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Review

Impacts of Habitat Quality on the Physiology, Ecology, and Economical Value of Mud Crab *Scylla* sp.: A Comprehensive Review

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Abstract: The water of the mangrove ecosystem and surrounding coastal areas are gradually shrinking due to the intense destruction. Therefore, the effects of the physicochemical properties of the habitat water on the in-habitant species must be studied. *Scylla* sp. is involved in the food chain and bioturbation structure formation in mangrove forests. Five major electronic databases, such as PubMed, Scopus, Web of Science, AGRICOLA, and Google Scholar, were systematically searched to review the cause and effects of influencing abiotic factors, mainly physicochemical properties of habitat water, including water pollution on *Scylla* sp. Responses of mud crabs at biochemical, molecular, physiological, growth, reproduction, and production level were independently reviewed or in relation to physicochemical properties of habitat water, pathogens, heavy metals, and harmful chemicals present in their habitat water. Review results suggest that these crabs are mostly under threats of overfishing, varied physicochemical properties of habitat water, pathogens, heavy metals, and chemical toxicants in water, etc. At low temperatures, the expression of calreticulin and heat shock protein-70 mRNA expression is elevated. Like melatonin, the hormone serotonin in mud crabs controls ecdysteroids and methyl farnesoate at 24 °C, 26 ppt salinity, and pH 7.2 of habitat water, facilitating their reproduction physiology. Xenobiotics in habitat water induce toxicity and oxidative stress in mud crabs. These crabs are prone to infection by white spot and rust spot diseases during the winter and spring seasons with varied water temperatures of 10–30 °C. However, elevated (65%) weight gain with higher molting at the juvenile stage can be achieved if crabs are cultured in water and kept in the dark. Their larvae grow better at 30 ± 2 °C with salinity 35 ppt and 12 hL/12 hD day length. So, monitoring habitat water quality is important for crab culture.

Keywords: abiotic factors; chemical pollutants; water-induced physiology; water physicochemical properties; mangrove habitat water; *Scylla* sp.

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1. Introduction

Saline water areas of mangrove ecosystems in coastal zones provide huge habitats worldwide for several aquatic and semiaquatic organisms. As per the latest update in the year 2023 by the Food and Agriculture Organization of the United Nations, 17,075,600 hectares of mangrove areas in the world give sustenance to various life forms in 112 countries [1]. The water quality of mangrove ecosystems can seasonally vary with 5–35 ppt salinity, 8–8.5 water pH, 3.5–8.3 sediemnt pH, 25–35 °C temperature, 3.37–3.89 mg/L dissolved oxygen, 2.65–4.46 biochemical oxygen demands, and 5.44–10.67 NTU turbidity, while the values are always specific and flexible to a specific water body [2]. Estuarine water bodies also vary seasonally in a similar way affecting their water pH, salinity, turbidity, hardness, temperature, dissolved oxygen, etc., and the variation is mainly due to tidal flows and day cycle [3,4]. Such a variable ecosystem imposes several cellular insults and physiological disturbances leading to hampering the growth, production, reproduction, immunity, etc., of the inhabitants [5,6]. The above responses or stress to the inhabitants by a change in their habitat water quality is magnified when pollutants and other chemicals or toxicants are added to the ecosystem mainly by anthropogenic activities followed by surface runoff [6–9]. Therefore, a detailed study on the impacts of the changing water quality on the life cycle, metabolism, growth, stress management strategies, production, and reproduction, including the economic values of any particular mangrove species, is warranted [10]. Results of such research on the water qualities and associated biotic and abiotic stressors/markers will lead to the draw appropriate policies to protect the mangrove/estuarine habitats and their inhabitants [11–13].

Mud crabs genus *Scylla* (*S. serrata*, *S. tranquebarica*, *S. olivacea*, and *S. paramamosain*) is an important member of mangrove/estuarine saline water ecosystems than other crustaceans due to its major activities (biological burrowing and bioturbation creation) in protecting and spreading mangrove forests [14]. Mud crabs are generally found in estuaries, especially in mangrove forests of India, Taiwan, Japan, China, South Africa, Indonesia, and the Philippines of Indo-Pacific places. Similarly, Malaysia, Singapore, Western Samoa, Salmon Island, Fiji, and New Caledonia are big mud crabs habitats. Generally, mud crabs have high demand worldwide for their nutritious and delicious taste of meat, which leads to overfishing at commercial bases across the coastal sites. The production of mud crabs surged from about 4000 to 175,000 t between 1990 and 2012. This compares with an estimated 10,000 t harvest worldwide in 1990 to 40,000 t in 2012 [15]. The world's fisheries produced 1,523,000 t of crabs and sea spiders from catch fisheries and 447,000 t from aquaculture in 2019, with an international export of a total of 588,110 t [1]. As a result of rising demand from consumers in recent years, the crab industry has flourished, and the market cost of mud crabs has increased. Wholesale prices average roughly USD 30 per kilogram, even in the high-yielding seasons, with the highest demand in the United States, China, South Korea, Thailand, and Japan [16]. In addition to overfishing, the availability of mud crabs is impacted by the fact that they depend on numerous abiotic factors at various stages of their lifecycle. Mud crabs spend their entire lifespan in water or water sediments of the intertidal and subtidal zones of estuaries and mangrove systems. This shallow water system is characterized by 150 days of the warm, wet season and 210 days of the cool, dry season, which result in the fluctuation of abiotic factors [17]. Therefore, study on the morphology, life cycle, growth, production, reproduction, and cellular physiology need to be studied with respect to the water qualities of these crabs for their better exploitation (Figure 1).

Figure 1 illustrates the evolution of mud crab research from biochemical to physiological to molecular studies from 1967 to 2022 [18]. It enables us to comprehend the transition of research on them from early biochemical to middle physiological to the contemporary molecular level. *S. serrata* has some distinguishable features, such as a convex body and broad carapace, which is present in a triangular shape at its abdominal side. There are 21 serrations prominently found at the line of fusion between the upper and lower body surface. One pair of antennae, antennules, and eyestalk is distinctly visible at the line of fusion at the anterior side in mud crab *S. serrata* [19]. In India, *S. serrata* has a carapace of 80–181 mm in width and body weight ranging from 0.68–0.83 kg [20]. Additionally, the mud crab habitat is quite more complex than other marine crabs because of its wide range of tolerance towards environmental factors, which makes mud crabs a significant organism for ecological studies.

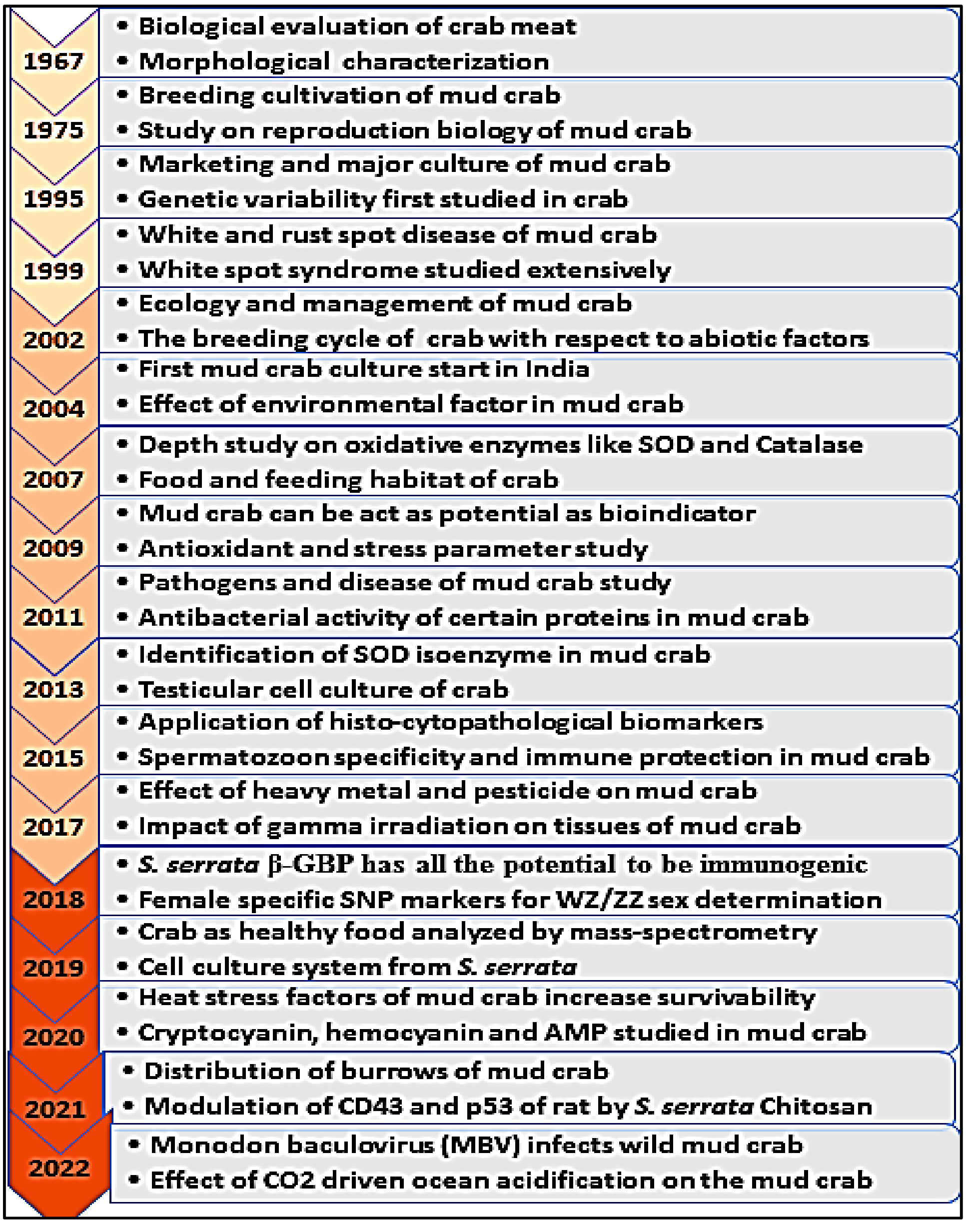

Figure 1. Major research findings on mud crabs in chronological order. Major studies have been conducted on mud crabs from the beginning to till date, and the sequence is as follows. Most studies focus on ecology, morphology, and reproduction in the early decade. The middle studies largely focus on pathogen and biochemical studies, while molecular and biotechnological-related studies are mostly conducted in this current decade.

Previous studies have proven that this animal model poses a high-stress resistance ability in addition to a well-defended immunological response to combat physiological stress under the changing habitat water qualities [21–26]. The innate immune system is well-observed in mud crabs, which also protects them from most pathogens [24]. However, water physicochemical factors, including temperature, salinity, pH, day length, tide height, and food availability, determine the growth and physiology of most crustaceans, including mud crabs [17]. For instance, variation in water temperature leads to stress response in aquatic organisms due to changes in their cellular metabolism. Mostly, it induces a stress response, irregular gene expression, pathogen spreading, and immune resistance against pathogens by down-regulating or up-regulating the synthesis of antimicrobial peptides and reproduction by hormonal changes in some cases [27]. Apart from this, high temperature for a prolonged period induces drought, which results in a rise of metal and toxicants in the water of a natural habitat that leads to bioaccumulation and bio-transfer of such toxicants in mud crabs and organisms depending on them [28].

Similarly, salinity or salt concentration in habitat water plays a significant role in several physiological processes of mud crabs, including the oxidative stress (OS) response. In turn, it influences the larval stages due to an increase in demand for oxygen during rapid growth and, to a lesser extent, immunity [29]. The growth, maturation, survival, and fecundity of mud crabs are well-maintained by abiotic factors such as natural diet, day length, and wind speed [30].

It is pertinent that abiotic factors, especially water physicochemical factors, directly affect an organism's body physiology, stress resistance, immunity, gene expression, reproduction, distribution, and bioaccumulation of toxic products [17]. Because water physicochemical factors have such a significant impact on the biochemical, molecular, and physiological processes of the mud crab, a comprehensive review is needed to explore the mechanisms from both its environmental water perspective and also for the aquaculture of the genus *Scylla*. Therefore, the scope of this research review compiles various sources to present their economic importance, unified environmental physiology, and environmental biotechnology, focusing more on the function of abiotic variables, especially water physicochemical factors (Figure 1). This systematic review provides the context necessary to evaluate the impact of key water physicochemical factors on mud crabs at the biochemical and molecular levels and information on their biotechnology that can be related to the environmental cause and effects in crabs in general and in mud crabs in particular. The review may be useful for both environmental water monitoring using *Scylla* sp. as indicator animals and also for the betterment of their aquaculture.

2. Materials and Methods

For a comprehensive review of the genus *Scylla* in relation to environmental and pollutant effects, key terms such as "*Scylla*", *S. serrata*", *S. tranquebarica*, *S. olivacea*, *S. paramamosain*, and "mud crabs" alone or along with "physiology", "stress", "biochemical", "molecular", biotechnological, medical, etc., were searched in PubMed, AGRICOLA, Scopus, Web of Science, and Google Scholar databases and only the peer-reviewed published literature was selected using traditional methods. The electronic databases were used to comprehensively search the literature on this topic related to *Scylla* sp., focusing on the literature written in English only.

2.1. Data Sources and Search Strategy

PubMed/MEDLINE is a large database in biomedicine, and the Google search engine eventually stores the entire published peer-reviewed and other articles, while AGRICOLA contains about 6 million records associated with agriculture and allied sciences. It is to be noted that *Scylla* sp. is exclusively available in cultivated as well as in natural brackish water, saline, or mangrove forest lands, so it is included in the AGRICOLA database. Similarly, Scopus and Web of Science also provide a large scope for peer-reviewed high-quality articles. The aforementioned factors played a role in our decision to use the above five databases. Of the papers available in all the above databases on mud crabs, only peer-reviewed literature published in English on "*Scylla* sp." was screened in relation to various additional search terms. Search terms such as "abiotic and biotic stressors, heavy metals, antibacterial proteins, antioxidant enzymes, behavior, bioindicator, breeding, biotechnology studies, chromosomes, culture, distribution, ecology, ecosystem importance, ecotoxic, endocrine system, environment, fisheries, food and feeding, genes, genomics, harvest, heavy metals, immunity, life cycle, migration, mitochondria, morphology, neurotransmitter, organic and inorganic waste, organophosphorus, pathogens, physiological responses, physiology, pollutants, polychlorinated biphenyls, poly-halogenated compounds, production, regulatory proteins, reproduction, respiration, salinity, temperature, and toxic chemical, along with "*Scylla* sp." or "mud crabs" were electronically searched in the above databases.

