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16 **Assessing individual muscle characteristics to enhance frozen-thawed meat**
17 **quality**

18

19 **Abstract**

20 This study assessed previous research aimed at mitigating the adverse effects of freeze-
21 thawing on meat quality. Specifically, it focuses on assessing the physicochemical alterations
22 in meat resulting from freezing, freeze-thawing, or technologies to minimize these alterations.
23 Recent studies have focused on conventional freeze-thaw technology applicable across
24 various livestock species and muscle types. However, recent research has indicated the
25 necessity for developing freeze-thaw technology considering the unique characteristics of
26 individual muscles. In this review, we summarize previous studies that have compared
27 alterations in the physicochemical properties of primary muscles owing to freezing or freeze-
28 thawing. Despite the introduction of various technologies to significantly reduce the adverse
29 effects on meat quality resulting from freeze-thawing, it is essential to consider the unique
30 characteristics (proximate composition, pH, and muscle fiber characteristics) of individual
31 muscles or cuts to develop enhanced the freeze-thaw processing technology.

32

33 **Keywords:** Freeze-thaw technology, meat quality, muscle type, muscle characteristics

34 **1. Introduction**

35 Freezing meat enables long-term storage and distribution, inhibits the growth of
36 microbes, and minimizes alterations in quality (Leygonie et al., 2012). However, thawing
37 frozen meat leads to adverse alterations in quality, such as excessive exudation of meat juice,
38 discoloration, and accelerated oxidation of proteins and lipids (Kim et al., 2013; Zhang et al.,
39 2017).

40 Persistent academic and industrial initiatives aim to develop technologies to mitigate
41 adverse alterations in meat quality by minimizing physicochemical changes during the
42 freeze–thaw process (Zhang et al., 2023). Various physical and chemical phenomena that
43 occur in meat during freezing or freeze-thaw processes have been observed, and their effects
44 on meat quality characteristics have been assessed (Leygonie et al, 2012). Additionally,
45 methods such as controlling freezing and thawing speed, brine injection, vitamin E treatment,
46 high-pressure, ohmic and electrostatic field treatments, and aging technology have been
47 introduced to enhance frozen-thawed meat quality (Cevik and Icier, 2020; He et al., 2014;
48 Hou et al, 2020; Kim et al., 2018; Zhu et al, 2004). Numerous studies have summarized and
49 reviewed the technologies developed over the last two decades (Zhang et al., 2023). Most of
50 these studies have focused on freeze-thaw technology, a widely applied method, regardless of
51 the livestock species and muscle type. However, meat exhibits characteristics (proximate
52 components, pH, and muscle fiber composition) unique to each muscle and displays varying
53 physicochemical characteristics before freeze-thawing (Park et al., 2022). Therefore, these
54 inherent variations in characteristics are anticipated to change depending on the muscle used
55 during meat processing, including freezing and thawing.

56 However, previous studies have not adequately assessed the variations in muscle or
57 meat cut characteristic-based freezing susceptibility and its influencing factors. Therefore, this
58 review summarized the research results regarding the physical and chemical alterations in

59 significant muscles owing to freezing or freeze-thawing. Moreover, we emphasize the
60 necessity of developing technology to minimize adverse alterations in meat quality owing to
61 freeze-thawing, depending on the characteristics of each muscle. To achieve this, we assessed
62 previous studies related to the freezing and freeze-thawing of meat, specifically focusing on
63 the results of muscles or comparative studies between various muscles or cuts.

64

65 **2. Formation of ice crystals through freezing and its effect on muscle tissues**

66 Freezing meat effectively prevents spoilage by inhibiting the growth of
67 microorganisms (Coombs et al., 2017). However, thawing meat following freezing gradually
68 eliminates its latent heat, resulting in altered physicochemical attributes, including reduced
69 juiciness and water-holding capacity (WHC), discoloration, increased rancidity, and texture
70 alterations (Cheng et al., 2020; Cheng et al., 2021; Park et al., 2012). This is because of the
71 effects of ice crystals that form between and within myofibrils during the freezing process
72 (Dang et al., 2021; Schudel et al., 2021). Meat contains approximately 75% water depending
73 on the species, muscle type, and fat content (Huff-Lonergan and Lonergan, 2005). Among the
74 different water types (bound, entrapped, and free) within meat, the entrapped and free water,
75 crucial for chemical and biochemical reactions in meat, are susceptible to freezing due to ice
76 crystal formation; however, bound water remains non-frozen in meat. Approximately 88% of
77 the total water content in meat is freezable (Xanthakis et al., 2013).

78 Ice crystal formation in meat typically begins at approximately -1°C , with
79 approximately 75% of the moisture of the forming ice crystals at -5°C (Cooke and Wien,
80 1971; Huff-Lonergan and Lonergan, 2005). When the core temperature of the meat drops to -
81 12°C , approximately 92% of the moisture forms ice crystals, and the residual moisture
82 maintains the ingredients in the meat, including proteins, in an unfrozen state (Cooke and
83 Wien, 1971; Huff-Lonergan and Lonergan, 2005). While meat is frozen, water initially

84 creates ice crystal nuclei both inside and outside the muscle fibers (myocytes), which then
85 gradually expand in the form of branches, producing large or small crystals (Xanthakis et al.,
86 2013). These ice crystals can physically damage muscle microstructure, resulting in Z-line
87 destruction, I-band weakening, and increased intermyofibrillar space (Añón and Calvelo,
88 1980; Cheng et al., 2020). The degree of physical destruction within the muscle varies
89 depending on the size of ice crystals (Dang et al., 2021; Schudel et al., 2021).

90 The freezing rate of meat determines the size and number of ice crystals, which affect
91 the muscle fiber structure (Fig. 1). Rapid freezing leads to the formation of smaller ice
92 crystals outside muscle fibers, whereas slow freezing leads to the formation of larger ice
93 crystals (Cheftel et al., 2002; Fernández et al., 2006; Su et al., 2014). The freezing rate is
94 linked to the heat transfer rate from the outside to core of the meat and is closely related to the
95 uniformity and non-uniformity of the histological and physicochemical properties of frozen or
96 frozen-thawed meat (Choi et al., 2016; Sanz et al., 1999). Drip loss inevitably occurs when
97 the frozen meat is thawed. During thawing, ice crystal formation varies based on the freezing
98 speed of meat, which determines the degree of muscle tissue destruction and drip loss (Dang
99 et al., 2021; Schudel et al., 2021). Additionally, the formation of ice crystals alters the solute
100 concentration both within and outside the muscle fiber, resulting in an imbalance, thereby
101 leading to biochemical and physical alterations in multiple meat components (Bevilacqua et
102 al., 1979; Huff-Lonergan and Lonergan, 2005; Love and Haraldsson, 1961). Therefore, ice
103 crystal formation and physicochemical alterations within the muscle tissue owing to freezing
104 are significant factors that directly or indirectly affect muscle food quality characteristics such
105 as WHC, meat color, flavor, and texture (Cheng et al., 2020; Cheng et al., 2021; Dang et al.,
106 2021; Wang et al., 2020).

