

Genetic Basis of Growth Traits in Shrimp Based on QTL and GWAS Studies

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Abstract Shrimps are an important part of global aquaculture, especially South American white shrimp and other varieties dominate the global aquatic supply, and their output accounts for more than half of the world's total crustacean production. Growth traits (such as body length, weight, etc.) are directly related to breeding yield and economic benefits, and are one of the core goals of aquatic breeding. In recent years, molecular genetic technologies such as quantitative trait locus (QTL) localization and genome-wide association analysis (GWAS) have made progress in the field of aquatic products and have been gradually applied to shrimp genetic breeding research. This study reviews the main growth traits of shrimp and their biological mechanisms, reviews the current application status of QTL localization and GWAS in the study of growth traits of shrimp, summarizes the research progress of key molecular markers and candidate genes, and discusses the combination of traditional breeding and molecular assistive means using Chinese shrimp as an example. Finally, future strategies and international cooperation in shrimp molecular breeding are expected.

Keywords Shrimp; growth traits; Quantitative trait loci (QTL); Genome-wide association analysis (GWAS); Molecular marker-assisted breeding

1 Introduction

Shrimp plays an important role in the global aquaculture industry. In particular, due to its fast growth and strong adaptability, *Litopenaeus vannamei* has become the world's highest-growing crustacean variety, accounting for more than 50% of the total global aquaculture crustacean production. Asia is the main production area, and the shrimp farming industry in China, Southeast Asia and India is booming, providing the world with a large amount of high-quality animal protein. Prawns are cultivated along the coast and inland China, and are one of the important industries for increasing fishery income and farmers to get rich. However, the development of different shrimp species is not balanced. For example, Chinese shrimps in China have plummeted due to disease outbreaks in the 1990s, while foreign vanabinoid shrimps have occupied the mainstream of breeding with higher survival and growth advantages (Ma et al., 2024; Wang et al., 2024).

Growth rate and final yield are one of the most concerned economic traits of aquaculture. For shrimp farming, individual weight and specifications directly determine market value. Faster-growing shrimps can shorten the breeding cycle, reduce feed and management costs. Studies have shown that shrimp growth traits have moderate to high heritability and can be significantly improved through breeding. In traditional breeding, breeders mostly use fast growth and large individual parent shrimp as the selection criteria. After continuous generations of family breeding, the growth rate of some shrimp varieties has been significantly improved. For example, the growth rate of new varieties such as vanabinoid shrimp "Kohai 1" and "Zhongxing 2" cultivated in China has significantly improved compared with the unbreeding groups (Huang et al., 2019).

With the development of molecular biology and genomics, breeders have begun to apply technologies such as QTL localization and GWAS to the genetic analysis of quantitative traits of aquatic animals. These methods have been successful in fish, such as Atlantic salmon, raw fish, etc., the growth, meat quality, disease resistance and other traits have been identified. QTL studies have constructed high-density genetic linkage maps to locate gene segments that control quantitative traits and provide molecular markers for important traits (Andriantahina et al.,

2013; Chen et al., 2022). GWAS uses a large number of markers across the genome-wide range to find trait-related alleles at the population level, with higher resolution and application range than traditional QTLs. In shrimp, early QTL studies were able to roughly localize regions containing thousands of genes due to their limited marker density. With the development of high-throughput sequencing, tens of thousands of SNP markers have been developed and applied to map construction and association analysis, improving positioning accuracy and efficiency.

2 Biological Basis of Shrimp Growth Traits

2.1 Main growth trait indicators: body length, weight, shell thickness, survival rate

Shrimp growth traits are usually characterized by several indicators that are phenotypically measurable, among which the most commonly used are body length and weight. Body length includes the full length and body length, etc., which can reflect the individual's morphological development. In genetic assessment, the average weight of a specific day age, daily weight gain or weight gain rate for a specific period is often used as a measure of growth rate. Shell thickness (shell hardness) is also a related trait. Although it does not directly represent growth rate, the thickness and weight of the shell will affect the net meat output ratio of shrimp, which has also been paid attention to in some breeding programs. In addition, survival rates are often regarded as important breeding traits and are closely related to growth (Yuan et al., 2018): Only under the premise of similar survival can it be practical to improve growth. Therefore, survival rate is sometimes used as an auxiliary indicator of growth tests. At the same time, there have been researches to include bait conversion rate, plumpness, etc. into the evaluation system of shrimp growth traits to more comprehensively measure growth performance. In QTL and GWAS analysis, these traits can be analyzed individually, or the overall growth phenotype can be extracted by comprehensive analysis methods such as principal components.