2.2. Study Selection

The entire published peer-reviewed articles in the English language in books, journals, periodicals, and various authentic reputed webpages till September of 2022 on "*Scylla*" in relation to the search terms in the above-mentioned electronic search engines were included. The word was searched with search terms as mentioned in Section 2.1 were screened in this review article. Articles not containing any of the above terms were not included in the review. Articles matching within the subject area of the *Scylla* sp. were included in the review, whereas any axillary article in which the above term(s) is merely used was excluded from the review. Because 895 and 17 articles were published on the crab *Scylla* in PubMed and AGRICOLA electronic engines, respectively, all the relevant articles were included in the screening while the articles were hugely filtered in the Google search engine that hit s about 10,800,000 numbers with the term "*Scylla*". Similarly, articles from Scopus and Web of Science were also screened as per the need of the topic. All the data from the published papers were independently extracted unbiasedly, irrespective of the geographical region. The published literature from all geographical areas was selected for screening. The filtering was performed by increasing the specific keywords or manually selecting the most relevant and recent articles published in peer-reviewed journals. For example, out of 895 articles present on *Scylla*, articles that describe the tissue culture from pancreatic cells of *Scylla*, the morphology of *Scylla*, etc., were excluded from the study, whereas articles that were relevant to the change in the species as a function of their environmental factors were included in the study. About 220 articles were included in this review article.

2.3. Data Extraction

In order to streamline the entire review process securely and to ensure the reliability and consistency of this arthropod species, we have covered various aspects, such as the economic importance, species origin, morpho-anatomical adaptive features, adaptations, biochemical and molecular responses against stress, cellular, organ-specific, metabolic, and behavioral adaptations against the biotic and abiotic stressors of the species *Scylla* species. In addition, we have extensively reviewed the effects of the specific chemicals and environmental parameters, such as water salinity, temperature, and pollutants, on its studied biochemical and molecular pathways. The role of this organism in its ecosystem as a disease carrier and ecologic relation with other co-habitants has also been reviewed for its better exploitation. It will extend the existing understanding of the link between enzymatic and pathophysiological activities or responses in lower animals and *Scylla* sp., in particular. The objective of this article was to systematically review information to elucidate for the first time the ecotoxic responses, such as redox regulatory activities, neurotransmitter enzyme levels, and responses to heavy metal exposure of this mud crab in their habitat water. As a result, it can be helpful for its conservation in general and environmental ecotoxic and environmental chemistry studies in particular.

2.4. Synthesis and Analyses

Once the authors were convinced of the peer-reviewed articles on these species, these were analyzed and filtered to a <200 number, and some of the repetition articles among all databases were considered only once. The subject area of each article was extracted and categorized to describe various aspects of *Scylla* sp. in relation to various environmental factors, which could be natural or anthropogenic in nature. However, the number of peer-reviewed articles on *Scylla* sp. indicates vast studies on these species, starting from physiological responses to life history trade-offs, which were emphatically included in the present review.

3. Economic and Biotechnological Values of *Scylla* sp. under Varied Water Physicochemical Factors

Apart from the economic aspect, mud crab is a key species for restoring the coastal water ecosystem; indeed, its activity help in spreading mangrove forest that indirectly contributes to the ecosystem as a whole for the survival of other species [31] and, in turn, it contributes to the artisanal culture and fishing in mangrove areas. The need to study a species is more dependent on its economic values, and *Scylla* sp. has tremendous environmental, food, and biotechnological values worldwide [15,16].

3.1. Nutritional Values of Mud Crab Meat

The mud crabs are well known for their nutritional value, and their delicious meat comprises 83.64% moisture, 22.77% protein, 1.35% lipid, and 2.09% ash when they are cultures in optimal saline water, which could be about 17 ppt salinity [32]. The nutritionally valuable element concentration was analyzed in pre-molt, hard-shelled, and newly molted (soft-shelled) crabs. Preferably, elements such as K, Ca, Mn, Cu, etc., were analyzed and present in the crab muscle tissue. Additionally, the exuvium of soft-shelled and the carapace of pre-molted hard-shelled crabs were collected for nutritional analysis. The analysis concluded that newly molted crabs are more valuable for consumption than hard-shelled ones due to the higher absorption efficacy of essential elements in soft-shelled crabs. Nonetheless, toxic elements such as Pb are excreted during exuviation, and elements such as Zinc are found in a balanced concentration in soft-shelled crabs [33]. Some facts, such as a high level of protein, lower fat content, balanced essential elements such as Fe, Zn, Mg, and Cu, and availability of free amino acids make crab meat nutritionally much valuable [34,35]. Thus, the demand for adopting advanced cultural techniques to optimize their complex environmental condition is the need of time.

3.2. Value and Environmental Water Management of Crab Shell Bio-Waste

Mud crab outer shell waste generated from fisheries markets and processing industries creates intense pollution in coastal areas. However, this waste is highly valuable as it primarily contains chitin, and according to studies, it can be converted into useful compounds [36,37]. *S. serrata* carapace management revealed that economical carapace could be used in industries as a catalyst for the transesterification of palm oil. Additionally, chitin plays a significant part in biodiesel production at a commercial level [38]. Apart from this, bioceramics have a high market value because of their use in the medical and dental industry as implants. Crab shell is enriched with calcium and other components, making it a potential material for bio-ceramics. The analysis of crab shells revealed the presence of 19.78% carbon, 24.53% oxide, 4.81% MgO, 3.98% P_2O_3, and 71.42% CaO. However, after calcination at 1000 °C, the above composition changes as 6.27% carbon, 28.96% oxide, 5.87% MgO, 5.65% P_2O_5, and 82.3% CaO [37]. Thus, the above composition can effectively employ the outer shell of mangrove crabs for bio-ceramic production.

In everyday life, the use of plastic leads to huge environmental pollution, especially in water bodies, and researchers try to resolve this problem by conducting studies to generate (micro)-bioplastics [39]. Huge quantities of biowaste (shell, scale, and carapace) are generated from aquatic animals like mud crabs. These waste materials are a high source of chitin and chitosan, which are well-known for their ability as natural biodegradable and biocompatible polymers. The yielding ability of chitin from waste can be enhanced by a mild extraction method, but it still needs some improvement to extract pure chitin [40].

3.3. Antimicrobial Proteins in Mud Crabs under Varied Water Temperature

Most aquatic organisms, including mud crabs, maintain their body fitness with an active immune system that indirectly depends upon water physicochemical factors, such as water precipitation, atmospheric humidity, water salinity, ultraviolet radiation, food availability, and wind speed. Infectious diseases significantly affect crabs by slowing down their growth and survivability rate. Despite the availability of various drugs and antibiotics against microbial diseases, emerging threats are also noticed against the health of organisms due to the rise in multiple drug-resistant pathogens. In order to reduce this infectious disease, the identification of immune molecules is indeed essential in crabs. In mud crabs, an insect-like innate immune system is recognized, which is confirmed by the presence of antimicrobial peptides (AMPs), antilipo polysaccharide factor (ALF), hemocyanin, cryptocyanin along with crustin-like immune proteins (Figure 2). These antimicrobial agents' expression and activity vary with abiotic factors, especially water physicochemical factors, as discussed in the following sections and shown in Table 1. Therefore, the exact role and their regulation under variable habitat water physicochemical conditions will provide a new window to protect such organisms with natural neutraceuticals rather than using any artificial medicines in aquaculture farms.

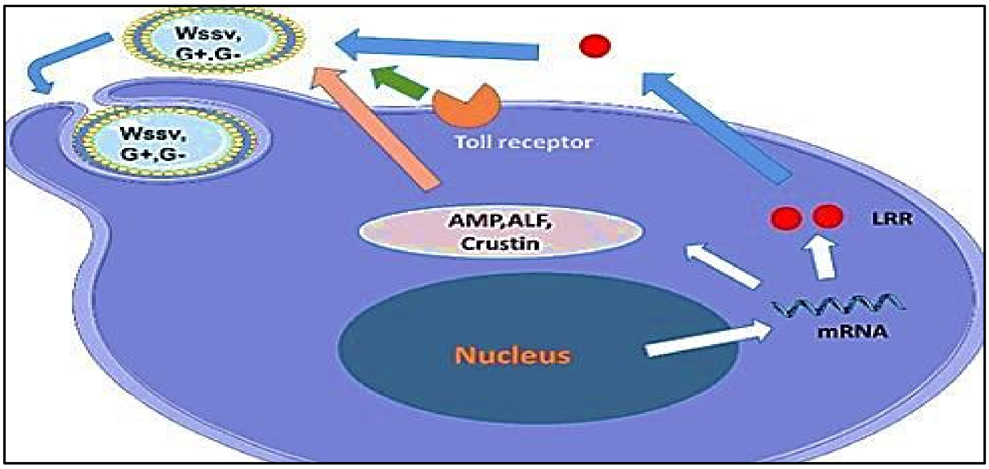

Figure 2. Phagocytosis is mediated by various immune proteins identified in mud crabs. The mud crab's innate immune system comprises both humoral and cellular responses. In cellular response, the peptidoglycan of bacteria and the protein coat of the virus trigger expression of AMPs. Antimicrobial peptides, anti-lipopolysaccharide factor (ALF), crustin-like factors, toll-like receptors, and leucine-rich repeat (LRR) work separately to phagocytose microbial pathogens. Phagocytosis occurs when these proteins bind on the surface of the pathogen leading to the engulfment of viruses and bacteria. The arrows indicate the direction of the movement or action of the molecules in cell.

The β-glucan binding protein (GBP) is an immunogenic agent present in the hemolymph of mud crabs. The antibiofilm efficacy of Ss-β-GBP was measured at different concentrations using light microscopy and confocal laser scanning microscopy, confirming that Ss-β-GBP is immunogenic to most pathogenic bacteria [41]. Multidrug resistance bacteria are generally treated through antibiotics, but amp-like arasin is also effective against infective disease-causing organisms. This peptide has 65 amino acids, molecular weight of 7 kDa, and an isoelectric point of 10.68. The N-terminal of this protein has a Gly/Arg-rich domain, and the C-terminal contains a cysteine-rich domain. It was observed that when the crab was subjected to lipopolysaccharide, Ss arasin mRNA of hemocyte expression increased, indicating its antimicrobial activity [42].

The gut bacteria of certain animals are novel sources of antibiotics as they can be used against multidrug-resistant pathogenic bacteria. The gut bacteria isolated from *S. serrata* were prepared and tested against gram-positive, gram-negative, and human cells (HaCaT) on bacterial-conditioned media, which showed significant antibacterial activities. Additionally, the antibacterial activity after heat inactivation suggests that the antibacterial property is maintained through bacterial metabolites or peptides [43]. However, human cells, on the other hand, recognize very little cytotoxic effect compared with gram-positive and negative bacterial cells, suggesting that gut bacteria are potential antibiotics for humans. Apart from this, carcinogenic agents are increasing, which also show a significant effect on crab health. The variations of the antimicrobial proteins, such as β-glucan binding protein in mud crabs, need to be studied as a function of water's physicochemical factors.

Marine invertebrates mostly depend upon AMPs to prevent pathogen invasion under various saline conditions (Table 1) [44,45]. The antimicrobial activity of these immune proteins mainly depends upon optimal temperature. The granular hemocyte of mud crabs contains an 11 kDa antimicrobial protein known as *S. serrata* antimicrobial protein, which resembles a protein scygonadin found in the ejaculatory duct of *S. serrata* and shows optimum activity at 35 °C. Techniques such as RT-PCR and Northern and Western blot analyses were employed to confirm that *S. serrata* antimicrobial protein is expressed in various tissues across the body, unlike scygonadin [46]. The hormonally active form of vitamin D3 is the only inducer of the AMPs family in higher-order animals, and no role of other biological, hormonal, microbial, and water physicochemical factors is recognized [46].

Table 1. Effects of temperature on AMP, crustin, and ALF-like innate immune molecule of *S. serrata*.

Innate Immune Molecules	Expression Upregulation at Temperature	M.W.	Highly Expressing Tissue	Response to Bacteria or Antigens	Response to WSSV	Antibacterial Activity	References
SSAPs	35 °C	11 kDa	Ejaculatory duct	UP: Bacteria	ND	G+, G-	[44]
Sc-ALF	25 and 35 °C	11.17 kDa	Hemolymph	UP: Bacteria, LPS	ND	ND	[47]
Ss Toll	ND	NA	NA	Up: Peptidoglycan, LPS	ND	ND	[48]
LRR	ND	NA	Various tissues	Up: Bacteria	Up-regulation	G-	[49]
Vg-2	25 °C	NA	Testicular spermatozoa	ND	Up-regulation	ND	[50,51]
Ss ALF	25 and 35 °C	NA	Hemocyte, heart and, muscle	Up: Bacteria and LPS	ND	G+, G-	[52]
B-GBP	ND	100 kDa	Hemolymph	Up: Bacteria	ND	G+, G-	[41]

Note(s): Immune proteins found in different parts of mud crabs significantly affect bacteria, viruses, and other antigenic molecules. Antibacterial activity on both gram-positive and gram-negative is found in most cases. (G+: gram-positive, G-: gram-negative, MW—molecular weight, ND—not detected, NA—not available, Up—upregulated, SSAPs—stage-specific activator protein, ScALF—anti-lipopolysaccharide factor in *Scylla*, LLR—leucine-rich repeat, GBP—glucan-binding protein, WSSV—white spot syndrome virus, LPS—lipopolysaccharide, and AMP—antimicrobial peptides).

Mud crab's heart, hemocytes, and muscle tissues are the sites of SsALF and crustin mRNA expression. mRNA expression of this immune protein regulation depends on factors such as time and temperature [53]. Antimicrobial activity was noticed when the purified SsALF protein was incubated against both bacterial and cell cultures [45]. A complete characterization of Sc-ALF (MW-11.17 kDa) was carried out, suggesting that ALF expression increases from 13 to 49 fold at 25 and 35 °C water temperature, while its expression remains normal at 30 °C [47,53]. This protein also exhibits lipopolysaccharide (LPS) binding ability that might indirectly regulate the human vaginal epithelial cell immune responses through modulation of LPS-TLR4 binding in the NF-kB pathway [52]. However, specific studies on Sc-ALF expression in relation to temperature are still missing. There are crustins characterized in different crab species that show a high similarity with mud crab crustin, a cationic antimicrobial protein with a molecular weight of 7–14 kDa present in the hemocyte of mud crabs [54]. Various studies confirm that this protein expression also varies with time and temperature. A significant up-regulation in crustin expression was seen in crabs acclimated to temperatures close to the extremes of winter (5 °C water temperature) and summer (20 °C water temperature) [55]. Therefore, during winter and summer, crabs are less susceptible to pathogen infections (Table 1).

It has been noticed that the mud crab, like all arthropods and mollusks, possesses hemocyanin, a component of the innate immune system found in the hemolymph [56]. Hemocyanin, a metalloprotein commonly found in crustaceans, is well-known as an oxygen-carrying protein [57]. This oxygen-carrying protein is a potent antimicrobial and anti-cancerous protein. Additionally, purified hemocyanin from crab hemolymph has agglutinative properties confirmed by affinity proteomic studies [24,58]. Cryptocyanin is another innate immune agent having a molecular weight of 79.11 kDa, observed in all stages from oocytes, embryos, and zoeas to adult mud crabs, and structurally similar to hemocyanin [59,60]. The hemocyanin expression in crab was found to be similar in conditions such as warm water (22 °C)/high food, warm water/low food, and cold water/high food fixed at pH of 7.4 and salinity 30–33 ppt. On the other hand, the expression of hemocyanin was found to be down-regulated in cold water (14° C)/low food conditions [61].

