DE GRUYTER
OPEN

J Vet Res 60, 301-307, 2016
DOI:10.1515/jvetres-2016-0046

Influence of post-mortem muscle glycogen content on the quality of beef during aging

Anna Onopiuk, Andrzej Półtorak, Agnieszka Wierzbicka

Department of Technique and Food Development, Faculty of Human Nutrition and Consumer Sciences, Warsaw University of Life Sciences, 02-776 Warsaw, Poland
anna_onopiuk@sggw.pl

Received: March 20, 2016 *Accepted: September 2, 2016*

Abstract

Introduction: Glycolic changes which occur post-mortem have an impact on the physical and sensory features of beef, which in turn determine the successive processes and influence such beef quality traits as colour, tenderness, and cooling loss. The aim of this study was evaluation of the post-mortem changes in bovine meat during aging, quantitative analysis of glycogen and lactic acid, as well as examination of their impact on technological and sensory quality of selected muscles from Holstein-Friesian × Limousin breed carcasses. **Material and Methods:** The study included three muscles of different metabolic qualities and sarcomere length: *m. semitendinosus*, *m. longissimus dorsi*, and *m. psoas major*, collected from nine bull carcasses aged 24 ±2 months. **Results:** Significant correlations were found between the volume of cooling loss on individual days of aging and the pH value of muscle tissue, lactic acid and glycogen content, as well as beef lightness. However, no significant dependency between the volume of glycogen and the intensity of red and yellow colours was detected. **Conclusion:** The colorimetric analysis of glycogen and lactic acid can be an effective tool in predicting the quality of beef.

Keywords: beef, glycogen, lactic acid, pH, shear force.

Introduction

Interruption of live metabolism as a result of slaughter and bleeding of the animal triggers the process of decomposition of most organic substances. Oxygen supply to the cells and tissues and, as a consequence, to all organs, is discontinued. Tissue enzyme reactions shift from processes of synthesis to the processes of decomposition. The degradation of muscle glycogen to lactic acid begins (21, 24). The later changes and indicators of meat quality depend on the level of glycogen and the speed of its decomposition in the process of the so-called anaerobic glycolysis (2, 22). Glycogen content significantly determines the final pH of meat (5, 6) and has a bearing on plenty of its indicators, such as hydration properties, shear force, colour, and cooling loss (4, 11, 23).

During anaerobic glycolysis, lactic acid acidifies the environment in a process that continues until inactivation of glycolytic enzymes in low pH or the depletion of majority of available glycogen. The formation of lactic acid and hydrogen ions lowers the intercellular pH of the muscles from pH 7.0, which is standard in a live animal, down to approximately 5.4–5.7 in the first 48 h post-mortem (14). Acidification of meat has an influence on proteolytic enzymes, which are important for stimulating both calpains and enzymes, whose activity reaches optimum in acidic environment. The activity of these enzymes in turn results in transformation of proteins, having an impact on the qualitative traits of meat. Lowering of the pH value has also an inhibitory impact on the development of proteolytic microflora, which increases the meat shelf-life. Sufficient concentration of glycogen in meat tissue is needed to reduce the pH level (11, 28). The rate of post-slaughter glycolysis depends on the type of muscle, its histology, and biochemical properties (types, number, and proportions of muscular fibres, and their glycolytic and oxidative properties). It is related to a specific growth rate and the number of fibre types (15, 26, 27).

The methods applied by the contemporary meat industry, including primarily pH measurement 45 min and 24 h after slaughter, prove to be insufficient in predicting meat quality. Due to the complexity of the transformations which occur in the meat tissue after

slaughter, the research conducted so far has additionally concentrated on the determination of glycogen disintegration. These changes are decisive for the rate of further post-slaughter transformations, and play a major role in development of final meat quality. With too fast post-mortem glycolysis the muscle proteins denature and the cell membranes are damaged, which results in too light colour of meat and a considerable reduction of meat water-holding capacity. The aim of this study was to evaluate the effect of post-mortem muscle's changes on glycogen and lactic acid contents, sarcomere length, as well as on selected quality features (pH value, colour, cooling loss, and texture) of beef *m. semitendinosus, m. longissimus dorsi*, and *psoas major* from Holstein-Friesian × Limousin breed carcasses during aging up to 21 d.

