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Meat and fish flesh quality improvement with proteomic applications



B. Picard,* F. Lefèvre,† and B. Lebret ‡§

* INRA, UMR1213 Herbivores, F-63122 Saint-Genès-Champanelle, France

† INRA, UR1037 Fish Physiology and Genomics, F-35042 Rennes, France

‡ INRA, UMR1348 Pegase, F-35590 Saint-Gilles, France

§ Agrocampus Ouest, UMR1348 Pegase, F-35000 Rennes, France

Implications

- Proteomics technologies have been used to better understand the development of complex phenotypic traits such as meat and fish flesh quality and identify biomarkers of these quality traits.
- Many protein biomarkers of beef tenderness have been highlighted and are currently under validation on different muscle and animal types. Biomarkers of fish flesh firmness, and of many sensory (tenderness) and technological (drip loss and pale, soft, and exudative defect) pork quality traits, have also been identified.
- Expected outcomes are to provide control tools of meat quality evaluation usable in the livestock sector and meat industries in the near future.

Key words: biomarkers, sensory quality, skeletal muscle, technological quality, texture

Introduction

Thanks to the sequencing of genomes, it is now possible to decode and locate many thousands of genes in a genome. This available information can be used for purposes of knowledge, diagnosis, or selection. The development of tools that accompanied this progress allows for the simultaneous analysis of thousands of genes (DNA chips), transcripts (transcriptomics), and proteins (proteomics; Figure 1).

The emergence of these functional genomic technologies enables the measurement of complex phenotypes, such as traits related to the quality of food products. Because meat quality traits result from genetic and environment interactions, working at the gene or protein expression level allows scientists to take both the genetic potential of animals and its modulation by the environment into account. Thus, biomarkers of gene expression appear more accurate than genetic markers to better understand biological processes determining phenotypes, and explain and predict meat quality variations (te Pas et al., 2011). The principle is to identify

genes and/or proteins whose expression or abundance is associated to the value of a phenotypic trait of interest, such as the quality of a product. These genes or proteins are thus considered as biomarkers that could be used to predict a given phenotype. In this review, we will focus on studies undertaken at the protein level, because proteins have the advantage to represent the final result of a complex gene expression system where different isoforms may exist although corresponding to a single gene because of post transcriptional modifications. Moreover, proteins are thought to be the main effector of some quality variables of great interest such as firmness. The significant interest of proteomic approaches in the field of animal and meat science to improve knowledge on biological mechanisms determining phenotypes and identify biomarkers of traits of interest has been highlighted in recent reviews (Hollung et al., 2007; Bendixen et al., 2011).

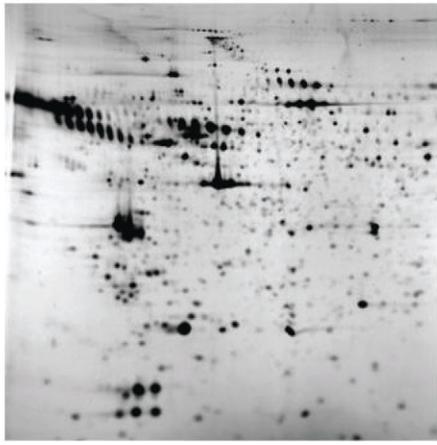
In this review we will focus on the recent proteomic studies conducted in relation with meat quality determination, evaluation, and improvement, in cattle, pig, and fish species by French INRA groups. In these three models, proteomics has been used to study specific questions according to each production sector.

Beef Quality: From Biomarkers to Phenotyping Tools

Although several biochemical factors are well known and a number of quantitative trait loci (QTL) have been determined, control of the variability in beef tenderness remains a major challenge for the beef industry. Beef tenderness presents a strong and uncontrolled variability that induces a consumer's dissatisfaction and partly explains the decrease in beef consumption. Moreover, this quality can be assessed only after slaughter by mechanical measurements such as the Warner-Bratzler test or by a sensory analysis panel. There is no technique for measuring tenderness on the living animal. So, the beef industry is waiting for tools to estimate the potential of tenderness from the live animal or carcass (Figure 2).

