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# Genetic Regulatory Mechanisms of Muscle Growth and Flesh Quality in *Oxyeleotris marmorata*

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**Abstract** *Oxyeleotris marmorata*, commonly known as the marbled sleeper or bamboo fish, is a high-value tropical freshwater species appreciated for its superior flesh quality and nutritional value. Despite increasing production, the long breeding cycle and slow growth rate hinder its industrial development. This study systematically summarizes the genetic and molecular mechanisms underlying muscle growth and flesh quality traits in *O. marmorata*, aiming to provide a theoretical basis for genetic improvement. Key topics include muscle development stages, fiber types and composition, regulatory pathways such as the GH/IGF axis and myogenic regulatory factors (MRFs), as well as roles of non-coding RNAs. The paper also explores genes related to intramuscular fat deposition, collagen synthesis, and flavor-related metabolism. Advances in omics technologies, QTL/GWAS findings, environmental and nutritional influences, and breeding strategies like MAS and CRISPR-based gene editing are also discussed. This study provides comprehensive insights into improving growth performance and meat quality through molecular breeding approaches.

**Keywords** *Oxyeleotris marmorata*; Muscle growth; Flesh quality; Genetic regulation; Non-coding RNA

## 1 Introduction

Marbled sleeper (*Oxyeleotris marmorata*), also known as bamboo fish, is a tropical freshwater fish in Southeast Asia. It grows slowly but has a huge body shape. It is popular for its delicious meat and rich nutrition. Bamboo shell fish has always been regarded as high-end edible fish, with high market prices and a certain breeding history in southwestern my country and Southeast Asia. With the advancement of breeding technology, the output of bamboo shoot shell fish farming industry has gradually increased, but problems such as long breeding cycle and relatively slow growth rate still affect their industrialization development. At present, the research on the genetic regulation of muscle growth and meat traits of bamboo shoot shell fish is still in its infancy, and it is urgent to systematically sort out relevant mechanisms to provide a theoretical basis for improved varieties.

For farmed fish, the growth rate of muscle directly determines the efficiency and economic benefits of farming, while the flavor and texture of meat determines consumer acceptance. Among the evaluation indicators of fish quality, intramuscular fat content and fatty acid composition play an important role (Dang et al., 2019). Studies have shown that increasing fat content in the body of fish can often significantly improve the taste and juiciness of fish meat (Listrat et al., 2016). For example, Xiong et al. (2016) pointed out that increasing intramuscular fat (IMF) content can enhance the flavor and juiciness of fish. Therefore, exploring the molecular regulatory mechanisms of muscle growth and fat deposition is crucial to improving the aquaculture benefits and product quality of bamboo shoot shell fish.

Based on the above background, this study reviews the biological basis and genetic regulation mechanism of muscle growth and meat traits of bamboo shoot shell fish. The content includes stage characteristics of muscle development, biological factors affecting meat quality, known key growth genes and non-coding RNAs, genes related to meat quality traits, and flavor metabolism pathways, omics research and QTL/GWAS progression, and the impact of environmental and nutritional factors on gene expression. In order to provide reference for the genetic breeding of bamboo shoot shell fish, it is of great significance to improving its growth performance and meat quality.

## 2 Biological Basis of Muscle Development in *Oxyeleotris marmorata*

### 2.1 Stages and types of muscle growth (hyperplasia and hypertrophy)

Fish are typical epigenetic and eternal animals, and their muscle development has a unique "dual mechanism". Most bone fish form new muscle fibers through the proliferation of muscle cells in the juvenile stage, while in the later stage, the growth and thickening of existing muscle fibers through hypertrophy (García-Pérez et al., 2022). In the early development stage, bamboo shoot shell fish mainly relies on satellite cells to proliferate and produce active muscle hyperplasia; as the body grows, muscle fibers mainly grow hypertrophy through protein synthesis. The combination of these two mechanisms allows fish to maintain muscle growth and growth for a long time. The muscle generation process involves the activation, proliferation and differentiation of satellite cells, as well as the regulation of myogenic regulatory factors (such as Myf5/MyoD, Myogenin, MRF4), so it has a highly complex molecular regulatory network.

