological development, reproduction, and growth stages of living things (Chainy et al., 2016).

Salinity and other environmental factors affect the development of fish embryos and larvae. Because they are located directly in the ecological environment, fish embryos can be exposed to stress factors. Embryonic exposure to salinity fluctuations is critical in shaping physiological resilience and survival outcomes (Chowdhury & Saikia, 2020). Studies have been conducted recently on exposure to environmental factors during embryonic and larval development (Kızılkaya et al., 2023; Turhan, 2023).

In a study conducted in 1956, brown trout were pretreated with growth hormone, and subsequent exposure to seawater showed increased hypoosmoregulation ability. This study reported that growth hormones are important in adaptation to a saline environment such as seawater (Smith, 1956). Changing environmental salinity levels can affect the growth of many fish species. Although the precise mechanism by which isoosmotic salinity promotes growth remains under investigation, it has been hypothesized that elevated glucose-6-phosphate dehydrogenase activity may enhance pentose phosphate pathway flux, promoting biosynthesis and growth. It is also claimed that these isoosmotic conditions affect macrophage phagocytosis by reducing the proteins produced as a due to stress in species such as sea bream (Narnaware et al., 2000; Deane & Woo, 2005).

A study on *Acipenser brevirostrum* observed that growth performance can be increased in juveniles gradually acclimated to salinity. However, it has been determined that fry development usually proceeds in salt water (Jarvis & Ballantyne, 2003). Rearing *Cynoscion nebulosus* larvae in hypersaline conditions can increase growth time to more than three days after hatching (Schacht et al., 2022). A study on growth, immunity, and the number of probiotics

in the intestine reached the highest level in fish exposed to 6‰ salinity (Ouyang et al., 2023). A study on the *Argyrosomus regius* species in 2024 determined that the increase in salinity level for 28 days increased growth (for 10 psu 16.2% weight increase; for 20 psu 25.0% weight increase; for 30 psu 24.6% weight increase), oxidative stress, and energy need (Lemos et al., 2024). At the same time, researchers point out that the increase in salinity level may reduce the resistance of aquatic animals against pathogens (Zhang et al., 2016).

A study showed that increased salinity can affect the average growth of *Micropterus salmoides* (Sun et al., 2023). It has been determined that with the increase in salinity, there is an increase in the mortality rate (salinity levels 0%, 5%, 10% 15%; survival rates 100%, 100%, 81.10%, 26.67% respectively), a decrease in the feed conversion ratio, a reduction in immunity with anomalies in intestinal villi and cells, and changes in the microbiota (Sun et al., 2023). A study on goldfish in 2013 revealed that increased salinity reduced food intake, followed by a decrease in growth (Küçük, 2013).

In a study conducted in 2017, the growth performance and feed utilization of *Anoplopoma fimbria* decreased significantly in low salinity. Antioxidant responses and immune values such as superoxide dismutase and catalase, also decreased with low salinity. As a result of this study, it was determined that the growth performance of *A. fimbria* was affected by environmental salinity (Kim et al., 2017). An experiment conducted with *Cyprinus carpio* found that growth parameters in 10‰ and 15‰ salinity groups were significantly lower than in 0 and 5‰ salinity groups, and survival rates were also significantly reduced in these high salinity values (Dawood & Sewilam, 2023). Salinity fluctuations serve as environmental cues modulating reproductive timing, gametogenesis, and migratory behavior in anadromous and catadromous fish species. A study on off-season spawning of Atlantic salmon determined that seasonally occurring salinity changes affected micronutrient content and growth level by gene regulation in the fry (Skjærven et al., 2020).

### 1.6. Tolerance and Adaptability of Fish to Salinity

According to their osmoregulatory mechanisms, animals are examined under two headings: osmoconformers and osmoregulators. Organisms that maintain osmotic equilibrium

without expending active energy are called osmoconformers. Marine invertebrates and some species of stenohaline fish, such as *Melanogrammus aeglefinus*, maintain their intracellular balance by minimizing the osmotic gradient during this regulation. Conversely, through ATP-dependent mechanisms, osmoregulators actively regulate ion transport and water balance, often against steep osmotic gradients. Species that mostly live in freshwater and some estuarine fish species are included in this group (Ramaglia et al., 2018). While some fish can tolerate fluctuations in salt levels, the tolerance level of most freshwater fish species is low (Nguyen et al., 2016).

