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Expression profile analysis of muscle regulation genes under growth and water flow stress in zebrafish

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ABSTRACT

Muscle is one of the important quality of fish. However, there is still a lack of sufficient understanding of the mechanism of muscle growth regulation in fish. In this study, the expression patterns of 10 reported muscle development related genes are analyzed in zebrafish during growth or under water flow stress. Myogenic regulatory factors (*MyoD*, *MyoG, MRF4*), myostatin regulatory genes (*Mstna*, *Mstnb*) and myoblast development-related genes (*Pax7*, *Prmt5*, *Desmin*, *MYHC*) are significantly increased expression at somite stage and muscle effect stage embryos in zebrafish. The mRNA levels of the muscle development related genes are up-regulated in 7-day fries and 30-day juvenile of zebrafish. And there are differences in the expression levels of seven muscle development related genes (*MyoD*, *Myf5*, *MyoG*, *Mstna*, *Mstnb*, *Desmin*, *MYHC*) between the large and small individuals of 20-day-old zebrafish. Results indicated that short-term water flow stressing can promote zebrafish muscle growth, while prolonged water flow stress may lead to motor fatigue and affect growth in zebrafish. This research provides a foundation for further exploration of the growth regulation mechanism in fish, and is helpful on fish farming.

1. Introduction

Muscle is not only involved in the construction of important organs in animals, but also an important source of food protein. The development of vertebrate skeletal muscle tissues begins from embryonic muscle progenitor cells and then muscle stemcells, myoblasts until myotubes formation and myofibers maturity [1,2]. In adults, muscle stem cells could be activated and start self-renewal upon intense exercise or external injuries, thereby increasing or restoring muscle tissue [1,3,4]. Myogenic regulatory factors are transcripts that regulate muscle-specific gene activation and play a major role in skeletal muscle formation and differentiation [5–7]. Muscle is one of the important quality of fish. Studies showed that early activation of the chimeric growth stage of fish muscle cell proliferation was essential for muscle development and individual weight gain in fry and juvenile fish [8]. However, the molecular mechanisms of muscle growth and development are still insufficient understanding in fish.

In fish, water flow is as an important and complex ecological factor, and plays significant roles in fish survival and reproduction [9–11]. There are reports of water flow affecting fish metabolism and feeding rate, and a negative correlation between fish growth rate with flow velocity, while others considered that continuous water flow promoted fish growth [12–14]. Moreover, it remains unclear whether the effects of water flow on fish growth differ among different age groups [12,15,16].

In this study, we selected 10 important genes which were reported related to muscle development in animal, including four myogenic regulatory factors (*MyoD*, *Myf5*, *MyoG*, *MRF4*), two myostatin regulatory genes (*Mstna*, *Mstnb*), and four myoblast development-related genes (*Pax7*, *Prmt5*, *Desmin*, *MYHC*) [6,7,17–20]. We analyzed these muscle regulation genes expression profile at different growth stages and under water flow stress conditions in zebrafish. This research meant to offer fish breeding methods for enhanced muscle growth in aquaculture.

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2. Materials and methods

2.1. Fish

Wild-type AB strain Zebrafish (*Danio rerio*) were obtained from the National Zebrafish Resource Center of China and fed at the State Key Laboratory of Developmental Biology of Freshwater Fish, College of Life Sciences, Hunan Normal University. All experiments in this study were performed in accordance with the guidelines of the Animal Ethical Review Committee of Hunan Normal University, Changsha, China.

Embryos at different stages of zebrafish development were collected, including the cleavage stage (1.5 h post-fertilization, 1.5 hpf), blastula stage (3 hpf), gastrula stage (6 hpf), somite stage (12 hpf), muscle effect stage (17 hpf), pharyngeal pouch period (24 hpf), and hatching period (72 hpf) [21]. The whole body embryo or fry before 15 days old, and the trunk of zebrafish after 20 days old were snap-frozen in liquid nitrogen and stored at −80 °C for subsequent RNA extraction.

