



## **EFFECT OF PIGLET BIRTH WEIGHT ON CARCASS MUSCLE AND FAT CONTENT AND PORK QUALITY – A REVIEW\***

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### **Abstract**

Piglet birth weight is determined by the maternal environment, intrauterine crowding, and nutrition, which influence embryonic and fetal survival and, as a result, fertility. The internal environment regulates prenatal myogenesis and muscle fibre number nutritionally and hormonally. The growth and metabolic differentiation of muscle fibres take place during the postnatal period. The effect of intrauterine undernutrition on myogenesis and on fetal growth and development (IUGR) is reflected in the low piglet birth weight and its high within-litter variation. Slaughter traits are determined by many factors, including genetic (breed), environmental (nutrition) and preslaughter handling. Slaughter traits and the physico-chemical and sensory characteristics of meat are dependent on prenatal myogenesis and neonatal weight. Optimized body weight of newborn piglets is conducive to improving quantitative traits (meatiness, fatness) and qualitative traits. However, slaughter traits are also influenced by many other differentiating factors, which is reflected in research results. Muscle fibres become metabolically differentiated during postnatal development, and one of the factors of large variation in pig meat quality traits is variation in the proportions of different fibre types in mature muscle. Considering the divergent opinions among scientists about the effect of prenatal myogenesis and piglet birth weight on slaughter value and pork quality, as well as the existence of areas that have received little investigation, it is justified to continue research in this area.

**Key words:** birth weight, myogenesis, slaughter value, pork quality

The effect of maternal undernutrition on weaker growth and development of embryos and fetuses in mammals or their organs during gestation (IUGR) and the effect of high prolificacy on neonatal weight were reviewed by Rekiel et al. (2014 b). The same review also provides information about the nutritional and hormonal factors that reduce IUGR. They are conducive to the development of muscle fibres and to

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the increased birth weight of piglets. The review (Rekiel et al., 2014 b) also describes postnatal growth in terms of carcass traits. The review cited above is part of a comprehensive study, with the present paper being its complementary part.

Pig carcass meat and fat content as well as pork quality are of importance for the meat industry and the consumers. Processing plants expect the slaughter products to have a high yield and be of good quality, while pork consumers expect pork to be low in fat and show very good quality parameters.

Studies performed in different research centres showed conclusive evidence that the quantity and quality of slaughter product and meat obtained from pigs depends on genetic and environmental factors (Chilibeck et al., 2005; Cagnazzo et al., 2006; Davoli and Braglia, 2007; Te Pas et al., 2010; Świątkiewicz, 2010; Wimmers et al., 2010; Wu et al., 2010; McNamara et al., 2011; Campos et al., 2012; Rehfeldt et al., 2012; Oksbjerg et al., 2013). The slaughter, quantitative and qualitative traits were found to be related to fetal developmental programming and prenatal myogenesis, and to changes occurring in muscle tissue and fibres during the postnatal period (Foxcroft et al., 2006, 2009; Markham et al., 2009; Du et al., 2010; Hill et al., 2010; Gonzalez-Bulnes et al. 2013; Oksbjerg et al., 2013).

The complexity of this research area is the basis of this review which attempts to answer how piglet birth weight is related to slaughter value and quality of the pork obtained.

### **Development of muscle fibres**

One of the first publications to discuss prenatal development of muscle fibres was written by Ashmore et al. (1973), who believed that primary (beta) fibres develop first, acting as a structural framework for the development of secondary (alpha) fibres. They put forward a hypothesis, which has been supported by many subsequent studies (Handel and Stickland, 1987; Mascarello et al., 1992; Wigmore and Dungleison, 1998; Rehfeldt et al., 2000; Rehfeldt and Kuhn, 2006; Bee, 2007; Sollero et al., 2011), that the characteristics of mature muscle fibres in the period before slaughter are traceable to fetal life.

Muscle fibres develop as two morphological populations and primary fibres that develop from early myoblast fusion establish a framework for subsequent development of secondary fibres. Handel and Stickland (1987) found no changes in the number of muscle fibres between birth and 128 days of age (around 50 kg b.w.), but citing work by Swatland and Cassens, they acknowledged that an apparent change in the number of muscle fibres is possible during the postnatal period. The change in numbers is apparent because it results from a reduction in the number of muscle fibres during the fetal period, which appear as interfascicular endings of muscle fibres in the sections of analysed muscles. Mascarello et al. (1992) reported a third form of muscle fibres (in addition to primary and secondary), which they detected during postnatal development of *longissimus dorsi* and *semitendinosus* muscles in growing pigs. Termed as “anti NE”, they were discovered in a reaction with type-specific antimyosin sera raised in rats. These fibres had a very small diameter and were scattered between large diameter fibres. They gradually decreased with increasing diameter of larger fibres, which progressed with age. The same authors hypothesized that

