APPROACHES TO MANIPULATE POST-MORTEM METABOLISM AND MEAT QUALITY

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Summary

The properties of meat that are of most interest to the consumer are strongly affected by perimortal treatments: the physical conditions that are imposed on the animal in the last few days of life and on the carcass in the first few hours post-mortem. The effects of these treatments are exerted through anaerobic glycolysis, the post-mortem breakdown of glycogen to lactic acid, and in this review are discussed with special reference to beef. The extent of glycolysis is a powerful influence on several meat qualities, but is important mainly because of its effect on colour: a low ultimate pH promotes a bright and attractive appearance. In beef, it is stress rather than under-nutrition that elevates ultimate pH; it is thus the prevention of stress (particularly in the few days preceding slaughter) that must be the goal if dark-cutting meat is to be eliminated. The rate of glycolysis is a major determinant of tenderness through its effects on cold shortening and (probably) proteolytic-enzyme activity. It depends primarily on cooling rate and use of electrical stimulation, and is thus largely controllable; an intermediate rate (one that produces a 3-hour loin pH of about 6) maximizes tenderness. It is suggested that the measurement of pH_3 may be of use to optimize stimulation parameters, predict eating quality, and reduce aging without quality reduction.

Introduction

The word *quality* can be defined in several ways: a distinguishing attribute, an essential property, a characteristic that determines rank, a degree of excellence. When applied to beef, however, quality has assumed another meaning, particularly in the United States where it is often used as a synonym (or even a definition) of *marbling*. The unfortunate confounding of these two very different words is due to the once-held belief that, among carcasses of similar maturity, it is marbling that determines (and can be used to predict) eating quality. This quaint notion, clearly implying that palatability is affected only by *live*-animal factors, is perpetuated in the U.S. quality-grading system, despite almost a half-century of evidence that eating quality is also strongly influenced by the *post-mortem* treatment imposed on the carcass.

In this review, *meat quality* means quality as perceived by the ultimate consumer: eating quality and colour. This definition is entirely compatible with the view expressed over 50 years ago -- I believe by John Hammond and E. H. Callow of Cambridge University -- that quality is what the customer wants and is prepared to pay a premium to receive: perhaps the simplest and most direct description yet devised. And among the several attributes that determine eating quality, tenderness will receive the most attention, for it varies much more widely than the other desirable properties.

Post-mortem muscle metabolism

The death of an animal does not coincide with the death of its musculature; the instant of slaughter marks only the start of the tissue's dying process, which in the bovine carcass may take 24 hours or more. Strong and orderly metabolic activity continues during this early-post-mortem period, though the end-products and their disposition are different than in life because of the cessation of blood

flow. Since oxygen cannot enter the tissue, oxidation can no longer take place, so the product of glycogen breakdown is now lactic acid and not carbon dioxide. Since waste can no longer leave the tissue, this lactic acid accumulates in the musculature, gradually lowering the pH from near neutrality to a more or less mildly acid value. Since the non-oxidative splitting of glycogen regenerates far less ATP than is formed oxidatively in life, cross-bridges form between the tissue's thick and thin filaments, locking them together in rigor mortis and sometimes causing significant shortening. And since considerable quantities of ions -- principally lactate and phosphate -- are produced by anaerobic glycolysis, the ionic strength rises appreciably.

The transition from muscle to meat -- from life to death -- is thus accompanied by quantitative changes in several metabolites (glycogen, ATP, lactic acid, phosphate) and physical properties (pH, ionic strength, extensibility, contractility). The glycolytic process varies widely among carcasses in its **extent**, and can be made to vary widely in its **rate**. The first of these parameters -- how far it goes -- is determined by live-animal factors, and is controllable to a limited degree; the second -- how fast it goes -- is determined (in beef) almost entirely by the treatment administered to the carcass in the early-post-mortem period, and is thus much more easily manipulated. Since both the extent and the rate of glycolysis can exert strong effects on beef quality, it is necessary to examine each of them in more detail.

