

## Global Genetic Flow and Population Structure of *Scomberomorus* spp.: Insights from Multi-Genomic Data Analysis

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**Abstract** The genus *Scomberomorus* spp. is an important middle- and upper-level economic fish with significant economic and ecological value. However, high-intensity development of global fisheries puts mackerel populations at risk of decreased genetic diversity and changes in population structure. This study reviews the progress of global gene flow and population structure in the genus Mackerel fish, and focuses on the role of multigenomic data in it. We also deeply explored the influence mechanisms of environmental factors such as ocean currents, seawater temperature salts, and overfishing on gene exchange and population structure of mackerel. Studies have shown that there is a certain degree of genetic differentiation between different geographical populations of mackerels, and it also maintains genetic communication through migration and currents; among which ocean currents can play a dual role in connecting populations and isolating populations. This study finally proposes that the genetic research on mackerel population still has shortcomings such as regional coverage imbalance and single marker types. In the future, research should be strengthened in combination with multigenomic data and ecological monitoring to support the sustainable management of marine fishery resources and the effective protection of mackerel species.

**Keywords** Mackerel; Gene flow; Population structure; Genetic diversity; Multigenomic data; Fishery management

### 1 Introduction

The genus *Scomberomorus* belongs to the family Scombridae, including about 20 species such as narrowband mackerel, Japanese mackerel, and broadband mackerel. It is an important middle- and upper-level predatory fish in tropical and temperate waters around the world. The meat of mackerel is delicious, rich in high-quality protein and unsaturated fatty acids, and has high economic value worldwide. For example, Japanese mackerel (*S. niphonius*) is a famous edible fish "mackerel" in China and East Asia. The narrow-band mackerel (*S. commercialis*) is widely distributed in the Indian Ocean-Western Pacific and is an important fishery resource for coastal countries. In the Western Atlantic Ocean, Brazilian mackerel (*S. brasiliensis*) and kingfish (*S. cavalla*) support local commercial and recreational fisheries (Gold et al., 2010). Since mackerels are generally located in the high trophic level of marine food networks, they play an important role in maintaining the health of marine ecosystems.

In recent decades, the global fishing intensity has continued to increase, and many mackerel populations have shown signs of decline. Brazilian mackerel production has dropped significantly along the northeastern coast of Brazil and is believed to have overfished (Siccha-Ramirez et al., 2018). Offshore China, the annual catch of Japanese mackerels has exceeded 400 000 tons in recent years, making it an important catch species in the Bohai Sea, the Yellow Sea and the East China Sea. However, with offshore environmental pollution and overfishing, its germplasm resources are facing decay, and the decline in genetic diversity may endanger population sustainability. Protecting the genetic resources of marine fish such as mackerels and maintaining the stability of their population structure has become one of the important tasks of fishery management. Genetic diversity is the basis for species to adapt to environmental changes and resist risks such as disease. Improving the understanding of the genetic structure of target fish can help formulate scientific management and conservation measures.

Traditionally, fishery science has studied the migration routes and population ownership of fish through marking release, catch statistics and ecological surveys. However, these methods often have difficulty accurately characterizing the degree of genetic communication. The development of molecular genetics technology provides a more direct tool for analyzing fish population structure. Since the end of the 20th century, some scholars have begun to use mitochondrial DNA sequence variation and nuclear DNA microsatellite markers to analyze the genetic diversity of mackerel populations (Johnson et al., 2021). Entering the 21st century, with the advent of high-throughput sequencing technologies, it has become possible to conduct population genetic research using genome-wide SNP markers and simplified genome sequencing methods (such as RAD-seq, etc.), allowing us to identify subtle population differentiation at the genome level (Joy et al., 2020).

Based on the above background, this study reviews the systematic classification and global distribution pattern of the genus Mackerel, introduces its main species and their respective geographical distribution ranges and ecological habits; summarizes the historical progress of genetic diversity and population structure research, including the early use of genetic markers such as mitochondrial DNA and microsatellites, as well as the application of nuclear genomic SNP and multigenomic technology in recent years. Comparing different seas around the world.

## 2 System Classification and Geographical Distribution of Mackerel

### 2.1 The main species of the genus *Scomberomorus* spp.

The genus *Scomberomorus* belongs to the family Macadidae, commonly known as Macadidae and Macadidae. It is a medium-sized migratory fish species, mainly distributed in the coastal areas of China, Japan and South Korea in the northwest Pacific, and also enters the Bohai Sea and the Yellow Sea. Broadband Macadidae (*S. guttatus*), distributed in the Indo-Western Pacific, including the South China Sea and Southeast Asia, commonly known as Spot Macadidae or Indo-Pacific King Macadidae; Pacific Spanish Macadidae (*S. maculatus*) and King Macadidae (*S. cavalla*), distributed along the western Atlantic Ocean; *S. brasiliensis*, distributed in the Caribbean Sea and the Atlantic Ocean in South America; and some regionally distributed species such as *S. semifasciatus* in Australia and West African Macadidae (*S. tritor*) etc. In addition, the "Korean mackerel" (*S. koreanus*) discovered in the Indian Ocean in recent years has been identified as an independent species through morphological and genetic identification, and is distributed along the northern coast of the Indian Ocean (Jeena et al., 2022; Zeng et al., 2022). These species are medium to large (usually 30 cm to more than 1 meter in length), have slender bodies, side flatness, sharp teeth, and have many spots or stripes on their backs. They are fierce predators. Despite the similar appearance, different species have differences in scales, tooth type, spine number and body color patterns, which can be classified and identified.

