Mucosal Health in Aquaculture

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Dedication

We dedicate this text to fish that have captivated us since youth.
Slimy and colorful. Resilient and enduring.
Fried, broiled, and blackened.

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Why mucosal health?

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Chapter Outline

1.1 Why mucosal health?

Aquaculture is the fastest growing sector of agriculture and is expected to maintain its rapid growth in coming decades in the face of rising world populations and declining wildcatch fisheries. Roughly half of all seafood for public consumption is now farmed. An ever-growing number of fish and shellfish species is either being grown commercially or being evaluated for aquaculture potential. The domestication of key species for aquaculture is still in its infancy, however, when compared with more established livestock industries such as poultry or cattle. Market demands for higher volumes of cultured product at lower prices have often come into conflict with the ability of near-wild species to cope with intensive aquaculture environments. Resulting disease outbreaks (whether virus, parasite, or bacteria) inflict significant economic, public perception, and marketing damage to the growing industry. Prioritizing the broad-based health of cultured species is critical in avoiding these boom/bust cycles and establishing the sustainable growth of the aquaculture industry worldwide.

Rather than recapitulating the more familiar textbook and cataloging fish pathogens and their treatments, here we choose to focus on the health and immunity of the cultured organism. *Ultimately, the goal of the aquaculture industry is to optimize environmental parameters, dietary regimens, and host genetics such that disease events are rare. These factors intersect in the mucosal surfaces of cultured aquatic organisms*. The mucosal surfaces (skin, gill, and intestine) constitute the first line of defense against pathogen invasion while simultaneously carrying out a diverse array of other critical physiological processes, including nutrient absorption, osmoregulation, and waste excretion. Aquaculture species depend more heavily on mucosal barriers than their terrestrial agricultural counterparts as they are continuously interacting with the aquatic microbiota. Unlike classical immune centers, such as the spleen and kidney, the accessibility of mucosal surfaces through immersion/dip treatments or dietary changes allows tailored chemical and nutritional strategies to maximize mucosal and, therefore, organismal health. Indeed, many areas of intense research in aquaculture over the last decade have hinged upon a better understanding of mucosal health. Nutritionists are hard at work studying the impacts of antinutritional factors in plant-based fish diets on gut mucosa and how to circumvent them. Feed companies are competing to produce superior immunostimulants, prebiotics, and probiotics that maximize mucosal health and decrease disease prevalence. Microbiologists and immunologists are studying mechanisms of pathogen adherence and entry through mucosal surfaces and designing attenuated mucosal vaccines to stimulate robust mucosal protection. This text cuts across all of these areas in order to capture and bring together our latest understandings of mucosal barriers in aquaculture species and their impacts on nutrition and immunity. Beginning with an in-depth overview of mucosal immunity in fish (Chapter 2, Castro and Tafalla), the book synthesizes our current understanding of the fish structure and function (Chapter 3, Peterson), fish skin (Chapter 4, Esteban and Cerezuela), gill (Chapter 5, Koppang, Kvellestad, and Fischer), and gut/intestinal (Chapter 6, Salinas and Parra) barriers, before looking at the impacts of the environment (Chapter 7, Sundh and Sundell), nutrition (Chapter 8, Trushenski), prebiotics and probiotics (Chapter 9, Caipang and Lazado), and the microbial community (Chapter 10, Merrifield and Rodiles) on these same surfaces. Chapter 11 (Soto, Griffin, and Tobar) considers the progress and potential of new vaccines seeking to protect aquacultured organisms at these barriers. Chapter 12 (Allam and Espinosa) provides a detailed investigation into mucosal health in shellfish.

Studies on immunity in aquacultured species, as a whole, have either been comparative in nature, seeking to catalog the presence or absence of components of immunity expected based on knowledge of mammalian immunology, or oriented around artificial disease challenges, with little or no examination of underlying mechanisms. However, an array of new cellular and molecular tools that has become available over the last several years is rapidly changing this. To close out the book, Chapter 13 (Beck and Peatman) focuses on new, promising approaches to understanding the mucosal interactome, a term used to describe the intricate co-regulation of host immunity, environmental signaling, pathogen dynamics, and the broader microbial community at mucosal surfaces.

The future looks bright for global aquaculture, with a growing middle class and an array of new, more sustainable production models and diets that promise to lower costs and reduce waste output. The key to continued success, however, rests in maintaining the health of cultured organisms season after season. Understanding how culture practices, system specifications, and nutrition can impact mucosal health and enhance or decrease disease prevalence puts control in the hands of producers and brings a needed predictability to a growing industry. It is our hope that this book serves as an important step in that direction.

