DOI: 10.12731/2658-6649-2025-17-6-2-1540 **EDN: RCUGTX**
UDC 577.218:595.3

Scientific Reviews

INFLUENCE OF STRESS FACTORS ON CRUSTACEAN GENE EXPRESSION

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Abstract

Background. This review systematizes current scientific data on the influence of abiotic (pH, temperature, hypoxia, ammonia, nitrite) and biotic (viral and bacterial infections) stress factors on gene expression in crustaceans of the order *Decapoda*. Molecular responses affecting key functional groups of genes associated with immunity, osmoregulation, antioxidant defense, chitin metabolism, and cellular homeostasis are analyzed. Stress-induced changes in gene expression are complex, tissue-specific, and time-dependent, representing key adaptive mechanisms. The results of this analysis have important practical implications for aquaculture, opening up prospects for identifying molecular markers of stress resistance and developing strategies for optimizing the maintenance conditions of commercially important species.

Purpose. This review aims to systematize and analyze current scientific data on the influence of abiotic (such as pH, temperature, hypoxia, ammonia, nitrites) and biotic (viral and bacterial infections) stress factors on expression of genes associated with immunity, osmoregulation, antioxidant defense, chitin metabolism and cellular homeostasis in crustaceans of the order *Decapoda*.

Materials and methods. The research was conducted in the scientific research laboratory "Center of Agrobiotechnology" of the Don State Technical University in 2024-2025**.**

Results. Complex changes in the expression of key genes regulating immunity, osmoregulation, antioxidant protection, chitin metabolism, and cellular homeostasis have been identified. It has been shown that these tissue-specific and time-dependent changes in expression are the central mechanism of the adaptive response to stress.

Conclusion. An analysis of current scientific data has allowed us to systematize information on the influence of abiotic and biotic stress factors on gene expression

in crustaceans, particularly in members of the order *Decapoda*. It has been established that changes in key environmental parameters (such as temperature, pH, ammonia and nitrite concentrations) and exposure to pathogens (viruses, bacteria) trigger complex molecular responses affecting genes associated with immunity, osmoregulation, antioxidant defense, chitin metabolism, and cellular homeostasis.

Keywords: crustaceans; stress factors; gene expression; immunity; aquaculture; transcriptome analysis; antioxidant system; chitin metabolism; osmoregulation; *Decapoda*

For citation. Kovalchuk, D. Yu., Sargsyan, D. S., Cholutaeva, E. E., & Shevchenko, V. N. (2025). Influence of stress factors on crustacean gene expression. *Siberian Journal of Life Sciences and Agriculture*, *17*(6-2), 112-132. https://doi.org/10.12731/2658-6649-2025-17-6-2-1540

Научные обзоры

ВЛИЯНИЕ СТРЕСС-ФАКТОРОВ НА ЭКСПРЕССИЮ ГЕНОВ РАКООБРАЗНЫХ

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Аннотация

Обоснование. В данном обзоре систематизированы современные научные данные о влиянии абиотических (pH, температура, гипоксия, аммиак, нитриты) и биотических (вирусные и бактериальные инфекции) стресс-факторов на экспрессию генов у ракообразного отряда Decapoda. Проанализированы молекулярные ответы, затрагивающие ключевые функциональные группы генов, связанные с иммунитетом, осморегуляцией, антиоксидантной защитой, метаболизмом хитина и клеточным гомеостазом. Показано, что стресс-индуцированные изменения экспрессии носят комплексный, тканеспецифичный и времязависимый характер, выступая ключевым механизмом адаптации. Результаты анализа имеют важное прикладное значение для аквакультуры, открывая перспективы для идентификации молекулярных маркеров стрессоустойчивости и разработки стратегий оптимизации условий содержания коммерчески важных видов.

Цель. Целью обзора является систематизация и анализ современных научных данных о влиянии абиотических (таких как pH, температура, гипоксия, аммиак, нитриты) и биотических (вирусные и бактериальные инфекции)

стресс-факторов на экспрессию генов, ассоциированных с иммунитетом, осморегуляцией, антиоксидантной защитой, метаболизмом хитина и клеточным гомеостазом, у ракообразного отряда *Decapoda*.

Материалы и методы. Исследования проводились в научно-исследовательской лаборатории «Центр агробиотехнологии» Донского государственного технического университета 2024-2025 гг.

