Chapter 3
Quantitative and physiological aspects of pig growth

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This chapter deals with:

- How and how fast the pig body develops from birth to maturity
- Age-dependent growth capacity
- Composition of growth in male, female and castrated pigs
- Mathematical descriptions of growth characteristics
- Fundamentals of growth physiology and growth regulation

1. Introduction

Animal growth can be defined as an increase in size and mass of the body. In commercial pig production and in production experiments, growth is mostly understood as whole body growth, while growth of body constituents (organs, tissues, chemical fractions) is of interest in developmental studies. Growth rate is defined as growth per time unit, e.g. daily weight gain. When pigs are kept in a non-limiting environment (thermoneutral and non-infectious conditions, ad lib access to water and feed of optimum nutrient composition), the obtained growth rates express the pigs' growth potential, i.e. their genetic capacity for growth. However, this is merely a theoretical concept because it is very difficult, if not impossible, to establish experimental conditions in which no environmental factor is limiting. Thus, actual growth rates are normally lower than potential growth rates as a result of sub-optimum environmental and nutritional conditions.

Growth can be visualized by growth curves, i.e. mass plotted against time, and growth curves can be quantitatively described by suitable mathematical functions. Differentiation of such functions with respect to time leads to time functions of growth rate. However, growth rates can also be expressed as functions of state, e.g. protein retention rate as a function of body protein mass.

Different body parts (chemical and anatomical fractions) develop at different rates resulting in changes of body composition during the lifetime of pigs. This can be described by quantitative relations between age or body mass and the mass of various body parts or by relating the mass

of different body parts to each other. The deposition rates of body protein, body lipid and body ash during the growth period determine the net nutrient requirements for growth. Quantitative descriptions of the changes in body composition are therefore useful for the estimation of nutritional recommendations during specific growth periods as they drive the demand for nutrients.

The first part of this chapter concerns the quantitative description of body mass development, prenatal as well as post-natal. The second part deals with the description of growth in major chemical fractions of the body, and the third part considers the development of various body tissues and organs emphasising their different rates of maturation. In these descriptions, the effect of gender on growth characteristics of pigs is underlined. As an attempt to explain the changing body composition during the growth period of pigs, the last part of the chapter is devoted to a discussion of how various regulating factors (hormones, signalling molecules etc.) may control protein and lipid deposition in different phases of growth.

2. Growth of body mass

2.1. Prenatal growth

The developmental performance of born pigs, such as birth weight, pre-weaning survival and post-natal growth capacity is primarily determined during gestation. In early gestation (<30 days), genetic control is the dominant factor determining embryonic loss and foetal growth, whereas during later gestation other factors, most notably substrate supply, influence the size of the foetal pig. The foetal growth period is characterised not only by rapid cell replication, but also tissue differentiation and formation of tissue matrices. These processes are influenced by genetic makeup and uterine capacity determining size, form and composition of the pig's body at birth. Emerging scientific evidence indicates that maternal energy and protein restrictions can severely affect the post-natal growth in the pig. This will not be discussed further, but interested readers are referred to reviews of Foxcroft et al. [12] on the biological basis for prenatal programming of post-natal performance in pigs, including effects on myogenesis and carcass characteristics. The time course of foetal growth is depicted in Figure 3.1, which shows that the weight of the foetus increases cubically as gestation progresses, indicating that foetal weight gain is accelerated during the last part of gestation [27]. Moreover, the weight of the foetus increases dramatically from day 70 in gestation suggesting that the nutrient requirement of the foetus increases correspondingly.

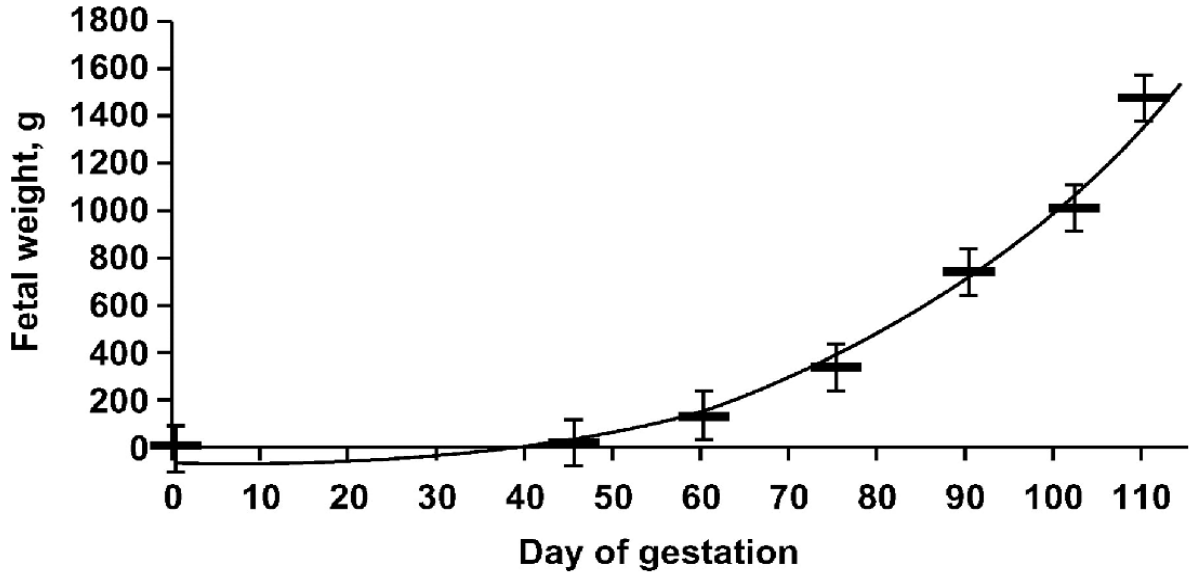

Figure 3.1. Foetal weight as a function of days in gestation. Adapted from [27].

2.2. Post-natal growth

Birth weight does not differ between genders, but it varies substantially between pigs and also between pigs within the same litter. The mean birth weight is approx. 1.5 kg and the associated phenotypic within litter coefficient of variation is around 15%, meaning that pigs from the same litter are quite variable in size. Piglets smaller than 1 kg at birth are termed runts and are the consequence of severe intrauterine growth retardation. These pigs of low birth weight show the poorest survival rate, the lowest growth performance and the lowest lean percentage at slaughter. In general, birth weight is correlated positively to the average daily gain (ADG) in the period from weaning to market weight around 100-120 kg. The relationship between birth weight and ADG is curvilinear, indicating that the effect of increasing birth weight follows diminishing return behaviour. Within a subset of birth weights, the relationship may be approximated by a straight line (the tangent to the curve) and it has been estimated that pigs weighing 1.5 kg at birth grow additionally 14 g/day from weaning to market weight compared with pigs weighing 1.4 kg [30]. Thus, heavy piglets have a competitive advantage at birth and usually remain heavier than their litter mates throughout the growth period until market weight.

A graphical presentation of growth curves of boars, gilts and barrows is given in Figure 3.2. A comprehensive growth trial on ad lib fed pigs provided the data (Danfær, unpublished).

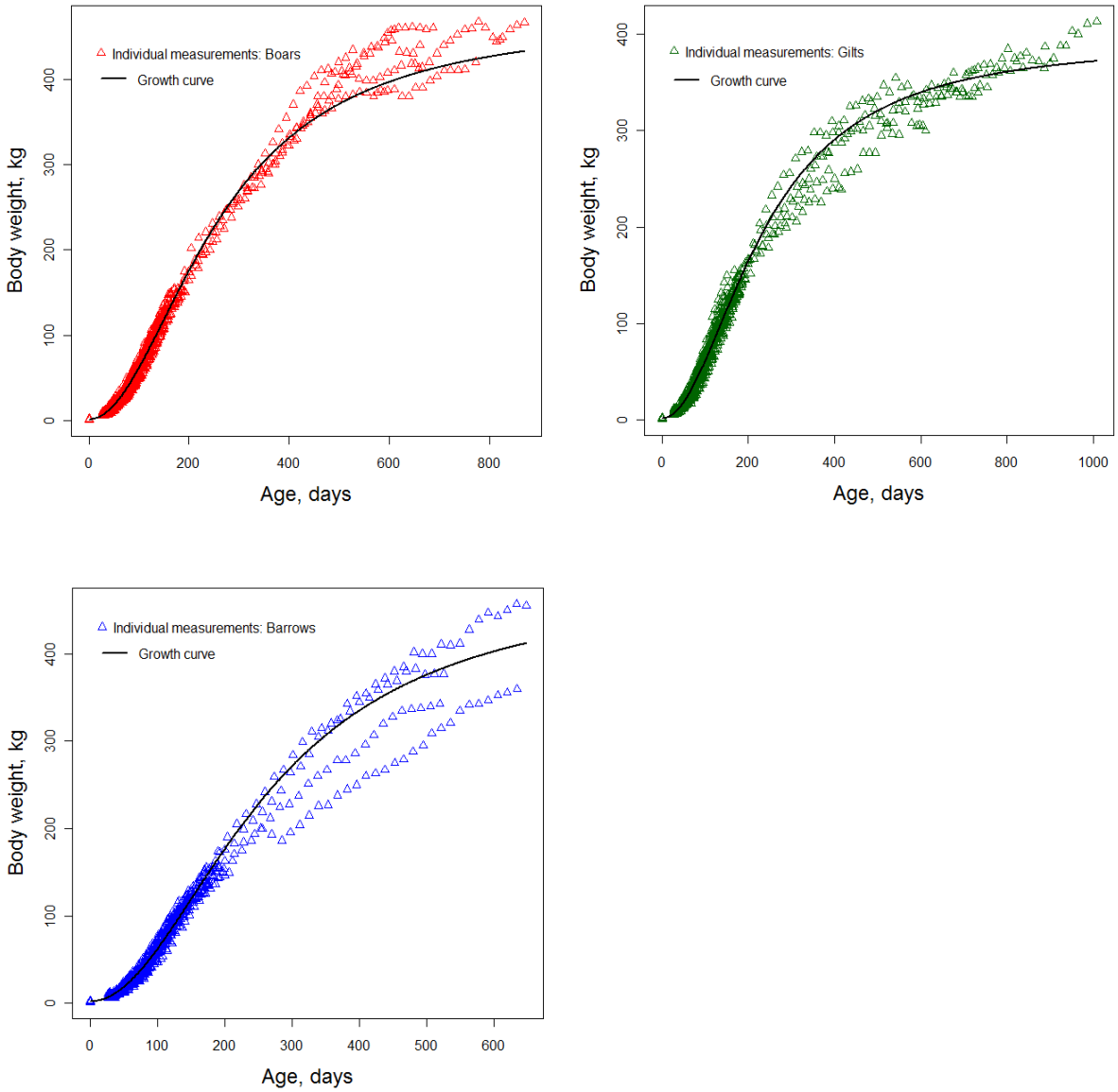

Figure 3.2.The time course of growth in modern meat type pigs fed ad lib. Data from Danfær (unpublished).

