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Longissimus from Berkshire pigs in a small-scale supply chain have increased oxidative metabolism, tenderness and water-holding capacity, compared with Large White × Landrace pigs in a modern commercial supply chain

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ABSTRACT

Context. Selection for leanness in the modern Australian pig has resulted in inconsistent quality, including a lack of pork tenderisation during ageing. Inconsistent quality is potentially a result of differences in supply chain and breed as well as the variation in muscle fibre-type proportion in pork *longissimus*. **Aim.** The aim was to investigate differences in fibre-type proportion and pork quality between Large White-Landrace pigs in a large supply chain and Berkshire pigs processed in a small supply chain. **Methods.** Pigs (n = 22) from two suppliers with different breeds (Supplier 1, Large White × Landrace, SC1-LWLR, n = 12, modern commercial pigs; Supplier 2, Berkshire, SC2-Berk, n = 10, heritage pigs) were slaughtered and samples from the *longissimus* were extracted at 3, 24, and 48 h postmortem for enzyme and pH analyses. *Longissimus* samples were subjected to ageing for either 2 or 16 days postmortem (Day 2, Day 16), assessed for colour, muscle fibre-type proportion (%), muscle fibre diameter (μm), water-holding capacity (purge, % and cook loss, %), Warner–Bratzler peak shear force (WBSF, N), and protein denaturation temperature using differential scanning calorimetry (DSC, peak temperature, °C). **Key results.** SC1-LWLR had higher purge than SC2-Berk (2.85% and 1.83% respectively; standard error of the difference (SED) = 0.33; P = 0.003), higher cook loss on Day 16 (24.63% and 16.79% respectively; SED = 1.62; P = 0.017) and higher WBSF on Day 2 and Day 16 (Day 2, 30.9 N and 26.7 N respectively; Day 16, 28.6 N and 22.0 N respectively; SED = 0.98, interaction P = 0.003). SC1-LWLR had a lower proportion of Type I (10.1% vs 16.0%; SED = 0.51) and Type IIA (14.0% vs 22.0%; SED = 0.77) and a higher proportion of Type IIB (75.9% vs 62.0%; SED = 0.74) (P < 0.001 for all) fibres. SC1-LWLR had lower DSC temperatures for two peaks. SC2-Berk had higher citrate synthase activity (P = 0.003) and glycolytic potential (P < 0.001) than SC1-LWLR. **Conclusions.** SC2-Berk *longissimus* had improved quality compared with SC1-LWLR pork, most likely owing, in part, to higher proportion of oxidative and intermediate fibres in the Berkshires. However, effects of differences in environmental conditions and/or processing conditions cannot be ruled out. **Implications.** The experiment increased our understanding of how variation in supply chains and muscle fibre-type proportion can impact the production of consistently high-quality pork.

Keywords: Berkshire, breed, cook loss, Large White × Landrace, muscle fibre type, oxidative capacity, pork, protein denaturation, supply chain, WBSF.

Introduction

The modern commercial pork industry uses breeding programs to select for leaner (Sellier 1998), heavier-muscled (Eggert *et al.* 2002), and faster-growing (Wojtysiak 2012) pigs. However, there has been a rise in inconsistent pork quality, including a failure of products to age postmortem (Hofmeyr 1998; Stollznow 2008). Heritage pig breeds are considered fatter and slower-growing (Park *et al.* 2007), yet often have superior quality compared with pork from the modern commercial pig (Weiler *et al.* 1995). Variations in

pork quality are affected by breed, muscle fibre-type proportion and size, nutrition, and antemortem stress, which all affect postmortem metabolism with subsequent effects on colour, water-holding capacity (WHC), tenderness (sensory and instrumental), and protein denaturation during cooking (Klont *et al.* 1998; Huff-Lonergan *et al.* 2002; Wood *et al.* 2004; Gispert *et al.* 2007; Scheffler and Gerrard 2007; Gil *et al.* 2008; Jiang *et al.* 2012; Kim *et al.* 2018; Zybert *et al.* 2019).

The proportion of different muscle fibre types in a muscle affects pork quality. Muscle fibre-type proportion is different between modern commercial and heritage pigs, where heritage pigs often have a greater proportion of oxidative Type I fibres and modern commercial pigs have a greater proportion of glycolytic Type IIB fibres (Rahelic and Puac 1981; Eggert *et al.* 2002). Muscles with a higher proportion of Type I fibres are generally associated with improvements in eating quality, tenderness, and WHC (Lefaucheur 2010; LeMaster *et al.* 2023). Protein denaturation temperatures are higher in muscles with a greater proportion of oxidative fibres than in muscles with a greater proportion of glycolytic fibres (Vaskoska *et al.* 2021).

Muscles with a greater proportion of Type IIB glycolytic fibres tend to have faster postmortem pH decline, than muscles with a greater proportion of oxidative fibres (Kang *et al.* 2011). However, a study by England *et al.* (2016) indicated that even with excess glycogen, oxidative muscles have a slow and limited extent of pH decline, because oxidative muscles have a lower glycolytic flux than glycolytic muscles, which limits the production of ATP (England *et al.* 2016). Antemortem and postmortem management of pigs and carcasses also influences the rate and extent of postmortem pH decline (Bendall 1973), muscle cell shrinkage, and WHC (Popp *et al.* 2015). Some modern commercial abattoirs use blast-chilling to rapidly chill carcasses to prevent inferior quality associated with prolonged elevated muscle temperatures. Elevated muscle temperature postmortem allows glycolysis to occur faster, resulting in rapid pH decline. Blast-chilling prevents rapid pH decline and can improve colour and other quality traits. However, blast-chilling has been related to increased muscle toughening owing to cold-shortening, in extremely lean pigs (Shackelford *et al.* 2012).

