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High-pressure processing of meat: Molecular impacts and industrial applications

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Abstract

High-pressure processing (HPP) has been the most adopted nonthermal processing technology in the food industry with a current ever-growing implementation, and meat products represent about a quarter of the HPP foods. The intensive research conducted in the last decades has described the molecular impacts of HPP on microorganisms and endogenous meat components such as structural proteins, enzyme activities, myoglobin and meat color chemistry, and lipids, resulting in the characterization of the mechanisms responsible for most of the texture, color, and oxidative changes observed when meat is submitted to HPP. These molecular mechanisms with major effect on the safety and quality of muscle foods are comprehensively reviewed. The understanding of the high pressure–induced molecular impacts has permitted a directed use of the HPP technology, and nowadays, HPP is applied as a cold pasteurization method to inactive vegetative spoilage and pathogenic microorganisms in ready-to-eat cold cuts and to extend shelf life, allowing the reduction of food waste and the gain of market boundaries in a globalized economy. Yet, other applications of HPP have been explored in detail, namely, its use for meat tenderization and for structure formation in the manufacturing of processed meats, though these two practices have scarcely been taken up by industry. This review condenses the most pertinent-related knowledge that can unlock the utilization of these two mainstream transformation processes of meat and facilitate the development of healthier clean label processed meats and a rapid method for achieving sous vide tenderness. Finally, scientific and technological challenges still to be overcome are discussed in order to leverage the development of innovative applications using HPP technology for the future meat industry.

KEYWORDS
cold pasteurization, high-pressure processing (HPP), meat products, meat tenderization, processed meats, structure formation

1 | INTRODUCTION TO THE CURRENT USE OF HIGH-PRESSURE PROCESSING IN THE MEAT INDUSTRY

High-pressure processing (HPP) has been the most successfully adopted alternative nonthermal processing technology in the food industry so far. Meat products constitute an important market share of the use of HPP in the food industry, with 25 to 30% out of the total high pressure (HP)-processed foods being meat products (Jung & Tonello-Samson, 2018). Furthermore, the number of HPP units in industrial operation is growing exponentially (Jung & Tonello-Samson, 2018). Hence, the number of HPP units in industrial operations doubled during the period of time from 2013 to 2016, from approximately 215 to 430 HPP units (Jung & Tonello-Samson, 2018). Overall, it can be estimated that approximately 400,000 tonnes (metric ton) of meat products were processed by HPP in 2019, with the United States currently being the biggest market user with around 50 HPP facilities dedicated to meat processing (Carole Tonello, Hiperbaric, personal communication). The technology has matured in the last 10 years (see photos of HPP equipment with main characteristics in Figure 1). HPP equipment manufacturers have launched to market HP vessels of higher volumes (i.e., ranging from 35 up to 525 L) and automation has been progressively incorporated into the processing lines. The largest production volume unit launched to market, which in addition permits a continuous process, is the Hiperbaric bulk (with 1,050 L). However, this revolutionary system (i.e., Hiperbaric 1,050 bulk) can only process liquid foods, and it is not applicable to solid foods such as meat and meat products. Recent advances in the technological development of HPP systems have enabled improvements in productivity, reduction of processing costs, processing times, and energy consumptions, which are directly related to the volume of the processing vessels, as well as yielded additional benefits associated with the robustness achieved when working with matured technologies in terms of more defined and secure procedures, breakdown frequency, spare parts, and after-sales services. Figure 1c shows a modern commercial HPP installation, which comprises three HPP units "in line" with vessels of 420 L each, and fully automated loading and unloading of product. This installation can process several tonnes of product per hour, which is a testament to the remarkable technological advances at industrial level of the HPP technology in the last years. Nowadays, HPP is a food processing technology that can be used by the meat industry to produce fresh, safe, innovative, nutritious, high-quality, clean label, convenience, and ready-to-eat (RTE) meat products that are attractive to the consumer and that can fulfill the future trends for healthy, natural, and minimally processed meats.

The utilization of HPP as a nonthermal pasteurization with minimal impacts on sensory quality and nutritional value is well-established, and a variety of meat products already benefit from the application of HPP to assure food safety and to extend shelf life. When HPP is used in certain finished meat products as an effective method to inactivate and control pathogenic bacteria such as *Listeria*, *Salmonella*, and *E. coli*, whereby preventing foodborne outbreaks and food recalls from taking place, the benefits of the application of HPP to ensure food safety are of great and irreplaceable value for the industry. However, the application of HPP under certain processing conditions (temperature [T], pressure [P] and time [t]) can affect

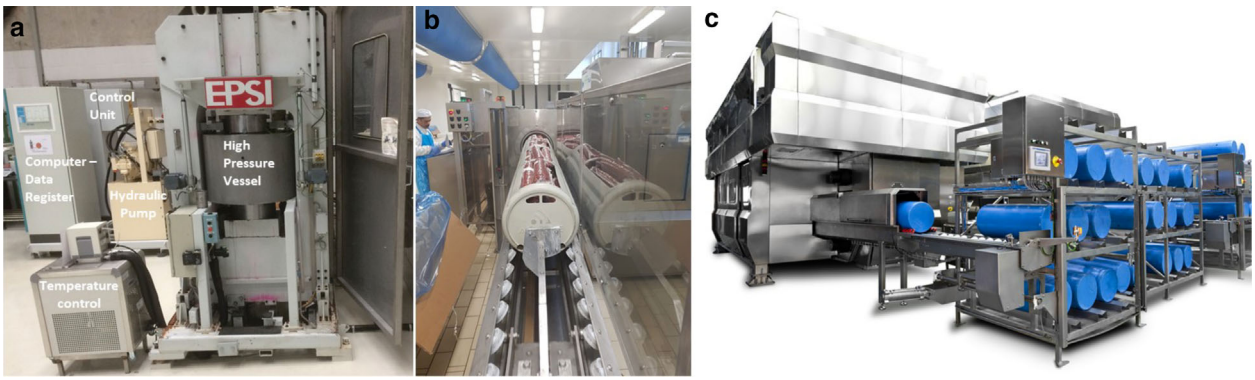


FIGURE 1 Examples of pilot and industrial high-pressure processing (HPP) units. (a) Pilot-scale HPP unit installed in Kulmbach (Germany) at the Department of Safety and Quality of Meat, Federal Research Institute for Nutrition and Food, Max Rubner Institute. Main parts of equipment are indicated in the picture. Equipment operates at a range of temperatures from –20 to 80 °C and pressures up to 900 MPa. (b) Industrial HPP unit with product (salami) being loaded into the pressure vessel. Equipment operates at room temperature and pressures up to 600 MPa. Courtesy of Marco Veroni (Veroni, Italy and USA). (c) Industrial HPP installation (Model Hiperbaric 420) with fully automated loading/unloading of product. Equipment operates at room temperature and pressures up to 600 MPa. Courtesy of Carola Tonello (Hiperbaric, Spain)

the labile nature of proteins, especially those in (nonprocessed) fresh meats. Depending on the applied conditions, HPP will result in moderate to severe adverse effects on the meat appearance and other quality traits, which, so far, have restricted a much broader implementation of the HPP technology in the meat industry.

This review describes the molecular impacts of HPP on meat systems and their implications for product quality, and provides discussion on key aspects to exploiting its full potential while minimizing the negative effects. Apart from its use as a cold pasteurization process, this review aims to point out that there are still namely two other potential applications of HPP, which could bring about massive benefits to the meat industry. These two applications are as follows: the use of HPP intended for meat tenderization, for instance of low value cuts, and its use for enabling structure formation in the manufacturing of processed meats. The former application will affect meat structure in a way that results in reduced shear force of cooked meat, and the latter mediates gelation processes involved in the formation of stable structures having good water and fat retention ability in processed meats. However, because the benefits of these two processes have not been as evident as for the case of a cold pasteurization for ensuring food safety, and due to the fact that their industrial implementation was not as straightforward, requiring important modification of process layout, they have not yet been embraced by the meat industry. This review provides a comprehensive, updated description of the use of HPP for meat tenderization and for structure formation in processed meats, serving as a guide document to understand the molecular impacts and leverage accordingly their practical implementation. Finally, current challenges and perspectives for the future uses of HPP in the meat industry will also be outlined.

2 | MOLECULAR IMPACTS OF HPP TO MEAT SYSTEMS

2.1 | HPP effect on microorganisms

Raw meat and meat products are regarded as easily perishable food with limited shelf life (Gill, 1996). For many years, several foodborne diseases have been associated with the consumption of contaminated meat and meat products, and it has been recognized as one of the major causes of foodborne infections (Fosse, Seegers, & Magras, 2008). One of the most recent outbreaks of *Escherichia coli* O103 with over 190 cases in the United States in 2019 was related to ground beef (Center of Disease Control and Prevention, 2019). Another outbreak of *Salmonella Newport* in 2018 was associated with the consumption of beef products, and resulted in recall of over 12 million pounds of beef in the United States and 400 consumers affected (Center of Disease Control and Prevention, 2018). HPP, as an inactivating technology of pathogenic bacteria such as *Salmonella*, *E. Coli*, and *Listeria* (Porto-Fett et al., 2010), has brought to the meat industry an excellent and reliable tool to prevent similar outbreaks from taking place without impairing product quality. However, it should be noted that HPP (without heat) cannot kill spores and additional measures have to be put in place to address this limitation (c.f. Section 2.1.1).

From a historical viewpoint, pioneering work on the application of HP to microorganisms was done by Bert Hite in the United States in 1899. In his work, he reported preservation of milk, which was "kept sweet for longer" if pressure of 650 MPa for 10 min at room temperature was applied (Hite, 1899). Hite also reported that HP can be used for shelf life extension of other products such as fruits and fruit juices, but abandoned vegetables as "hopeless," probably due to the presence of spore-forming bacteria (Hite, 1914). A few years later, Cruess (1924) reported the application of HP to be suitable technology for preservation of products in conditions, where growth of spores is inhibited, such as in juices with low pH value.

Increasing the shelf life of different foods is sometimes related to actions involving intensive treatments, which usually have detrimental effects on nutritional composition and organoleptic properties. HPP as a postpackaging preservation method is targeting the improvement of food safety and microbial quality of different food products, and aiming at keeping quality changes minimal. In meat products, HPP is used primarily for preservation purposes and shelf life extension (Guillou, Lerasle, Simonin, & Federighi, 2017). Therefore, several review papers report data on microbial inactivation rates in meat products submitted to HPP conditions (Bajovic, Bolumar, & Heinz, 2012; Hygreeva & Pandey, 2016; Simonin, Duranton, & De Lamballerie, 2012). These reviews normally present the inactivation rate as reduction in log of CFU/g and summarize the data, presenting it in tables. In general, pressure levels used for pasteurization of meats and meat products are in the range of 400 to 600 MPa with short processing times of 3 to 7 min at room or chilled temperature. International regulatory agencies require that pasteurization processes are designed to ensure a 5 log reduction. HPP standard treatments (at 400 to 600 MPa for 3 to 7 min), in most cases, lead to an inactivation level of more than 4 log reduction for the most common vegetative pathogenic and spoilage microorganisms resulting in an increased shelf life and improved safety. However, the change in visual appearance of fresh meat after HPP treatments due to protein denaturation and oxidation of myoglobin is considered undesirable. Consequently, the application of HPP in meat

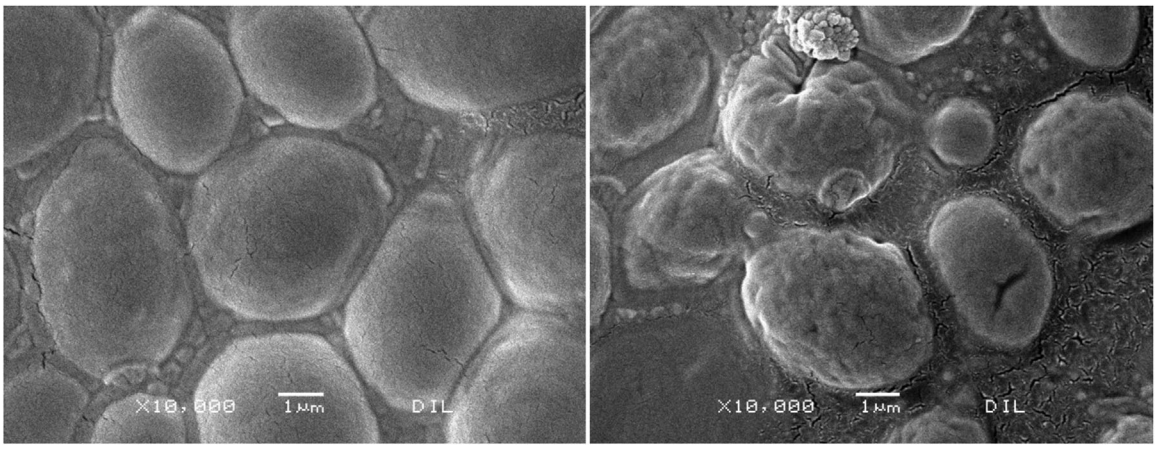


FIGURE 2 Scanning electron microscopic images of *Saccharomyces cerevisiae* and *Listeria innocua*, untreated (left) and after HPP treatment at 600 MPa for 3 min (right) in Ringer's solution

has been so far rather limited to RTE meals and processed meats (Warner et al., 2017).

2.1.1 | Mechanism of microbial inactivation

Moderate pressure levels (up to 180 MPa) decrease the rate of microbial growth and reproduction, and can result in sublethal cellular damages, whereas higher levels of pressure (over 200 MPa) can lead to cell death (Rademacher, 2006). Significant structural changes have been observed at pressure levels above 400 MPa (Smelt, Wouters, Guus, & Rijke, 1998). Inactivation of vegetative microbial cells usually takes place in the pressure range of 200 to 600 MPa at room temperature or chilled facilities, as often used in commercial and industrial scenarios (Georget et al., 2015; Rastogi, Raghavarao, Balasubramaniam, Niranjan, & Knorr, 2007). Pressure-induced microbial inactivation, and therefore, microbial stability of food, due to HPP treatment is the result of a combination of different factors, but is determined by pressure effects on microorganisms in a matrix and the possibility of those to recover after treatment. Changes in morphology and subcellular structures as well as biochemical, physiological, and genetic alterations are considered several factors leading to microbial inactivation (Cheftel, 1995; Hoover, Metrick, Papineau, Farkas, & Knorr, 1989). An example of morphological changes is given by scanning electron microscopy (SEM) images in Figure 2, showing that HP treatment of *Saccharomyces cerevisiae* and *Listeria innocua* suspended in Ringer's solution (pH 7.85 and conductivity 15.45 mS/cm) resulted in shrunk and wrinkled cell surfaces. Due to effects of pressure on the phospholipid bilayer, resulting in phase transition and/or phospholipid crystallization, changes of membrane permeability and fluidity and thus destabilization of the cell occur (Hazel & Williams, 1990; Shimada et al., 1993). Also, compression of gas vacuoles, separation of the cell membrane from the cell wall, contraction of the cell wall with the formation of pores, modifications of the cytoskeleton and strand formation, and modifications of the nucleus and of intracellular organelles are some of the effects responsible for cell death (Shimada et al., 1993). Another aspect assumed to be relevant is related to denaturation and agglomeration of cellular proteins (Farr, 1990), resulting in dissolution of membrane-bound enzymes and enzyme inactivation (Chong, Fortes, & Jameson, 1985; Hoover et al., 1989; Smelt, Rijke, & Hayhurst, 1994). Consequently, metabolic processes are affected (Mota, Lopes, Delgadillo, & Saraiva, 2013). Inactivation efficiency of spoilage and pathogenic bacteria strongly depends on endogenic (matrix characteristics) and exogenic (processing conditions) factors. Pressure and temperature are recognized as the most important processing parameters together with treatment duration, with numerous data available in the literature, clearly demonstrating the interrelationship between these two parameters (P and T) (Balasubramaniam, Barbosa-Cánovas & Lelieveld, 2016). In addition, microbial inactivation and, more particularly, protein denaturation under pressure, depends on matrix intrinsic parameters, such as pH value, water activity, and presence of other substances (salt, antimicrobial substances, fat, and others) (Cheftel, 1995). Pressure tolerance of microorganisms varies greatly, depending on several factors. The physiological status plays an important role, which is affected by the history of the microbial cell in the food matrix (Mañas & Pagán, 2005; Rendueles et al., 2011; Zhang, Jiao, Lian, Deng, & Zhao, 2015). Besides the growth status, intrinsic and extrinsic factors of the food

matrix can cause stress responses, for example, heat or cold shock, and osmotic or acidic stress responses, which might impair the efficiency of inactivation (Rendueles et al., 2011).

