INTERNATIONAL AWARD

Reducing High Rigor Temperature in Carcasses – Towards a Sustainable Meat Industry

Robyn Dorothy Warner

PREFACE

I dedicate this lecture to Bob Kauffman, who taught me about PSE, and with whom, according to Bob, we came up with the term RSE, one Saturday morning in the 1990's. I am deeply grateful to Suman Surendranath for nominating me for the award, and for the hard work that he and Bob Kauffman undertook in preparing my nomination for the award. I am truly humbled that AMSA selected me to be the recipient of this award and am also very grateful to the sponsors of the award.

It was because of the strong foundations of research in PSE in pig meat at the University of Wisconsin-Madison, that I came here to undertake my Ph.D. studies. To work alongside the stalwarts of meat science was inspirational. I took what I had learnt about PSE, muscle structure, muscle proteins and water-holding capacity, back to Australia and tested the concepts in ruminant muscle. After a few years, a few projects and a few collaborations around the world, enough research had accumulated to compile a special edition of the journal Animal Production Science. This lecture reports the highlights of this research. Of course, much of the research is based on the backbone of PSE and meat science research in the 1950's to 1970's.

INTRODUCTION

From as early as 1914, pale, watery pork has been creating problems for the fresh and processed pork industry (Wismer-Pedersen 1959). In the 1960's the term PSE (pale, soft, exudative;Briskey 1964) was used to name the quality condition that had previously been called 'pale, watery' pork or 'white muscle' disease (Lawrie 1960). Much research was devoted to understanding the occurrence of PSE in pigs (Barbut et al. 2008). The occurrence of PSE in poultry muscle has also been reviewed and the causative factors are similar to those in pigs, except a genetic test or mutation has not been identified (Barbut et al. 2008; Solomon, Van Laack, & Eastridge 1998).

The occurrence of pale, weepy meat has been reported in other species (eg. Beef; Hunt & Hedrick 1977a; Hunt & Hedrick 1977b; Tarrant & Mothersill 1977) but little is known regarding the causative factors in beef or sheep carcases. The muscle metabolism post-mortem associated with PSE, as measured by the rate of pH and temperature fall, is known to influence eating quality (Kim, Warner, & Rosenvold 2014; Marsh et al. 1987). In spite of this, the grading schemes for assuring beef and lamb quality, from major meat producing countries do not include this parameter (Polkinghorne & Thompson 2010). In Australia, inducement of rapid metabolism post-mortem using electrical stimulation (ES) was demonstrated to reduce beef eating quality (Hwang & Thompson 2001a; Hwang & Thompson 2001b;Polkinghorne et al. 2008). Thus in 1999, Meat Standards Australia (MSA) recommended the inclusion of a 'pH-temperature window' in the Australian beef eating quality scheme for assuring quality to the consumer (Webster et al. 1999). The prescribed pH-temperature window for beef carcasses stated that the muscle (striploin, longissimus lumborum) should commence rigor (defined as pH < 6.0) between 12^{o}C and 30^{o}C to avoid cold-shortening (≤ 12^{o}C) and 'high rigor temperature' (≥ 30^{o}C) respectively (Ferguson, Thompson, & Polkinghorne 1999). This was later revised to between 15^{o}C and 35^{o}C [see Figure 1 in Gutzke et al. (2014)].

Although a detrimental effect of rapid metabolism, induced by electrical stimulation (ES), on tenderness has not generally been reported in sheep carcasses, there have been some instances where ES produced detrimental effects. Shaw et al. (2005) demonstrated that high voltage electrical stimulation of sheep carcasses increased the percentage of 4 day aged lamb loins rated as unsatisfactory. Warner et al. (2005) showed that low voltage electrical stimulation of lamb carcasses resulted in lower consumer scores for smell, tenderness and overall liking, and attributed this to the 'heat toughening' (viz. higher rigor temperature). Finally, Thompson et al. (2005) showed the curvilinear relationship between consumer scores for sheep meat for overall liking and rigor temperature, with

Robyn Warner, Ph.D.
Melbourne School of Land and Environment
The University of Melbourne
Parkville, Vic., 3010, Australia
robyn.warner@unimelb.edu.au

the optimum rigor temperature being about 20°C. Thus for lamb carcasses, an optimal pH-temperature window for eating quality has been defined as 18-35°C for product aged for 5 days and 8-18°C for product aged for 10 days (Food Science Australia 2007).

On-farm feeding and slaughter practices have resulted in an increase in pale weepy beef in beef carcasses, some causative factors have been identified and these are discussed below. Recommendations for industry implementation for reducing the occurrence of pale, weepy beef and lamb meat are discussed as well as further research.

DEFINITIONS: PSE, DENATURING CONDITIONS AND RIGOR TEMPERATURE

Measuring PSE

For many years, the occurrence of PSE meat was identified by measuring the initial pH in pork muscle between 30 and 60 min, post-mortem. The most common criteria for defining a PSE carcase is that if the pH45 (pH measured at 45 min post-mortem) in the longissimus muscle is less than 6.0, the carcase is classified as PSE (Chadwick & Kempster 1983). This criteria has been used as recently as 2009 to define the occurrence of PSE in beef carcases in China (Du et al. 2009).

Protein denaturing conditions

With the possible exception of rigor formation, denaturation of myosin is one of the most dramatic early post-mortem events in muscle. Penny (1967a;1967b) demonstrated that myosin ATPase activity is the first enzyme/protein to be altered under pH and temperature conditions that mimic post-mortem muscle. The damage to both the myofibrillar and sarcoplasmic proteins that occurs is due to a combination of high temperature and low pH, with the rate of denaturation increasing exponentially as the muscle temperature increases above 30-35°C and the pH drops below 6 (Offer 1991;Scopes 1964).

Measuring rigor temperature

MSA uses a series of pH and temperature measurements in the loin muscle pre-rigor, to calculate the temperature at pH=6 (Warner et al. 2014a; 2014c), rather than using a single pH measurement at a specified time. MSA has also adopted the nomenclature 'high rigor temperature' to describe the conditions where the temperature is high (>35°C) when the muscle pH is < 6 (Warner et al. 2014a), conditions which have previously been described as heat-shortening or heat-toughening.

INFLUENCE OF HIGH RIGOR TEMPERATURE ON QUALITY TRAITS IN RUMINANTS

Carcases defined as 'high rigor temperature' are broadly comparable in metabolism and qualities to pig and poultry carcases which are labelled PSE. An occurrence of abnormally high pre-rigor temperature accompanied by a faster than normal pH decline in muscle (also known as a protein-denaturing condition) has been shown to have detrimental impacts on meat quality attributes of pork, poultry, venison, beef and lamb and these are reviewed in Kim, Warner, & Rosenvold (2014). Recent data on the effects of high rigor temperature on the meat quality of ruminants are presented below.