The strategy developed over the past 10 years has been 1) to search for biomarkers of tenderness by comparing extreme groups of animals on this criterion with genomic tools; 2) to validate the relationships between these markers and tenderness on large numbers of animals; 3) to precisely define the influence of management factors on the expression of these

First dimension: isoelectric point



Second dimension:
molecular weight

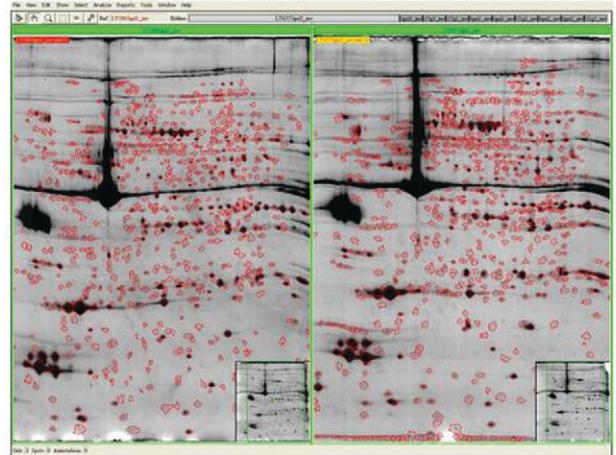
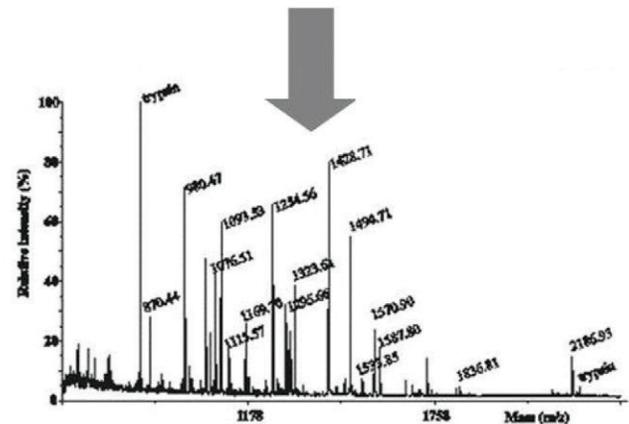


Image Analysis



Mass Spectrometry

MASCOT Peptide Mass Fingerprint

Your name: thibault Email: tchaze@yahoo.fr

Search title:

Database: MSDB

Taxonomy: All entries

Enzyme: Trypsin Allow up to: 1 missed cleavages

Fixed modifications: AB_old_ICATd0 (C), AB_old_ICATd8 (C), Acetyl (K), Acetyl (N-term), Amide (C-term)

Variable modifications: AB_old_ICATd0 (C), AB_old_ICATd8 (C), Acetyl (K), Acetyl (N-term), Amide (C-term)

Protein mass: kDa Peptide tol. s: 1.0 Da

Mass values: MH+ M_r Monoisotopic Average

Data file:

Query: NB Contents of this field are ignored if a data file is specified.

Overview: Report top: 20 hits

Identification of Protein

Figure 1. Different steps of proteomic analysis.

biomarkers; 4) to further analyze the biological functions involved in the development of tenderness; and finally 5) to use this knowledge to build tools used by industry to estimate the quality of an animal before or after slaughter.

Use of Genomic Tools for Identifying Biomarkers of Tenderness: Comparative Proteomics

Over the years, several proteomic analyses were performed in specific programs to better understand the mechanisms involved in tenderness or to provide biomarkers that can predict it. For that, the strategy has been to compare extreme groups of beef tenderness by proteomics (Picard et al., 2010, 2011) and/or transcriptomics (Bernard et al., 2007). For comparative proteomics, the proteins of muscles from two groups (very tender and not tender) were extracted and separated according to their isoelectric point by two-dimensional electrophoresis. The differences in spot volumes were analyzed by image analysis. Then the protein corresponding to the significant differential spots were identified by mass spectrometry (Figure 1). These studies established a list of biological markers of beef tenderness. The main results obtained in the *Longissimus thoracis* (LT) have demonstrated that fast glycolytic type proteins were more abundant in animals giving the less tender meat. Among these proteins, we identified: Phosphoglucomutase (PGM), lactate dehydrogenase B (LDHB), and Triphosphate isomerase in Charolais and Salers, the glyceraldehyde-3-phosphate dehydrogenase (GAPDH) in the Limousin, the fast troponin T (TnTf) isoforms in Charolais and Blond d'Aquitaine, and the β Enolase in Limousin and Blond d'Aquitaine breeds. Additional experiments led to similar conclusions about the positive relationships between oxidative metabolism and tenderness (Picard et al., 2010). Similar results have been observed for pigs. For example, D' Alessandro et al. (2011) reported PGM was more abundant in the muscle of pigs that produced more tender meat. Several proteins involved in calcium metabolism were also identified as positive markers for tenderness. For example, the amount of Parvalbumin peptides is considerably increased in tender muscles of Charolais and Limousin breeds. The calcium cycle proteins seem strongly involved in meat tenderness, in connection with the important role of calcium in meat ageing (Ouali et al., 2006). Accordingly, Bjarnadottir et al. (2012) recently found a relationship between Annexin 6, involved in the release of cal-



