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Review

Stress in Fish: Neuroendocrine and Neurotransmitters Responses

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Abstract: Farmed fish encounter persistent challenges stemming from a variety of environmental challenges and human activities that induce both acute and chronic stress, resulting in increased vulnerability to diseases and mortality. Therefore, it is essential to comprehend the stressors and corresponding stress responses in fish to recognize and mitigate harmful stress during aquaculture practices. In this review, we provide an overview of the various stressors present in aquaculture, along with the resultant alterations in neuroendocrine responses, including the BSC axis, HPI axis, and CNSS, as well as neurotransmitter levels within the nervous system, experienced by fish under different types of stress. Fish possess well-developed endogenous nervous and endocrine systems that respond to stress, with complex communication networks among these systems demonstrating distributed collaboration. An understanding of the neuroendocrine and neurotransmitter responses to stress may enhance our comprehension of fish stress mechanisms and facilitate the development of an integrated dietary supplementation strategy and improve their resilience against the diverse stresses encountered in aquaculture.

Keywords: stress; aquaculture; neural responses; neuroendocrine responses; fish

1. Introduction

Over the past few decades, the growing requirement for fish protein and the change in dietary habits have caused the explosive development of aquaculture [1,2]. However, the growth of aquaculture is limited by the various environmental and husbandry-related stress which results in the decline of disease resistance and subsequent death in fish. While the definition of stress remains a topic of debate, the most recent literature, acknowledged by the majority of researchers, suggests that the colloquial use of the term "stress" should be restricted to situations in which an environmental demand exceeds an organism's natural regulatory capacity and adaptive resources in a maladaptive manner [3,4]. It has been demonstrated that, in response to stress, fish exhibit a series of neural and neuroendocrine reactions aimed at participating in stressor recognition or alleviating the adverse effects of stressors and maintaining homeostasis [5,6]. Depending on the intensity and duration of the stressor, acute stress often shows beneficial effects, while chronic stress normally stands on the opposite side, that increases the fish vulnerability to fatal diseases [7]. The terms "acute" and "chronic" are context-dependent, which should be based on the duration of its consequences on the

physiology of the animal [8]. For instance, being caught in a net or escaping from a predator would typically be classified as “acute stress,” whereas being overcrowded in a tank or occupying a low position in the social hierarchy would generally be categorized as “chronic stress”. Therefore, it is crucial to address the understanding of the mechanisms of the neural and neuroendocrine responses when fish cope with stress. This article presents a comprehensive overview of the prevalent stressors in aquaculture, as well as the intricate interplay between neural and neuroendocrine responses in fish during periods of stress. It aims to facilitate a deeper understanding of fish stress and to illustrate an integrated adaptation strategy in fish that enhances their resilience against the multifaceted challenges they encounter.

2. Stressors in Aquaculture

Common stressors in aquafarming activities, such as unsuitable temperature (high or low temperature), pH (overacid or overalkali), dissolved oxygen (hypoxia or hyperxia), microorganisms (pathogenic parasite, bacteria or viruses), and overcrowding, etc., can be classified as environmental and anthropogenic stressors according to the stress sources, which can be further divided into physical, chemical, biological, and procedural stressors (Table 1). Changes in these stressors during the culture period can adversely affect the behavior, growth, immunity, and reproduction of fish, leading to economic loss to aquafarmers. Oxygen delivery limitations and cardiac failure have been known as the critical element in sublethal thermal stress [9]; however, stressor usually does not appear alone. For instance, increases in water temperature will not only elevate the fish oxygen demand and reduce the dissolved oxygen in the water, but also increase the toxicity of harmful substances (such as unionized ammonia, toxic microalgae, etc. [10,11]), and these will accelerate the homeostasis imbalance in fish. Meanwhile, unlike livestock, fish live in water, which make it hard for aquafarmers to detect anomalies in time. Therefore, the stress in aquaculture should not be overlooked, environmental monitoring and control are required the intensive and sustainable aquaculture. However, it is impossible to maintain an absolute stable condition without any stressors during farming processes. In addition, fish have a well-developed and complex endogenous neural and neuroendocrine regulation, which can induce a series of signaling cascades to deal with threatened homeostasis caused by stress. Understanding the cellular and molecular mechanisms of the neural and neuroendocrine responses and their network during stress, may help to reduce the negative effects of stress, improve disease resistance and develop strategies to mitigate the harmful effects of stress by regulating the neural and neuroendocrine system in fish.

Table 1. Common stressors in aquaculture.

