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Proteomic studies of the effects of processing techniques on properties of abalone muscles: a comprehensive review

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ABSTRACT

With the increasing per capita demand for animal protein, there is a growing interest in the abundant abalone protein resources. Abalone proteins are known for their nutritional and functional properties that contribute to flavor and texture. We systematically constructed the relationship between abalone protein, processing, and proteomics. This paper reviews the nutritional properties of abalone proteins and evaluates the effects of different thermal processing techniques, non-thermal processing, and freezing on abalone proteins. In addition, we synthesize published abalone proteomics studies and the use of proteomics technology to better elucidate the quality changes of abalone and its products, and as a technical basis for the study of blue food marker proteins. It is important direction to clearly explain the protein composition and meat quality mechanism of abalone in the processing and storage by proteomic. During various types of thermal processing, non-thermal processing, and freezing of abalone, the various chemical forces between protein molecules are disrupted, which in turn leads to different degrees of denaturation, aggregation, and gelation, which may have an impact on the organoleptic properties, bioavailability, and digestibility of abalone muscle. Proteomics is used in abalone biology studies to understand developmental biology, physiology, disease, stress, and species identification and can also be a powerful tool to characterize processing methods on abalone quality properties.

1. Introduction

Abalone (*Haliotis*), one of the most valuable marine gastropods, is widely farmed in China, Australia, Korea, and many other regions[1]. Chinese abalone has rich and full flesh and is considered tender and delicious. The well-developed gastropod muscles are rich in high-quality proteins and are mainly composed of myofibrillar protein (MP; 30%–50%) and collagen (10%–30%)[2]. It also has a complete range of amino acids, is rich in physiologically active substances, can be used as a functional health food, tonic, and medicine, and has physiological anti-fatigue and detoxification benefits[3].

Protein changes play an important role in the quality of food. Abalone gastropods are rich in MPs and collagen, both of which are structural proteins with important biological functions, mainly involved in muscle contraction. They affect muscle tenderness and have important effects on the water retention, elasticity, and texture of meat products[4]. Protein structure is maintained by chemical forces such as ionic, hydrogen, and disulfide bonds, as well as hydrophobic interactions[5]. During abalone processing, MP and collagen undergo

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dynamic structural changes in response to external conditions, which cause protein denaturation and affect the quality of abalone products. Food processing techniques, including cooking, pasteurization, pulsed electric fields (PEF), and high-pressure treatments, have a significant impact on the structure and function of proteins, which in turn changes the quality and nutritional value of the final product[6]. On this basis, it is important to identify and validate proteins using proteomics to characterize the degradation, polymerization, and denaturation processes in abalone muscle at the molecular level. Proteomic is an innovative combinatorial research approach that essentially links transcriptomic and proteomic databases to genes to proteins. Proteomics can provide valuable information about the protein properties and biological mechanisms underlying food quality[7-8]. The food industry is focusing on more subtle effects and mechanisms of interactions in order to make further progress in food quality and in determining the direct relationship between food and human health.

The basic research related to abalone protein in the world is nascent, the degree of understanding still needs to be deepened, and abalone protein has not been fully exploited. Here, we systematically review the relevant studies on abalone protein and introduce the research progress of abalone proteomics to provide the theoretical basis for the high-value utilization of abalone protein resources, which is of great significance to both enrich the supply of high-quality animal protein resources and exploit the marine biological resources.

2. Abalone protein content and composition

The basic chemical composition and protein content of abalone muscle are shown in Tables 1-2[9-10]. Apart from water, abalone is mostly composed of protein. Appropriate measures can effectively inhibit the action of enzymes and microorganisms in abalone, but fat and protein oxidation still proceed slowly, resulting in protein denaturation and degradation. As the main proteins constituting abalone muscles, the relative content and interactions of MPs and collagen proteins influences nutritional content and texture[11]. Studies have shown that myogenic fibronectin is mainly composed of myosin, actin, actinomycin, and pro-myosin, which has good gelation and water-holding capacity and plays an important role in the structural properties of abalone muscles[2]. In addition, as one of the main proteins of connective tissue, the collagen content directly affects the tenderness of abalone gastropods. The collagen of abalone and other aquatic invertebrates is mainly divided into two types: type I and type V[12].

Table 1
Proximate composition of abalone muscle.

Proximate composition	Content (%, wet weight)
Moisture	74.93 ± 0.25
Protein	15.87 ± 0.15
Carbohydrate	6.51 ± 0.06
Lipid	0.22 ± 0.02
Ash	0.36 ± 0.03

Table 2
Muscle protein composition of foot and middle adductor from reared abalone.

Muscle part	Protein fraction (%)			
	Sarcoplasmic	Myofibrillar	Alkali-soluble	Stroma
Foot	17.8 ± 3.1	33.2 ± 3.9	19.5 ± 4.1	29.6 ± 5.8
Middle adductor	17.3 ± 2.4	49.6 ± 1.9	20.1 ± 1.4	13.0 ± 2.8

The edge of the abalone foot and surface is mainly composed of connective tissue, while the middle adductor is mainly composed of myofibril[13]. The protein composition of abalone muscle is relatively high in MPs and stroma proteins (SP), among which MPs play an important role in the structural properties of the muscle and work together with SP to maintain the structural integrity of muscle cells[14-15].

The non-protein nitrogen in abalone muscle comes from free amino acids (FAA), nucleotides, and other substances that affect the flavor of abalone muscle. During abalone storage, denaturing hydrolysis occurs with the destruction of muscle fiber structure, and the content of alkali-soluble protein increases[16]. Abalone muscle contains the least amount of sarcoplasmic protein, which is related to muscle color, flavor, and water-retaining capacity[17], and is one of the factors that indirectly affect the quality of abalone muscle texture. Additionally, the energy value of abalone muscle is estimated to be 91 kcal/100 g, which is lower than that of low-fat meats such as beef and pork[18], making it a high-protein, high-carbohydrate, and low-fat food.