these fibres are formed through active proliferation of satellite cells, whose proliferative capacity during muscle regeneration after damage is well known. According to Mascarello et al. (1992), the proliferation of muscle fibres does not cease at birth, but also occurs, to a limited extent, in the neonatal period. Karlsson et al. (1993) and Petersen et al. (1998) concluded that the number and type of these muscle fibres are genetically determined. Current views on myogenesis, reported by Bee (2007) and Rehfeldt and Kuhn (2006), confirm and extend the results of earlier research. In pigs, myogenesis is a two-stage process involving migration, proliferation, apoptosis, differentiation and fusion of myoblasts into mature, multi-nucleated myofibres. These processes determine the number of muscle fibres in the prenatal period. Primary fibres develop in the first stage from 35 until 55 days of gestation, followed by a second generation of secondary fibres, which forms between 55 and 95 days of gestation (Lefaucheur et al., 1995). Every primary fibre is surrounded by around 20 secondary fibres. Because hyperplasia (an increase in the number of muscle fibres) in pigs takes place until 90 days of fetal life, the number of primary muscle fibres formed determines their number in neonates. This was confirmed by Dwyer et al. (1994). During the initial postnatal stage, muscle fibres in piglets mature, increase their volume and diversify into different types. In piglets aged between 1 and 4 weeks, all fibre types can be identified histochemically. Muscle fibre diameter increases by 100% until 25 days after birth, but at 4 months of age, i.e. from 100 to 125 days after birth, the increase is small, just 10% (Karlsson et al., 1999).

Muscle fibre hyperplasia in pigs is a developmental process that influences primary and secondary fibres. Wigmore and Stickland (1983) identified primary fibres in the semitendinosus muscle: around 12,000 on day 45 of fetal development and around 20,000 on days 60–79. Primary fibres are more resistant to environmental influences and are genetically determined (Dwyer et al., 1993). The number of secondary fibres depends on many factors, including nutritional ones, which cause variation in their number in littermates. The development of secondary fibres begins around 50 days of sow gestation and continues up to 85–90 days. Wigmore and Stickland (1983) observed the first secondary fibres (that could be identified and counted) at 54 days of gestation. There is also a population of myoblasts that do not take the form of fibres but remain closely associated; these are known as satellite cells. They are able to divide and provide a source of new myonuclei during postnatal growth. They contribute to fibre growth and take part in regeneration processes. The relationships between the different forms (primary and secondary fibres), depending on genetic factors, are not completely understood (Rehfeldt et al., 2000).

The increase in skeletal muscle mass during the postnatal growth period is due to hypertrophy of muscle fibres (Rehfeldt and Kuhn, 2006; Bee, 2007). The degree of myofibril hypertrophy depends in part on the number of myofibrils determined in the prenatal period. Myofibril size was found to be negatively correlated with myofibril number ( $r =$  from  $-0.3$  to  $-0.8$ ) (Bee, 2007; Rehfeldt et al., 2000). There is an antagonism between fibre thickness and size (Staun, 1968, 1972; Osterc, 1974; Fiedler et al., 1991; Larzul et al., 1997). The prenatally determined number of fibres and postnatal hypertrophy together determine muscle mass increase. Meatiness has positive genetic correlations with the number of muscle fibres and their cross-sec-

tional area (0.38 and 0.52, respectively) (Dietl et al., 1993; Larzul et al., 1997). Pigs with more muscle fibres are less fat. In modern pig breeds, larger fibres tend to have a smaller number of mitochondria, which helps to generate the energy needed for the muscles, mainly through the glycolytic pathway (Larzul et al., 1997; Fiedler et al., 1999). With a low energy status of the muscles prior to slaughter, this contributes to production of lactic acid (which is not removed) and results in Pale, Soft, Exudative (PSE) meat (Rehfeldt et al., 2000). Drip loss and pH<sub>45</sub> acidity show a correlation with muscle fibre number at  $r = -0.05$  and  $r = 0.13$ , respectively. These traits show a higher, unfavourable correlation with fibre cross-sectional area:  $r = 0.64$  and  $r = -0.37$ , respectively (Rehfeldt et al., 2000). The greater fibre area means a higher drip loss and lower pH, which is unfavourable.