### 2.2 Global distribution pattern and ecological habitat environment

The genus mackerel mainly lives in the continental shelf and coastal waters around the islands, and is a highly migratory fish. In the Indian Ocean-Western Pacific region, narrow band mackerels are widely distributed, from the Red Sea and the Arabian Sea, through the Indian coast to Southeast Asia and the South China Sea, and extending to the Melanesian Islands in northern Australia and the Western Pacific. Japanese mackerel mainly moves in the northwest Pacific Ocean, ranging from the Bohai Sea and the Yellow Sea to the north, through the East China Sea to the northern part of the South China Sea, and to the coast of Vietnam in the south. Broadband mackerel is common in the Indian Ocean and South China Sea and offshore Southeast Asia (Jeena et al., 2022), and is an important catch in the Gulf of Bengal, the Gulf of Thailand and the Malay Islands (Figure 1). In Atlantic waters, king fish (also known as narrow-tooth mackerel) is distributed in warm waters of the Western Atlantic Ocean, extending from the southeastern coast of the United States and the Gulf of Mexico to southern Brazil; Spanish mackerel (Flower Spot Mackerel) is more common on the Atlantic coast of the United States and the northern Gulf of Mexico; Sierra mackerel is mainly distributed in the Caribbean Sea and northern coast of South America (Cunha et al., 2020). Most species prefer warm sea areas with water temperatures of 20~30°C, and have significant seasonal migration patterns throughout the year: they migrate to higher latitude spawning grounds in summer, and return to lower latitude waters to overwinter in winter.

### 2.3 Brief description of the relationship between population characteristics and evolution

Due to geographical isolation and environmental differences, there may be differences in phenotypic characteristics and genetic composition of mackerel populations distributed in different sea areas. Through morphological research in the early days, some scholars divided Japanese mackerels along the coast of China into Yellow and Bohai Sea populations and East China Sea populations based on metrology characteristics, suggesting that the groups in these two major sea areas may be independent of each other. However, mitochondrial DNA sequence analysis did not detect significant genetic differentiation between the Yellow Sea and East China Sea populations, showing high genetic similarity (Zhu et al., 2016). This suggests that traditional morphological classifications may be affected by environmental shaping, and genetic markers can provide independent evidence. It is generally believed that Japanese mackerels along the coast of China may have genetic differentiation in the Yellow and Bohai Seas and the East China Sea, but the degree is relatively low. In the Indian Ocean region, studies have found that narrowband mackerels may have east-west differentiation across the "Wallace Line": East Indian populations are genetically different from Western Australian populations, similar to the pattern of differentiation of other Indo-Pacific marine organisms on both sides of this biogeographical boundary. The mackerel population along the Atlantic Ocean is completely different from the Indo-Pacific species because it is separated from the North and South American continents. But inside the Atlantic Ocean, populations in different regions are closely linked. Taking the Sierra mackerel on the coast of Brazil as an example, the populations from Kumana, Venezuela to the southern end of Brazil have low genetic diversity and frequent sharing of haplotypes, indicating that it is a single genetic library. This result suggests that the Sierra mackerel population on the western Atlantic Ocean is integrated and has no significant differentiation (Santa Brígida et al., 2007; Cunha et al., 2020).

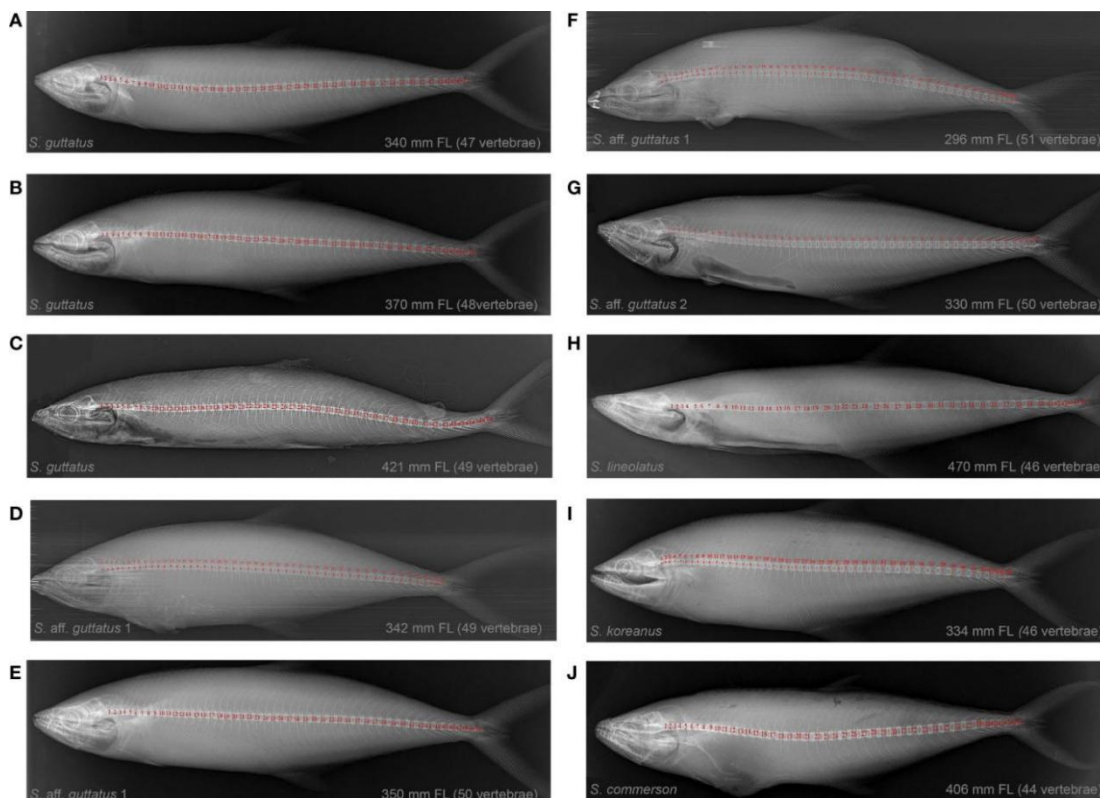


Figure 1 Digital X-ray images of *Scomberomorus* species (A-J) from the Northern Indian Ocean revealing the diversity, fork length (FL), and number of vertebrae (Adopted from Jeena et al., 2022)