2.2. Water flow stress stimulation program

The experiment project was designed which the water flow rate was set to a level that the fish continuously swam continuously against the current to water stress stimulation, named as the muscle stress group [22,23]. According to the pretest, zebrafish was run water training with 1.327 m/s water flow rate. The 30 day-old zebrafish with same size were randomly divided into the control groups and the exercise groups.

2.3. RNA isolation and cDNA synthesis

Total RNA was isolated from the aforementioned samples using the Trizol method and the quality of total RNA was detected using 1 % agarose gel electrophoresis and a nucleic acid analyzer. cDNAs were synthesized according to manufacturer's instructions the TaKaRa reverse transcription kit. Genomic DNA was first eliminated from the RNA, and the cDNAs were stored at −20 °C for future use.

2.4. Real-time quantitative PCR (qPCR)

Real-time quantitative PCR (qPCR) was performed to detect gene expression levels. The qPCR primers were designed using the Olig7 software and were listed in Table S1. Primer specificity was confirmed through RT-PCR, and NCBI blast was used to ensure sequence similarity above 99 % prior to their application in qPCR. For qPCR, a ten-fold dilution series of template cDNA was used. Each 10 μL qPCR reaction mixture contains 1 μL of cDNA (0.01 μg RNA), 5 μL of Brilliant SYBR Green qPCR Master Mix, 0.5 μL of forward and reverse primers working solution and 3 μL of DEPC water. Three biological replicates were performed for each sample, negative controls (NTC) for each sample, and each experiment was repeated three times. The thermal cycle consisted of an initial polymerase activation step at for 50 °C for 2 min, followed by 95 °C for 10 min, and then 40 cycles at 95 °C for 15 s and 60 °C for 1 min. The entire reaction was conducted using ABI 7500 real-time quantitative PCR system. The quantitative expression levels of the target genes were compared with the reference gene *β-actin*, and then the relative expression of genes was calculated using the $2^{-\triangle\triangle Ct}$ method.

2.5. Histochemical analysis of muscle samples

Using commercially available test kits (www.njjcbio.com), the Adenosine-5′- triphosphat (ATP) content, the succinate dehydrogenase (SDH) activity, and creatine kinase (CK) activity were measured in the dorsal muscle and tail handle muscles of the one-week and two-week experimental group, as well as the control group. Additionally, the combined enzyme activity of succinate dehydrogenase and cytochrome oxidase (combined SDH-COX) staining kit for frozen sections (HEPENG BIOLOGICAL) was used to measure the combined SDH-COX enzyme activity in the dorsal muscle of the experimental group and control group. The muscle tissue was sectioned using a frozen microtome, and the cross sections were stained and observed using the kit. For each sample, experiments were repeated at least three times.

3. Results

3.1. Expression levels of muscle development related genes in zebrafish embryos

As shown in Fig. 1, the mRNA levels of two myogenic regulatory factors (*MyoD*, *Myf5*) and myoblast development-related genes (*Pax7*, *Desmin*) were high at the cleavage stage embryos, then down-regulated at blastula or gastrula stages of zebrafish. After somite stage, the expression of two myogenic regulatory factors (*MyoD*, *MyoG*) and four myoblast development-related genes (*Pax7*, *Prmt5*, *Desmin*, *MYHC*) were up-regulated, and maintained a high expression level in the late stages of zebrafish embryos. While other myogenic regulatory factor (*MRF4*) and two myostatin regulatory genes (*Mstna*, *Mstnb*) were significantly increased expressed only at somite stage and muscle effect stage embryos in zebrafish.