We expected that heritage pigs would have a greater proportion of oxidative fibres, which would result in improved pork quality compared with modern commercial pigs. Thus, the aim of this study was to identify variations in pork quality between different supply chains that use either modern commercial or heritage pigs. We wanted to investigate the influence of breed and supply chain on muscle fibre-type proportion and size and the impact of muscle fibre-type proportion on the rate of postmortem muscle metabolism, WHC, instrumental tenderness, and protein denaturation during cooking. The supply chains used in this study were different in the transportation time from farm to slaughter, lairage duration, slaughter method and chilling procedures, which, we recognise, can affect quality. Ideally the different breeds would have been slaughtered at the same processing plant, so as to remove the effect of processing plant, but was not possible in this study. Thus, we focused on identifying differences between supply chains and the variations of muscle fibre-type proportion between modern commercial and heritage breeds, which could help the pork industry identify potential management and breeding strategies for improving pork quality.

Materials and methods

Sample collection

Sample collection occurred at two abattoirs, on two different days, for pigs from two suppliers and each used a different breed. Supplier 1 used Large White × Landrace (modern commercial supply chain) pigs approximately 21–22 weeks old (SC1-LWLR, $n = 12$ female carcasses), and Supplier 2 used Berkshire (small-scale supply chain) pigs, also approximately 21–22 weeks old (SC2-Berk, $n = 10$ female carcasses). The pigs from each supplier went through a different abattoir and processing procedure. SC1-LWLR pigs were despatched to a processing plant, underwent 4 h lairage, group CO_2 stunning, and the chillers used blast-chilling for the first 2.5 h. SC2-Berk pigs were despatched to a processing plant, underwent 24–30 h lairage, electric stunning was used, and chilling was conventional chilling. Muscle samples (9 g) from each carcass were excised from the *longissimus lumborum* (hereafter *longissimus*) at 3, 24 and 48 h postmortem with a metal corer attached to a drill, then immediately snap-frozen in liquid nitrogen. These samples were powdered in liquid nitrogen and storage was maintained at −80°C until analysis of muscle tissue pH and metabolites (glycogen, glucose, glucose-6-phosphate (G6P), lactate; see methods below). Samples taken at 3 h postmortem were also used to measure enzyme activity (citrate synthase, lactate dehydrogenase, isocitrate dehydrogenase) and these samples were also powdered in liquid nitrogen and storage was maintained at −80°C. The *longissimus* was excised from each animal between 24 and 30 h postmortem, stored at 0–2°C and shipped to the University of Melbourne meat laboratory. At 48 h postmortem, each *longissimus* was cut into four 2.5 cm thick (145 g ± 2.5) samples and these samples were randomly allocated to ageing for 2 or 16 days postmortem ($n = 2$ samples for each storage period from each carcass). All samples allocated for 16 days postmortem ageing were weighed, vacuum-packed, and stored at 1°C for 14 days, after collecting the samples at 2 days postmortem. For each 2- and 16-day-aged sample, measurements were taken for muscle pH, colour, purge (%, 16-day samples only), cook loss (%), and Warner–Bratzler peak shear force (WBSF, N) (see below). On the day of boning (2 days postmortem), three samples from each *longissimus* were also collected, including 1 g sample for measurement of peak protein denaturation temperature using differential scanning calorimetry (DSC, stored at 0–2°C until analysis on the day

of sampling), 1 g for myoglobin content, and a 10 mm^3 block for histochemical staining (snap-frozen in liquid nitrogen (see details below), and stored at −80°C).

Muscle tissue pH

Muscle pH was measured in duplicate according to previous methods (Bendall 1973). Muscle samples (100 mg ± 2) were powdered in liquid nitrogen and homogenised in a 1:8 (weight/volume) solution of 25 mM iodoacetic acid and 750 mM KCl (pH 7.0). Samples were centrifuged at 13,000*g* for 5 min at room temperature and measured immediately using a Hanna pH meter (HI 5221) with a semi-micro glass electrode (HI1093) (Hanna Instruments Inc., Woonsocket, Rhode Island, USA).

Postmortem metabolites and enzyme activity

Glycolytic metabolites

To determine glycolytic metabolite concentrations (glycogen, glucose, glucose-6-phosphate (G6P), and lactate; all expressed as μmol/g), samples were collected and processed according to previous methods (England *et al.* 2016) where all samples were powdered in liquid nitrogen and stored at −80°C. To measure glycogen, samples (100 mg ± 2, mean ± s.e.) were mixed with an equal volume of 2.5 M HCl and then were heated to 90°C for 2 h. After heating samples for 2 h, sample homogenate and HCl mixture was centrifuged at 13,000*g* for 5 min at room temperature. The supernatant was then neutralised with 1.25 M KOH (Keppler and Decker 1984) and stored at −20°C until further analysis. To measure lactate, glucose, and G6P concentration, 100 mg ± 2 was mixed with an equal volume of ice-cold 0.5 M perchloric acid, vortexed, incubated on ice for 20 min, and centrifuged at 13,000*g* for 5 min at room temperature. The supernatant was neutralised with 0.5 M KOH according to previous methods (Keppler and Decker 1984). Glycogen, G6P, glucose, and lactate were measured using previously reported methods (Keppler and Decker 1984) with modifications for a 96-well microplate (Hammelman *et al.* 2003). The enzyme reactions were conducted in borosilicate glass tubes (Thermo Fischer, Pittsburgh, Pennsylvania, USA) and metabolites were measured in triplicate spectrophotometrically at 340 nm, by using a 96-well microplate, with the Varioskan LUX Multimode Microplate Reader (ThermoScientific, Massachusetts, USA). Glycolytic potential (GP, expressed as μmol/g) was calculated as (see Monin and Sellier 1985):

$$GP = 2 \times (\text{glycogen} + \text{glucose} + \text{G6P}) + \text{lactate}$$