### 2.2 Structure and functional characteristics of skeletal muscle

Fish skeletal muscle tissue is mainly composed of muscle fibers and connective tissue. The muscle fiber content accounts for about 90% of muscle tissue, and the rest is a connective membrane and a small amount of fat. The muscle fibers are arranged in a layered lamellar shape, and the myomeres are separated from each other by the fascia. Fish muscles have high moisture content (≈75%), about 20% protein content, and generally have low fat content. Connective tissue (including inner membrane, outer membrane, etc.) is mainly composed of collagen, which plays an important role in the structural strength and toughness of muscle tissue (Nemova et al., 2021). The basic function of muscles is to contract movement and store energy, and its biochemical composition (protein, fat, carbohydrate ratio) directly affects the fleshy traits, such as texture and water retention (Figure 1).

Figure 1 Structural characteristics of marbled sleeper (*Oxyeleotris marmorata*)

### 2.3 Muscle fiber types and their influence on flesh quality

Fish muscle fibers can be divided into different types according to metabolic characteristics: fast muscle fibers (mainly glycolytic white muscles) and slow muscle fibers (oxidized red muscles rich in myoglobin). White muscle fibers are mainly responsible for rapid burst movement and are the main body of most farmed fish muscles; red muscle fibers contain hemoglobin, which supports long-lasting swimming, which is very important for fish body functions. Different fiber types have different performance in meat quality: studies have shown that in comparisons between fish, the diameter of muscle fibers is negatively correlated with the hardness of fish tissue, that is, the thinner the fibers, the more tender and firm the meat quality is usually (Wang et al., 2021). In addition, the content of collagen in muscles also has a significant impact on the hardness of meat. Several fish studies have found that collagen in muscles is positively correlated with the hardness of meat. Therefore, the type of fiber, its proportion, size and connective structure of muscle tissue together affect the texture and taste of the fish.

## 3 Identification and Function of Muscle Growth-Related Genes

### 3.1 Growth hormone/insulin-like growth factor axis (GH/IGF axis)

The growth hormone (GH)-insulin-like growth factor (IGF) axis is the core endocrine pathway that regulates fish growth. GH is secreted by the pituitary gland and promotes the synthesis and secretion of IGF-1 by promoting the liver and peripheral tissues, thereby stimulating the growth of muscles and other tissues. In bony fish, studies have confirmed that the GH/IGF system has an important regulatory effect on growth (Qing et al., 2024). For example, the triploid crucian carp study showed that the expression levels of GH, GH receptor (GHR) and IGF-1 genes in vigorously grown individuals suggest that enhanced GH/IGF axis activity can promote rapid growth of fish. In muscle, IGF-1 mediates the activation of signaling pathways such as PI3K/AKT through GHR, increasing protein synthesis and satellite cell proliferation, thereby accelerating muscle fiber growth. Therefore, gene variation or expression differences in the GH/IGF axis may directly affect the growth rate and final body shape of bamboo shoots.

### 3.2 Myogenic regulatory factors (MRFs)

Myogenic regulators (MRFs) include transcription factor families such as Myf5, MyoD, Myogenin and MRF4, which play a central role in the differentiation and formation of muscle cells. These factors initiate transcriptional procedures of muscle-related genes by binding to specific DNA sequences, driving myoblasts to differentiate into mature myofibers. Research points out that MyoD family members are crucial in the muscle formation process of vertebrates (Kim et al., 2008). In fish, these MRFs are equally highly conserved, able to identify non-myosinutrient cells and induce their transition to myosinutrient cell phenotype. In addition, the expression regulation and interaction of MRFs form a complex network to accurately control the spatiotemporal process of muscle development. There are currently no direct reports for bamboo shoot shellfish, but other fish species studies have shown that changes in MRFs expression will affect the rate of muscle growth and the number of fiber formation, and can be used as candidate targets for genetic breeding improvement.