Since early investigations on HP inactivation, great progress in understanding the inactivation principles along with kinetics of microbial and enzyme inactivation has been achieved. In most of the cases, HPP inactivation kinetics has been described as a continuously declining curve, showing a so called "tailing" effect at the end. It has been assumed that the tailing is the result of differences in heterogeneity of microbial populations or occurrence of tolerant cells due to stress adaptation and selection (Mota et al., 2013; Tay, Shellhammer, Yousef, & Chism, 2003). Mathematical models have been developed to predict the inactivation of microorganisms by HPP as a function of processing time. Numerous primary models being linear, concave, or sigmoidal have been developed to describe HP inactivation kinetics (Klotz, Pyle, & Mackey, 2007; Serment-Moreno, Barbosa-Canovas, Torres, & Welti-Chanes, 2014). The mostly observed nonlinear behavior supports the finding that microbial HP inactivation is multifactorial.

HP preservation at ambient temperatures includes inactivation of most vegetative microbial cells and partial or total inhibition of key enzymes (Farr, 1990; Simpson & Gilmour, 1997). It can be generally stated that yeasts and molds are more pressure sensitive compared to prokaryotic bacteria. Gram-negative bacteria (e.g., *E. coli* and *Salmonella*) seem to be more sensitive to HPP than Gram-positive bacteria (e.g., *Listeria*) (Considine, Kelly, Fitzgerald, Hill, & Sleator, 2008; Dumay, Chevalier-Lucia, & López-Pedemonte, 2010; Georget et al., 2015). Spores are generally known and recognized for their high tolerance against physical and chemical external factors such as heat, chemicals, radiation, and so on. The same holds true for their tolerance against HP as they can survive pressure of over 1 GPa at ambient temperatures (Ono, 2015). Spores usually found in food belong to species of *Bacillus* and *Clostridium*, causing spoilage and deterioration of food quality (Brown, 2000). Already in the 1960s, the study by Timson and Short (1965) showed that spores of *Bacillus subtilis* and *Bacillus alvei* can survive in milk treated at 1,034 MPa for 90 min at 35 °C, indicating their extreme pressure tolerance and that complete spore inactivation by pressure alone is not possible. Thus, different approaches to address the inactivation of spores in combination with HPP, such as the reduction of matrix's pH to prevent germination of spores, HP cycling, the combination of pressure with high and low temperatures and antimicrobial substances, and some other approaches, have been investigated (Black et al., 2007).

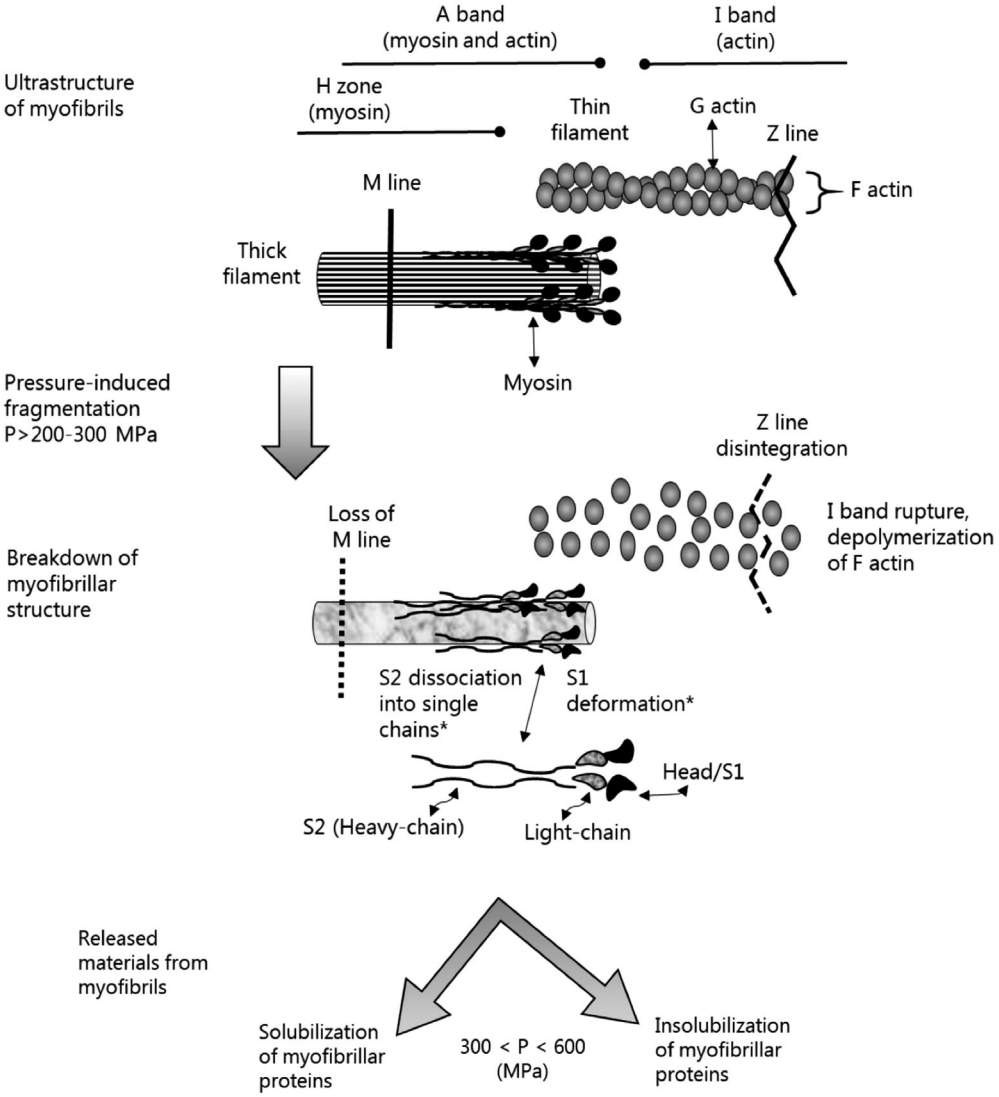
2.2 | HPP effect on proteins

HPP results in pressure-induced modification of muscle proteins giving the potential to manipulate the protein functionality and, thereby, the meat system. The future implementation of the HPP technology in the manufacture of meat product is based on the correct use of pressure to modify proteins. A large amount of scientific literature expresses the interest in unraveling the mechanism behind pressure-induced protein changes and how to use this pressure-modification effect in the processing of meat products. As a consequence, several reviews concerning the various aspects of the HP effects on meat proteins have been published (Bajovic et al., 2012; Bolumar, Middendorf, Toepfl, & Heinz, 2016; Buckow, Sikes, & Tume, 2013; Colmenero, 2002; Ma & Ledward, 2013; Olsen & Orlien, 2016, Chen et al., 2017; Simonin et al., 2012; Sun & Holley, 2009). In this section, the most important results and explanations regarding pressure-induced changes of meat proteins at a molecular level are presented.

2.2.1 | Muscle proteins

Meat consists mainly of three groups of protein fractions: connective tissue proteins (mostly insoluble in water), muscle sarcoplasmic proteins (soluble in water), and muscle myofibrillar proteins (soluble in saline solutions of moderate ionic strength). Collagen, the connective tissue, sometimes referred as "background toughness," is, thus, more related to the tenderness of meat (c.f. Section 3.2).

However, it should be noted that the total collagen content can vary from 1 to 15% of the muscle dry weight (Bailey & Light, 1989, as cited in Listrat et al., 2016). Some collagen content (1% dry weight) coming from the intramuscular connective tissue could then still be expected even in lean muscle clean of visible connective tissue bundles surrounding the muscle fibers, and could be relevant in nonlean muscle meat. The heme pigments and enzymes are the abundant proteins in the sarcoplasmic protein fraction, and constitutes around one third of the total proteins in lean muscle. Because the meat pigments define meat color, the HP effects on these proteins are presented in Section 2.3. The myofibrillar protein fraction is then two thirds of the total proteins in lean muscle and is made up mostly of myosin and actin, and less of α-actinin, tropomyosin, and troponin. Myosin is a heterogeneous hexamer constructed of two heavy chains (HCs) together with light chains (LCs) and two heads. Actin is a globular protein that forms microfilament structures. Myosin and actin are the most important functional and structural proteins that contribute to meat texture, and



Myofibrillar protein solubility (Meat type, pressure in MPa, and reference)	
Increase	Decrease
Bovine *Biceps femoris* myofibrils (300 ≤ P ≤ 600) Jung et al. (2000)	Bovine myofibrils (P ≤ 600) Chapleau et al. (2003)
Chicken myofibrils and pork (P ≤ 200) Iwasaki et al. (2006)	Chicken myofibrils and pork (P = 300) Iwasaki et al. (2006)
Bovine *semitendinosus* (P ≤ 400) Lee et al. (2007)	Bovine *semitendinosus* (P = 500) Lee et al. (2007)
	Minced turkey (P ≤ 200) Chan et al. (2011)
	Pork outside round (P = 600) Grossi et al. (2012, 2014)

FIGURE 3 Schematic representation and sequence of the effect of high pressure on myofibrillar muscle proteins. See S1 deformation:, where : indicates the graphic representation of the S1 deformation with pressure. Reprinted from Orlien (2019) with permission from Elsevier

for this reason, they have been investigated in detail to understand the effect and underlying mechanisms behind the pressure-induced changes. Figure 3 provides a schematic summary of the different studies on the effects of pressure on the myofibrillar proteins, myosin and actin, and forms the basis for the following explanation of the molecular mechanisms behind the protein changes.

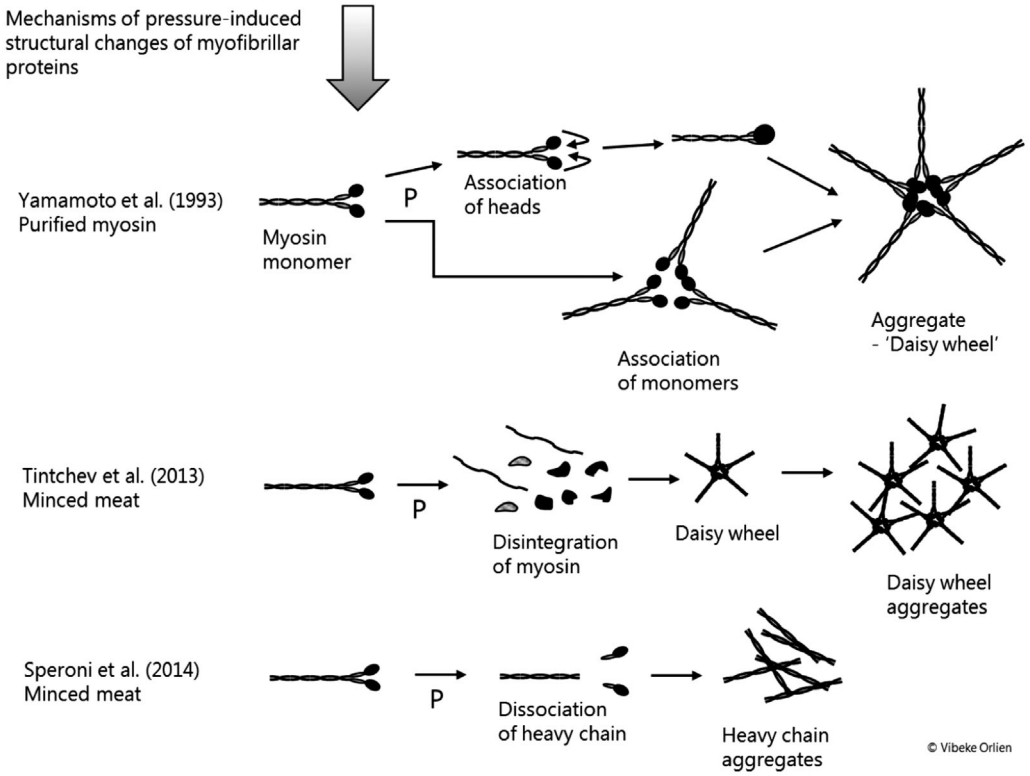


FIGURE 3 Continued

2.2.2 | Mechanistic description of the HP effect on muscle proteins

The HP-induced changes begin with fragmentation of the native myofibrils (Figure 3). The initial step is the I-band, M-line, and Z-line disruption when the pressure level reaches 200 MPa, resulting in the breakup of the myofibrillar structure (Jung, de Lamballerie-Anton, & Ghoul, 2000a; Noshiroya, Saitoh, Okano, & Yamamoto, 2006; Rusman, Gerelt, Yamamoto, Nishiumi, & Suzuki, 2007; Suzuki, Watanabe, Iwamura, Ikeuchi, & Saito, 1990). The I-band's rupture was shown to affect the thin filament, suggesting that depolymerization of F-actin may be causing fragmentation of the myofibrils (Suzuki et al., 1990). However, there is contradicting reports published, showing either remaining of the Z-line cohesion (Jung et al., 2000b; Rusman et al., 2007; Suzuki et al., 1990) or its dissolution (Iwasaki, Noshiroya, Saitoh, Okano, & Yamamoto, 2006). Loss of M-line was shown to affect the thick filament resulting in release of myosin (Iwasaki et al., 2006; Jung et al., 2000b). Iwasaki and Yamamoto (2002, 2003) observed that the myosin tail (S2) dissociated to single peptide chains and the head (S1), being the most pressure-sensitive part, was deformed (see : in Figure 3). It is noted in these studies that the subfragments, S1 and S2, were extracted from rabbit muscle prior to HPP treatment. Myosin's capacity to bind together and with water is very important for product quality being a determining factor of the water retention; thus, it has been one of the main interests concerning pressure effects. The myosin molecule is composed of two identical globular heads, which are connected to the light and the HCs as tail regions through the protein structure (Figure 3).

Myofibrillar protein solubilization due to HP-induced dissociation of the thin and thick filaments releases soluble materials from myofibrils. Depending on the protein system and pressure level, those proteins will either stay solubilized or alternatively become insoluble (Figure 3). As seen, a trend of decreased myofibrillar protein solubility is found in several published studies. The pressure impact on the individual proteins caused a decreased solubility as shown by several electrophoretic investigations (Angsupanich, Edde, & Ledward, 1999; Grossi et al., 2016; Speroni, Szerman, & Vaudagna, 2014; Tintchev et al., 2013). The HP-induced denaturation of the proteins resulted in modification either into larger insoluble protein aggregates, due to aggregation, or into small subfragments, due to further degradation, as shown by electrophoretic profiling. The general mechanisms behind the formation of insoluble aggregates are as follows: (a) the rupture of noncovalent interactions inside the molecules that result in protein denaturation and (b) formation of new intra- and/or intermolecular bonds due to the interaction

between the newly formed denatured protein's exposed areas. Formation of such new intermolecular disulfide bonds has been suggested to cause myosin HC aggregation (Angsupanich et al., 1999; Chattong & Apichartsrangkoon, 2009). However, it was also proposed that the aggregation of pressure-modified myosin was caused by hydrogen bonds (Angsupanich et al., 1999; Grossi et al., 2016; Ma & Ledward, 2004). The solubility loss was evaluated in detail by using a bond-targeting approach to elucidate the nature of these new protein–protein interactions behind the protein aggregation during pressurization (Grossi et al., 2016). It was concluded that aggregation was dominated by formation of hydrogen bonds, whereas the loss of protein solubility was not caused by increased disulfide cross-links and hydrophobic interactions in HP-treated meat. Figure 3 presents a more detailed description of the mechanisms of pressure-induced structural modifications of myofibrillar proteins based on previous studies (Speroni et al., 2014; Tintchev et al., 2013; Yamamoto, Hayashi, & Yasui, 1993). The first proposal was that of a daisy wheel, where the center is the association of the heads with the tails pointing outward, making up a myosin aggregate (Yamamoto et al., 1993). The two heads intramolecular association or head-to-head monomers intermolecular association was suggested to be the initial step upon pressurization. This results in one-headed species or small loosely bounded heads clusters resembling oligomers. Both types of species retain the ability to associate through hydrophobic interactions, deriving in oligomers shaped such as the daisy wheel (clumps) (Yamamoto et al., 1993; Yamamoto, Yoshida, Morita, & Yasui, 1994). It was reported that entangling of tails was not observed, which suggested that the tail resisted pressure and the helix structure was kept. The maximal number of myosin molecules contained in a daisy wheel oligomer seemed to be less than 20. Tintchev et al. (2013) based their mechanistic explanation on the findings of a full myosin disintegration into smaller fragments, *N*-terminal and *C*-terminal, upon HPP treatment of pork sausages at 200 and 300 MPa. After this initial myosin modification came a hydrophobic restructuring into similar types of daisy wheels, which further formed larger aggregates with actin and other muscle proteins into a protein network at pressures higher than 350 MPa. Nonetheless, the authors did not exclude that tail-to-tail interactions and entangling can be part of the further gel formation mechanisms at pressurization above 400 MPa. The third suggestion is also based on disintegration of the myosin molecules, but only partly dissociated into the myosin HCs and LCs (Speroni et al., 2014). They observed that the content of myosin HC increased, whereas no change in the myosin LC content was found when pressurizing beef patties at 300 MPa. Therefore, the authors concluded that aggregation due to pressure only involved myosin HC aggregations (Speroni et al., 2014). They emphasized that their extraction procedure may had disrupted other molecular interactions, and thus, aggregation with myosin LC and other proteins could not be completely discarded. The existence of three different suggestions for the protein–protein configuration of the formed aggregates expresses that it is still unknown. However, none of these mechanisms verify or reject the proposal that aggregation is caused solely by intermolecular disulfide bonding or H-bonding. The native solubility of myosin and actin was lost as shown by a target western blotting protein approach, meanwhile α-actinin and troponin-T were less affected at HPP treatment above 400 MPa (Grossi et al., 2016). This supports the hypothesis that myosin is very pressure sensitive and, under pressure it will dissociate and form aggregates, in agreement with the proposed mechanisms. Variations in the protein system under investigation, whole meat, minced meat, or myosin solution, will change the precise mechanism. Generally, the overall steps in the mechanism are as follows: (a) myofibrillar protein solubilization due to the thin and thick filaments dissociation as a result of the rupture of the filamentous structure, (b) protein denaturation caused by the noncovalent interaction rupture inside the molecules, and (c) formation of new intra- and/or intermolecular bonds because of the newly exposed areas of the denatured protein resulting in large aggregates. On top of that, HPP treatment induces as well protein oxidation events and promotes endopeptidase activity, both impacting myofibrillar protein structures and their functionalities (Grossi, Bolumar, Søltoft-Jensen, & Orlien, 2014; Grossi, Gkarane, Otte, Ertbjerg, & Orlien, 2012).

