



HAL
open science

Muscle Proteins

Mike Boland, Lovedeep Kaur, Feng Ming Chian, Thierry Astruc

► **To cite this version:**

Mike Boland, Lovedeep Kaur, Feng Ming Chian, Thierry Astruc. Muscle Proteins. Reference Module in Food Science, 2018, 10.1016/B978-0-08-100596-5.21602-8 . hal-02000883

HAL Id: hal-02000883

<https://hal.science/hal-02000883v1>

Submitted on 30 Jan 2019

HAL is a multi-disciplinary open access archive for the deposit and dissemination of scientific research documents, whether they are published or not. The documents may come from teaching and research institutions in France or abroad, or from public or private research centers.

L'archive ouverte pluridisciplinaire **HAL**, est destinée au dépôt et à la diffusion de documents scientifiques de niveau recherche, publiés ou non, émanant des établissements d'enseignement et de recherche français ou étrangers, des laboratoires publics ou privés.

Muscle Proteins

Mike Boland^a, Lovdeep Kaur^a, Feng Ming Chian^a, and Thierry Astruc^b, ^aMassey University, Wellington, New Zealand; and ^bINRA Auvergne-Rhône-Alpes, Saint Genès Champanelle, France

© 2018 Elsevier Inc. All rights reserved.

Introduction	1
Structure of Muscle	2
Myofibrillar Proteins	3
Contractile Proteins	3
Regulatory Proteins	5
Structural Proteins	5
Stromal Proteins	5
Collagen	6
Elastin	6
Sarcoplasmic Proteins	6
Calpains	6
Cathepsins	7
Myoglobin	7
Other Sarcoplasmic Proteins	7
From Muscle to Meat	8
Postmortem Biochemical Changes	8
Fast Postmortem Metabolism Effects on Muscle Proteins and Meat Quality	8
Postmortem Proteolysis	8
Proteolytic Systems	8
Postmortem Muscle Protein Degradation	8
Postmortem Protein Oxidation	9
Effects of Processing on Meat Proteins	9
Electrical Stimulation of Carcasses	9
Pulsed Electric Field	9
Exogenous Enzyme Technology	9
Shockwave Hydrodynamic Processing	10
High Pressure Processing	10
Effects of Cooking on Meat Proteins	10
Sous Vide Cooking	10
Other Cooking	11
Nutritional Value and Digestion	11
Sustainability of Meat as a Source of Protein	12
Real Cost of Meat, Water and Carbon Footprints	12
Importance of the Ruminant	12
The Future of Meat	12
References	13
Further Reading	16

Introduction

Muscle proteins are an important part of the diet in many cultures, as they make up the major proportion (other than water) of lean meat. These proteins provide most of the texture, color and nutritive value of meat and most meat products. In life, muscle proteins provide motive power to the animal. Following slaughter, muscle tissue forms meat.

Meat and meat products are today regarded in the developed world as a luxury, and in many Western countries meat consumption is on the decline due to both the price and the environmental cost. But strong demand for meat and meat products is expected to continue because of strong meat-eating traditions in many cultures, a general recognition of meat as one of the best sources of high quality bioaccessible protein and iron, and a general preference for the textures and flavors of meat-containing dishes. Further to this, meat plays an important part in many developing countries, particularly meat from pigs and chickens that can convert waste materials, and from ruminants that can convert plant materials that are inedible to humans, into high quality food.

Structure of Muscle

Skeletal muscles consist of multinucleated muscle fibers made up of bundles of elongated myofibrils in a parallel configuration (Fig. 1) (Gault, 1992; Strasburg et al., 2008). Depending on animal species, muscle size and anatomical location, muscle fibers differ in length (a few millimeters to 30 cm), diameter (10 μm to 100 μm), and orientation (parallel or at a specific angle to the length). Most of the skeletal muscles are composed of muscle fiber type I, IIA, IIX and IIB (Pette and Staron, 2000; Schiaffino and Reggiani, 2011; Spangenburg and Booth, 2003). These muscle fiber types are characterized based on their contraction speed (slow-twitch or fast-twitch) and preferred metabolic pathway for glycogen degradation (glycolytic or oxidative). Different muscle types vary in ATPase activity, which reflects their contractile characteristics as well as enzyme activities involved in their metabolic pathways. Type I fibers are slow-twitch, red, with oxidative metabolism; type IIA fibers are fast-twitch, red, with intermediate (oxidative glycolytic) metabolism; whereas type IIB and IIX fibers are fast-twitch, white, with glycolytic metabolism (Lefevre et al., 1999; Peter et al., 1972).

A muscle fiber is ensheathed by a fine connective tissue layer, the endomysium, which contains blood capillaries and nerves. Each muscle fiber is composed of a few dozen myofibrils and is enclosed by the muscle plasma membrane, called the sarcolemma, which is made up of a phospholipid bilayer with embedded proteins, glycoproteins and glycolipids. The myofibrils are bathed in

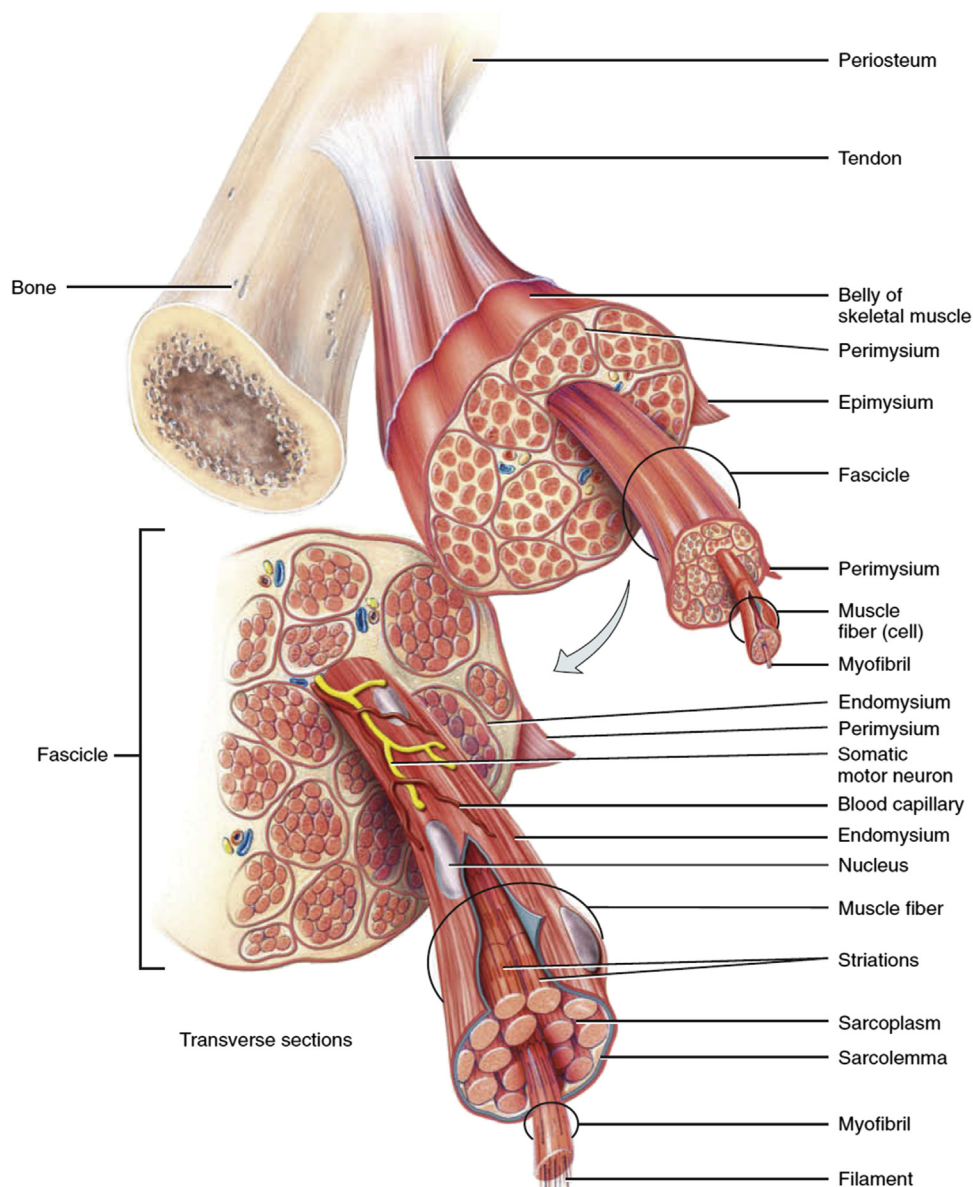


Figure 1 Structure of skeletal muscle. Adapted from Tortora, G.J., Derrickson, B.H., 2013. Principles of Anatomy and Physiology, fourteenth ed. Wiley Global Education, New York.

sarcoplasm containing several nuclei, sarcoplasmic reticulum, Golgi apparatus, mitochondria, lysosomes, glycogen granules, enzymes and other soluble constituents, that are vital for muscle function. The sarcoplasmic reticulum acts as a calcium ion reservoir for muscle contraction. Bundles of muscle fibers are organized into fascicles that are encased in another layer of connective tissue containing larger blood vessels and nerves called the perimysium. Several fascicles are assembled into a whole muscle by an outer layer of connective tissue known as the epimysium, which extends into tendons to join the muscles and bones together.

Unlike those of terrestrial animals, the muscles of fish are much shorter and are segmented into myotomes by a fine connective tissue layer called the myocommata, or myosepta, as depicted in [Fig. 2](#) ([Johnston, 2001](#); [Venugopal and Shahidi, 1996](#)). Each myotome consists of muscle fibers organized in parallel to the length axis of the fish body. Fish muscle fibers are enclosed by the sarcolemma. However, the connective tissue of the extracellular matrix in fish fuses with myocommata at the myotome-myocommata junction, in contrast to terrestrial animal muscles, that are tapered into a tendon.

Regardless of the animal species, myofibrils in muscle fibers consist of longitudinal myofilaments comprising thick and thin filaments ([Fig. 3](#)) ([Strasburg et al., 2008](#); [Tortora and Derrickson, 2013](#)). Thick filaments are made up of myosin molecules and several cytoskeletal proteins such as titin, while thin filaments are composed of actin, tropomyosin and troponin. Alternating light isotropic (I-band) and dark anisotropic (A-band) bands are seen on myofibrils under a polarized light microscope. At ultrastructural scale, each I-band is separated into two by a dark and narrow band called the Z-disk. The region between two Z-disks is known as a sarcomere, which is the repeating longitudinal contractile unit of the myofibril. A sarcomere comprises an I-band consisting purely of thin filaments, an A-band containing alternatively overlapping thin and thick filaments, an H-zone that is in the center region of the A-band, where the thin filaments are absent, and an M-line that is in the middle of the H-zone. When a muscle contracts, the Z-disks shift closer together due to shortening of the I-bands, and the length of the sarcomere is decreased ([Gault, 1992](#)).

Skeletal muscle proteins can be classified into myofibrillar (50%–60%), sarcoplasmic (30%) and stromal (10%–20%) proteins, based on their solubility at varying salt concentrations ([Strasburg et al., 2008](#)).

Myofibrillar Proteins

The myofibrillar proteins consist of contractile, structural and regulatory proteins ([Hopkins, 2014](#)). The contractile proteins are myosin and actin, which form the thin and thick filaments that control the skeletal muscle contraction and relaxation. The regulatory proteins include troponin and tropomyosin. The structural proteins comprise mainly titin, nebulin, α -actinin, β -actinin, tropomodulin, desmin, filamin, C-protein, H-protein and myomesin.

