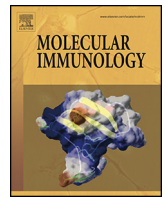




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Review

The mast cell plays a central role in the immune system of teleost fish[☆]

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ABSTRACT

The growing interest in fish models could raise an opportunity to better understand mast cell functions. The piscine mast cell, also known as eosinophilic granular cell, originates from haematopoietic organs, migrates to sites of maturation, and increases in injured tissues. Although there has been confusion arising from the different distribution in fish species and morphological and staining properties, there is a general agreement that the main functional roles, as those exploited in immunity, are quite similar. The aim of this review is to mainly focus on the roles of mast cells in teleost fish disease and in fish models of human diseases, with the attempt to give a comprehensive picture of their role in piscine immune function and their relationship to other immune system cells.

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1. Introduction

Stimulated by the growing business of aquaculture and the consequent interest in fish diseases, as well as the advent of the zebrafish as a tool and model to understand human diseases, the study of the teleost immune system has moved toward center stage. Current understanding shows that the mast cell (MC), a well-known effector of mammalian allergic disorders, is a critical component of the piscine immune response. However, recent study has also shown that the MC performs additional roles in fish that are not directly linked with the immunological functions, for example in oncology and tissue repair. Currently, major aspects about the nature of the MC and its role in fish disease remain unclear. Further, an increased knowledge of the biology and embryonic origin of mast cells may contribute to a greater understanding of human allergy, asthma and other mast cell-related diseases (Guiraldelli et al., 2013).

Fish are a heterogeneous group of vertebrates where the innate immune response is preferentially activated compared to the adaptive one, even though they possess all the components of the adaptive immune response. Immune organs in fish share homology with those of the mammalian immune system, with the exception

that fish lack bone marrow and lymph nodes. Moreover, it must be kept in mind that the immune system of fish is conditioned by the poikilothermic aquatic environment (Rauta et al., 2012). In view of earlier publications that have adequately reviewed the ontology, morphology, distribution, and functions of piscine MCs, this review will mainly focus on the roles of mast cells in teleost fish disease and in fish models of human diseases, with the attempt to give a comprehensive picture of their role in piscine immunity and their relationship to other immune system cells. The growing interest in fish models could raise an opportunity to better understand MC functions. With regard to the use of fish as a research model instead of mammals, zebrafish (*Danio rerio*) (Hamilton, 1822) has become a common research model in genetic, developmental, pharmacological and toxicological studies (Tavares and Santos Lopes, 2013). The zebrafish, at first viewed as a robust model for studying vertebrate hematopoiesis, has recently been exploited as a versatile organism for better understanding the complexity of both innate and adaptive immune responses (Rauta et al., 2012; Xu et al., 2012; Ellett and Lieschke, 2010; Meeker and Trede, 2008).

2. Ontogenesis and distribution

Several reviews have described ontogenesis, chemical features, and functions of mast cells in higher and lower vertebrates (Crivellato and Ribatti, 2010; Baccari et al., 2011), as well as fish alone (Reite and Evensen, 2006). Even though it is far from the aim of this review, a brief overview of mast cell biology in fish will be helpful. Prior comprehensive and detailed reviews reveal

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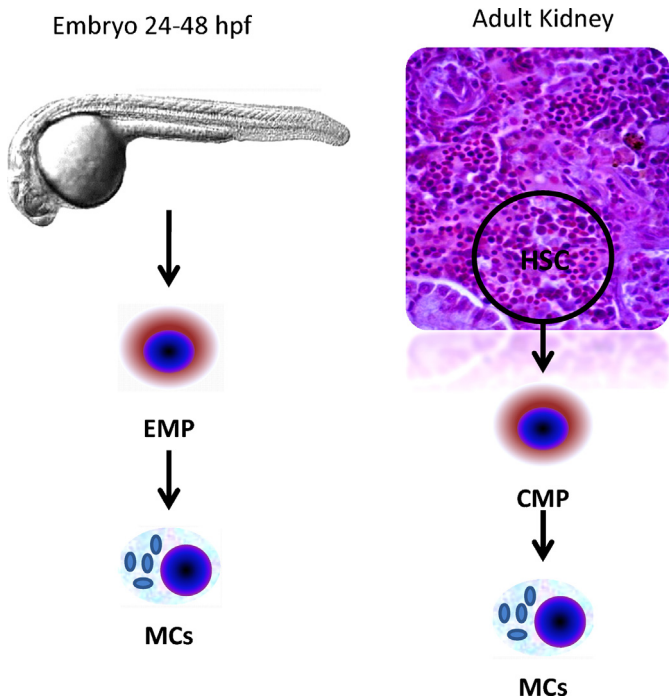


Fig. 1. MC ontogenesis in zebrafish. In embryos at 28–48 h post fertilization (hpf) mast cells originate from erythromyeloid progenitor cells (EMPs). In adult fish the kidney stroma is the main hematopoietic organ, where MC originate from a common myeloid progenitor (CMP) derived from hematopoietic stem cells (HSCs). Periodic acid-Schiff (PAS) stain, 20 \times .