Figure 2. The beef industry is currently in need of a tool to estimate the tenderness of live cattle (source: Rick Harrison).

cium, and tenderness. A set of proteins of the family of heat shock proteins (**Hsp**) was revealed as markers of tenderness at the transcript or protein level in the different experiments. For example, Bernard et al. (2007) have shown that gene expression of the DNAJA1 protein (protein Hsp40) was an appropriate indicator of meat toughness of Charolais young bulls. According to the hypothesis of Ouali et al. (2006), the anti-apoptosis DNAJA1 could slow down the process of cell death during the early stages of transformation of muscle into meat. Other family members were also identified as markers of tenderness in several programs (Hsp27, Hsp20, α B-crystallin, Hsp70). Proteins involved in oxidative stress, such as superoxide dismutase (**SOD1**) or Peroxiredoxin 6 (**PRDX6**), were found to be negatively related to tenderness. This is in contradiction with the data of D' Alessandro et al. (2011), which shows that SOD1 was more abundant in pork that was more tender and apparently had more protein degradation. A similar study conducted on *Semitenosus* (**ST**) muscle showed differences in the identified markers according to muscle type (Guillemin et al., 2012); breed-specificities for proteomic markers of tenderness were also reported (Chaze et al., 2009).

Validation of Biomarkers: Prediction of Tenderness

Comparative analyzes to identify biomarkers were conducted primarily in young bulls of different breeds. Currently, we want to validate the relationships between markers abundance and tenderness level over large numbers of cattle in French systems with cows, heifers, steers, bulls or beef, hardy breeds, and dairy breeds. In order to simultaneously analyze different biomarkers for several muscle samples, we developed the Dot-Blot technique (Guillemin et al., 2009). It consists of depositing the protein

extracts on a membrane (**PVDF**) and hybridizing the membrane with an antibody specific for the desired protein. Dot-Blot was used on 111 samples from LT and ST muscles from the Charolais bovine breed to quantify 24 proteins previously identified as biomarkers of tenderness by comparative proteomics (Guillemin et al., 2012). The main results showed that biomarkers better discriminated tenderness (evaluated by sensory or mechanical analysis) in ST than in LT muscle. This could be the consequence of different compositions of these muscles in characteristics such as total lipid content (higher in LT) or collagen content which are also involved in tenderness. Multiple regressions highlighted PRDX6 (cis-peroxiredox-6), LDHB (lactate dehydrogenase B), Hsp70-1B, Hsp70-GRP75 (Heat Shock Protein), and **MyHC** (Myosin Heavy Chain) II (IIa + IIx) as proteins explicative of ST tenderness (**WBSF**; $R^2=0,86$). In LT muscle, PRDX6, Hsp20, Hsp70-GRP75, and α B Crystallin (**CRY-**

AB) were the most explicative of tenderness ($R^2=0.69$; Guillemin et al., 2012). These predictive equations revealed that the PRDX6 protein is the main biomarker explaining the WBSF in both muscles ($P=0.003$). This enzyme is involved in the fight against oxidative stress which is caused by free radicals of oxygen, resulting in the formation of protein aggregates that impair tenderness (Morzel et al., 2008). Proteins of small Hsp family (Hsp27, Hsp20, and CRY-AB) are known to prevent the formation of these aggregates. Thus, the positive relationship between these Hsp and tenderness is quite concordant with the negative relationship between oxidative stress (PRDX6) and tenderness. We confirm that Hsp is important in tenderness determination, with Hsp70 as negative markers, in contrast to Hsp20 (Guillemin et al., 2012). Indeed, Hsp70 also sequester proapoptotic factors such as BCL-2 and inhibit apoptosis (Beere and Green, 2001). These proteins also have chaperone functions, but not on protein structure. This can explain why they are negative markers of tenderness in ST muscle, in contrast to Hsp20. Indeed, Guillemin et al. (2012) have shown that the ratio of the family of small Hsps/the family of Hsps70 appeared to explain variability of beef tenderness.

