

Responses of aquaculture fish to climate change-induced extreme temperatures: A review

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Abstract

Climate change-induced extreme temperature events are becoming more intense and frequent. For fish, temperature is the master abiotic factor that controls and limits fish development and physiology at all stages of aquaculture. Major physiological constraints at the individual level underpin changes in fish growth, hemato-physiology, metabolism, immune and molecular stress responses to extreme temperature events. Extreme temperature impacts on fish vary among and within the diverse species depending on stress magnitude and associated factors. This review synthesizes the impacts of climate change-induced extreme temperature events on neuroendocrine, oxidative, metabolic, osmotic, molecular, hemato-biochemical, and immune responses in fish related to aquaculture. Besides, overall aspects of extreme temperature impacts on fish growth and reproduction are also discussed. Possible mitigation measures to maintain the fish's physiological fitness during extreme temperature events are also addressed. However, studies on the interactive effects of extreme temperature events with other associated environmental stressors are needed across a broader range of species to gain a better understanding of fish response and aquaculture performance during extreme temperature events. Moreover, for fish, studies on alternative species, development of stress-

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tolerant strains, and the possibilities of nutritional mitigation measures as a potential option to combat extreme temperature stress are promising and should be pursued in future studies.

KEY WORDS

growth, metabolism, physiology, remediation, stress

1 | INTRODUCTION

As a result of climate change, global temperature patterns have changed markedly and are predicted to change and magnify more (Iona et al., 2018; Jeppesen et al., 2015; Mackenzie, Gislason, Möllmann, & Köster, 2007; Sarà et al., 2018). Temperature trend analyses indicate that the total global land surface area that experiences extreme cold (extreme winter stress) and extreme heatwaves (extreme warm stress) is increasing. In 2016, around the world, extreme cold and warm events were record-breaking, exceeding the previous record in 2010 (Jorgenson et al., 2019; Lazoglou, Anagnostopoulou, Tolika, & Kolyva-Machera, 2019; Lebel, Lebel, & Lebel, 2016; S. Xie, 2020). A vast range of fish species, environments, regions, and aquaculture systems are susceptible to climate change-induced extreme temperatures (heatwave and cold) events. Indeed, some of the concerned regions are the largest aquaculture producer nations, for example, China, Vietnam, Bangladesh, Egypt, and part of the Mediterranean (Spain, Italy, Turkey) are predicted to be highly vulnerable to extreme climatic events (G. Reid et al., 2019). For example, during mid-summer, southern Mediterranean water (e.g., shallow and semi-closed bays) temperatures sometimes exceed 32°C (Dülger et al., 2012). Whereas, in the northern part of the Mediterranean region, low winter temperatures with episodic frosts are now more frequent and sometimes winter temperatures plunge to <10°C from ~20°C (Aranda, Castro, Alía, Pardos, & Gil, 2005; Besson et al., 2016; Llorente & Luna, 2013). For Bangladesh, the frequency and intensity of the extreme heatwaves and cold events have increased significantly in recent decades because of climate change and global warming (Choi, Campbell, Aldridge, & Eltahir, 2021; Dastagir, 2015). Suggestions that linked aquaculture losses and extreme temperature events are now appearing in the reports for Vietnam (Thuy, Giang, Hoai, & Van Dan, 2017), Australia (Hobday et al., 2018), and Hawaii (McCoy et al., 2017). In Norway, the salmon aquaculture industry is facing more frequent extreme heatwave events than ever and enduring significant production loss (Calado, Mota, Madeira, & Leal, 2021). Moreover, some of the most prominent marine heatwaves happened in aquaculture and salmon farming areas of Tasmania, the Gulf of Maine (USA), Newfoundland (Canada), Iceland and Norway have been facing 3–8 days of extreme heatwaves with 4–12°C higher temperature than during normal summer (Calado et al., 2021; Rosa, Marques, & Nunes, 2012, 2014).

Further increases in extreme temperature events will amplify water quality fluctuation and hydrological stress (Albouy, Guilhaumon, Araújo, Mouillot, & Leprieur, 2012; Kharin, Zwiers, Zhang, & Wehner, 2013; Nowicki et al., 2019) to resident organisms. Shifts in ambient temperatures alter the overall fitness and performance of ectothermic fish with stark implications for global aquaculture (D'Abromo & Slater, 2019; Gaylord, MacKenzie, & Gatlin, 2001; Small & Peterson, 2005; Small, Soares, Woods, & Dahl, 2002). Fluctuations in temperature affect many aspects of physiology in fish, including feed intake, survival, growth, reproduction, behavior, distribution, energy acquisition, and physical properties of biomolecules (Chang et al., 2018; Islam, Kunzmann, Henjes, & Slater, 2021; Makrinos & Bowden, 2016; Maulvault et al., 2017; Wong, Walsh, & Morris, 2018). Studies have reported mass mortality of fish during winter and summer extremes by modifying the energetic cost for physiological homeostasis, osmotic, and ionic regulation (Madeira, Vinagre, & Diniz, 2016; Pörtner & Peck, 2010; Shen et al., 2018; Shrivastava, Sinha, Cannaeerts, Blust, & De Boeck, 2017). During summer heatwave and winter cold extremes, massive fish mortalities in aquaculture facilities and the wild have been reported for Asia (Roychowdhury, Aftabuddin, & Pati, 2020), the

Mediterranean region (Rosa et al., 2012, 2014), and Australia (Clarke et al., 2013; Roberts, Van Ruth, Wilkinson, Bastianello, & Bansemer, 2019; Rountrey, Coulson, Meeuwig, & Meekan, 2014). As a master abiotic factor, temperature controls and limits all physiological mechanisms in fish (Figure 1). Thermal tolerance of fish depends on species, genetics, age, developmental stages, physiological fitness, and prior thermal exposure histories (Chadwick & McCormick, 2017; Sunday, Bates, & Dulvy, 2012; Weinstein & Somero, 1998). Stress response magnitude also depends on the temperature progression rate towards the upper and lower limits and exposure duration (Crawshaw, 1977; Li, Leung, Bao, Lui, & Leung, 2015; van den Burg et al., 2005). In recent decades, climate change-induced temperature impacts on fish in the wild and aquaculture systems have been spotlighted. The general principles of fish thermal physiology and stress responses have been thoroughly reviewed (Alfonso, Gesto, & Sadoul, 2021; Faught, Hernandez-Perez, Wilson, & Vijayan, 2020; Feidantsis et al., 2021; Little, Loughland, & Seebacher, 2020; Schreck & Tort, 2016), thus they are not revisited here. Instead, this review is intended to summarize the research on climate change-induced extreme temperature impacts on aquaculture fish and offer possible mitigation measures. Emphasis is placed on neuroendocrine, antioxidants, metabolic, molecular, hemato-biochemical, immunity, growth, and reproductive performance of commercial aquaculture species while exposed to extreme temperature events.

2 | RESPONSES OF AQUACULTURE FISH TO EXTREME TEMPERATURE EVENTS

Initially, as a primary response to both acute and chronic thermal stress, fish activate brain centers and release a massive amount of catecholamines and corticosteroids. Secondary stress responses are the release of hormones in blood and tissues, metabolic impairment, energy mobilization, and hydromineral balance. Tertiary responses extend to organism and population levels, such as growth inhibition and reduction of reproductive and immune performance (Barton, 2002; Donaldson, Cooke, Patterson, & Macdonald, 2008; Tort, 2011; Yada & Tort, 2016). Acute temperature changes also result in sublethal physiological responses and mortality (Fan et al., 2019; Mateus et al., 2017; Niu,

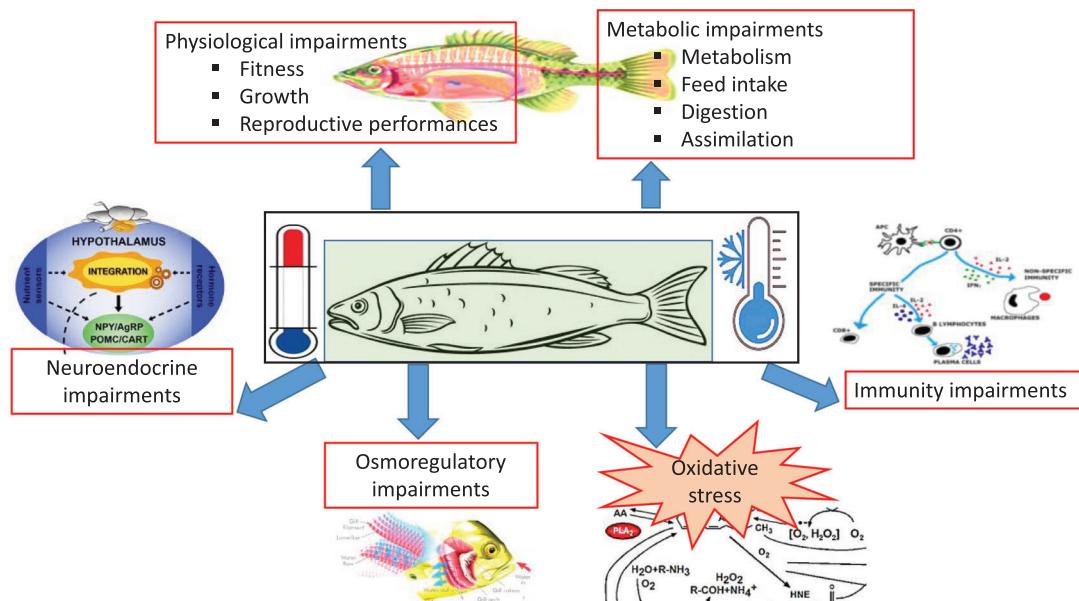


FIGURE 1 Temperature stress impacts in fish

Rummer, Brauner, & Schulte, 2008; Vargas-Chacoff, Regish, Weinstock, & McCormick, 2018). Chronic exposure beyond the optimal thermal window also impairs physiological fitness and can result in mortality. Cortisol responses during and after a sudden temperature increase have been described for several fish species. As secondary stress responses increased cardiac activity, glucose, and lactate are generally observed in response to acute temperature increases, as do changes in blood osmolality and other hematological variables (Donaldson et al., 2008; Schreck & Tort, 2016). Furthermore, inhibiting effects on the fish immune system may be observed (Tort, 2011; Urbinati, Zanuzzo, & Biller, 2020). Heat shock proteins (HSPs) release is also influenced by endocrine stress systems at the cellular level (Sopinka, Donaldson, O'Connor, Suski, & Cooke, 2016; Yamashita, Yabu, & Ojima, 2010). When stress becomes chronic or recurring, the reallocation of energy substrates may be detrimental to the fish's normal function. Long-term tertiary effects, such as impaired immune function, growth, or reproductive success (Eissa & Wang, 2016; Feidantsis et al., 2021; Schreck & Tort, 2016) can affect fish aquaculture performance (Figure 2).

2.1 | Neuroendocrine responses

Temperature affects many aspects of the nervous system, from brain organization to neurogenesis and functioning (Amiel, Bao, & Shine, 2017; O'Donnell, 2018; Pallotta et al., 2017). Species-specific variation in thermal plasticity may undermine fish's ability to cope with predicted global warming. The changes in neural systems are likely to be detrimentally compounding by other factors and affect fish feeding, immunity, behavior, and reproduction, which are of great concern for aquaculture production (Table 1). The catecholamine releases trigger systems that result in elevated oxygen transport, enhanced respiration, energy mobilization, and cardiac activity (Barton, 2002; Bonga & Sjoerd, 1997; S. G. Reid, Bernier, & Perry, 1998; Weyts, Cohen, Flik, & Verburg-van Kemenade, 1999). Acute exposure to higher temperature causes increased cortisol in Atlantic cod, *Gadus morhua* (Pérez-Casanova, Afonso, et al., 2008), European seabass, *Dicentrarchus labrax* (Goikoetxea et al., 2021), Nile tilapia, *Oreochromis niloticus*

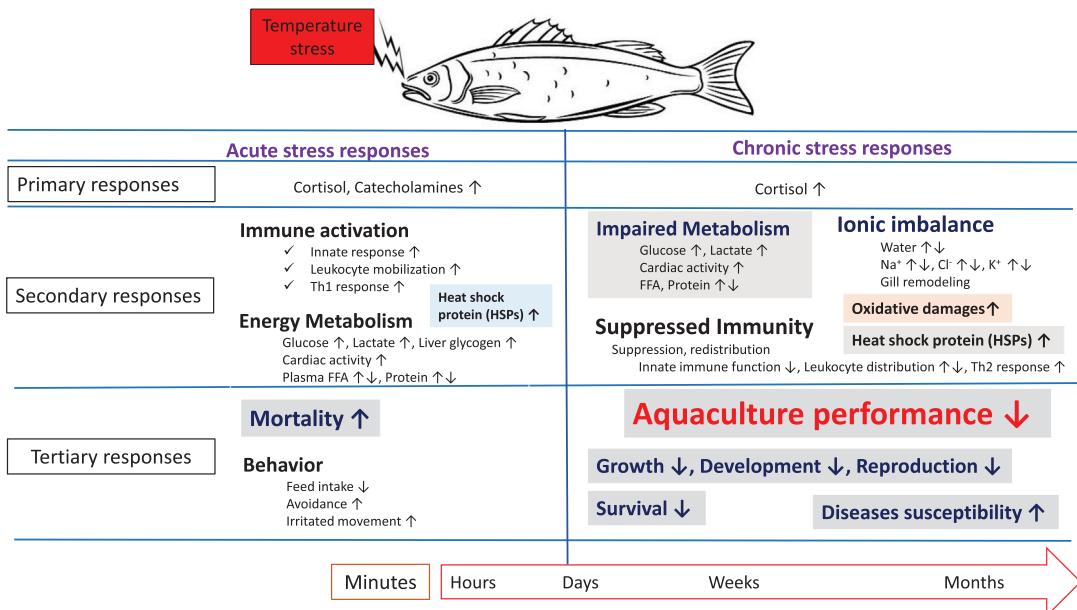


FIGURE 2 The primary, secondary, and tertiary responses of fish during temperatures stress. CRH, corticotrophin releasing hormone; FFA, free fatty acids; free fatty acids; Th1, Type-1 T-helper; Th2, Type-2 T-helper; ↑, stimulatory; ↓, inhibitory; ↓, activation

TABLE 1 Research on neuroendocrine stress responses of aquaculture fish during temperature stress^a

Species	Stress intensity	Stress duration	Stress type	Fish size/ fish age	Effects	Impacts on aquaculture	References
Atlantic cod, <i>Gadus morhua</i>	10–22°C	2 hr	Acute	~40 g	Cortisol [22°C] ↑	–	Pérez-Casanova, Afonso, Johnson, Currie, and Gamperl (2008)
Atlantic cod, <i>G. morhua</i>	10 (control), 16, and 19°C	45 days	Chronic	~40 g	Cortisol [P] (16°C, 19°C) ↑	↓ Growth performance at 16 and 19°C	Pérez-Casanova et al. (2008)
Atlantic salmon, <i>Salmo salar</i>	12 and 20°C	3 weeks	Chronic	140.3 ± 2.3 g	Heart rate (20°C) ↑, stroke volume (20°C) ↓	↓ Growth performance at 20°C	Gamperl et al. (2020)
Atlantic salmon, <i>S. salar</i>	12 (control), 16, and 20°C	99 days	Chronic	~70 g	Cortisol [P] (16°C, 20°C) ↑	–	Tramp et al. (2018)
Atlantic salmon, <i>Salmo salar</i>	12, 21, 22, 23, and 27.5°C	48 hr	Acute	–	Cardiac collapse starts at 21°C, heart rate (21–27.5°C) ↑	↑ Impaired movement at 23 and 27.5°C	Anttila et al. (2014)
Black porgy, <i>Acanthopagrus schlegeli</i>	20 and 30	2 weeks	Chronic	51.07 ± 6.0 g	Cortisol [P] (30°C) ↑, Wap65 [B, L, G, K, I] (30°C) ↑	↓ Metabolic performance at 30°C	Cheol, Kwang, Yong, Pi, and Byung (2008)
Black porgy, <i>Acanthopagrus schlegeli</i>	20 and 30°C	2 weeks	Chronic	51.07 ± 6.0 g	Cortisol (30°C) ↑	↓ Metabolic performance	Cheol et al. (2008)
Black Sea trout, <i>Salmo trutta labrax</i>	25 and 30°C	30 min	Acute	184.22 g	Cortisol (30°C) ↑	–	Dengiz Baltà, Akhan, and Baltà (2017)
Calfish, <i>Pangasianodon hypophthalmus</i>	25, 30, and 35°C	56 days	Chronic	10–20 g	Cortisol (35°C) ↑	↓ Growth performance at 25°C	Phuc, Mather, and Hurwood (2017)
Chinook salmon, <i>Oncorhynchus tshawytscha</i>	11, 16, 14, and 19°C	2 weeks	Chronic	0.887 ± 0.184 g	Brain Estradiol-17β, cortisol, triiodothyronine, and thyroxine (16.4°C, 19°C) ↑; brain dopamine, GnRH2, dopamine receptor 2A, growth hormone 1 (16.4°C, 19°C) ↓	↓ Reproductive performance at 19°C	Giroux, Gan, and Schlenk (2019)