107

108 **3. Effects of freezing and freeze-thawing on meat physicochemical properties**

109 Freezing is an effective method to extend the shelf life of meat. However, the
110 freezing and thawing processes have adverse effects on meat quality characteristics, such as
111 discoloration, reduction in WHC, and alterations in sensory properties (flavor, taste, and
112 texture) (Dang et al., 2021; Wang et al., 2020). A detailed overview of the alteration in color,
113 WHC, texture, and shelf life of meat owing to freezing and freeze-thaw cycles is described
114 below.

115

116 **3.1. Water-holding capacity (WHC)**

117 The shelf life of meat is usually determined by its appearance, color, flavor,
118 nutritional value, and microbial activity. The various ingredients of meat are crucial factors
119 that affect its quality characteristics and alterations (McMillin, 2008). The moisture of meat is
120 primarily retained in the interstices between the thick and thin myofibril filaments. This
121 occurs within and between myofibrils, and a small amount of water within the muscle is
122 retained through the electrostatic attraction between proteins (Bond et al., 2004; Cheng and
123 Sun, 2008). Additionally, the fat present in meat contains water, which contributes to
124 maintaining its moisture content (Joo et al., 2002). When meat releases moisture naturally or
125 owing to certain factors (cooking, freeze-thawing, and pressing), the exudate contains
126 nutrients and flavor components, such as vitamins, minerals, and amino acids (Añón and
127 Calvelo, 1980; Leygonie et al., 2012; Ngapo et al., 1999). Therefore, WHC (the ability of
128 meat to retain moisture) is synonymous with the effectiveness of retaining various useful
129 ingredients in meat. Additionally, WHC is commonly assessed by measuring the degree of
130 drip loss, thawing, cooking, and purging (Honikel, 1998; Honikel and Hamm, 1994; Huff-
131 Lonergan and Lonergan, 2005).

132 Freezing significantly reduces the WHC of meat. Thawing of the frozen meat results
133 in excessive exudation of its juices (Leygonie et al., 2012). Therefore, basic and applied

134 studies were conducted to minimize the amount of meat exudate, as listed in Table 1. The
135 primary results of previous studies on the loss of exudates and alterations in WHC in meat
136 based on freezing or freeze-thaw processes are summarized below.

137 Regardless of the animal species, increasing the freezing rate can reduce the size of
138 ice crystals and the thawing loss (Kim et al., 2020; Yun et al., 2021). Repeated freeze-thaw
139 cycles result in a significant deterioration of meat quality; additionally, a substantial alteration
140 in freezing temperature results in unfavorable WHC compared to a minor temperature
141 alteration (Wang et al., 2020). The WHC varies based on the order of aging (cold storage) and
142 freezing. When aged for approximately three weeks following freeze-thawing, more exudates
143 were lost compared to frozen-thawed following aging (Kim et al., 2018). In studies using
144 various cuts (muscles) of pork and beef, the loss of exudates owing to freeze-thaw may vary
145 based on the muscle type. Cooking loss of pork loin (*M. longissimus thoracis et lumborum*)
146 increased significantly following freeze thawing compared to that of other muscles (*M. psoas*
147 *major*, *M. semimembranosus*, and *M. semitendinosus*). However, in beef, tenderloin (*M.*
148 *psoas major*) exhibited significant WHC following freeze thawing compared to other muscles
149 (*M. longissimus lumborum*, *M. semimembranosus*, and *M. semitendinosus*) (Cheng et al.,
150 2020; Cheng et al., 2021). Additionally, it has been confirmed that cooking loss in beef
151 significantly increases when the freezing period increases, regardless of muscle type (Cho et
152 al., 2017). Freezing solutions consisting of sodium chloride, ethyl alcohol, and chitosan
153 reduce the size of ice crystals and the thawing-related loss in pork (Hou et al., 2020).

154 During thawing, meat undergoes protein breakdown, lipid oxidation, color changes,
155 and ice crystal melting, reducing its WHC (Gan et al., 2022; Min et al., 2016). Poudyal et al.
156 (2023) observed that shorter thawing times increased drip loss in porcine *M.*
157 *semimembranosus*, whereas longer thawing times enhanced the reabsorption of free water
158 from ice crystals, thereby reducing the final moisture loss. However, shorter thawing times

159 may result in inadequate water reabsorption, resulting in excessive water loss (Gonzalez-
160 Sanguinetti et al., 1985). Min et al. (2016) observed that thawing meat using pressure ohmic
161 thawing of up to 200 MPa with an electric field strength of 40 V/cm and pressure-assisted
162 thawing of up to 200 MPa reduced drip loss in beef psoas major compared to conventional
163 thawing methods.

164

165 **3.2. Meat color**

166 Consumers prioritize price and color when purchasing meat (Carpenter et al., 2001).
167 However, meat discoloration occurs during storage or retail displays. Based on previous
168 research, 15–20% of discoloration occurs during retail displays, resulting in an economic loss
169 of 50% or more (Hood and Riordan, 1973; Mancini and Hunt, 2005). The primary factors
170 influencing meat color are the myoglobin content and chemical state (Suman and Joseph,
171 2013). Myoglobin alters meat color based on redox phenomena (King et al., 2023). In its
172 unoxidized state containing iron molecules, myoglobin exists as deoxy-myoglobin
173 (deoxyMb), and the meat color appears purple. When deoxyMb reacts with oxygen in the air,
174 known as blooming, it transforms into oxy-myoglobin (oxyMb), which displays a bright
175 cherry-red color. When deoxyMb and oxyMb lose electrons or both electrons and oxygen,
176 they are converted into oxidized myoglobin (metmyoglobin; metMb), resulting in meat with a
177 brownish tint.

178 Therefore, meat color changes based on the chemical state (oxidation or reduction
179 states, bonding with oxygen or water molecules) of the heme iron molecule in myoglobin.
180 Additionally, the role of oxidation-reduction enzymes in altering the chemical state is crucial
181 (Tang et al., 2005a; Tang et al., 2005b; Tang et al., 2005c). External factors that affect the
182 oxidation-reduction states of myoglobin, such as packaging conditions (aerobic vs.
183 anaerobic), storage temperature (refrigerated vs. frozen), and storage period, directly alter the

184 oxidation, reduction, and oxygenation states (King et al., 2023). Moreover, it also affects the
185 activity of enzymes involved in the oxidation-reduction of myoglobin (Tang et al., 2005a;
186 Tang et al., 2005b; Tang et al., 2005c). Freeze thawing is one of the factors responsible for
187 these intricate alterations in meat color (Jeong et al., 2011).

188 As demonstrated in Table 1, a slow freezing speed correlated with an increase in the
189 lightness of the meat. Moreover, with an extended frozen storage period, the lightness of beef
190 tenderloin reduces (Cho et al., 2017; Hou et al., 2020; Kim et al., 2020). However, the redness
191 and yellowness of pork and beef do not vary during the freezing period (Cho et al., 2017; Hou
192 et al., 2020). Additionally, repeated freeze-thaw with significant temperature alteration results
193 in a reduction in the lightness and redness of beef, whereas the yellowness increases (Wang et
194 al., 2020).