## 3 Research Progress on Genetic Diversity and Population Structure

### 3.1 Early study of mitochondrial DNA and microsatellite markers

Molecular research on the genetic structure of mackerel populations began in the late 20th and early 21st century. Mitochondrial DNA (mtDNA) is widely used in fish population geography research due to its single parental

inheritance and high variability rate. One of the earliest related work was the analysis of the sequence of the Japanese mackerel mtDNA control region. The study found that the Japanese mackerel population in the Yellow Sea and East China Sea in China share a majority haplotype, with low nucleotide diversity and no significant geographical differentiation (Widayanti et al., 2024).

Nuclear DNA microsatellite (SSR) markers are also used in early population research of mackerels due to their high polymorphism. Radhakrishnan et al. (2018) developed 12 microsatellite sites and analyzed narrowband mackerel samples from five locations in the northern Indian Ocean (Arabic Sea and Bay of Bengal). The results showed that the alleles of each population were very similar, with the overall  $F_{ST}$  value only 0.0023~0.027, and AMOVA showed that most of the variations came from within the population. Bayesian clustering analysis failed to distinguish the geographical origin of the samples, supporting the conclusion that narrow-band mackerels in this area belonged to a single group. This is consistent with mtDNA research, indicating that the genetic connectivity of narrowband mackerel populations is very high along the coast of India. Experts used microsatellites to detect the differences between broadband mackerels in the northern and central South China Sea, and found that there were statistical differences in the frequency of alleles in the two groups, and speculated that it may have a certain degree of isolation due to coastal water mass barriers (Zeng et al., 2012).

### 3.2 Advances in the application of nuclear genome and SNP markers

With the advancement of molecular biology technology, researchers have begun to use single nucleotide polymorphism (SNP) markers in the nuclear genome to analyze the mackerel population structure. Nuclear DNA can reflect bi-line information of parents and has more advantages in exploring recent population dynamics. Shui et al. (2009) used AFLP (amplified fragment length polymorphism) for the first time to analyze the Yellow Sea and East China Sea Japanese mackerel. The results showed that the genetic differentiation index between the populations in the two sea areas was about 0.04, reaching a significant level. This is very different from the mitochondrial results, suggesting that the nuclear gene may have detected weak structures not reflected by the maternal marker (Li et al., 2024). Although AFLP is not as accurate as SNP, this study provides clues for the existence of hidden differentiation of mackerels. In the past decade, high-throughput sequencing has allowed people to develop thousands of SNP markers for population genetic analysis. Many recent achievements have taken advantage of this advantage (Siccha-Ramirez et al., 2018).

### 3.3 New perspectives brought by multigenomic technology (such as RAD-seq, WGS, ddRAD, etc.)

In recent years, high-throughput sequencing technology has developed rapidly, with a variety of simplified genome sequencing methods such as whole genome resequencing, RAD-seq (restriction enzyme fragment association sequencing), ddRAD, DArTseq, etc., which can obtain massive genetic markers at one time. These multigenomic technologies have revolutionized the genetics of marine fish populations. Compared with traditional research that relies on several gene fragments or dozens of microsatellite sites, the new technology can generate thousands of SNP markers, greatly improving statistical power, and is particularly suitable for detecting subtle population differentiation and gene flow patterns. For fish with high mobility such as mackerel, previous studies have often made it difficult to distinguish the population structure due to the low genetic differences, and the application of multigenomic data overcomes this problem. Widayanti et al. (2024) used environmental DNA technology combined with high-throughput sequencing to evaluate fish diversity in Taiwan Straits, and also detected the frequency difference in the occurrence of Japanese mackerels in different seasons, suggesting that population dynamics are related to seasonal changes in ocean currents (Widayanti et al., 2024). Although this study is not aimed at the genome of mackerel, it demonstrates new technologies that can provide information on group changes in mackerels on the ecological time scale. In terms of whole genome sequencing, Li et al. (2024) have constructed a high-quality chromosomal-level reference genome of broadband mackerel. This provides a basis for future group comparisons of mackerels in the whole genome-wide range. With the reference genome, gene variants associated with population differentiation and local adaptation can be more accurately located, identifying potential adaptive genetic markers (Siccha-Ramirez et al., 2018).