Material and Methods

Animals and muscle samples. The material used consisted of three muscles: *semitendinosus* (ST), *longissimus dorsi* (LD), and *psoas major* (PM), taken from bull carcasses (n=9) of Holstein-Friesian × Limousin meat bulls (commercial crossbred bulls) of pre-slaughter weight of 542 ± 32 kg, aged 24 ± 2 months. Differences in sarcomere length, and different characteristics of metabolic changes constituted the criteria of muscle selection. White fibres (type IIb, fast-twitch) and glycolytic nature of processes in live animals were predominant in the ST and LD muscles, while the fibres predominant in PM muscle were red (type I, slow-twitch) and of oxidative nature (7).

The studies of biochemical changes were conducted in defined time slots (2, 4, 6, 24, and 48 h post-mortem). The pH value was measured according to the PN-ISO 2917:2001/Ap1:2002 standard, using a portable Testo 205 series pH-meter (Testo AG, Germany). Each measurement was performed in three replications, taking the mean value as the assay result. Simultaneously, about 20 g of meat was removed with a scalpel for enzymatic analysis of glycogen and lactic acid. Meat samples were placed into tubes and stored in liquid nitrogen (at cryogenic VWR series XSS-36/6) during transport to the laboratory. The samples protected in this way were then stored in a freezer at -80°C (Ultra-low temperature freezer HERA freeze Thermo Scientific, USA).

Successive samples were collected from the remaining parts of the ST, LD, and PM muscles to be subjected to the process of wet aging. The samples were divided into four parts and vacuum packed in PE bags to be stored at 4 ±1°C. At 48 h post-mortem sarcomere length and glycolytic potential were measured in the samples. Moreover, colour, shear force, and cooling loss were additionally measured on the 7th, 14th, and 21st day of aging.

Glycogen, lactic acid, glycolytic potential. Enzyme assay kits (BioVision, USA) were used for determining glycogen content according to the procedure provided by the manufacturer. The 10 mg meat samples were weighed (XS 205 Dual RangeAnalytical Balance, Mettler Toledo, Spain), and later homogenised with 200 µL of distilled water for 2 min (Ultra Turrax homogeniser, IKA T18 basic, Germany). The homogenate was subsequently heated in a boiling water bath (WNB 7 Memmert, Germany) for 5 min to deactivate the enzymes. The samples were centrifuged at 13,000 rpm for 5 min (MPW-251, MPW Med. Instruments, Poland). A total of 10 µL samples were taken and filled up to 50 µL with Glycogen Hydrolysis Buffer (BioVision, USA). Next, 2 µL of Glycogen Hydrolysis Enzyme Mix was added to the samples and the mixture was blended and incubated at room temperature for 30 min. Each sample was then treated with 50 µL of solution containing Glycogen Development Buffer (46 µL), Glycogen Development Enzyme Mix (2 µL), and OxiRed Probe (2 µL) and incubated at room temperature for 30 min in darkness. Colorimetric measurements were performed using 415 nm wavelength (TecanSparkTM 10M, Männedorf, Switzerland). The method was based on enzymatic hydrolysis of glycogen to glucose by glucoamylase. The enzyme was obtained from fungi of *Rhizopus* sp. and *Bacillus* sp. bacteria. Optimum pH was ensured at all stages of the process thanks to the application of the aforementioned buffers, whose pH ranged from 4.0 to 7.4. The calibration curve was determined using commercial Glycogen Standard.

The lactic acid content was determined with enzyme assay kits (BioVision, USA). A 10 mg sample of meat was homogenised in 200 µL of distilled water for 2 min. The homogenate was heated in boiling water bath for 5 min to deactivate the enzymes. The samples were later centrifuged at 13,000 rpm for 5 min. Samples of 10 µL were taken and filled with lactate assay buffer to the volume of 50 µL. Subsequently, 50 µL of a solution containing Lactate Assay Buffer (46 µL), Lactate Enzyme Mix (2 µL), and Lactate Probe (2 µL) was added. The mix was incubated at room temperature for 30 min in darkness. The method was based on oxidisation of lactate in the presence of lactate dehydrogenase and colorimetric measurement at 450 nm wavelength. The enzymes used in the test for assaying lactic acid were obtained from rabbit muscles and pig heart. The optimum of pH reaction ranged from 7.5 to 8.1. The calibration curve was determined using commercial standard: L (+) - Lactate Standard.

