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Muscle fibre growth and quality in fish

Abstract

Striated muscle in fish is in parity with skeletal muscle in higher vertebrates made up of three major compartments - contractile proteins, lipids, and connective tissue, - all affecting the product and food quality of the muscle as meat. The most striking difference between striated fish muscle and that found in higher vertebrates is the separation of fibre types in to discrete layers in fish, where the high glycolytic and anaerobic type (Fast- White fibres) dominates constituting 90-95% of all muscle in most fish species. Red muscle fibres are commonly confined to a narrow strip along the lateral line and constitute less then 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. Salmonids seem not to have pink fibres. In contrast to other higher vertebrates in the majority of fish species growth continues through out life and the growth of muscle is the combined effect of formation of more muscle cells (fibres) and increase in size of already existing fibres. In spite of the apparent large connective tissue compartment of fish muscle, only 2-3 % of the protein is found here. All the above factors are believed to be in part under genetic control, but a gene x environment interaction seems to be evident. The current state of knowledge is reviewed here and the impact of muscle structure on quality is discussed.

Key Words: muscle fibre, fish, quality, growth, muscle structure

Zusammenfassung

Titel der Arbeit: **Muskelfaserwachstum und Qualität beim Fisch**

Quergestreifte Muskulatur bei Fischen besteht entsprechend der Skelettmuskulatur in höheren Wirbeltieren aus drei Hauptkomponenten, kontraktilen Proteinen, Lipiden und Bindegewebe, die die Produkt- und Nahrungsmittelqualität des Muskels als Fleisch beeinflussen. Der größte Unterschied zwischen Fischmuskel und dem höherer Wirbeltiere besteht in der Anordnung verschiedener Fasertypen in getrennten Schichten, von denen die mit glykolytischen und anaeroben Fasern (schnelle weiße Fasern) mit 90-95% den höchsten Anteil haben. Rote Muskelfasern sind allgemein auf einen schmalen Streifen entlang der seitlichen Linie begrenzt und kleiner und machen 10 % der myotomalen Muskulatur aus. Intermediäre- oder rosafarbene Fasern sind in der Übereinstimmung mit ihrem Namen, in Position zwischen den roten und weißen Muskelfasern angeordnet aber auch in vielen anderen Aspekten intermediär. Salmoniden scheinen rosafarbene Fasern nicht zu haben. Im Gegensatz zu anderen höheren Wirbeltieren setzt sich bei der Mehrheit der Fischspezies Wachstum durch das gesamte Leben fort und Muskelwachstum ist gekennzeichnet durch Hypertrophie und Hyperplasie. Trotz des offensichtlichen großen Bindegewebeanteils des Fischmuskels befinden sich nur 2-3 % des Proteins hier. Die oben genannten Faktoren unterstehen genetischer Steuerung, aber auch Genotyp x Umwelt Interaktion ist von Bedeutung. Der gegenwärtige Wissensstand sowie die Bedeutung der Muskelstruktur auf die Qualität werden hier diskutiert.

Schlüsselwörter: Muskelfasern, Fisch, Qualität, Wachstum, Muskelstruktur

Introduction

Striated muscle in fish is in parity with skeletal muscle in higher vertebrates made up of three major compartments all affecting the product and food quality of the muscle as meat. The contractile protein which is found organised in myofibrils inside the muscle fibres. The lipids which are found as the major component of cell membranes in the form of phospholipids, as storage lipids in adiposities or as lipid droplets in the cytoplasm of the muscle fibres. And the connective tissue which is made up of collagen and form the cytoskeleton of the muscle.

The main object for fish muscle are movement, unlike the mammals were the muscles also give important support to the skeleton. The most striking difference between striated fish muscle and that found in higher vertebrates is firstly the separation of fibre types in to discrete layers in fish, where the high glycolytic and anaerobic type dominates constituting 90-95% of all muscle in most fish species (Fig.1 and 2). Secondly in the majority of fish species growth continues through out most of the life and the growth of muscle is the combined effect of formation of more muscle cells (fibres) and increase in size of already existing fibres.

