Crustaceans: Microbes and Defense Mechanisms

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Asha Pillai

Abstract

Crustaceans are one of the most diverse arthropods that have successfully inhabited the aquatic ecosystems including freshwater, estuarine and marine. They have enormous benefits for the economy and human health and are of great significance to the aquaculture industry. Crustaceans are a rich source of protein and hence contribute to more than 70% of the world's economy through aquaculture. These animals are prone to many pathogenic species of microbes, especially bacteria. Most of the bacterial diseases in crustaceans are due to pathogenic strains belonging to *Vibrio* spp. *Pseudomonas* spp. and *Aeromonas* spp. that are known to cause blackspot diseases, necrosis and other shell diseases. To combat such infectious pathogens, crustaceans have developed simple but strong innate defense strategies. These innate immune mechanisms are activated upon specific recognition of molecules such as lipopolysaccharides, glycoproteins, glycolipids and peptidoglycans present in the invading microbes. An array of immune components both cellular and humoral are involved in the crustacean effector defense processes including phagocytosis, antibacterial activity, encapsulation and agglutination. This chapter presents an overview of the microbes infecting the crustaceans, especially the decapods and focuses on the various defense mechanisms adopted by them.

Keywords

Crustaceans microbes · Lectins · Phagocytosis · Encapsulation · proPO

A. Pillai (✉)
Department of Zoology, Ethiraj College for Women, Chennai, India
e-mail: asha_p@ethirajcollege.edu.in

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7.1 Introduction

Crustaceans are a key source of protein represented by a variety of edible species distributed throughout the world. The growing demand for wild or captive crustaceans has uplifted crustacean aquaculture as one of the most promising and commercially viable businesses to meet the requirements of the ever-growing human population. The expansion of crustacean aquaculture has always been accompanied by increased incidences of several diseases caused by infectious microbes, notably of bacterial or viral origin. To combat such pathogenic microbes, the crustaceans have developed simple but strong defense mechanisms. Several studies on these innate immune mechanisms of crustaceans have been made with great progress since the late 1970s (Hauton 2012). In the past two decades, this progress has accelerated with the isolation, characterization (Asha and Arumugam 2017; Chen and Wang 2019) and functional analysis (Asha and Arumugam 2021) of new classes of effector molecules.

In normal conditions, crustaceans maintain a healthy state and keep infections under control. Externally, they are covered by a hard, rigid exoskeleton that functions as an efficient physiochemical barrier against mechanical injury and microbe invasion. The cuticular coat, in combination with an acid environment rich in digestive enzymes, is able to inactivate and degrade most viruses and bacteria and forms the first line of defenses of the crustaceans. However, they lack the complex and highly specific adaptive immune system of vertebrates, which is based on lymphocytes, immunoglobulins and immunological memory.

Crustaceans possess an open circulatory system that distributes the essential nutrients, hormones, oxygen and cells through the hemolymph. The circulating cells of crustaceans known as hemocytes are functionally analogous to leukocytes of vertebrates and are mainly concerned with the recognition and elimination of non-self-molecules (Sritunyalucksana and Söderhäll 2000). The defense mechanisms of crustaceans become activated based on the nature and characteristics of the invading pathogen (Vazquez et al. 2009). Accordingly, different effector molecules are activated, such as proPO system, phagocytosis and encapsulation, which are mediated by proteins such as lectins, antimicrobial proteins and pattern recognition proteins (Luis et al. 2021).

This chapter provides a brief but broad overview of our current understanding of the crustacean immune system, especially of the decapods. This enables innumerable pathways that enable us to venture into new avenues for solutions to ensure global food security through crustacean aquaculture. Although the details of the immune pathways and their interrelations are not known, the limited data provide information on the disease combat in crustacean aquaculture through prophylaxis.

