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Genomic Selection Breeding in Abalone: Progress and Challenges

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Abstract Abalone is an important marine aquaculture shellfish in China, and its output accounts for about 90% of the world in recent years. Traditional breeding plays a key role in improving abalone yield and stress resistance, but faces bottlenecks such as slowing growth rate and inbreeding germplasm degradation. This study reviews the genetic basis and relationship between traits of the main economic traits of abalone, the proposal of emerging breeding goals, the accumulation of abalone genomic and omics data resources, the support of high-throughput phenotype and molecular detection technology, the research progress of the application of genome selection in abalone, and the breeding practice cases of industry-university-research cooperation. On this basis, we will explore the combination of cutting-edge technologies such as multi-omics fusion, intelligent algorithms and gene editing with abalone breeding, and look forward to the new models of targeted cultivation and personalized breeding in the future. Comprehensive analysis shows that important progress has been made in abalone genome selection breeding, but there are still challenges in improving the breeding system, accumulating data and integrating new technologies. Looking ahead, we should "hold on the germplasm chips" and drive the creation of abalone varieties through the integration of multi-dimensional technology to help the abalone industry continue to develop at a high-quality level.

Keywords Abalone; Economic traits; Genome selection; High-throughput breeding; Multiomic fusion; Breeding model

1 Introduction

Abalone (Haliotis) has been the first of the "four major seafood" in China since ancient times due to its high nutritional value and high market price. After decades of development, China has become the world's number one abalone breeding country. But while developing rapidly, the abalone industry also faces many challenges. Due to the long-term self-breeding of germplasm, inbreeding and germplasm degeneration of breeding groups, which are manifested as problems such as miniaturization of individuals, decreased stress resistance, and low production performance. Traditional breeding plays a role in improving the survival rate and growth rate of abalone, but it mainly relies on phenotypic selection, with a long cycle and limited efficiency (Liu et al., 2015). In order to solve the "bottleneck" problem of the abalone industry, it is necessary to use modern biotechnology to accelerate the breeding process.

Genome selection technology has triggered a revolution in the field of animal and plant breeding since its introduction in 2001. GS uses a large number of molecular markers across the genome-wide range to predict individual species values, which can significantly improve selection accuracy and genetic progress, and is regarded as an important means of molecular design breeding (Liu et al., 2023). Since 2016, China's aquatic products field has begun to explore GS methods, and has conducted research on varieties such as scallops, shrimps, yellow croaker, flounder, tilapia and abalone and established a GS technology system (Xu, 2024). Especially in abalone breeding, GS is expected to make up for the shortcomings of traditional breeding inefficiency and inability to make early selections for complex traits such as stress resistance. Starting from the 13th Five-Year Plan period, the country has provided key support for abalone genome sequencing and new variety cultivation through special scientific and technological investments such as "Blue Granary". The Ke Caihuan team of Xiamen University has successively cultivated three national new abalone varieties, "Dongyou No. 1", "Xipan Abalone" and "Lüpan Abalone", marking that China's abalone breeding level has ranked among the forefront of the international community.

Based on reviewing the genetic foundation of abalone's economic traits and traditional breeding experience, this study focuses on summarizing the research progress and application prospects of genome selection breeding technology in abalone, analyzing the current technical and industrialization challenges, and looking forward to the future direction of achieving the transformation of abalone breeding model through the integration of multi-dimensional technology. Through a systematic review of Chinese and foreign literature in the past five years, we hope to provide theoretical reference and practical reference for the cultivation and industrial upgrading of abalone varieties.

2 Genetic Basis and Breeding Objectives of Economic Traits of Abalone

2.1 The main economic traits of abalone and their genetic control modes

The main economic traits of abalone can be categorized into three major types: yield traits, quality traits, and stress resistance traits. Yield traits include individual weight, shell length, shell height, and meat yield ratio, which directly determine aquaculture profitability. Quality traits involve appearance (e.g., shell color) and nutritional components (e.g., taurine and protein content), which are closely related to market value and consumer preferences. Stress resistance traits refer to tolerance to high temperatures, low oxygen, and disease resistance, all of which are critical for survival rate and farming stability.

Most economic traits in abalone are controlled by quantitative genes, exhibiting polygenic inheritance and high environmental plasticity. Heritability estimates show substantial differences in the genetic control strength of different traits. For instance, studies on the growth traits of *Haliotis diversicolor* indicate that the heritability of shell length and body weight from juvenile to adult stages is moderate to moderately high (0.15~0.37). The heritability of heat tolerance traits in *Haliotis diversicolor squamata* (Wrinkled Disk Abalone) is moderate (0.35~0.42), while flesh quality traits such as taurine content also show moderate heritability (0.33~0.42) (Liu et al., 2023).

