

Compensatory growth from muscle structure to meat quality: a review

El crecimiento compensatorio desde la estructura muscular hasta la calidad de la carne: una revisión

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ABSTRACT

Compensatory growth and its effects on meat are relevant but remain controversial due to variable results. While muscle structure is well defined, the mechanisms underlying compensatory growth are still unclear, as they depend on multiple complex factors. Short nutritional restrictions allow higher recovery rates, which are influenced by the quality of post-restriction feeding. However, the duration of restriction periods can affect meat quality, particularly intramuscular fat, thereby influencing tenderness and consumer acceptance. This review defines compensatory growth and examines productive parameters, metabolic changes, and meat characteristics, providing a didactic approach for students and researchers interested in this topic.

KEYWORDS

Acceptance; nutritional restriction; feed efficiency; animal production

RESUMEN

El crecimiento compensatorio y sus efectos en la carne son relevantes pero controvertidos debido a la variabilidad de los resultados. Aunque la estructura muscular está bien definida, los mecanismos del crecimiento compensatorio siguen siendo poco claros, ya que dependen de factores complejos. Las restricciones nutricionales cortas permiten mayores tasas de recuperación, influenciadas por la calidad del alimento posterior. Sin embargo, los períodos de restricción afectan la calidad de la carne, especialmente la grasa intramuscular, influyendo en la ternura y aceptación del consumidor. Esta revisión define el crecimiento compensatorio, analiza parámetros productivos, cambios metabólicos y características de la carne, ofreciendo un enfoque didáctico para estudiantes e investigadores interesados en este tema.

PALABRAS CLAVE

Aceptación; restricción nutricional, eficiencia alimenticia; producción animal

INTRODUCTION

Muscle has long been a focus of scientific and technological interest, extensively studied to understand its structure and function. Animal production, zoo-technical management, and food science converge in exploring the relationship between muscle growth, muscle characteristics, and its potential as meat (Andújar et al., 2003). Muscle is a complex system essential for movement, digestion, and respiration, with its growth and composition tightly regulated. In meat production, *compensatory growth*—an accelerated growth response following a period of nutrient restriction—has gained increasing relevance (Lonergan et al., 2019). This physiological response can reduce feed costs, improves body composition, and enhance carcass yield and meat quality. Studies on compensatory growth have been conducted in aquaculture species (Hvas et al., 2020; Ortiz et al., 2008), mammals (Molina et al., 2007; Sun et al., 2020), and broilers (Butzen et al., 2013), but the results vary due to interacting factors (Lopes et al., 2018). This review provides foundational knowledge on muscle structure and growth, as well as the effects of compensatory growth on productivity and meat quality.

Muscle structure and composition

Muscle tissue plays a central role in animal physiology and meat production. It is classified into three types—smooth, cardiac, and skeletal—each with distinct functions and control mechanisms (Lonergan et al., 2019; Purslow, 2023). Smooth and cardiac muscles are involuntary and essential for internal organ function, while skeletal muscle, which is under voluntary control, is the primary tissue involved in locomotion and meat yield (Andújar et al., 2003). Skeletal muscle constitutes 35-60 % of carcass weight in mammals and is the main component of meat. It is organized hierarchically: muscle fibers are bundled into fascicles, which are surrounded by connective tissue layers—epimysium, perimysium, and endomysium). Muscle fibers are long, multinucleated cells that vary in diameter and structure across species. For example, fish generally have thicker fibers, while mammals possess longer ones (Lonergan et al., 2019). These fibers are classified into Type I, Type II α , and Type II β (Table 1), with their

distribution influencing meat properties such as color and texture. From a compositional standpoint, muscle tissue is composed of approximately 75% water, 18.5% protein, and varying amounts of lipids (1-13%), carbohydrates (mainly glycogen), and non-protein nitrogenous compounds such as creatine, free amino acids, and ATP (Toldrá, 2010). These components not only determine the nutritional and technological value of meat but also respond differently to nutritional strategies like compensatory growth, thereby influencing postmortem quality traits such as tenderness, water-holding capacity, and shelf life.