The extent of glycolysis

The pH of bovine muscle declines during the first 24 to 36 hours post-mortem because of the conversion of glycogen to lactic acid. The at-death (or initial) pH is about 6.8 to 7.0, though some muscles have values consistently above or below this range, and it may also be affected by fatigue or stress just prior to slaughter. The glycogen content of the muscles of reasonably well-fed, rested and unstressed cattle in life is usually 1 to 2% of the tissue's weight, and its post-mortem breakdown continues until a pH of about 5.4 to 5.6 is attained. Regardless of the amount of glycogen still remaining, glycolysis ceases at this point (Howard and Lawrie, 1956), presumably because the increasingly acid condition inhibits one or more of the participating enzymes. Several important and desirable properties of beef are favoured by attainment of a low ultimate pH (pH), including colour (MacDougall and Jones, 1981), flavour (Dransfield, 1981) and storage life (Newton and Gill, 1978).

A low at-death glycogen content results in a raised ultimate pH that, in extreme cases, can be near 7 (Howard and Lawrie, 1956; Warriss *et al.*, 1984). In contrast to several other species, cattle are very resistant to fasting-induced pH elevation. Even after 28 days without feed, steers studied by Howard and Lawrie (1956) still had enough glycogen in their muscles to give normal ultimate values of below 5.5. The same authors showed that various combinations of fasting, prolonged travel and enforced exercise were successful in producing somewhat higher values; but -- since a high pHu is clearly not due in general to animal abuse of this severity -- it became clear that some other factor must be largely responsible for the condition. This other factor is now recognized as stress, and it is obvious that animals vary widely in their individual abilities to resist it. It is appropriate to quote directly from Lawrie's classical paper on stress and dark-cutting beef (1958): *Certain steers were of an excitable temperament, and some short-range*

muscular tension, not manifested by external movement, reduced the glycogen reserves in their muscles to a chronically low level.

The incidence of high-pHu beef varies widely. In a nineteen-nation survey reported by Tarrant (1981), the occurrence of dark cutting -- the most obvious indicator of the condition -- ranged among countries from 0 to 11% in steers, heifers and cows, and from 1 to 20% in young bulls. Early studies on epinephrine-induced stress (summarized by Hedrick, 1981) and more recent investigations on behavioural stress (McVeigh and Tarrant, 1983) have demonstrated that remarkably high rates of muscle-glycogen depletion can be triggered by hormone treatment or (in susceptible animals) by exposure to stressful situations. The latter workers have also shown that several post-stress days are required for restoration of muscle glycogen in briefly stressed bulls.

Although a dark colour is the most easily detected consequence of a high ultimate pH, it is by no means the only one. The less acid pH encourages bacterial proliferation and thus shortens the product's shelf life (Newton and Gill, 1978). In addition, protein degradation (and thus the production of spoilage odors) starts earlier because of the virtual absence of glucose as preferred bacterial substrate (Gill and Newton, 1981). High ultimate pH does not appear to affect juiciness, but it certainly causes decreases in both flavour and acceptability (Bouton *et al.*, 1957). On the other hand, the high water-holding capacity of dark-cutting beef can be an advantage in the preparation of various processed-meat products.

The relationship between ultimate pH and tenderness is complex and still far from understood. Numerous investigators agree that beef of high pHu is very tender, the degree of tenderness increasing as pH 7 is approached (Bouton *et al.*, 1957, 1973; Penny *et al.*, 1963; Fredeen *et al.*, 1974; Dransfield, 1981; Yu and Lee, 1986; Purchas, 1990; Jeremiah *et al.*, 1991). Several explanations, based on established or probable consequences of elevated pH, have been offered: higher water-holding capacity, enhanced neutral-protease activity, reduced cooking shrinkage, and negligible cold shortening. A more likely explanation, I believe, is the smaller degree of protein denaturation that cooking causes in meat of higher ultimate pH. (Evidence for this conclusion is provided by the almost raw appearance of broiled steak from high-pH meat, and by the study of Trout (1989) on the highly pH-dependent heat denaturation of myoglobin.) Thus high-pH meat, cooked to the customary end-point temperature, corresponds in its denaturation extent to normal-pH meat that has been heated to a much lower temperature: a treatment known to produce a much more tender product (Davey and Gilbert, 1974). Whatever the reasons for the tenderness/high-pH association, the tenderizing effect is of little practical significance. The accompanying colour and flavour defects clearly outweigh the questionable advantage of greater (and sometimes excessive) tenderness; it is thus the prevention of high ultimate pH, and not its promotion, that is the goal.