(Continues)

TABLE 1 (Continued)

Species	Stress intensity	Stress duration	Stress type	Fish size/ fish age	Effects	Impacts on aquaculture	References
European seabass, <i>Dicentrarchus labrax</i>	16–21°C	4 days	Acute	17 days post-larvae	Cortisol [21°C] ↑	↑ Mortality at 21°C	Giroux, Gan, and Schlenk (2019)
European seabass, <i>D. labrax</i>	8, 16, 24 (control), and 32°C	30 days	Chronic	5.29 ± 0.30 g	Cortisol [P] (8°C;32°C) ↑	↓ Growth, immunity at 8 and 32°C	Islam et al. (2020)
European seabass, <i>D. labrax</i>	8 and 22°C	20 days	Chronic	24.5 ± 1.48 g	Cortisol [P] (8°C) ↑	↓ Growth, immunity at 8°C	Islam, Kunzmann, and Slater (2021)
European seabass, <i>D. labrax</i>	8 and 22°C	20 days	Chronic	24.8 ± 1.69 g	Cortisol [Mu] (8°C) ↑	↓ Growth, immunity at 8°C	Islam, Slater, Thiele, and Kunzmann (2021)
European seabass, <i>D. labrax</i>	24 and 33°C	10 days	Acute and chronic	12.28 ± 0.39 g	Cortisol [P] (33°C) ↓	↓ Growth, immunity at 33°C	Islam, Slater, and Kunzmann (2020)
Goby, <i>Gillichthys mirabilis</i>	9, 13, 19 (control), and 26°C	4 weeks	Chronic	27.31 ± 8.1 g	Creatine kinase, hexosaminidase (9°C;26°C) ↓	↓ Metabolism, cellular function at 9 and 26°C	Jayasundara, Tomanek, Dowd, and Somero (2015)
Hybrid tilapia, <i>Oreochromis</i> sp.	28 (control) and 31°C	28 days	Chronic	400–600 g	Cortisol (31°C) ↑; 11β-hydroxylase[P] (31°C) ↓	↓ Osmotic balance at 31°C	Musa, Ramly, Abdul Manaf, Razzak, and Musa (2017)
Largemouth bass, <i>Micropterus salmoides</i>	3 and 6°C	6 hr	Acute	333 ± 4 g	Heart rate (3°C) ↑, stroke volume (3°C) ↓	–	Cooke, Grant, Schreer, Philipp, and Devries (2003)
Mahi-mahi, <i>Coryphaena hippurus</i>	25, 27, and 30°C	6 hr	Acute	Post-hatch larvae (144 hr)	Heart rates, stroke volume (30°C) ↑	–	Perrichon et al. (2017)
Milkfish, <i>Chanos chanos</i>	18 and 28°C (control)	3 weeks	Chronic	13.7 ± 1.3 g	Cortisol (sw at 18°C) ↑	↓ Growth, immunity at 18°C	Hu, Chu, Hwang, and Lee (2019)
Mottled mojarra, <i>Eucinostomus leftroyi</i>	16, 18, 20, and 24°C (control)	6 hr	Acute	89 ± 7 mm	Ventilation rates, reflex impairments (16°C;18°C) ↑	–	Samson, Brownscombe, and Cooke (2014)

TABLE 1 (Continued)

Species	Stress intensity	Stress duration	Stress type	Fish size/ fish age	Effects	Impacts on aquaculture	References
Mozambique tilapia, <i>Oreochromis niloticus</i>	22–34°C	2 hr	Acute	14.7 ± 0.7 g	Cortisol (34°C) ↑	–	Basu, Nakano, Grau, and Iwama (2001)
Nile tilapia, <i>O. niloticus</i>	25, 23, 21, 1, and 13°C	3 days	Acute	120 ± 10.3 g	Cortisol (13°C) ↑	↓ Immunity at 13°C	Panase, Saemphet, and Saemphet (2018)
Nile tilapia, <i>O. niloticus</i>	25, 23, 21, 17, and 13°C	3 days	Acute	120 ± 10.3 g	Cortisol (13°C, 17°C) ↑	↓ Immune responses at 13 and 17°C	Panase et al. (2018)
Olive flounder, <i>Paralichthys olivaceus</i>	20, 22, 24, 26, 28, and 30°C	2 weeks	Chronic	27.96 ± 3.07 g	Cortisol [P], AChE [L, G] (28°C, 30°C) ↑	↓ Immunity at 28 and 30°C	J. H. Kim, Kim, and Hur (2019)
Olive flounder, <i>P. olivaceus</i>	20 (control), 26, 29, and 32°C	3 days	Acute	7.76 ± 1.82 cm	HSP70 [G] (26°C, 29°C, 32°C) ↑	↓ Survival at 29 and 32°C	Yifan Liu et al. (2017)
Rainbow trout, <i>Oncorhynchus mykiss</i>	13 and 25°C	1 hr	Acute		Cortisol (25°C) ↑	–	LeBlanc, Middleton, Gilmour, and Currie (2011)
Rainbow trout, <i>O. mykiss</i>	13–25°C	48 hr	Acute	295 ± 8 g	Plasma catecholamine, arterial CO ₂ tension (25°C); arterial O ₂ tension, arterial pH (25°C) ↓	↑ Impaired movement at 25°C	Currie, Ahmady, Watters, Perry, and Gilmour (2013)
Rainbow trout, <i>O. mykiss</i>	11 and 19°C	2 weeks	Chronic	8.5 ± 3.2 g	Cortisol (19°C) ↑; boldness (19°C) ↓; shyness (19°C) ↑	↑ Susceptible to predation at 19°C	Frost et al. (2013)
Rainbow trout, <i>O. mykiss</i>	12 and 25.3°C	3 weeks	Chronic	560 ± 1.78 g	Atrial and ventricular beating rate (25.3°C) ↑	–	Haverinen and Vornanen (2020)
Rainbow trout, <i>O. mykiss</i>	7, 9, 11, and 25°C	7 days	Acute/ chronic	7.8–13 g	Plasma cortisol (7°C > 11°C) ↑	–	Barton and Peter (1982)
Rainbow trout, <i>Salmo gairdneri</i>	6, 12, and 18°C	4 weeks	Chronic	150–450 g	Cardiac rate (18°C) ↑; blood flow distribution (18°C) ↓	–	Barron, Tarr, and Hayton (1987)
Ray finned fish, <i>Schizothorax prenanti</i>	11, 16, 21 (control), 26, and 31°C	24 hr	Acute	110 ± 10 g	AChE, cortisol (11°C, > 31°C) ↑	–	Yang et al. (2018)

(Continues)

TABLE 1 (Continued)

Species	Stress intensity	Stress duration	Stress type	Fish size/ fish age	Effects	Impacts on aquaculture	References
Senegalese sole, <i>Solea senegalensis</i>	20 and 25°C	10 min	Acute	13.3 ± 0.9 g	Cortisol (25°C) ↑	–	Conde-Sieira et al. (2018)
Steelhead trout, O. <i>mykiss</i>	11 (control), 16.4, and 19°C	2 weeks	Chronic	0.288 ± 0.037 g	Brain Estradiol-17β, cortisol, triiodothyronine, and thyroxine (16.4;19°C) ↑, brain gonadotropin (16.4°C;19°C) ↓	↓ Growth, reproductive performance at 19°C	Giroux, Vliet, Volz, Gan, and Schlenk (2019)
Sturgeon, <i>Acipenser fulvescens</i>	10 and 18°C	6 weeks	Chronic	11.54 ± 0.07 mm	Cortisol (18°C) ↓; predation (18°C) ↓	↓ Feed intake at 18°C	Wassink, Bussy, Li, and Scribner (2019)
Sturgeon, <i>A. fulvescens</i>	10 and 18°C	6 weeks	Chronic	11.54 ± 0.07 mm	Cortisol (18°C) ↑	↓ Immunity, survival at 18°C	Wassink et al. (2019)
Turbot, <i>Scophthalmus maximus</i>	18, 11, 4, and 0°C	3 weeks	Chronic	250–300 g	Cortisol [B] (0°C;4°C;12°C;18°C) →	↓ Osmotic balance at 0°C	Foss et al. (2019)

Abbreviations: 5-HIAA, 5-hydroxyindole-3-acetic acid; 5-HT, 5-hydroxytryptamine; AChE, acetylcholinesterase; B, blood; Br, brain; CTmax, critical thermal maximum; DA, dopamine; E, erythrocytes; G, gill; H, heart; I, intestine; L, liver; Ltmax, lethal thermal maximum; M, muscle; Mu, mucus; P, plasma; S, serum.

aSymbols represent an increase (↑) in the specified response; no change (↔); decrease (↓), increased trend (↗), decreased trend (↘).

(Panase et al., 2018), and Olive flounder, *Paralichthys olivaceus* (Yifan Liu et al., 2017). Both acute and chronic thermal changes disrupt cardiac rhythm because of alteration in ionic balance (Vornanen, 2016). For example, higher temperature stress limits reduce cardiac function in Atlantic salmon, *Salmo salar* (Anttila et al., 2014; Gamperl et al., 2020), sparid, *Chrysoblephus laticeps* (Skeelees et al., 2020), rainbow trout, *Oncorhynchus mykiss* (Haverinen & Vornanen, 2020), and decrease blood flow to brain, liver, kidney, and intestine in rainbow trout, *O. mykiss* (Barron et al., 1987). Low thermal stress also reduces the cardiac performance in largemouth bass, *Micropterus salmoides* (Cooke et al., 2003), and sculpin, *Myoxocephalus scorpius* (Filatova, Abramochkin, & Shiels, 2019). Mottled mojarra, *Eucinostomus lefroyi* showed significant increases in ventilation rate and reflex impairment at 18 and 20°C compared to 24°C (Samson et al., 2014). Proteomic analysis showed that cardiac proteins increased significantly in eurythermal goby, *Gillichthys mirabilis* when exposed to 9 and 26°C from 19°C during a 28-day thermal exposure (Jayasundara et al., 2015). The collapse of cardiac function may underlie both acute and longer-term thermal limits (Somero, 2010). Studies on proteomic responses in cardiac muscle to climate change-induced temperature may provide important insights into mechanisms supporting cardiac function's thermal plasticity.

Chronic temperature stress initiates neuroendocrine responses in the central nervous system and triggers releasing corticosteroids and catecholamine that can extend to secondary stress responses (Figure 2). Olive flounder, *P. olivaceus* exposed to 28 and 30°C for 2 weeks, resulted in a significantly higher amount of plasma cortisol and catecholamine derivatives [acetylcholinesterase (AChE)] release compared to fish at 20°C, indicating stressful conditions (J. H. Kim et al., 2019). Rainbow trout, *O. mykiss*, exhibit significant catecholamine release, a decrease in arterial O₂, and an increase in CO₂ when subjected to an acute heat shock (from 13 to 25°C for 4 hr) (Currie et al., 2013). Blood cortisol level was also increased in Nile tilapia, *O. niloticus* when exposed to 13°C from 25°C for 3 days (Panase et al., 2018). High-temperature (18°C) stress in sturgeon, *Acipenser fulvescens* resulted in whole-body cortisol content increase compared to fish at 10°C (J. H. Kim, Costa, Esteve-Codina, & Velando, 2017). The activity of monoaminergic neurotransmitters like dopamine (DA), noradrenaline (NE), and, especially, serotonin (5-HT) is likely involved in the organization and control of the stress state (Bonga & Sjoerd, 1997; Verburg-van Kemenade, Cohen, & Chadzinska, 2017). Juvenile chinook salmon, *Oncorhynchus tshawytscha* exposed at 16.4 and 19°C from 11°C for 14 days showed increased whole-body estradiol-17β (E2), testosterone, triiodothyronine, and thyroxine content in fish exposed to 16.4 and 19°C compared to 11°C. While brain dopamine, gonadotropin-releasing hormone receptor (GnRH2), dopamine receptor 2A, growth hormone 1, dopamine receptor 2A, and growth hormone 1 (GH1) decreased significantly in fish acclimatized at 16.4 and 19°C (Giroux, Gan, & Schlenk, 2019). Rainbow trout, *O. mykiss* exhibited increased brain Estradiol-17β, cortisol, triiodothyronine, and thyroxine in fish acclimatized at 16 and 19°C during an 11 day study period (Giroux, Vliet, et al., 2019).

Drawing a concise conclusion on the neuroendocrine responses of fish to temperature stress is not always possible. Only a small number of aquaculture species have been studied to understand fish neuroendocrine responses to climate change-induced extreme thermal events. Neuroendocrine responses varied to the ranges of stressors, species types (Alfonso et al., 2021; McKenzie et al., 2020), the experimental design followed, and parameters investigated. However, we found some common neuroendocrine stress reactions that impair growth, reproductive function and immune responses. Thus, in the future extreme temperature events scenario, fish growth and reproductive hormonal balance may be disrupted, which could hinder growth and reproduction. Still, there is a large gap in the full understanding of fish neuroendocrine responses along with growth and physiological performance at climate change-induced extreme thermal events. Studies with the vast number of species, multiple parameters, and environmentally realistic extreme thermal events are essential to evaluate the fish's neuro-physiological fitness at the population and individual level.

2.2 | Antioxidant responses

Although oxygen is required for metabolic activities, an excess amount can cause unwanted damage to cellular homeostasis and even cell death through the formation of reactive oxygen species (ROS) (Birnie-Gauvin, Costantini,

Cooke, & Willmore, 2017; Clotfelter, Lapidus, & Brown, 2013; Klein et al., 2017; Martínez-Álvarez, Morales, & Sanz, 2005). Animals, including fish, produce both enzymatic and non-enzymatic antioxidants to cope with ROS-generated stress (S. Chowdhury & Saikia, 2020; Islam, Kunzmann, Bögner, et al., 2020; Schreck & Tort, 2016). However, when these antioxidant defenses are insufficient to combat ROS, fish suffer from oxidative damage such as protein carbonylation and oxidation, DNA damage, lipid oxidation and peroxidation (Almroth et al., 2015; Madeira et al., 2016; Maulvault et al., 2017). Localization and actions of the enzymatic and non-enzymatic antioxidants system in fish during thermal stress exposure is a new contribution in this review (Table 2). In this section, this review discusses and summarizes the temperature events on the antioxidant response of fish and their impacts on aquaculture production (Table 3).

Acute thermal stress provokes an enormous antioxidant response in fish. A study by Madeira et al. (2016) reported increased superoxide dismutase (SOD), glutathione-S-transferase (GST), catalase (CAT), lipid peroxidation (LPO), and cytochrome (CYP1A) activities in gilthead seabream, *Sparus aurata* exposed to temperatures above 24°C for 48 hr. The same fish exposed to below 14°C for 10 days showed higher antioxidant enzymatic activities indicating a stressful situation (Kyprianou et al., 2010). Snakehead, *Channa punctata* stressed at 32°C for 3 hr showed a significant increase of glutathione (GSH), glutathione reductase (GR), CAT and GST (Clotfelter et al., 2013). Chronic exposure to temperature stress exposure also activates the antioxidant response. European seabass, *D. labrax*, and white seabream, *Diplodus sargus* exposed to both low (12–18°C) and high temperatures (28, 32, and 33.3°C) for 14 days showed higher GST, CAT, LPO and malondialdehyde (MDA) activities compared to fish at 24°C (Madeira et al., 2013; Vinagre et al., 2012). For the same species, significantly increased antioxidants responses were observed at 8 and >32°C compared to 16°C (Islam et al., 2021, 2021b; Islam, Kunzmann, Bögner, et al., 2020). Medaka, *Oryzias melastigma* showed higher glutathione peroxidase (GPx), CAT, SOD, GR, and LPO activities in fish exposed at 25°C for 3 weeks compared to fish at 18°C (Almeida et al., 2015). Carney Almroth et al. (2019) reported increased antioxidants activities and protein carbonyl (PC) activities in Atlantic halibut, *Hippoglossus hippoglossus* at 5°C compared to fish at 18°C during 96 days of thermal exposure study.

There is considerable variability in antioxidant response in fish to thermal stress. A deviation from normal antioxidants response to thermal stress can be expected to cause cellular and protein damages, which will, directly and indirectly, affect aquaculture production performance. More research is needed to determine antioxidant thresholds for both cultured and wild fish in order to determine the point at which performance and fitness are compromised during climate change-induced thermal changes.