Table 1. Characteristics of muscle fiber types

Type I	Type II β	Type II α
Slow contraction speed	Fast contraction speed	Fast contraction speed
Aerobic metabolism	Anaerobic metabolism	Aerobic and anaerobic metabolism
High myoglobin content	Low myoglobin content	Intermediate myoglobin content
High content of fatty acids	Low content of fatty acids	Intermediate fatty acid content
Small diameter fibers	Larger diameter fibers	Intermediate diameter fibers
Low glycogen concentration	High glycogen concentration	Intermediate glycogen concentration
Red color	White color	Pink color
Abundant blood supply	Low blood supply	Intermediate blood supply

Muscle growth

Postnatal muscle growth is characterized by changes in both the length and diameter of muscle fibers. The increase in muscle fiber diameter (*hypertrophy*) results from the incorporation of additional contractile proteins at the periphery of the myofibrils, as well as the longitudinal division of myofibrils to generate new

ones (Lonergan et al., 2019). Hypertrophy is achieved by increasing the number of myonuclei and accumulating muscle protein. During early postnatal life, the absolute growth rate increases significantly, with skeletal muscle protein accounting for most of this gain. As a result, muscle protein increases its share of the total body protein pool—from ~30 % in newborns to ~50 % in adults. The growth rate is highest at birth and decreases with development, due to a decline in the rate of protein deposition in muscle. These changes in protein deposition are regulated by the balance between protein synthesis and degradation, such that a reduced deposition rate is typically the result of a decreased rate of protein synthesis (Davis and Fiorotto, 2005).

Nutrition and muscle growth

Whole-body protein deposition in early postnatal life is achieved through highly efficient use of dietary. Evidence suggests that young animals utilize dietary amino acids more efficiently for muscle growth, as they are capable of greater increases in muscle protein synthesis in response to feeding. However, this anabolic response is absent in adult mammals (Tessari et al., 1996). Although feeding stimulates protein synthesis in all tissues during the neonatal period, the effect is most pronounced in skeletal muscle. In this regard, Gómez et al. (2008) state that while feed is the main exogenous factor influencing growth, achieving positive outcomes requires a constant and sufficient supply with an adequate nutritional quality to meet the metabolic demands of development.

Table 2. Average chemical composition of raw muscle tissue from different species.

Species	Water (%)	Protein (%)	Fat (%)	Minerals (%)	CHO (%)	Non-protein nitrogenous compounds	Vitamins and minerals
Beef	75-76	19-20	11	~1	<1	Creatine, ATP	B ₁₂ , iron, zinc
Pork	74-76	19-20	9-10	~1	<1	Creatine, ATP	Thiamine, phosphorus, B ₁₂
Chicken	74-77	20-21	10	~1	<1	Creatine, ATP	Niacin, B ₆ , selenium
Fish	66-81	16-21	0.2-25	1.2-1.5	<1	Creatine, ATP	Vit A, D, E, K, omega3, selenium

Toldrá (2010); United States Department of Agriculture (s.f. a,b), Zhang et al., 2025.

Table 3. Experimental conditions of some compensatory growth studies in various species.

Authors	Species	Age, weight, or size of the animals	Pre-experiment preparation	Tested treatments
Molina et al. (2007)	Cattle (<i>Bos taurus</i> × <i>Bos indicus</i>)	1.5 to 2 years	General clinical check-up and internal and external deworming	Stage I (dry season): 93 days of restriction followed by 93 days refeeding (total = 186 days) Stage II (rainy season): 62 days of restriction followed by 62 days of refeeding (total 124 days)