2.2 Physiological and metabolic regulation mechanisms

The growth of shrimp is regulated by a variety of endocrine and metabolic factors. From an endocrine point of view, shrimp lack growth hormones similar to vertebrates, but have hormone-like molecules such as insulin-like peptides (ILPs). The *ILPI* gene of vannamee shrimp was cloned and found that it is widely expressed in various tissues of the shrimp body, especially the highest among neuroendocrine organs (eye stems, etc.) (Su et al., 2024). This is similar to the role of insulin-like growth factors in regulating the growth and development of vertebrates, suggesting that *ILPI* has an important function in the growth and development of shrimps. In addition, ecdysterone (20E) and ecdysterone (MIH) in shrimps indirectly affect growth rate by regulating the molting cycle: shrimps only increase in volume and weight after molting, and shortening molting intervals can improve growth rate (Naidu et al., 2013). In terms of metabolism, growth speed is often related to nutritional metabolism and energy distribution. Studies have compared the molecular differences of fast-growing and slow-growing shrimps, and found that the genome-wide DNA methylation level of slow-growing individuals has significantly increased and is accompanied by upregulation of metabolic-related gene expression. These differential genes are enriched in carbohydrate and fatty acid metabolism pathways, and it is speculated that slow-growing shrimp will use more nutrients to maintain basal metabolism and stress rather than somatic growth. This finding suggests that epigenetic modifications (such as DNA methylation) participate in the regulation of shrimp growth phenotype by affecting the expression of metabolic genes.

2.3 Effect of environmental factors on growth traits

Environmental conditions largely determine the development of shrimp growth potential. Among them, water temperature is the most direct environmental factor affecting shrimp growth. The optimal growth temperature of vannamee prawns is about 28 °C~32 °C. Too low will reduce feeding and metabolic rates, and growth will slow down significantly, while too high may trigger a stress response and also inhibit growth (Heriyati et al., 2024). Studies have shown that under low temperature stress, the antioxidant enzyme activity and energy metabolism in shrimps change, and long-term low temperatures will lead to growth stagnation and even death. Dissolved oxygen levels are also crucial. Adequate dissolved oxygen keeps shrimps high intake and high metabolism. Conversely, hypoxia causes anorexia, growth stagnation, and weak shrimps are more susceptible to disease (Akbarurraiyid et

al., 2023). Water quality factors such as ammonia nitrogen and nitrite have a recessive effect on growth: chronic low-concentration ammonia nitrogen stress can reduce the feeding rate and digestive enzyme activity of shrimps, and the growth rate is significantly reduced (Li et al., 2024). A study of vanabinoid shrimp found that under the dual stress of sub-chronic ammonia nitrogen and salinity, the specific growth rate and intake of shrimp were inhibited and induced changes in stress-related gene expression. In addition, stocking density and nutritional level can also affect growth traits. High-density farming often leads to slow growth and small individuals, which is due to crowded stress and intra-species competition. In terms of bait nutrition, insufficient protein content will limit growth, and adding an appropriate amount of immune enhancer (such as astaxanthin) can improve digestive enzyme activity and growth-promoting gene expression, thereby improving growth performance.

3 Application of QTL Study in Shrimp

3.1 Basic principles and methods of QTL research

Quantitative trait loci (QTL) localization is a classic method to discover quantitative trait genes through genetic linkage analysis. The basic principle is to detect the linkage association between phenotypic traits and molecular markers on the constructed genetic linkage map. If the marker typing of a region is significantly correlated with the trait value, it is inferred that the region contains genol points that affect the trait. Traditional QTL mapping usually uses two-parent hybrid families, such as crossing parents with different growth traits, obtaining F2 or backcrossing populations, and then phenotyping and genotyping of population individuals. According to different mapping models, statistical methods such as interval mapping and composite interval mapping can be used to scan the map to locate the significance QTL. The accuracy of QTL positioning depends on the spectrum density and population size. The QTL map of early shrimps used microsatellite markers (SSRs), etc., and the number of markers was limited, resulting in a wide QTL interval. In recent years, second-generation sequencing technology has promoted the construction of high-density maps, each map can contain thousands to tens of thousands of marks, improving mapping accuracy (Huang et al., 2019).