Visual appraisal of a pig's growth curve is as follows: during the early stages of life, the growth is exponential up to a point where the growth rate peaks (the curve's point of inflexion) and then the rate slowly decreases towards zero as the animal matures. These characteristics lead to a sigmoid curve describing the body weight of the pig as a function of age. The empirical sigmoid pattern is present in Figure 3.2 and is evident for all three genders. The individual variation increases as the pigs age and thus they get more heterogeneous in weight as time progresses. This between-pig variability has obvious consequences for marketing pigs because meat processors want pigs that are uniform in size and weight. The cause of between-pig variability is partly of genetic origin, but environmental factors (e.g. disease, stocking rate, feeder allocation space, etc.) also play an important role in the progression of heterogeneity of body sizes.

2.3. Mathematical descriptions

The sigmoid growth pattern can be described quantitatively by appropriate mathematical equations relating body weight to time, i.e. growth functions. First order derivatives with respect to time of such functions describe the development of growth rate at increasing age. The point of inflexion in a growth function identifies the maximum growth rate and is therefore of interest for the study of pig growth, e.g. in comparisons between genders or genotypes and for genetic evaluations. The inflexion point of a growth curve is estimated by setting its second order derivative with respect to time (growth acceleration) equal to zero, enabling the calculation of age (T*) and body weight (W*) at the time point of maximum growth rate. The classical growth function for representing growth in pigs is the Gompertz equation [13], which has been favoured by many researchers [10]. The Gompertz growth function is defined as

$$W(t) = W_b \times \exp\left(1 - \exp(-kt) \times \log\left(\frac{W_f}{W_b}\right)\right)$$

where W(t) is the body weight at time t; W_f is mature weight; W_b is the birth weight; and k is the maturation rate constant.

The age and body weight at maximum growth rate is defined as described above resulting in the following equations

$$T^* = \frac{1}{k}\log(\log(\frac{W_f}{W_b})) \quad \text{and} \quad W^* = \frac{W_f}{e}$$

showing that the maximum growth rate occurs at a fixed body weight in relation to mature weight.

Another useful growth function that provides more flexibility due to an additional parameter is the generalized Michaelis Menten function [21], and Strathe [39] found that this function yielded good fits to the pig growth data shown in Figure 3.2. The generalized Michaelis Menten function is defined as

$$W(t) = \frac{W_b k^n + W_f t^n}{k^n + t^n}$$

where W(t) is the body weight at time t; Wf is mature weight; Wb is the birth weight; k is the approximate time to half mature size (more precisely the time at which W(t) = $(W_f + W_b)/2$); and n is a shape parameter controlling the steepness of the sigmoid curve. The age (T*) and the body weight (W*) at maximum growth rate is defined as

$$T^* = k(\frac{n-1}{n+1})^{1/n} \quad \text{and} \quad W^* = \frac{W_b(1+\frac{1}{n}) + W_f(1-\frac{1}{n})}{2}$$

Note that the point of inflexion does not occur at a fixed proportion of the mature weight as with the Gompertz function. If growth is studied within a narrow interval, say, 40-100 kg, then the growth curve is almost linear and can be described with good approximation as a straight line, i.e. $W(t) = W_0 + k \times t$ where W_0 is the initial body weight and k is growth rate. Hence, sigmoidal functions are useful when growth is studied from birth to late in life due to the S-shaped growth curve (Figure 3.2), and selection of the correct growth function is purely a statistical exercise. A detailed mathematical discussion of the presented growth functions and several more is given by Thornley and France [44].

Table 3.1. Growth triats of modern Danish meat type pigs with 95% confidence intervals estimated by using a generalized Michaelis Menten function based on data from Danfær (unpublished).

	Lower	Estimate	Upper
Mature weight, kg			
Boars	503.6	537.1	570.7
Gilts	354.8	382.1	409.3
Barrows	429.5	466.3	503.1
Birth weight	1.444	1.782	2.120
Approx. time to half mature weight (kg), days			
Boars	271.3	286.1	300.7
Gitls	219.5	232.5	245.6
Barows	247.5	264.3	280.8
Dimensionless exponent (n)	1.941	1.985	2.029
Body weight at maximum rate of groth (kg), inflexion point			
Boars	126.7	134.6	142.5
Gilts	89.6	96.1	102.7
Barrows	108.3	117.0	125.7

In a recent growth curve analysis [40], the experimental data presented in Figure 3.2 was analysed by fitting the two functions described above to the data. It was found that the generalized Michaelis Menten function was superior and results obtained using this function are presented in Table 3.1. The estimated weight of the mature body is 537, 382 and 466 kg for boars, gilts and barrows, respectively. These estimates are much higher than previously reported in the literature, which is mainly due to the length of the experimental period. It is clear that the availability of data describing the upper end of the growth curve has a large impact on the estimated mature weight [40], which explains some of the discrepancies found in the literature [19]. The dataset presented in Figure 3.2 is unique because pigs of all three genders were weighed regularly from birth to maturity. Experimental details such as diets and animal material are given by Strathe et al. [40]. The majority of growth trials reported in the literature examines growth and feed utilisation of barrows and gilts in a much narrower range of live weights, typically 20-100 kg, since there is little commercial interest in growth patterns of boars or at ages beyond standard market weight. In the future, scientific and commercial interest in the study of growth patterns and nutrient requirements beyond 100-120 kg live weight may be stimulated by considering the body weights at maximum growth rate and the fact that the maximum rate of lean tissue deposition is associated closely with maximum rate of gain. Table 3.1 shows that only gilts maximise their rate of growth at a slaughter weight of 100 kg, whereas boars and barrows still grow at a rate below maximum. However, as shown later in this chapter (Table 3.2) increasing the slaughter weight beyond 100 kg will affect the body composition (increase the fat content), especially in barrows.

Genetic selection during many decades has improved ADG, feed conversion ratio and lean meat percentage of slaughter pigs [34]. The effects of selection on mature weight are difficult to assess because there is little information available. To the knowledge of the authors, only few previous studies [48], [46] have monitored the weight of pigs during a period ending close to maturity, i.e. around 300 kg at 1000 days of age. If it is assumed that the age at maturity has not changed significantly as a result of selection, then selection for high growth rate will lead to larger and heavier pigs at maturity and furthermore, pigs slaughtered at standard market weight will be less mature.

The consequence for breeding and production sows in relation to genetic selection for high growth rate is increased body weight, length and height of sows, which may lead to changes in nutrient requirements related to maintenance processes as well as changes in housing designs.

Table 3.2. Estimated empty body weight and chemical composition of empty body at different body weights from birth to maturity in ad lib fed pigs (Danfær, unpublished).

Slaughter group	BW, kg	EBW, kg	Protein[1)]	Lipid[1)]	Ash1)	Water[1)]	Energy[2)]
Boars							
Birth	1.8	1.70	14.6	1.5	3.8	80.1	3.98
Weaning	7.9	7.49	16.5	12.2	3.3	68.0	8.83
25 kg	25	23.84	17.8	9.2	3.0	70.0	8.05
65 kg	65	62.26	19.3	13.9	3.1	63.7	10.14
100 kg	100	95.97	19.9	16.6	3.1	60.4	11.25
150 kg	150	144.24	19.5	19.7	3.2	57.6	12.40
300 kg	300	289.42	18.3	26.0	3.2	52.5	14.66
Mature	470	454.38	17.3	30.7	3.2	48.8	16.34
Gilts							
Birth	1.8	1.70	15.2	1.7	3.6	79.5	4.33
Weaning	7.9	7.49	17.0	11.1	3.4	68.5	8.38
25 kg	25	23.84	18.3	8.3	3.0	70.4	7.95
65 kg	65	62.26	20.4	15.0	3.1	61.5	10.82
100 kg	100	95.97	20.4	19.2	3.2	57.2	12.44
150 kg	150	144.24	19.0	24.4	3.2	53.4	14.18
300 kg	300	289.42	16.2	35.2	3.1	45.5	17.75
Mature	375	362.15	15.2	39.1	3.0	42.7	19.07
Barrows							
Birth	1.8	1.70	14.6	1.5	3.8	80.1	3.98
Weaning	7.9	7.49	16.6	12.2	3.3	67.9	8.83
25 kg	25	23.84	17.5	8.4	3.0	71.1	7.86
65 kg	65	62.26	19.7	16.0	3.1	61.2	11.09
100 kg	100	95.97	19.8	21.0	3.1	56.1	12.96
150 kg	150	144.24	18.1	27.2	3.1	51.6	15.00
300 kg	300	289.42	14.7	40.0	2.9	42.4	19.26
Mature	450	434.95	12.6	48.2	2.7	36.5	22.30

1) Per cent of empty body mass. 2) MJ/kg EBW.

