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Origins, Paleontological Evidence, and Global Dissemination Pathways of Abalone

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Abstract This study comprehensively explores the evolutionary history of abalones, the formation mechanism of biodiversity and the historical path of their global spread. As Marine gastropods with both ecological significance and economic value, the evolutionary origin of this group can be traced back to the middle of the Cretaceous period. By integrating the fossil records from ancient Marine regions with contemporary molecular system geographic information, the study confirmed that this genus has shown stable retention of morphological characteristics during the long-term evolution process, and further pointed out that the Indo-Pacific region is the main evolutionary hotspot for the diversity of its existing species. Through the analysis of the genetic lineage, it can be seen that the periodic climate changes during the glacial and interglacial periods, the diffusion strategies of the larvae, and the differences in the Marine environment jointly contributed to the complex geographical lineage structure of this species complex. This study proposes a three-dimensional and multi-level analytical framework, which can provide theoretical support and empirical basis for the scientific protection and sustainable development of abalone resources.

Keywords Abalone (Haliotis); Fossil record; Molecular phylogenetics; Biogeography; Conservation genetics

1 Introduction

Abalone, as a key economic species in Marine ecosystems, has attracted much attention for its unique shell structure and extensive temperate - subtropical distribution characteristics. This type of gastropod organism shows significant intraspecific morphological differentiation. Coupled with scattered fossil evidence, its systematic classification and origin research have long been controversial (Lee et al., 1995; Dominici et al., 2025). Analyzing the origin process, fossil evolution trajectory and global diffusion pattern of this group is an important basis for reconstructing its evolutionary history and formulating resource protection countermeasures.

As one of the main existing groups of the snail family, abalone's evolutionary history can be traced back to the Late Cretaceous period (approximately 66 to 75 million years ago) (Estes et al., 2005; Dominici et al., 2025). Relevant geographical analysis indicates that the early ancestors of abalone might have originated from the Tethys Ocean region or the continental margins of the North Pacific. After several rounds of local extinction during the Paleogene period, they gradually evolved into core areas of radiation and expansion in California and Southeast Asia. From the late Miocene to the early Pleistocene, with the development of the cold-water ecosystem, this group showed obvious adaptability to the trend of increasing body size (Lee et al., 1995). Although the fossil distribution of the Cenozoic Era is relatively scattered, through the systematic analysis of the shell structure, the evolutionary path of ancient European populations has been successfully reconstructed (Estes et al., 2005).

Research combining paleontological evidence and molecular data shows that abalone genus has multi-directional evolutionary characteristics during the diffusion process. Genetic analysis at the population level reveals that there are genealogical intersections among the existing groups, which are quite different from the traditional subspecies classification (Li et al., 2024; Dominici et al., 2025). The genetic composition in some parts of Europe indicates that this group experienced isolation and re-diffusion caused by climate fluctuations during the Pleistocene. Limited by geographical conditions, populations on some islands have developed unique genetic backgrounds. The genes of the populations on the west coast of North America show strong homogeneity, indicating that population expansion may have occurred recently. Overall, these pieces of evidence support the view that geological changes, ocean separation and reproductive mechanisms jointly influence the current distribution pattern (Estes et al., 2005; Dominici et al., 2025).

This study systematically constructed the origin and evolution framework of the genus Abalone by integrating paleontological stratigraphic records, molecular evolution data and biogeographic models, providing theoretical support for a deeper understanding of the formation mechanism of its biodiversity and sustainable utilization. The research results not only reveal the geographical diffusion paths and species differentiation patterns of the Abalone genus in different periods, but also reveal the driving role of key environmental factors in its evolutionary process. This framework is conducive to predicting the potential distribution and adaptation strategies of abalone resources under the background of global climate change, providing a scientific basis for resource conservation and germplasm innovation.

2 The Origin of Abalone

2.1 Origin of abalone in the cretaceous period of the mesozoic era

Paleontological studies have confirmed that the earliest representative species of abalone emerged in the Late Cretaceous (approximately 66~75 million years ago), and its evolutionary roots can be traced back to the end of the Mesozoic Era (Estes et al., 2005). The spatiotemporal distribution characteristics of these ancient shell fossils are consistent with the radiation expansion period of Marine primary producers (such as brown algae) at that time, suggesting that ecosystem reconstruction may have triggered its early phylogenetic differentiation.