Most studies of the pHu/tenderness relationship have revealed a toughness maximum at about pHu 6, but there is no agreement among them on the effects of lower ultimate pH. Bouton *et al.* (1957) and Jeremiah *et al.* (1991) reported appreciable tenderizing as pHu declined below 6, and Luckett *et al.* (1975) noted a very significant positive correlation between 6-day pH and Warner-Bratzler shear values within the range 5.3 to 5.8; on the other hand, Fredeen *et al.* (1974) and Dransfield (1981) detected no pHu influence at all below pH 6. The results of a recent Wisconsin study on the loins of 120 A-maturity steers agree with those

of the former workers, even though the ultimate pH values were all within a narrow range that would generally be considered normal (Table 1). A very highly significant mean difference in Warner-Bratzler shear value (1.57 unit, t = 5.9) was associated with a mean difference in ultimate pH of only 0.10 unit. These results strongly suggest a powerful pHu influence on quality, even within the normal ultimate-pH range, and raise several interesting and potentially important questions: Could quite small differences in ultimate pH be partly responsible for the puzzling tenderness variability so often encountered among similar and similarly treated carcasses? Or among different breeds or sexes? Could the apparent toughening effects of growth promoters, noted in several species (Jones *et al.*, 1985; Hamby *et al.*, 1986; Hanrahan *et al.*, 1987; Smith, 1987), be due to an elevation of pHu, as has been reported by Hanrahan *et al.* (1987) for cimaterol and by Beermann *et al.* (1990) for porcine somatotropin? If tenderness is indeed so dependent on quite small pHu differences, what determines the precise pH at which glycolysis ceases in muscles that contain plenty of glycogen? In this connection, it is to be noted that, even in muscles containing ample glycogen, the pH does not fall to a uniform low point, but attains a seemingly random value within the approximate range 5.35-5.7 (Howard and Lawrie, 1956; Warriss *et al.*, 1984).

Table 1. Tenderness and ultimate pH.

pHu range (n)	5.37-5.50(94)	5.51-5.65(26)
pHu mean (SD)	5.46 (.028)	5.56 (.041)
W-B shear (SD)	5.90 (1.06)	7.47 (1.52)

Further studies should be undertaken of this proposed pHu/tenderness relationship in the low-pH region, but credible results will be obtained only if pH measurements are made with extreme care to minimize errors. In particular, the iodoacetate/KCl homogenization procedure of Bendall (1973) is recommended; samples should be excised at 48 hours post-mortem (since at 24 hours the ultimate pH is often still unattained); buffer solutions and homogenates should be equilibrated to ambient temperature; and pH-meter standardization should be confirmed both before and after measurements have been taken. I believe these precautions will be necessary if such small pH differences are to be meaningful, and not merely reflective of inaccurate or insensitive procedures. Perhaps it is because these steps have not been taken routinely that this potentially important relationship has remained obscure and largely unsuspected to the present.

What can be done to manipulate the extent of early-post-mortem glycolysis? Despite significant advances in knowledge in recent years, we are still far from a complete understanding of the biological mechanisms involved: both those that control the glycogen content of muscle and those that are controlled by it. Feeding level is clearly not the primary determinant of ultimate pH (as it is, for instance, in the rabbit: Bate-Smith and Bendall, 1949). Indeed, it is scarcely a determinant at all. Stress, on the other hand, is now recognized as an extremely effective depletor of glycogen, the level of which may decrease by almost two-thirds within five hours (McVeigh and Tarrant, 1983). We also know that mixing stress and adrenaline-induced stress, although appearing to cause similar patterns of glycogen disappearance, are certainly not identical in nature (Lacourt and Tarrant, 1985). Thus the ß-adrenergic blocking agent propranolol (which prevents dark cutting in adrenaline-treated cattle: Ashmore *et al.*, 1973) is ineffective against

mixing-provoked stress (McVeigh and Tarrant, 1983). Reserpine and phenothiazine tranquilizers, administered prior to stress, are also unable to prevent dark cutting (Hedrick, 1981).

The avoidance of high ultimate-pH values is thus still highly dependent on the avoidance of stress, no matter what its cause: overcrowding, social regrouping, overexertion, adverse climatic conditions, excitement during loading and transport, dehydration, physical injury, etc. In this regard we may note with optimism two recent trends: one toward the construction of stock-handling and -holding facilities designed to reduce both physical and emotional trauma (e.g., Grandin, 1980), and the other toward a growing public concern that encourages (and will eventually demand) a more humane (and thus less stressful) treatment of animals.