It is possible to influence fibre characteristics genetically. Staun (1968, 1972), Fiedler et al. (1991) and Larzul et al. (1997) report that the coefficient of heritability for muscle fibre number ( $h^2$ ) averages 0.5 (from 0.22 to 0.88). Heritability estimates for muscle fibre size are lower and mostly lie between 0.2 and 0.3, which is logical because postnatal hypertrophy depends largely on the diet. To ensure high meat content without negatively affecting meat, it would be appropriate to select for fibre number, because general selection for meat content leads in particular to an increase in fibre size rather than number (Rehfeldt et al., 2000).

Rehfeldt et al. (2011 a) stated that skeletal muscle development in vertebrates is a highly integrated process. The studies in the field show that the processes are highly similar across mammals. The development stage tends to strongly affect the susceptibility of myogenesis to hormonal and environmental influences. With respect to genetic and environmental effects on muscle fibre development, the direct action of the growth hormone–insulin-like growth factor (GH–IGF) axis has been found to be of key importance. For mammals, the hypertrophy of the fibres formed during myogenesis and their metabolic and contractile properties have been found crucial for postnatal growth and function of muscles. Moreover, candidate genes have been found to be of importance in skeletal muscle development. Impaired myogenesis might be caused by undernutrition, but on the other hand increased maternal feed intake above the normal requirement does not seem to bring any additional benefits (Metges, 2005; Metges et al., 2008; Rehfeldt et al., 2011 a).

Extensive studies on both domestic and wild-type species have been conducted in order to get deeper insight into the genetic background of the skeletal muscle phenotype. It has been found that for mammals (including pigs) myofibre number, myofibre size, proportions of fibre types as well as the numbers and proportions of primary and secondary fibres differed with the increase in lean growth or quality of meat (Fiedler et al., 2004; Ruusunen and Puolanne, 2004; Lefaucheur et al., 2005; Lefaucheur et al., 2008; Rehfeldt et al., 2008 a). Next, some researchers including Ponsuksili et al. (2008) have pointed to the involvement of various factors in the selection responses in pigs. Among others, they indicated the importance of markers of satellite cell proliferation, metabolic enzyme activities, glycogen and fat contents as well as various proteins (i.e. AMPK $\alpha$ , IGF1 and IGF-binding proteins). Furthermore, genomic regions exhibiting quantitative trait loci controlling such traits as meat quality and muscle structure in pigs have been identified by means of genome scans

(Rehfeldt et al., 2011 b). Additionally, polymorphism in candidate genes (HMGA2, CA3, EPOR, NME1 and TTN) points to the relationship between genetic variation and carcass and meat quality. On top of it, also mutations in the IGF2 and RYR1 genes in pigs have been found of significance for carcass lean as well as muscle fibre traits (Cagnazzo et al., 2006; Stinckens et al., 2007; Wimmers et al., 2007; Gardan et al., 2008; Van den Maagdenberg et al., 2008). Eventually, the development and application of new analysis techniques is already providing and possibly will continue to provide new information about the meat and muscle fibre traits (Cagnazzo et al., 2006; Wu et al., 2008; Rehfeldt et al., 2011b).

Muscle fibres differentiate metabolically into different types during postnatal development (Maltin et al., 1997; Bee, 2007). In particular, three different types are commonly recognized, i.e. slow-twitch oxidative (SO), fast-twitch oxidative-glycolytic (FOG), fast-twitch glycolytic (FG). They mainly differ in the type of metabolism, the diameter of fiber, intensity of contraction or glycogen content (Picard et al., 2002). One of the factors responsible for differences in meat quality traits of modern pigs is variation in the percentages of fibre types in mature muscle (FOG, SO) (Maltin et al., 1997). This was confirmed in a study with 125 fatteners from 8 breeding companies. The investigated animals showed differences in the proportion of different muscle fibre types (FOG, FG, SO) (MLC, 1993). The diameter of FOG fibres was found to influence variation in texture. The proportion of SO fibres is positively correlated to juiciness, and an increase in their diameter is paralleled by a decrease in  $\text{pH}_{45}$  and a tendency for the formation of PSE meat.

Changes in muscle fibre number can be determined by breed differences (cross-breeding scheme), type of muscle, or sampling site. Muscle fibre diameter depends on the breed, body weight, and type of muscle. The internal environment which affects fetuses and is determined by the maternal nutrition and intrauterine crowding, influences myogenesis and has a residual effect on the weight of the progeny born to a sow (Rekiel et al., 2014 b). The effects of nutrition are still researched (Wu et al., 2010; McNamara et al., 2011; Campos et al., 2012; Rehfeldt et al., 2012; Oksbjerg et al., 2013). The size and number of different muscle fibre types determine the functional characteristics of the muscle, and thus its quality and technological and culinary value. Additionally, it is worth noting that sex has no effect on the composition of different muscle fibre types but influences their diameter (Migdał et al., 2005; Cagnazzo et al., 2006; Bee et al., 2007). Meat quality is partially genetically determined (Davoli and Braglia, 2007; Te Pas et al., 2010; Wimmers et al., 2010).