The drastic changes in the Marine environment during the Cretaceous period (including ocean current reorganization and changes in substrate types) profoundly influenced the evolutionary direction of this genus by creating new feeding niches. Although the fossil preservation is incomplete, the continuous occurrence record across geological periods indicates that abalone has a unique adaptability to drastic environmental changes, providing important clues for revealing the laws of long-term evolution.

2.2 Molecular evidence of abalone 100 mya

Multi-gene joint phylogenetic analysis shows that the phylogenetic separation of this genus from other primitive gastropods occurred approximately 100 million years ago and has a significant correlation with Mesozoic geological events (Yang et al., 2000; Carlisle et al., 2021). Selection stress analysis revealed that reproduction-related genes (such as the coding regions of ligand recognition proteins) underwent specific adaptations during evolution, corresponding to their rapid radiative evolution stages.

The replication events and subfunctionalization of key functional genes (such as sperm acrosomal enzyme gene clusters) constitute the molecular basis of environmental adaptation (Carlisle et al., 2021; Jia et al., 2022). These genetic mechanism innovations significantly enhanced their survival advantages in different physicochemical environments (such as fluctuations in pH).

2.3 The Indo-Pacific region is the ancestral cradle of abalone diversity

The analysis of biogeographic patterns indicates that this sea area, as the core area of the origin of existing species diversity, maintains the highest level of phylogenetic diversity (Hsu and Gwo, 2017). Its unique Marine topographic features (such as island arc systems and upwelling systems) provide ideal conditions for the speciation process by strengthening geographical isolation.

By analyzing the SSR marker data of typical sea areas such as the Philippine Sea and the Java Sea, the obvious genetic differentiation boundaries and the biological migration patterns with limited diffusion capabilities were revealed, which provided evidence for the view that the relevant sea areas undertake the driving sources of evolution at the genomic level. The high retention rate of ancient haplotypes in the region and the continuously discovered latent biological populations have strengthened the validity of this biogeographical theoretical framework from multiple dimensions.

3 Paleontological Evidence

3.1 Abalone shell fossils have been discovered in sediments from the Cretaceous period to the present, especially in the Tethys Sea region

Paleontological stratigraphic records show that the shell fossils of this genus were first preserved in the Maastrichdian stage (Late Cretaceous), and the early remains were concentrated in the west coast of North America and the Caribbean Sea area. After the Oligocene, they gradually appeared in the strata of New Zealand and Europe (Geiger and Groves, 1999). Since the Miocene, its fossils have been widely distributed in tropical and temperate seas around the world, especially enriched in areas such as the Mediterranean Sea, the west coast of North America and the east coast of Australia.

Although extant groups have the highest diversity in the Indo-Pacific Ocean, the fossil record in this area is extremely scarce, which may be due to diagenesis or insufficient sampling coverage. Based on the analysis of fossil distribution patterns and stratigraphic sequences, the Tethys Sea and its adjacent Pacific Ring transition zone are presumed to be the potential origin centers of this genus.

3.2 Morphological features such as breathing pores and shell structures are helpful for identifying fossil species and inferring evolutionary trends

Shell structural characteristics (such as the arrangement pattern of breathing pores and helical structure parameters) are the core basis for identifying fossil species (Geiger and Groves, 1999; Dominici et al., 2025). Multivariate analysis of ancient shells through geometric morphology measurement methods can effectively improve the classification accuracy of fossils and identify new evolutionary lineations (Figure 1) (Dominici et al., 2025).