Type of stressors	Examples	Reference
Physical	Water temperature;	[179–181]
	Photoperiod;	[182–184]
	Sound;	[185–187]
	Turbidity	[188–190]
	...	
Chemical	pH;	[191–193]
	Salinity;	[194–197]
	Dissolved Oxygen;	[198–200]
	Alkalinity;	[201,202]
	Carbon dioxide complexities;	[203–205]
	Nitrite;	[206–208]
	Ammonia;	[209–211]
	Hydrogen sulfide;	[212,213]
Iron;	[214,215]	
Heavy metal;	[216–218]	
Pesticides	[219–221]	

	...	
	Algal toxicosis;	[222,223]
	Microorganisms;	[224–226]
	Parasites;	[227–229]
Biological	Predators;	[230–232]
	Social rank;	[233–235]
	Environmental enrichment	[236–238]
	...	
	Overcrowding;	[239–241]
	Handling;	[242–244]
Procedural	Netting	[245,246]
	Feeding;	[247–249]
	Transportation	[250–252]
	...	

3. Neurotransmitters and Neuroendocrine Systems Respond to Stress in Fish

When fish are stressed, the primary stress responses are the neural and neuroendocrine responses. A perceived threat triggers the activation of the neural circuit in the brain, leading to the activation of downstream endocrine systems and other responsive organs [3,12]. The nervous system utilizes a variety of neurotransmitters in response to stress (Figure 1). In fish, three major neuroendocrine systems respond to stress: the brain-sympathetic-chromaffin cells (BSC) axis, the hypothalamus-pituitary-interrenal (HPI) axis, and the caudal neurosecretory system (CNSS) (Figure 2, Table 2).

Table 2. Comparison of neuroendocrine systems in fish.

System	Primary Components	Response Timing	Magnitude/Duration
Brain-Sympathetic-Chromaffin Cells (BSC) Axis	Brain (sympathetic neurons); Sympathetic nerves; Chromaffin cells (in head kidney; catecholamines)	Immediate (<1 min to hours)	Rapid onset; Short duration (minutes to hours); High peak magnitude
Hypothalamus-Pituitary-Interrenal (HPI) Axis	Hypothalamus (CRH/ACTH-releasing factors); Pituitary (ACTH); Interrenal tissue (cortisol/corticosterone)	Delayed (hours to days)	Slower onset; Long-lasting (days to weeks); Moderate to high magnitude (sustained)
Caudal Neurosecretory System (CNSS)	Dahlgren cell (urotensins, isotocin, CRH); Urophysis;	Variable (minutes to hours, depending on stimulus)	Moderate onset; Moderate duration (hours); Target-specific magnitude

3.1. Neurotransmitters During Stress

3.1.1. Acetylcholine (ACh)

ACh is a neurotransmitter released by cholinergic neurons and is found in both the peripheral nervous system (PNS) and central nervous system (CNS) of fish [13]. Cholinergic systems in the brain play a regulatory role in numerous physiological processes, including muscle contraction, autonomic regulation, cognitive function, and stress responses. Cholinergic neurons are distinguished by the presence of choline acetyltransferase (ChAT), which facilitates ACh synthesis, and the vesicular acetylcholine transporter (VACHT), which transports ACh into vesicles. The presynaptic release of ACh from vesicles into the synaptic cleft triggers the activation of nicotinic and muscarinic ACh receptors (nAChR and mAChR, respectively) before undergoing degradation by acetylcholinesterase (AChE) into acetate and choline. The latter is then transported back into the presynaptic neurons via the high-affinity choline transporter (HACT) [14].

It is widely acknowledged that the majority of stress leads to a rapid, transiently enhanced release of ACh in the cholinergic system [15,16]. The release of ACh may modulate the activation of stress-related signaling pathways. However, depending on the source and intensity of the stressors, the level of ACh may decrease following stress under certain conditions [17]. Due to the low concentrations and rapid turnover of ACh, measuring its levels in the fish brain has been challenging. Therefore, it is common practice to assess the activity of ACh-related enzymes and the expression of ACh receptors in order to evaluate the responses of the cholinergic system during stress. Positive correlations have been observed between the ACh content and the ChAT activity in various fish, including carp (*Cyprinus carpio*), rainbow trout (*Oncorhynchus mykiss*) and eel (*Anguilla anguilla*) [18], while inhibition in the expression and activity of AChE has been noted during different stress conditions, such as heavy mental load [19], temperature changes in carp (*C. carpio*) [20], pesticide exposure in tilapia (*Oreochromis mossambicus*) [21,22], parasite infestation in killfish (*Fundulus parvipinnis*) [23], and exposure to fired underwater currents in rainbow trout (*O. mykiss*) [24]. In addition, AChE is widely recognized as the primary neurotoxic biomarker that reflects cholinergic responses during various stressors in fish [25]. Reduced AChE activity implies a decline in cholinergic transmission and subsequent accumulation of ACh. A study by Jifa et al. (2006) reported no significant inhibition of AChE in the brain of Japanese seabass (*Lateolabrax japonicus*) exposed to benzo[a]pyrene (BaP) at concentrations of 2 and 20 $\mu\text{g L}^{-1}$ for 6, 12, and 18 days. This suggests that these concentrations had no appreciable effect on AChE activity [26]. Additionally, studies had shown that fish exposed to polycyclic aromatic hydrocarbons (PAHs) with a low molecular weight did not induce changes or cause stimulation of AChE activity [27]. It has also been reported that stress can induce the up-regulation of AChR in fish [28]. The activation of nAChR can induce anxiolytic like effects in zebrafish [29], while the antagonist of mAChR can disrupt the stress responses caused by organophosphorus exposure [30].