The glycolytic potential of muscles was determined in the samples taken 48 h after slaughter, according to an equation proposed by Monin and Sellier (17).

Sarcomere length determination. Sarcomere length measurement was performed by laser diffraction with the use of calcium-near laser (Optical Laser Device 633 nm, Optel, Poland) according to the

methodology adopted from Cross *et al.* (3). Meat samples of 2 g were placed in scintillation vials and infused in 5% solution of glutaraldehyde at 0.1 M $NaHPO_4$ with pH 7.2 (Sigma Aldrich, USA). After 4 h, the aldehyde was removed from the samples, and the meat was infused in 0.2 M sucrose solution (Sigma Aldrich, USA) and stored for 24 h at 4°C. The methodology involved irradiation of muscle fibres with laser light of 632.8 nm wavelength and observation of diffraction, which was the refraction of light on the spaces between the filaments building the sarcomere. Sarcomere length was determined on the 2nd d of aging based on the distance between the 0th and the 1st ray of diffracted light, according to the formula of Cross *et al.* (3).

Fresh meat colour. The colour of meat surface was measured after its 30-min exposure to oxygen at 4°C, using trichromatic colorimeter Minolta CR-400 (Konica Minolta, Japan) (19). Ten measurements were taken on the freshly cut surface of each sample after 30 min of blooming. The colour values were expressed according to the standards of the Commission International de l'Eclairage (CIE, 1976) system and reported as CIE L* (lightness), CIE a* (redness), and CIE b* (yellowness).

Warner-Bratzler Shear Force (WBSF). Meat samples of 80 g were heated in water at 75°C until the temperature of 72°C was reached in the geometric centre of the cylindrical samples with the diameter of the diagonal cross section of 1.27 cm and length of 2.5 cm. They were cut out from the pieces of meat subjected to heat treatment, along the fibres. The measurement of the shear force value was performed with Instron 5965 (Instron, Norwood, USA), equipped with a 500 N head, Warner-Bratzler measurement unit, and Bluehill® 2 software. Knife speed of 200 $mm \cdot min^{-1}$ was used for measurement purposes (16).

Cooling loss. Cooling loss was determined by weight, expressed as a percentage compared to the original weight of the sample (before vacuum packaging). The following formula was used for calculation purposes:

% cooling loss = sample mass before storage – sample mass after storage/sample mass before storage × 100% (25).

Statistical analysis. The results were statistically analysed using the Statistica 12.0 software (StatSoft Inc., USA). The Shapiro-Wilk test was used to verify the normality of data. For data with normal distribution one-way ANOVA test was used, and for non-normal data nonparametric Friedman ANOVA was applied, at significance level of $P \leq 0.05$. Additionally, the correlations between variables were made using Spearman correlation coefficient.

Results

The results of pH measurements are presented in Fig. 1. The pH value measured from 2 to 48 h post-mortem changed in the range from 6.82 to 5.41, and was consistently falling during the process of carcass chilling. The pH values differed significantly between the studied muscles, especially at 24 h. The highest pH value obtained 2 h after slaughter was observed in the LD muscle (6.20 ± 0.10). As early as at 6 h post-mortem, the pH dropped to 5.92 ± 0.14 (ST), 6.45 ± 0.25 (LD), and 5.69 ± 0.02 (PM) respectively. The differences between individual muscles were statistically significant ($P \leq 0.05$).

The results obtained showed the differences in the course of post-slaughter changes in individual muscles which differ significantly in sarcomere length and metabolic activity in live animals, as presented in Table 1. The slow-twitch PM muscle featured statistically longer sarcomeres (3.43 ± 0.07), and had higher pH and glycolytic potential at 48 h compared to fast-twitch SM and LD muscles ($P \leq 0.05$).