2.2.3 | Myofibrillar gelation under HPP

The most outstanding impact of HPP treatment of meat is the effect on the myofibrillar protein architecture, and the subsequent effect on the individual muscle proteins as described in Section 2.2. Pressure levels above 200 MPa lead to degradation of the myofibrils and releasing of soluble proteins. Higher pressure levels result in protein unfolding, prone to agglomeration, aggregation, and later on network formation. Thus, reactivity may change due to pressure modification of protein structure, and therefore, the functional properties. These pressure-induced structural modifications of the proteins lead to changes in the textural properties. Hydrogen and disulfide bonds, hydrophobic and interactions and disruptions, and subsequent reformation transform the native protein into a denatured protein and formation of aggregates. Three different approaches to myosin denaturation

following aggregation were presented in Section 2.2. Yet, other suggestions concerning the particular type of interaction(s) responsible for protein aggregation have been published: formation of disulfide and hydrophobic bonds (Chattong & Apichartsrangkoon, 2009), stabilization via hydrogen bonds and/or electrostatic interactions (Speroni et al., 2014), formation of hydrogen bonds first and then stabilization by disulfide bonds (Angsupanich et al., 1999), or only hydrogen bond stabilization (Grossi et al., 2016, Ma & Ledward, 2004). Nevertheless, release of protein material and denaturation are a precondition required for aggregation and structure formation in meat systems.

The aggregation of the myosin and actin structural proteins resulted in the loss of their native functionality above 400 MPa (Grossi et al., 2016). This indicated that the threshold for loss of solubility is around 400 MPa, and it is accompanied by a change of functionality. The elasticity of the thermal gel of chicken myofibrillar proteins was highest when the protein solution (20 mg/mL) had been pressurized at 200 MPa prior to heating (Iwasaki et al., 2006). Rheological behavior is often used to describe protein gelling functionality as it measures the gelation properties during increasing temperatures (20 to 80 °C), relevant for meat processing. The HP-induced structural changes of myofibrillar proteins and their relationships with the gelation properties were assessed for rabbit and chicken myosin solutions by investigating the microstructure and rheological properties (Cao, Xia, Zhou, & Xu, 2012; Zhang, Yang, Zhou, Zhang, & Wang, 2017). HPP treatment (100 to 400 MPa, 20 °C, 10 min) of rabbit myosin solutions (20 mg/mL) resulted in more solid and elastic gels compared to untreated myosin proteins, though increasing the pressure levels decreased the storage and loss modulus (Cao et al., 2012). This observation was explained by the formation of a gel network during the HPP treatment, especially at 400 MPa, thus this arranged aggregation and three-dimensional network was translated into decreased G' and G'' during heating, which agrees with the suggested threshold at 400 MPa. Similarly, it was found that low/moderate pressure (below 200 MPa, 10 min) of chicken myosin solution (30 mg/mL) following mild heating (65 °C, 20 min) raised the solubility and amount of denatured proteins, and thereby strengthened the gelation properties of myofibrillar proteins (Zhang et al., 2017). However, HPP treatment higher than 300 MPa induced severe protein unfolding, leaving few native molecules, and a heterogeneous gel microstructure was formed as the native protein unfolding speed was slower than aggregation, then it resulted in low hardness when heated for gelation. Hence, pressurization above 300 MPa impaired the heat-induced gelation ability of myofibrillar proteins. It was concluded that 200 MPa was the best pressure level to modify myofibrillar proteins for improving gelation functionality (Zhang et al., 2017).

The gelation features, gelation properties and texture, can be regarded as the macroscopic reflection of the microstructure of the gels. By using SEM, it was showed that myosin gels processed at 300 and 400 MPa with a following heat treatment led to a gel with many large gaps and globular aggregates, meanwhile gels formed at 100 and 200 MPa (i.e., below the pressure threshold) had many more voids of small-size and filament-like structures with many cross-links (Cao et al., 2012). Similarly, Zhang et al. (2017) found that gels formed after HPP treatment at 200 MPa had a denser and much more homogeneous protein network, bringing about a stronger gel than gels set after HPP pretreatment at pressures above 300 MPa, which were heterogeneous and presented large gaps. Iwasaki and co-workers (2006) also found that the elasticity of the pressure–heat-induced gels were higher for the 200 MPa gels than the 300 MPa gels. The heating/cooking of gels previously submitted to HPP treatment at 200 MPa enabled the formation of a finely dispersed, three-dimensional network of strands without any myofibrillar structure remaining (Iwasaki et al., 2006). The authors proposed that this gel type was the result of the depolymerization of the thin filaments: (a) the myosin filament (20 mg/mL in 0.2 M NaCl, pH 6.0) dissociated under pressure at 200 MPa and scattered myosin was reassociated to the myosin filament upon HPP treatment and (2) interaction among rearranged myosin filaments was promoted by the subsequent heating giving a strand-like type-gel (Iwasaki et al., 2006). Excessive protein denaturation is obtained at pressures higher than 300 MPa, which gives rise to other intra- and intermolecular interactions, resulting in an aggregated and irregular structure of the gels prior to heat treatment (Cao et al., 2012; Zhang et al., 2017). In agreement, Huang, Guo, Xiong, and Li (2016) observed that unfolding and aggregation processes counterbalanced each other with increasing pressures. They extracted the myosin proteins after pressure combined with heat treatment of pork *longissimus dorsi* and observed that the surface morphology became more uneven and rugged having openings and protein aggregates. Protein solubility and the gel microstructure are affected by adding salt to the myofibrillar protein solution. Hence, HPP treatment up to 400 MPa (15 min at room temperature) of chicken myofibrillar protein (40 mg/mL) in 0.1 M NaCl resulted in a gel mesh with structure of myofibrils, whereas disruption of the myofibril was observed in 0.2 M NaCl already at 200 MPa (Yamamoto, Yoshida, & Iwasaki, 2002). Moreover, the micrographs of the gels revealed that the surface of the myofibrils had a spiny structure formed by solubilized myofibrillar proteins. However, it was found that the strength of the gel set at 0.1 M NaCl increased with

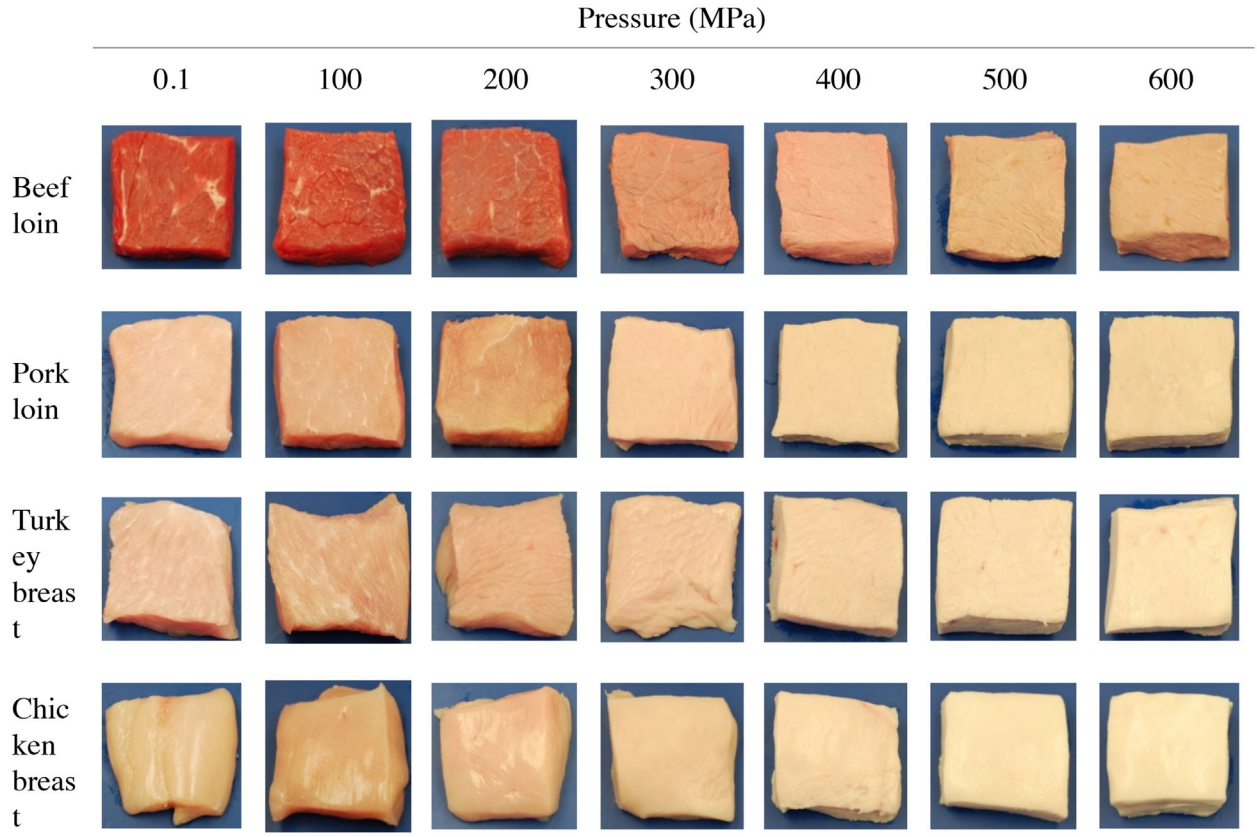


FIGURE 4 Color changes of beef loin, pork loin, turkey breast, and chicken breast upon high-pressure processing at the specific pressure for 5 min at room temperature (20 °C)

pressure (up to 500 MPa), thought was nearly not affected for the 0.2 M NaCl protein solution, which is in contrast to the former mentioned investigations. Overall, the protein concentration as well as the processing conditions, such as pressure level, time, and temperature, determines the outcome of pressure-induced gelation of myofibrillar protein systems. Therefore, HPP treatment of meat can be used to functionalize meat systems, which is presented in Section 3.3.

2.3 | HPP effect on color

Because HPP has an important effect on proteins (Section 2.2), it is no surprise that HPP affects meat color. The extent of the effect of an HPP treatment on fresh meat color depends primarily on the pressure level, the particular meat (species and muscle) being pressurized, and the initial oxidative state of myoglobin (Mb). In contrast, cured meats respond quite differently to HPP as compared to fresh meat, as nitrification will protect myoglobin from HP-induced oxidation.

2.3.1 | Effect of meat type

Meat types containing a high level of Mb ("red meat") are visually more affected by HPP than meat types with a low level of Mb ("white meat"). This is illustrated in Figure 4 and further details can be consulted in the review paper by Bak, Bolumar, Karlsson, Lindahl, and Orlien (2017).

Different meat animal species contain various levels of Mb (mg/g of meat), with "whiter meats" such as chicken and turkey containing 0.01 to 1.5 mg/g, pork 0.6 to 6.0 mg/g, and "red meats" such as sheep and beef 2.0 to 9.0 mg/g (Faustman & Suman, 2017; Young & West, 2001). It is seen from Figure 4 that HP treatment causes beef to fade to a brownish color, whereas pork, turkey, and chicken attain a paler appearance. Pressure-induced meat color changes are induced by denaturation of Mb and other meat proteins, alteration or disruption of the porphyrin ring, and changes in the redox chemistry of Mb (Bak et al., 2017; Cheftel & Culioli, 1997). This negative HP-induced effect on fresh meat color has been suggested to be used positively to produce fat replacers for their use in meat products, that is, raw poultry meat processed by HPP becomes white in appearance and optically similar to

fat particles (Kortschack, Heinz, & Bajovic, 2013), and has been used to manufacture fat-reduced Salami (Bolumar, Toepfl, & Heinz, 2015).

2.3.2 | Effect of pressure level and temperature

Pressure level affects denaturation of proteins. At pressure levels <200 MPa, there is only a very slight color change in comparison to unpressurized meat (0.1 MPa) (Figure 4), whereas application of pressures >200 MPa will make meat appear much paler than unpressurized meat due to muscle protein denaturation and coagulation. It has been reported that HPP (especially pressure levels >400 MPa) causes reduced water holding capacity (WHC) as well as lower sarcoplasmic protein solubility (Hughes, Oiseth, Purslow, & Warner, 2014; Marcos, Kerry, & Mullen, 2010) due to denaturation of myofibrillar proteins beginning at around 200 MPa, and of Mb at around 400 MPa, likely resulting in co-precipitation (Ma & Ledward, 2013). The structural modifications lead to changes in the ratios of absorbed, diffracted, and reflected light, resulting in increased light scattering, and hence, a paler appearance of the meat (Hughes et al., 2014). In appearance, HP-processed meat is quite similar to cooked meat, though with some particular molecular changes to Mb, which can be observed, for example, via surface reflectance measurements (Bak, Lindahl, Karlsson, & Orlien, 2012).

As a consequence of the adiabatic heating, HPP causes a temperature increase of water of approximately 2 to 3 °C per 100 MPa (Aertsen, Meersman, Hendrickx, Vogel, & Michiels, 2009; Knorr, 1999). Food products that have a high water content will experience a similar rise in temperature during HPP (Aertsen et al., 2009). However, temperature increases may be as high as 9 °C per 100 MPa, the exact increase depending on the composition of the food product in question (Patterson, Linton, & Doona, 2007). The extent of protein denaturation is directly connected to the combination of HP and temperature applied (Chen et al., 2017). But interestingly, the effect of processing temperature on meat color appears not to be dependent on the effect of pressure (Bak, Lindahl, Karlsson, & Orlien, 2012; Marcos et al., 2010). This is even though increasing pressure raises water temperature, which leads to increased protein denaturation, and therefore, increased lightness of the meat (Bak, Lindahl, Karlsson, & Orlien, 2012). The topic of protein modification in meat during cooking has been reviewed recently by Yu, Morton, Clerens, and Dyer (2017), who described denaturation of myofibrillar proteins beginning at 40 to 50 °C (Bouton, Harris, & Shorthose, 1976; Davey, & Gilbert, 1974), but denaturation may also occur at temperatures as low as 30 °C (Warriss, 2000).

2.3.3 | Effect of myoglobin chemical state

HPP also impacts the redox chemistry of Mb. Different myoglobin redox forms—deoxyMb, oxyMb, and metMb—have different susceptibilities to HP-induced denaturation. Thus, the proportions of the three Mb forms found in fresh meat prior to HPP are very important with regard to HP-induced color changes. At pressure levels <300 MPa, Mb is relatively stable to HPP, at least if deoxyMb is the predominant Mb form in the raw meat (Bak, Lindahl, Karlsson, & Orlien, 2012). Oxygenation as a result of HPP is sometimes reported, generally at low to moderate pressures (up to 300 to 350 MPa) (Bak, Lindahl, Karlsson, & Orlien, 2012; Jung, Ghoul, & de Lamballerie-Anton, 2003; Schenková et al., 2007), whereas oxidation to metMb is seen at higher pressures (pressure level above 300 MPa) (Carlez, Veciana-Nogues, & Cheftel, 1995). Yet, as reported in the review by Bak et al. (2017), this is an area where differences are frequently observed among studies. These inconsistencies in the meat color values likely stem from a number of reasons, mainly the original Mb form before HPP, the pressure level applied, and how long after the HPP treatment the instrumental color measurements were done, as an initially developed ferrous Mb form has been found to disappear within the first day after the HPP treatment (300 to 800 MPa) (Bak, Lindahl, Karlsson, & Orlien, 2012).

