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Global Biogeographic Patterns and Genetic Connectivity of Oyster Populations

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Abstract Oysters are widely distributed along coastal regions worldwide and serve as key ecological engineering species with significant value in maintaining coastal ecosystem functions and supporting fisheries. However, the biogeographic distribution patterns and genetic connectivity of oyster populations vary considerably across regions, influenced by a combination of paleoclimatic and geological history, oceanographic gradients, and human activities. This study provides a comprehensive overview of the systematics and distribution of major oyster groups globally, elucidates the biogeographic divisions and historical-ecological factors driving oyster population differentiation, and reviews recent advances in the application of molecular markers and population genomics in studying oyster genetic connectivity. Through case studies from representative regions-including Pacific oysters in the Northwest Pacific, eastern oysters in the North Atlantic of North America, and rock oysters in Europe and the Southern Hemisphere-we analyze the genetic structure and connectivity patterns of regional populations. The results reveal variations in genetic diversity and gene flow levels among oyster populations across different marine regions. Understanding genetic connectivity is crucial for biodiversity conservation and sustainable resource management, enabling the delineation of management units and guiding breeding, stock enhancement, and habitat restoration efforts. Under global climate change, oyster population distributions and connectivity patterns may undergo profound shifts, necessitating enhanced research on oysters' genetic responses to environmental changes. This study advocates for incorporating genetic connectivity into habitat conservation and aquaculture management decisions to enhance oyster populations' adaptability to environmental changes and ensure the long-term maintenance of their ecological functions and economic value.

Keywords Oyster; Biogeography; Genetic connectivity; Population genetics; Conservation genetics

1 Introduction

Oysters, belonging to the family Ostreidae, are mollusks widely distributed in shallow temperate to tropical coastal waters around the world. As foundational species in coastal ecosystems, oysters play a vital ecological role. By forming large reef structures or dense aggregations, they provide essential habitats for a variety of marine organisms, enhance local biodiversity, and contribute to water quality improvement through their filter-feeding activity. Moreover, oysters facilitate nutrient cycling and help stabilize shorelines (Reeves et al., 2020). However, due to historical overharvesting and habitat degradation, oyster reef ecosystems have suffered a dramatic global decline-an estimated over 85% of native oyster reefs have vanished in the past two centuries. This decline not only represents a loss of a critical food resource but also severely compromises coastal ecosystem functions. In response, numerous countries have initiated oyster reef restoration projects to rebuild their ecological service capacities.

Biogeographic studies provide insights into how historical climatic and geological events have shaped the current distribution and population structure of species, while population genetics offers tools to assess gene flow and connectivity among populations. For marine species with pelagic larval stages, such as oysters, genetic connectivity determines the extent of gene exchange between populations, which in turn affects local genetic diversity and adaptive evolutionary potential. Higher genetic diversity is often associated with greater resilience to environmental stressors, enhancing a population's capacity to adapt to climate change and other disturbances (Abecasis et al., 2024). Therefore, incorporating genetic connectivity into marine conservation planning-such as the design of marine protected area (MPA) networks-is crucial for maintaining long-term ecosystem stability and functionality.

Given the ecological and economic significance of oysters, and the marked regional variation in the genetic structure and connectivity of their populations, this study aims to provide a comprehensive review of the biogeographic distribution patterns and genetic connectivity characteristics of oyster populations worldwide. It seeks to analyze the underlying drivers of these patterns and explore their implications for conservation and management. Specifically, we introduce the major oyster taxa and their global distribution status, summarize observed population differentiation across biogeographic regions, and discuss the influence of historical climatic events and ecological factors on oyster distribution and connectivity. By examining representative populations in key marine regions-such as the Northwest Pacific, the Atlantic coast of North America, Europe, and the Southern Hemisphere-we analyze case studies of genetic structure and connectivity. Finally, we assess the potential impacts of future environmental change on oyster distribution and genetic patterns, and discuss possible mitigation strategies, including genetic enhancement and adaptive evolution approaches.

2 Systematics and Global Distribution of Oysters

2.1 Taxonomic classification and representative species of major oyster groups

The family *Ostreidae* encompasses most of the commonly recognized true oysters, also known as edible oysters. Based on morphological characteristics and molecular phylogenetic analyses, the *Ostreidae* can be further subdivided into several genera (or subgenera), with the most prominent groups including *Crassostrea*, *Ostrea*, *Saccostrea*, and the more recently proposed genus *Magallana*. The genus *Crassostrea* includes many economically important species, such as the Pacific oyster (*Crassostrea gigas*), the eastern oyster (*C. virginica*), and the Portuguese oyster (*C. angulata*). These species are generally characterized by their large, deep-cupped bivalve shells and typically inhabit estuarine bays, attaching to hard or muddy substrates.

