Muscle fiber, connective tissue and meat quality characteristics of pork from low birth weight pigs as affected by diet-induced increased fat absorption and preferential muscle marbling

Bimol C. Roy [a, *], Patience Coleman [a], Meghan Markowsky [a], Kun Wang [a, b], Yongbo She [a, b], Caroline Richard [a, b], Spencer D. Proctor [a, b] and Heather L. Bruce [a]

[a] Division of Animal Science, Department of Agricultural, Food and Nutritional Science, 4-10 Agriculture/Forestry Building, University of Alberta, Edmonton, Alberta, Canada, T6G 2P5.

[b] Division of Human Nutrition, Department of Agricultural, Food and Nutritional Science, University of Alberta, Edmonton, Alberta, Canada, T6G 2P5.

Running title: Meat and myofibers of low birthweight pigs

*Correspondence: Bimol C. Roy, Division of Animal Science, Department of Agricultural, Food and Nutritional Science, 4-10 Agriculture/Forestry Building, University of Alberta, Edmonton, Alberta, Canada T6G 2P5. E-mail: rimol@ualberta.ca and bcroy11@yahoo.com

Abstract

This study investigated how birth weight differences in piglets affected carcass and muscle fiber properties as well as meat quality at slaughter. Within litters, piglets were grouped according to their birth weight as either normal (NBW; 1.62-1.73 kg) or low (LBW; 1.18-1.29 kg). At 5 weeks of age, NBW piglets were randomly transitioned to control (C) or isocaloric high fat diets derived from non-dairy (HF), while LBW piglets were randomly transitioned to high fat diets derived from non-dairy (HF) or dairy sources (HFHD). Piglets were reared in individual pens under standardized housing and feeding conditions. Live weight was recorded weekly, and pigs were slaughtered at 12 weeks of age. Hot carcass weights, dressing percentages, lean meat yield, and primal cut proportions were determined. The m. *longissimus thoracis* was collected from the right side of the carcass for measurement of physical and chemical properties of meat and muscle fiber characteristics. Results indicated that LBW pigs compensated for their live weight compared to NBW pigs at 6 weeks of age. The mean muscle fiber diameter of LBW-HFHD group is significantly higher than NBW-C and NBW-HF group, and the type I muscle fiber diameter is significantly higher than NBW-C group. Dairy fat inclusion in LBW pig diet reduced carcass back fat thickness. This increased the calculated lean meat yield to be comparable to that of NBW pigs fed a commercial diet. Incorporating dairy-sourced high-fat into LBW pigs' diets appears to be an effective strategy for producing carcasses equivalent to NBW pigs.

Keywords: pig, pork, carcass quality, birth weight, muscle fibers, collagen

Introduction

Genetic selection strategies to increase prolificacy in polytocous pigs resulted in increased litter size which ultimately reduced the mean birth weight of piglets within-litter (Milligan et al., 2002; Quiniou et al., 2002) and led to intra-uterine growth retardation of the embryos due to limited placental capacity (Stange et al., 2020; Baur et al., 1998). It has been shown that low birth weight (LBW) piglets (0.95 - 1.3 kg) exhibit a reduced post-natal growth rate and finally a lower lean carcass percentage than normal birth weight (NBW) piglets (1.4 - 1.6 kg) at slaughter (Bee, 2004; Gondret et al., 2006; Morise et al., 2008). The total number of muscle fibers in a muscle is an important determinant of the total mass of a muscle (Luff and Goldspink, 1970; Miller et al., 1975) because fast growing pig strains tend to have a higher number of muscle fibers in their muscles than their slow growing counterparts (Ezekwe and Martin, 1975; Miller et al., 1975). There is some evidence that LBW (runt) piglets tend to grow more slowly and less efficiently than their NBW (larger) littermates (Powell and Aberle, 1980). As a result, piglets with LBW require a longer growth period than do the NBW piglets or their heavier littermates to reach the same slaughter weight (Wolter et al., 2002) and their growth is characterized by a lower feed efficiency that ultimately results in a reduced rate of weight gain as well as a lower lean meat yield and meat quality than NBW pigs at slaughter (Gondret et al., 2005a; Rehfeldt and Kuhn, 2006). Moreover, birth weight in pigs is related to post-natal muscle development, fat accretion, and ultimately meat quality (Bee, 2004; Poore and Fowden, 2004; Gondret et al., 2005b) although contradictions exist (Bérard et al., 2008). Chemical analysis revealed that at slaughter, muscles of LBW piglets contain less intramuscular fat and protein but more water than their NBW littermates (Rehfeldt and Kuhn, 2006) and this difference was more pronounced in locomotive (*semitendinosus*) muscle than in postural (*longissimus*) muscle (Gondret et al., 2005b) although contradictions exist for intramuscular fat content (Rehfeldt et al., 2008). In practice, LBW piglets are grown by fostering or feeding them individually from birth to slaughter. This might cause the carcasses to be fatter and have increased intramuscular fat compared with their NBW counterparts (Powell and Aberle, 1980). At weaning, LBW piglets weighed 12 % less than NBW piglets and required 12 more days to reach the same slaughter weight (Gondret et al., 2005b).

The total number of muscle fibers in a muscle is lower in LBW piglets than in NBW piglets or their heavier littermates, a characteristic fixed at birth (Wigmore and Stickland, 1983). Although

LBW piglets have fewer muscle fibers at birth, the muscle fibers they do have are larger in mean diameter or cross-sectional area at slaughter weight (Kuhn et al., 2002; Gondret et al., 2005b) which might contribute to increased meat toughness in *longissimus* muscle as tenderness score and muscle fiber diameter are negatively correlated (Gondret et al., 2006), although Maltin et al. (1997) did not find any relationship between muscle fiber cross-sectional area and meat tenderness in pork. The variation in the total number of muscle fibers in a muscle in relation to piglet birth weight is not always consistent (Dwyer et al., 1993). It was shown that muscles with a lower total number of muscle fibers that have large mean diameter or cross-sectional areas are prone to rapid post-mortem pH decline and high drip losses that ultimately alter meat tenderness (Lengerken et al., 1997) and lead to pale, soft exudative pork (Rosenvold and Andersen, 2001). Muscle characteristics such as muscle fiber type composition, intramuscular fat content, total collagen content and collagen heat-solubility differ with birth weight and influence meat quality (Lebret et al., 1999).

During the fetal and early post-natal stages, the development of different tissues in the animal body is prioritized according to nutrient supply (Lawrence et al., 2012). It has been demonstrated that ovine fetuses exposed to under nutrition *in utero* possess more intramuscular fat in their muscles (Bispham et al., 2003, 2005; Symonds et al., 2003). It was suggested that when muscle cannot form, intramuscular fat and connective tissue components increase in muscle as a default development pathway (Kablar et al., 2003). It is well accepted that LBW piglets, weighing less than 0.93 kg at birth, might exhibit slower post-natal muscle development, however they exhibit increased adipose tissue development during their lifetime (Gondret et al., 2006). It was observed that LBW piglets fed a high-fat diet were susceptible to insulin resistance (Fontaine et al., 2019). In fact, it has been shown that odd chain fatty acids (C15:0 and C17:0) from dairy fat sources are linked to a reduced risk of diabetes (Imamura et al., 2018). The addition of dairy products to the diet of LBW piglets may help to alleviate the metabolic consequences of insulin resistance in piglets. From the above discussion, we hypothesized that LBW piglets require a longer time to reach slaughter weight due to their lower growth rate and produce carcasses with lower yields of lean carcasses with inferior quality meat. This study investigated the influence of piglet birth weight on overall growth performance, carcass components and traits and muscle fiber characteristics, intramuscular fat content, collagen characteristics in the intramuscular connective tissue of *longissimus thoracis* muscle and the consequences for meat quality. Moreover, we would

like to determine the effect of high dairy fat diet compared with high fat diet on the development of adipose tissue in LBW piglets. This was part of the other study (Wang et al., 2023) previously published.

Materials and Methods

Animals and diets

The piglets used in this study were part of a human nutrition model study (She et al., 2022). As a result, replicate numbers were low due to the intensive nature of that research. The University of Alberta's animal care and use committee (AUP00001184) approved both studies. According to the guidelines of the Canadian Council for Animal Care (CCAC), piglets were cared for by trained personnel.

Landrace Large White × Duroc piglets were weighed within 24 hours of full-term birth and categorized as normal birth weight (NBW, 1.89 ± 0.02 kg, n = 11) and low birth weight (LBW, 1.05 ± 0.04 kg, n = 13). Piglets were categorized as LBW (below 95 % CI) or NBW (within or above 95 % CI) using confidence intervals (CI) (95 %). Randomly assigned NBW piglets received a standard commercial grower-control diet (NBW-C; 1.62 ± 0.07 kg SEM, n = 5) or a high fat diet (NBW-HF; 1.73 ± 0.09 kg SEM, n = 6). The LBW piglets were randomly assigned to either a high fat diet (LBW-HF; 1.29 ± 0.08 kg SEM, n = 8) or a high fat diet with dairy sources (LBW-HFHD; 1.18 ± 0.06 kg SEM, n = 5, 3 servings of 2000 kcal/day). Piglets were fed maternal milk until weaning (3 weeks of age) and a standard grower diet (control chow) thereafter until 5 weeks of age. All piglets were fed a transition diet for 1 week and a 6-week experimental diet for 6 weeks. A detailed description of the control chow and high fat diets has already been published (Fontaine et al., 2019). Briefly, the control diet provided 14 %, 17 % and 69 % of energy from fat, protein and carbohydrates, respectively. In contrast, the HF diets were 46 % (mainly lard), 21 % and 33 % (mainly fructose) with 1 % cholesterol. In the HFHD diet, the serving portion of dairy products contained whole milk powder (3.25 % fat, 33 g/serving; Bulk Barn, Canada), plain yogurt (10 % fat, 175 ml/serving portion; Liberté, Canada) and mozzarella cheese (28 % fat, 50 g/serving portion; No name® , Canada) and the diets were isocaloric. HF dairy sources were paired-fed with those on the HF diet, and daily feed intake was measured (She et al., 2022). Piglets for both NBW and LBW treatments were obtained from different dams and live weight were recorded at birth and then

weekly until 12 weeks of age (slaughter age).

Slaughter and carcass characteristics

At 12 weeks of age, pigs were euthanized by captive bolt and slaughtered by exsanguination and eviscerated. A blow torch was used to remove the hair from the carcasses and then the carcasses were transported to the food laboratory at Agri-Food Discovery Place (University of Alberta, Edmonton, Canada) within 10 minutes. Upon arrival at the laboratory, the carcasses were washed with cold tap water and the hot carcass weight (HCW) was recorded. The head was removed and the carcass was hung in a walk-in chiller (4 °C) and allowed to cool for 24 hours. After 24 hours, the cold carcass weight and carcass length (from the first cervical vertebrae bone atlas to the base of the tail) were measured and recorded. The carcass was then cut into halves and both sides were dissected into primal cuts (pork shoulder, pork belly, pork loin and pork legs) following the Canadian Food Inspection Agency Meat Cuts Manual (https://inspection.canada.ca/food-label-requirements/labelling/industry/meat-and-poultry-products/meat-cuts/eng/1300126276015/1300126349342). The weights of each primal cut were recorded, and their yields calculated as percentages of the HCW. The thoracic region of the pork loin was removed from the right side of the carcass, weighed, and retained for measurement of meat quality at 24 hours post-mortem. The pork loin thoracic region was fabricated for meat quality analysis as illustrated in Figure 1. One chop (Figure 1, steak A at 24 hours post-mortem) was analyzed to measure subcutaneous back fat depth and loin muscle depth following Teixeira et al. (2021) and described elsewhere in detail (Wang et al., 2023). These data were used to calculate the Canadian Lean Yield (CLY) percentage as described by Pomar and Marcoux (2003) using the following equation:

CLY (%) = 68.1863 − (0.7833 × fat depth in mm) + (0.0689 × muscle depth in mm) + (0.0080 × fat depth in mm^2) − (0.0002 × muscle depth in mm^2) + (0.0006 × fat depth in mm × muscle depth in mm).