2.3 | Metabolic and molecular stress responses

In ectotherms, metabolic rate increases two- to threefold with a 10°C increase in water temperature. However, the magnitude of these changes is not constant with every 10°C change, as usually there is a decrease at higher temperatures. Consequently, enzymatic reactions, cellular respiration, and metabolic rates vary with temperature (Kamunde, Sappal, & Melegy, 2019; Yang Liu et al., 2019; Volkoff & Rønnestad, 2020). Several studies have examined the effects of extreme ambient temperatures on the metabolic and molecular stress responses in fish. The present review summarizes extreme ambient temperature effects on metabolic and molecular stress responses; their impact on growth performance and disease resistance capacity in aquaculture fish (Table 4).

Temperature stress induces reallocation of metabolic energy required for growth and reproduction, massively impacting aquaculture aims. The relocated energy is used to restore physiological homeostasis (Barton, Schreck, Ewing, Hemmingsen, & Patiño, 1985; Heath, Iwama, Pickering, Sumpter, & Schreck, 1998; Schreck & Tort, 2016). Fish respond to thermal stress at the cellular, subcellular, and organ levels (Figure 3). These responses to thermal stress are through de novo synthesis of proteins and phospholipids, which activates nuclear and mitochondrial transcription (Guderley & St-Pierre, 2002; Lucassen, 2006; O'Brien, 2011). Both acute and chronic higher thermal stress is associated with changes in metabolic rate (Almroth et al., 2015; Benítez-Dorta et al., 2017; Tort, 2011). These

TABLE 2 Localization and actions of the enzymatic and non-enzymatic oxidative systems and their applications in fish

Antioxidants	Pathway location	Actions	Targets	Applications	References
Enzymatic					
Superoxide dismutase (SOD)	Mitochondria, cytosol	Lipid oxidation and peroxidation, protein oxidation DNA damage	Anion superoxide peroxynitrite	Insight into antioxidant defenses; higher activities may be associated with higher levels of O_2^-	Birnie-Gauvin et al. (2017); Ken, Lin, Shaw, and Wu (2003); Sevcikova, Modra, Slaninova, and Svobodova (2011)
Catalase (CAT)	Peroxisome, mitochondria, and cytosol	Membrane stabilization, ROS production	Hydrogen peroxide	Insight into antioxidant defenses; higher activities may be associated with higher levels of H_2O_2	Birnie-Gauvin et al. (2017); Slaninova, Smutna, Modra, and Svobodova (2009)
Glutathione peroxidase (GPx)	Cytosol and mitochondria	Lipid oxidation and peroxidation, protein oxidation DNA damage	Hydrogen peroxide, peroxynitrite	Insight into antioxidant defenses; higher activities may be associated with higher levels of ROS	Birnie-Gauvin et al. (2017); Sevcikova et al. (2011); Toppo, Vanin, Bosello, and Tosatto (2008)
Glutathione reductase (GR)	Cytosol and mitochondria	Lipid oxidation and peroxidation, protein oxidation DNA damage	Anion superoxide peroxynitrite, hydrogen peroxide. GR reduces GSSG and back to GSH	Insight into antioxidant defenses; GR reduces GSSG back to GSH; higher activities of GR may be associated with higher levels of GSSG	Birnie-Gauvin et al. (2017); Martinez-Alvarez et al. (2005)
Non-enzymatic					
Glutathione (GSH)	Mitochondria, cytosol	Lipid oxidation and peroxidation, DNA damage	Hydrogen peroxide, peroxynitrite	Provides insight into oxidative damage (GSH to GSSG ratio or vice versa) and antioxidant defenses (GSH)	Birnie-Gauvin et al. (2017); Guderley (2004)
Reduced glutathione (GSSH)	Mitochondria, cytosol	Lipid oxidation and peroxidation, DNA damage, protein oxidation	Anion superoxide peroxynitrite, hydrogen peroxide	Provides insight into oxidative damage (GSH to GSSG ratio or vice versa) and antioxidant defenses (GSH)	Birnie-Gauvin et al. (2017)
Glutathione alpha S-transferase (GST)	Mitochondria, cytosol	Lipid oxidation and peroxidation, DNA damage, protein oxidation	Hydrogen peroxide, peroxynitrite	Provides insight into oxidative damage	Lackner (1998)

(Continues)

TABLE 2 (Continued)

Antioxidants	Pathway location	Actions	Targets	Applications	References
Vitamin E (tocopherol)	Lipids/lipid peroxidation inhibition ROOH- $\cdot\text{O}_2$ cell/mitochondria membranes	Lipid peroxidation inhibition, membrane stabilization	$\text{ROOH}-\cdot\text{O}_2$	Insight into antioxidant defenses (peroxyl radical scavenger)	Bainy, Saito, Carvalho, and Junqueira (1996); Birnie-Gauvin et al. (2017); Puerto, Pichardo, Jos, and Cameán (2009)
Vitamin A (retinol)	Lipid cell membrane	Lipid peroxidation and reduction	$\cdot\text{O}_2-\text{ROOH}$	Insight into antioxidant defenses (peroxyl radical scavenger)	Bler, 2014; Sevcikova et al. (2011)
Vitamin C (ascorbic acid)	Aqueous middle, cytosol, and extracellular liquids	Regeneration of vitamin E regeneration, protection of LDL, provides an electron to quench ROS	$\text{OH}^\bullet-\text{O}_2^\bullet-$	Insight into antioxidant defenses (provides an electron to quench ROS)	Birnie-Gauvin et al. (2017); Lackner (1998); Lushchak (2011)
Glutathione	Aqueous middle	GPx substrate, regeneration of Vit-E, C	$\cdot\text{O}_2-\text{OH}^\bullet-$	Provides insight into oxidative damage (GSH to GSSG ratio or vice versa) and antioxidant defenses (GSH)	Donaldson et al. (2008); Toppo et al. (2008)
Coenzyme Q ₁₀	Mitochondria membranes	Regeneration of vitamin E regeneration, protection of LDL.	ROO [•]		Gornati et al. (2005)
Flavonoids	Linked with fluids	Inhibition of pro-oxidant enzymes, LDL protection	$\text{O}_2^\bullet-\text{OH}^\bullet-\text{ROO}^\bullet-\text{RO}^\bullet-$	Insight into total low molecular weight antioxidant defenses	Pickering & Pottinger (1995; Wendelaar Bonga (1997)
β carotene	Aqueous middle	Pro-vitamin, production of Vit-A	$\cdot\text{O}_2-\text{OH}^\bullet-$	Insight into total low molecular weight antioxidant defenses	Jha, Pal, Sahu, Kumar, and Mukherjee (2007); Lackner (1998)
Heat shock protein (HSP)	Aqueous middle	Protection of cellular protein	-	Extent of cellular damages	Basu et al. (2002); Maddeira, Narciso, Cabral, Vinagre, and Diniz (2012)
Manganese (Mn), Iron (Fe), copper (Cu), selenium (Se), and zinc (Zn)	Aqueous middle	Catalase cofactor, SOD cofactor (Cu-Zn-SOD), LDL and thiols protection, ROS production inhibition	-	Insight into total low molecular weight antioxidant defenses, extent of cellular damages	Atli, Alptekin, Tükel, and Canlı (2006); Martinez-Alvarez et al. (2005)

TABLE 3 Antioxidants stress response of fish during climate change-induced temperature stress^a

Species	Stress intensity	Stress duration	Stress type	Fish size/fish age	Effects	Impacts on aquaculture	References
Atlantic halibut, <i>Hippoglossus</i> <i>hippoglossus</i>	2°C (control) 5, 10, 12, 14, 16, and 18°C	96 days	Chronic	16.4 ± 0.2 g	SOD, CAT, GR, GST, GPx, AChE, BChE, CYP1A, PC [L] (5°C > 18°C) ↑	↑ Cellular and protein damage at 16 and 18°C	Carney Almroth, Bresolin de Souza, Jönsson, and Sturye (2019)
European seabass, <i>Dicentrarchus</i> <i>labrax</i>	12, 24, and 33.3°C	2 weeks	Chronic	86.00 ± 6.19 mm	GST[M] (33.3°C) ↑; CAT[M] (33.3°C) ↑; LPO[M] (33.3°C) ↑	↑ Cellular and protein damage at 33°C	Madeira, Narciso, Cabral, Vinagre, and Diniz (2013)
European seabass, <i>D. labrax</i>	18 and 25°C	4 weeks	Chronic	~5.6 g	CAT, GPx, SOD, GR, LPO, ChEs [L] (25°C) ↑; IDH, LDH [M] (25°C) ↑	↓ Growth, survival, at 25°C	Almeida, Gravato, and Guilhermino (2015)
European seabass, <i>D. labrax</i>	18, 24, and 28°C	30 days	Chronic	4.6–7.5 g	MDA, LPO, CAT [M] (18°C>28°C) ↑	↓ Growth, survival, condition factor at 28°C	Vinagre, Madeira, Narciso, Cabral, and Diniz (2012)
European seabass, <i>D. labrax</i>	8 and 22°C	20 days	Chronic	24.8 ± 1.69 g	SOD, CAT, GPx, GR (8°C) ↑	↓ Growth performance, immunity at 8°C	Islam, Slater, Thiele, and Kunzmann (2021)
European seabass, <i>D. labrax</i>	24 and 33°C	10 days	Chronic	11.62 ± 0.43	SOD, CAT, GPx, GR (33°C) ↑	↓ Growth performance, immunity at 33°C	Islam, Kunzmann, Thiele, and Slater (2020)
Fathead minnow, <i>Pimephales</i> <i>promelas</i>	7, 25, and 32°C	31 days	Chronic	6.41 g	SOD (25°C>32°C) ↑	–	Clotfelter et al. (2013)
Giltthead seabream <i>Sparus aurata</i>	10, 14, and 18°C	10 days	Chronic	150 ± 21 g	HK [H, WM, RM, L] (10°C,14°C) →, ALD (10°C,14°C) ↑, PK (10°C,14°C) ↑, CS (10°C) ↑, MDH (10°C) ↑, HOAD (10°C) ↑	↓ Growth and reproduction at 10 and 14°C	Kyprianou et al. (2010)
Giltthead Sea bream <i>S. aurata</i>	22, 24, 26, 28, 30, 32, 34, and 35.5°C	48 hr	Acute	12.2 ± 2.9 g	CAT [G, M, L, B, L] (22°C > 35.5°C) ↑, GST [G, M, L, L] (22°C > 35.5°C) ↑, SOD [G, M, L, B] (22°C > 35.5°C) ↑, LPO [M, L] (22°C > 35.5°C) ↑, CYP1A [L] (22°C > 35.5°C) ↑	–	Madeira et al. (2016)

(Continues)

TABLE 3 (Continued)

Species	Stress intensity	Stress duration	Stress type	Fish size/fish age	Effects	Impacts on aquaculture	References
Black goby, <i>Gobius niger</i>	12, 24, and 34.1°C	2 weeks	Chronic	98.70 ± 6.36 mm	GST[M] (34.1°C) ↑; CAT[M] (34.1°C) ↑; LPO[M] (34.1°C) ↓	-	Madeira et al. (2013)
Largemouth bass, <i>Micropterus salmoides</i>	20 (control) and 26°C	96 hr	Acute	150 ± 15 g	MDA [P, G, L] (26°C) ↑; SOD, CAT, and GSH-Px [G, L] (26°C) ↑; CAT, GSH [G, L] (26°C) ↑	-	Sun et al. (2020)
Thinlip mullet, <i>Liza ramada</i>	12, 24, and 38°C	2 weeks	Chronic	44.00 ± 3.90 mm	GST[M] (38°C) ↓; CAT[M] (38°C) ↑; LPO[M] (38°C) ↑	-	Madeira et al. (2013)
Pufferfish, <i>Takifugu obscurus</i>	25 (control) and 28°C	8 weeks	Chronic	8.3 ± 0.08 g	SOD, CAT, and HSP70 (28°C) ↑	↓ Feed intake at 18°C	C. H. Cheng, Guo, Ye, and Wang (2018)
Pufferfish, <i>T. obscurus</i>	25 (control), 21, 17, and 13°C	24 hr	Acute	15.4 ± 1.3 g	SOD, CAT, HSP90 (21°C > 13°C) ↑	-	C. H. Cheng, Ye, Guo, and Wang (2017)
Sablefish, <i>Anoplopoma fimbria</i>	8, 10, 12, 14, 16, 18, and 20°C	4 months	Chronic	68.5 ± 4.8 g	CAT, SOD (18°C) ↑	↓ Growth performance and feed intake at 12 and 14°C	Y. Kim et al. (2017)
Ray finned fish, <i>Schizothorax prenanti</i>	11, 16, 21 (control), 26, and 31°C	24 hr	Acute	110 ± 10 g	SOD, CAT [G, L, M] (11°C, 16°C, 26°C, 31°C) ↑; AChE (11°C, 31°C) ↓	-	Yang et al. (2018)
Seabream, <i>Diplodus vulgaris</i>	12, 24 (control), and 31°C	2 weeks	Chronic	74.89 ± 7.76 mm	GST [M] (31°C) ↑; CAT[M] (31°C) ↑; LPO[M] (31°C) →	-	Madeira et al. (2013)
Snakehead, <i>Channa punctata</i>	20 and 32°C	24 hr	Acute	70–80 g	GSH, GR, LPO [L, K, G] (32°C) ↓; CAT [L] (32°C) ↑; CAT [K, G] (32°C) ↓; GST [K, L] (32°C) ↑	-	Kaur, Atif, Ali, Rehman, and Raisuddin (2005)
Spotted seabass, <i>Lateolabrax maculatus</i>	18 (control), 20, 22, 24, and 28°C	3 days	Acute	22.9 ± 1.6 g	SOD [L, G, M] (20–28°C) ↑	-	Shin, Park, Yeo, and Han (2018)
Turbot, <i>Scophthalmus maximus</i>	16, 20, 23, 25, 27, and 28°C	7 days	Acute	160 ± 10.2 g	SOD [Mu] (20°C, > 28°C) ↑	-	Huang, Ma, and Wang (2011)

TABLE 3 (Continued)

Species	Stress intensity	Stress duration	Stress type	Fish size/fish age	Effects	Impacts on aquaculture	References
White seabream, <i>Diplodus sargus</i>	12, 24, and 33.8°C	2 weeks	Chronic	33.89 ± 9.07 mm	GST[M] (33.8°C) ↑; CAT[M] (33.8°C) →; LPO[M] (33.8°C) ↑	↓ Survival rate at 33.8°C	Madeira et al. (2013)
Yellow catfish, <i>Pelteobagrus fuscidraco</i>	25 (control) and 32°C	7 days	Chronic	2.21 ± 0.01 g	CAT, SOD (32°C) ↑	↑ Mortality at 32°C ↓ Growth, immunity performance at 32°C	F. Liu et al. (2019)
Meagre, <i>Argyrosomus regius</i>	17, 20, 23, and 26°C	90 days	Chronic	36.46 ± 0.08 g	SOD[H, M, L] (20°C) ↑; CAT[H, M, L] (17°C; 20°C; 23°C; 26°C) →, GR	↓ Cellular damage at 17 and 26°C ↓ Growth performance at 17 and 26°C	Antonopoulou, Chatzigiannidou, Feldantsis, Kounnas, and Chatzifotis (2020)

Abbreviations: ACAP, antioxidant capacity against peroxyl radicals; AChE, acetylcholinesterase; ALD, aldolase; B, blood; Br, brain; BChE, butyrylcholinesterase; CAT, catalase; CS, citrate synthase; CYP1A, cytochrome P450 1A; E, erythrocytes; G, gill; GCL, glutamate-cysteine ligase; GPx, glutathione peroxidase; GR, glutathione reductase; GST, glutathione S-transferase; H, heart; HK, hexokinase; HOAD, 3-hydroxy acyl CoA dehydrogenase; HSP, heat shock protein; I, intestine; L, liver; L-LDH, L-lactate dehydrogenase; LPO, lipid peroxidation levels; M, muscle; MDH, malate dehydrogenase; Mu, mucus; P, plasma; PC, protein carbonyls; PK, pyruvate kinase; S, serum; RM, red muscle; SOD, superoxide dismutase; WM, white muscle.

^aSymbols represent an increase (↑) in the specified response; no change (=); decrease (→); increased trend (↗), decreased trend (↘).

