A Review on Fish Growth and Physiological Properties of Fish Muscle Tissue Development

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Abstract- Fish muscle physiology is the scientific study of how the component parts of fish muscle function together in the living fish. It can be contrasted with fish anatomy, which is the study of the form or morphology of fishes. In practice, fish anatomy and physiology complement each other, the former dealing with the structure of a fish, its organs or component parts and how they are put together, such as might be observed on the dissecting table or under the microscope, and the later dealing with how those components function together in the living fish. Physiological properties of fish muscle therefore, is the total breakdown of the muscle components and their various role in the muscle. Muscle development cannot as well be left out in understanding of the muscle properties. Red muscle fibres are commonly confined to a narrow strip along the lateral line and constitute less than 10 % of the myotomal musculature. Intermediate or pink fibres are in accordance to their name not only intermediate in position between red and white muscle fibres but also in many other aspects. The current state of knowledge was reviewed here and the physiological properties of fish muscle ranging from its development (growth), structure, physical, biochemical and metabolic properties and impact on muscle structure and quality was discussed. It is recommended that more attention should be given to fish muscle physiology in order to enhance fish muscle formation which is directly proportional to fish fast growth. This is believed to help in manipulation of the muscle growth factors to quicken growth and maximize profits in an ideal environment and circumstance.

Indexed Terms- Fish muscle, physiological properties, muscle development, red muscle, white muscle, pink muscle

I. INTRODUCTION

Fish physiology is the scientific study of how the component parts of fish function together in the living fish (Prosser, 1991). It can be contrasted with fish anatomy, which is the study of the form or morphology of fishes. In practice, fish anatomy and physiology complement each other, the former dealing with the structure of a fish, its organs or component parts and how they are put together, such as might be observed on the dissecting table or under the microscope, and the later dealing with how those components function together in the living fish. Muscles are group of muscle tissues which contract together to produce a force. It is also a contractive form of tissue which animals use to effect movement (Astruc, 2014ab).

II. MYOGENESIS ROLE IN FISH MUSCLE DEVELOPMENT

Myogenesis (embryology)is the formation of muscle tissues through the differentiation of progenitor cells myoblasts into myocytes during the development of an embryo. Myogenesis pertains to the developmental process in embryo where the myoblast differentiates into a muscle cell. The myoblasts are the progenitor cells of the muscle tissue. During embryonic development, the myoblasts either divide mitotically to give rise to more myoblasts or differentiate into myocytes or muscle cells. The decision as to either proliferate or differentiate is still unclear but in vitro studies showed that the presence of sufficient growth factors in a culture medium would result in the cell division of the myoblasts. In contrast, less growth factors in the medium resulted in the differentiation of the myoblasts. The stages of myogenesis are the following: delamination (the formation of a gastrula by the splitting of the blastoderm), migration, proliferation, determination, differentiation, specific Muscle Formation, and satellite cells (Pestronk, 2013) (Fig. 1). In summary, the myoblasts begin to differentiate into myocytes by leaving the cell cycle and began expressing genes associated with the next stages. The myoblasts next align to one another and fuse. During the differentiation stage, certain genes (e.g., striated alpha-actin genes) are expressed and the myoblasts align with one another. The myoblasts, then, fuse with the recruitment of actin to the plasma membrane (Birbrair *et al.*, 2013). Genes that are essential during the fusion of myoblasts are myocyte enhancer factor-2 (Mef2) and twist transcription factor.