Pork meat quality characteristics

Pork meat quality characteristics were determined from chops removed from the m. *longissimus thoracis* (loin eye) muscle as described in Figure 1.

Meat color

Meat color was determined on a freshly cut cross section surface of a chop from the *longissimus thoracis* muscle after being exposed to air (bloom) for 20 minutes at room temperature. Surface color was measured using a CR-400 chroma meter (Konica Minolta Sensing, Inc., Japan) with the CIE standard color system where lightness (L*; ranging from 0 for black to 100 for ideal white), redness (a*; color coordinates where positive values indicate redness and negative values represent greenness), yellowness (b*; color coordinates where positive values reflect yellowness and negative values indicate blueness), and color intensity or saturation (C*; chroma and h*; hue) index (Commission Internationale de I'Eclairage, 1986) were recorded. The aperture area diameter was 8 mm with a 2° standard observer angle, and the D65 illumination setting was applied. The chroma meter was calibrated before the measurement using a white calibration ceramic tile provided by the manufacturer. The calibration index was used (Y = 93.1, x = 0.3160, y = 0.3324) and the readings from the white plate were recorded (L* = 97.55; a* = 0.04; b* = 1.89; Chroma = 1.89 and hue = 88.97). Three readings were performed on each chop, and the mean of the three readings was taken for statistical analysis. Readings were performed on the lean portion of each chop, avoiding intramuscular fat and connective tissue.

Intramuscular ultimate pH 24h

An Accumet AP71 pH meter (Fisher Scientific, Mississauga, Ontario) was used to measure the ultimate pH at 24 hours post-mortem with a pH electrode that was temperature compensated (Cat No. 655-500-30, FC210B, Canada-wide Scientific, Ottawa, ON) and calibrated with commercial pH standards 4.0 and 7.0. The glass electrode was inserted into cuts made in the muscle with a knife along with the temperature probe. The average of three readings was calculated and used for statistical analysis.

Drip loss

Drip loss was determined by the standard bag method according to Honikel (1994). For this, approximately 50-60 g of *longissimus thoracis* muscle trimmed off epimysium was suspended in an inflated plastic bag with a metal hook for 24 hours at 4 ℃. Drip loss was considered and calculated as the weight loss during the 24 hours suspension period as a percentage of the initial muscle weight.

Cooking of meat and cooking loss determination

After color measurement, the chops were weighed, penetrated with a thermocouple (Tiny-Tag View 2S, Gemini Data Loggers, Chichester, West Sussex, UK) at the geometric center of the chop to monitor the cooking temperature and then grilled on an electric clam-shell style grill (General Electric 4 in 1 Grill/Griddle, China) at 163 ℃. Chops were cooked until the temperature at the geometric center of each chop reached 71 ℃. At 71 ℃, the cooked chop was immediately removed from the grill, placed in a plastic bag, and immersed in ice water. This stop the cooking process. Once the chops cooled, the condensed fluid in the plastic bag was poured out. The chops were stored overnight in a plastic bag at 4 ℃. In the following day, the chops were patted dry with paper towels and weighed to determine the cooking loss using the following equation:

$$\text{Cooking loss (\%} = \frac{\text{(Meat chop weight before cooking} - \text{Meat chop weight after cooking and patted drying)}}{\text{Meat chop weight before cooking}} \times 100$$

Warner-Bratzler shear force determination

Warner-Bratzler shear force (WBSF) was measured on grilled chops stored in a cooler overnight. The grilled chops were taken out of the cooler and kept at room temperature (22-25 ℃) about 30 minutes for temperature equilibrium. A metal Cork borer was used to bore six 1.27 cm diameter cores with parallel to the muscle fibers direction from each cooked chop, avoiding thick visible fat or connective tissue. In order to measure peak force, a V-shaped shear blade was attached to a material testing machine (Lloyd Instrument LRX plus, AMETEK®, Digital Measurement Metrology Inc. Brampton, ON) and cut at a cross-head speed of 200 mm/min and a pre-load force of 2 N. A mean of six peak shear force values expressed as Newtons was obtained and used for statistical analysis.

Proximate composition of meat

Moisture

About 100 g of raw meat steak was trimmed off epimysium and cut into small cubes that were evenly distributed in a small aluminum tray. The tray covered with perforated aluminum foil, and then frozen at -20 ℃ until lyophilized for 5-7 days. After lyophilization the weight loss was reported as the moisture content (as a percentage of total raw meat weight) and was calculated by the equation:

$$\text{Moisture (\%)} = \frac{(\text{Raw meat weight} - \text{Lyophilized meat weight})}{\text{Raw meat weight}} \times 100$$

Crude fat

The crude fat content was measured with the Soxtec™ 2050 fat extraction apparatus (Foss® Analytical, Hilleroed, Denmark) following Roy et al. (2018) according to the Association of Analytical Communities Official Method of Analysis, 991.36 (Thiex et al. 2003). About 2.0 grams of lyophilized ground meat were weighed into a cellulose thimble (33 × 80 mm, Foss™ Thimbles for Soxtec™ 2055 Manual Fat Extraction System, Fisher Scientific, Cat No. TC15220045) and packed with defatted cotton (Foss™ Accessories for Soxtec™ Extraction Systems: Fisher Scientific, Catalog No.TC15290009). The extracted fat was calculated as a percentage from raw meat using the following equation:

$$\text{Crude fat (\%)} = [\text{Fat in lyophilized meat (\%)} \times \text{Dry matter (\%) in lyophilized meat}] \div 100$$

Crude protein

Based on the AOAC (1990) method, crude protein was determined with a LECO FP-2000 Nitrogen Determinator (Leco Corp., St. Joseph, MI). About 100 mg of lyophilized ground meat was weighed into a foil boat liner (Cat. No. 502-343, LECO) and the weight was recorded. Standards, blanks and calibration procedures were performed with LECO TruMac N with TruMac operating software as described in the manufacturer's operator instruction manual. Ethylenediaminetetraacetic

acid (EDTA, 9.65 % nitrogen, Leco Corporation) was applied as a standard for calibration after every 20 samples. Helium was used as a carrier gas, and nitrogen was measured with a thermal conductivity detector. Nitrogen was converted to protein concentration using the conversion factor of 6.25, which assumes meat protein contains 16 % nitrogen.

Ash

Approximately 2.0 grams of lyophilized ground meat were weighed into dried and pre-weighed Pyrex glass bottles. The glass bottles with lyophilized ground meat were then placed into an oven for 24 hours at 110 ℃ and then into a furnace at 490 ℃ for 24 hours to incinerate the meat into ash. Then, the glass bottles with ash were cooled at room temperature in a desiccator and checked for weight. The lyophilized ground meat content after incineration into the furnace was ash and calculated as a percentage on a raw meat basis. This was done according to the following equation:

Crude ash (%) = [Ash in lyophilized meat (%) × Dry matter (%) in lyophilized meat] ÷ 100

Total, soluble, and insoluble collagen determination

Soluble and insoluble collagen fraction separation

Soluble collagen was extracted from lyophilized ground meat according to the Hill (1966) method. About 2.00 grams of lyophilized meat were weighed, the weight recorded, and then the meat was heated with 18 mL ¼ Ringer's solution at 77 ℃ for an hour in a 25 mL Teflon-capped glass tube. Following heating, the tubes were cooled to room temperature, and then the supernatant (soluble collagen fraction) and residue (insoluble collagen fraction) were collected following centrifugation at 3500 *g* for 10 minutes. Extractions were performed in duplicate and means were used for statistical analysis.

Hydrolysis of soluble and insoluble collagen

An aliquot of two 1 mL of supernatants (for soluble collagen) and about 0.30 g of residue (for insoluble collagen) was hydrolyzed in 6 mL of 6M HCl for 20 h in a 20 mL glass Teflon-capped test tube. After hydrolysis, tubes were cooled in ice water to stop hydrolysis, and filtered (Whatman No. 4 filter paper, Fisher Scientific, Edmonton, AB). Filtered hydrolysates were evaporated to dryness, reconstituted in deionized water, and neutralized with NaOH. After neutralization, hydrolysates were evaporated to dryness, combined with 5 mL of deionized water, followed by the measurement of soluble and insoluble collagen content with a hydroxyproline assay.

Hydroxyproline assay for collagen estimation

Hydroxyproline content was determined following the Bergman and Loxley (1963) method for soluble and insoluble collagen quantification.

For hydroxyproline determination, 1.0 mL of soluble or insoluble collagen hydrolysate was obtained. The blank was prepared in the same manner as the samples using deionized water (1 mL). Absorbance was measured against the blank at 558 nm. Hydroxyproline standards (trans-4-Hydroxy-L-proline, Sigma-Aldrich) with concentrations of 2.5, 5, 10, 20 and 40 μg hydroxyproline/mL solutions were prepared. The hydroxyproline concentration in the sample was calculated using a standard curve determined by regressing the concentration of each standard against its absorbance. Multiply the concentration by the dilution factor for each sample. Hydroxyproline content was calculated based on the calculation of Stanton and Light (1987), where hydroxyproline content was converted into collagen concentration (mg/g raw meat) using a conversion factor of 7.14. Total collagen was determined by adding soluble and insoluble collagen together and collagen solubility was determined with the formula:

$$\text{Collagen solubility (\%)} = \frac{\text{Soluble collagen (mg/g raw meat)}}{\text{Total collagen (mg/g raw meat)}} \times 100$$

For each sample, duplicates were performed and their mean used for statistical analysis.

Muscle fiber type determination

Muscle fiber typing with histological and immuno-histological characterization of the *longissimus thoracis* muscles was conducted by collecting 1 cm^3 muscle samples from each muscle fabricated at 24 hours post-mortem. Muscle cubes were immersed in acetone previously cooled with dry ice as described by Roy et al. (2018). The muscle cubes were then stored at -80 ℃ until further processing. The muscle cubes were sectioned (10 µm thick) transverse to the muscle fiber direction in a cryostat (Leica CM1850 cryostat, Leica Biosystems Nussloch, Germany) at -25 ℃ and serial sections were mounted on dry slide glasses and stored at -80 ℃ until staining. At staining, the slide glass with mounted muscle sections was removed from storage and air-dried at room temperature for 30 minutes. Muscle fiber typing was performed using the myofibrillar adenosine triphosphatase (mATPase) staining method (Brooke and Kaiser, 1970) and the nicotinamide adenine dinucleotide dehydrogenase-tetrazolium reductase (NADH-TR) staining method (Roy et al., 2018). Confirmation of type I muscle fiber type was performed by immuno-fluorescence histochemistry using monoclonal antibodies (S58, skeletal muscle myosin antibody from Santa Cruz Biotechnology, Inc.) specific for the type I myosin isoform (Roy et al., 2018). Myofibrillar adenosine triphosphatase (mATPase) staining was done on muscle sections after pre-incubation in acid (pH 4.3) and alkali (pH 10.5). The classification of muscle fiber typing was carried out as presented in Figure 2 by following the different staining procedures in serial sections as mentioned above. Using the open-source software ImageJ (http://rsbweb.nih.gov/ij/), cross-sectional areas of muscle fibers were measured from three randomly captured images at 200x magnification, which included at least 300 muscle fibers from each sample and were converted to diameter. To determine the muscle fiber diameter class interval relative to frequency percentages, different class intervals of the diameter (10-20, 21-30, 31-40, 41-50, 51-60, 61-70, 71-80 and 81-90 µm) of total muscle fibers counted for diameter from each treatment group were considered.