3.1.2. Glutamate (Glu) and Gamma-Aminobutyric Acid (GABA)

Glu and GABA are the principal neurotransmitters in the central nervous system. Glu and GABA are synthesized not only in the brain, but also in peripheral tissues and organs [31,32]. Glu primarily functions as an excitatory neurotransmitter, whereas GABA serves as an inhibitory neurotransmitter. These two substances exhibit opposing yet complementary physiological roles, collectively regulating the normal functioning of the nervous system [33]. Glutamate is synthesized in neurons from intermediates of the glucose-derived tricarboxylic acid cycle and branched-chain amino acids, a process catalyzed by glutaminase utilizing glutamine (Gln) as a precursor. Within neurons, cytoplasmic glutamate is encapsulated into vesicles by vesicular glutamate transporters for subsequent extracellular release. Upon neuronal depolarization and the initiation of signal transduction, these glutamate-containing vesicles are released into the synaptic cleft, where they bind to three types of ionotropic glutamate receptors (iGluRs), N-methyl-D-aspartic acid receptor (NMDA), A-amino-3-hydroxy-5-methyl-4-isoxazole-propionic acid receptor (AMPA), and Kainate receptors [34] — as well as metabotropic glutamate receptors (mGluRs), before being removed and

converted into Gln through the action of glutamine synthetase [35]. The synthesis of GABA is facilitated by the enzymatic action of glutamic acid decarboxylase (GAD), which catalyzes the α -decarboxylation reaction using Glu as a precursor. GABA exerts its effects through GABAA and GABAB receptors, which are classified into two primary categories: ionotropic receptors and metabotropic receptors, respectively [36].

When subjected to stress, maintaining the balance of Glu and GABA is crucial for the physiological adaptation of fish. An imbalance between Glu and GABA can disrupt their homeostasis, leading to increased excitatory toxicity, which ultimately results in cellular swelling, irreversible neuronal damage, and even cell death [37,38]. It has been reported that glutamic acid effectively alleviates the adverse effects of saline-alkali environments on aquatic organisms such as grass carp and tilapia [39,40]. In response to heat stress challenges, rainbow trout activate the glutamate-glutamine metabolic pathway to mitigate oxidative damage caused by elevated temperatures [41]. Notably, under saline-alkali environmental stress conditions, disruption or blockage of the glutamate metabolic pathway directly affects ammonia excretion processes in crucian carp, resulting in nitrogenous waste accumulation within the body that may ultimately trigger an inflammatory response [42]. In aquatic animals, GABA plays a crucial role in regulating glucose homeostasis during fasting stress [43], alleviating symptoms of hyperglycemia, and enhancing the resilience of animals subjected to heat stress [44]. Further research has demonstrated that incorporating GABA into animal feed can significantly increase serum GABA levels while concurrently reducing serum concentrations of glucose and corticosterone hormones in stressful environments, thereby effectively mitigating the stress response [45,46]. In summary, Glu and GABA system plays an indispensable regulatory role under various environmental stresses.

3.1.3. Catecholamine (CA)

CAs are synthesized in the brain, in the adrenal medulla (head kidney in fish), and by certain sympathetic nerve fibers. These CAs, which include dopamine (DA), norepinephrine (NE), and epinephrine (E), are biosynthesized from tyrosine (Tyr). The process begins with hydroxylation catalyzed by tyrosine hydroxylase (TH), converting Tyr into dihydroxyphenylalanine (DOPA). Following this, DOPA undergoes decarboxylation mediated by aromatic amino acid decarboxylase (AADC) to yield DA. In certain neurons, DA functions directly as a neurotransmitter, whereas in others, DA may be further transported into chromaffin granules for additional processing. Within these granules, DA is further hydroxylated by dopamine- β -hydroxylase (DbH) to produce NE, which is then methylated through a reaction catalyzed by phenylethanol-N-methyl transferase (PNMT) to form E [47]. The activities of CAs are mediated by their binding to various receptors. In detail, the dopamine receptors are classified in two different families, D1-like (encompassing D1 and D5 subtypes) and D2-like (including D2, D3, and D4 subtypes), while adrenergic receptors are categorized into three different families, ADR α 1 (α 1A, α 1B, α 1D), ADR α 2 (α 2A, α 2B, α 2C) and ADR β (β 1, β 2, and β 3), based on their molecular structure and receptor pharmacological properties [48,49]. CAs play a pivotal role in intricate processes like behavior, movement, emotion, and memory [50–52].