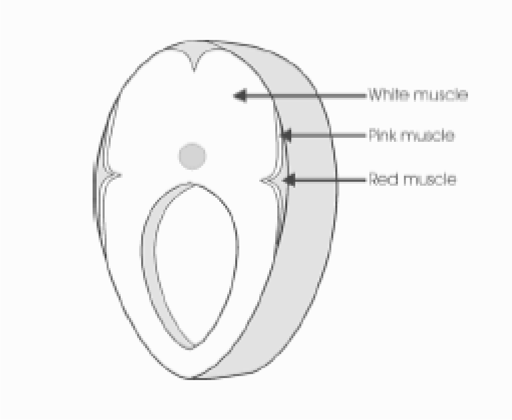

Fig. 1: A cross-section of a fish muscle showing the location of red (high aerobic, slow twitch), pink (high aerobic, high glycolytic and fast twitch) and white (anaerobic, high glycolytic and fast twitch) muscle fibres (Querschnitt durch Fischmuskel mit roter (aerob, langsam), intermediärer (aerob, schnell) und weißer (anaerob, glykolytisch, schnell) Muskulatur)

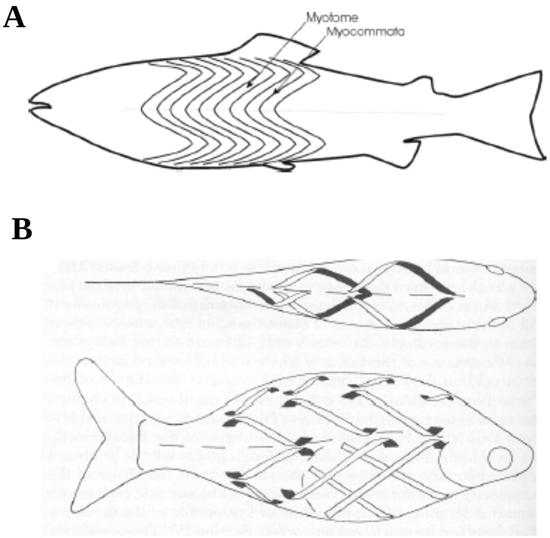

Fig. 3: A) Schematic drawing of somatic muscle in fish showing the arrangement of myotomes (muscle fibers) and myocommata (connective tissue). B) Schematic dorsal and lateral views of a typical teleost showing courses of myotomal muscle fibers in successive myotomes along the body. The helices shown where found by taking the origin of one muscle fiber from the point at which the muscle fiber in the myotome next anterior inserts onto the common myoseptum, and so on along the fish. From Alexander, 1969, *J. Mar. Biol. Assoc. U.K.* (**49**:263-290). (A) Anordnung der Myotome (Muskelfasern) und der Myokommata (Bindegewebe). B) Dorsale und laterale Ansicht eines Teleostfisches mit typischer Anordnung von Muskelfasern)

The striated muscle of teleost fish, which make up the fillet, consists of long sheets of muscles (myotomes) extending on both sides of the body from head to tail (Fig.3). Connective tissue makes up 2% to 5% of the muscle in bony fish and takes the form of fine membranes (myocommata) separating the long muscles into segments that are one cell deep (DUNAJASKI, 1979). Each myotome contains a superficial region lying directly beneath the skin, where the muscle fibres are run parallel to the body axis, and a deeper part where the muscle fibres are arranged in a helical fashion, forming angles of up to 40º (Fig. 3). This typical orientation of muscle fibres is associated with the need for constant amount of sarcomere shortening at different body flexures (SÄN-