3. Nutritional characteristics and evaluation of abalone protein

The composition of abalone protein determines its unique nutritional characteristics, and the basic physicochemical properties of its protein determine the processing characteristics of abalone products. The nutritional evaluation of abalone protein is usually considered by the content and proportion of essential amino acids (EAA) or through *in vitro* digestion and *in vivo* experiments. Abalone protein contains 8 EAA and 10 nonessential amino acids (NEAA). The total amount of EAA accounts for 34% of the total amino acids, while the amino acids account for 41% of the total amino acids. The highest content was of glutamic acid, followed by arginine, aspartic acid, leucine, and glycine (Table 3). Glutamate and leucine are important components of amino acids for umami peptides, which synergistically forms flavor with aspartic acid, enhancing the edible value of abalone[19]. Cysteine is the most abundant EAA in abalone muscle. As a sulfur-containing amino acid, cysteine participates in DNA transcription and RNA translation and can be converted into taurine and glutathione in the body, playing a key role in regulating metabolism[20]. In addition, the percent of sulfur-containing amino acids in abalone is higher than in the Food and Agriculture Organization of the United Nations (FAO)/World Health Organization (WHO) standard model diet for adults. Abalone consume a large amount of taurine to maintain normal life activities under high temperatures and enhance its resistance to the high-temperature environment in summer[21].

4. Abalone proteomics

Proteomics is a technique that allows high-throughput analysis of proteins expressed in biological systems under specific temporal and environmental conditions, mainly involving protein identification, localization, and quantification, as well as elucidation of protein modifications and protein-protein network interactions[22]. Proteomics technology can provide technical support to the marine industry for research on origin traceability, seafood farming, optimization of processing methods, functional ingredient detection, and food safety[23]. The advantage of proteomics technology is the high-throughput detection of seafood protein content level and dynamic

change information, which provides a reference for marine food quality evaluation methods[24]. In the past decade, more and more research based on the mass spectrometry (MS) platform has gradually replaced the traditional gel-based proteomics technology (Table 4). The schematic overview of a typical abalone proteomics experiment is shown in Fig. 1.

Table 3
Amino acid composition of abalone (%) and essential amino acid index (EAAI).

Amino acids	Muscle	Fractions		
		WF	MP	SP
Leu	6.07 ± 0.14^{b}	7.27 ± 0.48^{c}	8.52 ± 0.62^{d}	2.30 ± 0.42^{a}
Thr	4.67 ± 0.14^{c}	4.03 ± 0.18^{b}	4.76 ± 0.27^{c}	2.51 ± 0.06^{a}
Val	4.13 ± 0.08^{b}	4.86 ± 0.37^{c}	5.04 ± 0.41^{c}	2.36 ± 0.16^{a}
Ile	3.99 ± 0.08^{b}	4.06 ± 0.29^{b}	5.59 ± 0.67^{c}	1.55 ± 0.21^{a}
Phe	3.19 ± 0.08^{b}	3.95 ± 0.24^{c}	3.74 ± 0.29^{c}	1.74 ± 0.20^{a}
Tyr	3.47 ± 0.06^{b}	3.45 ± 0.27^{b}	3.92 ± 0.24^{c}	2.23 ± 0.38^{a}
Phe + Tyr	6.66	7.40	7.66	3.97
Met	2.35 ± 0.02^{b}	2.26 ± 0.33^{b}	3.08 ± 0.22^{c}	1.83 ± 0.17^{a}
Cys	1.36 ± 0.18^{b}	1.35 ± 0.13^{b}	0.80 ± 0.15^{a}	3.28 ± 0.28^{c}
Met + Cys	3.71	3.61	3.88	5.11
Lys	2.93 ± 0.76^{c}	5.04 ± 1.23^{d}	1.47 ± 0.21^{b}	0.85 ± 0.04^{a}
His	1.74 ± 0.26^{b}	2.76 ± 0.37^{c}	1.64 ± 0.18^{b}	0.12 ± 0.04^{a}
Trp	0.96 ± 0.03^{b}	1.17 ± 0.03^{c}	0.48 ± 0.03^{a}	0.50 ± 0.01^{a}
Total EAA	34.86 ± 1.76	40.21 ± 2.19	39.05 ± 4.83	19.27 ± 0.93
Arg	12.51 ± 0.22^{c}	14.86 ± 0.59^{d}	10.83 ± 0.50^{b}	9.91 ± 0.17^{a}
Asp	9.88 ± 0.44^{b}	11.81 ± 0.61^{c}	12.40 ± 0.61^{c}	8.28 ± 0.10^{a}
Glu	17.02 ± 0.54^{c}	15.90 ± 0.66^{b}	21.02 ± 1.08^{d}	14.81 ± 0.26^{a}
Ser	4.61 ± 0.18^{a}	5.20 ± 0.24^{b}	4.91 ± 0.25^{ab}	5.36 ± 0.38^{b}
Gly	8.90 ± 0.86^{b}	3.93 ± 0.29^{a}	3.51 ± 0.17^{a}	21.07 ± 0.57^{c}
Ala	5.61 ± 0.34^{b}	4.51 ± 0.19^{a}	6.65 ± 0.32^{c}	7.15 ± 0.05^{d}
Pro	3.89 ± 0.41^{c}	2.92 ± 0.37^{b}	1.17 ± 3.04^{a}	7.22 ± 0.14^{d}
Hyp	2.71 ± 0.42^{c}	0.66 ± 0.05^{b}	0.46 ± 0.08^{a}	6.93 ± 1.29^{d}
Total NEAA	65.14 ± 3.12	59.79 ± 2.46	60.95 ± 4.06	80.73 ± 2.18
EAAI	65.95	75.84	62.80	34.49

Note: Different letters in the same line indicate significant differences ($P < 0.05$). WF, water-soluble fraction.

Table 4
Proteomics investigations for abalone (*Haliotis* spp.) in the past decade.

