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Reconstructing the Phylogenetic Relationships of *Scomberomorus* spp.: Evolutionary History from Whole-Genome Data

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Abstract The genus *Scomberomorus* (mackerels) includes several important marine fish species of high economic value in global fisheries and aquaculture, particularly across Asia. However, due to the large number of species and their morphological similarity, traditional taxonomy has been ambiguous, hindering efforts in genetic improvement and resource conservation. In recent years, with the advancement of high-throughput sequencing technologies, phylogenetic studies have entered the "whole-genome era." This paper provides a comprehensive review of the latest developments in reconstructing the phylogeny of *Scomberomorus*, highlighting the application of whole-genome data in species classification, lineage delimitation, speciation mechanisms, and evolutionary timescales. Case studies on farmed populations in Asia are also discussed, evaluating the genetic structure of hatchery and released stocks relative to wild lineages, and proposing lineage-based population optimization strategies. Further analysis indicates that phylogenetic research contributes not only to the identification of genetic resources and resistance traits but also offers scientific support for molecular breeding, broodstock selection, and genetic improvement. The paper concludes by recommending expanded global sampling, multi-omics integration, and the application of phylogenetic findings in aquaculture management, aiming to bridge foundational evolutionary research with practical breeding applications.

Keywords *Scomberomorus*; Phylogeny; Whole-genome data; Genetic structure; Aquaculture breeding

1 Introduction

Scomberomorus is a species-rich group of fish in the Scombridae family, which can be found in tropical and temperate waters around the world. Most of them are fast-swimming and predatory, occupying a high position in the marine food chain and are considered key species to maintain the balance of coastal ecosystems (Andersson et al., 2024). There are currently about 18 species in this genus that are generally recognized. Although there are slight differences in morphology between different species, they are generally similar (Jeena et al., 2022). Due to its tender meat and rich in high-quality fatty acids such as DHA and EPA, *Scomberomorus* has long been in high demand in the market and has a high price (Gao et al., 2024).

However, the species classification of *Scomberomorus* has always been confusing. Traditional classification methods mainly rely on appearance, but the members of this genus are too similar in appearance and are easily affected by the marine environment and mutate, so it is often difficult to distinguish which category they belong to (Sun et al., 2022). Later, the application of molecular technology, such as the detection of mitochondrial genes such as *COI* and *Cytb*, made species identification more accurate (Yang et al., 2023). However, these mitochondrial genes can only reflect maternal genetic information, and they evolve rapidly, sometimes with deviations, and may not accurately reflect the true system relationship (Zhang, 2023).

In recent years, phylogenetic genomics has gradually emerged, bringing new solutions to this type of classification problem. Compared with the traditional method of only looking at one or two gene fragments, the study of integrating whole genome information can use tens of thousands of nuclear gene sites to provide higher-resolution pedigree results (Oliveira et al., 2021). For non-model marine fish such as Spanish mackerel, whole genome sequencing combined with high-throughput analysis technology is becoming the main tool for revealing the evolutionary relationship between species (Machado et al., 2022).

In actual production, Spanish mackerel also has significant fishery and aquaculture value. For example, Japanese Spanish mackerel (*S. niphonius*) is an important fishing target along the coasts of China, Japan, and South Korea. In the past, the annual production could reach hundreds of thousands of tons, which is an important economic support for offshore fisheries. However, with the overexploitation of resources and the intensification of environmental pollution, the number of wild populations has shown a downward trend, forcing countries to accelerate research and investment in artificial breeding and seed release (Lorenzen et al., 2021). At present, China has listed Spanish mackerel as a key target for reproduction and release, and widely promoted seedling and reproduction technology in the Bohai Sea, the Yellow Sea, the East China Sea and other regions (Sun et al., 2022).

This article aims to sort out the research progress of Spanish mackerel phylogeny, focusing on the application of whole genome data in species relationship analysis, and combined with aquaculture practices in Asia, to explore the practical significance of phylogenetic research in genetic improvement and breeding management.

2 Taxonomy and Species Diversity of *Scomberomorus*

2.1 Major species and distribution

Mackerel fish are widely distributed in warm temperate to tropical coastal waters around the world. Various species usually live along the continental shelf and near estuaries. According to the latest classification data, the genus currently contains 18 valid species (Jeena et al., 2022). Among them, the species distributed in the Indo-West Pacific region are relatively abundant, including: Blue-spotted Spanish mackerel (*S. niphonius*), mainly found in the East China Sea, Yellow Sea and the coast of Japan in the northwest Pacific; Indo-Pacific sharp-toothed Spanish mackerel (also known as narrow-banded Spanish mackerel, *S. commerson*), widely distributed in the tropical waters of the Indian Ocean and the western Pacific, is the most widely distributed species in the genus; Indo-Pacific Spanish mackerel (*S. guttatus*), found in the coastal waters of Southeast Asia and the Indian Ocean; Multi-lined Spanish mackerel (*S. plurilineatus*), distributed in East Africa and the western Indian Ocean, etc. In the Asia-Pacific region, there are also Korean Spanish mackerel (*S. koreanus)* distributed in the Korean Peninsula and surrounding waters, Queensland Spanish mackerel (*S. queenslandicus*) found in the northern waters of Australia, etc. There are also several species of Spanish mackerel in the Atlantic and along the coasts of the Americas, such as the Spanish mackerel (*S. maculatus*) in the western Atlantic and the Pacific mackerel (*S. sierra*) in the eastern Pacific, which are usually classified as "New World populations" and are morphologically and genetically different from the Old World populations (Jeena et al., 2022).