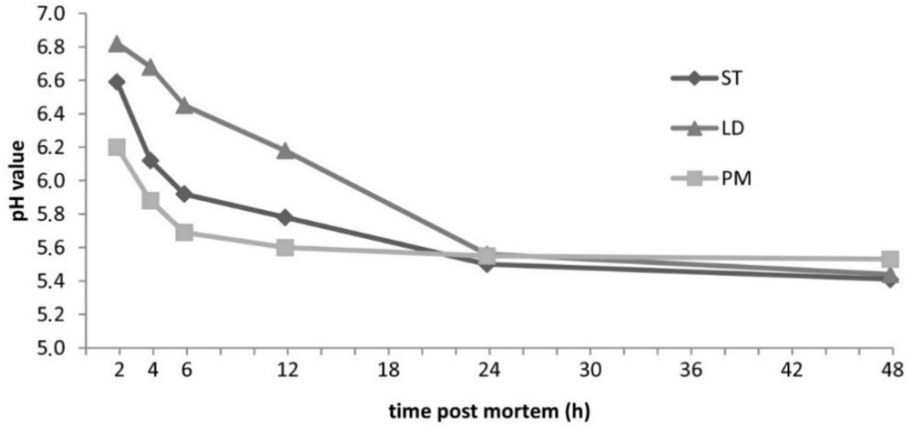

Fig. 1. The pH values for ST, LD, and PM muscles measured from 2 h to 48 h post-mortem, n = 9

Table 1. Type of muscle fibres, sarcomere length, glycolytic potential, and pH measured 48 h post-mortem, n = 9

	Semitendinosus (ST)	*Longissimus dorsi* (LD)	*Psoas major* (PM)
Type of muscle fibres	fast-twitch, glycolytic Mean ± SD		slow-twitch, oxidative Mean ± SD
sarcomere length (μm)	$1.76^{a} \pm 0.09$	$1.91^{b} \pm 0.05$	$3.43^{c} \pm 0.07$
pH_{48}	$5.41^{a} \pm 0.01$	$5.44^{a} \pm 0.02$	$5.53^{b} \pm 0.04$
GP_{48} (mg/g)*	$9.74^{a} \pm 0.94$	$10.14^{a} \pm 0.79$	$12.66^{b} \pm 0.61$

^{abc} – various letters in the same rows denote statistically significant differences between the mean values ($P \leq 0.05$).
*GP_{48} − glycolytic potential measured at 48 h post-mortem

Table 2. Glycogen and lactic acid content in ST, LD, and PM muscles measured from 2 h to 48 h post-mortem, n = 9

Time post-mortem, h	Glycogen (mg/g)			Lactic acid (mg/g)		
	ST Mean ± SD	LD Mean ± SD	PM Mean ± SD	ST Mean ± SD	LD Mean ± SD	PM Mean ± SD
2	$7.93^{a} \pm 0.39$	$7.79^{a} \pm 0.07$	$7.10^{b} \pm 0.13$	$3.41^{a} \pm 0.17$	$2.20^{b} \pm 0.12$	$3.27^{a} \pm 0.06$
4	$7.11^{a} \pm 0.27$	$6.24^{b} \pm 0.41$	$6.44^{b} \pm 0.28$	$3.74^{a} \pm 0.30$	$2.32^{b} \pm 0.09$	$3.80^{a} \pm 0.05$
6	$6.27^{a} \pm 0.06$	$4.73^{b} \pm 0.11$	$5.96^{c} \pm 0.18$	$4.26^{a} \pm 0.46$	$3.03^{b} \pm 0.24$	$4.09^{c} \pm 0.04$
24	$3.26^{a} \pm 0.29$	$3.33^{a} \pm 0.11$	$4.21^{b} \pm 0.15$	$4.84^{a} \pm 0.13$	$3.87^{b} \pm 0.07$	$4.81^{a} \pm 0.09$
48	$2.21^{a} \pm 0.17$	$2.89^{b} \pm 0.16$	$4.04^{c} \pm 0.18$	$5.09^{a} \pm 0.05$	$4.66^{b} \pm 0.07$	$5.05^{a} \pm 0.07$

^{abc} – various letters in the same rows denote statistically significant differences between the mean values ($P \leq 0.05$), one-way ANOVA

Table 3. Muscle colour parameters, shear force, and cooling loss measured at 2nd, 7th, 14th, and 21st d post-mortem for ST, LD, and PM muscles, n = 9