When fish and other vertebrates experience stress, they rapidly release CAs to elevate plasma glucose levels, thereby providing essential energy support for the instinctive 'fight-or-flight' response [53]. In marine organisms, environmental factors significantly influence their stress responses. For example, in response to fluctuations in seawater temperature and salinity, *Harpagifer antarcticus* exhibits significant alterations in various neurotransmitters and DA and NE levels within its system, further emphasizing the critical role of stress responses in the adaptation of marine organisms to environmental changes [54]. Zebrafish subjected to acute osmotic pressure changes and hypoxia exhibit significant reduction in NE and E levels within their brains, which subsequently affect their reproductive signaling processes, thereby revealing the potential impact of stress responses on fish reproductive health [55]. The hypoxia-tolerant tropical fish *Pygocentrus nattereri* experiences notable effects of endogenous myocardial NE and E on cardiac function when exposed to hypoxic conditions, facilitating its ability to sustain vital activities in low-oxygen environments [56]. Furthermore, E play

a crucial role in regulating energy balance in the livers of chondrichthyan fish, particularly under stressful conditions [57]. In aquaculture practices, the farming environment exerts a profound influence on fish stress responses. Gilthead seabream larvae, when subjected to adverse conditions such as high-density farming and fasting, exhibit significant alterations in their DA and NE levels and brain monoamines to adapt to these challenges [58]. Conversely, following exposure to low farming densities, *O. mykiss* experiences disruptions in the levels of brain CAs, leading to a series of physiological abnormalities such as reduced survival rates, impaired growth and feed efficiency, and dysregulation of immune and inflammatory systems [59]. Additionally, the CA levels in rainbow trout are also influenced by farming density, further affirming the significance of the farming environment on fish stress responses [59]. In addition to farming density, various environmental factors can also influence fish stress responses. For instance, exposure to AlCl_3 results in decreased levels of GABA, DA, and NE in zebrafish, while glutamate levels are elevated [60]. Similarly, in adult zebrafish exposed to methamphetamine (METH), their brain levels of DA and NE decrease in a time- and concentration-dependent manner, accompanied by an increase in anxiety-like behavior [61].

3.1.4. Serotonin

The monoamine serotonin, also known as 5-hydroxytryptamine (5-HT), is a major neurotransmitter in the CNS and PNS of fish. It plays a crucial role in vasoconstriction [62], hemostasis, intestinal motility [63], and stress responses [64]. 5-HT is synthesized from dietary L-tryptophan in a two-step process: first, it undergoes hydroxylation by tryptophan hydroxylase (Tph) to form 5-hydroxytryptophan (5-HTP), and then it is decarboxylated by aromatic amino acid decarboxylase (Aadc) to form 5-HT. 5-HT is further metabolized to 5-hydroxyindole acetic acid (5-HIAA) through a combination of monoamine oxidase (Mao) and aldehyde dehydrogenase (Ad) [65]. In addition, serotonergic neurons can also be identified based on 5-HT transporter (Sert) and 5-HT receptors.

Many studies have demonstrated that stress can induce hyperactivity of serotonin metabolism in fish [66,67]. In tilapia and zebrafish, social stress and acute isolation stress could lead to a reduction in the level of 5-HT and an increase in its metabolites 5-HIAA [68–70]. The tryptophan hydroxylase 1a (*tph1a*) gene was significantly upregulated in the gill of zebrafish after long-term exposure of microplastics and heavy metal [71]. Meanwhile, researches have also shown that after repeated heat stress and acute ammonia exposure, there is a significant reduction in the levels of 5-HT and the expression of *tph1* and *tph2* in the brain [72,73]. Acute social stress has been reported to downregulate the transcription of Mao A gene expression and enhance 5-HT metabolism in the brain of tilapia [70]. Additionally, a study on rainbow trout demonstrated that MAO activity decreased in the brain stem and telencephalon but increased in the optic tectum and hypothalamus during confinement stress [74]. Serotonin exerts its functions by binding to specific serotonin receptors. In fish, seven families of 5-HT receptors with at least 39 genes have been identified [75]. Many of the receptors were reported to response various stressors [75,76]. Inhibition of 5-HT receptors has been shown to attenuate stress responses in flatfish [77], salmon [78], tilapia [68], and zebrafish [79], while the agonists of 5-HT receptors can lead to enhanced stress responses in the non-stressed fish [80]. In addition, some of the agonists of 5-HT receptors (i.e. buspirone and MK-212) decreased stress-induced behavior in fish [78,79,81]. Emerging evidence suggests individual variability in sensitivity to serotonin fluctuations within the same species. Fish exhibiting divergent stress-coping styles, such as proactive versus reactive coping, display differences in 5-HT-related functions. These differences were reflected in a generally higher brainstem 5-HT concentration and a lower telencephalic 5-HT activity, i.e. the ratio of 5-HIAA to 5-HT, in proactive fish compared to reactive one [82].