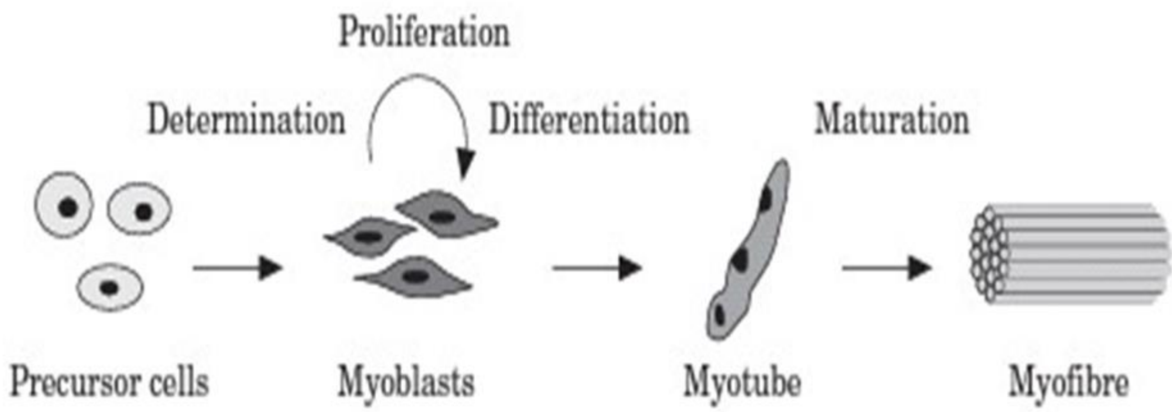


Figure 1: An illustration of Myogenesis of fish Muscle (Watabe, 1999)

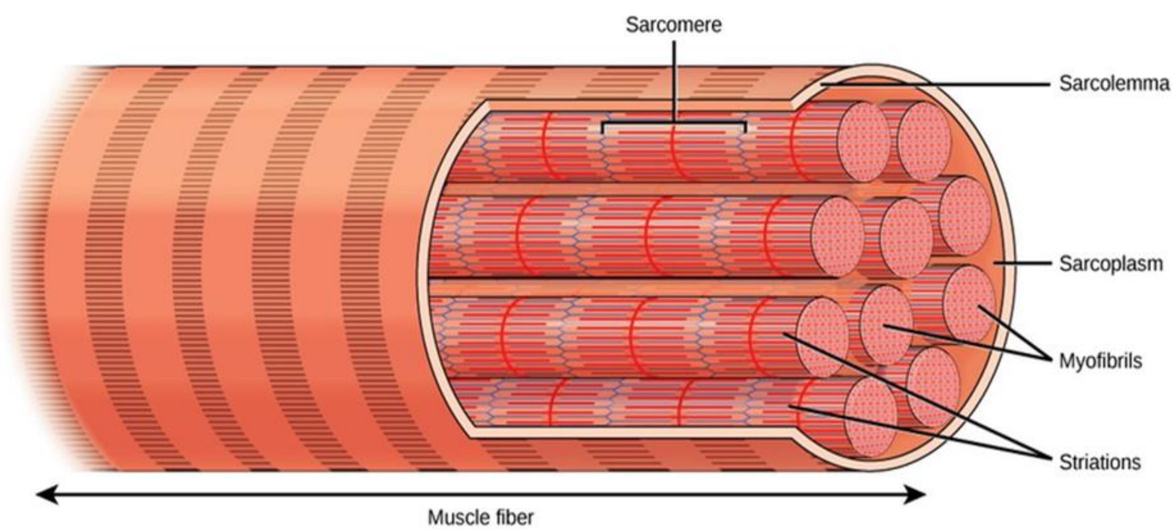


Figure 2: An illustration of Slow and fast muscle lineage from adaxial cells in the segmental plate of zebrafish (modified from Blagden *et al*., 1997).

III. EARLY MUSCLE DEVELOPMENT OF FISH

The trunk musculature of fish is derived from the segmental plate mesoderm flanking the notochord and lying underneath the presumptive spinal cord. Studies in zebrafish (*Brachydanio rerio*) have shown that the most medial cells in the segmental plate, called adaxial cells, commit to becoming myoblasts with a specific slow muscle lineage (Devoto *et al*., 1996), under the influence of the glycoprotein Sonic hedgehog (Shh) secreted from the notochord (Blagden *et al*., 1997) (Fig. 3). The fast muscle fibres derived from the lateral pre-somitic mesoderm, are formed from the fusion of several myoblasts to form multi-nucleated myotubes. Shh is not required for the commitment of the lateral pre-somitic cells to a fast muscle lineage as the *boz* mutant lacks Shh and yet contain fast muscle fibres throughout the somite (Blagden *et al*., 1997).

