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Review

Transcriptomic responses in the fish intestine

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ABSTRACT

The intestine, being a multifunctional organ central to both nutrient uptake, pathogen recognition and regulating the intestinal microbiome, has been subjected to intense research. This review will focus on the recent studies carried out using high-throughput gene expression approaches, such as microarray and RNA sequencing (RNA-seq). These techniques have advanced greatly in recent years, mainly as a result of the massive changes in sequencing methodologies. At the time of writing, there is a transition between relatively well characterised microarray platforms and the developing RNA-seq, with the prediction that within a few years as costs decrease and computation power increase, RNA-seq related approaches will supersede the microarrays. Comparisons between the approaches are made and specific examples of how the techniques have been used to examine intestinal responses to pathogens, dietary manipulations and osmoregulatory challenges are given.

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1. Introduction

The gastrointestinal tract of vertebrates along with its single layer of epithelial cells constitutes the largest and most important barrier against the external environment (Groschwitz and Hogan, 2009). The intestinal epithelium acts as a selectively permeable barrier for dietary nutrients, electrolytes and water, while maintaining an effective defence against pathogens and tolerance toward dietary antigens (Peterson and Artis, 2014). The epithelial cells are also crucial mediators of mucosal innate and adaptive immunity, important for distinguishing pathogens from commensal microbiota that live in the gut (Kinnebrew and Pamer, 2012; Donaldson et al., 2016). Fish and their immune system has received considerable attention from comparative immunologists, in part because of the unique position of this group to provide key insights into the evolution of immune systems (Trede et al., 2004; Cooper and Herrin, 2010; van Niekerk et al., 2015). While the innate immune mechanisms can be found in nearly all forms of life, the origins of mammalian-like (recombination-activating gene (RAG)-dependent) adaptive immunity reach back approximately 450 million years, coinciding with the emergence of the first jawed vertebrates (reviewed in Flajnik and Kasahara, 2010). The presence of convergently evolved system that is RAG-independent has been recently discovered in jawless vertebrates such as hagfish and lamprey (Pancer et al., 2004).

Fish are also known for their substantially higher exposure to pathogens than non-aquatic vertebrates, with typically a million of bacteria and 10 million of viruses per millilitre of seawater (Fuhrman, 1999). The pathogen exposure in fish starts immediately after hatching from their protective chorions, providing an interesting contrast to mammals protected during early development by maternal immunity (Trede et al., 2004). The exposure to pathogens is further enhanced during the mouth and gut opening stages and at the onset of exogenous feeding (Castro et al., 2015). However, the early life exposure to pathogens does not necessarily equip fish with the 'knowledge' of the microorganisms they may encounter in later life. Indeed, many fish species are exposed to different and unfamiliar pathogens when they switch between fresh and salt water environments (Jeffries et al., 2014). Evidence is also growing that some fish, including non-migratory species, are being exposed to novel pathogens as a result of climate change, because warmer environments are associated with an increase in the diversity of diseases, increased population growth rates of most microorganisms and increased vulnerability of coldwater fish (Crozier and Hutchings, 2014).

The transport of nutrients, solutes and pathogens across the epithelial barrier is controlled by two main mechanisms, either through the cells (transcellular transport) or between the cells (paracellular transport) (reviewed in Sundh and Sundell, 2015). Transcellular transport requires either active or passive transporters, intracellular trafficking and then excretion of the substances at the basolateral membrane of the cell, with amino acids, fatty acids and carbohydrates (mainly sugars) as the key substances being transported. Paracellular transport is controlled by cellular contact and the tightness of the contacts. The integrity and control of the intestinal barrier is often attenuated by both nutritional and immunological challenges in the fish.

Our knowledge of the fish immune system is advancing rapidly, with many of the cell types, humoral factors and regulatory molecules now identified (Collet, 2014; Castro and Tafalla, 2015) (Fig. 1). Within the intestine, immune activity is controlled by the gut associated lymphoid tissue (GALT) containing numerous immune cell types that are involved in both innate and adaptive responses (reviewed in Salinas and Parra, 2015). Of central importance is antigen sampling across the epithelial barrier, likely to involve antigen-sampling cells equivalent to mammalian microfold (M) cells and dendritic cells (DCs) (Fuglem et al., 2010). Although a specific DC subset has not yet been fully identified in fish, the presence of dendritic-like cells has been suggested in intestinal epithelium (Fuglem et al., 2010) and peripheral blood (Haugland et al., 2012) of Atlantic salmon as well as various non-intestinal tissues of rainbow trout (Johansson et al., 2012; Granja et al., 2015) and zebrafish (Lugo-Villarino et al., 2010). The intestinal dendritic-like cells are hypothesised to present luminal antigens to T and B cells ensuring the maintenance of the gut microbiome and identification of pathogens. B cells secrete different Ig molecules (Parra et al., 2013; Salinas, 2015) and are produced at high levels in the intestinal mucus to bind luminal antigens. The combination of B

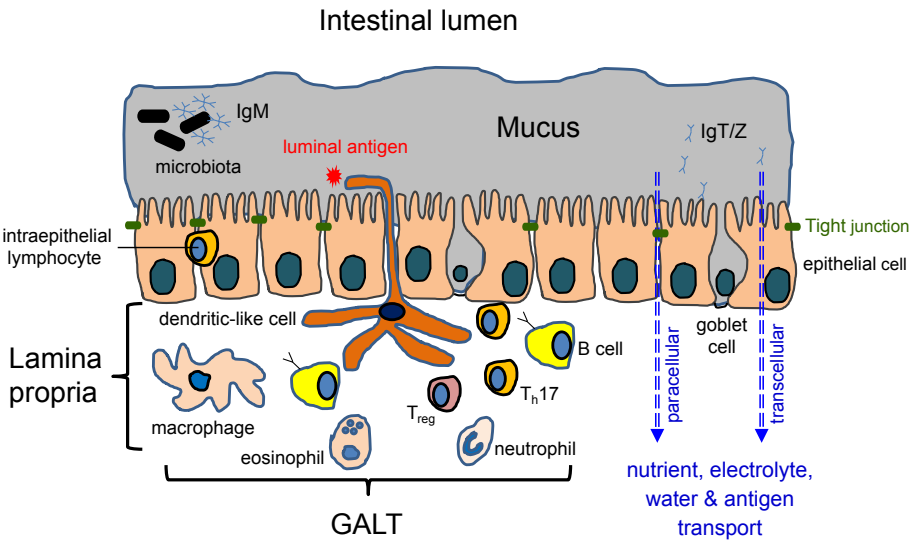

Fig. 1. Diagram of the intestinal mucosa in teleost fish. This complex tissue contains epithelial cells involved in the intestinal barrier function that control para- and transcellular transport, with associated genes regulating these processes. The gut-associated lymphoid tissue (GALT) is contained within the lamina propria and has a complex populations of immune cells. The presence of dendritic-like cells and T cell subtypes in fish has not yet been fully confirmed. Transcriptomics by its high-throughput nature, coupled with continually improving gene annotation, can reveal parallel changes in gut permeability and immune function.

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