3.2. Neuroendocrine Systems During Stress

Brain-Sympathetic-Chromaffin Cells (BSC) Axis

The autonomic nervous system provides the most immediate 'fight-or-flight' responses to stressor (in seconds) through its two divisions, the sympathetic nervous system (SNS) as well as the

parasympathetic nervous system (PNS). During stress, the sympathetic neurons in the spinal cord can release ACh and further activates acetylcholine receptors on chromaffin cells in the head kidney of the fish triggering depolarization and Ca^{2+} influx, which facilitates CAs release into the blood circulation and finally act on the peripheral target tissues [83,84]. In the PNS, efferent parasympathetic nerve signals are transduced from the central nervous system to their targets by preganglionic and postganglionic neurons. ACh is a major neurotransmitter in the PNS, and is activated when the stressful state is alleviated [85]. In general, the two systems usually regulate important functions in an antagonistic manner to achieve homeostasis during stress [84].

Glutamate is found to activate NMDA/AMPA receptors in brain regions (paraventricular nucleus, PVN) to increase sympathetic outflow [86], while the activation of mGluRs in PVN shows effectively reduce sympathetic outflow [87]. In addition, GABAergic inhibition in the PVN can reduce sympathetic activation by its GABAA and GABAB receptors [88]. Studies have demonstrated that chromaffin cells express various iGluRs and mGluRs, which exert distinct effects on the regulation of basal and glutamate-induced CA secretion through the nitric oxide/3',5'-cyclic guanosine monophosphate (NO/cGMP) pathway. Additionally, glutamate-mediated activation of neuronal nitric oxide synthase (nNOS) in chromaffin cells highlights the involvement of both PKA and PKC signaling pathways in the apoptotic effects induced by glutamate [89]. In chromaffin cells, GABA is synthesized, stored in granules, and released upon nicotinic ACh receptor activation. Exogenous GABA stimulates GABAA receptors, inducing CA secretion via action potentials while inhibiting trans-synaptically evoked excitation [32]. GABA facilitates secretion when synaptic excitation is low but inhibits it when excitation is high [90]. Although chromaffin cells do not synthesize 5-HT, they accumulate small amounts through SERT-mediated uptake [91]. Recent studies have demonstrated that 5-HT1A receptors inhibit catecholamine (CA) secretion and exocytosis from adrenal chromaffin cells via an atypical mechanism that does not involve the modulation of cellular excitability, voltage-gated Ca^{2+} channels, potassium channels, or intracellular calcium levels [92].

The BSC axis can rapidly increase blood pressure and heart rate during acute stress, and quickly subside after the stress due to reflex parasympathetic activation [93]. However, chronic stress continues to activate the SNS, leading to increased synthesis, storage, and basal levels of CAs, as well as decreased levels of ACh [85]. In fish, it has been recognized that both acute and chronic stressors such as air exposure [94], handling stress [76], and hypoosmotic shock [95], can induce CA biosynthesis and elevate plasma CA concentrations. In coral trout, acute stress can trigger rapid changes in body color through the activation of catecholaminergic signaling. *In vitro* incubation with NE induces aggregation of chromatosomes while intraperitoneal injection leads to lightening of body color [96]. In gilthead sea bream, the elevation of plasma CAs was observed to be induced by chronic high stocking density and food deprivation, suggesting an activation of the fish's BSC axis during chronic stress [58].

3.3. Hypothalamus-Pituitary-Interrenal (HPI) Axis

In the HPI axis, stress activates the hypophysiotropic neurons in the paraventricular nucleus (PVN) of the hypothalamus secreting arginine vasotocin (AVT) and the corticotropin-releasing hormone (CRH). These releasing hormones stimulate the anterior pituitary to generate pro-opiomelanocortin (POMC) which is processed into the adrenocorticotropic hormone (ACTH), also known as corticotropin, into the blood circulatory system. When ACTH reaches the head kidney, it binds with the melanocortin 2 receptor (MC2R) on cortisol-producing cells, resulting in the activation of steroidogenic acute regulatory protein (STAR) for the generation of corticosteroids, a class of steroid hormones [97]. Cortisol is a major corticosteroid in fish, which functions primarily to increase blood flow and heart rate, mobilize energy stores to muscle during stress by binding with corticosteroid receptors, namely the glucocorticoid receptor (GR) and mineralocorticoid receptor (MR), on the target cells [98]. Cortisol is the end-product of HPI axis activation and can also induce negative feedback on HPI axis, regulating the hypothalamic CRH and pituitary ACTH synthesis and secretion.