Contractile Proteins

Myosin (molecular weight of 520 kDa) is a filamentous protein that forms the thick filaments of muscle cells and is the principal protein of the A-band ([Gault, 1992](#); [Strasburg et al., 2008](#)). A myosin molecule has a quaternary structure consisting of six subunits, which include two myosin heavy chains (MHC), two essential myosin light chains (MLC1) and two regulatory myosin light chains (MLC2), with molecular weights (MW) of approximately 220 kDa, 23 kDa and 20 kDa correspondingly ([Clark et al., 2002](#); [Swartz et al., 2009](#)). Each myosin molecule can be hydrolyzed by enzymatic digestion into two portions, which are light meromyosin (LMM) and heavy meromyosin (HMM) ([Fig. 4](#)) ([Choi and Kim, 2009](#); [Pearson and Young, 1989a](#); [Strasburg et al., 2008](#)). LMM is important for the construction of thick filaments from myosin molecules while HMM is responsible for the regulation of ATPase activity and actin binding ability. HMM can be further broken down into fragment S1 and S2 where the former contains the globular myosin heads with the binding site of MgATP and actin, while the latter comprises the α -helix region which binds

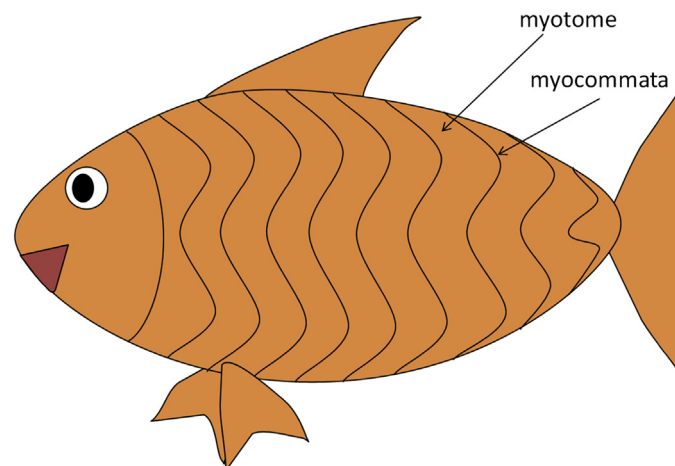


Figure 2 Schematic drawing of fish muscle displaying the orientation of myotomes and myocommata.

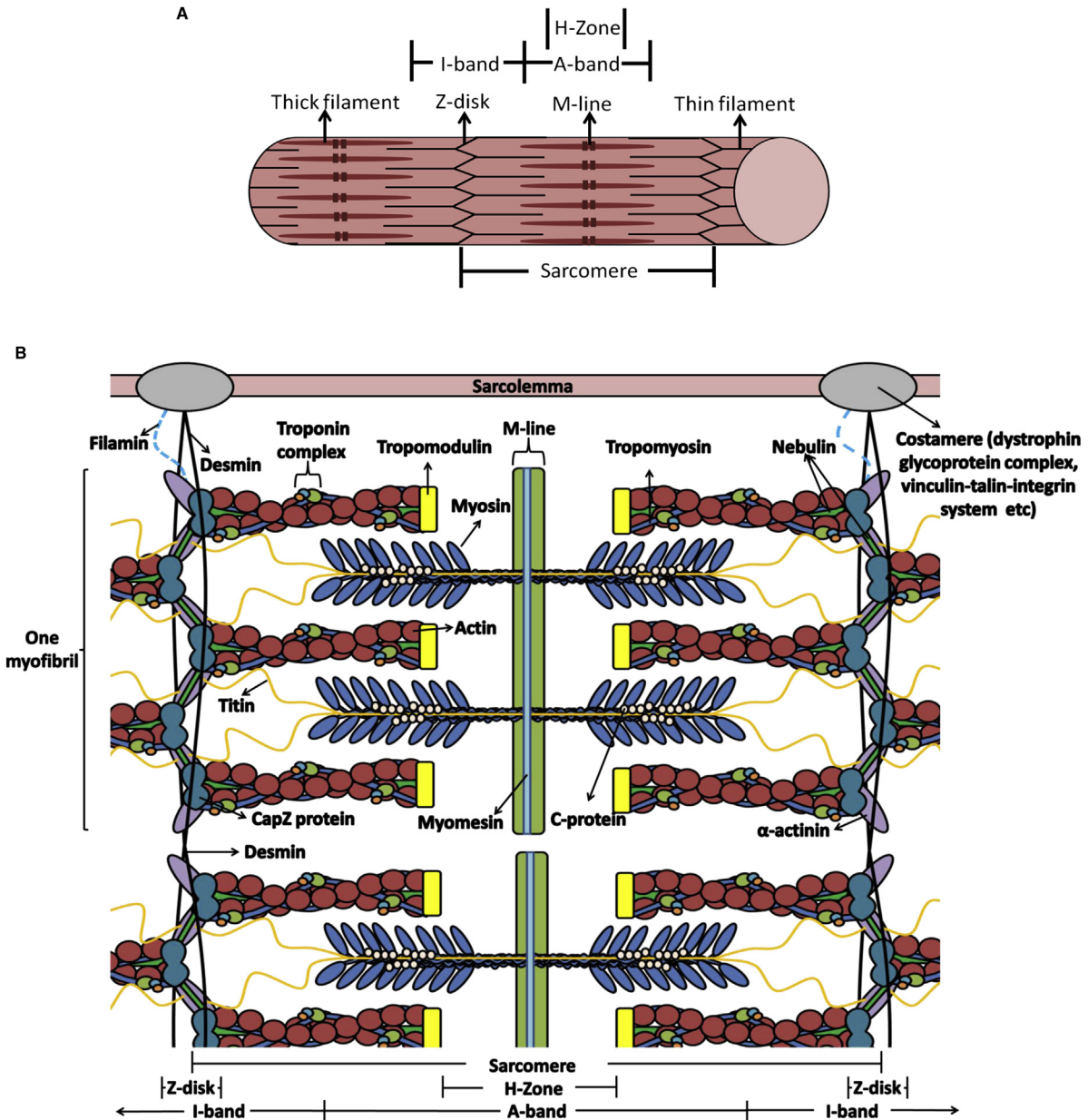


Figure 3 (A) Basic functional unit of a myofibril and (B) the arrangement of filaments within a sarcomere. Figure based on Au, Y., 2004. The muscle ultrastructure: a structural perspective of the sarcomere. *Cell. Mol. Life Sci.* CMLS 61, 3016–3033; Tortora, G.J., Derrickson, B.H., 2013. *Principles of Anatomy and Physiology*, fourteenth ed. Wiley Global Education, New York; Henderson, C.A., Gomez, C.G., Novak, S.M., Mi-Mi, L., Gregorio, C.C., 2017. Overview of the muscle cytoskeleton. *Compr. Physiol.* 7, 891–944.

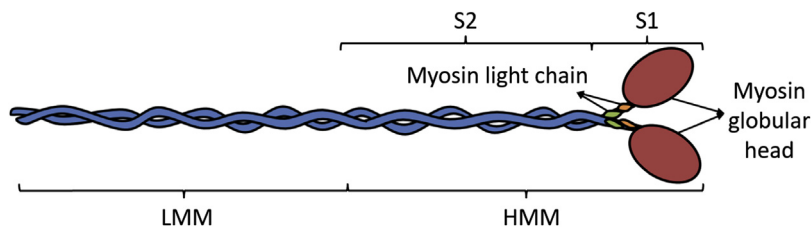


Figure 4 Schematic diagram representing a myosin molecule. Modified from Adamovic, I., Mijailovich, S.M., Karplus, M., 2008. The elastic properties of the structurally characterized myosin II S2 subdomain: a molecular dynamics and normal mode analysis. *Biophys. J.* 94, 3779–3789.

both MLC1 and MLC2. In adult mammalian skeletal muscle, there are primarily four MHC isoforms, namely MHC I, IIa, IIb, and IIx, which exist in pure slow-twitch fiber type I, fast-twitch fiber type IIa, IIb and IIx, correspondingly (Kohn et al., 2007; Pette and Staron, 2000). Hybrid fiber types containing different myosin isoforms have also been reported.

Actin (molecular weight of 42 kDa) is the building block of thin filaments and is present in two forms namely globular actin (G-actin) and filamentous actin (F-actin) (Gault, 1992; Strasburg et al., 2008). F-actin is formed by the polymerization of G-actin into double-stranded, coiled filaments. F-actin is bound to tropomyosin and troponin as shown in Fig. 5.

During muscle contraction, actin binds myosin to form actomyosin cross-bridges, which activate the myosin ATPase, leading to the pulling of thin filaments by myosin toward the M-line, resulting in shortening of the sarcomere (Lawrie, 2006).

Regulatory Proteins

Tropomyosin and troponin are two main proteins that regulate muscle contraction and relaxation (Choi and Kim, 2009; Zot and Potter, 1987). They prevent the activation of actomyosin ATPase in the absence of calcium ions by interacting with actin filaments to block the myosin binding site. Tropomyosin is a long, coiled protein (MW 65 kDa) that comprises two α -helix polypeptide subunits, called α - and β -tropomyosin. Tropomyosin molecules bind head-to-tail along the F-actin filament. Each tropomyosin molecule is attached to a troponin complex (MW 80 kDa) which is made up of troponin C (MW 18 kDa), troponin I (MW 21 kDa) and troponin T (MW 31 kDa) (Fig. 5). Troponin C acts as the calcium binding site; troponin T connects troponin complex to tropomyosin while troponin I inhibits actomyosin ATPase activity when it is bound to actin (Lehman and Craig, 2008). At high calcium ion concentration, calcium ions bind to Troponin C, which initiates a conformation change in the tropomyosin-troponin complex, dislocating troponin I, allowing the action of actomyosin ATPase for muscle contraction.

Structural Proteins

The structural proteins control the filamentous structure and integrity of myofibrils (Fig. 3) (Obinata et al., 1981). Titin, also known as connectin, with a molecular weight of 4200 kDa, serves as the backbone of thick filaments in the A-band. It also acts as a molecular spring in the I-band, which provides elasticity to the sarcomere during muscle contraction (Fig. 3) (Labeit and Kolmerer, 1995).

Nebulin (MW 800 kDa) is a structural protein that regulates the length of the thin filaments (McElhinny et al., 2003; Strasburg et al., 2008).

α -Actinin (MW 95 kDa) is the principal constituent of the Z-disk, supporting and attaching actin to the Z-disk (Obinata et al., 1981).

β -Actinin, also known as CapZ protein, is a heterodimer consisting of α - and β -subunits (MW 37 and 34 kDa respectively). It binds α -actinin in the Z-disk and prevents network formation between the actin filaments (Swartz et al., 2009).

Tropomodulin (MW 40 kDa) binds tropomyosin and actin as well as controlling the length of thin filaments by maintaining the number of G-actin monomers (Clark et al., 2002).

Both desmin (MW 55 kDa) and filamin (MW 300 kDa), play a major role in linking the myofibrils to the sarcolemma as well as stabilizing muscle structure (Capetanaki et al., 1997; Strasburg et al., 2008; Vander Ven et al., 2000).

C-protein (MW 140 kDa) and H-protein (MW 58 kDa) are myosin-binding proteins that are found in the A-band of thick filaments (Koretz et al., 1993; Xiong, 1997). These proteins are believed to contribute to the alignment and stabilization of the thick filaments.

Myomesin (MW 185 kDa) is the major protein in the M-line. It is responsible for the binding of titin and myosin and for maintaining the structure of the thick filaments.

Stromal Proteins

Stromal proteins constitute the connective tissue, which provides mechanical support and protection to the muscle in the form of tendons, epimysium, perimysium and endomysium (Fig. 1) (Gault, 1992). Connective tissue is composed mainly of collagen

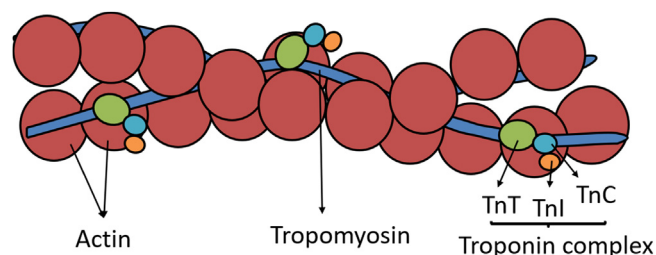


Figure 5 . Schematic diagram of a thin filament comprising actin, tropomyosin and troponin complex. TnT (troponin T), TnI (troponin I) and TnC (troponin C). Modified from Strasburg, G., Xiong, Y.L., Chiang, W., 2008. Physiology and chemistry of edible muscle tissues. In: Damodaran, S., Parkin, K.L., Fennema, O.R. (Eds), Fennema's Food Chemistry, fourth ed. CRC Press, Boca Raton FL, pp. 923–973.

(90%) along with other fibrous proteins including elastin, laminin and fibronectin, and proteoglycans (Chagnot et al., 2012; Voermans et al., 2008). Connective tissue contains different types of cells, including fibroblasts, macrophages, lymphoid cells, mast cells and eosinophils. Collagen and elastin are bound to an amorphous ground substance formed by proteoglycans and glycoproteins for the reinforcement of the connective tissue network.

Collagen

Collagen is the predominant stromal protein in skeletal muscles and is synthesized by fibroblasts (Bailey and Light, 1989; Duance et al., 1977; Gault, 1992). It is classified into four major types based on its aggregation characteristics: striated and fibrous (Types I, II, III, V and XI); non-fibrous and network forming (Type IV); microfibrillar or filamentous (Type VI), and fibril-associated collagen (Type VII) (Bailey, 1991).

