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Nutrition In Fish: Hematological Responses, Biochemical Aspects, And Impacts on Meat Quality

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Abstract

Animal nutrition directly impacts fish health and meat quality, affecting the hematological and biochemical responses of fish as well as the physicochemical characteristics of the meat, which are essential for consumer acceptance. This review article examines how nutrients and agro-industrial by-products used in fish feed influence the composition of the meat, which can be enriched with compounds beneficial to human health. Quality parameters such as color, tenderness, fatty acid profile, and lipid oxidation are discussed, as well as the potential of by-products in promoting sustainability and nutritional value, with implications for aquaculture and public health.

Keywords: Animal nutrition; Fish; Human health; nutraceutical; Physicochemical analyses

Introduction

In 2020, global fishery and aquaculture production reached a historic record of 214 million tons, 30% higher than the average of the 2000s and more than 60% above the average of the 1990s. It is estimated that global per capita consumption of aquatic foods increased from an average of 9.9 kg in 1960 to 20.2 kg in 2020. This increase could be attributed to factors such as population growth, changes in dietary habits, increased consumer income, improved distribution of production, better accessibility for the population [1], and advancements in technology that have introduced new by-products to the market.

Due to large-scale production, China, in addition to being the largest consumer, leads global fish production, accounting for more than 30% of the total volume [2].

A 13% increase in aquatic food production is projected by 2030. This reflects the expectation of continued demand for aquatic products. Therefore, it is essential that this productive growth be accompanied by sustainable practices and environmental conservation measures. Commitment to sustainability is crucial to ensure that the increase in production does not compromise aquatic ecosystems, biodiversity, and the livelihoods of communities dependent on fishing and aquaculture [1].

A trend observed in recent years is the stability of production from wild fisheries, in contrast to the growth of aquaculture [2]. The fact is that fishing often faces challenges related to overfishing, habitat degradation, and regulations to ensure the sustainability of fish stocks. Aquaculture, on the other hand, has grown due to its ability to meet the increasing demand for seafood in a controlled and sustainable manner. Improved aquaculture practices, including water recirculation systems and more sustainable farming approaches, have contributed to this growth.

Fish, whether produced through freshwater or saltwater farming, or caught via marine fishing, plays an important role in generating income for various communities around the world, in addition to being a valuable source of protein and essential nutrients for human health [2].

Fish farming in flooded areas, such as dams, reservoirs, irrigation channels, and dug ponds, emerges as a promising strategy to meet the growing demand for aquatic products. Species such as tilapia stand out in this context due to their adaptability, rapid growth, feed efficiency, and good commercial acceptance.

However, the success of this production model also depends on measures that ensure the health of the fish, especially in the face of stress associated with the farming environment, such as high population density, frequent handling, and fluctuations in water quality. Proper control of these factors is essential to prevent negative impacts on animal health, such as increased susceptibility to diseases, which could compromise productivity and the sustainability of the system.

This integrated approach allows the utilization of underused water resources, contributing to job creation, local economic development, and the sustainable increase in food supply. However, it is essential to adopt practices that preserve biodiversity and ecosystems, ensuring the economic, environmental, and sanitary sustainability of aquaculture production.

Lipid sources in diets and hematological and biochemical responses in fish

An adequate diet is essential to maintain fish homeostasis and ensure optimal productive performance. In nutrition, lipids play an important role. Therefore, for omnivorous fish like tilapia, a balanced amount of oils or fats in the diet constitutes an efficient form of body energy storage, which will be indispensable for various organic functions.

In addition to vegetable oils, fish oils from marine species are the most common source of essential fatty acids (EFAs) used in fish feed. These are important for maintaining the flexibility and permeability of cell membranes, the absorption of fat-soluble vitamins, among other functions. The oils and fats commonly used in feed formulations have different fatty acid profiles, which influence the digestive and metabolic processes of fish and affect the physiological mechanisms responsible for maintaining their health [3]. Among the functions of fatty acids, one can also mention their action on the immune system and their anti-inflammatory effects.

An important way to assess the nutritional condition of fish is through their hematological conditions, as blood, being a dynamic tissue, changes in response to variations in the diet consumed [4].

Hematology is a useful tool for assessing the influence of nutrition on fish health, showing a direct correlation between good nutrition and well-being. Although it is rarely explored in fish farming, it provides relevant data for health diagnosis, with the advantage of quick analyses through kits and the preservation of the animal's life.

Araújo et al. [5], for example, evaluated the effects of diets with different ratios of omega-6 and omega-3 polyunsaturated fatty acids on the hematological parameters of Nile tilapia (*Oreochromis niloticus*). The results indicated that fish fed a diet containing 6% flaxseed oil showed a reduction in the number of leukocytes after being subjected to cold stress, suggesting lower resistance to thermal stress. This highlights that the lipid composition of the diet can influence the immune response of the fish, reflected in hematological changes.

Changes in the blood count can be indicative of diseases. Therefore, the hematological profile of fish may be related to their nutritional status or the conditions of their environment [6]. These elements make it challenging to establish reference parameters for fish species, as these values can vary significantly depending on the natural environments in which they live or are raised [7].

In intensive farming, fish face various stress factors, such as water temperature, handling practices, capture, confinement, and transportation, which require adaptive responses to restore homeostasis and ensure survival. These challenges can lead to cumulative stress, affecting physiological and metabolic functions, compromising the immune system and resistance to pathogens, as well as reducing growth rates due to hormonal changes. Studies on hematological and biochemical parameters, in natural or artificial farming systems, are essential to assess the physiological conditions of fish and their responses to stress caused by environmental and nutritional factors, contributing to improvements in fish productivity and health [6] (Figure 1).



Figure 1: Factors influencing the hematological response in fish

In addition to affecting the overall health and performance of fish, changes in hematological and biochemical parameters can also have a significant impact on the composition of the animals' meat.