195 Meanwhile, during cold storage following freeze-thaw, a slower freezing speed
196 results in an increase in the lightness of pork loin and a reduction in yellowness (Kim et al.,
197 2018). Studies on the effects of freeze-thaw on pork and beef muscles have shown contrasting
198 results for the loin muscles of the two species. The lightness of beef was reduced and the
199 redness increased following freeze-thawing, whereas redness increased following freeze-
200 thawing (Cheng et al., 2020; Cheng et al., 2021). However, the lightness of pork loin tends to
201 be increased and redness is reduced following freeze-thawing (Cheng et al., 2021). In
202 contrast, semimembranosus exhibited an increase in redness owing to freeze-thawing,
203 regardless of the species. Moreover, psoas major exhibited a tendency to reduce yellowness
204 owing to freeze-thawing of beef. However, psoas major exhibited relatively smaller
205 alterations in meat color owing to freeze-thawing in both species compared to other muscles,
206 such as *M. longissimus thoracis et lumborum*, *M. semimembranosus*, and *M. semitendinosus*
207 (Cheng et al., 2020; Cheng et al., 2021). Furthermore, the meat color changes during thawing.
208 Min et al. (2016) demonstrated that thawing beef psoas major did not alter the lightness of

209 meat. However, the redness and yellowness reduced in all thawing treatments, such as
210 pressure-assisted thawing up to 200 MPa, pressure ohmic thawing up to 200 MPa, electric
211 field strength of 40 V/cm, and immersion thawing. Gan et al. (2022) observed that ultrasonic
212 thawing for beef, pork, and lamb *M. psoas major* resulted in minimal alterations in meat color
213 compared to other thawing methods, such as microwave, room temperature, and 25°C water
214 thawing. This indicates that ultrasonic thawing is significantly effective in preserving muscle
215 quality and reducing myoglobin and lipid oxidation in meat.

216

217 **3.3. Tenderness**

218 Meat tenderness is a crucial sensory quality, and its variations are caused by
219 alterations in the chemical composition and structural properties of muscle fibers and
220 connective tissues, which are influenced by the animal species, breed, slaughter method, and
221 postmortem processing of the meat (Pogorzelski et al., 2022; Zhang et al., 2023). Freezing
222 affects meat tenderness with a positive correlation between freezing and tenderness
223 (Lagerstedt et al., 2008). Ice crystals generated through freezing exert pressure on muscle
224 tissues, resulting in physical destruction and protein decomposition (Añón and Calvelo, 1980;
225 Cheng et al., 2020). When meat is frozen, larger ice crystals cause significant physical
226 destruction of the muscle tissue and meat tenderness (Leygonie et al., 2012; Zhang et al.,
227 2023). Thawing technique also affects meat tenderness. Min et al. (2016) demonstrated that
228 the pressure ohmic thawing technique results in minimal texture alteration, with shear forces
229 closely resembling those of fresh meat.

230 Aging the meat adequately before freezing negates the tenderizing effect of freezing
231 (Vieira et al., 2009). Enfält et al. (2004) discovered that beef subjected to initial aging for
232 seven days before freezing exhibited similar shear force to beef aged for 21 days in
233 refrigeration. Shanks et al. (2002) observed that frozen-thawed longissimus dorsi exhibited a

234 lower shear force than chilled meat over the same period. Freezing enhances tenderness
235 (reduction in shear force); however, the degree of enhancement varies based on the freezing
236 rate. Rapid freezing forms smaller ice crystals compared to slow freezing, resulting in
237 relatively less enhancement of tenderness (Kim et al., 2015; Kim et al., 2018; Yun et al.,
238 2021). Additionally, prolonged frozen storage enhances meat tenderness (Cho et al., 2017).
239 Furthermore, distinct tenderness patterns following freeze-thawing were observed among
240 various muscle types, with a reduction in the tenderness of porcine *M. semimembranosus* and
241 *M. semitendinosus*, and an enhancement in the tenderness of bovine *M. longissimus*
242 *lumborum* (Cheng et al., 2020; Cheng et al., 2021). Cheng et al. (2020, 2021) reported that
243 varied characteristics of the muscle fibers in each muscle may contribute to the varying
244 susceptibilities of muscle types owing to freezing. Additionally, freezing can physically
245 damage muscle tissue and enhance tenderness but weakens the WHC of meat. This leads to
246 excessive meat exudation upon thawing, resulting in a dry or tough meat texture. Because
247 excessive exudation of meat juice negatively affects tenderness, it can be enhanced or reduced
248 through freeze-thawing based on the characteristics of each muscle. In order to reduce the
249 negative changes in meat texture caused by the reduction in WHC, it is necessary to minimize
250 the destruction of the tissue through rapid freezing and high pressure treatments (Choi et al.,
251 2016; Min et al., 2016; Sanz et al., 1999).

252

253 **3.4. Microbial growth and oxidation in meat**

254 Freezing is a microbiologically safer and long-term meat storage method compared to
255 refrigeration. This is because microbial growth is inhibited at approximately -12 °C, cell
256 metabolism in animal tissue is inhibited at approximately -18 °C, and alterations in meat
257 quality are minimal at -55 °C (Dave and Ghaly, 2011; Hansen et al., 2004). Beef and lamb
258 can be stored at -18 °C for 12 months, pork for six months, and poultry meat for 9–12 months

259 (Valero D íaz et al., 2022). Freezing inhibits microbial growth and kills approximately 60% of
260 the microbial population. However, surviving microbes proliferate upon thawing, and fat
261 oxidation persists even during freezing (Dave and Ghaly, 2011; Zhou et al., 2010). Therefore,
262 freezing does not ensure the safety of meat. Lipid oxidation and meat spoilage bacteria are
263 significant factors that shorten the shelf life of meat. Meat products undergo oxidation during
264 processing, storage, and light exposure. This process deteriorates the nutritional and
265 organoleptic properties of meat and results in the formation of toxic compounds that are
266 harmful to humans (Papuc et al., 2017).

267 Thawing results in the conversion of solid ice crystals to liquid water, which raises
268 the surface temperature and can facilitate microbial reactivation by providing appropriate
269 temperature and humidity conditions (Marriott et al., 1980). Additionally, juices exuded
270 during freezing and thawing provide a nutritious environment and suitable medium for
271 microbes (Leygonie et al., 2012). Rapid thawing techniques are crucial for minimizing
272 microbial growth (Min et al., 2016) and reducing damage caused by thawing.

273 Bacteria significantly associated with meat spoilage include *Carnobacterium* spp.,
274 *Enterobacteriaceae*, *Lactobacillus* spp., *Leuconostoc* spp., *Shewanella putrefaciens*,
275 *Pseudomonas* spp., and *Brochothrix thermosphacta* (Borch et al., 1996). *Pseudomonas*
276 species are the primary cause of meat spoilage at temperatures between -1 °C and 25 °C in air.
277 *Pseudomonas* can penetrate meat because of its proteolytic activity (Gill and Penney, 1977;
278 Gupta and Nagamohini, 1992). Therefore, bacterial spoilage of meat results in odors, off-
279 flavors, discoloration, gas production, slime formation, and pH reduction, thereby causing
280 significant economic losses (Papuc et al., 2017).