3. Growth of major chemical components

3.1. The law of allometry

Allometry can be defined as the study of changes in the proportion of various parts of an organism during growth. The concept of describing relative growth mathematically is attributed to Huxley [16] who proposed the equation $Y = aX^b$ to relate the mass of individual body components (Y) to the mass of the whole animal (X). This allometric principle is also useful to express maintenance requirements for nutrients and energy as related to body weight (BW). By logarithmic transformation, the equation becomes linear: $\log(Y) = \log(a) + b \times \log(X)$. The scaling factor (b) can be defined as the growth coefficient of an organ or body pool. If the body part in question grows faster than the whole animal ($b > 1$) then its growth is positively allometric; if it grows at a slower rate ($b < 1$) then it is negatively allometric. Isometric growth is when a body component grows at the same rate as the whole animal ($b = 1$). An advantage of allometric analysis is that the growth coefficient is simply a ratio of instantaneous relative growth rate of Y to that of X, so that growth coefficients related to the same basis (e.g. empty body weight) can be compared across treatments, growth stages and even across species. These concepts have been widely used to study and characterise the differential growth and composition in relation to factors like genotype, gender, feeding level etc. [47]. Other practical applications of allometric scaling rules are the expression of requirements

for essential nutrients and energy to support maintenance processes because the requirement is constant when body size or pool is scaled to the power of b. It should be noted that use of the allometric equation assumes a constant growth coefficient (b) during the observed period. Schinckel and de Lange [37] argued that the augmented allometric equation ($Y = aX^b (c-X)^d$) can be a good alternative to the original equation. However, the biological interpretation of the parameters c and d is difficult. Alternatively, a multiphase function composed of two or more allometric relations can be used, but this requires that the breakpoints between different phases can be identified and, more notably, estimated.

3.2. Protein deposition

Protein deposition is the positive balance between protein synthesis and degradation. Together protein synthesis and degradation are included in the general concept of protein turnover [35]. Protein turnover is under hormonal and nutritional control and helps to modify diurnal variations in amino acid availability as a result of feeding being discontinuous. On a daily basis, protein turnover may involve as much as five times the requirement for dietary protein, but fortunately around 80% of the amino acids from protein breakdown are reutilized [35]. When changes in protein turnover during growth are considered, rates of synthesis and degradation are seldom expressed in absolute terms (e.g. g/day) as these rates are related to the mass of the body protein pool. It is often more useful to consider the fractional rate of protein synthesis or degradation, which is expressed simply as the rate of synthesis or degradation relative to the protein pool size, i.e. synthesis or degradation rate/body protein pool. Fractional protein synthesis rates in skeletal muscles at birth have been estimated as 12-14% per day, but decrease exponentially to around 6% per day at 25 kg and further to 4% per day at 80 kg live weight [28]. If a growing pig contains 18% protein at 25 kg then the absolute rate of protein synthesis can be equated as 0.18×25000 [g] $\times$ 0.06 [d^{-1}] = 270 [g d^{-1}]. Similarly, absolute rates of protein synthesis may be computed at other stages of growth. Fractional rates of synthesis decline more rapidly with age than those of degradation resulting in decreasing fractional rates of protein accretion. At maturity, the rate of protein synthesis equals the rate of degradation, which means that protein deposition becomes zero and protein turnover rates have reached a low, basal level. Hereby an upper limit for body protein mass is defined. Protein synthesis and degradation are technically more difficult to determine than protein deposition and therefore the latter is usually measured as an indicator of alterations of protein metabolism during growth and/or in response to dietary and environmental perturbations. The remaining of this section concerns protein deposition and body protein mass at various stages of growth. Effects of nutrition are dealt with later in this book and additional information is available in the review of Reeds and Davis [35].

During the foetal stage of growth, protein deposition is very limited until day 70 when protein deposition increases sharply. McPherson et al. [27] estimated the average foetus protein deposition rate to be 0.25 g/day until day 69 in gestation and then averaging 4.6 g/day afterwards until the end of study at day 110. If an average sow carries 15 foetuses then the daily amount of protein accumulated in foetal tissues is 3.75 g/day and 69 g/day before and after day 69 of gestation, respectively. Hence, dramatic changes occur in late gestational foetal protein deposition, which have obvious consequences for maternal protein requirements. These aspects are dealt with in later chapters.

A newborn pig contains approximately 250 g of protein, which seems to be constant across genders. It can also be expressed as 15% of the empty body weight (EBW), which is defined as the difference between body weight and the weight of the contents in the digestive tract and urine bladder.

An upper limit to daily protein deposition (PDmax), which is determined by the genetics of the pigs, is a central parameter because the pig's potential for depositing protein largely determines the pig's requirement for amino acids. Numerous dose-response type studies with growing pigs have demonstrated a plateau to body protein deposition that cannot be increased by feeding additional energy and balanced protein. Moreover, hyperalimentation studies have shown that increa-

sing feed intake (of a balanced diet) beyond ad libitum intake does lead to increased growth rate, but not to increased body protein deposition [24]. PDmax is dependent on the stage of growth [45] as the maximum rate of protein deposition changes during the course of growth. It is possible that in young pigs of high genetic merit, PDmax cannot be attained within limits of appetite. When this is the case, the upper limit to protein retention is determined by feed intake capacity and not by the synthetic capacity of the cells. Manipulating or changing the pattern of feed intake by means of nutrition or genetic selection becomes a key regulator of the body composition of the pig and this is discussed in more detail in later chapters. However, the existence of an upper limit to protein deposition can never be scientifically "proven" because it is impossible to demonstrate that an environment (a host of influencing variables some of which may be unknown) is non-limiting [11]. Nevertheless, definition of an upper limit to protein deposition is central to the description of the pig and for the understanding of key points that can be manipulated.

Description of the relationship between PDmax and age or live weight is important for the quantification of protein metabolism in pigs. As discussed previously, protein deposition is not constant during the foetal growth phase, which is dominated by hyperplasia, i.e. increase in number of cells or proliferation of cells. There is little, if any, information on the shape of the protein deposition curve from birth to weaning because such information is usually obtained from serial slaughter data where measurements are taken at birth and at weaning. Protein deposition during the post-weaning growth phase (7-120 kg live weight) is characterised by hypertrophy, i.e. an increase in cell mass and volume. The age-related protein deposition curve is curvilinear with an expected maximum in the above-mentioned weight interval. Published estimates of the maximum protein deposition for growing pigs vary considerably from around 80 to more than 200 g/day. Tauson et al. [41] investigated protein deposition patterns in boars of three breeds (Landrace, Duroc and Hamshire) and found that the breeds differed in the capacity for protein deposition with Duroc and Hampshire being superior to Danish Landrace boars. These Duroc and Hamshire boars of high genetic potential had a capacity for maximum protein deposition of about 230 g/day and there was a significantly quadratic relationship between protein deposition and metabolic body weight (MBW), showing that the shape of the PDmax curve was nonlinear. Furthermore, it was estimated that the maximum protein retention was not reached until 135 kg BW, which is beyond traditional market weight. The importance of a sufficient metabolisable energy (ME) supply early in the growth period was underscored by a lower protein accretion rate of boars given a daily energy supply below 1100 kJ ME/($kg^{0.75}$ × day) at an approximate live weight of 25 kg [41]. This finding illustrates the strong relationship between protein deposition and energy supply or ad lib intake as previously discussed.

The body protein mass in pigs develops according to a sigmoid curve as described for BW and the same mathematical methodology can be used for a quantitative description. It should also be expected that there are substantial differences between different genders within the same breed in their ability to deposit protein. In the study of Danfær (unpublished) designed to investigate the capacity for nutrient deposition in modern Danish meat type pigs (hybrids of Landrace x Large White sows and Duroc boars) fed ad lib, it was shown that the body protein content at birth is the same for the three genders. However, the form of the curve varies significantly with gender because the mature protein mass differs substantially. The generalized Michaelis-Menten function was fitted to the body protein versus age data, and based on the estimated parameters, the rates of protein deposition could be calculated. The rate of protein deposition is simply defined as the derivative of the body protein curve with respect to time (age). Such protein deposition curves are shown in Figure 3.3 for the three genders. It was estimated that the maximum protein deposition rate occurred at different stages of growth.

The barrows and gilts reached their maximum protein deposition potential around 120 days, whereas the boars' protein deposition rate continued to increase until approximately 150 days of age. The predicted maximum rates of protein deposition were 229, 197, 186 g/day at 113, 79 and 80 kg BW for boars, gilts and barrows, respectively (Danfær, unpublished). Part of the discrepancy between the results of Tauson et al. [41] and those obtained by Danfær can be explained by differences in experimental methodology. Tauson et al. [41] used the nitrogen balance technique to measure the protein deposition, and Danfær used the serial slaughter technique. It is well

documented that the nitrogen balance technique overestimates the amount of protein deposited because the deposition is calculated as the remainder after correcting for nitrogen loss in urine and faeces and thus any errors made in the determination of the other two components will affect the protein balance [33]. The serial slaughter technique will tend to underestimate the protein deposition because it measures protein deposition directly and hence small losses of body material will inevitably occur.