IV. LARVAL AND ADULT MUSCLE GROWTH

Both hyperplasia and hypertrophy occur during myogenesis in larval and adult muscle growth of fish such as sea bream (*Sparus aurata*), sea bass (*Dicentrarchus labrax*), carp (*Cyprinus carpio*), and rainbow trout (*Oncorhynchus mykiss*), all of which reaches a large adult size (Koumans *et al*., 1993; Alami-Durante *et al*., 1997; Johnston *et al*., 1998; Patruno *et al*., 1998; Stoiber and Sanger, 2001) (Fig. 4). In mammals, hyperplasia ceases near the time of birth (Watabe, 1999). Adult fish of those in which extensive post-larval muscle hyperplasia contributes to its large adult size have three main skeletal muscle phenotypes in their trunk musculature.

These are slow, intermediate and fast skeletal muscles, which have been shown to express different myosin heavy-chain (MyHC) isoforms (Watabe, 1999) and are located in three distinct muscle layers, red, pink and white, respectively. During the first half of larval life for sea bream, the presumptive fast muscle increases in thickness by the addition of new fibres derived from a germinal zone of presumptive myoblasts lying beneath the slow muscle layer (Veggetti *et al*., 1990).

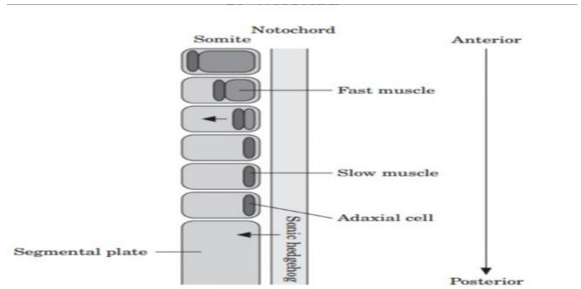
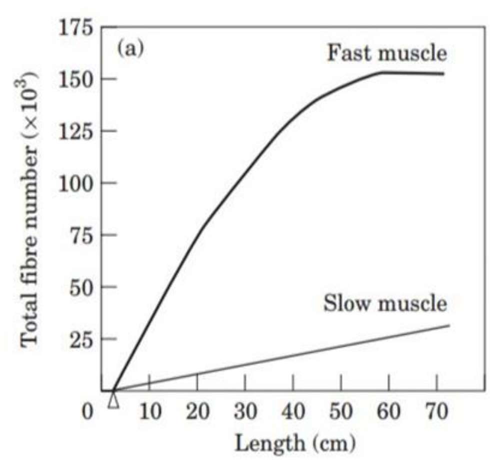


Figure 3: An illustration Early Muscle Development of Fish (Okwuosa and Ekeledo, 2019)

V. PHYSIOLOGICAL PROPERTIES OF FISH MUSCLE SWIMMING STRUCTURE

Muscle tissues generate and transmit power and can be formed by several types of muscle cells such as skeletal, cardiac or smooth muscle cells. Fish muscles are mostly striated, comprising from 40% to 75% of the animal’s weight (Carani *et al.*, 2008; Schmidt-Nielsen, 2010). In fish, muscle fibers are distributed in different areas or compartments, while in mammals there is mosaic pattern of distribution (Carani *et al.*, 2008). Another important characteristic of the fish muscular system is multiply innervated contractile fibers. Involving these fibers is connective tissue which holds them together and myomeres are separated by connective tissue sheaths called myosepts (Santos, 2007), though architectural details such as muscular and connective tissue anatomy and tissue relations in myomeres are not well known.



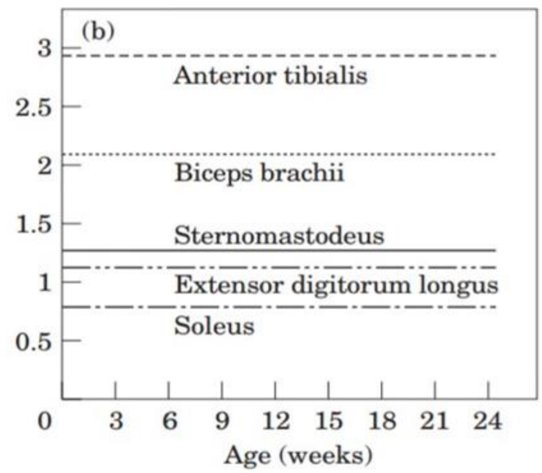


Figure 4: Fish muscle growth during development and their post-larval muscle growth involving hypertrophy and hyperplasia in comparison with mammalian muscle (modified from Watabe, 1999). An arrowhead indicates an approximate hatching period for rainbow trout. (a) Rainbow trout, (b) mouse.