Butzen et al. (2013)	COBB 500 broilers	1 day	Animals were kept in an environmentally controlled room under a 24-hour light program and had free access to water (<i>ad libitum</i>)	T1: No feed restriction; standard feed <i>ad libitum</i> T2: Quantity restriction (80 % of <i>ad libitum</i> intake) T3: Time-restriction (standard feed available for 8 h/day) T4: Quality restriction (standard feed containing 80 % of the limiting nutrients)
Sun et al. (2020)	Crossbred female piglets (Landrace × Large white as female parent, Duroc as the terminal parent)	32 days, 10.0 ± 0.73 kg	All weaned piglets were offered a diet containing 3.4 Mcal/kg of metabolizable energy, 80 g/kg lactose, 13.5 g/kg of lysine, 5 g/kg of methionine, 2.8 g/kg of tryptophan, 8.5 g/kg of threonine and 206 g/kg of crude protein until they reached the target body weight required for the experiment	30 days of restriction / 74 days of refeeding = 104 days
Miszura et al. (2021)	Nellore (<i>Bos indicus</i>)	Heifers weaned 8 ± 0.75 mo of age and 180 ± 8.6 kg	Not specified	Compensatory gain 6 months of feed restriction followed by 4 months of refeeding (total = 10 months) Alternated CG 2 months feeding / 2 months restriction, 2 months refeeding / 2 months restriction, 2 months refeeding (total = 10 months)
Jia et al. (2018)	Zebra fish (<i>Danio rerio</i>)	3 months, ≈1200 g, 46 cm	Acclimatization for 2 weeks	3 weeks of restriction / 2 weeks of refeeding (total = 5 weeks)
Stumpf et al. (2019)	Lobster (<i>Cherax quadricarinatus</i>)	Free juveniles 0.07 g	Stocked in tanks at an equivalent density of 96 crayfish/m ²	20 days divided into cycles of 4 days of restriction and 4 days of feeding, followed by 40 days of refeeding (total = 60 days)
Hvas et al. (2020)	Atlantic salmon (<i>Salmo salar</i>)	Post-smolt (Aquagen)	Acclimatization	8 weeks of restriction / 5 weeks of refeeding = total 13 weeks; harvest starts at 6 months
Prates et al. (2023)	Pacific white shrimp (<i>Litopenaeus vannamei</i>)	1.78 g (± 0.38 g) Stocking density = 300 shrimp/m ³	All experimental units (n = 18) were filled with 18 L (10 % of the total volume) of biofloc water obtained from a <i>Litopenaeus vannamei</i> grow-out. The tanks were completed with 162 L of seawater, previously treated with a chlorine solution (20 ppm) and neutralized using ascorbic acid powder (1 ppm)	Temperatures Optimum: 28 °C Intermediate: 24 °C Low: 20 °C Feeding regime: 36 days of restriction / 28 days of refeeding (total = 64 days)

Compensatory growth: definition and mechanisms of action

Compensatory growth is defined as a rapid increase in growth rate following a period of nutritional restriction, once animals receive adequate feeding (Molina et al., 2007). It typically occurs when food intake exceeds maintenance requirements and food efficiency improves significantly (Bores et al., 1988). Though commonly associated with nutrition, compensatory growth can also result from other stressors such as overcrowding, extreme temperature, or exposure to toxins (Prates et al., 2023). This phenomenon is particularly relevant in confined production systems, where it can enhance weight gain and feed efficiency, thereby increasing profitability (Lopes et al., 2018). In fish, it is often marked by hyperphagia, improved feed conversion, and rapid growth (Jia et al., 2018).

From a nutritional perspective—focus of this paper—compensatory growth only occurs when preceded by a catabolic phase, during which endogenous energy reserves are depleted. This phase is characterized by elevated circulating levels of growth hormone (GH), ghrelin and cortisol. During the subsequent anabolic (refeeding) phase, hyperphagia and accelerated growth occur, driven by increases levels of insulin-like growth factor-1 (IGF-1) (Mendez et al., 2018). Insulin levels also rise, enhancing the skeletal muscle's response to feeding and increasing protein deposition during the early post-natal development (Davis and Fiorotto, 2005). Although its underlying mechanisms are not fully understood, numerous studies in mammals, poultry, and aquatic species (Table 3) have explored its effects. The following sections summarize key findings.