Collagen consists of three polypeptide alpha chains with -Gly-X-Y- repeating units, where X is commonly proline and Y can be any amino acid (except tryptophan), but is often hydroxyproline, that coil to create a triple helix structure, forming tropocollagen (Astruc, 2014a; Bailey and Light, 1989; Gault, 1992; Strasburg et al., 2008). Tropocollagen molecules are polymerized into collagen fibers via covalent intermolecular cross-links that offer substantial tensile strength to collagen fibers. As the collagen fibers age, the divalent reducible cross-linkages interact to form mature trivalent, non-reducible, more heat-stable cross-links, which further enhances their stability and mechanical strength.

Collagen has been linked to the toughness of muscle-based food, and its content and extent of cross-linking differ among different animal species and breeds, age, muscle function, history of exercise and treatment with growth promoter (Strasburg et al., 2008). Small aquatic animals like fish generally have a lesser amount and less cross-linking of collagen compared to larger terrestrial animals that require higher weight-bearing strength. Some authors have reported an increase in meat toughness as the animal aged due to an increase in collagen cross-linking and a decrease in collagen solubility (McCormick, 1999; Purslow, 2005; Taylor, 2004). It was also found that the tender meat cut, bovine Longissimus dorsi, contains only half to two-thirds of the total collagen content and hydroxylysylpyridinoline cross-links of that found in the tougher cut, Biceps femoris. Various studies have shown improved meat quality by partial solubilization of collagen in tough meat cuts such as Semitendinosus (Christensen et al., 2011a,b; Combes et al., 2004; Sullivan and Calkins, 2010).

Elastin

Elastin is a minor constituent of connective tissue that offers elasticity to the blood vessels and ligaments in the muscles (Debelle and Alix, 1999). Elastin is an insoluble, hydrophobic, heat-stable and cross-linked protein fiber that behaves in a highly elastic manner in the presence of water. Elastin content varies among different muscle types. In Semitendinosus muscle, epimysium and perimysium are rich in coarse elastin fibers which are believed to be one of the contributors in meat toughness (Rowe, 1986). In contrast, Longissimus dorsi has limited coarse elastin fibers present in the epimysium and even less in the perimysium.

Sarcoplasmic Proteins

The sarcoplasmic proteins occur in the sarcoplasm surrounding the myofibrils (Pearson and Young, 1989b). They are involved in various metabolic functions such as protein metabolism, fatty acid oxidation, electron transportation, glycolysis, glycogenesis and glycogenolysis (Pearson and Gillett, 2012; Smith, 2000; Strasburg et al., 2008). The sarcoplasmic proteins include the heme pigments (myoglobin), the glycolytic enzymes (glyceraldehyde phosphate dehydrogenase), the mitochondrial oxidative enzymes (such as succinate dehydrogenase, cytochrome), the lysosomal enzymes (notably cathepsin), the nucleoproteins and others. Among them are the proteolytic enzymes that are involved in the post-mortem muscle tenderization process, and myoglobin that is responsible for meat color. The amount of different sarcoplasmic proteins is largely dependent on the muscle fiber type, which in turn depends on the animal species, breed, age, genetics, and muscle anatomical position and function (Strasburg et al., 2008). Sarcoplasmic proteases are vital in protein catabolism and post-mortem muscle softening. Both calpains and cathepsins are responsible for post-mortem proteolysis, with calpains and more specially calpain 1 or μ -calpain considered to be playing a major role (Ouali et al., 2006; Veiseth and Koohmaraie, 2005).

Calpains

The calpains are a family of calcium-activated, cysteine proteases that have maximum activity at neutral pH (Sentandreu et al., 2002). Calpains degrade myofibrillar proteins during protein turnover for muscle growth (Goll et al., 2008; Huang and Forsberg, 1998). There are two types of calpains responsible for post-mortem proteolysis, which are ubiquitous: μ -calpain and *m*-calpain (Table 1) (Raynaud et al., 2005; Strasburg et al., 2008). The calcium ion concentrations for the activation of μ -calpain and *m*-calpain are in the range of micromolar and millimolar respectively (Camou et al., 2007). Calpains are found and act along the Z-disk. Calpastatin is the natural inhibitor of μ -calpain and *m*-calpain.

Table 1 Characteristics of cathepsins and calpains associated with meat tenderness during ageing^{a,b}

	<i>Calpains</i>	<i>Cathepsins</i>
Nature	Cysteine proteases; calcium-dependent	Acid proteases
Occurrence	Cytosol	Lysosomes (in sarcoplasm)
Class/Isoform	<i>m</i> -Calpains, μ -calpains and calpain 3.	Main cathepsins involved in muscle ageing are cathepsins B, L, H and D
pH for optimum activity	Neutral	4–6.5 (varies with enzyme class)
Target proteins	Proteins in the Z-disk and cytoskeleton (mainly titin and desmin). Some breakdown of nebulin, troponin and tropomyosin.	Troponin T, collagen cross-links and mucopolysaccharides of connective tissue. Actin and myosin at pH < 5

^aWarriss (2010).^bKemp et al. (2010).

Cathepsins

Cathepsins are sarcoplasmic proteins that are released from the lysosomes in post-mortem muscle, which are active at an acidic pH (Table 1) (Geesink and Veiseth, 2008). Among the family of cathepsins, cysteine cathepsin B, H and L and aspartic cathepsin D are the most abundant in muscles. Cathepsins break down MHC, troponin T, troponin I, tropomyosin and collagen (Bechet et al., 2005) and collagen (Goll et al., 1983). The proteolytic activity of cysteine cathepsins and cathepsin D can be inhibited by cystatins (Geesink and Veiseth, 2008) and pepstatin (Bohley and Seglen, 1992) respectively.

Myoglobin

Myoglobin is a heme protein that acts as an oxygen carrier in muscle cells and is responsible for the color of both raw and cooked meat. The amount of myoglobin varies between different muscle types. Oxidative muscle fibers type I & IIA have higher myoglobin content than glycolytic muscle fibers type IIB and IIX (Hoekstra, 1969). Poultry has a paler appearance than beef due to a higher content of fast glycolytic fibers and consequently a lower level of myoglobin.

Four forms of myoglobin exist in the muscle, depending on the state of the heme group: deoxymyoglobin (purplish red), oxymyoglobin (cherry red), metmyoglobin (brown) and carboxymyoglobin (cherry red) (Fig. 6) (Suman and Joseph, 2013). The color of the muscle depends on the ratio of these forms of myoglobin (Baldwin, 2012). Cooking of meat results in denaturation of myoglobin and causes the oxidation of heme which induces a change in meat color.

Other Sarcoplasmic Proteins

Most of the enzymes involved in the metabolic processes in muscles are sarcoplasmic proteins (Pearson and Young, 1989b; Strasburg et al., 2008). For instance, the enzymes creatine kinase and adenylate kinase take part in the synthesis and dissociation of high energy phosphate compounds such as ATP, ADP and AMP. Caspases, metalloproteases, thrombin and plasmin have been reported to be involved in post-mortem proteolysis (Sentandreu et al., 2002). Other sarcoplasmic proteins such as hemoglobin play an essential role in the exchange of oxygen and carbon dioxide (Pearson and Young, 1989b; Tahergorabi et al., 2011).

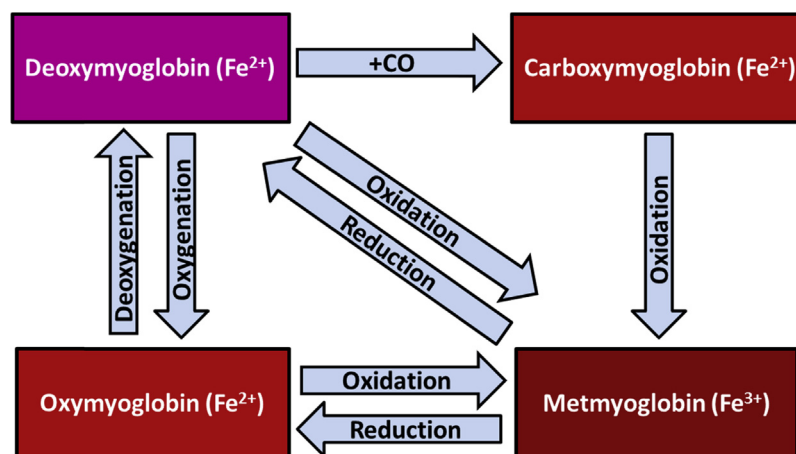


Figure 6 Interconversion of myoglobin redox forms in fresh meats. Modified from Suman, S.P., Joseph, P., 2013. Myoglobin chemistry and meat color. *Annu. Rev. Food Sci. Technol.* 4, 79–99.

From Muscle to Meat

Postmortem Biochemical Changes

Meat comes from the transformation of skeletal muscle after slaughter. After bleeding, cells survive for a short time by regenerating ATP (essential for maintaining ionic and potential membrane gradients) through anaerobic metabolic pathways. The synthesis of ATP is mostly based on the degradation of phosphocreatine and anaerobic glycolysis. When phosphocreatine is depleted, the poor performance of glycolysis does not maintain ATP at a constant value. Its cellular concentration gradually decreases. As the ATP level decreases and glycogen is degraded, protons and lactate molecules accumulate in muscle cells resulting in decreased muscle pH (Bendall, 1973; Greaser, 1986; Monin, 1988). When the ATP level falls by half the resting muscle content, the actin and myosin molecules bind to form an actomyosin complex. The relative sliding of the filaments becomes impossible and the whole of the myofibrillar apparatus is transformed into a rigid system called rigor. Subsequently, the muscle stiffness gradually fades, but not the inextensibility. This 'resolution' of rigor results from the lysis of the proteins constituting the myofibrillar structure during the so-called maturation period.

When the glycogen is depleted and/or when the enzyme co-factor AMP disappears, the pH stabilizes at a value called the ultimate pH (usually close to 5.7). The acidification of the muscle reduces the net charge of myofibrillar proteins and is close to their isoelectric point (around 5). The slightest repulsion of the proteins comprising the myofilaments leads to a tightening of the latter and a lateral contraction of the myofibrils (Pearce et al., 2011), which expels part of the intramyofibrillar water into the sarcoplasm that then migrates into the extracellular space. In addition to the decrease in pH, the osmotic pressure of the muscle evolves after slaughter. Its value doubles during the onset of rigor mortis (from 270–300 mosmoles to 500–600 mosmoles) (Ouali, 1990a, 1990b, 1992). This increase is directly related to the decrease in pH (Ouali, 1992). The resulting increase in ionic strength, close to 0.30, is sufficient to damage myofibrillar proteins and to promote the action of muscle proteases.

Fast Postmortem Metabolism Effects on Muscle Proteins and Meat Quality

Pronounced stress just prior to slaughter, coupled with the effects of stunning (especially electrical stunning), accelerates the muscle metabolism that continues after the animal dies and leads to a rapid drop in pH while the muscle temperature is still high (Charpentier and Goutefongea, 1963). The low pH/high temperature combination leads to the denaturation of the sarcoplasmic proteins (Bendall and Wismerpedersen, 1962; Charpentier, 1969; Charpentier and Goutefongea, 1963; Fischer et al., 1979; Lawrie et al., 1963; Scopes, 1964; Scopes and Lawrie, 1963) and the myofibrillar proteins, with myosin being the most sensitive (Bendall, 1973; Offer and Knight, 1988; Penny, 1967; Stabursvik et al., 1984). The denaturation of muscle proteins leads to reduction in their water holding capacity. The myofilament lattice retracts, expelling water to the extracellular space (Bendall and Swatland, 1988; Fialik, 1983; Guignot et al., 1993), increasing the ability of meat to reflect light (Macdougall, 1970, 1982). These meats are characterized by strong exudations, a lighter color and a soft texture, hence their name PSE (Pale Soft Exudative) (Adzitey and Nurul, 2011). This phenomenon was first observed in meat from pigs (Bendall and Wismerpedersen, 1962; Briskey, 1964; Hamm, 1960) and then in meat from poultry (Barbut, 2009; Owens et al., 2000; Swatland, 2008) and more recently in meat from sheep (Kim et al., 2014a,b; Warner et al., 2014) and cattle (Aalhus et al., 1998; Guignot et al., 1993; Warner et al., 2014).

Protein denaturation is also observed when the PSE trait is induced by maintaining a muscle at 37 °C for a few hours post slaughter (Penny, 1967, 1977).