3.2 Research progress on localization of QTL related to shrimp growth traits

In shrimp, the study of growth-related QTL has made some progress in recent years. The earliest attempt can be traced back to the QTL positioning study of the Chinese shrimp "Huanghai No. 1". Although those studies were published more than a decade ago, they demonstrated the possibility of genetic localization of shrimp growth traits for the first time. In the past five years, with the emergence of vannerbine shrimp genome sequencing and high-density maps, new achievements have been made in QTL localization for growth traits. Experts used a 268-individual shrimp family to detect 11 QTLs with significantly associated growth rates (Ma et al., 2024). These QTLs are distributed in multiple linkage groups of shrimp genomes. Each QTL can explain about phenotypic variations of about 5%~10%, with the sum of contribution rates exceeding 50%, indicating that growth traits are regulated by multiple genes and there are several main-effect sites. Some of these QTLs show colocalization among different traits, suggesting that there may be core genes that affect overall growth ability.

3.3 Comparison of QTLs in different population and genetic background

It should be emphasized that the QTL effect is often population-specific, and the same trait may be controlled by different sites in different genetic backgrounds. This is particularly evident among shrimps. The sites found in early single-line-based QTL studies were not necessarily significant in other strains or wild populations. This is due to the differences in allelic frequencies, linkage imbalance structures of different groups, and the growth traits themselves are affected by environmental and gene interactions. For example, Wang et al. (2019) found a candidate gene in different groups is the scavenger receptor Class C on the 13th linkage group. These results suggest that growth regulation in different breeding populations may be mediated by different gene pathways (Wang et al., 2019). Therefore, when applying QTL to molecular breeding, its population applicability needs to be taken into account, and it is best to be able to re-verify the QTL effect in the target breeding population. One way to improve the universality of QTL is to use multi-population joint maps or genome-wide associations to directly analyze natural populations or breeding populations, thereby localizing "shared sites" associated with traits. In fact, GWAS makes up for the limitations of single-family QTL to some extent and can be used for cross-validation of results in different contexts (Rio et al., 2020).

4 Application of GWAS in Shrimp

4.1 Theoretical framework and technical platform of GWAS

Genome-wide association analysis (GWAS) uses natural variation at the population level to discover trait-related genomic loci through statistical associations. Unlike QTL mapping-dependent families, GWAS is usually performed in groups with diverse genetic backgrounds (such as breeding groups or wild populations), each body is genotyped at high density and then the degree of association between each genotype and phenotype is detected. The theoretical basis of GWAS is that if alleles at a certain position in the genome affect traits, individuals carrying different alleles will have significant differences in the traits. By scanning the whole genome markers, these significant differential sites can be localized to identify potential functional genes. The implementation of shrimp GWAS is due to the advancement of classification technology. In the early days, due to the lack of a high-throughput classification platform, it was difficult to carry out GWAS in shrimp. The simplified genome sequencing methods that have emerged in recent years have greatly reduced the cost, and tens of thousands or even hundreds of thousands of SNP markers can be obtained in one sequencing, providing the possibility for GWAS. Yu et al. (2019) used RAD sequencing to obtain approximately 23 000 SNPs and performed GWAS analysis on 200 vanabinoid shrimps, demonstrating the feasibility of this method in crustaceans (Yu et al., 2019).

4.2 Common typing and statistical methods for correlation analysis

In the practice of shrimp GWAS, different studies have adopted a variety of classification strategies and statistical methods. In terms of typing technology, the most widely used SNP typing based on simplified genome sequencing. Some studies have used 2b-RAD data for GWAS. As genomic work advances, customized SNP chips for Vannebacteria prawns have also been released, such as the 55K SNP chip with more than 72 000 markers developed by the Chinese scientific research team. In terms of statistical methods, classic single-label tests (such as linear regression per SNP) are prone to false associations when considering population structure, so the common MLM model introduces inter-individual relationship matrix and structural matrix (Medrano-Mendoza et al., 2022).