As one of the important representatives of the genus Scolopendra, the Indo-Pacific Spanish mackerel has typical characteristics including: a slender, spindle-shaped body, a deeply forked caudal fin, and a silvery-white body with light-colored vertical stripes (Figure 1). These characteristics have a certain reference value for species identification. *S. guttatus* is widely distributed in the Indo-Pacific region and is an important economic species in the regional fishery (Gao et al., 2024).

Although most mackerels live in shallow offshore waters, their migration activities are somewhat limited, and most species have a limited distribution range and do not migrate long distances across oceans. This is in stark contrast to the tuna family of the same family - tuna often migrate across oceans, while mackerels tend to migrate in coastal waters. The only exception is the narrow-banded mackerel (*S. commerson*), which is distributed across the Indian Ocean and the western Pacific and is considered a highly migratory and widespread species. The geographic distribution and habitat range of each species determine its population structure to a certain extent (Yang et al., 2022). For example, Spanish mackerel populations living in semi-enclosed waters (such as the Gulf of Mexico and the Persian Gulf) may form independent evolutionary units due to geographical isolation. Spanish mackerels usually reproduce in waters with water temperatures above 20 °C and are sensitive to changes in water temperature. Take the Japanese Spanish mackerel as an example. Every spring, as the water temperature rises, they migrate from the East China Sea to the Yellow Sea and Bohai Sea to spawn, and then go south in autumn to hibernate. This seasonal migration may lead to reproductive isolation of groups in different waters, thereby promoting intraspecific population differentiation (Oliveira et al., 2021).

Figure 1 The appearance of Indo-Pacific king mackerel (Adopted from Gao et al., 2024)

2.2 Current status and challenges of genetic diversity

The genetic diversity of the Spanish mackerel genus is essential for its adaptation to the environment and long-term survival (Garner et al., 2020). However, due to pressures such as overfishing and habitat changes, the genetic diversity of many populations is under threat. Some regional studies have shown that Spanish mackerel populations often show low mitochondrial genetic diversity and limited genetic differentiation, suggesting that they may have experienced population bottlenecks or homogenization caused by continuous gene flow in history. For example, a study of narrow-band Spanish mackerel along the coast of Tanzania found that there was no significant genetic differentiation between sampling points, and the whole population constituted a single genetic pool. The high gene mobility may be due to the migration of adults and juveniles between different spawning and foraging grounds. For example, mitochondrial analysis of Brazilian Spanish mackerel (*S. brasiliensis*) in the southwest Atlantic showed that the genetic distance between its different geographical populations was limited and the population structure was relatively simple. These results indicate that many Spanish mackerel populations are connected at the regional scale, and the highly migratory life history leads to frequent gene exchanges between populations.

However, it is necessary to be vigilant that traditional molecular markers (such as mitochondrial genes) may underestimate the actual level of genetic differentiation. Recent higher-resolution data reveal that some species of Spanish mackerel, which were thought to be widespread, actually contain hidden genetic branches and population structures. For example, a multi-gene analysis of the Indo-West Pacific Spanish mackerel complex found that the Indo-Pacific Spanish mackerel (*S. guttatus*), which was originally considered a single species, actually includes two highly genetically differentiated lineages: one is restricted to the coast of the Bay of Bengal and was reconfirmed as a strictly defined Spanish mackerel (sensu stricto), and the other is widespread in the Indo-Pacific region and was restored to the name of Leopard Spanish mackerel (*S. leopardus*) (Gao et al., 2024).

The mitochondrial genetic distance between these two lineages exceeds 10%, which is enough to constitute different species. In addition, about 2% of genetic differences were detected within the Leopard Spanish mackerel, which was subdivided into two operational taxonomic units (MOTUs) in the Pacific and Indian Oceans. For another example, in the narrow-band Spanish mackerel (*S. commerson*), genetic data revealed two lineages that may be geographically isolated in the Indian Ocean and the Western Pacific. The existence of these cryptic lineages indicates that some widespread species of this genus are actually composed of several genetically differentiated populations or closely related species. Since they are difficult to distinguish by traditional morphology, they have been "hidden" under nominal species and were only discovered with the help of molecular methods. The existence of cryptic species not only means that we do not have enough knowledge about the actual species diversity of Spanish mackerel, but also poses a challenge to fishery management and aquaculture selection. If different genetic lineages differ in adaptive traits, ignoring their differences may lead to errors in management measures or breeding decisions.

3 Application of Whole-Genome Data in Phylogenetic Reconstruction

3.1 Advances in high-throughput sequencing

In the past two decades, high-throughput sequencing technology has developed rapidly, bringing a large amount of available data to phylogenetic research (Gao et al., 2024). Early "Sanger sequencing" could only obtain a single gene sequence at a time, while today's second-generation sequencing and third-generation sequencing can produce massive sequence information covering the entire genome in a short time. In the field of fish genome research, since the first fish genome (pufferfish) was published in 2002, hundreds of fish have completed genome sequencing. For non-model marine fish such as the genus *S. guttatus*, breakthroughs have also been made in recent years. For example, in 2024, researchers assembled a high-quality genome of this genus for the first time - the chromosome-level whole genome of the Indo-Pacific *S. guttatus*. The study combined PacBio HiFi long-read sequencing and Hi-C chromosome conformation capture technology to construct a genome map of 24 pairs of chromosomes with a total length of approximately 798 million bases, corresponding to 25,886 predicted protein-coding genes. This marks the first high-quality reference genome of the genus Spanish mackerel. In addition to Spanish mackerel, multiple genomes of other members of the Scomberidae family, such as tuna and mackerel, have also been published, such as bigeye tuna and true trevally.