Similarly to metalloproteins, phenoloxidase resembles the hemocyanin of 76 kDa with two homologous peptide chains. These enzymes exhibit higher activities during microbial pathogen-associated molecular pattern formation, where the metal center acts as an activator. However, a complete characterization of properties and the effect of water physicochemical factors on this protein can be revealed only after conducting in silico and in vitro experiments [62].

A toll-like receptor that recognizes pathogen-associated molecular patterns is constitutively expressed in all tissues and found in all life stages of mud crabs. The life of mud crabs is spent in various water habitats, especially salinities. Ligands like peptidoglycan and lipopolysaccharide modulate the expression pattern of SsToll. However, an up-regulation in SsToll was recognized when exposed to a virus [48]. Vg protein generally found in the female crab is responsible for vitellogenesis, but a separate variant detected in testicular spermatozoa, which is involved in immune protection during the spermatozoon maturation in mud crabs under normal water habitat (Figure 3.3, [50]). Leucine-rich repeat (LRR), like SsToll, is also involved in defense mechanisms and signal transduction in humans and mosquitoes [49]. The effects of temperature or any other factor on the expression of these proteins are still missing. Thus, a study on the differential expression of these proteins and mRNA will be helpful in determining the infection status of mud crabs under varied water physicochemical factors, such as temperature and salinity (Section 3.3 and Figure 4).

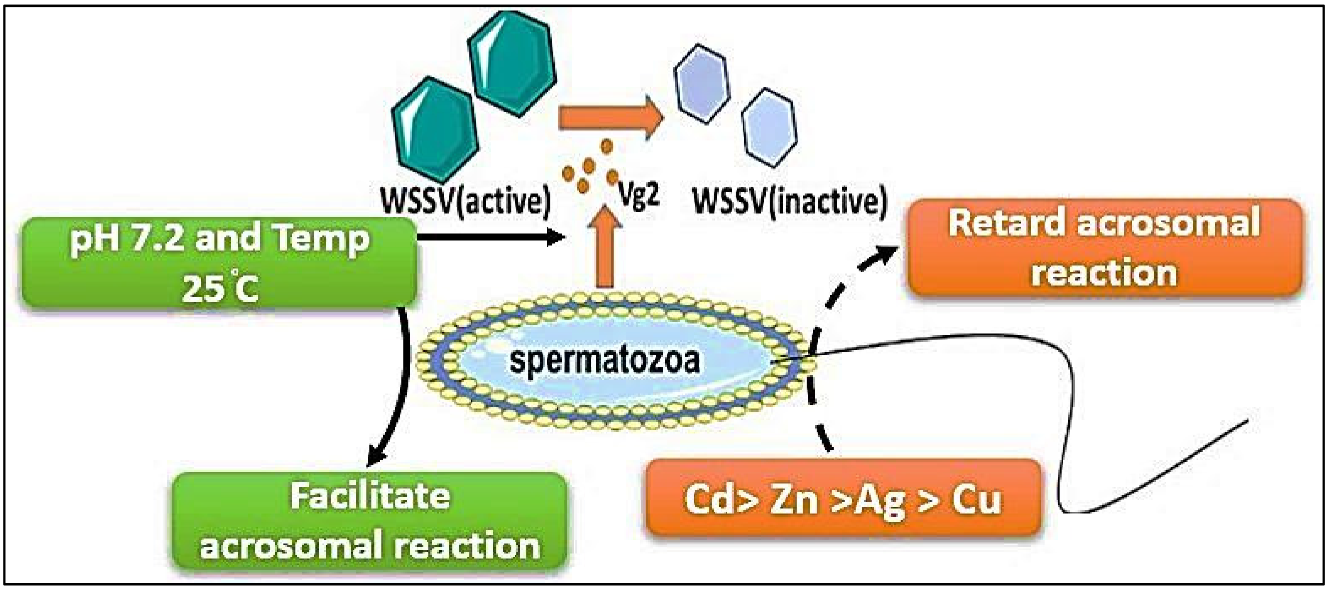

Figure 3. Impact of water temperature, salinity, and heavy metals on spermatozoa and role of Vitellogenin 2. The toxic effect of heavy metals on acrosomal reaction during the process of fertilization while optimum pH and temperature facilitate the acrosomal reaction. Vitellogenin is generally found in female crabs, which helps in egg maturation and production; however, male mud crabs also synthesize this protein in their spermatozoa. Vitellogenin 2, a separate variant detected in testicular spermatozoa, is involved in immune protection during spermatozoon maturation in mud crabs. Active WSSV in the presence of Vg2 becomes inactive.

An antimicrobial peptide, "rSparanegtin" was found to have an immuno-protective role in *S. paramamosain*, which is correlated to its increase in survival rate [63]. Similarly, Yang et al. (2020) [64] noticed that the antimicrobial peptide Scyreprocin present in *S. paramamosain* has a promising antifungal and anti-biofilm activity that could be used in aquaculture, including in mud crab culture. Similarly, many toxic chemicals, including Chlorpyrifos and Cypermethrin, and heavy metals such as Cd can induce stress in the above crab that leads to hampering the growth and production of the crabs [65,66]. Therefore, the water quality of mud crabs must be carefully monitored for their optimal growth and production.

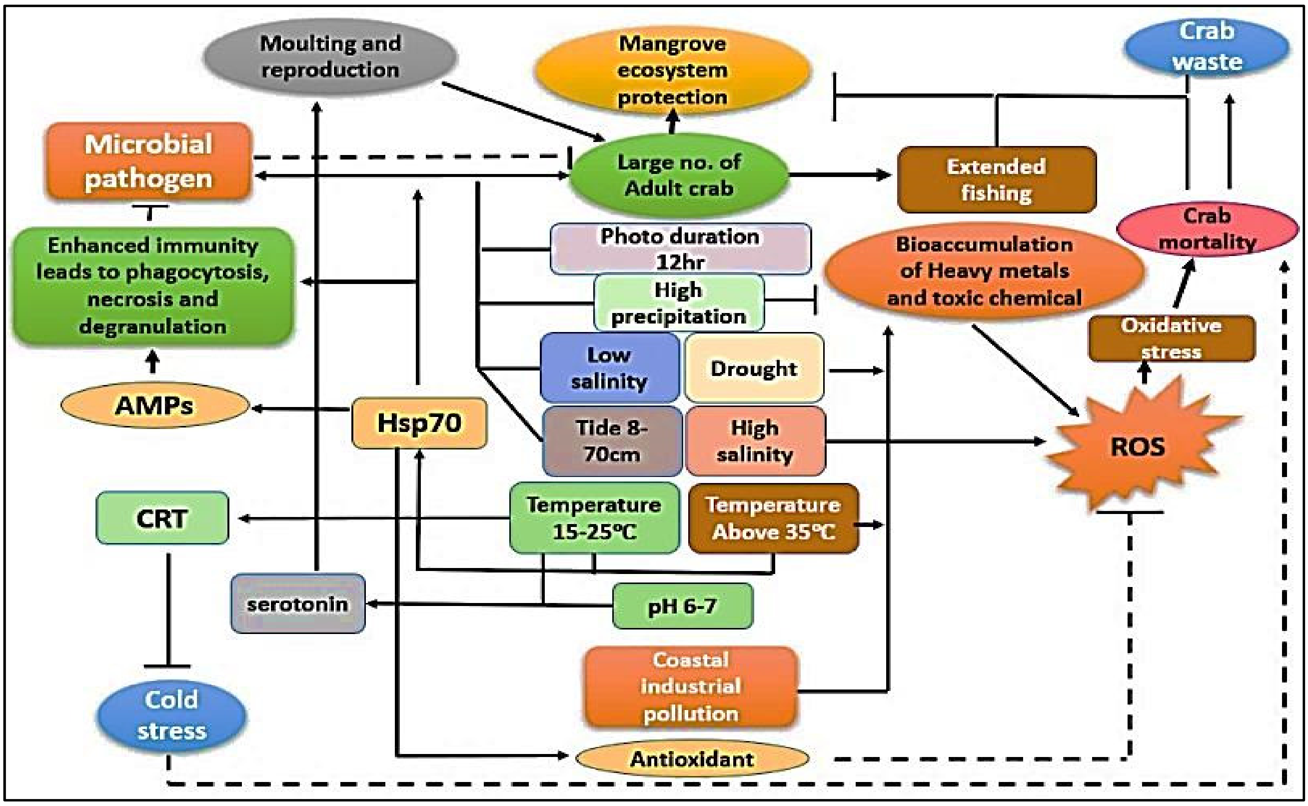

Figure 4. Biochemical and molecular responses of mud crab *Scylla serrata* in its natural environment. *S. serrata* is a mud crab and highly demanding worldwide. Many eco-physiological and molecular works have been done to enhance aquaculture in relation to its natural environment with highly fluctuating water physicochemical factors. For example, the involvement of molecules such as antioxidants, Hsp 70, is modulated under fluctuating environmental factors, including salinity, temperature, drought, photoperiod, etc. Such information and their pattern of involvement in cellular physiology, as shown in the figure, is extrapolated for its aquaculture.

3.4. Allergens in Mud Crab Meat and Their Modulation under Abiotic Factors

Most crustaceans are well-known for their delicious meat but also come with allergic reactions. Despite its delicious taste as food, it has some life-threatening effects; for example, an incident of death after consumption of crab meat was observed in China. The samples collected from the victim's different parts showed a high concentration of histamine in the intestine and a very high concentration of histamine in the crab sample [67].

Crustacean meat is mostly responsible for allergic reactions conducted through IgE. Recently, mud crab meat was identified with an allergen, arginine kinase. Mud crab arginine kinase also resembles other crustaceans, confirmed by sequence alignment studies. The native arginine kinase has a molecular weight of 40 kDa, and an isoelectric point of 6.5 was confirmed by a two-dimensional electrophoresis study, suggesting its similarity with other arginine kinases. It has been proven that serum from people with crustacean allergy positively reacted with the arginine kinase of mud crab, confirmed by immunoblotting analysis and colloidal gold immuno-chromatographic assay [68]. However, a complete high throughput method still needs to be included to identify crab meat allergens properly. Therefore, liquid chromatography-tandem mass spectrometry plays a major role in quantitatively detecting multiple allergens in crab meat and its product. Additionally, allergen proteins and peptides can be identified by analyzing data collected from the ion spectrum of polypeptide fragments through ultra-performance liquid chromatography-quadrupole/electrostatic. Thus, using such modern tools and techniques identification of allergens in crab meat will be helpful for health issues [69]. Nevertheless, the expressions of such allergens with respect to several water physicochemical factors need to be studied in mud crabs.

3.5. Anti-Cancer Molecules in Mud Crab and Their Variation under Habitat Water

The β-glucan binding protein in mud crabs was considered to make Ss-βGBP-ZnONPs and then tested against gram-positive *Enterococcus faecalis,* gram-negative *Pseudomonas aeruginosa,* and human MCF7 breast cancer cells. Both bacterial and cancer cells show a significant decrease in growth in the presence of this nanoparticle in the habitat water [70]. As described earlier in Section 3.5, amp-like arasin of mud crab is known for its effectiveness against multidrug-resistant pathogens and plays a great role in the inhibition of human cervical carcinoma (HeLa) and colon carcinoma (HT-29) cell growth [42]. However, cancer-related studies on mud crabs have not been investigated much so far.

Chitinase enzymes responsible for chitin digestion in mud crabs have an altered behavior in the presence of a dioxane solution. This solution is well-known for its carcinogenic effect and is mostly found in water bodies due to the discharge of toiletries, such as shampoo, body wash, bubble baths, foaming hand soap, cosmetics, deodorant, and skin lotion. Beta-N-acetyl-D-glucosaminidase cleaves N-acetylglucosamine polymers to simplify chitin into N-acetylglucosamine (NAG). It reversibly inactivates the enzyme NAGase, and the enzyme kinetics reaction is recorded with the help of the enzyme-substrate method. This enzyme is more prone to inactivation if it is not bound to its substrate, which means the substrate gives protection against inactivation by dioxane solution [71]. Therefore, environmental factors, especially habitat water parameters and pollution caused by humans, play a significant role in mud crab disease, reproduction, physiology, and gene expression, which motivates the need for research into strategies for protecting *Scylla* sp. Owing to the importance of the species, the crab industry reached a high level in most Asian countries that act as the hub for mud crabs.

4. Status of Mud Crab Industries in Asian Countries

The total coastal area of southern, southeastern, and eastern Asia is about 169,131 km, which includes several estuaries and mangrove areas that provide a huge potential area for large scalability of mud crab farming. Countries such as India, China, Japan, Vietnam, Cambodia, and the Philippines are examples where mud crab farming has been growing at a large scale [72]. Several Southeast Asian countries and wild-catching sectors source from the artisanal crab industries and export and meet 50% of mud crabs for the entire world's consumption. In 2021–2022, the mud crab landing all over India was 3291 mt from a total land area of 2998 ha. Additionally, the total crab export has increased from 5509 to 6938 mt in recent years, indicating a 25% growth from the previous year [72]. In a state-wise comparison, Andhra Pradesh and West Bengal are the major contributors to crab production in India. According to the World Bank report of 2019, Myanmar exported 15,649 mt mud crabs globally from 2016–2017, about 30% higher than the 2011–2012 [73]. Similarly, in the Philippines, the export value of mud crabs during 2017–2018 was 16,326 mt, which was found to be 33% higher than in 2009–2010 [74]. These hikes in mud crab export in recent decades suggest an overall increase in the rate of mud crab demand worldwide. However, the mud crab culture is still limited in most East, South, and Southeast Asian countries due to a lack of technical expertise, limiting the landing values mostly from wild catches from natural habitats [72].

Some countries, such as China, hovered over crab culture despite technical difficulties. The annual mud crab landing in mainland China was 60,000–70,000 mt, and the highest annual production from farming was 120,000 mt [75]. It indicates an exponential growth in mud crab production that could result from large-scale crab farming. Similarly, Thailand and Bangladesh have also started crab farming to enhance their export. The Thai Department of Fisheries estimated that the total mud crab production in 2010 was 2130 mt, and in the last decade, the production from coastal aquaculture was 6921 mt which showed about 200% elevated value than previous years [76]. Similarly, Bangladesh earns about USD 6 million annually by exporting 1500 metric tons of live mud crabs to Singapore, Hong Kong, China, Taiwan, and Japan. However, 95% of mud crab exported from Bangladesh is still collected from wild habitats because of limited technical difficulties for artisanal culture [77]. Great technical difficulties exist in crab seed supply to farmers in countries such as India. Though high-end technical advancement is still wanted in crab industries, mud crab production has risen from 134,000 to 407,000 t globally after including large-scale crab farming in coastal areas of East and Southeast Asia in the last decade [1]. Alternatively, it imparts a large-scale contribution to the mangrove ecosystems.