Song et al. [8] investigated the effects of fish oil (FO), soybean oil (SO), rapeseed oil (RO), peanut oil (PO), and lard oil (LO) on growth, immunity, and muscle quality in juvenile Largemouth bass (*Micropterus salmoides*). After 8 weeks of feeding, the results indicated that FO and RO promoted greater weight gain and increased levels of alkaline phosphatase and apelin in the serum of the fish compared to LO. Additionally, in these two groups, higher mRNA levels of immune defense molecules (lysozyme, hepcidin, and transforming growth factor β_1) were observed compared to PO ($p < 0.05$). Fish fed with FO and RO also showed a higher amount of n-3 polyunsaturated fatty acids (PUFAs) in the dorsal muscle and improved meat texture characteristics, such as firmness due to increased glycogen, chewiness, and elasticity due to an increase in collagen and hydroxyproline content. In contrast, SO was associated with a higher inflammatory risk, evidenced by an increase in leukocyte, platelet, neutrophil, and monocyte counts, as well as higher mRNA levels of interleukins (IL-1 β , IL-8, IL-12, and IL-15). These insights can thus contribute to the use of dietary lipid sources in bass and other fish species.

Nutrition, fish meat composition and human health

In fish farming, nutrition and feeding directly impact productivity, economic efficiency, fish health, performance, and the nutritional quality of the meat destined for the market.

The exploitation of aquaculture systems faces financial and environmental risks, with inadequate nutritional management being one of the main causes of reduced productivity and the generation of waste that compromises water quality. In confined fish farming, it is essential to provide commercial feeds that meet nutritional and energy requirements, aiming for satisfactory zootechnical performance and economic return.

Research and technologies aim to develop high-quality, balanced, and sustainable feeds to maximize productivity, reduce costs and environmental impacts, and improve product quality. Processes such as extrusion and density control minimize losses due to leaching, reducing waste and impacts on the aquatic environment.

Studies on nutrition in aquaculture can be challenging due to the great diversity of fish species, each with its own morphological, physiological, and behavioral peculiarities. Numerous factors must be considered when assessing their nutritional needs, such as sex, lineage, growth stage, physiological condition, production systems and regimes, water temperature, and others.

The fact is that fish are dependent on abiotic changes in the environment and exhibit metabolic fluctuations as ectothermic animals, whose body temperature varies according to water temperature. Therefore, the energy/nutrient balance suitable for one species may not be appropriate for another.

The formulation of balanced diets involves obtaining adequate energy and nutrients from a mix of ingredients, which requires knowing their composition and digestibility, the effects of any antinutritional factors present in the food, and possible additives that may be incorporated into the feed. However, the lack of precision in this knowledge is reflected in the existence of generalized commercial feeds based on the fish's feeding habits, whether carnivorous or omnivorous [9], thus demonstrating the scarcity of information on specific nutritional requirements by species.

Fish require numerous essential nutrients, including amino acids, energy, fatty acids, vitamins, minerals, and carotenoids. Proteins and amino acids, the most expensive components of feed, are prioritized because they provide metabolic energy, form enzymes and hormones, and directly influence growth [3].

Fish nutrition directly impacts meat quality, influencing attributes such as texture, color, aroma, flavor, nutritional value, shelf life, and contaminant levels. In this context, the formulation of complete and economical diets that improve meat quality has led to the search for high-quality ingredients, both animal and plant-based. Moreover, the use of nutraceuticals and additives, such as vitamins, minerals, antioxidants, pigments, enzymes, organic acids, probiotics, and hormones, has proven to be an effective strategy to optimize nutrient utilization, benefiting both fish health and the quality of the final product [10].

In this scenario, studies on fish diets and feeding habits have focused on evaluating the replacement of traditional protein and energy sources, such as fishmeal, with plant-based alternatives. These alternatives include by-products from oilseeds, such as soybean, flaxseed, and sunflower, as well as starchy ingredients like rice, cassava, and corn, and agro-industrial residues, such as those from beer production, yeast, fruits, and fish by-products. This not only reduces costs but also contributes to the reduction of the environmental impact of feed production.

Although plant-based ingredients are widely explored in research, their use must be done with caution, as excessive substitution may lead to adverse effects. Therefore, it is essential to assess whether these new ingredients used in fish feeding contain antinutritional factors that could harm the health and physiology of the animals. For example, phenolic compounds, such as tannins and phytic acid, present in plant-based ingredients, can inhibit digestive functions by

interfering with the action of digestive enzymes and affect the hydrolysis of proteins and starch [11]. Furthermore, it is important to consider whether any procedures, such as detoxification, need to be carried out on the ingredients before their inclusion in the feeds. An example of this is castor bean (*Ricinus communis*), an oilseed studied for monogastric nutrition [12], which contains three known antinutritional factors: ricin, a protein that causes cellular damage and inhibits protein synthesis; ricinine, an alkaloid that causes damage to the nervous system and digestive tract; and the allergenic factor CB-1A, which promotes allergic reactions in fish.

Therefore, ensuring that the ingredients used in fish feed do not compromise their health or meat quality is crucial for aquaculture, which aims to offer the market products that are nutritionally and sensorially comparable to wild-caught fish.

One of the main goals of fish farming is to offer the market products that are nutritionally and sensorially comparable to wild-caught fish. This goal arises due to the evident differences in nutrient composition and the physicochemical and sensory properties between the meat of "wild" fish and farmed fish, with diet being one of the key factors that determine these characteristics. Despite the efforts, many consumers still perceive farmed fish as lower quality compared to wild-caught fish. However, they recognize important advantages, such as greater control in production, more affordable prices, and better market availability [13].

Consumers, increasingly demanding in terms of quality, seek selected, flavorful foods that are convenient to use and produced sustainably, paying attention to the environmental impacts generated in their production. The growing concern with the food-health and well-being interaction, as well as the reduction of disease risks, leads consumers to seek functional foods in order to improve their health and quality of life [14].

Low in saturated fats, carbohydrates, and cholesterol, fish meat is an important source of lipids, proteins, easily digestible and of high biological value, as it contains essential amino acids such as lysine. It also has a wide range of micronutrients, such as vitamins, minerals, and polyunsaturated fatty acids (PUFAs) from the Omega-3 series, making it an unquestionably high-quality food [15]. In addition, fish production has a yield of about 30 to 60% (of edible parts), depending on the species and the type of processing it undergoes. The meat is composed of 60 to 80% moisture, approximately 20% crude protein, 0.5 to 5% ash content, and 6 to 20% lipids. However, this content is variable between species, sexual maturation cycle, food availability, and the fish's feeding habits [16].