TABLE 4 Metabolic and molecular stress responses of fish during climate change-induced temperature stress^a

Species	Stress intensity	Stress duration	Stress type	Fish size/fish age	Effects	Impacts on aquaculture	References
Atlantic cod, <i>Gadus morhua</i>	10 (control), 16, and 19°C	45 days	Chronic	~40 g	Glucose [P] (16°C, 19°C) ↑	↑ mortality at 16 and 19°C ↓ Immunity at 16 and 19°C	Pérez-Casanova, Rise, et al. (2008)
Atlantic halibut, <i>Hippoglossus</i> <i>hippoglossus</i>	8, 12, 15, and 18°C	3 months	Chronic	16.5 ± 2.4 g	Serum protein (18°C) ↑	↓ Immunity at 18°C ↓ Growth performance at 18°C	Langston et al. (2002)
Atlantic salmon, <i>Salmo salar</i>	(14, 17, 20, and 24°C) and freshwater (FW), seawater (SW)	8 days	Chronic	42 ± 7 g	Hsp70 (FW, SW at 24°C) ↑	↓ survival, growth at 15 and 18°C	Vargas-Chacoff et al. (2018)
Atlantic salmon, <i>S. salar</i>	12 (control), 16, and 20°C	99 days	Chronic	~70 g	Glucose and cholesterol (12°C, 16°C, 20°C) →; HSPs (4°C, 16°C) ↑	↓ Survival, growth at 16 and 20°C	Tramp et al. (2018)
Atlantic salmon, <i>S. salar</i>	4, 10 (control), and 16°C	30 days	Chronic	~96 g	HSPs (4°C, 16°C) ↑	↑ Disease susceptibility at 16°C	Jensen et al. (2015)
Black goby, <i>Gobius niger</i>	12, 24, and 34.1°C	2 weeks	Chronic	98.70 ± 6.36 mm	HSP70[M] (34.1°C) ↑	↓ Immunity at 16°C	Madeira et al. (2013)
Black porgy, <i>Acanthopagrus</i> <i>schlegeli</i>	20 and 30°C	2 weeks	Chronic	51.07 ± 6.0 g	Glucose [P] (30°C) ↑, Wap65 [B, L, G, K, I] (30°C) ↑	-	Cheol et al. (2008)
Catfish, <i>Horabagrus</i> <i>brachysoma</i>	26 (control), 31, 33, and 36°C	30 days	Chronic	23.01 ± 2.04 g	Glucose [B] (33°C, 36°C) ↑; G6PDH, glycogen [B] (33°C, 36°C) ↓; HSP70 [G, L, Br, M] (33°C, 36°C)	↓ Immunity at 33 and 36°C	Dalvi et al. (2017)
Catfish, <i>Pangasianodon</i> <i>hypophthalmus</i>	25, 30, and 35°C with (0, 6, 12 ppt)	56 days	Chronic	10–20 g	IGF-1 (35°C, 6 ppt) ↓; glucose (35°C, 12 ppt) ↑	↓ Growth, immunity at 25°C	Phuc et al. (2017)

TABLE 4 (Continued)

Species	Stress intensity	Stress duration	Stress type	Fish size/fish age	Effects	Impacts on aquaculture	References
European seabass, <i>Dicentrarchus labrax</i>	12, 24, and 33°C	2 weeks	Chronic	86.00 ± 6.19 mm	HSP70[M] (33.3°C) ↑	–	Madeira et al. (2013)
European seabass, <i>D. labrax</i>	8, 16, 24 (control), and 32°C	30 days	Chronic	5.29 ± 0.30 g	Triglycerides, lactate, cortisol [P] (8.32°C) ↑; glucose, protein [P] (8.32°C) ↓; HSP70[L, M] (8.32°C) ↑; IGF1 [L, M] (8.32°C) ↓	↓ Growth performance and immunity at 8 and 32°C	Islam, Kunzmann, Bögner, et al. (2020)
European seabass, <i>D. labrax</i>	8, 16, 24 (control), and 32°C	30 days	Chronic	5.68 ± 0.60 g	Triglycerides, lactate [P] (8°C; 32°C) ↑; glucose, protein [P] (8°C; 32°C) ↓	↓ Growth performance at 8 and 32°C	Islam, Slater, Bögner, Zeytin, and Kunzmann (2020)
European seabass, <i>D. labrax</i>	8 and 22°C	20 days	Chronic	24.5 ± 1.48 g	Lactate, BUN, glucose [P] (8°C) ↑; protein ↓; HSP70, (8°C) ↑	↓ Growth performance and immunity at 8°C	Islam, Kunzmann, and Slater (2021)
European seabass, <i>D. labrax</i>	8 and 22°C	20 days	Acute and chronic	24.8 ± 1.69 g	Protein [P] ↓	↓ Growth performance, immune response at 8°C	Islam, Slater, Thiele, and Kunzmann (2021)
European seabass, <i>D. labrax</i>	24 and 33°C	10 days	Acute and chronic	12.28 ± 0.39 g	Lactate, BUN, glucose [P] (33°C) ↑; protein [P] (33°C) ↓; HSP70 (33°C) ↑	↓ Growth performance and immunity at 33°C	Islam, Slater, and Kunzmann (2020)
European seabass, <i>D. labrax</i>	24 and 33°C	10 days	Acute and chronic	11.62 ± 0.43	Protein (33°C) ↓	↓ Growth performance and immune responses at 33°C	Islam, Kunzmann, Thiele, and Slater (2020)
Gilthead seabream <i>Sparus aurata</i>	10, 14, and 18°C	10 days	Acute and chronic	150 ± 21 g	Glucose, triglycerides [P] (10°C; 14°C) ↑, Hsp70 and Hsp90 (10°C; 14°C) ↑ in [H, WM, RM, L]	↓ Growth, immunity at 10°C	Kyriianou et al. (2010)
GiltHead Sea bream, <i>S. aurata</i>	18 and 27°C	90 days	Chronic	700–800 g	HSP70 [L, M] (18°C) ↑; HSP90 [L] (18°C) ↑,	↓ Growth performance at 27°C	Ekren (2019)

(Continues)

TABLE 4 (Continued)

Species	Stress intensity	Stress duration	Stress type	Fish size/fish age	Effects	Impacts on aquaculture	References
Hybrid tilapia, <i>Oreochromis</i> sp.	28 (control) and 31°C	28 days	Chronic	400–600 g (31°C) →;	11β-hydroxylase, protein [P] (31°C) ↑;	↓ Growth performance at 31°C	Musa et al. (2017)
Thinlip mullet, <i>Liza ramada</i>	12, 24, and 38°C	2 weeks	Chronic	44.00 ± 3.90 mm	HSP70[M] (38°C) ↑	–	Madeira et al. (2013)
Red snapper, <i>Lutjanus</i> <i>guttatus</i>	20, 23 (control), 26, 29, and 32°C	21 days	Chronic	20.0 ± 1.0 g	HSP70 [G, M] (29°C, 32°C) ↑; LDH-a gene [G, M] (29°C, 32°C) ↑,	↓ Thermal tolerance at 20, 23, and 32°C	Larios-Soriano et al. (2020)
Mahseer, <i>Neolissochilus</i> <i>hexagonolepis</i>	24, 27, and 30°C	45 days	Chronic	30.51 ± 0.52 g	Glucose (24°C) ↑	↓ Reproductive performance at 31°C	Majhi, Das, and Rajkhowa (2013)
Marine medaka, <i>Oryzias</i> <i>melastigma</i>	12, 13, 15, 25 (control), and 32°C	7 days	Chronic	0.078 ± 0.002 g (7 days larvae)	HSP70 (13°C, 13°C, 32°C) ↑	↓ Immunity at 12–15°C	Li et al. (2015)
Milkfish, <i>Chanos</i> <i>chanos</i>	18 and 28°C (control)	3 weeks	Chronic	13.7 ± 1.3 g	11β-hsd1 (fw at 18°C) ↓; 11β-hsd1 (sw at 18°C) ↑	↓ Growth, osmotic balance, immunity at 18°C	Hu et al. (2019)
Nile tilapia, <i>Oreochromis</i> <i>niloticus</i>	25, 23, 21, 17, and 13°C	3 days	Acute	120 ± 10.3 g	Protein and cholesterol (13°C) ↓	↓ Immunity at 13 and 17°C	Panase et al. (2018)
Nile tilapia, <i>O. niloticus</i>	28 (control) and 8°C	6 hr	Acute	–	Urea, glucose (8°C) ↑; TG (8°C, 28°C) →	–	Zhou et al. (2019)
Japanese halibut, <i>Paralichthys</i> <i>olivaceus</i>	20 (control), 26, 29, and 32°C	3 days	Acute	7.76 ± 1.82 cm	HSP70 [G] (26°C, 29°C, 32°C) ↑	↓ Growth and immune responses at 29 and 32°C	Yifan Liu et al. (2017)
Pufferfish, <i>Takifugu</i> <i>obscurus</i>	25 (control) and 28°C	8 weeks	Chronic	8.3 ± 0.08 g	HSP70 (28°C) ↑	↓ Growth responses at 28°C	(C.H. Cheng et al., 2018)

TABLE 4 (Continued)

Species	Stress intensity	Stress duration	Stress type	Fish size/fish age	Effects	Impacts on aquaculture	References
Pufferfish, <i>T. obscurus</i>	25 (control), 21, 17, and 13°C	24 hr	Acute	15.4 ± 1.3 g	Protein [P] (13°C < 21°C) ↓; HSP90 (21°C > 13°C) ↑; P53, caspase-9 and caspase-3 HSP90 [L] (21°C > 13°C) ↑	↓ Immune responses at 13 and 17°C	C. H. Cheng et al. (2017)
Rainbow trout, <i>Oncorhynchus mykiss</i>	7, 9, 11, and 25°C	7 days	Acute	7.8–13 g	Glucose (7°C > 11°C) ↑	–	Barton and Peter (1982)
Rohu, <i>Labeo rohita</i>	30 (control), 33, and 36°C	60 days	Chronic	15.96 ± 0.70 g	Glucose [P] (36°C) ↑	↓ Growth performance at 33°C	Ashraf-Ud-Doulaah et al. (2019)
Seabream, <i>Diplodus sargus</i>	12, 24, and 33.8°C	2 weeks		33.89 ± 9.07 mm	HSP70 [M] (33.8°C) ↓	–	Madeira et al. (2013)
Snakehead, <i>Channa punctata</i>	20 and 32°C	24 hr	Acute	70–80 g	Total protein (32°C) ↓	–	Kaur et al. (2005)
Sole, <i>Solea senegalensis</i>	18.7, 12, 4, and 0°C	3 weeks	Chronic	250–300 g	Glucose [B] (0°C < 4°C < 12°C < 18°C) →	–	Foss et al. (2019)
Spotted seabass, <i>Lateolabrax maculatus</i>	18 (control), 20, 22, 24, and 28°C	3 days	Acute	22.9 ± 1.6 g	HSP70 [L, M] (24°C > 28°C) ↑; HSP90 [L] (24–28°C) ↑; HSP90 [M] (20–28°C) ↑	–	Shin et al. (2018)
Striped catfish, <i>Pangasianodon hypophthalmus</i>	28, 32, and 36°C	7 days	Acute	12.34 ± 0.78 g	Glucose (36°C) ↑	–	Shahjahan, Uddin, Bain, and Haque (2018)
Thai pangas, <i>Pangasianodon hypophthalmus</i>	24, 28, 32, and 36°C	28 days	Chronic	12.34 ± 0.78 g	Glucose (36°C) ↑	↓ Growth performance at 24°C	Ariful, Uddin, Uddin, and Shahjahan (2019)
Sticklebacks, <i>Gasterosteus aculeatus</i>	13, 18 (control), 24, and 28°C	2 weeks	Chronic	–	TGF-β, HSP90, HSP70 (24°C, 28°C) ↓	↓ Immune responses at 13 and 28°C	Dittmar, Janssen, Kuske, Kurtz, and Scharsack (2014)

(Continues)

TABLE 4 (Continued)

Species	Stress intensity	Stress duration	Stress type	Fish size/fish age	Effects	Impacts on aquaculture	References
Turbot, <i>Scophthalmus</i> <i>maximus</i>	13 (control), 16, 17, 20, 27, and 28°C	7 days	Acute	160 ± 10.2 g	HSP70 [K, L] (16–28°C) ↑	↓ Immunity at 20°C or above	Huang et al. (2015)
Turbot, <i>S. maximus</i> ,	18, 11, 4, and 0°C	3 weeks	Chronic	250–300 g	Lactate [B] (0.4,12,18°C) →	–	Foss et al. (2019)
White seabream, <i>Diplodus</i> <i>vulgaris</i>	12, 24 (control), and 31°C	2 weeks	Chronic	74.89 ± 7.76 mm	HSP70 [M] (31°C) →	–	Madeira et al. (2013)
Yellow catfish, <i>Pelteobagrus</i> <i>Fulvidraco</i>	25 (control) and 32°C	7 days	Acute	2.21 ± 0.01 g	Total protein (TP) (32°C) ↓; HSP70 (32°C) ↑	↑ Mortality at 32°C ↓ Growth, immunity performance at 32°C	F. Liu, Qu, et al. (2019)
Meagre, <i>Argyrosomus</i> <i>regius</i>	17, 20, 23, and 26°C	90 days	Chronic	36.46 ± 0.08 g	HSP70 (17°C,20°C) ↑; HSP90(17°C,20°C) ↓	↓ Growth performance at 17 and 26°C	Antonopoulou et al. (2020)

Abbreviations: 11β-Hsd1L, 11β-hydroxysteroid dehydrogenase 1-like; ACP, acid phosphatase; B, blood; Br, brain; G, gill; G6PDH, glucose-6-phosphate dehydrogenase; H, heart; HSP, heat shock protein; HSP70, heat shock protein 70; I, intestine; L, liver; L-LDH, L-lactate dehydrogenase; M, muscle; P, plasma; RM, red muscle; S, serum; TG, triglycerides; TGF-β, transforming growth factor-beta; Wap65, warm temperature acclimation protein; WM, white muscle.

^aSymbols represent an increase (↑) in the specified response; no change (↔); decrease (↓), increased trend (↗), decreased trend (↘).

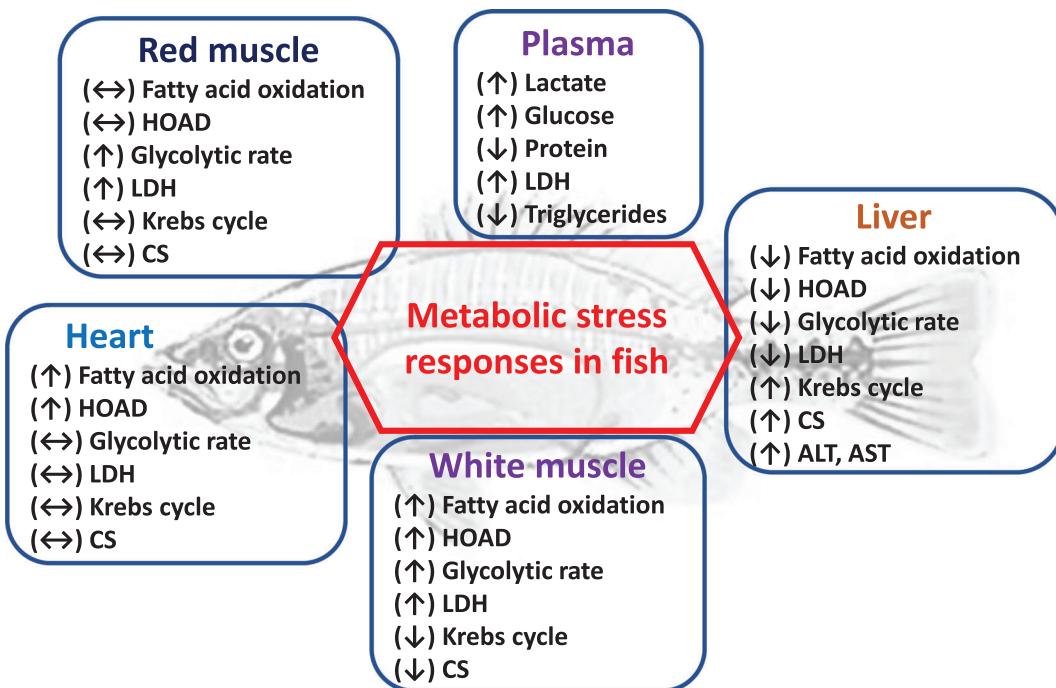


FIGURE 3 Metabolic stress responses of fish exposed to high temperature stress. (↔), indicates no change; (↑), indicates increase; and (↓), indicates decrease. ALT, alanine aminotransferase; AST, aspartate transaminase; CS, citrate synthase; HOAD, 3-hydroxy acyl CoA dehydrogenase; LDH, lactate dehydrogenase

changes in metabolic rate are further exacerbated by high respiratory rates and oxygen consumption (Araújo et al., 2018; Kyprianou et al., 2010). However, this review confined within temperature stress impacts on fish metabolic and molecular responses. Extreme winter (cold) stress response mechanisms in fish have been reviewed in detail by Donaldson et al. (2008), therefore they are not repeated here. During winter cold stress exposure, hyperglycemia is a standard indicator of cold shock responses, as blood glucose is directly associated with metabolism (Donaldson et al., 2008; Nie et al., 2019; Pickering, 1993). European common carp, *Cyprinus carpio* exposed at 7, 9, and 11°C from 25°C for 120 days showed increased glucose content at lower temperatures (7 and 9°C) (Tanck, Booms, Eding, Bonga, & Komen, 2000). A rapid temperature drop from 11 to 1°C resulted in increased plasma glucose levels in rainbow trout, *O. mykiss* during 7 days of extreme cold exposure (Barton & Peter, 1982). Cold shock also reduces physiological and enzymatic activity that drains lactate content and restores energy. Largemouth bass, *M. salmoides* exposed to cold temperature stress resulted in increased lactate content, impaired white muscle energy storage compared to fish at optimum temperature (Suski, Killen, Kieffer, & Tufts, 2006). Majhi et al. (2013) reported a 6°C cold shock significantly increased blood glucose in mahseer, *Neolissochilus hexagonolepis* compared to fish at 27 and 30°C. Tilapia, *O. niloticus*, exposed to 13°C had higher protein, cholesterol, and glucose content than fish exposed to 25°C (Panase et al., 2018). Plasma triglycerides and lactate content were significantly increased in European seabass, *D. labrax* exposed at 8°C for 30 days compared to fish reared at 16 and 24°C (Islam, Kunzmann, Bögner, et al., 2020). Higher temperature stress also caused impaired metabolism (Islam, Kunzmann, Thiele, & Slater, 2020; Islam, Slater, & Kunzmann, 2020; Shahjahan et al., 2018). Increased blood glucose content was reported for striped catfish, *Pangasianodon hypophthalmus* exposed at 36°C compared to fish at 24, 28, 32°C, and for 28 days (Ariful et al., 2019). In another study, increased blood glucose levels were reported for the same species exposed at 36°C for 7 days compared to fish at 30°C (Shahjahan et al., 2018). European seabass, *D. labrax* acclimated 32°C for 30 days had significantly lower triglycerides content than fish at 16 and 24°C (Islam, Kunzmann, Bögner, et al., 2020).