5. Mud Crab and Its Importance in the Brackish Water Aquatic Environment

5.1. Direct Contribution of Mud Crabs into Habitat

With the above economic values, mud crabs also contribute to the mangrove or estuarine water management indirectly. They form a bioturbation structure in sediment soil that helps in trapping the seeds of mangrove plants. It increases the chance of a mangrove forest area, and this has a positive impact on the management of water quality in the area as it leads to a green ecosystem in the area. Mud crabs play a significant role in changing nutrients, increasing mineralization, the oxygen-carrying capacity of the soil, and providing support for other aquatic organisms [31]. Extended fishing and dependency on natural sites gradually damage the number of crabs and natural habitats for other organisms. The purposive sampling method is generally used to analyze abundance, the frequency distribution of carapace, and the growth parameter of crabs by using FISAT 111 and Bengen statistics. Additionally, the carapace takes 4 and 6 months to mature in males and females, respectively [78]. Thus, extended fishing of mud crabs on a commercial basis should be avoided in their natural habitat. The exact role in protecting the mangrove ecosystem is quite interesting.

Mud crab plays a key role in balancing ecosystems by using their biological burrowing activity on the soil, making soil porous, laid to aeration, and nutrient flow in soil. They make burrows where the water level is below 100 cm, and the percentage of burrows increases by more than 40% with a lack of shade [79]. In the natural habitat, the porous soil makes mangrove forest conservation as the soil holds the seeds of the plant (bioturbation), which greatly impacts forest making and coastline protection [80]. Another dimension of facilitating aquatic life by mud crab is that they produce a large number of pelagic larvae that provides a great source of food for planktophagus aquatic organisms. Thus, from the above data and observation, it has been clear that mud crab plays a vital role in the food web by directly controlling the complex mangrove ecosystems.

The mangrove mud crabs that contribute to world fisheries are under-threat in many places due to varied water physicochemical factors, overfishing, pathogens, heavy metals, and chemical toxicants in water. Along with environmental factors, such as temperature and salinity, the effects of xenobiotics, heavy metals, and other toxicants must be checked in their habitat water and soil for their better growth, production, and reproduction [81]. Their omnivorous food habits have been experimentally proved, so the larval and adult care of these species under a suitable environment is suggested for their health management. Different behaviors of mud crabs, such as migration, reproduction, and breeding, are exclusively hormonally and environmentally regulated as a function of age [81]. Finally, mud crabs and their bio-waste are also used for various purposes, such as environmental monitoring, analyzing toxic loads, and in clinical and pharmaceutical sciences, indicating their demands. Therefore, the ecological interaction of these species during their life stages is environmentally important [81].

5.2. Role of Habitat Water on Ecology and Life Cycle of Mud Crabs

The lifecycle of mud crabs such as *S. serrata* comprises three primary stages: the dispersing larvae phase, the benthic juvenile stage, and the adult stage. In order to mature into adults, mud crabs generally migrate from the seawater to estuaries during their benthic juvenile stage [82]. Usually, in these stages, they inhabit a muddy mangrove forest with changing temperatures and salinities [15,83]. *S. serrata* in Okinawa inhabits marshy mangroves, and in Taiwan and the Philippines, it prefers sandy, muddy bottoms of seaward water [84]. According to some studies, they prefer varied habitats at various stages of their life cycle, from larvae to adults. Its larvae prefer stenohaline water and structurally complex habitats, which contain both refuge and food, but the seagrass habitat is preferred by crablets of *S. serrata* [15]. Extensive studies in this field proved that water physicochemical factors play a huge role in maintaining the variation among these habitats (Table 2).

Specifically, in India, it is noticed that mud crabs inhabit a variable benthic coastal region of different estuaries with fluctuating several abiotic and biological factors in the water of coastal sites. They can sustain in a varied range of soil sedimental and physio-chemical water parameters, such as pH, organic carbon, turbidity, temperature, and salinity affecting their growth and survivability (Table 2). *Scylla* sp. can thrive well in water temperatures ranging from 18–31 °C, 1–33 ppt of salinity range, alkalinity range from 70 to 119 mg L^{-1}, and the dissolved oxygen concentration in water fluctuating between 4–10 mg L^{-1} [85]. Tidal heights ranging from 8.60 to 72.52 cm are optimum for crab survivability and growth. Additionally, organic matter content in water between 1.91% to 3.25% and a slightly basic pH with an average pH of 7.04 is optimum for *Scylla* sp. [86]. Food availability also plays a major role in their survivability in varied environmental factors and habitats depending on their life cycle.

Table 2. Effect of pH, temperature, and salinity on the physiology of mud crabs.

Water Physicochemical Factors	Location	Ranges	Duration (days)	Effects on Crab	Reference
pH	Coimbatore, Tamil Nadu, India	8.2 7.8	60 days	Normal growth, feed intake, and survival rate	[87]
		7.6 7.2 7.0		Decrease in growth rate, survival rate, and feed intake	
	Chantaburi, Thailand			Hemolymph osmolality (%)	[88]
		4–6 6–12	10 days 10 days	11% decrease 15% increase	
Temperature	Terengganu, Malaysia			Growth rate (%)	[89]
		24 °C 28 °C 32 °C 27–30 °C	45 days 45 days 45 days 45 days	7.28 ± 1.31 9.69 ± 0.75 7.83 ± 0.56 9.48 ± 1.02	
	Northern Territory of Australia	20 °C/20 ppt 25 °C/20 ppt 30 °C/20 ppt 35 °C/20 ppt	1 day 1 day 1 day 1 day	7.75 ± 1.28 12.68 ± 0.77 15.98 ± 0.36 12.59 ± 0.60	[90]

Table 2. *Cont.*

Water Physicochemical Factors	Location	Ranges	Duration (days)	Effects on Crab	Reference
Salinity	Queensland, Australia			Hemolymph osmolality (mOsm kg^{-1})	[91]
		4 ppt 12 ppt 20 ppt 28 ppt	NA	415 ± 12 (hyperregulated) 312 ± 8 (hyperregulated) 194 ± 15 (hyperregulated) 122 ± 12 (hyperregulated)	
	Iilan, Taiwan	14 ppt 24 ppt 34 ppt 44 ppt	1 day 3 days 0 day 1 day	772.38 (stabilized) 803.50 (stabilized) 1034.50 (stabilized) 1274 (stabilized)	[21]
	Queensland, Australia	30 ppt	4 days	968.73 ± 8.85 (stabilized)	[92]
	Odisha, India			Mitochondrial respiration rate complex I and II (nmol)	[93]
		10 ppt 17 ppt 35 ppt	21 days 21 day 21 day	4.42 ± 0.88 and 6.41 ± 1.69 1.69 ± 0.41 and 4.04 ± 0.58 2.19 ± 0.55 and 4.42 ± 0.88	

Note(s): Mud crabs need 27–30 °C temperature and salinity of 34 ppt for better growth and acclimatization. In addition, the optimum pH of water is 7.8–8.2 for normal growth and other physiological activities of mud crabs, as concluded from different local studies.

5.3. Predatory Contribution to Food Chain under Varied Water Habitats

The gut analysis and presence of material remnants like 51% mollusks, 10% crustaceans, 22% fishes, and 4% plant products in adult mud crabs suggest that the crabs are predatory in nature [35,94]. The feeding pattern varies with each larval stage of mud crabs, but they prefer rotifers and *Artemia nauplii* (decapsulated cysts) as their food due to their non-motile nature [95]. Nutrients rich in essential fatty acids are beneficial for the growth and survivability of larval stages of crabs [96]. *Scylla* species tend to feed at night, making it difficult to spot during the day [94,97]. Reports on the dietary preferences of mud crabs indicate that it has both an animal and plant-feeding nature. However, seasonal and environmental changes in water quality have a major impact on the way the mud crab feeds and interact with other organisms and the ecosystem in which it lives [15].

5.4. Behavioural Contribution to Ecosystem

The nocturnal feeding habit of mud crabs' juveniles and their burrowing behavior helps them to escape from predators in deep water as well as marshy areas. Generally, hiding behavior is noticed in mud crabs' juveniles (e.g., they are found under the leaf and aquatic plants in order to avoid direct sunlight). Habitats of most aquatic animals are simple and have little interference with others, but in the case of mud crabs, *S. serrata* habitat is quite complex in structure [98] as mud crabs are not static to a particular zone, so they can change their habitat according to their favorable condition by covering a long distance of 219 m to 910 m in water per night. Male shows great care towards female mud crab protection during molting and shell casting in the mating season. Molting and food scarcity induce autobalism and cannibalism nature in *S. serrata.* Besides this behavior, mud crab shows abnormal development and physiology under varied environmental conditions.

5.5. Contribution as Biomarkers and Bio-Indicators

Biomarkers are essential to assess the health status of an aquatic animal with respect to varied water environmental conditions and for their monitoring. Polychlorinated biphenyls (PCB) and poly-halogenated compounds (PHC) are particles that gradually increase in water bodies and are consequently consumed by aquatic organisms like mud crabs. Enzymatic and non-enzymatic antioxidant assays in *S. serrata* show a considerable downregulation of the defense genes in summer with respect to the winter season when the PCB and PHC are at their peak concentration in water [99]. Additionally, ulcerative skin disease and parasitism epidemics in *S. serrata* were reported to coincide temporally and spatially with changes in water quality [100]. Another biomarker on mud crab was reported by Van Oosterom et al. (2010) [101], and it is an enzyme called Glutathione-S-transferase (GST) that can be used to study pollution impact assessment in saline water bodies.

Mud crab larvae are proposed to be used as an effective bioindicator for measuring the effects of sewage loads in saline water because they show a slower rate of larval development from stage I to stage II larval forms under pollution loads in habitat water. Secondary treated sewage has a significant role in toxicity in the zoea larva development of mud crabs, and it was observed when the progress of larval stages from stages I to II was examined [99]. Under a condition of constant photoperiod (12 hL/12 hD), a salinity of 35 ppt, and a temperature of 30 $\pm$ 2 °C, the growth of larval stages is found to be high when the habitat has sewage loads. Based on the aforementioned data, it is evident that mud crabs have a high potential to serve as bioindicator species. However, an extensive study of environmental factors and pollutants is essential to evaluate their impact on crab physiology.

6. Adaptive Responses of *Scylla* sp. to Water Physicochemical Factors

Major water physicochemical factors that are crucial to the survival of the coastal ecosystem and the organisms that rely on it include precipitation, atmospheric humidity, ultraviolet radiation (UVB), mineral nutrients, wind speed, salinity level, temperature, and the tides of the sea [102,103]. Out of all these factors mostly, temperature, salinity, and pH of water and soil affect ecosystems and organisms specifically [104].

Distribution at the population level and physiology, morphology, ecology, behavior, and life cycle at the individual level is highly influenced by water physicochemical factors such as strong katabatic winds, levels of salinity, tides of the sea, water temperature, dissolved oxygen levels [105], and nutrient availability in most invertebrate of the coastal aquatic ecosystem [106]. As invertebrates are poikilothermic species, temperature, salinity changes, and decreasing O_2 directly affect them by increasing their heart rate, lowering their respiration, and disrupting their osmotic balance [107]. The diurnal variation in sea tides maintains the aerial exposure timing of invertebrates at the coastline, by which respiration, morphology, and behavior are mostly affected [108]. Most invertebrates in the mangrove ecosystem are susceptible to oxidative stress (OS) exacerbated by water chemical factors. Factors such as temperature, O_2 level, and salinity induce free radical generation at the cellular level, resulting in physiological stress for organisms. In addition, gene expression and immunity of most invertebrates are also influenced by temperature, salinity, and solar radiation. Crustaceans, a major group of invertebrates common to coastal water bodies, are also affected by such factors [109]. Most crustacean mud crabs, especially *S. serrata*, have a special position in the whole mangrove ecosystem because of their special activities [110]. Before analyzing the effect of water physicochemical factors, it is essential to gather some general findings on these species of mud crabs.

6.1. Migration in Saline Water Bodies

The migration of mud crabs is generally environmentally specific, and the habitat water is changed where the crabs migrated. Mud crabs usually migrate to the open sea between November to March [111]. They are euryhaline in nature, facilitating their migration from marine water to estuaries, where they develop into the juvenile and return to marine water during the breeding season [19,82]. Thus, the crab is adaptive to both marine and estuary ecosystems. However, this dual property of the crab to cope with both environments may affect the lifecycle and development due to variations in water physicochemical and other habitat factors [19,95,112].

6.2. Reproduction Maturity in Natural Saline Water

The water physicochemical factors like temperature ranging from 30–35 °C, day length minimum of 12 h, and salinity 28 ppt play major roles in reproduction, with a distinct peak spawning season in the summer. Mating in mud crabs is species-specific, especially during the reproductive stage, with a sex ratio of male to female 3:1 [15]. Depending on specific geographical locations, the size of sex organs and carapace width in crabs are considered major indices through which reproductive maturity can be studied [83]. They attain reproductive maturity depending upon the size of carapace width, which varies across the different locations of the world, for example, 9 to 11 cm of carapace width in Australia and 9.2 cm carapace width in South Africa [113]. However, in the Indian subcontinent, a carapace width of 12.1 cm for *S. tranquebarica* and 7.9 cm for *S. serrata* is considered the mature reproductive stage in mud crabs [20]. Thus, in reference to the carapace width index, which decides the anatomical size of the sex organ, it will be easier to analyze the maturity of the sex organ in mud crabs.

Mud crab, *S. serrata*, is found to be exclusively intraspecific in mating and polygamy, generally in male species. The duration for copulation usually lasts for 2–3 days in their breeding season. The molting of the female starts during copulation when the male crab dorsally grasps the female for 3 to 4 days, leading to the shedding of the shell in the female crab. The male crab now moves for real mating by ventrally moving on the body of the female crab. The sperm transfer to a seminal female receptacle requires a minimum of 6 to 7 h during the mating season. However, it has been observed that the process of copulation lasts for 12 h or more than 24 h in some cases [114]. In addition, female crabs are capable of receiving sperm from two separate males during the process of copulation, and they are able to retain the spermatozoa of the second male crab for future use [82]. Inside the female seminal receptacle, sperm is stored in viable condition for 9 to 10 months, which is indeed helpful for the fertilization of 2 to 3 batches of eggs [82].

Fertilization is internal in mud crabs as it takes place inside the female body, and female mud crabs eject around 5 million eggs at one time. They usually come to the shoreline to lay eggs during spawning [82,115]. Environmental conditions and physical factors play a big role in the deposition of eggs, i.e., spawning [115]. The developmental life of a mud crab comprises five zoea stages and one megalopa stage (after hatching successfully from the egg). However, a clear distinction between sex and species is tough through compound microscopy in their larval stage [82].

In natural and/or artificial conditions, a formulated healthy diet is essential to attain the stage of reproductive maturity in mud crabs. The growth rate in mud crabs can be enhanced by supplementing adequate amounts of protein (45%) and essential fatty acids in the diet [96,116]. However, scarcity of food in natural conditions and lack of proper healthy food leads to stunted growth in most crabs [83]. However, age is also a relevant factor for the growth of crabs; as it grows older, the growth rate decreases. In *S. tranquebarica,* the size increases from 8 to 12 cm in one year, and in the second year, it increases from 14 to 15 cm. Similarly, in one year, the carapace of other *Scylla* sp. may grow from 2 to 9 cm. However, in the case of *S. serrata*, maximum growth occurs within a year after hatching in its natural habitat.