### **Effect of birth weight on slaughter traits**

The effect of piglet birth weight on slaughter characteristics such as muscling, fatness and intramuscular fat content, has been the subject of much research (Hegarty and Allen, 1978; Powell and Aberle, 1980; Wolter et al., 2002; Bee, 2004; Heyer et al., 2004; Gondret et al., 2005 a, b; Gondret et al., 2006; Rehfeldt and Kuhn, 2006; Bee et al., 2007; Lawlor et al., 2007; Rehfeldt et al., 2008 b; Beaulieu et al., 2010; Bérard et al., 2010; Schinckel et al., 2010; Alvarenga et al., 2012). The experiments showed different results. Beaulieu et al. (2010) found no effect of body weight at birth on slaughter traits, content of dissected meat and fat, and loin and

ham percentage in the weight of seven carcass cuts. Heyer et al. (2004) reported that carcass meat content and percentage of valuable cuts increase and backfat thickness decreases with increasing piglet birth weight. Bee (2004) observed that piglet birth weight has no considerable effect on carcass meat content and loin eye area, but has a statistically significant ( $P \leq 0.01$ ) effect on the content of depot fat, which showed a higher proportion in light piglets. Similar conclusions were reached by Bérard et al. (2008), who compared three groups of animals differing in birth weight and found it to have no statistically significant effect on meat content, proportion of subcutaneous fat and loin eye area. The only trait to be significantly ( $P \leq 0.05$ ) correlated to birth weight was dressing percentage, which was higher in light compared to medium and heavy weight piglets. The authors attributed this to lower gut filling and significantly lower ( $P \leq 0.01$ ) weight of the internal organs (liver and kidneys) in light compared to other piglets.

Alvarenga et al. (2012) found that compared to light (L) piglets, heavy (H) birth weight piglets had a higher mean daily gain at all stages of production. Growth rates became uniform in the finisher phase. The postmortem evaluation of intestinal epithelium showed that mucosal height was smaller in the L compared to H group, which decreased the absorptive area and the degree of nutrient utilization. This could have additionally contributed to a decrease in 5-month-old fatteners (L vs. H at birth) of muscle fibre number per  $\text{mm}^2$ , and of the muscle fibre percentage in relation to the connective tissue. H compared to L pigs were characterized by significantly ( $P \leq 0.01$ ) better slaughter indicators, dressing percentage and meat content of carcass, ham and shoulder (Alvarenga et al., 2012).

According to Gondret et al. (2005 a), piglet birth weight affects muscling and fatness traits in crossbred fatteners. Compared to heavy (H) pigs, light (L) pigs were characterized by higher backfat thickness and mesenteric fat content ( $P \leq 0.01$ ), higher meat content ( $P \leq 0.05$ ), but lower proportion of valuable cuts (loin  $P \leq 0.05$ , ham  $P \leq 0.01$ ). With the same slaughter weight, higher fat content and lower muscle content were found in fatteners that were light as piglets. Gondret et al. (2005 b), who determined meat content and backfat thickness in siblings from litters differing in birth weight, found no significant differences between groups L and H in slaughter traits ( $P > 0.05$ ). When investigating the activity of lipogenesis enzymes fatty acid synthase (FAS), malic enzyme and 6-phosphoglucose dehydrogenase in the adipocytes of subcutaneous fat tissue, they only found a significantly lower activity of the latter in L compared to H piglets. Compared to H piglets, L piglets showed a higher activity of lipid synthesis enzymes (including malic enzyme) in backfat ( $P \leq 0.01$ ) and a higher diameter of adipocytes in subcutaneous fat ( $P \leq 0.01$ ) and *semitendinosus* muscle ( $P \leq 0.01$ ) (Gondret et al., 2006). Compared to H piglets, the lipid content of *semitendinosus* muscle in L animals was 25% higher ( $P \leq 0.01$ ), with a 12% greater diameter of adipocytes ( $P \leq 0.01$ ). Access to feed was found to be conducive to deposition of fat in light piglets at birth (Gondret et al., 2006).