Postmortem Proteolysis

Proteolytic Systems

Conditions after slaughter and during carcass chilling favor degradation of intracellular muscle proteins by proteolytic systems. Calpains seem to represent the major system involved in tenderizing meat (Goll et al., 2003; Koohmaraie, 1994; Koohmaraie and Geesink, 2006; Raynaud et al., 2005; Taylor et al., 1995a). It has been concluded that post-mortem muscle tenderization is due mainly to the action of μ -calpain and to a lesser extent the action of m -calpain.

Cathepsins and proteasome seem less involved (Sentandreu et al., 2002; Koohmaraie and Geesink, 2006; Koohmaraie, 1994; Taylor et al., 1995b). Other proteolytic systems such as caspases, metalloproteases, thrombin or plasmin could also be involved in the postmortem degradation of muscle tissue (Sentandreu et al., 2002; Ouali et al., 2013).

It has been reported that low pH, elevated temperature and electrical stimulation can all accelerate the release of cathepsins from lysosomes and eventually facilitate muscle tenderization.

Postmortem Muscle Protein Degradation

The consequences of postmortem proteolysis on the ultrastructure of muscle are well understood (Davey and Dickson, 1970; Davey and Gilbert, 1969; Koohmaraie, 1994; Koohmaraie and Geesink, 2006; Ouali, 1990b; Taylor et al., 1995a). Surprisingly, myosin and actin are little affected by post mortem proteolysis, and it is rather the degradation of cytoskeleton proteins that causes a modification of myofibril ultrastructure and tenderness of the meat. Overall, post mortem proteolysis leads to a transverse rupture of the myofibrils at the connecting junction of the I-band to the Z-disks. This zone is essentially composed of actin, titin, and neb-ulin. Their postmortem degradation is likely to be responsible for myofibril breakdown (Koohmaraie and Geesink, 2006; Robson et al., 1997; Taylor et al., 1995a).

The cytoskeleton is also disorganized by the degradation of the desmin and the filamin, which bind the Z-disks of myofibrils to each other and also to the sarcolemma from peripheral myofibrils (Huff Lonergan et al., 2010; Taylor et al., 1995b; Koohmaraie and Geesink, 2006). The degradation of the constitutive proteins of the costamere (dystrophin-vinculin-talin-integrin) which constitutes the anchor point of desmin on the sarcolemma (Taylor et al., 1995a; Koohmaraie and Geesink, 2006) is also suspected to change the muscle fiber ultrastructure. The intermediate filaments which bind the myofibrils at the level of the M-lines are also partially hydrolyzed.

Deterioration of these major cytoskeletal proteins causes misalignment of the myofibrils relative to each other, detachment of the sarcolemma and rupture of the myofibrils along the Z-disks. Nevertheless, it appears that the degradation of desmin and titin are the most important of the mechanisms underlying development of tenderness during meat maturation (Koohmaraie and Geesink, 2006). Troponin T, incorporated into the thin filaments, is also degraded during the meat maturation phase, and its disappearance is related to the appearance of a 30 kDa peptide and the tenderness of the meat (Huff Lonergan et al., 2010). This protein is involved in the mechanism of muscle contraction, but it is also suspected to stabilize interactions between myofilaments. Its degradation may favor the disorganization of myofibrils.

Structural changes in intramuscular connective tissue become significant only after 10 days of maturation (Nishimura et al., 1995). In general, maturation increases the solubility of collagen (Purslow, 2005), causing an improvement in the texture of raw meat. However, the effects of postmortem changes in connective tissue on the texture of cooked meat are controversial (Nishimura, 2010; Purslow, 2005).

Postmortem Protein Oxidation

An increase in myofibrillar protein oxidation is observed during ageing (Martinaud et al., 1997; Rowe et al., 2004a,b), that results in carbonyl derivative formation (Levine et al., 1994; Martinaud et al., 1997) and protein disulfide cross-links (Martinaud et al., 1997; Stadtman, 1990). In general, both of these changes reduce the functionality of proteins (Xiong and Decker, 1995). Calpains are particularly susceptible to inactivation by oxidation (Lametsch et al., 2008). Therefore, oxidizing conditions in postmortem muscle decrease the calpain activity and are likely to affect the tenderization of meat. Myoglobin also undergoes oxidation during the refrigeration of carcasses and meat, with significant effects on the color of the meat (Renerre, 2000).

Effects of Processing on Meat Proteins

Meat processing affects the physical and chemical properties of the product by the action of physical forces, heat or the addition of salts, additives or processing aids (Lewis, 1992). For instance, meat tenderization through electrical stimulation, ultrasonic waves, blade tenderization and pressure treatment have been reported to modify the muscle structure and protein profile (Hopkins, 2014). These processes decrease the overlapping of actin and myosin, cause physical damage to the sarcomere and connective tissues or improve proteolysis rates through the activation of calpains by calcium ions released after membrane disruption.

Electrical Stimulation of Carcasses

Electrical stimulation of carcasses has no detectable influence on the degradation of desmin and troponin T (Ho et al., 1997), but could slightly accelerate the degradation of the cytoskeletal proteins titin and nebulin in postmortem muscle (Ho et al., 1996).

Pulsed Electric Field

There has been recent interest in meat tenderization applications of PEF. PEF causes the electroporation of muscle cell membranes, which potentially facilitates the meat ageing process by releasing the calcium ions from sarcoplasmic reticulum, which triggers the calcium-activated proteases and/or speeds up pre-rigor glycolysis, and also by releasing the cathepsins from the lysosomes (Warner et al., 2017). Compared to untreated muscles, PEF-treated cold- and hot-boned beef Longissimus lumborum muscles had increased degradation of troponin T and desmin (Suwandy et al., 2015a, b).

Exogenous Enzyme Technology

Exogenous proteases have been applied in meat tenderization for many years (Payne, 2009; Sullivan and Calkins, 2010). Most plant-based proteases can hydrolyze myofibrillar proteins efficiently (Bekhit et al., 2014; Kim and Taub, 1991). For the stromal proteins, under heating conditions, both papain and ficin were found to be effective in hydrolyzing elastin and collagen whilst bromelain degraded only collagen (more actively than papain and ficin) (El-Gharbawi and Whitaker, 1963; Miyada and Tappel, 1956; Payne, 2009). These enzymes have wide substrate specificity and can break down many of the peptide bonds present in meat proteins (Bekhit et al., 2014; Huff-Lonergan, 2014). Excessive proteolytic action can cause over-tenderization, leading to mushy meat texture (Ashie et al., 2002; McKeith et al., 1994; Weir et al., 1958).

Shockwave Hydrodynamic Processing

Hydrodynamic processing generates a shockwave up to 1 GPa which travels through water in fractions of a millisecond (Bolumar et al., 2014; Hopkins, 2014). A shockwave process can be set up by subjecting the sealed meat in a water-filled container to electrically-generated shockwaves (Hopkins, 2014). Shockwave treatment caused increased intramyofibrillar and endomysium spaces between muscle fibers (Zuckerman and Solomon, 1998; Bolumar et al., 2014) myofibrillar fragmentation alongside the Z-disk (Zuckerman and Solomon, 1998), destruction of collagen fibrils of the endomysium (Zuckerman et al., 2013) and degradation of C-protein, which is responsible for the integrity of the thick filaments (Spanier and Fahrenholz, 2005a). The physical disruption of muscles may lead to the release of endogenous proteases such as calpains and cathepsins, or their activators such as calcium ions, thus enhancing the tenderization effect. This was seen in a study where troponin T of shockwave-treated samples was degraded more than in an untreated control after ageing (Bowker et al., 2008a,b). Conversely, no enhancement in the activity of endogenous proteolytic enzymes (cathepsins and peptidases) was detected after the shockwave process, suggesting that the tenderization effect is mainly due to physical disruption. The effect of shockwave processing on the protein profile is debatable. It has been reported that there was no distinct difference in the myofibrillar, sarcoplasmic and stromal protein profiles between control and shockwave-treated samples (Bolumar et al., 2014; Schilling et al., 2002). However, it has also been reported that shockwave-treated muscle had higher myofibrillar solubility (Bowker et al., 2008a,b; Spanier and Fahrenholz, 2005a, 2005b) and increased collagen solubility.

High Pressure Processing

HPP is one of the technologies applied in the meat industry to improve shelf life, safety, and quality characteristics (texture and color) of foods (Bajovic et al., 2012). HPP subjects the meat to high pressure, usually ranging from 100 MPa to 800 MPa, via a surrounding liquid and is sometimes accompanied by heat treatment at 60 °C (Hopkins, 2014; Troy et al., 2016). HPP causes the destruction of microorganism, leads to protein denaturation and inactivation of endogenous enzymes (Sikes and Warner, 2016; Torres and Velazquez, 2005).

HPP alters protein secondary, tertiary and quaternary structures in the muscles by disrupting their conformations and molecular interactions (Campus, 2010; Sikes and Warner, 2016; Strasburg et al., 2008). For example, at pressures above 100 MPa protein tertiary structure unfolds and protein aggregation occurs (Cheftel and Culioli, 1997). However, covalent bonds are mostly unaffected. High pressure has been reported to denature myofibrillar proteins (Anderson and Parrish, 1989), cause depolymerization of actin (Ikkai and Ooi, 1966), and release cathepsins into the cytoplasm by degrading muscle membranes (Homma et al., 1994; Jung et al., 2000). For example, at pressures between 100 MPa and 300 MPa, myosin and actin were denatured (Angsupanich and Ledward, 1998; Sikes et al., 2010). The effect of high pressure on muscle structure depends on the applied pressure, processing temperature and time, and the muscle type (pre- or post-rigor) (Cheftel and Culioli, 1997). For instance, increases in intermyofibrillar spaces and myofibril shrinkage were observed in Atlantic salmon meat with increasing applied pressure (from 400 to 900 MPa) and time (Gudbjornsdottir et al., 2010).

The tenderness of pre-rigor meat can be improved by HPP (Sikes and Warner, 2016). Accelerated glycolysis of pre-rigor meat may occur when high pressure is applied, resulting in shear force reduction of myofibrillar-based food (Elgasim and Kennick, 1982; Hopkins, 2014; Kennick et al., 1980). The effect of high pressure on the texture of post-rigor meat depends on the processing temperature (Sikes and Warner, 2016). In most studies, high pressure treatment at 30 °C or below did not have a tenderization effect in post-rigor meat. The tenderness of post-rigor sheep muscle (Macfarlane et al., 1981; Macfarlane and Morton, 1978) and chicken breast (Kruk et al., 2011; Zamri et al., 2006) remained unchanged after high pressure, low temperature processing. In contrast, high pressure processing combined with heat treatment was effective in improving meat tenderness (Bouton et al., 1977; Rusman et al., 2007; Sikes et al., 2010).

High pressure processing affects the color of meat (Cheftel and Culioli, 1997). At pressures higher than 400 MPa, the oxidation of heme iron and denaturation of myoglobin in raw meat occur and cause an increase in lightness and decrease in the redness of meat. This increase in lightness was also observed in bluefish *Pomatomus saltatrix* as the applied pressure increased from 100 to 300 MPa (Ashie and Simpson, 1996).

Effects of Cooking on Meat Proteins

Sous Vide Cooking

Sous vide is a culinary technique developed in fine dining restaurants, where food is sealed under vacuum and cooked at a controlled temperature, usually in a water bath (Baldwin, 2012; Schellekens, 1996). Cooking in this way results in uniform and efficient heat transfer from the water to the food, overcoming the drawback of uneven heating encountered in conventional cooking processes, while retaining water, soluble components and volatiles in the food and avoiding oxidation. During the cooking process, heat denatures proteins, leading to physical changes in the meat. The effect of cooking on muscle texture largely depends on the cooking time and temperature as well as the heating rate.

The myofibrillar proteins (mostly myosin and actin) shrink during heating, causing the contraction and shrinkage of the muscle fibers (Baldwin, 2012; Christensen et al., 2011a,b). When meat is subjected to heat from 40 °C to 60 °C, muscle fibers shrink

transversely which causes a widening of the gap between them (Palka and Daun, 1999; Tornberg, 2005). As the temperature further increases, muscle fibers shrink longitudinally, and the water held between thick and thin filaments is expelled. The sarcoplasmic proteins start to aggregate and gel when heated at 40 °C to 60 °C (Baldwin, 2012). At sous vide cooking temperatures, most of the endogenous proteases remain active and contribute to enhancing the tenderness of the meat (Laakkonen et al., 1970a,b). At 55 °C, cathepsins B and L were found to be active during up to 24 hours of cooking, whereas both μ - and m -calpains were inactivated within 10 minutes (Ertbjerg et al., 2012). Connective tissues, such as collagen, denature at around 60 °C (Baldwin, 2012). This leads to the formation of water-soluble random-coiled gelatin, decreasing the adhesion between muscle fibers. Collagen in beef perimysium was observed to melt when cooked at 50 to 60 °C, while elastin remained heat stable at 100 °C (Taylor, 2004). DSC analysis showed that prolonged heating at 53 °C (for 19.5 hours) resulted in diminishing of myosin and collagen peaks of meat from bull Semitendinosus muscle in the thermograph, suggesting potentially improved meat tenderness (Christensen et al., 2013).