Proteomics	Species	Study field	Main finding	References
Label-free coupled with LC-MS/MS	*H. discus hannai* Ino	Food processing	A total 353 proteins were identified in fresh abalone muscle. The number was decreased to 233 (6 min) and 201 (30 min), and then increased to 271 (240 min) during boiling	[11]
iTRAQ coupled with LC-MS/MS	*H. discus hannai*	Growth	1 904 Proteins identified with 125 differentially expressed proteins (DEPs) in large specimens as compared to small specimens	[25]
TMT coupled with HPLC and LC-MS/MS	*H. discus hannai*	Food traceability	A total of 1 569 proteins were detected and 729 proteins were identified as DEPs in *H. discus hannai* cultured in Northern and Southern China	[26]
Two-dimension difference gel electrophoresis (2D-DIGE) coupled with MRM-MS	*H. laevigata*	Reproduction and development	Positive associations were observed between the abundance of specific proteins, such as heat shock cognate 70 and peroxiredoxin 6, and the propensity or failure to spawn in abalone	[27]
iTRAQ coupled with LC-MS/MS	*H. midae*	Environmental stress	A total of 227 DEPs were identified in *H. midae* haemocytes in response to varying degrees of exposure to ocean acidification conditions	[28]
2-DE	*H. diversicolor*	Populations	254 Spots showed differential expression among the three populations and 85 protein spots percentage volumes varied more than twofold	[29]

Note: TMT, tandem mass tagging; LC-MS/MS, liquid chromatography-tandem mass spectrometry; HPLC, high performance liquid chromatography; iTRAQ, isobaric tags for relative and absolute quantitation; MRM-MS, multiple reaction monitoring mass spectrometry; 2-DE, two-dimensional gel electrophoresis.

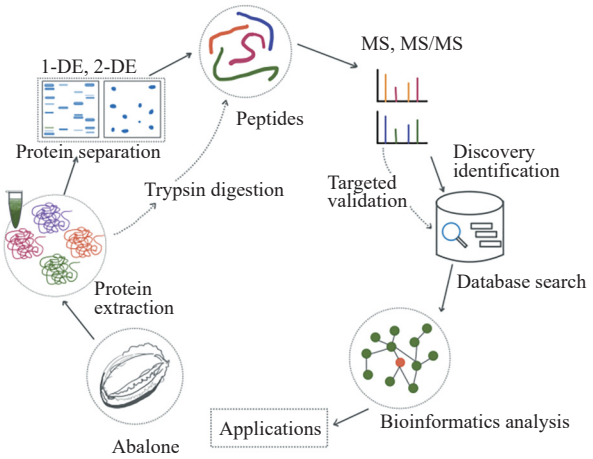

Fig. 1 Schematic overview for a typical proteomic experiment.

4.1 Proteomics for improving abalone hybridization

Hybridization is one of the widely used and effective methods in aquatic biological breeding, with the main purpose of producing new abalone cultivars with rapid growth and high resistance to adversity. Proteomic methods may be used to find pertinent biomarkers and define the molecular characteristics of hybrids in comparison to their parent species[30]. Proteomics, therefore, offers hope for a sustainable marine industry.

The 2-DE and MS methods were used to compare the proteomic differences between the Japanese and China Taiwanese populations and their inbred populations. The results showed that 46 DEPs in the populations were involved in major biological processes, including muscle contraction and regulation, energy metabolism, and stress response and showed additive properties in their progeny[29]. Di et al.[31] used 2-DE and matrix-assisted laser desorption/ionization time-of-flight/time-of-flight (MALDI-TOF-TOF) analysis to observe protein expression in hybrid and parental abalone muscle samples. A total of 136 DEPs spots were identified. These were mainly involved in energy metabolism and stress response. Most energy metabolism proteins were additive, and stress-induced proteins displayed additivity or overdominance. These data lay the foundation for future studies on the molecular mechanisms associated with advantages in hybrid abalone using proteomic approaches. However, the limitations of the application of proteomics technology come from the unstable proteome, high molecular weight, the presence of high abundant proteins[32], which make the current research of proteomics technology in sustainable aquatic development limited.

4.2 Proteomics for improving abalone breeding

Egg quality determines the overall reproductive fitness of an animal. Studying this topic can benefit the development of aquaculture and fisheries because healthy individuals are produced by high-quality eggs, and aquaculture development would benefit from a thorough understanding of the molecular foundation of reproduction. Further proteomic analysis of hybrid abalone eggs from *H. gigantea* (G) and *H. discus hannai* (D) and their parental abalone eggs was performed by Di et al.[33]. From the established 2-DE protein profile of abalone eggs, 112 protein gel sites were identified, and 59 were abalone proteins. Most of the differentially expressed protein sites involved in energy metabolism and stress response showed additivity or upregulation in GD (*H. gigantea* ♀ × *H. discus hannai* ♂). These findings suggest that protein expression levels may affect new abalone variety growth rates. Proteomic approaches can be useful tools for comparing the molecular phenotype of hybrid individuals with their parental species, which might identify relevant genetic markers and provide information for molecular breeding. Palmer et al.[34] provided an insightful report of candidate fertilization proteins by using the testis transcriptome and sperm proteome in combination. They identified 975 sperm proteins in abalone using shotgun mass spectrometry. In addition to the two proven sperm proteins (lysozyme protein and SP18), it is interesting that they identified the abundant and rapidly evolving homologous protein SP6. The acrosome localization and rapid evolution of SP6 suggest a possible role in abalone sperm-egg interactions to promote species-specific fertilization.

The expressed sequence tag and genomic resources predicted protein sequences that were used to establish a mollusk protein database. This database was used for a comprehensive abalone gonadal proteome analysis, which provided a basis for ongoing reproduction studies of cultured abalone[35]. Furthermore, spawning can be induced by a combination of thermal and UV irradiation. Mendoza-Porras et al.[27] used 2D-DIGE and MRM-MS to detect differences in protein expression in successfully and unsuccessfully spawned abalone after artificial induction. Many reproductive proteins, including vitellogenin, vitelline envelope zona pellucida domain 29, prohibitin, and metabolic proteins such as thioredoxin peroxidase, superoxide dismutase, and heat shock proteins, were identified. Positive associations were observed between the abundance of specific proteins, such as heat shock cognate 70 and peroxiredoxin 6, and the propensity or failure to spawn in abalone.