	Aging period (d)							
	2		7		14		21	
Variable	Mean	SD	Mean	SD	Mean	SD	Mean	SD
Semitendinosus								
Lightness (L*)	46.87 ^{Aac}	2.74	45.66 ^{Aab}	3.61	44.85 ^{Ab}	2.70	47.42 ^{Ac}	3.69
Redness a*	21.49 ^{Aab}	3.44	22.57 ^{Aa}	4.12	19.88 ^{Ab}	1.57	22.46 ^{Aa}	4.27
Yellowness b*	11.62 ^{Aa}	2.21	11.20 ^{Aa}	2.61	10.97 ^{Aa}	1.76	12.67 ^{Ab}	1.66
Shear force (N)	49.82 ^{Aa}	2.50	45.69 ^{Ab}	3.15	42.86 ^{Ac}	2.19	35.23 ^{Ad}	3.20
Cooling loss (%)	3.6 ^{Aa}	0.14	4.02 ^{Aa}	0.53	5.07 ^{Aab}	0.81	6.40 ^{Ab}	0.13
Longissimus dorsi								
Lightness (L*)	38.05 ^{Ba}	3.60	39.10 ^{Ba}	1.56	41.09 ^{Bb}	2.31	40.65 ^{Bb}	1.91
Redness a*	15.77 ^{Ba}	1.51	20.20 ^{Bb}	2.43	18.09 ^{Bc}	1.82	22.53 ^{Ad}	3.15
Yellowness b*	4.96 ^{Ba}	0.87	8.53 ^{Bb}	1.31	8.45 ^{Bb}	0.83	11.00 ^{Bc}	1.28
Shear force (N)	68.94 ^{Ba}	3.60	60.84 ^{Bb}	2.98	46.88 ^{Ac}	1.44	37.60 ^{Ad}	2.52
Cooling loss (%)	1.68 ^{Ba}	0.26	1.48 ^{Ba}	0.06	2.52 ^{Bab}	0.15	3.29 ^{Bb}	0.28
Psoas major								
Lightness (L*)	38.02 ^{Ba}	2.23	39.19 ^{Bb}	1.84	36.55 ^{Cc}	1.72	39.11 ^{Bb}	3.15
Redness a*	21.90 ^{Aa}	2.08	23.52 ^{Cb}	1.79	23.22 ^{Cb}	1.40	21.26 ^{Aa}	3.62
Yellowness b*	6.95 ^{Ca}	1.15	9.69 ^{Cb}	1.27	9.55 ^{Cb}	0.62	10.04 ^{Cb}	1.47
Shear force (N)	37.96 ^{Ca}	2.33	33.49 ^{Cb}	2.09	29.49 ^{Bc}	2.21	27.91 ^{Bc}	2.73
Cooling loss (%)	1.24 ^{Ba}	0.11	1.55 ^{Bab}	0.16	2.39 ^{Bb}	0.20	3.51 ^{Bc}	0.11

^{abc} – various letters in the same rows denote statistically significant differences between the mean values ($P \leq 0.05$)
^{ABC} – various letters in the same columns denote statistically significant differences between the mean values ($P \leq 0.05$), Friedman ANOVA

At 2 h post-mortem, the investigated muscles contained from 7.10 to 8.93 mg/g of glycogen (Table 2). The chilling contributed to a statistically significant ($P \leq 0.05$) decrease of glycogen content in the analysed muscles to the level of 4.73–6.27 already 6 h after slaughter. In the 24th h, the ST muscle contained 3.26 ± 0.29 mg/g of glycogen (41.11% of the initial value), LD – 3.33 ± 0.11 mg/g (42.75%), and PM – 4.21 ± 0.15 mg/g (59.30%). Further analysis of the changes in glycogen content in meat tissue proved that the pace of glycogen decomposition during 24 h post-mortem decreased significantly, and so did pH. The process continued far more slowly than during the first 12 h post-slaughter.

The content of lactic acid was in the range of 2.20–3.41 mg/g when measured at 2 h post-mortem. After 24 h of chilling, the lactic acid content increased significantly to the level of 3.87–4.84 mg/g (Table 2). In the following hours of cold storage, no significant increase in the volume of lactic acid was recorded. Its average content after 48 h was at the level of 4.66–5.09 mg/g of meat. The largest differences in the lactic acid content between the studied muscles were observed at 6 h after slaughter.