In a study conducted in 2004, it was determined that *Sarotherodon melanotheron* fish survived to approximately 120 ppt salinity levels when the salinity of the environment they lived in was increased by 2-8 ppt per day. According to the conclusion, some species can tolerate even maximum salinity when gradually exposed to high salinity (Lemarié et al., 2004). A study on the *Acipenser persicus* species determined that various metabolic stresses occurred in addition to physiological differentiation during the adaptation process to high salinity. It has been stated that water and ion loss through gills, increased water drinking rate, and increased Na<sup>+</sup>/K<sup>+</sup>-ATPase activity are physiological consequences (Shirangi et al., 2016).

When examining the effects of salinity stress, analysis of energy metabolism during its acute phase is generally preferred. Additionally, programmed cell death has become the focus of attention. Most studies on salinity-induced programmed cell death in fish have concentrated on osmoregulation-induced apoptosis in euryhaline species (Ching et al., 2013). Transcriptomic studies on *Dicentrarchus labrax*, a euryhaline fish species, have shown that salinity stress effectively regulates genes (Boutet et al., 2006). This physiological regulation may improve the mechanism of action on cellular cycles in the short and long term. Proteomic approaches can reveal the mechanistic basis of complex salinity stress responses. Integrating proteomic analysis with gene ontology and pathway enrichment tools enables detailed characterization of the stress response network (Li & Kültz, 2020). In fish adapted to extreme salinity, the identified genes were involved in transport activities, biological regulation, and metabolic processes, and higher metabolic

activity was determined (Tine et al., 2008). According to RNA sequencing analysis, studies on salinity adaptation in *Lateolabrax maculatus* determined that salinity stress induced alternative splicing events in key osmoregulatory and metabolic genes (Tian et al., 2020).

In a study on salinity tolerance, *Mugil cephalus* and *Chelon labrosus* were used as sample species. As a result of transferring these fish from 20 g/L salinity to 35, 40, 45, 50, 55, 60, 65, 70, 75, and 80 g/L salinity; it was determined that the tolerance level of *M. cephalus* could reach 53.1 g/L, and the tolerance level of *C. labrosus* could reach 50.4 g/L (Hotos & Vlahos, 1998). To study the high salinity effect, chronic salinity tolerance in *Carassius auratus* was investigated by gradually increasing the salinity by 2g/L every two days from 0g/L to 20g/L. While a high survival rate was observed in fish at 5 and 10g/L salinity, it was also noted that significant deaths occurred at 15 and 20g/L salinity (Schofield et al., 2006).

As salinity tends to increase in aquatic systems, euryhaline fish can be expected to gain an advantage over stenohaline fish soon. Therefore, the biochemical and physiological mechanisms enabling teleosts to cope with salinity fluctuations and hypersalinity must be better understood.

## 2. CONCLUSION

Salinity stress represents a critical environmental challenge increasingly intensified by climate change and human-induced disruptions. This review highlights the multifaceted impacts of salinity on aquatic organisms, particularly fish, encompassing physiological, biochemical, cellular, and molecular responses. It is evident that increased salinity exerts significant pressure on osmoregulatory mechanisms, demanding high energy expenditure for ion balance and water retention. The associated metabolic cost affects growth efficiency, reproductive performance, immune responses, and overall survival, particularly in species lacking high salinity tolerance. Tolerance and adaptation capacity are highly species-dependent, with euryhaline species demonstrating greater flexibility than stenohaline species. The emerging use of omics technologies, such as transcriptomics, proteomics and metabolomics, has facilitated the identification of key genes and proteins involved in salinity adaptation. These tools offer insights

into the molecular underpinnings of resilience and may support the development of salt-tolerant strains in aquaculture.

In conclusion, understanding the biological responses of aquatic species to increasing salinity is essential for biodiversity conservation, sustainable fisheries, and aquaculture practices. Proactive management strategies, including habitat protection, monitoring programs, and selective breeding, must be prioritized to mitigate the adverse impacts of salinization. Continued research using integrative and multidisciplinary approaches is necessary to fully unravel the adaptive potential of aquatic life under future salinity regimes.

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## CONFLICT OF INTEREST

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

## AUTHOR CONTRIBUTIONS

Fiction: HEED, ŞK; Literature: HEED; Methodology: HEED, FEK; Manuscript writing: HEED, ŞK, Supervision: FEK. All authors approved the final draft.

## ETHICAL STATEMENTS

Local Ethics Committee Approval was not obtained because experimental animals were not used in this study.

## DATA AVAILABILITY STATEMENT

Data sharing is not applicable for the present study as no new data was created or analyzed.

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