4.3 Current status and results of GWAS research on shrimp growth traits

Although it started late, several GWAS studies on the growth traits of shrimp have been published in recent years, revealing several key genes and molecular mechanisms. In vanabinoid shrimp, genome-wide association analysis was performed on 200 individuals in the breeding population, and four SNP sites significantly associated with body weight were identified, located in the linkage groups 19 and 39, respectively (Lyu et al., 2021). Further, they locked in two candidate genes: the *deoxycytidyl deaminase* gene (*DCD*) and the non-receptor type *tyrosine kinase* gene (*NRTK*), and found that specific SNPs of these genes were significantly associated with shrimp body weight. Using the screened SNPs, they predicted breeding values using a label-assisted BLUP method, with an accuracy of 9.4% higher than that of traditional BLUPs, indicating that these GWAS findings are of practical value. In another study, experts found that genes such as *protein kinase C- δ* (*PKC- δ*) and *Rap2a* may be involved in shrimp growth regulation through GWAS of a family offspring (Yu et al., 2019).

5 Molecular Markers and Candidate Gene Recognition

5.1 Application of molecular markers such as SSR and SNP in shrimp

Molecular markers are the bridge connecting genotypes to trait phenotypes and the basis for QTL and GWAS research. In early genetic studies of shrimp, simple repeat sequences (SSR) are a mainstream marker. SSR, also known as microsatellites, is widely used in the construction of genetic maps and population diversity analysis of shrimps due to its multi-allelic and highly polymorphic characteristics (Chen et al., 2024). The first genetic linkage map of Chinese shrimp is mainly composed of hundreds of SSR markers, which is limited in density but sets the starting point for QTL positioning. SSR labeling technology is mature and has low cost, but automated detection and throughput are relatively limited. At the same time, the genome distribution of microsatellites is uneven, which restricts fine localization. With the development of sequencing technology, single nucleotide polymorphism (SNP) markers have gradually become the preferred marker for shrimp molecular breeding. SNPs are abundant and widely distributed in the genome, and thousands of loci can be discovered at one time through

high-throughput sequencing. Compared with SSR, genotype interpretation of SNP is easier to standardize and is suitable for large-scale automated analysis (Du et al., 2010). In practical applications, SSR and SNP have their own advantages and disadvantages: SSR is suitable for paternity testing, small group linkage analysis, etc., and SNP is suitable for whole genome scanning, fine localization and breeding value prediction.

5.2 Key candidate genes identified by QTL and GWAS

With the help of QTL mapping and GWAS analysis, researchers have unearthed candidate genes closely related to shrimp growth from numerous molecular marker signals. These genes have a variety of functions and cover different links of growth regulation (Ma et al., 2024). *STEAP4* (Metal Reductase 4): Combining QTL localization with QTL expression (eQTL) analysis, the *STEAP4* gene was found to be highly correlated with growth rate in vannamee shrimp. *STEAP4* is involved in cellular iron ion metabolism, and the gene expression is significantly upregulated in rapidly growing individuals, and RNA interference experiments have shown that its silencing slows shrimp growth. Therefore, *STEAP4* is considered to be one of the important regulatory genes that affect shrimp growth.

Dnm1L (deoxycytidyl deaminase, or *DCD*): GWAS identified a significant association between SNP near the *DCD* gene and shrimp body weight. *DCD* plays a role in nucleotide metabolism, and mutation may affect the efficiency of DNA/RNA synthesis. *PTK2* (non-receptor type tyrosine protein kinase): Similar to *DCD*, researchers found that some variations in the *PTK2* gene were related to shrimp body weight. *PTK2* is a cellular signaling molecule and may affect growth by regulating cell proliferation and differentiation signals. Given that growth processes involve multiple cellular signaling pathways, the association of this gene implies the signaling network composition of shrimp growth regulated (Yu et al., 2019).

5.3 Potential function of candidate genes in regulation of growth traits

Based on the candidate genes identified above, the researchers further explored the mechanism of action of these genes in the regulation of shrimp growth. Overall, the genetic regulatory network for shrimp growth is very complex. These candidate genes each perform their own functions and may have interactions to form a multi-level regulatory system. Some candidate genes are directly involved in matter and energy metabolism, affecting the efficiency of nutrients required for shrimp growth. For example, *STEAP4* metal reductase affects iron metabolism and cellular respiration. Research has found that inhibiting *STEAP4* will reduce shrimp feeding and growth, which shows that energy metabolic activity is closely related to growth rate. Secondly, some candidate genes belong to signal transduction and cell cycle regulatory pathways. For example, PKC- δ , *PTK2*, *Rap2a*, etc., they belong to different signal cascades: PKC- δ participates in the MAPK pathway, *PTK2* involves cell adhesion and proliferation signals, and *Rap2a* is a small G protein, which participates in growth factor stimulation response (Figure 1) (Zhu et al., 2022). When the genes of these signaling molecules mutate, the rate of cell proliferation and differentiation process downstream may change, affecting the growth of tissues and individuals.