Overview of fish immunity

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Chapter Outline

Mucosal Health in Aquaculture

2.1 Introduction

Fish are a wide and heterogeneous group of vertebrates that comprise about 40,000 species, divided into three classes: Agnatha (jawless fish represented by hagfish and lampreys), Chondrichthyes (cartilaginous fish comprising sharks, rays, and skates), and Osteichthyes (bony fish). Fish heterogeneity is based on many aspects of their biology and habitats. There are fish species adapted to the most diverse aquatic environments with significant differences in morphology, size, physiology, and behavior. These differences evolved in parallel with the fact that fish have undergone a second whole-genome duplication event (2R), following the ancient genome duplication that occurred in early vertebrates (1R), and a further duplication in the teleostean lineage (3R), all of these leading to the subsequent duplication or deletion of various genome parts (Figure 2.1) (Danzmann et al., 2008; Meyer and Van de Peer, 2005; Ravi and Venkatesh, 2008). One of the first consequences of these genomic rearrangements during the evolution of the fish families is that some immune molecular families have expanded tremendously in some fish species, providing important differences with mammals and opening an exciting field to understand the functional effects of this molecular diversification.

In vertebrates, immunity was classically divided into two components: the innate immune response and the adaptive or acquired immune response. Innate immunity is the first line of defense against infection and includes both physical barriers as well as humoral and cellular responses. The adaptive immune response also has humoral and cellular players and is characterized by a specific antigen recognition that drives a stronger and faster secondary pathogen-specific immune response. In light of the discoveries from the past 20 years, an inseparable interrelationship among innate and adaptive components of the immune response has proven more complicated than previously thought, and many of the cells/molecules assigned to either the innate or acquired systems have specific roles in both of them. This is why, in this chapter, we will not make this distinction, but describe each immune cell type or factor indicating their role in either innate or acquired responses.

In a general view, the encounter with a pathogenic organism via mucosal tissues, such as gills, skin, or gut, is primary blocked or limited by physical barriers such as the mucus, the scales, and the epithelium. The mucosal layer interferes with the pathogen not only by trapping it, but also through the action of a variety of antimicrobial factors present in the mucus like lectins, lysozymes, pentraxins, complement proteins, antibacterial peptides, and immunoglobulins, which are destined to directly eliminate the

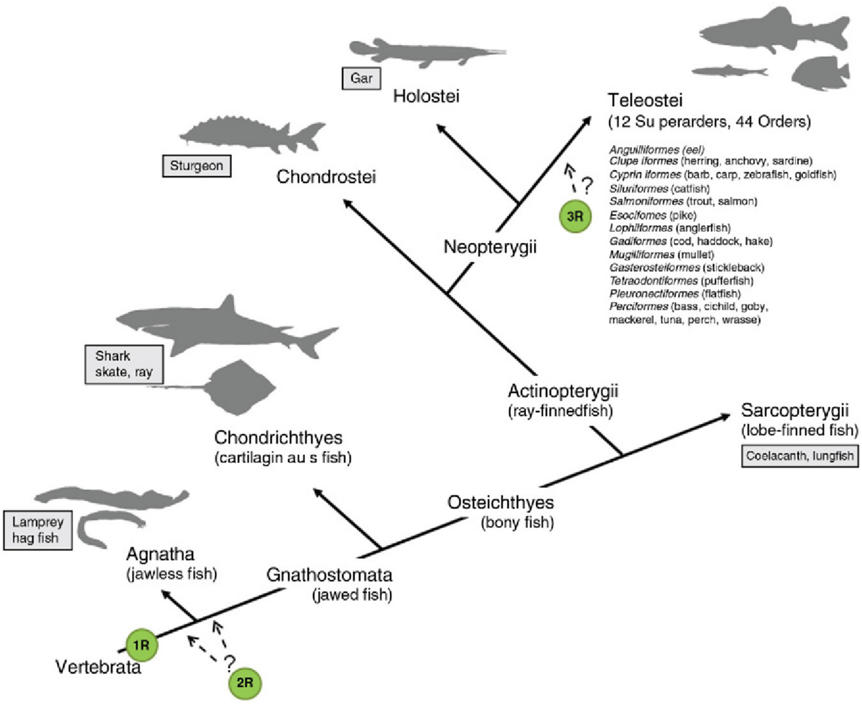

Figure 2.1 Schematic representation of the living-fish phylogeny (Near et al., 2012). Two rounds of whole-genome duplication (WGD) occurred early in the history of vertebrate evolution. WGD event in the ancestral vertebrate lineage duplicated the ancestral possibly cephalochordata-like genome to two (1R), and then to four genomes after a second WGD (2R) before the divergence of fish and tetrapods. Recent findings on lamprey genome sequentiation suggest that this second WGD occurred before the divergence of Agnatha and Gnathostomata (Smith et al., 2013). In the last 10 years evidence has accumulated for a ray-finned- (actinopterygii) specific genome duplication (3R) about 350 million years ago, leading initially to eight copies of the ancestral deuterostome genome. Most duplicated genes were secondarily lost or evolved new functions (Danzmann et al., 2008; Meyer and Van de Peer, 2005; Ravi and Venkatesh, 2008). Whether this third WGD occurred in the whole actinopterygian group or in part of the divergent lineages, in example salmonids and cyprinids, needs further investigation.