Statistical analysis

Data were analyzed by R (version 3.6.1) with the package lessR using one-way analyses of variance (ANOVA) where treatments (birth weight) were regarded as the sole source of variation. The Tukey's Honestly Significant Difference (HSD) test was used to detect significant differences between means when significant main effects were detected. All comparisons with $P < 0.05$ were considered statistically significant and $0.05 < P < 0.10$ were considered to approach significance.

Muscle fiber diameter class interval frequency percentages were analyzed by one-way analysis of variance (ANOVA) within each diameter interval class using piglets' birth weight groups as the sole source of variation. Where the model was significant ($P < 0.05$), Tukey's HSD test was used to determine mean differences between the treatments. Pearson correlation analysis was conducted to analyze the relationship between different measurements. The correlation coefficients were calculated using the package corrplot in R (version 3.6.2).

Results

Live weight of the piglets with age

The weekly mean live weights of the piglets by treatment are presented in Table 1. As planned, the birth weight of the piglets was significantly higher ($P = 0.0003$) in both NBW treatments (NBW-C and NBW-HF) compared with both LBW treatments (LBW-HF and LBW-HFHD) for the first 4 weeks of life. The NBW-HF pigs had heavier mean live weights than the LBW-HF and LBW-HFHD pigs up to 4 weeks of age, but by 6 weeks of age, mean live weights across the treatments were no longer different ($P > 0.05$). From 6 to 12 weeks, the difference in live weight between NBW-HF and LBW-HFHD pigs approached significance at 8, 9, 10 and 12 weeks ($0.05 < P < 0.1$) (Table 1). LBW pigs fed high fat diets (LBW-HF) had mean live weights similar to that of NBW-C pigs throughout (Table 1), while LBW-HFHD pigs had mean live weights similar to that of NBW-C and LBW-HF pigs throughout as well (Table 1).

Carcass characteristics

The carcass composition of the pigs at slaughter from the different treatments is presented in Table 2. Hot carcass weights were not different between the treatments, with the difference between the normal (NBW-HF) pigs and the low (LBW-HFHD) birth weight pigs approaching significance ($P = 0.0615$). Cold carcass weights were not different due to treatment, nor was carcass length, *longissimus thoracis* muscle depth and area, dressing percentage, pork shoulder weight percentage, pork loin weight percentage or pork belly weight percentage (Table 2). Mean subcutaneous fat depth was lower in the LBW-HFHD pigs than in the NBW-HF and LBW-HF

pigs but did not differ from the NBW-C pigs which indicated that inclusion of dairy fat as dietary fat source in the high fat diet of pigs significantly decreased subcutaneous fat depth (P = 0.0229). The pork leg proportion was significantly higher in LBW-HFHD than in NBW-C pigs but did not differ from pigs fed the other HF diets (LBW-HF and NBW-HF). The mean Canadian lean yield (CLY) percentage was significantly higher in LBW-HFHD pigs compared with pigs receiving other HF diets regardless of birth weight but not different from that of NBW-C pigs.

Physical properties of pork meat from *Longissimus thoracis* muscle at 24 h post-mortem

Meat quality characteristics in *longissimus thoracis* muscle are presented in Table 3. There were no significant differences in the color parameters lightness (L*), redness (a*), chroma, hue, ultimate pH at 24 h, cooking loss, and Warner-Bratzler shear force of the meat due to treatment. Differences that approached significance included yellowness (b*), with pork from LBW-HFHD pigs tending to have a higher yellowness (b*) value than that of NBW-C pork although it did not differ from pork from the NBW-HF and LBW-HF pigs (P = 0.0587). Also, drip loss tended to be higher for pork from NBW-HF pigs than NBW-C pigs but did not differ from LBW-HF and LBW-HDHF groups (P = 0.0985).

Proximate composition and collagen content of pork

Both the proximate composition and collagen content of pork were determined in *longissimus thoracis* muscle and results are presented in Table 4. There were no significant differences between birth weight treatments for muscle crude protein, intramuscular fat, ash, total collagen, soluble collagen, insoluble collagen content and collagen solubility percentage. Moisture content was significantly higher in pork from NBW-C pigs than NBW-HF and LBW-HF pigs but did not differ from that of LBW-HDHF pigs. The mean percentage of soluble collagen in pork from NBW-C pigs tended to be higher than that of NBW-HF pigs, with this difference approaching significance (P = 0.06).

Muscle fiber characteristics

Muscle histological cross-sections depicting the three muscle fiber types (I, IIA, and IIB) from pigs of different birth weight treatments are illustrated in Figure 2 and their properties are presented in Table 5. The total muscle fiber number in the whole cross-sectional area of the *longissimus thoracis* muscle was not significantly altered due to treatment, nor was the percentage of different muscle fiber types. LBW-HFHD pigs had a significantly increased mean muscle fiber diameter compared to NBW piglets receiving either control (NBW-C) or HF (NBW-HF) diets. The LBW-HFHD pig muscle showed a larger mean diameter of type 1 muscle fibers than NBW-HF pigs but did not differ from NBW-C and LBW-HF pigs. There was no difference in type IIA and IIB muscle fiber characteristics due to treatment.

The frequency distributions of type I, IIA, IIB and mean muscle fiber diameters across the different class intervals are presented in Figure 3. Type I muscle fiber diameter in the 31-40 μm class interval tended to be more frequent in NBW pigs than in LBW-HFHD pigs ($P = 0.0564$). The mean muscle fiber diameter in the class interval 11-20 μm appeared to be significantly more prevalent overall ($P = 0.0176$) and type IIB muscle fibers ($P = 0.0211$) in the NBW-HF pig muscle compared with that of the LBW-HFHD pigs. Also, the mean muscle fiber with diameters between 61-70 μm tended to be more prevalent ($P = 0.0741$) in LBW-HFHD and NBW-C pig muscles than in NBW-HF pig muscles ($0.05 < P < 0.1$).

Discussion

The implications of piglet birth weight on subsequent carcass characteristics have been a major subject of pig research in the past (Rehfeldt and Kuhn, 2006; Bee et al., 2007; Rehfeldt et al., 2008; Bérard et al., 2010; Alvarenga et al., 2012). The pork industry has increased swine litter size through genetic selection and has introduced highly prolific dam lines for commercial production that result in LBW piglets due to crowding in the dam's uterus (Quiniou et al., 2002). Also, due to the limited capacity of the uterus, the increased number of fetuses results in a reduced nutrient supply per fetus during gestation (Père and Etienne, 2000), hence LBW piglets are associated with a reduced growth rate during their lifetime (Quiniou et al., 2002; Rehfeldt et al., 2008; Zhang et al., 2018). The effect of a nutrient deficit diet during gestation on the myogenesis of a fetus is

strongly influenced by the time point in gestation at which the deficiency occurs. Nutrient deficiency during the early stages of pregnancy (35-60 days of gestation) hinders the development of primary muscle fibers but deprivation during late gestation (55-90 days of gestation) (Lefaucheur et al., 1995; Kalbe et al., 2017) reduces muscle fiber diameter (Greenwood et al., 1999). Consequently, nutrient deficiency at the early prenatal stage results in a lower total number of muscle fibers, altered composition of muscle fiber type, and ultimately a reduction in overall muscle mass (Ward and Stickland, 1991; Yates et al., 2012). During myogenesis, nutrient-deficient, growth-restricted fetuses reduce primary muscle fiber diameter (Wigmore and Stickland, 1983). The smaller diameter of primary muscle fibers presents a smaller surface area to serve as a scaffold for secondary muscle fibers to attach. This limits the number of viable secondary muscle fibers during myogenesis (Wigmore and Stickland, 1983). The reduction in primary muscle fiber numbers not only limits muscle growth, but also hampers formation of secondary fibers, which reduces the percentage of fast-twitch myofibers that will take on a glycolytic phenotype at maturity and results in an increase in a more oxidative phenotype in the muscle in LBW neonates (Wank et al., 2000; Lefaucheur et al., 2003). For growth, oxidative muscle fibers (Type I) exhibit greater rates of protein synthesis than glycolytic muscle fibers (Type IIA and IIB) and prefer to store energy as fat (Laurent et al., 1978; Bates and Millward, 1983; Kelly et al., 1984) which corroborate with the present study that the diameter of type I muscle fibers is larger in LBW-HFHD than NBW-C and NBW-HF ultimately help to catch-up the live weight of NBW piglets.

The results presented in this report disagreed with results from previous studies that showed that low birth weight piglets (Wolter et al., 2002; Gondret et al., 2005b) or lighter piglets at weaning (Mahan and Lepine, 1991; Wolter and Ellis, 2001; Gondret et al., 2005b) required more days compared to their heavier littermates to attain the same market weight. LBW neonates do not always remain smaller than their littermates throughout their growing period (Crume et al., 2014), and sometimes LBW piglets exhibit compensatory growth postnatally (Douglas et al., 2013; Rutherford et al., 2013; Rehfeldt and Kuhn, 2006). Consistent with previous studies (Bérard et al., 2008; 2010), LBW piglets in the present study exhibited compensatory growth as differences in live weight between the different treatments disappeared by 6 weeks of age. LBW-HFHD pigs showed no difference in mean live weights with NBW-C and LBW-HF pigs at weeks 8, 9, 10 and 12. This is a small study, with limited replication. The differences observed from week 5 onward most likely would be significant in a study with increased replication. Differences between the

treatments for live weight approached significance ($0.05 < P < 0.1$) at 5, 8, and 12 weeks, and would have been significant at 80 % power and 95 % confidence at a replication of greater than or equal to 8, 9 and 10, respectively.

Gondret et al. (2006) did not observe any significant differences in HCW and dressing percentages between NBW (1.89 ± 0.02 kg) and LBW (1.05 ± 0.04 kg) piglets when housed individually, and this was consistent with the results of the present study. Gondret et al. (2005b) speculated that LBW (0.80-1.10 kg) piglets grow slower than their NBW (1.75-2.05 kg) counterparts when placed in collective pens because LBW piglets compete less effectively for feed during the immediate post-weaning period. In this study, the piglets were individually penned and fed hence the LBW piglets had unfettered access to feed and showed compensatory growth relative to the NBW piglets which accounts for no differences due to diet being observed in HCW and dressing percentages. Other studies (Beaulieu et al., 2010; Gondret et al., 2006) did not find any differences in lean meat yield percentages between NBW and LBW pigs, whereas the present study showed that CLY percentage was higher in LBW-HFHD pig carcasses than in those from LBW-HF and NBW-HF pigs but did not differ from NBW-C pigs. Again, HCW differences were observed in the present study that may have been significant if replication was increased to greater than that used in the current study, but with the current replication complement, piglet birth weight had no significant effect on CLY percentage and loin muscle area in the present study, and this agreed with the results from previous reports (Bee, 2004; Bérard et al., 2008).

Heyer et al. (2004) reported that the percentage of primal pork cuts on an HCW basis increased. Subcutaneous (back) fat thickness decreased in NBW piglets compared to their LBW counterparts. Supplying dietary fat from dairy sources disrupted that relationship, decreasing the subcutaneous fat thickness of carcasses from the LBW-HFHD pigs compared to those from the LBW-HF and NBW-HF pigs. This may have been associated with dairy fat being the major source of energy in the diet. Gondret et al. (2006) observed that shoulder weight percentages did not differ between LBW and NBW piglets. However, but backfat depth and belly percentage were higher in LBW pigs and ham (leg weight) and loin weight were lower in LBW pigs. LBW pigs in previous studies had significantly higher intramuscular fat content as a result of being offered ad-libitum diets during growth (Kuhn et al., 2002; Poore and Fowden, 2004) or adjusted daily feed allowances during the rearing period (Bee, 2004) compared to pigs in the present study. It was reported that this compensatory growth may lead to extra fat deposition in muscle (Ibanez et al., 2011; Cho and

Suh, 2016) which was absent in the present study. Beaulieu et al. (2010) did not observe any significant effect of piglet birth weight on intramuscular fat content, which agrees with the present study results. There was no significant difference in total intramuscular fat content in the *longissimus thoracis* muscle among birth weight groups similar to Gondret et al. (2005b), although they observed a 25 % increase in intramuscular fat content in the *semitendinosus* muscle of LBW pigs.