Studies in terrestrial species

Molina et al. (2007) applied a 62-day nutritional restriction followed by refeeding with grass in beef cattle (*Bos taurus* × *Bos indicus*). The restricted group showed superior daily weight gain during refeeding, ending with a similar final weight to the control group (340.8 kg vs. 349.1 kg) and comparable body condition (6.1 vs 5.9).

Butzen et al. (2013) studied dietary quantity and quality restriction in COBB 500 broilers. While final weights were not significantly affected, females recov-

ered weight faster than males. Notably, quantitative restriction allowed slaughter at 35 days, while time-restriction delayed it to 42 days.

Sun et al. (2020) tested protein restriction (balanced for essential amino acids) in pigs. Despite no significant differences in final weight or performance, the restricted group had lower diarrhea incidence, higher nitrogen retention, and improved digestibility. Muscle showed reduced levels of histidine, methionine, and glycine, while gut and liver showed structural and protein content improvements—suggesting long-term metabolic adaptations.

Miszura et al. (2021) used partial restriction and alternate feeding in *Nellore* heifers over 10 months. The restricted group achieved full compensatory growth (100 % index), final weights similar to controls, and unaffected puberty onset (<18 months). This supports compensatory growth as a viable strategy for managing feed costs and pasture use in tropical systems.

Studies in aquaculture species

Jia et al. (2018) investigated liver function in *Danio rerio* (Hamilton-Buchanan) (zebrafish). After three weeks of restriction, refeeding enhanced mitochondrial function and ATP production, along with increased ROS levels. However, oxidative stress was transient and did not persist beyond 7 days. The study suggests that hepatic signals influence muscle growth via systemic pathways.

Stumpf et al. (2019) evaluated early-stage compensatory growth in *Cherax quadricarinatus* Von Martens (lobster) using intermittent feeding (4 days restricted / 4 days fed). Despite good survival (~65%), compensatory growth was partial, likely due to high density and insufficient refeeding duration. Hvas et al. (2020) studied *Salmo salar* L. (Atlantic salmon) post-smolt. After 8 weeks of restriction, fish reached control size within 6 months of refeeding. However, nutrient restriction delayed sexual maturation—potentially beneficial for production. Authors highlight the need for long-term studies to fully assess compensatory potential in fish.

Prates et al. (2023) tested partial restriction (40% ration) in *Litopenaeus vannamei* Boone (shrimp) across three temperatures. Full compensatory growth was observed, with better feed conversion and growth rates. Protein was preserved as an energy source, while

glycogen and triglyceride levels recovered by the end of refeeding.

Analysis of these studies confirms the three metabolic phases described by Hvas et al. (2020), during restriction-refeeding: glycogen mobilization, lipid utilization, and protein catabolism (severe starvation phase, potentially causing irreversible damage). Severe restriction, as shown by Stumpf et al. (2019), can limit compensatory capacity. According to Ali et al. (2003), growth responses vary by species, growth stage, environment, and restriction severity. Based on this, these authors establish that compensatory growth can occur as: 1) total compensation (same weight as controls); 2) partial compensation (improved growth but below control weight), 3) overcompensation (final weight exceeds controls) and 4) no compensation (no recovery in growth).

All reviewed studies indicate that compensatory growth results in a higher growth rates and improved feed efficiency during refeeding. It also enhances protein, reflected in better nitrogen retention and reduced waste, which is particularly advantageous in aquaculture systems like biofloc, where water renewal is limited.

