

Feature Review

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## Comparative Genomics of Oysters and Evolutionary Adaptation to Marine Environments

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**Abstract** Oysters are important for both marine ecosystems and aquaculture, but they are under threat from climate change, pollution, and disease. Recent studies of oyster genomes-such as the Pacific oyster (*Crassostrea gigas*) and the Hong Kong oyster (*Magallana hongkongensis*)-have uncovered key differences in their genetic structure, gene activity, and stress responses. These discoveries help explain how oysters manage to survive in environments with different salinity, temperature, and pathogens. The comparison between *C. gigas* and *M. hongkongensis* shows clear genetic divergence related to their habitats. By identifying genes linked to stress tolerance, researchers can support future breeding and conservation efforts-especially as climate conditions continue to change.

**Keywords** Oyster genomics; Environmental adaptation; Stress response; Salinity tolerance; Conservation genetics

### 1 Introduction

Oysters are not only delicious food on people's tables, they also have other important functions. They can purify seawater, provide habitats for small marine organisms, and help maintain the nutrient balance in coastal environments (Parker et al., 2023; Zapata-Restrepo et al., 2023). In many coastal areas, oyster farming has become part of the local economy, providing many jobs and food sources.

However, oysters are under growing pressure. Warmer oceans, heavier pollution, and the emergence of new diseases are making it harder for oysters to survive and reproduce (Xu et al., 2017; Brew et al., 2020). Different oyster species react in different ways-some can handle stress better than others.

To understand why some oysters can withstand these challenges, scientists began to study their genes. By comparing the genetic differences between different species and populations, researchers have found genetic characteristics related to disease resistance and environmental adaptation (Eierman and Hare, 2016; Farias et al., 2017; Sullivan and Proestou, 2021; Dupoué et al., 2023). These research results also provide a reference for future oyster breeding and resource protection.

### 2 Progress in Oyster Genome Sequencing

#### 2.1 Sequencing of *Crassostrea* and other related oysters

In recent years, oyster genome sequencing technology has been greatly improved. Several important oysters, including the Pacific oyster (*Crassostrea gigas*), the Yangtze River oyster (*Crassostrea ariakensis*), the European oyster (*Ostrea edulis*), and the Hong Kong oyster (*Magallana hongkongensis*), have completed chromosome-level genome assemblies (Li et al., 2020; Qi et al., 2021; Gundappa et al., 2022). For example, the genome of *C. gigas* is divided into 10 pseudochromosomes, showing complex structure and genetic diversity (Qi et al., 2021; Mrowicki and Uhl, 2024).

Different sequencing projects have different focuses. Some are used to study the evolution of oysters, while others directly provide data for breeding. For example, the genome of *C. ariakensis* can be used for conservation research and is also suitable for reference in aquaculture breeding (Li et al., 2024a). The genome of the European

oyster combines multiple sequencing methods to improve the accuracy of gene identification (Gundappa et al., 2022; Adkins and Mrowicki, 2023). The genome of the Hong Kong oyster helps study some ancient gene families, such as the homeobox gene (Li et al., 2020).

## 2.2 Common sequencing methods and existing problems

There is no single method that fits all oyster species. Researchers usually combine several sequencing technologies-such as long-read platforms like PacBio and Oxford Nanopore, short-read Illumina sequencing, and Hi-C mapping to assemble the genome (Qi et al., 2021; Gundappa et al., 2022).

However, assembling the oyster genome is not easy. Many oysters have a large number of repeated fragments in their DNA, sometimes even accounting for more than half, and the differences between genes are also large. In addition, some structural changes, such as gene duplication, will make the assembly process more complicated (Qi et al., 2021; Li et al., 2024b). To solve these problems, researchers will also introduce transcriptome information and genetic maps to help improve the accuracy of gene annotation (Gundappa et al., 2022).

Despite these difficulties, the recently completed oyster genome has a high level of completeness, and the identification of some important genes has become clearer. These data have begun to play a role in oyster biological research, adaptation analysis and breeding practices (Qi et al., 2021; Gundappa et al., 2022).