In contrast, the genus *Ostrea* consists of flat oysters, which are relatively smaller in size and possess flat, rounded shells. They often attach to rocks or shell substrates and can form low-profile, bed-like communities (Figure 1) (Richardson et al., 2022). Species in the genera *Saccostrea* and *Striostrea*, commonly referred to as rock oysters, include notable representatives such as the Sydney rock oyster (*Saccostrea glomerata*) from Australia and the hooded rock oyster (*S. cucullata*) from East Asia. These oysters are typically found in tropical and subtropical intertidal zones, residing on reef structures or mangrove roots, and are well adapted to high temperature and salinity conditions. In addition, related groups such as *Isognomon* and *Pinctada* (pearl oysters, which belong to the family *Pteriidae*) are also noteworthy. Some of these species can form reef-like ecological structures similar to those created by true oysters.

2.2 Global distribution regions and typical habitat environments

Oysters are naturally distributed across nearly all warm coastal regions worldwide, but distinct taxonomic groups exhibit clear regional patterns of distribution across the major oceans. The Indo-West Pacific region possesses the highest global oyster species diversity, particularly in tropical and subtropical seas, where numerous species of *Saccostrea* and *Crassostrea* are found (Narasimham et al., 2007). In areas such as Southeast Asia and northern Australia, multiple *Saccostrea* species co-occur and can form mixed-species oyster reefs in the same intertidal zones. In contrast, the temperate North Pacific, including the coastal waters of East Asia, supports fewer native oyster species. These are primarily composed of the Pacific oyster (*Crassostrea gigas*) and a limited number of *Saccostrea* species. However, due to the extensive availability of suitable habitats, these oysters occur in large numbers and exert significant ecological influence.

The native oysters of the North Atlantic region include the European flat oyster (*Ostrea edulis*) along European coasts and the eastern oyster (*Crassostrea virginica*) along the Americas. These two species have diverged into distinct genera as a result of prehistoric continental separation. In the temperate regions of the Southern Hemisphere-such as southern Australia, New Zealand, and South Africa-native oysters are mainly flat oysters and rock oysters. Historically, these regions harbored expansive oyster reef systems, but most have disappeared or exist only as remnant populations due to human impacts (Christianen et al., 2018). Despite regional differences, oysters commonly inhabit a set of typical coastal environments. Most oysters prefer shallow coastal and estuarine brackish environments, including estuarine bays, lagoons, mangrove swamps, and nearshore shallow seas. They typically attach to hard substrates such as rocks, shells, or artificial structures, or to shell debris on soft bottoms, which supports the formation of complex, three-dimensional reef structures (Qurani et al., 2020).

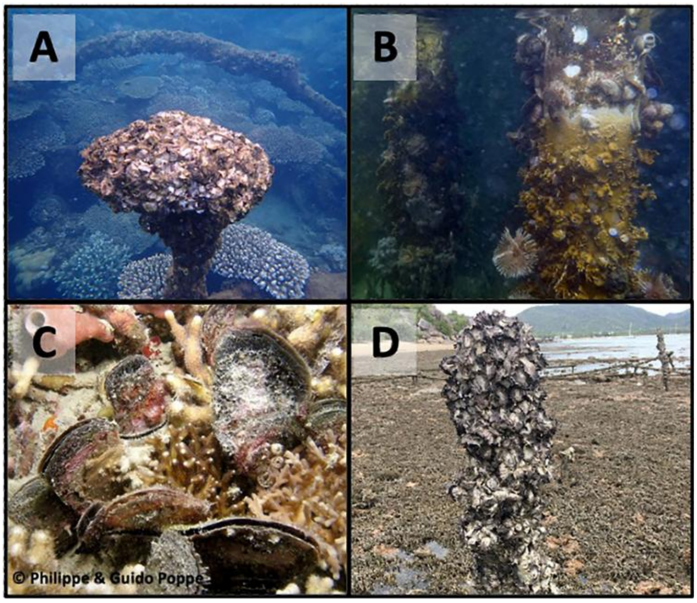

Figure 1 (A) *Saccostrea* sp. clustering above coral at Moreton Island, Queensland; (B) Oysters, coral, hydroids and sponges co-habiting a dock at the Smithsonian's Bocas Del Toro Marine Station in Panama; (C) *Isognomon* sp. and coral co-occurring on a reef in the Philippines; (D) Multiple *Saccostrea* species clustering on aquaculture furniture on a coral reef at Magnetic Island, Queensland (Adopted from Richardson et al., 2022)

Oysters exhibit a broad tolerance to variations in salinity and temperature. For example, *Crassostrea gigas* demonstrates strong adaptability and can thrive and reproduce across a salinity range of 20‰~35‰ and temperatures ranging from 10 °C in temperate zones to over 30 °C in subtropical waters. Many oyster species release planktonic larvae, with larval durations ranging from one to three weeks, enabling dispersal to nearby areas via ocean currents. However, extreme environmental conditions, such as the low salinity of the Baltic Sea or highly saline and hot conditions in certain tropical areas, may limit oyster distribution and define the boundaries of population ranges.

