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Effects of Low Temperature on Shrimp and Crab Physiology, Behavior, and Growth: A Review

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As important aquaculture species worldwide, shrimps and crabs are thermophilic animals with a feeble thermoregulation ability. Changes in environmental factors are the main reason for the decrease in the immunity and disease resistance ability of cultured organisms. Water temperature is one of the most common abiotic stress factors for aquatic ectotherms. It influences nearly all biochemical and physiological processes in crustaceans, resulting in an imbalance in ion and water homeostasis, neuromuscular function loss, cellular dehydration, and altered metabolic pathways. The present review summarizes the current knowledge on the effects of low temperature on the physiological response, and the behavior, development, and growth of shrimp and crab. We suggest a deeper research to understand the physiological processes involved in thermoregulation; this knowledge could be used to reduce the adverse effects in the shrimps and crabs during the culture.

Keywords: behavior, cold stress, crab, growth, physiology, shrimp

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INTRODUCTION

As important aquaculture species worldwide, crustaceans such as shrimp and crab have very weak cold regulation abilities. Since the 1980s, various diseases have caused huge losses in the aquaculture industry. Epidemiological surveys showed that shrimp and crab diseases mainly occurred in spring and summer, and the peak of the disease often occurred after drastic changes in environmental conditions. Changes in environmental factors are the main reason for the decline of biological immunity and disease resistance (Le Moullac and Haffner, 2000). For crustaceans such as shrimp and crab, the water temperature is an important survival-related environmental factor, which not only directly influences their metabolism, growth, molting, and survival, but also affects other environmental factors (e.g., dissolved oxygen) (Chen et al., 1995; Hennig and Andreatta, 1998; Saucedo et al., 2004). Therefore, the temperature has become an essential factor restricting shrimp and crab culture.

There has been significant research progress on how temperature affects crustacean growth, physiology, survival, energy metabolism, and biochemistry. In shrimps and crabs, cold shock can be discussed in the context of the general stress response. The present review used the definition of stress reported by Donaldson et al. (2008), which described stress as a cascade of physiological responses occurring in an organism that tries to re- disturbance its homeostasis after an insult. There are three broad categories of responses to environmental stress: primary (e.g., the release of corticosteroids and catecholamine and the neuroendocrine response), secondary (e.g., immunological, osmoregulatory, hematological, cellular, and metabolic changes), and tertiary (e.g., behavioral and physiological stress responses in the whole organism). This paper reviews the research progress of the effects of temperature from the three aspects (see **Figure 1**), which will enrich the basic physiological data of shrimp and crab, and to guide the artificial culture of shrimp and crab, providing a reference for related research in the future.

PRIMARY RESPONSES – THE NEUROENDOCRINE RESPONSE

The endocrine and nervous systems function synchronously to regulate many physiological processes and to maintain balanced organism-wide homeostasis in both normal and stressful conditions, *via* a process, termed neuroendocrine integration (Adamski et al., 2019). The neuroendocrine system and its related signaling molecules (e.g., biogenic amines (BAs) and neuropeptides) regulate many crustacea behavioral and physiological processes; therefore, they might also affect cold tolerance (Chen et al., 2014).

BAs identified in crustaceans include catecholamines [dopamine (DA), norepinephrine (NE), and epinephrine (E)] and indoleamine [5-hydroxytryptamine (5-HT)] (Chang et al., 2009, 2015). The stress response involves BAs (Zhao et al., 2016). For instance, low temperatures alter BA concentrations, allowing insects to survive in, or prepare for, unfavorable conditions such as prolonged stress. BAs have important functions in the regulation of fundamental life processes (Sinakevitch et al., 2018). Not only do BAs function as neuromodulators and neurotransmitters in nervous tissues, but also can act as neurohormones after their release into body fluids (Sinakevitch et al., 2018). According to the target tissue, BAs bind to different types of G protein-coupled receptors (GPCRs), resulting in the stimulation of various secondary messengers, such as Ca^{2+} or cyclic adenosine monophosphate (cAMP) (Farooqui, 2012). Research has identified four DA and five 5-HT receptor subtypes in crustaceans to date (Northcutt et al., 2016; Pang et al., 2019). Most of these receptors are member of a GPCR superfamily that activates cascades of second messengers, mainly protein kinase A (PKA) and cAMP (Costa et al., 2016). In crayfish (*Procambarus clarkii)*, agonistic behavior, such as the loser and winner effects is mediated by the cAMP-PKA signaling pathway (Momohara et al., 2016).

BAs' neuroprotective role in supporting muscle activity in various crustaceans in response to low temperature has been studied (Hamilton et al., 2007). In lobster and crayfish muscles, increased haemolymph 5-HT levels in response to cold resulted in an increase in the amplitude of the excitatory postsynaptic potential (EPSP). BAs' effects are frequently temperature-dependent; e.g., 5-HT-induced alterations of the EPSP occur only at suboptimal temperatures, which might aid the function of neuromuscular junctions under low temperature stress (Hamilton et al., 2007; Zhu and Cooper, 2018). This hypothesis was supported partially by the observation that in *Drosophila melanogaster* larval heart exposed to cold, only 5-HT had a strong excitatory effect (Zhu et al., 2016).