Effects on meat quality were limited, and how representative or applicable these results would be at commercial slaughter weight was not a hypothesis tested in the current study. We did not find any difference in ultimate pH at 24 h postmortem due to treatment, which contradicted the results of Gondret et al. (2006) who observed higher pH in *longissimus* muscle of LBW piglets compared with heavy birth weight piglets but found no difference in *semitendinosus* muscle though the slaughter age and weight of the LBW pigs were 153.9 ± 2.3 days and 101.5 ± 0.6 kg, respectively and LBW pigs required 12 days more to reach the same slaughter weight with their heavy birth weight counterparts. In some previous studies, it was observed that birth weight does not have a significant effect on drip loss and cooking loss (Beaulieu et al., 2010; Rekiel et al., 2014) in agreement with the present results although there are contradictory results from Bee (2004) and Gondret et al. (2005a) found that LBW pork meat had a higher drip loss than NBW piglets. There are reports that demonstrate that LBW piglets have fewer muscle fibers with larger diameters (Hegarty and Allen, 1978; Powell and Aberle, 1981; Gondret et al., 2005a) and Lengerken et al. (1997) claimed that meat from these muscles showed increased drip loss and lower ultimate pH which are generally associated with increased meat toughness (Minelli et al., 1995; Monin et al., 1999).

Beaulieu et al. (2010) observed that birth weight differences in piglets had no significant effect on the color characteristics (L*, a*, b*, chroma and hue values) of the meat, and this result agreed with the present study results. There are other studies that observed increased redness (higher a* values) (Bérard et al., 2008; Rekiel et al., 2014) and increased lightness (higher L* values) when measured at 1-day post-mortem (Gondret et al., 2006) in LBW piglets' *longissimus* muscles. The difference in pork color properties in the previous studies may be due to measurements conducted at different times post-mortem. Choi and Oh (2016) observed that pigs with heavier carcass weights had lower redness (a*) values and ultimate pH at 24 h in *longissimus* muscle compared to pigs with lighter carcass weights. They did not observe any difference between these two carcass

groups in lightness (L*) and yellowness (b*) values. According to Choi and Oh (2016) the higher growth rate associated with heavy carcasses produced larger muscle fiber cross-sectional areas in both types IIA and IIB muscle fibers and muscles had lower ultimate pH values at 24 h post-mortem.

In the present study, the loin WBSF did not show any significant differences between birth weight groups, which was inconsistent with the results of Gondret et al. (2005b) who concluded that LBW piglets produced less tender meat. Gondret et al. (2005b) found that mean muscle fiber diameter was negatively correlated with tenderness and that LBW piglets had a larger mean diameter than NBW pigs. In the present study, the WBSF of *longissimus thoracis* muscle did not differ between LBW and NBW treatments regardless of dietary fat supplementation. This agrees with Bérard et al. (2008) who did not find any differences in WBSF of cooked meat from *longissimus* muscle.

It is now an established idea that the number of total muscle fibers in a muscle is fixed before birth in pigs (Wigmore and Stickland, 1983) although contradiction exists as Mascarello et al. (1992) reported that proliferation of muscle fibers also occurs in the neonatal period. The total muscle fibers number in the whole cross-sectional area of the *longissimus thoracis* muscle was not significantly different due to treatment in the present study. There is evidence that hypertrophy of individual muscle fibers is higher in the post-natal period in muscles with a lower number of muscle fibers (Hegarty and Allen, 1978; Rehfeldt et al., 2000); therefore, differences in muscle fiber characteristics between LBW and NBW pigs were expected. Indeed, previous studies have shown that the mean muscle fiber diameter in the *semitendinosus* and *longissimus* muscles of pigs was higher in LBW compared with NBW at the same market BW (Handel and Stickland, 1987; Bee, 2004; Gondret et al., 2005b) or at the same age (Kuhn et al., 2002). In pig muscle, larger diameter muscle fibers and or a reduced total number of muscle fibers have been suggested to lead to a lower pH (Lengerken et al., 1997). The larger mean diameter of muscle fibers in *longissimus thoracis* muscle of LBW-HFHD piglets compared to NBW-HF agreed with other studies (Hegarty and Allen, 1978; Powell and Aberle, 1981; Gondret et al., 2005a) who found that muscles with a lower number of muscle fibers compensate growth through increased muscle fiber size. Rehfeldt et al. (2000) suggested that hypertrophy of muscle fibers might compensate for the decrease in muscle fiber number. In the present study, the total number of muscle fibers in the cross-sectional area of *longissimus thoracis* muscle did not differ significantly between birth weight treatments,

and this result agrees with other studies (Handel and Stickland, 1987; Dwyer et al., 1993). There is contradictory evidence of LBW piglets having a lower total number of muscle fibers in *longissimus* muscle than NBW piglets (Wigmore and Stickland, 1983; Dwyer and Stickland, 1991; Rehfeldt et al., 2004; Gondret et al., 2005a). It was observed in previous studies (Wigmore and Stickland, 1983; Bee, 2004; Gondret et al., 2006; Rehfeldt et al., 2008; Beaulieu et al., 2010) that LBW (around 1 kg) piglet muscle had a larger mean diameter for slow-twitch-oxidative (type I) muscle fibers similar to the present study. These studies also did not observe any adverse effect on meat quality with an increased mean diameter of type I muscle fibers. This agrees with the present study results. The results of this study confirmed that skeletal muscle mass is determined by the total number of muscle fibers and their cross-sectional areas (Dwyer et al., 1993). It has been reported that small pig fetuses have a reduced number of muscle fibers (Wigmore and Stickland, 1983) but these authors did not confirm that this persisted at slaughter. Moreover, it was shown that muscle fiber type composition is not always correlated with live weight at the time of slaughter, so carcass weight is often used for comparison (Jeong et al. 2012). It has been reported that piglet birth weight has no significant effect on muscle fiber type composition at slaughter weight of pigs (Bee, 2004; Gondret et al., 2005b; Rehfeldt and Kuhn, 2006), and the results of the present study agreed. Gondret et al. (2005b) explained that muscle fiber orientation in *longissimus* muscle is not parallel to the longitudinal direction, making the estimation of total muscle fibers counts crucial or relevant for this muscle. Also, skeletal muscle size is determined not just by the number of total muscle fibers it contains, but also by their combined variable cross-sectional area and length (Dwyer et al., 1993).

Gondret et al. (2006) observed increased insoluble collagen and a tendency for higher total collagen content in the *longissimus thoracis* muscle of LBW pigs compared to NBW pigs. However, there was no difference in collagen heat solubility percentages. Further, these authors did not observe any difference in collagen characteristics in the *semitendinosus* muscle regardless of birth weight. Clelland (2001) however found that *semitendinosus* muscle from LBW piglets in the same litter had a higher proportion of intramuscular connective tissue and Karunaratne et al. (2005) found an increase in collagen content associated with LBW. The present study confirmed that intramuscular collagen content and intramuscular fat were not affected by birth weight. This is an indication that the *longissimus* muscle may be less sensitive to the implications of birth weight than the *semitendinosus* muscle. It might also be that collagen content has no significant effect on

the toughness of pork from young pigs weighing less than 100 kg liveweight at slaughter (Kirkegaard et al., 1979). It is well established that muscle from LBW piglets contains more intramuscular fat and less lean muscle than NBW piglets (Bee, 2004; Poore and Fowden, 2004; Gondret et al., 2005b) which ultimately indicates that LBW piglets are prone to increased non-muscle components in their *semitendinosus* muscle mainly collagen type I and intramuscular fat at 86 days of gestation (Karunaratne et al., 2005). Intramuscular fat and connective tissue cells are the default differentiation pathway when muscle cells cannot form during gestation or the early post-natal period (Kablar et al., 2003). Increased intramuscular fat contents are due to larger mean adipocyte diameter in the skeletal muscle of LBW piglets than in NBW piglets (Powell and Aberle, 1981) although in the present study there was no observed difference in intramuscular fat content. When LBW pigs were fed the high fat diet, intramuscular fat contents increased in LBW pigs compared with NBW pigs (Liu et al., 2014). Other studies indicated that intramuscular fat content was similar among different birth weight pigs at slaughter (Powell and Aberle, 1980; Wolter et al., 2002; Gondret et al., 2005b) and this is consistent with the present study. Compared to NBW piglets, LBW piglets had lower subcutaneous fat depth when slaughtered at the same live weight (Rekiel et al., 2015), which contradicted the present study results, although the LBW-HFHD piglets showed decreased subcutaneous fat depth. Collagen content and intramuscular fat in muscle are important characteristics for the meat industry. An increased amount of collagen may increase meat toughness while higher intramuscular fat may improve meat tenderness (Gondret et al., 2005b; Fang et al., 1999). Discrepancies on the effects of birth weight with previous studies on live weight, carcass parameters, physical properties of meat, chemical composition (proximate and collagen content) probably arise from differences in genotype, birth weight delineation, nutrient composition in the diets, feeding level and fat content and sources of fat in the diet.

Some earlier studies showed that an increase in the mean diameter of muscle fibers has a negative influence on meat quality (Carpenter et al., 1963; Karlsson et al., 1993; Maltin et al., 1997) specifically increasing WBSF and drip loss (Minelli et al., 1995; Monin et al., 1999) but in the present study we did not observe any significant correlation between mean muscle fiber diameter with WBSF ($r = -0.14$) and drip loss ($r = -0.34$). Although there was no effect of birth weight or dietary treatment on meat quality in this study, dietary fat from dairy sources reduced subcutaneous fat depth and increased CLY percentage in LBW piglets that received a diet high in fat from dairy sources (LBW-HDHF) without compromising *longissimus* muscle depth. Rehfeldt and Kuhn

(2006) speculate that lower muscle fiber numbers in LBW piglets result in maximum hypertrophy in muscle fibers before reach to slaughter weight. This might divert available dietary nutrients towards fat storage instead of muscle accretion. LBW pigs have been reported to produce carcasses with excessive fat (Bérard et al., 2010) due to the ratio of protein and energy in diets suitable which is suitable for NBW pigs, but more energy is available for fat deposition in LBW pig muscle (Kerr et al., 2003; Wang et al., 2018). How the source of dietary fat could cause this is unknown, although dairy fat has a high proportion of saturated fats, which have been linked with high satiety (Kozimor et al., 2013). Milk saturated fats have a high proportion of medium chain triacylglycerols (Ruiz-Sala et al., 1996), which are linked to satiety and lower caloric intake in men (St-Onge et al., 2003). Wang et al. (2023) reported that the feed intake of the LBW-HFHD pigs was in fact lower than that of pigs receiving the other diets, confirming that dairy fats decreased feed intake. The inclusion of dairy fats in LBW pig diets may balance feed intake with protein synthesis capacity. This may decrease the amount of energy derived from the diet, reducing carcass fat and increasing lean meat yield. Further investigation of the impact of dietary fat sources on LBW pig growth and carcass quality is warranted in a larger study.