Influence of Management Factors on the Expression of Biomarkers of Tenderness

Our objective was to determine the precise effect breeding systems have on the abundance of protein biomarkers. First, a thorough analysis of the regulation of gene expression of DNAJA1 (coding protein Hsp40) was performed to show how its expression may vary according to muscle type and animal behavior. The main results showed that the greatest abundance of Hsp40 was observed in the youngest animal and the most oxidative muscles. No effect was detected for dietary treatment (pasture vs. maize based diet) or growth path (compensatory growth after a restriction period). Moreover, its abundance was not modified by pre-slaughter stress (Cassar-Malek et al., 2011).

The effect of muscle type (LT vs. ST) and animal type (bulls vs. steers) on the abundance of a list of 24 proteins was studied in Charolais cattle (67 young bulls and 44 steers). We detected muscle type effect on 14 of the 24 analyzed proteins and an animal effect on 15 of the 24 proteins. The main results showed that the family of small Hsp (27, 20, α B cristallin) varied according to these two factors. They are more abundant in young bulls than in steers and in LT than in ST muscle. On the contrary, Hsp70/GRP75 was more abundant in steers and showed no effect of muscle type. Proteins of calcium dependent proteolysis (M and μ -calpains) were more abundant in steers with no effect of muscle type. Contractile and metabolic proteins were more variable according to muscle than animal type (Guillemin et al., 2011a). This approach is being completed for various biomarkers and management factors. Altogether, this data will help provide advice on farming practices that could allow for optimal expression of tenderness biomarkers.

Biological Functions Governing Beef Tenderness

From the list of 24 proteins, we used bioinformatic tools to search for proteins interacting with other proteins identified as markers of tenderness (Guillemin et al., 2011b). This work highlighted cellular pathways strongly involved in the tenderization processes: apoptosis, Hsp functions, and oxidative stress resistance. We also demonstrated that the role of these pathways on the tenderization process differs according to muscle type. Moreover, this analysis revealed new data. For example, three proteins, never studied in tenderness, appeared to be at a crossroad of the tenderness interactome: SUMO4, H2AFX, and TP53. Direct relationships with tenderness is improbable. However, these proteins could be responsible for the balance between pathways, like apoptosis or stress response. So,

studying their relationship with tenderness could complete our knowledge on tenderness and help to better explain tenderness variability.

Development of Analytical Tools

From these data, the goal is to develop a routine application for the beef sector. The principle is the opposite approach of the Dot-Blot technique. It consists in depositing the interested antibodies on the membrane and hybridizing with the protein extract. This technology is called "antibody chip". This technology is already used for muscle proteins with medical applications in disease diagnostics (Sakanyan, 2005). Our challenge is to develop this technology for phenotyping bovine for tenderness. The advantages are that it is a fast, high-sensitive immunological technique that enables the simultaneous quantification of several proteins in samples obtained by biopsy live animals or carcasses. The expected outcomes are to provide the beef sector with a tool for "paddock" use to estimate the tenderness potential of a live animal or a meat cut. If we succeed in this challenge, this tool will improve the competitiveness of this industry by allowing it to provide the consumers with controlled quality beef.

Pig Meat Quality: Understanding the Development and Identifying Biomarkers of Complex Phenotypic Traits

Pork is the predominant meat consumed in the world (Figure 3), either as fresh meat or processed products, exhibiting a great diversity in

Figure 3. Pork at Palua Tikus Market in the coastal town of Penang, Malaysia (source: flickr.com/shebalso).



both the type of raw material (entire parts [hams] or minced meat [sausages]) and processing techniques used (cooking or dry-curing). Therefore, pork quality covers technological and sensory dimensions, including many traits like post-mortem (p.m.) pH, drip loss, color, intramuscular fat (IMF) content, tenderness, juiciness, and flavor. These pork quality traits result from interactions between genetic backgrounds, rearing and slaughtering conditions of animals, and meat processing. Even though many factors influencing pork quality have been identified, its variability remains high and muscle properties underlying good eating quality are still unclear. Thus, like for other animal species, identifying markers of quality traits is of significant interest in the pork industry. As a result, applications of proteomic approaches is increasing, generally based on two-dimensional electrophoresis and mass spectrometry for protein identification, in order to improve knowledge on biological mechanisms determining pork quality and identifying biomarkers of phenotypes. Studies consider either one important quality trait (e.g., IMF, color, shear force) in a differential animal design for a given trait, or many traits simultaneously (e.g., technological and sensory traits) using an experimental design leading to a range of variation for these traits. Most of the work concerns the *Longissimus* (LM), but the *Semimembranosus* (SM, ham muscle) has also been considered in relationships with the importance of cooked and dry-cured hams production.