2.2 Conflict between genetic correlations and selection between traits

In breeding practice, trade-offs are often needed between multiple target traits. When there is a positive genetic correlation between the two traits, homogeneous selection can lead to synergistic efficiency. Some studies have found that abalone shell length is significantly positively correlated with survival rate (genetically related 0.467), and the survival rate of abalone with faster growth is also relatively high. This means that certain traits can be improved simultaneously by co-selecting. However, selection conflicts occur when there is negative correlation between traits or antagonism. A typical example is the relationship between the shell color and growth of abalone: although abalone with red shell spots has ornamental or market value, its growth performance is worse than that of ordinary shell color individuals. Research on this phenomenon shows that the growth rate of red-shell abalone is significantly slower, and hybridization with ordinary strains can produce moderate-level hybrid dominance (Zhou et al., 2023). This suggests that a balanced genetic conflict is required when improving both appearance and growth traits. In addition, under the high-intensity selection of pursuing a single trait, other traits in the population may degenerate, such as one-sided pursuit of growth rate, which has led to adverse consequences such as the decrease in fertility of abalone and weakening of disease resistance. Therefore, modern breeding pays more attention to the application of comprehensive selection index and sets trait weights based on genetic correlations to avoid adverse correlation responses as much as possible.

2.3 Emerging breeding objectives: high temperature resistance, disease resistance and adaptability

With the changes in breeding environment and climatic conditions, the emerging goals of abalone breeding are gradually focusing on improving environmental stress resistance and disease resistance. High temperature resistance traits are increasingly valued. The sea temperature in southern production areas such as Fujian often rises to the upper limit of abalone tolerance in summer, resulting in large-scale deaths of abalone farmed. For example, the continuous high temperature has caused the survival rate of wrinkle plates to plummet, becoming a bottleneck that restricts industrial development. Studies in recent years have shown that genomic selection has significant effect in improving the heat resistance of abalone: using about 65 000 markers to perform GS analysis on 1 120 wrinkled disc abalones, the survival rate of selected high-heat-resistant families has been significantly improved (Yu et al., 2021). Secondly, disease-resistant breeding is becoming increasingly the focus. Under the conditions of tight breeding of abalone, bacterial sepsis, red meat diseases and other diseases are prone to outbreaks, posing a serious threat to yield. Traditional methods have achieved certain results through hybrid selection and breeding. For example, the new *Haliotis diversicolor* variety "Dongyou No.1" exhibits approximately 30% higher disease resistance compared to ordinary populations. However, disease resistance is usually controlled by polygenics and phenotype determination requires disease exposure, making breeding difficult (Zhou et al., 2023). GS provides a new idea for disease-resistant breeding: through genome-wide association analysis, disease-resistant SNP markers and candidate genes can be identified, so as to perform early genome-level seed selection. Broad-spectrum adaptability is also a new breeding direction, that is, improving the tolerance of abalone to multiple environmental stresses, including resistance to hypoxia and typhoons and waves. Low dissolved oxygen or even red tides often occur in nearshore aquaculture water bodies in summer and autumn, so the cultivation of hypoxic-resistant strains is increasingly attracting attention. An invention patent proposes a method to quickly determine the ability of abalone to resist hypoxia, which can be used to early screening of tolerant individuals. This phenotyping technique provides tool support for stress-resistant breeding. With accurate hypoxia-resistant phenotype data, combined with GS analysis, it is expected to cultivate new abalone products that are more adaptable to hypoxia environments.

3 Development of Abalone Genetic Resources and Accumulation of Omics Data

3.1 Progress in abalone genome sequencing and construction of reference genomes

The construction of high-quality reference genomes provides a fundamental information platform for genetic breeding in abalone. With the application of third-generation sequencing and advanced assembly technologies, the quality of abalone genome assemblies has improved significantly. In 2024, researchers assembled the genome of the tropical abalone (*Haliotis asinina*) to the chromosome level using PacBio HiFi long-read sequencing combined with Omni-C technology. This effort resulted in 16 pseudo-chromosomes covering 1.12 Gb-more than 98% of the total genome length-with a contig N50 of 67.09 Mb and genome completeness of 97.6%. A total of 25 422 protein-coding genes were annotated, providing a valuable resource for comparative genomic studies on heat tolerance mechanisms in abalone (Nguyen et al., 2022).

In addition to *H. asinina*, reference genomes of several other abalone species have been published. A U.S. research team constructed a reference genome for the red abalone (*H. rufescens*) as part of the California Conservation Genomics Project (CCGP); this genomic map aids in assessing the genetic diversity and adaptive potential of wild red abalone populations. Meanwhile, a high-quality reference genome for the endangered black abalone (*H. cracherodii*) was assembled using PacBio and Hi-C technologies, providing essential genetic data for species restoration efforts (Franchini et al., 2011). In Australia, researchers also reported a draft reference genome of the South African abalone (*H. midae*), with a total length of approximately 1.5 Gb and a contig N50 of 0.24 Mb. In practical breeding applications, reference genomes can be used to design capture chips or SNP arrays, enabling genome-wide scanning of breeding populations.

3.2 Acquisition and utilization of omics resources such as transcriptome and metabolomic group

In addition to genome sequencing, the accumulation of functionalomics data also provides important information for abalone breeding. In terms of transcriptomics, the abalone gene expression profiles under different developmental stages, tissues and treatment conditions have been widely analyzed. In the anti-pathogenic study, the researchers conducted transcriptome sequencing of the gill tissue after the pathogenic bacteria of wrinkle disc abalone infection, and identified 7 656 up-regulated and 2 789 down-regulated differentially expressed genes, which were enriched in redox processes, immune responses and other pathways. Among them, upregulated genes include pattern recognition receptors (such as C1q-like proteins, NOD-like receptors) and effector molecules (such as IL-17, lysozyme, superoxide dismutase, etc.), showing that abalone has initiated defense responses such as innate immunity and apoptosis regulation under the challenge of bacteria (Fang et al., 2022). Such transcriptomic data helps to lock in disease-related candidate genes (such as immune receptors, antimicrobial peptide genes), providing clues for molecular marker development and functional verification (Table 1). In the field of heat resistance, studies have compared the gene expression differences of hybrid abalone and their parents under heat stress, and found that hybrid abalone exhibits many non-additive expression genes, which may explain its heat resistance hybrid advantages (Boamah et al., 2024).