2.3 Population differentiation phenomenon under biogeographical zoning

Oyster populations in different regions around the world often show biogeographic differentiation genetically due to geographical isolation and environmental differences. On the one hand, intercontinental or interocean isolation has led to the evolution of oysters from different oceans into unique species. On the other hand, environmental gradients and physical barriers between different climatic zones and sea areas within the ocean also lead to population-level genetic structures. Studies have used the DNA of museum specimens to reconstruct the population structure of European flat oysters in the 19th century. It was found that there was a unique haplotype group along the North Sea to France at that time, while other groups were limited to narrower areas, which may reflect multiple shelters and regeneration processes after the last ice age. Although modern European flat oyster populations show a certain mixture due to large human transplants, wild populations in local regions (such as the UK and Nordic) still retain obvious genetic differences, suggesting their historically limited connectivity and environmental selection pressures (Monteiro et al., 2024).

3 Historical and Ecological Drivers of Biogeographic Pattern

3.1 Effects of paleoclimatic and geological events on the diffusion of oysters

The current distribution and genetic pattern of global oyster populations are deeply affected by repeated fluctuations in the Quaternary paleoclimate and earlier geological events. During the interglacial climate cycle of ice-age, drastic rise and fall of sea levels change the scope of coastal habitats and shapes the history of oysters' diffusion and isolation. The retreat during the ice age caused large-scale exposure of the continental shelf, many shallow sea oyster habitats disappeared, and populations were compressed to shelter areas; the sea during the interglacial period expanded the coastline again, providing new colonial space for oysters. Baker et al. (2019)'s study identified a unique haplotype of the 19th-century North Sea oyster through ancient DNA, supporting that the North Sea might have served as a post-ice shelter for independence and nurtured groups that were genetically distinct from other parts of the Atlantic Ocean (Baker et al., 2019).

In addition to climate change, geological tectonic events also have an irreversible impact on oyster distribution. From the late Miocene to the Pliocene, the gradual uplift of the isthmus of Central and American finally cut off the ocean connection between the Pacific and the Atlantic Ocean about 3 million years ago, contributing to the long-term isolation of the two oceanic oyster populations (Stange et al., 2018). The subsequent evolutionary differences formed a significant difference between the Atlantic flat oysters and the Pacific Cup oysters today. Group historical dynamic reconstruction shows that many oyster populations experienced obvious bottlenecks and expansions in the late Pleistocene. Monteiro et al. (2024) used the "Continuous Markov Model" (PSMC) analysis to find that the effective size of oysters in the northwest Pacific Ocean generally decreased about 100,000 years ago, and then slowly recovered from the glacial trough. This period corresponds to the harshest stage of the last ice age, which may reflect the adverse effects of the climate environment on oyster survival at that time, as well as the re-growth of populations when the interglacial period arrives.

3.2 The role of ocean currents, temperature-salt gradients and ocean obstacles

Physical and ecological factors in the marine environment continue to affect the connectivity and differentiation of oyster populations during the current climate period. Marine circulation and coastal currents are the main carriers driving the diffusion of phytoplankton juveniles. The juvenile stage of oysters can float in water for several days to weeks, and their diffusion distance depends to a large extent on the velocity and direction of the ocean current. For example, the Kuroshima tide system in the northwest Pacific flows from south to north, which helps transport oyster juveniles from Taiwan and South China to East China and southwestern Japan, thereby promoting population connectivity in these regions (Takeuchi et al., 2020). Secondly, environmental factors such as temperature and salinity gradients also affect the survival and settlement of oyster juveniles, thereby shaping the genetic connectivity pattern. Oysters are widely salty and warm species, but extreme conditions will exceed their tolerance range. Taking the Baltic Sea as an example, the surface salinity of this sea area gradually decreases from 20‰ at the entrance to below 5‰ of the inner bay. Although European flat oysters were once distributed in the western Baltic Sea, they were unable to reproduce in the lower salty central and eastern waters (Manuel et al., 2023).

Marine topography and ecological obstacles cannot be ignored. In addition to headlands, freshwater plumes in large estuaries, long sandbanks, strong tide straits, etc. may all become obstacles to the spread of oyster juveniles. The Skagrak Strait in Northern Europe connects the North Sea and the Baltic Sea. Its complex hydrology makes oyster juveniles prone to retention or are washed into the low-salt zone where discomfortable survival, forming a genetic boundary of populations.

3.3 The evolution of man-made activities and global oyster distribution pattern

Since modern times, the impact of human activities on the distribution of oysters and the genetic structure of population has become increasingly prominent. On the one hand, overfishing and habitat destruction have led to a significant decline in native oyster populations in many areas and even functional extinction. For example, native European oysters in the North Sea and Baltic Sea were almost extinct due to overcapacity and disease in the late 19th century (Pouvreau et al., 2023). On the other hand, artificial introduction and aquaculture have widely broken the original geographical isolation pattern of oysters. Since the end of the 19th century, Pacific oysters have been introduced as breeding varieties to the west coast of North America, Europe, Australia and other places, forming a naturalized population of "self-sustaining" (Lallias et al., 2013). These introduced Pacific oyster populations originated from the same ancestors as those of native Asian populations, and are therefore genetically similar.