The rate of glycolysis

In the first few post-mortem hours, skeletal muscle is a very sensitive tissue, responding strongly to a variety of administered insults. This quite brief period of vulnerability is a small window of opportunity in which quality-affecting treatments of several types can be applied: procedures that could not be attempted on the living animal, and that would be totally ineffective if used when the musculature was close to (or had attained) rigor mortis.

Several physical treatments exert marked effects on glycolytic rate and meat properties when applied to the pre-rigor tissue. A pressure of about 1000 atmospheres, even if used for only a minute at 30°C, causes extremely rapid glycolysis and very marked tenderizing despite considerable shortening; the phenomenon has been studied extensively, and has been reviewed by its discoverer (Macfarlane, 1985). The very rapid cooking of pre-rigor muscle arrests glycolysis and causes massive shortening, reduced cooking loss, and marked tenderizing (Cia and Marsh, 1976). Rapid pre-rigor freezing followed by fairly fast thawing can result in extremely fast glycolysis, shortening of up to 80%, excessive drip loss and appreciable tenderizing (Marsh and Thompson, 1957; Marsh and Leet, 1966). These treatments and their consequences are all of interest; the pressure technique, for instance, is a research tool that has contributed substantially to current knowledge of meat texture (Harris and Shorthose, 1988) and thaw shortening has been encountered in the commercial freezing of whalemeat (Sharp and Marsh, 1953). None of them, however, is at present either a practical problem or a practical solution to a problem.

By contrast, two other physical processes are of very real contemporary interest and concern: rapid and early cooling as a quality detractor, and electrical stimulation (ES) as a quality promoter. Neither of them is a recent finding; the ES patent application was filed in 1947 and became a public document four years later (Harsham and Deatherage, 1951), and the discovery of cold shortening was reported 30 years ago (Locker and Hagyard, 1963). Although hundreds of papers have been published on these two topics, there is still a strong need for research at both the basic and applied levels of inquiry, for there are many pertinent questions to be answered and many tentative answers to be questioned.

Before discussing the effects of ES on post-mortem metabolism, we must consider the consequences of the other controllable variable, cooling rate, for this largely

determines the pattern of several metabolic and physical changes undergone by the tissue. The best-known influence of cooling rate is on muscle length. Cold shortening occurs in beef or lamb if the pre-rigor muscle is cooled fairly rapidly (Locker and Hagyard, 1963), and is accompanied by a several-fold toughening if the contraction approaches 35% (Marsh and Leet, 1966). The time course of glycolysis and glycolysis-related changes is also strongly affected by the rate of cooling, particularly rigor onset and pH decline (Marsh, 1954). Because of its effects on temperature and pH, the rate also influences proteolytic-enzyme activity (Koohmaraie *et al.*, 1986; Dransfield, 1992), and for the same reason is at least a partial determinant in bovine muscle of the release of calcium ions (Lacourt, 1971; Pearson, 1977), which are needed for calpain activation. It is these cooling rate-induced differences in shortening, rigor-onset rate, calcium-ion release and proteolytic-enzyme activity that may be largely responsible for variability in beef eating quality.

In its first large-scale industrial application, ES was used for a single relatively simple purpose: to overcome a massive shortening-induced toughening caused by the early-post-mortem fast freezing of lamb carcasses (Locker *et al.*, 1975). Potentially complicating factors -- proteolytic-enzyme release, calcium-ion activation of proteolysis, temperature-dependent aging, etc. -- either did not exist or were of negligible consequence. The problem was a *pure* one of cold-provoked length change, uncluttered by other conceivable causes; the obvious solution was to accelerate glycolysis and rigor onset, and thus to *lock* the tissue into a relaxed configuration before it reached a temperature low enough to trigger a shortening response (Carse, 1973).

It was when the ES process was applied to beef that complications arose, though they were not recognized for some time. A light-weight lamb carcass, exposed to blast-freezing conditions (-18C, 3 m/s: Marsh *et al.*, 1968), obviously cools very much more quickly than a steer side undergoing the comparatively mild air-velocity and temperature conditions of a typical beef cooler. The bovine muscle's cold-shortening tendency is thus less than that of the lamb tissue because of both its slower attainment of a low internal temperature and its earlier start to cross-bridge formation. In addition, the slower cooling of the beef provides a more favorable environment for proteolytic-enzyme activation and activity. It is likely, therefore, that cold shortening is a less severe toughening agent in beef than in lamb, and that proteolysis plays a significant tenderizing role in bovine muscle.