6.3. Breeding and Induced Breeding in Mud Crab and the Role of Habitat Water

Mud crab shows a perennial breeding activity, and their spawning takes place all around the year, but the spawning rate seasonally varies. For example, during the rainy season in the Rasimi River of Kenya, a slight increase in the spawning of mud crabs was observed [117]. On the contrary, in South Africa, an increase in spawning was reordered in the early spring season [118]. In certain cases, such as in the Kabira Bay of Ishigaki Island, the summer season is commonly considered favorable, while early winter is unfavorable for spawning eggs by mud crabs. However, in India, specifically in the Chilika lagoon, the spawning season for *S. serrata* spreads all around the year, and for *S. tranquebarica*, it ranges between May to September. Similarly, the variation in breading period is recognized in *S. serrata* and *S. tranquebarica* at the Chilika Lagoon of India, ranging from August to November and March to June, respectively [20]. The above seasons are verified with specific habitat water conditions, such as high temperature and salinity in the summer seasons, then lower temperatures in the winter, and lower water salinity in the rainy season.

Induced breeding is commonly used in fishery culture to increase egg production for commercial use; this technique must be done under ambient water conditions and is essential to grow mud crab culture. Broadly two types of methods are used to perform induced breeding in mud crabs, i.e., unilateral and bilateral eyestalk ablation. In the case of mud crabs, the unilateral eyestalk ablation technique is used to perform induced breeding [119]. However, in both unilateral and bilateral eyestalk ablation, hyperglycaemic hormone physiologically stopped to achieve metabolic dysfunction. Simultaneously, eyestalk ablation also affects the secretion of the molting inhibition hormone, which facilitates the molting process in mud crabs during copulation and the subsequent breeding period [120]. Additionally, this eyestalk ablation directly acts on ovary maturation and hunger induction, facilitating faster growth in mud crabs at 28 °C and pH 7.6 [119]. This increases the oocyte number and causes great weight gain in the whole body, giving the proper female strength for the breeding process [121]. The induced breeding technique increases the production of eggs up to 4 million in *S. serrata*. However, water physicochemical factors, such as temperature, salinity, pH, etc., affect the survivability of eggs to some extent in culture conditions [93,102].

The risk of survivability is always high from the higher to the lower invertebrate group due to an unstable environment, especially varied water quality in aquatic animals. In order to overcome this kind of situation, mud crabs are adapted to breed in large no at a time so that a few juveniles may survive in the end. However, about 60% of mud crab attains a natural death in their natural habitat [122]. Although mud crab mortality is not observed up to the pre-zoeal stage, i.e., around 90% successfully viable till this stage, the next stage larvae become vulnerable to death. After the pre-zoeal stage, it enters the zoea stage and becomes a photo-tactic movement in the water, making these larvae vulnerable to predation by surface water predators and thus leading to a sharp increase in mortality. However, if they survive to the pre-adult stage, they strongly fight predators with their chelipeds and easily survive till natural death [82]. Meanwhile, specific proteins play a key role in countering variation in water physicochemical factor-induced stress during the entire life cycle of mud crabs.

6.4. Regulatory Proteins and Their Regulation in Reproduction

Many specific proteins play an effective role in growth, immunity, reproduction, molting, and development in crustaceans. In mud crabs, a special endoplasmic protein known as calreticulin (CRT) is involved in Ca^{2+} homeostasis and works through Ca^{2+} -dependent signal pathways in growth, immunity, reproduction, molting, and development. Additionally, CRT protein has multiple roles in homeostasis as it fights against low temperature and salinity stress. The expression of CRT is found to be higher in the hepatopancreas tissue of crabs [123]. At lower temperatures, i.e., below 10 °C, the expression of CRT mRNA increases, which supports the adaptability of mud crabs towards cold stress through the expression of CRT protein. Similarly, CRT mRNA expression is found to be higher at low salinity conditions. The male reproduction-related (Mrr) protein synthesized from the sex-specific gene in *Macrobrachium rosenbergii* (Mr-Mrr) is also recognized in mud crabs. This protein helps in sperm maturation processes in mud crabs and facilitates acrosome activation during fertilization [124]. The survival of mud crabs in hot climates against heat stress is determined by certain heat stress factors [125]. Thus, temperature has a big role in the expression and reproduction of regulatory proteins. However, endocrine physiology also plays an important role in regulating growth and reproduction in most crustaceans. It is because the harvesting or final production value is also dependent on the reproductive rate. Besides temperature, the effects of other water physicochemical parameters on the CRT-like proteins need to be studied in mud crabs.

6.5. Harvesting of Crabs as a Function of Seasonal Variation of Habitat Water

In eastern coastal sites, crab culture from April to October is suitable because different environmental factors are favorable in this period, as studied in Bangladesh. Collected data from various levels and discussions, as well as interviews with locals, suggested that a water salinity range of 2 to 10 ppt, a pH range of 7.8 to 8.6, and the silt-loam soil from April to October favors crab culture [126]. Thus, this survey suggests that harvesting should be done between April and October for those areas to produce better quality and landing quantity of crabs. In India and other coastal countries, similar studies need to be conducted in coastal areas to get the maximum harvesting from the crab culture.

Effectively managed crab culture can sustain a better livelihood for interested fish farmers as well as commercially dependent people in this field. Survey studies also confirmed that rearing crablets from <1.0 to 4.0 cm for 42 days or by phases is viable under a medium saline water state. Moreover, issues related to crab marketing, area ownership, and distance from the household need to be technically enhanced. Thus, a friendly environment needs to be established between farmers and intellectuals from the respective research institute to use technology to improve crab cultivation under the best water physicochemical conditions [127].

7. Mud Crab Physiology under Fluctuating Water and Pollution Stress

Mud crabs can tolerate a wide range of stressors, but when a threshold level is surpassed, then these species may become susceptible to respond to the effects generated by environmental factors, such as water temperature and salinity, etcetera [128,129]. Despite the high fluctuation in environmental water salinity and temperature, mud crabs are able to maintain physiological homeostasis, indicating their euryhaline and eurythermal nature [21,22,130,131].

7.1. Effects of Water Salinity

Out of all the environmental factors, water salinity has a significant role in the regulation of physiological activities in *S. serrata* [129]. For instance, small antioxidant levels and enzymatic antioxidant activities are found to be varied above 35 ppt of water salinity. Moreover, high water salinity also causes greater oxidative damage to lipid and protein molecules and deregulates the redox regulatory system in animals in general and in the mud crab in general [8,28]. However, no role in manipulation at the genetic level is observed under higher water salinity, such as 35 ppt [23].

A rare incident of shifting ammonotelism to ureotelism in excretion is well noticed in *S. serrata* when the salinity of water increases from lower to higher concentration [21,130]. However, an increase in salinity from 10 to 35 ppt causes an elevation in the excretion of ammonia and depletion in oxygen uptake and carbon dioxide release in the mud crab *S. serrata* [23]. The excretion of ammonia and associated studies always play a major role in aquatic body homeostasis maintenance [23]. Therefore, this field needs to be studied more to resolve the above ambiguities on the impact of salinity.

7.2. Effects of Water Temperature

The effect of water temperature and inorganic salt on the metabolism of mud crabs was studied by Ruscoe et al. [90], and they suggest that its larvae, zoea depends upon the rotifers as food, which is found in the maximum number in water salinity ranges, from ppt of 10 to 35 and temperature at 30 °C. Cold water stress data provide ideas for generating OS [132,133] and varied mitochondrial counts in mud crab tissue [60]. Factors such as temperature significantly affect mud crab physiology as it can increase or decrease the absorption capacity of drugs by the hemolymph [134].

The temperature of habitat water also affects the drug absorption rate, confirmed by enrofloxacin drug absorption in *S. serrata* at water temperatures of 19 and 26 °C. It has been observed that the absorption rate of drugs in the hemolymph is higher at 26 °C that decreases when the temperature is lowered down to 19 °C, but the rate of removal/excretion of drugs from the hemolymph of this crab is higher at 26 °C as compared with a lower temperature such as 19 °C [134]. The study suggested that the temperature of habitat water directly relates to the pharmacokinetics of enrofloxacin-like drugs.

The OS stress parameters and antioxidant enzyme systems are also greatly affected by variations in water temperature and other factors. To assess the environment, the OS parameters of *S. serrata* are most helpful as these are good ecotoxicological indices [102]. The result of OS analysis suggests that summer OS indices are higher in comparison with winter and rainy season OS indices. Thus, such findings indicate that temperature has a major role in maintaining the body's physiology, metabolism, and drug uptake. However, increasing industrialization and the discharge of untreated sewage into coastal water bodies cause major health hazards for aquatic and terrestrial organisms, including humans.

The salinity of water plays a major role in the physiology of aquatic animals in general [135]. The combined effects of both water temperature and salinity indicate that these environmental factors substantially affect its development, but water temperature induces more impacts on its growth than water salinity. It was identified in a study on the juvenile stone crabs *Menippe mercenaria* and *M. adina* that temperature (between 5 and 40 °C) has profound effect than salinity (between 10 and 40%) on molting frequency; however, both parameters have synergistic effects on their survivability [136]. The interaction of temperature and salinity on the growth and survival of juvenile mud crabs has been explored to determine optimal ranges for these factors [90]. Ruscoe et al. [90] grew two instar crablets separately at several temperatures (from 20 to 35 °C) and salinities (from 0 to 40 ppt) for 2.5 weeks. They observed that temperature had a major impact on the survival of the crablets than salinity because the rise in salinity from 5 and 40 ppt did not affect their growth and survivability. However, regardless of the temperature, the mortality of crabs was 100% when they were kept in freshwater, i.e., 0 ppt salinity. The authors reported in their study that the optimal conditions for weight-specific growth rate in the crab were 30 °C temperature and 10 to 20 ppt salinity [90].

7.3. Effects of Inorganic and Organic Metals/Pollutants in Habitat Water on Mud Crabs

The accumulation of heavy metals and other toxic chemicals in aquatic organisms occurs due to the direct discharge of industrial pollutants into these coastal water bodies. Heavy metals and toxic chemicals are the most pollutants found in the aquatic ecosystem, which is proved by the analysis of tissues collected from crustaceans, especially crabs, as they are benthic in nature ([137], Table 3).

7.3.1. Effects of Heavy Metal in Habitat Water on Crab Physiology

Mud crabs and other crustaceans exhibit a high rate of metabolism and smaller body size that favors higher metal accumulation (Table 3). The physicochemical nature of water and soil sediment factors, such as pH, temperature, salinity, nutrients, organic carbon, Ca, Mg, and environmental conditions, are the deciding factors of the bioaccumulation rate of metals by mud crabs [138]. Bioaccumulation of heavy metals, such as Mn, Zn, As, Co, Cu, Pb, and Cd, in habitat water lead to creating health hazards in humans and other organisms (Table 3). Several other factors are also responsible, such as sex and season, for the bioaccumulation of heavy metals. It has been observed that during pre-monsoon, Cr 11.4 mg L^{-1}, Pb 3.3 mg L^{-1}, and Cd 0.07 mg L^{-1} were found in the highest available concentration, while the lowest Cr 1.4 mg L^{-1}, Pb 2.4 mg L^{-1}, and Cd 0.04 mg L^{-1} during post-monsoon [139]. A recent study on this bioaccumulation with respect to sex carried out in Sri Lanka by Harris et al. [140] found that a high accumulation of As, Pb, Hg, and Zn with exceeding levels of Pb (0.2 mg kg^{-1}) and Hg (0.5 mg kg^{-1}) occur in mud crab. The metal Zn is commonly found in both sexes, with males having 40.76 mg kg^{-1} and females having 45.10 mg kg^{-1} body weight, while Cd and Sn are found in the lowest concentration.

The variation of Zn and Hg with respect to sex is insignificant, but in the case of Pb and As, the amount in the female is higher than male. Thus, aquatic food derived from contaminated estuaries, consumed at 7.7 kg $person^{-1}$ $year^{-1}$, causes various health issues [138]. Additionally, if people consume crab collected from those contaminated habitats, then the possibility of health hazards cannot be avoided. However direct effects of metals on sperm physiology described below are quite interesting.

The increasing pollution causes an increase in metal toxicity which subsequently interferes with sperm cell physiology in mud crabs [141]. The effect of metal toxicity was first confirmed in a sperm cell sensitivity test in mud crabs. Additionally, the sensitivity of metal toxicity is more stringent in mud crabs than in sea urchin sperm. The acrosomal reaction is directly affected by metallic ions, such as Cd, Cu, Ag, and Zn, as first studied by Zhang and colleagues [142]. The group observed structural changes in sperm and AR count after exposure to heavy metals. An increased rate of swelling, shape irregularities, and the acrosome filament of some sperm cells was crooked, ruptured, and even dissolved when heavy metal toxicity occurs. The intensity of metal toxicity in sperm cells of mud crabs is in the following order $Cd^{2+} > Zn^{2+} > Cu^{2+} > Ag^{+}$ [142]. Mud crabs can overcome cadmium toxicity with the help of metallothionein, a protein released during the resistance period [143]. Thus, the physiology of mud crab is heavily affected by heavy metals, and their subsequent consumption by human or other organism result in a health hazard. Apart from this, various toxic chemicals also affect crab physiology under various water physicochemical factors.

Table 3. Effects of heavy metals on body parts of mud crabs.

Inorganic Toxicants	Season	Site of Accumulation	Range of Accumulation	Effect	References
As, Cu, Zn	Wet	Muscle	High	Tissue damage	[138]
Cd, Cr, Pb	Wet	Na	Low	NA	[138]
Zn, Hg	Wet	Whole body	Balanced	Muscle damage	[144]
Pb and As	Summer	Whole body	High in female		[139]
Pb	Summer	Highest in hp, lowest in muscle	Too high	Body damage	[139]
Ag^{+2}, Cd^{+2}	Wet	Muscle	High	Structural changes in sperm	[142]

Note(s): Heavy metals listed using *S. serrata* as model organism under varied temperatures and salinity. All metals are more or less toxic to the crab in the summer and rainy seasons. Gill and hepatopancreas are mostly affected by heavy metals. Pb was found to be most toxic to mud crabs. The table indicates that mud crab responds quite well to toxicants and, therefore, may be used as biomarker species to study environmental status, including environmental pollution. HP—hepatopancreas.

7.3.2. Effects of Toxic Chemicals in Habitat Water on Mud Crab's Physiology

In addition to metals, toxic substances such as naphthalene, enrofloxacin, ciprofloxacin poly-, and perfluoroalkyl substances (PFASs) induce OS in mud crabs. The significant effect of naphthalene on the reproductive dysfunction of mud crabs was studied by manipulating the vitellogenesis [145–147]. Pharmacological compounds like enrofloxacin and ciprofloxacin were maximally retained for a longer duration in the hepatopancreas of mud crabs, and their elimination was quite slow [134]. When naphthalene level in habitat was studied in mud crabs, it was observed that levels of cytochrome P450, aryl hydrocarbon hydroxylase, glutathione-S-transferase, and UDP-glucuronyl transferase in hepatopancreas are elevated. DNA damage and cell necrosis are significant when exposed to naphthalene in the ovary, hepatopancreas, and hemolymph. This, in turn, suggests that naphthalene metabolism produces lethal oxidants [146,148].