In crustaceans subjected to cold stress, the BA levels are altered. For example, in the giant prawn *Macrobrachium rosenbergii*, variations in NE levels in the haemolymph, eyestalk, and thoracic ganglion, suggested that NE mediates cold shock-induced hyperglycemia (Hsieh et al., 2006). Higher haemolymph levels of DA were detected in 24°C-acclimated white shrimp (*Litopenaeus vannamei*) when shifted to a lower temperature (18 or 21°C) (Pan et al., 2008).

The crustacean hyperglycaemic hormone (CHH) family is an important endocrine hormone, comprising CHH, molt-inhibiting hormone (MIH), gonad-inhibiting hormone (GIH), and mandibular organ-inhibiting hormone (MOIH) (Chen et al., 2020). In particular, CHH, which mainly regulates the release of glucose, is involved in the mediation of stress responses. CHH is probably the most widely studied neuroendocrine mechanism that mediates the crustacean stress response (Wanlem et al., 2011). CHH is a neurohormone produced by the X-organ sinus gland complex, which is located in the eyestalk, and is regulated by several neuromodulators, e.g., catecholamines (Liu et al., 2008; Aparicio-Simón et al., 2010). DA's hyperglycemic effects involve CHH (Webster et al., 2012). A hyperglycemic response is also elicited by NE and E and to NE and E also elicit a hyperglycemic response; however, this effect is not dependent on the eyestalk, suggesting that this effect is not mediated by CHH or is mediated by non-eyestalk produced CHH (Si et al., 2019). A significant increase in CHH levels in the haemolymph in response to cold stress have been reported in several crustaceans, including the *L. vannamei* (Lago-Lestón et al., 2007) and the freshwater crayfish, *Cherax quadricarinatus* (Prymaczok et al., 2016).

SECONDARY RESPONSES – CHANGES IN METABOLISM, THE IMMUNE SYSTEM, AND OSMOREGULATION

Low temperature is closely related to the immune and antioxidant system of shrimps and crabs (see **Table 1**), and is the most important stress factor in aquaculture (Xu et al., 2019). Low temperature not only causes a disorder of free radical metabolism, damage the normal physiological function and immune defense ability of cells and tissues, and directly affects the metabolism of aquatic animals, but also affect dissolved oxygen and other environmental factors, thus leading to the susceptibility of shrimps and crabs to pathogens.

Effects of Low Temperature on Metabolism

Temperature can directly affect the respiration and energy metabolism of crustaceans. Under low temperature stress, on the one hand, energy consumption increases. On the other hand, neurohormone secretion and digestive enzyme activity decrease, and energy metabolism-related enzyme activity and

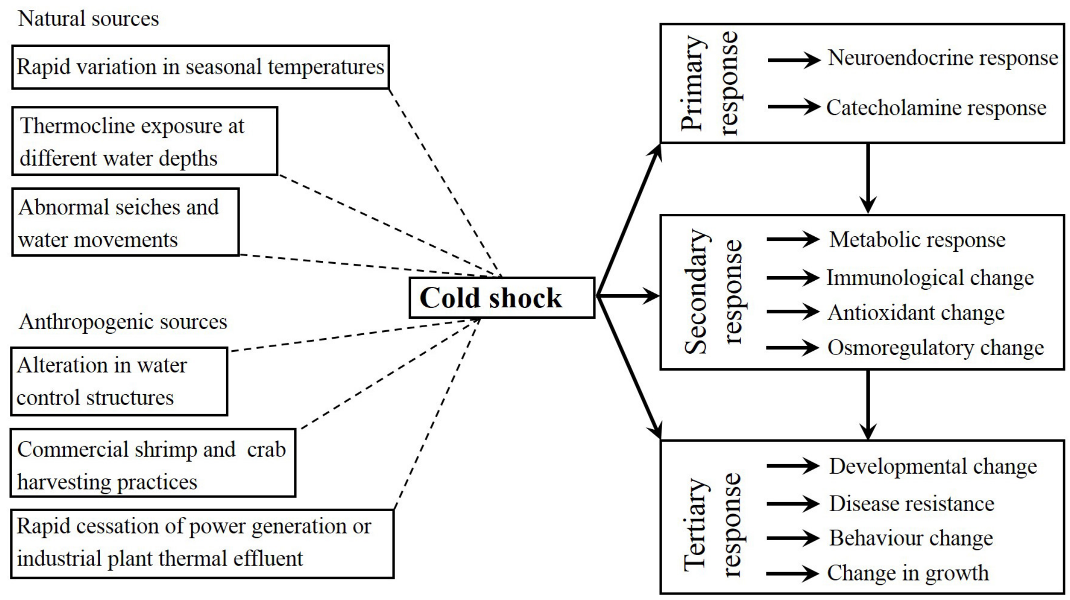

FIGURE 1 | Schematic representation of natural and anthropogenic sources of cold shock and the primary, secondary and tertiary responses to cold shock.

metabolic modes are altered, resulting in crustacean metabolic disorder (Anestis et al., 2008). Low temperatures are believed to have widespread effects on marine organisms' behavioral and physical traits, including their metabolism. Generally, crustaceans lack efficient regulators, making them sensitive to reduced temperatures.