Very low birth weights (<1 kg) of piglets have been a production problem for many years. When comparing muscle and fatness traits in piglets with a mean birth weight of 0.81 kg (runts, R) and those weighing 1.57 kg (normal, N), Hegarty and Allen (1978) found significantly ( $P \leq 0.05$ ) higher proportions of fat in the *biceps*

*brachii*, *longissimus dorsi* and *semitendinosus* muscles postmortem in the runts. Loin eye area and backfat thickness did not differ significantly between the groups. Lawlor et al. (2007) observed no significant differences in slaughter traits, backfat thickness and carcass meatiness between the groups with different birth weights except for loin muscle height, which was significantly ( $P \leq 0.05$ ) lower for the lightest compared to the other piglet groups. Nissen et al. (2004), who studied littermates with different birth weights, did not find any differences between the groups for meat percentage, weight of *semitendinosus* muscle and meat deposition rate ( $P > 0.05$ ). For higher birth weights, muscle mass and muscle deposition rate showed beneficial progressive changes (muscle mass: 41.7, 47.0, 50.4 kg; weight of *semitendinosus* muscle: 359, 413, 447 g; meat deposition rate: 268, 303, 324 g, for L, M and H pigs, respectively). The correlation ( $r$ ) estimated between birth weight and meat deposition rate was 0.28.

Table 1. Effect of birth weight and rearing system of suckling piglets on selected slaughter traits of fattening pigs (Powell and Aberle, 1980)

Group – piglet birth weight (kg)	Muscle (%)	Average backfat thickness (cm)	Loin eye area (cm <sup>2</sup> )
H – 1.56	58.2 a	3.00	36.6 a
R – 0.97	57.2 a	3.02	35.6 a
R – 0.79*	53.0 b	3.25	29.8 b

H – heavy, R – runt, \*fostered piglets; a, b –  $P \leq 0.05$ .

When comparing meat and fat content in three littermate groups differing in birth weight, Powell and Aberle (1980) observed no significant differences in slaughter traits. For this reason they divided runt piglets ( $R < 1.0$  kg) into subgroups, some piglets suckled with heavier littermates and the others were fostered to sows to make litters of 5–6 piglets; slaughter indicators were found to differ (Table 1). The carcasses of fostered runts had less meat and smaller loin eye area compared to R piglets that were raised with their littermates (Table 1), which was confirmed by dissection. Foster runts grew slower than the larger ones. They utilized the feed less efficiently and produced carcasses with higher fat proportion and with less meat, but the rearing conditions could enable their survival. Rehfeldt and Kuhn (2006) determined muscling and fatness traits of pigs at birth and at 6 months of age (Table 2). On the day of birth, L piglets were characterized by significantly lower meat content and muscle weight compared to piglets from the other groups ( $P \leq 0.05$ ). Creatine kinase (a proxy for muscular development) was the lowest in L piglets (3.57 IU/mg), compared to 4.12 and 4.19 IU/mg in M and H piglets ( $P \leq 0.05$ ). The DNA concentration was highest in L piglets, but total DNA content was lowest as well. Significant differences were also noted for total DNA content in *semitendinosus* ( $P \leq 0.05$ ), which was 3.87 mg in L piglets and 5.54 and 6.73 mg in M and H piglets, respectively. The total content of DNA reflects the differences in the muscle growth rates (Nissen et al., 2004).

Table 2. Effect of piglet birth weight on selected slaughter traits (Rehfeldt and Kuhn, 2006)

Item	Group – piglet birth weight (kg)		
	L – 0.94	M – 1.39	H – 1.80
<b>Birth</b>			
Muscle tissue (%)	42.5 a	44.6 b	45.2 b
Subcutaneous fat (%)	8.77	8.59	8.84
<i>Semitendinosus</i> weight (g)	2.00 a	3.11 b	3.92 c
<i>Psoas major</i> weight (g)	2.46 a	3.83 b	4.74 c
<b>6 month of age</b>			
Lean meat (%)	54.8	56.2	56.2
Fat (%)	24.6 a	22.6 b	22.9 b
Loin eye area (cm <sup>2</sup> )	44.9	48.7	49.1

Group: L – low, M – middle, H – heavy birth weight.

Muscle content and loin eye area were lower, and fat percentage significantly higher ( $P \leq 0.05$ ) in the group of L compared to M and H piglets at 6 months of age. Further experiments confirmed the lower muscle content and higher fat content of lighter compared to heavier piglets (Rehfeldt et al., 2008 b). According to Schinckel et al. (2010), an approximately 1% lower meat content should be expected in fattening pigs if they weigh an average of 1 vs. 1.5 kg as piglets. Wolter et al. (2002), who investigated the effect of birth weight and supplementing milk replacer or not on rearing and fattening performance and slaughter value, concluded that both birth weight and supplemental feeding created no differences in slaughter traits.