Large-scale cross-regional transport of seedlings and artificial seedling cultivation also have a direct impact on the genetic structure of oysters. In modern oyster farming, seedlings from one region are often transported to another region for breeding. Pacific oyster farming on the west coast of North America has long relied on seedling supply from Japan and the United States East Coast hatcheries. This practice may mix genes from different geographical sources, reducing genetic differences between regions. At the same time, seedlings often come from a few parents or are bred, and their genetic diversity and family structure are different from those of wild populations (Markus et al., 2021). Studies show that oyster populations in some farms in British Columbia, Canada have obvious family correlation and low nucleotide diversity, which show the characteristics of "artificial bottleneck" compared with local naturalized wild populations. When these farmed oysters are mixed with wild oysters, reproduction and infiltration may occur, affecting the gene pool composition of wild populations.

4 Genetic Connectivity Studies in Oysters

4.1 Development of molecular markers and high-throughput sequencing technologies

The research on genetic connectivity of marine shellfish such as oysters depends on the continuous advancement of molecular genetic marking technology. Early studies mostly used markers such as mitochondrial DNA sequences and isoenzymes to identify population differences. The phylogenetic relationship and general genetic differentiation pattern of oyster populations can be analyzed using mitochondrial COI gene sequences. However, the amount of information about a single gene marker is limited, making it difficult to accurately quantify connectivity. Since the 1990s, highly polymorphic nuclear loci such as microsatellite DNA have been widely used in the genetic research of oyster populations. Due to its co-dominance and high variation, microsatellite markers can provide rich information such as genetic differentiation (F_ST), heterozygation, etc., and are used to evaluate the genetic structure and diversity levels of different geographical populations such as European flat oysters.

Entering the 21st century, the rise of high-throughput sequencing technology has brought revolutionary changes to the genetic research of oysters. Simplified genome sequencing methods such as RAD-Seq (restricted cleavage site association sequencing) and GBS (genome degenerate sequencing) can obtain thousands of SNP markers across the genome, greatly improving resolution (Gutierrez et al., 2017). Going further, the huge whole-genome sequencing and genome assembly of oyster species have also made breakthroughs in recent years. Pacific oyster *C. gigas* sequenced the entire genome (about 0.59 Gb in size) as early as 2012. The genomes of species such as Eastern oyster *C. virginica*, turbidite oyster *S. cucullata* were successively published, providing a reference framework for population genomics research. Li et al. (2024) constructed the *Crassostrea ariakensis* genome at the Yangtze River Estuary at a near chromosome level. Combined with the whole genome resequencing data, they analyzed the genetic structure of the northern, central and southern groups of this species, as well as the effect of temperature salinity gradient on its adaptive variation. With the decline in sequencing costs, whole genome resequencing (WGS) has gradually been used in large sample population research of oysters.

4.2 Analysis model and evaluation index of population genetic structure

After obtaining molecular marker data, population genetic analysis models and statistical indicators need to be used to evaluate oyster population structure and connectivity. F_statistics (such as F_ST) are the most commonly used population differentiation metrics, reflecting the proportion of genetic variance among subpopulations. Lower F_ST (close to 0) means no obvious differentiation between populations and frequent gene communication; higher F_ST (close to 1) means that most of the variation exists between populations and limited communication. In oyster studies, differences among geographic populations are often quantified by calculating paired F_ST (Silliman, 2018).

Genetic diversity indicators are also important aspects of evaluating population status, including mean heterogeneity (H_O, H_E) and allelic richness. By comparing the diversity levels of different populations, it can be judged which populations have experienced bottlenecks or expansions. Under multigene marker data, clustering analysis and dimensionality reduction analysis are common tools for revealing implicit structures. Bayesian clustering methods such as STRUCTURE can attribute individuals to several genetic clusters based on the genotype to determine the most likely population composition number K. By testing different K values and calculating likelihoods, researchers can determine the number of genetic populations supported by the data (Thongda et al., 2018).

To detect the direction and extent of gene communication among populations, a mobility estimation model has also been applied. For example, using Migrate-n software based on co-ancestry processes, two-way mobility and historical population size can be estimated, or the recent gene flow ratio can be inferred by BayesAss. This type of approach is relatively rare in oyster studies, but is very helpful in understanding asymmetric current transmission (such as gene flows with stronger downstream directions). Some studies also used isolation-by-distance (IBD) analysis to examine the correlation between genetic distance and geographical distance to determine whether population structure meets a simple diffusion model. For contiguously distributed oyster coastal populations, significant IBD patterns can often be detected, meaning that gene flow decays with distance, for example, genetic differences are observed in oyster populations on the eastern coast of North America as the increase in coastline distance.

4.3 Gene flow, historical expansion and pedigree geographic modeling methods

In addition to describing the current population structure, the study of oyster genetic connectivity involves reconstruction of historical gene flows and population dynamics, as well as lineage geographic analysis in combination with geographical information. Genealogical geography methods analyze population historical expansion and migration routes by linking genetic branches with geographical distribution. In oyster studies, mitochondrial DNA haplotype networks and phylogenetic trees are commonly used pedigree geoanalysis tools. Researchers can construct haplotype network maps of different geographical groups to observe whether there are geographically clustered haplotypes and their divergence depths. The mitochondrial haplotype lineage of European flat oysters showed several regional branches, one of which extended from the North Sea to France as a mosaic distribution, presumably related to the mixing caused by artificial transplants, while several branches were limited to a small range and were interpreted as remains of ice age shelters. By combining this genetic evidence with paleoclimatic geography knowledge, the diffusion path and velocity of oysters after ice can be inferred.