Differential Proteomic Profiles Associated to Contrasted Levels for Quality Traits

Traits related to both technological and sensory qualities of pork [i.e., IMF content; pale, soft, and exudative (PSE) meat defect; or shear force] have been studied using comparative proteomics approaches to improve biological knowledge and identify potential biomarkers.

The IMF content is an important component of pork quality, and is highly variable among pig populations. To better understand its biological determinism and thereby help the design of genetic schemes for increasing IMF, contrasted groups for LM IMF content (1.36 vs. 4.58%) were compared by proteomic analyses (Liu et al., 2009). The expression of proteins of glucose and protein metabolic processes, cell communication, metabolites binding, and the response to stimulus functional categories were associated with IMF variation. Associated to transcriptomic data obtained on the same animals at similar and earlier age, these results indicate that variability in pig IMF content might arise essentially from differences in early adipogenesis and adipocyte development, thereby revealing biological processes to be considered for further studies on IMF control.

Pale, soft, and exudative meat, a major problem regarding pork quality, actually corresponds to various defects depending on both genetic and non-genetic factors, and originates from various physiological and biochemical mechanisms. In the SM, PSE zones result in low cohesiveness of meat that becomes unsuitable for cooked ham production, leading to important problems in pork industry. Using proteomic analyses, Laville et al. (2005) showed a decrease in protein solubility and p.m. proteolysis of myofibrillar proteins, and lower quantities of small Hsp (Hsp 27, CRY-AB) in the PSE zones compared with normal SM. The reduced protein solubility and abundance of Hsp 27 and proteins of oxidative metabolism were also observed in the SM of pigs of nn genotype at the RyR1 locus (halothane gene) that leads to the genetic PSE defect, compared with NN pigs (Laville et al., 2009), as well as in pigs exhibiting pale vs. dark color in the SM (61.3 vs. 43.2 L* value; Sayd et al., 2006). These studies open the way to markers of PSE defect by quantification of chaperones proteins

like small Hsp. In addition to the quantification of protein expression, proteomics has been used recently to quantify protein phosphorylation changes in p.m. porcine muscle in relation with pork quality. Huang et al. (2011) reported that fast pH decline muscles exhibited the greatest phosphorylation level (1 hour p.m.) and the least (24 hours p.m.), whereas slow pH muscles showed the reverse case. Studying another important defect of pork, the acid meat resulting from Rendement Napole- (RN-) genotype, Lametsch et al. (2011) reported greater phosphorylation levels of key enzymes of glycogenolysis and glycolysis during p.m. metabolism in RN- compared with wild-type pigs. This illustrates that proteomic approaches are relevant to characterize post-translational modifications of proteins, like phosphorylation levels that could be interpreted as metabolic fingerprints related to biological processes determining phenotypic traits such as meat quality.

Aimed at understanding the development of pork tenderness and identifying potential markers, Laville et al. (2007) compared two contrasted groups for LM WBSF of cooked meat. They showed that low WBSF group (i.e. tender meat) exhibited an overabundance of proteins of lipid metabolism, including adipocyte-fatty acid binding protein (FABP4), thus suggesting greater number of intramuscular adipocytes in these muscles. A greater FABP4 protein level was associated with greater IMF content in agreement with Damon et al. (2006), and could explain the increased tenderness. Laville et al. (2007) also reported a greater abundance of proteins involved in folding and polymerization, indicating increased protein synthesis in low WBSF group.