2.3.4 | Effect of curing

Different from fresh meat, cured meat color is significantly more stable to HPP (Bak, Lindahl, Karlsson, Lloret, et al., 2012; Goutefongea, Rampon, Nicolas, & Dumont, 1995). It has been suggested that the already stable cured meat pigment, nitrosylmyochromogen, is subsequently stabilized by HPP (Bak et al., 2013). Yet, it can still be sensitive to photooxidation during storage (Andrés, Adamsen, Møller, Ruiz, & Skibsted, 2006). Bak et al. (2013) have hypothesized that HPP results in stabilization of nitrosylmyochromogen as a result of the formation of intermolecular bonds with water. Because the effect of HPP is dependent on compression of water, it is surprising that a greater effect on color has been reported for meat products with higher content of water (Bak et al., 2013; Ferrini, Comaposada, Arnau, & Gou, 2012). The vast majority of studies investigating the effect of HPP on cured meats show no change in redness, confirming the stabilizing effect of HPP, whereas lightness tends to increase or stay stable (Bak et al., 2017). Concerning cooked, cured ham, HPP causes no additional increase

in lightness (Goutefongea et al., 1995) as muscle proteins were already in a denatured state after cooking. In contrast, meat that has been cured but not cooked may experience some increase in lightness as a consequence of HPP-induced protein denaturation (Bak et al., 2017). HPP has been useful to process an uncooked and nondried cured product such as carpaccio microbiologically safe, but in some cases a negative effect on color was observed (de Alba, Bravo, & Medina, 2012; Realini, Guàrdia, Garriga, Pérez-Juan, & Arnau, 2011; Szerman et al., 2011). Because of the dependence of the HPP effect on the water compression, carrying out HPP while the meat is in a frozen state will mitigate the negative effects of HPP on color (Szerman et al., 2011; Vaudagna et al., 2012). Particularly, there is a smaller increase in lightness due to a reduced extent of muscle protein denaturation (Szerman et al., 2011). In general, cured meat color is better stabilized by HPP, when HPP is applied after cured color has been allowed to fully developed (Serra et al., 2007).

2.4 | HPP effect on lipid and protein oxidation

Previous studies have reported that HPP treatments could trigger oxidation reactions in meat. In this context, the control of the level of pro- and antioxidant compounds is necessary to prevent these reactions (Guyon, Meynier, & de Lamballerie, 2016). Therefore, many authors have evaluated the extent of oxidation in HP-treated meat to understand the mechanisms and pathways that HPP favors.

2.4.1 | Lipid oxidation in pressurized meat

The effect of HP on lipid oxidation is mainly coupled with radical formation reactions, presence of catalysts such as enzymes, proteins, or metal ions, and the balance of antioxidant and pro-oxidants compounds (e.g., oxygen) in the product. Numerous authors have pointed that lipid oxidation induced by HP is initiated by the presence of low-molecular-weight iron compounds and myoglobin, hemoglobin, and ferritin in meat (Alves de Oliveira, Neto, Marcondes Rodrigues dos Santos, Ferreira, & Rosenthal, 2017). The amount of radicals formed during HPP treatment is potentially responsible of lipid oxidation and depends on the parameters of the treatment (P, T, and holding time) but also on the type of meat (species and muscle) (Bolumar, Skibsted, & Orlien, 2012). Thus, Schindler, Krings, Berger, and Orlien (2010) showed that volatile compounds from lipid oxidation are fewer in beef meat than in other types of meat. Likewise, in fish meat, pressures below 400 MPa have no major effect on the lipid oxidation, probably due to their low hemoprotein level and the presence of phenolic antioxidants (Gomez-Estaca, Gomez-Guillen, & Montero, 2007; Montero, Gimenez, Perez-Mateos, & Gomez-Guillen, 2005). The mechanisms of lipid oxidation induced by HP are poorly understood. However, the authors do agree to describe three preferential ways of induction of lipids oxidation by HP. The first mechanism would be an action of the HP on hemoproteins with increased accessibility of iron. Several works have showed that the level of lipids oxidation after HPP treatment was lower with the presence of a chelating agent like Ethylenediaminetetraacetic acid (EDTA). These results seem to show that preferential mechanisms of lipid oxidation induced by HP use metal ion catalysis (Beltran, Pla, Yuste, & Mor-Mur, 2004; Cheah & Ledward, 1996, 1997a, 1997b; Ma, Ledward, Zamri, Frazier, & Zhou, 2007). Although this hypothesis has not yet been fully confirmed experimentally, some authors have suggested that HP could also cause a release of ferric ions. The second mechanism would come from a membrane disruption, favoring enzymatic activities on unsaturated lipids from the membrane and at the same time promoting a catalysis of the lipid oxidation by metal cations (Bajovic et al., 2012). A third mechanism was suggested by Bolumar et al. (2012) in chicken breast, showing that the kinetic of radical species was different at pressures of 400 MPa and higher. These results seem to indicate that the induction of lipid oxidation by HP originates from the free radicals formed during the HPP treatment.

With regard to these mechanisms, the addition of antioxidants such as polyphenols, metal chelating agents, or proteins permits to control the oxidation of pressurized samples. Bragagnolo, Danielsen, and Skibsted (2007) evidenced that rosemary extract is effective to reduce the formation of free radicals in minced chicken (breast and thigh muscle) pressurized at 600 MPa.

The vacuum packaging, frequently used prior to the HPP treatment, can also reduce the effect of HP on the meat oxidation (Mariutti, Orlien, Bragagnolo, & Skibsted, 2008). Moreover, some authors have shown that during a cold storage, the formation of thiobarbituric acid reactive substances (TBARS) (a secondary product of lipid oxidation) in pressurized meat can be reduced by the use of antioxidant active packaging. However, whatever the packaging method (vacuum, with rosemary extract or oxygen scavenger) and the meat (chicken or pork), after HPP treatment the lipid oxidation is higher at the surface than at the inner part of the meat (Bolumar, Andersen, & Orlien, 2011; Bolumar, LaPena, Skibsted, & Orlien, 2016) (Figure 5).

In the literature, studies have evaluated the impact of HP on lipid oxidation immediately after HPP treatment and/or during the storage. Cheah and Ledward (1997)

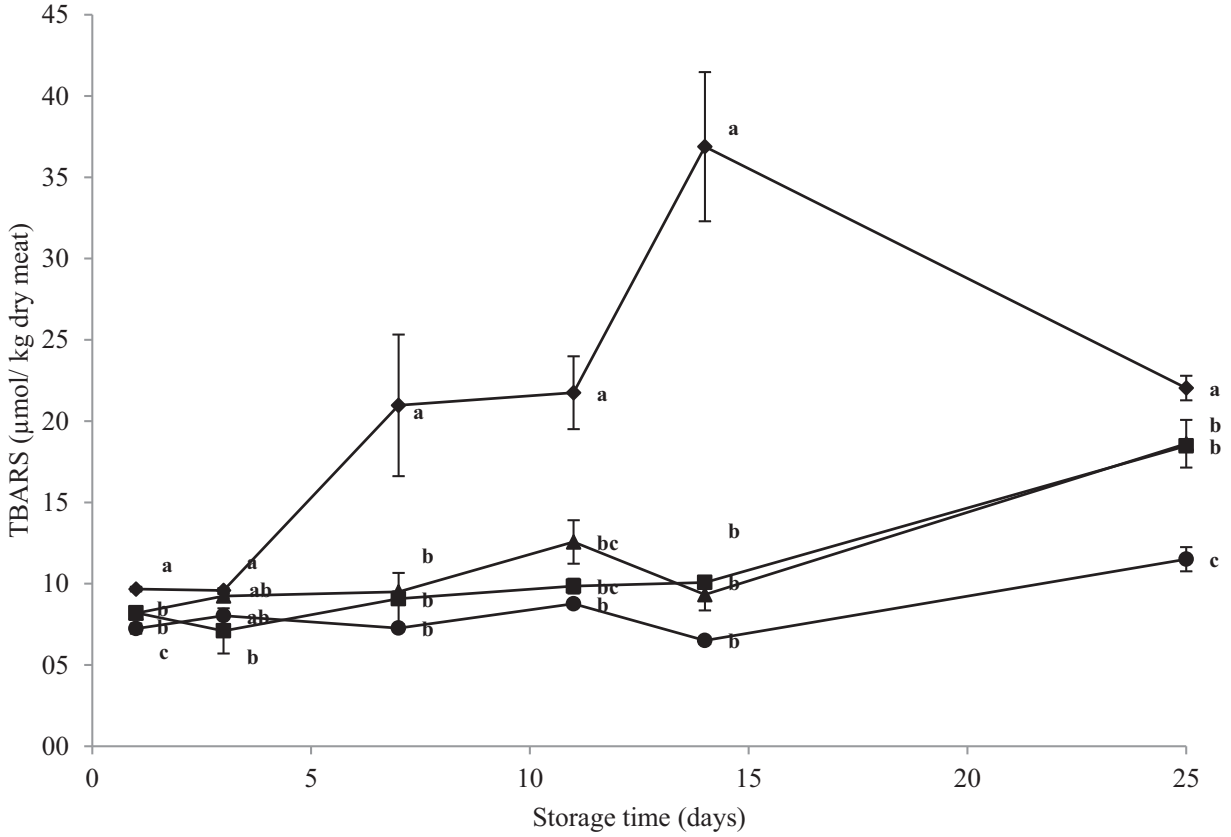


FIGURE 5 Oxidation products as thiobarbituric acid reactive substances (TBARS) at the surface part and the inner part of minced chicken breast patties packaged without (control) or with antioxidant active packaging pressurized at 800 MPa, 10 min, 5 °C during chill storage in the dark. (◆) control surface part; (■) control inner part; (▲) antioxidant packaging surface part; (●) antioxidant packaging inner part. A different letter within the same storage time means a significant difference at*p*-value <0.05 (Bolumar et al.,2011)

thus showed, in minced pork, that a threshold pressure between 300 and 400 MPa was required to observe a significant increase in lipid oxidation immediately after HPP treatment. In the same way, Beltran, Pla, Capellas, Yuste, and Mor-Mur (2004) showed a significant increase in the TBARS content of chicken muscle after a treatment at 500 MPa; these authors, in comparison with a thermal treatment (90 °C for 15 min), have shown that the level of hexanal was lower in pressurized samples until 300 MPa but higher in those treated at 500 and 900 MPa. These results confirm a threshold pressure beyond which the lipid oxidation mechanisms are different (Beltran, Pla, Yuste, et al., 2004).

Several authors have evaluated markers of lipid oxidation in different meats treated by HP during and/or after storage. The evolution of the substrates of lipid oxidation showed no change in the amount of triglycerides but a significant difference in the free fatty acids composition of phospholipids (Barba, Terefe, Buckow, Knorr, & Orlien, 2015; He et al., 2012; Huang, He, Li, Li, & Wu, 2012). Many authors have chosen to evaluate the amount of TBARS. Dissing, Bruun-Jensen, and Skibsted (1997) highlighted that the amount of TBARS was correlated with the pressure level, with a possible prediction of lipid oxidation in pressurized turkey meat. The TBARS content in chicken pressurized between 300 and 800 MPa, and then stored at 5 °C for 14 days, is more important, particularly at pressures up than 400 MPa (Orlien, Hansen, & Skibsted, 2000). In beef pressurized between 200 and 600 MPa and refrigerated for 7 days, the level of TBARS also increased (Ma et al., 2007). However, a recent study by Gimenez, Graiver, Califano, and Zaritsky (2017) on beef meat pressurized between 400 and 600 MPa and kept at 0 °C demonstrated that the TBARS value increased during storage after HPP treatment, but without exceeding a maximum level of 2 mg of malondialdehyde (MDA) per kg of meat product (Boles & Parrish, 1990; Campo et al., 2006). Conversely, the impact of HPP treatment on the volatile compounds (terminal products of lipid oxidation) is variable. For instance, HPP treatment did not cause severe changes in the aromatic profiles of raw beef and chicken meat treated at 400 and 600 MPa and stored at 5 °C for 14 days (Schindler et al.,

2010). However, the accumulation of volatile compounds (aldehydes) was lower in pressurized meat than in the control after refrigerated storage (Rivas-Canedo, Fernadez-Garcia, & Nunez, 2009), due to the decrease of the lipolytic activity of HP-sensitive bacteria.

Finally, the effect of HP on the lipid oxidation in dried meat products is enhanced by the postprocessing operations and the longer preservation time, and then is very different from other processed meat (Guyon et al., 2016).

2.4.2 | Protein oxidation in pressurized meat

The relevance of protein oxidation induced by HP has only recently obtained the same interest as lipid oxidation, which is showed by a growing number of studies dealing with this topic. The protein modifications under HP are complex and result from both conformational, as described in Section 2.2, and chemical changes.

Generally, the protein oxidation can be induced directly by reactive oxygen and nitrogen species, or indirectly by many species including radicals or reactive aldehydes and ketones (Mora, Gallego, Aristoy, & Toldra, 2019). Thus, a high complexity of pathways and a large variety of oxidation products have been described (Lund, Heinonen, Baron, & Estevez, 2011). The review of Soladoye, Juarez, Aalhus, Shand, and Estevez (2015) provides a summary of the different pathways leading to the protein oxidation. The protein oxidation process involves both carbonylation reactions and oxidation reactions of thiols with the formation of disulfide bridges and the formation of compounds involving irreversible bonds resulting from a protein rearrangement (polymerization, aggregation, and scission) and a modification of amino acid chains (Mora et al., 2019; Nagy & Winterbourn, 2010; Soladoye et al., 2015). Although the formation of disulfide bridges is often described as the only result of the oxidation of thiols, there are many thiol oxidation products, including highly reactive compounds able to dissociate and form stable compounds such as sulfonic acid (Nagy & Winterbourn, 2010).

The access of oxidative agents to their target can be modified by HP, which can, in some cases, favor the formation of compounds from oxidation (Guyon et al., 2016; Mora et al., 2019). The simultaneous evaluation of several indicators of protein oxidation (formation or dissociation of disulfide bridges, formation of carbonyl groups) is therefore essential to evaluate the overall impact of HPP on proteins. Thus, Grossi et al. (2014) showed an increase of the carbonyls content and a decrease of the free thiol groups content in a sarcoplasmic protein fraction of pork meat (*Semitendinosus*) vacuum packed and pressurized at 600 MPa upon 8 weeks of storage at 2 °C. Conversely, the content of free thiol groups in the myofibrillar protein fraction increased during the storage.

HPP treatment also modifies the amounts of free amino acids (FAAs) present in meat after storage (Guyon, Le Vessel, Meynier, & de Lamballerie, 2018), thus, FAA content was increased by the application of moderate pressures, namely, 200 and 300 MPa, and lowered by application of higher pressure, 500 MPa. The impact of HP on enzymatic activity, cofactors, and substrates has to be considered, but cannot explain all the phenomena. Thus, the position of amino acids within the protein structure greatly affects their exposure to oxidant factors (Mora et al., 2019). Figure 6 presents the amount of protein carbonyls, free thiol ratio, and FAAs in the protein extract of minced bovine meat immediately after HPP treatment. The impact of HP is perceptible from 200 MPa and is emphasized at 300 MPa.

In the absence of major structural changes at pressure under 100 MPa, the ionic interactions break under pressure and reform after the treatment (Ma & Ledward, 2013).

2.4.3 | The relationship between lipid and protein oxidation in pressurized meat

Lipid and protein oxidation are closely interconnected (Estevez, 2011). Various authors have shown a positive correlation between lipid and protein oxidation induced by HP. Ferryl species, from myoglobin, are better catalysts of the oxidation than protein radicals (Rao, Wilks, Hamberg, & Ortiz de Montellano, 1994). The oxidation is prevented when the chelators are more efficient than scavengers, so the implication of the ferrous ions seems to be a preferential way of the oxidation induced by HP (Bolumar, Andersen, & Orlien, 2014; Cheah & Ledward, 1997; Tume, Sikes, & Smith, 2010).

In dried meat products, the low water content and water activity limit protein oxidation. Thus, Cava, Ladero, Gonzales, Carrasco, and Ramirez (2009) followed during 90 days of storage at 4 °C the level of TBARS and 2,4-dinitrophenylhydrazine in dry cured products, pressurized at 200 to 300 MPa. They showed an increase in the level of lipid oxidation but no significant change in the level of protein oxidation. However, these results could be due to these particular type of meat products but also the low level of pressure applied in that study. Conversely, Fuentes, Ventanas, Morcuende, Estevez, and Ventanas (2010) have demonstrated in dry-cured ham treated at 600 MPa that lipid and protein oxidation were closely related, based on the correlation between the hexanal and the protein semialdehyde content.