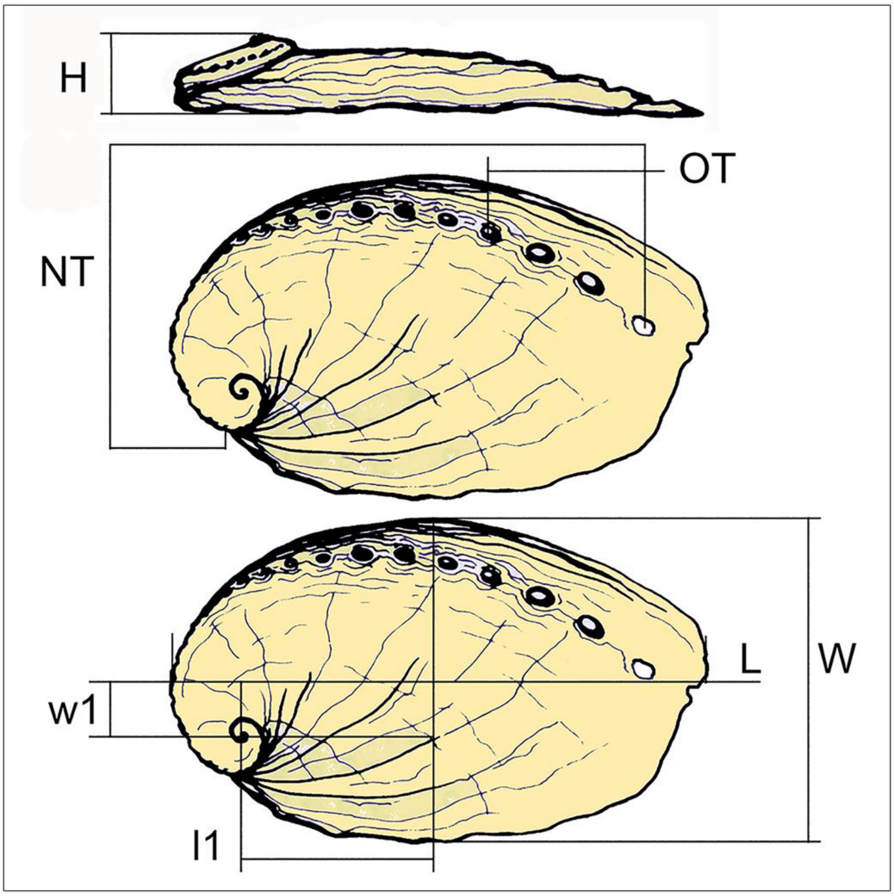

Figure 1 Haliotis shell morphometrics: L=maximum length (Adopted from Dominici et al., 2025)

Image caption: L=length from apex to L midline; W=maximum width; w1=width from apex to W midline; H=height from apex to aperture; NT=total number of tremata, from the contact of the whorl with the posterior labial margin to the anterior end of the row; OT=open tremata (Adopted from Dominici et al., 2025)

Such morphological evolution studies have successfully reconstructed the transition sequence from Haliotis ovata to *H. tuberculata*, revealing the response mechanism of shell characteristics to paleoenvironmental changes (Dominici et al., 2025). However, it should be noted that the phenotypic plasticity of current species may cause deviations in fossil interpretation, and correction should be carried out in combination with quantitative morphological indicators (Geiger and Groves, 1999).

3.3 The fossil record supports the long-term stability of shell morphology, but diversity undergoes regional changes over geological time

Morphological evidence of the shell indicates that since the Late Cretaceous, this genus has maintained significant structural conservation, and the core shell configuration has not undergone fundamental changes (Geiger and Groves, 1999). This evolutionary inertia may be closely related to the specialization of the ecological niche where its rocky reefs inhabit.

However, the regional species composition shows dynamic evolutionary characteristics, the differentiation event of the Mediterranean flora in the Pliocene was synchronized with the global cooling process (Dominici et al., 2025). Some ancient species (such as *H. antiqua*) only existed in specific geological periods, while widespread species such as *H. bertinii* continued into the Pleistocene, reflecting the differentiated survival patterns under the background of climate fluctuations.

4 Global Dissemination and Biogeographic Patterns

4.1 Abalones cross continents through plate movement and the spread of larvae affected by ocean currents

The formation of the global distribution pattern of abalones is regulated by both geological tectonic movement and the mechanism of larval migration. The separation of ancient land blocks and the development of new ocean basins provide channels for their diffusion. The planktonic larvae of them achieve transoceanic spread with the help of dominant ocean currents, facilitating long-distance genetic communication (Jeffrey et al., 2006; Mares-Mayagoitia et al., 2025). Although the planktonic period of the larvae of some species is relatively short, the dominant ocean current still maintains significant interpopulation connectivity. Molecular evidence shows that their gene flow even breaks through geographical barriers.

However, there is significant regional heterogeneity in the diffusion efficacy of the larvae, *Haliotis asinina* in the Indo-Pacific shows clear lineage boundaries among the main sea areas, but specific ocean currents still maintain gene infiltration between isolated populations (Jeffrey et al., 2006). The synergistic effect of ancient plate movement and existing Marine processes continuously shapes the modern distribution pattern and genetic structure of this genus (Jeffrey et al., 2006; Mares-Mayagoitia et al., 2025).

