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Maternal immune transfer in mollusc

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ABSTRACT

Maternal immunity refers to the immunity transferred from mother to offspring via egg, playing an important role in protecting the offspring at early life stages and contributing a trans-generational effect on offspring's phenotype. Because fertilization is external in most of the molluscs, oocytes and early embryos are directly exposed to pathogens in the seawater, and thus maternal immunity could provide a better protection before full maturation of their immunological systems. Several innate immune factors including pattern recognition receptors (PRRs) like lectins, and immune effectors like lysozyme, lipopolysaccharide binding protein/bacterial permeability-increasing proteins (LBP/BPI) and antioxidant enzymes have been identified as maternally derived immune factors in mollusc eggs. Among these immune factors, some maternally derived lectins and antibacterial factors have been proved to endue mollusc eggs with effective defense ability against pathogen infection, while the roles of other factors still remain untested. The physiological condition of mollusc broodstock has a profound effect on their offspring fitness. Many other factors such as nutrients, pathogens, environment conditions and pollutants could exert considerable influence on the maternal transfer of immunity. The parent molluscs which have encountered an immune stimulation endow their offspring with a trans-generational immune capability to protect them against infections effectively. The knowledge on maternal transfer of immunity and the trans-generational immune effect could provide us with an ideal management strategy of mollusc broodstock to improve the immunity of offspring and to establish a disease-resistant family for a long-term improvement of cultured stocks.

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1. Introduction

With the long time of evolution, animals have evolved different costly defense strategies which aim to reduce the infection by pathogens and improve their survival rate for further generation (Garnier et al., 2012; Sheldon and Verhulst, 1996). Like other invertebrates, mollusc exclusively relies on a sophisticated innate immune system to defense against the invading pathogens. Traditionally, the immune system in invertebrate is always considered to lack classical specific immunity that acquired from the clonal expansion of leucocytes (Rowley and Powell, 2007; Sadd et al., 2005). Recently, increasing evidences have revealed the existence of specific or "primed" immunity in invertebrates (Cong et al., 2008; Little et al., 2003; Rodrigues et al., 2010; Sadd and Schmid-Hempel, 2007; Yue et al., 2013b), and maternal transfer of immunity is one of the highlighted instances to favor the presence of specific immunity in invertebrate.

Maternal transfer of immunity is defined as the immunity transferred via eggs from mother to offspring which plays a crucial role in protecting the vulnerable offspring at early stages of life (Chucri et al., 2010; Shlichta and Smilanich, 2012; Swain and Nayak, 2009). The transmission of maternal immunity was initially found in mammals and birds about 100 years ago (Ehrlich, 1892), and now it has been well described in vertebrates (Malek et al., 1998; Poorten and Kuhn, 2009). In invertebrates, the transmission of maternal immunity has been reported in some species, such as insects (Moreau et al., 2012; Sadd et al., 2005; Zanchi et al., 2012), crustaceans (Huang and Song, 1999; Little et al., 2003) and molluscs (Yue et al., 2013b). Distinguished from the specific transfer of immunoglobulin in vertebrates, innate immune factors are the main molecules transferred from mother to offspring in invertebrates. Surprisingly, maternal immune experience has positive impact on the transfer of these immune factors endowing the enhancement of offspring immunity or disease resistance, and this phenomenon is termed as trans-generational immune priming (TGIP) (Sadd et al., 2005; Zanchi et al., 2012). Although the specific mechanisms underlying TGIP are not well described, it has been considered as a beneficial survival strategy of invertebrates and aroused great interest of many immunologists and ecologists.

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Fertilization and development is external in most of the molluscs, so the embryo is exposed to the environment that containing numerous potential pathogens. Therefore, the immunity vertically transferred from mother which has been verified the existence in molluscs (Yue et al., 2013b) is the foremost protective barrier for the eggs and embryos against the pathogen infection before the formation of their own immune system.

In the past decade, the economical and phylogenic importance of mollusc has promoted more investigations on the immune defense mechanism against diseases of developing embryos or larvae (Wang et al., 2012). Despite the accumulation of such information in recent years, it is still limited and preliminary for the understanding of maternal derived immunity. The present review attempts to summarize the current achievements accomplished in the maternal immunity of mollusc, mainly focusing on the transfer of maternally derived immune factors and its role in embryo and larval developmental stages as well as factors affecting the maternal transfer of immunity.

2. Transfer of maternally derived immune factors

The eggs and sperms of most molluscs, especially bivalves are broadcast spawners, are released into water for fertilization. And embryonic transcription in molluscs only starts at the compacted morula stage, the proteins and transcripts that exist in the eggs or early embryos should be maternal origin (Herpin et al., 2002; Tirapé et al., 2007). Previous studies on several molluscs have revealed that mollusc eggs possess remarkable antibacterial and lysozyme activities as well as agglutination against pathogens (Fiolka and Witkowski, 2004; Kamiya et al., 1986; Yue et al., 2013b). Recently, with the wide application of high throughput proteomic techniques, many maternally derived immune factors have been identified in mollusc eggs or embryos (Table 1).