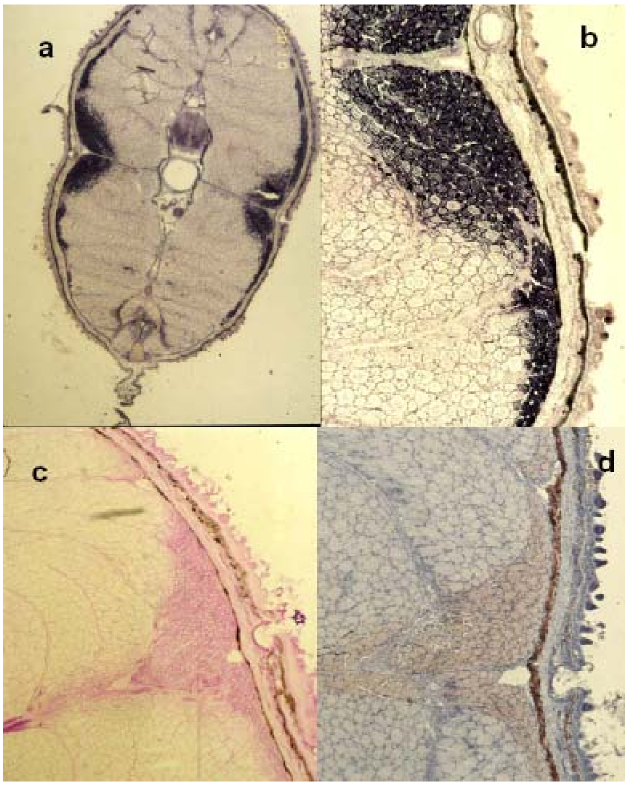

Fig. 2: a) Whole cross section of a fish muscle stained for oxidative capacity demonstrating localisation of red and white muscle. Sub cross sections of red and white muscle at the lateral line, demonstrating the metabolic characteristics of the two fibre types (b-d): stained for succinate dehydrogenase (mitochondria), glycogen (PAS-staining) and triglycerides (oil-o staining), respectively. The sections from a 2 gram Mahi Mahi (*latin)* larva in the study described in Kiessling and Ostrowski, (1997) (Querschnitte durch Fischmuskulatur gefärbt entsprechend oxidativer Kapazität als rote und weiße Muskulatur. Vergrößerungen des lateralen Abschnitts (b-d) mit Färbung der Fasern nach metabolischen Eigenschaften: Succinat-dehydrogenase-Aktivität (Mitochondrien), Glykogen- (PAS), Triglyceridgehalt (Öl-O-Färbung). Gewebe von Mahi Mahi Larve (nach Kiessling and Ostrowski, 1997))

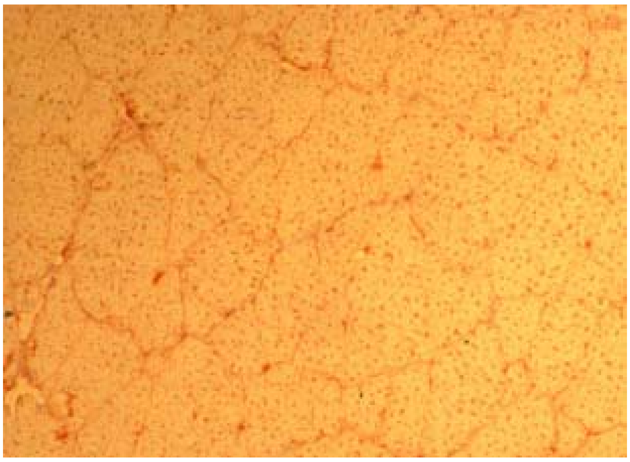

Fig. 4: Histochemical cross section of white adult rainbow trout muscle stained for Oil O (neutral lipids staining red). Photo from the study described in Kiessling et al. 1990 (Weiße Muskulatur einer adulten Regenbogenforelle Öl-O-gefärbt (neutrale Lipide rot) (nach Kiessling et al. 1990))

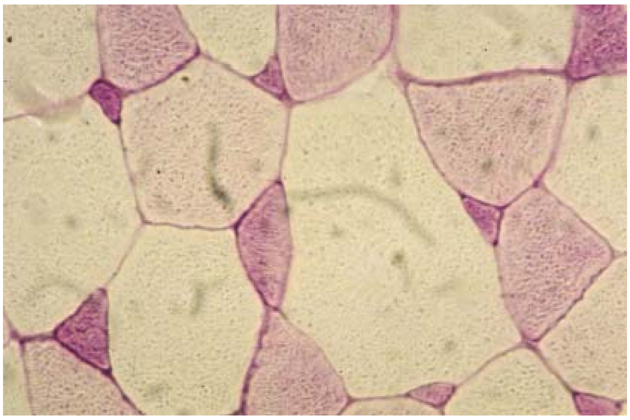

Fig. 5: White muscle in rainbow trout stained for glycogen (PAS-staining) demonstrating the difference in glycogen content between small (young) and large (old) fibres in a spawning migrating sockeye salmon (*Oncorhynchus nerka*). Photo A. Kiessling. (Glykogen-Färbung (PAS) weißer Muskulatur einer Regenbogenforelle zeigt unterschiedliche Glykogengehalte in kleinen (jungen) und großen (alten) Fasern in *Oncorhynchus nerka*. Photo A. Kiessling)