Conclusion

This preliminary study confirmed that LBW piglets exhibit compensatory growth and that growth is associated with hypertrophy of slow-twitch-oxidative (type I) muscle fibers and reflected by mean muscle fiber diameter which is larger in low birth weight groups at slaughter. Effects of birth weight on meat quality were limited, however, indicating that the pork quality is not compromised by low birth weight. Further studies should focus on modifying carcass composition, including decreased back fat thickness in LBW piglets on dairy-sourced high-fat diets.

Conflict of Interest Statement

The authors declare no conflict of interest.

Acknowledgements

The authors wish to thank Sharon Sokolik, Mirielle Pauline, Pamela Wizzard and the University of Alberta Swine Research and Technology Centre for their excellent technical assistance. The

assistance of Dr. Huaigang Lei during carcass dissection is gratefully acknowledged. This research was supported by grants from the Agriculture Funding Consortium, Dairy Farmers of Canada and the Natural Sciences and Engineering Research Council of Canada.

Author Contributions

Bimol C. Roy; Conceptualization, methodology, muscle sampling and meat quality determination, data curation, formal analysis, original draft preparation, review and editing, **Patience Coleman**; Assisted during muscle sampling and meat quality determination, review and editing, **Meghan Markowsky**; Assisted during muscle sampling and meat quality determination, review and editing, **Kun Wang**; Assisted during muscle sampling and meat quality determination, review and editing, **Yongbo She**; Conducted research experiments, review and editing, **Caroline Richard;** Project administration, funding acquisition, conceptualization, review and editing, **Spencer Proctor**; Project administration, funding acquisition, conceptualization, review and editing, **Heather L. Bruce**; Conceptualization, writing, review and editing. All authors have read and agreed to the submitted version of the manuscript.

Ethics Approval

The University of Alberta's Animal Ethics Committee approved all procedures involving animals under protocol number AUP00001184 in 2018, in compliance with the Canada Council on Animal Care (CCAC).

References

Alvarenga ALN, Chiarini-Garcia H, Cardeal PC, Moreira LP, Foxcroft GR, Fontes DO, Almeida FRCL. 2012. Intra-uterine growth retardation affects birthweight and postnatal development in pigs, impairing muscle accretion, duodenal mucosa morphology and carcass traits. Reprod Fertil Dev 25: 387-395.

Anderson GH, Luhovyy B, Akhavan T, Panahi S. 2011. Milk proteins in the regulation of body weight, satiety, food intake and glycemia. In: Milk and milk products in human nutrition. Eds. Clemens, R. A., Hernell, O., and Michaelsen, K. F. Nestlé Ltd., Vevey/S. Karger AG, Basel. Nutritional Institute Workshop Series Pediatric Program, 67: 147-159.

AOAC. (1990). Official methods of analysis of the AOAC, 15th ed. Methods. Association of official analytical chemists. Arlington, VA, USA.

Bates PC, Millward DJ. 1983. Myofibrillar protein turnover. Synthesis rates of myofibrillar and sarcoplasmic protein fractions in different muscles and the changes observed during postnatal development and in response to feeding and starvation. Biochem J 214(2): 587-592.

Bauer R, Walter B, Hoppe A, Gaser E, Lampe V, Kauf E, Zwiener U. 1998. Body weight distribution and organ size in newborn swine (sus scrofa domestica) - a study describing an animal model for asymmetrical intrauterine growth retardation. Exp Toxicol Pathol 50(1): 59-65.

Beaulieu AD, Aalhus JL, Williams NH, Patience, JF. 2010. Impact of piglet birth weight, birth order, and litter size on subsequent growth performance, carcass quality, muscle composition, and eating quality of pork. J Anim Sci 88(8): 2767-2778.

Bee G, Anderson AL, Lonergan SM, Huff-Lonergan E. 2007. Rate and extent of pH decline affect proteolysis of cytoskeletal proteins and water-holding capacity in pork. Meat Sci 76(2): 359-365.

Bee G. 2004. Effect of early gestation feeding, birth weight, and gender of progeny on muscle fiber characteristics of pigs at slaughter. J Anim Sci 82(3): 826-836.

Bérard J, Kreuzer M, Bee G. 2010. In large litters birth weight and gender is decisive for growth performance but less for carcass and pork quality traits. Meat Sci 86(3): 845-851.

Bérard J, Kreuzer M, Bee G. 2008. Effect of litter size and birth weight on growth, carcass and pork quality, and their relationship to postmortem proteolysis. J Anim Sci 86(9): 2357-2368.

Bergman I, Loxley R. 1963. Two improved and simplified methods for the spectrophotometric determination of hydroxyproline. Anal Chem 35(12): 1961-1965.

Bispham J, Gardner DS, Gnanalingham MG, Stephenson T, Symonds ME, Budge H. 2005. Maternal nutritional programming of fetal adipose tissue development: differential effects on messenger ribonucleic acid abundance for uncoupling proteins and peroxisome proliferator-activated and prolactin receptors. Endocrinol 146(9): 3943-3949.

Bispham J, Gopalakrishnan GS, Dandrea J, Wilson V, Budge H, Keisler DH, Broughton Pipkin F, Stephenson T, Symonds ME. 2003. Maternal endocrine adaptation throughout pregnancy to nutritional manipulation: consequences for maternal plasma leptin and cortisol and the programming of fetal adipose tissue development. Endocrinol 144(8): 3575-3585.

Brooke MH, Kaiser KK. 1970. Muscle fiber types: how many and what kind? Arch Neurol 23(4): 369-379.

Carpenter, Z. L., Kauffman, R. G., Bray, R. W., Briskey, E. J., and Weckel, K. G. (1963). Factors Influencing Quality in Pork A. Histological Observations. J Food Sci 28(4): 467-471.

Cho, W. K., and Suh, B. K. (2016). Catch-up growth and catch-up fat in children born small for gestational age. Korean J Pediatr 59(1): 1-7.

Choi YM, Oh HK. 2016. Carcass performance, muscle fiber, meat quality, and sensory quality characteristics of crossbred pigs with different live weights. Korean J Food Sci Anim Resour 36(3): 389-396.

Clelland A. 2001. Intra-litter variation in early porcine muscle development. Ph D thesis, The Royal Veterinary College, University of London.

Commission International de l'Eclairage (1986) Colorimetry. 2nd Edition. Commission International de l'Eclairage (CIE), Publication CIE 15.2, Wien.

Crume TL, Scherzinger A, Stamm E, McDuffie R, Bischoff KJ, Hamman RF, Dabelea D. 2014. The long-term impact of intrauterine growth restriction in a diverse U.S. cohort of children: the EPOCH study. Obes 22(2): 608-615.

Douglas SL, Edwards SA, Sutcliffe E, Knap PW, Kyriazakis I. 2013. Identification of risk factors associated with poor lifetime growth performance in pigs. J Anim Sci 91(9): 4123-4132.

Dwyer CM, Stickland NC. 1991. Sources of variation in myofibre number within and between litters of pigs. Anim Prod 52(3): 527-533.

Dwyer CM, Fletcher JM, Stickland NC. 1993. Muscle cellularity and postnatal growth in the pig. J Anim Sci 71(12): 3339-3343.

Ezekwe MO, Martin RJ. 1975. Cellular characteristics of skeletal muscle in selected strains of pigs and mice and the unselected controls. Growth 39(1): 95-106.

Fang SH, Nishimura T, Takahashi K. 1999. Relationship between development of intramuscular connective tissue and toughness of pork during growth of pigs. J Anim Sci 77(1): 120-130.

Fontaine MA, Diane A, Singh VP, Mangat R, Krysa JA, Nelson R, Willing BP, Proctor SD. 2019. Low birth weight causes insulin resistance and aberrant intestinal lipid metabolism independent of microbiota abundance in Landrace-Large White pigs. FASEB J 33(8): 9250-9262.

Imamura F, Fretts A, Marklund M, Ardisson Korat AV, Yang WS, Lankinen M, Qureshi W, Helmer C, Chen TA, Wong K, Bassett JK, Murphy R, Tintle N, Yu CI, Brouwer IA, Chien KL, Frazier-Wood AC, Del Gobbo LC, Djoussé L, Geleijnse JM, Giles GG, de Goede J, Gudnason V, Harris WS, Hodge A, Hu F; InterAct Consortium; Koulman A, Laakso M, Lind L, Lin HJ, McKnight B, Rajaobelina K, Risérus U, Robinson JG, Samieri C, Siscovick DS, Soedamah-Muthu SS, Sotoodehnia N, Sun Q, Tsai MY, Uusitupa M, Wagenknecht LE, Wareham NJ, Wu JH, Micha R, Forouhi NG, Lemaitre RN, Mozaffarian D. 2018. Fatty Acids and Outcomes Research Consortium (FORCE). Fatty acid biomarkers of dairy fat consumption and incidence of type 2 diabetes: A pooled analysis of prospective cohort studies. PLoS Med. 15(10): e1002670.

Gondret F, Lefaucheur L, Juin H, Louveau I, Lebret B. 2006. Low birth weight is associated with enlarged muscle fiber area and impaired meat tenderness of the longissimus muscle in pigs. J Anim Sci 84(1): 93-103.

Florence Gondret, Louis L. Lefaucheur, Isabelle Louveau, Bénédicte Lebret.

Gondret F, Louis L, Lefaucheur L, Louveau, I, Lebret B. 2005a. The long-term influences of birth weight on muscle characteristics and eating meat quality in pigs individually reared and fed during fattening. Archiv für Tierzucht 48: 68-73.

Gondret F, Lefaucheur L, Louveau I, Lebret B, Pichodo X, Le Cozler Y. 2005b. Influence of piglet birth weight on postnatal growth performance, tissue lipogenic capacity, and muscle histological traits at market weight. Livest Prod Sci 93(2): 137-146.

Greenwood PL, Slepetis RM, Hermanson JW, Bell AW. 1999. Intrauterine growth retardation is associated with reduced cell cycle activity, but not myofibre number, in ovine fetal muscle. Reprod Fertil Dev 11(4-5): 281-291.

Handel SE, Stickland NC. 1987. The growth and differentiation of porcine skeletal muscle fibre types and the influence of birthweight. J Anat 152: 107-119.

Hegarty PV, Allen CE. 1978. Effect of pre-natal runting on the post-natal development of skeletal muscles in swine and rats. J Anim Sci 46(6): 1634-1640.

Heyer A, Andersson HK, Linberg JE, Lundstrom K. 2004. Effect of extra maternal feed supply in early gestation on sow and piglet performance and production and meat quality of growing/ /finishing pigs. Acta Agric Scand A Anim Sci 54: 44-55.

Hill F. 1966. The solubility of intramuscular collagen in meat animals of various ages. J Food Sci 31(2): 161-166.

Honikel KO, Hamm R. 1994. Measurement of water-holding capacity and juiciness. In: Pearson A. M., Dutson T. R. (eds) Quality Attributes and their Measurement in Meat, Poultry and Fish Products. Advances in Meat Research, vol 9. Springer, Boston, MA.

Ibáñez L, Lopez-Bermejo A, Diaz M, and de Zegher F. 2011. Catch-up growth in girls born small for gestational age precedes childhood progression to high adiposity. Fertil Steril 96(1): 220-223.

Jeong JY, Kim GD, Ha DM, Park M J, Park BC, Joo ST, Lee CY. 2012. Relationships of Muscle Fiber Characteristics to Dietary Energy Density, Slaughter Weight, and Muscle Quality Traits in Finishing Pigs. J Anim Sci Technol 54(3): 175-183.

Kablar B, Krastel K, Tajbakhsh S, Rudnicki MA. 2003. Myf5 and MyoD activation define independent myogenic compartments during embryonic development. Dev Biol 258(2): 307-318.