Lactate dehydrogenase

Lactate dehydrogenase (LDH) was measured as a marker for glycolytic activity (Huber *et al.* 2007) by using the powdered tissue sample. LDH activity was measured using the LDH activity assay kit from Sigma Aldrich (lactate dehydrogenase activity assay kit, MAK066) manufactured by Sigma-Aldrich (Merck, Darmstadt, Germany). Following kit instructions, 100 mg ± 2 powdered tissue was homogenised in 500 μL of cold LDH assay buffer and then centrifuged at 10,000*g* for 15 min at 4°C. Next, samples were diluted 100:1 to ensure that the readings were within a linear range of the standard curve and then 5 μL of each sample was added to the 96-well plate in duplicate and each well was brought to a final volume of 50 μL using the LDH assay buffer. To each well, 50 μL of the reaction mix was added and initial measurements were taken spectrophotometrically at 450 nm. Following initial measurements, the plate was incubated at 37°C and spectrophotometric measurements were taken every 5 min during a 30 min incubation period. The LDH activity is expressed as micromoles per gram per minute.

Mitochondrial metabolites

Citrate synthase (CS) and isocitrate dehydrogenase (ICDH) were measured on powdered tissue samples stored at −80°C. Citrate synthase was measured using previously established methods (Scheffler *et al.* 2014) where 50 ± 1 mg powdered tissue was used and diluted with 20:1 in a 250 mM sucrose homogenisation buffer (pH 7.4), homogenised for 30 s, and sonicated for 10 s. Citrate synthase samples were diluted 10:1 in double-distilled water. The reaction buffer (48 mM, 2 μM oxaloacetate, 0.5 μM 5,5′-dithiobis (2-nitrobenzoic acid) (DTNB) was added to each sample and measured spectrophotometrically at 412 nm. Following initial absorbance readings, 30 μL acetyl Co-A (12 mM) was added to each sample and immediately analysed using a spectrophotometer at 412 nm every min for 7 min. ICDH activity was measured using the IDH activity assay kit from Sigma Aldrich (isocitrate dehydrogenase activity assay kit, MAK062) manufactured by Sigma-Aldrich (Merck, Darmstadt, Germany). Following the instructions from the kit, 50 ± 1 mg powdered tissue was homogenised with the IDH assay buffer, centrifuged at 13,000*g* for 10 min at room temperature and diluted 100:1 to ensure that the readings were within a linear range of the standard curve, and 5 μL of the sample was added to the 96-well plate for each sample, in duplicate. Next, wells were brought to a total volume of 50 μL using the IDH assay buffer, followed by the addition of 50 μL of reaction buffer to each well. Plates were mixed, incubated at 37°C for 30 min, and the plate was read on the spectrophotometer at 450 nm every 5 min during the 30 min incubation. The LDH and CS activities were expressed as micromols per gram per minute and ICDH was expressed as nanomols per gram per minute.

Muscle colour measurement

Surface colour (L^*, a^*, b^*) of the *longissimus* samples was measured 2 and 16 days of postmortem ageing. A fresh cut was made on each sample prior to colour analysis and samples were allowed to bloom for 30 min at 4°C and were then measured in triplicate on each sample (average of six

measurements from two samples for each carcass within each ageing period) using a CR400 Chromameter (Konica Minolta, Japan) with an 8 mm aperture, light source D65, and 0° viewing angle (Frank *et al*. 2017).

Purge loss

On Day 2 postmortem, two samples from each carcass, were weighed prior to storage, vacuum-packed and stored in a cooler at 0–2°C for 14 days. After 14 days of ageing in the vacuum bag, *longissimus* samples were removed from the bag, gently patted with absorbent paper to remove surface moisture, and weighed to determine purge loss. Purge loss was calculated using the final weight of each sample (two samples from each carcass for each ageing day) after the ageing period, subtracted from the initial weight, and expressed as a percentage (%) of the initial weight.

Cooking procedure and cook loss

After 2 and 16 days of postmortem ageing, two *longissimus* samples from each carcass were weighed prior to cooking to measure cooking loss. Before adding samples to the water bath for cooking, a 1.2 mm gauge injection thermometer (9FX1150, FusionChef Core Temperature Sensor (PT100) Diamond, Julabo) was placed in the geometric centre of a sample and used as an indicator for when the samples reached the target internal temperature of 70°C. Each sample was placed in a polyethylene bag and seven marbles were placed at the bottom of the bag to ensure samples were completely submerged for the entire cooking process. Each bag was fixed to a metal rack with clips (eight samples in each cooking cycle to allow for even distribution of temperature across all samples). Samples were placed in a preheated water bath (Julabo F38 Water Bath; John Morris Scientific, Melbourne, Vic, Australia) set to 80°C. Once the internal temperature of the indicator sample reached an internal temperature of 70°C, samples were removed from the water bath and placed in iced water for 30 min. Samples were covered and transferred to a 0–2°C chiller overnight. After cooking and chilling, samples (two samples from each carcass for each ageing day) were weighed to measure cook loss, using cooked weight subtracted from the raw weight, and expressed as a percentage (%) of the raw weight.

Warner–Bratzler peak shear force (WBSF)

Samples were measured for WBSF 24 h after cooking. Each cooked *longissimus* sample was cut parallel to the muscle fibres into six sections (each 25–40 mm × 10 mm × 10 mm). WBSF was measured using a Lloyd texture analyser (LS5; Amtek, Berwyn, Pennsylvania, USA) equipped with a Warner–Bratzler V-shaped blade fixed with a 60°angle (BesTech, Dingley, Vic, AUS) with a crosshead speed of 300 mm/min and a load cell of 500 N. Each 50 mm × 10 mm × 10 mm sample was oriented with the WBSF blade perpendicular to the muscle fibres. Data were obtained using the Nexygen software (ver. 3; Bestech, Dingley, Vic, Australia; https://www.bestech.com.au/products/sensors-instrumentation/materials-testers/nexygen-plus/) and reported as peak shear force (N). Data were averaged for each sample (six sections per sample; two samples for each carcass) and analysis was conducted using the average of six sections per sample, two samples per carcass for each ageing day.