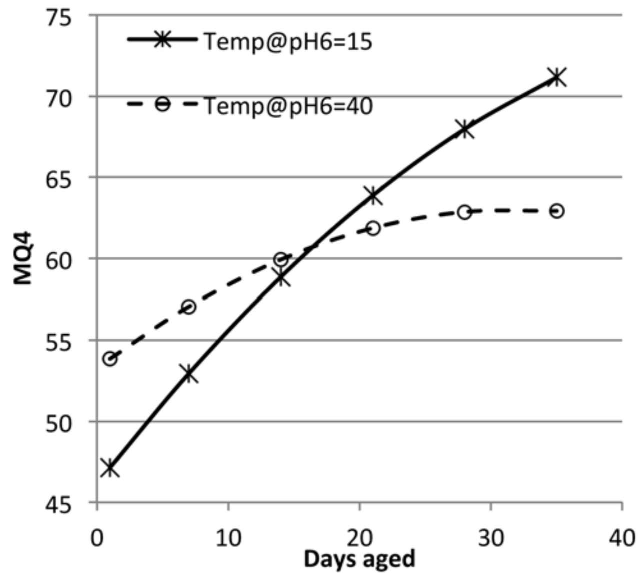

Figure 1: Effect of temperature at pH 6 (Temp@pH6; rigor temperature) and days aged on the predicted consumer MQ4 score (combined score for juiciness, tenderness, flavor and overall liking) for grilled striploin (*longissimus lumborum*) from a carcass which has been achilles hung. Source: Warner et al. (2014c).

Tenderness

Consumer sensory data collected from 3,865 beef striploins varying in days aged, rigor temperature and other traits was used to model the effect of rigor temperature on the consumer perception of tenderness and eating quality (Warner et al. 2014c). There was an interaction between rigor temperature and days aged (Figure 1). Striploins with an 'ideal' rigor temperature of ~15°C were marginally acceptable for tenderness at 1 day post-slaughter, and showed the expected improvement in tenderness with ageing for 4 weeks. Striploins that exhibited a high rigor temperature of 40°C were quite tender (and acceptable) at 1 day post-slaughter, but showed a failure to age beyond 14 days of ageing. This occurrence of heat-induced toughening of meat can be attributed to a combined effect of heat-induced additional sarcomere shortening and alterations of proteolytic enzyme activities (Kim, Warner, & Rosenvold 2014). In particular, the decrease in ageing potential (either early exhaustion of proteolytic enzyme activities or elevated protein denaturation, which consequently limits the proteolysis) could be a main factor in reduced tenderisation in meat from high pre-rigor temperature carcases (Dransfield 1994). The increased tender-

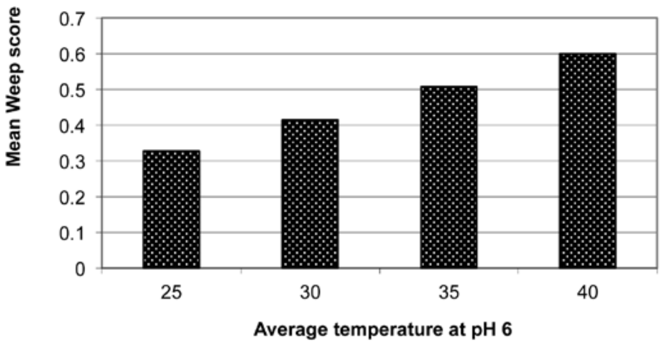

Figure 2: Effect of temperature at pH 6 (rigor temperature) on the weep score at grading (0 = no weep; 1 = weep present). The weep score is assessed on the beef striploin at about the 12th rib (*longissimus thoracis*), at grading, after a 2 hr bloom. It is an assessment of the amount of fluid oozing out of the meat surface. Source: Warner et al. (2014a).

ness seen in unaged meat (at 1–2 days post-slaughter) that has undergone high rigor temperatures may be explained by early activation of the calpain system and possibly changes to the collagen solubility (Dransfield 1994;McClain et al. 1969;Wu, Dutson, & Carpenter 1981).

Water-holding capacity

Many papers and reviews have been published on the impacts of rapid pH decline at a high muscle temperature on WHC in pork (for reviews, refer to Bendall & Swatland 1988; Huff-Lonergan & Lonergan 2005). However, there are a relatively few studies available on meat from ruminants, and until recently it has not been considered a serious problem in beef (Aalhus et al. 1998;Hamm 1986) The increase in 'weep' or 'exudate' from the surface with increasing rigor temperature in beef loin muscles is shown in Figure 2. The reduced WHC (purge, exudate, cook loss, drip loss) of lamb muscles undergoing high rigor temperature have also been demonstrated as shown in Figure 7a (Warner et al. 2014b) and by Kim et al. (2014).

The relatively low proportion of fast-twitch glycolytic muscle fibres in beef compared with pork muscle (Aalhus et al. 1998) has lead to the conclusion that beef and lamb muscles are not subject to the PSE condition. Thus few studies on beef and lamb muscles have included measurements of WHC when investigating the impact of a rapid pH decline, and even fewer have included biochemical measurements to understand the underlying mechanism. Kim, Warner, & Rosenvold (2014) suggest that the underlying mechanisms for PSE development in both ruminants and pigs appear to be similar, but that there is a lack of biochemical data in ruminants. They suggest that measurements of WHC should be included as standard measurements in beef and lamb studies, with a focus on the slaughter process. This would enable substantiation of whether the conditions are indeed identical for pigs and ruminants.

Colour

Pre-rigor muscles undergoing higher than normal temperature accompanied by a rapid pH decline result in paler colour and reduced colour stability of meat (Kim, Warner, & Rosenvold 2014). The decreased colour stability can be attributed to protein denaturation (particularly myoglobin and/or myofibrillar) as a primary factor (Zhu & Brewer 2003; Zhu & Brewer 2002), and possibly altered oxygen consumption by endogenous enzymes and/or metmyoglobin reducing ability (Faustman & Cassens 1990). The paler colour can also be attributed to light scattering (Swatland 2012). A higher temperature at rigor is known to result in an increase in pale coloured meat in both beef and lamb carcases (Hughes, Kearney, & Warner 2014; Kim et al. 2014; Warner et al. 2014c; Warner et al. 2014b) and this is shown in Figure 3.

Protein functionality and processed meats

The functional properties of PSE pork have been found to be inferior to those of normal pork in a range of processed meat products (Honkavaara 1988; Kauffman et al. 1978) but there is a lack of information on the effect of the PSE-like condition on the quality of beef or lamb processed products and it is recommended that R&D is undertaken on this topic.

OCCURRENCE OF HIGH RIGOR TEMPERATURE AND PSE-LIKE CONDITIONS IN BEEF AND SHEEP CARCASES

Although there has been many studies on the influence of high temperatures on the quality of excised muscles in ruminants (Kim, Warner, & Rosenvold 2014), there has been few reports of the occurrence of PSE-like high rigor temperature in carcases in beef or lamb processing plants. In a recent survey of 1,512 beef carcases in Australia, across seven processing plants, the incidence of high rigor temperature (striploin pre-rigor temperature >35°C when pH <6) carcases was 72% (Warner et al. 2014a). It is not possible to compare this directly to historical data in Australia or overseas as this is the first study to quantify the occurrence of high rigor temperature across a beef industry. In the 1970s in Canada, a survey of 1,200 beef carcasses reported that 15% of carcasses had a pH ≤ 6.25 in the semimembranosus muscle at 1 hr post-slaughter and defined these carcasses as 'faster rigor' onset (Khan & Ballantyne 1973). In their study, the semimembranosus muscle had a similar mean and range in the 1 hr post-mortem pH measurements to the longissimus dorsi muscle, thus their results can be compared to our data on the longissimus thoracis (~ dorsi). Using the first pH measurement at 30 to 60 min post-mortem in our study, 75% of the carcasses had a pH ≤ 6.25, clearly indicating faster rates of pH fall in our survey than in the 1970s study in Canada. In fact Rossi, Baldi, & Vandoni (2009) point out that compared to the occurrence of PSE in pork, PSE in beef is severely under-estimated. Using the standard definition of pH45 <6.0, the occurrence of PSE in the beef