In addition to metabolic impairments, temperature stress also activates regulatory networks responsible for mitigating and preventing further damage. For example, heat shock proteins (HSPs) as molecular chaperones have been reported to repair and prevent cellular damage from protein denaturation at both high and low temperatures (Donaldson et al., 2008; Nakano & Iwama, 2002; Werner et al., 2006; Werner, Smith, Feliciano, & Johnson, 2005). HSPs play essential roles in long-term stress adaptation, as these proteins increase after the initial stress exposure and thus protect cells and tissues from structural damage during subsequent exposures (Madeira et al., 2012; Maulvault et al., 2017; Reyes-López et al., 2018). Significantly increased HSP70 was reported for olive flounder, *P. olivaceus* exposed at 28 and 30°C for 2 weeks (J. H. Kim et al., 2019). European seabass, *D. labrax* acclimated at 8 and 32°C for 30 days had significantly higher HSP70 upregulation than fish at 16 and 24°C (Islam, Kunzmann, Bögner, et al., 2020). Olive flounder, *P. olivaceus* exposed at 29°C, and 32°C for 3 days showed significant increases of HSP70 compared to fish at 20 and 26°C (Yifan Liu et al., 2017). Shin et al. (2018) observed spotted seabass, *Lateolabrax maculatus* exposed at and above 22°C resulted in significant upregulation of HSP70 and HSP90 mRNA. In a recent study, European seabass, *D. labrax* was acclimatized at an extreme warm (33°C) temperature for 10 days and showed significantly higher upregulation of the HSP70 gene than at fish at 22°C (Islam, Slater, & Kunzmann, 2020). In another study, European seabass exposed to 8°C for 20 days prior acclimatized at different hyosalinities showed significant upregulation of HSP 70 than fish reared at 22°C (Islam, Slater, Thiele, & Kunzmann, 2021). To date, a number of “omics” approaches were used to understand the climate stress responses in fish (Cossins & Crawford, 2005). For example, microarray-based gene expression combined with metabolic, molecular, and proteomic data could be a useful approach to gain more insight into temperature stress physiology (Gracey, 2007). Gracey et al. (2004) acclimatized common carp, *C. carpio* for 22 days at 10°C and then responses were measured through a 13,440-probe cDNA microarray. The authors reported that 3,461 cold stress-regulated cDNA microarrays were differentially expressed among the tested tissues. Zhou et al. (2019) exposed Nile tilapia, *O. niloticus* at 8 and 28°C for 6 hr. Transcriptomic response in the kidney was characterized using RNA-seq. The authors reported that a total of 2,191 metabolic genes were annotated for significant expression. Pathway analysis showed that metabolic and cell adhesion molecules were significantly down-regulated at low temperatures. Moreover, significant pathway changes were also observed in ferroptosis for Nile tilapia for the first time (Zhou et al., 2019). Taken altogether, cDNA microarrays could be an important tool to understand underlying system-wide gene expression in response to thermal shock and adaptation.

As shown above, a large number of thermal stress studies for fish have reported metabolic and molecular stress responses in fish. Considering future climate scenarios, metabolic and molecular impairments in fish will affect growth, immunity and disease resistance through energy offset during extreme temperature events, which are of great concern for aquaculture. Because of many variables that influence the levels of response in fish, combined with intra- and interspecific variations, this profoundly challenges generalization. It was difficult to establish the limit for metabolic and molecular responses concerning optimum growth and disease resistance capability.

2.4 | Changes in hematological and biochemical parameters

Many studies have reported temperature as an important factor in influencing hemato-biochemical responses (Table 5). Higher thermal exposure can also influences blood cell counts and morphology (Islam, Slater, Thiele, & Kunzmann, 2021; Mofizur Rahman & Baek, 2019). Hematological responses to thermal stress are reflected through cellular and nuclear morphology (Islam, Kunzmann, Bögner, et al., 2020; Islam, Kunzmann, Thiele, & Slater, 2020; Islam, Slater, Bögner, et al., 2020). These result in lipid miscibility and increase thermo-stability to thermal stress as a general cellular stress response mechanism (Ashaf-Ud-Doulah et al., 2019; Shahjahan, Kitahashi, & Ando, 2017; Shahjahan, Rahman, Islam, Uddin, & Al-Emran, 2019). European seabass, *D. labrax* exposed at low temperatures (<8°C) and high temperature (>24°C) for 10–30 days exhibited significantly increased white blood cells (WBC) while red blood cells (RBC), hematocrit, hemoglobin (Hb) exhibited the inverse trend compared to fish at 16 and 24°C

TABLE 5 Hematological and biochemical responses of fish during climate change-induced temperature stress^a

Species	Stress intensity	Stress duration	Fish size/ fish age	Effects	Impacts on aquaculture	References
Nile tilapia, <i>Oreochromis niloticus</i>	25, 23, 21, 17, and 13°C	3 days	Acute	120 ± 10.3 g ALT, AST, (13°C) ↑; RBC hematocrit (%), Hb, mean corpuscular volume, mean corpuscular hemoglobin (13°C) ↓; WBC (1°C) ↑	↓ Immunity at 13, 17, and 21°C	Panase et al. (2018)
Striped catfish, <i>Pangasianodon hypophthalmus</i>	28, 32, and 36°C	7 days	Acute	12.34 ± 0.78 g Hb, RBC (36°C) ↓; WBC, ECA, ENA (36°C) ↑	↓ Immunity at 28°C	Shahjahan et al. (2018)
Thai pangas, <i>Pangasianodon hypophthalmus</i>	24, 28, 32, and 36°C	28 days	Chronic	12.34 ± 0.78 g Hb, RBC (36°C) ↓; WBC, glucose, ECA, ENA (36°C) ↑	↓ Growth performance and immunity at 24 and 28°C	Ariful et al. (2019)
European seabass, <i>Dicentrarchus labrax</i>	8, 16, 24 (control), and 32°C	30 days	Chronic	5.68 ± 0.60 g WBC (8°C, 32°C) ↓; RBC (8°C, 32°C) ↓; ECA, ENA (8°C, 32°C) ↑	↓ Growth performance and immunity at 8 and 32°C	Islam, Kunzmann, Bögner, et al. (2020)
Rohu, <i>Labeo rohita</i>	30 (control), 33, and 36°C	60 days	Chronic	15.96 ± 0.70 g; WBC (36°C) ↑; RBC, Hb (36°C) ↓; ENA, ECA (36°C) ↑	↓ Immunity at 36°C	Ashraf-Udd-Doulah et al. (2019)
Atlantic salmon, <i>Salmo salar</i>	16–12, 8, 6, 4, 2, and 1°C	14 days	Chronic	72.89 ± 3.12 g AST, ALT, LDH, ALP [P] (16°C, 14°C) ↑	↓ Immunity at 16°C	C. Liu et al. (2020)
Catfish, <i>Pangasianodon hypophthalmus</i>	25, 30, and 35°C with (0, 6, 12 ppt)	56 days	Chronic	10–20 g RBC, Hb (35°C) ↓	↓ Growth, immunity at 25°C	Phuc et al. (2017)
Pufferfish, <i>Takifugu obscurus</i>	25 (control), 21, 17, and 13°C	24 hr	Acute	15.4 ± 1.3 g Blood cell count (13°C > 21°C) ↓; AST, ALT, LDH (21°C > 13°C) ↑	↓ Immune responses at 13 and 17°C	C. H. Cheng et al. (2017)
Atlantic halibut, <i>Hippoglossus hippoglossus</i>	8, 12, 15, and 18°C	3 months	Chronic	16.5 ± 2.4 g Leucocytes (18°C) ↑	↓ Immunity at 18°C ↓ Growth performance at 18°C	Langston et al. (2002)

(Continues)

TABLE 5 (Continued)

Species	Stress intensity	Stress duration	Stress type	Fish size/ fish age	Effects	Impacts on aquaculture	References
Three-spined sticklebacks, <i>Gasterosteus aculeatus</i>	13, 18 (control), 24, and 28°C	2 weeks	Chronic	—	Leucocytes (24°C, 28°C) ↓; lymphocyte proliferation (24°C, 28°C) ↓	↓ Immune responses at 13 and 28°C	Dittmar et al. (2014)
Perch, <i>Perca fluviatilis</i>	5, 10, 16 (control), 20, 24, 27, and 30°C	5 weeks	Chronic	~85 g	Serum opsonin (5°C, 10°C, 27°C, 28°C, 30°C) ↓	↓ Growth, immunity at 24, 27, and 30°C	Marnia and Lilius (2015)
Shortnose sturgeon, <i>Acipenser brevenostrum</i>	11 and 20°C	14 weeks	Chronic	15.64 ± 4.34 g	WBC (20°C) ↑	↓ Growth and immunity at 20°C	Gradil et al. (2014)
Orange-spotted grouper, <i>Epinephelus coioides</i>	19, 27 (control), and 35°C	96 hr	Acute	190 ± 4.6 g	Leucocyte (19°C, 35°C) ↓; phagocytic activity (19°C, 35°C) ↓	↓ Immunity at 19 and 35°C	A. C. Cheng, Cheng, Chen, and Chen (2009)
Japanese medaka, <i>Oryzias latipes</i>	5 and 25°C (control)	14 days	Chronic	300–450 mg	Spleen cellularity (5°C) ↓; phagocytes (5°C) ↑	↓ Immunity at 5°C	Prophete et al. (2006)
Barramundi, <i>Lates calcarifer</i>	22, 28 (control), and 36°C	3.5 months	Chronic	48 ± 1.5 g	Stress-related genes expression were observed through next- generation transcriptome profiling	↓ Growth and immunity at 22°C	Newton, Zenger, and Jerry (2013)
Rainbow trout, <i>Oncorhynchus mykiss</i>	5, 10, and 20°C	65 days	Chronic	~18.7 g	Respiratory burst, opsonin (5°C, 10°C) ↓	↓ Immunity at 5 and 10°C	Nikoskelainen, Bylund, and Lilius (2004)
European seabass, <i>D. labrax</i>	8 and 22°C	20 days	Chronic	24.5 ± 1.48 g	γGGT, GOT, GPT, LDH [P] (8°C) ↑	↓ Growth and immunity at 8°C	Islam, Kunzmann, and Slater (2021)
European seabass, <i>D. labrax</i>	8 and 22°C	20 days	Acute and chronic	24.8 ± 1.69 g	Hematocrit, Hb, BRC (8°C); WBC, ECA, ENA (8°C) ↑	↓ Growth and immunity at 8°C	Islam, Slater, Thiele, and Kunzmann (2021)

TABLE 5 (Continued)

Species	Stress intensity	Stress duration	Fish size/ fish age	Effects	Impacts on aquaculture	References
European seabass, <i>D. labrax</i>	24 and 33°C	10 days	Acute and chronic	12.28 ± 0.39 g γ GGT, GOT, GPT, LDH [P] (33°C) ↑	↓ Growth and immunity at 33°C	Islam, Slater, and Kurzmann (2020)
European seabass, <i>D. labrax</i>	24 and 33°C	10 days	Acute and chronic	11.62 ± 0.43 WBC, ECA, ENA (33°C) ↑	↓ Growth performance and immunity at 33°C	Islam, Kunzmann, Thiele, and Slater (2020)

Abbreviations: ALT, alanine aminotransferase; AST, aspartate transaminase; ECA, erythrocytic cellular abnormalities; ENA, erythrocytic nuclear abnormalities; Hb, hemoglobin; LDH, L-lactate dehydrogenase; P, plasma; RBC, red blood cells; WBC, white blood cells.
^aSymbols represent an increase (↑) in the specified response; no change (↔); decrease (↓), increased trend (↗), decreased trend (↘).

(Islam, Kunzmann, Bögner, et al., 2020; Islam, Slater, Bögner, et al., 2020; Islam, Slater, Thiele, & Kunzmann, 2021). Striped catfish, *Pangasianodon hypophthalmus* exposed to 36°C for 7 days caused significant reduction of Hb and RBC content compared to fish at 28°C, where WBC showed opposite trends (Shahjahan et al., 2018). Tilapia, *O. niloticus* exposed at 13°C showed significantly lower RBC, hematocrit, Hb, mean corpuscular volume, and mean corpuscular hemoglobin (Panase et al., 2018).

Temperature stress can also alter blood cell counts and cellular morphology through changes in lipid layer and energy storage. Several recent studies have reported erythrocytic cellular and nuclear abnormalities from climate-induced temperature events (Ariful et al., 2019; Ashaf-Ud-Doulah et al., 2019; Islam, Kunzmann, Bögner, et al., 2020; Shahjahan et al., 2018). Shahjahan et al. (2018) examined the effects of high temperature on erythroblasts (Ebs), erythrocytic cellular abnormalities (ECA), and erythrocytic nuclear abnormalities (ENA) in striped catfish, *Pangasianodon hypophthalmus* exposed to 28, 32, and 36°C for 7 days. Frequencies of Ebs, ECA, and ENA were found to be elevated at increased temperatures. In another study, the same fish exposed to 24, 28, 32, and 36°C for 28 days exhibited significantly higher ECA and ENA at the highest temperature (Ariful et al., 2019). For European seabass, *D. labrax* both ECA and ENA frequencies were significantly higher in fish reared at 8 and >32°C compared to 16 and 24°C during the 10–30 days exposure (Islam, Kunzmann, Bögner, et al., 2020; Islam, Slater, Bögner, et al., 2020; Islam, Slater, Thiele, & Kunzmann, 2021). Mofizur Rahman and Baek (2019) evaluated the morphometric indices of erythrocytes in red-spotted grouper, *Epinephelus akaara* exposed at higher water temperatures (31 and 34°C) for 42 days showed significantly decreased erythrocyte major axis and nucleus major axis compared to fish at 25°C, 28°C (Panase et al., 2018).

