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## Q6 Immune and stress responses in oysters with insights on adaptation

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## ABSTRACT

Oysters are representative bivalve molluscs that are widely distributed in world oceans. As successful colonizers of estuaries and intertidal zones, oysters are remarkably resilient against harsh environmental conditions including wide fluctuations in temperature and salinity as well as prolonged air exposure. Oysters have no adaptive immunity but can thrive in microbe-rich estuaries as filter-feeders. These unique adaptations make oysters interesting models to study the evolution of host-defense systems. Recent advances in genomic studies including sequencing of the oyster genome have provided insights into oyster's immune and stress responses underlying their amazing resilience. Studies show that the oyster genomes are highly polymorphic and complex, which may be key to their resilience. The oyster genome has a large gene repertoire that is enriched for immune and stress response genes. Thousands of genes are involved in oyster's immune and stress responses, through complex interactions, with many gene families expanded showing high sequence, structural and functional diversity. The high diversity of immune receptors and effectors may provide oysters with enhanced specificity in immune recognition and response to cope with diverse pathogens in the absence of adaptive immunity. Some members of expanded immune gene families have diverged to function at different temperatures and salinities or assumed new roles in abiotic stress response. Most canonical innate immunity pathways are conserved in oysters and supported by a large number of diverse and often novel genes. The great diversity in immune and stress response genes exhibited by expanded gene families as well as high sequence and structural polymorphisms may be central to oyster's adaptation to highly stressful and widely changing environments.

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## 1. Introduction

Mollusca is a phylum of ancient protostome bilaterians that emerged in early Cambrian about 542 mya [1]. During its long evolutionary history, Mollusca has greatly diversified and expanded in the number of species. With about 100,000 living species [2,3], Mollusca stands as the second most speciose phylum of animals after Arthropoda. Mollusca is a major group of lophotrochozoans whose biology and evolutionary history remain poorly understood. How molluscs have survived major extinction events over half a billion years of evolution and become one of the most successful

colonizers of marine, freshwater and terrestrial environments is of wide interest. Their success as indicated by species richness and adaptation to diverse environments suggests that molluscs are remarkably adaptive and may possess advanced molecular machineries and mechanisms for host-defense against biotic and abiotic stresses.

Oysters are representative bivalve molluscs that are widely distributed in world oceans. They are sessile filter-feeders inhabiting bottoms of estuaries and coastal oceans, well adapted for life in the intertidal zone. As sessile organisms thriving in estuaries and intertidal zones, oysters can tolerate wide fluctuations in temperature and salinity [4]. They can survive extended periods out of water. Oceans especially estuaries are rich in microbes, many of which are potential pathogens. As filter-feeders, oysters and other bivalve molluscs face tremendous exposure to pathogenic

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microbes. Invertebrates such as molluscs have no adaptive immune systems and rely solely on innate immunity for defense against pathogens. The fact that oysters without adaptive immunity can thrive in microbe-rich environments as filter-feeders is a testament of the strong capability of oyster's innate immune systems. Understanding oyster's amazing resilience against biotic and abiotic stressors may provide insights to the evolution of the immune and stress response systems in protostome invertebrates.

Oysters are also of ecological and economic importance. They are keystone species in estuarine ecology and provide important ecological services as filter-feeders and reef-builders. Oysters support major aquaculture and fishery industries worldwide. Aquaculture production of oysters amounted to 4.7 million metric tons [5]. Because of their economic and ecological importance plus suitable biological characteristics, oysters are popular models to study molluscan biology, development, innate immunity and stress adaptation. Oysters face considerable challenges from diseases and unexplainable mortalities probably caused by multiple stressors. Studies on oysters' immune and stress responses may contribute not only to our understanding of host-defense and adaptation, but also to the development of superior stocks for aquaculture [6].

Genes involved in immune and stress responses have been identified by traditional cloning and sequencing of individual genes. Recent advances in genomics have provided tools and opportunities for in-depth studies on oysters' immunity and stress responses. Genomic studies are particularly helpful in studying immune and stress responses as they involve interactions among many genes and pathways that are best studied through genome-wide approaches, instead of one gene at a time. The sequencing of the Pacific oyster genome [7] has provided a complete catalog of oyster genes that serves as a valuable reference for genome-wide analyses. The reference genome has greatly empowered transcriptome studies by facilitating easy mapping and accurate annotation. There has been rapid accumulation of genomic and transcriptomic data relevant to oysters' immune and stress responses. As thousands of oyster genes have been implicated in immune and stress responses, this review does not attempt to catalog all genes or studies, but focus on key genes and pathways that are related to important diseases and stressors, as well as basic mechanisms underlying oyster's immune and stress adaptation.

