

## A Review on the Impact of Thermal Stress on Fish Biochemistry

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### ABSTRACT

Fish are an important resource for humans, providing food, economic support, and ecological services. However, rising global temperatures and subsequent increases in their habitat water temperature, pose a significant challenge. We conducted a systematic review to understand the biochemical responses of thermal stress on fish. Stress can be acute (rapid exposure for a short duration) or chronic (repetitive long-term exposure). Stress responses occur at neurotransmitter and hormonal levels, progressing to peripheral and organism-wide effects. Prolonged stress leads to reduced growth, reproductive impairments, heightened infection susceptibility, and mortality. Elevated temperatures serve as abiotic stressors, triggering biotic stress responses. Fish employ strategies to cope with thermal stress, including altering gene expression, metabolite profiles, cellular signaling, and enzyme activity. Cumulative effects of thermal stress induce oxidative stress, causing cell death, organ failure, and mortality. Stressors increase the energy demand, prompting changes in hormonal, enzymatic, and biomolecular responses. Cortisol alters gene expression, stimulating glucose synthesis (gluconeogenesis). Other hormones (thyroid hormones, epinephrine, norepinephrine, insulin, glucagon) also play roles in the thermal stress response. Enzymes involved in metabolic pathways have optimal temperature and pH ranges altered by thermal stress. Heat shock proteins and warm acclimation proteins act as protective mechanisms by preserving the structural integrity of proteins, which is crucial for maintaining proper functionality and cellular responses. Further research is needed to expand on these molecular mechanisms to evaluate proper mitigation strategies.

**Keywords:** Fish stress, Global warming, Thermal stress, Biochemical responses, Molecular mechanism

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### INTRODUCTION

#### Importance of fishes

Fish are very important aquatic animals to humans as they provide different health benefits, economic support, and ecological services (FAO, 2016). As per the [www.fishbase.de](http://www.fishbase.de) website, there are a total of 33,230 fish species in the world (Fishbase, 2020). Direct or indirect beneficial impacts of fish on the human population are numerous and have prevailed from ancient ages; only a few of these are discussed here. Fishes are important nutritional food for humans as well as for other animals. Fish are a low-cost protein source for humans and nearly

3.1 billion humans depend on fish to the tune of at least 20% of their total animal protein intake. Fish are the source of different essential amino acids such as lysine, valine, and functional amino acids, such as leucine and arginine (Ganguly et al., 2018). Fish are also a source of important vitamins, minerals, and other nutrients such as A, D, E, K, B12, sodium, potassium, magnesium, zinc, calcium, iron, copper, iodine, selenium, and fish oils ([http://www.fao.org/fileadmin/user\\_upload/newsroom/docs/BlueGrowthNutritionRev2.pdf](http://www.fao.org/fileadmin/user_upload/newsroom/docs/BlueGrowthNutritionRev2.pdf)). Fish oils are rich in important PUFAs, such as linoleic acid,  $\alpha$ -linolenic acid, arachidonic acid, EPA and DHA. Fish oils have different physiological benefits in several patho-



logical conditions such as heart problems, atherosclerosis, rheumatoid arthritis, bipolar disorder, osteoporosis, asthma, etc. (Mohanty et al., 2019). Ornamental fish also are used in pet therapy to reduce mental depression (Gardiánová & Hejrová, 2015). Fish spas are also very popular nowadays (Riyaz & Arakkal, 2011). Fish are also used in the production of feed for other animals including other fish (Tacon & Metian, 2008).