Fish meat is an excellent source of minerals such as calcium, phosphorus, sodium, potassium, zinc, manganese, iron, and iodine (in marine fish). Its low connective tissue content and collagen gelatinization at lower temperatures provide greater tenderness and nutritional value compared to other meats. In addition, the consumption of fish, especially marine fish rich in omega-3, helps with weight loss, cholesterol control, prevention of cardiovascular diseases, and other health benefits. It is a relevant nutritional option in light of contemporary eating habits associated with sedentary lifestyles and excessive consumption of saturated fats and sugars.

Influence of nutrition on the physicochemical characteristics of fish meat

Complete and balanced diets are essential to ensure productivity, profitability, and high-quality meat that meets market demands, as feeding directly influences the sensory and physicochemical attributes of fish meat and accounts for up to 70% of production costs. A viable alternative is to identify, through rural diagnostics, the main regional cultivated products and agroindustries with potential use in fish nutrition, in order to reduce costs with commercial feeds and mitigate the environmental impacts of improper waste disposal. Da Silva et al. [17] investigated the use of alternative

foods from family farming, such as residues from the main local activities (açai, acerola, banana, cacao, cupuaçu, guava, mango, passion fruit, and pupunha), as a proposal for Tambaqui (*Colossoma macropomum*) feed, highlighting the potential of these residues.

However, it is essential that studies not only focus on reducing production costs but also evaluate the impacts on the quality of fish meat. Therefore, continuous studies on nutrition and the physicochemical attributes of meat are essential to keep up with trends and improve efficiency in aquaculture. Understanding the dietary effects on the nutritional composition of the product allows for adjustments in feeding practices, also aiming to optimize the final product's quality.

Table 1 presents some studies conducted to evaluate alternative feed ingredients in fish farming.

Ingredient	Species	Index analyzed in meat	Some main changes	Reference
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Insect Meal (<i>Acheta domesticus</i>)	Meagre (<i>Argyrosomus regius</i>)	Muscle and liver composition	Higher lipid content in the fish; higher muscle protein compared to the control. Higher content of monounsaturated fatty acids (MUFA) and n-6 PUFA, mainly oleic acid (18:1n-9) and linoleic acid (18:2n-6).	18
Microalgae (Mixture of 4 marine microalgae)			Improvement in the composition of MUFA and n-6 PUFA, but requires adjustment in the inclusion rate.	
Protein and lipid from tuna cooking water			Increase in protein content in the liver and muscle; improvement in DHA and n-3 PUFA content.	
Mixture of the three ingredients			Higher content of saturated fatty acids (SFA), especially palmitic acid (16:0).	

<p>Yellow mealworm (<i>Tenebrio molitor</i>) (YM / TM) – as a replacement for soybean meal</p>	<p>Mirror carp (<i>Cyprinus carpio</i> var. <i>specularis</i>)</p>	<p>Muscle texture and physicochemical parameters (chewiness, hardness, cohesiveness, gumminess, adhesiveness, and springiness)</p>	<p>Increase in total antioxidant capacity (T-AOC) of the muscle in YM30, which corresponds to 30% replacement of soybean meal in the diet, and in the activity of superoxide dismutase, an antioxidant enzyme that plays a key role in neutralizing free radicals.</p> <p>Improvement in skin color, with increased yellowish tone.</p> <p>Muscle texture parameters (such as chewiness, hardness, cohesiveness, gumminess, adhesiveness, and elasticity) initially increased with the inclusion of TM in the diet, but then decreased.</p>	<p>19</p>
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Black cumin (<i>Nigella sativa</i>)	Rainbow Trout (<i>Oncorhynchus mykiss</i>)	Protein content, fatty acids, digestibility, amino acid profile	Increase in protein content and essential amino acids, improvement in texture and flavor.	20
Clostridium autoethanogenum protein (CAP) in substitution of soybean meal	Grass carp (<i>Ctenopharygodon idella</i>)	Muscle nutritional value and sensory characteristics	<p>Improved pH, cohesiveness, elasticity, adhesiveness, and chewiness of the muscle.</p> <p>Increased content of essential and non-essential amino acids ($P < 0.05$), improving the nutritional value of the muscle.</p> <p>Increased expression of genes such as regulators of myogenesis.</p> <p>Improved sensory characteristics, such as the umami taste of the muscle, while reducing the content of volatile compounds that regulate the fishy odor.</p>	21

Marine Microalga Schizochytrium sp. as a replacement for fish oil	Nile Tilapia (Oreochromis niloticus)	Fatty acid deposition	Higher levels of DHA (22:6n3), resulting in greater DHA deposition in the fillets and a higher DHA:EPA ratio. Improved levels of long-chain omega-3 polyunsaturated fatty acids (n3 LC-PUFA) in the fillets.	22
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It is important to emphasize that the use of alternative ingredients, such as those discussed, should be complemented by rigorous tests on digestibility and nutrient bioavailability to improve diet formulation in aquaculture. These tests allow for the evaluation of how efficiently fish utilize the ingredients in the feed, ensuring that essential nutrients are properly absorbed and metabolized. Furthermore, they contribute to optimizing diets, helping to reduce costs and develop more sustainable and effective feeds, which can result in better zoosanitary performance and improved product quality.

According to Grigorakis [23], the sensory and nutritional aspects of fish meat depend on its physicochemical composition, which can be influenced by numerous factors that affect its quality, such as intrinsic characteristics [species, age, and sex], environmental conditions [temperature, salinity], and dietary history, including feeding rate and diet composition.

The feed used in freshwater fish farming contains various types of animal and vegetable-derived meals and oils. It is this diversity of ingredients that makes it essential to understand how they affect the fillet, the main product to be marketed.

The undesirable taste in fish, associated with the use of commercial feeds, is rarely observed. According to Kubitza [24], the grains, meals, and flours of animal and plant origin used in fish feed do not alter the taste and odor of fish fillets in a way that is detectable by consumers. However, depending on the type of ingredient used and its inclusion level in the feed, they may cause differences in pigmentation (color) and texture of the meat.

According to the influences of the diet on the physicochemical characteristics of fish muscle, it is possible to evaluate not only its sensory characteristics but also its biological value, based on the increase of nutrients beneficial to human nutrition, such as high protein content, vitamins, minerals, and others.

It is also from the composition of fish meat obtained through a specific diet that the amount of unsaturated fatty acids can be analyzed, as well as their role in the conservation process and the production of derived products, through analysis of changes resulting from their oxidation. These characteristics, responsible for the good acceptance of this meat in the market, can be altered by inadequate feeding of the fish.