Despite being a widespread physiological phenomenon, the expression of compensatory growth is highly species-specific, influenced by digestive physiology, hormonal regulation, and metabolic flexibility. In mammals, it involves protein turnover and hormonal shifts. In poultry, fast growth is possible, though limited by early slaughter and skeletal constraints. In fish, indeterminate growth and ectothermy allow for full compensation even after extended restriction.

Finally, although the concept is well-documented, mechanisms remain partially understood. Shorter restriction periods are generally more effective, and the timing of restriction onset is critical, depending on species and production context (Madsen and Bee, 2015). During hyperphagia, hormonal changes boost feed efficiency, allowing recovery rates up to 114%, while longer-term compensation relies on increased dry matter intake.

Converting muscle to meat

Once the animal reaches optimal size, it is slaughtered, and the process of muscle conversion into meat begins.

After death, the disruption of homeostasis triggers a series of energetic, biochemical, and physical changes in the muscle. As the animal is exsanguinated and oxygen is depleted, skeletal muscle shifts to anaerobic metabolism, using glycogen and high-energy phosphates anaerobically to produce ATP (Toldrá, 2010). This process is inefficient and leads to rapid ATP depletion, causing myosin to bind to actin, and triggering rigor mortis within 1-12 hours postmortem, depending on the species and environmental conditions (Matarneh et al., 2017). Anaerobic glycolysis also generates lactic acid, reducing the pH from approximately 7.2 to 5.6 (Matarneh et al., 2017). If this pH drop is too fast or insufficient, it can negatively affect meat color, texture, and water-holding capacity. Factors such as handling before an after slaughter can significantly influence this pH trajectory. During storage, proteolysis—primarily driven by enzymes like calpains—reduces muscle tension, contributing to improved tenderness and flavor (Devine, 2014; Lonergan et al., 2010; Pomponio and Ertbjerg, 2012). Maintaining low storage temperatures is essential to preserve these sensory qualities. Importantly, pre-slaughter nutritional strategies, including compensatory growth, can influence postmortem processes such as pH decline and proteolytic activity, ultimately affecting meat quality and shelf life.

Compensatory growth and meat quality

Until now, the muscular structure, mechanisms of muscle development, and the use of compensatory growth as a strategy to produce animal species of interest for meat supply have been described. At this stage, the various factors involved in muscle growth and the associated metabolic responses have been reviewed. These are mainly related to feeding strategies, which can extend their effects even after slaughter, and are intricately interrelated with the factors influencing the conversion of muscle to meat, thereby affecting key quality parameters. Most studies in the literature focus on the effects of compensatory growth on production performance; however, few have rigorously evaluated its impact on meat quality. The following section discusses the main findings reported in the available studies.

In general, Therkildsen et al. (2011) reported that compensatory growth strategies can improve meat quality in dairy cows, as well as enhance economically relevant traits such as slaughter weight, dressing percentage, EUROP conformation, and intramuscular fat content, along with texture and flavor—without affecting meat color or carcass technological characteristics. Conversely, Butzen et al. (2013) observed that compensatory growth in broilers did not significantly influence carcass composition (back, leg, and breast fractions) or parameters such as thawing loss, cooking loss, shear force or lipid oxidation in breast fillets. It is important to note that water-holding capacity—reflected by thawing and cooking losses—is a key determinant of meat texture, color, flavor, and nutritional value. Low water retention leads to excessive fluid and nutrient loss, resulting in dry, tough, and less palatable meat of inferior quality. These findings should be interpreted with caution. Trocino et al. (2015) demonstrated that although sex and compensatory growth affect the final body weight of chickens, they may also be associated with the onset of myopathies that impair meat quality, highlighting the need for further research.

Hansen et al. (2006) and Keady et al. (2017) found that meat from cattle subjected to compensatory growth exhibited greater hardness (lower tenderness), both instrumentally (shear force) and sensorially (chewiness). The authors suggested that dietary restriction decreases the rate of protein degradation as a compensatory mechanism, which persists postmortem and results in fibers more resistant to proteolysis. In contrast, meat from animals fed *ad libitum* contained more intramuscular fat and showed increased tenderness. However, Therkildsen et al. (2011) reported the opposite trend in beef and pork, respectively: meat from compensatory growth animal was more tender, associated with higher myofibrillar fragmentation index values indicating greater protein degradation at slaughter. No significant differences in intramuscular fat content were observed in those studies.