In order to more quantitatively characterize historical gene flows and population dynamics, researchers began to use Bayesian inference methods based on the co-alescent model. For example, Approximate Bayesian Computation (ABC) can simulate different historical scenarios (such as population separation at different times, different mobility, etc.), compare the simulated genetic indicators with the measured data to calculate the likelihood, and thus select the best possible historical models. In terms of gene flow direction, migration models (such as MLE method) can estimate the size and direction of continuous gene flow between branches after ancestral population division under the shared aliascent framework.

5 Case Studies: Analysis of Oyster Population in Typical Sea Areas in Global

5.1 The genetic structure of Pacific oysters in the northwest Pacific (China, Japan, South Korea)

Pacific oysters (*Crassostrea gigas*) are native to the northwest Pacific coast, including eastern China, the Korean Peninsula, Japan and the Russian Far East. They are the most representative oyster species in the region. Historically, due to widespread continuous coastal distribution and long-distance floating juveniles, the Northwest Pacific Pacific oysters were considered to be a highly connected single group. However, genetic research in recent years has found that there is still a certain geographical structure and differentiation within it. Early analysis based on mitochondrial and nuclear DNA markers showed that Pacific oysters (sometimes called "*Portuguese oysters*") in southern China were slightly genetically different from populations in northern Japan, and was speculated to be a result of Pleistocene Ice Age. This view is further supported by higher resolution genome-wide data. Qi et al. (2017) used SNP markers to compare Pacific oysters introduced in China, Japan and Europe, and found that the F_ST between the Chinese and Japanese populations was about 0.024, which was significantly higher than the F_ST indirectly close to 0 in Japan and European or North American breeding populations. This suggests that within the native distribution area, Pacific oysters along the Chinese coast have experienced mild genetic differentiation with Japanese populations (Qi et al., 2017). The reasons for this differentiation may include changes in the paleomarine environment (such as the Taiwan Strait was exposed during the last ice age, thus isolating the north-south population) and the restrictions on the north-to-north transmission of juveniles in the current East China Sea and Yellow Sea circulation pattern.

5.2 Population connectivity and management of oysters along the Eastern Atlantic coast of North America

The eastern oyster (*Crassostrea virginica*) along the Atlantic coast of North America is distributed from the vast coastal zone between the Gulf of Canada and the Gulf of Mexico. It is the cornerstone species of local coastal ecological and fishery resources. The genetic connectivity pattern of its population is deeply affected by coastline topography and hydrological conditions. It can be summarized as: the Atlantic coast and the Gulf Coast are relatively independent, while the coastal interior shows a certain gradient change. RAD markers and genome-wide studies consistently show that there is a dividing line between the genetic structure of the eastern oysters near the Florida Peninsula. The Atlantic coastal populations and the Gulf of Mexico populations allele frequencies were significantly different at multiple nuclear loci, with F_ST reaching above 0.05, showing significant genetic differentiation.

Inside each side, the eastern oyster population is generally higher in connectivity but with regional gradients and estuary effects. Along the Atlantic coast, from New England, Chesapeake Bay to the northeastern coast of Florida, the gene flow is continuously distributed, but due to the long coastline, genetic differences between populations will rise slightly with the increase of distance, which is the classic "isolation distance-by-distance" model. As the largest estuary bay on the east coast of the United States, Chesapeake Bay also has certain differences between its internal oyster subgroup and its offshore coast (Hornick and Plough, 2021).

Based on these pattern characteristics, North America adopted a strategy of regional partitioning and localized recovery for the management of oyster resources in the eastern region. Due to the obvious differences in ethnic groups in the Atlantic and Gulf of Mexico, managers usually avoid transporting oyster seedlings across these two regions to avoid potentially undermining the adaptive balance of the local gene bank. Disease control and genetic breeding are also key points in management (Proestou et al., 2016). Eastern oysters are susceptible to MSX and Dermo diseases, and for this purpose, disease-resistant strains have been cultivated and used for breeding and recovery. However, it should be noted that artificial breeding may reduce population genetic diversity. Therefore, when large-scale release of disease-resistant seedlings, the management department will supervise their genetic composition to avoid excessive proportion of single-class families.

5.3 Isolation and recovery potential of rock oyster populations in Europe and the Southern Hemisphere

The native oysters along the coast and southern hemispheres mostly belong to the genus Flat Oyster and the genus Rock Oyster. Their populations often experience a severe decline after historical over-catching. They are currently mainly isolated populations, but they also show certain recovery potential and management value. European native oysters were once widely distributed in coastal waters from Norway, the United Kingdom to the Mediterranean, forming a large number of oyster beds (Figure 2). However, since the late 19th century, European flat oysters have become functionally extinct in many sea areas due to factors such as over-digging and disease. Currently, there are only a few sporadic wild populations, such as Loch Ryan in Scotland, the west coast of Sweden with colder water temperatures, and the local Gulf areas in France, Spain and other places. These surviving populations are limited in size, far apart from each other, and are basically in genetic isolation (Monteiro et al., 2024).