Studies, such as that of Duarte et al. [25], demonstrate that supplementation with fish oil, for example, results in Nile tilapia fillets with more favorable fatty acid profiles, showing lower n-6/n-3 ratios and higher proportions of PUFA compared to saturated fatty acids, in comparison to control diets. However, these changes in lipid composition can directly influence the oxidative stability of the products.

Furthermore, the inclusion of lipid sources in the feed can lead to a considerable increase in body fat depending on the levels of inclusion, with a proportional equivalence to the added amounts. An excess of fat in the carcass, even if composed of high-quality lipids, is currently undesirable as it not only affects the sensory characteristics of the meat but also decreases the fillet yield percentage due to fat accumulation in the abdominal cavity's adipose tissue, negatively impacting the fish's commercial value [26].

For Bridi et al. [27] the term meat quality is comprehensive and involves sensory aspects (color, tenderness, flavor, juiciness, odor), functional aspects (pH, water-holding capacity), and nutritional aspects (amount of fat deposition, fatty acid profile, oxidation level, protein, vitamin, and mineral content). Moreover, it involves sanitary measures to ensure the absence of contagious agents, food safety against biological, physical, and chemical hazards (food free from antibiotics, hormones, or other contaminating substances), as well as ethical principles related to human and animal welfare, environmental preservation (sustainability of the system and environmental impacts), and social issues (such as the prohibition of child or slave labor).

Among the sensory aspects, color is one of the main quality parameters evaluated by consumers, as it is directly associated with the perception of freshness and the visual appeal of the product. Changes in meat coloration can indicate alterations in the physicochemical state, such as pigment oxidation or variations in myoglobin levels, reflecting the nutritional condition of the fish, pre-slaughter handling, and processing. These factors directly influence the acceptability of the product in the market.

In this work, we aim to gather and discuss the main methodologies applied in the evaluation of fish meat quality (**Figure 2**), emphasizing their practical applications and contributions to the improvement and acceptability of products in the production chain.



Figure 2: Physicochemical parameters for evaluating fish meat quality.

In general, the various fish species have their own characteristic coloration in muscle, body fluid, viscera, skin, and scales. This diversity of colors is related to the presence of various natural pigments (substances that give color to animal tissues or cells) such as myoglobin, hemoglobin, bilins, hemocyanin, carotenoids, melanins, pteridines, purines, and others [28]. Being unstable, these pigments participate in various reactions. Therefore, a change in the color of a given food is an indicator of possible chemical and biochemical alterations resulting from processing and/or storage [29].

Melanin, for example, is responsible for the dark coloration seen in fish. Carotenoids, which are fat-soluble, give yellow to red colors to the meat. Pteridines, on the other hand, are water-soluble compounds, resulting in brighter colors, although they play a lesser role compared to carotenoids. Purine compounds, predominantly guanine, are generally found in the belly skin of most fish species, giving a silver coloration. These basic pigments can combine with other components, such as proteins, producing colors in fish that range from blue and violet to shades of green [29].

The color of fresh meat is due not only to hemoglobin, which remains in the tissue as residual blood, but primarily to the concentration and chemical state of myoglobin [30]. Additionally, the method of slaughter and bleeding plays an important role in meat quality, as proper bleeding reduces the retention of hemoglobin in the muscle, improving the product. The color of the meat is not influenced only by the slaughter and bleeding process, but also by the fish species and the diet to which it has been subjected. These factors can cause variations in coloration, ranging from white and soft pink to vivid red tones.

The discoloration of fish meat can occur due to the oxidation of myoglobin, influenced by factors such as muscle pH, redox potential, activity of metmyoglobin reductase, oxygen consumption, lipid oxidation, exposure to light, and storage temperature [31]. In the early stages of lipid oxidation, the formation and accumulation of hydroperoxides, a primary product of oxidation, occurs. This phenomenon is observed both between different fish species and between white and dark muscles [32].

Additionally, changes in meat color can be attributed to intrinsic factors of the animal, such as muscle type, species, age, and sex, as well as extrinsic factors, such as diet and physical exertion prior to slaughter. Post-mortem factors, including pH, temperature, and anatomical region, also play an important role in this process [33].

The color of a food directly influences the consumer's perception, having a significant impact on them and influencing their choice and purchasing behavior of a particular product. According to Francis and Clydesdale [34], color can be defined as the sensation visualized by an individual when light energy corresponding to the visible spectrum reaches the retina of the eye, with the region of the electromagnetic spectrum sensitive to the human eye located in the wavelength (λ) range between 390nm and 750nm. The colors corresponding to the visible range of the spectrum can, therefore, be described from the perspective of sensory perception resulting from the detection of light after interaction with an object, that is, subjectively, through an observer who analyzes the color as "red," "green," "yellow"; or it can be objectively evaluated according to its wavelength through instruments.

In order to standardize color measurement, the Commission Internationale de l'Eclairage (CIE) in 1931 adopted methods for measuring and specifying color using light sources standardized by the CIE, exact provisions for observation, the use of appropriate mathematical units for expressing color, and the standard observer [35].

Color measurement, or colorimetry, can be performed using instruments such as the spectrophotometer and tristimulus colorimeters, as well as additive or subtractive visual colorimeters. The spectrophotometer provides measurements by reflectance and/or transmittance of a sample at each wavelength. The tristimulus colorimeter generates measurements correlated to human eye perception based on tristimulus values, using the XYZ color model and Lab* color model. Visual additive colorimeters rely on the addition of three primary colors (red, green, and blue) to form any color, while visual subtractive colorimeters involve the removal of parts of the visible spectrum through filters with primary colors [35].

In 1976, the CIE recommended the use of the CIE Lab* color scale, or CIELAB, in order to provide a uniform relationship between color differences and visual differences. This method is represented by a color scale, where the maximum value of L*, referring to lightness, is 100, corresponding to perfect diffuse reflection, and the minimum value is zero, representing black. The a* and b* axes do not have specific numerical limits. The a* coordinate ranges from red (+a*) to green (-a*), and the b* coordinate ranges from yellow (+b*) to blue (-b*). The delta values (ΔL^* , Δa^* , and Δb^*) indicate how much the sample deviated from the standard for L*, a*, and b*, and are frequently used in quality control and formulation adjustments. They are also used to calculate the total color difference (ΔE^*) [36].