Metabolomics also plays an increasingly important role in the study of abalone’s adaptability and quality. By analyzing the changes in small molecule metabolites of abalone under different environmental conditions or nutritional levels, we can gain an in-depth understanding of its physiological metabolic mechanism. Some studies have compared the metabolites spectrum of wrinkle disc abalone after acute high temperature stress in the low-temperature domestication group and the room-temperature domestication group. It was found that high temperature will lead to impaired mitochondrial function, incomplete oxidation of amino acids and fatty acids, and accumulation of large amounts of unstable metabolic intermediate products (Nguyen et al., 2022). This metabolomic evidence reveals the biochemical adaptation mechanism of abalone's heat-resistant domestication, which is of guiding significance for cultivating heat-resistant strains.

Table 1 Summary of transcriptome data quality

Sample	Raw Reads	Clean Reads	Q20 (%)	Q30 (%)
A0h_1	49 956 086	48 345 146	97.80	93.78
A0h_2	60 683 246	59 898 532	97.87	93.80
A0h_3	61 470 694	60 069 372	97.92	93.99
A8h_1	51 587 050	50 699 510	97.92	94.03
A8h_2	52 928 692	49 932 234	97.59	93.30
A8h_3	58 296 146	55 617 338	97.99	94.16
A48h_1	56 932 668	55 630 668	97.81	93.76
A48h_2	53 354 632	49 324 524	97.97	94.06
A48h_3	51 494 542	50 737 750	98.01	94.12

3.3 Genetic marker development: comparative analysis of SNP, SSR and InDel

Molecular genetic markers are a key tool to connect genomic information with breeding practices. Early molecular breeding research on abalone mainly relies on microsatellite markers (SSR) and amplified fragment length polymorphisms (AFLP), etc., for population genetic diversity analysis, genetic linkage map construction and pedigree identification. Due to its co-dominant and multi-allelic characteristics, SSR markers have played an important role in small-scale genetic monitoring (Liu and Huang, 2024). However, the number of SSRs is limited, unevenly distributed, and the detection throughput is low, making it difficult to automate. With the improvement of abalone reference genomic data, it is possible to develop high-density SNP markers. For example, based on high-deep resequencing data, hundreds of thousands of high-quality SNP sites can be screened out in the wrinkle disc abalone genome. The abalone SNP chip developed in recent years has greatly improved the efficiency and consistency of genotyping: Korean researchers have developed a 60K abalone custom chip containing 65,740 SNP sites, and the average classification success rate is 90.47%, and the polymorphic SNP ratio is 76.03% (Kho et al., 2021). China also has an independently developed 40K liquid phase capture chip to achieve target capture and sequencing of nearly 88 000 SNP sites in the abalone genome. Compared with traditional SSR markers, SNP chips have the advantages of high flux, wide coverage, good stability and easy to detect automatically; compared with conventional solid-phase SNP chips, liquid-phase capture chips are easier to operate, lower cost and have high flexibility. Therefore, in the whole genome selection of abalone, SNP markers have become the main force. A patent has reported a method to identify the inherited male and female wrinkle disc abalone by detecting base deletion at specific sites (Luo et al., 2021). InDel markers tend to have the advantage of being simple and intuitive (electrophoretic and discernible length differences), but are relatively small in number.

4 High-Throughput Technical Support System in Abalone Breeding

4.1 High-throughput phenotypic analysis platform and underwater imaging technology

Phenotype determination is the basis of breeding, but as marine shellfish, the traditional measurements of abalone (such as shell length, weight, survival, etc.) often require manual operation, which is inefficient and easily stressful to individuals. To meet the needs of large-scale family breeding, high-throughput, non-invasive phenotypic acquisition technology is gradually being applied in abalone breeding. Among them, underwater imaging and image analysis are important directions. By installing a high-definition camera or scanner in the breeding pond, images of abalone individuals are collected regularly, and then using image analysis algorithms to automatically measure growth indicators such as shell length, shell width and volume, the growth tracking of thousands of individuals can be achieved without taking measurements one by one (Dai et al., 2024). This method has been verified in some aquaculture, such as the prediction of fish length and behavioral monitoring. For attached growing abalone, combined with special lighting and background plates, an automatic shooting and size recognition system is expected to be established to significantly improve the efficiency of phenotypic data acquisition. In addition, technologies such as ultrasonic imaging have also introduced abalone breeding. Studies have tried to use ultrasound to non-invasively detect the gonad development status of abalone to distinguish gender and maturity. This method avoids the harm caused by traditional anatomy examination to pro-balm, making screening of breeding groups more efficient. Furthermore, environmental sensors and intelligent monitoring platforms are also under development, which can record breeding environmental parameters and phenotypic behavioral data such as abalone feeding and exercise in real time (Williams et al., 2018). Through the Internet of Things, this data is integrated into a breeding database, breeding experts can monitor the growth and health of each family in real time during the busy season and adjust their breeding strategies in a timely manner.