The temperature of sous vide cooking should be set where it is high enough for collagen solubilization and microbiological inactivation, yet has minimum myofibrillar shrinkage to achieve optimum tenderization action (Ruiz et al., 2013). When a tough meat cut is cooked at a temperature between 55 °C and 60 °C for 24 hours, the tenderness is improved as the collagen is converted to gelatin and the myofibrillar proteins are hydrolyzed by the endogenous proteolytic enzymes (Bouton and Harris, 1981; Tornberg, 2005). A decrease in shear force was observed with an increase in cooking temperature from 50 °C to 65 °C, but the shear force increased when the temperature exceeded 65 °C and up to 80 °C (Baldwin, 2012). It has been suggested that the reduction in shear force is due to the gel formed from the sarcoplasmic protein, which filled the channels between fiber bundles, resulting in a decrease in elastic modulus that requires lesser tensile stress to fracture the meat (Tornberg, 2005).

Other Cooking

Cooking of meat other than sous vide does not have the same precise control of temperature and generally exposes at least part of the meat to much higher temperatures than encountered in sous vide cooking, although other parts may be hardly heated at all (for example in the center of a “blue” steak). Chefs and consumers often judge the “doneness” of meat by its color, and this is mostly due to the degree of heme oxidation of myoglobin. During the cooking process, deoxymyoglobin, metmyoglobin and oxymyoglobin undergo oxygenation, oxidation and reduction reactions, and the ratio between them determines the color of final product (Liu and Chen, 2001). The color of the cooked meat also depends on the rate in achieving the designated core temperature and the duration held at that temperature. Cooked meat tends to be redder when the rate of heating is faster and paler when it is held at specific temperatures longer (Baldwin, 2012).

Important temperature effects are summarized in Table 2 (McGee, 2004).

Nutritional Value and Digestion

Muscle-based food is an excellent source of protein nutrition. The compositions of lean tissue in muscle-based foods are consolidated in Table 3 (Foegeding et al., 1996; Strasburg et al., 2008; Williams, 2007). About 17% to 23% of lean muscle is made up of protein that contains all the dietary essential amino acids. Consuming meat together with plant-based foods, such as cereals and legumes, can compensate for the lower levels of lysine (cereals), and sulfur amino acids (legumes) in the diet (Bodwell and

Table 2 Effects of heat on meat proteins and qualities

Temperature (°C)	Meat qualities	Proteolytic enzymes	Fibrillar proteins	Collagen	Protein-bound water	Myoglobin status
40	Soft Smooth Translucent	Active	Beginning to unfold		Begins to escape	
50	Firming Becoming opaque	Very active	Myosin begins to denature			
55	More fibrous, Juicy when cut	Denature and lose activity	Myosin coagulated			
60	Shrinking Losing resilience Losing juice Pink		Other proteins denature	Collagen sheaths shrink, squeeze cells	Flows from cells under collagen pressure	Begins to denature (“medium” doneness)
70	Shrinking Stiff Little juice Gray-brown			Begins to denature and dissolve	Flow ceases	
80			Actin denatures Cell contents compacted			

Adapted from McGee, H., 2004. On Food and Cooking – The Science and Lore of the Kitchen, second ed. Scribner, New York.

Table 3 Composition of lean muscle tissues

Species	Proximate composition (%)			
	Water	Protein	Lipid	Ash
Beef ^{a,b,c}	70–73	20–23	3–8	1
Pork ^{b,c}	68–70	19–20	9–11	1.4
Chicken ^{b,c}	73.7	20–23	4.7	1
Lamb ^{a,b,c}	73	20–22	5–6	1.6
Cod (lean fish) ^{b,c}	81.2	17.6	0.3	1.2
Salmon (fatty fish) ^{b,c}	64	20–22	13–15	1.3

^aWilliams (2007).^bStrasburg et al. (2008).^cFoegeding et al. (1996).

Anderson, 1986). Protein from meat is highly digestible and bioavailable compared to plant protein (Černá, 2011), except after severe processing which can modify amino acid side chains (Soladoye et al., 2015). Muscle-based foods, especially red meats, are a rich source of highly bioavailable iron, due to their myoglobin content.

Protein digestibility, which is largely dependent on the source and processing history of food, is considered to be an important factor determining the amount of undigested dietary protein reaching the large intestine (Yao et al., 2016). It has been reported that increasing cooking temperature and time can decrease meat protein digestibility (Astruc, 2014b; Li et al., 2017; Kaur et al., 2014). High pressure-treated meat was found to be more digestible than the untreated control sample, both in vitro (Kaur et al., 2016) and in vivo (Elgasim and Kennick, 1980). Long-time salting and drying rendered the meat protein to be less digestible by pepsin in the stomach (Li et al., 2017).

Sustainability of Meat as a Source of Protein

Real Cost of Meat, Water and Carbon Footprints

There has been much comment on the environmental cost of producing meat. A commonly quoted “fact” is that it takes 10 kg of plant protein to produce 1 kg of meat protein. This is a worst-case figure and largely incorrect because:

- It assumes the animal is eating food that could otherwise have been used by humans
- It ignores other contributions made by the animal – often a lifetime of milk or egg production or of providing motive power, as well as the other products from the carcass – offal, hides and gelatin, for example
- Animals are often farmed on land that is too steep or inaccessible to use for cropping, thus any opportunity cost for land use is, in the case of these animals, illusory
- In developing countries (and increasingly in developed countries) animals are fed on waste food that is no longer fit for human consumption.

Production of meat requires a lot of water. Meat animals are often farmed in regions where there is an excess of water available through plentiful rainfall – where no opportunity cost for water exists. Water management will be an increasingly important consideration for all kinds of farming. Farming for animal products, including meat, is appropriate under certain conditions.

The carbon footprint of meat production arises mostly because of production of methane by the animals during their lifetime. Methanogenesis occurs mostly in the rumen from the metabolism of methanogenic bacteria in the rumen population. It is generally undesirable, not only because it produces atmospheric methane, but because it results in lost energy and carbon that could otherwise benefit the animal. Research is underway globally to address this issue and there is hope that in the future ruminants will be able to be largely methanogen-free.

Importance of the Ruminant

It is a simple fact that almost all food must originate from plant material, because photosynthesis is the ultimate source of almost all organic material. The route by which this material can become food for humans depends on the palatability and digestibility of the plant material. Ruminant animals, by virtue of their completely different digestive systems, can consume plant material such as grasses and the leaves of bushes and trees and convert it into forms that can be valuable nutrition for humans (milk and meat). Without the intervention of the animal, these food sources would be lost to us.

The Future of Meat

The future of meat and the prospects of meeting future demand for meat and other animal-based sources of protein have been addressed by several groups, and potential solutions include more production through intensification and increasing grasslands

(at an environmental cost that may be unacceptable), recycling food waste to feed animals and using alternative sources of animal fodder, such as insects. Laboratory-grown meat has also made an appearance, albeit only as a prototype, but may be expected to have an influence in the future, as will plant-origin meat substitutes, but meat will continue to occupy an important place in the planet's food ecosystem.

References

- Aalhus, J.L., Best, D.R., Murray, A.C., Jones, S.D.M., 1998. A comparison of the quality characteristics of pale, soft and exudative beef and pork. *J. Muscle Foods* 9, 267–280.
- Adamovic, I., Mijailovich, S.M., Karplus, M., 2008. The elastic properties of the structurally characterized myosin II S2 subdomain: a molecular dynamics and normal mode analysis. *Biophys. J.* 94, 3779–3789.
- Adzitey, F., Nurul, H., 2011. Pale soft exudative (PSE) and dark firm dry (DFD) meats: causes and measures to reduce these incidences - a mini review. *Int. Food Res. J.* 18, 11–20.
- Anderson, T., Parrish, F., 1989. Postmortem degradation of titin and nebulin of beef steaks varying in tenderness. *J. Food Sci.* 54, 748–749.
- Angsupanich, K., Ledward, D.A., 1998. High pressure treatment effects on cod (*Gadus morhua*) muscle. *Food Chem.* 63, 39–50.
- Ashie, I.N.A., Simpson, B.K., 1996. Application of high hydrostatic pressure to control enzyme related fresh seafood texture deterioration. *Food Res. Int.* 29, 569–575.
- Ashie, I.N.A., Sorensen, T.L., Nielsen, P.M., 2002. Effects of papain and a microbial enzyme on meat proteins and beef tenderness. *J. Food Sci.* 67, 2138–2142.
- Astruc, T., 2014a. Connective tissue: structure, function, and influence on meat quality. In: Devine, C., Dikeman, M. (Eds.), *Encyclopedia of Meat Sciences*, second ed., vol. 1. Academic Press, London, pp. 321–328.
- Astruc, T., 2014b. Muscle structure and digestive enzyme bioaccessibility to intracellular compartments. In: Boland, M., Golding, M., Singh, H. (Eds.), *Food Structures, Digestion and Health*, first ed. Academic Press, London, pp. 193–222.
- Au, Y., 2004. The muscle ultrastructure: a structural perspective of the sarcomere. *Cell. Mol. Life Sci. CMLS* 61, 3016–3033.
- Bailey, A.J., 1991. The chemistry of natural enzyme-induced cross-links of proteins. *Amino Acids* 1, 293–306.
- Bailey, A.J., Light, N.D., 1989. *Connective Tissue in Meat and Meat Products*. Elsevier Applied Science, London.
- Bajovic, B., Bolumar, T., Heinz, V., 2012. Quality considerations with high pressure processing of fresh and value added meat products. *Meat Sci.* 92, 280–289.
- Barbut, S., 2009. Pale, soft, and exudative poultry meat - reviewing ways to manage at the processing plant. *Poult. Sci.* 88, 1506–1512.
- Baldwin, D.E., 2012. Sous vide cooking: a review. *Int. J. Gastron. Food Sci.* 1, 15–30.
- Bechet, D., Tassa, A., Taillandier, D., Combaret, L., Attaix, D., 2005. Lysosomal proteolysis in skeletal muscle. *Int. J. Biochem. Cell Biol.* 37, 2098–2114.
- Bekhit, A.A., Hopkins, D.L., Geesink, G., Bekhit, A.A., Franks, P., 2014. Exogenous proteases for meat tenderization. *Crit. Rev. Food Sci. Nutr.* 54, 1012–1031.
- Bendall, J.R., 1973. Post mortem changes in muscle. In: Bourne, G.H. (Ed.), *Structure and Function of Muscle*. Academic Press, New York, pp. 243–309.
- Bendall, J.R., Swatland, H.J., 1988. A review of the relationships of pH with physical aspects of pork quality. *Meat Sci.* 24, 85–126.
- Bendall, J.R., Wismerpedersen, J., 1962. Some properties of fibrillar proteins of normal and watery pork muscle. *J. Food Sci.* 27, 144–159.
- Bodwell, C.E., Anderson, B., 1986. Nutritional composition and value of meat and meat products. In: Bechtel, P.J. (Ed.), *Muscle as Food*. Academic Press, London, pp. 321–369.
- Bohley, P., Seglen, P.O., 1992. Proteases and proteolysis in the lysosome. *Experientia* 48, 151–157.
- Bolumar, T., Bindrich, U., Toepfl, S., Toldra, F., Heinz, V., 2014. Effect of electrohydraulic shockwave treatment on tenderness, muscle cathepsin and peptidase activities and microstructure of beef loin steaks from Holstein young bulls. *Meat Sci.* 98, 759–765.
- Bouton, P.E., Harris, P.V., 1981. Changes in the tenderness of meat cooked at 50–65°C. *J. Food Sci.* 46, 475–478.
- Bouton, P.E., Harris, P.V., Macfarlane, J.J., O'Shea, J.M., 1977. Effect of pressure treatments on the mechanical properties of pre- and post-rigor meat. *Meat Sci.* 1, 307–318.
- Bowker, B.C., Fahrenholz, T.M., Paroczay, E.W., Eastridge, J.S., Solomon, M.B., 2008a. Effect of hydrodynamic pressure processing and aging on the tenderness and myofibrillar proteins of beef strip loins. *J. Muscle Foods* 19, 74–97.
- Bowker, B.C., Fahrenholz, T.M., Paroczay, E.W., Solomon, M.B., 2008b. Effect of hydrodynamic pressure processing and aging on sarcoplasmic proteins of beef strip loins. *J. Muscle Foods* 19, 175–193.
- Briskey, E.J., 1964. Etiological status and associated studies of pale, soft, exudative porcine musculature. *Adv. Food Res.* 13, 89–178.
- Camou, J.P., Marchello, J.A., Thompson, V.F., Mares, S.W., Goll, D.E., 2007. Effect of postmortem storage on activity of μ - and m-calpain in five bovine muscles. *J. Anim. Sci.* 85, 2670–2681.
- Campus, M., 2010. High pressure processing of meat, meat products and seafood. *Food Eng. Rev.* 2, 256–273.
- Capetanaki, Y., Milner, D.J., Weitzer, G., 1997. Desmin in muscle formation and maintenance: knockouts and consequences. *Cell Struct. Funct.* 22, 103–116.
- Černá, M., 2011. Chapter 24-Seaweed proteins and amino acids as nutraceuticals. In: Kim, S.-K. (Ed.), *Advances in Food and Nutrition Research*, vol. 64. Academic Press, London, pp. 297–312.
- Chagnot, C., Listrat, A., Astruc, T., Desvaux, M., 2012. Bacterial adhesion to animal tissues: protein determinants for recognition of extracellular matrix components. *Cell. Microbiol.* 14, 1687–1696.
- Charpentier, J., 1969. Influence de la température et du pH sur quelques caractéristiques physico-chimiques des protéines sarcoplasmiques du muscle de porc: conséquences technologiques. *Ann. Biol. Anim. Biochim. Biophys.* 9, 101–110.
- Charpentier, J., Goutefongea, R., 1963. Comportement électrophorétique des protéines sarcoplasmiques du muscle de porc normal et exsudatif. *Ann. de Biol. Animale de Biochimie de Biophysique* 3, 381–389.
- Cheftel, J.C., Culioli, J., 1997. Effects of high pressure on meat: a review. *Meat Sci.* 46, 211–236.
- Choi, Y.M., Kim, B.C., 2009. Muscle fiber characteristics, myofibrillar protein isoforms, and meat quality. *Livest. Sci.* 122, 105–118.
- Christensen, L., Bertram, H.C., Aaslyng, M.D., Christensen, M., 2011a. Protein denaturation and water-protein interactions as affected by low temperature long time treatment of porcine *Longissimus Dorsi*. *Meat Sci.* 88, 718–722.
- Christensen, L., Ertbjerg, P., Aaslyng, M.D., Christensen, M., 2011b. Effect of prolonged heat treatment from 48°C to 63°C on toughness, cooking loss and color of pork. *Meat Sci.* 88, 280–285.
- Christensen, L., Ertbjerg, P., Løje, H., Risbo, J., van den Berg, F.W.J., Christensen, M., 2013. Relationship between meat toughness and properties of connective tissue from cows and young bulls heat treated at low temperatures for prolonged times. *Meat Sci.* 93 (4), 787–795. <https://doi.org/10.1016/j.meatsci.2012.12.001>.
- Clark, K.A., McElhinny, A.S., Beckerle, M.C., Gregorio, C.C., 2002. Striated muscle cytoarchitecture: an intricate web of form and function. *Annu. Rev. Cell Dev. Biol.* 18, 637–706.
- Combes, S., Lepetit, J., Darche, B., Lebas, F., 2004. Effect of cooking temperature and cooking time on Warner–Bratzler tenderness measurement and collagen content in rabbit meat. *Meat Sci.* 66, 91–96.
- Davey, C.L., Dickson, M.R., 1970. Studies in meat tenderness 8. ultra-structural changes in meat during aging. *J. Food Sci.* 35, 56–60.
- Davey, C.L., Gilbert, K.V., 1969. Studies in meat tenderness 7. Changes in fine structure of meat during aging. *J. Food Sci.* 34, 69–74.
- Debelle, L., Alix, A.J.P., 1999. The structures of elastins and their function. *Biochimie* 81, 981–994.
- Duance, V.C., Restall, D.J., Beard, H., Bourne, F.J., Bailey, A.J., 1977. The location of three collagen types in skeletal muscle. *FEBS Lett.* 79, 248–252.
- El-Gharbawi, M., Whitaker, J.R., 1963. Factors affecting enzymatic solubilization of beef proteins. *J. Food Sci.* 28, 168–172.
- Elgasim, E., Kennick, W., 1982. Effect of high hydrostatic pressure on meat microstructure. *Food Microstruct.* 1, 75–82.