In shrimp and crab, proteins are the primary energy source (Cuzon et al., 2010). In cold-adapted *L. vannamei*, fat absorption and digestion, and the protein pathways were enhanced significantly (He et al., 2018). Similarly, under cold stress (23°C), plasma lipids (especially total cholesterol and triglycerides) and total proteins increased significantly; there were no significant changes in glucose levels (Wu et al., 2020). Therefore, it was speculated that in crustaceans under acute cold-stress, lipids and proteins are the main energy sources (Wang et al., 2019). A metabolic study of the black tiger shrimp (*Penaeus monodon*) cultured under low temperature revealed that its amino acid and trehalose contents increased significantly (Jiang et al., 2019). Under low temperature stress, in addition to the fatty acid composition of tissues and cells, the content of free amino acids (FAA) in tissues also changed. The content of total FAA increased in spring and autumn, but decreased rapidly in winter. As an important nutrient in the body, protein may be automatically decomposed into amino acids under low temperature stimulation. On the one hand, amino acids are used for protein synthesis and turnover, and on the other hand, they might have anti-stress functions. To improve the metabolic rate and oxygen carrying capacity of the body, or to meet the needs of protein synthesis, the structure and synthesis rate of hemocyanin in shrimp and crab will change significantly in response to stress.

The fatty acid metabolism of crustaceans is sensitive to temperature. Cold temperature mainly affects membrane fluidity by affecting the saturation of fatty acids in the cell membrane. Membrane fatty acid desaturation is considered an important mechanism by which crustaceans adapt to low temperature, and is crucial to maintain membrane fluidity, enzyme activity, and normal cell function (Pruitt, 1990; Suprayudi et al., 2004). Cold stress leads to a change in the fatty acid (FA) composition in crustacean cells, which usually leads to the decrease in the saturated fatty acid (SFA) ratio and a rapid increase in the unsaturated fatty acid (UFA) ratio, which is conducive to the maintenance of cell membrane fluidity (Azra et al., 2020a,b). In *Scylla serrata*, *Cancer pagurus*, and *Carcinus maenas*, the SFA content decreased significantly at low temperature (Cuculescu et al., 1995; Wang et al., 2007). In the crayfish cultured at low temperatures, the haemolymph cholesterol and triglyceride contents were reduced significantly, suggesting that under cold stress, these two substances are consumed to release energy (Wu et al., 2020). UFAs are important components of cellular membranes and participate in energy metabolism (Nemeth et al., 2014). Under cold stress, UFA levels increased in *L. vannamei* (Fan et al., 2019), the Chinese fleshy shrimp (*Fenneropenaeus chinensis*) (Meng et al., 2019), and the kuruma shrimp (*Marsupenaeus japonicas*) (Ren et al., 2020). Desaturase enzymes play an important role in the synthesis of unsaturated fatty acids. In *C. quadricarinatus* low temperature treatment increased Δ6 desaturase mRNA expression and enzyme activity with decreasing water temperature (Wu et al., 2018). However, the mechanisms for the induction of Δ6 desaturases at low temperature remain unclear.

As an important energy source, sugar plays a vital role in the low temperature stress of shrimp and crab. A decrease in temperature led to an increased blood glucose content and a decreased glycogen content in *M. rosenbergii*, *S. serrata*, *Pachygrapus crassipesran* Dall, *Paranephrops planfrons*, and *L. vannamei* (Hsieh et al., 2006; Kong et al., 2008;

Valle et al., 2009; Zhou et al., 2011). This change in sugar levels in shrimp and crab is an adaptation to low temperature. During cold stress, glucose is consumed as a fast energy source, and the hepatopancreas continuously decomposes glycogen to meet the needs of maintaining the metabolic energy supply. When the temperature rises, or the crustacean adapts to low temperature, the haemolymph glucose level will gradually recover.