Aquatic organisms (crustaceans) generally store lethal substances in their tissues in the freshwater system but generally depurate them when moving to decontaminated water. The migratory nature of mud crabs exposes them to several toxic products, such as perfluorooctyl sulfonate (PFOS), perfluorohexanesulfonic acid (PFHxS), and perfluorooctanoic acid (PFOA). These products can be depurated from mud crab if transferred into uncontaminated water, but each toxicant has a different depuration rate. PFOA is depurated from crab within 72 h of exposure to decontaminated water. However, depuration from PFHxS and PFOS were not recognized in mud crab, indicating its harmful effect on organisms connected in that food chain [149]. These health risks can be slowed down if mud crabs facilitate to migrate away from contaminated water.

The larvae of mosquitoes are considered to be one of the major food sources of mud crabs; however, the nano-formulated larvicides have a harmful effect on its physiology by inhibiting the action of antioxidant enzymes like acetylcholinesterase (AChE) and GST [150]. Thus, like heavy metals, these toxic compounds have similar harmful effects on crab physiology. The effects of these chemicals on biomolecule degradation and biomarker level in water have been summarized under varied temperatures and salinity conditions in Table 4. However, the effect of water physicochemical factors on mud crab physiology will be incomplete without going through the mechanism of its reproductive cycle.

Table 4. Effect of toxicants on biomarker molecules of mud crabs under different abiotic setups in habitat water.

Pollutants Level in the Water	Temperature and Salinity	Effect on Biomolecule	Levels of Biomarker	Mortality %	Reference
Naphthalene (10 µg mL^{-1})	28 °C, 30 ppt	DNA-16%, RNA-20%	ADP-5.38% ↓, ACP-30% ↓, ALP-38% ↓, AST-35% ↓, and ALT-13% ↓	50%	[145]
Perfluorooctyl sulfonate (30 µg mL^{-1})	21 °C, 30 ppt	NA	SOD-73%, CAT-71%, and Gpx-50%	66%	[151]
Carbon dots (8 µg mL^{-1})	25 °C, 30 ppt	NA	AChE-12% and GST-50%	55%	[150]

Note(s): Toxicants listed using *S. serrata* as a model organism under varied temperatures and salinity. All pollutants are more or less toxic to crabs at high temperatures and low salinity. DNA and RNA are mostly affected by these toxicants, and crab mortality is higher in the case of PFOS. Naphthalene was found to be the most toxic to mud crabs. The table indicates that mud crab responds quite well to toxicants and, therefore, may be used as biomarker species to study environmental status, including environmental pollution. SOD—superoxide dismutase, CAT-catalase, GST—glutathione-S-transferase, GPx—glutathione peroxidase, AChE—acetylcholinesterase, ACP—acid phosphatase, ALP—alkaline phosphatase, AST—aspartate transaminase, ALT—alanine transaminase, and lactate dehydrogenase, ACP—acetylcholine, NA—not available, and ↓—decreased.

7.4. Endocrine Systems under Habitat Water Fluctuation

According to studies, mud crab has a similar kind of endocrine system as other crustaceans. However, a difference is observed in mud crab heart growth from the rest of the crustaceans. The molting hormone is solely responsible for the growth of crustaceans, but in mud crabs, heart growth is regulated by both the molting hormone of Y-organ and eyestalk factors, confirmed by analyzing eyestalk extractions and bilateral eyestalk ablations (Figure 5). It also confirms that the rate of heart growth is 1.78% faster in males than in female mud crabs [120].

In crustaceans, melatonin activity significantly modulates physiological functions, such as reproduction, molting, and glucose homeostasis [152]. Melatonin causes hyperglycemia in mud crabs and other crustaceans, hence considered a hyperglycemic hormone [153]. Additionally, in mud crabs, melatonin works as a reproductive hormone as it regulates the levels of methyl farnesoate and ecdysteroid, and in the presence of melatonin, secretion of juvenile hormone and ecdysteroid increases in the mandibular organ and Y-organ, respectively. Thus, melatonin induces the secretion of methyl farnesoate and ecdysteroid, which subsequently induce reproduction in mud crabs [154].

In addition to melatonin, the hormone serotonin also regulates the levels of juvenile hormone and ecdysteroids in the mud crab at a temperature of 24 °C, salinity of 26 ppt, and pH of 7.2 and thus considered a reproductive hormone. Like melatonin, serotonin also induces Y-organs to increase the secretion of ecdysteroids up to 132%, but mandibular organs have no direct effect on methyl farnesoate synthesis. However, due to the presence of serotonin, an increased level of methyl farnesoate was detected during circulation. Serotonin induces the release of methyl farnesoate from the mandibular organ, which is triggered by the inhibiting hormone secreted from eyestalk, further leading to a rise in the level of methyl farnesoate up to 86.5% [155]. Apart from this, the effect of neurotransmitter levels on the cerebral physiology of mud crabs was observed by administering pentylenetetrazole (PTZ) drugs.

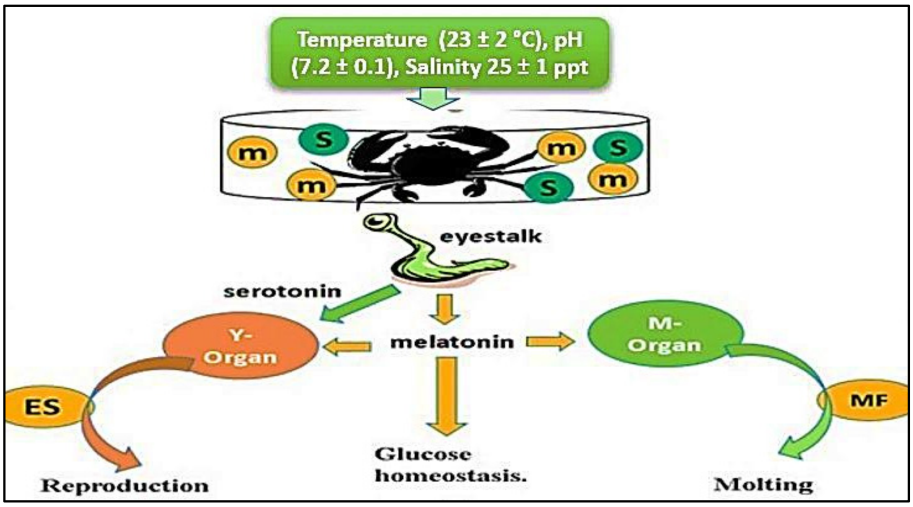

Figure 5. Effect of water physicochemical factors on melatonin and serotonin on the endocrine system of mud crab. The endocrine system of mud crab comprises eyestalk that releases melatonin and serotonin, which induce mandibular organ (MO) and Y-organ (YO) to produce methyl farnesoate and ecdysteroid, respectively together, they help in reproduction, glucose homeostasis, and molting. Physicochemical parameters such as temperature, pH, and salinity play a critical role during such induction. The Y-organ is influenced by serotonin and melatonin, while the M-organ only depends on melatonin. When left in a medium containing melatonin and serotonin, the crab shows an increase in farnesoate and ecdysteroid secretion (ES).

7.5. Neurotransmitter Changes under Habitat Water Fluctuation

The mud crab neural network is quite similar to other crab neural systems, but a complete structural and functional analysis still needs to be included. Convulsant drugs like PTZ directly affect cerebral ganglion by inducing epileptiform activities in mud crabs. The presence of an antiepileptic drug, i.e., sodium valproate in habitat water, induces sedative action in cerebral ganglion and prevents PTZ-mediated epileptiform discharges. Additionally, drugs like PTZ and sodium valproate significantly affect glutamate and gamma-aminobutyric acid (GABA) discharge in the cerebral ganglion of mud crabs. Administration of PTZ decreases GABA concentration; on the other hand, it increases the level of glutamate. Similarly, sodium valproate decreases GABA concentration and does not affect glutamate levels. Thus, epileptic seizures are inducible by administrating convulsant drugs in cerebral ganglion in *S. serrata* [156]. The possibility of bioaccumulation of these drugs rises during drought conditions. However, the direct role of water physicochemical factors still needs to be investigated in the endocrine regulation of mud crabs through genetic analysis.

7.6. Immunity and Disease Aspects under Habitat Water Fluctuation

Immunity can also be affected by water physicochemical factors and inorganic contaminants such as Ni and Hg in aquatic organisms (Figures 6 and 7). The immune-associated impact in crabs exposed to environmentally relevant concentrations of Hg can be detected by analyzing the effect on hemocyte, lysosomal membrane stability, phenoloxidase, superoxide generation, and phagocytosis. Additionally, OS resulting from Hg exposure increased lipid peroxidation levels and decreased the activity of the antioxidant enzymes, including SOD, CAT, and glutathione-mediated enzymes in serum. After observing and analyzing the above parameters, it can be concluded that Hg significantly reduces the immune-associated factors in hemolymph and reduces antioxidants [157]. The detrimental effect of metals on aquatic life has been discussed in the previous sections. In coastal water bodies, xenobiotic contaminants, especially metals such as Ni, exhibit immuno-toxic effects in mud crabs. Superoxide anion generation and phagocytosis activity in the hemolymph were considerably higher when exposed to Ni than the normal one. Additionally, the accumulation pattern of xenobiotic contaminants was shown to be high in gills compared w the hepatopancreas and ovary [148]. Apart from these, other proteins also show antimicrobial activities where the effects of water physicochemical factors on its expression pattern have not been studied yet.

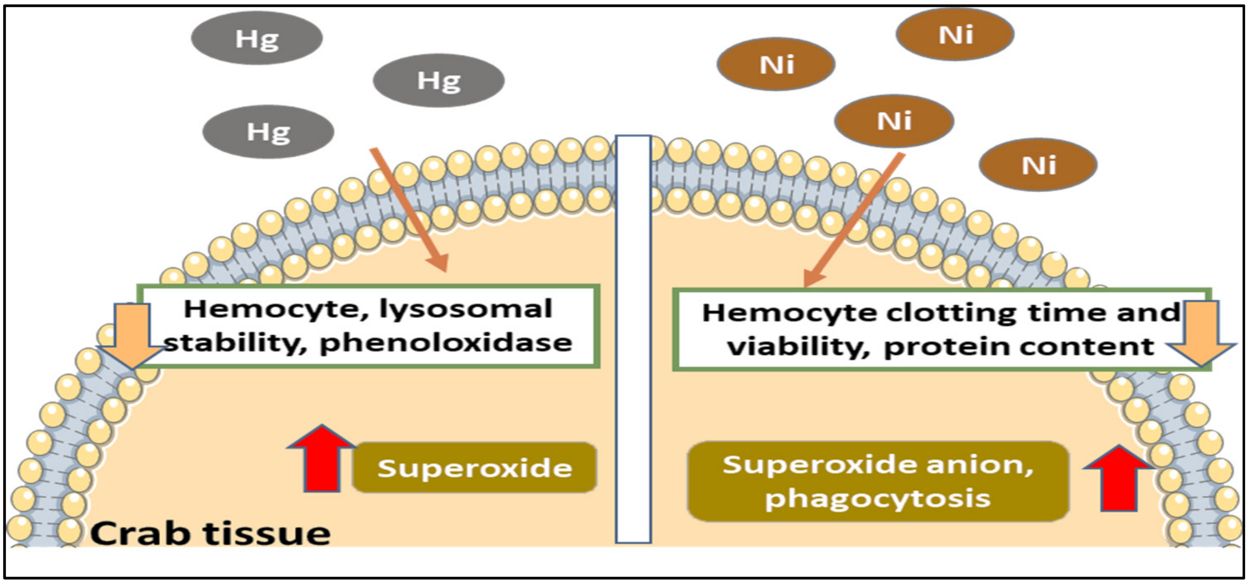

Figure 6. Effect of heavy metal on the immunity of mud crab. Bioaccumulation of heavy metals is highly toxic for mud crabs, of which mercury and Nickel cause serious health issues in mud crabs. Mercury and Nickel induce oxidative stress by producing superoxide anion, and meanwhile, Hg decreases hemocyte and membrane stability, and Ni reduces hemocyte clotting time and viability. The arrows indicate the direction of movement or action of the respective molecules.

The majority of aquatic organisms, including mud crabs, are susceptible to a wide range of diseases. The infection rate of mud crabs by microbial pathogens is highly dependent upon water physicochemical factors, such as precipitation, atmospheric humidity, host availability, levels of salinity, solar radiation (UVB), strong katabatic winds, seasonal and diurnal variations in temperature, etcetera [158]. Some common diseases of mud crabs include bitter crab disease, white spot syndrome, rust spots, and algal diseases. The "bitter crab" disease, caused by dinoflagellates, is commonly found in Alaska, characterized by a bitter flavor in the flesh of crabs [1,74]. Similarly, dinoflagellate *Hematodinium* sp. infects tissue and hemolymph, which leads to the clotting of hemolymph and eventually results in the death of mud crabs in Australia. The dominancy of different pathogens in Alaska and Australia suggests the role of varied water physicochemical factors in facilitating diseases [1,74].

The first viral disease detected in mud crabs is the white spot syndrome virus (WSSV), characterized by white patches on its shell surface. The viral disease was confirmed by injecting the respective viral strain, and the subsequent appearance of the symptoms in laboratory conditions was maintained at 30–32 °C and a salinity range of 25–30 ppt [159]. Some common symptoms of this syndrome include inactiveness, shoreward movement, and the appearance of white patches. However, the crab may overcome the deadly effect of this syndrome with time but continue as a carrier of the white spot syndrome virus for other crabs or crustaceans [160].