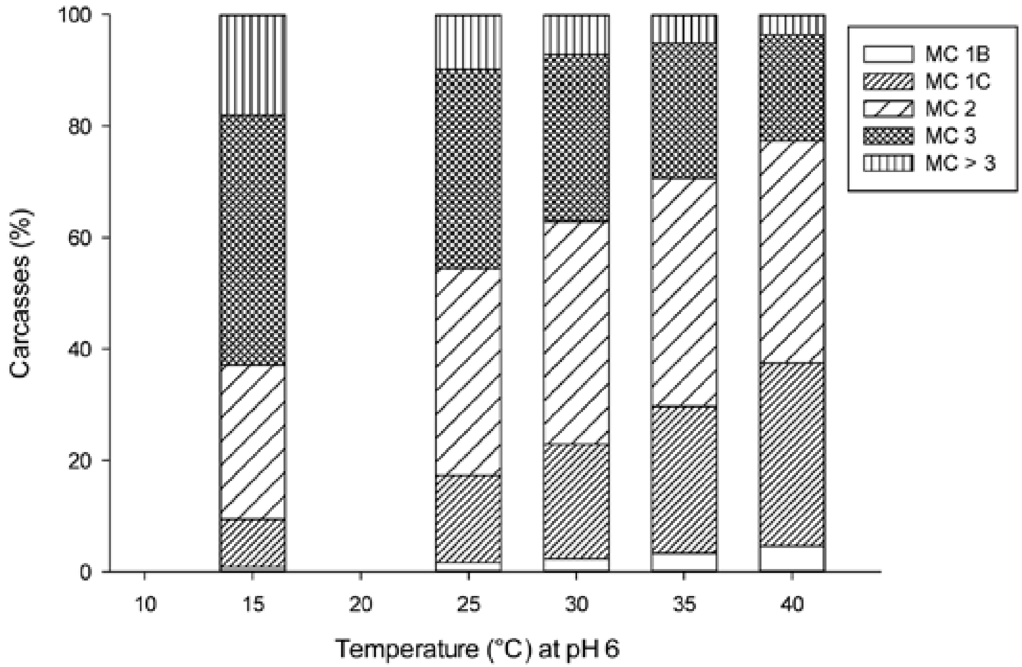

Figure 3: Predicted percent of beef carcasses (total number = 1512) with each meat colour score (AUSMEAT colour score at grading; 1B being palest to >3 being unacceptably dark) in the *longissimus thoracis* for a range in temperature at pH 6 (rigor temperature) from 15 to 40°C. Source: Hughes, Kearney, & Warner (2014).

carcases in the study of Warner et al. (2014a) was 14%. Using this traditional definition for PSE clearly underestimates the impact of high rigor temperature in beef carcases on quality.

Given the size of sheep carcasses, the risk of cold-shortening is considered to be greater than the risk of high rigor temperature. Yet studies in Australia and in the UK have quite clearly shown that sheep carcasses can have a high temperature at rigor (temperature at pH 6 >35°C) (Australia - Pearce et al. 2010; Thompson, Hopkins, D'Souza, Walker, Baud, & Pethick 2005) (UK - Matthews 2011). In the UK, no cold-shortening was found in the small survey of sheep carcases but enough high rigor temperature carcases were identified to recommend more extensive testing (Matthews 2011). As abattoirs generally use stimulations systems to prevent cold-shortening in sheep carcases, they need to be made aware of the risk of inducing high rigor temperature. There are no large scale surveys showing the incidence of high rigor temperature in sheep carcases and we recommend these are undertaken.

ANIMAL FACTORS OF INFLUENCE FOR HIGH RIGOR TEMPERATURE POST-MORTEM

Grain-feeding

The incidence of high rigor temperature in beef carcases derived from cattle that have been grain-fed for longer than 100 days is 84-95% compared to 46-52% occurrence in carcases that are derived from grass-fed cattle or cattle fed grain for 60-70 days (Warner et al. 2014a). Fat grass-fed cattle (fat depth >20 mm) also have a higher incidence of high rigor temperature than lean grass-fed cattle (Figure 4; Warner et al. 2014a). The reasons that grain-fed cattle, and fat grass-fed cattle, have a higher occurrence of PSE-like (high rigor temperature) meat are multi-factorial. Grain-fed cattle have recently been shown to have 0.3-0.4°C higher core body temperature than grass-fed cattle (Figure 5; Jacob et al. 2014). Furthermore, an association between blood insulin, indicators of insulin resistance, and the occurrence of high rigor temperature post-mortem in beef cattle has been reported (Warner et al. 2014a). As long grain feeding is known to increase fat deposition, and is postulated to increase circulating insulin, this may contribute to, or explain, the decreased ability to dissipate heat in these cattle (DiGiacomo, Dunshea, & Leury 2014; Warner et al. 2014a). Cattle on a grain diet exhibit muscles with an increase in anaerobic metabolism and a decrease in aerobic metabolism relative to cattle on a grass-based, or grass/grain diet. (Johnston et al. 1981;Shibata et al. 2009). Finally the rate of temperature decline post-mortem would be slower for fatter, heavier carcases, resulting from grain feeding. Glycolytic enzymes exponentially increase their rate of metabolite turnover at higher temperatures (Marsh 1954) and glycolysis is also faster in muscles containing predominantly anaerobic fibre types compared to muscles containing more aerobic fibre types (Ryu & Kim 2006). Thus all of these factors above, alone or in combination, can potentially explain the increased incidence of PSE-like, high rigor temperature, beef meat in grain-fed, and fatter grass-fed, cattle.

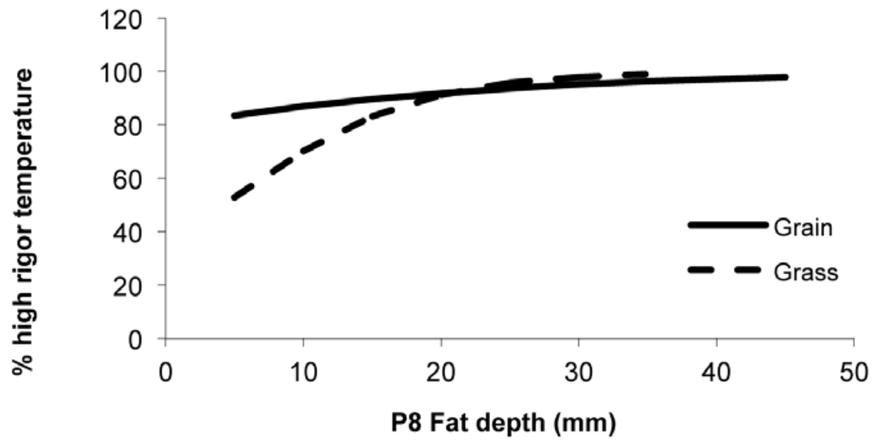

Figure 4: The effect of feed type (grass vs grain) and P8 fat depth on the % high rigor temperature (high rigor temperature; muscle temperature >35°C when pH<6). Source: Warner et al. (2014a).