## 4 Comparison of Mackerel Population Structure in Different Sea Areas Around the world

### 4.1 Differences in the Indian Ocean and Western Pacific populations

The Indian Ocean and the Western Pacific waters are integrated, but they contain a complex semi-closed marginal sea and island system. For highly migratory fish such as mackerel, the population structure in this vast area has always attracted much attention. Through the aforementioned high resolution studies, we have known that the narrowband mackerel (*S. commercialis*) has a distinct genetic differentiation pattern in the northern Indian Ocean. It is reported that narrowband mackerels sampled in the North Indian Ocean-East Indian Ocean can be divided into at least four genetic groups. Among them, groups in the northeastern Indian Ocean (the Gulf of Bengal), the eastern (near the Malay Peninsula), and the central and northern Indian Ocean were all identified as belonging to different gene clusters, and the F<sub>ST</sub> analysis also supported significant differences between the groups (Vineesh et al., 2018). In particular, the study found that population genetic differences are positively correlated with geographical distance, showing a clear isolation by distance pattern. This means that even without absolute geographical barriers, distant groups gradually accumulate differences in gene frequencies due to limited migration individuals.

### 4.2 Genetic pattern of the Atlantic and Caribbean

Compared with the high diversity of the Indo-Western Pacific, there are fewer species of mackerel in the Atlantic, and their population structure studies are mainly focused on kingfish and Sierra mackerel along the Western Atlantic coast. Previous studies of *S. brasiliensis* have shown that the species may constitute a genetic unit throughout the southwestern Atlantic Ocean (Venezuela to southern Brazil). Mitochondrial analysis found that samples from different sampling sites (Cumana, Venezuela, northeastern Brazil, southeastern Brazil) shared most haplotypes, with the interpopulation differentiation index Phi<sub>ST</sub> and the AMOVA results were not significant. Haplotype networks have a star topology, suggesting that population expansion has been experienced historically (Figure 2) (da Cunha et al., 2020). All these evidences support that the Western Atlantic Sierra mackerel is a single genetic population. However, the application of nuclear DNA markers has revised this conclusion. By comparing microsatellite or SNP data from north-south Brazilian samples, there are signs of slight allelic frequency differences between the southern Brazilian population and the northern Brazilian population (Soeth et al., 2022). The reason may be related to the current system along the Brazilian coast: the North Brazilian warm current and the Malvinas cold current intersect in southern Brazil, forming a hydrological barrier, which restricts the exchange of fish in the north and the south. Similar phenomena may also exist on kingfish (*S. cavalla*). Kingfish is widely distributed in the East Coast of North America and the Gulf of Mexico, and traditional views regard it as a single management unit. However, trace element trace element trace and microsatellite studies suggest that there is a certain separation between the king fish in the Gulf of Mexico and the king fish along the Atlantic coast (Gold et al., 2010), and may each lay eggs and return to its original position, thus forming two relatively independent subgroups.

### 4.3 Localized population characteristics of coastal waters in Southeast Asia and China

Southeast Asia and China's offshore in the western Western Pacific are important spawning and fishing areas for mackerels, and are also one of the hot spots for population structure research. The population structure of the major species, Japanese mackerel, has been controversial along the coast of China. Traditionally, it is divided into the Yellow-Bohai Group and the East China Sea Group according to the spawning ground and the fishing flood. There are certain differences in the spawning time and growth parameters of the two. Yang Linlin and others analyzed the otolithic morphology of Japanese mackerels in different spawning sites in China. The results showed that the shape differences in the breeding groups of the three major sea areas of the Bohai Sea, the Yellow Sea and the East China Sea were extremely significant. This shows that Japanese mackerels living in different sea areas have ecologically measurable differentiation characteristics, supporting their relative independence of their breeding populations. Further, the otolith morphological discrimination formula was established using discriminant analysis, which allowed the correct distinction rate of Xiangshan Port (East Sea) and Laizhou Bay (Huang and Bohai Sea) samples to reach 71%, providing a morphological basis for population discrimination. Mitochondrial studies of broadband mackerels in the Gulf of Thailand have shown that there is no obvious genetic

differentiation between the populations in the Gulf of Thailand, which may be due to the fact that the bay is a semi-enclosed water body, and the internal water mass circulation causes the fish to mix (Radhakrishnan et al., 2018).