Результаты. Выявлены комплексные изменения в экспрессии ключевых генов, регулирующих иммунитет, осморегуляцию, антиоксидантную защиту, метаболизм хитина и клеточный гомеостаз. Показано, что эти тканеспецифичные и времязависимые изменения экспрессии являются центральным механизмом адаптационного ответа на стресс.

Заключение. Проведенный анализ современных научных данных позволил систематизировать информацию о влиянии абиотических и биотических стресс-факторов на экспрессию генов у ракообразных, в частности у представителей отряда *Decapoda*. Установлено, что изменения ключевых параметров окружающей среды (таких как температура, pH, концентрация аммиака и нитритов) и воздействие патогенов (вирусов, бактерий) вызывают сложные молекулярные ответы, затрагивающие гены, связанные с иммунитетом, осморегуляцией, антиоксидантной защитой, метаболизмом хитина и клеточным гомеостазом.

Ключевые слова: ракообразные; стресс-факторы; экспрессия генов; иммунитет; аквакультура; транскриптомный анализ; антиоксидантная система; хитиновый метаболизм; осморегуляция; Decapoda

Для цитирования. Ковальчук, Д. Ю., Саркисян, Д. С., Чолутаева, Э. Э., & Шевченко, В. Н. (2025). Влияние стресс-факторов на экспрессию генов ракообразных. *Siberian Journal of Life Sciences and Agriculture*, *17*(6-2), 112-132. https://doi.org/10.12731/2658-6649-2025-17-6-2-1540

Introduction

Aquatic crustaceans, particularly commercially and ecologically important species from the order *Decapoda* (shrimp, crayfish, crabs, lobsters, and spiny lobsters), represent valuable economic resources. Their global cultivation is continually challenged by disease outbreaks caused by pathogen infection and exposure to unfavorable environmental factors [5]. These problems lead to immune suppression, mass mortality, and, consequently, significant economic losses [5]. When grown in aquaculture, these organisms are exposed to the complex effects of a number of abiotic and biotic stress factors, the parameters of which (temperature, pH, salinity, dissolved oxygen concentration, ammonium, etc.) often fluctuate outside optimal ranges [13]. Such fluctuations

negatively impact the physiological state, immune status, and overall health of the organism [5; 13]. Changes in key environmental parameters, as well as exposure to pathogens, trigger complex stress and immune responses at the molecular and cellular levels [5]. However, the underlying mechanisms by which these stressors mediate changes in immune parameters are not fully understood [13]. In recent years, advances in molecular biology techniques such as RNA sequencing (RNA-seq) and real-time PCR have made it possible to thoroughly investigate the transcriptomic responses of crustaceans to various stressors [5; 13].

Thus, the aim of this review is to systematize and analyze current scientific data on the influence of abiotic and biotic stress factors on the expression of immunity-associated genes in crustaceans of the order *Decapoda*.

Purpose. The aim of the review is to systematize and analyze current scientific data on the influence of abiotic (such as pH, temperature, hypoxia, ammonia, nitrites) and biotic (viral and bacterial infections) stress factors on expression of genes associated with immunity, osmoregulation, antioxidant defense, chitin metabolism and cellular homeostasis in crustaceans of the order *Decapoda*.

The influence of abiotic factors on gene expression

Abiotic factors are non-living environmental conditions that directly or indirectly affect living organisms. These factors are essential for the existence of agroecosystems, but at the same time, these conditions can become extreme (for example, changes in water temperature or pH from optimal to suboptimal). These changes can have a significant impact on the productivity of aquaculture species. Therefore, a better understanding of the genes that control responses to stress factors will allow us to optimize the production of commercially farmed crustaceans under varying water parameters [5; 17].

he hydrogen ion concentration (pH) characterizes the acid-base balance of water. For most crustacean species, the optimal range lies in the neutral or slightly alkaline zone, approximately 7.5 - 8.5. Deviations from this range trigger a cascade of stress reactions. Under low pH conditions, that is, in an acidic environment, the most dangerous thing for crustaceans occurs – demineralization of their exoskeleton. Calcium carbonate, the main structural component of the shell, begins to dissolve, weakening the existing shell, making the process of molting and forming a new one extremely difficult and often fatal. The new shell becomes soft, unable to protect the animal from mechanical damage, pathogens, and cannibalism. At the same time, the acidic environment damages the gill filaments, disrupting gas exchange and osmoregulation, and reduces the effectiveness of hemocyanin, the respiratory pigment that carries oxygen [5].