## 3 Genomic Architecture and Species Variation

### 3.1 Genome size and repetitive elements

Oyster genomes vary greatly in size, and many contain a large number of repetitive sequences. For example, the genome of the Pacific oyster (*Crassostrea gigas*) has many transposable elements. These “jumping genes” may increase genetic diversity and help improve adaptability (Zhang et al., 2012). Another case is the Sydney rock oyster (*Saccostrea glomerata*), whose genome is about 784 Mb and also rich in repetitive sequences (Powell et al., 2018). These repetitive features aren’t random noise. In marine bivalves generally, they seem to have a function: helping the organisms adapt quickly to environmental changes. That said, not every species shows the same pattern in the same way, and the relationship between genome architecture and adaptability is still being investigated (Zhang et al., 2012; Powell et al., 2018).

### 3.2 Species-specific genes and structural features

Gene families that help oysters deal with stress and pathogens have expanded in some species more than others. In both *C. gigas* and *S. glomerata*, for example, researchers have found more copies of genes like heat shock proteins and apoptosis inhibitors-proteins that help deal with stress, salinity swings, or infections (Zhang et al., 2012; Zhang et al., 2016; Powell et al., 2018). In *Crassostrea ariakensis*, certain genes-especially those from solute carrier families that help cells manage salt and temperature stress-show clear signs of being favored by natural selection (Zhang et al., 2022). It’s not just the genes themselves that matter. The regions that control when and how these genes are activated also differ, which can influence how oysters respond to their environment.

## 4 Genomic Features of Adaptation to Marine Environments

### 4.1 Genes related to temperature and salt tolerance

To survive in complex and changing marine environments, oysters have evolved several key gene families related to temperature and salinity tolerance. These include solute carrier genes, heat stress response genes, and various regulatory elements. In multiple oyster species, these genes exhibit signs of adaptive evolution, indicating their critical role in responding to environmental stress (She et al., 2018).

For example, in the estuarine oyster, several solute carrier genes under positive selection-such as *Slc23a2* and *Mct12*-have been identified. These genes are primarily located on chromosome 9 and form distinct gene clusters. As shown in the CIRCOS plot below, these clusters are highlighted in purple-red arcs, indicating a concentrated distribution. This pattern suggests that these regions may be under directional selection, playing a specialized role in salinity adaptation (Figure 1) (Li et al., 2021).