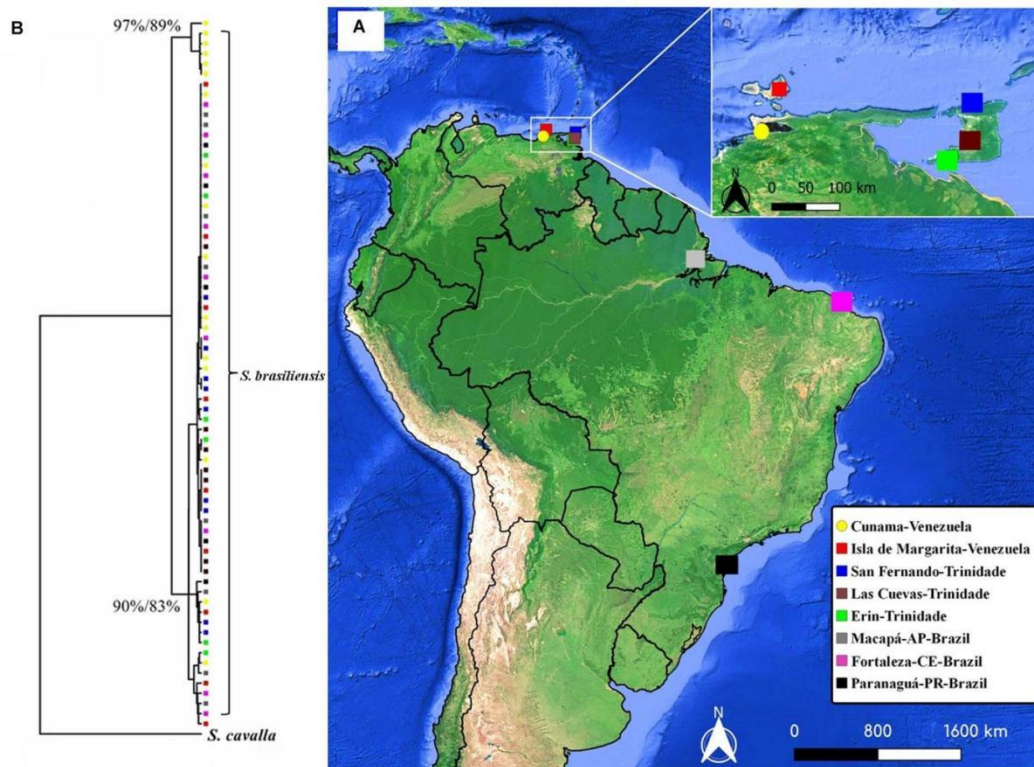


Figure 2 (A) Map of South America showing the eight sites from which the specimens of *S. brasiliensis* analyzed in the present study were obtained: 1- Cumana; 2- Isla de Margarita; 3- San Fernando; 4- Las Cuevas; 5- Erin; 6- Macapá; 7- Fortaleza and 8- Paranaguá. (B) Neighbor-Joining and Maximum Likelihood trees for the *Scomberomorus brasiliensis* haplotypes of the *MT-ND4* gene. Each haplotype is represented by a different color, yellow circles = 1- Cumana, red squares = 2- Isla de Margarita, blue = 3- San Fernando, brown = 4- Las Cuevas, green = 5- Erin, gray = 6- Macapá, pink = 7- Fortaleza and black = 8- Paranaguá (Adopted from da Cunha et al., 2020)

## 5 Factors and Ecological Driving Mechanisms of Gene Flow

### 5.1 The influence of ocean currents and migration pathways on gene communication

#### 5.1.1 The dual role of ocean currents as population connection channels

Ocean currents are a key factor affecting the gene flow of marine fish populations. For mackerels, ocean currents can not only act as "highways" to promote long-distance gene exchange, but also may form environmental barriers and limit the mixing of different groups. In promoting gene flow, strong currents can carry floaty eggs and juvenile fish, making them cross distances that were originally difficult to cross independently. For example, the Kuroshima and its tributaries flow through the East China Sea and Taiwan Straits, bringing the Japanese mackerel fish produced in the southern part of the East China Sea to the northerly Yellow Sea, thus emerging new individuals supplemented by the East China Sea (Sassa and Tsukamoto, 2010).

However, ocean currents also have a barrier effect. When there are water currents of very different natures between the two sea areas, the migration and early life history stages of fish are restricted. Studies show that in cases of low genetic connectivity among populations in the Yellow Sea and East China Sea, the Yangtze River flush water may be an important factor. There are large areas of low-salt water mass in the Huangdonghai summer, separating the northern and southern waters at the plankton level. Through the review of 137 literatures, it was found that more than 65% of the cases believed that there was significant genetic differentiation between the Yellow Sea and the East China Sea marine protection zone, and the freshwater front of the Yangtze River was

considered to be one of the six obstacles. For mackerel, Japanese mackerel spawns mainly in nearshore low-salt water environments (such as Hakka Bay). Once a juvenile fish enters the range of flushed water, it is difficult to go further north, thus forming a partially isolated breeding group in the Yellow Sea and the East China Sea. In addition to freshwater fronts, the intersection of hot and cold flows can also form similar barriers (Yu et al., 2022).

#### 5.1.2 Dynamic regulation of population structure by seasonal changes of ocean currents

Many ocean currents have seasonal characteristics and periodically change with monsoon or climate factors. This seasonal change can have a dynamic impact on fish migration pathways and gene flow. Taking China's coastal areas as an example, in winter, the northeast monsoon is strong, the cold current goes south, the main body of the black tide is eastward away from the shelf, and the water exchange between the Yellow Sea and the East China Sea weakens; in summer, the southwest monsoon prevails, and the warm current goes north to the coast, promoting the connection of water clusters in the two sea areas. Correspondingly, most Japanese mackerels retreat to the East China Sea to overwinter in winter, and go north to the Yellow Sea to lay eggs in summer. Seasonal changes in ocean currents just guide this migration cycle, causing fish in the two sea areas to mix briefly in summer and return to their respective positions in winter (Cheng et al., 2015). This periodic intersection helps maintain genetic exchange between groups without completely confusing the population, because it is not consistent throughout the year. Similarly, in the northern Indian Ocean, the currents in winter and summer reverse under the monsoon drive. Narrow-band mackerels may follow ocean currents and travel to the Arabian Sea and the Bay of Bengal in different seasons to feed or breed. During the alternation of monsoons, fish from different regions may converge in open waters to exchange genetic material (Gwak, 2025).

### 5.2 Genetic response to changes in marine environment

Differences and changes in marine environmental factors will have an impact on the genetic structure of highly migratory fish such as mackerel. On the one hand, different environmental conditions may drive local populations to produce adaptive genetic differentiation; on the other hand, changes in marine environment caused by global climate change will also change population distribution and gene communication patterns. Temperature is one of the important factors. The tolerance range of water temperatures of various species of the genus Mackerel is slightly different. For example, Japanese Mackerel can tolerate lower temperatures in the Yellow Sea for winter, while broadband Mackerel prefers warmer waters. In the long run, temperature gradients may become genetic selection pressures, causing populations of different temperature bands to accumulate different allelic frequencies. For example, Japanese mackerels in higher northern latitudes may present selectable markers on genes associated with cold resistance, distinguishing them from southern populations (Guo et al., 2021). Although this "adaptive differentiation" may not be obvious in neutral markers, it may be detected by genome-wide scans (Figure 3) (Lee et al., 2023). Similar findings have been observed in related groups such as tuna. Salinity is also an influencing factor. Mackerels usually do not enter fresh water, but lay eggs in low-salt areas of the estuary. The low saline environment at the Yangtze River estuary has different selection pressures on embryonic development compared with the outer sea, which may lead to differences in the genetic composition of the egg-laying population in the Yangtze River estuary with the population in higher salinity waters. The spatial differences between environmental factors such as oxygen content and pH in the distribution of mackerel are not extreme, so it is generally believed that the impact is small.