Kalbe C, Lösel D, Block J, Lefaucheur L, Brüssow KP, Bellmann O, Pfuhl R, Puppe B, Otten W, Metges CC, Rehfeldt C. 2017. Moderate high or low maternal protein diets change gene expression but not the phenotype of skeletal muscle from porcine fetuses. Domest Anim Endocrin 58: 63-75.

Karlsson A, Enfält AC, Essén-Gustavsson B, Lundström K, Rydhmer L, Stern S. 1993. Muscle histochemical and biochemical properties in relation to meat quality during selection for increased lean tissue growth rate in pigs. J Anim Sci 71(4): 930-938.

Karunaratne JF, Ashton CJ, Stickland NC. 2005. Fetal programming of fat and collagen in porcine skeletal muscles. J Anat 207(6): 763-768.

Kelly FJ, Lewis SE, Anderson P, Goldspink DF. 1984. Pre- and postnatal growth and protein turnover in four muscles of the rat. Muscle Nerve 7(3): 235-242.

Kerr BJ, Southern LL, Bidner TD, Friesen KG, Easter RA. 2003. Influence of dietary protein level, amino acid supplementation, and dietary energy levels on growing-finishing pig performance and carcass composition. J Anim Sci 81(12): 3075-3087.

Kirkegaard E, Moller AJ, Wismer-Pedersen J. 1979. Relationship between fat content, connective tissue and objective tenderness measurements in porcine longissimus dorsi. 25th European Meeting Meat Research. Workers, Budapest, 2: 311-317.

Kozimor A, Chang H, Cooper JA. 2013. Effects of dietary fatty acid composition from a high fat meal on satiety. Appetite, 69: 39-45.

Kuhn G, Rehfeldt C, Hartung M, Ender K. 2002. Heavy newborn piglets develop a high carcass quality. Fleischwirtschaft-Frankfurt, 82(9): 128-129.

Laurent GJ, Sparrow MP, Bates PC, Millward DJ. 1978. Turnover of muscle protein in the fowl (Gallus domesticus). Rates of protein synthesis in fast and slow skeletal, cardiac and smooth muscle of the adult fowl. Biochem J 176(2): 393-401.

Lawrence T, Fowler V, Novakofski J. 2012. Growth of Farm Animals, 3rd Edn. Oxford: CABI. Prenatal and postnatal growth in mammals. In: Lawrence, T. L. J., Fowler, V. R., Novakofski, J. E. chapter 11 pp. 225.

Lebret B, Lefaucheur L, Mourot J. 1999. La qualité de la viande de porc. Influence des facteurs d'élevage non génétiques sur les caractéristiques du tissu musculaire. Productions animales, Institut National de la Recherche Agronomique 12(1): 11-28.

Lefaucheur L, Ecolan P, Barzic YM, Marion J, Le Dividich J. 2003. Early postnatal food intake alters myofiber maturation in pig skeletal muscle. J Nutr 133(1): 140-147.

Lefaucheur L, Edom F, Ecolan P, Butler-Browne GS. 1995. Pattern of muscle fiber type formation in the pig. Dev Dyn 203(1): 27-41.

Lengerken GV, Wicke M, Maak S. 1997. Stress susceptibility and meat quality-situation and prospects in animal breeding and research. Arch Anim Breed 40 (Suppl.): 163-171.

Liu J, He J, Yu J, Mao X, Zheng P, Huang Z, Yu B, Chen D. 2014. Birth weight alters the response to postnatal high-fat diet-induced changes in meat quality traits and skeletal muscle proteome of pigs. Br J Nutr 111(10): 1738-1747.

Luff AR, Goldspink G. 1970. Total number of fibers in muscles of several strains of mice. J Anim Sci 30(6): 891-893.

Mahan DC, Lepine AJ. 1991. Effect of pig weaning weight and associated nursery feeding programs on subsequent performance to 105 kilograms body weight. J Anim Sci 69(4): 1370-1378.

Maltin CA, Warkup CC, Matthews KR, Grant CM, Porter AD, Delday MI. 1997. Pig muscle fiber characteristics as a source of variation in eating quality. Meat Sci 47(3/4): 237-248.

Mascarello F, Stecchini ML, Rowlerson A, Ballocchi E. 1992. Tertiary myotubes in postnatal growing pig muscle detected by their myosin isoform composition. J Anim Sci 70(6): 1806-1813.

McGilchrist P, Greenwood PL, Pethick DW, Gardner GE. 2016. Selection for increased muscling in Angus cattle did not increase the glycolytic potential or negatively impact pH decline, retail colour stability or mineral content. Meat Sci 114: 8-17.

Miller LR, Ganvood VA, Judge MD. 1975. Factors affecting porcine muscle fiber type, diameter and number. J Anim Sci 41(1): 66-77.

Milligan BN, Fraser D, Kramer DL. 2002. Within-litter birth weight variation in the domestic pig and its relation to pre-weaning survival, weight gain, and variation in weaning weights. Livest Prod Sci 76(1): 181-191.

Minelli G, Culioli J, Vignon X, Monin G. 1995. Postmortem changes in the mechanical properties and ultrastructure of the longissimus in two porcine breeds. Journal of Muscle Foods, 6(4), 313-326.

Monin G, Larzul C, Le Roy P, Culioli J, Mourot J, Rousset-Akrim S, Talmant A, Touraille C, Sellier P. 1999. Effects of the halothane genotype and slaughter weight on texture of pork. J Anim Sci 77(2): 408-415.

Morise A, Louveau I, Le Huërou-Luron I. 2008. Growth and development of adipose tissue and gut and related endocrine status during early growth in the pig: impact of low birth weight. Animal 2(1): 73-83.

Père MC, Etienne M. 2000. Uterine blood flow in sows: effects of pregnancy stage and litter size. Reprod Nutr Dev 40(4): 369-382.

Picard B, Lefaucheur L, Berri C, Duclos MJ. 2002. Muscle fibre ontogenesis in farm animal species. Reprod Nutr Dev 42(5): 415-431.

Pomar C, Marcoux M. 2003. Comparing the Canadian pork lean yields and grading indexes predicted from grading methods based on Destron and Hennessy probe measurements. Can J Anim Sci 83(3): 451-458.

Poore KR, Fowden AL. 2004. The effects of birth weight and postnatal growth patterns on fat depth and plasma leptin concentrations in juvenile and adult pigs. J Physiol 558(Pt 1): 295-304.

Powell SE, Aberle ED. 1981. Skeletal muscle and adipose tissue cellularity in runt and normal birth weight swine. J Anim Sci 52(4): 748-756.

Powell SE, Aberle ED. 1980. Effects of birth weight on growth and carcass composition of swine. J Anim Sci 50(5): 860-868.

Quiniou N, Dagorn J, Gaudré D. 2002. Variation of piglets' birth weight and consequences on subsequent performance. Livest Prod Sci 78(1): 63-70.

Rehfeldt C, Tuchscherer A, Hartung M, Kuhn G. 2008. A second look at the influence of birth weight on carcass and meat quality in pigs. Meat Sci 78(3): 170-175.

Rehfeldt C, Kuhn G. 2006. Consequences of birth weight for postnatal growth performance and carcass quality in pigs as related to myogenesis. J Anim Sci 84(Suppl): E113-E123.

Rehfeldt C, Fiedler I, Stickland NC. 2004. Number and size of muscle fibres in relation to meat production. M. F. W. Te Pas, M. E. Everts, H. P. Haagsman (Eds.), Muscle Development of Livestock Animals: Physiology, Genetics, and Meat Quality, CAB Int., Wallingford, Oxon, UK. 1-37.

Rehfeldt C, Fiedler I, Dietl G, Ender K. 2000. Myogenesis and postnatal skeletal muscle cell growth as influenced by selection. Livest Prod Sci 66(2): 177-188.

Rekiel A, Więcek J, Batorska M, Kulisiewicz J. 2015. Effect of Piglet Birth Weight on Carcass Muscle and Fat Content and Pork Quality - A Review. Ann Anim Sci 15(2): 271-287.

Rekiel A, Bartosik J, Więcek J, Batorska M, Kuczyńska B, Łojek A. 2014. Effect of piglet birth weight on selected characteristics of pork. Ann Anim Sci 14: 967-975.

Rosenvold K, Andersen HJ. 2003. Factors of significance for pork quality-a review. Meat Sci 64(3): 219-237.

Roy BC, Walker BB, Rahman MM, Bruce HH, McMullen L. 2018. Role of myofibers, perimysium and adipocytes in horse meat toughness, Meat Sci 146: 109-121.

Ruiz-Sala P, Hierro MTG, Martínez-Castro I, Santa-María G. 1996. Triglyceride composition of ewe, cow, and goat milk fat. JAOCS 73: 283-293.

Rutherford KM, Baxter EM, D'Eath RB, Turner SP, Arnott G, Roehe R, Ask B, Sandøe P, Moustsen VA, Thorup F, Edwards SA, Berg PB, Lawrence AB. 2013. The welfare implications of large litter size in the domestic pig I: biological factors. Anim Welf 22: 199-218.

She Y, Wang K, Makarowski A, Mangat R, Tsai S, Willing BP, Proctor SD, Richard C. 2022. Effect of high-fat and low-fat dairy products on cardiometabolic risk factors and immune function in a low birthweight swine model of diet-induced insulin resistance. Front Nutr 9: 923120.

Stange K, Miersch C, Sponder G, Röntgen M. 2020. Low birth weight influences the postnatal abundance and characteristics of satellite cell subpopulations in pigs. Sci Rep 10: 6149.

Stanton C, Light N. 1987. The effects of conditioning on meat collagen: Part 1- evidence for gross in situ proteolysis. Meat Sci 21: 249-265.

St-Onge MP, Ross R, Parsons WD, Jones PJH. 2003. Medium-chain triglycerides increase energy expenditure and decrease adiposity in overweight men. Obes Res 11: 395-402.

Symonds ME, Gopalakrishnan G, Bispham J, Pearce S, Dandrea J, Mostyn A, Ramsay MM, Stephenson T. 2003. Maternal nutrient restriction during placental growth, programming of fetal adiposity and juvenile blood pressure control. Arch Physiol Biochem 111(1): 45-52.

Teixeira A, Silva SR, Hasse M, Almeida J, Dias L. 2021. Intramuscular Fat Prediction Using Color and Image Analysis of Bísaro Pork Breed. Foods (Basel, Switzerland), 10(1): 143.

Thiex NJ, Anderson S, Gildemeister B. 2003. Crude fat, hexanes extraction, in feed, cereal grain, and forage (Randall/Soxtec/submersion method): collaborative study. J AOAC Int 86(5): 899-908.

Wang Y, Zhou J, Wang G, Cai S, Zeng X, Qiao S. 2018. Advances in low-protein diets for swine. J Anim Sci Biotechnol 9: 60.

Wang K, She Y, Mangat R, Alexander Makarowski A, Roy BC, Bruce HL, Dyck MK, Richard C, Proctor SD. 2023. Preferential deposition of dairy derived fatty acids in muscle tissue is partially due to the upregulation of CD36 in a low-birth-weight swine model. J Anim Sci 101: skad113.

Wank V, Bauer R, Walter B, Kluge H, Fischer MS, Blickhan R, Zwiener U. 2000. Accelerated contractile function and improved fatigue resistance of calf muscles in newborn piglets with IUGR. Am J Physiol Regul Integr Comp Physiol 278(2): R304-R310.

Ward SS, Stickland NC. 1991. Why are slow and fast muscles differentially affected during prenatal under nutrition? Muscle Nerve 14(3): 259-267.

Wigmore PM, Stickland NC. 1983. Muscle development in large and small pig fetuses. J Anat 137(Pt 2): 235-245.