Collagen is the main constituent of connective tissue in fish muscles. Firmness of the muscle is directly related to its collagen content (Suarez *et al*., 2005). Skeletal muscle constitutes the majority of edible parts of fish and in addition, striated muscle includes muscles associated with fin movement (Mumford *et al.,* 2007). Physiological roles of red muscle are different from those of white muscle. Red muscle is laterally located in the animal's body, it extends toward the spine and turns dark red in sites of high myoglobin concentration (Mumford *et al.,* 2007; Carani *et al.,* 2008). In fish, red muscle has a higher lipid content than white muscle, a greater number of mitochondria per cell and higher respiratory rate; red fibers are aerobic with slow contraction (Mumford *et al.,* 2007). Red muscle is used to power slow sustainable swimming, however, when swimming speed increases, there is progressive recruitment of white muscle, representing a power reserve for short high-speed swimming (Wardle *et al.*, 1995). In some species of fish white muscle is an important fraction of an animal's total mass, and may represent from 80% to 100% at a given point of a transversal section. White muscle is responsible for short, strong bursts of motion, which occur during food capture or predator escape. White fish muscles have low amounts of mitochondria, lower respiratory rates and get fatigued faster than red fibers; furthermore, they are anaerobic, with glycolytic metabolism (Mumford *et al.,* 2007; Carani *et al.,* 2008). Red/white fiber ratio in a fish's body is related to lifestyle, thus pelagic fishes have higher proportions of red fibers while white muscle fibers predominate in benthic fishes (Mumford *et al.*, 2007).

VI. TYPES OF FISH MUSCLES FIBRES

Fish muscles come in three different types as follows;

- Red Muscle

Red muscle, also known as slow muscle, is red because it has a high number of capillaries present in it and thus has a high haemoglobin content. Being well supplied with oxygen red muscle is used for steady, constant-effort swimming and is found in active fish, particularly those that live in the open waters of seas and oceans, nevertheless red muscle seldomly makes up even as much as 20% of a fish's total muscle mass (Birbrair *et al.*, 2013).

- Pink Muscle

Pink muscle is intermediate between the two, and is good for continued swimming efforts lasting a few tens of minutes at a relatively high speed. Of course, like all animals, fish use all their muscles in concert as they go about their daily lives (Birbrair *et al.*, 2013).

- White Muscle

White muscle, or fast muscle, has thicker fibres than red muscle and possesses many less capillaries, and so it has a much reduced blood flow, and therefore, a reduced oxygen availability. Most white muscle activity is anaerobic (glycogen is converted to lactate). White muscle fibres can produce tensions that are up to 2.7 times greater than those of red muscle, but they are more energetically wasteful and therefore the cost to the animal is higher. Finally, white muscle can only work for short periods of time, a couple of minutes maximum is not unusual, before they exhaust their supply of glycogen and need to rest. All this means that white muscles are convenient for short quick bursts of movement, in which capacity they out compete red muscle easily, but that they are no good for prolonged swimming (Astruc, 2014b; Birbrair *et al.*, 2013).

Most fish have a mixture of two, or all three, types of muscle, but keep the types in discrete groupings, however in the salmonid fishes the red and white muscle types are mixed to form a mosaic type of muscle. The colours these muscles show is related to the amount of haemoglobin present in the muscles, with red muscle having plenty of haemoglobin present and white very little, if any. However, when looking at fish muscles it is well to be aware that some fish, that feed on crustaceans, particularly salmonids, develop a pink colour to their muscles as a result of a carotenoid pigment they acquire from their food, in the same way that flamingoes get their pink colour from the crustaceans they eat (Pestronk, 2013).