The HPP treatment generally promotes the oxidation of lipids and proteins. However, oxidation mechanisms

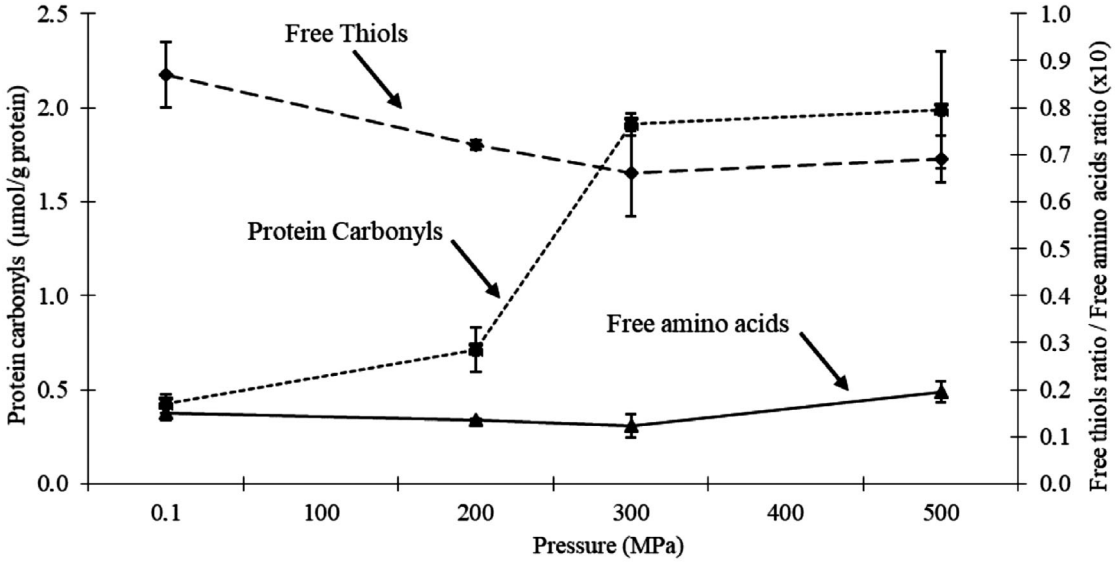


FIGURE 6 Protein carbonyls (■), free thiol ratio (◆), and free amino acids ratio (▲) in the protein extract of minced bovine meat just after (day 0) high-pressure treatment for 5 min at the specified pressure ($n = 3$). Free thiol and free amino acids ratios were calculated by dividing the concentration of free and total for each component (Guyon et al.,2018)

are also modulated by external factors, such as the type of packaging used and the commercial presentation. In a recent study of vacuum-packaged ground beef processed between 200 and 500 MPa, the coupled monitoring of indicators of lipid and protein oxidation immediately after pressurization showed a positive correlation between the increase in hexanal content, the increase of carbonylated proteins, and the decrease of free thiols with an apparent decrease of TBARS (Guyon, 2016). The decrease in TBARS combined with the loss of protein solubility probably comes from the interaction between the compounds from lipid oxidation and the oxidized proteins under HP. Campus, Flores, Martinez, and Toldra (2008) also showed a lack of correlation between the TBARS level and the occurrence of volatile compounds in vacuum-dried pork loin treated by HPP, with a decrease in TBARS from 300 MPa, counterbalanced by an increase of the hexanal. The low oxygen concentration in meat stored under vacuum slows down the production of compounds derived from lipid oxidation, and the speed of the TBARS generation is probably slower than the formation of MDA–protein complexes. Thus, Gobert et al. (2010) confirmed that the promotion of oxidation in beef meat is dependent on the oxygen concentration in the packaging atmosphere. The commercial meat presentation has an impact on the promotion of oxidation too. Hence, oxidation in dry-pre-sliced ham, pressurized and stored at refrigerated temperature, was enhanced compared to nonsliced vacuum-packaged ham (Fuentes et al., 2010), likely because of increased surface area, which facilitated the contact between oxygen and meat product.

Then differences in the type of meat, the packaging, the HPP treatment, and the type of storage induce conflicting results. But overall, the application of an HPP treatment to meat has consequences on lipid and protein oxidation, and further on the aromatic profiles during refrigerated storage, which will have to be carefully considered for certain applications when designing appropriate protective strategies to preserve product's flavor quality. It is foreseeable to believe that there may exist interconnections between lipid and protein oxidation on a molecular level. However, the complexity of these chemical reactions and the meat matrix structure and composition makes the precise characterization of the particular underlying mechanisms extremely difficult in many cases, and further research is warranted in this area.

3 | APPLICATIONS OF HPP IN THE MEAT INDUSTRY

3.1 | Cold pasteurization for safety assurance and shelf-life extension

Meat composes favorable conditions for microbial growth. Yet, safety and quality of the products must be ensured (Biswas, Kondaiah, Anjaneyulu, & Mandal, 2011). Due to high water content and presence of nutrients, meat represents a suitable medium for growth of a wide range of microorganisms, including spoilage bacteria and pathogens (Hayman, Baxter, O'riordan, & Stewart, 2004; Naidoo & Lindsay, 2010; Nicolaou, Xu, & Goodacre,

2012). The most prevalent pathogens in fresh and frozen meat and related products are *Salmonella* sp., serovars of enterohemorrhagic *E. coli* (EHEC) (e.g., O157:H7), *Listeria monocytogenes*, *Staphylococcus aureus*, and *Clostridium botulinum* (Mor-Mur & Yuste, 2010; Omer et al., 2018). However, there are other so-called emerging pathogens that potentially represent a risk to consumers such as *Campylobacter jejuni*, *Salmonella typhimurium* DT 104, *Arcobacter butzleri*, *Mycobacterium avium* subsp. *paratuberculosis*, *Aeromonas hydrophila*, and prions (Mor-Mur & Yuste, 2010).

It has been generally recognized that HPP is more suitable for preservation of processed meat, rather than raw meat. As already discussed, the HP-induced color changes are a result of denaturation of myoglobin. Several studies have reported significant color changes in the pressure range above 200 to 300 MPa (Carlez et al., 1995; Kruk et al., 2011; Bak, Lindahl, Karlsson, & Orlien, 2012), generally reporting increased brightness (*L*: values) and reduced red color (*a*: values). Schmidgall, Hertel, Bindrich, Heinz, and Toepfl (2011) investigated HPP as a possible technology for shelf life extension of marinated poultry meat. The study included several spoilage and pathogenic strains, as target microorganisms. The authors reported that *Leuconostoc gelidum* exhibited the highest tolerance against pressure and was suggested as a relevant spoilage microorganism, and *Arcobacter* was suggested as a relevant target strain for pathogenic microorganism. Some raw meat products are currently commercialized (Bajovic et al., 2012) and some examples are discussed here. Minced meats usually present a higher risk of microbial contamination than entire meat cuts, with the microbial contamination generally on the surface, and easily destroyed during cooking. The Dutch company Zwaneberg applies HPP to inactivate hazardous bacteria in the production of steak tartare, and thus, increases safety and extends shelf life, without compromising quality and flavor. The company Cargill from the United States uses HPP in beef patties, also for safety purposes, under the commercial name "Fressure." This type of products is used in foodservice and as such not displayed to the consumer prior to cooking, and in that case, color change after cooking is of much less importance. After preparation, the HP-treated patties exhibit the same appearance and taste as untreated patties. As such, the HPP represents a tool to provide an extra decontamination step in the supply chain of some HPP-suitable raw meat products, allowing a further assurance of food safety.

Food preservation by HPP is a physical postpackaging preservation treatment that can be applied to various foods, provided they have the necessary water content to transmit the hydrostatic pressure and no air voids are present. HPP has been successfully applied in the food industry since 1990 to inactivate microorganisms, with approvals of the Food and Drugs Administration (FDA), the United States Department of Agriculture (USDA), the European Food Safety Authority (EFSA), Health Canada, and other regulatory agencies in many countries. From a total of around 420 HPP machines installed worldwide at the moment, around 30% is used for preservation of cooked and cured meat products (Tonello, 2018). The most commonly HPP-produced commercial products include dry cured ham, dry-fermented sausages, cooked ham, sausage minced meat, and beef (Simonin et al., 2012ÿ Meloni, 2019).

3.1.1 | Combination of HPP with other hurdles

Suitability of HPP as a postpackaging treatment for processed meat does not come into question. However, in the case of raw meat, changes in elasticity, hardness as well as color at mid to HP intensities have been well documented (Carlez et al., 1995; Simonin et al., 2012; Tintchev et al., 2010, 2013). These effects limit the commercial potential of HPP as a single solution for preservation of raw meat, unprocessed seafood, and similar protein-rich food. Furthermore, it should be noted that HPP is not an effective treatment against spore-forming bacteria, and therefore, additional control measures such as nitrite addition, refrigeration during storage, addition of 2% w/w sodium lactate, use of protective cultures, or use of oxygen-permeable packaging or combinations thereof would have to be implemented to assure food safety of the product over an extended storage period under the light of the toxin-forming spore *Clostridium Botulinum* risk (Linton, Connolly, Houston, & Patterson, 2014; Ramaroson et al., 2018). Another possibility, which is not currently commercially viable, would be the use of heat combined with high temperatures to attain commercial sterilization (c.f. Section 5). Besides, HPP is often associated with higher processing costs, mainly due to energy required to build up the pressure, the batch nature of the processing, and the inability to recover the applied energy (Aganovic et al., 2017; Rodriguez-Gonzalez, Buckow, Koutchma, & Balasubramaniam, 2015). Thus, any reduction of processing time and pressure level or increase of treatment volume and filling ratio would positively reflect on the process efficiency. In this context, a "hurdle" approach could be introduced as a solution to address the minimally processed food with increased safety and moderate costs. Hurdle technology represents a combination of different preservation factors with the aim to produce stable food while minimizing the damage to the nutritional and functional properties of foods (Leistner, 2000). Furthermore, the resistance of microorganisms to a combined preservation approach is lower as the different preservation

methods may have different modes of action and affect certain microflora in a different way. In theory, HPP can be combined with several approaches, such as heat, antimicrobial substances, phages, changes in formulations, and others.

3.1.1.1 Antimicrobials

The combination of HPP with antimicrobials added to foods is a preservation concept that has been investigated in a variety of foods. Different organic acids, plant extracts, bacteriocins, lysozyme, lactoperoxidase system, chitosan, and some others have been investigated for inactivation ability or to permit the control of pathogens and extend shelf life of different products. Certain studies showed that combinatory effects of HPP and antimicrobials were successful against *Listeria monocytogenes*, *Salmonella enterica*, *Escherichia coli* O157:H7, spore-forming bacteria, and other targets (Barba, Criado, Belda-Galbis, Esteve, & Rodrigo, 2014; Chung & Yousef, 2010; Garcia-Graells, Masschalck, & Michiels, 1999; Whitney, Williams, Eifert, & Marcy, 2008). In a meat model based on cooked ham, the use of bacteriocins (enterocins A and B, sakacin K, pediocin AcH, or nisin) in combination with HPP (400 MPa, 10 min, 17 °C) was investigated and the development of bacterial cell counts during storage at 4 °C was monitored (Garriga, Aymerich, Costa, Monfort, & Hugas, 2002). Compared to the other bacteriocins, lower cell counts of *Staphylococcus aureus* during storage were obtained when nisin A was included. Remarkably, a >1 log higher inactivation of *E. coli* by HPP was observed when nisin was present in the product and the counts of surviving cells remained unchanged during storage for 61 days. In the same study, low counts (10^2 CFU/g) of *Listeria monocytogenes* were reported in treatments with sakacin, enterocins, or pediocin after a storage for 61 days. Combination of nisin (200 ppm), acidification, and HP (450 MPa) showed a great decrease in counts of the mesophilic and psychrotrophic microbiota of poultry meat (approximately 5 to 7 log reduction) (Yuste, Pla, Capellas, & Mor-Mur, 2002). In the study of Marcos, Jofré, Aymerich, Monfort, and Garriga (2008), the effect of HPP (400 MPa, 10 min) and antimicrobials (enterocins and lactate–diacetate) on the growth of *L. monocytogenes* in sliced cooked ham during chilled storage was assessed. The results of the study pointed out that lactate–diacetate provided a bacteriostatic effect against *L. monocytogenes* during the 3 months of storage at 1 and 6 °C, even with temperature abuse. The effectiveness of nisin, lactate salts, and HPP to inhibit the growth of *L. monocytogenes* and *Salmonella* was studied in sliced cooked ham (Aymerich, Jofre, Garriga, & Hugas, 2005). A synergistic effect for potassium lactate and HPP (400 MPa, 17 °C, 10 min) along with refrigerated storage temperature was found to inhibit the growth of *L. monocytogenes* and *Salmonella*. Bacteriocins have great potential to be used in combination with HPP to deliver extended shelf life. Currently though in Europe, only nisin is yet approved for its use in food applications, with pediocin also approved in the United States. In Europe, nisin is considered a food additive and then has to be declared on the label (i.e., E-234). The advantage of using bacteriocins is that they are added to the product at a very low concentration, and consequently, they have no adverse effects on the sensory quality, which is paramount in commercial products. Albeit nisin can be exposed to loss of part of its antimicrobial activity due to HP treatment (Modugno et al., 2018). Sulfites and nitrites are effective antimicrobials commonly used in meat products that exert a hurdle to microbial growth of spoilage and pathogen bacteria. Their removal from meat product's recipes can become problematic, and requires taking additional control measures during manufacturing (e.g., working with highly strict microbial standards) and the commercial shelf life (e.g., refrigeration) in order to manage microbial risks. HPP as a postslicing and postpackaging decontamination treatment can reduce microbial loads in end products ready for dispatch, and potentially contribute to assuring shelf life, when no or reduced amounts of salt, sulfites, and nitrites are added into the formulations (Mizi et al., 2019; Myers, Cannon, et al., 2013; Myers, Montoya, Cannon, Dickson, & Sebranek, 2013; O'Neill, Cruz-Romero, Duffy, & Kerry, 2018). Furthermore, the reduction or removal of nitrite and sulfites from meat product formulations not only will affect microbial growth but can also bring additional issues that will have to be addressed adequately to maintain and assure product quality. In the case of nitrite, the potential growth of *Clostridium Botulinum* will have to be prevented by applying additional control measures in the process and different approaches will have to be explored (as described before). Nitrites contribute as well to the development of the traditional color and flavor of cured meat products, and differences in these attributes can be expected in the final product when nitrite is not present or reduced. Equally important is the functionality of both, nitrite and sulfite, as antioxidants in meat products. Their reduction can result in higher levels of oxidation. In such cases, the addition of antioxidant (plant) extracts can help. Despite of the technical difficulties to accomplish a proper and safe substitution of those food additives, there is nowadays a consumer demand for using less additives and E-numbers in foodstuffs, which challenges the industry. The use of natural extracts and biopreservation methods to control microbial growth in combination with other processing technologies such as HPP can aid processors to meet this important consumer demand. Yet, despite the very promising results that have been reported in the literature regarding microbial inactivation by using combined hurdles with HPP, it seems

that the full potential of HPP application in combination with antimicrobials to fight pathogenic and spoilage bacteria in different meat products is far from being fully researched and uncovered.

3.1.1.2 Bacteriophages

Up to this moment, there is a limited number of studies addressing the relationship between bacteriophages and HP. One of the early studies that addresses this topic is from the 90s (Brauch, Hänsler, & Ludwig, 1990). This study reported that the number of phages was considerably reduced at pressure of around 300 MPa and temperatures of 25 and 40 °C. At the same time, it has also been reported that a smaller fraction lost its infectivity much more slowly. It should be noted that pressure treatments of several hours were investigated, still concluding that a stable fraction of phages occurs even when pressure was applied for 24 hr. This could open the possibility of using pressure-resistant phages, as a biopreservation method, in combination with HPP. These phages still active after HPP treatment would target certain pathogens, and would act as an additional inhibition hurdle to bacterial growth during storage. Later studies reported partial inactivation of phages of 2 log reduction after 5 min treatment in a pressure range of around 300 MPa, and increasing inactivation with increasing treatment time (Dilek Avsaroglu, Buzrul, Alpas, Akcelik, & Bozoglu, 2006). In another study, lactococcal phages P001 and P008 in calcium-enriched M17-broth were heated at 55 to 80 °C, and compared to HP-treated ones (up to 600 MPa). The phages were inactivated by means of heat and HP in the pressure–temperature region of 0.1 to 600 MPa and 25 to 80 °C. In particular, phage P008 was very heat and pressure tolerant (Müller-Merbach, Rauscher, & Hinrichs, 2005). However, the tolerance of different bacteriophages under different processing conditions is under scrutiny up to this moment. For example, up to now only few data are available on the effect of foods or food components on the pressure tolerance of phages. Own investigations by Hertel and coauthors indicated that some food components, for example, sugar and proteins, do not affect the biological activity of *Salmonella* phages, whereas components such as salt may negatively affect the activity. In addition, HPP up to 250 MPa did not affect the activity of *Salmonella* phages in minced pork meat. This is a promising future research area in food safety.

