



Host–parasite interactions: Marine bivalve molluscs and protozoan parasites, *Perkinsus* species



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ABSTRACT

This review assesses and examines the work conducted to date concerning host and parasite interactions between marine bivalve molluscs and protozoan parasites, belonging to *Perkinsus* species. The review focuses on two well-studied host–parasite interaction models: the two clam species, *Ruditapes philippinarum* and *R. decussatus*, and the parasite *Perkinsus olseni*, and the eastern oyster, *Crassostrea virginica*, and the parasite *Perkinsus marinus*. Cellular and humoral defense responses of the host in combating parasitic infection, the mechanisms (e.g., antioxidant enzymes, extracellular products) employed by the parasite in evading host defenses as well as the role of environmental factors in modulating the host–parasite interactions are described.

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1. Introduction

Protozoan parasites are common pathogens of many marine bivalve molluscs. Due to their economical and ecological impacts, the interactions of *Perkinsus* species with several economically important marine bivalve molluscs have been studied extensively. *Perkinsus* spp. were recently included in the new phylum Perkinsozoa as part of the infra-kingdom Alveolata. Although their systematic position has long been controversial inside the Alveolata, Perkinsozoa is now considered to be the earliest group diverging from the lineage leading to dinoflagellates, branching close to the line shared by dinoflagellates and apicomplexans (Bachvaroff et al., 2011; Zhang et al., 2011; Robledo et al., 2012).

Based on gene sequencing, there are currently 7 accepted species in the genus *Perkinsus*: *P. marinus*, *P. olseni*, *P. qugwadi*, *P. cheasapeaki*, *P. mediterraneus*, *P. honshuensis*, and *P. beihaiensis* (Villalba et al., 2004; Moss et al., 2008). Most described *Perkinsus* species have been found to infect only bivalve species with the exception of *P. olseni*, which also infects abalones in Australia (Villalba et al., 2004).

Among *Perkinsus* spp., *P. marinus* and *P. olseni* are the most destructive species. Diseases caused by them are collectively referred as perkinsosis (Villalba et al., 2004). They have been associated with massive mortalities resulting in significant economic

losses, in eastern (American) oysters *Crassostrea virginica*, and clams *Ruditapes philippinarum* and *R. decussatus*, respectively.

The eastern oyster, *C. virginica*, propagates along the east, and Gulf coasts of North America and Mexico, and is one of the most commercially and ecologically important shellfish species in these regions. The Manila clam, *R. philippinarum*, is also one of the most commercially important bivalve species worldwide as it is extensively cultivated and exploited in Asian and European countries. The carpet-shell clam, *R. decussatus* L., is another important fishery resource with high economic value in European countries, but unlike Manila clams, its distribution is restricted to Western Europe and North Africa.

Perkinsus marinus causes perkinsosis also referred as “dermo” disease in eastern oysters along the East and Gulf of Mexico coasts of the United States, particularly in the mid-Atlantic regions (see Burreson and Ragone-Calvo 1996; Ford, 1996; Soniat, 1996). Massive disease associated mortalities (usually exceeding 50% often over 90% per year according to environmental conditions) have caused not only heavy losses for the oyster industry (Burreson and Ragone-Calvo, 1996; Gutierrez et al., 2003), but also result in the degradation of oyster reefs, subsequently loss of natural habitats and reducing water clarity, affecting adversely the overall health of the ecosystem (Gutierrez et al., 2003; Tolley and Volety, 2005).

Perkinsus olseni, formerly named *P. atlanticus*, parasitizes Manila clams in Europe and Asia and also the carpet shell *R. decussatus* in Europe as well as in northern Africa (Tunisia) (El Bour et al. 2012). It also infects other clam species including *Paphia rhomboides*,

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P. aurea, and *Venerupis pullastra*, to a lesser extent in terms of prevalence and infection intensity. *P. olseni* has caused mortalities in clam populations in southern Portugal and NW Spain (Ruano and Cachola, 1986; Azevedo, 1989; Villalba et al., 2005; Villalba, 2008) and in coastal regions of Korea, Japan and China (Choi and Park, 1997; Hamaguchi et al., 1998; Park and Choi, 2001). Perkinsosis was associated with 50–80% of *R. decussatus* mortality in Algarve (S. Portugal) (Ruano and Cachola, 1986) and with a maximum of 40% of *R. philippinarum* annual cumulative mortality in Galicia (NW Spain) (Villalba et al. 2005). In Korea, perkinsosis was associated with an 80% decrease in *R. philippinarum* landings (Park and Choi 2001).

Disease-associated mortalities are particularly severe at times when environmental conditions are favorable to the parasites like *P. marinus*. Elevated temperatures and increasing salinity significantly advance its development and activity in the external environment and within the host. Likewise, harmful pollutants in the environments could impact adversely the host physiology and defense mechanisms (de Montaudouin et al., 2010).