On the other hand, the high pH characteristic of an alkaline environment has a direct toxic effect on gill tissue and disrupts the excretion process. In crustaceans, ammonia is the end product of nitrogen metabolism, and it is normally excreted through the gills by diffusion. However, in alkaline water, the chemical equilibrium shifts toward the formation of highly toxic free ammonia (NH_3), which, instead of being excreted, begins to passively diffuse back into the body's tissues, causing severe internal poisoning [17].

Thus, at the School of Earth, Environmental and Biological Sciences (Queensland University of Technology, Brisbane, Queensland, Australia), expression of genes controlling osmoregulation in the Australian red-claw crayfish *Cherax quadricarinatus* (von Martens, 1868) was studied [2]. The animals were distributed into three separate glass containers with water temperature of 25.5 °C and conductivity of 521 μS/cm [2]. A total of nine crayfish (average length 131.9 mm and body weight 56.3 g) were used in the experiment. The crayfish were placed in three different pH levels: 6, 7 and 8 conventional units [2]. RNA was isolated from gill tissues. Isolation was performed using the guanidine thiocyanate-phenol-chloroform extraction method (TRIZOL/Chloroform method) [2]. The yield and quality of RNA were checked using agarose gel electrophoresis, spectrophotometry and a bioanalyzer using the RNA 2100 nanochip chip [2]. The obtained RNA was then used to construct a cDNA library and subsequent sequencing on the Illumina platform. The obtained sequences were assembled into longer chains using bioinformatics tools [2].

Real-time PCR (qPCR) analysis was performed to test the expression of the identified genes [2]. Specific primers developed based on sequencing data were used, with 18S rRNA serving as the reference gene for normalization. The statistical significance of differences in gene expression between the three pH groups was determined using one-way analysis of variance [2].

As a result, five transcripts belonging to the carbonic anhydrase (CA) gene family were identified [2]. Among them, three full-length isoforms were described: cytoplasmic CA (ChqCAc), membrane-bound (GPI-anchored) CA (ChqCAg), and beta-class CA (ChqCA-beta), which represents the first complete sequence of the β-CA gene in cancer [2]. Two partial sequences (ChqCA-p1 and ChqCA-p2) were also found that showed high similarity to the GPI-linked isoform, suggesting a duplication of this gene. In addition to the CA genes, numerous other key osmoregulatory genes were found in the transcriptome, such as various subunits of Na+/K+-ATPase and V-type H+-ATPase [2].

A key finding was that when gene expression was examined in response to changes in the pH of the surrounding water, significant differences were

found only for cytoplasmic carbonic anhydrase (ChqCAc) [2]. Its expression was highest at pH 6, where the mRNA level was approximately 2-fold higher than at pH 7, and 6-fold higher than at pH 8 [2]. Expression of the GPI-linked and beta isoforms of CA, as well as other tested osmoregulatory genes (with the exception of an increase in V-type H+-ATPase), did not show statistically significant changes depending on the pH level. These results suggest that cytoplasmic carbonic anhydrase (ChqCAc) plays an important role in the systemic acid-base balance in crayfish [2].

The influence of pH on gene expression was also studied at the Key Laboratory of Experimental Marine Biology of the Chinese Academy of Sciences, where a bioinformatics analysis of chitin metabolism gene expression was conducted. Specifically, the glutamine and fructose-6-phosphate aminotransferase (GFAT) gene was analyzed in *Litopenaeus vannamei*. GFAT is the first and key rate-limiting enzyme of the hexosamine biosynthetic pathway, which directs metabolic flux toward the synthesis of chitin precursors [18]. The study indicated that LvGFAT gene expression was significantly upregulated in shrimp hepatopancreas when exposed to two abiotic stress factors: alkaline pH and the toxic heavy metal cadmium [18]. The hepatopancreas, as a central organ of digestion, metabolism, and detoxification, plays a key role in stress response [18]. The increased LvGFAT expression under these conditions suggests that this gene and the entire hexosamine pathway may be involved in cellular defense mechanisms. One possible molecular mechanism is that activation of this pathway provides a substrate for O-GlcNAcylation, an important post-translational modification of proteins that regulates the cellular response to various stressors, including toxins and changes in redox status [18]. Thus, chitin metabolism appears to be not limited to the construction of structural components but can also be integrated into complex biochemical networks that respond to adverse environmental conditions. The work was based on a comprehensive analysis of genomic and transcriptomic data [18]. Published genomic sequences of more than twenty crustacean species were used as materials, including economically important species such as *Litopenaeus vannamei*, *Penaeus monodon* and *Portunus trituberculatus*, as well as model and ecologically significant species such as *Daphnia magna* and copepods. In addition, multiple transcriptome (RNA-Seq) datasets obtained from publicly available databases such as NCBI were analyzed, covering various tissues, developmental stages, physiological states (e.g., molting cycle), and exposure conditions [18].