Wolter BF, Ellis M. 2001. The effects of weaning weight and rate of growth immediately after weaning on subsequent pig growth performance and carcass characteristics. Can J Anim Sci 81(3): 363-369.

Wolter BF, Ellis M, Corrigan BP, DeDecker JM. 2002. The effect of birth weight and feeding of supplemental milk replacer to piglets during lactation on preweaning and postweaning growth performance and carcass characteristics. J Anim Sci 80(2): 301-308.

Yates DT, Macko AR, Nearing M, Chen X, Rhoads RP, Limesand SW. 2012. Developmental programming in response to intrauterine growth restriction impairs myoblast function and skeletal muscle metabolism. J Pregnancy 2012: 631038.

Zhang L, Wang Y, Kong Y, Ahmad H, Yan R, Dong L, Zhang J, Wang T. 2018. Effects of Intrauterine Growth Retardation on Growth, Meat Quality and Muscle Fiber Composition of Pigs. Pak J Zool 50(3): 1137-1146.

Table 1. Live weight (kg) of piglets at birth and weekly with increasing age in different treatment birth weight groups

Age (Weeks)	Treatment groups				P-value
	NBW-C (kg)	NBW-HF (kg)	LBW-HF (kg)	LBW-HFHD (kg)	
n	**5**	**6**	**8**	**5**	
At birth	1.62 ± 0.07a	1.73 ± 0.09a	1.29 ± 0.08b	1.18 ± 0.06b	0.0003
1	2.94 ± 0.30 ab	3.57 ± 0.39a	2.50 ± 0.33ab	2.10 ± 0.16b	0.0351
2	4.5 ± 0.34ab	5.52 ± 0.59a	3.75 ± 0.49b	3.74 ± 0.21ab	0.0470
3	6.58 ± 0.29ab	7.52 ± 0.43a	5.65 ± 0.57b	5.36 ± 0.40b	0.0234
4	9.08 ± 0.74ab	9.95 ± 0.42a	7.31 ± 0.81b	6.24 ± 0.13b	0.0045
5	11.22 ± 1.23xy	13.05 ± 1.17x	9.51 ± 1.03y	8.90 ± 0.32y	0.0502
6	14.44 ± 1.57	15.33 ± 1.70	12.51 ± 1.46	12.40 ± 0.52	0.4237
7	19.60 ± 1.64	21.52 ± 1.87	16.91 ± 1.90	15.70 ± 0.70	0.1252
8	25.92 ± 2.03xy	28.87 ± 2.10x	23.95 ± 2.02y	21.12 ± 1.23y	0.0884
9	32.36 ± 2.08xy	35.38 ± 2.21x	29.57 ± 2.40xy	26.82 ± 1.10y	0.0788
10	37.66 ± 2.27xy	43.48 ± 2.54x	37.08 ± 2.73xy	32.54 ± 1.21y	0.0537
11	42.78 ± 2.93	46.85 ± 2.29	41.59 ± 2.71	37.34 ± 1.25	0.1223
12	48.44 ± 2.23xy	53.62 ± 1.97x	48.10 ± 2.05xy	45.64 ± 1.22y	0.0960

Data represents Mean ± standard error (SE)

Different letters (a, b) in the same row are significantly different in different animal groups at the 0.05 level of probability ($P < 0.05$).

Different letters (x, y) in the same row indicate differences approached significance ($0.10 > P > 0.05$) in different animal groups

NBW = Normal birth weight; LBW = Low birth weight; C = Control (chow diet); HF = High fat diet; HFHD = High fat dairy source

The dark shaded area of the table shows that the transitional diet was provided

The light shaded area of the table shows that the experimental diets were provided

Table 2. Effect of birth weight of piglets on carcass characteristics of pork at 24 h post-mortem

Parameters	Treatment groups				P-value
	NBW-C	NBW-HF	LBW-HF	LBW-HFHD	
n	**5**	**6**	**8**	**5**	
Hot carcass weight (kg)	37.08 ± 2.40xy	40.77 ± 2.27x	36.26 ± 1.49xy	33.44 ± 2.40y	0.0615
Cold carcass weight (kg)	34.84 ± 2.66	39.07 ± 2.52	35.23 ± 1.65	33.26 ± 2.66	0.2248
Carcass length (cm)**	77.50 ± 2.18	79.68 ± 2.06	75.78 ± 1.35	76.00 ± 2.18	0.2749
Subcutaneous fat depth (cm)	1.21 ± 0.17bc	1.45 ± 0.16ab	1.40 ± 0.10ab	0.90 ± 0.17c	0.0229
Longissimus thoracis muscle depth (cm)	3.76 ± 0.42	4.62 ± 0.39	4.56 ± 0.26	4.56 ± 0.42	0.1925
Longissimus thoracis muscle area (cm^2)	11.56 ± 2.73	17.18 ± 2.59	15.36 ± 1.70	19.03 ± 2.73	0.1140
Canadian lean yield (CLY, %)	62.51 ± 0.82ab	61.69 ± 0.78b	62.00 ± 0.52b	64.79 ± 0.82a	0.0085
Dressing (%) on HCW basis	73.57 ± 2.81	76.17 ± 2.66	72.37 ± 1.74	73.28 ± 2.81	0.5592
Pork shoulder weight (%) on HCW basis	29.99 ± 2.11	30.12 ± 2.00	26.88 ± 1.31	27.50 ± 2.11	0.3083
Pork leg weight (%) on HCW basis	21.70 ± 3.10b	22.99 ± 2.94ab	29.22 ± 1.93ab	31.97 ± 3.10a	0.0148
Pork loin weight (%) on HCW basis	25.33 ± 1.64	25.08 ± 1.56	22.27 ± 1.02	22.79 ± 1.64	0.1773
Pork belly weight (%) on HCW basis	16.77 ± 0.81	17.52 ± 0.77	18.01 ± 0.50	17.20 ± 0.81	0.4824

Data represents Mean ± standard error (SE)

Different letters (a, b, c) in the same row are significantly different in different animal groups at the 0.05 level of probability ($P < 0.05$).

Different letters (x, y) in the same row indicate differences approached significance ($0.10 > P > 0.05$) in different animal groups

NBW = Normal birth weight; LBW = Low birth weight; C = Control (chow diet); HF = High fat diet; HFHD = High fat dairy source

HCW = Hot carcass weight

** Carcass length was measured from the first cervical vertebrae bone atlas to base of the tail.

Table 3. Physical properties of pork from *Longissimus thoracis* muscle at 24 h post-mortem from different birth weight groups

Parameters	Treatment groups				P-value
	NBW-C	NBW-HF	LBW-HF	LBW-HFHD	
n	**5**	**6**	**8**	**5**	
CIE L*	50.17 ± 1.27	53.41 ± 1.20	52.12 ± 0.79	52.83 ± 1.27	0.1311
CIE a*	8.14 ± 0.48	8.32 ± 0.46	8.25 ± 0.30	8.08 ± 0.48	0.9649
CIE b*	0.95 ± 0.49y	1.54 ± 0.46xy	1.53 ± 0.30xy	2.52 ± 0.49x	0.0587
Chroma values	8.21 ± 0.51	8.56 ± 0.49	8.44 ± 0.32	8.42 ± 0.51	0.9331
Hue values	6.59 ± 3.08	10.34 ± 2.92	9.98 ± 1.91	15.03 ± 3.08	0.1359
Ultimate pH at 24 h postmortem	5.53 ± 0.06	5.52 ± 0.05	5.47 ± 0.03	5.52 ± 0.06	0.6784
Drip loss (%)	1.87 ± 0.95y	4.40 ± 0.90x	3.43 ± 0.59xy	2.54 ± 0.95x	0.0985
Cooking loss (%)	19.91 ± 1.86	18.02 ± 1.76	18.60 ± 1.15	16.82 ± 1.86	0.5138
Warner-Bratzler shear force (N)	31.86 ± 3.43	25.94 ± 3.25	30.94 ± 2.13	26.55 ± 3.43	0.2595

Data represents Mean ± standard error (SE)

Different letters (x, y) indicate tendency (0.10 > P > 0.05) in different animal groups

NBW = Normal birth weight; LBW = Low birth weight; C = Control (chow diet); HF = High fat diet; HFHD = High fat dairy source

Table 4. Proximate composition and collagen content of pork from *Longissimus thoracis* muscle at 24 h post-mortem from different birth weight groups

Parameters	Treatment groups				P-value
	NBW-C	NBW-HF	LBW-HF	LBW-HFHD	
n	**5**	**6**	**8**	**5**	
Crude protein (%)	20.97 ± 0.26	21.12 ± 0.25	21.08 ± 0.16	20.86 ± 0.26	0.7955
Moisture (%)	75.82 ± 0.33a	74.67 ± 0.32b	74.89 ± 0.21b	75.11 ± 0.33ab	0.0229
Crude fat (%)	1.59 ± 0.37	2.40 ± 0.35	2.38 ± 0.23	2.51 ± 0.37	0.1213
Ash (%)	1.17 ± 0.03	1.12 ± 0.03	1.16 ± 0.02	1.17 ± 0.03	0.2375
Total collagen (mg/ g raw meat)	3.57 ± 0.50	3.20 ± 0.47	2.72 ± 0.31	2.40 ± 0.50	0.1764
Insoluble collagen (mg / g raw meat)	2.36 ± 0.41	2.27 ± 0.39	1.86 ± 0.25	1.71 ±0.41	0.3873
Soluble collagen (mg / g raw meat)	1.21 ± 0.17x	0.93 ± 0.16xy	0.86 ± 0.10xy	0.69 ± 0.17y	0.0673
Collagen solubility (%)	35.24 ± 1.45	28.87 ± 4.22	31.62 ± 2.76	28.63 ± 4.45	0.5035

Data represents Mean ± standard error (SE)

Different letters (a, b) in the same row are significantly different in different animal groups at the 0.05 level of probability ($P < 0.05$).

Different letters (x, y) in the same row showed a tendency in different animal groups at the 0.05 level of probability ($P > 0.05$)

NBW = Normal birth weight; LBW = Low birth weight; C = Control (chow diet); HF = High fat diet; HFHD = High fat dairy source

Table 5. Muscle fiber characteristics in the *Longissimus thoracis* muscle at 24 hours post-mortem in piglets of different birth weight groups

Parameters	Treatment groups				P-value
	NBW-C	NBW-HF	LBW-HF	LBW-HFHD	
n	**5**	**6**	**7**	**5**	
Total muscle fibers in loin muscle area	79152 ± 20129	128875 ± 19125	87888 ±12993	95396 ± 20129	0.1073
Type I muscle fibers (%)	10.32 ± 2.10	9.27 ± 2.00	9.66 ± 1.36	6.05 ± 2.10	0.2642
Type IIA muscle fibers (%)	16.40 ± 3.10	19.04 ± 2.95	17.00 ± 2.00	18.03 ± 3.10	0.8436
Type IIB muscle fibers (%)	73.28 ± 3.41	71.69 ± 3.24	73.34 ± 2.20	75.92 ± 3.41	0.6970
Mean muscle fibers diameter (µm)	42.57 ± 2.80b	39.833 ± 2.66b	46.757 ± 1.81ab	51.032 ± 2.80a	0.0057
Type I muscle fibers diameter (µm)	38.86 ± 2.67ab	37.36 ± 2.54b	43.21 ± 1.73ab	44.86 ± 2.67a	0.0401
Type IIA muscle fibers diameter (µm)	38.91 ± 3.06	36.30 ± 2.90	39.38 ± 1.97	40.85 ± 3.06	0.5379
Type IIB muscle fibers diameter (µm)	49.94 ± 3.19	45.85 ± 3.03	51.09 ± 2.06	53.25 ± 3.19	0.1723

Data represents Mean ± standard error (SE)

Different letters (a, b) in the same row are significantly different in different animal groups at the 0.05 level of probability ($P < 0.05$).