Influencing the conditions created for fetuses in the uterus is part of fetal developmental programming, which was described in the review by Rekiel et al. (2014 b). Research on fetal developmental programming has been carried out in different species of animals (pigs, rodents, ruminants) and described in the literature (Foxcroft et al., 2006; Wu et al., 2006; Du et al., 2010; Rehfeldt et al., 2012; Du, 2014). Du et al. (2010) analysed the possibility of fetal programming in cattle in terms of the development of skeletal muscles and intramuscular fat content. The authors quoted above found that undernutrition reduces the level of myogenesis, limits muscle hypertrophy, and decreases the content of intramuscular fat. Gonzalez-Bulnes et al. (2013) conducted research using prenatal programming, in which they fed the sows a diet providing 50% and 160% of the daily maintenance requirements for pregnancy. They observed that fetal growth conditioned by malnutrition from periconceptional stages is mainly regulated at the end of the pregnancy, to ensure proper body weight and size of the piglets, hence the survival of the offspring. Moreover, regardless of the nutrition scheme, the early postnatal development of piglets is affected by their sex, with males growing in a faster manner than the females.

In summing up the results of studies on the effect of slower prenatal growth and development, which is reflected in lower newborn piglet birth weight, and its effect on carcass meat and fat traits, it is concluded that they vary. The findings of Wolter et al. (2002), Lawlor et al. (2007), Bérard et al. (2008) and Beaulieu et al. (2010) indicate that piglet weight at birth has no considerable influence on muscling and fatness traits. The results of Alvarenga et al. (2012) provide evidence that it does have

some effect because light piglets show a slower growth rate and poorer development of intestinal epithelium, and heavy piglets achieve better indicators of muscling. The results of other experiments (Powell and Aberle, 1980; Bee, 2004; Heyer et al., 2004; Gondret et al., 2005 a, b; Rehfeldt and Kuhn, 2006; Rehfeldt et al., 2008 b; Schinckel et al., 2010) provide information that the carcasses of light piglets are heavier than those of heavy piglets. The higher fatness may be due to the higher activity of lipid synthesis enzymes or because with less muscle fibres, the plateau of lean growth is reached earlier, after which energy is stored as fat (Gondret et al., 2006). According to some researchers, the higher fat content of light piglets only concerns intramuscular fat (Hegarty and Allen, 1978; Powell and Aberle, 1980; Beaulieu et al., 2010).

### **Piglet birth weight and pig meat quality**

The effect of piglet birth weight on the physicochemical and sensory characteristics of meat quality was investigated and the results obtained were analysed (Powell and Aberle, 1980; Wigmore and Stickland, 1983; Heyer et al., 2004; Nissen et al., 2004; Gondret et al., 2005 a; Foxcroft et al., 2006; Rehfeldt and Kuhn, 2006; Bee, 2007; Bérard et al., 2008; Rehfeldt et al., 2008 b; Beaulieu et al., 2010; Schinckel et al., 2010; Świątkiewicz, 2010; Rekiel et al., 2014 a).

Reduced fetal growth and prenatal myogenesis are one of the more important determinants of neonatal weight and have a residual effect on muscling, fatness and meat quality of pigs (Powell and Aberle, 1981; Dwyer et al., 1994; Lefaucheur, 2006; Bérard et al., 2008). With a small number of secondary fibres formed during fetal life and the rapid increase in their size during the later period, the unused energy is used for deposition of fat. Underfed sows during gestation give birth to lighter piglets, which after growth and fattening produce carcasses with limited muscle development, lower weight of primal cuts, and poorer meat quality (Bee, 2004; Gondret et al., 2005 a; Karunaratne et al., 2007; Lösel et al., 2009). Research results also suggest that hormones, including the growth hormone (GH), somatotropin (ST) and insulin-like growth factor (IGF-1) all contribute to fetal nutrition, piglet birth weight, piglet growth and postnatal development (Gatford et al., 2010). Therefore, the experiments performed in recent years are comprehensive in nature (McNamara et al., 2011; Campos et al., 2012; Rehfeldt et al., 2012). They account for the fact that during the primary and/or secondary fibre formation in fetuses, sows receive different amounts of feed (Cerisuelo et al., 2009; McNamara et al., 2011), protein (Rehfeldt et al., 2012), protein and energy (Świątkiewicz, 2010), and supplemental L-carnitine (Lösel et al., 2009; Nissen and Oksbjerg, 2009, cited from Oksbjerg et al., 2013) or arginine (Mateo et al., 2007, cited from Oksbjerg et al., 2013; Wu et al., 2010, 2013). In the study by Wu et al. (2013), piglet weight and the proportion of muscle tissue in the neonates were highest when pregnant sows received feeds with optimum protein level (12.1%). These parameters were reduced when the feed was too high or too low in protein; similar conclusions were drawn by Gonzalez-Bulnes et al. (2013). These findings suggest that research efforts should be directed at optimizing neonatal weight as well as the quality of carcasses and pork from slaughter animals.