### 3.3 Roles of non-coding RNAs such as miRNAs and lncRNAs in muscle development

In addition to the above-mentioned coding genes, non-coding RNAs (such as miRNA and lncRNA) are also involved in regulating muscle development. In recent years, studies have found that a large number of miRNAs are expressed in fish muscle development, and typical muscle-specific miRNAs (miR-1, miR-133, miR-206, etc.) can regulate myogenic cells proliferation and differentiation. In addition, some lncRNAs indirectly regulate the expression of muscle-related genes by binding to miRNA or proteins. García-Pérez et al. (2024) showed that in sea bream satellite cells, amino acid-rich and IGF-1-enhancing treatment can change the expression profiles of more than 100 miRNAs (including miR-133a/b, miR-206, etc.) and multiple lncRNAs, and found that 8 lncRNAs are negatively correlated with muscle-specific mRNAs, indicating that these non-coding RNAs may participate in muscle gene regulation through the "sponge" mechanism (García-Pérez et al., 2024). These findings suggest that muscle growth of bamboo shoot shell fish may also be significantly affected by miRNA and lncRNA, revealing a new dimension of gene expression regulation.

## 4 Genetic Basis of Flesh Quality Traits

### 4.1 Genes related to fat deposition and intramuscular fat

Fish body fat mainly exists in the form of liver, abdominal fat and intramuscular fat. The content of intramuscular fat is considered an important factor affecting the flavor and juiciness of meat. In terms of related genes, the hormone-sensitive lipase (*HSL*) gene is a key enzyme for fat mobilization, and its expression is closely related to fat storage. In addition, transcription factors such as PPARγ, FABP (fatty acid binding protein) and lipid metabolic enzyme genes are also involved in fish adipogenesis and distribution. Dang et al. (2019) pointed out that "the fat content of fish body and the composition of fatty acids are one of the important criteria for evaluating the quality of fish meat. Studies have shown that increasing the fat content in muscle can effectively improve the taste of meat", emphasizing the importance of intramuscular fat to meat quality. The genetic polymorphism and expression regulation of these genes may explain the differences in intramuscular fat deposition capacity of different strains or varieties, and is also a potential marker for improving fish meat quality.

### 4.2 Regulatory factors influencing muscle texture and water-holding capacity

The texture (hardness, firmness) and water-holding properties of fish are affected by a variety of factors, among which the diameter, number of muscle fibers and connective tissue structure play a major role. Studies have shown that the diameter of muscle fibers is negatively correlated with the hardness of meat among different fish species (the larger the fiber diameter, the looser the meat is), while the content of collagen and connective tissue is positively correlated with the hardness of raw meat (Gui et al., 2020). Intramuscular proteases (such as cysteine proteases calpain, cathepsin, etc.) and aquaporin proteins in the sarcoid reticulum may also affect muscle contraction status and water retention. Differences in gene expression of these factors can lead to meat quality differences in different breeding conditions or genetic backgrounds. There is currently a lack of reports on genes directly related to the muscle texture and water retention of bamboo shoot shell fish. Related studies can refer to relevant genes of other economic fish, such as collagen family and protease genes, to provide clues for subsequent research.

### 4.3 Flavor-associated metabolic pathways and their genetic regulation

The flavor of fish is mainly determined by a variety of metabolites such as free amino acids, nucleotides (such as sweet glutamic acid, umami inosine IMP, etc.) and fatty acid components. The accumulation of these flavor substances depends on the corresponding metabolic pathways, such as amino acid metabolism, ATP degradation pathways, etc., and the enzyme gene mutation or regulatory status on these pathways will directly affect the content of flavor substances (Dai et al, 2024). Although few studies have been shown specifically in fish to reveal the genetic mechanisms of taste component metabolism, studies have shown that intramuscular fat abundance can lead to a stronger taste by increasing flavor fatty acids (EPA, DHA) and bringing a stronger taste (Li et al., 2024). This aspect of research can be explored in depth by linking metabolomics and genomic data.

## 5 Application of Omics Technologies in *O. marmorata* Research

### 5.1 Transcriptomic analysis of differentially expressed genes

Omics technology is widely used in fish genetic research, providing a new perspective for muscle development and meat quality research. For example, muscle transcriptome sequencing was performed on the fast-growing and slow-growing groups of *Sinocyclocheilus grahami*, and a total of 1 647 differentially expressed genes were identified (Yin et al., 2023). These differential genes are enriched in functional categories such as extracellular matrix (ECM)-receptor interactions, intracellular metabolic pathways. Further weighted gene co-expression network analysis (WGCNA) points out that the type I collagen gene (col1a1, col1a2, etc.) may be an important candidate gene that affects growth performance. Similar studies can discover new regulatory genes for rapid growth of bamboo shoot shell fish muscles and improvement of fiber structure.