The study methodology relied on bioinformatics tools. Homology searches against known sequences using protein alignment and domain architecture

analysis tools were used to identify genes associated with chitin metabolism [18]. Protein structural characteristics such as molecular weight and isoelectric point were predicted using computational tools such as ExPASy Compute pI/Mw [18]. Phylogenetic analysis was performed to classify genes and establish evolutionary relationships between them [18]. Gene expression pattern analysis was performed using RNA-Seq data to determine tissues and molt stages where genes are active [18]. Regarding stress data, the results were apparently taken from cited experimental studies that likely used quantitative PCR (qPCR) methods to accurately measure gene expression levels in shrimp subjected to controlled stress conditions [18].

A genomic analysis revealed systemic features of chitin metabolism in crustaceans. A key discovery was the fundamental difference between synthesis and degradation genes: biosynthesis genes, such as chitin synthase (CHS), are highly conserved and typically present in one or two copies, while degradation genes, particularly the chitinase family (CHT), are significantly expanded and form multi-copy families, highlighting their functional diversity [18]. The general pathways of chitin metabolism were found to be similar to those in insects, but possess specific features, including groups of chitinases unique to crustaceans [18]. Expression analysis revealed that these genes have distinct tissue-specific and temporal regulation, closely linked to the molting cycle [18]. In addition, their role in the response to stress, both abiotic (increased GFAT gene expression under the influence of alkaline pH and cadmium) and biotic (changes in chitinase expression during immune response to pathogens) was confirmed [18]. Thus, chitin metabolism is not only a growth mechanism, but also a multifunctional system integrated into the processes of adaptation and defense of the organism [18].

Environmental temperature is the dominant factor determining the rate of metabolic processes in poikilothermic animals, which include crustaceans. Each species has a specific temperature optimum. Temperatures exceeding the species optimum induce the development of a stress response [5,6].

When temperatures reach critical values, an exponential acceleration of metabolic activity is observed. Despite the potential increase in growth rate, this process leads to a number of physiological dysfunctions. The increasing metabolic demand for oxygen conflicts with the decreasing solubility of gases in water. An imbalance arises between the body's energy expenditure and the availability of resources (oxygen and nutrients), which can lead to heat shock. At the cellular level, heat shock is characterized by disruption of the catalytic function of key enzymes, denaturation of protein structures, and subsequent systemic homeostasis failure, which is a common cause of mortality [5; 6].

Suboptimal temperatures, in turn, act as a limiting factor, inhibiting physiological functions. A decrease in environmental temperature causes a slowdown in metabolism, which is manifested by a significant reduction in feeding activity and motility. This leads to the cessation of feeding and, consequently, to growth arrest. Digestive processes are disrupted due to a decrease in the catalytic efficiency of enzymes at low temperatures [5; 6].

The Center for the Study of Food and Development (CIAD) conducted a study on the effects of high temperatures and hypoxia on the expression of selenium-dependent CqGPx3 isoforms. The study was also conducted on C. quadricarinatus. Two isoforms of glutathione peroxidase 3 (CqGPx3a and CqGPx3b) were examined. This enzyme protects against oxidative damage by catalyzing the reduction of hydrogen peroxide to water, thereby neutralizing this potentially dangerous oxidant [12].

Methods included exposure to stress factors, RNA isolation from various tissues, gene cloning, quantitative PCR, and bioinformatics analysis [12].

Two distinct isoforms were discovered: CqGPx3a was expressed predominantly in the nervous system, while CqGPx3b was expressed in pereiopods (walking legs). Under stress, CqGPx3a expression was significantly increased by hypoxia and high temperature, while CqGPx3b expression remained unchanged. Bioinformatics analysis revealed that CqGPx3b contains a proline-rich C-terminal domain with potential antimicrobial activity [12].

Thus, the isoforms exhibit tissue-specific expression and distinct responses to stress: CqGPx3a plays a role in antioxidant defense in the nervous system, while CqGPx3b likely performs dual functions in peripheral tissues [12].