Differential scanning calorimetry (DSC)

From each Day 2 (48 h) postmortem *longissimus* sample, 1 g of tissue was used for DSC ($n = 10$ samples for SC1-LWLR; $n = 10$ samples for SC2-Berk). Samples were kept on ice and stored at 4°C until analysis. Each 1 g sample was prepared according to methods in previous studies (Vaskoska *et al*. 2021), where 20 ± 1 mg was dissected from each 1 g sample, placed into individual hermetically sealed aluminium pans and then placed in a furnace for DSC (Model 8000, Perkin Elmer, Waltham, Massachusetts, USA). A blank hermetically sealed aluminium pan was used as a reference. Heating for the DSC was conducted with a 1 min isothermal step to allow samples to equilibrate to 25°C. The isothermal step was followed by a heating step of 5°C/min from 25°C to 90°C. Once 90°C was reached, a rapid cooling step cooled the sample to 25°C at a rate of 30°C/min. The Pyris software (Version 11 Perkin Elmer, Waltham, Massachusetts, USA; https://www.perkinelmer.com/product/pyris-software-n5340092) was used to calculate the maximum heat input for protein denaturation (peak temperature, degrees Celsius) and enthalpy (the heat of transition ΔH, Joules per gram).

Histological staining and analysis

Histological characterisation of myosin fibre types was conducted on six animals from each supply chain ($n = 12$ total). Samples for histological analysis were cut from Day 0 *longissimus* samples into 10 mm^3 cubes and each cube was attached to a wooden cork board by using optimal cutting-temperature compound (OTC, Leica, Wetzler, Germany) and immersed in prechilled isopentane solution chilled in liquid nitrogen. The cubes were stored at −80°C until further analyses. While samples were still frozen, the cubes were sectioned into 10 μm sections with a cryostat (Model 1860, Leica, Wetzler, Germany) at −20°C, ensuring that cross-sections of muscle fibres were obtained. Once cut, the sections were collected using superfrost glass microscope slides (Thermo Fisher Scientific, Waltham, Massachusetts, USA) and six slides were made for each animal. The sections were stored in microscope boxes and kept at −80°C until processing for nicotinamide adenine dinucleotide tetrazolium reductase (NADHTR) and myosin adenosine triphosphatase (mATPase) staining.

The determination of Types I, IIA, and IIB muscle fibres was conducted using mATPase staining procedures, with the use of NADHTR staining as verification of muscle fibre-type

classification. The mATPase staining was conducted following previous procedures (Vaskoska *et al.* 2021). Samples were preincubated in formic acid (pH between 4.35 and 4.4), which allows for the separation between muscle fibre types. Black-stained fibres are classified as Type I oxidative fibres, white-stained fibres are classified as Type IIB glycolytic fibres, and grey fibres are classified as Type IIA intermediate fibres. The proportion and fibre diameter for each muscle-fibre type was calculated at five random locations across each muscle slide using ImageJ (Java 1.8.0_172 64-bit). For NADHTR staining, muscle sections were thawed by incubation at 37°C in nitroblue tetrazolium (mass concentration 1.25%, Merck, Kenilworth, NJ, USA) and β-nicotiaminde adenine dinucleotide (mass concentration 1% Merck, USA) in Tris buffer (0.2 M, pH 7.4) for 30 min. Following incubation, samples were processed through acetone:water solutions (30:70, 60:40, 90:10) and then rinsed in distilled water. White–blue staining indicated glycolytic Type IIB fibres, pale blue staining represented intermediate Type IIA fibres, and dark blue staining indicated oxidative Type I fibres. The NADHTR images were used to verify fibre types identified using mATPase staining from each serial image. Briefly, proportion was calculated as the number of fibres counted for each muscle fibre type across each slide within an animal and expressed as a percentage of the total muscle fibre number counted. Muscle fibre diameter was determined using Feret diameter (the minimum distance of parallel tangents at opposing borders of the muscle fibre) and was calibrated using a haemocytometer in ImageJ at ×10 magnification, resulting in muscle fibre diameter (μm). The measurement of Feret diameter is similar to previous methods where the muscle fibre diameter, along with proportion, allowed for detection of subtle differences among muscle samples (Briguet *et al.* 2004). The staining methods used for histology can distinguish three muscle fibre types, namely Types I, IIA, and IIB/IIX, but cannot differentiate between IIB and IIX; hence, all fast-glycolytic fibres (IIX and IIB) are expressed hereafter as IIB. Therefore, muscle fibres were allocated to Fibre-types I, IIA, or IIB on the basis of mATPase staining after confirming classification with NADHTR staining.

Myoglobin content analysis

The myoglobin content in pork samples was determined using the method described by Wadhwani *et al.* (2010) with a few modifications, previously described by Li *et al.* (2023). Lean pork tissue (0.6 ± 0.05 g), from 2 days postmortem, was homogenised in a 5 mL of ice-cold 40 mM sodium phosphate buffer at pH 6.8, by using an Ultra-Turrax T25 homogeniser (IKA, Shaufen, Germany) at 27,000*g* for 30 s at room temperature. The homogenate was immediately placed on ice and incubated for 1 h, and then centrifuged at 20,000*g*, at 2°C, for 30 min. The supernatant was collected and read at A525 and A700 against phosphate buffer by using a Thermo Scientific Multiskan Spectrometer (Thermo Fisher Scientific Australia, Melbourne, Vic, Australia). The concentration of myoglobin was compared with a myoglobin standard curve constructed using 0–1.2 mg/mL myoglobin in the same 40 mM phosphate buffer as used for sample extraction, and expressed as milligrams of myoglobin per gram of tissue.