4.2 Automation and scale development of molecular marker detection technology

The advancement of genotyping technology has greatly promoted the transition from experience to precise seed selection. In abalone breeding, molecular marker detection has evolved from the past low-throughput manual operation to a highly automated large-scale process. First of all, the high-density SNP classification technology based on chips has been applied. By customizing the SNP chip, genotypes of tens of thousands of loci can be detected on each abalone in one experiment. Secondly, the popularity of the next generation of sequencing (NGS) technology provides solutions for simplifying methods such as genome sequencing and target sequence capture. Using RAD-seq or GBS technology with restriction enzyme digestion, thousands of abalones can be sequenced in parallel, and thousands of SNP marker data can be obtained for genetic evaluation and selection. Compared with traditional methods, the data analysis process can be completed automatically, and data between different batches and laboratories have good consistency (Zhao et al., 2023). Furthermore, laboratory automation equipment greatly improves detection efficiency and accuracy. The adoption of fully automatic DNA extractor and PCR loading system enables 384 or even 1536 samples to be processed simultaneously per round of molecular detection, reducing artificial error and working intensity. In some large domestic aquatic breeding centers, the equipment of high-throughput sequencing platforms and computing servers makes it a reality to process tens of thousands of abalone samples each year. Finally, as the cost decreases, the application of whole-genome resequencing in breeding has also been explored. Some studies have conducted whole-genome sequencing of dozens to hundreds of abalones to identify functional mutations and provide a basis for marker-assisted selection.

4.3 The role of bioinformatics and cloud computing in data analysis

As abalone breeding enters the genome era, the analytical and processing ability of large-scale data has become one of the keys to the success or failure of breeding. On the one hand, the amount of data generated by genome sequencing and large population typing is extremely large, requiring powerful bioinformatics tools for management and interpretation. A genome-wide association analysis (GWAS) may involve tens of millions of genotypes and trait data of thousands of individuals, and its computational complexity is very high. To this end, researchers have developed bioinformatics software specifically for aquaculture breeding, such as the "AquaGS" system based on a graphical user interface, which can support users to conveniently perform GS prediction model construction and cross-validation analysis. This type of software integrates a one-stop process from data import, quality control, model training to result visualization, greatly reducing the technical threshold for breeding experts to apply GS (Liu et al., 2023). At the same time, more and more research relies on high-performance computing (HPC) and cloud platforms to process breeding data. Uploading huge genomic data to the cloud can quickly complete tasks such as genome assembly, variation detection and breeding value prediction using the parallel computing power of cloud servers. Another important aspect is the application of big data and artificial intelligence technologies in breeding decision-making. Analyzing multi-generation breeding data through machine learning algorithms can optimize the optional solutions, control the growth of in-kin coefficients, and predict genetic progress under different breeding schemes. Big data analysis can be used to identify key environmental factors that affect the growth and survival of abalone, thereby guiding the precise delivery of good varieties in different breeding areas.

5 Research Progress of Genome Selection (GS) Technology in Abalone

5.1 Analysis of the applicability of GS principle in abalone

Genome selection uses molecular markers to cover the entire genome to predict individual breeding values, which have achieved remarkable results in domestic livestock, poultry and some aquatic animals. For abalone with longer generation intervals, the application of GS has a clear potential advantage. Wrinkle disc abalone is generally sexually mature in 2 to 3 years. If traditional phenotype breeding is adopted, the selection cycle of one generation often takes more than 3 years. GS allows early selection based on genotype at the larval stage, thereby shortening generational intervals and improving genetic progress. Secondly, the abalone has strong fertility (single females can lay millions of eggs), and a large enough reference group can be established to support GS model training. Taking heat tolerance as an example, one study assessed heat tolerance phenotypes in over a thousand *Haliotis diversicolor squamata* (Wrinkled Disk Abalone) individuals and conducted a genome-wide scan, and estimated that the breeding value was as accurate as possible. This accuracy has been significantly higher than the traditional genealogical BLUP method, greatly increasing the choice credibility. Some target traits of abalone (such as disease resistance) cannot be directly measured on candidate abalone, and the species-using individual must be selected through family measurement of siblings. GS can use data on survival or disease-challenged individuals, train the model and then predict the disease-resistant breeding value of healthy abalone, thereby achieving the selection of untested individuals, which is particularly important for improving disease-resistant breeding efficiency. Of course, some special factors need to be considered in the application of GS: the cost of abalone larvae cultivation and family construction is high, and the size of the training group will affect the accuracy of the model; the environment of different abalone breeding varies greatly, and the GS model may have an extrapolation risk of environmental adaptability.