281 The primary factor that causes the deterioration of stored meat is lipid oxidation,
282 which is caused by enzymes produced by microbes and meat enzymes or autoxidation (Zhang
283 et al., 2010). Among microbes, certain isolates produce lipid-oxidizing enzymes, such as

284 lipoxygenase, linoleate, oxygen oxidoreductase, and hydroperoxide lyase (Brash., 1999).
285 Meat oxidation is a significant factor in the deterioration of meat quality, affecting flavor,
286 texture, nutritional value, and color. Lipid oxidation in fresh meat, known as autoxidation,
287 occurs during cold or frozen storage and is induced by oxygen and lipid free radicals (Soyer et
288 al., 2010). Free radicals are atoms or molecules characterized by unpaired electrons that are
289 inherently unstable and reactive in nature. When they attract electrons from stable
290 compounds, they become free radicals, creating a continuous cycle (Fang et al., 2002;
291 Škrovánková et al., 2012). The resulting hydroperoxides cause biological damage to lipids,
292 hexanes, enzymes, and proteins, thereby resulting in the production of detrimental
293 compounds, such as malondialdehyde and cholesterol oxidation products (Morrissey et al.,
294 1998). Numerous factors influence lipid oxidation in meat, including heat, light, antioxidants,
295 oxygen, phospholipid, and unsaturated fatty acid contents (Guyon et al., 2016). Gan et al.
296 (2022) observed that freeze-thawing of psoas major from bovine, porcine, and lamb increased
297 lipid oxidation in meat across all animal species. However, ultrasonic thawing resulted in
298 significant stable alterations. The degree of lipid oxidation increases with longer thawing
299 times (Fioramonti et al., 2017; Gan et al., 2022). Microwave thawing has a shorter thawing
300 time; however, because of the energy and heat generated, it is excessive and facilitates lipid
301 oxidation (Gan et al., 2022; Lorentzen et al., 2020). Phospholipids present in cell membranes
302 are highly sensitive to oxidation because of their higher unsaturation compared with other fats
303 in meat (Domínguez et al., 2019). Lean meat contains a relatively high proportion of easily
304 oxidized phospholipids. Therefore, phospholipids are the primary cause of fat oxidation in
305 lean meats (Domínguez et al., 2019). Additionally, phospholipid fat oxidation results in
306 noticeable alterations in the meat quality. Lipase-mediated phospholipid degradation has also
307 been observed in frozen meat. These reactions occur at various freezing temperatures and
308 storage periods (Pikul et al., 1985). Therefore, the degree to which packaging reduces air

309 exposure during frozen storage plays a crucial role in determining fatty acid oxidation. Protein
310 oxidation, assessed through carbonyl and sulfhydryl content, is significantly correlated with
311 lipid oxidation (Mercier et al., 1998; Renerre et al., 1999). Meat, specifically chicken, has a
312 high unsaturated fatty acid content. Therefore, lipid and protein oxidation are more prevalent
313 during frozen storage. Moreover, the degree of oxidation is highly significant in chicken legs
314 than in chicken breasts (Soyer et al., 2010).

315

316 **4. Assessing individual muscle characteristics to enhance meat freezing/thawing** 317 **technologies**

318 The quality of meat subjected to freezing and thawing depends on pretreatment,
319 freezing, storage, and thawing conditions. Freezing is the primary process that significantly
320 influences the overall quality of frozen muscle food (Nakazawa and Okazaki, 2020). Rapid
321 freezing and the formation of small ice crystals are crucial for meat freezing because they
322 reduce muscle tissue damage and drip loss during thawing (Li and Sun, 2002). Kim et al.
323 (2018) demonstrated that total exudate loss was reduced in pork loin muscle subjected to
324 rapid freezing (-80 °C) compared to slow freezing (-20 °C). Moreover, aging before freezing
325 and rapid freezing contributed to reduced deterioration. Additionally, rapid freezing reduces
326 the purge and drip loss in beef loins (Kim et al., 2015). Kim et al. (2020) discovered that
327 preserving pork neck and chicken leg meat at varying storage temperatures (-18, -50, and -
328 60 °C) for six months revealed that maintaining the quality of fresh meat without any
329 degradation for the complete duration was achieved through freezing at -60 °C. High-pressure
330 freezing is anticipated to achieve significant supercooling effects that can form uniform ice
331 crystals within meat products (Cheftel et al., 2002). Upon pressure release, an increase in
332 pressure results in the transformation of type-I ice crystals (less dense than liquid water) to
333 type-IV ice crystals (Cheftel et al., 2000). Type IV ice crystals, which are smaller and denser

334 than water, exhibit no expansion upon freezing, in contrast with the 9–13% typical expansion
335 observed in type I crystals. They can produce high-quality freeze-thawed meat with minimal
336 cell structure damage. However, high-pressure freezing is expensive and has limitations on
337 meat size (Chevalier et al., 2000; Fernández et al., 2007). Additionally, static electric field
338 freezing (Fallah-Joshaqani et al., 2019) and ultrasonic technology (Patist and Bates, 2008)
339 have been proposed, with ultrasonic technology reducing the thawing time and structural
340 damage to muscle fibers owing to freezing (Guo et al., 2021).

341 The degree of alteration in meat quality owing to freezing and freeze-thaw varies
342 based on the moisture and fat content and muscle fiber characteristics (Huff-Lonergan and
343 Lonergan, 2005; Song et al., 2020). Among the muscle fiber types, type I is less susceptible to
344 freezing than type II. Therefore, muscles with a higher type I distribution exhibit less
345 deterioration in meat quality when subjected to freezing and thawing (Cheng et al., 2020;
346 Cheng et al., 2021; Song et al., 2020). Moreover, various cuts/muscles exhibit distinct muscle
347 fiber characteristics, including muscle fiber composition, resulting in distinct freezing
348 susceptibilities. Variations in freezing susceptibility based on muscle fiber type have been
349 confirmed in major cuts (loin or strip loin, tenderloin, round, and eye of round) of beef and
350 pork (Cheng et al., 2020; Cheng et al., 2021). Beef tenderloin (*M. psoas major*) with a high
351 proportion of type I muscle fibers exhibited a relatively lower degree of reduction in WHC
352 and discoloration owing to freeze-thawing compared to round (*M. semimembranosus*) and eye
353 of round (*M. semitendinosus*) with a high proportion of type II muscle fibers. This pattern was
354 also observed in the WHC and tenderness of pork. Therefore, these results emphasize the
355 significance of freeze-thaw that considers the components or muscle fiber characteristics of
356 each muscle/cut, regardless of the animal species.