4.2 Main diversification centers: Indo-Pacific, South Africa, North Pacific

As a key source of evolution, the Indo-Pacific region ranks first in the world in terms of genetic diversity dimensions and population structure complexity (Jeffrey et al., 2006). The Cape of Good Hope waters in South Africa and the marginal area of the North Pacific Ocean (Sea of Japan/Gulf of California) served as key evolutionary hubs, each evolving specific evolutionary branches and adaptive traits (Mares-Mayagoitia et al., 2023; Mares-Mayagoitia et al., 2025). These regions are maintained by a stable supply of genetic matrix and environmental gradients, supporting the continuous survival of organisms and the process of ecological differentiation.

Genomic scanning revealed that the species clustering patterns in these hotspot regions were significantly associated with environmental factors such as temperature and dissolved oxygen (Sandoval-Castillo et al., 2018; Mares-Mayagoitia et al., 2023). For example, although the abalone population in the California cold current region maintained a high genetic homogeneity, adaptive differentiation to local environmental heterogeneity was still detected. These regions provide key samples for analyzing the evolutionary potential and climate response mechanisms of this genus.

4.3 Climate events (such as glaciers) and sea level changes have played a crucial role in isolating populations and promoting speciation

The Pleistocene ice age cycle and the resulting sea level rise and fall events had a profound impact on the biogeographic pattern of this genus, driving the heterologous species formation process through periodic isolation effects (Jeffrey et al., 2006). The drop in sea level during the ice age led to shelf exposure and habitat fragmentation, prompting genetic divergence among isolated populations (Jeffrey et al., 2006; Wang, 2024). Interglacial Marine transgressions triggered secondary contacts, forming a complex pattern of genetic infiltration.

These paleoclimate signals are completely preserved in the genetic structure of modern populations, manifested as the coexistence of isolated residual characteristics and expansive imprints (Jeffrey et al., 2006; Dimond et al., 2024). For example, the genetic fault zone of the H. asinina population in the Indo-Pacific is highly consistent with the paleogeographic barrier, while the contemporary gene flow pattern is jointly regulated by reproductive characteristics and ocean current dynamics (Jeffrey et al., 2006). Such events have profoundly shaped the modern diversity spatial pattern of this genus.

5 Molecular Phylogenetic and Genetic Evidence

5.1 Mitochondrial DNA and nuclear markers help clarify species relationships and differentiation times

Mitochondrial genomes (such as the COI coding region) and nuclear genomic markers (such as lysozyme genes and the 18 kDa protein coding region) have become key tools for analyzing the relationships and differentiation sequences among abalone populations (Lee et al., 1995; Metz et al., 1998; Hsu and Gwo, 2017; Tshilate et al., 2023). Analysis based on the joint establishment of multiple genes can accurately identify genetic differences at the species/subspecies level and effectively reveal latent diversity units (Lee et al., 1995; Hsu and Gwo, 2017).

Taking the COI sequence as an example, its haplotype network analysis shows that there are significant genetic distances among geographical populations such as the Taiwan Strait and the Sea of Japan, and the taxonomic status of some abalone populations needs to be redefined (Hsu and Gwo, 2017). Nuclear gene selection stress testing further supports this conclusion. The rapid evolution patterns of reproductive-related genes (such as the coding regions of gamete recognition proteins) provide new evidence for germline differentiation mechanisms (Lee et al., 1995; Metz et al., 1998; Tshilate et al., 2023).

5.2 Genetic evidence of ancient radiation and recent diversification

Whole-genome sequencing revealed that this genus presented bimodal evolutionary characteristics. In the Indo-Pacific hotspot region, paleodifferentiation events and recent species formation events show spatio-temporal coupling (Lee et al., 1995; Botwright et al., 2019; Chiappa et al., 2022). Typically, the estimated time point for the phylogenetic differentiation between the green abalone and the striped abalone is 71 million years ago, corresponding to the geological records of key evolutionary nodes at the end of the Cretaceous period (Botwright et al., 2019).