7.2 Crustaceans and Their Importance

Crustaceans are primarily marine organisms and compose a large, ancient and diverse animal group that includes many well-known, commercially exploited members, such as shrimps, crabs, crayfish and lobsters that form a vital link in food web (Szaniawska 2018). They are the most abundant animals inhabiting the world's oceans and include freshwater, terrestrial and semi-terrestrial species. Crustaceans form the fourth largest diverse group among animals comprising approximately 75,000 species, including barnacles and beach fleas. They are mostly aquatic in habitat with majority of the species inhabiting marine waters. Diversity of crustaceans is also witnessed in freshwaters but on land the diversity is low. Studies have estimated a total of 14,756 species and 2725 genera of extent decapods and about 3047 species of shrimps and prawns worldwide (Susanto 2021).

Crustaceans possess a hard exoskeleton due to the deposition of calcium carbonate in the cuticle. The body and appendages are specialized into the thoracic and abdominal region with the head bearing the feeding and sensory organs. In a few crustaceans, the head and thorax are merged to form the cephalothorax secured by an expansive carapace. These animals possess remarkable survival due to the presence of a large number and assortment of joint appendages occurring in every segment of their body.

Crustaceans being rich in proteins, serve as valuable food sources and are therefore of substantial economic importance in aquaculture. They are the highest-valued seafood next to freshwater fishes with a global production of 8.5 million tonnes (Boenish et al. 2021; Azra et al. 2021).

Malacostracans (crabs) are the most cultivated class of crustaceans accounting for 20% of the marine crustacean species captured, reared, and used worldwide. This is followed by shrimps and prawns, the majority of the penaeid species (*Penaeus monodon, Litopenaeus vannamei*) that are mainly cultivated in Asia (Pratiwi 2008). Among the freshwater prawns, *Macrobrachium is* the only species that is cultured.

Apart from these, the shells of crabs and other crustaceans are used in the treatment of inflammatory disorders. Crustaceans also serve as bioindicators as they successfully inhabited numerous environments. *Palaemonetes argentinus* serves as a bioindicator for pollution in freshwater bodies (Bertrand et al. 2018). Besides, copepods are used as live feeds in aquariums, baits for game fishing and for compost production.

7.3 Disease-Causing Microbes of Crustaceans

The expansion of aquaculture has always been accompanied by an increase in the incidence of diseases caused by microbes. The crustacean aquaculture industry is no exemption and faces heavy losses due to disease-causing microbes. An insight into the various pathogenic strains of microbes infecting crustaceans revealed that bacterial strains dominated the scenario. Studies have shown that crustaceans inhabiting freshwater as well as marine habitats are equally prone to such infectious microbes (Odeyemi et al. 2021; Rowley 2022). These microbes invade a series of host tissues and organs including gut (Zhao et al. 2018; Le et al. 2019; Cicala et al. 2020), hemolymph, hepatopancreas (Gainza et al. 2018; Landsman et al. 2019) gills, muscles as well as gonads.

Accordingly, a highly pathogenic bacterium *Aeromonas hydrophila* has been isolated from the freshwater crayfish, *Pacifastacus leniusculus* (Jiravanichpaisal et al. 2009), which causes necrosis of the gill, heart, hepatopancreas and the circulatory system. Endotoxins released by these bacteria were found to be the causative agent for the crayfish mortality. In the bluecrab *Callinectus sapidus* gram-negative bacteria viz., *Vibrio sps (*gut, hepatopancreas, gills) and *Clostridium botulinium* (hemolymph) were observed to cause necrotic centers in arteries, heart and hemal sinuses resulting in fatalities (Sizemore and Davis 1985). Several bacteremias in crabs have been attributed to *Vibrio sps*., *Aeromonas sps*., and Rhodobacteriales like chitinolytic and chitinoclastic bacteria which may cause shell diseases in these crabs (Wang 2011). Novel pathogens like *Spiroplasma sps* identified in the Chinese mitten crab (Wang et al. 2004) have inflicted a huge loss to the crustacean aquaculture industry. Potential spoilage bacteria have also been identified in the farmed shrimp *Litopenaeus vannamei* (Don et al. 2018). In the freshwater prawn *Macrobrachium rosenbergii* more than 186 bacterial isolates related to 7 bacterial genera causing midcycle disease and black spot disease which are highly infectious have been identified. These bacterial spp. were *V.alginolyticus, A.hydrophila, P.fluorescens, C.freundii* and *E.aerogens* (Stephen 2022) which caused a heavy loss to the freshwater aquaculture industry.