GER and STOIBER, 2001). Length of muscle fibres decreases in length towards the tail end of the fillet (LOVE, 1988); and the muscle fibre cross sectional area is smaller at the tail and head than in between (LOVE, 1988; SIGURGISLADOTTIR, 2001).
All fish have two main types of locomotor muscle fibres, red and white, specialized for either low speed cruising or short bursts of maximum speed, respectively (BONE, 1978). In several fishes there are more than these two fibre types (SÄNGER and STOIBER, 2001). The organization found in teleosts is as follows: the axial muscle consists mainly of fast white fibres, covered by a thin layer of slow-red muscle fibres, with a layer of pink intermediate muscle fibres in between them (Fig. 4). Salmonids lacks this intermediate fibre type (MARTINEZ et al., 1993; KIESSLING et al., 1995)

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 (Fig. 2). 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 (Fig. 4) (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 and 5, KIESSLING et al. 1990; KIESSLING et al. 1991a; 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 through out 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).

Muscle growth; 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 (MOYLE and CECH, 1982). 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. STICKLAND, 1983; WEATHERLEY et al., 1988; KIESSLING et al., 1991a; rev: ROWLERSON and VEGETTI, 2001). As the fibres increase in size they get packed with myofibrils. Fibres also acquire additional nuclei as they grow (JOHNSTON, 1993; USHER et al., 1994; 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 (Fig. 4) (JOHNSTON, 2001). 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 (WEATHERLEY et al., 1979; WEATHERLEY and GILL, 1984; HIGGINS and THORPE, 1990; KIESSLING et al., 1991a; VEGETTI et al., 1993; 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 (Fig. 5). 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 (WEATHERLEY et al., 1988; STICKLAND, 1983; 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).

Muscle structure and quality

Important quality factors in fish are texture, colour, fillet gaping, taste and flavour. We will look into how the muscle structure affects some important quality traits below.

Texture; Texture is one of the criteria of flesh quality. It is a sensory characteristic for the consumer and an important attribute for the mechanical processing of fillets. Very soft texture is frequently reported and the industry is requesting methods able to measure fish texture, and is also seeking answers to what causes fillet softness.

Textural properties depend on the chemical composition and the structural properties, in particular the myofibrillar and connective tissue proteins. The connective tissue forms a supporting network through the whole fish muscle. The content of connective tissue is lower and more evenly distributed in fish muscle compared with warm-blooded animals, though there is increased firmness along the anterior-posterior axis of the fillet.

The fibre distribution of the muscle has been found to affect the texture in fish (Fig. 6, KIESSLING, RUOHONEN, BJØRNEVIK and ESPE, submitted 2005). Intra-species comparison has shown that muscle fibres measured as average fibre cross-section area, increases with decreasing sensory firmness in cooked fish (HATAE, 1990; HURLING et al., 1996). Also in fresh and smoked Atlantic salmon and in fresh brown trout, studies have shown a weak decrease in flesh firmness as the size of the fibres increases (or the fibre density decreases) (JOHNSTON et al 2000, 2004; BUGEON et al., 2003). On the other hand there are also studies on Atlantic salmon and Atlantic cod that was not able to confirm this finding (SIGURGISLADOTTIR, 2001; BJØRNEVIK et al., 2003). An underlying rational for this discrepancy between studies may firstly be found in the fact that texture varies as a factor on the rostral-caudal location n the fillet (SIGURGISLADOTTIR, 2001; BJØRNEVIK et al., 2003).