5.2 Construction and evaluation methods of prediction model

The core of genomic selection is to build reliable genomic breeding value (GEBV) prediction models. Currently in the abalone GS study, the main statistical methods used include GBLUP (Genome Optimal Linear Unbiased Prediction) and various Bayesian models. GBLUP uses all markers to construct a genomic affinity matrix to directly predict GEBV, and is computationally efficient and suitable for traits that are mainly additive genetic. Bayesian model assumes that different markers have different effect distributions, which can give greater weight to a few large-effect QTLs, and may perform better when traits are affected by major genes. Data simulation studies on abalone show that Bayesian models have better prediction accuracy than GBLUP when there are a few large effect sites; however, in real data applications, Bayesian methods often perform comparable or slightly advantageous to GBLUP.

In terms of model evaluation, cross-validation or independent validation set methods are usually used to measure prediction accuracy, that is, to calculate the correlation coefficient of GEBV to the actual phenotype (or traditional breeding values). The reference population is randomly divided into training sets and verification sets, and multiple cycles of verification can be obtained to know the average correlation coefficient of the model on unknown individuals. In the example of abalone heat resistance traits, the average accuracy of the BayesB model with 5-fold cross-validation reached 0.55±0.05, indicating that the model has high robustness (Liu et al., 2022). Furthermore, direct evaluation of the selection response can be used, i.e. the phenotypic advantage of species abalone selected according to GEBV compared to unselected populations.

5.3 GS cases of key traits (such as growth, disease resistance)

Research on the application of genome selection technology in abalone is still in its infancy, but some cases of key traits have made encouraging progress. In terms of growth traits, some experts conducted genome-wide association analysis on the growth-related traits (shell length, shell width, total weight, etc.) of the wrinkle disc abalone population, and identified multiple significantly associated SNP sites and candidate genes. These growth-related markers explain a proportion of phenotypic variation that can be incorporated into the GS model to improve the accuracy of prediction of growth traits.

In terms of disease-resistant traits, taking the common resistance to Vibriopathy as an example, domestic scientific research teams are building large-scale family lines and genotyping the activity, hoping to find molecular markers that resist disease and use them for GS model training. Referring to the successful experience of other aquatic animals, such as the anti-sea lice and anti-bacterial cold water disease traits of salmon, which have achieved a genetic gain of about 20% to 30% through GS, and the prospect of anti-disease GS of abalone is also widely optimistic (Zhao et al., 2023). Genomic selection has shown feasibility in response to environmental stress resistance traits. GS application of high-temperature traits is the most advanced: Liu et al. successfully bred a heat-resistant abalone breeding line using genome prediction, which not only verified the effectiveness of GS in this trait, but also provided an example for other stress-tolerant traits. In this study, they measured the heat-resistant phenotype (adhesion time under high temperature exposure) on 1120 tail wrinkle disc abalone and obtained approximately 64,788 high-quality SNP genotype data (Brokordt et al., 2017). The BayesB model constructed with these data has a prediction accuracy of 0.55 (GBLUP is 0.40), and the accuracy rate is further improved by selecting a significant SNP subset. The highly heat-resistant individuals selected from this are used for reproduction and the heat-resistant survival of their offspring is expected to be significantly higher than that of control systems without GS selection.

6 Practical Applications and Case Studies of Genomic Selection Breeding in Abalone

6.1 Comparative breeding strategies based on different germplasm backgrounds

Abalone breeding strategies can vary based on different germplasm resources, primarily including three models: intra-population selection and improvement, hybridization among closely related species to develop new varieties, and distant hybridization to create heterosis. Intra-population selection relies on the genetic variation within the target species, using family selection to accumulate favorable alleles. Hybridization among closely related species utilizes genetic differences between geographical populations, with directional crosses to cultivate new varieties. A representative case is the "Xipan Abalone" bred by Xiamen University: this variety was developed by crossing the imported Japanese disk abalone (*Haliotis discus discus*) as the female parent with a selectively bred local Jinjiang line of the wrinkled disk abalone (*Haliotis discus hannai*) as the male parent. After four generations of selection, a new line was obtained that combined the superior traits of both subspecies while overcoming hybrid sterility and instability (Zhao, 2014).

Distant hybridization-crosses between different species-has attracted significant attention in abalone breeding. It enables the realization of strong heterosis and breaks through the limitations inherent in the original species. The “Lüpan Abalone” is a successful example of such distant hybridization. It was developed by crossing a selectively bred line of *H. discus hannai* (wrinkled disk abalone) as the female parent with the introduced American green abalone (*H. fulgens*) as the male parent, and took 11 years of breeding efforts. This new variety combines the large body size of green abalone with the desirable meat flavor of *H. discus hannai*. Its growth size is more than double that of ordinary wrinkled disk abalone, with 30% of individuals exceeding 500 grams. It also demonstrates an increased heat tolerance of 2.26 °C and a nearly halved farming cycle (Figure 1) (Guo et al., 2023).

This breakthrough enabled China to possess a domestically bred variety comparable to large abalones imported from South Africa and Australia. The main challenges of distant hybridization lie in reproductive isolation and offspring fertility. However, once successful, the resulting hybrids often carry trait combinations that are impossible to achieve through conventional breeding (Xiao et al., 2022). The development of the Lüpan Abalone clearly illustrates that interspecies hybridization, combined with post-hybrid selection, provides a viable “path of transcendence” for abalone, effectively addressing challenges such as small body size and slow growth in domestic strains.