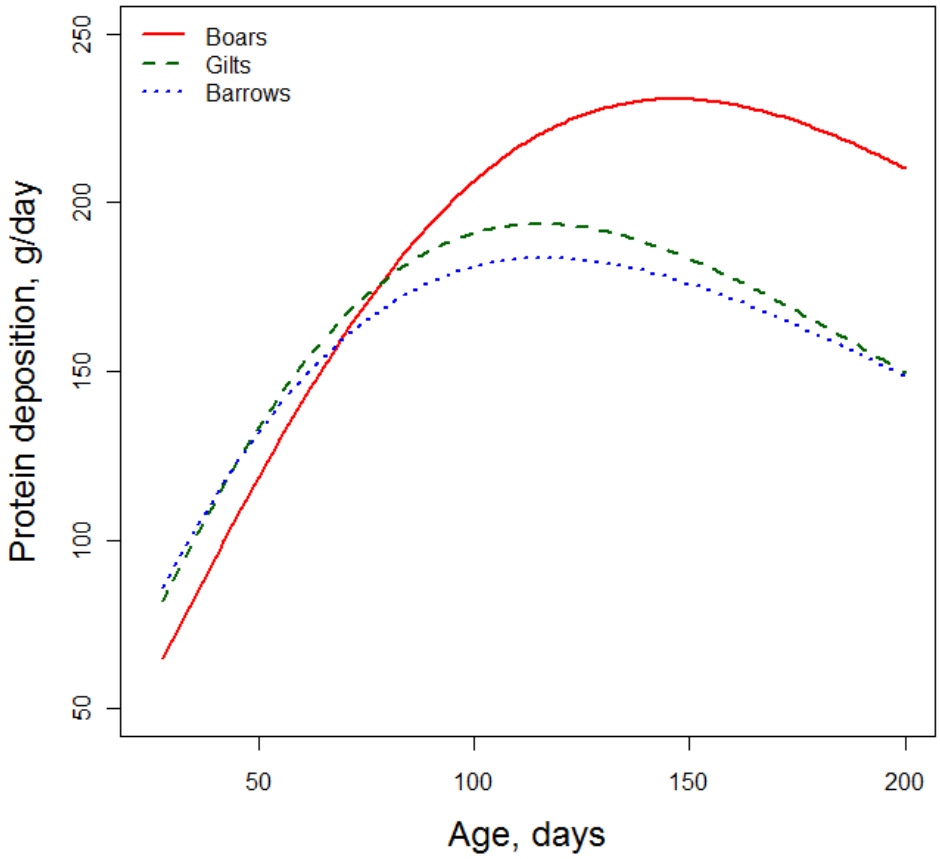

Figure 3.3. Gender specific protein deposition curves based on the generalized Michaelis Menten function. Data from Danfær (unpublished).

Modern Danish meat type pigs accumulate large amounts of protein during lifetime, and body protein masses at maturity were estimated to be 80 kg for boars and around 60 kg protein for barrows and gilts (Danfær, unpublished). Chemical composition data is presented in Table 3.2 for the three genders at increasing age and BW, i.e. at birth, weaning, 25, 65, 100, 150, 300 kg and maturity. The protein content increases from 15% at birth to 20% of EBW at 100 kg live weight and then decreases towards maturity to 17, 15 and 13% in boars, gilts and barrows, respectively.

3.3. Lipid deposition

The rate of lipid deposition in adipose tissue is determined by genotype, gender, dietary energy intake as well as degree of maturity. When protein deposition rate decreases, lipid deposition becomes the major component of the weight gain. The chemical body composition changes continuously during growth with increasing lipid deposition as shown in Table 3.2. Here lipid content of pigs is presented for all three genders. The body lipid mass is subjected to dramatic changes from birth to maturity, i.e. from 1.5% to 31, 39 and 48% of EBW in boars, gilts and barrows, respectively. Between weaning and 25 kg BW there is a distinct decrease in the lipid content from about 12 to 8-9% in all three genders. This finding may reflect the dietary and environmental challenges the piglets are subjected to at weaning combined with the high priority of modern genotypes for lean tissue growth as nutrient metabolism is directed towards growth of muscle tissue. The mass of body lipid at increasing age can be described as a sigmoid curve with an accelerating phase, inflexion point, decelerating phase and mature mass like that of body protein.

The lipid mass at maturity is about 145 kg in boars and gilts, but substantially higher, i.e. 225 kg, in barrows (Danfær, unpublished). The point of inflexion, i.e. when the maximum rate of deposition is obtained, was estimated for this population of pigs to occur later in barrows (250 days) than in boars and gilts (213-216 days of age). The estimated maximum rates of lipid deposition are 337, 402 and 406 g/day, and the live weights at which maximum rates of lipid deposition take place are 189, 167 and 213 kg in boars, gilts and barrows, respectively (Danfær, unpublished). In general, it can be stated that daily lipid accretion rates increase significantly from around 50 kg live weight until they peak at around 200 kg, but it should be noted that the shape of the daily lipid deposition curve is strongly dependent on pig genotype and feed intake level.

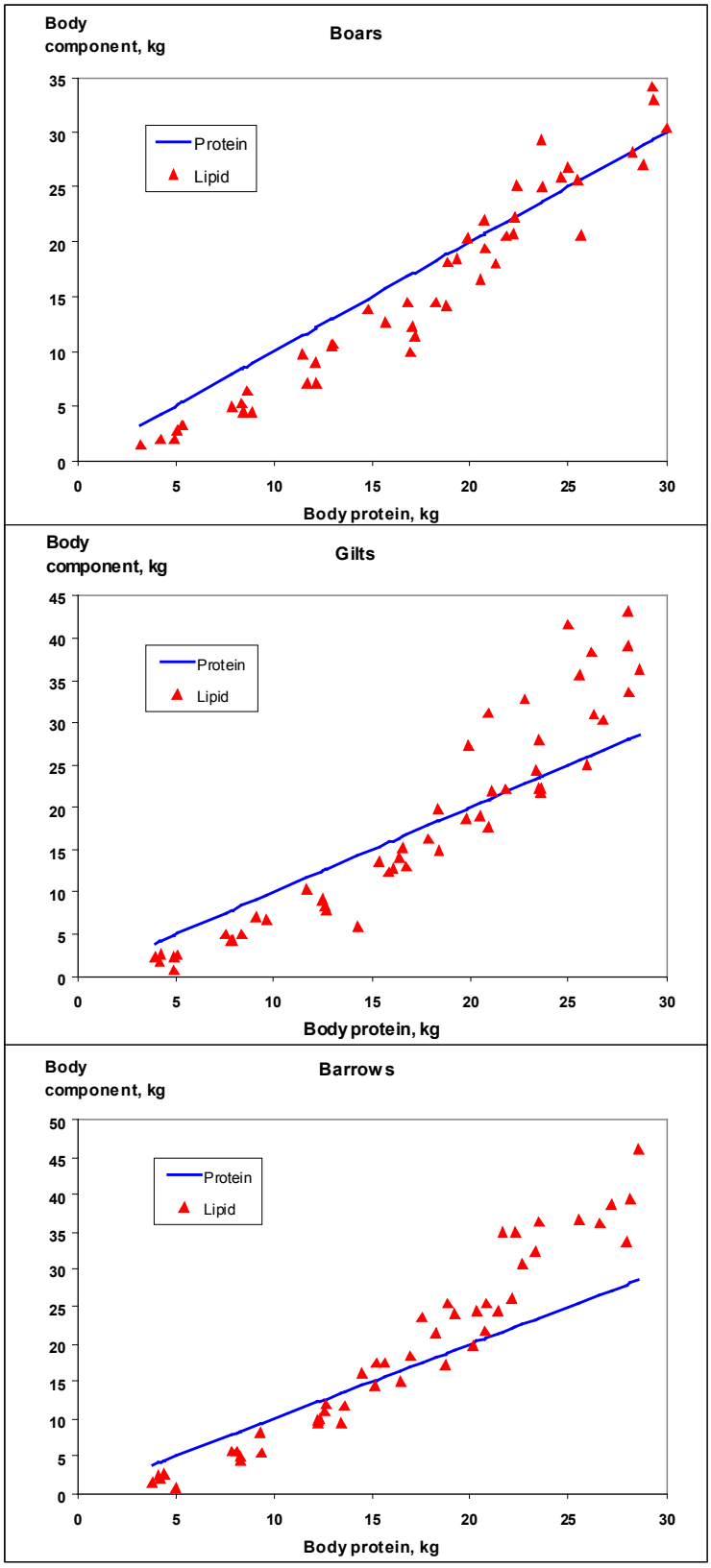

Figure 3.4. Relations between body protein and body lipid from weaning to 150 kg live weight in 3 genders. The lipid mass equals the protein mass at 25.9, 19.7 and 15.5 kg body protein in gilts, boars and barrows, respectively. Data from Danfær (unpublished).

Young pigs contain more protein than lipid in their bodies, but the lipid content increases faster than the protein content and at some point, depending on genotype, gender and nutrition, the lipid mass will exceed that of protein. The relations between body protein and body lipid from weaning until 150-160 kg live weight in boars, gilts and barrows (Danfær, unpublished) are shown in Figure 3.4 illustrating the effect of gender on the point at which the masses of lipid and protein are equal.

The data in Figure 3.4 can be described quantitatively by allometric equations relating body lipid (Y) to body protein (X), and from these relations the point of equal protein and lipid content could be determined as 25.9, 19.7 and 15.5 kg corresponding to 136, 101 and 80 kg live weight for boars, gilts and barrows, respectively. These estimates clearly show that the lipid content in barrows reaches the protein content much earlier (actually before standard market weight) than in boars, and that gilts in this respect are intermediates. The allometric parameters were (a): 0.251, 0.175, 0.163 and (b): 1.424, 1.584, and 1.662 for boars, gilts and barrows, respectively.

These parameter values confirm that the lipid mass grows at a faster rate than the protein mass (b>1) and that this difference in growth rate is highest in barrows and lowest in boars.

A thorough discussion of energy partition in growing pigs is presented in a later chapter in this book.

3.4. Body water and ash contents

The last two major chemical components in the pig body are water and ash (a general term for all minerals). The percentage of water and ash at various stages of growth is given in Table 3.2. The ash content is rather constant about 3% of EBW throughout the lifetime of pigs, although it is highest at birth. The newborn empty body contains 80% water, but this is decreased in the mature empty body to 49, 43 and 36% in boars, gilts and barrows, respectively. The overall lifetime trend in the chemical composition of pigs shows that water and ash are positively related to protein and can be described by allometric functions of the protein content. From the data of Danfær (unpublished), water content (Y, kg) in the body from weaning to maturity can be related to body protein (X, kg) by the following equations: $Y = 4.33 \cdot X^{0.89}$, $Y = 4.27 \cdot X^{0.87}$ and $Y = 4.52 \cdot X^{0.86}$ for boars, gilts and barrows, respectively. De Lange et al. [6] suggested that the scaling parameter (b) is constant across studies and pig types, i.e. about 0.86 in good agreement with these equations, which shows that the water-to-protein ratio in the body decreases as the pigs grow older. On the other hand, this ratio does not seem to be affected by energy intake level or by dietary induced variations in the body lipid to body protein ratio [1], [6].