### Increment in water temperature

'Climate change' is a nightmare for the whole world and one of the most challenging hazards to be faced on the Earth in the coming future. Climate change results in a rise of the global surface temperature, known as 'Global warming'. The mean temperature of Earth's surface so far has risen by 1.4 °F over the last century and is expected to rise more (2 to 11.5 °F) over the coming hundred years (<http://www.epa.gov/climatechange/basics/>). Global warming is not only an increase in the temperature but also an alteration of different parameters of water bodies (Ficke et al., 2007, Brander, 2010). The surface temperature of the Earth has already increased (nearly +0.93 °C in the past 150 years) and is predicted to increase a few degrees more (1–4 °C) up to the end of this century (IPCC, 2007). Other than the increment in the Earth's surface temperature, experts have predicted some regional variations in temperatures (IPCC editor, 2012). Thus, impacts will vary in different parts of the globe. More events of extreme, abrupt, and frequent changes in temperature are documented in past decades (1991–2000) compared to earlier decades (1971–1990) (Dash & Mamgain, 2011). Different researchers (Diffenbaugh et al., 2007; Ray et al., 2012) also have found extreme events earlier. A heatwave was observed in Ahmedabad, India when the temperature rose to 46.8 °C during May 2010 (Azhar et al., 2014). Increments in the air temperature also led to a rise in the water temperature. Jurgelėnaitė and Jakimavičius (2014) have established a good positive correlation between air temperature and water temperature. The IPCC (2013) in their fifth assessment report estimated ocean warming by 0.09 to 0.13 °C per decade over the past 40 years. There will be an increment in the temperature of water bodies that will alter the habitat of different aquatic animals. Fishes are temperature-sensitive animals (poikilotherms); therefore, increments in the habitat temperature in the coming future beyond the adaptation capacity may exert abiotic stress among them.

## STRESS BIOLOGY

### General stress in animals

Cannon (1929) was the pioneer researcher who proposed the concept of stress as an "emotionally stimulation situation". Later, Selye (1936) explained the stress in the biological point of view. He demonstrated stress as a "non-specific pathological" response to different "noxious agents". However, several researchers encountered the concept of "the non-specific nature" of stress and proposed it is as highly specific (Mason, 1971; Pacak & Palkovitis, 2001). Stress is the discomfort state of the body under a threat where coordinated responses of physiological, biochemical, and behavioral processes cumulatively help the organism to overcome the situation (Chrousos & Gold, 1992). The initial response is to adapt to the situation by changing different biological processes of the body to a new normal situation in response

to external as well as internal stimuli, which are cumulatively known as "allostatic load" (Schreck, 2001). The term "allostatic" denotes the body's capacity to attain stability amid change, with "load" signifying the toll or expense incurred by the body in adapting to stress (McEwen, 2013). Conceptually, stress can be defined as an alteration of physiological, biochemical (in the lower and higher organism), and mental (only in higher organisms) states due to different external (environmental factors), internal (body imbalance), or emotional stimuli that in the long-run effect performance and create physiological disorders, which every organism tries to avoid although it is nearly impossible.

### Stress responses

Under stress, fish initially respond at the neurotransmitter and hormonal level (primary response) then at the peripheral level (secondary response) (Mazeaud et al., 1977), and finally to the whole organism or population level (tertiary responses) (Wodemeyer & McLeay, 1981). The primary responses are the "alarming stages" and two hormonal axes are involved in any kind of stress response in fish. The sympathetic-chromaffin (SC) axis and the hypothalamic-pituitary-interrenal (HPI) axis regulate oxygen uptake, transfer, and energy metabolisms (Wendelaar, 1997, Roychowdhury et al., 2020b). The secondary responses are the stages of "resistance". During that stage, fish try to engage all the available mechanisms to cope with the situation. The tertiary response of an organism is the "stage of exhaustion" where fish are unable to fight against the stress, reflected in their performance, and finally may cause even death (Roychowdhury et al., 2020a, Roychowdhury et al., 2020b). Therefore, the primary responses occur at a systemic level whereas secondary responses occur at the peripheral level, and the tertiary response affects the whole organism (Wodemeyer & McLeay, 1981). Once a fish receives stress stimuli, its sensory neurons in the brain activate the hypothalamus to release different hormones and neurotransmitters. Releasing hormones (RHs) such as CRH and TRH are the most important. These RHs act on the pituitary to release different hormones such as ACTH and  $\alpha$ -MSH. ACTH further helps to release cortisol, an important hormone under stress. Cortisol is produced from an internal gland whereas catecholamines are produced in a chromaffin gland and interestingly both of them are found in the kidneys of fish (Milano et al., 1997). These hormones further alter the biochemistry, immunology, and physiology of fish under stress and induce the secondary responses (Weyts et al., 1999). These effects, in the long term, are reflected in fish performance as a reduction in growth, reproduction, susceptibility to infection, and ultimately mortality (Schreck et al., 2001).