Statistical analyses

Data analysis was conducted using restricted maximum likelihood (REML) in GenStat (ver. 22.1.0.532, 64-bit edition, VSN International), where the fixed model for the quality characteristics (colour, WHC, and WBSF) included the Supply_chain + Ageing_Day + Supply_chain.Ageing_Day and the random model included the carcass number (Carcass). For enzyme, metabolite and pH analysis (3, 24, and 48 h pH; glucose, glycogen, G6P, lactate, CS, LDH, and ICDH, all at 3 h postmortem), the fixed model included the Supply_chain + Time_postmortem + Supply_chain.Time_postmortem and the random model included carcass number (Carcass). For muscle fibres (muscle fibre-type proportion; muscle fibre diameter), the fixed model included Supply_Chain and the random model included Carcass. For DSC peak temperature, the fixed model included Supply_Chain and the random model included Carcass. Data were expressed as adjusted least-squares means (LSM) and standard errors of the difference (SED) for the main effect, or interaction where two treatments were included in the analysis. The Fisher's least significant difference (l.s.d.) was used to compare differences between means. Differences were considered significant if the *P*-value was <0.05, and were considered a trend if *P* was <0.10.

Results

Carcass data

There were no differences in hot carcass weight between SC1-LWLR and SC2-Berk ($P = 0.20$; Table 1). However, SC2-Berk had a greater fat depth than SC1-LWLR ($P < 0.001$).

Table 1. Effect of supply chain (Supply chain 1, Large White × Landrace, SC1-LWLR; Supply chain 2, Berkshire, SC2-Berk) on carcass parameters and *longissimus* biochemistry traits.

Item	SC1-LWLR	SC2-Berk	SED	*P*-value
Animals sampled	12	10	–	–
Carcass weight (kg)	81.4	77.6	2.83	0.20
Fat depth (mm)	11.0	16.8	1.20	<0.001
CS (μmol/g.min)	4.41	6.31	0.569	0.003
LDH (μmol/g.min)	3322	3685	208.5	0.40
ICDH (nmol/g.min)	3.66	4.40	0.423	0.088
Myoglobin (mg/g tissue)	0.773	0.921	0.0625	0.16

Least-squares means are shown as well as the standard error of difference (SED) and *P*-values.
CS, citrate synthase; LDH, lactate dehydrogenase; ICDH, isocitrate dehydrogenase.

Changes in muscle pH, metabolites and enzymes postmortem

Muscle pH

There was an interaction between supply chain and time postmortem for muscle pH ($P < 0.001$; Table 2). Muscle pH was higher for SC2-Berk at 3 h postmortem than for SC1-LWLR; however, at 24 h postmortem, SC2-Berk had similar pH to SC1-LWLR.

Glycolytic metabolites

There was an interaction between supply chain and time postmortem for lactate ($P = 0.047$; Table 2). Lactate was similar in SC2-Berk and SC1-LWLR at 3 and 48 h postmortem, but SC2-Berk had higher lactate at 24 h postmortem. There was an interaction between supply chain and time postmortem for G6P ($P = 0.002$), where SC1-LWLR had a higher G6P concentration at 3 h postmortem than SC2-Berk, whereas the G6P concentration was similar between supply chains at 24 and 48 h postmortem. Glucose concentration increased significantly ($P < 0.001$) between 3 and 24 h postmortem for both supply chains. There was an interaction between supply chain and time postmortem for glycogen ($P = 0.01$), where glycogen concentration decreased over time and was higher at 3 h postmortem in SC2-Berk than in SC1-LWLR and SC1-LWLR had a much lower glycogen content at 48 h than SC2-Berk. Glycolytic potential (GP) was significantly ($P < 0.001$) different between supply chains where SC2-Berk had a higher GP than SC1-LWLR.

Enzyme activity and myoglobin content

SC2-Berk had higher CS activity than SC1-LWLR at 3 h postmortem ($P = 0.003$) (Table 1). SC1-LWLR tended to have a lower ICDH activity than SC2-Berk ($P = 0.088$). LDH activity (Table 1) was not different between supply chains ($P = 0.40$). There was no difference in myoglobin content between SC1-LWLR and SC2-Berk ($P = 0.16$).

Quality traits

There were differences in colour between supply chains and ageing day (Table 3). There was an interaction between supply chain and ageing day ($P = 0.03$) for b^*, where b^* was similar between supply chains on Day 0, but increased to a greater extent after 16 days postmortem ageing in SC2-Berk. There was a difference between supply chains ($P = 0.028$) and ageing days ($P < 0.001$) for L^*, where L^* was higher for SC1-LWLR than for SC2-Berk and L^* increased after 14 days for both supply chains. There was a difference in a^* over the ageing period, where a^* increased after 14 days of ageing ($P = 0.02$).

There was a difference in purge (%) between supply chains ($P = 0.003$) (Table 3). SC2-Berk had lower purge (%) than SC1-LWLR. There was an interaction ($P = 0.017$) between supply chain and ageing day for cook loss (%) (Table 3); SC2-Berk and SC1-LWLR had similar cook loss (%) on Day 2 whereas on Day 16 postmortem, SC1-LWLR had much higher cook loss than SC2-Berk.

There was a significant ($P = 0.0026$) interaction between supply chain and ageing day for WBSF (Table 3). SC2-Berk had lower WBSF (N) on Days 2 and 16 postmortem, than SC1-LWLR, and the difference in WBSF was larger (N) on Day 16 postmortem (Day 2, difference of 4.2 N; Day 16, difference of 6.6 N). This indicates increased tenderisation after ageing for SC2-Berk compared with SC1-LWLR.

Muscle fibre-type proportion (%) and muscle fibre diameter (µm)

Muscle fibre-type proportion and muscle fibre diameter were different between supply chains ($P < 0.001$ for all; Table 4). The *longissimus* from SC2-Berk had a higher proportion of Types I and IIA fibres and a lower proportion of Type IIB fibres than SC1-LWLR. The muscle fibre diameter for all muscle fibre types was smaller in SC2-Berk than in SC1-LWLR.