6 Case Analysis: Study on Growth Traits of Chinese Prawns

6.1 Research progress on QTL localization of growth-related traits of Chinese shrimp

Chinese prawns were once the pillar species of coastal farming in northern China, and the genetic improvement of their growth traits is related to industrial revitalization. After the disease hit the industry hard at the end of the last century, scientists carried out the family breeding of Chinese prawns, and in 2003 it became China's first new breed of marine aquaculture animals - "Huanghai No. 1" Chinese prawns. For this breeding line, early research constructed a genetic linkage map of Chinese shrimp, and QTL analysis of growth traits was performed for the first time. Results QTLs related to body weight and body length were found on several chromosomal segments, and some SSR markers closely linked to QTL were screened out (Liu et al., 2010). These markers were once believed to be used for molecular assisted breeding of Chinese shrimp. In the past five years, with the promotion of molecular tools in aquatic products, there have been new trends in the study of growth traits of shrimp in China. The first is the study of population genetic diversity and differentiation. More importantly, they identified a group of SNP sites with significant frequency differences between breeding and wild populations (significant to *Fst*).

These differential sites may be related to the traits of artificial breeding, suggesting that targeted allelic modifications have occurred in Chinese shrimp.

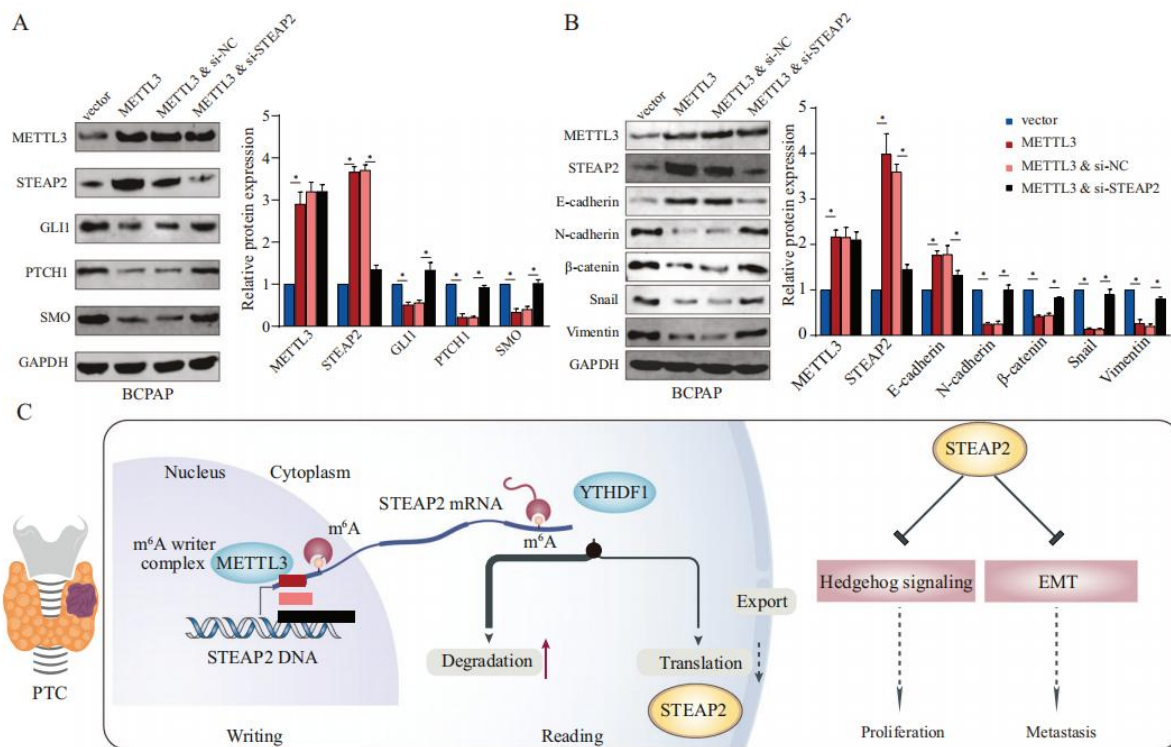


Figure 1 BCPAP PTC cell lines were transfected with METTL3-overexpression (METTL3) plasmids and siRNA targeting STEAP2 (si-STEAP2) as indicated (Adopted from Zhu et al., 2022)