### Acute stress and chronic stress

Stress responses in fish depend on the types of stressors, the duration of exposure, the rate of introduction to stressors, and the amount of the stress (Barandica & Tort, 2008; Wedemeyer, 1997). Stresses are of two types, acute and chronic, based on the duration of exposure time. Acute stress involves rapid exposure for a short duration of exposure time (hours). Chronic stress is due to constant or repetitive exposure to the stressor for long periods (Barandica & Tort, 2008).

Acute stress is mainly the "fight or flight" response and is initiated mostly in the primary response. Acute stress in Black Sea trout

(*Salmo trutta labrax*) due to thermal exposure may involve an alteration in blood glucose, cortisol, total protein, serum ion concentrations, and lysozyme activity (Dengiz Balta et al., 2017). Acute stress is sometimes helpful for an organism. However, chronic stress can be viewed as repetitive exposure to stressors and the central nervous system (CNS) does not get sufficient time to recover (Sapolsky, 1996). It generally causes secondary and even tertiary responses (health issues). Under any kind of chronic stress, the body changes to 'a new normal' state. Chronic stress impacts nearly all physiological processes, and experimental conditions have been devised to induce such stress, revealing varying durations in different fish species. For instance, it necessitated 15 days in zebrafish (Chakravarty et al., 2013) and Nile tilapia (Volpato & Barreto, 2001), 28 days in rainbow trout (Moltesen et al., 2016), and 8 days in zebrafish (Golla et al., 2020). Intriguingly, chronic stress elicits a more intricate set of responses compared to acute stress. While acute stress predominantly triggers primary and secondary responses, chronic stress encompasses all three types of stress responses. This complexity underscores the multifaceted nature of physiological adaptations in animals under prolonged stress conditions (McEwen & Gianaros, 2011).

## THERMAL STRESS IN FISH

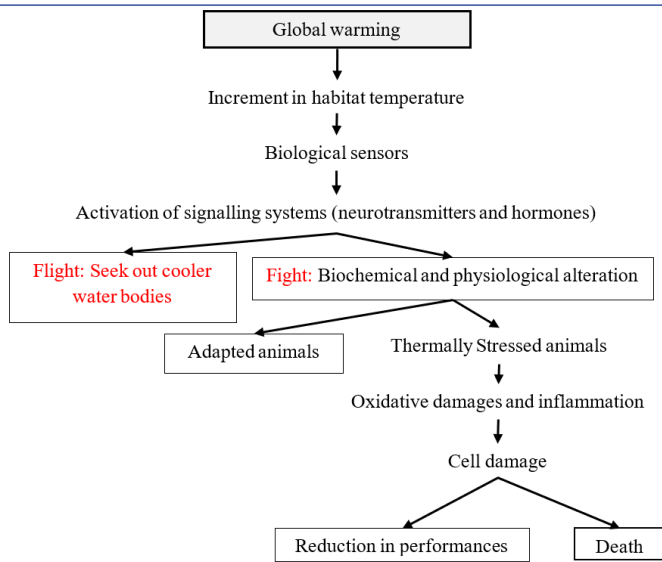
In the earlier section, it was discussed that fishes are temperature-sensitive animals, therefore, an increment in the habitat temperature beyond the thermal tolerance capacity causes fish to feel abiotic stress. Thermal tolerance is the range of temperatures encompassing minimum to maximum levels where fish can survive and perform all their physiological functions. The upper-temperature tolerance limit (UTTL) of fish is the highest temperature up to which fish can survive (Daniel et al., 2008, Roychowdhury et al., 2019). The UTTL of fish depends on geographical location (Sorte et al., 2011), previous thermal history (Beitinger et al., 2000), transgenerational acclimatization (Donelson et al., 2012), the type of feed consumed (Kumar et al., 2014), and the rate of temperature increments (Camilo & Maria, 2006). The most commonly employed tools for studying the UTTL in fish are the lethal temperature maximum (LT<sub>max</sub>) and critical temperature maximum (CT<sub>max</sub>) (Beitinger et al., 2000). Thermal plasticity in fish refers to the capacity of fish species to adjust their physiological and behavioral traits in response to temperature changes (Comte & Olden, 2017). Fish exhibit thermal plasticity through alterations in metabolism, enzyme activity, gill function remodeling, changes in spawning time, and behavioral adaptations (Angiulli et al., 2020; Das et al., 2012; Farrell, 2009; Roychowdhury et al., 2020b). Parameters like warming temperature (WT) and thermal safety margin (TSM) are crucial for studying thermal plasticity in ectothermic animals (Becker & Genoway, 1979; Madeira et al., 2007). In fish physiology, aerobic space refers to the volume of oxygen available for aerobic metabolism, crucial for energy production (Jobling, 1995). Factors influencing this space include dissolved oxygen levels, gill efficiency, and metabolic rate (Farrell, 2009). Elevated water temperature often results in decreased dissolved oxygen (DO), leading to hypoxic conditions. Understanding aerobic space helps assess fish adaptation to environmental conditions and stressors (Eliason et al., 2013). The Tem-