It is worth mentioning that in 2022, researchers published the genome assembly results of Atlantic horse mackerel (*Scomber colias*), using third-generation sequencing and graphical assembly methods to construct a highly continuous reference genome. The accumulation of these genomic resources has laid the foundation for comparative genomic and phylogenetic studies of scomber fish.

In addition, there is genome skimming technology, which can recover high-copy sequences such as mitochondrial whole genomes and ribosomal genes through shallow sequencing, which can be used to quickly construct phylogenetic frameworks. The emergence of third-generation long-read sequencing (PacBio, Nanopore) also provides a new perspective for phylogeny: its long read length can not only better assemble genomes and capture structural variations, but also directly perform phylogenetic analysis of k-mer frequency or non-paired assembly. For example, studies have shown that species relationships can be reconstructed without alignment by comparing the repetitive sequence composition or k-mer sharing of different genomes.

3.2 Coordinated analysis of nuclear and mitochondrial genomes

In phylogenetic studies, nuclear and mitochondrial genomes have their own characteristics. Coordinated analysis of the information of the two can obtain more comprehensive and reliable evolutionary signals (Sun et al., 2022). Mitochondrial DNA (mtDNA) is widely used in animal phylogenetic and population genetic studies due to its high mutation rate and maternal haplotype nature. However, mtDNA only represents the maternal evolutionary history and is easily affected by factors such as hybridization and mate preference, resulting in phylogenetic trees that are inconsistent with the true relationship of species (called "gene tree/species tree inconsistency").

In the phylogenetic study of the genus Mackerel, mitochondrial and nuclear genes were often used for analysis separately in the past. Now, whole genome sequencing enables us to obtain mitochondrial whole genome sequences and tens of thousands of nuclear gene markers at one time. For example, through low-depth genome sequencing (genome skimming), a complete mitochondrial genome can be assembled from sequencing data, and a large number of single-copy nuclear gene sequences can be detected at the same time. The phylogenetic tree constructed using the mitochondrial whole genome usually has a high resolution and can effectively identify closely related species and cryptic lineages (Jeena et al., 2022).

A recent study reported the mitochondrial genome characteristics of two species of Spanish mackerel in the family Scombridae, and reconstructed the phylogenetic relationship of the family Scombridae based on the complete mitochondrial sequence. The results are basically consistent with the traditional classification (Lorenzen et al., 2021). On the other hand, the nuclear genome provides a huge number of independent sites, and supermatrix (connecting many genes) or consensus methods (such as multi-gene co-alescent models) can be used to infer species trees, which usually obtain highly supported phylogenetic results and quantify potential conflict signals on lineages. Comparing the results of nuclear DNA and mtDNA, if the topological structure is inconsistent, it often indicates a potential biological reason: it may be caused by historical hybridization causing the replacement of mtDNA, or it may be caused by the independent evolution of mitochondrial lineages.

3.3 Data processing and phylogenetic tree construction process

Reconstructing phylogenetic relationships based on whole genome data usually requires multiple steps from raw data processing to phylogenetic tree inference. The first is sample collection and genome sequencing: select representative species and individuals for research questions, extract genomic DNA and perform high-throughput sequencing. The sequencing platform can be selected according to needs, such as Illumina short read length to obtain high coverage sequences, or PacBio/ONT long read length to facilitate crossing complex regions. After obtaining the original sequence, quality control is required to filter low-quality reads and adapter contamination .(Machado et al., 2022)

For whole genome sequencing data, two strategies can be used: first, de novo assembly of the genome of each species, and then positioning and extracting conserved sequences on the genome for comparison; second, direct alignment to the reference genome without assembly or comparison through the k-mer matrix. In the study of the Spanish mackerel genus, since there is no perfect reference genome, the de novo assembly of mitochondria or specific genes has been used in the past. However, with the release of the reference genome of Spanish mackerel (such as *S. guttatus*), reads of other species can be aligned to the reference in the future, and homologous sites can be extracted from them for phylogeny.

The next step is to identify and align homologous sequences. If there is a reference genome annotation, a list of single-copy orthologous genes shared by all species can be directly extracted, and then sequences can be extracted from each genome assembly or reads alignment for these genes. Subsequently, multiple sequence alignments are performed for each homologous gene or sequence, and regions with poor alignment quality are eliminated. In order to reduce computational pressure, supermatrices are often screened: for example, only single-copy genes or sites with rich variation information are retained. Then, phylogenetic analysis methods are selected according to the research purpose: splicing supermatrices to construct a "species tree" or a consensus method based on gene tree summary. The supermatrix method connects all gene alignments into long sequences and uses maximum likelihood (ML) or Bayesian methods to infer the overall phylogenetic tree. The advantage of the supermatrix method is that all data are used, and the disadvantage is that it may mask conflicts between different genes. Finally, the resulting phylogenetic tree is evaluated and corrected (Yάñez et al., 2023). It is necessary to pay attention to the support of each branch on the tree (such as bootstrap or posterior probability). Nodes with low support may require more data or different model testing.

4 Phylogenetic Reconstruction Results and Evolutionary Patterns

4.1 Optimization of classification structure and phylogenetic relationships

With the help of whole genome data and multi-gene joint analysis, the phylogenetic relationship of the genus *S. punctatus* has been reconstructed more clearly recently. Overall, the new study supports the monophyletic origin of the genus *S. punctatus* and divides the internal species into several clades, optimizing the previous classification structure based on morphology or limited genes (Jeena et al., 2022). For example, multi-locus phylogenetic analysis roughly divides the species of this genus into two main evolutionary lineages: one includes the complex population of *S. punctatus* (*S. guttatus* and its cryptic relatives), *S. multilineata*, *S. koreana*, etc., and the other includes the Queensland *S. punctatus* and *S. commerson*, etc. Among them, the first lineage is further subdivided into multiple subbranches: the study found that the original broad Indo-Pacific horse mackerel (*S. guttatus* sensu lato) is actually composed of true horse mackerel (*S. guttatus* sensu stricto) and leopard horse mackerel (*S. leopardus*), and the two are clearly distinguished on the phylogenetic tree. True horse mackerel is mainly confined to the Bay of Bengal, which is consistent with the historical model origin, while leopard horse mackerel is widely distributed in other waters of the Indo-Pacific (Yang et al., 2023).