infectious agent (Alexander and Ingram, 1992b; Ellis, 2001). If the pathogen succeeds in penetrating the epithelium, it then encounters the complete cellular and humoral machinery of the immune system, triggered first by cell types bearing invariable receptors called pattern recognition receptors, which are able to recognize common conserved molecular characteristics of many microbial agents. Simultaneously, the primary responses of antigen-specific lymphocytes bearing variable receptors that are able to specifically recognize molecules distinctive of a pathogen will also be activated, setting the basis for further secondary responses (Figure 2.2).

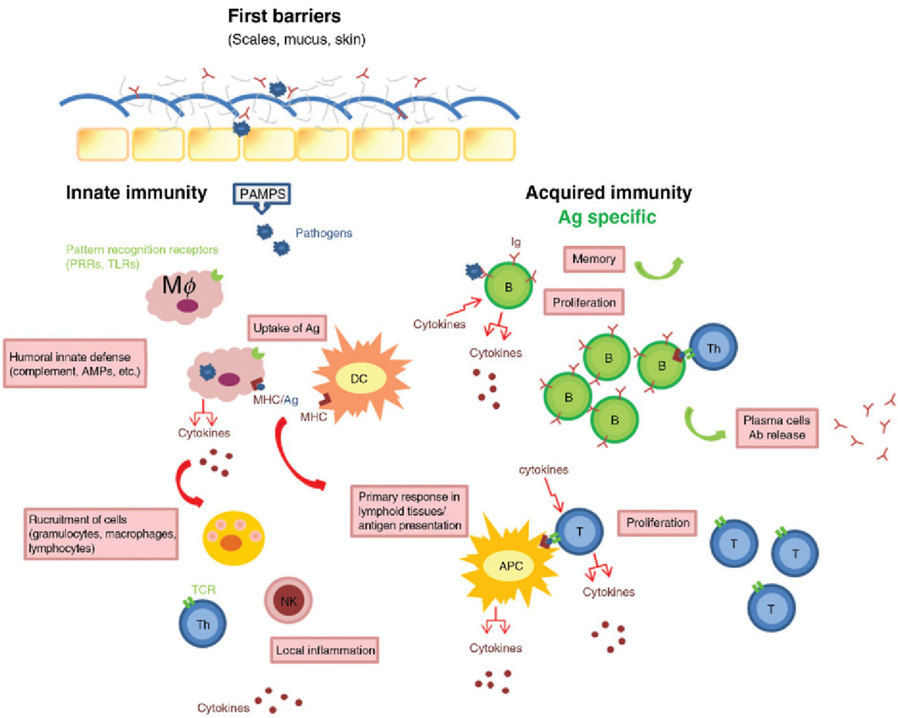

Figure 2.2 General mechanisms of the fish immune response. The encounter with a pathogenic organism via mucosal tissues, such as gills, skin, or gut, is primarily blocked or limited by physical barriers such as the mucus, the scales, and the epithelium. The mucus contains different humoral components with antimicrobial activity such as complement factors, lysozyme or Igs. In case the pathogen succeeds to penetrate the epithelium, it encounters the innate cellular machinery, triggered in a first step by those cell types bearing invariable receptors called pattern recognition receptors (PRRs), able to recognize common conserved molecules (PAMPs) characteristic of many microbial agents. The uptake of the antigen leads, on one hand, to the release of cytokine mediators and attractants for different cell types to unleash the inflammatory process and, on the other hand, to the antigenic presentation through the MHC in the lymphoid tissues for the activation of the primary responses of antigen-specific lymphocytes bearing variable receptors able to specifically recognize molecules distinctive of the pathogen, setting the bases for further secondary responses and memory.

2.2 Organs, tissues, and general structures

In higher vertebrates, the immune system consists of primary (lymphocyte-generating) and secondary (immune response-generating) lymphoid organs. The fetal liver, thymus and bone marrow constitute the primary lymphoid organs, while the spleen, lymph nodes, and mucosal-associated lymphoid tissue (MALT) comprise the secondary lymphoid organs. Fish organization of immune organs is slightly different from higher vertebrates. The main difference is that fish lack bone marrow and lymph nodes and the