perature Coefficient (Q<sub>10</sub>) measures the temperature sensitivity of physiological or biochemical processes, indicating the rate of change with a 10-degree Celsius temperature increase. In the context of oxygen consumption in fish, the Q<sub>10</sub> value describes how oxygen consumption rates vary with temperature changes. Researchers use Q<sub>10</sub> values to understand thermal dependence in fish and other ectothermic organisms, providing insights into the temperature's influence on metabolic processes and aiding predictions of climate change impacts on fish physiology and ecology. Variations are observed among fish species based on their adaptations to specific environmental conditions (Claireaux & Lefrançois, 2007; Farrell, 2009; Pörtner & Farrell, 2008).

'Fight or flight' is the initial strategy for most organisms in a hostile environment. Fish try to move toward the more preferable environment but if they fail to do so, they will feel stress (Kovach et al., 2012). A warmer temperature is abiotic stress that causes different biotic stress in organisms (Nakano et al., 2014). However, data on the impacts of thermal stress on different biochemical pathways are limited in carp fish. Therefore, previous literature on thermal stresses on fish and other organisms needs to be reviewed to understand the thermal stress biology of an organism. Besides, this information can help to design proper methodology and selection of different biomolecules expected to be altered under thermal stress in fish. The process of adaptation and stress are difficult to distinguish at the initial stages as fish try to fight the stress by altering their biochemical pathways in higher temperatures. Patterns of the expression of different biomolecules are changed initially due to adaptation and later on due to stress (Bijlsma & Loeschcke, 2005). The consequence of an event depends on the extent of stress, the genetic makeup of the organisms, and previous history of exposure (Beitinger et al., 2000). A higher temperature is known to increase the kinetic properties of molecules causing a higher diffusion rate for micro-molecules (Bag et al., 2014) and denaturation of macromolecules (Wu, 1995). Maintenance of the native three-dimensional structure of a protein is very much essential for proper functioning, and interaction with other biomolecules involved in cellular response, and any randomness beyond certain limits may lead to cellular death (Nakamura & Lipton, 2009). Fish try to cope with the situation by changing gene expression patterns and are reflected in alteration in metabolites (biomolecules), cellular signaling systems (hormones and others), and enzyme activity (Lancaster et al., 2016). The stress is tolerable to a certain extent after the performance of the species drops (La & Cooke, 2011; Pörtner & Knust, 2007). Due to the cumulative impacts of the different effects of thermal stress, oxidative stress begins to occur and results in cellular death, organ failure and ultimately death of the organism (Figure 1).