Figure 1 The new abalone variety of national review A Dongyou No. 1; B Xipan abalone; C Lüpan abalone (Adopted from Guo et al., 2023)

6.2 Experience in pilot projects in cooperation with enterprises and scientific research

Abalone breeding is a systematic project that cannot be separated from the close cooperation between scientific research institutes and enterprises. In recent years, China has carried out a number of pilot projects in the cultivation of abalone varieties through industry, academia and research, and has accumulated valuable experience. The cooperation between Fuda Abalone Company and Xiamen University is one of the examples. Under the guidance of Xiamen University’s expert team, Fuda Abalone Company, located in Fujian, started from the first few breeding ponds and gradually established a modern breeding workshop of 3 500 square meters. Schools and enterprises jointly implemented a number of major provincial and ministerial scientific research projects, and built the world's first-class and largest abalone breeding base - the "Fujian Province Abalone Genetic Breeding Center" (Figure 2). The center currently preserves 7 species of abalone, 3 national new varieties and 33 breeding lines, and has established more than 320 families, becoming the library with the most complete living germplasm resources and the strongest seed production capabilities (Xu, 2024). In terms of creating new varieties, the school-enterprise teams complement each other’s strengths: the scientific research party is responsible for genetic evaluation, hybridization plan design and marking development, and the enterprise party is responsible for large-scale seedling breeding, breeding comparison experiments and promotion and application. After the new variety passes the national approval, enterprises will use their own channels to quickly pilot the demonstration and promote it, and transform the advantages of the good varieties into productivity as soon as possible. After years of hard work, Fuda Abalone Company was approved as a national wrinkle plate abalone seed farm in 2023, achieving a "zero" breakthrough in the national seed farm of Fujian aquatic companies. This success proves that the strong alliance between scientific research and enterprises can effectively open up the entire chain of abalone seed cultivation. From the formulation of breeding plans, germplasm innovation to large-scale seedling production and promotion and application, each link has professional division of labor and coordination, thus accelerating the output and industrialization of new varieties.

6.3 Establishment and optimization of integrated breeding system of industry, academic and research

In order to make abalone breeding sustainable development, it is crucial to build a good breeding system that integrates production, education and research. The integrated breeding system emphasizes the organic connection between breeding, seedling breeding and promotion, and realizes the closed loop of "breeding and promotion". In the process of breeding good varieties, it is necessary to continue to develop new varieties and maintain genetic progress. Fujian and other places have jointly built genetic breeding centers through scientific research institutions and leading enterprises, ensuring the long-term and stable development of breeding work (Lai et al., 2023). For example, Zhangzhou City and the Provincial Aquatic Products Research Institute jointly built the southern Fujian fishery germplasm resource library, committed to the protection and rational utilization of high-quality germplasm such as abalone. Only with core breeding units can we continuously provide excellent parents and technical support for the entire industry. In the seedling breeding process, it is necessary to integrate seedling breeding resources and increase the supply ratio of good seedlings. At present, there are still problems with scattered seedling farm layout and insufficient number of good seed farms. The solutions include: planning a centralized seedling cultivation base, promoting the creation of high-quality seed farm certification, and improving the standardization level of seedling production. By formulating technical and quality standards for abalone seedling cultivation, each seedling farm is encouraged to strictly implement unified breeding procedures for good seedlings to ensure stable seedling quality (Gan et al., 2022). At the same time, we support advantageous enterprises to take the lead in forming a seedling breeding consortium to change the situation where many seedling farms fight independently. In the promotion of good varieties, it is necessary to establish a smooth channel from core groups to commercial breeding. Under the integrated system, breeding units provide good-bred parents or fertilized eggs, professional hatcheries cultivate naive abalone, intermediate cultivation grounds cultivate large seedlings, and finally breed commercial abalone, with all links closely connected and division of labor and cooperation. Under this model, breeding units ensure the recycling and supply of good seedlings through the contract system, while the breeding end verifies the effect of new varieties through demonstration points, accelerating the improvement of good seed coverage.

Figure 2 Marine breeding in the sea area of Dajian village, Huangqi town, Lianjiang county, Fuzhou city (Photo credit: Wang W.W.)

7 Future Breeding Model of Abalone Driven By the Integration of Multidimensional Technology

7.1 Synergistic effect of genome selection and gene editing

Genome selection and gene editing are the two core technologies of molecular breeding, each with unique advantages. GS is able to handle overall improvements in quantitative traits, while gene editing can accurately modify individual genes. The collaborative application of the two is expected to accelerate abalone breeding to a new level. On the one hand, GS can be used to discover and evaluate key genes of traits and indicate targets for gene editing. The main effect QTL or candidate genes identified through GS analysis can be directed edited using tools such as CRISPR/Cas9 (Li et al., 2024). On the other hand, new variants created by gene editing can also be included in GS evaluation to achieve combination optimization. For non-modal organisms such as abalone, current gene editing efficiency and larval survival remain challenges. However, studies have proved the feasibility of abalone gene editing: through microinjection of TALEN tool, researchers have successfully achieved directed mutations in the abalone fertilized egg gene and cultivated surviving D-shaped larvae. This shows that abalone has the basis for carrying out functional gene knockout and knock-in experiments. With the improvement of gene editing technology (such as the use of efficient CRISPR/Cas systems and optimized embryo microscopy), it is entirely possible to create new traits that are difficult to obtain in traditional breeding in abalone.