On the phylogenetic tree, true horse mackerel is close to Korean horse mackerel (*S. koreanus*) and multi-line horse mackerel, while leopard horse mackerel and multi-line horse mackerel form a sister group relationship. It is worth noting that two genetic branches (named *aff. guttatus* 1 and *aff. guttatus* 2) appeared within the leopard horse mackerel, corresponding to the two major regional populations of the Pacific and Indian Oceans. This discovery suggests that the leopard mackerel may be further differentiated and may even represent two geographical subspecies or species. For the second largest lineage, the phylogenetic tree shows that the sharp-toothed mackerel (*S. commerson*) and the Queensland mackerel (*S. queenslandicus*) are clustered into one branch. This is consistent with the above speculation based on mitochondria, suggesting that there may be regional population differentiation of sharp-toothed mackerel frontiersin.org (Hashemi and Doustdar, 2022).

4.2 Discussion on the mechanism of speciation

The reconstruction of the phylogenetic relationships of the Spanish mackerel provides a new perspective for understanding its speciation mechanism. According to the latest molecular evidence, geographic isolation (allopatric speciation) plays an important role in the evolution of species in this genus. The distribution areas of many Spanish mackerel species or lineages are separated by marine geographical barriers, which have led to independent evolution and genetic differentiation (Oliveira et al., 2021).

This geographic isolation led to the differentiation of Spanish mackerel and Leopard Spanish mackerel. Similarly, the populations of Spanish mackerel in the Indian Ocean and the Western Pacific are blocked by the Southeast Asian Land Bridge and the Australian continent. Today, genetic data have detected the differentiation of its Pacific and Indian Ocean subpopulations. This suggests that the isolation of the two ocean environments and different ocean current systems may have contributed to the lineage differentiation within the Spanish mackerel.

Different environmental pressures may lead to differences in physiology and behavior among populations, thereby promoting the formation of reproductive isolation. Although there has been no clear case of ecological differentiation speciation reported in Spanish mackerel, similar evidence has been found in other closely related fishes. For example, in some populations of Perciformes, differences in the number of individuals that develop under different water temperature conditions and misaligned reproduction times can lead to limited gene exchange and gradually lead to species differentiation. In recent years, extreme climate events (such as the El Niño phenomenon) may change the population connectivity pattern of Japanese mackerel and others. Model predictions show that if climate change continues, some mackerel populations (especially those distributed at the edge of the climate) may gradually become alienated from the core population, thus embarking on an independent evolutionary path (Lorenzen et al., 2021).

Finally, it is worth mentioning the potential impact of human activities on the evolution of mackerel. The high-intensity fishing in modern fisheries may have a fishery-induced evolution (FIE) effect on some species, such as genetic responses such as early sexual maturity and smaller body size. Although such changes mainly occur within populations, they may also change the adaptation pattern of populations under long-term effects, thereby affecting the genetic differences between different populations. If some populations undergo obvious genetic trait changes due to fishing pressure, while other populations are not affected, then the reproductive barriers between the two may gradually increase, similar to "human-driven speciation (Pan et al., 2024)。

4.3 Phylogenetic differentiation on a time scale

By calibrating the phylogenetic tree of the genus *S. regalis* using molecular clock methods, we can infer the time frame of its phylogenetic differentiation in geological history. Recent phylogenetic studies have used mitochondrial whole genome data to time the main lineages of the genus, revealing that the evolution of the genus *S. regalis* spanned a long period from the Paleocene to the Pleistocene (Oliveira et al., 2021).

In the subsequent Eocene to Oligocene (about 56 million to 34 million years ago), the first major lineage differentiation occurred within the genus *S. regalis*. Clock analysis shows that the Old World group (mainly including species in today's Indo-West Pacific) and the New World group (American species, such as *S. regalis*, etc.) may have separated at the end of the Eocene to the beginning of the Oligocene.

During the Miocene (23 million to 5.3 million years ago), the genus *S. regalis* ushered in the second peak of diversification. The ancestral lineages of many living species originated from this period. For example, the time calibration results show that in the Eastern population, the common ancestor of Japanese and Montenegrin mackerels appeared about 42 million years ago (late Eocene), and then the differentiation of *S. niphonius* and *S. munroi* occurred about 15 million to 10 million years ago (middle Miocene). In the Indo-West Pacific group, the differentiation of the multi-lined mackerel and the leopard mackerel-Korean mackerel-true mackerel complex was concentrated in the late Oligocene to the early Miocene (roughly 30 million to 20 million years ago) (Gao et al., 2024.

5 Case analysis: Phylogenetic Relationships of Aquaculture-Related Populations

5.1 Genetic structure of common aquaculture populations in Asia

In Asia, *Scomberomorus niphonius* (also known as blue-spotted Spanish mackerel) in the Spanish mackerel genus is an important target for aquaculture and stocking, especially in coastal areas of China. Every year, a large number of artificially bred juveniles are released into natural waters, making it a typical representative for studying the genetic interaction between aquaculture populations and wild populations. Understanding its genetic structure is of great significance for evaluating the effect of stocking, optimizing parent selection and maintaining genetic diversity (Pan et al., 2024).