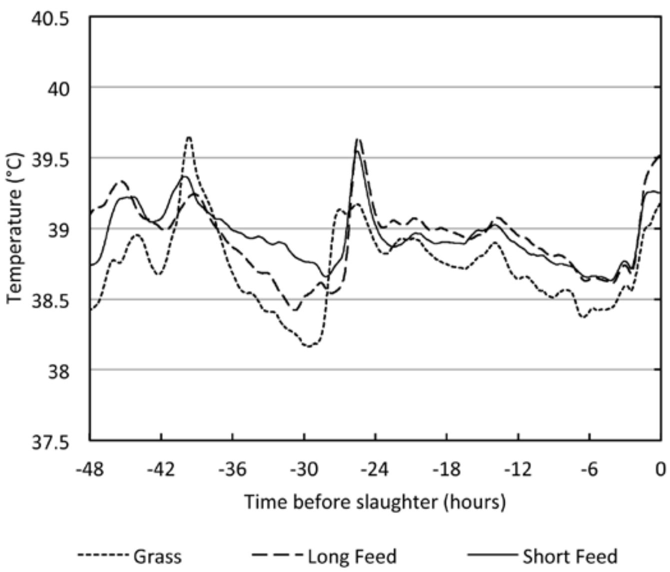

Figure 5: Core body temperature during the curfew and lairage period 48 hours before slaughter for steers from grass after (300 days pasture), short grain feeding (Short Feed, 150 days pasture, 150 days grain feeding) and long grain feeding (Long feed; 300 days grain feeding) treatments. Values are moving averages calculated at intervals of 60 minutes. Source: Jacob et al. (2014).

Environmental temperatures

Higher environmental temperatures, which are more prevalent during summer months, cause an increase in the occurrence of PSE in broilers and turkeys (Petracci, Bianchi, & Cavani 2009) and pigs (Guardia et al. 2004;Santos et al. 1994). There is also limited evidence for an increase in PSE-like meat in beef carcases in summer (Du, Zhang, Hu, & Luo 2009).

Stress and stunning pre-slaughter

In pigs, the incidence of PSE is known to be exacerbated by pre-slaughter stress, especially by the use of electric prodders (Channon, Payne, & Warner 2000;D'Souza et al. 1998b;D'Souza et al. 1998a). But in cattle and sheep, although the stressors associated with slaughter result in elevated body temperature (Jacob et al. 2014;Pighin et al. 2014), acute stress induced by the use of electric prodders does not appear to change the body temperature or the rate of metabolism, as measured by pH decline (Warner et al. 2007). In sheep, pre-slaughter exercise influences the temperature of several muscles and sometimes (but not always), the pH decline (Bond, Can, & Warner 2004;Bond & Warner 2007;Warner, Ferguson, Cottrell, & Knee 2007).

A lack of stunning (for religious reasons, called Islam/Muslim in the citation) has been found to increase muscle temperature post-slaughter in beef carcases, compared to stunning with a high pressure air gun, although there is little change in initial muscle pH (Du et al. 2009). Also, the same authors reported a higher incidence of PSE beef (defined as pH45<6.0), in summer, in carcases from 'Islam' cattle relative to carcases from cattle that were stunned prior to exanguination (Du et al. 2009).

POST-MORTEM FACTORS OF INFLUENCE FOR HIGH RIGOR TEMPERATURE

Electrical inputs

An increase in the incidence of % PSE-like beef meat (% high rigor temperature) with longer duration of electricity input at the hide puller (rigidity probe or back stiffener) has been demonstrated (Warner et al. 2014a) (Figure 6). This is logical as the frequency at which the rigidity probe on the hide puller operates (40-50 Hz; Food Science Australia 2006) is also known to generally cause the post-mortem pH fall to increase (Devine et al. 2004; Food Science Australia 2006). In the study by Warner et al. (2014a), the effect of the rigidity probe was specifically identified as the main contributor to the occurrence of high rigor temperature beef carcasses. Different electrical inputs speed up the process of glycolysis through their impact on the rate of pH fall and thus will impact

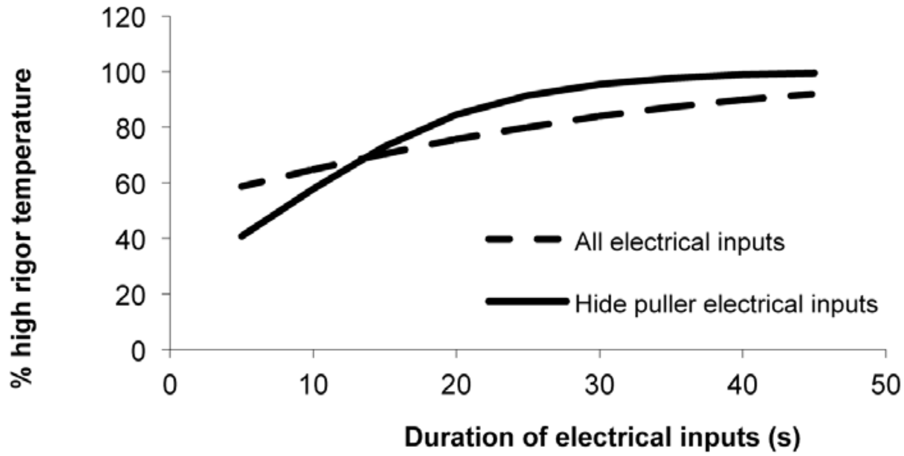

Figure 6: The effect of the duration of electrical inputs (all electrical inputs v. Hide puller electrical inputs) on the predicted % high rigor temperature (high rigor temperature; muscle temperature >35°C when pH<6). Source: Warner et al. (2014a).

on temperature at rigor (Simmons et al. 2006). Electrical inputs can occur at the immobiliser, stimulation or bleed rail and also at the hide puller, where the rigidity probe delivers the current. The large forces involved with beef downward hide pullers can be sufficient to cause 'broken backs' and damage to the muscle, which can be overcome by applying an electrical current to the back of the carcass (Food Science Australia 2006). In order to get sufficient energy into the back muscle for adequate contraction, large AC voltages are applied (typically 180V RMS, 50 Hz; Food Science Australia 2006) which is in the range for muscle stimulation and pH fall (Devine et al. 2004). Immobilisers are used to limit the risk of injury to workers, after the stunned animal falls out of the 'knocking' box, and enable shackling of the leg while holding the animal relatively immobile (Food Science Australia 2006). In Australia, the immobilisers used on cattle are generally high frequency (>500 Hz) and thus will have minimal effect on the rate of pH fall, in comparison to low frequency immobiliser systems (Simmons et al. 2008; Lombard et al. 2008; Warner et al. 2014a).

Petch and Gilbert (1997) showed that the combination of electrical inputs during the different stages of the slaughter floor needs to be monitored in order to optimise meat quality and prevent over-stimulation and high drip losses in both beef and lamb carcases. Warner et al. (2014a) recommend that the electrical inputs at the rigidity probe, during hide pulling, should be minimised if possible. For example, in their study, reducing the duration of electrical input at the rigidity probe from 20 to 10 sec, reduced the % high rigor temperature from 84 to 58%.

Stretching

Tenderstretch, which involves hanging the carcase by the aitch bone, has clearly been shown to improve tenderness in most hindquarter muscles and usually (not always) in loin muscles (Bouton et al. 1973). Interestingly, tenderstretch, or stretching, has been shown to protect not only tenderness but also water-holding capacity, against the damaging effects of high rigor temperature. This has been demonstrated for tenderness and WHC in Figure 7a for sheep and for tenderness in beef cattle in Warner et al. (2014c).