3.2. Expression profile analysis of muscle development related genes in growth stage zebrafish

Zebrafish of 8 different ages (1, 3, 7, 15, 20, 25, 30 and 60 days old) were used to be investigated the expression of 10 muscle development related genes. Compared to other early stages fries, the 7-day zebrafish exhibited higher levels of expression in most muscle development related genes (Fig. 2A). In juvenile zebrafish, the expression levels of muscle development related genes were significantly up-regulated after 25-day old and 30-day old in particular (Fig. 2A). Meanwhile, the general observations indicated that size difference was existed among zebrafish raised together in the same batch. As shown in Fig. 2B, the body length of 20-day old zebrafish ranged from 0.45 cm to 0.93 cm, and those of 30 day-old zebrafish ranged from 0.50 cm to 1.19 cm. We tested the genes expression of 20-day zebrafish, and founded that the expression levels of three myogenic regulatory factors (*MyoD*, *Myf5* and *MyoG*), two myostatin-regulated genes (*Mstna*, *Mstnb*), and two myoblast development-related factors (*Desmin*, *MYHC*) were significantly higher in the big groups (body lengths between 0.70 cm and 0.93 cm) than those of small groups (body lengths between 0.45 cm and 0.69 cm), while *MRF4* was down-regulated in the large population (Fig. 2C).

3.3. Effect of water flow stress on muscle development related genes expression in zebrafish

Water flow exercise training was conducted on 30-day-old zebrafish.

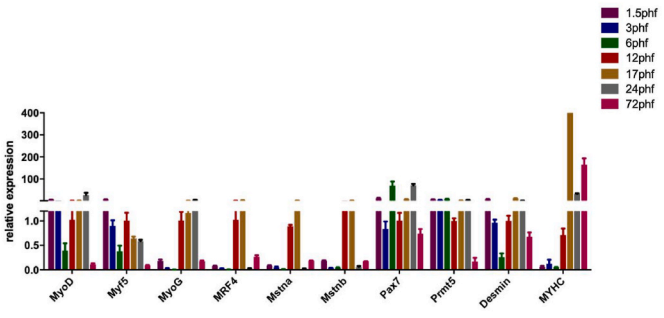

Fig. 1. Expression levels of muscle development related genes in zebrafish embryos at different stages. 1.5 phf: cleavage stage; 3hpf: blastula stage; 6hpf: Gastrula stage; 12hpf: Somites stage; 17hpf: Muscle effect stage; 24hpf: Pharyngeal pouch period; 72hpf: hatching period.

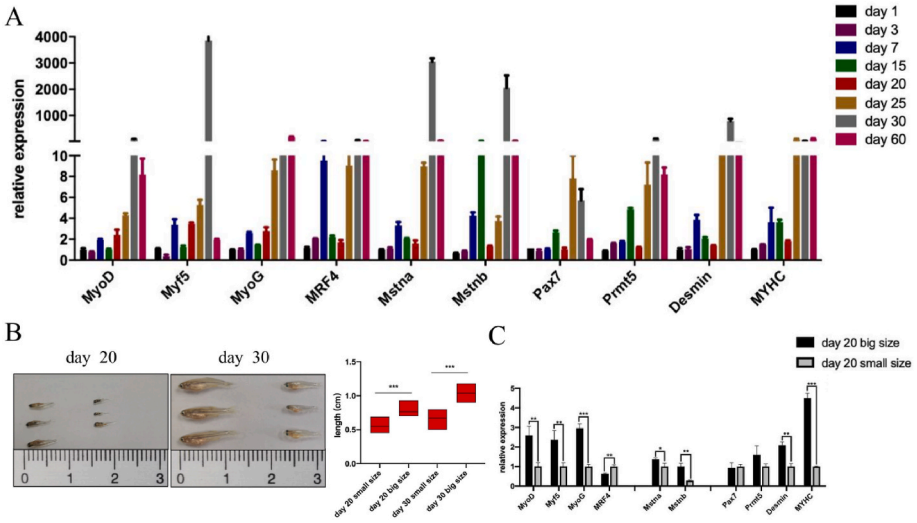

Fig. 2. Size observation of zebrafish and the expression levels of muscle development related genes in growth stage zebrafish. (A) The qPCR analysis of the expression levels of myocyte development related genes in zebrafish of different ages. (B) 20-day and 30-day old zebrafish of different sizes; left: 20-day and 30-day old zebrafish of different sizes; right: 20-days and 30-days zebrafish body length statistics. (C) Expression of muscle development related genes in muscle tissue of the growth differential zebrafish population (*$p < 0.05$, **$p < 0.01$, ***$p < 0.001$).