In fish, various stressors, such as temperature [99], crowding [100], hypoxia [101], light-dark cycles, and fasting [102], have been shown to activate the HPI axis, with cortisol levels widely recognized as indicators of the stress response. In rainbow trout and lake whitefish, the cortisol response to stressors immediately after hatching is absent when siblings experience stress during the embryonic stage [101,103]. The activation of the HPI axis typically occurs in response to acute and high-intensity stress, depending on both intensity and duration. Conversely, under chronic stress conditions, the capacity of the HPI axis to mount an appropriate stress response is diminished, particularly within the pituitary gland [104]. Notably, chronic heavy metal exposure has been found to alter the HPI axis and inhibit cortisol responses to acute stressors [105,106]. However, in Atlantic salmon, chronic stress was also observed to prolong HPI axis activation during eight weeks of daily crowding [100]. Additionally, the response of the HPI axis to stress has been shown to be influenced by maternal conditions. For example, maternal cortisol exposure or sequestration during embryogenesis can mediate the development and sensitivity of the HPI axis in their offspring [107,108].

Moreover, the neural and neuroendocrine system have largely complementary actions during stress. For instance, noradrenergic and adrenergic projections to the hypophysiotrophic zone of the PVN can participate in HPI activation [109]. ACh was known to stimulate cortisol secretion through mAChR in adrenal cells [110,111]. Meanwhile, cortisol was also reported to induce ACh accumulation and result in tissue damage and impairs regeneration [112]. CRH-releasing neurons have projections to the locus coeruleus which can directly send projection to the sympathetic and parasympathetic preganglionic neurons for enhancing the sympathetic activity and reducing the parasympathetic activity [85].

Strong evidence indicates that glutamate drives hypothalamic-pituitary-adrenal (HPA) axis stress responses through excitatory signaling mediated by iGluRs activity [113]. Meanwhile, other studies have shown that Glu may participate in the feedback loop of the HPA axis via kainate receptors and mGluRs, which inhibit HPA activation [114]. Additionally, cortisol secretion during acute stress induces the release of glutamate in limbic and cortical regions [115], while inhibition of glutamate receptors results in the stimulation of adrenocorticotrophic hormone (ACTH) release during stress [116]. Taken together, these findings suggest that glutamate plays a complex role in the excitation of corticotropin-releasing hormone (CRH) neurons, acting at multiple levels to both drive HPA axis responses and limit over-activation. The role of GABA in HPA axis has been well established. CRH neurons have been shown to be regulated by both phasic and tonic GABAergic inhibition, which are distinct types of GABAergic inhibition mediated by specific subtypes of GABAA receptors [117]. Meanwhile, the cortisol also increase GABAergic signaling through changes in the expression of postsynaptic GABAARs and tonic GABAergic inhibition, contributing to the inhibition of CRH neurons [118]. These results provide novel negative feedback onto the HPA axis.

NE and E are known to stimulate hypothalamic CRH secretion via alpha 1 and alpha 2 receptors, while CA may also contribute to the feedback loop of HPA axis. Study investigated corticosterone's long-term regulation of Crh and Avp gene expression in the PVH using a saporin-based immunocytotoxin targeting catecholaminergic neurons. In adrenalectomized animals with corticosterone replacement, corticosterone's suppression of Crh expression required intact catecholaminergic innervation. Avp expression elevation post-adrenalectomy was similarly suppressed in lesioned animals. These findings demonstrate that corticosterone-catecholamine interactions critically modulate hypothalamic Crh and Avp expression [119]. In addition, another CA, DA is also found to regulate the activation of HPI axis during stress. By contacting with their receptors on CRH-containing neurons in the PVN, DA can regulate the HPI axis during stress [120]. Dopaminergic neurons are the primary source of DA, which also seems to regulate HPA axis [121]. Meanwhile, several dopaminergic regions in the brain express glucocorticoid receptors and administration of glucocorticoids can increase the level of extracellular DA [121].

Study has shown that midbrain serotonin neurons directly innervate CRH cells in the hypothalamic PVN to stimulate CRH and POMC release. This subsequently leads to ACTH secretion

and activation of the hypothalamic-pituitary-adrenal (HPA) axis, mediated by 5-HT_{1A}, 5-HT_{2A}, 5-HT_{2C}, and possibly also 5-HT_{1B} receptors [122,123]. In human colonic enterochromaffin (EC) cells, EC cell-specific CRH1 expression and their activation pathways driving serotonin release/synthesis [124]. Meanwhile, chronic corticosterone exposure elevates TPH2 protein expression and mediate hypersensitivity of stress/anxiety circuits via opposing CRH receptor actions on serotonin synthesis [125].