Effects of Low Temperature on Immune System

The crustacean immune system mainly functions *via* innate immune mechanisms comprising humoral and cellular responses. Cellular innate immunity comprises all hemocyte-mediated reactions (e.g., phagocytosis, nodule formation, and encapsulation). Humoral innate immunity comprises mainly lysozyme, phosphatases, antimicrobial peptides (AMPs), protease inhibitors, agglutinins, and the prophenoloxidase-activating system (Kenneth and Lage, 1992; Kulkarni et al., 2020). In the humoral response, AMPs, lysozyme, or phenoloxidase (PO) concentrations increase markedly under stress conditions, e.g., invasive pathogens, disease outbreaks, and environmental hazards. Hemocytes comprise the major component of the crustacean cellular immune system, and their levels will change according to the condition of the organism and the environment (Wang and Chen, 2006). Thus, stress-induced immune system activity is conveniently assessed using the total haemocyte count (THC) (Xu et al., 2019). Fan et al. (2013) found that the THC in *L. vannamei* was reduced when the temperature decreased from 28 to 13°C. These results indicated that the THC of crustaceans is closely related to temperature. The lower the temperature, the lower the enzyme activity and the lower the THC. In lobsters, the hemocyte phagocytic activity was affected negatively by low temperature (Steenbergen et al., 1978). The evolutionarily conserved cellular process of autophagy involves maintaining homeostasis by recycling damaged or excess cellular components (e.g., misfolded proteins, intracellular pathogens, damaged organelles, and damaged DNA) (Bolliet et al., 2017). In *L. vannamei*, autophagy is associated with low temperatures (Liang et al., 2020).

In invertebrates, the important innate immune response mechanism, melanization, functions *via* the prophenoloxidase (proPO)-activating system and is catalyzed by PO (Amparyup et al., 2013). In shrimp, melanization has been suggested to be an antiviral response (Zhao et al., 2020). Meanwhile, PO functions in cellular defense in association with phagocytosis-enhancing factors; therefore, PO is used frequently to assess the effect of environmental stress on the invertebrate immune system (Ellis et al., 2011). In brown shrimp (*Penaeus californiensis*) exposed to increasing temperature (18−32°C), the hemocyte proPO system activity decreased at 32°C (Vargas-Albores et al., 2008). In the crab (*Carcinus aestuarii*), when incubated at 4°C, the PO activity in cell-free haemolymph was significantly higher than that in the control crabs incubated at 17°C ($p < 0.05$) (Matozzo et al., 2011).

In addition, immune parameters, such as antibacterial activity, are suppressed by low temperature. Taken together, these previous studies show that low temperature has important effects on shrimp disease tolerance and survival. However, to date, there have been few studies investigating the immune regulatory mechanisms in shrimp exposed to low temperature. Lysozyme (LSZ), as a kind of hydrolase, is the basis of phagocyte sterilization, existing widely in different tissues, body fluids, and secretions of various organisms, and can be used to measure the non-specific immune capacity of organisms (Mock and Peters, 1990). Low temperature can affect the activity of LSZ. Ding et al. (2010) reported that temperature change could inhibit the LSZ activity of *S. serrata*. In the red claw crayfish, LSZ was inhibited significantly following low temperature exposure (Wu et al., 2019). Hemocyanins are extracellular negatively charged proteins that are involved in numerous physiological functions, such as protein storage, osmoregulation, oxygen transport, and enzyme activities (Ishwarya et al., 2018; Coates and Costa-Paiva, 2020). In the crayfish *P. clarkii* and *P. zonangulus*, the acclimation temperature directly affected the hemocyanin binding affinity (Powell and Watts, 2006). Thus, it is believed that shrimp are more susceptible to pathogens under low temperature conditions.

Effects of Low Temperature on the Antioxidant System

In healthy organisms, the production and elimination of free radicals are in a dynamic balance; however, in adversity, stress will induce a reaction from the enzyme systems and non-enzyme systems of mitochondria, microsomes, and the cytoplasm, resulting in the production of excess reactive oxygen species (ROS) and oxygen free radicals, thus breaking the balance of reactive oxygen metabolism (Wade et al., 2017). In cells and tissues, oxidative stress's effects on cellular damage can be indicated by the level of lipid peroxidation (Mensah et al., 2012). To reduce oxidative stress and repair damaged cells, the primary defense response comprises the production of enzymatic and non-enzymatic antioxidants to scavenge ROS and free radicals (El-Gendy et al., 2010). In all organisms, the main antioxidative enzymes that detoxify ROS are glutathione S-transferase (GST), glutathione reductase (GR), catalase (CAT), glutathione peroxidase (GPx), and superoxide dismutase (SOD), in addition to the non-enzymatic antioxidant molecule, reduced glutathione (GSH) (Lesser, 2006; Zheng et al., 2019).

In mud crabs subjected to cold stress, the CAT, SOD, and GPX activities increased over 2 h, and then decreased gradually; the content of malondialdehyde (MDA) also increased gradually under cold stress (Kong et al., 2007). In *S. paramamosain* acclimated at 5, 10, 15, and 27°C (control group), the SOD, CAT, and GPx activities, and the MDA content decreased gradually with lowering temperatures and were significantly reduced at 5 and 10°C compared with those in crabs incubated at 27°C (Kong et al., 2012). Qiu et al. (2011) evaluated the physiological effects of continuous temperature decrease on *L. vannamei*. The MDA level increased when water temperature decreased from 23 to 12°C.