Infectious diseases among the cultivated penaeid prawns in the Northeast Asian countries of Hawaii and Japan and along the coasts of Central America were caused by viruses. Most of them belonged to the baculovirus species that infected the midgut, exoskeleton and the hepatopancreas of the penaeid prawns (Lee et al. 2022). In India, the myxobacterial infection, reported in *Penaeus indicus, Penaeus monodon, Metapenaeus affinis* and *Metapenaeus dobsonii*, is caused by *Chondrococcus* spp. and *Flexibacter succicans* (Rao and Soni 1986). Several chitin-destroying bacteria, such as *Pseudomonas* spp. and *Aeromonas* spp., known to cause brown spot disease have been identified in the juveniles as well as adults of *Penaeus indicus*. Vibriosis caused by *Vibrio anguillarum* is the most important disease of *Penaeus indicus* cultivated in brackish water fields (Nilla et al. 2012; Newman 2022) while *Escherichia coli* infects the larvae of these penaeids.

7.4 An Overview of Crustacean Immunity

Invertebrates, unlike vertebrates, do not possess true adaptive immune mechanisms and are hence totally dependent on their innate immune system to defend themselves against invading pathogens. In these animals, an inquiry into the nature of basic immune mechanisms underlying the defense network against invading pathogens has led to the identification of an apparently simple and primitive defense system consisting of humoral and cellular components (Smith and Chisholm 1992; Cerenius and Söderhäll 1995; Zhang et al. 2019). It is notable that crustaceans have been one of the most extensively studied group of arthropods and are capable of maintaining a healthy state by mounting exclusive defense mechanisms against potential pathogens (Kulkarni et al. 2020). A complex system of innate immune mechanisms involving cellular and humoral components is triggered in the host upon entry of a pathogen.

In crustaceans, the cellular immune components primarily include certain fixed maintaining cells such as branchial podocytes, nephrocytes, and circulating blood cells or hemocytes (Smith and Ratcliffe 1980; Johnson 1987; Stara et al. 2018). Various soluble substances detected in the hemolymph of these animals constitute the humoral immune system in crustaceans. These include β-1,3 glucan binding proteins (bacterial lipopolysaccharides (LPS)-binding proteins) (Yu and Kanost 2002; Chaosomboon et al. 2017), antimicrobial peptides (Destoumieux et al. 1997; Vazquez et al. 2022), lectins or agglutinins (Maheswari et al. 2002; Asha and Arumugam 2017), hemolytic components (Milochau et al. 1997), antifungal proteins (Iijima et al. 1993) and a series of cytotoxic molecules. These innate immune mechanisms are activated upon specific recognition of molecules such as lipopolysaccharides, glycoproteins, glycolipids and peptidoglycans present in the invading microbes (Chen and Wang 2019).

7.4.1 Cellular Immunity in Crustaceans

The circulating cells (coelomocytes or hemocytes) represent the primary effector component during the immune response of crustaceans (Beck et al. 1994; Söderhäll and Junkunlo 2019). There are three types of circulating hemocytes found in crustaceans viz., (1) hyaline cells—which are small, spherical and lesser in number which varies among different crustacean species; (2) semigranular cells—which possess small eosinophilic granules and also contain prophenoloxidase activators; (3) granular cells—which are filled with numerous granules in their cytoplasm and can attach and spread on the foreign bodies (Wu et al. 2019; Liu et al. 2021; Li et al. 2021; Asha and Arumugam 2021). These cells have been have shown to interact with a range of foreign materials and mediate different types of immune reactions such as phagocytosis, nodule formation, encapsulation, cytotoxicity and exocytosis of immune-reactive substances (Leippe and Renwrantz 1988; Liu et al. 2018; Junkunlo et al. 2018, 2020). In addition, crustaceans possess fixed cells in their gills (Smith and Ratcliffe 1978), which plays a vital role in cellular defense mechanisms.