In the late seventies, when ES technology was under development for beef-quality enhancement, proteolysis in post-mortem muscle was assumed to be due exclusively to the lysosomal enzymes (cathepsins), which require quite acid conditions for release and activation. In addition, it was widely held that aging could start only with rigor completion (see Marsh (1983) for numerous references to this concept). Both of these beliefs -- the enzymes' need for an acid environment, and the aging process's need for rigor -- led to the view that ES would be most effective if it produced the fastest possible rate of glycolysis. It was argued that a great acceleration of rigor onset and pH fall would eliminate cold shortening, provoke strong catheptic activity, and allow the early initiation of proteolysis while the tissue -- though in rigor -- was still warm (Savell *et al.*, 1977; Dutson *et al.*, 1980). Yet another incentive to maximize glycolytic rate was revealed when a very rapid pH fall was shown to give better lean color, improved marbling scores, and (sometimes) higher U.S. quality grades (Smith *et al.*, 1980; Smith, 1985), particularly when a higher voltage (550 vs 150) was used (McKeith *et al.*, 1981). [This cosmetic factor is more important in the United States than

elsewhere, and has been quoted (Terrell *et al.*, 1982) as the principal incentive for U.S. use of stimulation.] It was largely these observations and suppositions that guided the commercial development of stimulators in the U.S. (Savell, 1985).

It soon became apparent, however, that these concepts could not entirely explain the observed effects of ES. In a series of studies using 2-Hz stimulation for five minutes and very mild early-post-mortem cooling conditions, all putative tenderizing mechanisms were eliminated except rapid acidification; the stimulated sides were found to be significantly tougher than both the controls (Marsh *et al.*, 1981; Takahashi *et al.*, 1984) and other sides receiving 60-Hz stimulation for 10 seconds (Takahashi *et al.*, 1987). Later studies in Wisconsin (Marsh *et al.*, 1987, 1988) and Nevada (Pike *et al.*, 1993) have confirmed and considerably extended these observations. It is now clear that peak tenderness -- at least in bovine *longissimus* muscle -- requires an intermediate rate of glycolysis, and not the fastest possible rate as earlier believed. This conclusion is supported by results of Unruh *et al.* (1984; 1986) and Pommier *et al.* (1987), all of whom have demonstrated beef toughening when sides were both stimulated and subjected to delayed or very slow cooling: treatment combinations that induce very high glycolytic rates.

Partial data from Marsh *et al.* (1987) are presented in Table 2 to illustrate the desirability of achieving an intermediate rate of glycolysis.

Table 2. Tenderness and glycolytic rate.

pH3 range (n)	***5.70***	***<5.90-6.29***	***6.50***
Tenderness:			
Panel (unaged)	4.53^{a}	5.38^{b}	4.01^{a}
W-B shear (unaged)	4.79^{b}	4.27^{b}	5.84^{c}
W-B shear (aged)	4.24^{a}	3.27^{b}	3.90^{a}

^{a,b,c} Within each horizontal line, values with different superscripts are significantly different.

The very wide range of glycolytic rates was obtained by varying the early-post-mortem cooling conditions, the duration of ES, and the electrical frequency of the stimulating current. Panel tenderness was assessed on a scale of 1 (extremely tough) to 8 (extremely tender); unaged meat received no aging beyond the standard 48-hours chilling, whereas aged meat was held for an additional 14 days at 2°C.

For several reasons, this concept -- if confirmed -- might be of some practical interest and significance:

First, it would indicate that it is not only unnecessary to achieve an extremely rapid glycolytic rate for tenderness optimization: it is also undesirable. (This would not be the only unfortunate consequence of very fast pH fall in beef; it is already believed to cause a decrease in water binding: Eikelenboom and Smulders, 1986). It would thus become rather easier to integrate stimulation into plant operations, since a shorter ES duration would suffice.

Second, aging would be more effective; Table 2 shows that an intermediate pH_3 not only gives a more tender unaged product but also encourages more aging than does a very low one.

Third, the occasional or periodic determination of pH_3 would provide works' personnel with a simple measure of stimulator effectiveness, and would indicate if ES duration should be altered to give the most effective rate of pH fall.

Fourth, the pH_3 concept just might provide an entirely new basis for the quality grading of beef.