Differential scanning calorimetry

There were four protein denaturation peaks from the thermograms of the *longissimus* for both SC1-LWLR and SC2-Berk (Table 5). Protein denaturation peak temperatures (T_{max}) for Peak I and Peak III were higher ($P = 0.002$ and

Table 2. Effect of supply chain (SC; Supply chain 1, Large White × Landrace, SC1-LWLR; Supply chain 2, Berkshire, SC2-Berk) and time postmortem (T; 3, 24, 48 h) on *longissimus* pH and glycolytic intermediates (µmol/g).

Item	SC1-LWLR			SC2-Berk			SED	*P*-value		
	3 h	24 h	48 h	3 h	24 h	48 h		SC	T	SC × T
pH	5.90	5.83	5.68	6.14	5.71	5.66	0.011	0.21	<0.001	<0.001
Glycogen (µmol/g)	37.2	30.7	19.6	45.3	26.3	25.5	1.54	0.55	<0.001	0.01
Glucose (µmol/g)	8.15	10.6	10.8	6.71	9.75	9.51	0.784	0.45	<0.001	0.32
Glucose-6-phosphate (µmol/g)	6.63	5.48	5.01	3.40	5.10	5.04	0.820	0.12	0.71	0.002
Lactate (µmol/g)	86.5	98.7	122	90.6	117	122	3.02	0.004	<0.001	0.047
Glycolytic potential (µmol/g)	190	192	192	201	199	201	2.7	<0.001	0.73	0.15

Least-squares means are shown as well as the standard error of difference (SED) for the interaction and *P*-values.

Table 3. Effect of ageing (A; 2, 16 days postmortem) and supply chain (SC; Supply chain 1, Large White × Landrace, SC1-LWLR; Supply chain 2, Berkshire, SC2-Berk) on colour (*L*, a*, b**), cook loss (%), and Warner–Bratzler shear force (WBSF, N) of the *longissimus*.

Item	SC1-LWLR		SC2-Berk		SED	*P*-value		
	2 days	16 days	2 days	16 days		SC	A	SC.A
CIE-*L**	51.0	54.0	49.1	52.3	0.74	0.028	<0.001	0.71
CIE-*a**	6.65	7.01	6.83	7.33	0.430	0.60	0.020	0.72
CIE-*b**	4.8	5.74	4.70	6.53	0.407	0.47	<0.001	0.003
Purge (%)	–	2.85	–	1.83	0.330	0.003		
Cook loss (%)	18.6	24.6	15.7	16.8	1.62	<0.001	<0.001	0.017
WBSF (N)	30.9	26.7	28.6	22.0	0.98	<0.001	<0.001	0.003

Least-squares means are shown as well as the standard error of difference (SED) for the interaction and *P*-values.

Table 4. Effect of supply chain (SC; Supply chain 1, Large White × Landrace, SC1-LWLR; Supply chain 2, Berkshire, SC2-Berk) on muscle fibre-type proportion (%) and muscle fibre size (fibre diameter, μm) of the three muscle fibre types (I, IIA, and IIB).

Item	Fibre type	SC1-LWLR	SC2-Berk	SED	*P*-value
Fibre proportion (%)	I	10.1	16.0	0.51	<0.001
	IIA	14.0	22.0	0.77	<0.001
	IIB	75.9	62.0	0.74	<0.001
Fibre diameter (μm)	I	440	327	15.3	<0.001
	IIA	414	332	13.7	<0.001
	IIB	543	496	9.7	<0.001

Least-squares means are shown with the standard error of difference (SED) and *P*-values.

Table 5. Effect of supply chain (SC; Supply chain 1, Large White × Landrace, SC1-LWLR; Supply chain 2, Berkshire, SC2-Berk) on transition temperature T_{max} (°C) and denaturation enthalpy (ΔH; J/g) of the major differential scanning calorimetry peaks on the thermograms for *longissimus lumborum*, using a heating rate of 5°C/min.

Item	Peak	SC1-LWLR	SC2-Berk	SED	*P*-value
T_{max} (°C)	I	52.0	55.8	0.96	0.002
	II	64.1	65.1	1.43	0.50
	III	74.3	78.4	0.66	0.001
	IV	82.4	81.2	0.71	0.11
Enthalpy (ΔH; J/g)	I	1.05	0.278	0.8512	0.037
	II	0.135	0.154	0.1223	0.88
	III	0.109	0.235	0.0526	0.030
	IV	0.962	1.170	0.0825	0.055

Least-squares means are shown with the standard error of difference (SED) and *P*-values.

$P = 0.001$ respectively) for SC2-Berk than for SC1-LWLR. Peak enthalpy was higher for SC1-LWLR than for S2-Berk for Peak I ($P = 0.037$), but was lower, or tended to be lower, for SC1-LWLR for Peak III ($P = 0.03$) and Peak IV ($P = 0.055$).

Discussion

The principal findings of this study were that the *longissimus* from SC2-Berk pigs in the small-scale supply chain had superior meat quality, in terms of higher water-holding capacity (purge, cook loss), lower shear force (lower WBSF at 2 and 16 days postmortem, indicating improved tenderness) and improved surface colour (lower lightness and higher redness), compared with the SC1-LWLR pigs in the large-scale supply chain. The differences can be attributed to a dominating effect of differences in aerobic capacity between the breeds, but differences between the supply chains also need to be considered. The increased aerobic capacity of the *longissimus* from the SC2-Berk pigs, relative to the modern commercial SC1-LWLR pigs, was evident from the higher citrate synthase and ICDH activity as well as higher proportion of aerobic Type I fibres and a reduced proportion of glycolytic Type IIB fibres. These differences in aerobic metabolism between the pigs from the two supply chains are reflected in higher muscle pH at 3 h postmortem in the SC2-Berk pigs, which would have contributed to the differences in meat quality.