Body ash content (Y, kg) from weaning to maturity can be described as $Y = 0.149 \cdot X^{1.03}$, $Y = 0.132 \cdot X^{1.07}$ and $Y = 0.138 \cdot X^{1.06}$ (X = kg body protein) for boars, gilts and barrows, respectively (Danfær, unpublished). Hence, the ash-to-protein ratio is almost constant in boars, but increases slightly towards maturity in gilts and barrows.

4. Body tissues and organs

Gut fill including urine in the bladder represents the difference between BW and EBW and is often assumed to be constant at 5% of the live weight [1]. However, factors such as feeding level, diet characteristics and time off-feed are known to influence gut fill [38]. Intake of fibre is likely to mediate the effect of feed intake and diet composition on gut fill [17]. An allometric equation common for all three genders from birth to maturity can be derived from the dataset of Danfær (unpublished) as $EBW = 0.939 \cdot BW^{1.005}$, $R^2 = 1.000$. The value of the b parameter is significantly different from 1, which means that gut fill is not a constant fraction of BW, but decreases from about 6% at birth to about 3% at maturity. The main tissues in the EBW of growing pigs are muscle (edible lean tissue), fat, bones, visceral organs, blood and skin. Other tissues, including nervous, lymphatic and vascular tissues, contribute less than 10% of EBW in growing pigs. The development of major tissues like muscles, fat, bones and visceral organs is discussed in more detail in the following sections.

4.1. Muscle growth and development

The ultimate goal of pig production is the production of meat for human consumption. The development of muscle tissue in the embryonic phase is characterised by hyperplasia, which is a rapid increase in the number of muscle fiber cells and thereby an increase in the DNA content of the tissue. As the embryo and foetus continue to grow and develop, myoblasts divide and the volume of muscle tissue increases. Myoblasts fuse to become primary myotubes, which are later surrounded by secondary myotubes. The multinucleated myotubes become enclosed in a sheath of connective tissue that forms a framework of the muscle. From day 35 in gestation, it can be observed that skeletal muscle bundles start to form in the pig embryo. At the time of birth, the number of muscle cells is nearly fixed. However, the number of nuclei in muscle cells continues to increase for some time as a result of satellite cell proliferation and subsequent fusion with muscle cells [36].

Post-natal muscle growth is dominated by hypertrophy, which is an increase in size and volume of muscle fibers, or by an increase in the number of myofibrils. These may show a ten to fifteen-fold increase in number within in a muscle fiber during the lifetime of an animal [20]. For a more detailed review of muscle cell development and physiology, the reader is referred to a later chapter in this book.

Muscle tissue represents the largest proportion of BW except in very obese animals. Muscles have a higher protein content than any other tissue in the body. In market weight pigs, between 45 and 60% of the whole-body protein is present in lean tissue and approximately 15% of body protein is present in visceral organs [6]. Many dynamic factors influence muscle growth. During early post-natal development, the elongation of skeletal bones has a major effect on muscle growth, but other factors such as genetic potential, physical activity and nutrition, become increasingly important [20].

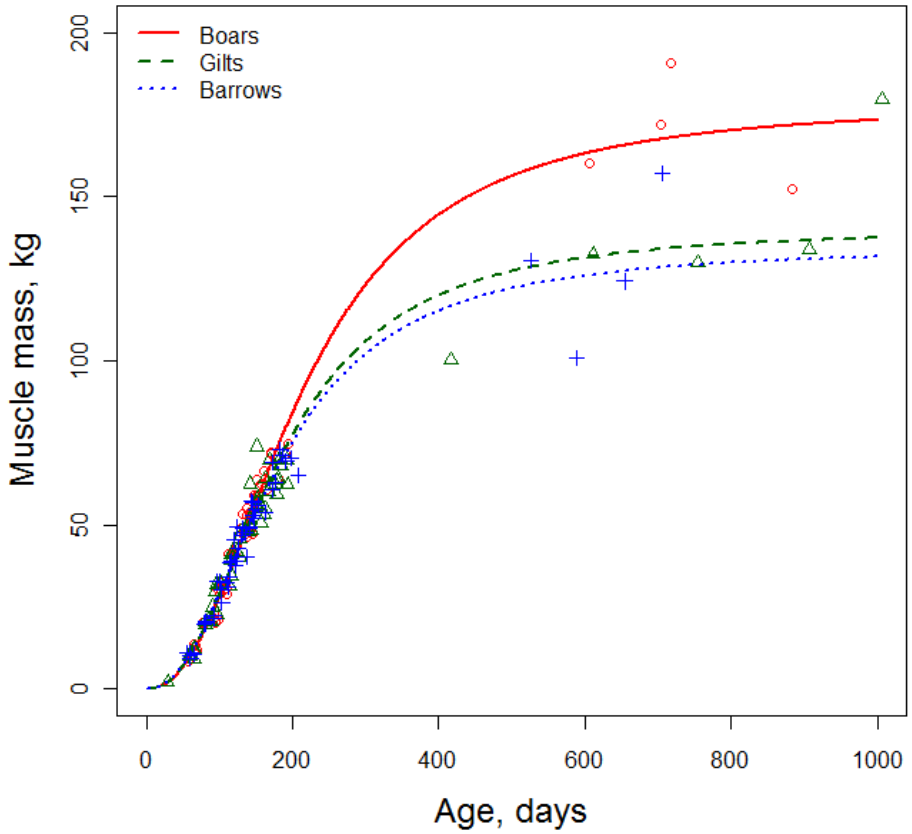

Figure 3.5. Development of muscle tissue (dissected meat) in boars, gilts and barrows. The sigmoid curves are estimated by use of generalized Michaelis Menten functions. Data from Danfær (unpublished).

In Figure 3.5, the relationship between muscle mass (dissected meat) and age is depicted (Danfær, unpublished). First it should be noted that the time course of the data closely resembles that of the whole body, i.e. a sigmoid curve. The generalised Michaelis Menten function was fitted to the data resulting in curves for the three genders in Figure 3.5.

For comparison of different growth curves, the points of inflexion are useful, and from the data presented in Figure 3.5 it was estimated that the maximum rate of muscle growth is 586, 532 and 515 g/day at 137, 120 and 115 days of age for boars, gilts and barrows, respectively. The ranking of these growth characteristics according to gender is similar to the protein deposition data as might be expected because the muscle data originate from the same study (Danfær, unpublished). As shown in Table 3.3, muscle tissue growth is nearly isometric with empty body growth because the growth coefficient is close to 1, indicating that the ratio of dissected meat to EBW is almost constant throughout the entire growth period.

In the study of Mohrmann et al. [29], lean percentage for barrows was at its maximum at a mean BW of 60 kg and for gilts at 119 kg. Using magnetic resonance imaging, Kastelic [18] showed in a study with 57 Landrace pigs in a weight range from 21 to 92 kg that the highest percentages of lean tissue occurred at 55 kg live weight for barrows and at 72 kg for gilts. Lean percentage of both sexes was higher in the study of Mohrmann et al. [29], but both studies confirmed higher lean percentages for gilts. The sex differences in the percentage of lean tissue became more apparent as the pigs approached market weight, in particular from 90 kg to 120 kg BW. Barrows showed the largest decrease in lean percentage between 90 and 120 kg BW. Growth of total lean tissue was almost isometric to the development of live weight as the growth coefficients were close to unity [29] in accordance with the data of Danfær (unpublished).

Table 3.3. Allometric equations relating tissues and organs (Y, kg) to empty body weight (X, kg) from birth to maturity in ad lib fed pigs: $Y = a \times X^b$. The inflexion point (IP) identifies the age at max. growth rate. Data from Danfær (unpublished.)

	Boars			Gilts			Barrows		
Y, kg	a	b	IP (days)	a	b	IP (days)	a	b	IP (days)
Muscles	0.49	0.99	137	0.423	1.03	120	0.58	0.96	116
Adipose	0.037	1.33	193	0.031	1.38	195	0.024	1.46	202
Bones	0.23	0.84	120	0.22	0.84	105	0.23	0.83	106
Heart	0.007	0.85	99.6	0.008	0.83	82.4	0.012	0.74	80.6
Liver[1]	0.023	1.04	70.4	0.028	0.98	64.5	0.048	0.83	66.5
Liver[2]	0.42	0.34	-	0.27	0.42	-	0.50	0.28	-
Kidneys[1]	0.007	0.93	74.8	0.007	0.92	55.5	0.014	0.76	51.3
Kidneys[2]	0.044	0.49	-	0.052	0.43	-	0.061	0.39	-
Stomach[1]	0.003	1.26	72.9	0.004	1.165	66.2	0.012	0.90	66.8
Stomach[2]	0.065	0.49	-	0.032	0.649	-	0.094	0.42	-
Small int.[1]	0.003	1.26	52.6	0.004	1.17	51.7	0.012	0.90	51.6
Small int.[2]	0.065	0.49	-	0.032	0.64	-	0.094	0.41	-
Brain	0.018	0.24		0.025	0.15		0.02	0.19	

1) Before change point. 2) After change point (see text).

4.2. Adipose tissue development

From the perspective of pork production, the deposition in adipose tissue is largely an undesired by-product. However, adipose tissue is very important to the welfare of animals because the subcutaneous fat provides protection and insulation against the environment, which is especially important in domesticated pigs as they have a sparse hair coat. Adipose tissue is the major energy storage in mammalian systems and is therefore an important element of carbohydrate and lipid homeostasis on a day to day basis. Fatty acids can be mobilized from adipose tissue to be used as a dense oxidative fuel by many peripheral tissues, especially skeletal muscles.