The results of colour parameters, shear force, and cooling loss measurements are presented in Table 3. The analysis of the L value demonstrated that colour lightness differed between individual muscles. The highest value of the L value, and therefore the highest lightness was recorded for the ST muscle on the 21st d of aging (47.42 ± 3.69). LD muscle was characterised by the lowest a and b parameters on the 2nd d after slaughter. During the 21-d period of LD storage, the intensification of yellow and red colours increased markedly, and they were comparable to the respective colours in the other two muscles.

Moreover, a beneficial impact of cold aging at 2 ± 1°C on the textural features of the muscles was observed. A three-week period of wet aging made it possible to obtain high tenderness. During the 21-d period of cold aging, the shear force value was reduced by 29.29%, 45.46%, and 26.48% for ST, LD, and PM muscles respectively.

Furthermore, the results demonstrated that an increase in the cooling loss occurred in parallel to the duration of meat aging. The largest cooling loss was observed in the glycolytic ST muscle, and the lowest in the LD. The differences were statistically significant ($P \leq 0.05$). No differences were noted, however, in the cooling loss between LD and PM muscles.

Discussion

Falling back on earlier studies conducted by Moltimer *et al.* (18), pH measurement is one of the most common criteria of meat quality assessment, as it informs about the rate of post-slaughter glycolysis, which is an efficient prognosticating tool. The pH measurement results point to the correct course of post-slaughter transformations in the assessed beef muscles. The final value of pH after 48 h post-mortem lay in the range of 5.41–5.53, which according to literature (10) attests to the correct development of anaerobic glycolysis. Post-slaughter transformations of glycogen under oxygen-free conditions led to the accumulation of lactic acid and in consequence to the lowering of meat pH. The lowering of glycogen content in the ST, LD, and PM muscles and increase in the lactic acid concentration contributed to the development of acid content typical of normal meat. The content of glycogen and lactic acid depends on the type of muscle as well as time of slaughter. The same relationship was observed by Hambrecht *et al.* (8) for pork *longissimus* and *supraspinatus* muscles.

The scope of post-mortem glycogenolysis depends on glycogen reserves at the time of slaughter. The reason behind divergences in energy transformations among various muscles in the same carcass is physical activity at lifetime and metabolic changes taking place therein. In the initial post-slaughter phase, glycogen decomposed quickly, yet later the process slowed down, which among others resulted in changing the activity of glycogenolytic enzymes: amylo-α-1, 6-glucosidase, 4-α-glucanotransferase, also known as glycogen debranching enzymes (GDE) (20). The drop in the GDP activity occurred more quickly in red than in white muscles, which was also confirmed by Kyla-Puhju*et et al.* (12). The faster the GDE became inactive, the more of residual glycogen remained in the muscles. Hence the oxidative, slow-twitch PM muscle, classified among the white muscles, featured a greater amount of glycogen at 48 h post-mortem, and at this time had higher final pH and glycolytic potential. Value of glycolytic potential depends on the size, type, and number of muscle fibres which constitute the muscle structure (15, 26).

The analysis of colour parameters showed that the muscles differed in colour, especially in their L* value, since the colour depends on the volume and degree of oxidisation of haem stains (13). Being of fast-twitch, glycolytic white muscle type, the ST and LD muscles contained less myoglobin and were characterised by higher brightness (L* value) and a lower redness (a* value). The pH change triggered by glycolytic transformations and the synthesis of lactic acid resulted in the change of meat colour, and especially its lightness. Lowering meat pH resulted in a statistically significant ($P \leq 0.05$) increase in the lightness of its colour, which was also found by Abril *et al.* (1). The statistical analysis proved the existence of a linear dependency between pH and brightness measured at 48 h post-mortem ($r = –0.887$ for ST muscle).