357 Thawing meat results in ice crystal melting, thereby reducing WHC. Therefore, it is
358 crucial to use appropriate thawing techniques to enhance the quality of thawed meat (Alonso

359 et al., 2016), prevent damage to the muscle structure, minimize fat and protein oxidation, and
360 reduce water retention (Zhang et al., 2023). Generally, meat is thawed using air or water at
361 refrigeration or room temperature, which provides a cost-effective approach without physical
362 treatment (Gan et al., 2022; Lan et al., 2021). Advanced thawing technologies, including
363 high-pressure, microwave, ohmic, ultrasonic, electrostatic field, and radiofrequency field and
364 combinations of these techniques (Zhang et al., 2023), can effectively reduce the thawing time
365 and minimize the deterioration of meat quality compared to traditional thawing techniques.
366 Gan et al. (2022) reported that ultrasonic thawing, a physical technique, can effectively
367 prevent muscle structure deformation in meat. Although shorter thawing times are known to
368 reduce meat deterioration, Lan et al. (2021) demonstrated that microwave thawing results in
369 serious muscle damage owing to regional heating. However, a study discovered that
370 radiofrequency thawing can reduce alterations in the structure and properties of proteins,
371 thereby increasing the thawing efficiency.

372 Each skeletal muscle has its own morphological, physiological, kinematic, and
373 functional characteristics. However, muscle cells (fibers) exhibit varying physicochemical
374 characteristics (Park et al., 2022). As demonstrated in Table 2, representative porcine skeletal
375 muscles were identified based on their varying compositions of muscle fiber types (I, IIA,
376 IIX, and IIB), resulting in varied pH, meat color, WHC, and tenderness (Chang et al., 2003;
377 Park et al., 2022; Ruusunen and Puolanne, 2003). Moreover, various bovine skeletal muscles
378 have been profiled and their fiber characteristics and physicochemical properties were
379 differentiated (Joo et al., 2017; Lang et al., 2020; Von Seggern et al., 2005). As reported by
380 Cheng et al. (2020, 2021), various levels of quality alterations through freeze-thaw process
381 are anticipated between various muscle types exhibiting varying muscle fiber characteristics
382 and meat quality. Specifically, porcine skeletal muscles with a higher type II fiber
383 composition and lower type I fiber composition, such as *M. longissimus dorsi*, *M. gluteus*

384 *superficialis*, *M. semimembranosus*, and *M. semitendinosus* should avoid freezing because
385 type II fibers are highly susceptible to freezing than type I fibers (Chang et al., 2003; Park et
386 al., 2022; Ruusunen and Puolanne, 2003; Song et al., 2020). For bovine skeletal muscles, *M.*
387 *psoas major* and *M. superficialis flexors* are anticipated to remain stable when frozen owing
388 to their higher type I fiber composition than that of type II fibers. In contrast, bovine *M.*
389 *semitendinosus*, *M. semimembranosus*, and *M. gluteus medius*, which consist predominantly
390 of type IIB fibers, are anticipated to be susceptible to freezing (Joo et al., 2017; Lang et al.,
391 2020). The muscles are prone to instability during freezing, specifically in pork loin and
392 round cuts, in contrast to the highly stable muscles during freezing, such as tenderloin and a
393 part of the shank. Until recently, with only limited studies, alterations in meat quality owing
394 to freezing and thawing, considering the muscle fiber composition of each cut, have not been
395 adequately assessed. Furthermore, no freezing and thawing technologies were introduced.

396 However, the effects of meat components, such as moisture, fat, protein, and collagen
397 on alterations in muscle tissue and quality characteristics during freezing and thawing have
398 not been assessed. In pork and beef, various muscles exhibit distinct characteristics, resulting
399 in diverse proximate compositions and meat quality properties (pH, color, tenderness, and
400 WHC) (Table 2). For example, the porcine *M. psoas major* has a higher pH than *M.*
401 *longissimus dorsi*, whereas biceps femoris has a lower moisture content and higher fat content
402 compared to *M. biceps brachii* and *M. rectus femoris* (Park et al., 2022; Ruusunen and
403 Puolanne, 2003). Additionally, *M. superficialis flexor* exhibits higher moisture and collagen
404 content, whereas *M. longissimus lumborum* exhibits lower moisture and collagen content
405 compared to the major bovine muscles (Table 2; Joo et al., 2017). Among the various muscles
406 of beef chuck and round cuts, a higher fat content was observed in *M. cutaneous omo*
407 *brachialis*, *M. longissimus costarum*, *M. multifidus*, *M. spinalis dorsi*, *M. serratus ventralis*,
408 and *M. superficial pectoral* (Table 2; Von Seggern et al., 2005). Moreover, pH, moisture, fat,

409 collagen, WHC, and shear force are anticipated to influence the freeze-thawed meat quality
410 characteristics.

411

412 **5. Conclusion**

413 Methods such as rapid freezing, high-pressure treatment freezing and thawing,

414 electric field, ultrasonic treatment thawing, and adjusting the sequence of aging and freezing

415 reduce the degradation of the quality of meat subjected to freezing or freeze-thawing.

416 Regardless of the type of species and cuts (muscle type), improved quality can be expected in

417 the frozen-thawed meat by applying these technologies. Additionally, susceptibility to

418 freezing and quality alterations in meat vary based on the characteristics of each muscle (meat

419 cut). Proper freezing or thawing treatment considering the unique characteristics of each

420 muscle (specifically the muscle fiber characteristics) is expected to further reduce the

421 deterioration in meat caused by freezing. Therefore, additional research is required to assess

422 the effects of unique muscle characteristics (proximate composition, pH, WHC, tenderness,

423 muscle fiber characteristics, etc.) on alterations in the quality of frozen-thawed meat. In

424 conclusion, freezing is a hygienic and safe method to extend the shelf life of meat. However,

425 it is essential to consider unique meat characteristics when implementing technical

426 enhancements to minimize the adverse effects of freeze-thawing on meat quality.

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ACCEPTED

669 **Figure Legends**

670 **Fig. 1: Schematic diagram of the physical destruction of meat tissue due to differences in**
671 **freezing speed.** Rapid freezing creates relatively small ice crystals within muscle, resulting in
672 less tissue destruction, while slow freezing creates large ice crystals within muscle, resulting
673 in severe tissue destruction.

ACCEPTED

Table 1. Previous studies on changes in physicochemical properties of meat due to freeze-thawing.