4.3 Proteomics for abiotic stress and stress response

Proteomics has also been used in the study of fish cultures under different environments and different toxic substances, and since proteins are biologically active molecules, the determination of different concentrations of specific proteins in cells exposed to altered environmental states represents a relatively direct measure of molecular stress response mechanisms[36]. Proteins are constantly influenced by environmental conditions, and the proteome of abalone is dynamic, which is beneficial for gaining insight into molecular phenotypes that represent functional adaptations to environmental changes.

Many of these studies compared the proteomes of control abalone and abalone exposed to abiotic stressors, such as endocrine-disrupting chemicals (EDCs). In abalone, the effects of EDCs (diallyl phthalate (DAP) 50 μg/L and bisphenol-A (BPA) 100 μg/L) were studied by proteomic analysis of hepatopancreatic tissue[37]. DAP or BPA exposure alters abalone hepatopancreatic protein physiological functions, including detoxification, oxidative stress, hormonal regulation, cellular metabolism, and innate immunity. Liu et al.[38] investigated the acute toxic effects of two typical EDCs, nonylphenols (NPs) and BPA, on abalone embryos at different developmental stages and their mechanisms. Proteomics results showed that as NPs and BPA alter multiple functional proteins in abalone larvae, they significantly affect a variety of physiological functions such as energy and substance metabolism, cell signaling, formation of the cytoskeleton

and cilium, and immune and stress responses, which eventually leads to the failure of their abalone larval formation.

Two-dimensional polyacrylamide gel electrophoresis (2D-PAGE) methods can be limited in detecting proteins outside the pI range or in low abundance, and with advances in gene expression analysis, new proteomics techniques are being more widely used in seafood research. iTRAQ is a relatively new technique wherein isobaric tags with known *m*/*z* values are covalently attached to peptides and depends on the MS/MS fragment of the peptide for quantification. It has the advantages of high throughput, accurate quantification, and high resolution and has gained attention in recent years[25]. For instance, Kang et al.[39] observed differences in protein expression between abalone exposed to prolonged high temperatures (26 ℃) and those exposed to fluctuating temperatures (20–26 ℃) based on iTRAQ and quantitative MS. Exposure of abalone to fluctuating temperatures resulted in a significant down-regulation of 20 proteins related to enzyme activity and a significant up-regulation of 20 structural proteins compared to prolonged 26 ℃ exposure. In addition, this biological response to high-temperature stress is also dependent on exposure time, and adjusting the thermal regime mitigated the potential risk to abalone at peak summer temperatures by reducing exposure time and increasing the upper thermal limit.

To further understand the immune system and pathophysiological mechanisms in abalone, Beltran[40] used a comparative shotgun proteomics approach using iTRAQ coupled with LC-MS/MS to characterize the proteomic changes in blood cells in the medium-term after bacterial infection. Alterations in the immune activation state alter the blood cell proteome and involve a range of molecular and biological processes. This study broadened the understanding of the innate immune response in marine invertebrates.

Climate change is making global ocean acidification increasingly common, and the effects of abiotic stresses and disease outbreaks are adversely affecting the need to maintain or increase annual abalone farm production[41]. Therefore, understanding the abalone immune system and stress response will help devise strategies to maintain its viability under changing climatic conditions during aquaculture. A study by Carroll et al.[28] identified key pathways and protein/effectors in response to ocean acidification stress by using a high-throughput shotgun proteomics approach to quantify the expression of hemocyte proteins. A total of 56 of 227 differentially expressed hemocyte proteins identified were biologically and statistically significant, primarily affecting key components of central metabolic pathways, stress, immune responses, and the cytoskeleton.

4.4 Proteomics for abalone population differences

The quality and nutritional value of species are known to be influenced by their geographic distribution, and the assessment of seafood's origin and the inheritance of variation between populations is consistent with the need to avoid fraudulent deception in order to maintain market transparency and consumer health. Proteomics plays a significant role in the field of biomarker detection and analysis for food certification because it is a suitable and potentially useful method for testing critical factors like food quality and safety[42].

To further elucidate the differences in gastropod muscle tissue proteins among different regional abalone populations, Di et al.[29] used 2-DE combined with MALDI-TOF-TOF/MS to comparatively analyze protein expression differences in three geographic populations (Japan, Taiwan (China), and Vietnam). The expression of 254 protein spots differed among the three abalone populations, and 85 DEPs were identified based on MALDI-TOF-TOF/MS as being mainly involved in energy production, storage, and stress responses. In addition, Luan et al.[26] distinguished abalone from Southern and Northern China based on TMT-based proteomics. A total of 729 differential abundance proteins were identified, of which 110 and 619 were up- and down-regulated, respectively. After bioinformatics analysis and western blot validation, fatty acid (FA) synthase, troponin I, calpain small subunit 1, and myosin light chain 6 were selected as candidate biomarkers for abalone culture in different regions. Although there are certain challenges, such as the absence of abalone protein sequences in the database that may reduce the effectiveness of protein identification, proteomics is becoming a feasible approach for abalone confirmation due to these successful applications. Hence, new algorithms, advances in bioinformatics, and improved MS equipment are needed to help correctly identify adulteration of marine species and their derived foods to ensure quality, quantity, and sustainability in the food industry.

5. The mechanism of protein changes during processing, and the quality of abalone

Proteins contribute to the texture and taste of foods in addition to providing nutrition. Proteins have a vital role in imparting nutritional value and organoleptic attributes to abalone. For fresh abalone, which is difficult to store and transport, various processing methods and products have been developed to enable distribution.