It has become clear that organisms share a common adaptation mechanism, termed the heat shock response (HSR), to cope with temperature-induced stress, which results in a dramatic change in gene expression patterns and leads to the elevated synthesis of a range of molecular chaperones and the induction of other cell-protective pathways (Richter et al., 2010). The heat shock protein (HSP) and heat shock factor (HSF)- mediated regulation pathways play crucial roles in the HSR, and have been studied intensively in terms of HSR mechanisms and the cold-tolerance of organisms (Gbotsyo et al., 2020).

HSPs are regulated by heat shock elements (HSEs), HSFs, and other factors to control their cellular levels (Morimoto and Santoro, 1998). HSF1 is an important transcription factor that regulates the heat shock response, and is expressed widely in eukaryotes, playing an important role in maintaining intracellular homeostasis during heat stress (Anckar and Sistonen, 2011). When the body is subjected to cold stress, it combines with HSE. In addition, HSPs are conserved at the evolutionary level. In a study of high temperature stress of *Penaeus monodon*, *PmHSF1* expression was elevated. The expression levels of HSPs and other heat tolerance related genes in *P. monodon* changed significantly after the *PmHSF1* gene was knocked down (Sornchuer et al., 2018). In *M. japonicas*, *MjHSF1* transcription was upregulated under heat stress (Zheng et al., 2020). To date, most of the studies on the related functions of HSF1 have focused on the interaction between HSF1 and HSPs, and there are few studies on the expression of immune related factors associated with HSF1. Several HSP genes are downstream targets of HSF1, which are involved in crustacean resistance to adverse environments.

HSPs comprise molecular chaperones that are produced during the exposure to, and recovery from environmental or physiological stress, including cold stress (Johnston et al., 2018). HSPs, also referred to as molecular chaperones or stress proteins, comprise a group of highly conserved proteins that are present ubiquitously in both prokaryotic and eukaryotic organisms (Roberts et al., 2010). HSPs protect cellular functions and structures and from the effects of stress and have important functions in the maintenance of cellular homeostasis (Morimoto and Santoro, 1998). Based on their molecular weight, HSPs are generally classified into five families, HSP100, HSP90, HSP70, HSP60, and small HSPs (Ahn and Im, 2020). In *F. chinensis*, the levels of *FcHSP90* mRNA were induced sensitively in response to heat shock (from 25 to 35°C), reaching a maximum level after 6 h of heat shock (Li et al., 2009). In other crustaceans (*S. serrata* and *L. vannamei*) mRNA levels of *HSP40*, *HSP70*, or *HSP90* were increased in response to cold or heat shock (Fu et al., 2013; Chen et al., 2018; Sung et al., 2018; Fan et al., 2019).

Apoptosis, a cell death process, has a crucial function in maintaining tissue hemostasis and disease protection. As a component of inflammatory reactions, the physiological function of apoptosis helps to remove damaged or harmful cells from immune tissues (Johnstone et al., 2002). Li et al. (2014) evaluated the effect of continuous temperature decrease on hemocyte apoptosis of *L. vannamei*, which showed an increase in the apoptotic cell ratio and a decrease in caspase-3 activity when the water temperature was reduced from 27 to 17°C. Cold temperature led to increase caspase-3 expression in the swimming crab (*Portunus trituberculatus*) (Meng et al., 2014). A previous study from our group demonstrated that in *M. japonicus*, the expression of *p53* increased significantly under cold stress, which suggested that cold-induced apoptosis might involve p53 (Ren et al., 2020). Significant changes in p53 signaling pathways under cold stress were also observed in the hepatopancreas of the red claw crayfish under cold stress (Wu et al., 2019).

Low Temperature's Effects on Osmoregulation

During cold acclimation (or low temperature adaptation), shrimps and crabs change the composition and concentration of intracellular ions by regulating the number and distribution of various ion channels on the cell membrane and changing the composition and concentration of intracellular ions to maintain normal physiological activities (Masroor et al., 2018). On the gill cell membrane of *S. serrata*, four kinds of adenosine triphosphatases (Ca^{2+}/Mg^{2+}-ATPase, Ca^{2+}-ATPase, Mg^{2+}-ATPase, and Na^{+}/K^{+}-ATPase), which are involved in ion uptake and osmotic pressure regulation, were upregulated during the process of adaptation to a lower temperature (Kong et al., 2012). In the hepatopancreas of *M. nipponense*, the Na^{+}-K^{+} ATPase activity in the temperature range 16−22°C was enhanced by 1.38-fold compared with that in the temperature range 25−32°C (Wang et al., 2006). In *Procambarus clarkia*, exposure from room temperature (23°C) to 4°C for 28 days resulted in a significant increase in Ca^{2+}-ATPase activity (Gao et al., 2009). Thus, in a cold environment, shrimps and crabs can reduce heat loss by adjusting the ionic concentration and osmotic pressure of their body fluid to reduce the difference between their body temperature and that of the outside water.