7.4.2 Phagocytosis

In crustaceans, intracellular destruction of microbes is accomplished through phagocytosis and the mechanism is similar to other animals. In the process, the microbe is trapped, ingested, destroyed and eliminated from the host with the help of phagocytic cells. Fixed phagocytic cells are seen in pericardial sinuses, gills and the base of appendages, whereas circulating/mobile phagocytes are observed in the hemolymph in continuous circulation (Liu et al. 2020). Phagocytosis is a phenomenon in which hemocytes recognize and ingest foreign bodies such as bacteria, spores or dead cells of the organism itself. Most of the circulating pathogens such as Gram -ve *Pseudomonas* spp. and *Escherichia coli* in the hemocoel of the freshwater crab *Parachaerabs bicarinatus* and *Cherax destructer* are destructed and eliminated by the phagocytic hemocytes (McKay and Jenkin 1970). A similar situation has been observed in the American lobster *Homarus americanus* (Mori and Stewart 2006). Although in the blue crab *Callinectus sapidus,* both Gram +ve as well as Gram −ve bacteria are eliminated by the hemocytes (Cassels et al. 1986). The rate of phagocytosis by the hemocytes of crustaceans also appears to vary with other parameters including diet as observed in the larvae of tiger shrimp *Penaeus monodon* where the resistance due to infection was high in larvae fed on *Vibrio* spp. (Bechteler and Holler 1995).

7.4.3 Encapsulation

Pathogens of larger size like parasites cannot be phagocytosed and hence need to be eliminated through a different mechanism. The phenomenon of encapsulation involves the formation of compact layers of hemocytes especially the semigranular cells that congregate and surround the invader, thereby preventing them to enter into the muscle or hemocoel. Typically, a hemocyte capsule comprises several layers (10–30) of hemocytes tightly packed without intercellular spaces. The layer of hemocytes immediately in contact with the surface of the foreign particle lies extremely flattened on it almost resembling a myelin sheath. Interestingly the granular hemocytes rupture upon adherence to the foreign particle surface thereby releasing the granular material. The material also contains enzymes that signals the hemocytes to flatten and conjoin to form capsules and are referred to as encapsulation-promoting factors (EPF) (Ratner and Vinson 1983). In vitro encapsulation of foreign particles by separated hemocytes from several crustaceans have been reported including crayfish *Pascifastacus leniusculus* (Söderhäll et al. 1984), *Astacus leptodactylus* (Persson et al. 1987) and the horseshoe crab *Carcinus maenas* (Söderhäll et al. 1986).

7.4.4 Clottable Proteins

These are defense molecules with multifunctional properties mostly found in the hemolymph plasma rather than hemocytes. The formation of intravascular and extracellular clots prevents the loss of hemolymph as well as the entry of invading pathogens by rapid sealing of wounds in injured animals (Morales et al. 2019). In some malacostracans, a hemocyte-derived clotting cascade is triggered by the lipopolysaccharide of bacteria which activates the clotting enzyme that catalyzes the conversion of a soluble coagulogen into insoluble clot, coagulin (Kawabata et al. 1996). In crustaceans like shrimps, lobsters and cray fishes, the transglutaminase released from hemocytes upon entry of a pathogen, catalyzes the linking of clottable protein into insoluble aggregates in the presence of calcium, which results in clotting and trapping of pathogens. Clottable proteins with sequence identities have been found in freshwater crayfish, *Penaeus leniusculus, Littopenaeus setiferus* and *Penaeus monodon*. Although crustacean clottable proteins exhibit similarities in function, they do not share structural similarities (Hall et al. 1999).

7.4.5 Cytotoxicity

Similar to the cytotoxic mechanisms accomplished by the mammalian NK cells, the semigranular and granular cells of crustaceans destroy the tumor cells present in the host by attaching themselves to the target tissue and releasing the cytotoxic chemicals (Parrinello and Arizza 1992).