5.1 Thermal processing techniques

Thermal processing of food requires heating the food above 70 ℃. The most widely used methods are grilling and boiling, roasting, and deep-frying. Boiling extends the shelf life of abalone by inhibiting the growth of microorganisms and inactivating enzymes. However, high-intensity heat treatment may cause degradation and reduce the quality and sensory appeal of the treated products, especially for muscular food like abalone. Yu et al.[43] assessed the impact of different cooking temperatures and times on the muscle texture of the abalone. During the relatively milder heat treatments (60 ℃ for 10 min and 70 ℃ for 10 min), the cross-sectional area of the muscle fibers increased, and the cross-sectional apertures decreased, which led to an increase in the shear force and hardness of the abalone. Relatively strong heat treatment (70 ℃ for 30 min, 80 ℃ for 10 min, and 100 ℃ for 10 min) caused degeneration of myosin and contraction of myofibrils, eventually increasing the shear force and hardness of abalone muscles. The degradation of tropomyosin, paramyosin, and actin resulted in changes in the diameter, density, and cross-sectional area of muscle fibers[44]. The smaller diameter and cross-sectional area of muscle fibers and the higher density indicate higher tenderness and meat quality of abalone muscles[45]. Furthermore, an increase in temperature promoted multiple chemical changes: the exposed sulfhydryl groups were oxidized into disulfide bonds, myoglobin denaturation led to the formation of a newly ordered three-dimensional network structure, and the elasticity and hardness of the protein gel were enhanced[46].

A study by Yu et al.[4] investigated the differences in texture and digestive properties of different abalone parts (adductor and transition part) during boiling. With an increase in boiling time, the shear force and hardness of the abalone adductor first increased and then decreased, whereas the transition fraction continued to decrease after 6 min of boiling. At the same time, the degree of protein hydrolysis, protein digestibility, and peptide translocation levels of the adductor decreased significantly, while the protein digestion and transport indexes of the transitional fraction first decreased significantly (6 and 30 min) and then increased (240 min). In general, the difference in protein composition and structure between the adductor and transition part of the abalone gastropod results in more significant differences in texture and digestive properties. The adductor contains more MPs, and the transition part contains more collagen[47]. There is a good correlation between the collagen content and the toughness of abalone[48]. Increasing temperature weakens the hydrogen bonding between collagen molecules and increases the hydrophobic effect. Further heating loosens the triple helix structure of collagen molecules, degrades collagen into gelatin gel and loosens it with dehydration, and reduces the muscle toughness in the transition part[10]. To better understand the water-protein interactions after heating in abalone, Dong et al.[46] used nuclear magnetic resonance (NMR) and magnetic resonance imaging (MRI) to examine the dynamic distribution of water and the gel properties of proteins. The T_1 and T_2 weighted images and the corresponding histogram of the relative intensity of the T_1 and T_2 weighted images of abalone MP for different temperatures are shown in Fig. 2. The water distribution became relatively uniform throughout the abalone MP gels above 60 °C.

Li et al.[49] used *in vitro* gastric digestion simulation to evaluate the three cooking methods: steaming, boiling, and frying, and used NMR spectroscopy combined with multivariate statistical analysis to understand the nutritional changes of abalone. The results showed that boiling preserved more amino acids and FAs than steaming and deep-frying, making it the optimal choice among these cooking methods. In general, deep-frying promotes substantial lipid oxidation and protein degradation. In high-temperature frying, hydrophobic groups become exposed, leading to contraction and fracture of MPs and poor water retention in abalone muscle[50]. The release of FAA and short peptides increases the flavor of fried abalone. In addition, protein cross-linking and deamidation rates affect flavor and taste properties[51].

5.2 Non-thermal processing techniques

Non-thermal processing technologies such as ultrasound (US), PEF, high hydrostatic pressure (HHP), and atmospheric cold plasma (ACP) are gradually becoming emerging technologies in the food processing industry[52]. Non-thermal processing technologies have less impact on food nutrients than traditional heat treatment and can maintain the color, flavor, and texture of food[53]. In addition, non-thermal techniques can affect the structural and functional properties of proteins and can influence their digestibility either positively or negatively depending on their processing conditions[54]. HHP, US and PEF are other vital non-thermal processing technologies for abalone and related products (Fig. 3).

5.2.1 HHP

In addition to increasing food safety and shelf life in seafood applications, HHP, a type of non-thermal processing, has also been shown to increase meat tenderness[55]. Briones-Labarca et al.[56] treated abalone with HHP (500 MPa for 8 min and 550 MPa for 3 and 5 min), placed them in a 4 °C environment for storage, and compared the quality changes (microstructure, color, texture, and biochemistry) of abalone during refrigeration. Results have shown that the protein and fat content of treated abalone were significantly lower ($P < 0.05$); however, all HHP treatments had a less negative impact on muscle tissue color than untreated abalone during the refrigeration time. Another significant study examined the effect of HHP treatments (200, 300, 400, and 500 MPa for 5 min) on secondary structure changes and digestibility of abalone muscle and concluded that the

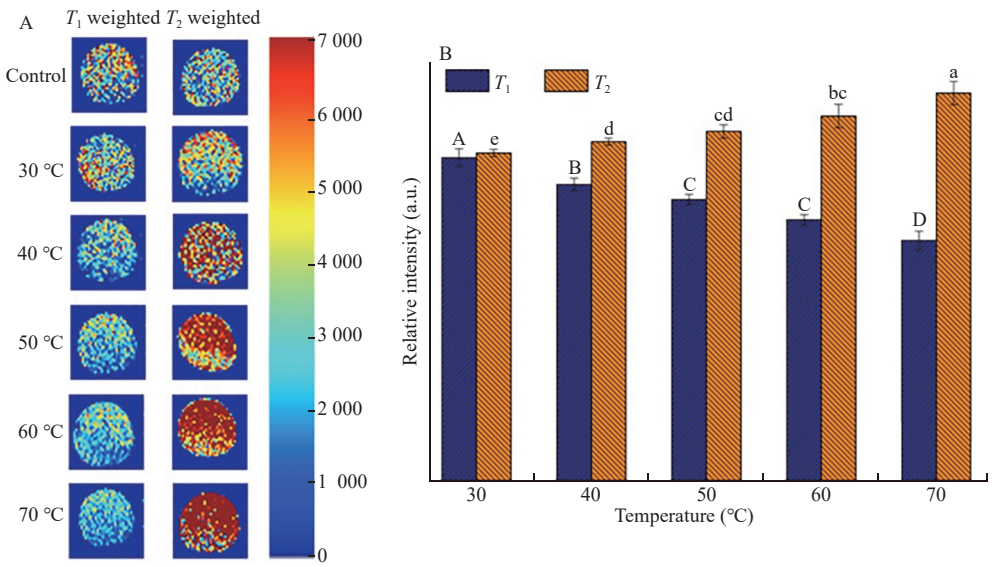

Fig. 2 (A) T_1 (longitudinal relaxation time) and T_2 (transverse relaxation time) weighted images of abalone MP gels heated at 30–70 °C and (B) the corresponding histogram of the relative intensity of the T_1 and T_2 weighted images[46]. Different letters for the same parameter indicate significant differences ($P < 0.05$) between treatments.