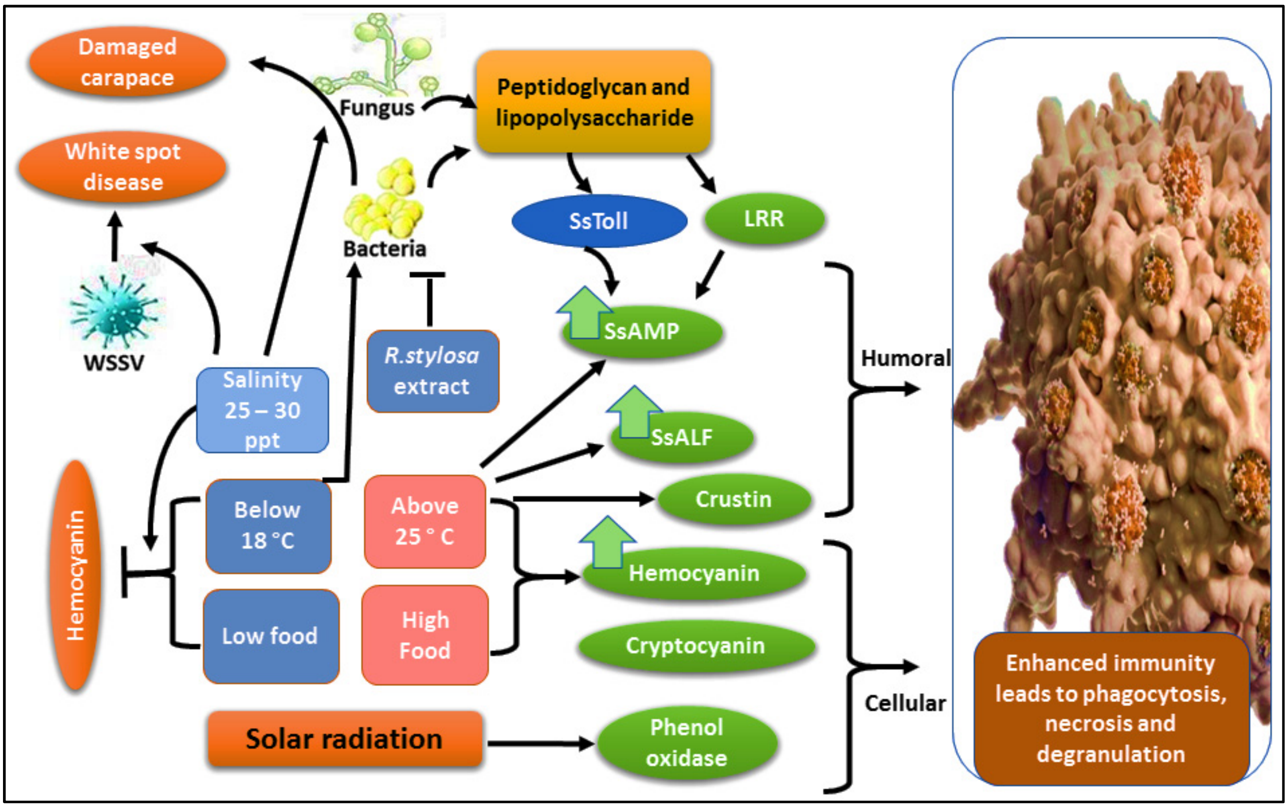

Figure 7. Role of water physicochemical factors and radiation in regulating innate immunity of mud crabs. White spot syndrome virus (WSSV), bacteria, and fungi depend upon abiotic variations. For example, temperature below 18 °C and salinity below 25 ppt help in propagating disease in mud crabs. Above 25 °C temperature facilitates antimicrobial agents and strengthens humoral immunity of innate systems such as SsAMP, SsALF, and crustin. Both 25 °C and high food enhance hemocyanin level, while below 18 °C and low food reduce hemocyanin level, solar radiation help in activating phenol oxidase activity in mud crabs, making cellular immunity of the innate system. Peptidoglycan from bacteria and lipopolysaccharide from fungal colonies induce SsToll and LRR proteins that lead to an increase in SsAMP synthesis. These altogether lead to phagocytosis, necrosis, and degranulation-like activity in mud crabs. *Rhizophora stylosa* extract from mangrove fruits works as a natural antibacterial agent. The arrows indicate the direction of movement or action of the respective molecules.

Next to the white spot, rust spot disease is also common in mud crabs during the winter and spring seasons (10–30 °C) and is represented by rust spots over the body surface of the crab. It is a bacterial-born disease with a significant effect on crab health and growth as it causes physical damage to the carapace by weakening the chitin with the help of a specific fungus. This exposes the crab's internal organs to the outer oxidizing environment as well as other harmful bacterial agents where salinity and high nutrients in the medium play a damaging role for the crab [161]. However, in this condition, neither below 20 ppt nor above 30 ppt salinity is favorable for mud crabs, as in both cases, bacterial and dinoflagellate infection significantly rises [162]. Studies on disease related to crabs led to the discovery of mud crab reovirus (MCRV), which causes great damage in crab culture and harvesting and propagate largely in 20 ppt salinity and temperature at 28 °C [112]. Thus, water physicochemical factors like temperature and salinity have a major role in viral, bacterial, fungal, and algal diseases of mud crabs. However, little information is available on other water physicochemical factors' role in crab microbial diseases, which need to be explored.

Highly pathogenic viruses, such as *S. serrata* reovirus (SsRV) and mud crab-specific virus McRV genome, are completely sequenced using molecular characterization methods. The virus has 12 dsRNA, out of which seven are sequenced earlier and have sequence similarities with other members of the family, while all the remaining segments contain an open reading frame on the positive strand, and the terminal sequence is conserved [163]. Out of all segments, S4 is bicistronic, and comparisons between S4–S6 and S8–S12 and other reovirus genes show a very low homology. Moreover, all remaining segments of SsRV have higher sequence similarity with McRV, indicating that these two viruses belong to the same species. SsRV virus has a total of eight structural proteins encoded in S1, S3, S6, S9, S11, and S12 segments. However, a non-structural protein p35 (viroporin) is encoded by the S10 segment of SsRV. The role of the p35 protein is found to be crucial in the SsRV replication cycle, which is confirmed by screening a cDNA library derived from *S. serrata* [164]. Thus, several proteins that play a key role in these viruses can be targeted for future drug design.

Gram-negative, rod-shaped, yellow colony-forming *Aquimarina hainanensis* bacterium is highly pathogenic to mud crabs as it degrades chitin and gelatin, which are structural and integral parts of tissue and carapace. The homology of the gram-negative bacterium with the *Aquimarina* genus has been confirmed by analyzing the 16 s rRNA gene [165]. Additionally, mud crabs are prone to *Vibrio* bacterial diseases, but fruits are available in mangrove forests with antimicrobial activities. The minimum inhibitory concentration test of methanol and chloroform extract from *R. stylosa* and *Acaryochloris marina* suggests that these antimicrobials are safe to apply to mud crabs [166]. However, studies on antimicrobial and other pathogen-related drugs under varied water physicochemical factors are still not clearly observed.

8. Molecular Response under Physicochemical Variation of Water Quality

The total number of haploid chromosomes in *S. serrata* was found to be 47–53(n) [167]. Initially, the haploid chromosome numbers in *S. serrata* were estimated to be 53 by Niiyama [168] and 47 by Vishnoi [169]. Although a complete genome analysis is missing in mud crab, only some studies on specific genes have been carried out in the last decade. Complete sequence analysis of the mitochondrial genome has been conducted to measure the length of the genome, types of protein-coding genes, number of ribosomal genes, and percentage of adenine and thiamine contents. The above data can be used to analyze population and phylogenetic studies of other crab species [170]. Apart from this, sex-specific markers are identified in mud crabs, which are crucial for sex determination in organisms. A genomic study performed by Shi et al. [171] on *Scylla* sp. considering (female-specific) SNP markers (from 335.6 million raw reads, out of which 204.7 million reads were observed in 10 females and 130.9 million reads were observed from 10 males) indicates that WZ/ZZ sex determination system for mud crabs *S. paramamosain, S. tranquebarica,* and *S. serrata* can also be useful for rapid genetic sex identification in mud crabs. Twenty sex determination markers were identified as sex-specific through sequence assembly and female-male comparison to date. Half of these markers are heterozygous in females while homozygous in males [171]. A complete study on these sex-specific markers confirmed that mud crabs could have WZ/ZZ sex-determination system. So, chromosomal differences accompanying sex determination in mud crabs seem to be through XY and ZW chromosomal arrangements [171,172]. However, the latter system needs a wide range of studies to be confirmed.

Several genes play crucial roles in the analysis of phylogenetic, evolutionary, and biomarker studies, and their expression directly or indirectly vary with temperature, salinity, and nitrate concentration. The mud crab Hsp70 gene is a key gene for stress resistance, disease resistance, and phylogenetic as well as evolutionary analysis [173–176]. The immuno-defense activity of cytosolic Hsp70 cDNA of mud crab is confirmed by reverse transcriptase-polymerase chain reaction coupled with cDNA amplification. The level of Hsp mRNA expression was analyzed in various tissues at different temperatures, salinity, and nitrite concentration, suggesting that the expression of mRNA is 85% higher at 4 °C and 78% higher at 40 °C than 25 °C ([174], Figure 8). Similarly, mRNA expression was found to be 85% higher at 0 ppt and 75% higher at 45 ppt than at 25 ppt. However, mRNA expression rises to 88% with rising nitrate concentration [174]. Additionally, genes can be used as tools to understand genetic diversity as well as enzyme functionality.

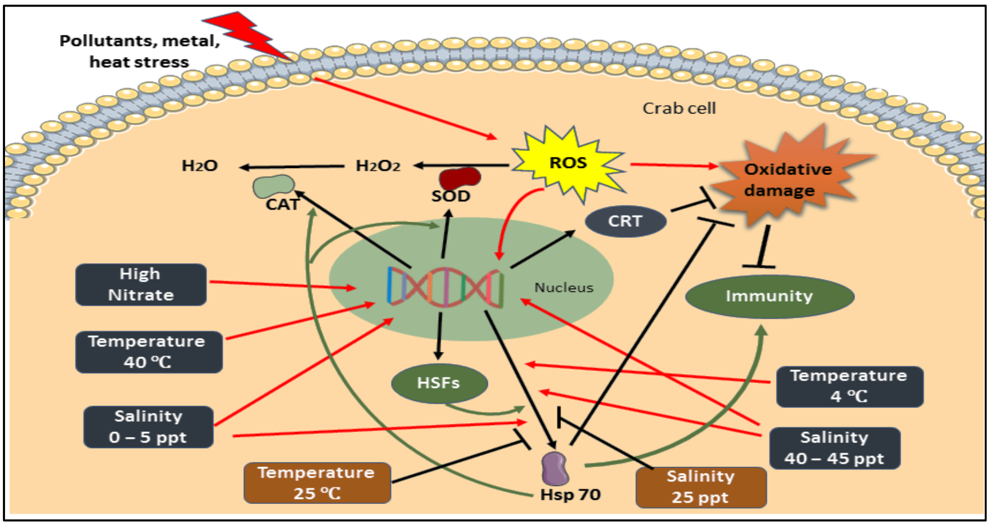

Figure 8. Expression of the gene under the influence of different salinity and temperature. Low salinity, high temperature, and high nitrate are the inducing factors for heat stress. Hsp 70 induced by these factors and HSFs also increase antioxidants like SOD and CAT mRNA expression. Below 4 °C, cold stress response induces CRT mRNA expression that neutralizes oxidative damage also. Hsp 70 also induces immunity in mud crabs. Temperature below 25 °C and salinity below 25 ppt inhibit Hsp 70 expression.

Overexploitation of historical bottleneck of an organism's population can be analyzed based on DNA sequences, which will help in understanding genetic diversity and connectivity among the population of different zones. Microsatellites and cytochrome oxidase genes are considered for analyzing population connectivity. On analyzing these genes, it was confirmed that the mud crab population is under overexploitation or historical bottlenecks [177]. In order to design a marine protected area observing the pattern of connectivity and measuring genetic diversity is indeed essential [178,179].

In order to counter superoxide activity, an enzyme like superoxide dismutase plays a major role, without which OS cannot be regulated, which leads to big damage to the crab body. Toxicants, temperature above 35 °C, salinity above 35 ppt, and below 5 ppt are common factors of reactive oxygen species (ROS) production at the cellular level leading to damage of biomolecules like proteins, lipids, and nucleic acids [180]. A complex antioxidant system is activated to neutralize the effect to counter ROS. This antioxidant system comprises several enzymes and proteins, out of which superoxide dismutase (SOD) and catalase (CAT) play a major role in ROS neutralization [181]. Thus, it is essential to know the physiological effect of SOD and CAT, such as major antioxidant enzyme inhibition by various kinds of inhibitors, as well as the role of water physicochemical factors involved in enzyme expression. Molecular docking was conducted in order to know the mode of binding of different inhibitors of SOD, such as hydrogen peroxide, potassium cyanide, and sodium dodecyl sulfate. The result suggested that potassium cyanide was not bound to the predicted structure of MnSOD, but hydrogen peroxide and sodium dodecyl sulfate showed a significant interaction. These data give an idea about the presence of some specific amino acids in the active site of the enzyme, which leads to the prediction of the binding modes of the proteins [182].

In silico study on this enzyme gives an idea about its structural character and also provides data on amino acids in the active site of the enzyme. Several inhibitors exist for this enzyme, but information on their binding with the enzyme on a structural basis is still unclear. However, using inhibitors of SOD such as hydrogen peroxide, potassium cyanide, sodium dodecyl sulfate (SDS), β-mercaptoethanol, and dithiocarbamate, the cleavage sites on this enzyme and blocking the activity of inhibitors were established. SOD-SDS complex interactions reveal that residues such as Pro72 and Asp102 of the predicted crab extracellular-SOD as common targets of inhibitors [26]. Thus, this study will give an idea about the inhibitors which can interact on these sites, and subsequently, this information can be used to perform other enzymatic studies in crabs.

Similarly, another important antioxidant enzyme, CAT, has been structurally analyzed. It plays a significant role in keeping an organism healthy by protecting it from oxidation and peroxidation. A predicted three-dimensional structure of catalase in the mud crab is revealed by using a comparative modeling approach. The template PDBID: 7CAT of beef liver catalase of *Bos taurus* having NADPH binding site was used to construct this prediction. In order to know the binding properties of catalase with hydrogen peroxide, they use molecular docking. With the help of molecular dynamics, the structure of the receptor for docking and from which it is revealed that Arg 68, Val 70, and Arg 108 in catalase are responsible for binding with H_2O_2 [183]. Thus, the structural detail of specific enzymes will be helpful in monitoring the effect of organic and inorganic compounds and drug design. As important as it is to design drugs to protect the mud crab from various diseases, it is necessary to first address common diseases and the immune system that leads to its production.

9. Habitat Water Quality Management and Techniques to Enhance Mud Crab Production

Now crab culture is rapidly growing in coastal areas due to the rise of global demand, but this is still challenging as it has a long period of fattening and complex water physicochemical factors variation throughout the culture process [184]. A nutritious, rich protein diet plays an important role in the rapid growth of the mud crab. Studies conducted to optimize the nutritional composition of the diet of mud crabs suggest that 55–79% protein, 6% lipid, 1% cholesterol, and 3–4% phospholipid are highly effective for the growth of its larval (megalopa) stage. Similarly, for optimal growth during the juvenile stage, 32–40% protein, 6–12% lipid, 0.51–1% cholesterol, and 13.5–27% carbohydrate are effective [185]. In addition, a micro-bound probiotic diet is useful for growth in different stages of mud crabs [185]. Besides the nutritional approach, water physicochemical factors significantly influence the growth rate of mud crabs. During the culture process, the zoeal larvae must be maintained between a salinity of 30–35 ppt and a temperature of 28–32 °C. However, megalopa larvae survive well in 25 °C/35 ppt conditions, and the mean larval development time is found to be increased from 16 days to 25 days when the temperature decreases from 34 to 20 °C (Table 5, [186]). In captive conditions, the time taken during the hardening of the shell of mud crabs is 2 to 3 weeks which needs a high cost for its maintenance during the rearing of the crab [187].

Table 5. Optimum temperature, salinity, pH, and light in habitat water on survivability at different stages of mud crab.