### 5.2 Proteomic profiling of key regulatory proteins

Proteomics studies can supplement transcriptome information and reveal changes in protein levels during growth and meat formation. Through differential proteome analysis, researchers can identify proteins related to muscle development, lipid metabolism, connective tissue formation, etc. There have been studies using proteomics technology to analyze the effects of feed additives on muscle protein expression in zebrafish or trout, and found that growth regulators and stress-related proteins have significant differences (Jury et al., 2008). Although the proteomic data on bamboo shoot shellfish are still missing, referring to the results of other fish, we can focus on myofibers, membrane transporters, and energy metabolism-related proteins.

### 5.3 Metabolomic insights into variations in flesh quality traits

Metabolomics provides intuitive indicators for flavor and texture research by detecting small molecule metabolites in muscles. By comparing the fish muscle metabolite spectrum under different strains or feeding conditions, key metabolites related to taste and flavor (such as free amino acids, inosine content, etc.) can be identified (Du et al., 2020). For example, metabolomic analysis of grass carp with different feeding methods can be found that changes in amino acid metabolism pathways and triacylglycerol metabolism are correlated with meat quality differences (Mabuchi et al., 2019). Future metabolomic studies on bamboo shoot shellfish can be integrated with transcriptome and proteome data to systematically identify metabolic regulatory networks that affect meat quality.

## 6 Advances in QTL Mapping and Association Analysis

### 6.1 Quantitative trait loci (QTL) mapping for muscle growth traits

Quantitative trait loci (QTL) localization is an important means to reveal the genetic basis of complex traits. Muscle-related QTL has been reported in freshwater fish such as tuna and bass. For example, in rainbow trout, researchers found QTLs related to muscle yield on chromosomes 14 and 16, which could explain up to 28.4% of phenotypic variation. In addition, a 7-month-old fish weight QTL detected in the same study was located on chromosome 9, explaining about 1.5% of the variation (Blay et al., 2021). Similarly, multiple pairs of QTL regions related to body weight and meat quality have also been found in other breeding fish species such as salmon and bass. These results indicate that growth traits are usually regulated by multiple genes, and QTL studies provide important clues for candidate gene screening.

### 6.2 Genome-wide association studies (GWAS) for flesh quality traits

In recent years, with the development of high-throughput genotyping technology, genome-wide association research (GWAS) has been used to genetic analysis of fish meat traits. For example, in Atlantic salmon, GWAS analysis identified multiple loci on chromosomes 13, 18, and 20 related to muscle yield (bone loss yield) and found QTLs related to muscle fat content on chromosomes 9 and 10 (Blay et al., 2021). These findings suggest that specific chromosomal regions may contain key genes that affect fat deposition and muscle growth. Through GWAS, more accurate genetic markers can be identified at the population level, providing a basis for breeding plans for species such as bamboo shoots, shellfish, etc.

### 6.3 Candidate gene screening and functional validation

Based on QTL and GWAS results, candidate genes in the associated region can be screened and functionally verified. Common muscle growth candidate genes include *IGF1*, *GH* receptors, myogenic regulators, etc. In addition, emerging candidate genes such as collagen family, muscle protein degradation enzymes and fat metabolic enzymes have also been concerned. The emergence of gene editing technologies such as CRISPR/Cas9 has provided convenience in verifying the function of candidate genes. For example, after targeted knockout of the *MRF4* gene in tilapia, relevant studies have shown that the expression of the downstream myogenin factor Myogenin has almost doubled (Sukhan et al., 2024), demonstrating the regulatory effect of this gene on muscle development. This type of research model will have potential application value in bamboo shoot shell fish breeding.

