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Review

Reprint of "Evolution of specific immunity in shrimp – A vaccination perspective against white spot syndrome virus" ☆

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ABSTRACT

Invertebrates lack true adaptive immunity and it solely depends on the primitive immunity called innate immunity. However, various innate immune molecules and mechanisms are identified in shrimp that plays potential role against invading bacterial, fungal and viral pathogens. Perceiving the shrimp innate immune mechanisms will contribute in developing effective vaccine strategies against major shrimp pathogens. Hence this review intends to explore the innate immune molecules of shrimp with suitable experimental evidences together with the evolution of "specific immune priming" of invertebrates. In addition, we have emphasized on the development of an effective vaccine strategy against major shrimp pathogen, white spot syndrome virus (WSSV). The baculovirus displayed rVP28 (Bac-VP28), a major envelope protein of WSSV was utilized to study its vaccine efficacy by oral route. A significant advantage of this baculovirus expression cassette is the use of WSSV-immediate early 1 (ie1) promoter that derived the abundant expression of rVP28 protein at the early stage of the infection in insect cell. The orally vaccinated shrimp with Bac-VP28 transduced successfully in the shrimp cells as well as provided highest survival rate. In support to our vaccine efficacy we analysed Pattern Recognition Proteins (PRPs) β-1,3 glucan lipopolysaccharides (LGBP) and STAT gene profiles in the experimental shrimp. Indeed, the vaccination of shrimp with Bac-VP28 demonstrated some degree of specificity with enhanced survival rate when compared to control vaccination with Bac-wt. Hence it is presumed that the concept of "specific immune priming" in relevant to shrimp immunity is possible but may not be common to all shrimp pathogens.

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1. Introduction

The animal kingdom includes, more than 95% of invertebrates and about 4% vertebrate species. Invertebrates occupy such a huge space in animal life with immense diversity of organisms ranging from unicellular to multicellular. In general, production of immune response plays a predominant role for effective survival of all living organisms. Invertebrates lack true adaptive immunity and they solely depend on the primitive immunity called innate immunity (Hoffmann and Reichhart, 2002). Nevertheless, there are various immune mechanisms exerted by invertebrates that act potentially against various bacterial, fungal and viral pathogens. Recently much interest has been focused on the invertebrate immune system. In this review, we emphasize on the innate immune mechanisms in shrimp, a crustacean species and strategies for baculovirus vaccine development against shrimp viral pathogen.

Shrimp are the major aquaculture species generating higher revenue in most of the developing countries. In 2010, shrimp export has generated revenue of USD 11.3 billion in trades in shrimp growing countries (FAO, 2010). It also provides a source of employment for one million people involved in shrimp culture industry. However, diseases are major impacts on the successful production of these cultured species, especially bacterial and viral diseases. It was estimated that global production losses due to disease over the preceding 15years had amounted to approximately US$15 billion (Flegel, 2012). Besides white spot syndrome virus (WSSV), which appears to be a constant threat for the last two decades, the recently emerging early mortality syndrome (EMS) is also responsible for such devastating loss in shrimp culture industry (FAO, 2013).

The WSSV infected shrimp population succumbed to death within 2–5days of onset of clinical symptoms (Chou et al., 1995a,b; Lightner, 1996). Also, WSSV infects broad range of arthropods including copepods and insects which act as carriers (Sánchez-Paz, 2010). These significant factors of WSSV render researchers to get involved in the development of anti-viral target as well as the identification of shrimp immune mechanisms against this virus. Several published research articles stated to combat this killer virus by various vaccination regimens such as inactivated vaccine, immunostimulants from plant and chemicals, protein and DNA vaccine and dsRNA treatment (Namikoshi et al., 2004; Witteveldt et al., 2004a,b; Robalino et al., 2004; Balasubramanian et al., 2006; Citarasu et al., 2006; Jha et al., 2006; Rout et al., 2007; Kim et al., 2007). Certainly, in all these vaccinations the protection achieved against WSSV hints that there are possible specific immune responses playing crucial roles in invertebrate defense mechanisms. Thus understanding the shrimp defense system will contribute in developing new vaccines against WSSV and other shrimp pathogens. Hence, the intention of this review is to discuss on the generalised innate immune system of shrimp together with evolution of specific immunity also known as "specific immune priming" of invertebrates, development of recombinant baculovirus vaccination for shrimp and finally future research perspectives.

2. The immune system of invertebrates

The innate immunity of invertebrates in response to pathogen invasion is comprised of both cellular and humoral immune responses. The innate immunity of shrimp is activated upon recognition of pathogen associated molecular patterns (PAMPs) by germline-encoded pattern recognition receptors (PRRs). This recognition step directly or indirectly triggers various defense mechanisms in shrimp in a complicated manner to eliminate the pathogen (Söderhäll, 1999; Sritunyalucksana and Söderhäll, 2000). The cellular immune responses include phagocytosis, nodule formation, encapsulation and apoptosis, whereas humoral immune responses contain prophenoloxidase cascade, clotting cascade, antimicrobial peptides (AMPs), lectins, Dscam, Toll and IMD pathways.

3. Cellular immune responses

Cellular immune responses in invertebrates are carried out by haemocytes, which are present in hemolymph, the open circulatory system of shrimp. Three main types of hemocytes can be identified in most decapod crustacean, namely hyaline cells, semigranular cells and granular cells. Each cell participates in various cellular events such as phagocytosis, apoptosis, encapsulation and nodule formation, wound repairing and clotting. Besides its participation in cellular responses, hemocytes supplies different antimicrobial peptides, lectins, proteinase inhibitors and opsonins such as the cell adhesion protein peroxinectin (Cerenius et al., 2008).

3.1. Phagocytosis

Phagocytosis is a main cellular defense mechanism in invertebrates carried out by hyaline cells. It is involved in the internalization of foreign materials such as bacteria, protozoans, fungi and viruses. The phagocytic activity of penaied shrimp has been demonstrated by the use of bacteria (*Vibrio parahemolyticus* and *Vibrio vulnificus*) and surface microbial antigens (β-1,3 glucan, Peptidoglycans (PGN), Lipopolysaccharides (LPS) and Zymosan), as both increase the phagocytic capacity of hemocytes to destroy pathogens (Itami et al., 1998; Campa-Cordova et al., 2002). From the evidence of Nyholm et al. (2009), it was observed that the interaction between microorganisms and hemocytes of invertebrates can be highly specific and is important for the establishment and maintenance of symbioses. The molecules involved in the phagocytosis have been identified as Rab gene and Ran protein. Rab gene identified from *Penaeus japonicus is* called *Pj*Rab, which exhibited high homology with Rab6 of other species. The silencing of *Pj*Rab by RNA interference (RNAi) increased the WSSV copies, indicating that *Pj*Rab might be an intracellular virus recognition protein employed by a host to