The obtained results showed that the muscles from commercial crossbred bulls (HF × Limousine), with higher glycogen levels measured at 2 h post-slaughter had higher lactic acid content, which indicates a higher degree of meat tissue acidification. The ST muscle,

which had the highest level of glycogen measured at 2 h (7.93 ± 0.39 mg/g of muscle tissue), demonstrated the highest L value and consequently the highest lightness and cooling loss on each day of aging. Consistently with earlier research (9, 29), it was demonstrated that the reduced water binding capacity and resultant cooling loss are higher when the pH of meat is lower. The PM muscle contained least glycogen at 2 h post-mortem, which resulted in a statistically higher pH (5.53 ± 0.04), the lowest shear force (37.96 ± 2.33 N), and the lowest cooling loss (1.24 ± 0.11%).

To sum up, the quantitative glycolytic analysis of beef muscles up to 48 h post-mortem from the Holstein-Friesian x Limousine bull carcasses can be an effective tool in predicting the quality of meat. Glycolytic compounds, such as glycogen and lactic acid, develop appropriate pH, which provides information about the occurrence or lack of technological defects. The results of this study indicate that the glycogen content is closely dependent on muscle type. The colorimetric analysis of glycogen and lactic acid development, based on enzyme reactions, made it possible to quickly obtain precise results, which may be useful in predicting technological beef quality.

Conflict of Interests Statement: The authors declare that there is no conflict of interests regarding the publication of this article.

Financial Disclosure Statement: The research was performed within the Project no POIG.01.03.01-00-204/09 Optimising of Beef Production in Poland. According to ”From Farm to Fork” Strategy co-financed by the European Regional Development Fund under the Innovative Economy Operational Programme 2007–2013.

Animal Rights Statement: The authors declare that the experiments on animals were conducted in accordance with local Ethical Committee laws and regulations as regards care and use of laboratory animals.