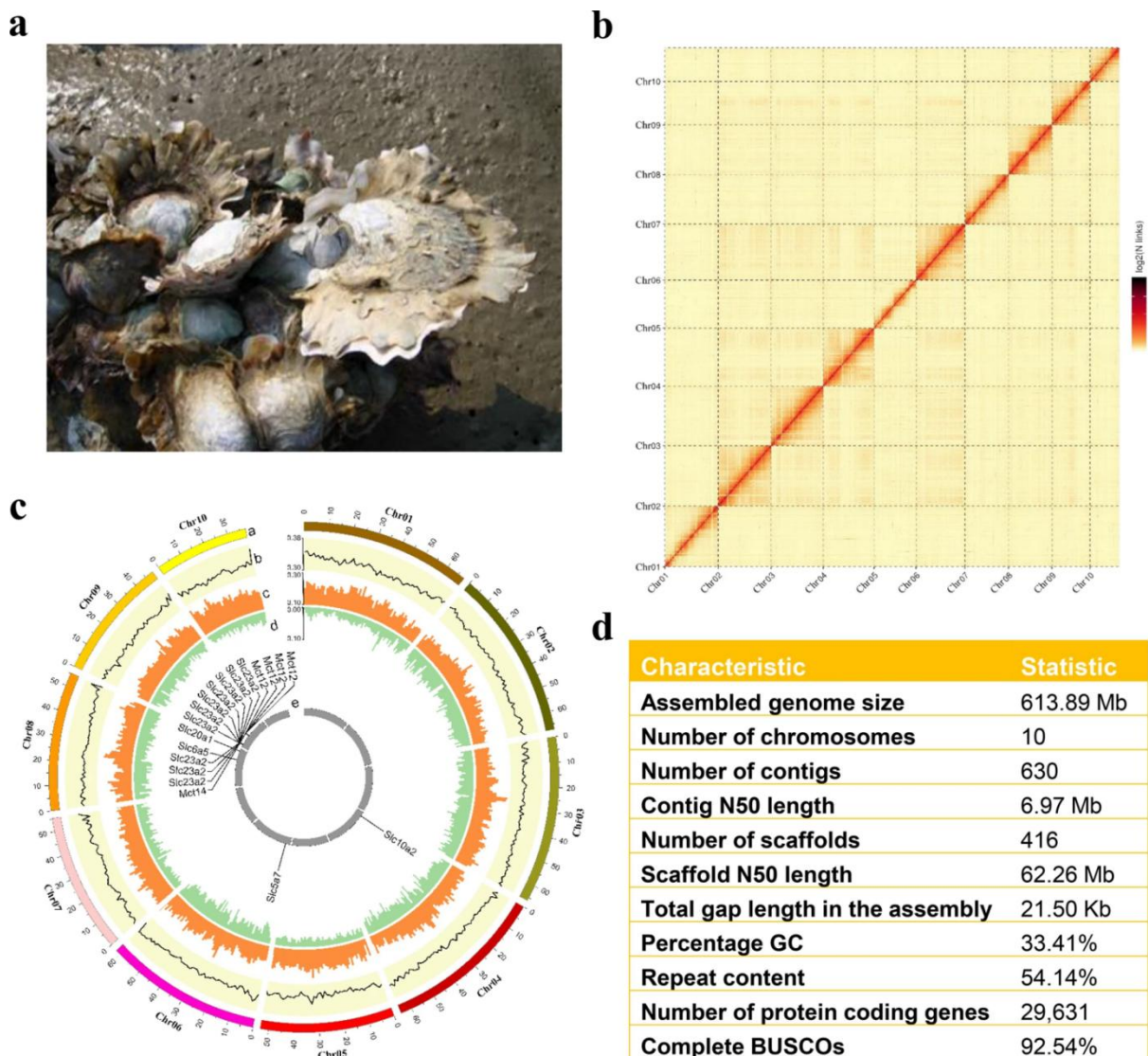


Figure 1 a Estuarine oyster (photo by Lumin Qian). b Hi-C interaction heatmap showing 10 chromosomes of the estuarine oyster. c CIRCOS plot showing 10 chromosomes (a), the distribution of GC content (b), transposable elements (c), coding sequences (d), and duplicated gene cluster of the solute carrier families showing selection signals (e, also see Supplementary Figure 13). d Summary statistics of the genome assembly (Adopted from Li et al., 2021)

In addition, classic stress-related genes are also involved in environmental responses. For instance, *Cg\_CLCN7* is responsible for chloride ion transport, and *Cg\_API* regulates apoptosis; both are significantly upregulated under high-salinity conditions (She et al., 2018). However, the distribution of these functional genes is not uniform across populations. Oysters from high-salinity or high-temperature habitats often carry more favorable gene variants (Li et al., 2020), reflecting a genetic basis for local adaptation. Nonetheless, differences at the genetic level do not always lead to observable phenotypic changes, as environmental context and gene-environment interactions remain important factors.

#### 4.2 Metabolic and antioxidant response mechanisms

In addition to activating stress-related genes, oysters also adjust their metabolism when facing harsh environments. For example, some oysters living in high-salinity seawater will activate pyruvate and taurine metabolism more frequently. These metabolic processes help cells maintain normal function and reduce damage caused by salinity stress (She et al., 2018; Zhang et al., 2022). Some gene families, such as GPCRs, are frequently duplicated and show different responses depending on the type of stress-whether heat, salinity, or pollutants (Fu et al., 2022). These flexible responses may explain why oysters are so widely distributed.