Water Physicochemical Factors	Zoea-II	Zoea-III	Zoea-IV	Zoea-V	Megalopa	First Crab Stage	Adult Crab	Reference
Temperature	25–28 °C	25–28 °C	25–28 °C	25–28 °C	28–34 °C	22–25 °C	22–25 °C	[186]
Salinity (ppt)	30	35	30–34	30–34	34	24	20–21	[186]
pH	8.1–7.8	8.1–7.8	8.1–7.8	8.1–7.8	8.1–7.8	7.8–7.5	7.3–6.4	[188]
Light condition	Low light	Low light	Low light	Low light	Full light	Full light	Full light	[189]
Survivability	86%	85%	82%	78%	60%	85%	90%	[186]

Note(s): Larval stages of zoea need high temperature and salinity for better survivability, while low temperature and salinity are required for the subsequent stages of the lifecycle. The pH of water and light duration also affect the larval and adult stages of mud crabs. High pH and low light induce larval stages, and low pH and full light induce later stages of the lifecycle of mud crabs.

As crab absorbs water during the molting process, incorporating minerals in water lowers the hardening period of the crab's soft shell. However, minerals through diets, drinking, and direct absorption via gills and epidermis play an important role in hardening the soft shell [190]. The fattening period varies according to the condition of the crab habitat and food quality. It has been shown that brackish water is most favorable for shortening the fattening period of around 30 days [191]. This information explains how minerals, temperature, and salinity play a key role in the shell hardening and survival of larval stages (Figure 9). Additionally, if crabs are reared in high salinity and in the presence of significant minerals, such as $CaCO_3$, $MgSo_4$, and KCl, the hardening of the shell occurs within nine days [187]. In order to forecast fishing industries about the standing stocks of eggs and larvae, DNA barcoding of different life stages of mud crabs is essential, which is possible by using specific genes such as mitochondrial cytochrome oxidase subunit 1 [192]. Based on these findings, although advanced culture systems are developed, the major obstacle to culturing these crabs is cannibalism during larviculture from megalopa to crablet stages during the nursery. It leaves this potential crab industry with challenges, especially those dependent on capturing wild crabs, which has serious sustainability issues [89]. Therefore, challenges still exist in studying food and feeding behavior, especially cannibalism during the above early stages in the life of mud crabs [89]. Special attention must be paid to their cultural techniques under the control of environmental factors for better production of mud crabs [89].

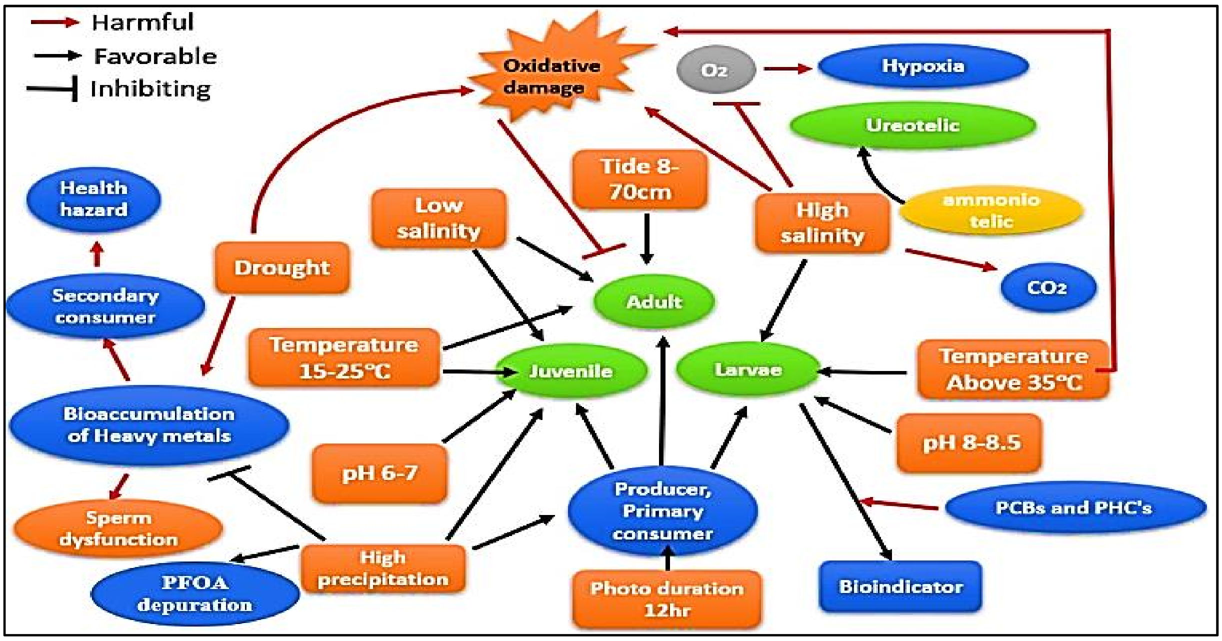

Figure 9. Effect of water physicochemical factors on life stages and physiology of mud crab. Temperature range between 15–25 °C, low salinity, and pH range from 6–7 favors both juvenile and adult stages of mud crab. High precipitation and photo-duration increase the producer and primary consumer of the aquatic food chain, which are essential for the growth of mud crabs. Bioaccumulation of heavy metals and toxicants increases in drought conditions, while high precipitation reduces the bioaccumulation rate in mud crabs. Bioaccumulation of heavy metals leads to sperm dysfunction and health hazard. PCBs and PHCs retard larval development from stages 1 to 2, which makes larvae a bioindicator. Temperature 30–34 °C, a high pH, and high salinity favor larval stages. High salinity and temperature cause oxidative stress, hypoxia, and carbon dioxide content. High salinity also changes excretion of mud crabs from ammoniotelic to ureotelic. Arrows indicate the direction of action while −∣ symbol indicates the inhibitory action of the respective molecules.

The box culture system for mud crabs is one of the most reliable culture systems. The weight gain rate was 65.0 ± 26.3%, and the molting of the juvenile is significantly higher when crabs are grown in a light-proof environment. However, it has been shown that the adult crab growth rate of 37.6 ± 20.6% fastens in the presence of light inside the culture box provided by the solar power generator. Growing mud crabs in highly dense conditions will raise the probability of cannibalism. Shelters with specific density, i.e., recirculation aquaculture systems, can increase the growth and production rate of mud crabs [189]. Because metabolic waste, fecal matter, and wasted food management are major issues during the crab culture period, a physical filtration system has been employed using Malang sand to overcome the above problems. This system enables the clearance of bottoms in the culture area from waste products and increases the availability of nitrifying and denitrifying bacteria in the medium [193]. The major components of a healthy crab diet include seaweeds, poultry waste, earthworms, and fish meal as food products such as seaweeds provide 57.18% of carbohydrates, while fish meal contains 61% protein and poultry waste provides 25% lipid content [97]. Adopting all these techniques shall be helpful to improve the culture system and production even under deadly pathogen attacks.

Although crab culture in artificial conditions is rarely affected by infectious diseases, still information on pathogens needs to be investigated. The milky disease of crab has been reported since 2005 when the mud crab was cultured along the coast of southeastern China. The disease mainly occurs between September and November [162]. Similar kinds of symptoms are noticed in the case of bitter crab disease or pink crab disease caused by members of the genus *Hematodinium* are common in cultural sectors. Thus, lowering the fattening period, implementing the box culture system, and maintaining proper environmental conditions will enhance crab culture.

10. Future Prospective of *Scylla* sp. with Respect to Mangrove/Estuarine Habitat Water

Owing to the importance of the crab industries, more research in different aspects has been done recently on *Scylla* sp. The comparative evaluation of proximate compositions in mud crabs suggests that females are more nutritionally rich, i.e., 17.07 ± 1.52% protein content, while males are rich in mineral content, especially Ca (1199.71 ± 343.43 mg/100 g) and Fe (14.21 ± 1.28 mg/100 g). So, a combined intake of male and female mud crabs will be more beneficial in terms of nutrition [194]. It has been studied that the mud crab can be edible till 240 min after death at normal room temperature. The crab postmortem investigation on ATP catabolism and succession of the bacterial community suggests that the muscle K value could be used as an optimal nucleotide freshness indicator for the freshness of mud crabs, with a proposed threshold of 20%. The muscle K value can be influenced by *Photobacterium*, *Peptostreptococcaceae*, average path distance, OTU richness, and Shannon index of bacterial muscle community [195].

Recent toxicological studies indicate that the effect of marine diesel oil on mud crabs under ocean acidification and warming conditions has been investigated, suggesting a decreased ingestion and absorption rate whereas a significant increase in the rate of respiration and ammonia excretion [196]. Similarly, human activities and natural sources, such as the weathering of Uranium-bearing rock, lead to contamination of marine ecosystems. Uranium exposure can lead to hemocyte reduction, mitochondrial anomaly, lamellar disruption of the gill, necrosis of hepatopancreas, and disruption and rupture of muscle bundles mud crab tissues [197].

Studies on the disease and immunity of mud crabs have been done recently. The SpBAG3, a Bcl2-associated athanogene 3, plays a key role in regulating apoptosis, development, cell movement, etc., and has been characterized in *Scylla* species. Specifically, it has a crucial role in assisting WSSV by inhibiting hemocyte apoptosis in mud crabs [198]. The WSSV infection in mud crab downregulates SpBNIP3, a BCL2 and adenovirus E1B 19-kDa-interacting protein 3. This leads to an increase in the apoptosis rate and Caspase 3 activity but decreases the mitochondrial membrane potential and hemocytes autophagy levels [199]. Mud crab reovirus (MCRV) infection in mud crabs induces phagocytosis, apoptosis, and unsaturated fatty acid biosynthesis, as well as other metabolic enzymes that give novel cellular mechanisms in crustaceans with respect to MCRV infection [200].

Recently, investigations on growth and reproduction have been done to elevate their production value. The ovarian development of mud crabs can be regulated through Vitellogenin (Vtg) and Vitellogenin receptor (VtgR) genes, which are involved in oocyte maturation. Both genes can be targeted with the help of agomiR-34, which binds at 3′-UTR and leads to inhibiting the expression of the genes [201]. The female reproductive output in mud crabs has been investigated by Fazhan and colleagues [202]. It indicates that sand type can influence the weight of the egg clutch, total egg number, fecundity, and clutch size. They observed that fine sand (<70 μm) substrate could maximize female reproductive output. Photoperiod plays a critical role in mud crab growth, survival, and metabolism. In constant darkness, lipogenesis-related genes are found to be up-regulated, while lipolysis-related genes are down-regulated. Thus, in order to utilize the lipid as an energy source, mud crab needs an optimum photoperiod [203].

The mangrove mud crab *Scylla* sp. plays a pivotal role in maintaining mangrove ecosystems in coastal areas. Being an ectothermic animal, these crabs exhibit altered physiological responses, including metabolic depression under the changing climate, global warming, and associated changes that affect the physicochemical properties of their habitat water. The mangrove ecosystems are also vulnerable to insults from various biotic and abiotic factors, including water physicochemical factors that may come out under climatic and anthropogenic activities. The contribution of *Scylla* sp. to the food chain and bioturbation activity in mangrove areas is commendable. Therefore, it is reviewed to compare biochemical, molecular, and physiological responses, growth, reproduction, and production of *Scylla* sp. independently or in relation to water physicochemical factors, pathogens, heavy metals, and harmful chemicals. Fluctuation of water physicochemical factors greatly impacts on physiology, reproduction, immunity, and other vital processes of mud crabs. So, necessary steps for conserving these species and their habitat, especially the mangrove ecosystems, are needed. As these crabs are under frequent overfishing threats, the current review may be useful to improve the production and management of mud crabs through a detailed analysis of several biomarkers to set up possible climatic resilient strategies.

Nevertheless, crab seed supply is a major challenge in Asian countries like India. On the one hand, importance on the physicochemical factors of water, such as salinity and pH, and hormonal regulation in broodstock along with infectious diseases must be carefully regulated for mud crab culture; on the other hand, this crab can be used as a bioindicator species as physicochemical properties of habitat water including temperature, salinity, pH, heavy metals, and chemical toxicants regulate their specific proteins expression. Therefore, environmental factors, especially habitat water parameters and pollution caused by humans, play a significant role in mud crab disease, reproduction, physiology, and gene expression, which motivates the need for research into strategies for protecting *Scylla* species. Owing to the importance of the species, the crab industry reached a high level in most Asian countries, which needs to be expanded in other crab-consuming countries.

11. Conclusions

The current review extensively discusses mud crab physiology, reproduction, immune system, and ecotoxicology in response to water physicochemical factors, which could be useful for its management in aquaculture and fisheries. Induced breeding, culture technique, bio-waste management, and the protection of gravid females are needed for the enhanced production of mud crabs under abiotic environmental insults. Environmental factors, such as temperature, salinity, pH, and infectious diseases, affect mud crab growth and survivability in the natural and culture system (Figure 9). Due to its ectothermic nature, the role of the endocrine system, namely eyestalk factors, M-organs, and Y-organs, for induced breeding of mud crabs under low temperatures is important, but maintaining a balanced titer for induced serotonin and melatonin is required. Drought and high temperature are the deciding factors of bioaccumulation of heavy metals, such as As, Cd, Co, Cu, Mn, Pb, and Zn, and toxic products, such as PFASs, PFOS, PFHxS, and PFOA, lead to health hazards. The toxic effects of organic and inorganic pollutants create health hazards not only in mud crabs but also in other predator organisms by entering the food chain system, which can be overcome by lowering pollution levels in coastal water bodies. The pathogen of mud crab ranges from virus to algae, but there are several innate immune proteins and natural drugs that boost the immune system to combat harmful pathogens of mud crab under varied water physicochemical factors. Certain key genes under the influence of temperature and salinity play a significant role in immuno-defense activity, sex determination, and phylogenetic analysis, leading to a better understanding of its distribution and survivability. Components of crab shells can be used as biodiesel, bio-ceramic, naturally biodegradable, and biocompatible polymer production, leading to biowaste management in coastal areas. Crab culture can be commercially enhanced by adopting techniques, such as box culture, recirculation aquaculture system, and providing a healthy composite diet. In their natural habitat, they play a crucial role using their biological burrowing activity, making soil porous like earthworms, leading to the sustenance of mangrove forests and the whole ecosystem. Additionally, the expression pattern of biomolecules under the influence of water physicochemical factors makes mud crabs a potential organism for biomarker studies. Thus, being an environmentally and economically significant species, the mud crab draws special attention to its stress physiology for its aquaculture management.

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Abbreviations

ALF—antilipo polysaccharide factor, AMPs—antimicrobial peptides, CRT—calreticulin, CAT—catalase, Hsp—heat shock protein, H_2O_2—hydrogen peroxide, LPS—lipopolysaccharide LPx—lipid peroxidation, MCRV—mud crab reovirus, OS—oxidative stress, PFOA—perfluorooctanoic acid, PFOS—perfluorooctyl sulfonate, PPT—parts per thousand, PTZ—pentylenetetrazol, ROS—reactive oxygen species, SOD—superoxide dismutase and WSSV—white spot syndrome virus.

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