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Review

Mucosal immunoglobulins and B cells of teleost fish

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ABSTRACT

As physical barriers that separate teleost fish from the external environment, mucosae are also active immunological sites that protect them against exposure to microbes and stressors. In mammals, the sites where antigens are sampled from mucosal surfaces and where stimulation of naïve T and B lymphocytes occurs are known as inductive sites and are constituted by mucosa-associated lymphoid tissue (MALT). According to anatomical location, the MALT in teleost fish is subdivided into gut-associated lymphoid tissue (GALT), skin-associated lymphoid tissue (SALT), and gill-associated lymphoid tissue (GIALT). All MALT contain a variety of leukocytes, including, but not limited to, T cells, B cells, plasma cells, macrophages and granulocytes. Secretory immunoglobulins are produced mainly by plasmablasts and plasma cells, and play key roles in the maintenance of mucosal homeostasis. Until recently, teleost fish B cells were thought to express only two classes of immunoglobulins, IgM and IgD, in which IgM was thought to be the only one responding to pathogens both in systemic and mucosal compartments. However, a third teleost immunoglobulin class, IgT/IgZ, was discovered in 2005, and it has recently been shown to behave as the prevalent immunoglobulin in gut mucosal immune responses. The purpose of this review is to summarise the current knowledge of mucosal immunoglobulins and B cells of fish MALT. Moreover, we attempt to integrate the existing knowledge on both basic and applied research findings on fish mucosal immune responses, with the goal to provide new directions that may facilitate the development of novel vaccination strategies that stimulate not only systemic, but also mucosal immunity.

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1. Introduction

Higher metazoans have different barriers that separate themselves from the surrounding environment. Whereas some animal species evolved non-mucosal barriers (i.e. the cuticle of arthropods), others, such as teleost fish, developed mucosal surfaces as their strategy to protect themselves from the aggressions of the environment. In addition to being physical barriers, mucosal surfaces are also active immunological sites armed with cellular and humoral defences. Since these surfaces represent the interface between each animal and the external environment, they are exposed more than any other site, to a continuous bombardment of microbes and stressors. The mucosa-associated lymphoid tissue (MALT) contains B cells and immunoglobulins, which play a pivotal role in the maintenance of mucosal homeostasis (reviewed by Brandtzaeg, 2009). In higher vertebrates, secretory immunoglobulins (sIg) as well as their importance in innate and adaptive immunity, are fairly well characterized. Despite the fact that sIg in mammals has been classically associated with IgA and to a lesser degree with IgM, there is a growing appreciation that all immunoglobulin classes are in fact relevant at mucosal sites (Baker et al., 2010).

In lower vertebrates, and in particular teleost fish, the presence of immunoglobulins in mucosal secretions was first reported in plaice (*Pleuronectes platessa*) in the late 1960s (Fletcher and Grant, 1969). Until recently, there has been a general belief that IgM was the only functional immunoglobulin in teleosts, both in systemic and mucosal compartments. Recent breakthroughs in the field of fish immunoglobulins have added two new players to the scene, IgD (Edholm et al., 2010a) and IgT/IgZ (Danilova et al., 2005; Hansen et al., 2005). Significantly, IgT has been reported to be an immunoglobulin specialized in gut mucosal immunity (Zhang et al., 2010), a novel finding that makes the field of mucosal immunoglobulins and mucosal B cells in fish even more appealing. As commented by Flajnik (2010) in reference to recent findings on IgT, all GOD's (generation of diversity) creatures, even fish!, appear to have dedicated mucosal immunoglobulins. To our delight, there is still much to discover about these immunoglobulins and their immune functions. The present review summarises our current knowledge on teleost B cells and immunoglobulins found in mucosal surfaces. It also examines, with an evolutionary and comparative eye, the parallelisms and dissimilarities of sIg in bony fish versus higher vertebrates. Moreover, this review attempts to integrate past and current basic and applied research findings of fish mucosal immune responses as a platform to provide new directions that facilitate the future development of novel vaccination strategies. These strategies should target stimulation not only of systemic, but also of mucosal immunity.

2. Gross anatomy of MALT

Obvious physiological, anatomical and histological differences exist between terrestrial and aquatic vertebrates, which clearly translate into the presence of distinct MALT in fish and mammals. It is accepted that the mucosal immune system is more complex than its systemic counterpart both in terms of effectors and anatomy (Brandtzaeg, 2009; Cerutti and Rescigno, 2008; Fagarasan, 2008; Macpherson et al., 2008) and, as a consequence, its nomenclature also becomes more intricate. The Nomenclature Committee of the Society of Mucosal Immunology proposed a standard nomenclature for both secretory immune-function molecules and mucosa-associated immune-cell compartments. Table 1 includes the nomenclature for mucosa-associated immune-cell compartments accepted in mammals (summarised in Brandtzaeg et al., 2008) as well as those thus far used in fish. It is important to note that no standard nomenclature has yet been proposed for fish MALTs and therefore, we recommend adopting the mammalian one in those cases where it is applicable. MALT uniquely present in teleosts has its own terminology but unfortunately there has not been a general agreement on it by the scientific community. The three main mucosal immune compartments found in bony fish are: (1) the gut-associated lymphoid tissue (GALT) with the lamina propria (LP) and intraepithelial (IEL) compartments; (2) the skin-associated lymphoid tissue (SALT); (3) the gill-associated lymphoid tissue (we propose to abbreviate it as GIALT) which includes the gills and the interbranchial immune tissue (ILT).

2.1. The gut-associated lymphoid tissue (GALT)

Herbivorous, detritivorous, omnivorous and carnivorous fish species differ from each other in terms of the presence or absence of a stomach, the length of the intestine (from 1 to more than 20 times the body length), and the presence and number of pyloric caeca, intestinal loops and valves (Evans, 1998). The GALT is strikingly diverse across vertebrate groups. For instance, chickens have caecal tonsils not present in mammals, and even within mammals, their GALT exhibit a significant structural diversity (Fagarasan, 2008; Finke and Meier, 2006). Generally speaking, the GALT of higher vertebrates consists of both scattered and organised lymphoid tissue. Fish, however, lack an organised GALT, and thus, have no peyer's patches (PP) or mesenteric lymph nodes (MLNs) (Rombout et al., 2010), whereas the presence of PP or MLN in amphibians remains to

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