3.1.1.3 Salt

Salt is broadly used in food production because of its diverse contributions, such as flavor, texture, and extending shelf life of food products by reducing water activity. However, high salt consumption (8 to 10 g/day) in Western countries is associated to high blood pressure and other cardiovascular diseases (He & MacGregor, 2009; Ruusunen & Puolanne, 2005). A large part of the human salt intake comes directly from processed foods, meat products being an important contributor. Accordingly, there is an increasing trend and need for reducing the amount of salt used in meat and other products, while at the same time maintaining the same level of quality attributes (structure and flavor) and without compromising safety. The beneficial effects of HPP on myofibrillar gelation could help reduce the salt content in meat products. But at room temperatures, those effects occur primarily at low pressure levels (~200 MPa) where there is little significance for microbial inactivation. The present section thus focuses on the effect of salt on microbial inactivation and how HPP could aid in assuring food safety and extend shelf life when reducing the content of salt. Reduction of salt concentration would not have a major impact on initial microbiological load, but might influence the survival and ability of microorganisms to grow during storage. Toleration of stress induced by salt is dependent on a microorganism's characteristics and matrix attributes (Inguglia, Zhang, Tiwari, Kerry, & Burgess, 2017). Hayman et al. (2004) reported that increased salt concentration from 0.5 to 3.6% in tryptic soy broth enhanced tolerance of *Listeria* against HPP at 600 MPa for 2 min. In a following study, neither NaCl nor sodium lactate significantly influenced the time to inactivation of *Listeria monocytogenes*, which in contrast was highly dependent on initial load and pressure level (Youart, Huang, Stewart, Kalinowski, & Legan, 2010). Combinations of HPP with other hurdles such as the additions of organic acids or salt replacers have been investigated with success as a hurdle strategy for extending the shelf life and safety of low-salt processed meat products such as frankfurters (with a reduction in the salt content from 2.5 to 1.3%) and cooked ham (with a reduction in the salt content from 2.6 to 1.4 %) (O'Neill, Cruz-Romero, Duffy, & Kerry, 2018). Due to the ongoing exigency and challenge for the industry to reduce the salt contents in meat products, similar strategies could play a role as possible approaches to reach safe products with the highest quality. Particularly helpful could be when significant reductions in the salt content (e.g., 50%) are undertaken, which would likely require of methods to assuring the safety of the meat product for a similar shelf life span. HPP could be one of the technologies to tackle this particular problem associated with drastic salt reductions in meat products.

So far HPP is applied by several meat processors demonstrating a great potential in ensuring meat safety (Campus, 2010). However, microbial cells that are only sublethally injured could represent a potential risk for microbial quality. If no other hurdles are provided, the microbial cells could recover, and jeopardize the safety and reduce the shelf life of the product. Validation studies and challenge

tests over storage time must be conducted to ensure that the product is stable during the entire shelf life.

3.2 | Meat tenderization

The use of HPP for altering functionality during food processing is interesting because modifications in the properties of foods processed by HP proceed differently to that of processing using heat (Hayashi, Kawamura, Nakasa, & Okinaka, 1989). Macfarlane (1985) has shown that muscle proteins are the most sensitive of all food constituents to HP. Meat tenderization by HPP depends on the time postmortem when HPP is applied, the muscle type, and the HPP processing conditions such as pressure level, temperature, and to a lesser extent, the treatment duration.

3.2.1 | Impact of HPP on meat structure resulting in tenderization

The gross structure through to the individual constituent protein molecules of muscle is highly ordered but very complex. As pressure modifies the noncovalent interactions of proteins, this results in changes to the properties of the muscle proteins (c.f. Section 2.2 and Figure 3).

The solubility and aggregation of actin, myosin, and actomyosin is influenced by HP and has been described in Section 2.2.2. The depolymerization of F-actin has been extensively reported and generally occurs at lower pressures, 100 and 300 MPa (Garcia, Amaral, Abrahamsohn, & Verjovski-Almeida, 1992; Ikkai & Ooi, 1966; Jung, Ghoul, & de Lamballerie-Anton, 2000; Ikeuchi et al., 2002). Pressure-induced changes of myosin filaments have been described previously (Davis, 1981; Josephs & Harrington, 1967; Messens, Van Camp, & Huyghebaert, 1997; Yamamoto, 1996; Yamamoto, Miura, & Yasui, 1990). Association of monomeric myosin heads has been shown to form tight aggregations due to hydrophobic bonds at pressures between 100 and 300 MPa, and surface hydrophobicity was not increased with higher pressures (Chapleau & de Lamballerie-Anton, 2003; Chapleau, Mangavel, Compoint, & de Lamballerie-Anton, 2003; Yamamoto et al., 1994). This indicates that denaturation of the myosin head does not occur at higher pressure. Another method for identifying denaturation of individual muscle proteins is differential scanning calorimetry (DSC) (Wright, Leach, & Wilding, 1977), which records the maximum temperature at which a protein denatures, as well as changes in the total denaturation enthalpy associated with the denaturation. These parameters relate to distinct changes in the texture of the meat (Fernandez-Martin, 2007). Although actin has a high thermal stability, it appears to be the most sensitive myofibrillar protein, probably as a result of the F-G depolymerization at low pressures (Fernandez-Martin, 2007) (as depicted in the two first steps from Figure 3). The pressure sensitivity of myofibrillar proteins is also dependent on the temperature of processing, as denaturation occurs more quickly at higher temperatures. Muscle fibers contain many parallel myofibrils (1 to μm in diameter) that have a striated appearance. This is due to isotropic bands (I-bands) that have a light appearance, and anisotropic bands (A-bands), which are darker. The loss of structural organization due to damage to sarcomeric structures, including I-bands, M-line components, and A-bands, has been observed in myofibrils with increasing pressure applied to both pre- and postrigor muscle (Bouton, Harris, Macfarlane, & O'Shea, 1977; Buckow et al., 2013; Elgasim & Kennick, 1982; Rusman et al., 2007) (Section 2.2.2).

Although the focus of research on the effects of HPP has been on myofibrillar proteins, in general, sarcoplasmic protein denaturation has been shown to affect meat quality properties, such as WHC (Lawrie, 1998), and a decrease in solubility of sarcoplasmic proteins with applied HP has been reported and correlated with a reduction in WHC (Kim, Lee, Lee, Kim, & Yamamoto, 2007; Marcos & Mullen, 2014; Marcos et al., 2010). This insolubilization of individual sarcoplasmic proteins has been hypothesized to be one of the mechanisms impacting the pressure-induced changes in muscle (Marcos & Mullen, 2014). Sarcoplasmic proteins were correlated with reduced WHC, but surely, the reduction in WHC was likely also due to an overall effect on protein denaturation including myofibrillar proteins, disruption of muscle structures, and their effects on the compartmentalized water holding in meat.

Collagen, which is the main component of connective tissue, has a triple-helix structure and is primarily stabilized by hydrogen bonds. As hydrogen bonding is enhanced under pressure (Heremans, 1982), it was proposed that collagen is not greatly affected by HP (Gekko & Koga, 1983). However, contrasting results have been reported, and the effects of pressure on connective tissue are dependent on the temperature of pressure application, as well as the extraction state of the collagen, that is, pressure applied to intact muscle or isolated connective tissue. Using DSC, Ma and Ledward (2004) found no effect on the collagen component when pressure (0.1 to 800 MPa for 20 min) was applied at 20 °C to beef muscle. This study also showed that when pressure was combined with heat (40 to 60 °C), the transition temperature and enthalpy of collagen decreased with 400 MPa at 60 °C and were still evident at pressures of 600 to 800 MPa at 60 °C. On the other hand, Sikes, Tornberg, and Tume (2010) concluded from DSC studies of beef *sternomandibularis* that pressure treatment

combined with heat (200 MPa at 60 °C for 20 min) stabilized the collagen component, with an increase in enthalpy compared to raw muscle. HP has also been shown to protect collagen from subsequent heat denaturation (Beilken, Macfarlane, & Jones, 1990; Fernandez-Martin, 2007). To date, results are inconclusive, differing with regard to the stabilization/destabilization of collagen by HPP treatment, and further research is warranted to clarify this point. Microscopic investigations of bovine intramuscular connective tissue structures have shown disruption of the endomysium (Ueno, Ikeuchi, & Suzuki, 1999) and separations of the perimysial sheet into collagen fibers (Ichinoseki, Nishiumi, & Suzuki, 2006, 2007) when HP (up to 500 MPa) was applied at low temperatures (4 to 8 °C).

HPP of prerigor muscle has been proposed to manipulate glycolysis early postmortem that has subsequent impacts on texture. Pressures of 100 to 200 MPa applied to prerigor beef and lamb have been shown to cause intense muscle contraction as a result of the release of calcium, which accelerates glycolysis, and a rapid pH decline and a decrease in shear force of the final product, most likely from fragmentation and disorganization of the myofibrillar structure (Bouton et al., 1997b; Kennick & Elgasim, 1981; Kennick, Elgasim, Holmes, & Meyer, 1980; Macfarlane, 1973). Warner et al. (2017) recently reviewed the application of HPP to pre- and postrigor meats for meat tenderization purposes. Studies applying HPP to prerigor pork has shown that HPP partially inhibits postmortem metabolism through the denaturation of glycolytic enzymes, resulting in a higher pH at 24 hr of chilled storage (Smit, Summerfield, & Cannon, 2010; Souza et al., 2011, 2012). More recent studies on prerigor beef has shown that pressure at 175 MPa produced meat at 1 day postmortem as tender or more tender than muscles aged for 28 days (Morton et al., 2017), and that pressure-treated muscle had a lower myofibrillar fragmentation index, shorter sarcomeres, reduced calpain 1 activity, and a higher pH at 24 hr (Morton, Lee, Pearson, & Bickerstaffe, 2018). Similar to the reports in the 1970 to 1980s (Bouton et al., 1977; Elgasim & Kennick, 1982), microscopic evaluation of pressure-treated prerigor muscle showed structural disorganization of the sarcomeric components (Morton et al., 2018). The higher pH at 24 hr was attributed to the loss of glycogen phosphorylase activity from the sarcoplasm, which would result in stopping glycolysis. These authors postulated from their data that the mechanism of tenderization of HPP prerigor meat was different to that of tenderization of chilled, aged meat, and that the contributing factor to tenderization was due to physical disruption of muscle structure (Morton et al., 2018).

Many theories on the mechanism of the effect of HPP for tenderization of postrigor meat have been suggested. Some of these are based on the disorganization of the meat structure resulting in tenderization (Sun & Holley, 2010). Others support the theory of the increased release of enzymes and subsequent increased proteolytic activity (Homma, Ikeuchi, & Suzuki, 1994; Ma & Ledward, 2004), and further alternate mechanisms are postulated to be a combination of structural and enzymatic events (Sikes et al., 2010). Many studies by Macfarlane's group (Macfarlane, McKenzie, & Turner, 1981; Macfarlane & Morton, 1978) led to the hypothesis that the depolymerized actin is free to shift in the A-band region and associates with myosin on the release of pressure (Macfarlane, 1985). This theory centered on the disaggregation of actin, as well as other I-band proteins such as troponin and tropomyosin. However, the Z-disk structure was not altered. In addition, these changes within the sarcomeric structure were not correlated to an improvement in tenderness in cooked (80 °C for 60 min) meat (Macfarlane et al., 1981). Other proteins belonging to costameric and cytoskeletal structures with a linking function within the muscle fiber's structure were therefore suggested to be involved in the tenderization of postrigor meat using HPP (Cheftel & Culioli, 1997).

Similarly, Japanese researchers reported disorganization of rabbit muscle structure when exposed to HPP (100 to 300 MPa) at ambient temperatures that resulted in tenderization. These changes involved the I-band and M-line, and led to the conclusion that tenderization of postrigor muscle using HPP was caused by different mechanisms to that of ageing of muscle (Suzuki et al., 1990; Suzuki, Suzuki, Ikeuchi, & Saito, 1991; Suzuki, Watanabe, Ikeuchi, & Saito, 1992).

Although Jung, de Lamballerie-Anton, and Ghoul (2000a) found modifications to the ultrastructure of postrigor beef *biceps femoris* muscle when treated with 325 MPa at 10 °C for 4.3 min, they also reported swelling and disruption of lysosomes that resulted in an increase in free lysosomal enzymes (Jung, Ghoul, & de Lamballerie-Anton, 2000). There was no improvement in tenderness reported in these series of studies. Therefore, neither changes to the ultrastructure nor increased proteolysis from lysosomal enzymes resulted in tenderization under the HPP conditions (up to 520 MPa at 10 °C for 260 s) used in those studies.

3.2.2 | Processing conditions required to achieve tenderization

HP applied to prerigor muscle has been shown to be effective for tenderization when pressures are applied around 200 MPa for up to 4 min at 30 to 35 °C. The magnitude of pressure appears to be species specific, with pressures below 200 MPa reported for beef and lamb, and above

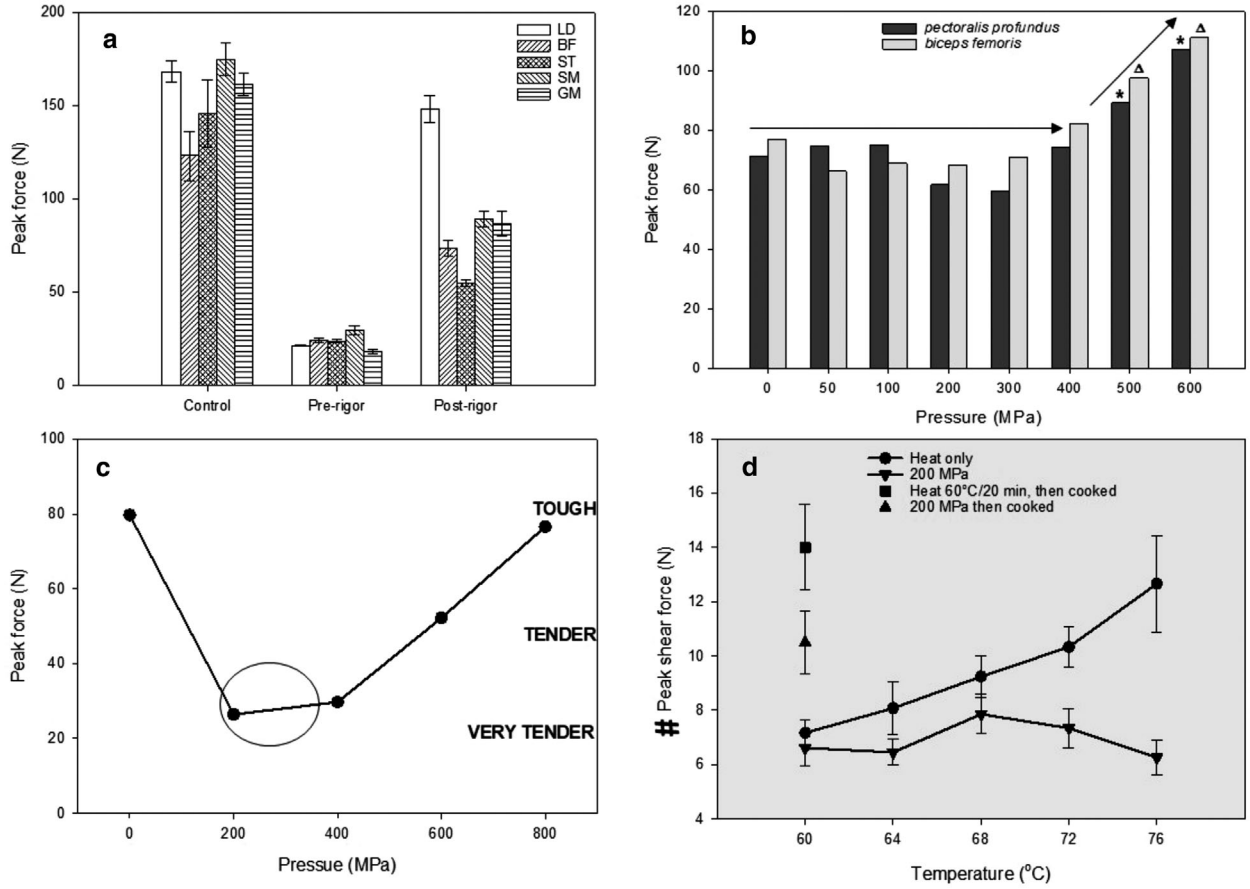


FIGURE 7 Summary of meat tenderization effects by high-pressure processing (HPP). (a) Warner–Bratzler peak force values of control (excised prerigor, no treatment), prerigor (excised prerigor and pressurized at 103 MPa at 35 °C for 2 min), and postrigor (conventional processing, 24 hr postslaughter) beef muscles. Abbreviations: LD,*longissimus dorsi*; BF,*biceps femoris*; ST,*semitendinosus*; SM,*semimembranosus*; GM,*gluteus medius*(Source: Macfarlane,1973). (b) Effect of high pressure (0 to 600 MPa at 4 to 8 °C for 5 min) on the texture (peak force) of low-value beef muscles,*pectoralis profundus*and*biceps femoris*. : and Δ indicate significance (p-value <0.05) for each muscle. Adapted from Sikes (2014) with permission from Meat and Livestock Australia. (c) Effect of HPP (0 to 800 MPa) combined with temperature at 60 °C on the peak force value of postrigor beef*sternomandibularis*muscle. Reproduced from Sikes and Tume (2010) with permission from Meat and Livestock Australia. (d) Peak shear force (left) of steaks following various temperature, pressure and cook treatments. Note that Figure 7d has different absolute values of peak shear force than Figures 7a–c due to the different dimensions of the particular block of meat measured in each case, but the relative values of peak shear force are representative for the effect of temperature (under high pressure) on the shear force. The dimensions for the standard Warner-Bratzler shear force (WBSF) were 15 mm × 6.7 mm, giving a cross-sectional area of 1 cm^2(for Figures 7a–c), whereas the dimensions of the samples measured for Figure 7d were 6.42 mm × 3 mm, giving a cross-sectional area of 0.2 cm^2. Reproduced from Sikes and Tume (2014) with permission from Elsevier

200 MPa (up to 225 MPa) for pork. This pressure optimum for tenderization could also be related to the pressures that impact the color of meat. It is known that pressures above 200 MPa denature myoglobin (Bak et al., 2017; Carlez et al., 1995; Cheah & Ledward, 1997; Ma & Ledward, 2013), and therefore, it is important, particularly in meat with a higher myoglobin content, to prevent any deterioration in color due to processing. Morton et al. (2017) showed that even though pressure at 250 MPa produced more tender prerigor beef *longissimus thoracis* than pressure at 175 MPa, the color of the steaks from the 250 MPa treatment was lighter and to some extent, unacceptable to consumers.