Studies have analyzed Spanish mackerel populations along the Yellow Sea and East China Sea coasts of China using mitochondrial DNA and microsatellite markers. The results showed that the genetic differences between populations in these areas were low, the gene mobility was strong, and the overall structural differentiation between populations was low. This shows that a large amount of genetic variation is shared between different geographical populations, and no obvious local branches or subspecies divisions have been found. Therefore, if wild broodstock are collected from adjacent waters for reproduction, their offspring will have a high genetic compatibility with the local wild population, and it is not easy to introduce foreign genes after release, which is conducive to maintaining ecological stability (Jeena et al., 2022).

However, high migration does not mean that there is no population structure at all. Higher-resolution genetic tools, such as SNP whole-genome scanning, may reveal subtle genetic differentiation between different spawning populations of Japanese Spanish mackerel. This refined analysis is expected to reveal genetic heterogeneity that cannot be detected by mitochondrial markers, especially regional adaptive variation formed under different habitats or ecological pressures.

Figure 2 shows the phylogenetic relationships of several representative species and cryptic lineages of Spanish mackerel, clearly showing that the Indo-Pacific Spanish mackerel (*S. guttatus* sensu lato) includes multiple different genetic branches, such as true Spanish mackerel (*S. guttatus*), leopard Spanish mackerel (*S. leopardus*) and other subtypes (*aff. guttatus* 1/2). This result reinforces the view of this article: individuals with similar phenotypes may come from lineages with significant genetic differences (Figure 2). If these differences are not identified during parent selection or release, problems such as genetic mixing and reduced adaptability may occur. Therefore, phylogenetic information should be used as an important reference for population management to improve the genetic adaptability and ecological safety of farmed populations (Jeena et al., 2022).

In addition, there is inevitably selection pressure in the process of artificial breeding, such as high-density environment and artificial feed conditions, which may cause the allele frequency associated with certain traits to shift. Although there is no whole-genome study on the released Japanese mackerel, there is evidence in marine fish such as large yellow croaker that artificially released individuals often have low genetic diversity and are enriched in certain genes related to adaptation to artificial environments. Therefore, it is recommended to strengthen genome monitoring of farmed and released populations in the future to prevent genetic erosion of wild populations caused by long-term release (Yáñez et al., 2023).

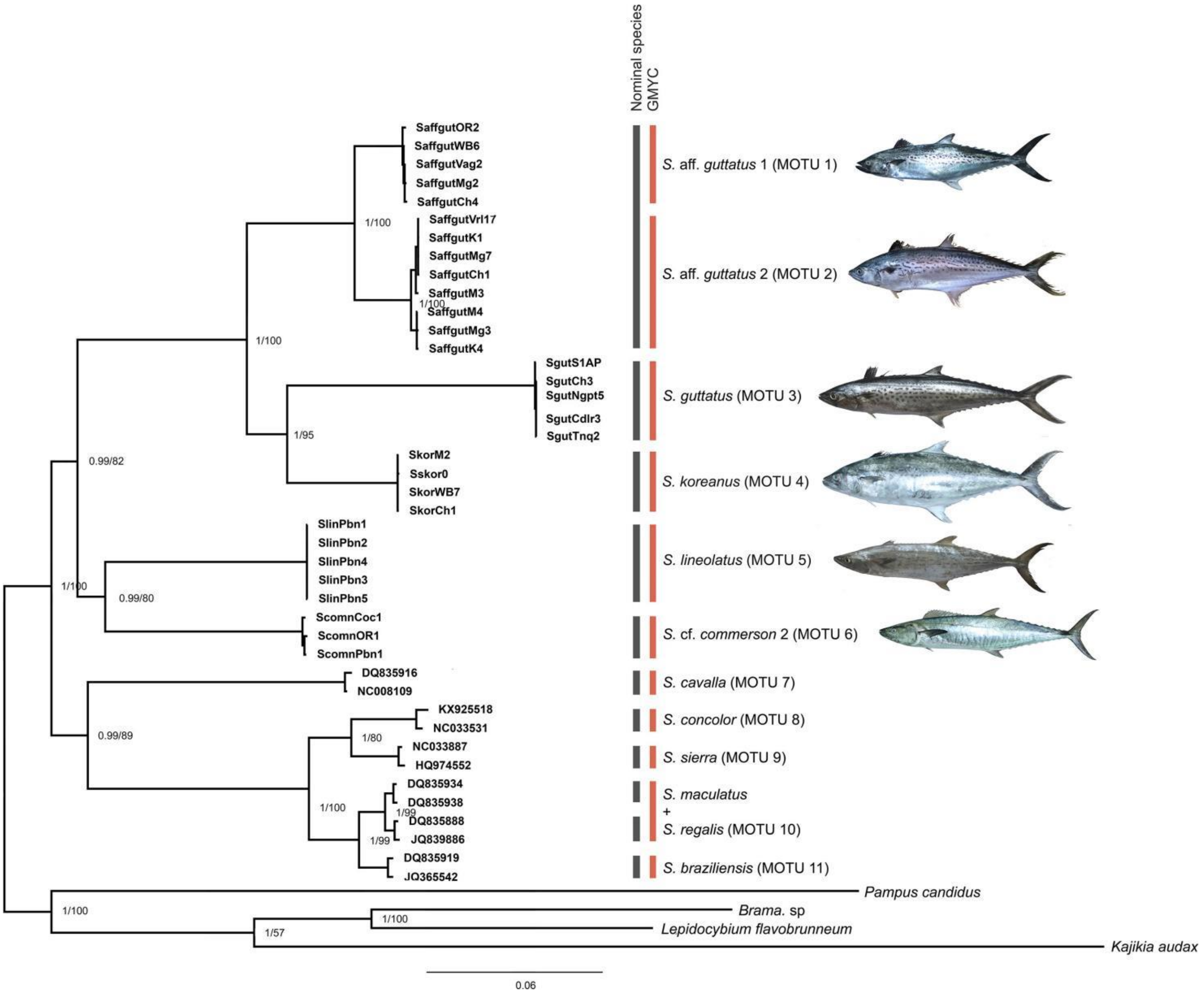

Figure 2 Phylogenetic tree of *Scomberomorus* species based on multilocus data integrating bayesian inference and maximum likelihood analyses (Adopted from Jeena et al., 2022)