### 4.3 Epigenetics and environmental response

Genetics isn't the whole picture. Epigenetic changes-especially DNA methylation—are now seen as another layer of adaptation. For example, intertidal oysters tend to show lower methylation levels and more flexibility in methylation patterns when exposed to heat stress. In contrast, subtidal species have higher, more stable methylation profiles. These methylation changes affect the expression of genes involved in cell death, development, and ion balance. In other words, it's not just about what genes oysters have-but also how they're regulated. This may give oysters the ability to respond quickly to environmental changes (Wang et al., 2020).

## 5 Functional Insights from Transcriptome Analyses

### 5.1 Expression in intertidal and subtidal species

Not only does the environment affect the characteristics of oysters, but their gene expression also shows how they adapt step by step. The activity of some genes in different salinities is often related to the growth rate or survival rate of oysters (Wang et al., 2020; Zhang et al., 2022). However, this relationship is not absolute. Different species have different responses, and the interaction between genes and environment cannot always be accurately predicted (Liu and Huang, 2024).

### 5.2 Response to pollution and pathogens

When oysters encounter pollution or infection, some specific genes are activated. For example, the GPCR gene family will produce different responses when facing heavy metals or pathogens (Zhang et al., 2016; Fu et al., 2022). These genes can help oysters reduce stress and are important for them to survive in harsh or polluted waters. But adaptation isn't just controlled by one or two genes. Many of these responses involve multiple genes working together, and the effect can depend on the environment. This is known as polygenic adaptation, and it shows how complex oyster responses to stress can be (Bernatchez et al., 2018; Fu et al., 2022).

## 6 Evolution of Oyster Immune Systems

### 6.1 Innate immune gene expansions

In the intertidal zones where pathogens are abundant and environmental conditions fluctuate frequently, oysters have gradually evolved a complex innate immune system. Studies have shown that several immune-related gene families have expanded in oyster genomes, particularly Toll-like receptors (TLRs), inhibitor of apoptosis proteins (IAPs), and caspases. These key genes exhibit both increased copy numbers and enhanced expression across multiple oyster species (PZhang et al., 2016; Owell et al., 2018). Such expansions help oysters recognize a wide range of pathogens and improve their ability to regulate cellular stress responses.

### 6.2 Pathogen recognition systems

The Toll-like receptor (TLR) family has expanded considerably in oysters. This helps explain their ability to sense a wide range of pathogens in environments where microbial diversity is high (Zhang et al., 2016; Powell et al., 2018). But again, not all TLRs act the same, and some are more responsive than others depending on the challenge. Lectins and antimicrobial peptides are another major line of defense. These molecules identify and neutralize pathogens directly. Oysters show a great deal of variation in these genes, which is thought to support their survival across different microbial landscapes (Zhang et al., 2016; Powell et al., 2018).

## 7 Case Study: Genetic Comparison of Pacific and Hong Kong Oysters

### 7.1 Genetic differences and salinity adaptation

There are obvious genetic differences between Pacific oysters (*Crassostrea gigas*) and Hong Kong oysters (*Crassostrea hongkongensis*). Pacific oysters are more adapted to living in seawater with higher salinity, while Hong Kong oysters are more adapted to environments with lower salinity (Zhang et al., 2022). This difference is not only reflected in their distribution areas, but also in their growth rates and survival rates, and each performs better in the environment they are adapted to. When faced with salinity changes, the genes activated by the two oysters are also different. They respond to stress through different gene regulation methods. This difference is closely related to the environment in which they live for a long time, indicating that they gradually adapt to their respective living conditions through genetic changes.



## 7.2 Genetic pathways related to stress adaptation

The genes of the two oysters also differ in the part that controls the response to salinity changes. Pacific oysters can activate some specific metabolic pathways under high salinity conditions, while Hong Kong oysters show similar coping mechanisms under low salinity conditions (Zhang et al., 2022). This shows that their genetic systems have formed ways to adapt to various environments, which is the result of long-term natural selection.