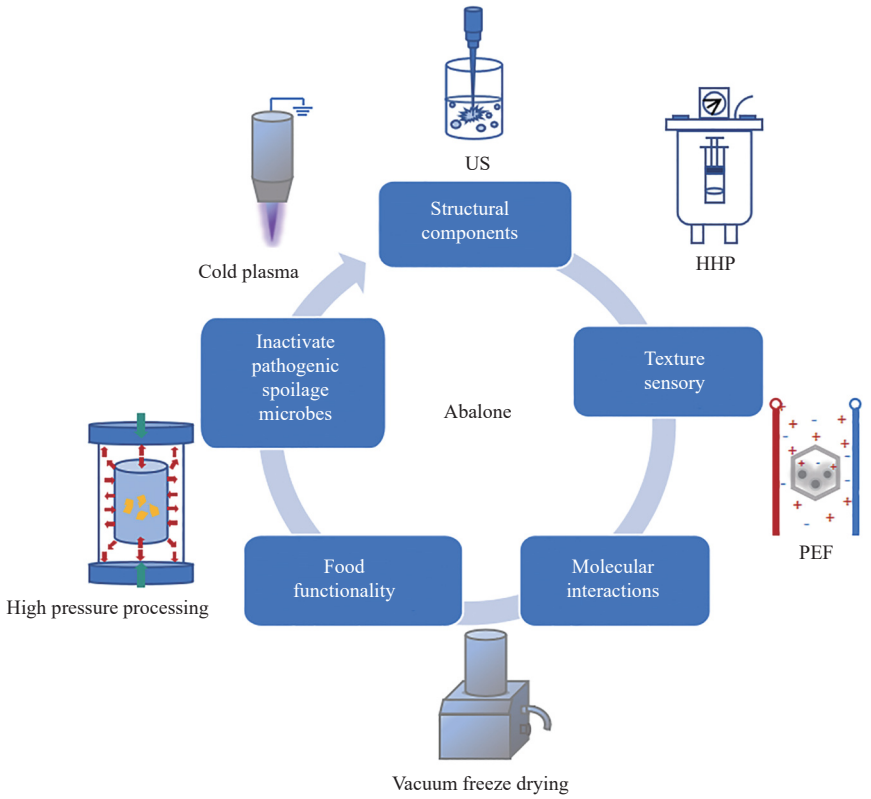

Fig. 3 Schematic representation of the impact of different non-thermal processing technologies on abalone.

HHP improved the hydrolysis of abalone through the change of β-sheet and β-turn conformations[57].

During HHP, ionic, hydrophobic, and hydrogen bonds are dissociated, leading to changes in the protein quaternary, tertiary, and secondary structures[58]. High-pressure treatment disrupts electrostatic interactions and stimulates sulfhydryl-disulfide exchange, which in turn leads to protein unfolding and exposure of side chains. Hydrogen, hydrophobic, and disulfide bond interactions promote protein refolding, which ultimately preserves the protein structure[59-60]. The schematic diagram of the mechanism of pressure-induced protein denaturation is shown in Fig. 4[61]. HHP induces water penetration into the protein cavities, and hydrogen bonds between protein molecules are disrupted due to hydrogen bonding interactions between protein and water molecules, which leads to the conversion of α-helices into β-sheets, β-turns, and random coils[62]. Hence, abalone proteins partially unfolded, making it easier for pepsin to carry out protein hydrolysis. In addition, HHP destroys the non-covalent bond structure of proteins, leading to the denaturation of abalone proteins and a decrease in the stability of connective tissue structure[63], which improves the digestibility of abalone proteins. Barrios-Peralta et al.[64] extracted MPs from abalone using phosphate buffer and determined their emulsification properties to evaluate the

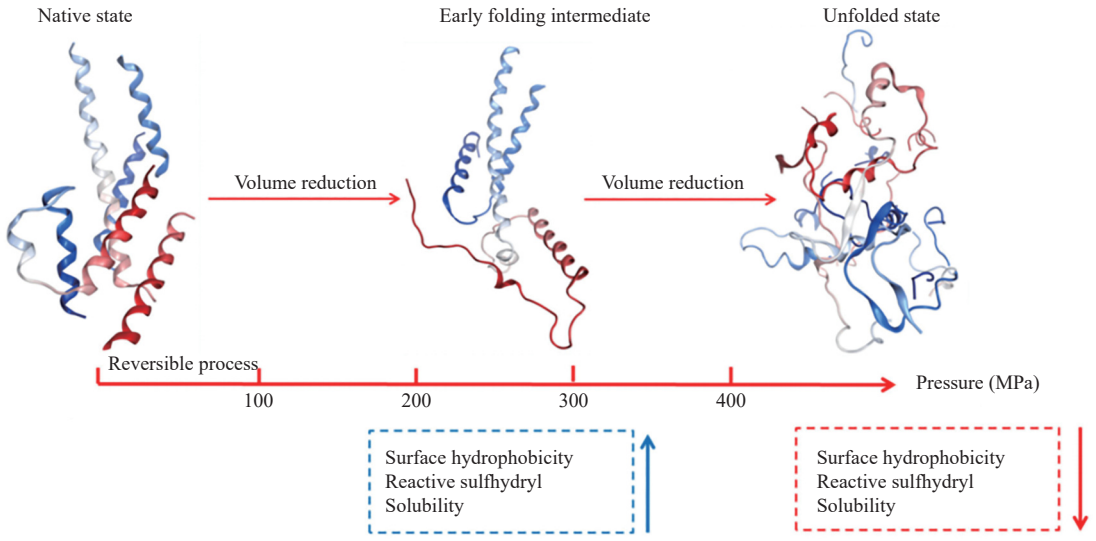

Fig. 4 Schematic diagram of the mechanism of pressure-induced protein denaturation[61].

effect of HHP processing on the salt-soluble proteins of abalone and the changes induced by the interaction with selected food additives (potato starch, dried egg whites, and agar). The results show that HHP alters the structure of abalone MPs and improves its functional properties when some food additives are added.