The *longissimus* from the SC1-LWLR pigs had a higher proportion of Type IIB fibres and a lower proportion of Types I and IIA fibres than from the SC2-Berk pigs, indicating the SC2-Berk had more oxidative muscles. In support of our results, many other studies have found that modern commercial pigs have a higher proportion of Type IIB/IIX glycolytic fibres, and a lower proportion of Type I oxidative fibres than heritage/wild/native pigs; the *gracilis* in wild pigs had a higher proportion of Types I and IIA fibres and a lower proportion of Type IIB fibres than in Landrace × Pietrain modern commercial pigs (Weiler *et al.* 1995), the *longissimus* of the Korean native pig had a higher proportion of Type I fibres than the Landrace pig (Park *et al.* 2007), and the *longissimus* of the Lantang pig (native Chinese pig breed) had less Type IIB fibres and a greater proportion of Type IIA than the modern commercial Landrace pigs Dai *et al.* (2009), the *longissimus* from Large White and Landrace pigs had a higher proportion of Type IIB fibres and less of Type I and Type IIA fibres than from the semi-wild Mangulica pig (Rahelic and Puac 1981). Dai *et al.* (2009) found that the Landrace breed had an overexpression of Type IIB mRNA, resulting in a greater proportion of glycolytic Type IIB fibres in the *longissimus* of Landrace than in the native Lantang pig. Guo *et al.* (2019) also reported that the *longissimus* of semi-wild Mashen pigs had a lower expression levels of myosin heavy-chain IIB (glycolytic), and a higher expression of myosin heavy-chain I (oxidative)

and IIA (intermediate), than that of Large White pigs. In summary, muscle fibre-type proportion varies in muscles from different breeds, where muscles from modern commercial pigs generally have a greater proportion of glycolytic fibres and heritage, native, or wild pigs have less of Type IIB fibres and a greater proportion of Types I and IIA fibres.

Separate to muscle fibre-type proportions, the size/diameter of muscle fibres is known to affect quality measurements (Ouali *et al.* 2005). In our study, the muscle fibre diameter for all muscle fibre types in SC2-Berk pigs was smaller than in SC1-LWLR pigs. This agrees with other studies where, in general, native, heritage or wild pigs have smaller muscle fibres than modern commercial pigs (Rahelic and Puac 1981; Weiler *et al.* 1995; Crawford *et al.* 2010; Guo *et al.* 2019), regardless of fibre type. Dai *et al.* (2009) attributed differences in muscle fibre cross-sectional area of the *longissimus* between heritage and modern commercial breeds to differences in carcass weight and growth rate, which does not explain the differences in our study, because age and carcass weight were similar for pigs from both supply chains.

Mitochondrial enzymes, measured from samples extracted early postmortem, are good indicators of whether the predominant metabolism of a muscle is oxidative or glycolytic. For example, Gil *et al.* (2003) found that when proportion of Type I fibres increases, ICDH activity also increases. Citrate synthase (CS) activity is also an indicator of oxidative activity in muscles (Scheffler *et al.* 2014; Lebret *et al.* 2023). In our study, the *longissimus* of SC2-Berk samples tended to have increased ICDH activity, and had increased citrate synthase activity, compared with the SC1-LWLR pigs, likely because of the increased composition of Types I and IIA fibres. Plastow *et al.* (2005) found that Duroc and Pietrain pigs had higher ICDH activity than the Meishan × Large White and Large White. The lack of difference in LDH activity between SC1-LWLR and SC2-Berk is likely due to the small sample size. Increased muscle CS activity has been related to increased sensory tenderness in pork *longissimus* (Essén-Gustavsson and Fjelkner-Modig 1985) and improved WHC (Brunner *et al.* 2012), which are both discussed further below.

Muscle fibre-type proportion influences WHC, especially purge and cook loss (Ryu and Kim 2005). There were differences in purge and cook loss between supply chains, where SC2-Berk pigs had improved WHC with less purge and cook loss than the SC1-LWLR pigs, which is similar to the increased water-holding capacity (lower drip loss and purge) found in muscles of heritage/wild/native pig breeds relative to modern commercial highly selected pigs (Suzuki *et al.* 2003; Lee *et al.* 2012). Increased proportions of Type IIB fibres in porcine muscles are often associated with poor quality, with increased L^* values, lower WHC and higher WBSF (tougher), whereas increased proportions of Type I fibres are associated with improved WHC and tenderness (Ryu and Kim 2005, 2006; Kim *et al.* 2013; LeMaster *et al.* 2023). Pork from SC2-Berk in the current study had a lower cook loss after 16 days of postmortem ageing than the SC1-LWLR pigs, which is similar to the results of Lee *et al.* (2012). Choi *et al.* (2014) found that the muscles from fatter carcasses, predominantly from heritage breeds, have improved WHC compared with the muscles from very lean, modern, commercial pork carcasses. Muscle fibre size also influences WHC and tenderness (Ouali *et al.* 2005) where, as muscle fibre diameter increases, WHC decreases, and toughness increases. The current study found that heritage pork from the SC2-Berk had increased WHC with lower purge and lower cooking loss after 16 days of postmortem ageing, which is supported by findings from other studies (Florowski *et al.* 2006; Tang *et al.* 2008; Crawford *et al.* 2010; Men *et al.* 2012; Shen *et al.* 2014; Chen *et al.* 2018). Although differences in WHC and WBSF between the supply chains in the current study are likely to be due to differences in muscle fibre-type proportions in the *longissimus*, variation in feeding, handling and pre- and post-slaughter management cannot be excluded.