Using the Pacific oyster (*Crassostrea gigas*) as a model, the core stress and immune pathways activated under various stress conditions—including high temperature, heavy metals, low salinity, and pathogen exposure—are illustrated (Figure 2) (Zhang et al., 2016). Gene families marked with bold black borders in the figure, such as HSPs, SODs, and IAPs, represent expanded genes that are significantly upregulated under multiple stress scenarios. This capacity to respond to diverse stressors is a clear sign of the evolutionary enhancement of the oyster's innate immune system. When exposed to salinity stress, each species activates a different set of genes. These differences in gene expression show that they rely on distinct biological responses to adapt. Their genetic patterns line up with their home environments, pointing to the strong influence of local adaptation on their evolution.

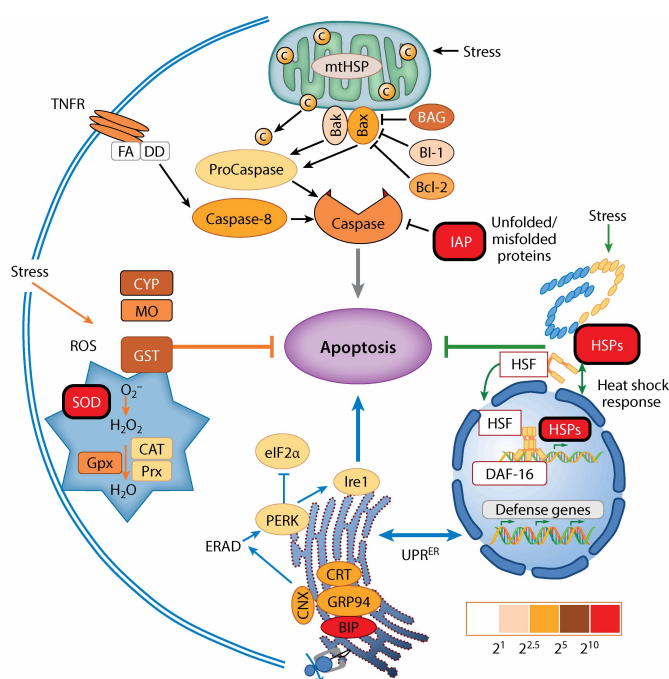


Figure 2 The major stress-responsive pathway-related genes in *Crassostrea gigas* (Adopted from Zhang et al., 2016)

Image caption: Protein folding systems included HSPs and HSF in the heat shock response and GRP78, GRP94, PERK, CRT, CNX, eIF2 $\alpha$ , and Ire1 in the endoplasmic reticulum unfolded-protein response (UPR<sup>ER</sup>). Apoptotic pathways included IAPs, BAG, Bcl2 like, caspases, BI-1, TNFR, and FADD. The xenobiotic biotransformation and antioxidant systems included CYP450, MO, SOD, Gpx, Prx, and CAT. Boxes with bold black borders indicate oyster expanded gene families, including HSPs, IAPs, and SODs, and the filled colors represent the degree of upregulation in RPKMtreatment/RPKMcontrol by stress, using transcriptomes from oysters challenged with nine different types of stressors (Adopted from Zhang et al., 2016)

## 8 Implications for Conservation and Aquaculture

### 8.1 Breeding applications of genetic markers

With more is known about stress tolerance genes, especially those linked to temperature and salinity, practical applications are emerging. Molecular markers—such as adaptive SNPs—are now being used to select oyster strains better suited for particular environments. It's not just theory anymore. High-throughput genotyping has made these tools available on a broader scale. That said, selective breeding isn't a one-size-fits-all solution. The usefulness of certain markers can vary by location and environmental condition, so there's still a need for local adaptation strategies.

## 8.2 Building resilience to climate pressure

Genomic studies have revealed more than just interesting patterns—they've made it possible to think about resilience in a more structured way. Variations in gene regulation, family expansion, and population-level adaptation all play into how oysters cope with climate stress. This knowledge helps managers and breeders alike. If we know which populations have the genetic tools to tolerate future conditions, conservation and aquaculture planning can be more targeted. In a time of rising sea temperatures and unpredictable salinity shifts, that information could make a real difference.

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## Conflict of Interest Disclosure

The authors confirm that the study was conducted without any commercial or financial relationships and could be interpreted as a potential conflict of interest.

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