Research on the effects of low temperatures was conducted at the Jiangsu Provincial Institute of Freshwater Fisheries. This study examined the effects of long-term (8 weeks) acclimation to low temperatures (10, 15, 20, 25, and 30 °C) on *C. quadricarinatus*. A number of physiological, biochemical, and molecular methods were used to comprehensively assess the organism's response. Growth parameters (weight and length gain, molting frequency) were measured, and the activity of key antioxidant enzymes (glutathione-S-transferase, GST; glutathione reductase, GR) and antioxidant content (total, reduced, and oxidized glutathione) were determined in the hepatopancreas. Gene expression of heat shock proteins (HSP20, HSP21, HSP60, HSP70, HSP90) and cold shock protein (CSP) was analyzed using quantitative PCR. To identify global molecular changes, transcriptome analysis (RNA-Seq) of the hepatopancreas of crayfish from the 10°C and 25°C groups was performed, followed by bioinformatics analysis to identify expressed genes and affected biological pathways [20].

Results showed that low temperatures (15 and 10°C) inhibited crayfish growth, reducing the rate of weight and length gain, and disrupted normal molting dynamics. Biochemically, the activity of the antioxidant enzyme GST decreased, but the content of reduced glutathione (GSH) and the GSH/GSSG ratio increased, indicating activation of non-enzymatic antioxidant defenses. Gene expression analysis revealed a specific response of different HSPs: the expression of *HSP60* and *HSP70* was significantly increased at low temperatures, while HSP20 was suppressed. Expression of the cold shock protein (*CSP*) gene was also significantly increased. Transcriptome analysis identified 589 differentially expressed genes. Long-term cold exposure was shown to disrupt the endocrine system (steroid and thyroid hormone biosynthesis), glucose metabolism, and suppress immune function (reduced expression of genes associated with the antibacterial response and inflammation). At the same time, defense mechanisms were activated, including glutathione metabolism and expression of genes associated with longevity. Thus, adaptation of *C. quadricarinatus* to cold is achieved by slowing growth and basal metabolism while simultaneously activating specific molecular defense mechanisms, which ensures survival [20].

Ammonia nitrogen and nitrite, which are formed through bacterial nitrification of ammonia or denitrification of nitrate, are common toxicants in aquaculture. These elements are a serious problem in aquatic ecosystems, as they accumulate from a number of anthropogenic sources, such as wastewater from metal, dye, and celluloid industries, municipal wastewater, and aquaculture. Being a stress factor similar to temperature and pH fluctuations, they can affect gene expression [3, 9].

The Key Laboratory of Mariculture at Ocean University in China conducted a study to investigate the effects of ammonia nitrogen (ammonia-N) on the molecular immune mechanisms of *Litopenaeus vannamei* [3].

Healthy shrimp were acclimatized for two weeks and then divided into four groups: control (0 mg/L) and three experimental groups (2, 10 and 20 mg/L ammonia-N) for 48 hours [3].

Hemolymph was collected at different time points (0, 3, 6, 12, 24 and 48 h). Quantitative real-time PCR (qRT-PCR) was used to determine the expression level of a wide range of genes in hemocytes, including genes encoding complement components, a cascade system of proteolytic enzymes designed to protect the body from foreign agents (*C1q, MBL, Ficolin, A2M, Integrin*), C-type lectins, which are involved in intercellular interactions, immune response and apoptosis (*C-lectin 1, 2*), intracellular signaling factors (*PLC, NF-κB, PKA, CREB*), phagocytosis (*ROCK, Myosin, Cubilin, Peroxinectin, Dynamin*) and

exocytosis (*SNAP, Syntaxin, VAMP*) [15, 16]. Expression of genes of the propenol oxidase system (*PPAE, PPO3*), immune factors (*Pen3, Crustin, Stylicins, ALFs, LYC*) and inflammatory factors *(*HSP90, TNFa, IL-16**) was also analyzed. Functional immune parameters were also assessed in parallel: phagocytic activity of hemocytes, total hemocyte count (*THC*), and in plasma – serine proteinase activity, phenol oxidase (*PO*), antibacterial and bacteriolytic activity. Statistical analysis of the data was performed using one-way analysis of variance (*ANOVA*) followed by Duncan's test [3].