There were differences in WBSF (tenderness) between the supply chains and with ageing. The *longissimus* from SC2-Berk had lower WBSF, and more reduction in WBSF with ageing, than from the SC1-LWLR pigs. This indicates less tenderisation for the SC1-LWLR pigs between 2 and 16 days of postmortem ageing. It is well recognised that genes play a small (but significant) role in meat tenderness, and that other endogenous and environmental factors usually dominate the factors influencing meat tenderness (Warner *et al.* 2010). The reasons for these differences are likely to be a combination of all the differences between the supply chains, as well as differences in fibre-type proportion between the breeds. These results for the modern commercial SC1-LWLR pigs are not dissimilar to findings by Channon *et al.* (2016) who reported a noticeable lack of improvement in pork *longissimus* WBSF after an ageing period of 14 days. According to Dransfield *et al.* (1981), tenderisation of pork *longissimus* occurs rapidly, where 50% of pork tenderisation occurs within 24–48 h, rather than over a period of days or weeks (Lundberg *et al.* 1987; Koohmaraie *et al.* 1991). Similarly, Crawford *et al.* (2010) compared WBSF of Berkshire and Landrace and found that the Berkshire *longissimus* had lower WBSF values than Landrace *longissimus* (21 - 25 N vs 29 - 33 N, respectively), further suggesting that improved tenderness occurs in muscles with lower proportions of glycolytic fibres. Park *et al.* (2007) found the *longissimus* from Korean Native pigs is more oxidative and demonstrated greater tenderisation after ageing, with lower WBSF values than the *longissimus* from Landrace pigs. Increased proportions of Type-I fibres in a muscle are associated with a more active calpain system (Ouali and Talmant 1990). Several factors influence quality, including environmental differences and supply-chain differences. Unfortunately, in this study, it was not possible to raise the two breeds on the same farm, nor was it possible to slaughter the two breeds at the one processing plant.

Protein denaturation temperatures using DSC indicate the peak denaturation temperatures for various proteins. Protein

denaturation occurred at lower temperatures for myosin (peak I) and actin (peak III) in the *longissimus* of SC1-LWLR pigs than in the *longissimus* of SC2-Berk, indicating that fibre shrinkage occurs at lower temperatures during cooking, which explains the increased cook loss and WBSF in the SC1-LWLR pigs compared with SC2-Berk. The denaturation temperatures for the *longissimus* from the SC1-LWLR were similar to thermal denaturation peaks of pork *longissimus* in other studies (Xiong *et al.* 1987; Xiong 1994; Vaskoska *et al.* 2021). The increased proportion of oxidative fibres in the *longissimus* from SC2-Berk was associated with higher thermal denaturation peaks than the thermal denaturation peaks from the SC1-LWLR pork, which agrees with other studies (Zielbauer *et al.* 2016; Vaskoska *et al.* 2021), and was most likely causative in lower cook loss and lower WBSF, improving tenderness in the SC2-Berk.

Differences in environmental factors and supply-chain logistics, such as transportation time and lairage, influence glycolytic potential because glycogen stores are depleted during transportation owing to time off-feed and heightened stress (Čobanović *et al.* 2016). Because of logistics, and minimisation of pig movement for disease control in the pig industry, it was not possible to standardise these factors in this study. In our study, the SC2-Berk had increased glycolytic potential, an increase in lactate between 3 h and 24 h postmortem and higher glycogen content at 3 h than the commercial SC1-LWLR pigs. The differences in glycolytic potential could be due to differences in transportation and lairage between the supply chains (Gajana *et al.* 2013; Driessen *et al.* 2020). Warner *et al.* (2015) found that in lamb *longissimus*, G6P generally increases overtime postmortem, and it increases faster when carcasses are chilled rapidly. Owing to the differences in transportation, lairage, stunning, and chilling between the supply chains, the rate of glycolysis and the production and consumption of glycolytic metabolites varied. Supply-chain differences influence the rate and extent of postmortem metabolism and, thus, pork quality (Shackelford *et al.* 2012; Rybarczyk *et al.* 2015; Zybert *et al.* 2019). Scheffler *et al.* (2013) indicated that glycolytic metabolite concentrations are highly variable in pork postmortem and suggested that glycolytic metabolites might not be reliable quality indicators because of different factors between supply chains, but mitochondrial enzymes may be more reliable indicators of oxidative activity and quality.

Colour is an important characteristic for consumers. Overall, SC1-LWLR had higher lightness and lower redness and yellowness, than SC2-Berk. This was expected because the SC1-LWLR had a lower proportion of oxidative myoglobin-rich fibres, which are paler in colour, and have a faster pH fall, both of which are usually associated with lighter and less red meat (Bocian *et al.* 2012; Listrat *et al.* 2016). It is unlikely that these colour differences between supply chains were due to chilling; SC1-LWLR had blast-chilling, which usually results in a slower pH fall and lower lightness (L^*) (Swatland 2002; Savell *et al.* 2005; Lebret *et al.* 2015; Purslow *et al.* 2021), which is opposite to what we observed for SC1-LWLR.

Conclusions

The *longissimus* from the SC2-Berk pigs had a higher proportion of oxidative and intermediate fibres, and higher mitochondrial enzyme activity, than pork from the SC1-LWLR pigs, which had a higher proportion of glycolytic fibres. This increased oxidative metabolism in SC2-Berk *longissimus* was associated with improved WHC and WBSF, compared with pork from the SC1-LWLR pigs. Pork from SC2-Berk had higher glycolytic potential, likely being a result of pre-slaughter conditions that were different between the supply chains. Because of variations between supply chains in pre-slaughter conditions, it was evident that mitochondrial enzyme activity, particularly citrate synthase, was a more robust measurement of the oxidative/glycolytic metabolism of a given muscle than were glycolytic metabolites. Protein denaturation temperatures were higher for the SC2-Berk than for the SC1-LWLR pigs, which is the likely cause of the increased cook loss and toughness. Thus long-term selection in the modern commercial pig is associated with an increased proportion of glycolytic fibres which is likely causative in a decline in pork quality.

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Data availability. Data are contained within the article.

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