- Elgasim, E.A., Kennick, W.H., 1980. Effect of pressurization of pre-rigor beef muscles on protein quality. *J. Food Sci.* 45, 1122–1124.
- Ertbjerg, P., Christiansen, L.S., Pedersen, A.B., Kristensen, L., 2012. The effect of temperature and time on activity of calpain and lysosomal enzymes and degradation of desmin in porcine longissimus muscle. In: Proceedings 58th International Congress of Meat Science & Technology Montreal, Canada, p. 358.
- Fairlie, S., 2011. Meat: A Benign Extravagance. Chelsea Green Publishers, White River Junction, VT.
- Fialik, E., 1983. The histological differentiation of PSE-muscle by means of extracellular region and fiber diameter. *Wien. Tierärztliche Monatsschrift* 70, 403–407.
- Fischer, C., Hamm, R., Honikel, K.O., 1979. Changes in solubility and enzymic activity of muscle glycogen phosphorylase in PSE-muscles. *Meat Sci.* 3, 11–19.
- Foegeding, E., Lanier, T., Hultin, H., 1996. Characteristics of edible muscle tissues. *Food Chem.* 3, 879–942.
- Gault, N., 1992. Structural aspects of raw meat. Chemistry of muscle-based foods. Special Publ. Royal Soc. Chem. Lond. 106, 79–105.
- Geesink, G., Veiseth, E., 2008. Muscle Enzymes. Handbook of Muscle Foods Analysis. CRC Press, Boca Raton FL, pp. 91–110.
- Goll, D.E., Netti, G., Mares, S.W., Thompson, V.F., 2008. Myofibrillar protein turnover: the proteasome and the calpains 1 & 2. *J. Anim. Sci.* 86, E19–E35.
- Goll, D.E., Otsuka, Y., Nagainis, P.A., Shannon, J.D., Sathe, S.K., Muguruma, M., 1983. Role of muscle proteinases in maintenance of muscle integrity and mass. *J. Food Biochem.* 7, 137–177.
- Goll, D.E., Thompson, V.F., Li, H., Wei, W., Cong, J., 2003. The calpain system. *Physiol. Rev.* 83, 731–801.
- Greaser, M.L., 1986. Conversion of muscle to meat. In: Bechtel, P.J. (Ed.), *Muscle as Food*. Academic Press, New York, pp. 37–102.
- Gudbjornsdottir, B., Jonsson, A., Hafsteinsson, H., Heinz, V., 2010. Effect of high-pressure processing on *Listeria spp.* and on the textural and microstructural properties of cold smoked salmon. *LWT Food Sci. Technol.* 43, 366–374.
- Guignot, F., Vignon, X., Monin, G., 1993. Postmortem evolution of myofilament spacing and extracellular-space in veal muscle. *Meat Sci.* 33, 333–347.
- Hamm, R., 1960. Biochemistry of meat hydration. *Adv. Food Res.* 10, 355–463.
- Henderson, C.A., Gomez, C.G., Novak, S.M., Mi-Mi, L., Gregorio, C.C., 2017. Overview of the muscle cytoskeleton. *Compr. Physiol.* 7, 891–944.
- Ho, C.Y., Stromer, M.H., Robson, R.M., 1996. Effect of electrical stimulation on postmortem titin, nebulin, desmin, and troponin-T degradation and ultrastructural changes in bovine longissimus muscle. *J. Anim. Sci.* 74, 1563–1575.
- Ho, C.Y., Stromer, M.H., Rouse, G., Robson, R.M., 1997. Effects of electrical stimulation and postmortem storage on changes in titin, nebulin, desmin, troponin-T, and muscle ultrastructure in *Bos indicus* crossbred cattle. *J. Anim. Sci.* 75, 366–376.
- Hoekstra, W., 1969. Energy metabolites in red and white striated muscles of the pig. *J. Agric. Food Chem.* 17, 29–33.
- Homma, N., Ikeuchi, Y., Suzuki, A., 1994. Effects of high-pressure treatment on the proteolytic enzymes in meat. *Meat Sci.* 38, 219–228.
- Hopkins, D.L., 2014. Tenderizing mechanisms. Mechanical. In: Devine, C., Dikeman, M. (Eds.), *Encyclopedia of Meat Sciences*, second ed. Academic Press, London, pp. 443–451.
- Huang, J., Forsberg, N.E., 1998. Role of calpain in skeletal-muscle protein degradation. *Proc. Natl. Acad. Sci.* 95, 12100–12105.
- Huff-Lonerger, E., 2014. Tenderizing mechanisms enzymatic. In: Devine, C., Dikeman, M. (Eds.), *Encyclopedia of Meat Sciences*, second ed. Academic Press, London, pp. 438–442.
- Huff Lonerger, E., Zhang, W., Lonerger, S.M., 2010. Biochemistry of postmortem muscle - lessons on mechanisms of meat tenderization. *Meat Sci.* 86, 184–195.
- Ikkai, T., Ooi, T., 1966. The effects of pressure on FG transformation of actin. *Biochemistry* 5, 1551–1560.
- Johnston, I., 2001. Implications of muscle growth patterns for the colour and texture of fish flesh. In: Kestin, S.C., Warriss, P.D. (Eds.), *Farmed Fish Quality*. Blackwell Science Ltd, Oxford, pp. 13–30.
- Jung, S., Ghoul, M., de Lamballerie-Anton, M., 2000. Changes in lysosomal enzyme activities and shear values of high pressure treated meat during ageing. *Meat Sci.* 56, 239–246.
- Kaur, L., Maudens, E., Haisman, D.R., Boland, M.J., Singh, H., 2014. Microstructure and protein digestibility of beef: the effect of cooking conditions as used in stews and curries. *LWT Food Sci. Technol.* 55, 612–620.
- Kaur, L., Astruc, T., Vénien, A., Loison, O., Cui, J., Irastorza, M., Boland, M., 2016. High pressure processing of meat: effects on ultrastructure and protein digestibility. *Food Function* 7, 2389–2397.
- Kemp, S., Bardsley, R.P., Buttery, P.J., Parr, T., 2010. Tenderness - an enzymatic view. *Meat Sci.* 84, 248–256.
- Kennick, W.H., Elgasim, E.A., Holmes, Z.A., Meyer, P.F., 1980. The effect of pressurisation of pre-rigor muscle on post-rigor meat characteristics. *Meat Sci.* 4, 33–40.
- Kim, H.-J., Taub, I.A., 1991. Specific degradation of myosin in meat by bromelain. *Food Chem.* 40, 337–343.
- Kim, Y.H.B., Kerr, M., Geesink, G., Warner, R.D., 2014a. Impacts of hanging method and high pre-rigor temperature and duration on quality attributes of ovine muscles. *Anim. Prod. Sci.* 54, 414–421.
- Kim, Y.H.B., Warner, R.D., Rosenvold, K., 2014b. Influence of high pre-rigor temperature and fast pH fall on muscle proteins and meat quality: a review. *Anim. Prod. Sci.* 54, 375–395.
- Kohn, T.A., Hoffman, L.C., Myburgh, K.H., 2007. Identification of myosin heavy chain isoforms in skeletal muscle of four Southern African wild ruminants. *Comp. Biochem. Physiol. A. Mol. Integr. Physiol.* 148, 399–407.
- Koohmaraie, M., 1994. Muscle proteinases and meat aging. *Meat Sci.* 36, 93–104.
- Koohmaraie, M., Geesink, G.H., 2006. Contribution of postmortem muscle biochemistry to the delivery of consistent meat quality with particular focus on the calpain system. *Meat Sci.* 74, 34–43.
- Koretz, J.F., Irving, T.C., Wang, K., 1993. Filamentous aggregates of native titin and binding of C-protein and AMP-deaminase. *Arch. Biochem. Biophys.* 304, 305–309.
- Kruk, Z.A., Yun, H., Rutley, D.L., Lee, E.J., Kim, Y.J., Jo, C., 2011. The effect of high pressure on microbial population, meat quality and sensory characteristics of chicken breast fillet. *Food Control.* 22, 6–12.
- Laakkonen, E., Sherbon, J.W., Wellington, G.H., 1970a. Low temperature, long time heating of bovine muscle 3. collagenolytic activity. *J. Food Sci.* 35, 181–184.
- Laakkonen, E., Wellington, G.H., Sherbon, J.N., 1970b. Low temperature, long time heating of bovine muscle 1. changes in tenderness, water binding capacity, pH and amount of water soluble components. *J. Food Sci.* 35, 175–177.
- Labeit, S., Kolmerer, B., 1995. Titins: giant proteins in charge of muscle ultrastructure and elasticity. *Science* 270, 293–296.
- Lametsch, R., Lonerger, S., Huff-Lonerger, E., 2008. Disulfide bond within mu-calpain active site inhibits activity and autolysis. *Biochimica Biophysica Acta Proteins Proteomics* 1784, 1215–1221.
- Lawrie, R.A., 2006. Chemical and biochemical constitution of muscle. In: Lawrie, R.A., Ledward, D. (Eds.), *Lawrie's Meat Science*, seventh ed. Woodhead Publishing, Cambridge UK, pp. 75–127.
- Lawrie, R.A., Penny, I.F., Scopes, R.K., Voyle, C.A., 1963. Sarcoplasmic proteins in pale, exudative pig muscles. *Nature* 200, 673.
- Lefevre, F., Culioli, J., Joandel-Monier, S., Ouali, A., 1999. Muscle polymorphism and gelling properties of myofibrillar proteins from poultry, mammals, and fish. In: Xiong, Y.L., Chi-Tang, H., Shahidi, F. (Eds.), *Quality Attributes of Muscle Foods*. Springer, New York, pp. 365–391.
- Lehman, W., Craig, R., 2008. Tropomyosin and the steric mechanism of muscle regulation. In: Gunning, P. (Ed.), *Tropomyosin*. Springer, New York, pp. 95–109.
- Levine, R.L., Williams, J.A., Stadtman, E.R., Shacter, E., 1994. Carbonyl assays for determination of oxidatively modified proteins. *Methods Enzym.* 233, 346–357.
- Lewis, D.F., 1992. Structural aspects of processed meat. In: Johnston, D.E., Knight, M.K., Ledward, D.A. (Eds.), *Chemistry of Muscle-based Foods*. Royal Society of Chemistry, London, p. 203.
- Li, L., Liu, Y., Zou, X., He, J., Xu, X., Zhou, G., Li, C., 2017. In vitro protein digestibility of pork products is affected by the method of processing. *Food Res. Int.* 92, 88–94.
- Liu, Y., Chen, Y.-R., 2001. Analysis of visible reflectance spectra of stored, cooked and diseased chicken meats. *Meat Sci.* 58, 395–401.
- Maddougall, D.B., 1970. Characteristics of appearance of meat 1. Luminous absorption, scatter and internal transmittance of lean of bacon manufactured from normal and pale pork. *J. Sci. Food Agric.* 21, 568–571.