Cases of late differentiation were simultaneously detected. Although the phenotypic differences of the specific groups in the Mediterranean were significant, the level of genomic differentiation was relatively low (Lee et al., 1995; Chiappa et al., 2022). Microsatellite data analysis indicates that speciation in this area is limited by geographical isolation and presents rapid speciation characteristics (Chiappa et al., 2022).

5.3 Population genetics indicates that due to larval retention and habitat specificity, gene flow between species with longer geographical distances is limited

Analysis of the genetic structure of transocean populations shows that genetic connectivity among geographically isolated populations is generally limited, mainly attributed to the retention effect of larvae and habitat specialization (Hsu and Gwo, 2017; Walton et al., 2022; Chiappa et al., 2022. If significant Fst values were detected between populations in the Taiwan Strait and the Sea of Japan, SNP markers revealed the existence of diffusion barriers and independent evolutionary units (Hsu and Gwo, 2017).

Each archipelago maintains a unique genetic branch, confirming the evolutionary background of geological historical isolation and limited gene exchange (Walton et al., 2022). The research conclusion confirms the synergistic effect of geographical isolation and niche conservation, jointly regulating the formation of the global genetic pattern of this genus (Figure 2) (Hsu and Gwo, 2017; Walton et al., 2022; Chiappa et al., 2022).

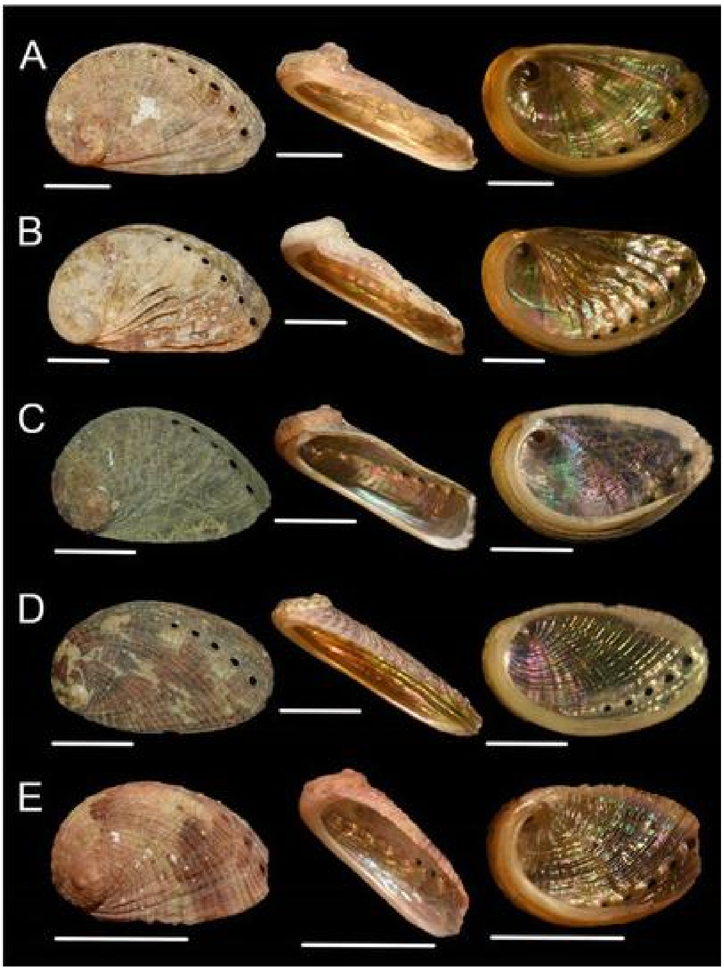

Figure 2 Voucher shells of the Haliotis investigated in this work with their morphological identification (Adopted from Chiappa et al., 2022)

Image caption: (A) Haliotis tuberculata tuberculata BAU 1391. (B) Haliotis tuberculata tuberculata with lamellae (formerly Haliotis lamellosa) BAU 676.3. (C) Haliotis mykonosensis BAU 657.3. (D) Haliotis tuberculata coccinea BAU 717.3. (E) Haliotis stomatiaeformis, juvenile BAU 699. All scale bars are 1 cm (Adopted from Chiappa et al., 2022)

6 The Value of Human-Mediated Diffusion and Protection

6.1 The influence of abalone farming and directional migration on natural distribution and gene pool

Intensive aquaculture and artificial migration activities have profoundly reconstructed the original distribution framework and genetic composition of the species of this genus. The regional restocking project (taking Baja California, Mexico as an example) has an increased degree of genetic homogenization in the released population due to the single parental source, resulting in a significant divergence from the surrounding wild population (Munguia-Vega et al., 2015). Such artificial regulatory behaviors may trigger the infiltration of heterologous genotypes, threatening the genetic integrity and environmental adaptation potential of indigenous populations.