Like muscle cells and connective tissue cells, adipocytes develop from the embryonic mesoderm. Growth of adipose tissue involves proliferation of connective tissue, nerves and blood vessels, but the main contribution is growth of adipocytes. Adipose cell growth has different phases, i.e. hyperplasia (division of preadipocytes), differentiation of preadipocytes into adipocytes, and hypertrophy (increase in size) of differentiated adipocytes. Cell division is restricted to preadipocytes; once they have differentiated, they loose their ability to divide.

In skeletal muscle tissues, cell division only takes place prenatally and around the time of birth, and post-natal muscle growth is restricted to hypertrophy of existing cells. This feature does not apply to adipose tissue, where division of preadipocytes also occurs post-natally and even in older animals, especially with excessive energy intake. Hypertrophy of adipocytes is characterized by intracellular accumulation of triacylglyceride leading to increasing cell size.

For a detailed discussion of metabolic regulation in peripheral tissues, see a later chapter in this book. A quantitative approach (mathematical model) to the description of carbohydrate and lipid metabolism in growing pigs is given by Danfær [3].

The subcutaneous adipose tissue (backfat) is the most prominent fat depot in the pig at all stages of growth including the newborn [28]. The growing pig has three distinct layers of back fat separated by layers of connective tissue. The outer layer integrates with the dermis of the skin and surrounds the base of the hair follicles. The middle layer integrates with the skeletal muscle directly beneath it, and the third layer is placed in the region dorsal to the longissimus muscle. The measurement site for determination of thickness of the subcutaneous fat layers is at the last rib on the right side, 7 cm from the midline, referred to as the P2 site. The individual layers do not grow at the same rate or in the same proportion to the whole body of the pig. When absolute rates of growth are considered, the middle layer has been identified as the most rapid growing of the three. This was demonstrated by McEvoy et al. [25] who by means of ultrasound measured the change in thickness of the individual layers per unit change in live weight and thereby ranked the middle layer (0.0040 cm/kg) first followed by the outer layer (0.0031 cm/kg) and the third layer (0.0020 cm/kg). These numbers refer to crossbred Landrace x Large White gilts, but it is expected that the absolute levels depend on the breed and gender of the pig. Evaluation of individual layers is not normal practice. Instead, a single measurement is made of skin plus total subcutaneous fat thickness, which is simply referred to as “back fat thickness”. It is an important parameter, which is used to make decisions during pig production on optimal growth, on longevity in gilts and on meat quality control.

In addition, there are small amounts of fat deposited in the retroperitoneal, perirenal depot and in the suspending mesenteries of the stomach, small and large intestines, and around the heart. Fat is also deposited between muscles, which is referred to as intermuscular fat and represents approximately 15% of carcass fat [28]. The extent and distribution of various fat depots, including the subcutaneous depot, vary with breed and gender, but are also related to energy intake and to demands for energy use.

The growth of adipose tissue is positively allometric as related to the growth of EBW. Based on the dataset of Danfær (unpublished), the growth coefficient (b) was estimated as 1.33, 1.39 and 1.46 for boars, gilts and barrows, respectively (see Table 3.3). The growth coefficient is the slope of the line (on logarithmic scales) when adipose tissue mass is regressed on EBW, and as the ratio of the b values for barrows and boars is 1.10 (1.46/1.33), the data suggest that the rate of adipose tissue growth is 10% faster in barrows than in boars. This estimate may be taken as a direct hormonal effect of testicular hormones (androgens) on energy partitioning in boars versus barrows.

4.3 Bone tissue development

Development of the skeleton is an integrated part of growth in pigs, but from the viewpoint of meat production it represents little more than a by-product. Bones function as a means to support the musculature and thus providing form and enabling movement. The formation of bone is a process usually referred to as osteogenesis and occurs both in prenatal and post-natal life by transformation of connective tissue. Bone tissue is formed by either endochrondral ossification or by intramembranous ossification in the absence of a cartilaginous template [43].

Different cell groups are involved in formation of bones:

- osteoblasts are directly involved in bone matrix formation and are derived from mesenchymal cells,
- osteocytes are mature osteoblasts and are responsible for the formation and maintenance of the bone matrix,
- chondroblasts form cartilage that is connected with bone and in some cases required for bone formation, and
- osteoclasts are involved in bone breakdown (resorption) and remodelling.

Thus, bone growth, repair and maintenance are orchestrated processes involving all four cell types within the bone. For a detailed description of cellular development, growth and function of bone tissues, the reader is referred to the review of Thompson and Loveridge [43]. As growth continues from the time of birth, a center of ossification is established in the epiphysis, which is the primary elongation site of the long bones. Longitudinal growth of these bones involves action of both chrondrocytes and osteoblasts at the epiphyseal growth plate. Elongation of a long bone will continue until the epiphyseal growth plate closes, which will occur when this ossifies. When the epiphyseal growth plate is closed, the bone tissue is still metabolically active due to resorption and formation that replaces the old bone matrix. Apart from their mechanical functions, bones serve as reservoir of calcium and phosphorus, and thus constitute vital buffer systems for maintenance of calcium and phosphorus homeostasis. These aspects are dealt with in a later chapter.

Allometric parameters (a and b) for bone growth as related to EBW are presented in Table 3.3 showing that the growth coefficient is less than 1 for all three genders, i.e. 0.84, 0.84 and 0.83 for boars, gilts and barrows, respectively (Danfær, unpublished). Bones mature slightly faster than muscle tissues as the growth rate of bones peaks (point of inflexion) earlier than that of muscles indicating that muscle growth is tightly linked to and dependent on the development of bone structure.

4.4. Comparative aspects of organ and tissue development

From a viewpoint of growth biology, it is interesting to analyse how different organs and tissues evolve during the lifetime of pigs. Again, the inflexion point is an important parameter because the age at which the maximum rate of growth occurs will rank the development and priority between organs and tissues. In Figure 3.6, the growth rate relative to the maximum rate of growth is depicted as a function of time for seven tissues/organs (Danfær, unpublished). Expression of the growth rates relative to their maxima scales, the rates between 0 and 1 and the height of the growth waves are then equal for all tissues and organs. This makes it easier to visually compare the development of different organs and tissues. The curves are constructed by fitting the generalized Michaelis Menten function to serial slaughter data obtained from Danish meat type barrows (Danfær, unpublished). These relative growth curves may also be viewed as growth waves, a concept first introduced by Hammond [14].

From Figure 3.6, it can be concluded that the visceral organs (stomach, small intestine, liver and heart) have a high priority during early development, whereas the adipose tissue clearly has the lowest priority. The relative growth rates of muscle and bone tissues are strongly interconnected as their relative growth rates peak almost simultaneously, although slightly earlier for bones.

Comparisons of growth coefficients (b) estimated for different organs within different populations of pigs indicate that the small intestine, lungs and liver are relatively early-developing organs, while blood and the large intestine develop later [42], (Danfær, unpublished). For the large intestine, this may reflect the pig's increased capacity with age for fermentation of feedstuffs in the lower gastrointestinal tract. Davey and Bereskin [4] reported that within Large White and Duroc breeds at 100 kg live weight, obese pigs had lighter livers, hearts, kidneys and stomachs than lean pigs, although differences were not always significant. The stomach, small intestine, liver and kidneys are essential organs for the pig's ability to digest, absorb, metabolise and excrete nutrients and minerals. It

is therefore important that these organs are functioning at the earliest possible stage. The optimal function of these organs is important to achieve efficient feed utilization and a high growth rate. On the other hand, these organs have high energy expenditures and thus contribute to a large proportion of the maintenance requirement. Hence, the consequence of a rapid development of the stomach, small intestine, liver and kidneys is that the pig obtains optimal conditions for growth, but at the risk of lower feed efficiency. Some researchers suggest that compensatory growth after a period of restricted feeding could be a result of a lowered energy requirement for maintenance due to delayed growth of visceral organs with muscle growth being almost unaffected [15].

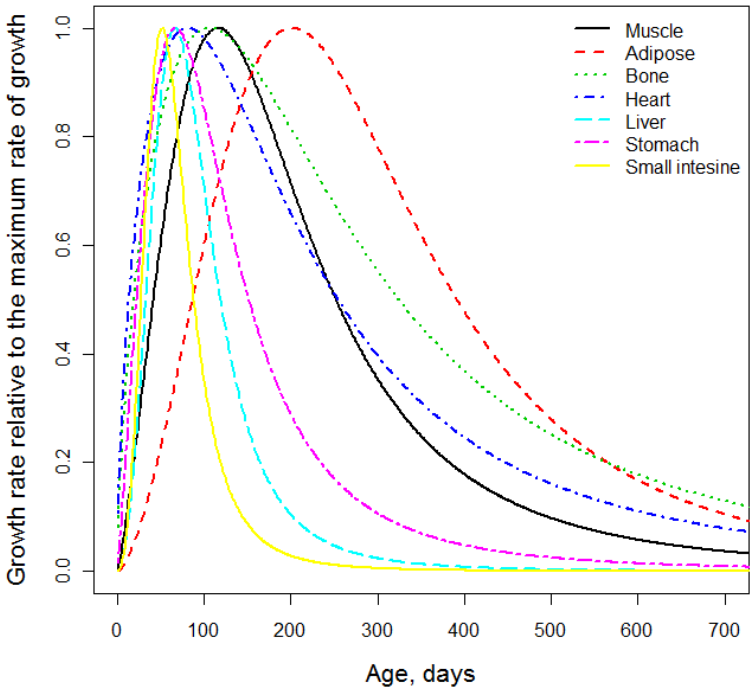

Figure 3.6. Tissue and organ growth rates in barrows expressed relative to the maximum rate of growth. The curves are based on generalized Michaelis Menten functions. Data from Danfær (unpublished).