- Macdougall, D.B., 1982. Changes in the color and opacity of meat. *Food Chem.* 9, 75–88.
- Macfarlane, J.J., McKenzie, I.J., Turner, R.H., Jones, P.N., 1981. Pressure treatment of meat: effects on thermal transitions and shear values. *Meat Sci.* 5, 307–317.
- Macfarlane, J.J., Morton, D.J., 1978. Effects of pressure treatment on the ultrastructure of striated muscle. *Meat Sci.* 2, 281–288.
- Martinaud, A., Mercier, Y., Marinova, P., Tassy, C., Gatellier, P., Renner, M., 1997. Comparison of oxidative processes on myofibrillar proteins from beef during maturation and by different model oxidation systems. *J. Agric. Food Chem.* 45, 2481–2487.
- McCormick, R.J., 1999. Extracellular modifications to muscle collagen: implications for meat quality. *Poult. Sci.* 78, 785–791.
- McElhinny, A.S., Kazmierski, S.T., Labeit, S., Gregorio, C.C., 2003. Nebulin: the nebulous, multifunctional giant of striated muscle. *Trends Cardiovasc. Med.* 13, 195–201.
- McGee, H., 2004. *On Food and Cooking – The Science and Lore of the Kitchen*, second ed. Scribner, New York.
- McKeith, F.K., Brewer, M.S., Bruggen, K.A., 1994. Effects of enzyme applications on sensory, chemical and processing characteristics of beef steaks and roasts. *J. Muscle Foods* 5, 149–164.
- Miyada, D.S., Tappel, A.L., 1956. The hydrolysis of beef proteins by various proteolytic enzymes. *J. Food Sci.* 21, 217–225.
- Monin, G., 1988. Evolution postmortem du tissu musculaire et conséquences sur la qualité de la viande de porc. *Proc. Journées de la Recherche Porcine en France Paris* 20, 201–214.
- Nishimura, T., 2010. The role of intramuscular connective tissue in meat texture. *Anim. Sci. J.* 81, 21–27.
- Nishimura, T., Hattori, A., Takahashi, K., 1995. Structural weakening of intramuscular connective-tissue during conditioning of beef. *Meat Sci.* 39, 127–133.
- Obinata, T., Maruyama, K., Sugita, H., Kohama, K., Ebashi, S., 1981. Dynamic aspects of structural proteins in vertebrate skeletal muscle. *Muscle Nerve* 4, 456–488.
- Offer, G., Knight, P., 1988. The structural basis of water holding in meat. Part 2: drip losses. In: *Lawrie, R. (Ed.), Developments in Meat Science*, vol. 4. Elsevier Science Publishers, London, pp. 173–243.
- Ouali, A., 1990a. La maturation des viandes: Facteurs biologiques et technologiques de variation. *Viandes Produits Carnes* 11, 281–290.
- Ouali, A., 1990b. Meat tenderization: possible causes and mechanisms. A review. *J. Muscle Foods* 1, 129–165.
- Ouali, A., 1992. Proteolytic and physicochemical mechanisms involved in meat texture development. *Biochimie* 74, 251–265.
- Ouali, A., Herrera-Mendez, C.H., Coulis, G., Becila, S., Boudjellal, A., Aubry, L., Sentandreu, M.A., 2006. Revisiting the conversion of muscle into meat and the underlying mechanisms. *Meat Science* 74 (1), 44–58. <https://doi.org/10.1016/j.meatsci.2006.05.010>.
- Ouali, A., Gagaoua, M., Boudida, Y., Becila, S., Boudjellal, A., Herrera-Mendez, C.H., Sentandreu, M.A., 2013. Biomarkers of meat tenderness: present knowledge and perspectives in regards to our current understanding of the mechanisms involved. *Meat Sci.* 95, 854–870.
- Owens, C.M., Hirschler, E.M., McKee, S.R., Martinez-Dawson, R., Sams, A.R., 2000. The characterization and incidence of pale, soft, exudative Turkey meat in a commercial plant. *Poult. Sci.* 79, 553–558.
- Palka, K., Daun, H., 1999. Changes in texture, cooking losses, and myofibrillar structure of bovine *M. semitendinosus* during heating. *Meat Sci.* 51, 237–243.
- Payne, C.T., 2009. Enzymes. In: *Tarté, R. (Ed.), Ingredients in Meat Products: Properties, Functionality and Applications*. Springer New York, New York, NY, pp. 173–198.
- Pearce, K.L., Rosenvold, K., Andersen, H.J., Hopkins, D.L., 2011. Water distribution and mobility in meat during the conversion of muscle to meat and ageing and the impacts on fresh meat quality attributes - a review. *Meat Sci.* 89, 111–124.
- Pearson, A.M., Gillett, T.A., 2012. *Composition and Nutritive Value of Raw Materials and Processed Meats*. Springer, New York.
- Pearson, A.M., Young, R.B., 1989a. Proteins of the thick filament. In: *Pearson, A.M. (Ed.), Muscle and Meat Biochemistry*. Academic Press, San Diego, pp. 66–97 (Chapter 3).
- Pearson, A.M., Young, R.B., 1989b. Sarcoplasmic proteins. In: *Pearson, A.M. (Ed.), Muscle and Meat Biochemistry*. Academic Press, San Diego, pp. 296–337 (Chapter 11).
- Penny, I.F., 1967. The influence of pH and temperature on properties of myosin. *Biochem. J.* 104, 609–615.
- Penny, I.F., 1977. Effect of temperature on drip, denaturation and extracellular-space of pork *Longissimus-dorsi* muscle. *J. Sci. Food Agric.* 28, 329–338.
- Peter, J.B., Barnard, R.J., Edgerton, V.R., Gillespie, C.A., Stempel, K.E., 1972. Metabolic profiles of three fiber types of skeletal muscle in Guinea pigs and rabbits. *Biochemistry* 11, 2627–2633.
- Pette, D., Staron, R.S., 1990. Cellular and molecular diversities of mammalian skeletal muscle fibers. *Rev. Physiol. Biochem. Pharmacol.* 116, 1–76.
- Pette, D., Staron, R.S., 2000. Myosin isoforms, muscle fiber types, and transitions. *Microsc. Res. Tech.* 50, 500–509.
- Purslow, P.P., 2005. Intramuscular connective tissue and its role in meat quality. *Meat Sci.* 70, 435–447.
- Raynaud, F., Fernandez, E., Coulis, G., Aubry, L., Vignon, X., Bleimling, N., Gautel, M., Benyamin, Y., Ouali, A., 2005. Calpain 1–titin interactions concentrate calpain 1 in the Z-band edges and in the N2-line region within the skeletal myofibril. *FEBS J.* 272, 2578–2590.
- Renner, M., 2000. Oxidative processes and myoglobin. In: *Decker, E.A., Faustman, C., Lopez-Bote, C.J. (Eds.), Antioxidants in Muscle Foods: Nutritional Strategies to Improve Quality*. John Wiley & Sons, Inc., New York, pp. 113–134.
- Robson, R.M., Huff-Lonergan, E., Parrish, F.C., Ho, C.-Y., Stromer, M.H., Huiatt, T.W., Bellin, R.M., Sernett, S.W., 1997. Postmortem changes in the myofibrillar and other cytoskeletal proteins in muscle. In: *Proceedings of the 50th Annual Reciprocal Meat Conference*, Iowa State University, Iowa State University, Ames, Iowa.
- Rowe, R.W.D., 1986. Elastin in bovine *semitendinosus* and *longissimus dorsi* muscles. *Meat Sci.* 17, 293–312.
- Rowe, L.J., Maddock, K.R., Lonergan, S.M., Huff-Lonergan, E., 2004a. Influence of early postmortem protein oxidation on beef quality. *J. Anim. Sci.* 82, 785–793.
- Rowe, L.J., Maddock, K.R., Lonergan, S.M., Huff-Lonergan, E., 2004b. Oxidative environments decrease tenderization of beef steaks through inactivation of mu-calpain. *J. Anim. Sci.* 82, 3254–3266.
- Ruiz, J., Calvarro, J., Sánchez del Pulgar, J., Roldán, M., 2013. Science and technology for new culinary techniques. *J. Culin. Sci. Technol.* 11, 66–79.
- Rusman, H., Gerelt, B., Yamamoto, S., Nishiumi, T., Suzuki, A., 2007. Combined effects of high pressure and heat on shear value and histological characteristics of bovine skeletal muscle. *Asian Australas. J. Anim. Sci.* 20, 994.
- Schellekens, M., 1996. New research issues in sous-vide cooking. *Trends Food Sci. Technol.* 7, 256–262.
- Schiaffino, S., Reggiani, C., 2011. Fiber types in mammalian skeletal muscles. *Physiol. Rev.* 91, 1447–1531.
- Schilling, M.W., Claus, J.R., Marriott, N.G., Solomon, M.B., Eigel, W.N., Wang, H., 2002. No effect of hydrodynamic shock wave on protein functionality of beef muscle. *J. Food Sci.* 67, 335–340.
- Scopes, R.K., 1964. The influence of post-mortem conditions on the solubilities of muscle proteins. *Biochem. J.* 91, 201–207.
- Scopes, R.K., Lawrie, R.A., 1963. Post-mortem lability of skeletal muscle proteins. *Nature* 197, 1202–1203.
- Sentandreu, M.A., Coulis, G., Ouali, A., 2002. Role of muscle endopeptidases and their inhibitors in meat tenderness. *Trends Food Sci. Technol.* 13, 400–421.
- Sikes, A., Tornberg, E., Tume, R., 2010. A proposed mechanism of tenderising post-rigor beef using high pressure–heat treatment. *Meat Sci.* 84, 390–399.
- Sikes, A.L., Warner, R., 2016. Application of high hydrostatic pressure for meat tenderization. In: *Knoerzer, K., Juliano, P., Smithers, G.W. (Eds.), Innovative Food Processing Technologies: Extraction, Separation, Component Modification and Process Intensification*. Woodhead Publishing, Cambridge, pp. 259–290.
- Smith, D.M., 2000. Functional properties of muscle proteins in processed poultry products. In: *Owens, C.M., Alvarado, C.Z., Sams, A.R. (Eds.), Poultry Meat Processing*. CRC Press, Boca Raton FL, pp. 231–244 (Chapter 11).
- Soladoye, O.P., Juárez, M.L., Aalhus, J.L., Shand, P., Estévez, M., 2015. Protein oxidation in processed meat: mechanisms and potential implications on human health. *Compr. Rev. Food Sci. Food Saf.* 14, 106–122.
- Spangenburg, E., Booth, F., 2003. Molecular regulation of individual skeletal muscle fibre types. *Acta Physiol. Scand.* 178, 413–424.
- Spanier, A.M., Fahrenholz, T.M., 2005a. Changes in protein distribution in beef *semitendinosus* muscle (ST) in samples showing varying response to hydrodynamic pressure (HDP)-treatment. In: *Spanier, A.M., Shahidi, F., Parliment, T.H., Mussinan, C., Ho, C.T., Contis, E.T. (Eds.), Food Flavor and Chemistry: Explorations into the 21st Century*. Royal Society of Chemistry, London, pp. 418–430.