Associations between Proteomic Profiles and Variations in Technological or Sensory Traits for Identification of Biomarkers

Experimental designs are aimed at associating between, or within, breed or rearing condition variations in pork quality and the muscle proteomic profile in order to understand underlying biological processes and identify biomarkers of quality. In an experiment associating two contrasted pure breeds (local Basque, corresponding to premium quality products, and conventional Large White) reared in various production systems (conventional, alternative, or extensive), associations between biochemical, physico-chemical, and sensory traits, and transcriptomic and proteomic profiles of LM revealed biological mechanisms and metabolites, transcripts, and proteins associated to the variations of many pork traits (Salmi et al., 2010; Lebret and Damon, 2011; Damon et al., 2012). As an example, sarcoplasmic proteome analyses revealed that protein oxidation generated during meat ageing and cooking, which might impair tenderness, water holding capacity, and technological properties of raw meat, relied on proteins involved in antioxidant protection (selenium binding protein and mitochondrial superoxide dismutase; SOD) and on iron containing proteins (myoglobin isoforms and serotransferrin; Promeprat et al., 2011). Proteins of antioxidant pathways were negatively associated with drip and cooking losses and positively associated with tenderness, whereas opposite associations were found between proteins of energy metabolism and these traits (Sayd et al., 2009). In agreement, greater levels of antioxidant enzymes such as SOD1 were found in tender meat from Casertana pigs compared with tougher meat from Large White pigs (D'Alessandro et al., 2011). Combining proteomics and transcriptomics results, these authors hypothesized that antioxidant enzymes could play a role in protecting the proteolytic enzymes cathepsins and calpains during

p.m. proteolysis, thereby enhancing meat tenderization in Casertana pigs. In addition to studies performed on samples taken early p.m., proteome degradation during meat ageing in relation with technological and sensory pork quality traits has also been investigated by proteomics approaches (Lametsch et al., 2002; te Pas et al., 2009). Post-mortem proteolysis of actin and metabolic enzymes has thus been demonstrated (Lametsch et al., 2002), providing new insights on the biochemical phenomena occurring during meat ageing and tenderization. Altogether, these results improve knowledge on pork quality variation and the protein targets identified can be considered for further development of biomarkers of quality. However, validation of potential markers for use in various breeds or pork chains may be a difficult task. When associating LM protein abundance and pork quality variations using multiple regressions analyses, Kwasiborski et al. (2008) found that the abundance of 1 or 2 proteins could explain up to 85% of variability of traits like ultimate pH (muscular creatine kinase and dimeric dihydrodiol dehydrogenase, 83%), drip loss (pyruvate kinase isoform M1, 65%), or thawing loss (actin interactin protein, 85%). Nevertheless, protein-trait associations displayed significant gender and breed differences, indicating that the identification of 'robust' (i.e., generic) proteomic markers of pork traits for wide use in pork industries deserves further research.

Fish Quality: Towards a Better Understanding of Flesh Texture

In fish, flesh quality is dependent on environmental factors, mainly water and food quality for product safety and food composition for flesh

nutritional quality. Nevertheless, amongst sensory quality, flesh texture is mainly determined by biological factors such as muscle organization, protein content, and composition. In fish, the best quality is firm and cohesive flesh with good water holding capacity. These traits are mainly determined by proteins' nature and properties, so proteomic tools appear especially of interest to study fish flesh quality. However, very few studies were undertaken to identify flesh quality biomarkers, probably due to the small number of research teams working in that topic.

Post-mortem Changes

The first studies analyzed muscle proteome p.m. changes in relation to flesh softening. Cod muscle proteome observed in 2D-PAGE during 8 days p.m. revealed a limited degradation compared to mammal muscles, with 9 spots in which intensity increased and 2 spots in which intensity decreased (Kjaersgard and Jessen, 2003). In this study, protein identification was not reported and very little genomic data are available illustrating the limitations of proteomic approaches for species in which the genome was not sequenced. More recently, the evolution of rainbow trout muscle protein was studied during 5 days p.m. by sodium dodecyl sulfate polyacrylamide gel electrophoresis (SDS-PAGE), and gel band intensity was found to be related to flesh firmness. Proteins from both myofibrillar [i.e., α -actinin, actin, Myosin Light Chain (MyLC) 1 and 2, MyHC fragment] and sarcoplasmic (creatine kinase, glycogen phosphorylase, triose phosphate isomerase) fractions closely correlated with firmness (i.e., Godiksen et al., 2009). In these cases, proteomic approaches allowed scientists to explore new targets of post-mortem proteolysis and to study the possible implications of the different proteolytic systems in flesh quality.

Figure 4. A rainbow trout harvest. Only 15 min of crowding stress of rainbow trout can lead to increased flesh firmness (source: flickr.com/spikefi/).