5.2 Phylogenetic comparison with wild populations

Comparison of phylogenetic relationships between farmed (or released) populations and wild populations can reveal the impact of human intervention on the genetic pattern of species (Johnson et al., 2021). For highly migratory fish such as Spanish mackerel, large-scale artificial breeding and release may change the gene pool composition of wild populations to a certain extent (Pan et al., 2024). Phylogenetic analysis can be used as an assessment method: if a large number of released fish survive and integrate into the breeding population, theoretically, the genetic structure of the wild population should be observed to be close to that of the released fish. On the contrary, if the released fish fail to integrate successfully due to poor adaptability, their genetic components will not be able to accumulate in the wild population. Taking the Japanese Spanish mackerel as an example, the genetic diversity of the wild population is still high, and there is no obvious evidence that release leads to a decrease in genetic diversity or changes in population structure.

Phylogenetic and population structure analysis often finds some typical differences between farmed/released fish and wild fish: one is the level of genetic diversity, such as the number of alleles and heterozygosity. Farmed populations are usually less diverse than wild populations due to limited parental sources and artificial selection pressure. Second, there are unique alleles. Wild populations often have some rare alleles that are missing in farmed populations. There are not many such analyses on Spanish mackerel at present. However, a study on seahorse release found that the number of alleles and heterozygosity of the released population were significantly lower than those of the wild population, and the FST values of both reached statistically significant levels. It can be inferred that if a whole-genome SNP analysis is conducted on the Japanese Spanish mackerel population released along the coast of China in recent years, subtle but existing signals of population differences may be found, which deserves further study.

In addition to genetic diversity, phylogenetic analysis can also compare population adaptive genetic variation. For example, it can be screened whether some key gene variants related to disease resistance and migratory behavior are missing in farmed populations. These variants may be retained by natural selection in wild populations, but lost under artificial conditions due to different selection pressures. The phylogenetic tree cannot directly reflect the differences in specific genes, but it can be combined with methods such as GWAS to locate sites with functional significance, and then look at their degree of differentiation between populations. For example, if it is found that the farmed population has a single allele on immune-related genes, while the wild population is diverse, it needs to be taken seriously. Existing literature has pointed out that artificial continuous breeding may cause hidden inbreeding depression and domestication selection effects, which may reduce the competitiveness of released fish in the wild (Yáñez et al., 2023).

5.3 Phylogenetic-based population optimization recommendations

First, enrich the breeding germplasm and maintain genetic diversity. Phylogenetic analysis emphasizes the importance of genetic diversity for population health. Therefore, in the selection of artificial breeding broodstock, a sufficient number of wild individuals should be caught from the target sea area, covering different subpopulations and families, to avoid over-reliance on a few populations or close relatives as parents. The more broodstock there are, the richer the genetic variation of the offspring population, and the lower the risk of inbreeding degeneration in the future release or breeding population. In particular, if phylogenetic studies have revealed that the target species has genetic branches (for example, there are two lineages in leopard mackerel), the lineage homologous to the local wild population should be used as the parent to avoid problems such as foreign gene invasion or hybrid sterility caused by mixed breeding of different lineages (Zeng et al., 2022).

Secondly, strengthen pre-release domestication and selection to improve the survival rate of release. Phylogenetic relationships can tell us the differences between farmed fish and wild fish, but how to bridge this gap requires efforts in breeding management. Some studies have pointed out that by conducting "survival skills training" before release, such as simulating predation and escape scenarios in the wild, the survival rate of released fish in the wild can be significantly improved (Gao et al., 2024).

Third, regular genetic monitoring and feedback improvement. It is recommended to establish a genetic monitoring archive for the Spanish mackerel release project, and sample and analyze the genetic structure of the population before and after each batch of release, including allele frequency, heterozygosity, and phylogenetic clustering relationship with historical samples. Once it is found that the seedlings of a certain breeding are too genetically deviated from the wild population (for example, obvious grouping appears in cluster analysis), the parental composition or breeding method should be adjusted in time (Da Cunha et al., 2020).

Finally, for farms with fully artificial closed breeding (such as the development of Spanish mackerel factory breeding in the future), phylogenetic and genomic selection technologies can also be used to accelerate strain breeding. With the help of genomic data, whole genome selection for growth, disease resistance and other traits can be carried out to quickly select dominant individuals from many families for breeding. At the same time, molecular markers can be used to avoid inbreeding, maintain a certain effective population size, and maintain genetic diversity. Gene editing technologies (such as CRISPR) have been successfully used to improve growth and disease resistance traits in some aquatic animals, and may also be used in mackerel in the future (Wang, 2024).