5.2.2 PEF

PEF treatment can change the microstructure of meat and the interaction between biomolecules such as proteins and is used extensively in several fields, including meat safety, tenderization, and salt reduction. PEF treatment of meat products is not as effective as in liquid food and can only reduce some Gram-negative bacteria on the surface of meat. Considering the limitations of PEF treatment of meat sterilizationu[65-66], it usually needs to be combined with other methods to ensure the safety of meat products. Luo et al.[67] investigated the effects of PEF treatment (0.66, 1.38, and 2.00 kV/cm, 50 Hz) with and without heat treatments (70, 80, and 90 ℃ for 15 min) on abalone muscle color, texture, lipid oxidation values, and FAA and FA content. The results showed that the PEF treatment had little effect on the physical and chemical properties of heated and non-heated abalone. There were almost no significant differences between non-PEF-treated control and PEF-treated abalone in terms of hardness, cohesiveness, elasticity, and chewiness values. Also, the changes in FAA content in abalone muscle tissue depended on the pulse intensity of PEF treatment, and a low pulse intensity did not cause significant protein hydrolysis. Protein hydrolysis can be accelerated by PEF treatment due to the release of Ca^{2+} that triggers calcium-dependent cysteine protease activation[68]. Meanwhile, the free radicals generated by PEF break the non-covalent bonds and electrostatic interactions of proteins, induce the unfolding of protein molecules, enhance the interaction between protein and water molecules, and finally improve the solubility of proteins[69]. Protein hydrolysis results in a degradation of the myogenic fiber structure and a decrease in shear force, which improves the tenderness of the meat.

Anais et al.[70] preceded the freeze-drying process of Chilean abalone with different PEF treatment conditions (0.5, 1.0, and 2.0 kV/cm) and evaluated their effects on protein quality, microstructure, and digestibility of the freeze-dried products. The analysis showed that PEF and cooking pretreatment significantly modified the protein structural bonds of Chilean abalone. Pretreatment with 2.0 kV/cm PEF combined with cooking had the most significant effect on the quality change of Chilean abalone samples, with samples treated with 2.0 kV/cm PEF also having higher values in the digestibility study. PEF treatment induces protein unfolding in an acidic gastric environment and enhances meat protein sensitivity by affecting the interaction of protein substrates and protease active sites[71-72]. In addition, the applied electric field causes cell rupture when it exceeds a critical threshold value, which can significantly improve the digestibility of proteins and the utilization of FAA in meat[73].

5.2.3 US

US is considered a green non-thermal processing technology and is widely used in the meat industry for processes that include emulsification, extraction, and physicochemical modification[74-75]. US can be classified into high-frequency (≥1 MHz) and low-frequency US (20 kHz to 1 MHz) and is used in food physicochemical inspection and food modification, respectively[76]. After ultrasonic treatment, the protein molecular chain is transformed into a disordered and loosely stretched structure, which affects the interactions between protein molecules, manifested in changes in the hydration capacity and solubility of proteins[77]. The cavitation, thermal, and mechanical effects of US change the structural and functional properties of proteins when applied to food[78].

Bagarinao et al.[79] reported the effects of US treatments on abalone texture, microstructure, and *in vitro* protein digestibility. The results showed that sonication in water for 5 min followed by soaking in water at 4 ℃ for 24 h exhibited the best effect on improving the texture of cooked abalone meat. The total release of free amino N and the overall protein breakdown during digestion were significantly higher in the US-treated cooked abalone than in the cooked control. During the US treatment, cavitation increases the surface area of solid-liquid contact, and the rupture of a large number of cavitation bubbles increases the pressure around the protein particles, prompting protein structure unfolding, peptide bond breaking, exposure of hydrophilic amino acid residues, and protein solubility increases[80]. It has been suggested that the cavitation effect of US may destabilize the degree of cross-linking and mature cross-linking of collagen, thereby increasing the solubility of collagen[81]. The mechanical action of US damages muscle fibers, causing damage to muscle cells and water molecules to enter cells[82], thus improving the water retention of muscles and increasing the tenderness of the abalone.

In a study of softened abalone offered to the elderly, Lin et al.[83] found that alkali soaking combined with ultrasonic cleaning had a significant softening effect, and the combined application of enzyme soaking and ultrasonic treatment reduced the hardness of the abalone by 16.32%. The pH of the meat after US combined with NaOH treatment was above the isoelectric point[84], which improved the water-retaining capacity of the protein and made the abalone muscle tender and juicy. Moderate sonication can effectively promote the unfolding of proteins, which can be more easily attack by enzymes, and at the same time, can improve enzyme activity by changing the intermediate conformation of enzyme molecules through cavitation effects[85]. Exposure of abalone to protein hydrolases released peptides and FAA, resulting in lower pH and greater muscle tenderness in abalone.

5.3 Freezing technology

Compared with other foods, seafood is high in moisture content, rich in protein, tender, and easily spoiled. In the processing and preservation of seafood, frozen is an important weight for the reserve and regulation of the seafood industry and is the main product form for the import and export trade and intra-regional circulation of seafood[86]. Ice crystals inevitably damage the cellular tissue structure and accelerate the freezing and denaturation of proteins in the process of freezing and storage, which leads to the deterioration of muscle texture and reduction in the abalone quality.