As shown in Fig. 3A, after 1 week treated, comparing to the control groups, the mRNA levels of *MyoD*, *Pax7*, *Desmin* were up-regulated in the dorsal and tail handle muscle of experimental group, and those of *MyoG*, *Prmt5*, *MYHC* were only significantly up-regulated in the dorsal muscle, while *Myf5* was significantly up-regulated only in the tail handle muscle. However, two myostatin-regulated genes (*Mstna*, *Mstnb*) were showed significant down-regulation in the dorsal muscle but were up-regulated in the tail handle muscle. After 2 weeks of water flow stress, compared to the control group, the mRNA levels of *Desmin* was still up-regulated in the dorsal and tail handle muscle of experimental group, and those of *MyoD* and *MYHC* were up-regulated in the dorsal muscle. However, the expression of *MyoG* and *Prmt5* were up-regulated in the dorsal muscle but down-regulation in the tail handle muscle, while those of *Mstnb* were down-regulated in the dorsal muscle. Meanwhile, *MRF4* and *Pax7* were significantly down-regulated in the tail handle muscle. Those of *Myf5* and *Mstna* were down-regulated in the dorsal and tail handle muscle. After 4 weeks of water flow stress, the expression levels of three myogenic regulatory factors (*Myf5*, *MyoG*, *MRF4*), two myostatin-regulated genes (*Mstna* and *Mstnb*), and myoblast development-related genes (*Pax7*, *Prmt5*, *Desmin* and *MYHC*) were all down-regulated in the dorsal and tail handle muscles (Fig. 3A).