Rate of cooling and interventions

For prediction of carcase quality, measurements of muscle pH and temperature are generally made in the longissimus muscle. Deep muscles in heavy carcasses are predisposed to the conditions of high temperature (>35°C) and low pH (<6). The semimembranosus muscle of the beef carcase can remain above 40°C for 2 hrs post-mortem and above 35°C for 3 hrs post-mortem (see Figures 8a and 8b; Jacob et al. 2014). The semimembranosus and gluteus medius muscles also can be 16°C higher in temperature than the loin muscle at 3 hrs post-mortem (Figure 8b; Jacob et al. 2014). Meat has a low coefficient of thermal conductivity (Van Moeseke et al. 2001) and heat pipes are a way of increasing the rate of heat loss from low conductivity materials (James et al. 2005). Heat pipes have been shown to decrease the semimembranosus temperature at a depth of 100 mm by up to 4° C at 2 hrs post-mortem, as shown in Figure 8a (Jacob et al. 2014). Targeting these muscles for intervention rather than the whole carcase could provide a solution for high rigor temperature under commercial conditions with cold deboning.

SUMMARY - INCLUDING COMPARISON TO PIGS AND POULTRY

In pigs, the predominant factors influencing the occurrence of PSE pig meat are genetic (mainly RYR1 gene), high environmental temperatures, pre-slaughter stress and post-mortem chilling rates (Barbut et al. 2008). In

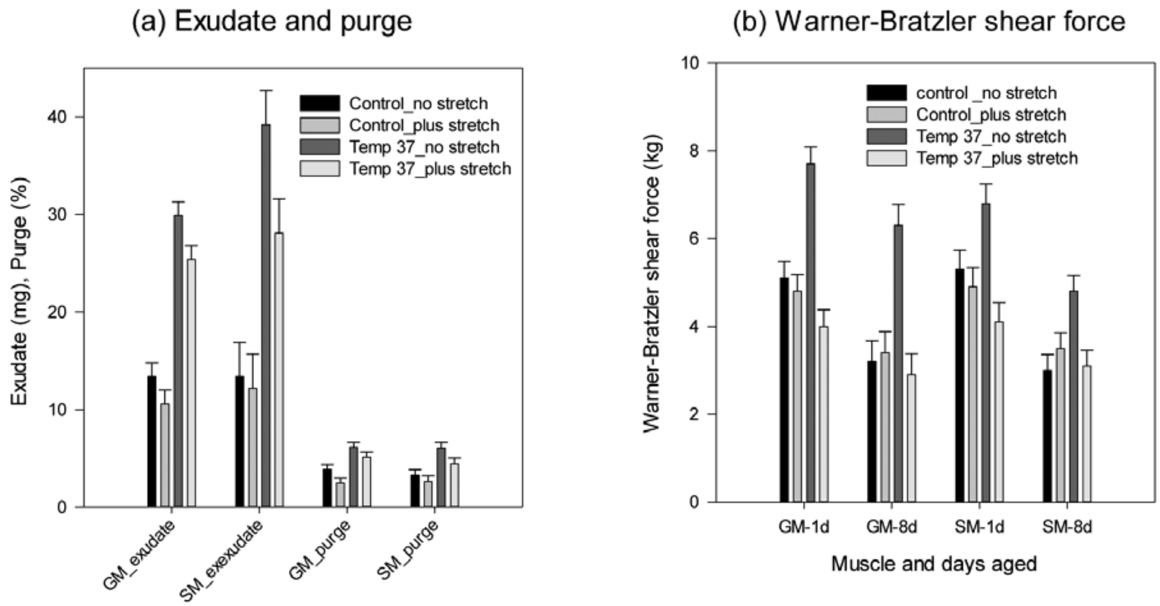

Figure 7: Effect of temperature conditioning (Control, 2°C chilling v. High temp 37°C for 4.5 hrs) and stretching of sides (no stretch v. plus stretch) for the *Gluteus medius* (GM) and *Semimembranosus* (SM) on (a) Exudate and purge and (b) Warner-Bratzler shear force at 1 or 8 days (1d, 8d) post-slaughter. The SED for comparison within muscles and time post-slaughter is shown as a vertical bar. Derived from Warner et al. (2014b).

poultry, the main causative factors for PSE appear to be similar to pigs including genetic selection for rapid lean tissue growth, stress pre-slaughter, chilling rates and environmental temperatures (Barbut et al. 2008;Petracci et al. 2009). In poultry, no specific genes associated with PSE meat have been identified but stress-induced, idiopathic and focal myopathies have been implicated (Barbut et al. 2008;Petracci et al. 2009).

In beef carcases, the occurrence of high rigor temperature (PSE-like) meat appears to much higher than expected. The incidence is difficult to compare to the occurrence of PSE in pigs and poultry as different methods are used for definition. Using the standard of pH45<6, PSE in beef carcases in Australia (14%) is generally comparable to the occurrence of 0 to 40% in the poultry industry and the 3-10% PSE reported for the USA pig industry (Barbut et al. 2008;Cannon et al. 1996). High rigor temperature in beef carcases appears to be associated with slow cooling in deep muscles in the hindquarter, electrical stimulation of the carcase post-slaughter, fatness of the carcase, grain feeding of cattle for longer than 70 days and possibly environmental temperatures. There has been little data collected on the factors influencing the occurrence of high rigor temperature in sheep carcases.

Strydom & Rosenvold (2014) suggest that it is possible to target several points along the supply chain, to reduce the occurrence of high rigor temperature in beef carcases. They suggest utilising an entire supply-chain approach to establish the most efficient and cost-effective ways to reduce the incidence.

RECOMMENDATIONS

In order to reduce the occurrence of high rigor temperature carcases in ruminants and ensure the impacts on quality are understood and quantified, the following recommendations are presented for industry implementation and further research.

Industry implementation

1. The increasing occurrence of PSE beef with fat depth, in grass-fed carcases, suggests that fat trimming should be an option for reducing high rigor temperature in these carcases.
2. Reducing the duration of electrical inputs into the beef carcase, particularly at the hide puller, will be beneficial. Evidence suggests that high frequency electrical inputs at the immobiliser should have minimal effect on rates of metabolism, but this may need testing in individual scenarios.
3. Accelerating rigor with electrical stimulation for both sheep and beef carcases remains controversial, as it appears to exacerbate the occurrence of high rigor temperature and associated negative meat quality attributes. Eliminating any electrical stimulation (ES) will be beneficial for beef carcases. If there is any tendency for cold-shortening in sheep carcases, the benefits of ES for preventing cold-toughening most likely outweigh the risks of high rigor temperature.