Species	Muscles	Freezing/thawing/storage conditions	Outcome	References
Porcine	<i>M. longissimus dorsi</i>	Sequence of freezing and aging: freezing without aging (FT), aging prior to freezing (AFT), and freezing and aging (FTA) Slow-freezing: -20°C for 8 weeks and thawing 1 °C for 2 days Fast-freezing: -80 °C and stored -20°C for 8 weeks and thawing 1°C for 2 days Aging: 1°C for 19 days	pH: FTA ≤ FT < AFT ↓ WBSF in FTA with slow-freezing ↑ Purge/thaw loss in FTA unrelated with freeze rate ↑ L* in FTA with slow-freezing ↓ a* in slow-freezing ↓ b* in FTA with slow-freezing	Kim et al. (2018)
Porcine	<i>M. longissimus dorsi</i> <i>M. psoas major</i> <i>M. semimembranosus</i> <i>M. semitendinosus</i>	Fresh: 4°C for 7 days Freeze-thawing: -20°C for 5 days and thawing at 4°C for 2 days	- pH in all muscle cut and freeze-thawing - Purge loss ↓ L* in LTL and ST ↑ a* in LTL and SM ↑ b* in LTL and ↓ in PM and ST ↑ WBSF in SM and ST ↑ Cooking loss in LTL ↓ Drip loss in SM and ST ↓ WHC and toughness in SM and ST ↑ Muscle type I and IIA size in ST ↑ Muscle type IIXB amount in SM	Cheng et al. (2021)
Bovine	<i>M. longissimus thoracis et lumborum</i>	Fresh: aging at 4°C for 2, 7, and 14 days Freeze-thawing: aging for 2, 7, and 14 days at 4°C, freezing at -20°C for 2 months, and overnight thawing at 4°C	↓ WBSF over time ↓ WHC in freeze-thawing ↑ Tenderness, juiciness and meat taste in fresh - Panel preference	Lagerstedt et al. (2008)
Bovine	<i>M. longissimus thoracis et lumborum</i> <i>M. psoas major</i> <i>M. semimembranosus</i> <i>M. semitendinosus</i>	Fresh: 4°C for 5 days Freeze-thawing: -20°C for 3 days and thawing at 2°C for 2 days	- pH in all muscle cut and freeze-thawing ↑ L* in LT with freeze-thawing ↓ a* in LT, ↑ a* in SM and ST with freeze-thawing ↓ b* in SM with freeze-thawing ↓ WBSF in LT with freeze-thawing ↑ Purge losses in LT, SM and ST with freeze-thawing	Cheng et al. (2020)

		<p>↓ Drip loss in all cuts except PM with freeze-thawing ↓ Cooking loss in LT and PM, ↑ cooking loss in SM with freeze-thawing ↑ WHC and ↓ discoloration in PM than SM ↑ Muscle type I amount in PM than SM</p>
Porcine Porcine neck Chicken Chicken leg	Freeze-thawing: frozen at -18°C, -50°C, and -60°C for 0.5, 1, 2, 3, 4, 5, and 6 months and then thawed at 2°C	<p>↓ Thawing loss at -60°C, ↑ thawing loss at -18°C during 6 months in porcine neck and chicken leg with freeze-thawing - Cooking loss in pork neck and chicken leg with different temperature ↑ L*, a*, and b* in pork neck frozen at -18°C</p> <p>Kim et al. (2020)</p>
Bovine <i>M. longissimus thoracis et lumborum</i>	<p>A4: ageing at -1.5°C for 4 weeks A4F2: ageing at -1.5°C for 4 weeks and freezing at -18°C for 2 weeks with fast freezing in freezing solution or slow freezing in air-blast at -18 °C A3F2: ageing at -1.5°C for 3 weeks and freezing at -18°C for 2 weeks with fast freezing in freezing solution or slow freezing in air-blast at -18 °C F2: fast freezing in freezing solution or slow freezing in air-blast at -18 °C for 2 weeks</p>	<p>- pH, cooking loss, drip loss, purge loss and WBSF by freeze rate pH: A4F2 > F2 > A4 > A3F2 Purge loss and drip loss: F2 > A3F2 > A4F2 > A4 Cooking loss: A4 > A4F2 > A3F2 > F2 WBSF: F2 > A4 > A3F2 = A4F2 L*, a*, and C: A4 > A4F2, A3F2, and F2 Hue angle: A4 < A4F2, A3F2, and F2</p> <p>Kim et al. (2015)</p>
Bovine Hind legs	<p>A: Freezing at -18°C with freezing fluctuation cycles repeat for 3 days B: Freezing at -18°C and -17°C; stored at -18°C for 4 hours, raised to -17°C, then returned to -18°C for another 4 hours with freezing fluctuation cycles repeat for 3 days</p>	<p>Free drip loss and cooking loss: A < B < C < D Centrifuge drip loss: A = B < C < D L*: A > C > B > D a*: A > B > C > D b*: A < B < C < D</p> <p>Wang et al. (2020)</p>

		<p>C: Freezing at -18°C and -15°C; stored at -18°C for 4 hours, raised to -15°C, then returned to -18°C for another 4 hours with freezing fluctuation cycles repeat for 3 days</p> <p>D: Cycled between -18°C and -13°C; stored at -18°C for 4 hours, raised to -13°C, then returned to -18°C for another 4 hours with freezing fluctuation cycles repeat for 3 days</p>	
Bovine	<p><i>M. longissimus thoracis</i></p> <p><i>M. longissimus lumborum</i></p> <p><i>M. psoas major</i></p> <p><i>M. semimembranosus</i></p>	<p>Fresh: aging at 2°C for 0, 7, and 14 days</p> <p>Freeze-thawing: frozen at -18°C for 0, 3, 6, and 9 months</p>	<p>↓ L* in PM with increase of freezing period</p> <p>- a* and b* by aging and freezing period</p> <p>↑ WHC in LL, PM, and SM by freezing for 3 months and in LT by freezing for 3 and 6 months</p> <p>↑ Cooking loss in LL, LT, PM, and SM with an increase of freezing period</p> <p>↓ WBSF in LL, LT, and SM with aging period</p> <p>Cho et al. (2017)</p>
Porcine	<i>M. longissimus dorsi</i>	<p>Freeze-thawing: -20°C, -30°C, and -40°C in airflow velocities of 0, 1.5, and 3 m/s and thawing at 2°C over night</p> <p><i>Ice crystal size</i></p> <p>Category I: slow freezing in <0.4 cm/h</p> <p>Category II: intermediate freezing in 0.6–0.7 cm/h</p> <p>Category III: rapid in >0.96 cm/h</p>	<p>Ice crystal size: slow freezing (<0.5 cm/h) > rapid freezing (>0.5 cm/h)</p> <p>↓ Thawing loss in category III > II > I</p> <p>↓ Drip loss and cooking loss in category III > II > I</p> <p>↓ a* and b* in category I</p> <p>↓ WBSF in category II and III than at -20°C with no air</p> <p>Yun et al. (2021)</p>
Porcine	<i>M. longissimus dorsi</i>	<p>ISF: fast freezing in freezing solution at -22°C consisting of 16% sodium chloride, 25% ethyl alcohol, 1.2% chitosan, 0.8% antifreeze protein, and 57% water and thawing at 1, 31, 61 and 91 days at 4 °C for 12 h</p> <p>AF: slow freezing in air-blast at -22 °C and thawing at 1, 31, 61 and 91 days at 4 °C for 12 h</p>	<p>↓ Ice crystal formation in ISF</p> <p>↓ WBSF in AF</p> <p>↑ Myofibrillar damage and lipid oxidation in AF</p> <p>- L*, a*, and b* in ISF and AF with thawing for 91 days</p> <p>↑ pH in AF at 91 days, - pH in ISF</p> <p>↑ Thawing loss in AF for 1, 31, and 91 days</p> <p>≡ Cooking loss in AF and ISF</p> <p>Hou et al. (2020)</p>
Bovine	<i>M. longissimus thoracis</i>	<p>Fresh: aged at 2°C for 2, 3, 4, 5, 6, 7, 10, 14, 21, and 35 days</p>	<p>Cooking loss: fresh < frozen-thawed for 1, 3, 4, 5, 6, 7, and 10 days</p> <p>WBSF: fresh > frozen-thawed for all days</p> <p>Shanks et al. (2002)</p>