Furthermore, we investigated the impact of water flow stress on

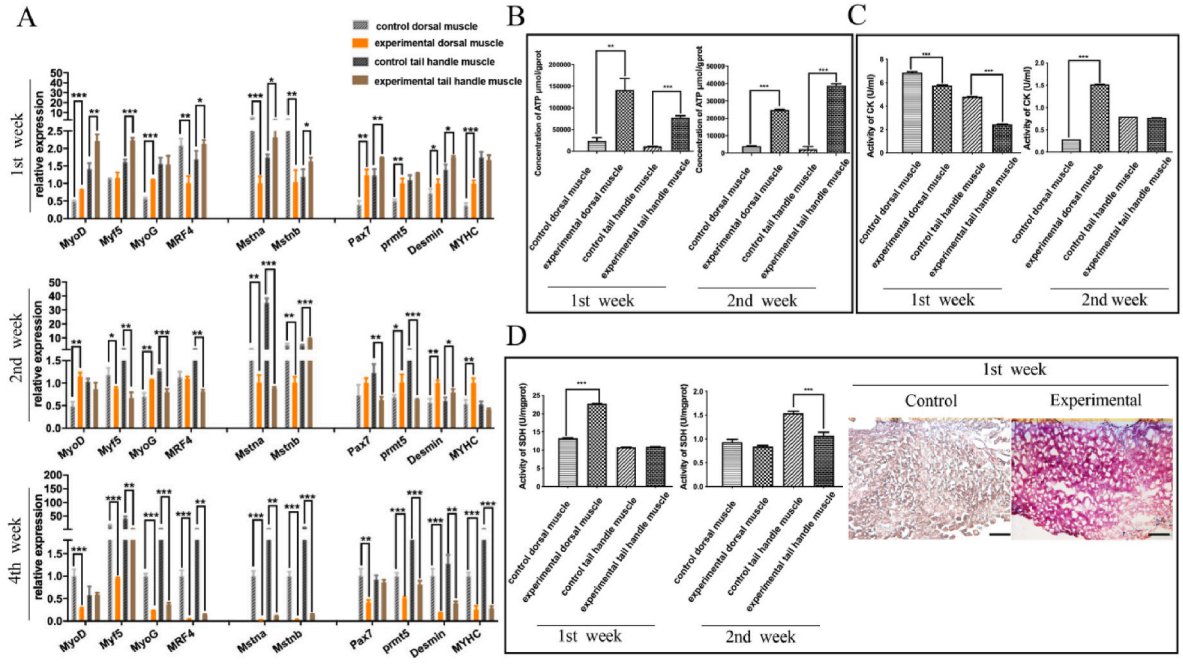

Fig. 3. Effect of water flow stress affected on muscle development in 30-day old zebrafish. (A) qPCR analysis of the expression of 10 muscle development-related genes in the dorsal and tail handle muscle under water flow stress. (B) Concentration of ATP in the dorsal muscle and tail handle muscle of zebrafish after 1st and 2 nd weeks of water stress. (C) Activity of CK in the dorsal muscle and tail handle muscle of zebrafish after 1st and 2 nd weeks of water stress. (D) Left: activity of SDH in the dorsal muscle and tail handle muscle of zebrafish after 1st and 2 nd weeks of water stress. Right: activity of combined COX-SDH enzyme in zebrafish dorsal muscle after 1 week of water stress. All the scale bars represent 25 μm (*p < 0.05, **p < 0.01, ***p < 0.001).

muscle energy metabolism in zebrafish. Following 1–2 weeks of water flow stress treatment, the experimental groups exhibited a significant increase in ATP content compared to the control groups in the muscle tissue (Fig. 3B). Additionally, the CK activity decreased in both the dorsal muscle and tail handle muscle compared to the control group after 1 week of water flow stress. But after 2 weeks of water flow stress, the CK activity in the dorsal muscle significantly increased compared to the control groups (Fig. 3C). Furthermore, compared to the control groups, SDH activity increased in the dorsal muscle and tail handle muscle after 1 week of water flow treatment, and significantly increased in the dorsal muscle (Fig. 3D). Consequently, the activity of combined SDH-COX was further detected. After 1 week of water flow stress, the activities of combined SDH-COX in the dorsal muscle of the experimental groups were higher than those in the control groups, indicating a high content of mitochondria (Fig. 3D).

4. Discussion

In this study, the mRNAs of *MyoD*, *Myf5, Pax7* and *Desmin* were as maternal factors in zebrafish embryos, with which were high levels at the cleavage stage then down-regulated at blastula or gastrula stages. And myogenic regulatory factors (such as *MyoD*, *MyoG*, *MRF4*), myostatin regulatory genes (eg. *Mstna* and *Mstnb*), and myoblast development-related genes (eg. *Pax7*, *Prmt5*, *Desmin*, *MYHC*) were significantly increased expressed at somite stage and muscle effect stage embryos, fry and juvenile growth in zebrafish. Our results indicated that 7-day old, and 30-day old might be important growth stages for zebrafish. Interesting, among the zebrafish raised together in the same batch, distinct size differences were observed, and these different were associated with the expression of muscle development-related genes.

Myogenic regulatory factors (*MyoD*, *MyoG*, *MRF4*), two myostatin regulatory genes (*Mstna*, *Mstnb*), and four myoblast development-related genes (*Pax7*, *Prmt5*, *Desmin*, *MYHC*) were involved in the regulation of muscle development. Study shows that skeletal muscle cells are determined by the expression of muscle regulatory factors (*MyoD*, *Myf5*, *MyoG*, *Myf4*), which are transcription factors that regulate the activation of muscle-specific genes and are the dominant regulatory genes in vertebrate embryonic muscle development [4,6,7,24,25]. At the somite stage, the differentiation stage of skeletal muscle occurs, with mesodermal cells aggregate to form somites, myotome cells in somites then transform into muscle progenitor cells and form proliferating muscle cell lines. Subsequently, only the expression of muscle-specific factors, such as myogenic regulatory factors, enables the development into muscle [5,7]. Muscle satellite cells originated from embryonic mesoderm stem cells, *Pax7* is a marker for satellite cells in a wide range of vertebrates from fish to humans [5,24]. *Prmt5* is critical for regulating the proliferation of satellite cells and plays an important role in transforming satellite cells into functional muscle fibers. Studies have shown that *Prmt5* is not indispensable for the proliferation and differentiation of pax7-positive myogenic progenitor cells, and there are significant differences in the process of muscle formation between embryonic and adult stage [17,26,27]. Desmin is an intermediate filament protein closely related to muscle tissue development and structural stability [28]. Meanwhile, *MYHC*, the encoding gene for myosin heavy chain and a major component of muscle fibers , *MYHC* plays a crucial role in muscle cell contraction and force generation and plays a crucial role in the formation and functional performance of muscle fibers [18,29]. Myostatin (MSTN) is an important negative regulator of muscle cell growth. Unlike mammals, *MSTN* are more widely expressed in fish, the functions of fish *MSTN* genes are diverse [30]. Studies have revealed significant differences in tissue-specific expression of *Mstna* and *Mstnb* genes during fish development and expression at different developmental stages [31,32]. Studies have shown that knockout of mstnb can significantly improve the growth performance of zebrafish, while knockout of mstna has the opposite results [33,34]. These genes were indeed involved in the regulation of muscle development during zebrafish growth, the muscle development-related genes screened in this study can be considered as candidate genes for studying the regulation of zebrafish muscle development, we can further reveal their functions by knocking down or overexpressing, and the relevant regulatory mechanisms also need to be further analyzed.

