Fish & Shellfish Immunology xxx (2015) 1–14

Contents lists available at ScienceDirect

Fish & Shellfish Immunology

journal homepage: www.elsevier.com/locate/fsi

The immune system and its modulation mechanism in scallop

Linsheng Song [a, *], Lingling Wang [b], Huan Zhang [b], Mengqiang Wang [b]

[a] Dalian Ocean University, Dalian 116023, China
[b] Key Laboratory of Experimental Marine Biology, Institute of Oceanology, Chinese Academy of Sciences, Qingdao 266071, China

ARTICLE INFO

Article history:
Received 24 January 2015
Accepted 7 March 2015
Available online xxx

Keywords:
Scallop
Immune recognition
Signal transduction
Effector synthesis
Immune response
Cellular immunity
Neuroendocrine regulation

ABSTRACT

Scallops are a cosmopolitan family of bivalves, and some of them are highly prized as dominant aquaculture species. In the past decades, there have been increasing studies on the basic biology and immunology of scallops, and this review summarizes the research progresses of immune system and its modulation mechanism in scallop. As invertebrate, scallops lack adaptive immunity and they have evolved an array of sophisticated strategies to recognize and eliminate various invaders by employing a set of molecules and cells. It is evident that basic immune reactions such as immune recognition, signal transduction, and effector synthesis involved in immune response are accomplished in a variety of ways. They rely upon an extensive repertoire of phagocytosis, apoptosis and encapsulation of the circulating hemocytes for eliminating invasive pathogens, as well as the production of immune effectors that are active against a large range of pathogens or sensitive for the environmental stress. Furthermore, the molecular constitutions, metabolic pathways and immunomodulation mechanisms of the primitive catecholaminergic, cholinergic, enkephalinergic system and NO system in scallop are also discussed, which can be taken as an entrance to better understand the origin and evolution of the neuroendocrine-immune regulatory network in lower invertebrates.

1. Introduction

Scallops are a cosmopolitan family of bivalves (Mollusca: Bivalvia: Pectinidae), widely distributed from the intertidal area to the depth of ~7000 m. They can attain sizes over 24 cm, and occupy cold water areas with reduced salinity near the seaward end of glaciers, sub-tropical and temperate estuarine bays, and tropical shallow seas [1]. Many scallop species are highly prized as a food source, and some of them are farmed in the industry of aquaculture. Over the last few years, there have been large increasing studies about the biology and pathology of scallops, predominantly in addressing the molecular constitutions and responses of their immune systems.

Molluscs are characterized by a coelomatic cavity, which makes it possible to distinguish a well-defined cellular and humoral component in the immune system. In the majority of molluscs, there are two circulating immunocytes, amoeboid blood cells that are large and highly phagocytic and granular cells of various sizes, which control the main immune responses, i.e. phagocytosis, cell shape changes (cell motility), chemotaxis (cell migration), and cytotoxicity [2]. In recent years, interest in scallop immunity has been increasing continuously due to their economic importance of aquaculture and key position in animal phylogeny and evolution. It is generally assumed that scallop, as invertebrate, lacks the complexity of adaptive immune system, and relies solely on innate immunity mediated by both cellular and humoral components [3]. The former includes phagocytosis and encapsulation, while the latter involves recognition to microbes, signal transduction and the production of various effectors, such as antimicrobial peptides (AMPs), lysozymes, antioxidant enzymes, cytokines and heat shock proteins [4]. Recently, the fundamental elements of neuroendocrine system have been identified in mollusk, suggesting that a primordial 'neuroendocrine system' is also present in mollusc, which would help to further investigate the evolution of neuroendocrine-immune regulatory network in invertebrates [5,6]. Here we summarize the research progress of scallop immunity, focusing on the molecular constitutions of innate immune system, the mechanism of immune response and the immunomodulation of neuroendocrine system.

2. The molecular constitution of scallop immune system

As invertebrates, scallops rely exclusively on an innate, non-lymphoid immune system to execute cellular and humoral

* Corresponding author.
E-mail address: lshsong@dlou.edu.cn (L. Song).

http://dx.doi.org/10.1016/j.fsi.2015.03.013
1050-4648/

immune reactions [3]. The cellular immune reactions including encapsulation and phagocytosis are performed by different hemocytes, and the humoral immune responses are consisted of the reaction cascades of recognition to microbes, signal transduction and production of immune effectors. Recently, a high content and variety of immune related gene homologs have been characterized in scallops [7,8]. The following text details our current knowledge on the molecular constitution of immune recognition, signal transduction and effector synthesis involved in cellular and humoral immunity.