Tenderness

Although at the time of purchasing meat other aspects such as color, visible fat, price, and cut are relevant, tenderness is considered by consumers as the most important sensory characteristic, as it is related, along with flavor and juiciness, to satisfaction at the time of product consumption [37].

Variations in meat tenderness involve several factors, with three being considered the most important: post-mortem proteolysis, connective tissue (collagen and elastin), and the state of muscle contraction [38].

After the fish's death, chemical, biochemical, and physical reactions occur that promote the development of post-mortem tenderness. A more applied understanding of these changes would be essential to assist in the production of higher-quality products. On the one hand, the denaturation and degradation of myofibrillar proteins and the cytoskeleton in mammals would be ideal for meat tenderization, but for fish, such changes in muscle structure would be undesirable. This is because texture is one of the most important qualities affecting the acceptance of the product. Therefore, while tenderness is desirable for beef, firmness is considered a key factor for fish meat quality [39].

Considering firmness of the muscle as an important indicator of fish freshness, softening would indicate deterioration and depreciation of the meat's properties. Therefore, to prevent such occurrences, it is essential to understand the mechanisms involved in this process in order to develop preventive measures to be used in aquaculture and the food industry, minimizing the loss of texture quality in the meat.

Fish meat softens after 24 hours of storage at low temperatures. Thus, a soft, crumbly texture limits the shelf life of the product, preventing its commercialization. This softening occurs as a result of the degradation of fish and shellfish proteins by both endogenous and microbial proteases, with prolonged storage under inadequate conditions intensifying the autolysis of nucleotides and nitrogenous compounds [40].

Some studies aim to investigate the effects of cooling and identify the mechanisms that cause softening and loss of texture post-mortem in fish meat, observing the intense hydrolysis of myofibrillar and collagen proteins and the subsequent changes that affect the muscle's microstructure [41,42]. Understanding the role of proteases, especially

those with collagenolytic activity in the fish meat softening phenomenon, is essential to prevent and delay quality losses associated with post-mortem handling or storage. This knowledge helps increase the market value of the product and minimize economic losses.

The textural quality of fish meat can be evaluated through a combination of physical, chemical, and sensory methods, each with its specific contributions to understanding the texture and tenderness of the product. Shear force, evaluated by the Warner-Bratzler method, stands out as the primary instrumental tool in texture studies [38], showing a good correlation with consumers' sensory perception. However, sensory analysis is indispensable to evaluate subjective attributes such as flavor, aroma, and juiciness, which cannot be measured by mechanical methods. On the other hand, chemical methods provide detailed information about the structural and biochemical components that influence texture, such as collagen, water retention capacity, and enzymatic activity.

Shear force (SF)

The tenderness of meat can be evaluated subjectively through sensory testing with a panel of tasters. However, due to the multifactorial characteristics, complexity, and uncertainty of this attribute, it is difficult to make an accurate judgment. Sensory testing is time-consuming and more expensive and labor-intensive compared to instrumental measurements [43].

Texture analysis can be applied both near the production line in the industry and in individual laboratory tests, measuring the elasticity, resistance, and specific hardness of fish products.

Tenderness analysis is performed using a texture analyzer, an equipment that measures the force required to cut the meat. The resulting value is expressed in kilogram-force (kgf). The test simulates the large deformations involved in chewing; therefore, a higher shear force, or force required to break the sample, indicates greater meat hardness.

Shear force is applied to both raw and cooked meats, with the Warner-Bratzler blade being the most efficient for evaluating firmness and texture. This instrumental analysis helps identify fillets with excessively soft consistency, an undesirable characteristic that compromises the quality perceived by consumers. Additionally, it aids in controlling structural defects, predicting tears and fissures in the muscle tissue, which make the fillets unsuitable for processing and industrial handling demands, resulting in downgraded or rejected products.

Collagen

The interstitial space in muscle cells is occupied by three proteins: collagen, reticulin, and elastin, which together are called connective tissue. In fish, the distribution of muscular connective tissue is specific to each species, with the concentration of collagen varying according to behavior and the activity performed during swimming movements [44].

The main structural protein of connective tissue, representing about 20 to 25% of the total muscle proteins, is collagen [45], a glycoprotein. Among the nineteen types of collagen, six (I, II, III, IV, V, and VI) can be found in meat. Of these, types I and III are the most studied in relation to their direct influence on tenderness [46]. Therefore, considering collagen as the main component of connective tissue, the texture of the meat is significantly influenced by it.

Numerous attempts to correlate the total collagen content in animal muscle with the final texture and tenderness of the meat have resulted in conflicting conclusions. Dransfield [47] demonstrated a relationship between the total muscle collagen and its role in meat hardening. However, other studies have found that the qualitative nature of collagen, rather than its quantity, affects the initial texture of the meat. In other words, it was not only the collagen content that was responsible for variations in meat hardness, but rather a combination of collagen crosslinking (cross-links between fibers), differences in content, and the diameter of the perimysial fibers that influenced the hardness between muscles [44].

On the one hand, collagen directly influences the texture of mammalian meat, affecting tenderness depending on its quality or quantity in the muscle tissue (location, size, solubility). However, the contribution of connective tissue to the texture of fish meat remains poorly understood. Fish have a lower collagen content, with lower solubility temperatures, which facilitates cooking in less time. In contrast, mammalian meats require longer cooking times and higher temperatures due to the complexity of their cross-linking [48,49].

Collagen is a heat-sensitive protein that undergoes chemical changes that impact the quality of meat products. During cooking, type I collagen, found in the epimysium, is more affected by heat due to its weaker cross-links, while type III collagen, with intramolecular disulfide bonds, is more stable. According to Bailey [50], a balance in collagen cross-links is essential for an acceptable meat texture, as both a lack of and an excess of these cross-links result in meat that is either too soft or too tough.

Chemically, collagen exhibits a composition rich in the amino acids glycine, hydroxyproline, and proline. Thus, in addition to observing the microstructure of collagen fibers through electron microscopy, and considering the prominent presence of hydroxyproline in collagen, chemical methods can also be used to assess meat texture. These methods are based on determining the connective tissue content through the quantification of hydroxyproline, which is extracted from the meat sample using acid or enzymatic digestion techniques [49].

Myofibrillar Fragmentation Index (MFI)

The texture of fish meat is influenced by several factors, including species, the quantity and properties of proteins, dietary management, and stress conditions during handling for slaughter. The various post-mortem reactions resulting from the rate and extent of pH decline, rigor mortis, the extent of proteolysis causing degradation of myofibrils and connective tissue, storage temperature, and others, are directly linked to the expression of the final qualitative attributes of the meat.