3.4. Caudal Neurosecretory System (CNSS)

In addition to the common systems, fish possess a distinct neuroendocrine system located at the caudal end of the spinal cord, referred to as the CNSS. This system includes a neurohemal organ known as the urophysis and magnocellular peptide-synthesizing neuroendocrine neurons, termed Dahlgren cells, which were first described in 1914 [126]. CNSS plays the important roles in osmoregulation [127], thermoregulation [128], and other stress responses (such as ammonia, hypoxia, isolation and subordination) [129]. Studies have shown that the activities of the CNSS are innervated by the midbrain and medulla [130], then release neuropeptides into the circulation from tail vein. Recent studies demonstrated that some neurotransmitters, including DA [131], adrenaline [132], serotonin [133], taurine [134], nitric oxide [127], Glu [135] and GABA [136], were found to regulate the firing activities of Dahlgren cells through their receptors in CNSS, reflecting the crosstalk between nervous system and CNSS. The major synthesized neuropeptides in the CNSS are AVT, Isotocin (IT) [137], CRH, Urotensin I (UI, *uts1*) [138] and Urotensin II (UII, *uts2*) [139], parathyroid hormone related protein (PTHrP) [140]. It has been proved that the CNSS is the major circulating source of CRH, UI, UII, and PTHrP in fish [140–142].

Research has demonstrated that various stressors, including handling, osmotic pressure, thermal conditions, hyperammonemia, hypoxia, isolation, and subordination, can influence the expression of *crh*, *uts1*, and *uts2* synthesized in the CNSS [127,129,143–145]. The expression changes of these genes in CNSS varied depending on the type of stressor: handling stress resulted in an increased expression of all three genes; acute seawater/freshwater transfer experiments elevated the expression of *uts1* while decreasing that of *uts2*; acute hypothermal stress, but not hyperthermal stress, enhanced the expression of all three genes; subordination had no significant effect; isolation led to a reduction in the expression of *crh* and *uts1*, whereas hyperammonemia and hypoxia increased the expression levels of *crh* and/or *uts1*. In addition, both *in vivo* and *in vitro* studies showed that administration of UI and UII cause the increase in cortisol secretion [146]. In comparison to the individual administration of ACTH, UI, or UII, the enhanced release of cortisol following perfusion with a combination of ACTH and either UI or UII is significantly greater, indicating that interrenal UI and UII potentiate the steroidogenic effects of ACTH [147]. Given that fish possess relatively low blood pressure and slow fluid circulation velocity, the CNSS may play a role in stress responses by providing complementary regulation through the control of circulating levels of stress-related hormones and modulating cortisol production in relation to specific stressors. Current studies indicate that the contributions of the brain and CNSS to stress responses appear to be dependent on factors such as the type of stressor, duration, intensity, and specific regions within fish [148].

4. Dietary Supplements on Stress Mitigation Through Neuroendocrine and Neurotransmitters Regulations

Traditional pharmaceutical therapy in aquaculture normally focuses on the substance in the water that induces the infection after the onset of the disease, which is often palliative and induces secondary environmental pollution, for instance, using antibiotics and malachite green to treat bacterial and fungal infections. However, most of the infections occur after the failure of stress regulations. Using dietary supplements to preserve the beneficial effects and reduce the harmful effects of stress is more environment friendly and seems to be a viable and sustainable strategy to develop immunocompetence and disease resistance in aquatic animals. According to their components, they are divided into nutritional and non-nutritional supplements.

4.1. Nutritional Supplements

Recently, dietary intervention of amino acids, such as phenylalanine, has been considered to reduce the stress-induced physiological injury in fish through neuroendocrine and neurotransmitters regulations [149].

Phenylalanine (Phe) and tyrosine (Tyr) is the precursor of the neurotransmitters, catecholamines (NE, E and DA) [150–152]. Oral administration of the Phe-enriched diet is found to induce a high level of DA and minimize the effect of repeated handling stress in juvenile soles (*Solea senegalensis*) [153]. Dietary supplementation with 5% of Phe supplementation diet, shows a reduction on several stress markers (glucose, cortisol, NE, E, and DA) in meagres (*Argyrosomus regius*), but not in gilthead seabreams (*Sparus aurata*), during netting/chasing stress [154]. However, gilthead seabreams (*S. aurata*) fed with diets supplemented with 5% of Phe or Tyr showed a reduction in various stress markers during chronic confinement and netting/chasing stress [155]. In addition, phenylalanine could also eliminate the reactive oxygen species (ROS) and mitigate the oxidative damage during stress [155,156]. However, it is still unclear that whether the stress mitigation is caused by amino acids themselves or their metabolites.