LEVEL THREE – CHANGES IN BEHAVIORAL AND GROWTH RESPONSES

Temperature is a basic environmental factor that limits species distribution, affecting individual growth and determining the reproductive cycle. How shrimps and crabs adapt to temperature change and maintain a steady state of life process is a long-term scientific problem. Low temperature has adverse effects on the growth and development of organisms (Shields, 2019). The temperature adaptation range of an organism is an important character in aquaculture. Improving tolerance to temperature stress is a challenging problem in aquaculture breeding. In the rock crab (*Cancer irroratus*), progressive temperature increase caused their heart rate to increase between 12 and 26°C, peaking at 153 ± 27 beats min^{-1} at 26°C (Frederich et al., 2009). The molting and reproduction of crustaceans are also affected by temperature. The lower the taxonomic position of the organism, the more susceptible it is to temperature. Therefore, to regulate the reproductive physiology of crustaceans, water temperature is an important factor.

Effect of Temperature on Shrimp and Crab Embryonic Development

The embryonic development of crustaceans is a dynamic physiological process. In addition to the influence of the

TABLE 1 | Effects of low temperature on immune and antioxidant parameters in shrimp and crab.

Organism	Species	Size/life stage	Temperature	Factor	Tissue	References
Shrimp	*Litopenaeus vannamei*	11 g, 4 cm	13°C	SOD, POD, CAT, GSH-Px, T-AOC	Hepatopancreas, haemolymph	Xu et al., 2018
	Litopenaeus vannamei	4.59 ± 0.5 g	13°C	IAP, p53, HSP70	Intestine	Wang et al., 2020
	Litopenaeus vannamei	1.91 ± 0.22 g	15°C	CGL, GSH, TBARS	Hepatopancreas, haemolymph	de Souza et al., 2016
	Litopenaeus vannamei	5.0 1 ± 0.46 g	12 ± 2°C	MDA	Haemolymph	Qiu et al., 2011
	Litopenaeus vannamei	7.09 ± 3.22 g	13°C	Ser/Thr kinase signal pathway	Muscle	Huang et al., 2017
	Penaeus monodon	16.5 ± 0.6 g	15°C	$O_2^{-\cdot}$ SOD, GSH, NOS, NO	Hepatopancreas	Jiang et al., 2019
	Penaeus monodon	3.96 ± 0.82 g	20°C	SOD, ACP, PO	Haemolymph	Yang et al., 2013
	Marsupenaeus japonicus	13.034 ± 0.88 g	10°C	p53, CYCS, Bax, Bcl2, caspase-3	Hepatopancreas	Ren et al., 2020
	Fenneropenaeus chinensis	P40	4°C	GST, C-type lectin, ASAH,	Whole body	Meng et al., 2019
	Macrobrachium rosenbergii	30.2 ± 4.1 g	22°C	THCs, PO, proPO, RBs, LGBP, PE, a_2-M, SOD	Haemolymph	Chang et al., 2015
	Macrobrachium nipponense	0.66 ± 0.03 g	29°C	ALT, SOD, CAT, MDA, INOS	Hepatopancreas, haemolymph	Lv et al., 2021
	Cherax quadricarinatus	22.56 ± 1.25 g	9 ± 2°C	ACP, AKP, LSZ, PO	Hepatopancreas	Wu et al., 2019
	Cherax quadricarinatus	22.56 ± 1.25 g	9°C	HSP21, THC, SOD, T-AOC, GPx, MDA	Hepatopancreas, haemolymph	Wu et al., 2018
Crab	*Scylla serrata*	145 ± 20 g	4°C	SOD, CAT, GPX, MDA	Gills	Kong et al., 2007
	Portunus trituberculatus	213.8 ± 21.6 g	3°C	SOD, CAT, MDA, PC, caspase-3, HSP70, HSP90	Hepatopancreas, muscle	Meng et al., 2014
	Carcinus aestuarii	4 cm	4°C	CAT, THC	Gills, haemolymph	Matozzo et al., 2011
	Carcinus aestuarii	1–1.7 g	4°C	THC, DCH, NRRT	Haemolymph	Qyli et al., 2020