## BIOCHEMICAL MECHANISM

Any kind of stressor increases the requirement of physiological energy that can be fulfilled by alteration of hormonal, enzymes and bimolecular responses. In general, glucose, triglycerides and protein act as energy molecules depending upon the nature and quantity of energy needed (Mergenthaler et al., 2013). Glucose serves as an immediate energy source, while triglycerides provide major energy, and protein provides energy during hun-



**Figure 1.** Conceptual representation of the consequences of thermal stress in fish.

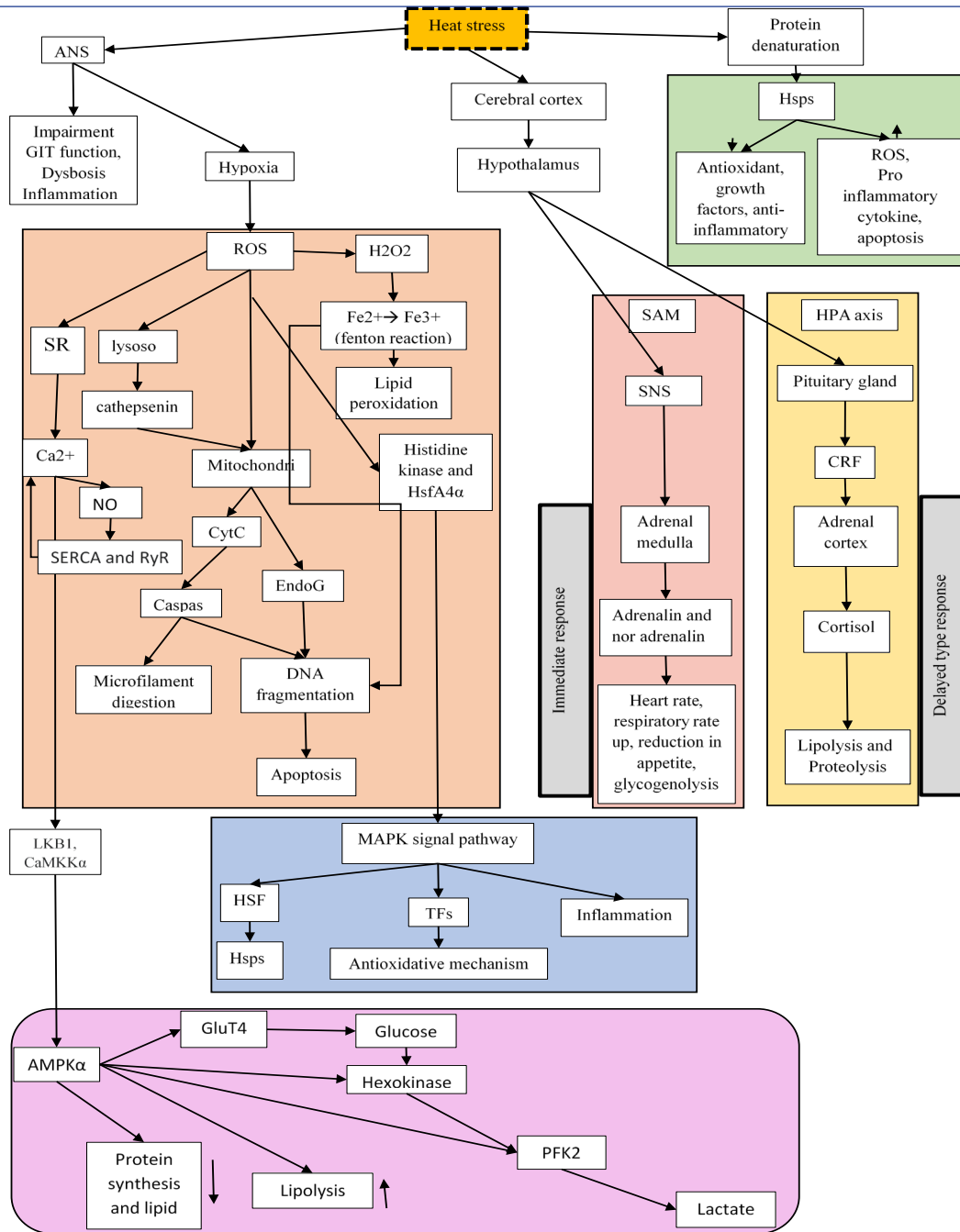
ger or in some physiological disorders and stress. In stressful situations, fishes try to increase blood glucose to provide more energy to vital organs including the brain by changing the metabolism of biomolecules under the control of hormones (Mergenthaler et al., 2013). The steroid hormone, cortisol alters the pattern of gene expression (transcription level) and increases the expression of the different enzymes required for the synthesis of new glucose molecules (gluconeogenesis) (Babitha & Peter, 2010; Vijayan et al., 1997) and breakdown of the stored glycogen (glycogenolysis) (Vijayan et al., 1993 and 1996) during stress to increase blood glucose concentration in serum. Cortisol converts the non-essential proteins of muscle to amino acids and transports them through the blood to the liver for gluconeogenesis (Vijayan et al., 1993; Vijayan & Moon, 1994; Freeman & Ilder, 1973). Cortisol is also documented to mobilize stored lipids in teleost species (Dave et al., 1979). Thyroid hormones, T3 and T4 are produced in the thyroid gland and normally maintain a positive nitrogen balance, but T3 inhibits protein synthesis in higher concentrations (Murray et al., 1996). Like cortisol, thyroid hormones are also known to act at the transcriptional level and modify its function or 'fine-tune' the actions of cortisol and adrenaline in a stressful situation (Peter, 2011). Epinephrine and norepinephrine, released from chromaffin cells, are recognized by their immediate elevation of plasma glucose levels (Arends et al., 1999; Ruane et al., 2001). Their roles encompass enhancing glucagon secretion, facilitating glycogen breakdown (glycogenolysis), initiating new glucose synthesis (gluconeogenesis), mobilizing fatty acids (beta oxidation), and concurrently suppressing insulin production, glycogen synthesis (glycogenesis), and glucose breakdown (glycolysis) (Nelson & Cox, 2001). Their primary targets are muscle, adipose tissue, and liver, and increase the supply of oxygen to tissue by increasing heart rate, blood pressure, and respiratory passage (Nelson & Cox, 2001). Cortisol plays a role mostly in chronic stress, while epinephrine and norepinephrine act as emergency hormones and are involved in immediate responses. Insulin and glucagon maintain glucose homeostasis in blood in