The freezing process disrupts the structure of myogenic fibronectin due to the formation of ice crystals and the increase in intracellular ion concentrations, exposing the hydrophobic groups buried within the protein molecules to the molecular surface, enhancing the protein-protein intermolecular hydrophobic

interactions, intermolecular aggregation, and decreasing solubility[87]. The primary purpose of abalone freezing is to inhibit the change of MP conformation, prevent the oxidation of sulfhydryl groups to disulfide bonds, and delay the oxidation of abalone MP[88]. It is difficult to achieve the desired preservation effect using a single cryopreservation technique. To improve this issue, researchers usually use cryopreservation techniques in combination with auxiliary techniques such as preservatives and pressure to extend the shelf life of frozen abalone products.

Abalone may have food safety issues during refrigeration due to the influence of microorganisms or long storage times. In response to this phenomenon, Hao et al.[89] used rosemary extract in combination with sodium alginate coating to prepare edible films that effectively altered the microbial composition in frozen abalone, which in turn affected the final microbial community composition and levels, pH, and total volatile basic nitrogen (TVBN) content. High pressure had potential advantages as a cold-pasteurization technique in delaying microbial growth as well as the production of TVBN. Pressurization at 200 MPa was the optimum pressure condition in which the shelf-life of abalone was extended to approximately 10 days, compared to 3 days in the control[90]. Furthermore, Hong et al.[91] investigated the effects of high-pressure sub-zero temperature and pressure-shift freezing on the quality characteristics of abalone and showed that variable-pressure freezing effectively reduced the effects of the freezing process on the quality of abalone.

6. Application of proteomics in abalone processing

Generally, proteomics studies focus on abalone reproduction and development, but the effects of different processing methods at the molecular mechanistic level that translate into differences in abalone muscle quality are still unclear. With the improvement of protein separation and identification techniques such as 2-DE-MS, LC-MS/MS, and iTRAQ, proteomics is becoming more popular for studying muscle quality. Yu et al.[11] used a non-labeled proteomic analysis to identify and quantify water-soluble proteins in abalone muscle during boiling. A total of 353 water-soluble proteins were identified in fresh abalone muscle, and with the extension between heating, cyanidin, protein kinase, dehydrogenase, phosphorylase, and others were not detected. After further heating, the newly identified proteins were mainly collagen and myogenic fibronectin. Proteomics is a feasible approach for studying abalone muscle quality and can provide insight into protein function, structure, biological properties, and protein-protein interactions (Fig. 5). Food composition changes significantly during processing, the differential or comparative proteomics provides quantitative and other valuable information on specific proteins during food processing to determine the effects of different processing conditions on food quality and nutrition. Currently, although the application of proteomics in abalone processing is limited, proteomics has been applied to explore the mechanisms for improving the texture of refrigerated *Litopenaeus vannamei*[92], meat quality of tilapia fillets during post-mortem storage[93], and the texture of the adductor muscles of boiled scallops[94]. Proteomics analysis can not only improve the understanding of biochemical mechanisms related to muscle quality changes but also help the meat industry to develop new technologies for meat product quality enhancement.

7. Conclusion and future direction

The nutritional and muscle texture characteristics of abalone are indicative of several factors: growth environment, management, and processing. Among them, the processing method greatly changes the structure, water-retaining capacity, and sensory properties of abalone proteins, thus affecting the quality of abalone products. 1) Further research is still needed regarding high-quality abalone processing systems. 2) Compared with other commercially valuable invertebrates, limited proteomic studies and incomplete databases are still obstacles in abalone research. 3) Proteomics needs further development to fully

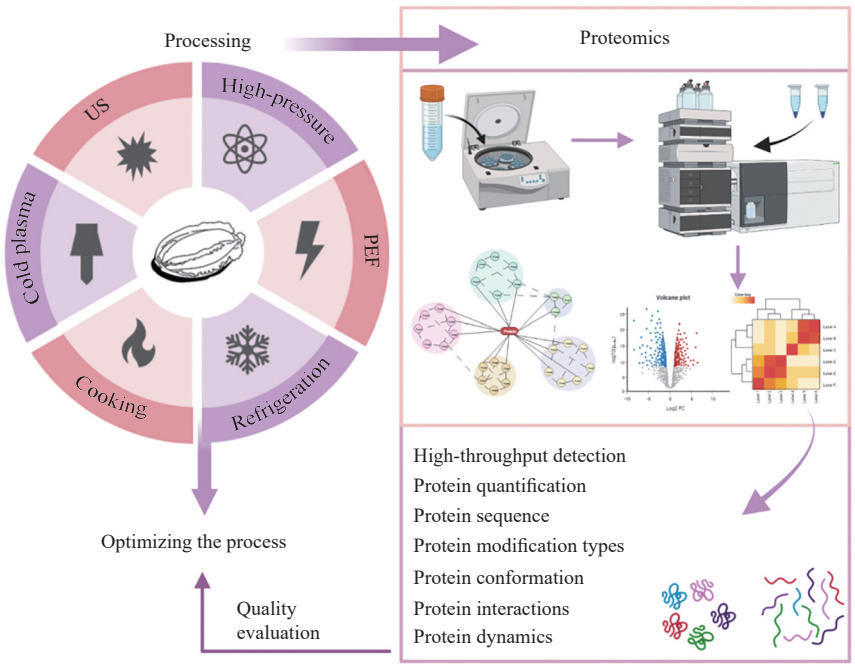

Fig. 5 System of abalone processing, proteomics, and quality evaluation (created with BioRender.com).

enable mechanistic studies and process optimization for sustainable abalone processing. 4) In addition, an integrated approach to proteomics and other omics technology may be useful to understand or influence physiological and quality changes in abalone.

Conflict of interest

Hongliang Zeng is an editorial board member for *Food Science and Human Wellness* and was not involved in the editorial review on the decision to publish this article. The authors declare no conflict of interest.

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