a_2-M, a_2-macroglobulin; AChE, acetyl cholinesterase; ACP, acid phosphatase; ALP/AKP, alkaline phosphatase; ALT, alanine aminotransferase; Bcl2, B-cell leukemia/lymphoma-2; Bax, Bcl-2-associated X protein; CAT, catalase; CSP, cyclophosphamide; Cu/Zn-SOD, Cu/Zn superoxide dismutase; CYCS, cytochrome C; DCH, differential hemocyte count; GCL, glutamate-cysteine ligase; GSH, glutathione; GSH-Px/GPx, glutathione peroxidase; GST, glutathione s-transferase; HSP21, heat shock protein 21; HSP70, heat shock protein 70; HSP90, heat shock protein 90; IAP, inhibitor of apoptosis protein; INOS, inducible nitric oxide synthase; LDH, lactate dehydrogenase; LGBP, lipopolysaccharide- and b-1,3-glucan binding protein; LSZ, lysozyme; MDA, malondialdehyde; NO, nitric oxide; NOS, nitric oxide synthase; NRRT, neutral red retention time; O_2^-, negative ions of oxygen; p53, a tumor suppressor gene; PC, protein carbonyl; PE, peroxinectin; PO, polyphenol oxidase; POD, peroxidase; RBs, respiratory bursts; ROS, reactive oxygen species; SeGpx, Selenium containing glutathione peroxidase; SOD, superoxide dismutase, T-AOC, total antioxidant capacity; TBARS, thiobarbituric acid reactive substance; THC, total hemocyte count; Trx, thioredoxin reductase.

TABLE 2 | Tolerance and behavior characteristics of shrimp and crab in response to temperature.

Species	Temperature interval (°C)	Symptoms under low temperature stress	References
Litopenaeus vannamei	16 to 38°C	<18°C, they will stop feeding; <9°C they will die	Jesus et al., 1997
Penaeus monodon	18 to 34°C	<18°C, they stop feeding and swimming; <12°C, they will die	Wang et al., 2006
Marsupenaeus japonicus	17 to 29°C	<10°C, food intake decreased and they died below 5°C	Dong et al., 2020
Fenneropenaeus chinensis	18 to 30°C	water temperature dropped to 4°C, the shrimp lost its balance, fell to one side and lost its response to external stimuli	Meng et al., 2019
Procambarus clarkii	20 to 30°C	Stopped feeding below 14°C, and died below 1°C	Chen et al., 1995
Macrobrachium rosenbergii	15 to 34°C	<18°C, the shrimp will be impatient, swim wildly along the pool wall, their reactions will be slow, and they will not eat; <14°C, they will die after a few days	Cheng and Chen, 2000
Cherax quadricarinatus	24 to 30°C	<14°C, they did not grow and died after 4 weeks	Haubrock et al., 2021
Macrobrachium nipponense	24 to 27°C	Stopped feeding below 14°C	Wang et al., 2006
Scylla paramamosain	18 to 25°C	Died below 5°C	Huang et al., 2019
Portunus trituberculatus	12 to 35°C	Food intake decreased below 10°C	Meng et al., 2014
Portunus pelagicus	14 to 36°C	<17°C, the food intake decrease; <14°C, little activity; <12°C, it will cause death	Azra et al., 2018
Charybdis feriatus	20 to 30°C	<14°C, the food intake begins to decline; < 9°C, the food intake stopped	Baylon and Suzuki, 2007
Eriocheir sinensis	20 to 26°C	<19°C, crawls with low frequency and eats a little; <10°C, it stops growing and molting; <5°C, it hibernates and does not eat	Song et al., 2004

parents, the external environmental conditions also have an important impact on embryonic development. In particular, the temperature not only affects the time of embryonic development, but also affects the quality and speed of embryo development (Yamamoto et al., 2017). Studies have shown that only when the temperature of organisms is above zero can they begin to develop and grow (Hartnoll and Abele, 1982). The biological zero of embryonic development of *Exopalaemon carinicauda*, *S. serrata*, and *P. clarkii* are 12.18°C, 11.70°C, and 5.60°C, respectively (Wu, 1991; Lv et al., 2004; Liang et al., 2013).

In the suitable temperature range, the higher the temperature, the faster the embryo develops. Wang et al. (1998) found that the embryonic development time of *Thenus orientalis* was shortened from 43 to 21 days with an increase in temperature from 22 to 31°C. Liang et al. (2013) found that in the ridgetail white prawn *E. carinicauda*, the incubation time of embryos shortened with the increase in temperature when the temperature was between 18 and 28°C. Cooler water retards growth and delays maturity, causing crabs to begin maturation when they are at larger sizes (Azra et al., 2020a).

Gonadal Development of Crustaceans in Response to Temperature

During evolution, crustaceans have formed a relatively perfect reproductive regulation system, involving neuropeptides, hormones, neurotransmitters, and other hormones (Nguyen et al., 2016). The levels of these hormone are adjusted with the changes in temperature, salinity, and other environmental factors, such that crustaceans can reproduce under the best environmental conditions. Among them, temperature is involved in gonadal maturation by regulating hormone synthesis and secretion (Qian et al., 2015).

Xu et al. (2008) studied *P. clarkii* and found that an increase in water temperature from 22 to 28°C could promote gonadal maturation. Carmona-Osalde et al. (2004) found that in the range of 16–25°C, the ovary development of *P. llamasir* could be promoted by increasing the temperature. When the water temperature was between 15 and 25°C, the egg holding rate of *S. serrata* increased as the temperature increased (Yao et al., 2005). These studies confirmed that the water temperature is a major factor that influences crustacean gonadal development. In a certain temperature range, the higher the water temperature, the better the quality of gonadal development of crustaceans.