normal conditions but their direct involvement in heat stress is limited. Insulin increases the utilization of glucose by increasing glucose transportation in cells and increasing the rate of glycolysis in extrahepatic tissues and glycogenesis in hepatic tissue but glucagon plays the counter role of insulin by producing glucose through gluconeogenesis and glycogenolysis thus increasing blood glucose (Nelson & Cox, 2001).

Blood glucose is used to monitor general stress for different species. Energy-rich molecules like ATP, GTP, phosphocreatine, succinate, and ketone bodies are also known to play an important role during thermal stress and can be used as possible markers for thermal stress (Dijk et al., 1999). Metabolism of biomolecules is under hormonal control necessitating monitoring of the hormones cortisol, T3, T4, epinephrine, norepinephrine, insulin, and glucagon during stress.

Every enzyme has an optimum temperature and pH and thermal stress is known to change these parameters for cold-blooded fish. Enzymes involved in the metabolism of energy-rich biomolecules alter their activity by changing their concentration (expression) or affinity (modification) towards the substrate under a stressed condition. Enzymes catalyzing the irreversible steps of carbohydrate metabolism (hexokinase, phosphofructokinase1, pyruvate kinase, citrate synthase, glucose 6 phosphatase, fructose-1,6 bis-phosphatase, etc.), protein metabolism (glutamate-pyruvate transaminase and glutamate-oxaloacetate transaminase), lipid metabolism (lipase), and creatinine metabolism (creatinine kinase) are important from this perspective (Dhanasiri et al., 2013, Abbaraju & Rees, 2012; Ton et al., 2003).