Proteolysis is one of the most significant biochemical changes during the conversion of muscle into meat and continues throughout the storage of the product. In mammals, proteolytic systems such as cathepsins and calpains have been widely studied due to their role in the degradation of myofibrils, particularly the actin-myosin bonds, proteins essential for muscle contraction. These enzymes help weaken the bonds between proteins, contributing to meat tenderization. However, the study of these systems in fish muscle still receives little attention [51], despite their importance in the maturation process of the meat.

It is known that post-mortem proteolysis in fish, while contributing to the release of bioactive peptides with potential health benefits for humans [52], can lead to the softening of fish muscles, depending on its extent, resulting in a loss of quality [53] and consequently causing the product to be rejected by consumers.

Several methods, such as the Myofibrillar Fragmentation Index (MFI), can be used to estimate the degradation of muscle structure post-mortem. The MFI reflects the extent of myofibrillar proteolysis and serves as a fast and efficient tool in evaluating meat texture, correlating with Warner-Bratzler shear force.

According to Watanabe et al. [54] the measurement of the MFI provides more direct results about the maturation process of meat than shear force analysis in cooked samples. This is because, being assessed from raw samples, the MFI avoids distortions in results caused by the effects of cooking processes, such as the denaturation of myofibrillar proteins and collagen, which, in addition to interacting with pH, affect the meat's tenderness.

As post-mortem aging affects the texture, tenderness, and water retention of meat, it is essential to control the time-temperature variables to optimize the action of enzymes for ideal meat tenderization and the development of other desirable sensory characteristics such as aroma and flavor.

Considering that the MFI is usually measured in fresh meat samples, and that low refrigeration temperatures could influence myofibrillar fragmentation due to enzyme activity inactivation, Veiseth et al. [55] aimed to compare the MFI values obtained from frozen muscle and fresh muscle, concluding that there was no significant difference between the results of both analyses. Therefore, MFI could also be evaluated in samples that had been frozen.

Water holding capacity (WHC)

One of the most evident changes in post-mortem muscle is water loss or exudation [39]. The texture of the meat, including its tenderness and firmness, is related to the amount of intramuscular water and its water holding capacity (WHC). WHC directly influences the commercial presentation of the product, its qualitative characteristics, and its behavior during processing, affecting both the appearance of the meat before and during cooking, as well as its juiciness during mastication.

Water loss in fish fillets is directly related to pH, as higher pH values result in less protein denaturation and greater WHC. Pressure and heat are also factors that affect the WHC of fish, and therefore, they must be controlled during industrial processing to ensure the preservation of the raw material's quality.

According to Flores and Bermell [56], all factors that affect myofibrillar proteins have a fundamental influence on WHC. Therefore, in addition to pH, other post-mortem changes and the effect of certain salts also play a role.

Meat during the pre-rigor period has a high WHC [39], meaning it retains its moisture when subjected to external forces such as cutting, grinding, pressing, and heating. This higher WHC may be related to the increasing ability of myosin to bind with water at a pH above the isoelectric point of the main myofibrillar proteins. Under these conditions, the electrostatic repulsive forces between proteins increase, forming a less compact myofibrillar matrix, thereby retaining more water molecules.

In the early hours after the animal's death, during the development of rigor mortis, a significant reduction in the WHC is observed, reaching its lowest point. This minimum level corresponds to the final post-mortem pH, between 5.3 and 5.5, known as the isoelectric point [39]. Thus, it is clear that the WHC is influenced, among other factors, by pH, ionic strength, and osmotic pressure.

In fish muscle, however, the pH tends to be higher than that of mammalian meat, rarely falling below 6.0, even in full rigor. Nevertheless, considerable water losses are reported in the muscles of animals that exercised excessively due to handling and slaughter. This may be associated with the characteristic decrease in pH in fish meat due to the accumulation of lactic acid produced during exercise, causing protein insolubility and promoting a condition known as gredosidade, meaning the formation of pale, soft, and exudative meat similar to PSE (pale, soft, exudative) [39].

In addition to excitability during exercise due to post-capture handling, it has also been found that water temperature, season, and sexual maturity affect gredosidade. It is essential, after capture, for the fish to remain in water for a certain period to stabilize and achieve normal muscle pH after slaughter [39].

A lower WHC affects the appearance of the meat and reduces its nutritional value, as the exudate released contains lipids, vitamins, soluble proteins, and minerals, making the meat drier and tougher.

As an important variable regarding meat quality, it is essential that WHC can be analyzed using certain techniques. Among them, there are methods without the application of mechanical force (gravimetric or evaporation methods), measuring weight loss due to the leakage of extracellular water; methods involving mechanical force (centrifugation, absorption, pressure on filter paper) through positive or negative pressure to force the leakage of intracellular and extracellular water, showing only trends that may occur during meat commercialization; or methods using thermal force (weight loss measurement during meat cooking), measuring the release of intracellular and extracellular water from samples subjected to cooking, which denatures the meat proteins. Therefore, it is noted that the comparison between obtained results will depend not only on the choice of the most suitable and convenient method but also on the standardization of its use [57].

In general, methods have certain peculiarities and limitations depending on the type of meat product being evaluated. Gravimetric methods are quite accurate; however, they require more time to complete the analysis. On the other hand, methods that apply mechanical force are faster, but the pressure applied causes damage to the structure of the meat sample. Therefore, the amount of water evaluated is not solely free water but a combination with other components.

Thus, the evaluation of water loss during cooking, water loss during thawing, and water-holding capacity are physical indicators of meat quality.

Lipid Oxidation

Lipid oxidation is an autocatalytic process that causes changes in meat quality, affecting its texture, flavor, odor, and color. In addition to impairing structural integrity and nutritional quality, making the meat less acceptable for consumption, this reaction also compromises food safety due to the formation of toxic compounds harmful to health.

This reaction is, therefore, the source of problems related to unpleasant tastes and odors, characteristic of rancidity. This occurs because meat is rich in triglycerides and phospholipids, which, due to the interruption of blood supply after slaughter, begin to undergo oxidation [58].