Early studies on prerigor muscle showed enhanced tenderness when beef *longissimus dorsi* was pressure treated at 103 MPa (85% improvement; Figure 7a) (Macfarlane, 1973) and in beef (64%) and sheep (70%) *longissimus dorsi* (Kennick et al., 1980). Recently, this improvement in tenderness has been confirmed, with a 60% lower shear force value in beef steaks with pressure treatment at 175 MPa and aged for 1 day (Morton et al., 2017). However, this tenderization effect of HPP was lost after 28 days ageing, with control and HPP meat having similar tenderness at that time. The manipulation of glycolysis using HPP (175 to 225 MPa, 10 to 35 °C, 5 to 180 s) in prerigor pork sides or primal cuts (*longissimus dorsi*) resulted in an improvement in

tenderness (up to 30%) of pork chops (Souza et al., 2011, 2012), with these data being the basis of a patent by Hormel (Smit et al., 2010).

The improved tenderness of prerigor beef *longissimus dorsi* by HPP observed by Macfarlane (1973) came along with a concomitant reduced cooking loss. This higher yield was confirmed in beef by Morton et al. (2017). Kennick et al. (1980) showed that although HPP at 103 MPa of prerigor beef and sheep *longissimus dorsi* resulted in increased weep and reduced WHC, the cooking loss was lower than for the controls. Therefore, the overall moisture loss during HPP was no different to the controls. Other studies on HPP of prerigor pork muscle reported that drip loss and cook loss were reduced, indicating an increased WHC (Souza et al., 2011, 2012).

Despite some reports indicating that HP applied at low or ambient temperature (0 to 25 °C) to postrigor muscle can improve texture (Ichinoseki et al., 2006; Kim et al., 2007; Suzuki, Kim, Homma, Ikeuchi, & Saito, 1992), it is well-known that to ensure consistent tenderization of postrigor muscle, HP combined with temperatures greater than 25 °C is required (Bouton, Ford, Harris, Macfarlane, & O'Shea, 1977; Bouton, Harris, et al., 1977; Ma & Ledward, 2004; Zamri, Ledward, & Frazier, 2006; Sikes et al., 2010; McArdle, Marcos, Kerry, & Mullen, 2011; McArdle, Marcos, Mullen, & Kerry, 2013; Sikes & Tume, 2014; Sikes & Warner, 2016). In contrast, the application of HPP at lower temperatures has been reported to increase the toughness of meat from several species (Duranton, Simonin, Cheret, Guillou, & de Lamballerie, 2012; Grossi et al., 2014; Hong, Park, Kim, Lee, & Min, 2005; Jung, de Lamballerie-Anton, & Ghoul, 2000b; Jung, Ghoul, & de Lamballerie-Anton, 2000; Kruk et al., 2011; Ma & Ledward, 2004; Macfarlane et al., 1981). In a recent study, HP (0 to 600 MPa) applied at low temperature (0 to 8 °C) for 5 min to low-value beef muscles, *pectoralis profundus* and *biceps femoris*, was shown to have no impact on texture (as measured by a modified Warner–Bratzler method) with pressures lower than 500 MPa (Figure 7b). However, at pressures of 500 to 600 MPa, the meat had significantly ($p < .001$) higher peak force values, suggesting reduced tenderness of the meat with HPP treatment at low temperature (Sikes, 2014).

Optimum tenderness of postrigor muscle has been reported at pressures of 100 to 200 MPa combined with temperatures of 60 to 80 °C (Ma & Ledward, 2004; McArdle et al., 2013; Rusman et al., 2007). If higher pressures (>200 MPa) at 60 °C were applied to postrigor beef *sternomandibularis*, it was shown that pressures above 400 MPa at this temperature toughened the meat (Figure 7c) (Sikes & Tume, 2010). General duration of pressure treatment is up to 30 min in these type of studies, but much shorter time (5 min) has also proved to result in tenderization (Rusman et al., 2007). Sikes and Warner (2016) reviewed 13 studies on HPP of postrigor meat, from a range of muscles across different species (beef, lamb, pork, and chicken) and, in all of the studies, the improvement in tenderness ranged from 30% to 80% when pressure was applied at 150 to 400 MPa at temperatures higher than 50 to 60 °C (Beilken et al., 1990; Bouton, Ford, et al., 1977; Bouton, Harris, et al., 1977; Bouton, Harris, & Macfarlane, 1980; Ma & Ledward, 2004; McArdle et al., 2011; McArdle et al., 2013; Ratcliff et al., 1977; Rusman et al., 2007; Sikes & Tume, 2014; Sikes, Tornberg, & Tume, 2010).

In addition to a 50% reduction in the peak force value of beef *semimembranosus* and *biceps femoris* muscles, with pressure 200 MPa at 76 °C for 20 min, Sikes and Tume (2014) also showed a significant increase in product yield (Figure 7d). With applied pressure at relatively high temperatures (60 to 76 °C), the weight loss of pressure-treated steaks was greatly reduced: about 8% at 76 °C compared with 30% in the heat alone control sample. This improvement in yield was attributed to HPP.

As discussed for HPP of prerigor muscle, pressure applied to postrigor meat will also impact meat color. An obvious color change in beef muscle is apparent when pressure is applied above 200 MPa, even at low temperatures, but will be pronounced when high temperatures are concomitantly applied as required (Buckow et al., 2013; Bak et al., 2019; Carlez et al., 1995; Hughes et al., 2014; Jung, Ghoul, & de Lamballerie, 2003; Ledward, 2000). This change in color is generally manifested as an increase in lightness (L: value) and a decrease in redness (a: value). This color change is a limitation for the use of HPP to postrigor meat for tenderization.

The application of a combined pressure–heat process to produce innovative value-added products with ensured eating quality, such as RTE meat products, meal solutions, and foodservice benefits, has potential in the meat industry (Figures 8c and 8d). However, one of the challenges for commercialization of this technology for tenderization of meat is to achieve the target temperatures required for the process to be effective. A container and system for HP thermal processing have been developed (Knoerzer, 2017). This multilayered canister is applicable for use with current commercial HP units (cold HPP machines) and achieves the required conditions for meat tenderization. The canister optimizes heat retention through thermal insulation and selective adiabatic heating of the multilayer configuration sealed with a floating piston that locks out cold water and allows pressure transmission.

This section has highlighted the effect of HPP on modifications to muscle ultrastructure, proteolytic enzymes, and individual muscle proteins and their interactions within the muscle structure. These modifications have been related to tenderization and effects on other quality attributes, namely, color and water binding. The

FIGURE 8 Demonstration of products of the different applications of high-pressure processing (HPP) in the meat industry. (a and b) Photos of traditional meat products cold pasteurized by HPP. (a) Dry-cured fermented Salami, ready for being HP-processed vacuum packaged as an entire piece (photo courtesy of Marco Veroni, Veroni, Italy, and USA), and (b) cooked ham, cold pasteurized with HPP in the retail package (photo courtesy of Neus Quintana, Esteban Espuña, Spain). (c and d) Photos of professionally prepared concept HPP meat products developed and tenderized applying HPP to postrigor meat. (c) Goat curry and (d) beef chuck soft taco. Reproduced with permission from Meat and Livestock Australia (MLA). (e) Photos of traditional German sausage, Bratwurst, manufactured with varying amount of salt (NaCl) added in the formulation (1 and 2%) and application of HPP (200 MPa for 4 min at room temperature, 20 °C): e1, control Bratwurst containing 2% of added salt; e2, salt-reduced Bratwurst containing 1% of added salt; and e3, salt-reduced Bratwurst containing 1% of added salt and application of HPP treatment (200 MPa for 4 min at room temperature, 20 °C) prior to cooking

application of HPP for tenderization of meat is dependent on the postmortem state of meat at which HPP is applied, the muscle type, and the HPP conditions used, such as the magnitude of pressure, the temperature of processing, and to a lesser extent, the pressure treatment time. HPP can be an alternative further processing technology to low-temperature (50 to 65 °C) long-time (hours) treatments, also known as cook-in-bag (under vacuum) technique or sous vide (Dominguez-Hernandez, Salaseviciene, & Ertbjerg, 2018), but with much shorter processing times in the case of using HPP (within the order of magnitude of minutes rather than hours) to achieving consistent tenderization of meat.

3.3 | Structure formation in processed meats

With the HPP effect on proteins and on myofibrillar gelation (Section 2.2) in mind, HPP is in fact a very interesting processing technology for improving functional properties in the manufacturing of processed meats. Section 3.2

describes how HPP can be used to tenderize whole meat pieces. In this section, examples of how HPP can be used to bind proteins together to produce meat gels and obtaining the desired texture are presented. Using HPP for enabling structure formation in meat systems is a counterbalanced action between solubilization and aggregation of proteins, because pressure increases myofibrillar proteins solubility, thereby improving their functional properties, but pressure also results in protein denaturation and aggregation, thereby impairing solubility of the main myofibrillar proteins, myosin and actin. Thus, the use of HPP to promote protein solubility and induce aggregation has been examined thoroughly as an alternative method to produce firm meat products, especially sausages. It should be noted that meat is minced as an initial process step in the preparation of meat batters, thereby a mechanical filament disruption is introduced prior to HPP treatment.

Normally, a high salt concentration (typically NaCl > 1.5%) is used to guarantee the technological, microbial, and sensory properties in sausage manufacturing. The former covers the desirable functional and eating quality characteristics such as cohesive consistency, firm texture, and water binding. The relationship between food and health has gained increasing attention, and challenges the meat industry to produce low-salt meat products. The ability of HPP to foster protein solubilization and gelation has been investigated to aid or further improve meat binding that is acceptable in the production of sausages, and to possibly avoid, or considerably reduce, the salt content as described by Bolumar et al. (2016) and Olsen and Orlien (2016). Vaudagna et al. (2012) found that HPP treatment at 350 MPa (6 min, 20 °C) had a significant hardening effect on pork meat batters without salt and phosphates. However, the addition of salt (1.5 and 3.0% NaCl) and polyphosphate (0.25% and 0.5% $Na_4P_2O_7$/$Na_5P_3O_{10}$) neutralized the pressure effect, and this time the HPP treatment had a softening effect on the product's texture. It was suggested by the authors that pressure-induced protein denaturation proceed differently from salt-induced denaturation, and thus, the type of denaturation was more important than the amount of denatured proteins to determining the texture formation (Villamonte, Simonin, Duranton, Chéret, & Lamballerie, 2013). Even when pressure and heat were combined (400 MPa, 55 and 70 °C, 30 min), a significant decrease of the textural properties of pork sausages with salt and phosphate in comparison to heat treatment alone has been found (Fernandez-Martın, Fernandez, Carballo, & Jimenez-Colmenero, 1997; Fernandez-Martín, Cofrades, Carballo, & Jimenez-Colmenero, 2002). An HPP pretreatment (150 and 300 MPa, 5 min, 20 °C) of beef meat prior to sausage formulation (1.5 or 2.5% salt and 0.25% polyphosphate) and cooking (75 °C, 30 min) also produced a lower hardness for the high-level salt frankfurters (Crehan, Troy, & Buckley, 2000). It seemed that both low pressure level (150 MPa) and low salt level (1.5%) resulted in improved frankfurters regarding cook loss, emulsion stability, texture and liking (Crehan et al., 2000). Guo and colleagues (2017) decided to find the lowest salt level (varying from 0.6 to 1.4% NaCl) needed for production of HP-processed (600 MPa, 5 min, 40 °C) chicken sausages. Increasing salt content up to 1.2% increased the texture characteristics and resulted in either rough, disorganized structure (with 0.6 and 0.8% salt) or rigid, solid-stranded morphology (with 1.0 to 1.4% salt) (Guo et al., 2017). In combination with sensory analysis, it was concluded that a content of 1.2% NaCl was sufficient for general acceptability. Iwasaki et al. (2006) reported that low-salt (1%) pork sausages' rheological properties were boosted by pressurization at 200 MPa before heat treatment. Similar low-salt (1%) beef sausage with improved texture and sensory acceptability was produced by HPP treatment (up to 400 MPa, 2 min, 10 °C) following cooking (76 °C, 25 min), with the best water retention achieved at 200 MPa (Sikes, Tobin, & Tume, 2009). Controlling the gradient of pressurization had marked impact on the functional properties of pork meat batters, and, thus, was used to reduce salt content by 50% without impairing meat gel product quality (Tintchev et al., 2013). An example of a traditional German sausage, Bratwurst, manufactured with varying amounts of cooking salt (NaCl) added in the formulation (1% and 2%) and application of HPP (200 MPa for 4 min at room temperature) is shown in Figure 8e. The reduction of the salt content to 1% has terrible effects on the Bratwurst's structure, whereas this deleterious effect is counterbalanced by the targeted use of an HPP treatment.

There is an increasing interest in using compounds from the plant kingdom due to both the health aspect and the concern regarding the anticipated world's meat protein deficiency. The use of plant-based functional ingredients has been shown to be an approach to help improve meat texture when reducing the salt content in HPP meat products. The addition of carrot fiber (0.5 and 1.5%) or potato starch (2 and 3.8%) to a meat-emulsified batter enabled a lowering of the salt content to 1.2% (with no added phosphates) in HP-treated (400, 600, or 800 MPa, 5 min, 5 or 40 °C) pork sausages (Grossi, Søltoft-Jensen, Knudsen, Christensen, & Orlien, 2012). Furthermore, the addition of starch or fiber had greater effect on the textural properties compared to the level of salt. The protein binding was enhanced by HPP treatment and the addition of starch or fiber, which improved hardness (with starch being better than fiber) (Grossi et al., 2012). Moreover, a synergistic action of mild heating (40 °C) during HPP treatment enhanced even further the sausage

hardness (Grossi et al., 2012). Likewise, it was possible to substitute part of the NaCl (from 2.5 to 1.0%) with β-glucan in chicken meat sausages following temperature-assisted HPP (400 and 600 MPa, 30 min, 40 or 60 °C) (Omana, Prastow, & Betti, 2011). However, incorporation of hydrocolloids, such as xanthan gum, locust bean gum, and carboxymethylcellulose, was found to weakening the gel network after a harsh HPP treatment (600 MPa, 40 min, 50 °C) of ostrich meat sausages (Chattong, Apichartsrangkoon, & Bell, 2007). Other types of ingredients have also been investigated to reduce and replace salt in HPP meat products. Trespalacios and Pla (2007) reported that the combined use of microbial transglutaminase with egg protein and HPP treatment (700 or 900 MPa, 30 min, 40 °C) resulted in chicken meat gels with reduced salt (and no phosphates) and enhanced textural properties compared to meat gels without enzyme or only heat treated. Fulladosa, Serra, Gou, and Arnau (2009) reported a positive substitution of NaCl with potassium lactate in the manufacturing process of restructured dry-cured hams with application of HPP (600 MPa, 6 min, 10 °C).