In fish and other animals, during thermal stress, functional tissues and organ damage release some specific cellular enzymes into the bloodstream and can be used as stress indicators (Krajnovic-Ozretic & Ozretic, 1987; Roychowdhury et al., 2020). Significantly higher accumulation of glutamic-pyruvate transaminase (GPT), glutamic oxaloacetic transaminase (GOT), lactic acid dehydrogenase (LDH), gamma-glutamyl-transaminase (γ GGT) in European seabass, *D. labrax* exposed at cold (8°C) temperature (Islam, Kunzmann, Henjes, & Slater, 2021) and high (>32°C) temperature (Islam, Slater, & Kunzmann, 2020) indicate reduced liver function because of damaged hepatocytes and other cellular injuries. Tilapia, *O. niloticus* exposed to 13°C caused increased alanine transaminase (ALT), aspartic transaminase (AST) content compared to fish at 25°C (Panase et al., 2018). Catfish, *Horabagrus brachysoma* exposed at 33 and 36°C for 30 days reported increased LDH, malate dehydrogenase (MDH), ALP, ACP, AST, and ALT activities. Decreased RBC, hematocrit, Hb, mean corpuscular volume, mean corpuscular hemoglobin have also been reported for the same fish (Dalvi et al., 2017). ALT, AST, and WBC values were increased significantly in Nile tilapia, *O. niloticus* stressed at 13°C from 25°C for 3 days (Dalvi et al., 2017). Overall, these results suggest that rapid decreases in water temperature may induce stress responses and have the potential to cause impairment of hematological parameters. Thus, along with other hematological parameters, ECA and ENA could be used as important thermal stress indicators (Table 5).

Numerous results reported on extreme temperature events can disturb the hemato-biochemical parameters of fish. Significant cellular damage and abnormalities occur during extreme temperature events. To repair this damage and regain cellular homeostasis, fish need to offset a significant amount of energy, which ultimately affects growth, immunity and disease resistance capability. However, still, some paradoxes exist because of differences in fish species, differential thermal stress (cold, warm, duration, and magnitude), physiological knowledge, and lack of ecophysiological understanding during extreme thermal events. Besides, the complexity of interaction among biotic and abiotic factors, pre-exposure history, compensatory adaptive mechanisms are also responsible for stress response variation from the vast number of species and even for the same species, different strains, size, age, and location have to be considered for further studies.

2.5 | Immune responses

Out of the preferred temperature range, both acute and chronic temperature changes negatively affect fish immune functions and the ability to fight against pathogens (Makrinos & Bowden, 2016; Wright & Cooper, 1981). The

TABLE 6 Growth performance, osmoregulatory and immunological stress responses of fish during climate change-induced temperature stress^a

Species	Stress intensity	Stress duration	Stress type	Fish size/ fish age	Effects	Comments	References
Atlantic cod, <i>Gadus morhua</i>	10 (control), 16, and 19°C	45 days	Chronic	~40 g	IL-1β /β2-M, MHC class, IgM-L (16°C;19°C) ↓	↓ Growth and immunity at 19°C	Pérez-Casanova, Rise, et al. (2008)
Atlantic cod, <i>G. morhua</i>	10 (control) and 16°C	5 days	Acute	52.6 ± 2.5 g	DHX58, STAT1, IRF7, ISG15, RSAD2, and IkBα (16°C) ↑	↓ Immunity at 16°C	Hori, Gamperl, Booman, Nash, and Rise (2012)
Atlantic halibut, <i>Hippoglossus hippoglossus</i>	8, 12, 15, and 18°C	3 months	Chronic	16.5 ± 2.4 g	Leucocytes, LSZ, serum protein (18°C) ↑	↓ Growth and immunity at 18°C	Langston et al. (2002)
Atlantic salmon, <i>Salmo salar</i>	(14, 17, 20, and 24°C) and freshwater (FW), seawater (SW)	8 days	Acute	42 ± 7 g	Mortality (sw;24°C) ↑; Na ⁺ -K ⁺ - ATPase (sw) ↑; Na ⁺ -K ⁺ - ATPase (fw;sw;14°C → 24°C) ↓; NKCC (sw;24°C) ↓	↓ Survival, growth and immunity at 24°C	Vargas-Chacoff et al. (2018)
Atlantic salmon, <i>S. salar</i>	5, 8, 15, and 20°C	90 days	Chronic	~23.1	Na ⁺ /K ⁺ ATPase [G] (8°C;8°C) ↑; Na ⁺ , Cl ⁻ [P] (8°C;8°C) ↑	↓ Growth at 15 and 20°C	Bernard, Mandiki, Duchatel, Rollin, and Kestemont (2019)
Atlantic salmon, <i>S. salar</i>	18 and 23°C	150 days	Chronic	—	Growth, feed intake (18°C;22.9°C) Na ⁺ , Cl ⁻ , K ⁺ [P] (18°C;22.9°C) ↑	↓ Growth at 23°C	Wade et al. (2019)
Atlantic salmon, <i>S. salar</i>	4, 10 (control), and 16°C	30 days	Chronic	~96 g	Growth, SGR (16°C) ↑; epidermal thickness (16°C) ↓; immunosuppression (4°C) ↓; HSPs (4°C;16°C) ↓	↓ Growth at 16°C	Jensen et al. (2015)
Catfish, <i>Pangasianodon hypophthalmus</i>	25, 30, and 35°C	56 days	Chronic	10–20 g	Growth (35°C) ↓, FCR, IGF-1 (35°C) ↑	↓ Growth and immunity at 25°C	Phuc et al. (2017)
European seabass, <i>Dicentrarchus labrax</i>	8, 16, 24 (control), and 32°C	30 days	Chronic	5.29 ± 0.30 g	Serum protein [P] (8°C;32°C) ↓	↓ Growth and immunity at 8 and 32°C	Islam, Kunzmann, Bögener, et al. (2020)
European seabass, <i>D. labrax</i>	8, 16, 24 (control), and 32°C	30 days	Chronic	5.68 ± 0.60 g	WG, SGR, FCR, HSI, VSI, ISI, SSI (16°C;24°C) ↑, WBC (8°C;32°C) ↑; serum protein	↓ Growth and immune performance at 8 and 32°C	Islam, Slater, Bögener, et al. (2020)

(Continues)

TABLE 6 (Continued)

Species	Stress intensity	Stress duration	Stress type	Fish size/ fish age	Effects	Comments	References
European seabass, <i>D. labrax</i>	18°C (temperate)/FW, SW and 24°C (warm)/ FW, SW	4 weeks	Chronic	86.87 ± 20.23 g	Na^+ / H^+ -ATPase, Na^+ / H^+ -exchanger 3 [G] (24°C, SW) ↑; ncc2a [G] (18°C, 24°C, FW) ↑, NKCC1, CFTR, Rh-glycoproteins, RHCG1, RHBG, V- H^+ -ATPase, vha-a and b 3 [G] (24°C, SW) ↑	-	Masroor et al. (2019)
European seabass, <i>D. labrax</i>	8 and 22°C	20 days	Acute and chronic	24.5 ± 1.48 g	WG, SGR, FI, SUR (8°C) ↓; serum protein, Na^+ , K^+ , Cl^- [P] (8°C) ↓; TNF- α , CFTR, ATPase, NKCC1 (8°C) ↑; IGF1 (8°C) ↓	↓ Growth and immunity at 8°C	Islam, Kunzmann, and Slater (2021)
European seabass, <i>D. labrax</i>	8 and 22°C	20 days	Acute and chronic	24.8 ± 1.69 g	WG, SGR, PER, FI, SUR (8°C) ↓; serum protein ↓, WBC (8°C) ↑; RB, LSZ (8°C) ↓; TNF- α (8°C) ↑	↓ Growth and immune responses at 8°C	Islam, Slater, Thiele, and Kunzmann (2021)
European seabass, <i>D. labrax</i>	24 and 33°C	10 days	Acute and chronic	12.28 ± 0.39 g	WG, SGR, PER, FI, SUR ↓; Na^+ , K^+ , Cl^- [P] (33°C) ↓; TNF- α , CFTR, ATPase, NKCC1 (33°C) ↑; IGF1 (33°C) ↓	↓ Growth and immune performance at 33°C	Islam, Slater, and Kunzmann (2020)
European seabass, <i>D. labrax</i>	24 and 33°C	10 days	Acute and chronic	11.62 ± 0.43	WG, SGR, PER, FI, SUR (33°C) ↓; serum protein, BRC (33°C) ↓; RB, LSZ (33°C) ↓; TNF- α (33°C) ↑	↓ Growth and immune responses at 33°C	Islam, Kunzmann, Thiele, and Slater (2020)
Hybrid tilapia, <i>Oreochromis</i> sp.	28 (control) and 31°C	28 days	Chronic	400–600 g	Ca^{2+} , Na^+ , Cl^- , Mg^{2+} and K^+ [P] (31°C) ↑; serum protein [P] (31°C) ↑	↓ Immune responses at 31°C	Musa et al. (2017)
Japanese medaka, <i>Oryzias latipes</i>	5 and 25°C (control)	14 days	Chronic	300–450 mg	Spleen cellularity (5°C) ↓; phagocytes (5°C) ↑; ROS (5°C) ↑	↓ Immune responses at 25°C	Prophete et al. (2006)

TABLE 6 (Continued)

Species	Stress intensity	Stress duration	Stress type	Fish size/ fish age	Effects	Comments	References
Largemouth bass, <i>Micropterus</i> <i>salmoides</i>	20 (control) and 26°C	96 hr	Acute	150 ± 15 g	TNF-1α, IL-1β, IL-8 mRNA [G, L] [26°C] ↑; lysozyme [G, L] [26°C] ↑; IL-10, Hepcidin-1, Hepcidin-2 [26°C] ↓	↓ Immune responses at 26°C	Sun et al. (2020)
Milkfish, <i>Chanos</i> <i>chanos</i>	18 and 28°C (control)	3 weeks	Chronic	13.7 ± 1.3 g	Na ⁺ , K ⁺ -ATPase, 11β-hsd1 [18°C] ↓; Na ⁺ , K ⁺ -ATPase, 11β-hsd1 [18°C] ↑	↓ Immune responses at 18°C	Hu et al. (2019)
Nile tilapia, <i>Oreochromis</i> <i>niloticus</i>	25, 23, 21, 17, 13, and 13°C	3 days	Chronic	120 ± 10.3 g	Serum protein (13°C) ↓; WBC (13°C) ↑.	↓ Immune responses at 13°C	Panase et al. (2018)
Nile tilapia, <i>O. niloticus</i>	18.4 (control), 23, 28, and 33°C	4 weeks	Chronic	18.2–21.7 g	LSZ (33°C) ↓	↓ Immune responses at 33°C	Dominguez, Takemura, and Tsuchiya (2005)
Nototheniod, <i>Eleginops</i> <i>maclovinus</i>	10 (control), 14, and 18°C.	2 weeks	Chronic	136.7 ± 21.1 g	Na ⁺ , K ⁺ -ATPase [G, K, I] (10°C, >18°C) ↑	–	Oyarzún, Muñoz, Pontigo, Morera, and Vargas- Chacoff (2018)
Olive flounder, <i>Paralichthys</i> <i>olivaceus</i>	20, 22, 24, 26, 28, and 30°C	2 weeks	Chronic	27.96 ± 3.07 g	IgM, LSZ [P] (28 & 30°C) ↓	↓ Immune responses at 28 and 30°C	J. H. Kim et al. (2019)
Orange-spotted groupers, <i>Epinephelus</i> <i>coioides</i>	19, 27 (control), and 35°C Pathogen: <i>Vibrio</i> <i>diginolyticus</i>	96 hr	Acute	190 ± 4.6 g	Mortality (19°C, 35°C) ↓; leucocyte (19°C, 35°C) ↓; ACh ₅₀ : LSZ (19°C, 35°C) ↓; phagocytic activity (19°C, 35°C) ↓	↓ Immune responses at 19 and 35°C	A. C. Cheng et al. (2009)
Perch, <i>Perca</i> <i>fluviatilis</i>	5, 10, and 20°C	3 weeks	Chronic	199.9 ± 49.7 g	Na ⁺ , Cl ⁻ [P] (sw.5°C, 10°C, 20°C) ↑; Na ⁺ /K ⁺ -ATPase [G] (sw.5°C, 10°C, 20°C) ↑	–	Christensen, Svendsen, and Steffensen (2017)
Perch, <i>P. fluviatilis</i>	5, 10, 16 (control), 20, 24, 27, and 30°C	5 weeks	Chronic	~85 g	Serum opsonin (5°C, 10°C, 27°C, 28°C, 30°C) ↓	↓ Immune responses at 5, 10, 27, 28, and 30°C	Marnila and Lillius (2015)

(Continues)

TABLE 6 (Continued)

Species	Stress intensity	Stress duration	Stress type	Fish size/ fish age	Effects	Comments	References
Puffer, <i>Takifugu obscurus</i>	19, 25, and 31°C	4 days	Acute	Larvae	Na^+, K^+ -ATPase [G, K, I] (19°C, 23°C) ↓	-	Wang et al. (2019)
Pufferfish, <i>T. obscurus</i>	25 (control), 21, 17, and 13°C	24 hr	Acute	15.4 ± 1.3 g	Serum protein, (13°C > 21°C) ↓	↓ Immune responses at 13–21°C	C. H. Cheng et al. (2017)
Rainbow trout, <i>Oncorhynchus mykiss</i>	8 (control), 13, and 18°C	3 hr	Acute	13–50 g	Na^+, Cl^- (18°C) ↓	-	Onukwufor and Wood (2018)
Rainbow trout, <i>O. mykiss</i>	12 and 15°C with pathogen <i>Tetracapsuloides bryosalmonae</i> for PKD	7 weeks	Chronic	8–10 g	Leukocytes, pathogen load, lymphocytes, Th1, NKEF [K] (15°C) ↑	↓ Immune responses at 15°C	Bailey, Segner, Casanova-Nakayama, and Wahli (2017)
Rainbow trout, <i>O. mykiss</i>	5, 10, and 20°C	65 days	Chronic	~18.7 g	Respiratory burst, opsonin (5°C, 10°C) ↓	↓ Immune responses at 5 and 10°C	Nikoskelainen et al. (2004)
Sablefish, <i>Anoplopoma fimbria</i>	8, 10, 12, 14, 16, 18, and 20°C	4 months	Chronic	68.5 ± 4.8 g	Growth (12°C, 4°C) ↓, FCR (18°C) ↓, LSZ (18°C) ↓	↓ Growth and immune responses at 12, 14, and 30°C	J. H. Kim, Park, et al. (2017)
Schizothorax <i>prenanti</i>	11, 16, 21 (control), 26, and 31°C	24 hr	Acute	110 ± 10 g	Na^+, K^+ -ATPase [G, L, M] (11°C, 16°C, 26°C, 31°C) ↓	-	Yang et al. (2018)
Shortnose sturgeon, <i>Acipenser brevirostrum</i>	11 and 20°C Pathogen: <i>Dicheelostium oblongum</i>	14 weeks	Chronic	15.64 ± 4.34 g	IRF-1, IRF-2 (20°C) ↑; WBC (20°C) ↑	↓ Immune responses at 20°C	Gradil et al. (2014)
Snakehead, <i>Channa punctata</i>	20 and 32°C	24 hr	Acute	70–80 g	Serum protein (32°C) ↓	↓ Immune responses at 32°C	Kaur et al. (2005)
Sole, <i>Solea senegalensis</i>	18.7, 12, 4, and 0°C	3 weeks	Chronic	250–300 g	Na^+, K^+ [B] (0°C, 4°C) ↑; pH, Ca^{2+} [B] (0°C, 4°C, 12°C, 18°C) →	-	Foss et al. (2019)

TABLE 6 (Continued)

Species	Stress intensity	Stress duration	Stress type	Fish size/ fish age	Effects	Comments	References
Striped catfish, <i>Pangasianodon</i> <i>hypophthalmus</i>	28, 32, and 36°C	7 days	Acute	12.34 ± 0.78 g	Hb, RBC (36°C); WBC, glucose, ECA, ENA (36°C) ↑	↓ Immune responses at 36°C	Shahjahan et al. (2018)
Sturgeon, <i>A. brevirostrum</i>	5, 10, 15, and 20°C	3 days	Acute	~150 g	Na ⁺ , Cl ⁻ [SW] (5°C:10°C) ↑	–	Downie, Wallace, Taylor, and Kieffer (2018)
Thai pangas, <i>Pangasianodon</i> <i>hypophthalmus</i>	24, 28, 32, and 36°C	28 days	Chronic	12.34 ± 0.78 g	WG, SGR, FCR (28°C and 32°C) ↑, Hb, RBC (36°C); WBC, glucose, ECA, ENA (36°C) ↑	↓ Growth and immune responses at 32 and 36°C	Ariful et al. (2019)
Three-spined sticklebacks, <i>Gasterosteus</i> <i>aculeatus</i>	13, 18 (control), 24, and 28°C	2 weeks	Chronic	–	Leucocytes (24°C:28°C); lymphocyte proliferation (24°C:28°C); IL-1β, TNF-α, TGF-β (24°C:28°C) ↓	↓ Immune responses at 24 and 35°C	Dittmar et al. (2014)
Tilapia, <i>Oreochromis</i> <i>moorii</i>	19, 23, 27 (control), 31, and 35°C	96 hr	Acute	41.2 ± 5.03 g	Leucocytes, respiratory burst, phagocytic activity, phagocytic index, LSZ, ACH ₅₀ (19°C:33°C:35°C) ↓	↓ Immune responses at 19, 23, and 35°C	Ndong, Chen, Lin, Vaseeharan, and Chen (2007)
Turbot, <i>Scophthalmus</i> <i>maximus</i>	16, 20, 23, 25, 27, and 28°C	7 days	Acute	160 ± 10.2 g	IgM, IL-1β, hepcidin, transferrin, lysozyme, ACP [Mu] (20°C:28°C) ↑	↓ Immune responses at 20 and 28°C	Huang et al. (2011)
Turbot, <i>S.</i> <i>maximus</i>	13 (control), 16, 17, 20, 27, and 28°C	7 days	Acute	160 ± 10.2 g	IgM [K, L] (16-28°C) ↑	↓ Immune responses at 28°C	Huang et al. (2015)
Yellow catfish, <i>Peteobagrus</i> <i>Fulvidraco</i>	25 (control) and 32°C	7 days	Acute	2.21 ± 0.01 g	Total protein (TP) (32°C); thyroxin (T4), immunoglobulin (Ig), complement 3 (C3) and complement 4 (C4) concentrations (32°C) ↑; hepcidin, IgM, LSZ (32°C) ↑	↓ Immune responses at 32°C	Foss et al. (2019)