In conservation practice, migration management programs are applied to the rejuvenation of endangered populations. For example, due to the wide-area genetic structure and high genetic heterogeneity characteristics of the black abalone population, ex-situ conservation and population reconstruction have become low-risk implementation paths (Wooldridge et al., 2024). However, it is necessary to strictly prevent and control biosafety risks such as pathogen transmission and the loss of specific adaptive characteristics.

6.2 Overfishing and diseases threaten population conservation

The pressure of high-intensity fishing continues to threaten the resources of this genus, and most economic species have been included in the list of threatened species (Peters et al., 2024). Overdevelopment leads to population collapse, decline in genetic diversity and increased vulnerability to environmental stress. Although the spread of larvae may temporarily increase the genetic diversity level of declining populations, its natural recovery rate is difficult to meet conservation requirements (Miller et al., 2009).

Disease outbreaks (such as the wilt syndrome that led to a 90% reduction in the California black abalone population) have exacerbated the difficulty of conservation (Peters et al., 2024; Wooldridge et al., 2024). The synergistic effect of pathogen - climate - interspecific competition forms complex stress, highlighting the need to establish a multi-factor integrated management model.

6.3 Importance of natural and artificial distribution for management

Distinguishing between the effects of natural diffusion and artificial migration is the prerequisite for formulating scientific management plans. Molecular traceability technology can identify the genetic imprints generated by management measures (such as the establishment of Marine protected areas), providing biomarkers for evaluating conservation effectiveness (Munguia-Vega et al., 2015). Studies have shown that the protected area network can effectively maintain the level of genetic diversity and enhance population connectivity as a hub for juvenile diffusion.

Optimal management requires the integration of genomic data, ecological models and ocean dynamic parameters to construct a genetic adaptive protection framework (Munguia-Vega et al., 2015; Mares-Mayagoitia et al., 2025). It is suggested to establish a cross-jurisdiction-jurisdiction collaboration mechanism and develop an SNP marker traceability system to ensure the sustainability of resources in the context of environmental changes (Munguia-Vega et al., 2015; Peters et al., 2024; Mares-Mayagoitia et al., 2025).

7 Conclusion

The evolutionary origin of abalones can be traced back to the Cretaceous period, and their shell fossils have completely preserved the continuous evolutionary trajectory from ancient oceans to modern nearshore ecosystems. This adaptive resilience throughout geological eras has been confirmed at the genetic level. The deep divergence among the main evolutionary branches reveals the evolutionary buffering capacity of this group in response to geological upheavals and climate oscillations. The synergy of paleontological remains and molecular evidence indicates that their evolutionary steady-state characteristics and widely adaptable phenotypes are the core driving forces for the successful colonization of global seas.

The existing geographical distribution pattern of abalones is jointly shaped by natural forces and human disturbances. The larvae rely on the natural diffusion of ocean currents and are restricted by geographical barriers and ecological gradients, forming a coupled population structure of "high connectivity - local specialization". However, human activities such as intensive fishing and escape from aquaculture have disrupted the natural gene flow pattern, triggering ecological responses such as the invasion of heterologous genes or the decline of indigenous genetic diversity. Modern conservation planning needs to take into account the dual effects of the historical evolution path and human activity stress.

Integrating paleoecological evidence, refined genomic analysis and ecosystem simulation can systematically reveal the deep mechanism by which abalones adapt to radiation. For example, environmental genomics can decipher the spatiotemporal patterns of ocean current regulation on gene flow, and physiological threshold studies can analyze the critical parameters of species' habitat requirements. The key technologies supported by such research include optimizing the network topological configuration of Marine protected areas, constructing dynamic prediction models for population rejuvenation, and formulating eco-friendly aquaculture procedures, etc. The establishment of a cross-regional collaborative governance framework and a DNA barcode traceability system will become the core countermeasures to address the challenges of global changes.

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Conflict of Interest Disclosure

The authors affirm that this research was conducted without any commercial or financial relationships that could be construed as a potential conflict of interest.

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