2.1. Immune recognition

As the first step in activating immune response, immune recognition discriminates non-self from self-substances and plays an important role in initiating the immune response. Immune responses begin when the specialized, soluble or cell-bound pattern recognition receptors (PRRs) recognize the major targets, called pathogen-associated molecular patterns (PAMPs) [9,10]. So far, seven groups of distinct PRRs have been identified in scallops, including peptidoglycan recognition proteins (PGRPs) [11–13], Gram-negative binding proteins (GNBPs), C-type lectins (CTLs) [14], galectins [15,16], thioester-containing proteins (TEPs) [17], scavenger receptors (SRs) [18] and Toll-like receptors (TLRs) [19] (Table 1). Some other protein families, such as fibrinogen-related proteins (FREPs) [20,21] and C1q domain-containing (C1qDC) proteins [22–25], were also found to act as PRRs in scallop immune system. Scallops have developed a sophisticated repertoire of PRRs, and most of them serve as multi-functional proteins, not only in the immune recognition against various microbes, but also in the elimination of invading microbes. The structural characteristics and recognition patterns of some scallop PRRs including lectins, PGRPs, LGBPs and C1qDC proteins are briefly introduced in this review.

2.1.1. Lectins

CTLs are a superfamily of diverse proteins with one or more carbohydrate-recognition domains (CRDs) of approximately 130 amino acid residues [26]. They are most abundant PRRs in scallops and serve important roles in innate immunity. More than fifteen CTLs have been so far identified in scallops, mainly in zhikong scallop *Chlamys farreri* and bay scallop *Argopecten irradians* [14]. Most scallop CTLs contain single CRD, while there are three or four CRDs in CfLec-3 and CfLec-4 from *C. farreri* and AiCTL-9 from *A. irradians* [27–29] (Fig. 1), respectively. The architecture and phylogenic analysis revealed that multi-domain CTLs in different lineages did not arise from a common multi-domain progenitor, and these proteins served distinct functions in different animal lineages [27].

The scallop CTLs possess multifunction and play vital roles in host immune defense against invading pathogens. They could

Table 1
The pattern recognition receptors reported in scallops.

Gene name	Accession no.	Species	Domain	Reference
C-type Lectins				
Cflec-1	DQ209290	*C. farreri*	CRD	[66] [31]
Cflec-2	DQ209289	*C. farreri*	CRD	[67] [32]
Cflec-3	DQ209291	*C. farreri*	3 CRDs	[28]
Cflec-4	DQ209292	*C. farreri*	4 CRDs	[27] [33]
Cflec-4b	DQ209293	*C. farreri*	4 CRDs	–
Cflec-5	GU002543	*C. farreri*	CRD	[160]
AiCTL1	EU277646	*A. irradians*	CRD	[68]
AiCTL2	FJ469995	*A. irradians*	CRD	–
AiCTL-3	FJ469996	*A. irradians*	CRD	[30]
AiCTL-4	FJ469997	*A. irradians*	CRD	–
AiCTL-5	HM113531	*A. irradians*	CRD	[72]
AiCTL-6	GQ202279	*A. irradians*	CRD	[71]
AiCTL-7	HM149769	*A. irradians*	CRD	[70]
AiCTL-9	JN166712	*A. irradians*	4 CRDs	[29]
Ailec	EU590646	*A. irradians*	CRD	[69]
Galectins				
AiGal-1	FJ469998	*A. irradians*	4 CRDs	[15]
AiGal-2	FJ469999	*A. irradians*	4 CRDs	[16]
PGRP				
CfPGRP	AY987008	*C. farreri*	PGRP + Ami_2	[12]
AiPGRP	AY437875	*A. irradians*	PGRP + Ami_2	[11]
LGBP				
CfLGBP	AY259542	*C. farreri*	Glyco_hydro_16	[42]
Toll-like receptor				
CfToll-1	DQ350772	*C. farreri*	LRR_5 + LRR + LRR_TYP+10LRR + LRRCT + LRRNT + 2LRR + LRR_TYP + LRR + LTTCT + transmemebrane region + TIR	[19]
C1q domain containing proteins				
CfC1qDC	EF536358	*C. farreri*	C1q	[25]
AiC1qDC-1	GU475113	*A. irradians*	C1q	[22]
AiC1qDC-2	GU475114	*A. irradians*	C1q	[23]
Scavenger receptors-like				
CfSR	GQ260639	*C. farreri*	6 SRCR + UPAR-like + ShK toxin-like	[18]
CfLRP	–	*C. farreri*	5 LY + SRCR+5LY	[170]
Thioester-containing proteins				
CfTEP	EF210036	*C. farreri*	A2M_N + A2M_N2+A2M + Thiolester_cl + A2M_comp + A2M_recep	[17]
Fibrinogen-related proteins				
AiFREP	EU399719	*A. irradians*	FBG	[21]
AiFREP-2	KJ101557	*A. irradians*	FBG	[20]

Please cite this article in press as: L. Song, et al., The immune system and its modulation mechanism in scallop, Fish & Shellfish Immunology (2015), http://dx.doi.org/10.1016/j.fsi.2015.03.013