The quality of meat is determined by genetic, nutritional and slaughter factors. Quality traits are attributed to the differences in muscle tissue structure, which is

determined by prenatal myogenesis influenced by fetal programming (Foxcroft et al., 2006, 2009; Du et al., 2010; Hill et al., 2010; Wu et al., 2010; Gonzalez-Bulnes et al., 2013). In the context of meat quality, researchers draw particular attention to the amount, size and proportion of different muscle fibre types (Lengerken et al., 1997; Maltin et al., 1997; Klont et al., 1998; Karlsson et al., 1999; Lefaucheur et al., 2001; Kristensen et al., 2002; Gentry et al., 2004; Migdal et al., 2005; Gondret et al., 2006; Bereta and Eckert, 2010; Oksbjerg et al., 2013; Du, 2014). Selection for lean meat content increased the total number and diameter of fibres as well as the proportion of type IIB fast-twitch fibres in the total number of muscle cells, which had a negative effect on meat quality (Larzul et al., 1999; Oksbjerg et al., 2000). Nutrient deficiency impairs pre- and postnatal muscle tissue development. During fetal life the development of secondary muscle fibres and cell size are reduced, and after birth the underdevelopment concerns the size and maturity of muscle fibres. Impaired hyperplasia of glycolytic muscle fibres slows down the metabolic processes and the maturation of muscle cells (Dwyer et al., 1994; Du et al., 2010). The available knowledge in this area shows that the meat quality of adult animals can be influenced pre- and postnatally (Lefaucheur et al., 2003; Wu et al., 2006; Markham et al., 2009).

The basic chemical composition of meat from animals with different birth weights that have reached slaughter weight is analysed much less frequently than the physical and organoleptic characteristics.

When studying the meat of fatteners differing in birth weight, Rekiel et al. (2014 a) found no statistically significant differences in its chemical composition. Rehfeldt and Kuhn (2006) confirmed significantly higher water content and significantly lower protein and fat content in the meat of neonatal L piglets compared to M and H piglets. They also found that creatine kinase (CK) activity and total DNA content were significantly ( $P \leq 0.05$ ) lower in the group of lightest piglets. However, after reaching slaughter weight, L pigs had a higher fat content of meat compared to pigs from M and H groups ( $P > 0.05$ ). These results conform with the observations of Nissen et al. (2004), according to whom the differences in muscle development are due to muscle fibre number and size, which results from the differences in satellite cell proliferation and protein metabolism. This is confirmed by the differences in the DNA content of fibres and in RNA, which reflects protein metabolism and the synthesis of specific muscle proteins. The smaller number of muscle fibres in lighter piglets leads us to assume that this is the consequence of intrauterine undernutrition, which results in poorer meat quality. However, not all research findings are conclusive. Wigmore and Stickland (1983), Bee (2004), Gondret et al. (2006), Rehfeldt et al. (2008 b) and Beaulieu et al. (2010) found in the group of lightest piglets (around 1 kg or <1 kg) an increase in the mean area of fibres, especially slow-twitch oxidative, but observed no deterioration in meat quality.

The results of studies on meat acidity are not completely conclusive. Maltin et al. (1997) hold the view that the ratio of oxidative to glycolytic fibres is critical to meat quality. They showed that the higher the diameter of SO fibres, the lower the  $\text{pH}_{45}$  was. This was paralleled by an upward trend for PSE meat. Lengerken et al. (1997) found a higher postmortem decrease in pH for samples collected from the muscles

with a small number of fibres and a large cross-section area, typical of light piglets at birth, whereas Gondret et al. (2005 a) observed body weight to have no effect on muscle tissue acidity.