The chemical composition, high water activity, pH close to normal, and the levels of easily oxidizable unsaturated fats make fish meat a highly perishable product. The deterioration process of fish, consisting of enzymatic activity, fat rancidification, and the action of microorganisms from the surface, gills, and intestinal tract, begins immediately after the

animal's death. Its speed will depend on both exogenous factors, such as handling conditions, slaughter practices, processing, exposure time, storage, and preservation, as well as endogenous factors, such as the physicochemical characteristics of the fish [59].

Lipid oxidation reactions primarily occur when reactive chemical compounds with oxygen promote the breaking of double bonds in the phospholipid fractions of cell membranes, being more likely to occur in fish due to their higher degree of unsaturation. This mechanism causes the rupture of membranes and subcellular structures, altering their function as a semipermeable barrier due to the loss of essential polyunsaturated fatty acids (PUFAs) and the formation of hydroperoxides, aldehydes, and other secondary toxic products [60].

Thus, the extent of the oxidation phenomenon will depend not only on the number and nature of the unsaturations present in the lipid structure but also on the environment in which it is found, considering factors such as exposure to light and heat, the presence of pro-oxidant metal ions, and the presence of reactive oxygen species, known as free radicals [61], such as hydroxyl radicals, nitric oxide, superoxide, peroxy, or even non-radicals like hydrogen peroxide, hypochlorous acid, and ozone.

In all lipid oxidation mechanisms, the presence of a free radical is a rule, which reacts with the hydrocarbon chain of the fatty acid, forming a peroxide. This peroxide will react with another hydrocarbon chain, extracting hydrogens and forming a hydroperoxide. The carbon chain from which the hydrogens were extracted will act as a new peroxide, perpetuating the cycle [62].

Therefore, in an effort to prevent or delay oxidative rancidity, the meat industry has been using various technologies to preserve sensory characteristics and extend the shelf life of products, including vacuum packaging, modified atmosphere, and the use of antioxidants.

Chilled or frozen storage is another strategy that has been widely used to maintain the appearance and nutritional properties of fish meat while minimizing oxidative effects. However, the presence of highly unsaturated lipid composition and a high content of pro-oxidant molecules in certain fish species promote the progressive development of both enzymatic and non-enzymatic rancidity, even at low temperatures, as storage time increases.

Fatty marine fish, such as salmon, mackerel, and herring, and their oils have attracted consumers for being rich in polyunsaturated fatty acids (n-3), which are essential for health. Due to the high lipid content, it is important to control factors that accelerate oxidation, such as oxygen, light, and storage temperature [63], as the higher the temperature, the faster the oxidation of unsaturated fats.

Aubourg et al. [64], investigated through biochemical and sensory analyses the effect of lipid content in mackerel on the quality loss of whole fish and fillets during frozen storage, monitored for up to 12 months. Hydrolysis and increasing lipid oxidation were observed in both samples. Due to the higher rate of these reactions, the fillet had a shorter shelf life, approximately 1 to 3 months, compared to the whole fish, which lasted for 5 months.

Other factors that influence lipid oxidation include the presence of catalysts, known as pro-oxidants, which accelerate the oxidation reaction (such as metals and the heme group of myoglobin), and the water activity [aw] of the food. The presence of free water intensifies the catalytic activity of metals, and therefore, the risk of oxidation increases as water activity rises.

The resistance of meat to rancidity depends not only on the level of unsaturation and concentration of fatty acids but also on the balance of antioxidants in the animal tissues. Tocopherols are important substances with antioxidant properties that stabilize free radicals. Vitamin E is part of the tocopherol group. In nature, several forms of vitamin E are found: α , β , δ , and γ tocopherols, as well as tocotrienols, which act on the cell membrane by donating electrons and preventing membrane damage caused by reactive substances [61]. For this reason, they play an important role in reducing meat deterioration and exerting a stabilizing effect on color, delaying the oxidation of myoglobin.

Kasapidou et al. [65] observed that the antioxidant effects promoted by vitamin E, however, depend on its dietary concentrations. Thus, various studies are conducted with the aim of analyzing the effects of vitamin E supplementation on antioxidant activity in meat.

This is why the application of antioxidants directly to meat products or in animal diets to extend shelf life has received so much attention recently, particularly natural antioxidants. Substances such as butylated hydroxytoluene (BHT), butylated hydroxyanisole (BHA), and tert-butylhydroquinone (TBHQ) have strict limits for inclusion in food products [66].

Tocher et al. [67] evaluated the increase in vitamin E levels in muscle and its relationship with the antioxidant system in fish, observing that lower supplementation of this vitamin in the diet also resulted in decreased levels in the meat, consequently leading to an increase in oxidative reactions with a high production of lipid peroxides. Thus, it was possible to demonstrate the essential role of vitamin E in the nutrition of aquatic organisms, preserving fish quality, improving conservation, and ensuring a satisfactory texture in fillets and fish-derived products.

Lipid oxidation can be evaluated through physico-chemical methods aimed at quantifying the formation of compounds resulting from this reaction, such as the determination of peroxide values, conjugated dienes (produced in the early stages of autoxidation), thiobarbituric acid-reactive substances (TBARS), high-performance liquid chromatography (HPLC), among others. The most frequently measured products are hydroperoxides and conjugated dienes for primary oxidation, and volatile substances for secondary oxidation [63]. Among them, there are advantages and disadvantages, but the simplest and fastest methods are based on the quantification of pigments measured spectrophotometrically.

One of the most commonly used methods to assess lipid stability in meat products is the 2-thiobarbituric acid (TBA) test. It is known that hydroperoxides formed by oxidation reactions are rapidly broken down in secondary oxidation processes, producing aldehydes, ketones, alcohols, and carboxylic acids, which give the meat a strong characteristic odor and sometimes a yellowish color. Malondialdehyde is the most commonly found aldehyde resulting from lipid oxidation, produced during the autoxidation of PUFAs. In this context, malondialdehyde can be quantified in meat through the TBA test, where a reaction occurs between both to form a reddish-colored compound that can be measured spectrophotometrically at a wavelength of 532 nanometers (nm), or between 500 and 550 nm depending on the methodology chosen for the analysis [63].

With the result of the test, it is possible to quantify malondialdehyde based on the values obtained from a calibration standard curve with known concentrations of this compound. For preparing the curve, standards such as 1,1,3,3-tetramethoxypropane (TMP) or 1,1,3,3-tetraethoxypropane (TEP) are used, which, in combination with the acidic medium of the test, undergo hydrolysis releasing malondialdehyde. The results are expressed in units of absorbance per unit of sample mass or in "TBA value" or "TBA number," defined as the mass, in mg, of malondialdehyde per kg of sample [63].