Image caption: A, B Effect of METTL3/STEAP2 axis on the expression of Hedgehog signaling pathway-related proteins (Smo, Gli1, and PTCH1) and EMT markers (E-cadherin, N-cadherin, snail, vimentin, and β -catenin) in PTC cells were quantified by western blot assay. C The graphic illustration of METTL3-mediated m6A modification modulating malignant phenotype of PTC through enhancing STEAP2 expression and then restraining Hedgehog signaling pathway and EMT. All data are presented as the mean \pm standard deviation of three independent experiments. * $P < 0.05$, ** $P < 0.01$, and *** $P < 0.001$ (Adopted from Zhu et al., 2022)

6.2 GWAS reveals the molecular mechanism of key growth traits of Chinese shrimp

Compared with vannamee prawns, there are fewer studies on whole genome association analysis (GWAS) of Chinese prawns. The genetic background differences in Chinese prawns may lead to different growth regulation mechanisms from those of vannamee prawns. Chinese prawns are more tolerant of low temperatures but grow slowly, which may mean that their growth may be controlled by some genes related to energy metabolism and stress response. According to population comparison research, some of the differences between Chinese shrimp breeding population and wild population are located on immune and stress-resistant genes. This suggests that in order to improve survival rate and disease resistance during the breeding process, it may indirectly affect growth-related pathways—faster-growing families are often families with better stress resistance, because improving health status is conducive to growth.

Further, drawing on the discovery of vannamee shrimp, we can pay attention to some common candidate genes. For example, the insulin-like peptide ILP pathway is highly conserved in crustaceans, and similar growth hormones are likely to exist in Chinese shrimp. If differentially expressed genes of fast-growing families can be screened through transcriptome sequencing, ILP, its receptors, downstream signals, etc. are potential targets of concern (Su et al., 2024). In recent years, studies have conducted transcriptome and metabolomic analyses on Chinese shrimp, trying to reveal the molecular characteristics of rapidly growing individuals. The results show that fast-growing Chinese shrimps have a series of metabolic enzyme genes upregulated in muscle tissue, such as

genes related to amino acid metabolism and mitochondrial respiration, which is contrary to the finding that individuals with slow-growing vannameid shrimps have increased metabolism (Figure 2) (Gao et al., 2022). This may be a different adaptation strategy caused by species differences: individuals with slow growth of vannameid shrimps improve metabolism and response stress, while individuals with fast growth of Chinese shrimps improve metabolism and make full use of limited growth seasons.