References

1. Abril M., Campo M.M., Önenę A., Saňudo C., Alberti P., Negueruela A.I.: Beef colour evolution as a function of ultimate pH. Meat Sci 2000, 58, 69–78.
2. Coombes S.V., Gardner G.E., Pethick D.W., McGilchrist P.: The impact of beef cattle temperament assessed using flight speed on muscle glycogen, muscle lactate and plasma lactate concentrations at slaughter. Meat Sci 2014, 98, 815–821.
3. Cross H.R., West R.L., Dutson T.R.: Comparison of methods for measuring sarcomere length in beef *semitendinosus* muscle. Meat Sci 1981, 5, 261–266.
4. Díaz M.T., Vieira C., Pérez C., Lauzurica S., González de Chávarri E., Sánchez M., De la Fuente J.: Effect of lairage time (0 h, 3 h, 6 h or 12 h) on glycogen content and meat quality parameters in suckling lambs. Meat Sci 2014, 96, 653–660.
5. England E.M., Matarneh S.K., Oliver E.M., Apaoblaza A., Scheffler T.L., Gerrard D.E.: Excess glycogen does not resolve high ultimate pH of oxidative muscle. Meat Sci 2015, 114, 95–102.
6. England E.M., Matarneh S.K., Scheffler T.L., Wachet C., Gerrard D.E.: pH inactivation of phosphofructokinase arrests postmortem glycolysis. Meat Sci 2014, 98, 850–857.
7. Fernandez X., Lefaucheur L., Candek M.: Comparative study of two classifications of muscle fibres: consequences for the photometric determination of glycogen according to fibre type in red and white muscle of pig. Meat Sci 1995, 41, 225–235.
8. Hambrecht E., Eissen J.J., Newman D.J., Smits C.H.M., Verstegen M.W.A., den Hartog L.A.: Preslaughter handling effects on pork quality and glycolytic potential in two muscles differing in fiber type composition. J Anim Sci 2005, 83, 900–907.
9. Huff-Lonergan E., Baas T.J., Malek M., Dekkers J.C.M., Prusa K., Rothschild M.F.: Correlations among selected pork quality traits. J Anim Sci 2002, 80, 617–627.
10. Immonen K., Puolanne E.: Variation of residual glycogen-glucose concentration at ultimate pH values below 5.75. Meat Sci 2000, 55, 279–283.
11. Immonen K., Ruusunen M., Puolanne E.: Some effects of residual glycogen concentration on the physical and sensory quality of normal pH beef. Meat Sci 2000, 55, 33–38.
12. Kyla-Puhju M., Ruusunen M., Puolanne E.: Activity of porcine muscle glycogen debranching enzyme in relation to pH and temperature. Meat Sci 2005, 69, 143–149.
13. Lee N., Sharma V., Singh R., Mohan A.: Effects of injection enhancement carrageenan, sea-salt, and potassium lactate on beef *longissimus lumborum* muscle sensorial characteristics and color stability. J Food Process Technol 2014, 5, 1–9.
14. Maltin C., Balcerzak D., Tilley R., Delday M.: Determinants of meat quality: tenderness. P Nutr Soc 2003, 62, 337–347.
15. Młynek K., Janiuk I., Dzido A.: Effect of growth intensity of bulls on the microstructure of *musculus longissimus lumborum* and meat quality. Acta Vet Brno 2012, 81, 127–131.
16. Moczkowska M., Półtorak A., Wierzbicka A.: Impact of the ageing process on the intensity of post mortem proteolysis and tenderness of beef from crossbreeds. Bull Vet Inst Pulawy 2015, 59, 361–367.
17. Monin G., Sellier P.: Pork of low technological quality with a normal rate of muscle pH fall in the immediate post-mortem period: the case of the Hampshire breed. Meat Sci 1985, 13, 49–63.
18. Mortimer S.I., van der Werf J.H.J., Jacob R.H., Hopkins D.L., Pannier L., Pearce K.L., Gardner G.E., Warner R.D., Geesink G.H., Hocking Edwards J.E., Ponnampalami E.N., Ball A.J., Gilmour A.R., Pethick D.W.: Genetic parameters for meat quality traits of Australian lamb meat. Meat Sci 2014, 96, 1016–1024.
19. Półtorak A., Wyrwisz J., Moczkowska M., Marcinkowska-Lesiak M., Stelmasiak A., Rafalska U., Wierzbicka A., Da-Wen Sun.: Microwave heating of bovine *gluteus medius* muscle: impact on selected physical properties of final product and cooking yield. Int J Food Sci Technol 2014, 50, 958–965.
20. Przybylski W., Monin G., Koćwin-Podsiadła M., Krzęcio E.: Glycogen metabolism in muscle and its effects on meat quality in pigs – a mini review. Pol J Food Nutr Sci 2006, 3, 257–262.
21. Pöso A.R., Puolanne E.: Carbohydrate metabolism in meat animals. Meat Sci 2005, 70, 423–434.
22. Ryu Y.C., Kim B.C.: Comparison of histochemical characteristics in various pork groups categorized by postmortem metabolic rate and pork quality. J Anim Sci 2006, 84, 894–901.
23. Scheffler T.L., Gerrard D.E.: Mechanisms controlling pork quality development: The biochemistry controlling postmortem energy metabolism. Meat Sci 2007, 77, 7–16.
24. Šimek J., Vorlova L., Malota L., Steinhauserova I., Steinhauser L.: Post-mortal changes of pH value and lactic acid content in the muscles of pigs and bulls. Czech J Anim Sci 2003, 48, 295–299.

25. Strydom P.E., Frylinck L., Montgomery J.L., Smith M.F.: The comparison of three β-agonists for growth performance, carcass characteristics and meat quality of feedlot cattle. Meat Sci 2009, 81, 557–564.
26. Vestergaard M., Therkildsen M., Henckel P., Jensen L.R., Andersen H.R., Sejrsen K.: Influence of feeding intensity, grazing and finishing feeding on meat and eating quality of young bulls and the relationship between muscle fibre characteristics, fibre fragmentation and meat tenderness. Meat Sci 2000, 54, 187–195.
27. Wegner J., Albrecht E., Fiedler I., Teuscher F., Papstein H.J., Ender K.: Growth- and breed-related changes of muscle fiber characteristics in cattle. J Anim Sci 2000, 78, 1485–1496.
28. Young O.A., West J., Hart A.L., van Otterdijk F.F.H.: A method for early determination of meat ultimate pH. Meat Sci 2004, 66, 493–498.
29. Żelechowska E., Przybylski W., Jaworska D., Sante-Lhoutellier V.: Technological and sensory pork quality in relation to muscle and drip loss protein profiles. Eur Food Res Technol 2012, 234, 883–894.