7.4.6 Humoral Immunity in Crustaceans

The innate defense mechanisms of crustaceans also involve several factors, occurring in the serum or plasma, which act against foreign bodies. Naturally occurring bioactive molecules are activated to bring about certain important immunological phenomena such as agglutination (Sima and Vetvicka 1993; Bouallegui 2021), lysis, precipitation and stasis (Boman et al. 1991) of nonself particles. These molecules that form the humoral defense of crustaceans include lectins, β-1,3 glucan-binding proteins (Duvic and Söderhäll 1990; Chai et al. 2018), proPO system, antifungal proteins (Chen et al. 2018) and antimicrobial proteins (Destoumieux et al. 1997; Vazquez et al. 2022). Although most of these humoral factors belong to the category of genuine humoral defense, some of them are derivatives of the circulating hemocytes that operate in conjunction with the cellular network. Agglutinins/lectins, antimicrobial peptides and prophenoloxidases are the most widely studied humoral components mainly due to their universal distribution, opsonophagocytic properties and well-known antimicrobial activity.

7.4.7 Agglutinins/Lectins

Agglutinins/lectins are proteins or glycoproteins capable of specifically binding to a whole sugar, a part of the sugar, a sequence of sugars, or their glycosidic linkages (Goldstein et al. 1980; Gabius 1994). In crustaceans, agglutinins have been detected against vertebrate erythrocytes (Hall and Rowlands Jr 1974a, b; Ratanapo and Chulavatnatol 1990), bacteria, invertebrate sperm, protozoans and other cells. In general, agglutinins do not occur in every crustacean species (Smith and Chisholm 1992) and compared to other invertebrates, the titers are often quite low. Several agglutinins may be present in any one species but levels of activity may differ considerably between individual animals (Adams 1991).

Most of the lectins reported in crustaceans belong to the C type as they are dependent on calcium for their functioning (Runsaeng et al. 2018; Snigdha et al. 2022). Identification of a 9.5 kDa lectin with N/O acetylated sugar specificity, in the freshwater prawn *Macrobrachium rosenbergii,* have been found to be produced in the hemocytes and remain on their membrane and participate in the recognition of foreign bodies (Vázquez et al. 1997). Although lectins from decapod crustaceans have been found to exhibit heterogeneity in molecular mass and subunit conformation, they possess preserved carbohydrate-binding specificities for N/O acetylated sugars, thus indicating the conservation of such sugar-binding specificities throughout evolution (Kilpatrick 2002; Alpuche et al. 2005; Vasta et al. 2007). Bacterial species like *Aeromonas* spp. and *Bacillus cereus*, which possess O- acetyl groups of sugars in their cell wall is recognized by lectins in *Macrobrachium rosenbergii* (Vázquez et al. 1994, 1996). In a similar way, LPS from *Escherichia coli* is identified by a lectin from *Carcinoscorpius cauda* (Dorai et al. 1982). Studies have also shown that the synthesis of lectins in different organs of the crustaceans might be activated by the entry of the pathogenic bacteria or viruses. Thus, in the swimming crab *Portunus trituberculatus,* the main source of lectins is the hepatopancreas followed by the gills, hemocytes and ovary (Kong et al. 2008). In the case of post-larvae of *Penaeus monodon* infected with White Spot Syndrome Virus (WSSV), the expression of lectin gene has been traced to the muscle, eye stalk and cuticle apart from hepatopancreas (Leu et al. 2007). Lectins have also been observed to show structural and functional diversity within the same species as reported in *Litopenaeus vannamei* (Viana et al. 2022).

In addition, many experimental studies have attributed a variety of biological functions to lectins including feeding, symbiosis, larval settlement and diverse endogenous functions, such as cell aggregation, embryonic development, metamorphosis, wound repair and transport of carbohydrates (Yeaton 1981; Beck et al. 1994; Ahamed et al. 2022). Agglutinins present in the hemolymph of crustaceans are proposed to act as carriers for sugars, glyco-conjugates, or antibody-like molecules, or as opsonins involved in humoral responses against pathogens. These agglutinins present on hemocyte surfaces as in crayfish and bluecrab have been proposed to participate in cellular recognition and trigger phagocytosis, nodulation and encapsulation responses. Naturally occurring agglutinins serve as opsonins and facilitate the phagocytic uptake of target cells precoated with the serum-purified agglutinins (Kondo et al. 1992; Maheswari 2000; Ogutu 2003). It has also been demonstrated (Asha and Arumugam 2016) that the ability to agglutinate target cells is also associated with one of the most important physiological phenomena in crustaceans viz., stages of moult cycle.