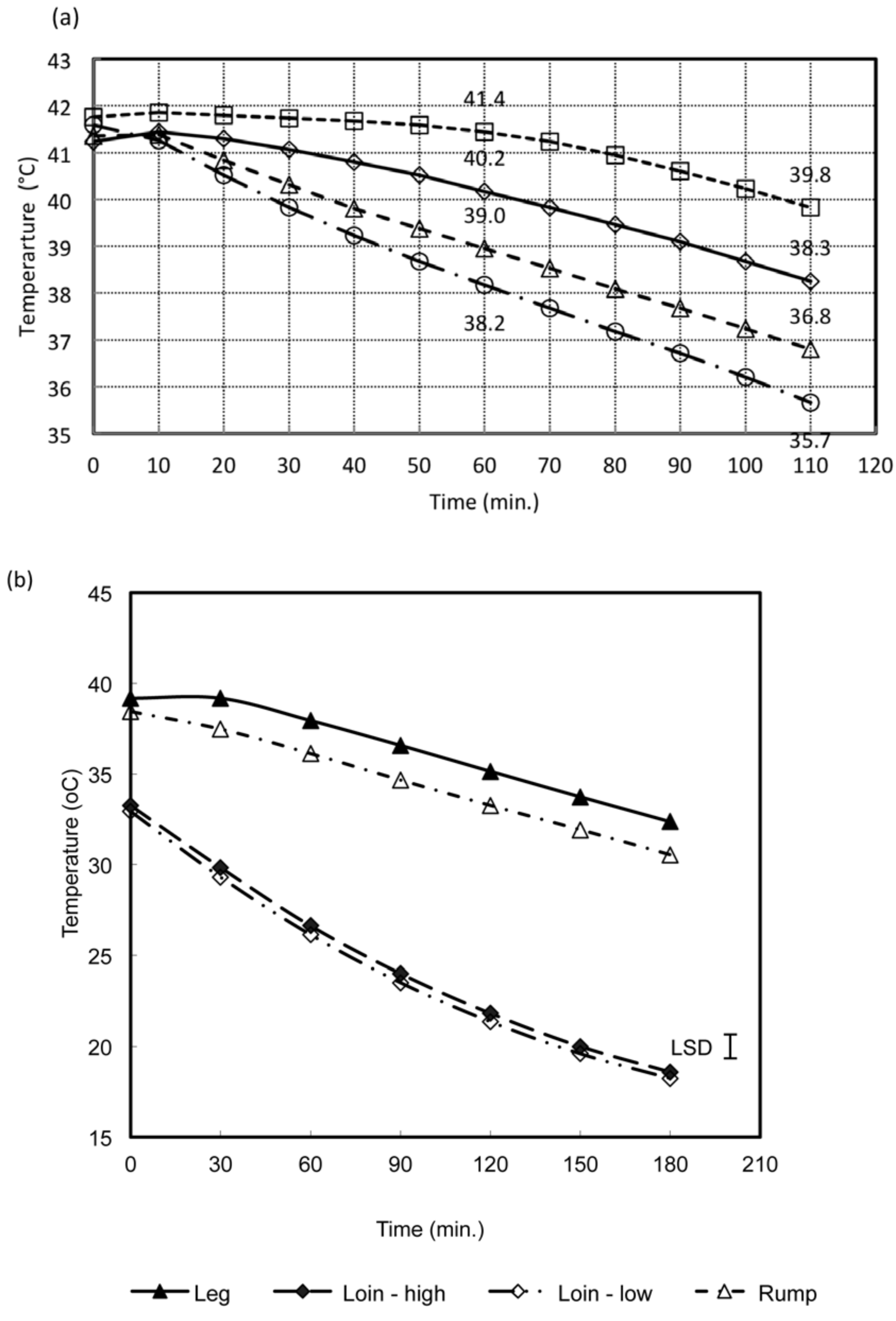

Figure 8: (a) The temperature (°C) of the fascial seam in a beef carcase between the *semimembranosus* and *semitendinosus* at a depth of 100 mm, measured in the control side and at radial distances from a heat pipe of 20, 40 and 80 mm, at 10 minute intervals for 110 minutes, t ~1 hr post-mortem. (b) The effect of probe location (leg, region of *semimembranosus* and *semitendinosus*; rump, region of *gluteus medius*; loin high and low, *longissimus lumborum* and *thoracis* respectively) in a beef carcase on the temperature (°C), ~1 hr post-mortem and measured at intervals for 180 min. Source: Jacob, Beatty, & Warner (2014).

4. Ante mortem and post mortem solutions that increase the rate of carcass cooling would be beneficial for reducing the occurence of PSE in beef carcases. Possible ante mortem solutions include access to feed and water, showering with water and provision of shade, as discussed in Jacob & Hopkins (2014). Possible post mortem solutions for carcase cooling include vascular flushing, hot fat trimming, opening seams and possibly use of heat tubes, hot boning, spray chilling, blast chilling, immersion cooling, and very fast chilling and these options are discussed in Jacob & Hopkins (2014).
5. Tenderstretch of carcases successfully overcomes the tenderness and WHC problems of PSE, high rigor temperature, meat in hind quarter, but not loin muscles. It is recommended as an option for companies to consider.
6. Combinations of different techniques, that suit the specific requirements of a particular processing plant, is the likely best solution to the occurrence of high rigor temperature and PSE in beef carcases, but further development of commercial solutions is suggested.

Further R&D

7. Surveys of the longissimus rigor temperature in beef, sheep and other species' carcases will indicate the extent of the problem. These surveys should include measurements in several other muscles, including deep muscles in the hind quarter of the carcase, such as the semimembranosus. These surveys should also collect other data, to enable causative factors to be identified.
8. Routine collection of data on the water-holding capacity in ruminant animal and meat experiments, particularly in relation to consumer perceptions of juiciness, will enable the underlying biochemical and structural mechanisms to be determined (Kim, Warner, & Rosenvold 2014).
9. The high occurrence of PSE meat in grain-fed beef carcases suggests that interventions in the feedlot are required. Several dietary treatments could be investigated as means of reducing high rigor temperatures in beef carcases. The most promising dietary treatments are dietary betaine, chromium and magnesium either alone or in combination and these are reviewed in DiGiacomo, Dunshea, & Leury (2014).
10. Unlike the pig industry, the limited large scale studies on PSE and high rigor temperature in ruminant carcases have not considered whether genetic selection for muscle growth has an impact on the occurrence of high rigor temperature. Thus this certainly warrants further investigation.
11. There is a lack of information on the effect of the PSE-like condition on the quality of beef or lamb processed products and it is recommended that R&D is undertaken on this topic.

ACKNOWLEDGEMENTS

The contributions of Brad Kim, David Gerrard, Drewe Ferguson, Robin Jacob, Joanne Hughes, Katja Rosenvold, Phil Strydom, Dario Pighin, Gavin Kearney, Geert Geesink, Brian Leury, Kristy Digiacomo, Frank Dunshea, Philip Franks and Chris Anderson to the work which is reported in this paper are gratefully acknowledged as well as the funding provided by Meat and Livestock Australia. Also, before me, go the 'Giants of Meat Science' who laid the foundations of much of the research which is reported here. Many of these 'Giants' undertook some of their research at the Muscle Biology Laboratory at University of Wisconsin-Madison. I was grateful for the opportunity to undertake my PhD studies at this laboratory and gain insights and experience from these people, and others, in the USA.

REFERENCES

Aalhus, J. L.; Best, D. R.; Murray, A. C.; Jones S.D.M. 1998, A comparison of the quality characteristics of pale, soft and exudative beef and pork, *Journal of Muscle foods*, 9 (3) pp. 267-280.

Barbut, S.; Sosnicki, A. A.; Lonergan, S. M.; Knapp, T.; Ciobanu, D. C.; Gatcliffe, L. J.; Huff-Lonergan, E. J.; Wilson, E. W. 2008, Progress in reducing the pale, soft and exudative (PSE) problem in pork and poultry meat, *Meat Science*, 79 pp. 46-63.

Bendall, J. R.; Swatland, H. J. 1988, A review of the relationships of pH with physical aspects of pork quality, *Meat Science*, 24 pp. 85-126.

Bond, J. J.; Can, L. A.; Warner, R. D. 2004, The effect of exercise stress, adrenaline injection and electrical stimulation on changes in quality attributes and proteins in Semimembranosus muscle of lamb, *Meat Science*, 68 pp. 469-477.

Bond, J. J.; Warner, R. D. 2007, Ion distribution and protein proteolysis affect water holding capacity of Longissimus thoracis et lumborum in meat of lamb subjected to antemortem exercise, *Meat Science*, 75 pp. 406-414.

Bouton, P. E.; Fisher, A. L.; Harris, P. V.; Baxter, R. I. 1973, A comparison of the effects of some post slaughter treatments on the tenderness of beef, *Journal of Food Technology*, 8 pp. 39-49.