## 2. The oyster genome

Oysters belong to Class Bivalvia, Order Ostreoida and Family Ostreidae. Most of the common oysters are found in the genus *Crassostrea*. Among all oysters and possibly all molluscs, the Pacific oyster *Crassostrea gigas* and eastern oyster *Crassostrea virginica* are among the most extensively studied species due to their economical and ecological importance. *C. gigas* is native to China, Japan and Korea, but has been introduced to many countries for aquaculture [8]. *C. virginica* is native to Atlantic coast of North America, ranging from Canada to Mexico. In addition to their economic and ecological importance, these oysters have several characteristics making them good model species for biological research. Both oysters have separate sexes, high fecundity and external fertilization. They are widely available and can be easily produced and cultured under laboratory conditions.

The genomes of Pacific and eastern oysters are relatively small compared with other bivalve molluscs [9,10]. Both oysters as well as all other oysters studied so far have a haploid number of 10 chromosomes, compared with a haploid number of 19 in most clams and scallops [11,12]. The DNA content of oysters is also lower than that of most other bivalve molluscs. The Pacific oyster has a genome size of 637 Mb [7], and the genome of the eastern oyster is about 672 Mb [13]. The fact that the haploid number and DNA content of

oysters are about half of that of clams and scallop has led to the suggestion that whole genome duplication may have occurred during the evolutions of bivalve molluscs, and oysters may represent the diploid lineage [12]. However, it is also possible that the oyster genomes represent a degenerated genome from an ancestor with 19 chromosomes. Further studies on chromosome rearrangements may help to elucidate the evolutionary history of oyster genomes. Nevertheless, the relative small genomes of oysters make them good candidates for whole genome sequencing and other genomic studies [6,9].

An international Oyster Genome Project was initiated in 2008 to sequence the genome of *C. gigas*, and the publication of the oyster genome [7] has provided unprecedented insights to a molluscan genome and opportunities to study all aspects of molluscan biology including immune and stress responses. The *C. gigas* genome is highly polymorphic and complex, with repetitive sequences accounting for 36.1% of the genome [7]. It is particularly rich in miniature inverted-repeat transposable elements (MITEs, 157,007 copies or 8.82% of the genome), some of which may still be active and play a significant role in shaping genome diversity in *C. gigas*. The frequency of single-nucleotide polymorphism (SNP) as determined by re-sequencing of a wild oyster is 1.224% (82 bp/SNP), which is about 10 times of that found in an average human individual (Table 1). The frequency of indels is 0.077% compared with 0.015% in humans. On average, the genome of an oyster has a polymorphism (SNPs and indel) frequency of 1.301% or one every 77 bp. In comparison, the polymorphism frequency in humans is about 0.140% or one every 714 bp per individual (Table 1). The *C. virginica* genome is even more polymorphic than *C. gigas*, with a high SNP frequency of 5% (20 bp/SNP) being estimated at population levels [15]. Another study found a SNP frequency of 1.98% at population levels in expressed sequences of *C. virginica* [16]. These data suggest that oyster genomes are highly polymorphic and probably among the most polymorphic genomes we know. As we will discuss, the exceptionally high polymorphism in oysters may underlay functional diversity that is essential for oysters' adaptation to highly variable and challenging environments.

The oyster genome has a large set of 28,027 protein-coding genes including 8654 that are oyster or mollusc-specific [7]. Among the oyster-specific genes, genes related to protein binding, apoptosis, cytokine activity and inflammatory response are highly enriched, indicating a rich gene set related to host-defense. Many gene families related to immune and stress response are expanded compared with other sequenced genomes [7,17]. The expanded gene families included many involved in immune and/or abiotic stress responses such as *heat shock proteins (HSPs)*, *cytochrome P450 (CYP450)*, *globular head C1q domain containing protein (C1qDC)*, *inhibitors of apoptosis (IAPs)*, *C-type lectin domain containing protein (CTLDC)*, *extracellular superoxide dismutase (ecSOD)*, *fibrinogen-related protein (FREP)*, *transmembrane protein 173 (MITA)*, *myeloid differentiation primary response gene 88 (MyD88)*, *RIG-1-like receptors (RLRs)*, *Toll-like receptors (TLRs)*, and *tumor necrosis factors*

**Table 1**  
Polymorphism in the *C. gigas* genome compared to that in *Homo sapiens*.

Parameter	<i>C. gigas</i>	<i>H. sapiens</i>
Sample size	1	179
Bases covered (Mb)	308	2420
SNP sites/individual	3,764,864	3,019,909
SNP frequency/individual (%)	1.224	0.125
Indel sites/individual	238,182	361,669
Indel frequency/individual (%)	0.077	0.015
SNP + indel frequency/individual (%)	1.301	0.140

Calculations are based on [7] and [14].

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