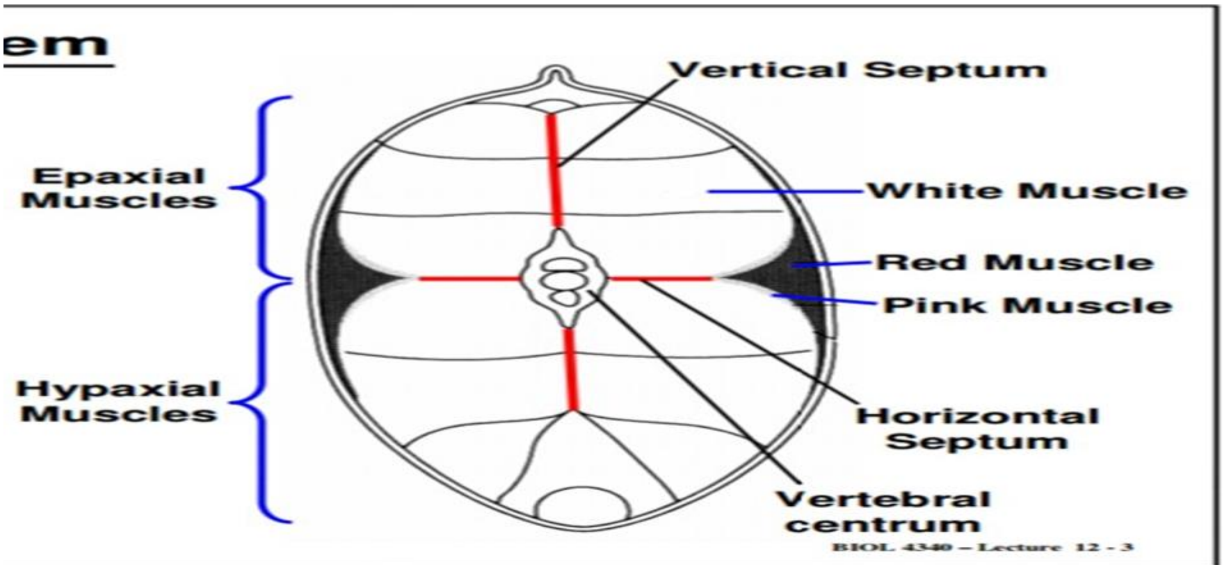


Figure 5: An illustration Types of Fish Muscles Fibres (Okwuosa and Ekeledo, 2019)

- Slow-Red fibres

Red muscle fibres are commonly confined to a narrow strip along the lateral line. Red muscle fibres usually constitute less then 10 % of the myotomal musculature and are small in diameter (25-45 μm). The red muscle fibres are also called slow fibres and are used mainly for sustained energy efficient swimming. The characteristic of this muscle type are good capillary supply, high amount of mitochondria, lipid droplets and glycogen stores. Concentration of myoglobin and cytochromes are high. The energy metabolism in red muscle is almost entirely aerobic, based mainly on lipid as fuel complemented with carbohydrates (Sänger and Stoiber, 2001).

- Fast- White Fibres

White muscle fibres compose the major part of the skeletal muscle in fish and constitute never less than 70% (Sänger and Stoiber, 2001). The white fibres show the largest fibre diameter ranging between 50 and 100 μm or even more. The proportion of the cross-sectional area of the skeletal muscle that is comprised of white muscle varies along the length of the fish, being greatest in the anterior of the animal and declining caudally. Generally, the white muscle type is used at high swimming speeds e.g., in fast-start burst swimming for prey capture and escape response, though there is an overlap of labour between red and white muscles in most teleosts. White muscle fibres are tightly packed with myofibrils occupying between 75 and 95% of the fibre volume. Organelles such as mitochondria which interrupt the arrays of myofibrils, are few and both lipid droplets and myoglobin are present in very low levels in most species. Salmonids and a few other fatty fish constitutes the exception with significant amounts of intrafibrilar fat (Kiessling *et al.,* 1990; Zhou *et al.,* 1995). Vascularization in white glycolytic muscle is poor. Glycogen content is also low with granules mainly located between the myofibrils. However, there seems to be a marked heterogeneity in glycogen content between different sized white fibres, with a significantly higher content in the smaller fibres (Figs. 2, Kiessling *et al.,* 1990;

Kiessling and Ostrowski, 1997). The energy for white muscle, operating in a nearly closed system, dominates by anaerobic breakdown of intramuscular glycogen with small contribution from cytosolic phosphocreatine (PCr) and ATP. In addition to this glycolytic based system is energy likely also provided via the slower but more efficient aerobic break down of lipids. Enzymatic activity levels β-oxidation and respiratory chain in the range of 10% of that found in red muscle is reported throughout life in white muscle of rainbow trout (Kiessling *et al.,* 1991b), Atlantic salmon (Frøyland *et al.*, 1998) and migrating sockeye salmon (Kiessling *et al.,* 2004a).