The results demonstrated a marked suppression of immune function under the influence of ammonia-N [3]. The expression of key complement components (*C1q, MBL, Ficolin, A2M*) and their receptor Integrin was significantly reduced, especially at 6-24 hours of exposure [3]. The C-type lectin genes demonstrated opposite dynamics: C-lectin 1 was suppressed, while C-lectin 2 was transiently activated at 3 and 6 hours with a subsequent decrease. In signaling pathways, a decrease in NF-κB and transient activation of *PLC*, *PKA* and *CREB* were observed. This correlated with a significant decrease in expression of genes associated with phagocytosis (*ROCK, Myosin, Cubilin, Dynamin*), and a drop in phagocytic activity itself and the total number of hemocytes. Humoral immunity was also impaired: the expression of exocytosis genes (*SNAP, Syntaxin, VAMP*) and the proPO system (*PPAE, PPO3*) was suppressed, which was accompanied by a decrease in PO and serine proteinase activity in plasma. Plasma antibacterial and bacteriolytic activities also significantly decreased. The expression of many antimicrobial peptides (*Pen3, Crustin, Stylicins*) was suppressed, while ALFs and LYC showed a transient increase. Inflammatory factors (*HSP90, TNFa, IL-16*) demonstrated complex changes, indicating the development of an immune imbalance [3].

This study demonstrates that nitrogen stress leads to profound suppression of both cellular (phagocytosis) and humoral (exocytosis, proPO system, antimicrobial peptides) immunity in shrimp. The authors suggest that this suppression is mediated by coordinated changes in the expression of complement components and C-type lectins, which, in turn, affect intracellular signaling pathways (NF-κB, PKA/CREB) regulating key immune behaviors of hemocytes [3].

The study on the effects of nitrite was conducted at the Key Laboratory of Aquatic Live Feed Production and the Key Laboratory of Biodiversity and Biotechnology, Jiangsu Provincial College of Life Sciences. The effect of acute nitrite exposure on gene expression was studied using Australian red-claw crayfish [9]. Juveniles with an average weight of 20 ± 2 g were used in the study [9]. After acclimation for four weeks, the crayfish were exposed to four nitrite

concentrations (NO_2-N: 0.5, 1, 1.5, and 2 mg/L) and a control for 48 h, while maintaining a constant chloride level (10 mg/L) [9]. The temperature was 26 ± 1 °C, pH 7.1 ± 0.5, and dissolved oxygen concentration was approximately 5.0 mg/L. Gill tissue samples were collected after 12, 24, and 48 h. Relative mRNA expression of ten genes was measured using real-time reverse transcription-PCR (RT-PCR): antioxidant enzymes (mitochondrial and cytosolic Mn-SOD, extracellular Cu/ZnSOD, catalase CAT, glutathione-S-transferase GST) and metabolic enzymes (arginine kinase AK, glutamate dehydrogenase GDH, mitochondrial malate dehydrogenase mMDH, α-subunit of Na^+/K^+-ATPase and phosphoenolpyruvate carboxykinase PEPCK) [9]. Statistical significance was determined using two-way analysis of variance and Post Hoc tests [9].

As a result, it was found that the expression of antioxidant enzyme genes increased significantly after 12 and 24 hours of exposure in all experimental groups, indicating the activation of oxidative stress defense system [9]. However, after 48 hours at high nitrite concentrations (1.5 and 2 mg/L), their expression was suppressed, indicating a breakdown of compensatory mechanisms [9]. The genes of metabolic enzymes (AK, GDH, mMDH, Na^+/K^+-ATPase) demonstrated similar dynamics: an increase in expression at early stages, probably to meet increased energy needs, and a subsequent decrease after 48 hours [9]. In contrast, the expression of the PEPCK gene was significantly suppressed throughout the experiment at high nitrite concentrations. The obtained data indicate that acute exposure to nitrite causes dose- and time-dependent oxidative and metabolic stress in crayfish [9].