		Freeze-thawing: aged for 3, 4, 5, 6, 7, 10, 14, 21, and 35 days at 2°C, frozen at -16°C for 2 months and thawed at 1°C for 24 h	≅ WBSF for 3, 6, and 7 days aged-frozen meat with aged for 14 to 21 days fresh meat	
Bovine	<i>M. longissimus thoracis et lumborum</i>	Pelvic suspension: carcasses hung in pelvic bone Achilles suspension: carcasses hung in Achilles tendon Both suspensions treated at 4°C, aged for 2, 4, 7, 14, and 21 days and frozen at -20°C for 7 days, and thawed at 4°C overnight	- Tenderness in both suspensions ↓ WBSF in pelvic suspension for 2 days ageing ≅ WBSF between suspensions after ageing for 14 and 21 days ≅ pH in both groups during ageing ↓ WHC in Achilles suspension	Enfält et al. (2004)
Bovine	<i>M. longissimus thoracis</i>	Fresh: aged at 4°C for 3 and 10 days Freeze-thawing: aged at 4°C for 3 and 10 days and frozen at -20°C and -80°C for 30, 75, and 90 days, and thawed at 4°C for 48 h	↓ L*, a*, and chroma in Fresh aged for 3 and 10 days ↓ a*, b*, and chroma, and ↑ hue in Freeze-thawing for 90 days ↑ Freezing loss and press loss in Fresh aged for 3 and 10 days - Cooking loss in Freeze-thawing for storage periods ↑ Press loss in Freeze-thawing for 90 days ↑ Cooking loss in Freeze-thawing for 30, 60 and 90 days ↓ WBSF in Fresh aged for 3 days and Freeze-thawing for 75 and 90 days - WBSF in Fresh aged for 10 days ↑ Tenderness in Freeze-thawing aged for 3 days and frozen for 30, 75 and 90 days	Vieira et al. (2009)
Porcine	<i>M. psoas major</i>	<i>Freezing</i> Fresh: stored in 4°C for further analysis SR: -10°C supercooled rapid freezing in static air freezer at -80°C NR: non-supercooled rapid freezing at -80°C SS: -10°C supercooled slow freezing at -20°C NS: non-supercooled slow freezing at -20°C <i>Thawing</i> RT: room temperature thawing in 20°C	- Hardness in all freeze-thawing condition Drip loss: IW and RF < TW and RT ↑ Drip loss in NS ↓ Size ice crystal in SR	Poudyal et al. (2023)

	IW: ice water thawing at $0 \pm 0.5^\circ\text{C}$ RF: refrigerator thawing at 4°C TW: tap water thawing under $12 \pm 2^\circ\text{C}$ running water		
Bovine <i>M. psoas major</i>	<p><i>Freezing</i> Fresh: stored at 4°C for 2 days Freezing: frozen at -40°C for overnight</p> <p><i>Thawing</i> POT: pressure ohmic thawing up to 200 MPa and electric field strength of 40 V/cm PAT: pressure-assisted thawing up to 200 MPa Ohmic thawing: ohmically thawed to 8°C under electric field of 40 V/cm to 4°C at 0.1 MPa Conventional thawing: thawed to 4°C by immersion thawing</p>	<p>↓ Drip loss in PAT, POT and Ohmic thawing Cooking loss: POT < PAT < Ohmic thawing < Conventional thawing ↑ WBSF in PAT - L* in all condition ↓ a* and b* in PAT, Ohmic thawing and Conventional thawing</p>	Min et al. (2016)
Bovine Porcine <i>M. psoas major</i> Lamb	<p><i>Freezing</i> Fresh: refrigeration temperature Freezing: at -80°C for 2days</p> <p><i>Thawing</i> MT: microwave thawing UT: ultrasonic thawing IT: infrared thawing at 60°C and the power of the infrared tube to 12 W RTT: thawed at room temperature SWT: thawed in still water at 25°C</p>	<p>↓ Thawing loss and cooking loss in UT ↑ Cooking loss in RTT ↑ L* in RRT ↓ L* in UT ↑ b* in UT ↓ Lipid oxidation in UT</p>	Gan et al. (2022)

WBSF, Warner-Bratzler shear force; WHC, Water-holding capacity; L*, lightness; a*, redness; b*, yellowness.

≈, approximately equal; -, no significantly different; ↑, increase; ↓, decrease; >, higher; <, lower; =, equal; ≥, higher or equal.

Table 2. Previous studies on muscle fiber characteristics and physicochemical properties in various porcine and bovine skeletal muscles.

Species	Breed	Sex/age/carcass weight	Muscles	Outcome	References
Porcine	Berkshire Tamworth Duroc Large white	Male/NP/NP	<i>M. longissimus dorsi</i> <i>M. psoas major</i>	<p>↑ Type I, muscle fiber proportion in <i>M. psoas major</i> of the Berkshire</p> <p>↑ Type I, muscle fiber proportion in <i>M. longissimus dorsi</i> of the Large White</p> <p>↑ Type IIA, muscle fiber proportion in <i>M. psoas major</i> than in <i>M. longissimus dorsi</i></p> <p>↑ Type IIB and ↓ type IIA, muscle fiber amount in <i>M. longissimus dorsi</i> of Berkshire, Duroc and Tamworth</p> <p>↓ Type I, muscle fiber amount in Large White and ↑ type I amount in both muscles of Duroc</p> <p>↑ Type IIA, muscle fiber amount in Duroc and ↓ type IIA amount in Large White and Tamworth</p> <p>↓ Type IIB and ↓ type IIX, muscle fiber amount in <i>M. psoas major</i> of Large White</p> <p>↓ pH at 45min, drip loss, L*, and hue value in <i>M. psoas major</i> than <i>M. longissimus dorsi</i></p> <p>↑ pH at 24 h, a* and b* in <i>M. psoas major</i> than <i>M. longissimus dorsi</i></p>	Chang et al. (2003)
Porcine	Wild Domestic	Male and female/165±2 days/105.1±8.8 kg	<i>M. longissimus dorsi</i> <i>M. gluteus superficialis</i> <i>M. semimembranosus</i> <i>M. infra spinam</i> <i>M. masseter</i>	<p>↓ Type IIB and ↑ type IIA, muscle fiber area % in <i>M. longissimus dorsi</i>, <i>M. gluteus superficialis</i>, and <i>M. semimembranosus</i> of wild pig</p> <p>↑ Type IIB, muscle fiber area % in <i>M. longissimus dorsi</i>, <i>M. gluteus superficialis</i>, and <i>M. semimembranosus</i> in domestic pig</p> <p>↑ Type IIA and ↓ type IIB, muscle fiber area % in <i>M. infra spinam</i> of wild pig</p> <p>↑ Type I, muscle fiber area % in <i>M. masseter</i> of wild pig</p>	Ruusunen and Puolanne (2003)