Effects of Low Temperature on Behavior and Growth of Crustaceans

Behavioral modifications comprise changes in microhabitat use, abundance and distribution, feeding, predation, migration and spawning behaviors. In crustaceans grown under low temperatures, decreased activity and a decrease or cessation of feeding are the most frequently observed in behavior (Matheson and Gagnon, 2012). Fighting behavior increases the heart rate and metabolic rate of animals, and has a certain impact on their ability to withstand high temperature (Wang et al., 2020). Crustaceans are intolerant to low temperature and lack the ability to regulate their body temperature. In a low temperature environment of 9°C, the body of *L. vannamei* lost its balance and was slow to respond to external stimuli. Temperature has more complicated effects on locomotor activities (e.g., swimming or walking), which form part of the normal behavior of an animal, and are thus controlled by the central nervous system (Lagerspetz and Vainio, 2006).

Temperature is a growth limiting factor for all living things, but especially for aquatic organisms (Lushchak, 2011). All shrimps and crabs have a temperature tolerance range (see **Table 2**). When the water temperature exceeds the regulatory capacity of shrimp and crab, low temperatures will slow down their growth rate and even cause death. Temperature optima can be defined as the temperature at which shrimp grow fastest and most efficiently (González et al., 2010). The tolerance of different crustaceans to temperature is shown in **Table 1**. At low temperatures, shrimp and crabs need more energy to cope with stress, resulting in a significant reduction of reserves used for the growth process. Studies have shown that temperature is closely related to the growth of *L. vannamei* (Wyban et al., 1995) *P. monodon* (Deering et al., 1995), and *Macrobrachium nipponense* (Wang et al., 2006).

Temperature can affect the growth of crustaceans by altering two factors, the molt increment (the increase in duration between successive molts) and the intermolt period (the time interval between successive molts). Increasing temperature usually decreases the intermolt period; however, its effect on the molt increment is unknown. In early juvenile mud crabs, *S. paramamosain*, temperature-induced autotomy influenced the molting of early juvenile mud crabs, and changes in the levels of mRNA encoding the ecdysone receptor (EcR) seemed to play an important regulatory role in the molting process (Gong et al., 2015). Juvenile dungeness crabs (*Metacarcinus magister*) at different stages of molting (12, 19, or 26 days post-molting) were moved from ambient temperature (15°C) to temperatures of 5°C and 20°C for 14 days. From 5 to 20°C, survival ranged from 97 to 100% Molt stage progression increased from 5 to 15°C, but not at 20°C (Wittmann et al., 2018). *L. vannamei* incubated at 13°C showed significant reductions in swimming and feeding behaviors, and more deaths were observed at this temperature (Huang et al., 2017).

PERSPECTIVES

Climate change is causing alterations to oceans, rivers, and lakes; therefore, it is vital to determine the mechanism by which crustaceans tolerate low temperatures, to gain a deeper understanding of the effects environmental fluctuation on biology. This will allow us to implement the required measures to conserve aquatic organisms. However, we lack sufficient detail of the biological responses of crustaceans to low temperatures. To gather these data, it is important to study the expression and functions of genes and proteins that are influenced by temperature changes. The temperature adaptation range of an organism is an important agricultural character of an aquaculture variety. Improving the tolerance to low temperature stress is an important issue in aquaculture breeding. However, it is precisely because of the wide range of physiological effects of low temperature that involves many genes, which important genes determine the temperature tolerance is obviously a question that needs to be answered first. With the completion of the whole genome sequencing of shrimp and crab (Zhang et al., 2019; Tang et al., 2020; Jin et al., 2021; Yuan et al., 2021; Zhao et al., 2021), it has become an important research method to mine the key regulatory genes from the temperature responsive gene regulatory network.

CONCLUSION

Short- and in long-term temperature fluctuation has become a major stress factor responsible for altering the distribution patterns of marine crustaceans. The accumulated literature shows that the physiological parameters of crustaceans are influenced significantly by temperature changes. To adapt to environmental temperature alteration, crustaceans must invoke endocrine responses, changes in their metabolic rate, immune responses, and antioxidant responses. Despite having a good general grasp of the effects of temperature on crustaceans' responses, there are still gaps in our knowledge. However, obtaining a complete understanding of crustaceans' temperature adaptation mechanisms will permit us to predict future changes and will augment our knowledge of their physiological and ecological requirements. Current research provides a basis for future studies of the responses of crustaceans to low temperatures. The specific FAA metabolism pathways and ROS signal transduction pathways that are triggered in response to low temperature variation should be investigated in the future.

AUTHOR CONTRIBUTIONS

XR, QW, and JL conceived the idea, performed the literature search, and wrote the manuscript, with input and suggestions from the other authors. All authors contributed to the article and approved the submitted version.

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