Briskey, E. J. 1964, Etiological status and associated studies of pale, soft, exudative porcine musculature, *Advances in Food Research*, 13 pp. 89-178.

Cannon, J. E.; Morgan, J. B.; McKeith, F.K.; Smith, G.C.; Sonka, S.; Heavner, J.;Meeker, D.L. 1996, Pork chain quality audit survey: quantification of pork quality characteristics, *Journal of Muscle foods*, 7 pp. 29-44.

Chadwick, J. P.; Kempster, A. J. 1983, A repeat national survey of muscle ph values in commercial bacon carcasses, *Meat Science*, 9 pp. 101-111.

Channon, H. A.; Payne, A.; Warner, R. D. 2000, Halothane genotype, pre-slaughter handling and stunning method all influence pork quality, *Meat Science*, 56 pp. 291-299.

D'Souza, D. N.; Dunshea, F. R.; Warner, R. D.; Leury, B. J. 1998a, The Effect of Handling Pre-Slaughter and Carcass Processing Rate Post-Slaughter on Pork Quality, *Meat Science*, 50 pp. 429-437.

D'Souza, D. N.; Warner, R. D.; Leury, B. J.; Dunshea, F. R. 1998b, The Effect of Dietary Magnesium Aspartate Supplementation on Pork Quality, *Journal of Animal Science*, 76 pp. 104-109.

DiGiacomo, K.; Leury, B. J.; Dunshea, F. R. 2014, Potential nutritional strategies for the amelioration or prevention of high rigor temperature in cattle - a review, *Animal Production Science*, 54 pp. 430-443.

Dransfield, E. 1994, Modelling post mortem tenderisation - V: Inactivation of calpains, *Meat Science*, 37 pp. 391-409.

Du, Y.; Zhang, J.; Hu, T.; Luo, X. 2009, Effect of Pre-Slaughter Conditions on Beef Quality, *Scientia Agricultura Sinica*, 42 (10) pp. 3625-3632.

Faustman, C.; Cassens, R. G. 1990, The biochemical basis for discoloration in fresh meat: A review, *Journal of Muscle foods*, 1 pp. 217-243.

Ferguson, D. M.; Thompson, J. M.; Polkinghorne, R. 1999, Meat Standards Australia. A 'PACCP' based beef grading scheme for consumers. 3) PACCP requirements which apply to carcass processing, *International Congress of Meat Science and Technology, Yokohama, Japan*, 45 pp. 18-19.

Food Science Australia 2007, Producing Quality Sheep Meat, 06/07 edn, *Food Science Australia*, Brisbane, Australia.

Food Science Australia 2006, Electrical inputs during beef processing, *Meat Technology Update*, 1 (February) pp. 1-4, Brisbane Australia.

Guardia, M. D.; Estany, J.; Balasch, S.; Oliver, M. A.; Gispert, M.; Diestre, A. 2004, Risk assessment of PSE condition due to pre-slaughter conditions and RYR1 gene in pigs, *Meat Science*, 67 pp. 371-375.

Gutzke, D. A.; Franks, P.; Hopkins, D. L.; Warner, R. D. 2014, Why is muscle metabolism important for red meat quality? An industry perspective, *Animal Production Science*, 54 p. iii-iiv.

Hamm, R. 1986, "Functional properties of the myofibrillar system and their measurements," in *Muscle as Food*, P. J. Bechtel, ed, Academic Press, New York, pp. 135-199.

Honkavaara, M. 1988, Influence of pse pork on the quality and economics of cooked, cured ham and fermented dry sausage manufacture, *Meat Science*, 24 pp. 201-207.

Huff-Lonergan, E. J.; Lonergan, S. M. 2005, Mechanisms of water-holding capacity of meat: The role of postmortem biochemical and structural changes, Meat Science, 71 pp. 194-204.

Hughes, J. M.; Kearney, G.; Warner, R. D. 2014, Improving beef meat colour scores at carcass grading, *Animal Production Science*, 54 pp. 422-429.

Hunt, M. C.; Hedrick, H. B. 1977b, Histochemical and histological characteristics of bovine muscles from four quality groups, *Journal of Food Science*, 42 pp. 578-582.

Hunt, M. C.; Hedrick, H. B. 1977a, Chemical, physical and sensory characteristics of bovine muscle from four quality groups, *Journal of Food Science*, 42 pp. 716-720.

Hwang, I. H.; Thompson, J. M. 2001a, The effect of time and type of electrical stimulation on the calpain system and meat tenderness in beef longissimus dorsi muscle, *Meat Science*, 58 pp. 135-144.

Hwang, I. H.; Thompson, J. M. 2001b, The interaction between pH and temperature decline early postmortem on the calpain system and objective tenderness in electrically stimulated beef longissimus dorsi muscle, *Meat Science*, 58 pp. 167-174.

Jacob, R. H.; Surridge, V. S. M.; Beatty, D. T.; Gardner, G. E.; Warner, R. D. 2014, Grain feeding increases core body temperature of beef cattle, *Animal Production Science*, 54 pp. 444-449.

Jacob, R. H.; Beatty, D. T.; Warner, R. D. 2014, A preliminary study into the use of heat pipes to prevent high rigor temperature in beef carcasses by increasing cooling rate, *Animal Production Science*, 54 pp. 504-509.

Jacob, R. H.; Hopkins, D. L. 2014, Techniques to reduce the temperature of beef muscle early in the post mortem period - a review, *Animal Production Science*, 54 pp. 482-493.

James, C.; Araujo, M.; Carvalho, A.; James, S. J. 2005, The heat pipe and its potential for enhancing the cooking and cooling of meat joints, *International Journal of Food Science & Technology*, 40 pp. 419-423.

Johnston, D. M.; Moody, W. G.; Boling, J. A.; Bradley, N. W. 1981, Influence of Breed Type, Sex, Feeding Systems, and Muscle Bundle Size on Bovine Fiber Type Characteristics, *Journal of Food Science*, 46 pp. 1760-1765.

Kauffman, R. G.; Wachholz, D.; Henderson, D.; Lochner, J. V. 1978, Shrinkage of PSE, normal and DFD hams during transit and processing, *Journal of Animal Science*, 46(5) pp. 1236-1240.

Khan, A. W.; Ballantyne, W. W. 1973, Post-slaughter pH variation in beef, *Journal of Food Science*, 38 pp. 710-711.

Kim, Y. H. B.; Kerr, M.; Geesink, G.; Warner, R. D. 2014, Impacts of hanging method and high pre-rigor temperature and duration on quality attributes of ovine muscles, *Animal Production Science*, 54 pp. 414-421.

Kim, Y. H. B.; Warner, R. D.; Rosenvold, K. 2014, Influence of high pre-rigor temperature and fast pH fall on muscle proteins and meat quality: a review, *Animal Production Science*, 54 pp. 375-395.

Lawrie, R. A. 1960, Post-mortem glycolysis in normal and exudative longissimus dorsi muscles of the pig in relation to so-called white muscle disease, *Journal of Comparative Pathology*, 70 pp. 273-295.

Marsh, B. B. 1954, Rigor mortis in beef, *Journal of The Science of Food & Agriculture*, 2 pp. 70-75.

Marsh, B. B.; Ringkob, T. P.; Russell, R. L.; Swartz, D. R.; Pagel, L. A. 1987, Effects of early postmortem glycolytic rate on beef tenderness, *Meat Science*, 21 pp. 241-248.

Matthews, K. 2011, Evaluation of the pH fall in English lamb abattoirs against the Meat Standards Australia pH/temperature window, Report to EBLEX. Available at http://www.eblex.org.uk/wp/wp-content/uploads/2013/04/evaluationofthephfallinenglishlambabattoirs_271011- final-report.pdf [Verified 31 March 2014].