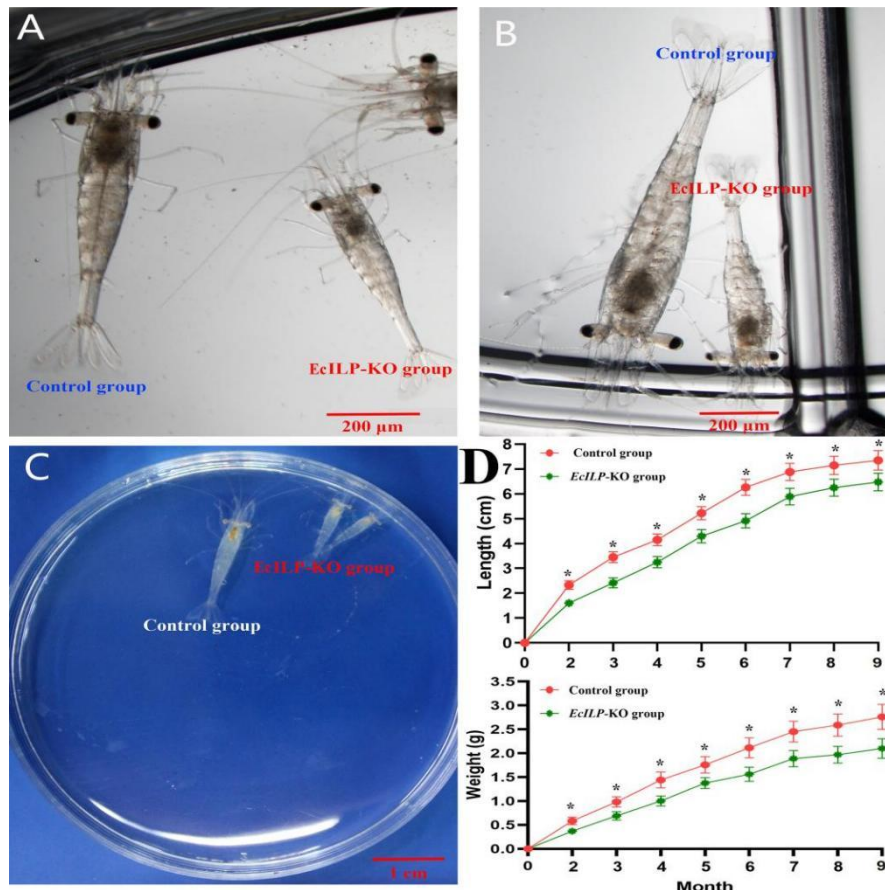


Figure 2 Growth comparison of *EcILP-KO* and control group individuals (Adopted from Gao et al., 2022)

Image caption: (A) 18 days after hatching, (B) 22 days after hatching, (C) One month after hatching, (D) Statistical changes in body length and body weight from 2 to 9 months after hatching. Error bars refer to the standard deviation. P values are denoted: $*P < 0.05$ (Adopted from Gao et al., 2022)

6.3 The response of molecular marker assisted breeding in Chinese shrimp

Chinese shrimp breeding has always been dominated by traditional phenotypic selection, but the concept of molecular marker assisted breeding (MAS) has begun to be gradually introduced. On the one hand, during the breeding process of "Huanghai No. 1", due to the lack of mature molecular markers, breeding mainly relies on family selection and phenotypic screening. But breeding experts have long realized that the introduction of molecular markers can improve the accuracy of seed selection and shorten generation intervals. SSR markers screened in early QTL studies have tried to track allelic frequency changes in excellent families. However, due to the weak association effect of these markers with traits, the effect is not obvious in actual MAS. In recent years, with the enrichment of China's shrimp molecular marker resources, the prospects for MAS application have become clearer. The differential SNP sites identified by Liu Xu et al. can be used as candidate markers for monitoring breeding progress. If the allelic frequency changes at these loci are shown to be consistent with improvements in growth phenotypes, they can be used for early family screening. In addition to MAS, Chinese shrimp breeding may also apply genome-wide selection (GS) strategies. GS uses a large number of markers across the genome to predict individual sports species values, and does not rely on the identification of specific genes. It has been widely used in animal husbandry (Liu et al., 2023).

7 Comprehensive Strategy of Combining QTL and GWAS

7.1 Multiomics joint analysis methods (genomics, transcriptomics, epigenetics)

One of the development directions of modern molecular breeding is to integrate different "omics" information and build a comprehensive trait regulation network. For shrimp growth traits, it is often difficult to fully explain the genetic mechanism by relying solely on a single QTL or GWAS, so data from multiple angles such as genomics, transcriptomics, and epigenetics need to be combined (Zhang et al., 2022). A successful case is Chen et al. (2024) combining traditional QTL analysis with transcriptome expression QTL (eQTL) to discover STEAP4, a hidden key gene. They determined the differentially expressed genes of fast-growing shrimp through the transcriptome, and then screened the differentially expressed genes within the QTL interval, and finally locked in STEAP4 and verified with RNA interference. This QTL+ transcriptome strategy greatly improves the efficiency and accuracy of candidate gene discovery and also provides examples for other traits. For non-modal species such as shrimp, multiomic association also facilitates functional annotation and pathway analysis. Since shrimp genome annotation is not as perfect as model organisms, the transcriptome can determine which genes in the QTL interval are expressed in the target tissues, and the locations of important regulatory elements can be found through ATAC-seq, etc., and the dispersed genes can be integrated into a collaborative network through co-expression analysis (Zhao et al., 2020). This information can help researchers identify the "core" gene nodes that truly drive traits in massive correlation signals. In addition, multiomics combination also provides tools for the study of hybridization advantages and interaction effects.

7.2 Advantages of combining QTL and GWAS in precision breeding

Combining genetic analysis methods such as QTL and GWAS can give full play to the effect of complementary advantages in breeding practice, thereby promoting precise breeding. First, QTL studies are usually conducted at the family level, and can use high heritability to find main effect sites, but are limited to specific parent combinations; GWAS searches for natural variant influence traits at the population level, and the results are more applicable (Banka et al., 2024), but are more sensitive to small effect sites. By combining the two, on the one hand, the reliability of QTL positioning can be verified through GWAS, and on the other hand, the QTL results can be used to guide GWAS screening.