## 7 Environmental and Nutritional Influences on Gene Expression

### 7.1 Effects of feed composition and nutritional regulation

Feed nutritional composition has a significant effect on fish muscle growth and meat quality. For example, in the study of grass carp, the effects of forage and artificial feed were compared, and it was found that individuals who were raised in forage were larger in diameter, higher in muscle density, and tighter in meat; while the artificial feed feed group deposited more body fat and loose muscle tissue structure (Zhao et al., 2018). In addition, experiments on increasing the phosphorus content in feed showed that appropriate increase in phosphorus content can significantly improve the protein content and water-holding properties of grass carp muscles. These studies show that different feed formulas affect muscle mass by regulating metabolic pathways and gene expression levels. For bamboo shoot shellfish, optimizing the proportion of protein, fat and minerals, as well as supplementing specific functional nutrients (such as collagen or feed additives that induce muscle growth) may effectively improve growth performance and meat quality.

### 7.2 Impact of environmental factors such as temperature and dissolved oxygen

Environmental conditions such as water temperature and dissolved oxygen will affect muscle growth and quality by affecting metabolic rate and stress levels. Higher water temperatures usually speed up metabolism and promote growth rates, but excessive or fluctuating temperatures can cause stress and affect muscle fiber development. Conversely, a low temperature environment may prolong the growth cycle but may increase the muscle fiber density. Insufficient dissolved oxygen can cause hypoxia stress, induce expression changes of related genes (such as HIF-1α), which in turn affects energy metabolism and muscle production. Although specific mechanisms vary by species and conditions, the apparent effects and metabolic reprogramming of these environmental stress factors have been reflected in studies such as bass and trout (Jiang et al., 2021), and the impact on the meat quality of bamboo shoot shell fish deserves in-depth research.

### 7.3 Epigenetic regulation and gene-environment interactions

Epigenetic mechanisms are an important link to explain the long-term impact of environmental factors on gene expression. Environmental stress (such as temperature changes, nutritional levels) can affect gene activity by inducing DNA methylation, histone modifications and changes in non-coding RNA expression, thereby affecting the phenotype. Lin et al. (2018) review pointed out that environmental stimulation causes hereditable changes in gene expression patterns through epigenetic modification. For bamboo shoot shellfish, epigenetic spectrum research under different breeding environments will help understand population genetic variation and breeding responses, and provide new ideas for choosing excellent varieties such as high temperature tolerance and density tolerance.

## 8 Genetic Breeding Strategies and Molecular Marker Development

### 8.1 Application of marker-assisted selection (MAS) in breeding

Based on the above genetic information, molecular markers associated with the target trait can be developed for assisted selection. Currently, commonly used markers in fish breeding include SNP, SSR, etc. For example, studies have identified genetic markers related to rapid growth and higher bone-to-female ratios. Applying markers of relevant QTL regions to breeding can accelerate the seed selection process (Cuiyun et al., 2013). For bamboo shoot shellfish, establishing a marker-trait association database for muscle growth and meaty traits is the basis for promoting MAS.

### 8.2 Potential of gene editing technologies such as CRISPR/Cas

Gene editing technologies such as CRISPR/Cas9 show great potential in the field of aquatic breeding. It can knock out, insert or replace target genes directly at the genome level, verify gene function and improve traits. Cai et al. (2020) used CRISPR technology to knock out the tilapia *MRF4* gene and observed significant changes in muscle gene expression. Similar methods can be used for functional gene research and breeding improvement of bamboo shoot shellfish, such as precise regulation of growth inhibitors (such as myostatin) or enhance flavor-related gene expression (Sukhan et al., 2024). As the technology matures, this strategy is expected to be used to optimize the growth rate and meaty traits of bamboo shoot shell fish.

### 8.3 Integrated breeding strategies for improving muscle and flesh quality traits

Future breeding can combine traditional breeding, molecular marking and gene editing methods. On the one hand, excellent alleles can be enriched through MAS or genotype selection, and on the other hand, gene editing can be used to directly improve the function of key genes. During comprehensive breeding, we also need to pay attention to the coordination of environment and management, such as optimizing feed density, adjusting feed formula, etc., to realize the genetic potential. Overall, the combination of interdisciplinary means will promote the continuous improvement of the muscle and meat performance of bamboo shoot shell fish.

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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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