Thermodynamics explains life as the maintenance of organized cellular structures through energy generated by oxidizing energy-rich nutrients by enzyme(s) that act at an optimum temperature under the control of hormones. Temperature changes directly affect these activities. Proteins are the mediators of diverse types of cellular functions (Alberts et al., 2002) including enzymatic action to scale formation, body growth to reproduction, and digestion to excretion. The function of a protein depends on its native structure that gets denatured due to the rise in temperature causing more vibration in molecules and related disturbance. Heat shock proteins (Hsps), which are highly conserved, are the molecular chaperones required for the proper folding of the protein and are also involved in protein transport to cellular compartments (Alberts et al., 2002; Shi & Thomas, 1992). At higher temperatures Hsps refold the denatured protein to its original native structure and the heat shock factor (Hsf) induces the expression of various Hsps in the process (Wu, 1995). There are various types of Hsps within the cell such as Hsp10, HspB group (Hsp27, hspB1, hspB6), HspA group (Hsp70, Hsp71, Hsp72, Hsp78), HspC group (Hsp90, hsp94), Hsp40, Hsp60, Hsp104, and Hsp110 (Antonova et al., 2007; Benjamin & McMillan, 1998; Li & Srivastava, 2004; McLemore et al., 2005; Salinthon et al., 2008; Schlesinger, 1990). Hsp30, Hsp27, and Hsp47 are identified in goldfish (Wang et al., 2007) while Hsp78 and Hsp100 are found in *Poeciliopsis lucida* (Norris et al., 1995). Warm acclimation protein (wap) is another candidate that plays an important role during heat stress (Kikuchi et al., 1997) (Figure 2).

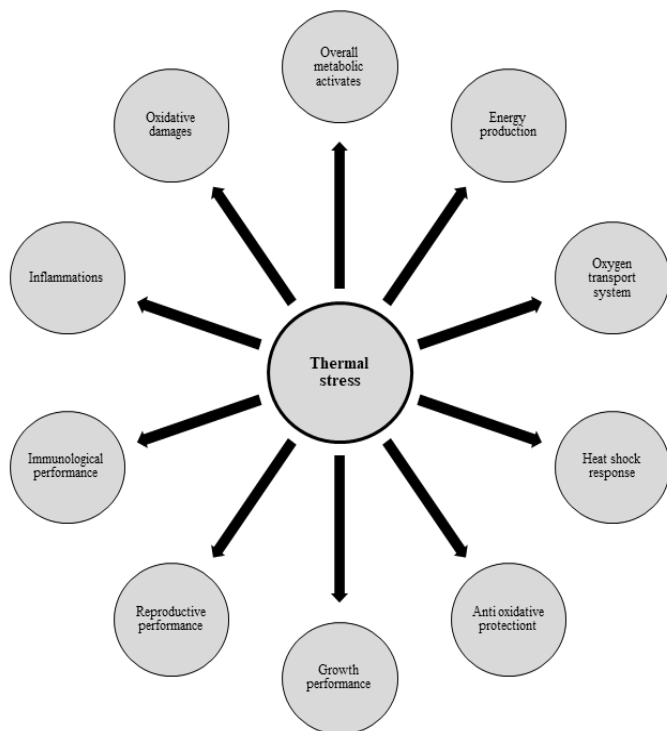


**Figure 2.** Impact of thermal stress at the molecular biology level (Antoun et al., 2017; Cui et al., 2016; Kourtis and Tavernarakis, 2011; Kültz, 2015; Xing et al., 2019).

Numerous experiments have been conducted to study the impacts of heat stress on fish and a few of them are cited here: rahu (Akhtar et al., 2013; Kumar et al., 2015; Mohapatra et al., 2014), common carp (Ouellet, et al., 2013), rainbow trout (Recsetar et al., 2012), blenny species (Camilo and Maria, 2006), salmon (Dengiz Balta et al., 2017; Nakano et al., 2014), *Channa punctatus* (Kaur et al., 2005), pacific sardine (Kaur et al., 2005), and *Danio dangila* and *Brachydanio rerio* (Majhi & Das, 2013). The selected temperatures for treatments were mostly sub-lethal with no fish death (Das et al., 2002; Das et al., 2005; Nakano et al., 2014).