Water flow is an important environment factor for fish, as it affects fish movement and metabolism, ultimately influencing their growth and development [9–11,35]. The contraction of skeletal muscles plays a crucial role in fish movement [36], and muscle cells, particularly myofibers, are the primary cell type involved in this process [1,2]. Early activation of the muscle cell proliferation through the chimeric growth stage is essential for muscle development and individual weight gain in fry and juvenile fish [8]. The dorsal muscle is one of the largest and most important muscle tissues in zebrafish, responsible for supporting and promoting body movement [36]. Swimming exercise has been found to enhance skeletal muscle oxidative capacity, which is crucial for muscle function and dependent on ATP production, as well as the calcium cycle within the muscle cells [33,37]. Previous studies on highland sprinters have also showed that only a certain intensity of exercise load caused significant changes in serum CK activity in athletes [38,39]. In this study, after 1 week of water flow treatment, the expression levels of muscle development-related genes such as *MyoD*, *Pax7*, and *Desmin* were significantly up-regulated in muscle tissue. However, after 2 week of treatment, the expression of *MyoG*, *Prmt5, MRF4* and *Pax7* were down-regulation in the tail handle muscle. After 4 weeks of treatment, 9 muscle development-related genes were all down-regulated in the dorsal and tail handle muscle. These findings suggested that the tail handle muscle may be more sensitive to water stress than the dorsal muscle in zebrafish. Additionally, the increased ATP content, CK activity, SDH activity and combined SDH-COX activity after water flow stress indicated enhanced energy metabolism in zebrafish. In conclusion, our results demonstrated that appropriate water flow stress exerted a positive influence on muscle growth in zebrafish. Understanding the effects of water flow stress on muscle development and energy metabolism could contribute to the optimization of fish breeding conditions and the promotion of efficient growth in aquaculture systems.

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Data availability

Data will be made available on request.

CRediT authorship contribution statement

Xiudan Yuan: Writing – original draft, Methodology, Investigation, Formal analysis, Data curation. **Leiting Tao:** Investigation, Formal analysis, Data curation. **Xiaoli Hu:** Software, Methodology, Conceptualization. **Ruoyu Lin:** Software, Data curation, Conceptualization. **Jingping Yang:** Funding acquisition, Data curation, Conceptualization. **Mengzhe Feng:** Software, Methodology, Conceptualization. **Mei Peng:** Methodology, Formal analysis, Conceptualization. **Wenbin Liu:** Writing – review & editing, Supervision, Funding acquisition. **Yamei Xiao:** Writing – review & editing, Supervision, Project administration, Funding acquisition, Formal analysis.

Declaration of competing interest

The authors declare the following financial interests/personal relationships which may be considered as potential competing interests: The authors confirm that this article content has no conflicts of interest.

Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.repbre.2023.12.004.

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