### 5.3 The interference of fishing pressure and artificial isolation on genetic structure

The impact of human activities on the genetic structure of marine fish has attracted widespread attention in recent years. For mackerels, overfishing and man-made isolation are two main human interference factors that may have important implications for their population genetic structure. First, overfishing will lead to a sharp decline in population size and a change in age structure. From a genetic point of view, it is equivalent to a significant reduction in the effective population size ( $N_e$ ), aggravate inbreeding and genetic drift, thereby reducing genetic diversity. For example, Gwak (2025)'s research pointed out that as the number of Sierra mackerels increases in southern Brazil, the genetic diversity indicators of local populations have a downward trend (such as a



decrease in haplotypes). Although the decline is not large at present, long-term high-pressure fishing may trigger genetic bottlenecks (Gwak, 2025). Fishing also tends to remove larger mature fishes in individuals, disrupt the original mating system, and make the actual gamete contribution more tilted to a few small, high-reproductive individuals, which will also reduce the effective transmission of alleles.

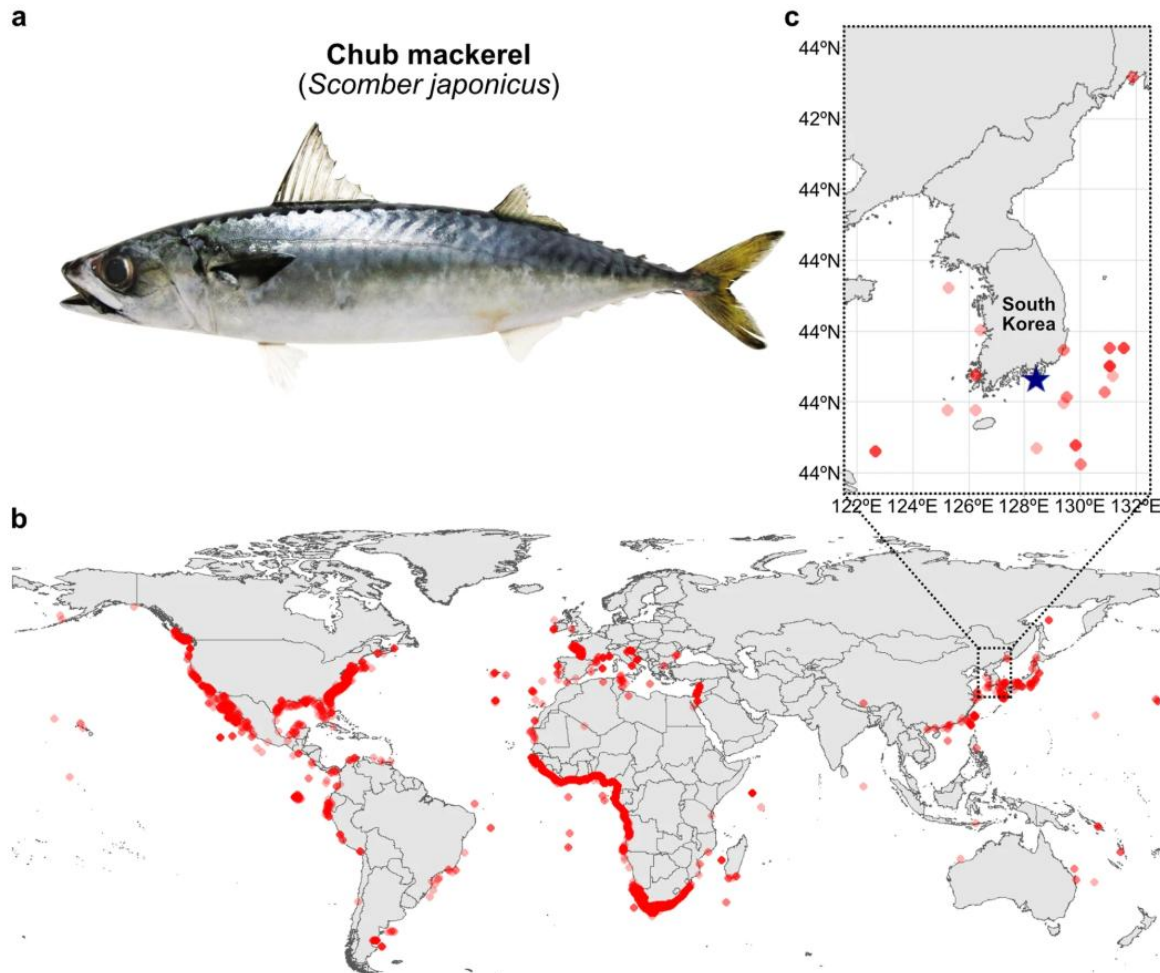


Figure 3 Morphological features, worldwide occurrences and sampling location of chub mackerel (Adopted from Lee et al., 2023)  
 Image caption: (a) Morphology of chub mackerel provided from the Marine Fish Resource Bank of South Korea (MFRBK). (b) Locations of worldwide occurrences of chub mackerel. (c) Local map of the sampling location of the chub mackerel individual of fScoJap1 assembly marked as a blue star mark in South Korea (34°46'15.8" N, 128°23'54.0" E). Each red dot on the map represents an occurrence location. Some dots were shaded (30% transparency) to display overlapping dots (Adopted from Lee et al., 2023)