For example, when QTL is located in a certain chromosomal region, focus on the apical signal in that region in GWAS, reducing the burden on multiple tests, and thus making it easier to reach significant levels. Secondly, in the prediction of breeding value, fusion QTL markers and genome-wide markers also have advantages. In actual breeding, several large-effect markers can be locked according to the GWAS results to implement MAS to quickly eliminate families with obvious slow growth, and then use genome-wide breeding value prediction (GBLUP, etc.) to make fine selections (Altaf and Tatar, 2024). This two-stage selection utilizes efficient screening of GWAS and comprehensive accuracy of genome-wide selection, allowing for better genetic gain than using one method alone. Combining QTL and GWAS helps resolve genetic architectures of complex traits, thereby developing multitrait improvement strategies (Francisco et al., 2021). Growth traits tend to be genetically related to other traits, such as growth and survival may be negatively correlated.

7.3 Future prospects for genetic improvement of shrimp

Looking ahead, shrimp genetic improvement will enter a new era driven by molecular technology. Driven by studies such as QTL and GWAS, the genetic basis of our shrimp growth traits is gradually becoming clear. This provides a scientific basis for formulating a new generation of breeding programs. Molecular marker assisted selection (MAS) will be more widely used in shrimp breeding fields. Once the key site effect is verified, breeders can use molecular marker screening at the larval stage to accelerate the turnover of generations and improve the breeding accuracy. Meanwhile, genome-wide selection (GS) is expected to be carried out in large breeding companies. As mentioned earlier, SNP chips and supporting analysis methods have been developed in China. Combined with the characteristics of large reproduction and large family size of shrimps, as long as investment is guaranteed, GS can significantly improve the genetic progress rate. In addition to growth itself, future breeding goals will become more diverse, such as disease resistance, hypoxia resistance, high-quality meat quality, etc.

How to ensure growth advantages while taking into account these traits is a major challenge. This requires comprehensive selection based on methods such as the genome-wide selection index, and also requires us to deeply understand the genetic correlation between traits.

8 Conclusion

Quantitative trait localization (QTL) and genome-wide association analysis (GWAS) have made important contributions to elucidating the genetic basis of shrimp growth traits. QTL study used family mapping to successfully locate several genomic regions that affect growth, providing clues for the discovery of main-effect genes. GWAS identified a batch of molecular markers and candidate genes significantly related to growth through high-density scanning of the breeding population, which gave us a more comprehensive understanding of the multigene control of shrimp growth. These two methods complement each other: QTL provides a reliable framework for verifying associations, and GWAS expands the scope and accuracy of genetic analysis. Thanks to QTL and GWAS research, scientists have identified a series of key growth-related candidate genes, such as *STEAP4*, *MMD2*, *DCD*, *PKC- δ* , etc., and have preliminarily clarified their functional role in metabolism, signaling, etc.

The progress in genetic research on shrimp growth traits has important implications for future molecular breeding. Growth traits are regulated by multiple genes and are significantly affected by the environment, which suggests that breeding work needs to consider multiple factors in a comprehensive way. Using important gene loci identified by QTL/GWAS, marker-assisted selection can be carried out to improve the efficiency and accuracy of growth improvement. Secondly, the study proves the importance of integrating multiomic data and combining different analytical methods. Future breeders should be good at combining genomic data with phenotypic data, and through technologies such as whole genome selection, they can achieve accurate prediction and early selection of shrimp growth traits. Furthermore, these studies highlight the value of genetic diversity for improvement. Whether it is Chinese prawns or vannamee prawns, maintaining certain genetic variations can provide space for continuous breeding. For the industry, the application of molecular breeding technology will cultivate a batch of new varieties of shrimp with faster growth and higher bait conversion rate, thereby improving breeding benefits and reducing unit output costs.

Research on the genetic basis of shrimp growth is a typical interdisciplinary field, involving many aspects such as genetics, genomics, statistics, and aquaculture. Future breakthroughs depend on the deep integration and collaboration of various disciplines. On the one hand, we need genetic breeders, molecular biologists and breeding experts to work closely together to design research plans to ensure that the experimental results have practical application value. On the other hand, international cooperation will provide us with a broader platform. Shrimp farming is carried out globally, and the scientific research forces of each country have their own strengths. Through international cooperation, we can complement each other's advantages and share resources.

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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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