In view of the extreme recession of European flat oysters, countries are currently actively advancing their recovery plans. For example, Germany piloted the deployment of artificially bred young oysters in the North Sea to rebuild reef beds; the United Kingdom, the Netherlands and others established the "Native Oyster Restoration Alliance" (NORA) to coordinate international cooperation. These recovery projects emphasize two aspects in genetic management: one is to use local legacy oysters as parents as possible to preserve regional unique genotypes; the other is to maintain a high number of parents and balanced family contributions during the proliferation process to increase diversity. Preliminary results show that artificial assistance can help break the vicious cycle of "small group-low reproductive rate" (Pouvreau et al., 2023).

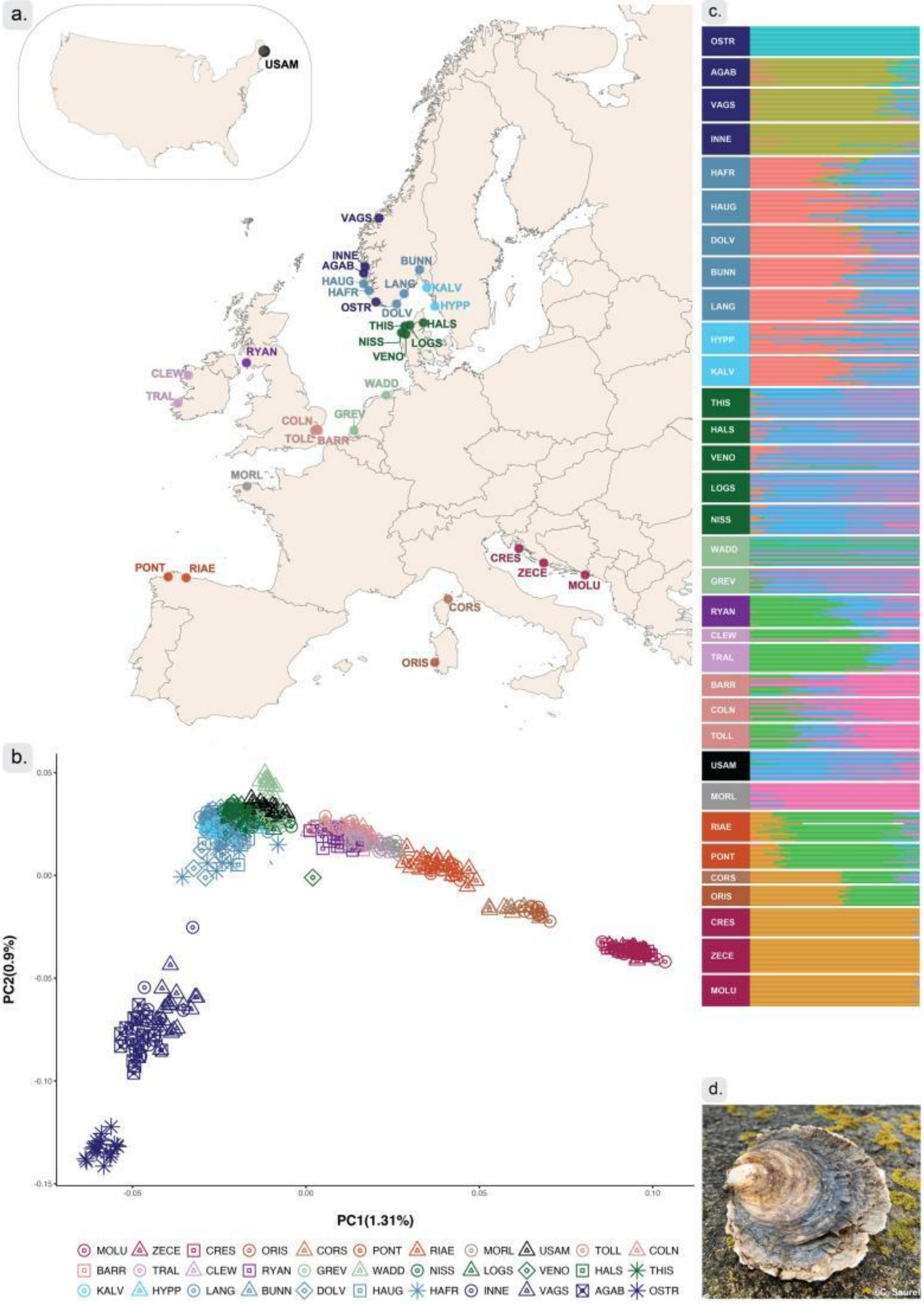

Figure 2 Sampling sites and genetic clusters. (a) Sampling sites for *O. edulis*; colours match the clustering in the PCA. (b) PCA plot of the first two principal components using 1 404 180 LD-pruned genome-wide SNPs. (c) Individual admixture proportions by sampling site, using LD-pruned genome-wide SNPs, for ten ancestral (K) clusters. (d) *Ostrea edulis* adult, Limfjorden, Denmark (2024) (Adopted from Monteiro et al., 2024)

6 Application of Genetic Connectivity in Protection and Resource Management

6.1 The significance of genetic diversity on adaptability and population recovery

Genetic diversity is known as the basic level of biodiversity and plays a decisive role in species adapting to environmental changes and long-term population survival. For a wide range of species like oysters, sufficient genetic variation means more possible phenotypic combinations in the population, thus having a greater chance of genotypes adapted to new environmental conditions such as temperature rise, salinity changes, or new pathogens (Puritz et al., 2022). Studies have shown that oyster populations with high genetic diversity tend to be more resistant to disease outbreaks or extreme climate events and recover faster after disasters.