Pre-slaughter Stress Effect

Pre-slaughter stress is difficult to avoid in aquatic species because of fishing, and it was shown that even a short time stress of 15 min crowding (high density stocking) impairs product quality (Lefèvre et al., 2008). Some studies reported changes in muscle proteome analyzed by two-dimensional polyacrylamide gel electrophoresis. Pre-slaughter stress associated with intense muscle activity was shown to affect both proteins involved in muscle metabolism (i.e., triose phosphate isomerase, enolase, pyruvate dehydrogenase) and structural proteins (i.e., desmin, cap-Z, MyHC fragment). Moreover, desmin appeared persistently under-represented in stressed fish, suggesting that muscle integrity was affected (Morzel et al., 2006). In Atlantic salmon, 40 min crowding stress altered the abundance of 27 protein spots, including both structural proteins (i.e., actin, MyLC, MyHC, tropomyosin) and sarcoplasmic proteins, especially enzymes involved in energy production (i.e., creatine kinase, enolase, phosphoglycerate kinase), suggesting accelerated p.m. metabolism (Veiseth-Kent et al., 2010). A 15 min crowding stress applied to high- or low-stress-responsive rainbow trout before slaughter (Figure 4) led to an over-representation of spots identified as desmin, MyLC3, myeloperoxidase, malate dehydrogenase, apolipoprotein A1, nucleoside diphosphate kinase (Nme), and parvalbumin but with no difference between low-responsive and high-responsive fish strains. Principal component analysis of proteomics data and flesh texture parameters showed that desmin and FABP-H were positively correlated with raw flesh firmness, whereas myeloperoxidase and apolipoprotein A1 were negatively correlated. Firmness of cooked flesh was positively correlated to apolipoprotein A1, Nme, and parvalbumin.

Effect of Plant-based Diet

Currently, one of the main challenges in fish culture is implement a vegetable-based diet without affecting production efficiency and product quality. Indeed, in a recent study, reduced raw flesh firmness of rainbow trout fed an all-vegetable diet was associated with a decrease in MyHC and changes in several glycolysis enzyme bands in SDS-PAGE analysis of muscle proteins (Lefèvre et al., 2010).

The identification of biomarkers of flesh quality in fish species is much less documented than in terrestrial species. Interestingly, identified biomarkers are different than those found for meat quality, suggesting that the determinants of quality would be distinct. All the studies mentioned above are based on gel separation of proteins, limiting biomarker identification to soluble proteins. Matrix proteins, while difficult to study, also seem to be major determinants of flesh texture.

Conclusion

The approaches developed during the past years, with financial support from professionals and national and international research policies, has led to substantial progress in our understanding of genes and proteins involved in the determination of meat quality traits, with a major focus on the technological and sensory traits, particularly tenderness. The results confirm the complexity of the determination of phenotypic traits determined by genetic and environment interactions. However, they improve our understanding of the biological mechanisms that determine meat quality and provide elements (markers) to move from knowledge to the development of tools for field evaluation of these complex traits.

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About the Authors



Dr. Brigitte Picard is a meat scientist. She obtained a Ph.D. degree in biochemistry in 1990 and is currently developing research on muscle growth and cattle meat quality. She is the head of an INRA team of 26 people with currently six thesis and two post-doc students. She manages programs on markers of beef tenderness (biological integrative approach associating biochemical studies, functional genomics [proteomics] and modelling). Her competences are: muscle physiology, analysis of proteins (electrophoresis mono and two-dimensional, western-blot, ELISA, and immunohistochemistry), primary cultures of muscle cells (myoblasts and satellite cells), and the proteomic analysis of muscle.

Correspondence: brigitte.picard@clermont.inra.fr



Dr. Bénédicte Lebret is a meat scientist. She has Ph.D. degree in biology and agronomy. Her main research topics are the determination of technological and sensory quality of pork with a special emphasis on production systems and genotype effects on these traits. Her skills are in animal (pig) science, muscle biochemistry, and meat science. She has been head of the Research Group Growth and Meat Quality of INRA-UMR PEGASE (15 permanent staff, Ph.D.'s and post-docs) for 10 years. She manages research programs on the influence of production systems on pork quality and on identification of biomarkers of pork quality and is supervisor of Ph.D. and post-doc students.



Dr. Florence Lefèvre is a fish flesh quality scientist. She obtained her Ph.D. degree in food science in 1997. She works in the INRA Fish Physiology and Genomics Laboratory, more precisely in the Fish Growth and Flesh Quality Group. She is involved in research programs aimed to understand the determinants of fish flesh quality, especially the role of muscle structure and nature of proteins in trout muscle texture.