Powell and Aberle (1981) did not find any differences in the colour of meat from slaughter pigs from the groups differing in birth weight. Different results were reported by Bérard et al. (2008), who concluded that neonatal weight has an effect on the colour intensity of *longissimus dorsi* muscle. They found colour saturation to be significantly ( $P \leq 0.01$ ) higher in L compared to H piglets. Similar conclusions were drawn by Rekiel et al. (2014 a). For the groups differing in birth weight (I  $\leq 1.30$  kg, II  $1.31$ – $1.70$  kg, III  $\geq 1.71$  kg) they showed differences in redness, with the highest value obtained for the lightest piglets (I vs. II –  $P \leq 0.01$ ; I vs. III –  $P \leq 0.05$ ). However, similar to Beaulieu et al. (2010), Rekiel et al. (2014 a) noted no differences in the lightness of the meat samples, whereas Rehfeldt et al. (2008 b) demonstrated this value to decrease in heavier piglets. In a study by Świątkiewicz (2010), the meat of pigs with higher birth weights was of poorer quality (including lighter colour) compared to the samples obtained from lighter animals.

A significantly ( $P \leq 0.05$ ) higher intramuscular fat content (IMF) was noted by Beaulieu et al. (2010) in light piglets weighing  $< 1.2$  kg. The same authors found no differences among the other, heavier piglets.

The intramuscular proteins titin, nebulin and troponin maintain the structural integrity of myofibrils under *in vivo* conditions. Their postmortem degradation weakens myofibril structure, which improves tenderness of meat and changes its water holding capacity. An experiment (Bérard et al., 2008) found higher titin and nebulin proteolysis 24 and 72 h after slaughter of pigs that were heavy at birth, which partially explains the differences in tenderness and drip loss. Calpains are responsible for degradation of proteins postmortem. Higher activity of  $\mu$ -calpains is associated with meat tenderness. In the described study, their level did not explain whether piglet birth weight and litter size had an effect on meat tenderness. In the experiments of Gondret et al. (2005 a, 2006), samples of roasted loin from H piglets were significantly more tender in sensory assessment compared to those from L piglets. When hyperplasia during fetal development was reduced (smaller number of fibres), hypertrophy was higher (greater fibre cross-sectional area) in L piglets to compensate for lower hyperplasia. The results of the study support the argument that fibre cross-sectional area is greater in pigs with low birth weight. A greater fibre cross-sectional area may adversely affect sensory tenderness. Lengerken et al. (1997) showed that muscles with a small number of fibres and a large diameter are characterized by lower tenderness; this trait is typical of the light piglets. According to Maltin et al. (1997), a greater diameter of the fast-twitch oxidative-glycolytic fibres (FOG) changes texture parameters by increasing instrumental shear force. Rekiel et al. (2014 a) failed to confirm significant differences in this parameter, but the values obtained were around 10% higher for the group of L compared to H piglets. Nissen et al. (2004) believe that the higher protein metabolism in heavier piglets is associated with increased synthesis of proteolytic enzymes which have a positive effect on tenderness. Świątkiewicz (2010) found higher shear force and greater meat toughness in pigs whose mothers were fed intensively during gestation and gave birth to heavier piglets.

According to Beaulieu et al. (2010), piglet birth weight has no substantial effect on drip loss and cooking loss, although their results were slightly higher for the group of lighter piglets. No differences for this parameter were reported by Rekiel et al. (2014 a). However, Lengerken et al. (1997) claim that muscles with a small number of fibres and large diameter have a tendency for higher drip loss. This is supported by the findings of Rehfeldt and Kuhn (2006), Karunaratne et al. (2007), Rehfeldt et al. (2008 b) and Lösel et al. (2009), but contradicted by Świątkiewicz (2010). Bee (2004) and Gondret et al. (2005 a) demonstrated that underfed piglets with lower birth weight produce poorer quality meat characterized by high drip loss.

### Conclusions

We may conclude from the results of different studies that muscle fibre number and type are determined during fetal life. The effect of intrauterine undernutrition on myogenesis and fetal growth and development (IUGR) is reflected in the low birth weight of piglets and high within-litter weight variation.

To ensure high meat content without negatively affecting the quality parameters, it seems appropriate to select for the number of fibres, because general selection for lean meat content increases fibre size rather than number. Muscle fibres become metabolically differentiated during postnatal development, and one of the factors of large variation in pig meat quality traits is variation in the proportions of different fibre types in mature muscles.

Muscle fibre number is determined by breed (genotype), type of muscle and sampling location. Muscle fibre diameter depends also on breed, muscle, the diets of animals and their slaughter weight. The size and number of muscle fibre types determine the functional characteristics of the muscle, and thus its quality and technological and culinary value.

The results of studies investigating the effect of piglet birth weight on muscling and fatness traits are inconclusive, although the overwhelming majority shows that light piglets grow more slowly and their carcasses are fatter; moreover, the meat from these animals is characterized by poorer quality, higher drip loss and lower tenderness.

It appears that production of litters with uniform, high birth weights could be most advantageous for optimizing fattening as well as the slaughter, quantitative and qualitative traits of pigs.

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