These experiments were mainly focused on the recovery responses (Kumar et al., 2015), adaptation strategies (Das, 2002), gene expression pattern (Ouelle et al., 2013), oxidation-reduction state (Nakano et al., 2014), thermal tolerance, growth and oxygen consumption (Das et al., 2005), and search for bio-markers (Purohit et al., 2014). Different experimental conditions were used for warmer water exposure to induce heat stress in fish. The three main determinants to introduce thermal stress to fish are the amount of temperature, duration of exposure, and rates of temperature increment, and all of them varied in the experi-

ments (Akhtar et al., 2013; Das et al., 2005; Dengiz Balta et al., 2017; Kaur et al., 2005; Kumar et al., 2015; Majhi & Das, 2013; Mohapatra et al., 2014; Nakano et al., 2014; Recsetar et al., 2012). Fish may feel both acute stress and chronic stress based on events that will occur in future (IPCC, 2014). Different researchers have studied the impacts of both acute and chronic thermal stress among other animals including fish (Hernández-López et al., 2018) but data is very limited for IMC. Thermal stress is expected to alter the different physiological and biochemical processes of the body and that may be reflected in different pathways and performance of fish (Figure 3).



**Figure 3.** Abiotic thermal stress affects different physiological pathways (Aftabuddin et al., 2017; Aftabuddin and Roychowdhury, 2019).

## DISCUSSION

The review revealed that thermal stress has substantial effects on fish, leading to reduced growth, reproductive impairments, increased susceptibility to infections, and even mortality. These consequences can have profound ecological and economic implications, considering the vital role of fish in providing food, supporting economies, and maintaining ecosystem balance. The study highlights the distinction between acute and chronic stressors, with acute stress resulting from short-term rapid exposure and chronic stress arising from long-term repetitive exposure. Understanding this differentiation is crucial for developing effective strategies to mitigate the impacts of thermal stress on fish populations. The elevated water temperatures associated with global warming act as abiotic stressors, triggering various biotic stress re-

sponses in fish. It was observed that fish employ a range of mechanisms to cope with thermal stress, including alterations in gene expression patterns, metabolite profiles, cellular signaling pathways, and enzyme activity. These adaptive responses enable fish to maintain their physiological balance and attempt to counteract the detrimental effects of thermal stress. However, the cumulative impact of thermal stress can induce oxidative stress, leading to cellular death, organ failure, and ultimately mortality. This highlights the urgent need to address the challenges posed by rising temperatures and the associated thermal stress on fish populations. The study emphasizes the role of hormonal, enzymatic, and biomolecular responses in the fish's attempt to meet the increased energy demands caused by stressors. Hormones such as cortisol play a significant role in altering gene expression and stimulating glucose synthesis through gluconeogenesis. Other hormones, including thyroid hormones, epinephrine, norepinephrine, insulin, and glucagon, are also involved in the fish's response to thermal stress. Enzymes associated with metabolic pathways in fish have optimal temperature and pH ranges that can be altered by thermal stress. Maintaining the proper structure and functionality of proteins is crucial for cellular responses and overall fish health. Heat shock proteins and warm acclimation proteins act as protective mechanisms, helping to preserve protein integrity and mitigate the adverse effects of thermal stress.

The findings of this systematic review emphasize the importance of further research to enhance our understanding of the molecular mechanisms underlying these responses. Such knowledge can guide the development of targeted conservation and management strategies to safeguard fish populations in the face of a rapidly changing environment.

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**Author Contribution:** This review is part of the first author's Ph.D. thesis, and he conducted most of the work for manuscript preparation. The other two authors are the Ph.D. supervisors; they have provided scientific input and assisted in the preparation of the manuscript.

**Ethical Statement:** We certify that this is our original research work and it has neither been submitted or published elsewhere as a whole or in part. The authors are responsible for all the data and content in the Manuscript.

**Declaration of Generative Ai in Scientific Writing:** During the preparation of this work the author(s) used [https://chat.openai.com/] in order to improve English language such as checking grammar, spelling and for finding some references. After using this tool/service, the author(s) reviewed and edited the content as needed and take(s) full responsibility for the content of the publication.

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