Secondly, artificial isolation refers to human activities that change habitat connectivity. For example, large-scale offshore projects and increased shipping noise may hinder the traditional migration routes of fish, and the actual effect is similar to that of geographical barriers. Although mackerel has strong swimming ability and no evidence has been shown that human maritime activities have significantly prevented its migration, with the intensification of offshore development, it is not ruled out that local populations have reduced their interactions with other groups due to avoiding human interference, thus gradually genetic differentiation (Cheng et al., 2015). Another human factor is release and breeding escape. If fish from non-homologous groups are artificially introduced into a region and cross with local fish, it may change the genetic structure. Although mackerels usually do not undergo artificial proliferation and release, it is not ruled out that future breeding or breeding trials can cause escape, such as artificially cultivated broadband mackerels escape into the wild and mated with wild groups, which will introduce artificially selected genotypes and "dilute" the wild gene bank. Studies have confirmed the effect of this infiltration on the genetic diversity of wild populations in other fish.



## 6 Advantages and Challenges of Multigenomic Data in Population Research

### 6.1 Application cases of high-throughput sequencing in mackerel research

The rise of high-throughput sequencing (HTS) technology has injected strong impetus into research on marine fish populations, including mackerels. In the study of mackerel, HTS mainly plays a role in two types: one is genome assembly and comparison, and the other is population genome diversity analysis. The former represents the construction of the reference genome of mackerel. Gao et al. (2024) combined PacBio and Hi-C technologies to assemble the chromosomal genome of broadband mackerel (Indo-Tai Mackerel). The genome is about 798 million bp, divided into 24 chromosomes, which are highly collinear with other fishes of the Macadae family (such as tuna). Gene annotation predicts 25 886 protein-encoded genes (Gao et al., 2024). This is the first high-quality whole genome of the genus Mackerel, which is of great significance to subsequent research. Researchers can use it to compare genes across species to find important genes that regulate growth, adapt to temperature, etc. With more mackerel species genome sequencing, mutual comparisons will reveal the genetic basis of the evolutionary history and adaptive differentiation of the genus. The second type of HTS application is population diversity analysis, that is, obtaining massive SNPs through simplified genome sequencing (such as RAD-seq, GBS, DArT-seq, etc.) to calculate population genetic parameters and detect structures.

### 6.2 Problems of data integration, standardization and interspecies comparison

Although multigenomic data present unprecedented opportunities, there are also some challenges. One of them is the integration and standardization of data obtained from different researches. Since each study may use different sequencing platforms, different types of markers (such as ddRAD vs GBS vs whole genome resequencing), and different analyses of Pipeline, it is not easy to directly compare the results. Taking mackerel as an example, if one study uses RAD-seq to find some significant differentiated SNPs in Region A, and another study uses a genome-wide method to find some markers in Region B, we hope to compare the two to see if they have any commonalities. However, due to the different sequencing fragments, the marker coordinates are difficult to correspond directly, and the data need to be located on the reference genome for comparison (Huang et al., 2024). This requires high-quality reference sequences and annotation of each SNP. Fortunately, there is a broadband mackerel reference genome now, and studies should be encouraged to anchor data to the genome in the future, so that a public coordinate framework can be established to facilitate cross-research integration. Another standardization problem is the comparison of the traditional group plot results. The sample size and number of sites of different studies vary, and the calculated diversity indicators (such as  $H_e$ ,  $\pi$  values) and differentiation indicators (such as  $F_{ST}$ ) are comparatively limited. Certain standardized methods should be used, such as recalculating the metrics using the same downsampled set of sites, or introducing reference populations for calibration. In addition to data integration, comparability among different species is also a challenge. Although the genus Mackerel species have a relatively close relationship, they may have significant differences in genetic variation levels and population history. For example, Japanese mackerels may have experienced more serious historical bottlenecks leading to low diversity, while narrowband mackerels may remain large and effective. If compared indiscriminately, wrong conclusions will be drawn. Researchers should avoid directly comparing the  $F_{ST}$  equivalent values of different species, but should pay more attention to the patterns and reasons within each species. At the same time, parallel research designs are also needed among species.

### 6.3 The influence of genetic marker selection and research design on conclusions

In population genetic research, the selected type of genetic marker and research design framework often directly affect the final conclusion, and research such as mackerel is no exception. Different genetic markers have their own biases. For example, mitochondrial DNA is only one-quarter of the effective population size of nuclear DNA due to maternal haploid inheritance, so it is more sensitive to bottlenecks and drift changes, and its ability to detect population differentiation is also different from that of nuclear markers (Canino et al., 2010). This can explain why mtDNA did not find differentiation of the Yellow Sea and East China Sea Japanese mackerel, while nuclear markers such as AFLP were detected. Because if the differentiation time is short, the maternal gene may not have fixed differences, and slight frequency changes in nuclear genes can be measured.