7.2 Intelligent breeding: AI algorithms and big data decision-making support

The development of modern information technology has injected new vitality into traditional breeding. The application of artificial intelligence (AI) and big data in abalone breeding will drive the breeding model from experience-driven to intelligent-driven. Artificial intelligence algorithms can be used to analyze complex breeding data, mine potential laws and optimize decisions. Some studies have introduced deep learning algorithms in GS to capture nonlinear genetic effects and gene interactions that are difficult to characterize in traditional linear models. Preliminary results show an improvement in the prediction accuracy of low hereditary traits. Big data integration analysis can assist breeding decisions. Abalone breeding involves genetic, environmental and management data. For example, by integrating the production big data of different breeding farms over the years, AI algorithms can identify which families perform better in specific environments (such as high temperature and high density ponds), thereby guiding the targeted promotion of the strains and achieving matching of "good varieties and good methods". For example, when using computer vision technology to monitor the feeding and exercise behavior of young abalone in the seedling cultivation stage, and to judge the health status early based on behavioral abnormalities, it will greatly improve the survival rate and selection intensity of breeding populations. If blockchain and other technologies are introduced into breeding data management, it can ensure that the breeding process data is authentic and traceable, making it easier for AI to learn more trustworthy information (Liu et al., 2022). The vision of intelligent breeding is to build a "digital twin" breeding scenario: simulate different assembly schemes and breeding environments in a computer, conduct virtual evaluations of each candidate scheme, and screen out most suboptimal schemes before real-life experiments. This will greatly compress the test cycle and cost.

7.3 Exploration of targeted breeding and personalized marine breeding

Faced with the diversified market demands in the future and the complex and changeable breeding environment, abalone breeding is developing towards directional and personalization. The so-called targeted breeding refers to the targeted cultivation of varieties or strains that meet the target based on specific breeding goals and conditions. For example, in order to adapt to the high-temperature sea areas under the background of global warming, new heat-resistant abalone varieties can be selected in a directional manner; in order to meet the demand for super-large abalone in the high-end market, extremely fast-growing and large individual varieties can be cultivated in a directional manner; for the deep sea cage breeding model, abalone types that are resistant to waves and flows and have stronger adhesion can be selected. The implementation of targeted breeding is inseparable from the support of the aforementioned GS, gene editing and AI technologies. Genome selection allows us to accelerate selection at the molecular level for a target trait without waiting for complete multitrait improvement.

Based on targeted breeding, the concept of personalized marine aquaculture has gradually emerged. Different farmers and industries may have different preferences for abalone varieties: some focus on growth rate, some emphasize the meat yield and flavor, and some focus on the ornamental shell color. In the future breeding system, breeding plans can be customized for the needs of the main categories. For example, for the leisure agriculture of "yard abalone" can provide ornamental products with gorgeous shell colors but slightly slow growth; for the processed dry abalone industry, it can provide special products with huge individual and dense fleshy texture suitable for sun drying. The cultivation of these personalized lines was difficult to take into account in the past due to resource constraints, and with the help of genomic technology, it was possible to advance multiple breeding programs in parallel (Arai and Okumura, 2013).

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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.

References

Arai K., and Okumura S., 2013, Aquaculture-oriented genetic researches in abalone: current status and future perspective, African Journal of Biotechnology, 12: 4044-4052.
https://doi.org/10.5897/AJB12.2178

Boamah G.A., Huang Z., Ke C., You W., Ayisi C.L., Amenyobge E., and Dropenu E., 2024, Preliminary analysis of pathways and their implications during salinity stress in abalone, Comparative Biochemistry and Physiology Part D Genomics and Proteomics, 50: 101224.
https://doi.org/10.1016/j.cbd.2024.101224

Brokordt K., González R., Farías W., Winkler F., and Lohrmann K., 2017, First insight into the heritable variation of the resistance to infection with the bacteria causing the withering syndrome disease in *Haliotis rufescens* abalone, Journal of Invertebrate Pathology, 150: 15-20.
https://doi.org/10.1016/j.jip.2017.08.014

Dai Y., Shen Y.W., Liu Y.B., Xia W.W., Hong J.W., Gan Y., Huang J., Luo X., Ke C.H., and You W.W., 2024, A high throughput method to assess the hypoxia tolerance of abalone based on adhesion duration, Aquaculture, 590: 741004.
https://doi.org/10.1016/j.aquaculture.2024.741004

Fang Y., Yang X.Y., Zhang S.J., Chen X.Y., Lin G., Zhang Y.Q., Wang M.J., and Li M.Z., 2022, Transcriptome study on immune response against *Vibrio parahaemolyticus* challenge in gill of abalone *Haliotis discus hannai* Ino, Frontiers in Marine Science, 9: 956317.
https://doi.org/10.3389/fmars.2022.956317

Franchini P., Van Der Merwe M., and Roodt-Wilding R., 2011, Transcriptome characterization of the south African abalone *Haliotis midae* using sequencing-by-synthesis, BMC Research Notes, 4: 1-11.
https://doi.org/10.1186/1756-0500-4-59