Tryptophan (Trp) is an essential amino acid that plays critical roles in the regulating the stress response. It serves as a precursor for serotonin and melatonin synthesis. Studies had demonstrated that dietary Trp at 0.72 % level supplementation could reduce serum cortisol levels and oxidative stress responses during thermal stress in rohu (*Labeo rohita*) [157]. Additionally, dietary Trp at 5g kg⁻¹ levels had been shown to enhance intestinal antioxidant capacity and modulated inflammatory responses under high-stocking density conditions in rainbow trout (*Oncorhynchus mykiss*) [158]. Tryptophan supplementation had also been associated with decreased levels of POMC b-like peptides, which were involved in adrenocorticotrophic hormone and cortisol secretion. When stressed fish (*Dicentrarchus labrax*) fed a Trp-supplemented diet were subjected to an inflammatory stimulus, plasma cortisol levels decreased and the expression of genes involved in the neuroendocrine response was altered, which seemed to be mediated by altered patterns in serotonergic activity [159].

Except the amino acids, some fatty acids and vitamins are also found to regulate cortisol release during stress. For instance, prostaglandin (PGE₂) has been reported to be involved in modulating the HPI axis and affect the cortisol release in fish [160]. Vitamins are being used to mitigate various husbandry and physical stressors in aquaculture. For instance, dietary administration of vitamin C and E can protect the fish from death or other negative effects induced by various stressors, such as heat, hypoxia and handling [161–163]. More importantly, vitamin C and E seem to mitigate the stress by modulating the neuroendocrine and immune reactions. High dose vitamin C and E can block steroidogenesis by preventing the conversion of unsaturated lipids into cholesterol esters, and hindering the formation of cortisol [163–165].

4.2. Non-Nutritional Supplements

Except the nutritional additives, some non-nutritional compounds are also known to modulate immune function and enhance stress tolerance in fish. Levamisole, a synthesized phenyl imidazothiazole, has been reported to improve the stress tolerance [165,166]. Even with low supplementation of levamisole (0.1%), rainbow trout fingerlings show a higher tolerance during the crowded stress [167]. After 15-days oral administration of levamisole, it has been found that levamisole can modulate the plasma cortisol and enhance the innate immune responses against the bacterial infection in air-exposure-stressed pacu (*Piaractus mesopotamicus*) [168]. Clinical results in human showed that levamisole was helpful in reducing or stopping steroids and affecting the glucocorticosteroids level [169]. Another *in vitro* experiment showed that levamisole could significantly suppress the elevation of ROS, triggered by glutamate through stabilizing mitochondrial membrane potential, and protect the cell death [170]. However, levamisole mechanism of action in fish is poorly understood.

Recently, application of some biological derivatives, such as prebiotics and probiotics, also show a mitigation of stress via increasing the level of neurotransmitters in brain and modifying host-

microbial community in fish intestine [171,172]. The application of mixed water probiotic is reported to reduce cortisol levels, improve tolerance to various husbandry stressors in fish [173,174].

In addition, some herbal medicines are also reported to demonstrate anti-stress effects in aquatic animals. The emodin, as the active component of anthraquinone extract, can protect the Wuchang bream (*Megalobrama amblycephala*) from the crowding stress not only by reducing the serum cortisol [163], which is also proved in common carp (*Cyprinus carpio*) [175]. By targeting the NF- κ B signaling, the emodin improves the antioxidant capacity [176]. The *in vitro* experiment shows that the emodin can induce antioxidant defenses in peripheral blood leukocytes by Nrf2-Keap1 signaling [177]. Moreover, dietary supplementation with 1% turmeric can significantly reduce the plasma cortisol and enhance the lysozyme levels during transportation, which is used as an excellent feed additive to ameliorate the adverse effects of transportation in common carp (*C. carpio*) [178].

5. Conclusions and Perspectives

The steadily increasing demand for fish-derived protein necessitates the expansion and intensification of aquaculture practices, which in turn has heightened various environmental and husbandry-related stressors affecting fish. Fish possess well-developed endogenous nervous and endocrine systems that respond to stress, with complex communication networks among these systems demonstrating distributed collaboration. The nervous system plays a crucial role in detecting challenges, facilitating neural regulation, and innervating the endocrine system. Concurrently, the endocrine system subsequently releases a variety of stress-related hormones to reorganize energy resources, modify metabolic processes, and regulate immune responses. Future research on fish neural and neuroendocrine stress responses should focus on: 1) Investigating the specific mechanisms and differences in neuroendocrine stress responses across different fish species; 2) Understanding the coordinated regulatory mechanisms of the neuroendocrine stress system as fish respond to multiple stressors; 3) Enhancing and elucidating the interactions between the nervous system and neuroendocrine system in fish; 4) Exploring strategies to enhance aquaculture efficiency and improve survival rates by modulating neuroendocrine stress responses.

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