Secondly, the sampling layout in the research design is crucial to whether the structure can be discovered. If the sampling points are unevenly distributed or the sample size is insufficient, the key genetic pattern is easily missed. For example, many early studies only took two or three location samples and came to the conclusion that "no significant structure". However, Feutry and others discovered the isolation mode with distance through six samples. If the sampling point is too thin, it is likely that the demarcation will be missed. The selection of data analysis methodology will also affect the conclusion. For example, the commonly used STRUCTURE clustering is not sensitive to detecting weak differentiation. If you rely too much on it, you may misjudge the same group. Some early studies did not find that the structure was partly limited by the method used. To avoid method deviation, it is best to combine multiple analyses, such as F<sub>ST</sub>, AMOVA, principal component analysis, and cluster analysis to obtain a consensus. In particular, it should be noted that population differentiation may be extremely low and sufficient statistical power must be used to identify it (Yan et al., 2015).

## 7 Conclusion

### 7.1 Problems and research gaps in current research

Although important progress has been made in the research on the genetic diversity and population structure of the genus Mackerel in recent years, there are still several problems and gaps that need to be resolved. First, the area coverage is unbalanced. Currently, research on the inheritance of mackerel populations is mostly concentrated in a few areas and species. For example, there have been some results in the coastal areas of China, the narrowband mackerel of the Indian Ocean, and the Western Atlantic Sera mackerel of the West, but data is lacking for many other distribution areas and species. Second, marking and method limitations. Looking back at previous literature, it can be found that most studies use limited markers (mtDNA fragments, microsatellites at several sites, etc.), and lack resolution. High-resolution multigenomic means are just in the beginning and are only used in individual cases. Therefore, some early conclusions need to be re-evaluated.

Third, there is a lack of long-term monitoring. The genetic structure of the population is not static, and may change with changes in resources, climate, etc. However, most of the current studies are one-time sampling analysis and lack cross-year comparisons. This prevents us from understanding the genetic structural dynamics of mackerel. Fourth, adaptive genetic research is missing. Almost all existing studies focus on the structure of neutral markers, and there is no systematic study on local adaptation or functional gene differentiation of mackerel. Mackerels are widely distributed in many environments, but the problems of which genes help them adapt to different temperature and salts and why some groups have different growth speeds and slow growth have not been analyzed at the gene level.

### 7.2 Potential of multigenome integration in future research

The development of multigenomic data and comprehensive analysis methods will bring breakthrough progress to future research on mackerel population structure. Applying genome-wide scanning based on global sampling will allow us to build a comprehensive genetic map of the genus Mackerel. Through international cooperation, samples from major species and key sea areas were obtained and genome-wide association analysis was conducted, which can simultaneously examine the differences in neutral marker differentiation and adaptive marker. The introduction of ancient DNA and population history models will enrich our understanding of the evolutionary history of mackerel. If the DNA of mackerels from fishery archives or sediments can be extracted decades ago or even earlier, compared with contemporary populations, the genetic structure can be directly observed to change over time. Population dynamic models (such as Coalescent modeling, DIYABC, etc.) can be used to infer the expansion and bottleneck situations of populations during the Ice Age, Holocene and other periods based on modern data. This will extend our understanding of the current structure to the historical dimension and explain more accurately the causes of the current pattern (Wang et al., 2024). New sequencing strategies such as environmental DNA metabarcoding technology also have potential. By collecting water samples at different time and sequencing mackerel DNA fragments, their distribution changes and rough genetic diversity can be monitored at high frequency. If this non-invasive method is combined with traditional fishing investigations and genomic analysis, it will form a new monitoring system. Multidisciplinary intersections such as combining telemetry,

ecological models and genetic data will greatly expand the analysis dimension. Multigenome integration can not only parse and differentiate, but also use it to identify snap-ins. By comprehensively analyzing genomic data, we may objectively delineate genetically independent population units and evaluate the effective population size and mobility of each unit, providing a scientific basis for demarcation of fishery management departments.

### 7.3 Suggestions on marine fisheries management and species protection

Based on the findings of this study, we put forward the following suggestions for fishery management and species protection of fishes in the genus Mackerel: Implement regional management based on population units. Genetic studies show that some mackerel species have geographical differentiation, and traditional administrative regional demarcation may not necessarily match the actual population boundaries. Therefore, it is recommended that the fishery sector refer to genetic evidence to manage genetically connected populations as units.

Establish a network of marine protected areas to cover key genetic units. Highly migratory fish such as mackerels often lay eggs, scavenge, and overwinter all over the country, requiring habitat protection from multiple locations. Genetic research helps identify key reproductive populations and connect corridors. It is recommended to set up protected areas or fishing moratoriums in the main spawning grounds and migration channels, and form a network to ensure that all genetic units are protected. Include genetic diversity monitoring indicators. Traditional fishery management is mostly based on resource quantity and biomass indicators, but the decline in genetic diversity may be an early signal of resource degradation. Fisheries research institutions are advised to regularly collect genetic samples of mackerel fish to monitor allelic diversity and population differentiation indicators.

Prevent foreign gene infiltration and gene destruction. If artificial breeding of mackerels is developed in the future, release activities should be managed carefully to avoid putting seedlings with large genetic differences into wild populations, causing genetic pollution. At the same time, engineering construction should minimize interference to migratory routes to avoid artificial isolation of groups. For situations where genetic structural changes have occurred (such as speculated that the population of the Yellow and Bohai Seas has been reduced), artificial breeding of local seedlings should be considered to assist in recovery, but it is necessary to ensure that local parent fish breeding is used to maintain genome adaptability. Strengthen publicity and international cooperation. Improve the public's awareness of the importance of protecting marine fish genetic resources, so that fishermen understand that protecting breeding groups and young fish is not only for the purpose of fishing next year, but also for the continuation of genetic bloodline.

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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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