Genetic connectivity is one of the key mechanisms to maintain diversity. Through gene flow, alleles in different regional populations can be recombined, thereby increasing genetic variation locally. In the context of habitat fragmentation, promoting moderate connectivity among populations can help alleviate the decline in diversity caused by inbredness and genetic drift. In management practice, this means avoiding over-isolating oyster populations. A Korean Pacific oyster study is an example: they strengthened the local population by introducing Japanese oysters with different genetic backgrounds, and the population diversity metrics created were increased by about 10%~15%, and achieved a 4-fold increase in effective population size (Hughes et al., 2019). However, attention should also be paid to balance "genetic rescue" and "external gene invasion".

In addition to natural population protection, the management of genetic diversity should also be paid attention to in breeding and recovery situations. During artificial breeding, as many parents as possible should be used and their contributions should be balanced to prevent the effective population size of the offspring population from being too small. Experts point out that aquaculture often tends toward a few high-yield lines, which will lead to a significant decline in genetic diversity and will need to be alleviated by rotating broodstock or introducing wild bloodlines. For restoration projects, such as artificial reef building, it is necessary to ensure that the young oysters released have sufficient genetic variation to adapt to the on-site environment, otherwise the restoration population may be difficult to maintain itself.

6.2 Connectivity protection strategies in the context of habitat fragmentation

With coastal development and environmental degradation, many oyster habitats are fragmented and the risk of populations being isolated from each other increases. In this context, specialized protection strategies need to be developed to maintain or restore genetic connectivity networks. The first is to optimize the protection space pattern. Based on the knowledge of existing oyster reefs and population distributions, a systematic planning approach can be used to establish a network of interconnected protected areas rather than an isolated single area. Research shows that controlling the protection zone spacing within the average diffusion distance of oyster juveniles helps ensure sufficient genetic exchange between protected zones. For example, when planning for the recovery of native oysters in Europe, NORA recommends establishing multiple recovery points within a range of dozens of kilometers, so that oyster juveniles in one area can achieve genetic exchange through phased diffusion. For those areas that are "functionally extinct", genetic connectivity can be gradually restored from zero to near-natural state through continuous reef construction in adjacent seas.

Secondly, the construction of habitat corridors is also a feasible strategy. Under natural conditions, oyster reefs are often distributed in chains along the estuary bay, which itself acts as a "corridor" for gene flow. If these continuous belts are destroyed, artificial construction of alternative corridors can be considered. In terms of controlling human activities, it is also necessary to focus on maintaining connectivity (Powers, 2025). It should be pointed out that in the case of severe habitat fragmentation, sometimes auxiliary migration is also a last resort. When both populations are geographically close to isolation but both face the risk of extinction, artificial transfer of some individuals can introduce new genetic variations, reduce inbredness and improve overall survival opportunities. This is called "genetic rescue" and has successful cases in other species. However, the differences in adaptability of the two groups must be carefully evaluated when implementing oysters to avoid causing genetic contamination or disease transmission.

6.3 Genetic interference and management measures of wild and breeding populations

Because oysters have both fishery and breeding values, it is inevitable that there will be mutual influence between wild populations and breeding populations, causing potential genetic interference problems. It is mainly reflected in two aspects: First, artificial selection and inbreding during the breeding process may cause the genetic structure of farmed oysters to deviate from the wild population. If the two reproductive and mating occurs, it will change the genetic frequency of the wild population; second, farmed oysters introduced by foreign strains or species will escape and compete with local oysters or hybridize, causing gene invasion or germplasm to become mixed.

In response to wild-cultural genetic interference, various measures can be taken to alleviate it. The first is to use sterile or semi-sterile breeding strains, such as breeding triploid oysters, which are widely used to prevent summer reproduction and improve meat quality. Due to their extremely low fertility, these triploids significantly reduce the possibility of hybridization with wild oysters and fundamentally reduce the risk of infiltration. Secondly, optimizing the breeding layout and avoiding the establishment of large-scale farms near important wild oyster beds is also a way to reduce interference. Third, it is very necessary to establish a genetic monitoring plan. Regular sampling and analysis of wild populations in the breeding area and surrounding areas. If the genetic diversity or endemic allelic frequency of wild populations is found to be significantly reduced, the breeding management strategy needs to be adjusted. In addition, for the problem of the spread of imported alien oyster species (such as Pacific oysters in Europe) in the wild, management is usually based on prevention and control, and it is necessary to limit its competition for local oysters and habitat occupation as much as possible. If the alien species cannot be eradicated, it should be monitored for signs of hybridization with the local species.