In parity with glycogen levels aerobic activity seems to be concentrated to small rather than large fibres (Kiessling *et al.,* 1990). It has therefore been speculated if this heterogeneity between fibres of different sizes is related to regeneration of glucose in small fibres from lactate formed during anaerobic glycolysis in the large fibres and/or from an aerobic catabolism of pyrovate from glycolysis to fuel contraction in small fibres during intermediate swimming speeds (Kiessling *et al.,* 2004a).

- Intermediate -Pink Fibres

Intermediate or pink fibres is in accordance to their name not only intermediate in position between red and white muscle fibres but also in many other aspects. In juveniles and adults of most teleost species, a zone of intermediate or pink fibres is inserted between red and white fibres. The mean fibre diameter lies between those of red and white. Pink fibres are characterized as fast contracting with intermediate resistance to fatigue and intermediate speed of shortening between red and white muscles. Salmonids on the other hand seems not to have pink fibres, but only white and red (Martinez *et al.*, 1991 re Arctic charr; 1993 re Atlantic salmon; *Kiessling et al.*, 1995 re rainbow trout).

- Fish Muscle Growth Mechanism

Most fishes continue to grow throughout their lives. Growth in fish has been studied intensively because it is a good indicator of health. Rapid growth indicates abundant of food and other favourable conditions, whereas slow growth is likely to indicate just the opposite. Growth is commonly measured as changes in body weight, length or condition factor (i.e. weight/length relationship) over time. Post-embryonic growth of the muscle tissue involves an increase in the number and diameter of the fibres and a contemporary remodeling of the associated connective tissue, nerve and blood supply. Muscle growth can therefore be studied as the contribution of hyperplasia (increase in fibre number) and hypertrophy (increase in fibre size) to muscle growth by various forms of histological methods combined with morphometric analysis (Rowlerson and Vegetti, 2001). Muscle fibre morphometric variables most commonly used are diameter or cross-sectional area and number of muscle fibres measured within a representative area of the musculature. From this, size distribution histograms are made or a probability density function (pdf) where the increase in fibre size describes hypertrophic growth and the increase of small fibres denotes hyperplastic growth, i.e. recruitment of new fibres.

Growth is usually positive, in that the fish increase in size over time. The principal factor controlling the growth processes are growth hormones secreted by the pituitary and steroid hormones from the gonads. However, the rate of growth of fish is highly variable because is it greatly dependent on a variety of interacting environmental factors such as water temperature, levels of dissolved oxygen and ammonia, salinity and the photoperiod (*Kiessling et al.*, 2004). Such factors interact with each other to influence growth rates, and with others such as the degree of competition, the amount and quality of food ingested, and the age and state of the maturity of the fish.

- Hypertrophy

In fish the muscle grows by enlargement of existing fibres (hypertrophy) throughout post-embryonic life until they reach a functional maximum diameter, which is in the range 100-300 μm for white fibres in most fish (Rowlerson and Vegetti, 2001). Hypertrophic growth persists long after hyperplastic growth has ceased (e.g. *Kiessling et al.*, 1995; Rowlerson and Vegetti, 2001). As the fibres increase in size they get packed with myofibrils. Fibres also acquire additional nuclei as they grow (Nathanilides *et al.*, 1996; Alami-Durante *et al.*, 1997). The new nuclei are supplied by a population of satellite cells (already present in the muscle), which fuse with existing muscle fibres to provide the additional nuclei (Johnston *et al.*, 2000). To supply the number of nuclei required during growth, this population must be capable of proliferation. In fish, a major uncertainty is whether there are separate muscle stem cell populations for fibre recruitment and fibre hypertrophy.