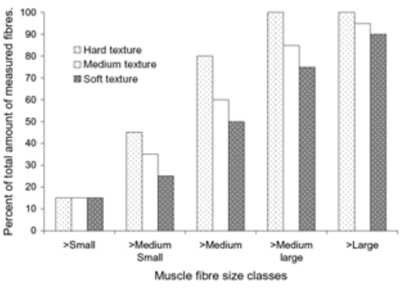

Fig. 6: Percent of fibres accounted for (accumulated, y-axis) in each fibre size class (cross section) in farmed Atlantic salmon (*Salmo salar*) displaying either hard, intermediate or soft texture, as measured by transverse cutting (shear force) with a Warner Bratzler type blade. Based on data from Kiessling, Ruohonen, Bjørnevik and Espe, (In progress 2006).(Anteil an Muskelfasern an der gemessenen Gesamtzahl (akkumuliert, Y-Achse) in jeder Fasergrößen-klasse (Querschnitt) mit weicher, intermediärer oder harter Textur (Scherkraft, Warner Bratzler Messer))

Muscle fibre size may only partly explain the variation in mechanical resistance of the flesh (40% with the mean fibre size diameter is found in brown trout) (BUGEON et al., 2003). Muscle structure is more complex than a physical structure based on muscle fibre, and other factors could explain flesh texture characteristics. An increase in insoluble collagen with increasing texture firmness has been seen indicating that connective tissue also may contribute to the firmness of fish flesh (ESPE et al. 2004).

Gaping; Fillet gaping is a well known quality problem in fish. Gaping in fillets occurs as slits between muscle blocks. The slits can range from slight separation at the cut surface to complete separation right down to the skin of the fillet. This phenomenon is of considerable economic importance to the fish industry, as gaping significantly decreases the technological and market value of the fish, spoils the appearance of fillets and make skinning difficult or impossible.

The relationship between fibre area and occurrence of gaping has been studied, and contradictory results have been reported. JOHNSTON (2001) found a negative relationship between fibre density and occurrence of gaping in Atlantic salmon, i.e. increasing gaping score with larger mean white fibre area, whereas BJØRNEVIK et al. (2004) found a negative relationship between fibre area and gaping, while KIESSLING, RUOHONEN, BJØRNEVIK and ESPE, (submitted 2005) report a lower

number of intermediate fibres in Atlantic salmon displaying severe gaping compared to fish with no or intermediate gaping (compare with Fig. 6 for texture).
Each muscle fibre is surrounded by reticular fibres, the "endomysium", and it has been speculated that a fish with many small fibres would have a relatively larger amount of connective tissue, compared with a fish with larger and fewer muscle fibres. And that this larger amount of connective tissue would prevent the fillet from gaping.

Flesh colour; Visual appearance is a very important property in the food industry. In salmonids the red colour of the flesh is of particular importance, and for white fishes, a delicate white appearance is preferred. It has been argued that a perceived change in flesh colour can be caused by an altered reflection due to the change in surface properties with altered fibre area. Different studies have so far not been able to verify this hypothesis. JOHNSTON et al (2000) reported a positive relationship between Roche colour score and fibre density in Atlantic salmon, whereas no such relationship was found in other studies (BJØRNEVIK et al., 2004; ESPE et al., 2004). A weak positive relationship is found between lightness and fibre density in Atlantic salmon, higher density and more intermediate sized fibres coincides with a darker flesh (KIESSLING, RUOHONEN, BJØRNEVIK and ESPE, submitted 2005, compare with Fig. 6), whereas no such relationship was seen in cod (BJØRNEVIK et al., 2003).

In conclusion; muscle fibre growth in fish consist of two distinct phases. The first during early larvae age, comparable to that seen in higher vertebrates during the embryonic stage, and a second during adult life signified by a combined hyperplasia and hypertrophy. Growth during both these stages are under a combined of genetic and environmental control. Several studies are under way in order to determine the genetic component of this control (e.g. EU project "Progress" as well as the control mechanisms (see ASHTON et al., 2005 for a review). The relationship between final muscle fibre composition and size has long been debated but only recently the target for systematic research. Undoable a relationship exist, however, the predictive power is weak using the fibre component alone. Based on available data the degree of explanation varies from 0-25% depending on species, life stage and variable studied. The majority of variation measured in quality of the fish fillet is probably an effect of the connective tissue, the lipid component and naturally also to handling of the flesh post mortem.

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