The growth and development of visceral organs (liver, kidneys, stomach and small intestine (see Table 3.3 and Figure 3.7) in relation to the empty body during the lifetime of pigs seem to be biphasic, although there is little information in the literature to support this finding, e.g. Tess et al. [42]. The primary cause is that only few studies have investigated the growth of visceral organs beyond 120 kg BW.

As shown in Figure 3.7, the growth of the liver occurs in two phases that can be described on log-log scales by two straight lines that intersect at the change point. This change point was estimated at 68 kg EBW as a pooled estimate for all three genders. The gender-specific estimates of the slope of the lines (growth coefficients, b) are listed in Table 3.3, and show that the liver grows nearly isometrically with the rest of the body during the first phase and then negatively allometric during the second phase, which indicates that liver development is stagnating later in life. Similar developmental trends can be observed for the stomach, small intestine and kidneys (Danfær, unpublished).

It can be concluded that pigs develop organs and tissues most critical for life prior to those organs and tissues that are less essential for the survival of the animal. Note in Table 3.3 that postnatal development of the brain is exceedingly negatively allometric with a growth coefficient around 0.2 for the three genders. Furthermore, no point of inflexion could be estimated for the brain as it

simply does not exist post-natally. The growth rate of the pig's brain peaks prenatally and is continuously decreasing after birth (Danfær, unpublished).

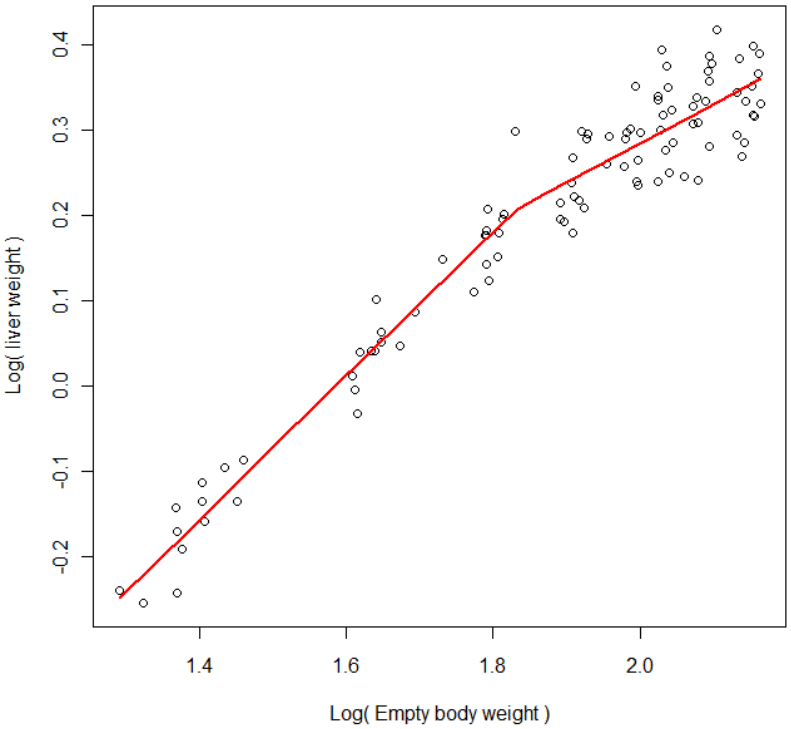

Figure 3.7. Biphasic development of liver mass in relation to empty body weight. The change point is estimated as 1.83 on a log scale (equivalent to 68 kg empty body weight). Data from Danfær (unpublished).

McKeegan [26] was probably the first researcher to describe the order of growth between muscle, bone and adipose tissues in pigs. His results were based on the pioneer work of Hammond [14] who presented the ordering of tissue growth in sheep. Both Hammond's [14] and McKeegan's [26] arguments for the sequence of tissue growth are somewhat unclear and based only on the mass of muscle, bone and adipose tissues and not on their actual growth rates. It has not been possible to find any literature sources that discuss relative growth rates of different tissues as those presented in Figure 3.6. In that sense, the age-related order of the relative growth rate curves from the study of Danfær (unpublished) is unique.

5. Regulation of body tissue growth

It has been stated in this chapter that the composition and energy content of the pig body undergo considerable changes from birth to maturity. It has also been stated that these changes differ between genders. The most pronounced changes are increases in the empty body percentage of lipid and energy, and a decrease in the content of water, whereas the percentage of ash only decreases slightly. The percentage of protein increases until approximately 100 kg BW and then decreases (see Table 3.2). The magnitude of the changes in lipid, energy and water content is highest in barrows and lowest in boars. The rate of protein retention reaches its maximum around market weight (100 kg) or earlier, but at this time the rate of lipid retention is higher than that of protein, and it is still increasing. This is why the percentage of protein in the body decreases from market weight to mature weight. From birth to maturity the lipid:protein ratio in the empty body increases from 0.1 to 1.8, 2.6 and 3.8 in boars, gilts and barrows, respectively.

This illustrates clearly that the patterns of protein and lipid growth are regulated differently and also that the regulation of growth rates and growth composition differs between genders. It is therefore pertinent to ask the following:

- which are the major regulating factors responsible for the changing growth pattern and growth composition as related to age and gender?
- what are the modes of action of the regulating factors?

These questions will be elucidated in the following.

5.1. Protein and lipid turnover

Body protein retention is determined by rates of protein synthesis and protein degradation as lipid retention is determined by rates of lipogenesis and lipolysis. In this context, it is important to distinguish between absolute rates (g/d) and fractional or relative rates (fraction of body pool per day, d-1). The fractional rate of protein retention decreases continuously from birth to maturity (Danfær, unpublished), but the absolute rate increases until 110-140 days of age depending on gender (see Figure 3.3) and then decreases. The fractional and absolute rates of lipid retention follow the same patterns as for protein retention with the maximum absolute rate at 215 days for boars and gilts, and at 250 days of age for barrows.

The age-dependent decline in the fractional rate of body protein retention is primarily due to a developmental decline in the fractional rate of muscle protein synthesis. The fractional rate of protein synthesis (FRS) in pig muscles is about 3-fold higher at birth than at weaning, and this rate of decline is decreasing with age [5]. The fractional rate of protein degradation (FRD) also decreases with age, but at a slower rate than FRS, and at maturity, FRD equals FRS. Chronic changes in FRS are thought to be a result of changes in ribosome numbers. In the newly differentiated muscle, the high ribosomal abundance is the principal factor that enables high rates of protein synthesis, and its reduction with maturation is one mechanism responsible for the general decline in FRS observed for all muscle proteins.

During growth, myofibrillar proteins accumulate faster than sarcoplasmic (i.e. cytoplasmic) proteins due to a higher FRS. As compositional maturity approaches, the rate of synthesis of myofibrillar proteins decreases faster than that of sarcoplasmic proteins, and in the mature muscle, the protein synthesis rate is highest in sarcoplasmic proteins. This means that as pigs get older, the priority in muscle protein synthesis changes from growth of muscle fibres towards turnover of enzymes and other regulatory proteins in the cytoplasma. The stimulation of protein synthesis by insulin in adult porcine muscle appears to be limited to mitochondrial proteins, and the developmental decrease in muscle protein synthesis rates is dominated by myofibrillar proteins [5]. The decline in FRS is more rapid in muscles dominated by fast, glycolytic fibres than in muscles dominated by slow, oxidative fibres.

Very few data on in vivo lipid turnover rates in growing pigs have been published. In one study, Dunshea et al. [8], [9] estimated fractional rates of lipogenesis, lipolysis and lipid retention in 80 kg pigs as 2.3, 0.8 and 1.5%, respectively, of the body lipid pool per day.

5.2. Growth hormone

The secretion of growth hormone (GH) from the anterior lobe of the pituitary is controlled by the hypothalamic factors, GH releasing hormone (GHRH) and somatostatin (SRIF). GHRH stimulates GH secretion through a G-protein, which is a membrane protein coupled to a hormone receptor. Activation of the G-protein/receptor complex by GHRH increases the intracellular concentration of cAMP, which in turn stimulates GH secretion. SRIF inhibits the release of GH from the pituitary somatotrophs and also inhibits a number of gastro-intestinal and pancreatic hormones. In the pituitary somatotrophs, SRIF decreases cAMP, inhibits Ca^{++} channels and activates K^{+} channels, which will decrease synthesis and secretion of GH.

GH is an important regulator of nutrient partitioning among the body tissues as it stimulates bone and skeletal muscle growth, but it reduces or inhibits adipose tissue growth. The effects of GH on tissue metabolism may be direct or indirect via the insulin-like growth factor (IGF-I). The classical somatomedin hypothesis proposes that the indirect effects of GH on growth are mediated by IGF-I produced in the liver. However, this hypothesis has been challenged by the idea that IGF-I is also produced locally in response to GH. For example, when hepatic IGF-I production is blocked by genetic engineering, the concentration of circulating IGF-I levels is decreased to 25% of normal with no immediate effect on the growth rate [2]. This indicates that locally produced IGF-I can compensate - at least temporarily - for lacking production in the liver.

GH increases protein turnover, but the rate of synthesis increases more than the rate of degradation. Muscle protein as well as whole body protein syntheses are stimulated. Thus, GH increases muscle mass as well as skeletal and internal organ masses; this contributes to an increase in heat production, which together with increased organ masses results in higher maintenance requirements. GH promotes the translation step of protein synthesis initiation by stimulating the binding of both met-tRNA and mRNA to the ribosome complex. GH decreases anabolic lipid metabolism and thereby retention of fat. Administration of GH in pigs results in a decreased rate of lipogenesis that does not seem to be mediated via IGF-I, and it does not appear that GH alters lipid retention by increased rate of lipolysis [8], [9].

GH increases the masses of bone and skin as well as the proportion of total visceral mass in all genders. The stimulation of cell division in the growth plate of long bones may involve local production of IGF-I.