(Continues)

TABLE 6 (Continued)

Species	Stress intensity	Stress duration	Stress type	Fish size/ fish age	Effects	Comments	References
Zebrafish	15 and 28°C Pathogen: Poly I:C	24 hr	Acute	-	IL-1β, iNOS, TNF-α, TLR3, IFN-1, IFN γ , IRF3, MDA-5, Mx (20°C) \uparrow	↓ Immune responses at 20°C	Dios, Romero, Chamorro, Figueiras, and Novoa (2010)

Abbreviations: 11 β -Hsd1L, 11 β -hydroxysteroid dehydrogenase 1-like; ACP, acid phosphatase; ALP, alkaline phosphate; B, blood; Br, brain; CFTR, cystic fibrosis transmembrane conductance regulator; DHX58, DExH-Box Helicase 58; E, erythrocytes; FCR, food conversion ratio; G, gill; GCSF, granulocyte colony-stimulating factor; H, heart; HIS, hepatocyte somatic index; I, intestine; IFN, interferon; IgM, immunoglobulin; IL, interleukin; iNOS, inducible NO synthase; IRF, interferon regulatory factor; ISG15, interferon-stimulated gene 15; ISI, intestine somatic index; I κ B α , inhibitor of nuclear factor kappa B; I κ B-delta; L, liver; LSZ, lysozyme activities; M, muscle; MU, mucus; Mx1, myxovirus (influenza virus) resistance 1; NF- κ B signal transduction cascade; NKCC, Na-K-Cl cotransporter; NKEF, natural killer cell enhancement factor; RHCg1, Rh-glycoproteins; RSAD2, radical S-adenosyl methionine domain containing 2; P, plasma; S, serum; SGR, specific growth rate; SOCS1, suppressor of cytokine signaling 1; SSI, spleen somatic index; STAT1, signal transducer and activator of transcription 1; Th1, T helper type 1; TLR3, toll-like receptor 3; TNF, tumor necrosis factor; VSI, viscera somatic index; WG, weight gain.
^aSymbols represent an increase (\uparrow) in the specified response; no change ($=$); decrease (\downarrow), increased trend ($/\nearrow$), decreased trend ($/\searrow$).

intended scope of this review section is to encompass only extreme temperature events that can affect immune function in aquaculture fish (Table 6). The most common characteristic of immune responses to temperature stress is increased antibody content (Bowden, 2008; Makrinos & Bowden, 2016; Pascoli et al., 2011; Yada & Tort, 2016). Serum lysozyme activities (LSZ) are important innate immune defense molecules in teleosts that are responsible for the cell wall breakdown of both gram-positive and gram-negative bacteria (Saurabh & Sahoo, 2008). This enzyme is opsonic and activates complementary systems and phagocytosis (Bowden, 2008; Dominguez et al., 2005; Saurabh & Sahoo, 2008). Besides, immunoglobulin M (IgM) is a predominant antibody commonly found in fish (Mashoof & Criscitiello, 2016; Uribe, Folch, Enriquez, & Moran, 2011; Warr, 1995). Hepcidin is a cysteine-rich antimicrobial peptide produced and secreted by the liver during inflammation; involved in the antimicrobial function (Álvarez, Guzmán, Cárdenas, Marshall, & Mercado, 2014; Z.-H. Huang et al., 2011; Reyes-López et al., 2018; J. Xie, Obiefuna, Hodgkinson, McAllister, & Belosevic, 2019). Moreover, interleukin (IL)-1 β and tumor necrosis factor-alfa (TNF- α) are considered important mediators for the inflammatory response in fish (Chen et al., 2019; Guo, Tang, Sheng, Xing, & Zhan, 2018; Huisng, Stet, Savelkoul, & Verburg-Van Kemenade, 2004). For instance, turbot, *Scophthalmus maximus* exposed to high temperatures (20, 23, 25, 27, and 28°C) resulted in a significant increase of mucus immunity, namely IgM, IL-1 β , hepcidin, transferrin, LSZ, and acid/alkaline phosphatase (Z.-H. Huang et al., 2011). Total leucocyte count, respiratory burst, phagocytic activity, phagocytic index, LSZ, alternative complement pathway (ACH₅₀) activities were decreased significantly in Mozambique tilapia, *Oreochromis mossambicus* exposed at low (19°C, 23°C) and high (35°C) temperatures compared to fish at 27°C during the 96 hr exposure experiment (Ndong et al., 2007). In another study a significant decrease in LSZ activity was found in Nile tilapia, *O. niloticus* reared at 33°C after 4 weeks of exposure (Dominguez et al., 2005). Significantly increased plasma IgM and LSZ were also reported for olive flounder, *P. olivaceus* exposed at 28 and 30°C for 2 weeks (J. H. Kim et al., 2019).

Temperatures beyond the preferred thermal window increase disease susceptibility in fish. In a study, rainbow trout, *O. mykiss* exposed to 12 and 15°C for 7 weeks lost immune performance against *Tetracapsuloides bryosalmonae*, a pathogen responsible for proliferative kidney disease. At 15°C, infection prevalence, pathogen load, lymphocytes, and upregulation of Th1-like signature cytokines and natural killer cell enhancement factors (NKEF) have been observed (Bailey et al., 2017). Gill and liver lysozyme activities, TNF-1 α , IL-1 β , IL-8, IL-10, Hepcidin-1, 2, and transforming growth factor (TGF- β 1) were found significantly lower in largemouth bass, *M. salmoides* stressed at 26°C compared to fish at 20°C (Sun et al., 2020). Atlantic cod, *G. morhua* exhibited increased beta-2 microglobulin (b2-M), major histocompatibility complex (MHC) class 1, IgM-L genes upregulation at 19°C compared to fish 10°C (Pérez-Casanova, Afonso, et al., 2008). A study on turbot, *S. maximus* reported increased IgM at 17, 20, 27, and 28°C after 7 days exposure, indicating the importance of temperature as an immune competence driver (Z. Huang et al., 2015). Atlantic halibut, *H. hippoglossus* exposed at 8, 12, 15, and 18°C for 3 months exhibited considerable influence on leucocyte population, LSZ, and serum protein content in fish reared at 18°C (Langston et al., 2002). It has been assumed that teleosts depend on nonspecific immunity during low-temperature stress, while at higher temperature stress, they rely on specific immune responses (Cabillon & Lazado, 2019). For example, in perch, *Perca fluviatilis* glucan binding proteins (nonspecific response) are predominant during low-temperature acclimated fish. Simultaneously, opsonin (specific response) was more effective during higher temperatures stress (Marnila & Lilius, 2015). In Atlantic salmon, *S. salar*, IL-1B, IL-8, and TNF- α genes were upregulated in fish skin acclimatized at 4 and 16°C compared to 10°C (Jensen et al., 2015). Atlantic cod, *G. morhua* acclimatized at 10 and 16°C showed significantly different cytokine gene expression in 16°C fish compared to 10°C (Hori et al., 2012). Short nose sturgeon, *Acipenser brevirostrum* showed upregulation of interferon regulatory factors (IRF 1 and 2) during high thermal exposure (Gradil et al., 2014). Abrupt temperature changes from 25 to 30°C resulted in the decreased respiratory burst (RB) and lymphocyte proliferation in Japanese medaka, *Oryzias latipes*. European seabass, *D. labrax* exposed to an extremely warm temperature (33°C) for 10 days showed increased TNF-1 α , RB, and leucocytes counts (Islam, Kunzmann, Thiele, & Slater, 2020). Barramundi, *Lates calcarifer* showed downregulation of immune genes in cold water (22°C) fish and upregulation in warm water (36°C) compared to fish at 28°C during 30 days exposure (Nikoskelainen et al., 2004).

These results highlight that climate change-induced environmentally relevant extreme temperature events resulted in diverse outcomes in immune responses, altering the types of interactions between hosts and pathogens. Fish become susceptible to potential pathogens and disease because of reduced immunity at both extreme cold and warm temperatures. Although for fish, immune responses exhibited some trends in the reported literature, however, there are still exceptional, contrasting, and contradictory reports. Extra caution should be taken when interpreting fish immune responses during extreme temperature events.

2.6 | Changes in ionic balance

Generally, fish in saline water gain more ions while in freshwater lose electrolytes (Imsland, Gunnarsson, Foss, & Stefansson, 2003; Kang, Chen, Chang, Tsai, & Lee, 2015; Strydom, Whitfield, & Paterson, 2002; Vargas-Chacoff et al., 2018). During extreme temperature events, ion transportation depends on metabolic energy rather than passive ion diffusion between the fish body and the environment and can lead to osmotic failure (Christensen et al., 2017; Evans & Kültz, 2020; Gonzalez & McDonald, 2000). Temperature change reduces the ion influx in freshwater fish, resulting in net ion loss, while in seawater fish, the opposite happens. To compensate for ion loss (freshwater) and ion gain (saltwater), fish increase $\text{Na}^+ \text{-K}^+$ ATPase and $\text{Na}^+ \text{-K}^+ \text{-Cl}^-$ cotransporter (NKCC) activities in gills, kidneys and intestine. Besides, fish decrease epithelium permeability in freshwater to slow down the loss, while increases in saltwater to accelerate ion outflow (Gonzalez & McDonald, 2000; Kang et al., 2015; Lorin-Nebel, Boulo, Bodinier, & Charmantier, 2006; Vargas-Chacoff et al., 2020). As a consequence, because of ionic imbalances, the central nervous system (CNS) function is compromised. For example, synapse transmission efficiency decreases, provoking primary stress responses and thus affecting all physiological functions in fish (Donaldson et al., 2008; Stewart, Aboagye, Ramee, & Allen, 2019; Vargas-Chacoff et al., 2018). Table 6 summarized the research on the impact of extreme temperature events on osmoregulatory ability. Temperature affects gills' plasticity through impairments of $\text{Na}^+ \text{-K}^+$ ATPase activities. Generally, $\text{Na}^+ \text{-K}^+$ ATPase activity is reduced at low temperatures and increased at higher temperatures (Chadwick & McCormick, 2017; Giffard-Mena, Lorin-Nebel, Charmantier, Castille, & Boulo, 2008; Vargas-Chacoff et al., 2018). $\text{Na}^+ \text{-K}^+$ ATPase activity affects branchial and renal chloride cells responsible for Na^+ and Cl^- uptake based on electrochemical gradients between blood and the surrounding water environment (Giffard-Mena et al., 2008; L'Honoré, Farcy, Blondeau-Bidet, & Lorin-Nebel, 2020; Lorin-Nebel et al., 2006). European seabass exposed to 33°C from 24°C resulted in increased Na^+ , Cl^- , and K^+ (Islam, Kunzmann, Bögner, et al., 2020). Vargas-Chacoff et al. (2018) investigated the interaction of temperature and salinities on osmo-tolerance and gill osmoregulatory proteins in Atlantic salmon, *S. salar* smolts. Warm stress was applied to fish in freshwater (FW) and seawater (SW) for 8 days at temperatures ranging from 14 to 17, 20, and 24°C. Fish exposed to SW and 24°C experienced 100% mortality, whereas no mortality occurred in any other group. Gill $\text{Na}^+ \text{-K}^+$ -ATPase activity and NKCC increased in SW fish compared to FW fish and decreased with higher temperatures (24°C) in both high and low salinities. Hu et al. (2019) reported that in milkfish, *Chanos chanos* acclimatized with hypothermal stress (18°C) for 21 days showed increased Na^+ , K^+ -ATPase and 11 β -hydroxysteroid dehydrogenase 1 and 2 (11 β -Hsd1 and 2) activities in gills compared to 28°C fish. Turbot, *S. maximus*, and Sole, *Solea senegalensis* acclimatized at 18 and 11°C, for 21 days showed a significant decrease in plasma Na^+ and Cl^- ions concentration compared to fish reared at 4 and 0°C (Foss et al., 2019). Bernard et al. (2019) reported the increased $\text{Na}^+ \text{-K}^+$ ATPase activity and plasma Na^+ , Cl^- in Atlantic salmon, *S. salar* reared at 5 and 8°C than fish at 15 and 20°C during 90 days of exposure. In recent studies, European seabass, *D. labrax* exposed to 8 and 32°C exhibited significantly increased $\text{Na}^+ \text{-K}^+$ ATPase, NKCC1, Cystic fibrosis transmembrane conductance (CFTR) upregulation while acclimatized at both low and high saline water (Islam, Kunzmann, Henjes, & Slater, 2021; Islam, Slater, & Kunzmann, 2020).

Unlike body temperature, ionic balances need to be adjusted and maintained in response to thermal stress to function efficiently. Temperature stress further exacerbates osmotic stress and salinity tolerance ability in fish. Fish that encounter both thermal and osmotic stressors seem to suffer excessively. Ion regulatory failure is inevitable

during acute extreme low and high thermal stress. With the threat of increased extreme temperature events, further studies are required to understand detailed mechanisms underlying ionic balance in fish along with other physiological parameters.

2.7 | Growth and reproductive performance

In ectotherms, environmental temperatures influence feed intake, digestion, absorption, and assimilation (Fu, Fu, Qin, Bai, & Fu, 2018; Person-Le Ruyet et al., 2004; Volkoff & Rønnestad, 2020). Fish trade-off extra energy in regaining homeostasis to endure extreme temperature events. In fish under non-stressed conditions, energy supply is proportionately distributed to maintain storage, development, growth, activities and body maintenance. However, during a stressful situation, maintenance costs increase to cover extra energy requirements in stress minimization and cellular damage repair, which offset energy allocated for growth, development, immunity, storage and reproduction. Thus, growth, reproduction and immune performance are decreased. Growth inhibition and changes in reproduction performance and sex ratio during temperature stress have been reported and reviewed (Geffroy & Wedekind, 2020; Islam, Kunzmann, Henjes, & Slater, 2021; Tort, 2011; Vandeputte et al., 2020). However, for some teleosts within their preferred thermal window, temperature increases within the aerobic scope are likely to be advantageous (Enes, Panserat, Kaushik, & Oliva-Teles, 2006; Handeland, Imsland, & Stefansson, 2008; Imsland, Sunde, Folkvord, & Stefansson, 1996). A slight temperature increase (eustress) results in higher energy and metabolic activities, higher absorption and assimilation rates and faster physiological activities lead to a higher growth rate (Pörtner et al., 2001; Sotoyama et al., 2018; Takasuka & Aoki, 2006; Zanuy & Carrillo, 1985). In contrast, laboratory-controlled temperature studies demonstrated that temperature could reach the deleterious point for growth performance (Angilletta, Huey, & Frazier, 2010; Bowden, 2008; Islam, Kunzmann, Bögner, et al., 2020; Mateus et al., 2017; Neuheimer, Thresher, Lyle, & Semmens, 2011). Reduced growth, feed intake, and food conversion efficiency are commonly observed during temperature stress (Table 6). Striped catfish, *Pangasianodon hypophthalmus* exposed at 25°C exhibited decreased growth performance compared to fish at 30 and 35°C during the 56 days study (Phuc et al., 2017). European seabass, *D. labrax* acclimatized at extreme cold (8°C) and high (32°C) temperatures resulted in significantly reduced growth performance during 30 days of thermal exposure (Islam, Kunzmann, Bögner, et al., 2020). Atlantic salmon, *S. salar* exhibited decreased growth performance at 17 and 22°C compared to 10°C during the 5 months of study (Wade et al., 2019). In another study, the same fish exposed to 16 and 20°C showed significantly lower growth performance than fish at 12°C during 99 days study (Tromp et al., 2018).