Four more investigations of the pH_3/tenderness relationship have been undertaken in Wisconsin since the first study was reported (Marsh *et al.*, 1987). In total, 400 experimental sides from 340 A-maturity steers of three breeds have been examined after various early-post-mortem treatment combinations that used differing cooling rates and a wide variety of ES voltages, frequencies, durations, PM times of application, and electrode systems. In all of them, very significant correlations were found between pH_3 and all three tenderness measures: panel unaged, and Warner-Bratzler both unaged and aged. Quadratic (second-order) correlations were always appreciably higher than simple (linear) correlations; thus in the first study (n=120), r (linear) was .28 while r (quadratic) was .53. By contrast, the correlation between tenderness and marbling (which is the sole quality-grade determinant in carcasses of the same maturity) failed to achieve significance in every case. (This result is in full agreement with that of Smith *et al.* (1988), who observed a low (-.08) marbling/tenderness correlation in A-maturity carcasses of limited marbling range: slight-modest.)

In our earlier studies of the glycolytic-rate influence on eating quality, pH_3 was determined on small excised loin samples homogenized in the iodoacetate/KCl reagent of Bendall (1973). Although this procedure is accurate and permits later rechecking of values, it is slow, destructive, and totally impractical for in-plant use. In the latest study, pH_3 was determined both by the homogenate method and by spear (glass) electrode, measurements by the latter method being made at electrode-tip depths of 1.3, 2.5 and 3.8 cm into the loin at the 10-11 rib level, adjacent to the homogenate-sample site. The comparisons revealed very gratifying correlations between the two methods at each of the electrode-penetration depths (r=.92, .94, and .89 respectively), but they also showed a remarkably high pH_3 dependence on sampling depth. The mean difference between the 1.3 and 3.8 cm readings was 0.76 pH unit; in several of the (unstimulated) muscles that were still actively glycolysing at all depths at three hours, the difference was more than one unit.

The strong influence of depth, of course, is due to the steep temperature gradient that exists in the loin by three hours post-mortem (Ringkob *et al.*, 1989), for glycolytic rate in beef is highly temperature dependent (Marsh, 1954). Appreciable pH and temperature gradients in several muscles of the cooling beef carcass have been described by Tarrant and Mothersill (1977). The depth effect on pH_3 is eliminated if the electrode is always inserted to the same depth into the musculature. In our recent experience, an electrode-tip depth of 2.5 cm gives pH_3 readings that are close to the values obtained by the homogenate method. Unless precautions are taken to ensure a constant penetration depth (e.g., with a collar on the electrode), it is likely that only a very poor pH_3/tenderness correlation will be observed, and highly probable that the toughening effect of very low pH_3 values will be undetected.

Table 3. pH_3 and marbling as tenderness predictors.

Comparison (n=35)	*Correlation coefficient: Linear*	*Quadratic*	*pH_3 at peak*
pHiodo/Panel	-.38	.57	5.97
pHiodo/W-B	+.50	.66	5.92
pHprobe/Panel	-.49	.63	5.94
pHprobe/W-B	+.62	.75	5.88
Marbling/Panel	-.10		
Marbling/W-B	+.28		

The results of our latest study, designed specifically to compare the two methods of determining pH_3, are shown in Table 3. The 35 carcasses, all from the same source, were A-maturity and of fairly similar marbling (Tr70--Sm60). Their early-PM treatments varied widely: 12-Hz ES at 25 or 380 V for 0, 9, 25 or 120 sec., and widely differing cooling rates that gave three-hour mid-loin temperatures of 22.0-34.8°C. The loins were unaged beyond the usual 2day post-mortem at 0-2°C. For n=35, correlation coefficients of .33, .43 and .53 are significant at probability levels of .05, .01 and .001 respectively. (The r value of +.28 for the marbling/Warner Bratzler correlation was numerically much higher than in our other studies (0.10); fortunately, it still failed to achieve significance, for its positive sign indicated greater toughness with increased marbling!) The pH_3 values at peak tenderness were calculated from the computer-generated quadratic equations, and conformed with those of all our studies: invariably between 5.8 and 6.1, and almost always in the range 5.9-6.05.

Conclusion

Whatever may be the bases of current quality-grading systems, it is now very clear that meat quality does not depend solely on live-animal factors. Indeed, recent evidence strongly suggests that eating quality is determined more by events in the first day post-mortem than in the entire lifetime of the animal. Much remains to be learned if we are to improve our basic understanding of quality attainment and our practical knowledge to achieve it routinely. If present concepts are validated and extended, however, the meat packer and processor will have a much greater ability -- and responsibility -- to enhance and maintain the eating quality of meat.

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