The effect of nitrite on gene expression in *Litopenaeus vannamei* (Boone, 1931) was also studied at the Key Laboratory of Ecology and Environmental Science of Guangdong Province Higher Education Institutions. Shrimp with an average weight of 4.41 ± 1.80 g, which were acclimated for two weeks under laboratory conditions, were used as experimental animals [19]. Exposure to nitrite nitrogen at a concentration of 20 mg/L, which is considered suitable for aquaculture conditions, was carried out for different periods of time: 0, 4, 8, 12, 24, 48, and 72 hours [19]. The control group was kept in water without the addition of nitrite. Hemolymph was collected from the shrimp at specified time points for analysis [19]. Flow cytometry with Annexin V-FITC and propidium iodide (PI) staining was used to assess hemocyte apoptosis, allowing the use of viable, early and late apoptotic, and necrotic cells [19]. Concurrently, total RNA was isolated from the hemolymph cell pellet for gene expression analysis [19]. mRNA levels for seven key genes were determined using quantitative real-time PCR: two apoptosis-related genes (caspase-3 and cathepsin B (CTSB)), one stress protein (HSP70), and

four antioxidant enzymes (manganese superoxide dismutase (MnSOD), catalase (CAT), glutathione peroxidase (GPx), and thioredoxin (TRx)) [19]. Statistical significance of differences between the control and experimental groups was determined using one-way analysis of variance (ANOVA) [19].

The study found that nitrite exposure caused a significant increase in the proportion of apoptotic hemocytes, but this effect was only evident at late stages of exposure – 48 and 72 hours. Gene expression analysis revealed complex, temporal dynamics of the molecular response. Genes responsible for antioxidant defense and the immediate stress response were activated first. Thus, the expression of MnSOD, GPx, and the heat shock protein HSP70 was significantly increased as early as 8 hours after exposure. GPx expression then decreased, while MnSOD demonstrated a second peak of activation at 48 hours. A later response was demonstrated by catalase (CAT), whose mRNA level increased at 24 and 48 hours, and thioredoxin (TRx), whose expression increased sharply at 48 hours. Regarding apoptotic genes, caspase-3 expression increased significantly at 24 and 48 hours, preceding the visible increase in the number of apoptotic cells. Cathepsin B (CTSB) expression was also significantly increased at later stages – 48 and 72 hours – correlating with the peak of apoptosis [19].

Thus, the obtained results indicate that the toxic effect of nitrite on shrimp hemocytes is mediated by oxidative stress. The cells trigger a cascade of protective molecular reactions: first, fast-acting antioxidant enzymes (GPx) and the chaperone HSP70 are activated, followed by the involvement of other components of the antioxidant system (MnSOD, CAT, TRx). Long-term exposure to stress leads to the activation of apoptotic pathways, in which caspase-3 and, possibly, cathepsin B play a key role, which ultimately leads to cell death and can weaken the shrimp immune system [19].

The influence of biotic factors on gene expression

Innate immunity is characteristic of both invertebrates and mammals. In crustaceans, innate immunity is considered the primary defense factor, playing a critical role in identifying viral infections and initiating antiviral responses [5; 8]. Defense mechanisms against pathogens are directly mediated through changes in gene expression. Diseases, such as viral infections, have a direct and powerful effect on the transcriptome, inducing increased expression of genes encoding antimicrobial peptides and immune system components. Thus, studying which genes are turned on or off during disease allows us to uncover molecular mechanisms of immune response and pathogenesis, providing key insights into crustacean resistance to infections [7; 10].

A study on the molecular response to white spot syndrome virus (WSSV) infection was conducted at the State Key Laboratory of Marine Ecology, College of Oceanography and Environmental Sciences, Xiamen University [10]. Hematopoietic tissue (Hpt) cell culture isolated from *C. quadricarinatus* was used in the experiment [10]. The cells were infected with WSSV, and suppressive subtractive hybridization (SSH) was used to identify genes with altered expression, creating two libraries: L1 (1 hour after infection) and L12 (12 hours after infection) [10]. Differential expression was further confirmed using semi-quantitative real-time PCR (RT-PCR) [10].

As a result, 366 genes were identified whose expression levels were statistically significantly increased in response to infection [10]. Among them, the genes were divided into functional groups: immune response (e.g., anti-lipopolysaccharide factor ALF, apoptosis gene ALG-2), cytoskeletal system (actin, tubulin), signal transduction (various kinases, transcription factors), stress (heat shock proteins), metabolism and homeostasis, and protein synthesis and processing. An important result was that 176 of these genes were described in the context of WSSV infection for the first time [10]. Confirmed overexpression of eight randomly selected genes (such as DNA helicase, coatomer, and TRIM32) by RT-PCR revealed that WSSV infection activates a complex cellular response involving not only classical immune pathways but also cytoskeletal remodeling, the ubiquitination system, and intracellular transport [10].