NBW = Normal birth weight; LBW = Low birth weight; C = Control (chow diet); HF = High fat diet; HFHD = High fat dairy source

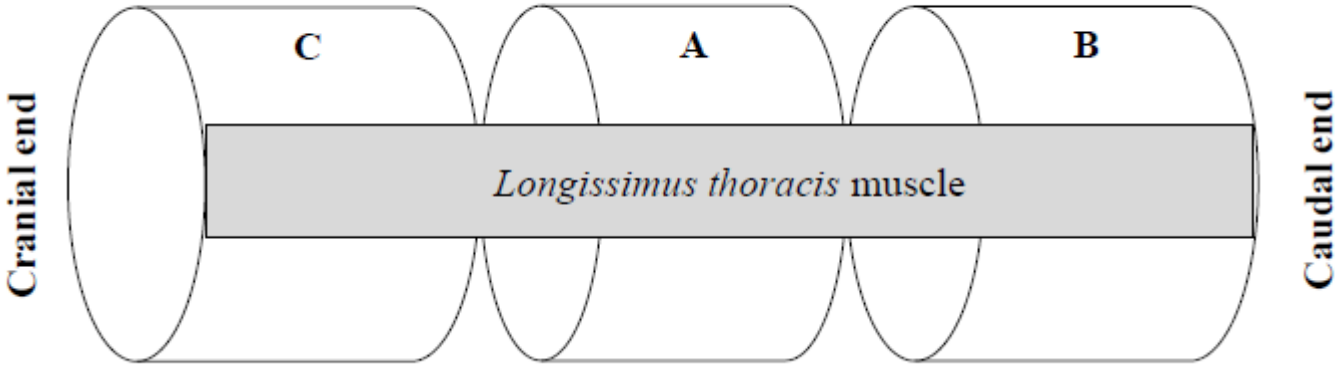

Fig.1. Breakdown of *Longissimus thoracis* muscle from the right side of pork carcasses for meat quality characteristics determination at 24 hours post-mortem. One chop (about 2.54 cm) (A) was utilized for calculating the *Longissimus* muscle area from subcutaneous (backfat) fat depth, and muscle depth measurement, and objective meat color and drip loss determination. The other chop (B) was used for cooking, measuring cooking loss, and determining Warner-Bratzler shear force. Muscle cubes from the center of the third chop (C) were sampled for muscle fiber characterization, thereafter the epimysium was removed from the chop, cut into small cubes, lyophilized, ground, and used for proximate composition and collagen solubility determination.

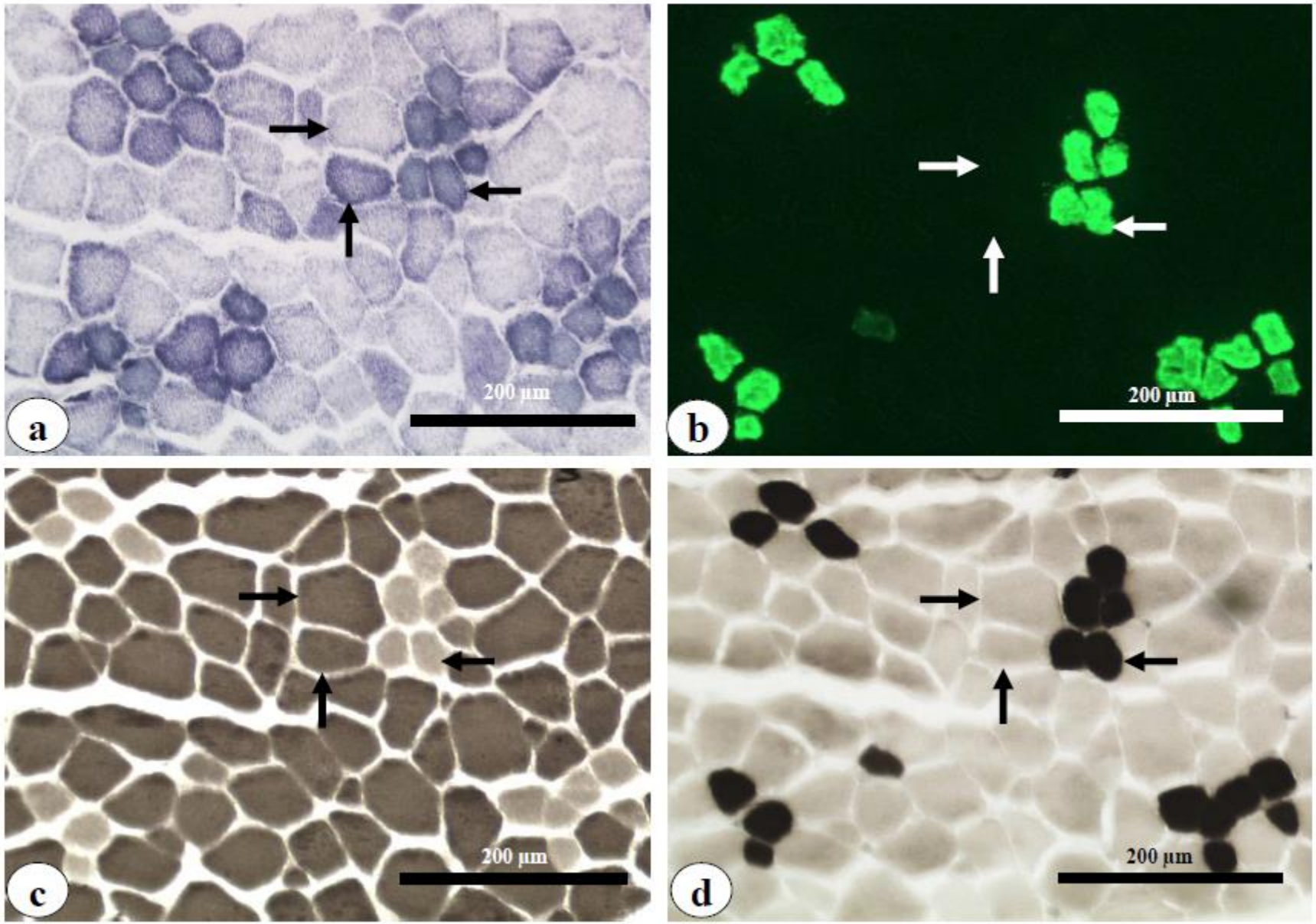
a
200 µm
b
200 µm
c
200 µm
d
200 µm

Fig. 2. Histochemistry and immunohistochemistry of muscle fibers typing in muscle serial sections from *Longissimus thoracis* of pork (a) NADH-TR; (b) myosin heavy chain type I primary antibody S58 and Alexa fluor488 green secondary antibody; (c) myosin ATPase activity after alkaline pre-incubation (pH 10.5) and (d) after acid pre-incubation (pH 4.3). Three types of muscle fibers were identified namely fast-twitch-glycolytic (IIB), fast-twitch-oxidative-glycolytic (IIA) and slow-twitch-oxidative (type I) indicated by right arrow, up arrow and left arrow, respectively. Bars = 200 µm.

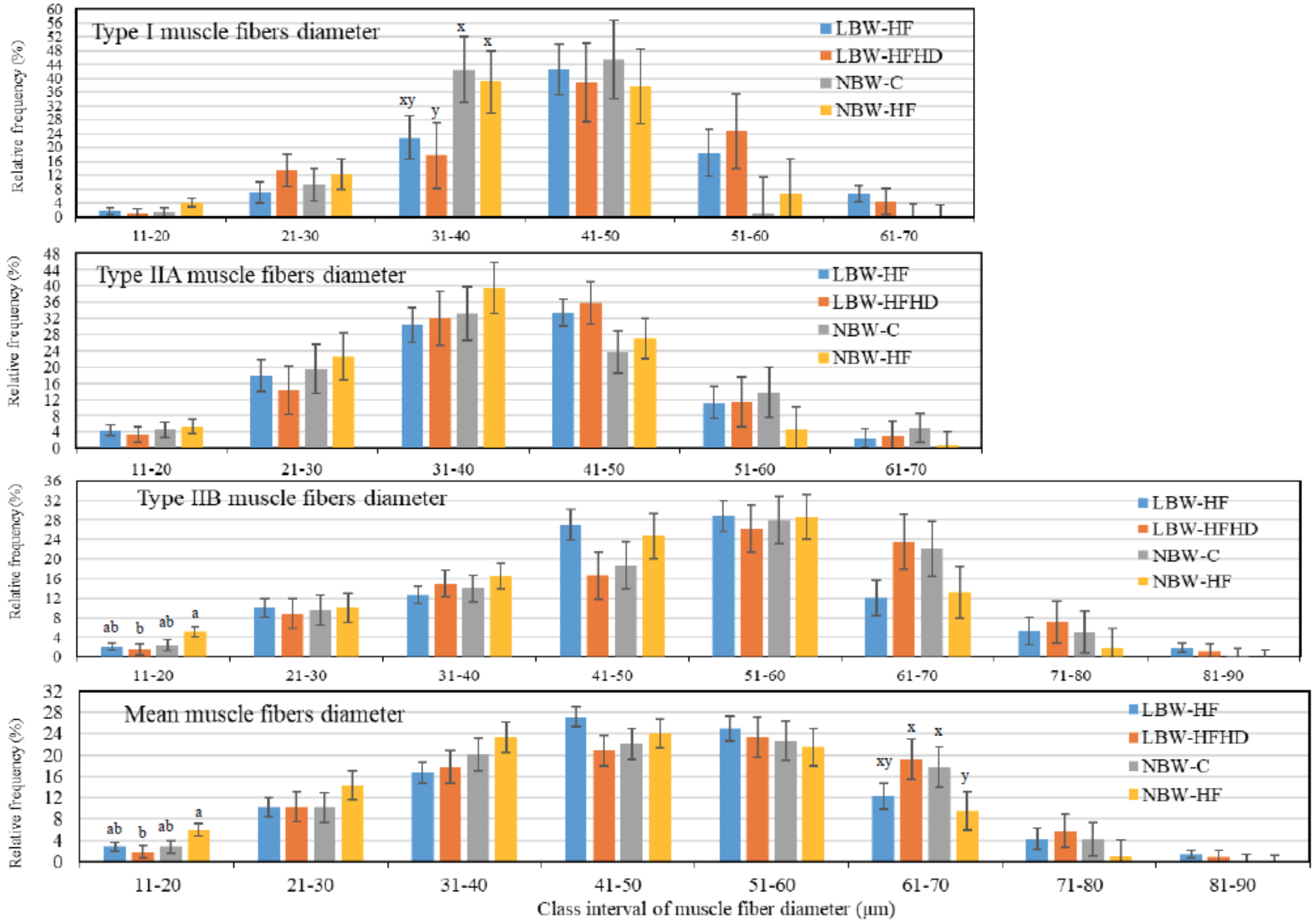
Type I muscle fibers diameter
Type IIA muscle fibers diameter
Type IIB muscle fibers diameter
Mean muscle fibers diameter
LBW-HF
LBW-HFHD
NBW-C
NBW-HF
Relative frequency (%)
11-20
21-30
31-40
41-50
51-60
61-70
71-80
81-90
Class interval of muscle fiber diameter (μm)

Fig. 3. The relative frequency of types I, IIA, IIB and mean fiber diameters of *Longissimus thoracis* muscle among pig carcasses of various birth weight groups. The different letters (a, b) indicate significance ($P < 0.05$) in the same class interval within muscle fiber type, whereas the different letters (x, y) indicate differences approaching significance ($0.10 > P > 0.05$) in the same class interval within muscle fiber type. The error bars indicate the standard error of the mean.