The inconsistencies in tenderness among studies can be explained by differences in feeding regimens affecting muscle protein turnover. Diets rich in energy toward the end of the feeding period can increase soluble collagen content, influencing meat hardness. Other factors such as the duration and severity of the

restriction period, animal sex, and the specific muscle analyzed also contribute to variability.

The physiological variability following compensatory growth likely stems from species-specific responses and differences in nutritional managements. Protein turnover is a key factor: restrictive diets may suppress proteolysis, producing tougher meat due to intact muscle fibers (Hansen et al., 2006), whereas intensive refeeding may trigger postmortem proteolysis (Therkildsen et al., 2011). Hormonal regulation, including changes in growth hormone, insulin, IGF-1, and cortisol, also plays a critical role in modulating muscle protein synthesis and degradation, influencing intramuscular fat deposition, fiber-type distribution, and enzymatic activity during meat aging. Additionally, muscle fiber composition contributes to variation: animals with a higher proportion of oxidative fibers exhibit lower redness (a^* values), whereas glycolytic fibers accumulate more glycogen, affecting pH and water retention postmortem. Therefore, discrepancies across studies reflect not only experimental differences but also the complex interplay endocrine and muscular adaptations during and after compensatory growth.

Although tenderness is a major determinant of eating quality, color remains the most influential attribute for consumer selection, as it provides the first visual impression of the product. The reviewed studies agree that compensatory growth significantly affects color parameters. Keady et al. (2017) reported that meat from restricted animals presented lower a^* and C^* values compared with non-restricted animals, resulting in a paler, less vivid appearance. This is likely due to a higher proportion of glycolytic fibers with reduced myoglobin content following nutritional restriction. From a commercial standpoint, such discoloration can negatively affect consumer perception, as color serves as a key indicator of freshness and quality. Lehnert et al. (2006) suggested that this effect is linked to nutrient deprivation during restriction, which favors the preservation of fast-twitch (Type II α and II β) fibers with lower myoglobin content. Sensory analyses consistently indicate that meat from non-restricted animals is more acceptable, being easier to cut and chew, and exhibiting higher tenderness—all directly associated with higher intramuscular fat content.

In summary, the impact of compensatory growth on meat composition is variable but commonly involves changes in intramuscular fat content and water-holding capacity—critical attributes for consumer acceptance and technological performance. While some studies report improved carcass yield and nutrient retention, others note increased toughness or altered color characteristics. Furthermore, metabolism adjustments and modified protein turnover associated with compensatory growth influence postmortem enzymatic activity, affecting meat aging, oxidation, and shelf life. Therefore, although compensatory growth can enhance production efficiency, its implications for meat quality must be evaluated on a species-specific basis, considering both the severity and duration of the restriction period.

CONCLUSIONS

The study and understanding of postnatal muscle development in animals of commercial importance, as well as the design of feeding strategies that promote greater meat production with optimal quality, are essential for improving efficiency in the meat industry. Although further research is needed to clearly elucidate the physiological mechanisms underlying compensatory growth across different species, existing evidence support its use as an effective strategy to reduce production costs—particularly in systems facing seasonal feed shortages, as often occurs in tropical regions. From a purely productive perspective, this approach is advantageous; however, from a sustainability standpoint, important findings highlight improved nutrient utilization and reduces waste generation. These aspects may attract further scientific interest and encourage new studies integrating a sustainability framework. Finally, it is concluded that identifying consistent patterns is crucial to ensure that meat reaching the consumer maintains high quality, without overlooking intangible quality parameters such as animal welfare.

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