Porcine	LYD	Castrated/NP/79. 2±3.5 kg	<p><i>M. infrahyoid</i> <i>M. rectus abdominis</i> <i>M. gracilis</i> <i>M. psoas major</i> <i>M. semitendinosus</i> <i>M. semimembranosus</i> <i>M. vastus</i> <i>M. diaphragm</i> <i>M. longissimus dorsi</i> <i>M. biceps brachii</i> <i>M. biceps femoris</i> <i>M. rectus femoris</i> <i>M. subscapularis</i> <i>M. superficialis digital flexor</i></p>	<p>↓ Moisture content, and high L*, cooking loss, and WBSF in <i>M. semitendinosus</i> than in <i>M. psoas major</i> and <i>M. vastus</i> ↑ Moisture, crude protein, and WBSF but ↓ fat content, pH, a*, and b* in <i>M. longissimus dorsi</i> than in <i>M. diaphragm</i> ↓ Moisture content, higher crude fat content, and ↑ b* in <i>M. biceps femoris</i> than in <i>M. biceps brachii</i> and <i>M. rectus femoris</i> ↑ pH and WBSF, and ↓ drip loss in <i>M. subscapularis</i> than in <i>M. superficialis digital flexor</i> ↑ All muscle fiber area in <i>M. psoas major</i> than in <i>M. semimembranosus</i>, <i>M. vastus</i>, and <i>M. semitendinosus</i> ↓ Type I, relative fiber area in <i>M. semitendinosus</i> ↓ Type IIA and IIXB, relative fiber area in <i>M. semimembranosus</i> ↑ Type IIA, relative fiber area in <i>M. diaphragm</i> than in <i>M. longissimus dorsi</i> ↑ Type IIX and ↓ type IIB in <i>M. biceps brachii</i> than in <i>M. biceps femoris</i> and <i>M. rectus femoris</i> ↓ Type IIA, muscle fiber density in <i>M. biceps femoris</i> ↑ type IIX and ↓type IIB in <i>M. biceps brachii</i> than in <i>M. biceps femoris</i> and <i>M. rectus femoris</i> ↓ type IIA, muscle fiber density in <i>M. biceps femoris</i></p>	Park et al. (2022)
Bovine	Chinese Simmental cattle	Bull/26 months/378±30 kg	<p><i>M. longissimus thoracis</i> <i>M. psoas major</i> <i>M. semitendinosus</i></p>	<p>↑ Type I, IIA, and IIB muscle fiber density in <i>M. longissimus thoracis</i> and <i>M. semitendinosus</i> than in <i>M. psoas major</i> ↑ Type I, muscle fiber number % in <i>M. psoas major</i>. ↓ Type I, muscle fiber number % in <i>M. semitendinosus</i> ↑ Type IIB, muscle fiber number % in <i>M. semitendinosus</i>. ↓ Type IIB, muscle fiber number % in <i>M. psoas major</i> ↑ WBSF in <i>M. semitendinosus</i> and <i>M. longissimus thoracis</i> than in <i>M. psoas major</i> ↓ WBSF, hardness, and chewiness values in <i>M. psoas major</i> than in <i>M. semitendinosus</i> and <i>M. longissimus thoracis</i> ↓ Pressing loss in <i>M. semitendinosus</i> and <i>M. longissimus thoracis</i> at 1, 3, and 21 days of aging</p>	Lang et al. (2020)

				<p>↑ Cooking loss in all muscles at 1 and 3 days of aging ↑ L* in <i>M. semitendinosus</i> at 1 and 21 days of aging ↑ a* in <i>M. psoas major</i> at 1 and 3 days of aging ↑ b* in <i>M. semitendinosus</i> than in <i>M. psoas major</i> at 7, 14, and 21 days of aging</p>	
Bovine	Hanwoo	Steer/NP/NP	<p><i>M. longissimus lumborum</i> <i>M. psoas major</i> <i>M. semimembranosus</i> <i>M. semitendinosus</i> <i>M. gluteus medius</i> <i>M. triceps brachii</i> <i>M. rectus abdominis</i> <i>M. superficialis flexor</i></p>	<p>↑ Type I, muscle fiber number % in <i>M. superficialis flexor</i> ↑ Type IIA, muscle fiber number % in <i>M. psoas major</i> and <i>M. triceps brachii</i> ↓ Type IIA, muscle fiber number % in <i>M. rectus abdominis</i> Type IIB fiber area %: <i>M. semitendinosus</i> > <i>M. semimembranosus</i> > <i>M. longissimus lumborum</i> ↓ Type IIB, muscle fiber number % in <i>M. superficialis flexor</i> ↑ Type I, muscle fiber area % in <i>M. superficialis flexor</i> and ↓ Type I, muscle fiber area % in <i>M. semitendinosus</i> ↑ Type IIA, muscle fiber area % in <i>M. gluteus medius</i> and ↓ Type IIA, muscle fiber area % in <i>M. longissimus lumborum</i> ↑ Moisture and collagen contents in <i>M. superficialis flexor</i> and ↓ moisture and collagen contents in <i>M. longissimus lumborum</i> ↑ a* in <i>M. psoas major</i> and <i>M. superficialis flexor</i> and ↓ a* in <i>M. semimembranosus</i> ↑ L* in <i>M. longissimus lumborum</i> and ↓ L* in <i>M. superficialis flexor</i> ↑ Drip loss and cooking loss in <i>M. semimembranosus</i> ↓ Drip loss and cooking loss in <i>M. longissimus lumborum</i> and <i>M. psoas major</i> ↑ WBSF in <i>M. superficialis flexor</i> and ↓ WBSF in <i>M. psoas major</i></p>	Joo et al. (2017)
Bovine	NP	NP/NP/ 250-431 kg	<p>Chuck 27 muscles Round 12 muscles</p>	<p>↑ Fat content in <i>M. cutaneous omo brachialis</i>, <i>M. longissimus costarum</i>, <i>M. multifidus</i> and <i>spinalis dorsi</i>, <i>M. serratus ventralis</i>, and <i>M. superficial pectoral</i> ↑ WHC in <i>M. deltoideus</i> and <i>M. supraspinatus</i></p>	Von Seggern et al. (2005)

↑ WBSF in *M. biceps brachii*, *M. infraspinatus*, *M. levatores costarum*, *M. multifidus* and *spinalis dorsi*, *M. serratus ventralis*, *M. subscapularis*, and *M. teres major*
↑ pH in *M. dorsalis oblique*, *M. longissimus costarum*, *M. levatores costarum*, *M. multifidus* and *spinalis dorsi*, *M. rhomboidus*, *M. serratus ventralis*, *M. subscapularis*, *M. supraspinatus*, and *M. trapezius*

WBSF, Warner-Bratzler shear force; WHC, Water-holding capacity; L*, lightness; a*, redness; b*, yellowness; ↑ and >, higher or increase; ↓, lower or decrease; LYD, Yorkshire × Landrace × Duroc; NP, not provided.

Fig. 1