2.1. Lectins

Lectin is a family of carbohydrate-binding proteins that play significantly diverse roles in nonself-recognition and clearance of invaders in invertebrates as PRRs (Arason, 1996). Based on their structures and functions, lectins are broadly classified as C-, P-, I-, R-, L-type lectins, galectin and calnexin and so on (Kim et al., 2009). In mollusc species, several lectins, especially the C-type lectins, have been well documented (Song et al., 2010) and they are found to mediate various innate immune responses such as pathogen recognition (Janeway Jr. and Medzhitov, 2002), agglutination (Song et al., 2011), opsonization (Yang et al., 2011) and phagocytosis (Canesi et al., 2002).

The maternal transfer of lectins from mother to offspring has been reported in some molluscan species. *Helix pomatia* agglutinin (HPA) is an N-acetylgalactosamine (GalNAc) binding lectin which exists in roman snail eggs as a constituent of perivitelline fluid to protect them from bacteria invasion (Sanchez et al., 2006). Several other lectins such as C-type lectin, D-galactose binding lectin, anti-B-like agglutinin and scalarin have been identified in the egg or egg mass fluid of different molluscs like snail *Biomphalaria glabrata*, *Pomacea scalaris* and *Pila ovata* and sea hare *Aplysia kurodai* (Hathaway et al., 2010; Ituarte et al., 2012; Kawsar et al., 2009; Uhlenbruck et al., 1973). In oyster *Crassostrea gigas*, galectin was also detected in the oocyte and 2–4 cell embryos (Tirapé et al., 2007).

2.2. Lysozymes

Lysozyme is an ancient and ubiquitous enzyme existing in diverse organisms, which catalyzes the hydrolysis of β-1, 4-glycosidic linkage between N-acetylmuramic acid and N-acetylglucosamine of peptidoglycan and causes bacterial cell lysis. So far, three distinct types of lysozyme (i-type, g-type and c-type lysozyme) have been identified and characterized in molluscs (Ding et al., 2011; Xue et al., 2004; Zhao et al., 2010, 2007). All these lysozymes were verified to exhibit remarkable antimicrobial activity against either Gram-positive or Gram-negative bacteria, indicating their involvement in the immune response of molluscs against pathogens.

Primarily maternally derived lysozyme was found in snail eggs *Helix aspersa* maxima and *Achatina achatina* (Fiolka and Witkowski, 2004). Recently, the existence of maternally transferred lysozyme was also found abundantly in the eggs and 4-cell embryos of scallop *Chlamys farreri* (Yue et al., 2013b). With the development of embryo, the protein level of maternal lysozyme decreased gradually to the undetected level at blastula stage and then increased dramatically at trochophore stage, suggesting the coordinated relationship between the maternal investment and offspring's own synthesis of immune factors (Yue et al., 2013b).

2.3. LBP/BPI

LBP/BPI is a number of acute phase plasma proteins playing crucial roles in the innate immune response to Gram-negative bacteria (Elsbach and Weiss, 1998). It recognizes and binds LPS directly,

Table 1
The main maternally derived immune factors in molluscs.

Type	Gene name	Role	Source
Pattern recognition receptors (PRRs)	Lectins (agglutinin, C-type lectin, D-galactose binding lectin, anti-B-like agglutinin and scalarin)	Agglutinating activity	Hathaway et al. (2010) and Kawar et al. (2010)
Immune effectors	Lysozyme	Antimicrobial activity	Diz et al. (2013), Hathaway et al. (2010), Sun et al. (2012) and Yue et al. (2013b)
	LBP/BPI	---	
	Antioxidant enzymes	---	
	Vitellogenin	---	Corporeau et al. (2012) and Hathaway et al. (2010)
	Aplysianin A and E	Antimicrobial activity	Jimbo et al. (2003), Kamiya et al. (1986), Kisugi et al. (1987), Kisugi et al. (1989) and Lijima et al. (1995)
	LPS/β-1,3-glucan binding protein (LGBP)	---	Yue et al. (2013b)
	Gram-negative bacteria-binding protein	---	Hathaway et al. (2010)
	Aplysianin/achacin-like protein	---	Kisugi et al. (1989)
	Scavenger receptor cysteine-rich protein	---	Sun et al. (2012)
	C1q domain containing protein	---	Sun et al. (2012)
	Protease inhibitors	---	Sun et al., 2012
	Phenoloxidase	---	Bai et al. (1997) and Thomas-Guyon et al. (2009)
	Heat shock protein 70 (HSP70) and so on	---	Corporeau et al. (2012)

"---" The immune functions are remaining untested.

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