McClain, P. E.; Pearson, A. M.; Brunner, J. R.; Crevasse, G. A. 1969, Connective Tissues from Normal and PSE Porcine Muscle. 1. Chemical Characterization, *Journal of Food Science*, 34 pp. 115-119.

Offer, G. 1991, Modelling of the formation of pale, soft and exudative meat: Effects of chilling regime and rate and extent of glycolysis, *Meat Science*, 30 pp. 157-184.

Pearce, K. L.; Van De Ven, R.; Mudford, C. R.; Warner, R. D.; Hocking-Edwards, J. E.; Pethick, D. W.; Hopkins, D. L. 2010, Case studies demonstrating the optimisation of medium voltage electrical stimulation of lamb carcases, *Animal Production Science*, 50 pp. 1107-1114.

Penny, I. F. 1967a, The effects of postmortem conditions on the extractability and adenosine triphosphatase activity of myofibrillar proteins of rabbit muscle, *Journal of Food Technology*, 2 pp. 325-338.

Penny, I. F. 1967b, The influence of pH and temperature on the properties of myosin, *Journal of Biochemistry*, 104 pp. 609-615.

Petracci, M.; Bianchi, M.; Cavani, C. 2009, The European perspective on pale, soft, exudative conditions in poultry, *Poultry Science*, 88 pp. 1518-1523.

Pighin, D. G.; Brown, W.; Ferguson, D. M.; Fisher, A. D.; Warner, R. D. 2014, Relationship between changes in core body temperature in lambs and post-slaughter muscle glycogen content and dark-cutting, *Animal Production Science*, 54 pp. 459-463.

Polkinghorne, R.; Thompson, J. M.; Watson, R.; Gee, A.; Porter, M. 2008, Evolution of the Meat Standards Australia (MSA) beef grading system, *Australian Journal of Experimental Agriculture*, 48 pp. 1351-1359.

Polkinghorne, R. J.; Thompson, J. M. 2010, Meat standards and grading: A world view, *Meat Science*, 86 pp. 227-235.

Rossi, C. A. S.; Baldi, G.; Vandoni, S. 2009, Evaluation of factors influencing PSE and colour alteration in beef cattle, Engineering 4 Food, November p. 36.

Ryu, Y. C.; Kim, B. C. 2006, Comparison of histochemical characteristics in various pork groups categorized by postmortem metabolic rate and pork quality, *Journal of Animal Science*, 84 pp. 894-901.

Santos, C.; Roseiro, L. C.; Goncalves, H.; Melo, R. S. 1994, Incidence of different pork quality categories in a Portuguese slaughterhouse: A survey, *Meat Science*, 38 pp. 279-287.

Scopes, R. K. 1964, The influence of post-mortem conditions on the solubilities of muscle proteins, *Biochem J.*, 91 pp. 201-207.

Shaw, F. D.; Baud, S. R.; Richards, I.; Pethick, D. W.; Walker, P. J.; Thompson, J. M. 2005, New electrical stimulation technologies for sheep carcasses, *Australian Journal of Experimental Agriculture*, 45 pp. 575-583.

Shibata, M.; Matsumoto, K.; Oe, M.; Ohnishi-Kameyama, M.; Ojima, K.; Nakajima, I.; Muroya, S.; Chikuni, K. 2009, Differential expression of the skeletal muscle proteome in grazed cattle, Journal of Animal Science, 87 pp. 2700-2708.

Solomon, M. B.; Van Laack, R. L. J. M.; Eastridge, J. S. 1998, Biophysical basis of pale, soft, exudative (PSE) pork and poultry muscle: a review, *Journal of Muscle Foods*, 9 pp. 1-11.

Strydom, P. E.; Rosenvold, K. 2014, Muscle metabolism in sheep and cattle in relation to high rigor temperature - overview and perspective, *Animal Production Science*, 54 pp. 510-518.

Swatland, H. J. 2012, Optical properties of meat, *Reciprocal Meat Conference, 65* pp. 1-7.

Tarrant, P. V.; Mothersill, C. 1977, Glycolysis and associated changes in beef carcasses, *Journal of Science in Food and Agriculture*, 28 pp. 739-749.

Thompson, J. M. 2002, Managing meat tenderness, *Meat Science*, 62 pp. 295-308.

Thompson, J. M.; Hopkins, D. L.; D'Souza, D. N.; Walker, P. J.; Baud, S. R.; Pethick, D. W. 2005, The impact of processing on sensory and objective measurements of sheep meat eating quality, *Australian Journal of Experimental Agriculture*, 45 pp. 561-573.

Van Moeseke, W.; De Smet, S.; Claeys, E.; Demeyer, D. 2001, Very fast chilling of beef: effects on meat quality, *Meat Science*, 59 pp. 31-37.

Warner, R. D.; Dunshea, F. R.; Gutzke, D.; Lau, J.; Kearney, G. 2014a, Factors influencing the incidence of high rigor temperature in beef carcasses in Australia, *Animal Production Science*, 54 pp. 363-374.

Warner, R. D.; Ferguson, D. M.; Cottrell, J. J.; Knee, B. W. 2007, Acute stress induced by the pre-slaughter use of electric prodders causes tougher beef meat, *Australian Journal of Experimental Agriculture*, 47 pp. 782-788.

Warner, R. D.; Ferguson, D. M.; McDonagh, M. B.; Channon, H. A.; Cottrell, J. J.; Dunshea, F. R. 2005, Acute exercise stress and electrical stimulation influence the consumer perception of sheep meat eating quality and objective quality traits, *Australian Journal of Experimental Agriculture*, 45 pp. 553-560.

Warner, R. D.; Kerr, M.; Kim, Y. H. B.; Geesink, G. 2014b, Pre-rigor carcass stretching counteracts the negative effects of high rigor temperature on tenderness and water-holding capacity - using lamb muscles as a model, *Animal Production Science*, 54 pp. 494-503.

Warner, R. D.; Thompson, J. M.; Polkinghorne, R.; Gutzke, D.; Kearney, G. A. 2014c, A consumer sensory study of the influence of rigor temperature on eating quality and ageing potential of beef striploin and rump, *Animal Production Science*, 54 pp. 396-406.

Webster, J.; Gee, A.; Porter, M.; Philpott, J.; Thompson, J.; Ferguson, D.; Warner, R. Trout, G.; Watson, R.; Shaw, F.; Scott, J.; Chappell, G.; Strong, J. 1999, *Meat Standards Australia. Grading for Eating Quality. Development of the Meat Standards Australia Grading System - Volume 1*. Meat and Livestock Australia, North Sydney, Australia.

Wismer-Pedersen, J. 1959, Quality of pork in relation to rate of pH change post mortem, *Food Research*, 24 pp. 711-727.

Wu, J. J.; Dutson, T. R.; Carpenter, Z. L. 1981, Effect of Postmortem Time and Temperature on the Release of Lysosomal Enzymes and Their Possible Effect on Bovine Connective Tissue Components of Muscle, *Journal of Food Science*, 46 pp. 1132-1135.

Zhu, L. G.; Brewer, M. S. 2002, Effects of pH and temperature on metmyoglobin solubility in a model system, *Meat Science*, 61 pp. 419-424.

Zhu, L. G.; Brewer, M. S. 2003, Effects of urea denatureation and pH on the ability of porcine myoglobin to undergo reduction, *Meat Science*, 63 pp. 427-432.