7.4.8 Antimicrobial Peptides

Antimicrobial peptides (AMPs) are one of the major components of the innate immune defense of crustaceans. AMPs are primarily known as natural antibiotics, which play a role in host defense response including self or non-self-recognition, cell-to-cell communication, superoxide anion activity, melanization, phagocytosis, cytotoxicity and encapsulation (Xiao et al. 2018). Penaeidins, a family of antimicrobial components, have been identified in shrimps and they have been shown to possess both antibacterial and antifungal properties (Vazquez et al. 2022). In crabs, a low molecular weight antimicrobial peptide called crustin which is immunologically effective against Gram-positive bacteria has been isolated (Du et al. 2019). The pathological and clinical backgrounds have prompted researchers to investigate novel and potent antioxidant peptides from crustaceans that are of therapeutic use. The regulation of expression and distribution of penaeidins during microbial challenges is done through hemocyte reactions and hemocyte proliferation process. Thus, these antimicrobial peptides in penaeid shrimps protect the tissues from infections and aid in wound healing (Xiao et al. 2020).

7.4.9 Prophenoloxidase System

Phenoloxidase (PO) is a copper-containing enzyme capable of catalyzing the hydroxylation and oxidation of phenols into quinones and a series of steps leading to the synthesis of melanin. It is the terminal enzyme of proPO which is a cascade that is activated by the extremely low levels of microbial cell wall components such as LPS and β-1,3 glucans. This stimulation of immune responses by the proPO system is achieved by specific interactions with receptors on the hemocytes (Li et al. 2018). The concept of pattern recognition receptors (PRPs), which are a group of germlines encoded receptors, recognize surface antigens on microbes like LPS, peptidoglycans, mannans and β-1,3 glucans (Habib and Zhang 2020; Tran et al. 2020). This results in the production of melanin pigment which is seen accumulated as dark spots in the cuticle of arthropods. The toxic metabolites that are formed during melanin formation are known to exhibit antifungal activity. Enzymes of the proPO system are localized in the hemocytes of penaeid shrimps, especially in the semigranular and granular cells (Perazzolo and Barracco 1997). Studies on *Penaeus monodon* hemocytes have confirmed this showing the expression of proPO mRNA only in the hemocytes. The proPO cascade culminating in melanization plays a vital role in preventing the bacteria from proliferation and becoming deleterious to the host. Studies on the kuruma shrimp *Marsupenaeus japonicus* have shown that the inactivation of proPO results in a significant increase in the amount of bacteria and a sharp increase in shrimp mortality (Fernand et al. 2009). A bacteria-induced β-1,3-glucan binding protein has been isolated from red swamp crayfish *Procambarus clarkii*, which appears to protect the host from *Aeromonas hydrophila* infection (Chai et al. 2018). Furthermore, it has been demonstrated that the expression of genes encoding LPS binding protein in hemocytes of the white shrimp *L.vannamei* is upregulated in infections caused by *Vibrio sps* (Cheng et al. 2005) and viruses (Roux et al. 2002).

7.5 Future Perspectives

Crustaceans as a source of animal protein are much relied upon by the increasing global population demanding an expansion of their aquaculture. However, this demand for the expansion of crustacean aquaculture has to be met along with several challenges, especially the spread of potential disease-causing microbes. Opportunistic pathogens cause diseases that severely affect crustaceans resulting in irreparable economic losses. The simple but strong innate immune mechanisms possessed by these animals have enabled them to overcome an unfavorable and life-threatening attack by the microbes. Several physiological factors like developmental stages, ecdysis and stress conditions also play a vital role in modulating these immune mechanisms. In recent years, there has been a lot of progress in the understanding of the crustacean defense systems. Novel defense molecules, some of which have been found to be homologous proteins to C Reactive Proteins (CRPs) and complement factors in human immune systems, have been discovered in crustaceans. This chapter highlighted the general immune mechanisms adopted by some of the disease-sensitive species of crustaceans, especially decapods. At this juncture, it is of utmost importance and relevance to focus on the modifications in the immune mechanisms of crustaceans to avoid losses in aquaculture production sectors.

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