Changes in ambient water temperatures and other factors have been reported to affect spawning, reproduction, phenology, sexual maturity, and sex differentiation by interfering with the steroidogenesis and gametogenesis process (Chang et al., 2018; Pörtner et al., 2001; Seebacher & Post, 2015; Servili, Canario, Mouchel, & Muñoz-Cueto, 2020). Teleost reproductive performance is expected to be affected by climate change-induced temperature events (Miranda, Chalde, Elisio, & Strüssmann, 2013; Pankhurst & King, 2010; Servili et al., 2020). Temperature changes either advance or retard gametogenesis and maturation through endocrine disruption (Mateus et al., 2017; Wurtsbaugh & Davis, 1977; Zanuy & Carrillo, 1985). Atlantic salmon, *S. salar* exposure to increased temperature during gametogenesis resulted in impairment in steroid synthesis in gonads, liver vitellogenin production, and alteration of hepatic estrogen dynamics (Takasuka & Aoki, 2006). These changes ultimately result in reduced reproductive investment and gamete viability (H. King & Pankhurst, 2003; H. R. King & Pankhurst, 2004a). During different gonadal maturation phases, high-temperature exposure impairs gonadal steroidogenesis, causes delays, or inhibits pre-ovulatory shift (H. King & Pankhurst, 2003; H. R. King & Pankhurst, 2004b; Pankhurst & King, 2010; Pörtner et al., 2001; Żarski et al., 2017). In Northern pike, *Esox lucius* (Cejko, Krejszeff, Judycka, Targońska, & Kucharczyk, 2019), Atlantic salmon, *S. salar* (Taranger et al., 2003), rainbow trout, *O. mykiss* (Dadras, Dzyuba, Golpour, Xin, & Dzyuba, 2019) and hound, *Mustelus schmitti* (Elisio, Awruch, Massa, Macchi, & Somoza, 2019) inhibition of spermiation was observed during elevated temperature exposure. Sperm motility and quality were also

affected by climate change-induced temperatures in coruh trout, *Salmo coruhensis* (Tunçelli & Memiş, 2020), rainbow trout, *O. mykiss* (Dadras et al., 2019), sturgeon, *A. brevirostrum* (Gilroy & Litvak, 2019) and streaked prochilod, *Prochilodus lineatus* (Paula et al., 2019). Thus, from the above discussion we can assume that growth, reproductive performance, and physiological fitness of aquaculture species in captive environments and the wild will be affected by climate change-driven extreme temperature events. More studies on commercial aquaculture species and climate change-induced extreme temperature events along with other environmentally realistic parameters are required to understand the growth and reproductive performances.

3 | MITIGATION MEASURES FOR FISH DURING EXTREME TEMPERATURE EVENTS

Few strategies are currently available to mitigate climate change impacts on fish arising from extreme low and high-temperature events (Table 7). It is essential to find ways to improve fish physiological fitness where water temperatures fluctuate largely (D'Abramo & Slater, 2019; Islam, Kunzmann, Henjes, & Slater, 2021). Temperature control could be an option to keep fish healthy during extreme temperature events, which is only possible in highly controlled aquaculture systems. Pond coverings or increased pond depth (Al-Deghayem & Suliman, 2019; Hassaan et al., 2019; Kemski, Wick, & Dabrowski, 2018), as well as using recirculating aquaculture system (RAS) and biofloc technology (El-shebly, 2016; Gallardo-Collí, Pérez-Rostro, & Hernández-Vergara, 2019) could be other important considerations. However, in large captive water (lake, ponds) and cage culture systems in open water (lagoons, bay, sea, offshore farm), water temperature control is not always possible. Thus, alternatives are required to fare fish better during extreme temperature events. Development of temperature stress tolerant fish species and strains, farming of alternative culture species, species with short production cycle, even shifting of aquaculture sites could be adopted as possible options to mitigate extreme temperature events (D'Abramo & Slater, 2019). However, applied research is needed to identify the most favorable alternative option to minimize extreme thermal events. Besides, dietary and nutritional management strategies could be another promising option to ameliorate thermal stress in fish. For example, the synthetic luteinizing hormone-releasing hormone has been found to improve reproductive performance and mitigate the inhibitory effects of elevated temperature in both sexes of *S. salar* (H. R. King & Pankhurst, 2004a, 2004b), *O. niloticus* (Dussenne, Gennotte, Rougeot, Mélard, & Cornil, 2020), and freshwater eels, *Anguilla* spp. (Burgerhout, Lokman, van den Thillart, & Dirks, 2019). A recent study by Fei et al. (2020) reported that dietary amino acids could enhance sex steroid hormone synthesis and growth performance of yellow catfish, *Pelteobagrus fulvidraco*. Dietary manipulation also improved physiology of African Catfish, *Clarias gariepinus* (Al-Deghayem & Suliman, 2019), pearl gourami, *Trichogaster leeri* (Ghosí Mobaraki, Abedian Kenari, Bahrami Gorji, & Esmaeili, 2020), red seabream, *Pagrus major* (M. S. Hossain et al., 2019), butter catfish, *Ompok bimaculatus* (G. Chowdhury et al., 2020) and amberjack, *Seriola dumerili* (S. Hossain et al., 2018). However, the use of endocrine therapy and a nutritional management approach as potential thermal mitigation measures to support natural gametogenesis is still unexplored.

Functional and supplementary feed additives are also promising for fish to cope with climate change-induced extreme temperature events (de Mattos et al., 2019; Hassaan et al., 2019; Herrera, Mancera, & Costas, 2019; Schrama et al., 2017). For example, essential oils could be used as stress-reducing agents as reviewed in De FreitasSouza et al. (2019), or dietary selenium nanoparticles (Kumar et al., 2019), zinc nanoparticles (Kumar, Chandan, Wakchaure, & Singh, 2020), mushrooms (Dawood et al., 2020), fennel seeds (Al-Sagan, Khalil, Hussein, & Attia, 2020), carotenoids (Yang Liu, Liu, et al., 2019) and vegetable oil (El Asely et al., 2020) have been reported to mitigate thermal stress (both low and high) in different fish species. Essential oils can also be used to mitigate thermal stress responses in fish (reviewed in De FreitasSouza et al., 2019). Gilthead seabream, *S. aurata* fed with a high oil content diet before the onset of winter improved fish health conditions (Ibarz et al., 2010). Growth performance and metabolic responses of barramundi, *L. calcarifer* were improved significantly fed with polyunsaturated fatty acid

TABLE 7 Research on dietary and nutritional mitigation measures to mitigate thermal stress

Species	Ingredients/diets	Temperature stress intensity	Stress duration	Fish size/age	Comments	References
African catfish, <i>Clarias gariepinus</i>	Fishmeal-based diet (D1), soymeal-based diet (D2), pea-meal based diet (D3)	24, 28 (control), and 32°C	16 weeks	101–104 g	Fishmeal or soy-meal positively improved the health status during thermal stress	Al-Deghayem and Suliman (2019)
Barramundi, <i>Lates calcarifer</i>	Long-chain (\geq C20) polyunsaturated fatty acids (LC-PUFA); Stearidonic and γ -linolenic acid	20 and 30°C (control)	5 weeks	50 ± 1.4 g	Stearidonic and γ -linolenic acid-enhanced low-temperature tolerance	Alhazzaa, Bridle, Nichols, and Carter (2013)
Pufferfish, <i>Takifugu obscurus</i>	Astaxanthin (0 (control), 20, 40, 80, 160, and 320 mg/kg)	25 (control) and 35°C	8 weeks	8.3 ± 0.08 g	80, 160, and 320 mg/kg astaxanthin improve resistance against high-temperature stress	C. H. Cheng et al. (2018)
Nile tilapia, <i>Oreochromis niloticus</i>	Dietary fatty acids (fish, linseed, sunflower, olive, and coconut oils)	28 (control) and 22°C	12 weeks	9.22 ± 0.81	Dietary source containing more PUFA and less SFA improves performance	Corrêa, Nobrega, Mattioni, Block, and Fracalossi (2017)
Nile tilapia, <i>O. niloticus</i>	Plant oil, fish oil, and mixes of plant oils as fish oil	28 (control) and 22°C	9 weeks	8.43 ± 1.60 g	Fish oil performed best during cold exposure	Corrêa, Nobrega, Block, and Fracalossi (2018)
Nile tilapia, <i>O. niloticus</i>	White button mushroom (WBM): 0, 0.5, 1, 2, and 4%	26 (control) and 32°C	60 days	17.62 ± 0.06 g	WBM is recommended to cope with heat stress	Dawood et al. (2020)
Nile tilapia, <i>O. niloticus</i>	Fish oil (FO), corn oil (CO), sunflower oil (SFO), and linseed oil (LnO)	28 (control) and 22°C	8 weeks	7.31 ± 0.05 g	FO with either CO or LnO could maintain the normal growth performance and feed utilization with enhanced antioxidant capacity under suboptimal temperature	El Asesy, Reda, Salah, Mahmoud, and Dawood (2020)
Nile tilapia, <i>O. niloticus</i>	Propolis extract (0 (control), 1, 2, 3 and 4 g kg ⁻¹)	16, 17, and 19°C	60 days	25.40 ± 0.84 g	Propolis at 3 and 4 g kg ⁻¹ could enhance fish resistance to cold temperature stress during the winter season	Hassan, El Nagar, Salim, Fitzsimmons, and El-Haroun (2019)

(Continues)

TABLE 7 (Continued)

Species	Ingredients/diets	Temperature stress intensity	Stress duration	Fish size/age	Comments	References
Atlantic cod, <i>Gadus morhua</i>	Amino acid supplementations: Tryptophan (Trp) and phenylalanine (Phe)	5 (control), 10, and 15°C	7 days	31.8 ± 1.22 g	During thermal stress, both Trp and Phe supplementations reduced the stress markers in the cod; hence, they could be used as additives for the stress attenuation	Herrera et al. (2017)
Rainbow trout, <i>Oncorhynchus mykiss</i>	Dietary tryptophan (Trp): 0% (control), 0.5% (T0.5), and 1% (T1)	5, 14 (control), and 20°C	70 days	~50 g	The 0.5% Trp was found to be related to stress suppression	Hoseini et al. (2020)
Pangasianodon hypophthalmus	Dietary selenium nanoparticles (0 [control], 5, 10, 15 mg/kg) and riboflavin (0.5 mg/kg)	25, 28 (control), and 34°C	95 day	5.35 ± 1.02 g	Diets supplemented with riboflavin @ 5 mg/kg diet and se-NPS @ 0.5 mg/kg diet could confer protection to the fish against thermal stress	Kumar et al. (2019)
Yellow catfish, <i>Percobagrus fulvidraco</i>	Dietary carotenoid: 0 (control), 50, 100, 150, 200 or 250 mg/kg	25 (control) and 32°C	60 days	2.21 ± 0.01 g	A basal diet with 150–200 mg/kg carotenoids enhances immune responses to disease and imparts resistance to high-temperature stress	F. Liu, Qu, et al. (2019)
Giltthead seabream, <i>Sparus aurata</i>	Additional Vit C, E, non-essential amino acids	8, 15 (control), and 20°C	116 days	87 ± 5 g	Winter feed diet tested seems to have positive effects during thermal stress	Schrama et al. (2017)
Barramundi, <i>L. calcarifer</i>	Dietary n-3 highly unsaturated fatty acid (n-3 HUFA) content	20, 28, and 32°C	6 weeks	176 ± 3.3 g	Feed that is high in dietary energy and n-3-HUFA improves productivity and physiological performances	Williams, Barlow, Rodgers, and Agcopra (2006)
Yellow catfish, <i>Plateosaurus multitrack</i>	Dietary linolenic acid (LNA) and linoleic acid (LA) ratios: D0.27, D0.82, D1.71, and D2.63	27 (control) and 36°C	8 weeks	~22.88 g	Higher-level dietary LNA/LA ratios are beneficial for HUFA-rich gonadal development and steroid synthesis of yellow catfish during high-temperature stress	Fei et al. (2020)

TABLE 7 (Continued)

Species	Ingredients/diets	Temperature stress intensity	Stress duration	Fish size/age	Comments	References
Giltthead seabream, <i>Sparus auratai</i>	Winter feed (marine-derived protein sources and supplemented in phospholipids, vitamin C, vitamin E, and taurine)	7.6–16.5°C	116 days	87 ± 5 g	Winter feed counteracts on thermal stress	Richard et al. (2016)

supplemented diet during suboptimal temperature stress exposure (Alhazza et al., 2013; Williams et al., 2006). Improved immune status has been reported for gilthead seabream, *S. aurata* fed with a winter feed enriched with vitamin C, E, propolis, phycocyanin, minerals, choline, highly unsaturated fatty acids inositol, and phospholipids (Islam, Kunzmann, Henjes, & Slater, 2021; Jia, Jing, Niu, & Huang, 2017; Schrama et al., 2017; Tort et al., 2004). Nile tilapia, *O. niloticus*, fed diets rich with vitamin E, C and polyunsaturated fatty acids have been reported to curb both winter cold and summer heatwave stress (Corrêa et al., 2017, 2018; Marston, 2010). Dietary astaxanthin improves growth, nonspecific immune responses, antioxidant defense system, and improves resistance against high-temperature stress in pufferfish, *Takifugu obscurus* (C. H. Cheng et al., 2018). Nonspecific immunostimulants, such as beehive extracts and propolis, have been reported to mitigate thermal stress by stimulating nonspecific immunity in Nile tilapia, *O. niloticus* and rainbow trout, *O. mykiss* (Acar, 2018; Morsy et al., 2013). C. H. Cheng et al. (2018) investigated the effects of dietary astaxanthin on growth performance, biochemical parameters, ROS production, and immune-related gene expressions in pufferfish, *T. obscurus* under high-temperature stress at 25–28°C for 8 weeks. The results showed that those fish fed with astaxanthin significantly improved growth performance, immune activities and decreased antioxidant activities. F. Liu, Qu, et al. (2019) evaluated the dietary carotenoid supplementation during high-temperature stress (25°C, 32°C for 60 days) and disease resistance ability in yellow catfish, *P. fulvidraco*. Increased growth, total antioxidant capacity, CAT, SOD, hepcidin, IgM, and lysozyme G were observed in carotenoid supplemented fish groups. The authors concluded that carotenoids enhance immune responses to disease and impart resistance. In face of global climate change and frequently occurring extreme temperature events, nutritional mitigation of thermal stress in fish is important to develop climate-smart environmentally sustainable aquaculture. Dietary vitamins C and E, propolis, fatty acids, astaxanthin, carotenoids can be used to feed aquaculture fish to ameliorate extreme thermal stress events. However, dietary and nutritional manipulation's effectiveness depends on species, types of ingredients, concentration, dosages, duration, and mode of administration. However, these topics are poorly studied. Future studies are needed on a range of aquaculture species, stress-specific ingredients, dose, and concentration to maximize benefits and avoid suppressive impacts.

4 | CONCLUSIONS

It is essential to know how fish will cope with future climate change-induced extreme temperature events, along with other environmental challenges, to understand the impacts on aquaculture and fisheries production. Based on this review, it is apparent that extreme temperature events can significantly impair fish growth, reproduction, metabolism, physiology, behavior, future fitness and survival. Although fish can cope with a certain degree of thermal stress by offsetting growth and physiological fitness, only minimal data exist on coping within the context of extreme temperature events. It is essential to conduct more species-specific and environmentally realistic studies to understand future climate change-induced fish ecophysiology. It is also necessary to select a broader range of stressors and model fish species to understand unexpected outcomes under different climate scenarios. Additional research on non-lethal endpoints to trace stress events in fish is required. No studies exist with a comparative-collective approach to investigate fish stress responses along with life cycles, feeding strategies, or behavioral responses under diverse culture conditions or regimes. Exploring these areas could open a new window for climate-smart aquaculture research and production. Moreover, attention should be given to mitigating extreme temperature events impacting fish in open aquaculture systems. Development of stress-tolerant fish species and strains, farming of alternative species, shifting of aquaculture sites could be options to mitigate extreme temperature events. More applied research is required to identify the most favorable alternative options to minimize the negative effects of extreme climatic events. In addition to these, dietary and nutritional mitigation measures could be a promising option to manage thermal stress. However, this research area is understudied among diverse fish species groups. A wide range of studies with a range of supplementary ingredients is required to understand nutritional measures as a mitigation option to combat climate change-induced thermal stress. Another important point to mention is that most of the climate change impact

studies have been conducted on American and European aquaculture species. Only a few studies are available for a few flagship aquaculture species in Asia, the major global seafood supplier. Particular attention should be given to research on the vastly understudied Asian aquaculture species to prepare better in the face of global climate change.

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