- Hyperplasia

Hyperplastic growth of muscle refers to the increase in muscle fibre number due to the formation of new fibres. After the initial two muscle layers have been formed during embryonic life, hyperplastic growth continuous in two successive and distinct phases. The first phase is a continuation of embryonic myogenesis and completes the formation of the definitive muscle layers (slow red, pink and fast white), followed by a second and quite different hyperplastic process resulting in a large increase in the total number of fibres in all muscle layers, especially in the white muscle layer (Rowlerson and Vegetti, 2001). New presumptive fast white fibres during embryonic and into larval life, appear in a germinal layer or proliferation zone located just under the superficial monolayer and extends dorsally from the horizontal septum into the apex of the myotome. In many fish species which remain small, this second hyperplastic growth phase is lacking, whereas fast-growing fish generally show greater hyperplasia than slow-growing fish of the same age (Kiessling *et al.*, 1991a; Valente *et al.*, 1999). In most fish, which grow to a large final size, the majority of muscle fibres are formed in a long-lasting hyperplastic growth process disseminated throughout the entire myotome. This process gives rise to the typical mosaic appearance of muscle cut in transverse section, with fibres of different ages (and therefore diameter) intermingled. Mosaic hyperplastic muscle growth, which occurs principally during juvenile life, is of great interest in commercial aquaculture because it contributes to the market size of the fish. The intensity of mosaic hyperplastic growth is most pronounced in early juvenile life: later it decreases gradually until the fish reaches a characteristic fraction of body size after which further growth occurs by hypertrophy only (Rowlerson *et al.*, 1995). There is indirect evidence for the existence of a distinct population of myogenic cells supporting mosaic hyperplastic growth (Rowlerson and Vegetti, 2001).

CONCLUSION

The three main components of muscle (i.e., muscle fibers, connective tissue, and adipose tissue) are involved in the determination of various physiological functions of the muscles which ranges from movement (swimming), capturing of prey to meat formation via muscle growth. Muscle fibers comprises of White, Red and Pink. While red helps in fish maintenance of steady and stable movement and White get recruited when fish needs to move faster either to capture prey or escape from danger or even any other movement that requires fast quick jump/movement. Pink muscle fiber in other hand are characterized as fast contracting with intermediate resistance to fatigue and intermediate speed of shortening between red and white muscles. Fish muscle growth mechanism has been related to the biochemical and metabolic activities that happen to the fish starting from breeding point to growing stages based on what the fish inherited and what is fed with couple with environmental factors like temperature, water purity etc. However, most fishes continue to grow throughout their lives. Growth in fish has been studied intensively because it is a good indicator of health. Rapid growth indicates abundant of food and other favourable conditions (which are measured as mentioned above), whereas slow growth is likely to indicate just the opposite. Growth is commonly measured as changes in body weight, length or condition factor over time. Post-embryonic growth of the muscle tissue involves an increase in the number and diameter of the fibres and a contemporary remodeling of the associated connective tissue, nerve and blood supply. Muscle growth have been studied as the contribution of hyperplasia (increase in fibre number) and hypertrophy (increase in fibre size) to muscle growth by various forms of histological methods combined with morphometric analysis. The quality and muscle dimensions varies at different degrees depending on species, muscle type, and posts laughter meat-processing techniques. The relative independence among the characteristics of these three major muscle constituents suggests that it is possible to independently manipulate these characteristics by genetic, nutritional, and environmental in order to control the physiological properties and quality of muscle and thus better fulfill the expectations of producers, meat processors and consumers.

RECOMMENDATION

Base on the knowledge acquired from the reviewed literatures and text books, it is therefore recommended that:

- More attention should be given in the studies of fish muscle physiological properties to enable emergence of new innovative researches and findings that will be implemented in order to manipulate the fast growth of fish muscle fibers for a better yield and good return of investment.
- Muscle growth should be studied as the contribution of hyperplasia (increase in fibre number) and hypertrophy (increase in fibre size) to muscle growth by various forms of histological methods combined with morphometric analysis.
- Precise knowledge regarding the fish physiological properties, structural and biochemical characteristics of each muscle component and their relationships with physiological functions, growth performance and meat quality dimensions is a prerequisite to understanding and controlling the biological basis of the quantity and quality of animal meat products of fish origin. Future research should also focus on the modulation of muscle properties that determine the major components of meat quality in the different species: tenderness in cattle, water-holding capacity and tenderness in flesh texture in fish.

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