6 Implications for Aquaculture Research

6.1 Genetic resource protection and genetic improvement

The first implication of whole genome phylogenetic research for aquaculture is the re-recognition of the importance of genetic resource protection. As molecular data reveal the complex pedigree structure and high level of cryptic genetic diversity within the Spanish mackerel genus, we are more aware that each pedigree and each population may contain unique adaptive genetic resources. Once these genetic units disappear due to overfishing or improper release, it will be an irreversible loss (Jeena et al., 2022; Yang et al., 2023). Therefore, in the development of aquaculture, the protection of wild genetic resources must be considered simultaneously. Specifically, a germplasm resource bank can be established, such as live seed preservation or frozen sperm/embryo preservation of Spanish mackerel from different geographical groups, in preparation for future breeding and population recovery. At the same time, organizations such as IUCN are also calling for the inclusion of genetic diversity indicators in species red list assessments to encourage countries to take genetic conservation actions (Lorenzen et al., 2021).

On the other hand, phylogenetic research also provides direction for genetic improvement (breeding). Genomic data can help us discover useful genetic variations and accelerate the cultivation of high-yield and high-quality aquaculture varieties. For example, by comparing the genomes of different lineages, candidate genes related to traits such as growth, disease resistance, and environmental tolerance can be located. If a lineage is found to have unique dominant alleles on these genes, it is possible to consider introducing the pedigree of the lineage during breeding to enhance these traits. For example, assuming that a lineage of Spanish mackerel in the Indo-Pacific region has a high tolerance to warm water hypoxia, its genes can be integrated into the breeding program to meet the aquaculture challenges brought about by rising water temperatures. Breeding in the genomic era has shifted from traditional phenotypic selection to whole genome selection (GS), using tens of thousands of molecular markers to predict individual breeding values. Although there is no dedicated GS research on emerging aquaculture varieties such as Spanish mackerel, it is entirely possible to learn from the successful experience of other species (Yáñez et al., 2023). For example, in farmed fish such as salmon and tilapia, GS has significantly improved the selection efficiency of disease resistance and growth traits.

6.2 Disease resistance and environmental adaptability breeding strategies

The two eternal themes in aquaculture are disease prevention and control and environmental adaptation. Phylogenetic and genomic studies provide us with scientific basis for improving mackerel breeding strategies in these two aspects. First, in terms of disease resistance breeding, genome-wide association analysis (GWAS) can help identify genetic markers associated with disease resistance. Although mackerel farming has not yet been carried out on a large scale, it is foreseeable that under intensive farming conditions, common diseases such as bacterial sepsis and parasitic infections may pose a threat to mackerel (Oliveira et al., 2021； Pan et al., 2024), The use of genomic selection to improve disease resistance traits has been successful in other species: for example, the application of GS in Pacific oysters has improved resistance to Vibrio disease; selective breeding in Atlantic salmon has significantly reduced the incidence of ISA virus.

In terms of environmental adaptability, global climate change and environmental fluctuations require farmed varieties to have a wider tolerance range. Phylogenetic information can guide us to find potential environmental tolerance gene pools. For example, Japanese mackerel is distributed in the northern edge and survives and reproduces at lower water temperatures, so it may have genes related to cold resistance; while narrow-banded mackerel reproduces in high-temperature, high-salinity tropical waters and may have stronger resistance to high temperatures. If the lineages with different environmental adaptation characteristics can be hybridized to cultivate new strains with both wide temperature and wide salt tolerance, it will be beneficial to expand the breeding area and improve the robustness of breeding (Gao et al., 2024).

In breeding for disease resistance and environmental adaptability, in addition to traditional breeding, gene editing can also be used to accelerate the realization of target traits. CRISPR-Cas9 technology has demonstrated its power in the field of aquaculture. For example, editing specific genes in carp can enhance disease resistance, and editing growth-related genes in zebrafish can double the growth rate. For mackerel, if key disease resistance or environmental tolerance gene sites have been identified, such as mutation sites of genes encoding immune receptors, targeted editing can be attempted. However, sufficient basic research is needed before this to clarify the functions of these gene sites and whether they will have negative effects (Machado et al., 2022). At the same time, factors such as supervision and public acceptance need to be considered. At present, the application of gene editing in food fish is still in the experimental stage, but its potential cannot be ignored. When the technology and regulations mature in the future, gene editing is expected to quickly give new species such as Spanish mackerel excellent traits such as disease resistance or high tolerance.

6.3 Molecular tools to improve breeding efficiency

The advent of the whole genome era provides a powerful molecular toolbox for aquatic breeding. These tools can greatly improve breeding efficiency and reduce the cost of breeding trial and error. For marine fish such as Spanish mackerel, we can make full use of the following new technologies:

Genomic selection: Traditional breeding selects parents through phenotypic determination, which has a long cycle and is affected by environmental interference. Whole genome selection uses individual whole genome marker information to predict its breeding value, and can select potential excellent individuals in the juvenile stage. It is particularly effective for high heritability traits such as growth. With the reduction of sequencing costs, low-coverage whole genome sequencing plus genotype filling has become a more economical solution than SNP chips (Yáñez et al., 2023). A review shows that the application of GS in multiple farmed species such as tilapia and Atlantic salmon has significantly improved selection accuracy and genetic progress. Therefore, in the future, it is entirely possible to implement GS breeding plans for target traits of Spanish mackerel (such as growth rate and feed conversion rate).

Molecular assisted selection (MAS) and marker development: For some important traits, if clear major effect genes or linked markers are known, MAS can be implemented to accelerate the fixation of favorable alleles. Phylogenetic studies can help us discover potential candidate genes, such as comparing the genomes of individuals at different lineages or phenotype extremes to find sites with extremely high allele frequencies in excellent populations. Subsequently, specific PCR markers or microarray chips can be developed for genotype screening in conventional breeding. For example, if a single nucleotide polymorphism (SNP) is found to be highly correlated with muscle fat content in Spanish mackerel, a molecular test can be designed for the SNP to select individuals with ideal genotypes in young fish and retain them (Yáñez et al., 2023).