All these examples demonstrate the applicability of the HPP technology for commercial processed meat products. Generally speaking, the use of HPP in the manufacturing of processed meats is owing to the ability of HPP to improve the functional properties of the myofibrillar proteins through denaturation, solubilization, aggregation, and gelation, thereby affecting textural properties, WHC, and sensory perception. Actually, the final outcome is affected by the nature of the batter/protein system (meat type and particular formulation, especially the use of binders such as fibers, starches, and other protein sources) and the HPP settings (such as pressure level, pressurizing gradient, treatment duration, temperature, pressure and temperature combinations, and the particular sequence of application). A comprehensive review by Chen and colleagues (2017) reports on both earlier studies and recent advances in structural modification of myofibrillar proteins for improved functionality of processed meats by using HPP treatments.

4 | PROCESSING COSTS, CONSUMER AND MARKET ACCEPTANCE, AND SUSTAINABILITY

Processing costs, consumer and market acceptance, and, more recently, sustainability are important determinants for the uptake of new processing technologies by the food industry.

Regarding HP-processing costs, it can generally be stated that HPP requires a high initial investment and a relatively high operative and maintenance cost (e.g., a high electricity consumption), both of which are significantly higher than the corresponding costs for thermal processing systems alone (Aganovic et al., 2017; Cacace, Bottani, Rizzi, & Vignali, 2020; Sampedro, McAloon, Yee, Fan, & Geveke, 2014). Thus, HPP is usually applied to high-value meat products, but also where other drivers come into place, for instance to ensure food safety, to extend shelf life, or to develop clean label products.

New technologies must overcome the natural resistance to change. Public acceptance of HP-treated food is in general high, and HPP normally results in a strongly positive influence on consumer receptiveness and perception (Cardello, Schutz, & Lesher, 2007). The main benefits perceived by consumers from HP-treated products are naturalness, improved taste, and higher nutritional value (Nielsen et al., 2009). In a study by Sorenson and Henchion (2011), consumers' aptitudes toward HP-processed chilled ready meals were evaluated. The vast majority of consumers have a positive attitude toward HP-processed chilled ready meals and believed that over-processing reduces the nutritional value—an aspect that represented a strong leverage factor for differentiation from existing products. However, it was also revealed that food safety concerns due to low awareness levels of the technology represented a strong perceptual barrier to consumers' acceptance of HPP. Specifically, thermal processing was positively associated with assurance of food safety. In contrast, HPP as a new and nonthermal technology was perceived as potentially posing a greater risk in terms of food safety (Sorenson & Henchion, 2011). Thus, the main barriers for the acceptance of new food processing technologies, including HPP, concern the potential perceived risks associated with the use of new technologies (Olsen, Grunert, & Sonne, 2010), and hence, adequate provision of information to consumer, through education and adequate food labeling, reduces resistance toward acceptance. Consumers recognize the benefits of HPP when information about the technology is provided on the food labels, and, as a result of these indications, not only their concerns toward HPP are reduced but also a higher intention to purchase the product is obtained (Bruhn, 2016). However, from a consumer perspective, there is still a widespread lack of trust of food regulators and industry that may ultimately contribute to a general skepticism. Thus, an important factor to bear in mind in dealing with consumers' attitudes toward new products is to design appropriate labels and select the information these contain to appropriately communicate information about the benefits of HPP (and any other novel technology) (Lavilla, 2019).

In addition, a lower environmental impact can also be seen as an advantage by a growing number of consumers and is becoming increasingly important for the

meat industry in order to obtain its social license to operate. However, the number of studies dealing with the evaluation of the environmental sustainability of HPP treatments in the food industry, and particularly in meat products, is rather scarce. Most of the few studies are related to juices (Aganovic et al., 2017; Sampedro et al., 2014); and the very few dealing with meat product are reported below. We appreciate that more studies are definitely required to make sound conclusions in this area. This is because the specific product and process features included in the numerical calculations, namely, among others; product's volume and weight, temperature process profile, inclusion/exclusion of down- and upstream operations, and specific amount of packaging, as well as the system boundaries of the life cycle assessment (LCA) methodology applied in the study, that is, the use of "gate to gate" or a "cradle to gate" methodologies, have a profound impact in the respective estimated values of the environmental impact, and consequently, it is of utmost importance in order to make sensible and "realistic" comparisons.

Nevertheless, Villamonte, de Lamballerie, and Jury (2014) examined the use of HPP in meat processing using an LCA methodology. They reported that the contribution of an HPP treatment, as an additional step, to the life cycle of cooked ham was nearly negligible. The environmental footprint of HPP was equal or less than a 0.1% increase to parameters such as global warming potential, acidification, eutrophication, and photochemical oxidation. The environmental burden of different impact categories decreased about 16% for the HP-treated cooked ham in comparison to the traditional process. The comparison of the value performance with regard to the environmental impact is defined as ecoefficiency. The use of HPP as a postpackaging cold pasteurization step in the production of cooked ham improved the ecoefficiency of the product. Improving food security and an extended shelf life can clearly compensate for the minimal environmental impact of an HPP treatment (Villamonte, de Lamballerie, & Jury, 2014). A recent comparison of the costs and the environmental performance using an LCA methodology was performed in Parma ham, which was processed either by HPP or by modified atmosphere packaging (MAP). This study revealed that HPP was not only less expensive but also had a lower impact in most of the impact categories, as MAP requires a significant amount of packaging materials and food gases (Cacace et al., 2020). In some cases, reducing packaging and increasing shelf life can pay off for a higher energy consumption during processing. If it is considered the resource-intensive nature of our food supply chain, a technology that can double shelf life keeping the nutritional value offers immediate and significant environmental benefits.

5 | CURRENT LIMITATIONS, TRENDS, AND FUTURE OPPORTUNITIES

The intense research conducted in the last decades has resulted in a detailed characterization of the HP-induced molecular impacts in meat systems. However, some HP-induced molecular changes still remain elusive. This is partially due to the complexity of muscle structure and the interconnections between the meat components itself, specially the proteins, and their dynamic changes taking place during HPP treatment within the particular chemical and physical surroundings under the specific treatment conditions (P, T, t, and their gradients during processing) and the resultant structural rearrangements. In particular, a better molecular characterization of the HP-induced changes on the muscle cell structure, the disassociation of the actomyosin complex and/or disorganization of other potential muscle structures happening at around 200 MPa, and the effect of HP on collagen-based structures, which to date has been largely neglected, could leverage our understanding of the HP-induced structural changes determinants with major impact on product quality, and further, pave the way for full utilization of HPP for meat tenderization and structure formation purposes.

Commercial sterilization of meat products using HPP is not readily available at the moment. HPP (without heat) is unable to inactivate bacterial spores, which is required to reach commercial sterilization. To tackle this challenge, different strategies and processes combining HP with heat have been assayed with varying degrees of success (Black et al., 2007). One of these processes is the use of HP (assisted) thermal sterilization, which, so far, is only doable in pilot-scale HPP units. This process makes use of the self-generated heat when compression is applied to reach sterilizing temperatures. But the use of high temperatures combined with HPs is a technological barrier that has not been fully overcome in industrial units. The operation of HP equipment in continued production cycles in a wide range of operation temperatures (20 to 120 °C) is a rather stressful condition potentially affecting physical structure, mechanical properties, and the stability of a high-pressure vessel in the long run, which could be the cause of a work safety incident. Hence, HPP using moderate to high temperatures is not currently possible and still requires the development of validated industrial equipment, though it could be a breakthrough in the future of advanced food preservation technologies. The use of canisters with the product externally heated could be an alternative process to overcome this technological challenge and attain commercial sterilization (Knoerzer, 2017), but this will require an additional step for loading/unloading of product inside/outside the canisters and heating to the required temperature before HPP treatment. The use of

canisters would achieve the pressure–temperature combinations required for many applications, such as pasteurization and sterilization of low-acid food products (essentially the elimination of bacterial spores), as well as product texture modification, for example, meat tenderization. HPP of muscle foods at moderate to high temperatures could have clear implications not only in the development of sterilized products that are stable at room temperature, but also for tenderization of meats and for structure formation of processed meats. Advances in equipment enabling the combined use of HP and moderate to high temperatures could bring about significant advantages and facilitate new processes that are currently not viable due to technological limitations.

HP effects on meat systems proceed in a different manner to temperature driven processes and, as such, offer possibilities to industry that cannot be achieved by common thermal procedures. Hence, it has the potential to be applied to develop novel transformative processes, which can be utilized during the conversion of muscle into meat and further into meat products. For instance, HPP applied at the prerigor state of meat can modify functional properties of meat such as WHC and emulsifying ability, and as a result, boosting the properties and abilities of meat for further processing. This route could open new possibilities for using HPP in combination with hot-boning practices at abattoirs developing more efficient transformation processes of meat than are currently employed.

The use of the hurdle technologies concept for preservation can contribute to an even further shelf life extension (Leistner & Gorris, 1995). In this sense, the use of different antimicrobials combined with HPP treatment has been extensively investigated with good outcomes (Section 3.1.1). The most recent research has put a focus on the combined use of HPP with bacteriocins and lactic acid bacteria strains aimed to be used as bioprotective cultures to control vegetative cells of spore-forming bacteria in cooked ham after application of HPP (Ramaroson et al., 2018). Process validation of such approaches should be prioritized for future research, targeting pertinent microorganisms in the appropriate matrixes. These strategies can contribute to extend further shelf life and improve safety, all in all, facilitating logistics and reducing waste.

Moreover, HPP has been useful to reduce the salt content and chemical additives from meat products' formulations due to a guaranteed shelf life extension. For instance, in the United States, HPP is one of the technologies that have been successfully applied in commercial scenarios to deliver safe naturally cured meat products to market when combined with antimicrobials against spore-forming bacteria (e.g., cultured celery as a natural nitrite source against *Clostridium Botulinum*). This has permitted the industry to enter the market of "natural and organic products." HPP reinforces the microbiological quality assurance in conditions of "naturally cured" meat products or where less nitrite is used (Myers et al., 2013; Sebranek, Jackson-Davis, Myers, & Lavieri, 2012). The use of natural extracts with antimicrobial and antioxidant properties in combination with HPP has also been tested with success (Mizi et al., 2019; O'Neill et al., 2018). These strategies that combine HPP treatment and additional technological aids provide new ways for further improvement of microbial control and extension of shelf life in meat products, allowing clean labeling and natural protection.

An extended shelf life can help processors reduce food waste by providing the industry with a longer time frame to manage logistics and extension of expiration or "consume by" dates, thereby achieving a more sustainable food supply. Overall, not only product quality and safety of meat products can be improved by using HPP without an important contribution to the environmental impact, but also an extended shelf life can bring about environmental benefits as it can help the industry to reduce food waste, for instance, in some segments such as short-lived minimally processed meat products.

The use of HPP can also be applied to attempt to reduce the allergenicity of meat products and to improve digestibility, particularly because of the HP-induced effects on protein structure (Pottier, Villamonte, & de Lamballerie, 2017). However, this is yet an incipient research field, and the same authors highlighted that there is a lack of in vivo studies needed to assess the improvement of digestibility and reduction of allergenicity in humans, which are required in order to validate these potential novel HPP applications.

The development of vessels of higher volumes along with the implementation of automation solutions in the processing lines for loading, unloading, and handling of meat products will result in higher processing outputs, and most likely also in the reduction of processing cost per kilogram. This will make HPP technology more accessible to large companies. Indeed, an outstanding increase of the industrial vessel volumes has been already accomplished in the last 10 years, with vessels of up to 520 L being currently available. Moreover, the instantaneous transmission of HP throughout the entire system, together with the considerably lower processing times compared to traditional thermal processing methods, makes it a unique technological ally for the industry in its endeavor to gaining processing efficiencies in the food supply chain (Pardo & Zufia, 2012; Toepfl, Mathys, Heinz, & Knorr, 2006). The establishment and consolidation of tolling facilities in many countries over the globe may allow the access to the benefits that HPP technology can bring to small producers and provide flexibility of use to large meat companies in the near future. This could leverage the adoption of the HPP technology

as subcontracted manufacturing services, many times integrated within national and overseas logistic platforms.

Overall, sliced RTE meat products with ensured safety (free of *Listeria*), minimally processed meats, and with reduced amount and number of additives have been the main market drivers of HPP technology in the meat industry so far. Evolution to equipment capable of higher productions with more automation incorporated in the processing line is forecasted. This will allow the HPP technology to penetrate into large companies. Applications adding up microbial inactivation benefits, the primary goal of the technology, along with some of the various benefits that this technology can offer, such as improved or desired texture and clean labeling, could result in more added value, facilitating the uptake of HPP's costs.

6 | CONCLUSIONS

The use of HPP as a cold pasteurization method is nowadays a standard practice in many meat companies to assure food safety and extend the shelf life of minimally processed, RTE and premium cold cuts and meat products. Meat history and processing steps prior to HPP treatment, as described along this review, may greatly affect product quality (e.g., WHC, color, susceptibility to oxidation, protein functionality, and texture), and therefore, must be carefully considered in order to make the best possible use of the HPP technology. Furthermore, the fundamental principles of the application of HPP for meat tenderization and for structure formation in the manufacturing of processed meats are to a large degree very well laid down, and its adoption by industry depends heavily on other factors such as initial capital investment, payback periods, cost–benefit analysis, and a reorganization of the industrial processes and plant layouts within the meat processing plants. Future research and industrial applications with HPP technology in meat industry can be outlined into two main category groups of meat products:

1. HPP for fresh meat products. HPP discolors fresh meat, hence, its role in tenderization and microbial decontamination comes with a very important inherent limitation difficult to overcome. Because the application of HPP to prerigor meat for tenderization purposes requires no heat application, which often results in a reduced impact on meat color, this approach could be more plausible and should be explored more intensively. In reality though, the hot-boning practices that would be required for a prerigor application of HPP are very unusual in present meat processing plants, which so far has precluded a greater interest in this approach. On the other hand, application of HPP to postrigor meat intended for tenderization has to be combined with heat, but can constitute a rapid technique to achieve sous vide tenderness. This novel HPP-based process could be used for tenderization of low-value cuts in cooked applications, for instance as a pretreatment in the development of "extra-tenderized" steaks for food service applications.
2. HPP for value-added or further-processed meat products. The multiple functionality of HPP technology on microbial inactivation as well as a concomitant method for increasing water binding, reducing additives, and/or obtaining a desired texture can make HPP one of the methods of choice by industry to develop microbiologically stable processed meats with a similar or extended shelf life when reducing the content of salt (NaCl) and additives such as nitrites, sulfites, and phosphates commonly employed in meat formulations. The removal of food preservatives such as salt, nitrite, and sulfites will have to be done adopting a holistic approach addressing the adequate replacement of all of the functionalities required (i.e., mainly antimicrobial, antioxidant, and water retention). Some of the basic principles to attain that goal are briefly described in this review, but more research exploring the combination of extracts (generally from plant sources) having those cited functionalities and bioprotection methods in combination with HPP will have to be carried out in order to gain in our knowledge of specific hurdle strategies that at the same time maintain product quality, all-in-all enabling real progress toward the reduction of food additives/preservatives in meat products. Besides that, HPP could also play a role in the development of convenience, minimally processed RTE meals and pet food containing meat and/or meat co-products with moderate shelf life span and distributed under refrigeration conditions, while enduring a much lower heat load.

To sum up, HPP can help processors increase innovation across the meat sector, providing the industry with alternatives for healthier clean label processed meats, salt reduction, facilitating access to organic markets, valorization of low-value cuts, and to develop stable meat products with higher nutritional value, retained quality, enhanced food security, and better sustainability of meat supply chains.

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AUTHOR CONTRIBUTIONS

TB and DB contributed to the design of the manuscript's architecture; collected and merged all the contributed sections; and wrote the abstract, introduction, Sections 4 and 5, and the conclusions. VO contributed Sections 2.2 and 3.3 regarding the effect of HPP on texture formation. AS contributed the section related to meat tenderization. KB wrote section related to color changes. KA, A-SS, and CH contributed the Sections 2.1 and 3.1 related to microbial inactivation and shelf life extension. CG and ML contributed the Section 2.4 regarding oxidation with HPP. TB, VO, KB, KA, CG, and AS proof-read the entire manuscript.

CONFLICTS OF INTEREST

The authors declare no conflicts of interest.

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