7 Future Threats and Response: Genetic Response in Environmental Change

7.1 Prediction of the impact of climate change on distribution range and gene flow

Global climate change is changing the marine environment at an unprecedented rate, which will profoundly affect the distribution pattern and genetic connectivity of oysters. Sea water heating is one of the most direct influencing factors. As the average temperature rises, suitable habitats for many oyster species will experience geographical displacement, which is expected to move towards higher latitudes overall. The model predicts that by the mid-21st century, the distribution of temperate oysters (such as European flat oysters and eastern oysters) may expand by hundreds of kilometers, while habitats on the southern edge may shrink due to excessive water temperature and frequent hypoxia events. This means that genetic exchanges between currently distant populations may be possible in the future through new mediated habitats (Abe, 2021).

Changes in the current pattern are also an important aspect of climate change affecting gene flow. Global warming may cause weakening of ocean circulation or offsetting paths. For example, if the Kuroshio pathway moves northward or changes in intensity, the northwestern Pacific Pacific oyster juvenile transport chain may be disturbed, thereby changing the gene exchange rate between the Chinese-Japanese populations (Scanes et al., 2021). Sea level rise will flood new lowlands, creating new coastal lagoons and mangrove habitats, which may play a role in increasing oyster habitat continuity and promoting genetic connectivity in certain areas. But on the other hand, too fast sea level rise may exceed the rate of upward growth of oyster reefs, causing the reef to be submerged and killed, causing the original continuous distribution to break, and close attention is needed. The increasing frequency of extreme weather events is also part of climate change. Hurricanes, warm winters, ocean heat waves, etc. will cause great ups and downs in the oyster population. Frequent large-scale deaths will significantly reduce the effective size of the population, aggravating genetic drift and loss of diversity.

7.2 The perturbation mechanism of marine acidification and heat stress on genetic structure

In addition to temperature changes, ocean acidification and heat stress are another set of environmental stresses brought about by climate change, which may have hidden and long-term effects on the genetic structure of oysters. Marine acidification directly affects the calcification and survival of oyster juveniles. A large number of experimental studies and a series of meta-analysis have confirmed that elevated water pCO_2 will reduce the growth rate of oyster juveniles and increase early mortality. Long-term observations of the Sydney Rock oysters in Australia show that the average shell length of the offspring of oysters propagated under high CO_2 conditions significantly reduces the average shell length and the survival rate is reduced. This selective pressure means that specific genotypes that can survive an acidification environment will increase in the proportion of the next generation, thereby changing the allelic frequency of the population.

The effects of heat stress on oysters are more intuitive and can lead to large-scale thermal death and reproduction failure of shellfish. In recent years, unprecedented ocean heat waves have occurred on the northwest coast of North America, causing high mortality rates of local farming and wild oysters, which has attracted attention. In addition to the immediate blow to population size, such events also have potential genetic effects. Extreme high temperatures may quickly eliminate families with poor heat tolerance, and surviving individuals tend to carry specific heat-tolerant alleles or phenotypes (Zhao et al., 2024). The study found that after experiencing a heat wave, the frequency of specific alleles of certain heat shock protein genes in the wild Pacific oyster population in Canada's BC province has increased significantly, suggesting a strong choice. Ocean acidification and heating also have a composite effect. On the one hand, heating can aggravate the adverse effects of acidification on juveniles, because juvenile metabolism accelerates at high temperatures and requires more stable calcification. On the other hand, it is interesting that certain studies have shown that cross-generational exposure may induce partial relief: allowing parental oysters to live under acidified conditions, and their offspring exhibit higher survival rates in acidified water than controls. This means that there are mechanisms of epigenetic adaptation or phenotypic plasticity that can offset the problem of insufficient genetic diversity to some extent. However, this plasticity is not infinite and needs to be supported by genetic mutation in more severe situations.

7.3 Research on genetic improvement and adaptive evolution in coping with environmental stress

Faced with multiple pressures such as climate change and environmental pollution, research and application of genetic means to improve the adaptability of oyster populations has become an important direction. Choosing breeding is one of the most realistic and feasible ways at present. By breeding oysters in controlled environments for generations, people can target favorable variants, thereby cultivating more high temperature, acid or disease-resistant strains. Advances in genomics and molecular breeding technology provide new tools for accelerating genetic improvement. Genome-wide selection can predict its adult resistant phenotype by marking at the juvenile shellfish stage, thereby screening the best seedlings and greatly shortening the breeding cycle. Gene editing techniques (such as CRISPR/Cas9) have the potential to target the modification of known antiresistance-related genes in the oyster genome (Guo et al., 2018). In addition to artificial improvement, promoting natural adaptive evolution is also one of the strategies to enhance population stress resistance. The so-called "adaptive evolution" refers to the process of accumulation of favorable genes in wild populations under natural selection. To this end, we need to create conditions to allow as many different genetic types as possible to participate in reproduction and guide the selection of directions through environmental management.

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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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