that a debate has raged whether the mast cell of teleost fish is homologous to the mammalian counterpart, since it greatly differs in histochemical staining as well as distribution among different tissues and between fish species. For example in some species MCs are metachromatic only when fixed in alcoholic fixatives and stained with alcoholic thionin, toluidine blue at low pH or Alcian blue; in other species after fixation with water-based fixatives they appear eosinophilic after hematoxylin and eosin staining (Reite and Evensen, 2006). More recently published works on zebrafish, by the mean of immunochemistry, have helped in a better identification of mast cell (Dobson et al., 2008). In 1971, Roberts et al. introduced the term “eosinophilic granule cells” (EGC) to indicate some epidermal cells resembling mast cells morphologically, but with red granules upon staining with hematoxylin and eosin (Baccari et al., 2011). Following several histochemical studies focused on *Esox lucius*, a species belonging to Salmoniformes, Reite (1996) stated that EGC are homologous of mast cells. Subsequently, piscine mast cells are also named EGC/MCs. Although there has been confusion arising from the different distribution in fish species and morphological and staining properties, there is a general agreement that the main functional roles, as exploited in immunity, are quite similar (Reite and Evensen, 2006; Vallejo and Ellis, 1989). In mammals, MC progenitors originate from the bone marrow and mature in peripheral tissues where they acquire different characteristics (Gurish and Austen, 2012). Fish, even if lacking a bone marrow and lymph nodes, have a lymphatic system that is mainly composed by the head kidney followed by spleen, thymus and mucosa-associated lymphoid tissue (Press and Evensen, 1999). In teleosts, it seems likely that MCs originate in the haematopoietic organs and reach target tissue where they mature and acquire different functions. More recently, at least in zebrafish, this enigma has been resolved (Da’as et al., 2012) (Fig. 1). MCs are normally found around vessels and nerves in the connective tissues of the tegumentary, urinary, gastrointestinal, respiratory and reproductive systems of some

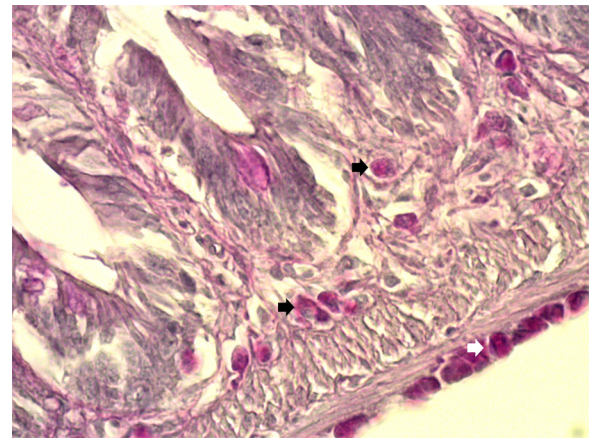


Fig. 2. MC localization in the digestive tract. MCs (black arrow) in the submucosa and eosinophils (white arrow) in the serosal layer of the digestive tract of parasitized zebrafish. Periodic acid-Schiff (PAS) stain, 40 \times .

fish species, as well as in all vertebrate groups (Mulero et al., 2007). Reports exist about their presence even in eye (McMenamin and Polla, 2013), hypothalamus (Weiss, 1979), pancreas (Dezfuli et al., 2009), and corpuscles of Stannius (Ahmad et al., 2001). Further, it appears that the digestive tract of many fish species is the richest source of MCs (Fig. 2). In salmonids, it is possible to detect the so called “stratum granulosum” consisting of one or a few rows of granule cells with the staining properties of MCs (Reite, 1997). Given the cytochemical features and location of MCs in fish host tissues, it has been suggested that they are analogous, both in the structural and functional properties, to mammalian mucosal MCs (Reite, 1996). It is widely accepted that MCs have a role in the immune response of fish and that the different environments within which the huge number of teleost species live, could explain the MC/EGC distribution pattern and function.

MCs are motile (Reite and Evensen, 2006) and they migrate to the site of infection, especially during parasitosis (Dezfuli et al., 2013a). Reite (1998) suggested that in species subjected to a less intense pathogenic pressure it may have been energetically “economic” to keep few MCs/EGCs in the “standing force” and rely on an efficient “mobilization force”. There is evidence that in healthy subjects few mast cells are interspersed in connective tissues, often in close association or inside blood vessels, and that they increase around and within capillaries during parasite infections (Dezfuli et al., 2012a,b). Thus it is reasonable to consider the co-existence of a resident population and a circulating population that can reach the site of infection whenever needed (Dezfuli et al., 2012a,b). MCs are often in close association, and share several functions with other elements of the fish innate immune system such as eosinophils, neutrophils and rodlet cells in defense against pathogens (Fig. 3). Eosinophils are granulocytic leucocytes involved in the defense against parasites; in zebrafish they have been well differentiated from other granular cells, represents more than 50% of peritoneal leukocytes and share periodic acid-Schiff (PAS) positivity with MCs (Balla et al., 2010). Neutrophils are phagocytic cells that migrate to and accumulate in response to parasitic infection or injury (Henry et al., 2013; Matsuyama and Iida, 1999). Rodlet cells (RCs), are exclusively found in bony fish and are commonly located at epithelial, mesothelial and endothelial linings. There is evidence that they are endogenous cells (Laura et al., 2012) that increase in number as a response to a variety of stressors and tissue injuries caused by viruses, parasites, toxins, neoplasia. However, their function is still unclear (Manera and Dezfuli, 2004).

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