In the fed state, GH acts on the liver to stimulate expression of genes for IGF-I and its most important binding protein, IGFBP3. IGF-I is transported in the blood tightly bound to its binding protein, which will keep IGF-I in circulation for a longer time, i.e. increase its half-life. It appears that GH also stimulates expression of IGF-I genes in skeletal muscles, but it is unclear whether GH acts directly on skeletal muscle to stimulate growth. The direct effect of GH on adipocytes is an inhibition of their sensitivity to insulin. This effect, which is not exerted in muscle cells, is closely dependent on the amount of GH in circulation and is consistent in all genders.

The plasma level of GH is very high at birth and decreases sharply during the next 2-3 days. The high GH level contributes to the high rate of protein accretion in the newborn, even in negative energy balance. The plasma level increases again from 10 to 45 days and then decreases from 45 to 140 days of age [22]. The age-dependent decline towards market weight in rates of GH synthesis and secretion seems to be caused by a decrease with age in the sensitivity of the somatotrophic cells to GHRH [7].

Circulating GH is not affected by gender in animals younger than two months. In older pigs, plasma GH concentration is higher in intact males and in females than in castrated males [22].

5.3. IGF-I

GH stimulates transcription of IGF-I and IGFBP3 in the liver, but skeletal muscles and other tissues may also be significant sources of IGF. The hormone stimulates proliferation of satellite cells, increases synthesis and reduces degradation of muscle protein. These effects are modulated by IGF-binding proteins (IGFBP3) and to exert its effects, type I IGF receptors are required. There is considerable homology in structure and function between receptors for IGF-I and insulin, but IGF-I is most likely a long-term regulator in contrast to insulin. Both hormones stimulate protein synthesis initiation by increasing the formation of the active eIF4E-eIF4G complex, which regulates the binding of m-RNA to the ribosome. IGF-I also stimulates bone elongation, which will have a stimulatory effect on muscle growth.

The IGF-I concentration is rather low in the foetus, but increases post-natally, whereas the concentration of IGF-II is high in the foetus and decreases after birth. Thus, IGF-II seems to be more important in the foetus than IGF-I. In prepubertal gilts, the serum levels of IGF-I and IGFBP3 increase with age until about 100 kg BW or 150 days of age, and then the concentration is more or less constant within the observed period of growth, i.e. until 180 days of age [31]. Louveau et al. [22] found that the IGF-I plasma level did not change from 10 to 45 days, but increased between 45 and 140 days of age. In a later study, the plasma concentration of IGF-I in gilts increased from 70 to 168 days and decreased slightly thereafter until 224 days of age [32]. The IGF-I receptor abundance in muscles increases sharply during the suckling period and then decreases in a fashion similar to the fractional rate of protein synthesis, while the receptor affinity is not related to age at any time from 5 to 180 days of age [31]. In older animals, a decrease in skeletal muscle IGF-I and IGFBP3 mRNA with age has been observed, and the number of capillaries per unit of muscle area decreases with age implying that the blood flow per unit of muscle tissue decreases with age. The incorporation of nuclei into muscle fibres seems to level off with age, which could be explained, at least partly, by a decrease in IGF-I receptor number in the muscles.

Serum from male pigs has a 1.77-fold higher level of IGF-I than serum from female pigs at 100 kg BW, but there is no effect of gender on the abundance of IGFBP3 [31]. In older pigs (140 days), the IGF-I level is higher in males than in females and castrated males [22]. Several studies indicate that the difference in muscle growth rate between male and female animals may at least partly be explained by differences in satellite cell proliferation. The effect of testosterone may be permissive with regard to the effect of IGF-I. Thus, the higher muscle growth rate in males compared with females may partly be due to increased satellite cell proliferation caused by elevated plasma IGF-I and testosterone levels.

Circulating IGF-I is directly related to energy intake both in neonatal pigs and in older animals. Increasing milk intake of suckling piglets during seven days after birth results in increased expression of GH receptor mRNA and GH binding in the liver, higher plasma concentrations of IGF-I and IGFBP3 as well as higher growth rates [23].

5.4. Insulin and adrenalin

The secretion of the anabolic hormone insulin from the pancreatic β-cells is stimulated by an increased plasma glucose concentration. Adrenalin is secreted from the adrenal medulla upon stimulation via the sympathetic nervous system in emergency situations. Insulin and glucagon are the major controlling factors of the blood glucose level. Insulin stimulates glucose uptake in muscle and adipose tissues, and glucagon from the pancreatic α-cells promotes gluconeogenesis and glycogenolysis in the liver. Adrenalin stimulates glycogenolysis in muscles and lipolysis in adipose tissue.

Apart from its effect on glucose transport across cell membranes, insulin stimulates amino acid uptake, increases protein synthesis and reduces protein degradation in muscle tissue. Insulin activates formation of a protein complex (initiation factors), which in turn stimulates initiation of protein synthesis. Insulin downregulates muscle protein degradation possible by inhibition of the ubiquitin pathway, but insulin may also affect other pathways of protein degradation by decreasing mRNA levels for cathepsin D and m-calpain. Insulin deficiency leads to poor growth both pre- and post-natally. For example in pigs, a lack of insulin can inhibit normal growth by up to 50%.

Anabolic and catabolic processes in adipocytes are mainly regulated via insulin and adrenergic receptors. The two types of adrenergic receptors are αAR and βAR. In many situations, stimulation of αAR leads to actions antagonistic to stimulation of βAR. The insulin receptor tends to work opposite to βAR to provide the major adipocyte regulatory system. Thus, insulin stimulates the anabolic lipid metabolism, while βAR agonists inhibit these metabolic pathways. Insulin increases the activity of lipoprotein lipase (LPL) and thereby the uptake of fatty acids in adipocytes, which in turn together with the increased glucose availability stimulates lipogenesis. Activation of βAR decreases LPL activity, decreases lipogenesis, and increases lipolysis via stimulation of cAMP. Lipolysis

is also regulated by inhibitory receptors. Stimulation of α2AR inhibits lipolysis as coupled to the Gi protein, which is an inhibitory factor. Adrenalin has both βAR and αAR activity, and the effect of this hormone on lipolysis depends on the relative abundance of βAR and α2AR on the adipocyte. In pigs, there are few α2AR in adipose tissue, so this inhibitory mechanism is not important. The major hormone in this respect is probably insulin, which stimulates cAMP-phosphodiesterase to decrease the intracellular concentration of cAMP.

In neonatal pigs, there is a positive relationship between the postprandial increase in plasma insulin concentration and the rate of muscle protein synthesis. However, the stimulating effect of insulin on muscle protein synthesis and growth decreases with age, and in adult animals the response is small or absent. The abundance of insulin receptor proteins and the downstream signalling proteins in pig muscles are two-fold higher in the early suckling period than at weaning. The developmental decline in the capacity of the intracellular insulin signalling pathway to stimulate initiation of protein synthesis seems to be responsible for the decreasing postprandial effect on muscle protein synthesis.

5.5. Sex hormones

Growth rates in both males and females increase around puberty. In the male, testosterone and dihydrotestosterone are the main testicular hormones that control growth and increase lean muscle mass. Entire males in most species grow faster and contain more skeletal muscle mass and less fat than castrated males. These differences are attributed to higher concentrations of testosterone in the circulation, and intact males exhibit higher rates of protein gain at equal feed intakes. Testosterone appears to have two modes of action. Its direct action on striated muscles is through specific intracellular receptors. Testosterone circulates in the blood bound to specific proteins that assist the entry of the hormone into cells. The indirect effect of androgens on lean muscle growth is thought to be associated with GH. In the female, oestrogens are secreted from the ovary during menstrual cycles. The stimulatory effects of oestrogens on growth are thought to be mediated through an increase in GH. However, actions on the IGF-I axis independent of GH have been identified, and oestrogens may also have direct effects on muscle tissues by binding to oestrogen and androgen receptors.

Sex steroids exert a long-term regulation on tissue metabolism, and significant age and gender effects are associated with the onset of puberty. Differences in fatness between genders become most pronounced at puberty and beyond when testosterone in males and oestrogens in females strongly influence growth and metabolism. Testosterone reduces fat synthesis and deposition, whereas estradiol enhances fat synthesis and deposition in females. Oestrogens are responsible for the inhibition of cell divisions in the growth plate of long bones, and the irreversible conversion of this into compact bone takes place earlier in females than in intact or castrated males. Thus, females have smaller skeletal stature and mature size compared with intact or castrated males.

5.6. Leptin

Adipose tissue has endocrine properties and export many peptides that can modify the biological function of adipocytes and other tissues. Among these is leptin, a cytokine-like peptide. There are leptin receptors in many tissues, e.g. hypothalamus and adipose tissue. As adipose tissue increases in size, more leptin is secreted and hence signals to the brain to decrease feed intake are amplified. In adipose tissue, leptin decreases lipid synthesis and increases lipolysis in pigs. However, the quantitative importance of this in the regulation of growth rate and body composition is not clear.

6. Summary

Until around market weight, age effects on growth rate and body composition in pigs can be rather well explained by developmental changes in plasma levels and activity of hormones, and other

regulating factors. In later growth periods from market weight towards maturity, very few data on the activity of growth regulating hormones in pigs are available.

The GH/IGF-I axis constitutes together with insulin the major regulating system during the accelerating phase of protein and body weight gain (see Figures 3.2 and 3.3). From puberty and onwards, testosterone and oestrogens in concert with GH are responsible for the developing differences between genders in rate and composition of growth (see Table 3.2 and Figure 3.4). Apart from hormonal influences, the much higher rates of lipid retention as compared with protein retention towards maturity in ad lib fed pigs are also caused by histological differences between skeletal muscle and adipose tissue. Muscle fibre cells do not increase in number after birth, and their capacity to increase in size is limited. On the other hand, adipose tissue maintains the ability post-natally to develop new preadipocytes, which can differentiate into adipocytes capable of lipid storage and increased cell volume. This higher capacity for expansion in adipose compared with muscle tissues leads to increasing or excessive fatness in older pigs fed ad lib.

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