- Spanier, A.M., Fahrenholz, T.M., 2005b. Hydrodynamic pressure (HDP)-treatment: influence on beef striplolin proteins. In: Spanier, A.M., Shahidi, F., Parliament, T.H., Mussinan, C., Ho, C.T., Contis, E.T. (Eds.), *Food Flavor and Chemistry: Explorations into the 21st Century*. Royal Society of Chemistry, London, pp. 391–404.
- Stabursvik, E., Frøtheim, K., Frøystein, T., 1984. Myosin denaturation in pale, soft, and exudative (pse) porcine muscle-tissue as studied by differential scanning calorimetry. *J. Sci. Food Agric.* 35, 240–244.
- Stadtman, E.R., 1990. Metal ion-catalyzed oxidation of proteins - biochemical-mechanism and biological consequences. *Free Radic. Biol. Med.* 9, 315–325.
- Strasburg, G., Xiong, Y.L., Chiang, W., 2008. Physiology and chemistry of edible muscle tissues. In: Damodaran, S., Parkin, K.L., Fennema, O.R. (Eds.), *Fennema's Food Chemistry*, fourth ed. CRC Press, Boca Raton FL, pp. 923–973.
- Sullivan, G.A., Calkins, C.R., 2010. Application of exogenous enzymes to beef muscle of high and low-connective tissue. *Meat Sci.* 85, 730–734.
- Suman, S.P., Joseph, P., 2013. Myoglobin chemistry and meat color. *Annu. Rev. Food Sci. Technol.* 4, 79–99.
- Suwandy, V., Carne, A., van de Ven, R., Bekhit, A.E.-D.A., Hopkins, D.L., 2015a. Effect of pulsed electric field treatment on hot-boned muscles of different potential tenderness. *Meat Sci.* 105, 25–31.
- Suwandy, V., Carne, A., van de Ven, R., Bekhit, A.E.-D.A., Hopkins, D.L., 2015b. Effect of pulsed electric field treatment on the eating and keeping qualities of cold-boned beef loins: impact of initial pH and fibre orientation. *Food Bioprocess Technol.* 8, 1355–1365.
- Swartz, D., Greaser, M., Cantino, M., 2009. Muscle structure and function. In: Du, M., McCormick, R.J. (Eds.), *Applied Muscle Biology and Meat Science*. CRC Press, Boca Raton FL, pp. 1–45 (Chapter 1).
- Swatland, H.J., 2008. How pH causes paleness or darkness in chicken breast meat. *Meat Sci.* 80, 396–400.
- Tahergorabi, R., Hosseini, S.V., Jaczynski, J., 2011. Seafood proteins. In: Phillips, G.O., Williams, P.A. (Eds.), *Handbook of Food Proteins*. Woodhead Publishing, Cambridge UK, pp. 116–149 (Chapter 6).
- Taylor, R.G., Geesink, G.H., Thompson, V.F., Koohmaraie, M., Goll, D.E., 1995a. Is z-disk degradation responsible for postmortem tenderization. *J. Anim. Sci.* 73, 1351–1367.
- Taylor, R.G., Tassy, C., Briand, M., Robert, N., Ouali, A., 1995b. Proteolytic activity of proteasome on myofibrillar structures. *Mol. Biol. Rep.* 21, 71–73.
- Taylor, R.G., 2004. Connective tissue structure, function and influence on meat quality. In: *Encyclopedia of Meat Sciences*. Elsevier, Oxford, pp. 306–314.
- Tornberg, E., 2005. Effects of heat on meat proteins - implications on structure and quality of meat products. *Meat Sci.* 70, 493–508.
- Torres, J.A., Velazquez, G., 2005. Commercial opportunities and research challenges in the high pressure processing of foods. *J. Food Eng.* 67, 95–112.
- Tortora, G.J., Derrickson, B.H., 2013. *Principles of Anatomy and Physiology*, fourteenth ed. Wiley Global Education, New York.
- Troy, D.J., Ojha, K.S., Kerry, J.P., Tiwari, B.K., 2016. Sustainable and consumer-friendly emerging technologies for application within the meat industry: an overview. *Meat Sci.* 120, 2–9.
- Vander Ven, P.F., Obermann, W., Lemke, B., Gautel, M., Weber, K., Fürst, D.O., 2000. Characterization of muscle filamin isoforms suggests a possible role of γ -filamin/ABP-L in sarcomeric Z-disc formation. *Cell Motil. Cytoskeleton.* 45, 149–162.
- Veiseth, E., Koohmaraie, A., 2005. Beef tenderness: significance of the calpain proteolytic system. In: Hocquette, J.F., Gigli, S. (Eds.), *Indicators of Milk and Beef Quality*. EAAP European Association for Animal Production Publication, pp. 111–126, 112.
- Venugopal, V., Shahidi, F., 1996. Structure and composition of fish muscle. *Food Rev. Int.* 12, 175–197.
- Voermans, N.C., Bonnemann, C.G., Huijting, P.A., Hamel, B.C., van Kuppevelt, T.H., de Haan, A., Schalkwijk, J., van Engelen, B.G., Jenniskens, G.J., 2008. Clinical and molecular overlap between myopathies and inherited connective tissue diseases. *Neuromuscul. Disord.* 18, 843–856.
- Warner, R.D., Dunshea, F.R., Gutzke, D., Lau, J., Kearney, G., 2014. Factors influencing the incidence of high rigor temperature in beef carcasses in Australia. *Anim. Prod. Sci.* 54, 363–374.
- Warner, R.D., Kerr, M., Kim, Y.H.B., Geesink, G., 2014. Pre-rigor carcass stretching counteracts the negative effects of high rigor temperature on tenderness and water-holding capacity - using lamb muscles as a model. *Anim. Prod. Sci.* 54, 494–503.
- Warner, R.D., McDonnell, C.K., Bekhit, A.E.D., Claus, J., Vaskoska, R., Sikes, A., Dunshea, F.R., Ha, M., 2017. Systematic review of emerging and innovative technologies for meat tenderisation. *Meat Sci.* 132, 72–89.
- Warriss, P.D., 2010. *Meat Science: An Introductory Text*, second ed. CABI, Wallingford, UK; Cambridge, MA.
- Weir, C.E., Wang, H., Birkner, M.L., Parsons, J., Ginger, B., 1958. Studies on enzymatic tenderisation of meat. II Panel and histological analyses of meat treated with liquid tenderising containing papain. *J. Food Sci.* 23, 411–422.
- Williams, P., 2007. Nutritional composition of red meat. *Nutr. Dietetics* 64, S113–S119.
- Xiong, Y.L., Decker, E.A., 1995. Alterations of muscle protein functionality by oxidative and antioxidative processes. *J. Muscle Foods* 6, 139–160.
- Xiong, Y., 1997. Structure-function relationships of muscle proteins. In: Damodaran, S., Paraf, A. (Eds.), *Food Proteins and Their Applications*. Marcel Dekker, New York, pp. 341–392.
- Yao, C.K., Muir, J.G., Gibson, P.R., 2016. Review article: insights into colonic protein fermentation, its modulation and potential health implications. *Alimentary Pharmacol. Ther.* 43, 181–196.
- Zamri, A.I., Ledward, D.A., Frazier, R.A., 2006. Effect of combined heat and high-pressure treatments on the texture of chicken breast muscle (*Pectoralis fundus*). *J. Agric. Food Chem.* 54, 2992–2996.
- Zot, A.S., Potter, J.D., 1987. Structural aspects of troponin-tropomyosin regulation of skeletal muscle contraction. *Annu. Rev. Biophys. Biophys. Chem.* 16, 535–559.
- Zuckerman, H., Bowker, B.C., Eastridge, J.S., Solomon, M.B., 2013. Microstructure alterations in beef intramuscular connective tissue caused by hydrodynamic pressure processing. *Meat Sci.* 95, 603–607.
- Zuckerman, H., Solomon, M.B., 1998. Ultrastructural changes in bovine longissimus muscle caused by the hydrodyne process. *J. Muscle Foods* 9, 419–426.

Further Reading

- Adzitey, F., Nurul, H., 2011. Pale soft exudative (PSE) and dark firm dry (DFD) meats: causes and measures to reduce these incidences - a mini review. *Int. Food Res. J.* 18, 11–20.
- Baldwin, D.E., 2012. Sous vide cooking: a review. *Int. J. Gastron. Food Sci.* 1, 15–30.
- Bekhit, A.A., Hopkins, D.L., Geesink, G., Bekhit, A.A., Franks, P., 2014. Exogenous proteases for meat tenderization. *Crit. Rev. Food Sci. Nutr.* 54, 1012–1031.
- Bendall, J.R., 1973. Post mortem changes in muscle. In: Bourne, G.H. (Ed.), *Structure and Function of Muscle*. Academic Press, New York, pp. 243–309.
- Boland, M.J., Rae, A.N., Vereijken, J.M., Meuwissen, M.P.M., Fischer, A.R.H., van Boekel, M.A.J.S., Rutherford, S.M., Gruppen, H., Moughan, P.J., Hendriks, W.H., 2013. The future supply of animal-derived protein for human consumption. *Trends Food Sci. Technol.* 29, 62–73.
- Fairlie, S., 2011. *Meat: a benign extravagance*. Chelsea Green Publishers. ISBN:10:1603583246.
- Huff Lonergan, E., Zhang, W., Lonergan, S.M., 2010. Biochemistry of postmortem muscle - lessons on mechanisms of meat tenderization. *Meat Sci.* 86, 184–195. <https://doi.org/10.1016/j.meatsci.2010.05.004>.
- Knoerzer, K., Juliano, P., Smithers, G.W. (eds.), *Innovative Food Processing Technologies: Extraction, Separation, Component Modification and Process Intensification*, pp. 231–258. Woodhead Publishing, Cambridge. Particularly Chapters 9 and 10.
- Koohmaraie, M., Geesink, G.H., 2006. Contribution of postmortem muscle biochemistry to the delivery of consistent meat quality with particular focus on the calpain system. *Meat Sci.* 74, 34–43. <https://doi.org/10.1016/j.meatsci.2006.04.025>.

- McGee, H., 2004. *On Food and Cooking – The Science and Lore of the Kitchen*, second ed. Scribner, New York.
- Nollet, L.M.L., Toldra, F., 2006. *Advanced Technologies for Meat Processing*. CRC Press, Taylor & Francis, Boca Raton, FL.
- Pearce, K.L., Rosenvold, K., Andersen, H.J., Hopkins, D.L., 2011. Water distribution and mobility in meat during the conversion of muscle to meat and ageing and the impacts on fresh meat quality attributes - a review. *Meat Sci.* 89, 111–124. <https://doi.org/10.1016/j.meatsci.2011.04.007>.
- Strasburg, G., Xiong, Y.L., Chiang, W., 2008. Physiology and chemistry of edible muscle tissues. In: Damodaran, S., Parkin, K.L., Fennema, O.R. (Eds.), *Fennema's Food Chemistry*, fourth ed. CRC Press, Boca Raton FL.
- Warriss, P.D., 2010. *Meat Science: An Introductory Text*, second ed. CABI, Wallingford, UK; Cambridge, MA.