Fatty acid profile

Lipids, composed primarily of fatty acids, are divided into two main groups: saturated and unsaturated. The saturation state of these fatty acids is an important chemical and nutritional characteristic. Fatty acids form triglycerides, which are lipids with the main function of providing and storing energy for the body.

The levels of lipids and the fatty acid profile significantly contribute to the quality attributes of meat, influencing its palatability, nutritional value, and tenderness [45].

Numerous studies highlight fish lipids as a rich source of polyunsaturated fatty acids, associating the consumption of these acids, particularly from marine species, with a low incidence of cardiovascular diseases. This link was first observed in the Greenland Eskimos, who followed a fish-rich diet [68].

In addition to preventing vascular diseases, acting as an antithrombotic and anti-atherogenic, lipids help reduce inflammation, prevent diabetes, nervous disorders, and vision problems. Their protective role has led consumers to adopt healthier eating habits, preferring meats with low cholesterol levels.

The lipid content in fish is variable and depends on the species, food availability, sexual maturation cycle, and nutritional management of the fish. Lipids play an important role in the organisms of living beings [69], serving functions ranging from structural and energetic to coenzymatic and hormonal.

In natural foods, the most commonly found fatty acids are those formed by chains with an even number of carbon atoms, ranging from 12 to 22 carbon atoms. These fatty acids are classified into four families/series: omega-9 (n9), omega-7 (n7), omega-6 (n6), and omega-3 (n3), with n6 and n3 being considered essential as they are important in energy balance [70].

Polyunsaturated fatty acids, such as linoleic acid (LA), C18:2 n6, which forms the n6 fatty acid family, and especially alpha-linolenic acid (ALA), C18:3 n3, are considered essential because mammals cannot synthesize them and must obtain them through their diet [68].

In particular, the omega-3 fatty acids eicosapentaenoic acid (EPA) and docosahexaenoic acid (DHA) have various beneficial properties for human health.

The composition of fatty acids in fish tissues reflects the diet, and its profile can be altered through nutritional management by adjusting the types of fats and oils used in the feed, with the goal of increasing the levels of EPA and DHA in farmed fish.

Farmed fish can have their diet enriched either through natural food created by fertilizing the tank with organic or chemical fertilizers, aimed at increasing benthic organisms or phytoplankton rich in PUFAs, or through supplementation with animal and plant oils rich in PUFAs. This strategy aims to increase the concentration of PUFAs in the flesh of the fish, which naturally have lower levels of these acids compared to wild species.

Several enzymes are involved in both biochemical cascades related to the metabolism of n6 and n3 fatty acids, making them interconnected and interdependent.

One of the main functions of ALA is its role as a precursor in the synthesis of EPA and DHA, allowing the human body to synthesize other essential n3 fatty acids. This synthesis is achieved from glucose and amino acids through enzymatic reactions of elongation (which add two-carbon units) and desaturation (which create new double bonds) [71]. Humans, however, have desaturase enzymes responsible for adding the double bond only at positions $\Delta 4$, $\Delta 5$, $\Delta 6$, and $\Delta 9$, meaning they cannot introduce unsaturations further from the carboxyl group than C9 [72]. However, fatty acids containing unsaturations beyond C9, such as $\Delta 12$ (n6), linoleic acid, and $\Delta 15$ (n3), are essential for these organisms.

The competition between ALA and LA for the same desaturation and elongation enzymes makes the conversion of ALA into EPA and DHA inefficient. For this reason, it is recommended to incorporate EPA and DHA into the diet from sources that naturally contain them. When ingested, LA and ALA need to have their chains desaturated and elongated to form physiologically active n3 and n6 LC-PUFAs (long-chain polyunsaturated fatty acids), or long-chain polyunsaturated fatty acids (20 carbon atoms or more).

The $\Delta 6$ desaturase enzyme is considered a key regulatory enzyme in the process of converting ALA to DHA, as it participates in two distinct points in the metabolic pathway [73].

The competition between essential n3 and n6 fatty acids occurs at the level of the same desaturase enzymes ($\Delta 6$ desaturase). The $\Delta 6$ desaturase enzyme prefers alpha-linolenic acid (omega 3) over linoleic acid (omega 6). As a result, the conversion products of alpha-linolenic acid, the EPA and DHA fatty acids, block the action of $\Delta 6$ desaturase, thus inhibiting the conversion of linoleic acid to arachidonic acid (omega 6), which prevents the production of eicosanoids from the series 2, prostaglandins, and leukotrienes 4. In this context, eicosanoids from the series 2 are prevented from exerting their harmful effects on the body, such as promoting cell proliferation in cancerous cell lines, invasion, and metastasis of tumors, due to the protective action of n3 fatty acids [74].

It is essential to conduct studies on the fatty acid composition in meat, as it affects both the product quality and consumer health. Moreover, it is important to investigate the relationship between n3/n6 and saturated/unsaturated fatty acids, improving the techniques for identifying and quantifying these fatty acids.

In conclusion, the analysis of fatty acids in fish meat as methyl esters (FAME) by gas chromatography stands as an effective and accessible methodology for the lipid characterization of these products. The rapid preparation of FAMEs and the use of different types of capillary columns with stationary phases of varying polarities enable efficient separation of fatty acids, depending on the sample characteristics. Identification is based on retention times, and quantification is obtained through peak area analysis, using an internal standard to ensure accuracy in determining the absolute concentration of fatty acids present. This technique provides a detailed and reliable evaluation of the lipid profile, crucial for understanding the quality attributes of fish meat [75].

Conclusion

Although animal nutrition is a tool used to generate economic gains in production and improve biometric indices in aquaculture, attention must be given to the influence it has on important qualitative attributes of the meat. Therefore, ingredients, especially those recycled from other industries, should be carefully studied for their applicability in animal production, with consequent implications for human nutrition and their relevance to environmental sustainability. Similarly, analytical methods should be explored with the aim of mapping physiological changes in fish and their

reflections on meat characteristics. For the development of science and technological innovation, it is necessary to standardize specific analytical methods for the food class in question, leading to more accurate and efficient analyses of its composition and nutritional quality.

Disclosure statement

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