Another study on the impact of diseases was conducted at the Key Laboratory of Freshwater Aquaculture Genetics and Breeding of Zhejiang Province, Zhejiang Institute of Fisheries [7]. The study examined changes in gene expression in Australian red-claw crayfish infected with the iridescent virus (Decapod iridescent virus 1, DIV1).

In this study, clinically healthy crayfish were artificially infected with DIV1 by intramuscular injection, and naturally infected individuals were also collected from farms to investigate the response of *C. quadricarinatus* to virus infection [7]. Nested PCR and histopathological examination of tissues (gills and hepatopancreas) with hematoxylin and eosin staining were used to confirm infection [7]. The expression profile of 90 immune genes in hemocytes was analyzed using a qRT-PCR array [7]. The composition of the intestinal microbiota was studied by high-throughput sequencing of the 16S rRNA gene (V3–V4 regions) followed by bioinformatics processing in QIIME2 [7]. Statistical analysis included alpha diversity assessment, Student/Welch tests, and Spearman correlation analysis to identify relationships between gene expression and microbiota composition [7].

As a result, it was found that DIV1 infection causes characteristic histopathological changes in tissues (eosinophilic inclusions and karyopyknosis) [7]. Gene expression analysis revealed significant activation of 27 immune genes associated with antimicrobial peptides (e.g., *Crustin2, lyz*), Toll-like and JAK-STAT signaling pathways, as well as with stress response (*Hsp70*) [7]. Analysis of the microbiome revealed a decrease in alpha diversity (Chao1 and Faith's PD indices) and significant changes in its composition: an increase in the proportion of Enterobacter and Acinetobacter bacteria and a decrease in the proportion of Fusobacterium and Bosea at the genus level [7]. Correlation analysis revealed a close relationship between changes in the abundance of certain bacterial genera (e.g., *Enterobacter, Hyphomicrobium*) and the expression level of immune genes (such as *Toll and Foxn*), indicating a complex impact of infection on immune system and the host's symbiotic microbiota [7].

The influence of abiotic factors on chitin metabolism gene expression has been described previously; however, these are not the only factors affecting its regulation.

In addition to their central role in molting and growth, chitin metabolism genes exhibit a pronounced response to biotic stress factors, serving as an important component of the crustacean immune system. Numerous studies confirm the activation of these genes in response to pathogens. In particular, upregulation of shrimp chitinase genes is observed during viral infection with white spot syndrome virus (WSSV) [18]. It has been shown that individual enzymes, such as endo-beta-N-acetylglucosaminidase (NAG) in *Penaeus monodon*, can directly interact with viral proteins (e.g., VP41B of WSSV), which in some cases may facilitate infection, while in others, it may be part of a defense response [18].

Similarly, bacterial infections with pathogens such as *Vibrio parahaemolyticus* and *Aeromonas hydrophila* induce expression of genes encoding chitin-degrading enzymes, as demonstrated for the NAG gene in *Exopalaemon carinicauda*. Key immune tissues such as hemocytes and hepatopancreas are the main sites of expression of these immune-associated genes [18]. Knockdown experiments with chitinases (e.g., LvCHT5 in *Litopenaeus vannamei*) result in significant changes in the expression profile of a wide range of immune genes, including antimicrobial peptide genes, suggesting a regulatory role for chitin metabolism in immune networks [18]. Thus, chitin metabolism system is integrated into overall defense mechanisms of crustaceans, maintaining cuticle integrity as a physical barrier and participating in both direct and indirect responses to viral, bacterial, and potentially fungal pathogens [18].

Conclusion

An analysis of current scientific data has allowed us to systematize information on the influence of abiotic and biotic stress factors on gene expression in crustaceans, particularly in members of the order *Decapoda*. It has been established that changes in key environmental parameters (such as temperature, pH, ammonia and nitrite concentrations) and exposure to pathogens (viruses, bacteria) trigger complex molecular responses affecting genes associated with immunity, osmoregulation, antioxidant defense, chitin metabolism, and cellular homeostasis [2; 3; 7; 9; 10; 12; 18].

Sponsorship information. The study was supported by a grant within the framework of the "Nauka-2030".

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ВКЛАД АВТОРОВ

Все авторы сделали эквивалентный вклад в подготовку статьи для публикации.

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Поступила 08.11.2025 Received 08.11.2025
После рецензирования 20.11.2025 Revised 20.11.2025
Принята 01.12.2025 Accepted 01.12.2025