To develop means and strategies to prevent and control diseases caused by *P. marinus* and *P. olseni*, time and effort have been directed to investigating the interactions between these parasites and their hosts. This review focuses on these two well-studied host–parasite interaction models: the two clams (*R. philippinarum* and *R. decussatus*) and the parasite *P. olseni*, and the eastern oyster *C. virginica* and the parasite *P. marinus*, with emphases on (1) host defense mechanisms and humoral and cellular responses to *Perkinsus* spp. infection; (2) *Perkinsus* spp. metabolic biochemistry and virulence factors; (3) physiological and immunological changes upon infection by *Perkinsus* spp., and (4) host–parasite interactions in variable and adverse environments.

2. Host defense mechanisms

There is a fairly wide consensus that *Perkinsus* spp. pathogenicity and virulence increase when its host becomes immunologically compromised (Chu, 2000). As the focus of this review is on bivalve–*Perkinsus* interactions, description of bivalve defense mechanisms is first presented in a general manner (for detailed reviews, see Cheng, 1996; Chu, 2000; Bachère, 2003), and then the more specific immune mechanisms known to be specifically affected by *Perkinsus* spp., are discussed in more detail.

2.1. Cellular factors

Molluscan bivalves have an open circulatory system and possess an innate immune system composed of humoral factors and cell-mediated mechanisms. Humoral factors include lectins

(agglutinins, opsonins), lysosomal enzymes (acid phosphatase, lysozyme and various hydrolytic enzymes), antimicrobial peptides, and protease inhibitors, etc. (see Cheng, 1996; Chu, 2000; Bachère, 2003). Cell-mediated defense mechanisms are mainly carried out by hemocytes, which move freely amongst all tissues. Hemocytes are considered to be the primary cellular effectors because of their ability to ingest or encapsulate and then destroy microorganisms. Hemocytes are chemotactic, mobile, phagocytic and able to aggregate (Hine, 1999; Canesi et al., 2002).

Bivalve hemocytes can be classified into two main categories: granulocytes (containing many granules) and hyalinocytes or agranulocytes (containing few or no granules) (Cheng, 1981; Fisher, 1986; Auffret, 1988; Chu, 2000; Lambert et al., 2003; Hégaret et al., 2003; Soudant et al., 2004).

Along with these morphological differences, specific abilities are attributed to these two categories of hemocytes. Granulocytes have a higher phagocytic capacity than hyalinocytes (Fisher, 1988; Cajaraville and Pal, 1995; Lopez et al. 1997a; Chu, 2000). This is consistent with the fact that granulocytes contain more lysosomal enzymes (Pipe, 1990; Pipe et al., 1997; Lopez et al., 1997b). Thus, granulocytes are believed to be more efficient in killing microorganisms than hyalinocytes and have been demonstrated to produce more reactive oxygen species in both stimulated and non-stimulated conditions (Pipe, 1992; Lambert et al., 2003, 2007). Hyalinocytes, in contrast, are thought to be more specialized in clotting and wound healing (Ruddell, 1971; Suzuki et al., 1991).

Major differences in terms of hemocyte morphology (size and internal complexity) have been observed as measured by flow cytometry between clam and oyster hemocytes (Fig. 1). Thus, immune responses to *Perkinsus* spp. infection possibly diverge between the two bivalve sub-classes, Eulamellibranchia and Filibranchia, to which clams and oysters belong, respectively.

2.2. Humoral factors

Humoral factors are also involved in the elimination of pathogenic microorganisms. Various constitutive or inducible humoral defense factors including lectins, antimicrobial peptides, lysosomal enzymes (e.g., β -glucuronidase, acid and alkaline phosphatase, lysozyme, aminopeptidase, and lipase), major plasma proteins, protease inhibitors, and cytokine-like molecules have been described in bivalves, but their respective and specific roles against pathogen infection are not yet fully elucidated (Chu, 2000; Tiscar and Mosca, 2004).

2.2.1. Lectins

Lectins were first found free in serum or bound to hemocyte membranes of bivalves (Fisher and DiNuzzo, 1991; Olafsen et al.,

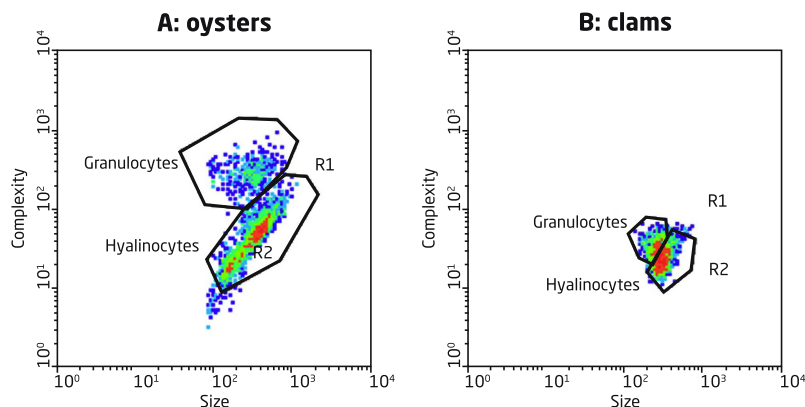


Fig. 1. Density plot of circulating hemocytes from oysters (A, *Crassostrea gigas*) and clams (B, *Ruditapes decussatus*) analyzed by Flow Cytometry using the same instrument settings. Granulocytes and hyalinocytes were differentiated on the basis of cell diameter and internal complexity.

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