Gene editing and synthetic biology: Gene editing technologies such as CRISPR-Cas9 allow us to modify target sites at the genome level, achieving targeted improvements that are difficult to achieve with traditional breeding. For example, if you want to breed a non-spawning triploid Spanish mackerel population to improve growth, you can edit genes related to germ cell formation to achieve sterility (similar to what was done with salmon in the past). Another example is that muscle growth can be promoted by knocking out the myostatin gene (MSTN) - this method has been used to obtain "bodybuilding fish" strains in carp and crucian carp. Gene editing can also be used to verify the function of candidate genes, thereby better guiding MAS and GS. For example, by knocking out or overexpressing a candidate gene, observing the growth or disease resistance changes of Spanish mackerel to confirm whether the gene is worthy of consideration in breeding (Halasan et al., 2021).

Pan-genome and big data AI applications: As the genome data of different Spanish mackerel species and individuals accumulate, we can construct a pan-genome of the Spanish mackerel genus, covering all genetic variations in all strains. This will help us understand genetic diversity more comprehensively and use information such as structural variation to improve breeding. For example, studies have found that the loss of structural variation (such as large fragment deletions) during breeding may affect traits. Through pan-genome analysis and machine learning algorithms, we may be able to discover the regulatory network of complex traits, thereby improving the accuracy of phenotype prediction. AI technology has been used to analyze massive genomic and phenotypic data to find the optimal combination.

7 Conclusion

7.1 Significance of phylogenetic reconstruction

The reconstruction of the phylogenetic relationship of the genus Mackerel based on whole genome data not only clarifies the evolutionary context of the species in this genus, but also provides an important scientific basis for fishery resource management and aquaculture. By integrating multiple molecular evidences, researchers optimized the classification system of the genus Mackerel and confirmed the existence of cryptic lineages and new species, such as the resurrection of the leopard mackerel and the internal regional differentiation of the sharp-toothed mackerel. These findings enrich our understanding of marine biodiversity and highlight the unrecognized genetic diversity in marine fish. The phylogenetic tree combined with molecular clock analysis depicts the evolutionary process of the genus Mackerel for tens of millions of years since the Paleogene, revealing that its multiple radiations and differentiations are closely related to geological and climatic events. These macro perspectives help us understand the historical reasons for the formation of the current species distribution pattern and provide a reference for predicting future changes.

More practically, phylogenetic research points out the direction for the conservation and management of species and populations: which lineages are the most unique and need to be protected first, and which populations have important genetic value and should avoid mixed use. This information is especially important when formulating plans for stocking or transplanting across regions. At the same time, this review illustrates how whole genome technology can be used for genetic improvement in aquaculture. From maintaining genetic diversity to trait selection, coupled with the introduction of molecular tools, traditional aquaculture has entered a new stage of refinement and scientificization. The case study of Spanish mackerel shows that the intersection of evolutionary biology and aquatic science can produce huge synergistic effects. The evolutionary perspective can enhance our understanding of the genetic nature of farmed species, and the needs of aquaculture practice also provide new topics for evolutionary research.

7.2 Outlook for future research directions

Although the whole genome phylogenetic study of the genus Spanish mackerel has made important progress, there are still many issues that deserve further exploration. In future research, we propose the following prospects:

(1) Comprehensive pan-genome and adaptive evolution research: In the future, genome sequencing can be performed on more species and different geographical groups of Spanish mackerel to construct a "pan-genome" map of the genus. This will help identify species-specific gene variants and adaptive genetic markers, and further reveal the genetic mechanism of Spanish mackerel's adaptation to different environments (such as temperature and salinity).

(2) Hybridization and gene flow research: Phylogenetic trees show that some Spanish mackerel species have overlapping geographical distributions, which provides the possibility of potential interspecific hybridization. In the future, genomic data can be used to detect whether interspecific hybridization and gene introgression have occurred historically or currently. For example, the contact area between the leopard Spanish mackerel and the true Spanish mackerel lineage distributed in the waters of Southeast Asia can be studied in detail, and genome colinearity analysis and gene tree inconsistency detection can be used to identify whether there is gene fragment exchange between them. This is not only related to species definition, but also meaningful for genetic risk assessment to prevent hybridization of different species in aquaculture.

(3) In-depth functional gene research and molecular breeding practice: On the basis of obtaining the genome and phylogenetic framework, in-depth functional gene research should be carried out, including gene editing to verify the function of key genes, transcriptome analysis of changes in gene expression of fish under different conditions, etc. In particular, around economic traits such as growth, disease resistance, and reproduction, find major effect gene sites and analyze their action pathways.

(4) Ecogenomics and climate change response: In the face of global climate change, it is recommended to use the Spanish mackerel genus as a model to carry out ecological genomics research on marine fish to environmental changes. For example, long-term monitoring data can be combined with genomes to analyze whether the rise in

seawater temperature in the past few decades has caused detectable changes in the allele frequency of populations such as Japanese Spanish mackerel (indicating the occurrence of adaptive evolution). It is also possible to construct population genome simulations under different climate scenarios to predict the potential evolutionary response path of Spanish mackerel. If it is found that some key adaptive genes may be lost under extreme scenarios, this is very important for formulating seed conservation and aquaculture strategies.

(5) Interdisciplinary integration and data sharing: The study of Spanish mackerel brings together the interests of multiple fields such as systematics, population genetics, ecology and aquaculture science. Future research should promote closer cooperation among these fields. For example, genetic parameters can be introduced in fishery management decisions, or ecological adaptability can be considered in the formulation of breeding programs. The establishment of an open Spanish mackerel genome and environmental database is encouraged to allow researchers and institutions in different regions to share data and conduct joint analysis.

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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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