Gan Y., Wang Y., Yu F., Xiao Q.Z., Luo X., Han Z.F., Ke J.W., You W.W., and Ke C.H., 2022, Genotype by environment interactions for productive traits of purebred and crossbred abalone strains under different rearing modes, Aquaculture, 563: 738966.
https://doi.org/10.1016/j.aquaculture.2022.738966

Gao X.L., Zhang M., Luo X., You W.W., and Ke C.H., 2023, Transitions challenges and trends in China's abalone culture industry, Reviews in Aquaculture, 15(4): 1274-1293.
https://doi.org/10.1111/raq.12769

Kho K.H., Sukhan Z.P., Hossen S., Cho Y., Kim S., Sharker M.R., Jung H.J., and Nou I.S., 2021, Construction of a genetic linkage map based on SNP markers QTL mapping and detection of candidate genes of growth-related traits in pacific abalone using genotyping-by-sequencing, Frontiers in Marine Science, 8: 713783.
https://doi.org/10.3389/fmars.2021.713783

Lai X., Xiao Q., Ji H., Huang Z., Huang H., You W., Luo X., and Ke C., 2023, Comparative analysis of the growth and biochemical composition of backcrosses and their parents in abalone, Aquaculture, 570: 739445.
https://doi.org/10.1016/j.aquaculture.2023.739445

Li R., Xu Y., Wu F., Peng Z., Chan J., and Zhang L., 2024, Easy-to-use CRISPR-Cas9 genome editing in the cultured pacific abalone (*Haliotis discus hannai*), The CRISPR Journal, 7(1): 41-52.
https://doi.org/10.1089/crispr.2023.0070

Liu H., and Huang S.Q., 2024 The role of immune function in longevity and adaptation in vertebrates, International Journal of Molecular Zoology, 14(4): 197-210.
https://doi.org/10.5376/ijmz.2024.14.0018

Liu J., Lai Z., Fu X., Wu Y., Bao X., Hu Z., and Lai M., 2015, Genetic parameters and selection responses for growth and survival of the small abalone *Haliotis diversicolor* after four generations of successive selection, Aquaculture, 436: 58-64.
https://doi.org/10.1016/J.AQUACULTURE.2014.10.046

Liu J.Y., Yin Z.Z., Zhou M.Z., Yu W.C., You W.W., Chen Y.X., Luo X., and Ke C.H., 2023, Genetic parameters and genomic prediction for nutritional quality-related traits of Pacific abalone (*Haliotis discus hannai*), Aquaculture, 579: 740118.
https://doi.org/10.1016/j.aquaculture.2023.740118

Nguyen T.V., Alfaro A.C., Mundy C., Petersen J., and Ragg N.L.C., 2022, Omics research on abalone (*Haliotis* spp.): current state and perspectives, Aquaculture, 547: 737438.
https://doi.org/10.1016/j.aquaculture.2021.737438

Xu T., 2024, Improving abalone farming in fujian: genetic environmental and disease management solutions, MedScien, 35(3): 703-710.
https://doi.org/10.61173/3mwghy58

Yu F., Peng W., Tang B., Zhang Y., Yi W., Gan Y., Luo X., You W.W., Gwo J., Chen N., and Ke C.H., 2021, A genome-wide association study of heat tolerance in Pacific abalone based on genome resequencing, Aquaculture, 536: 736436.
https://doi.org/10.1016/J.AQUACULTURE.2021.736436

Zhao C.N., and Yan Z.L., 2014, Hybrid technology of discus abalone *Haliotis discus hannai* and *H. discus discus*, 2014: 654-657.

Zhao Z., Gan H., Lin X., Wang L., Yao Y., Li L., Wang Y., and Zhang Z., 2023, Genome-wide association screening and MassARRAY for detection of high-temperature resistance-related SNPs and genes in a hybrid abalone (*Haliotis discus hannai* ♀×*H. fulgens* ♂) based on super genotyping-by-sequencing, Aquaculture, 573: 739576.
https://doi.org/10.1016/j.aquaculture.2023.739576

Zhou M.C., Zhang J.P., Huang M.Q., You W.W., Luo X., Han Z.F., and Ke C.H., 2023, Genetic variation between a hybrid abalone and its parents (*Haliotis discus hannai* ♀ and *H. fulgens* ♂) based on 5S rDNA gene and genomic resequencing, Aquaculture, 579: 740173.
https://doi.org/10.1016/j.aquaculture.2023.740173

Xiao Q.Z., Shen Y.W., Gan Y., Wang Y., Zhang J.P., Huang Z.K., You W.W., Luo X., and Ke C.H., 2022, Three-way cross hybrid abalone exhibit heterosis in growth performance thermal tolerance and hypoxia tolerance, Aquaculture, 555: 738231.
https://doi.org/10.1016/j.aquaculture.2022.738231

Williams D., Aitkenhead M., Karley A.J., Graham J., and Jones H.G., 2018, Use of imaging technologies for high throughput phenotyping, Raspberry: Breeding, Challenges and Advances, 2018: 145-158.
https://doi.org/10.1007/978-3-319-99031-6_9

Luo H., Xiao J., Jiang Y., Ke Y., Ke C., and Cai M., 2021, Mapping and marker identification for sex-determining in the Pacific abalone *Haliotis discus hannai* Ino, Aquaculture, 530: 735810.
https://doi.org/10.1016/j.aquaculture.2020.735810