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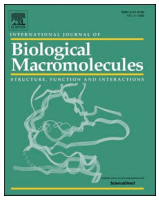

Review

New insights on health benefits, interactions with food components and potential application of marine-derived sulfated polysaccharides: A review

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ABSTRACT

Sulfated polysaccharides refer to polysaccharides containing sulfate groups on sugar units. In nature, sulfated polysaccharides are widely distributed in marine organisms, and the variation in sulfation sites, monosaccharide composition, and branched chain distribution among different species results in differences in the physicochemical properties and biological activities. From the latest perspective, this review summarized the types, structural characteristics, and potential health benefits of sulfated polysaccharides in marine foods. In recent years, marine-derived sulfated polysaccharides have been widely used as stabilizers and antimicrobial agents applied in nutraceutical delivery systems and food packaging, which depend on their interactions with food components. Hence, we outlined the non-covalent/covalent interactions of marine-derived sulfated polysaccharides with food components (e.g., proteins, polysaccharides, and polyphenols) as well as the application in food industry. Additionally, the prospects and potential development for sulfated polysaccharides are concluded, aiming to provide a deep understanding of marine-derived sulfated polysaccharides to promote the industrial application in food health.

1. Introduction

Oceans cover approximately over 70 % of the total surface area of the Earth. Marine food (also called "blue food") supply not only high-quality proteins for human beings, but also multiple novel structural and functional ingredients [1]. Notably, the sustainable development of marine foods can mitigate the environmental burdens associated with the production of numerous terrestrial foods.

Sulfated polysaccharides are another main component of marine food and widespread in algae, invertebrates, and marine microorganisms. In terms of structure, sulfate groups are present in a majority of polysaccharides derived from marine foods, which allows numerous potential health benefits, such as antioxidant, immunomodulatory, and anti-inflammatory activities [2]. Furthermore, the presence of sulfate groups allows sulfated polysaccharides (SPs) with polyanionic properties to interact with other positively charged compounds. For instance, protein–SP complexes with superior physicochemical properties can be obtained below the isoelectric point of protein. On the basis of the multiple advantages of marine–derived sulfated polysaccharides (MSPs), a widespread application has also been achieved in the food industry: serving as carriers for targeted delivery of bioactive ingredients to improve the bioaccessibility and as food processing additives to optimize the sensory and nutritional properties of food [3].

Although the origins and structures of MSPs have been reported in scientific literature [4,5], these works mainly focused on the biological activities of MSPs (e.g., antitumor and antioxidant activities) and their biomedical applications. However, the information on the application of MSPs in food is scattered. In general, interactions between sulfated polysaccharides and other components in multi-component food systems will inevitably take place in several ways, and these interactions may have a significant impact on the structure and properties of the foods. Therefore, this work first reviewed the structure, origin, and biological activities of natural SPs in marine food. Susequently, the possible noncovalent/covalent interactions among MSPs and food components (especially proteins) are summarized, and the applications of MSPs in the food industry are discussed. Moreover, the challenges and possible perspectives of MSPs are presented, aiming to facilitate their utilization in the food industry.

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2. Types and physicochemical properties of MSPs

2.1. SPs in marine plants

2.1.1. Fucoidan

Fucoidan is a water-soluble heterogeneous polysaccharide that is rich in fucose and sulfate groups, mainly found in brown seaweeds and invertebrate marine animals. In terms of structure, fucoidan possesses nonspecific chemical structure and is differentiated by species, and fucoidan derived from different species presents many structural similarities. In particular, the skeleton of fucoidan can be divided into two forms: a long chain formed with only α-(1 → 3)-linked-L-fucopyranose residues as repeating units and an alternating form of α-(1 → 3)- and α-(1 → 4)-linked-L-fucopyranose (Fig. 1A) [6]. The sulfate group is usually positioned at C2 and/or C4, and sometimes at C3 of L-fucopyranose. Simultaneously, the backbone may be linked to monosaccharides (e.g., galactose, mannose, xylose, and rhamnose), allowing the formation of more sophisticated conformations [7].

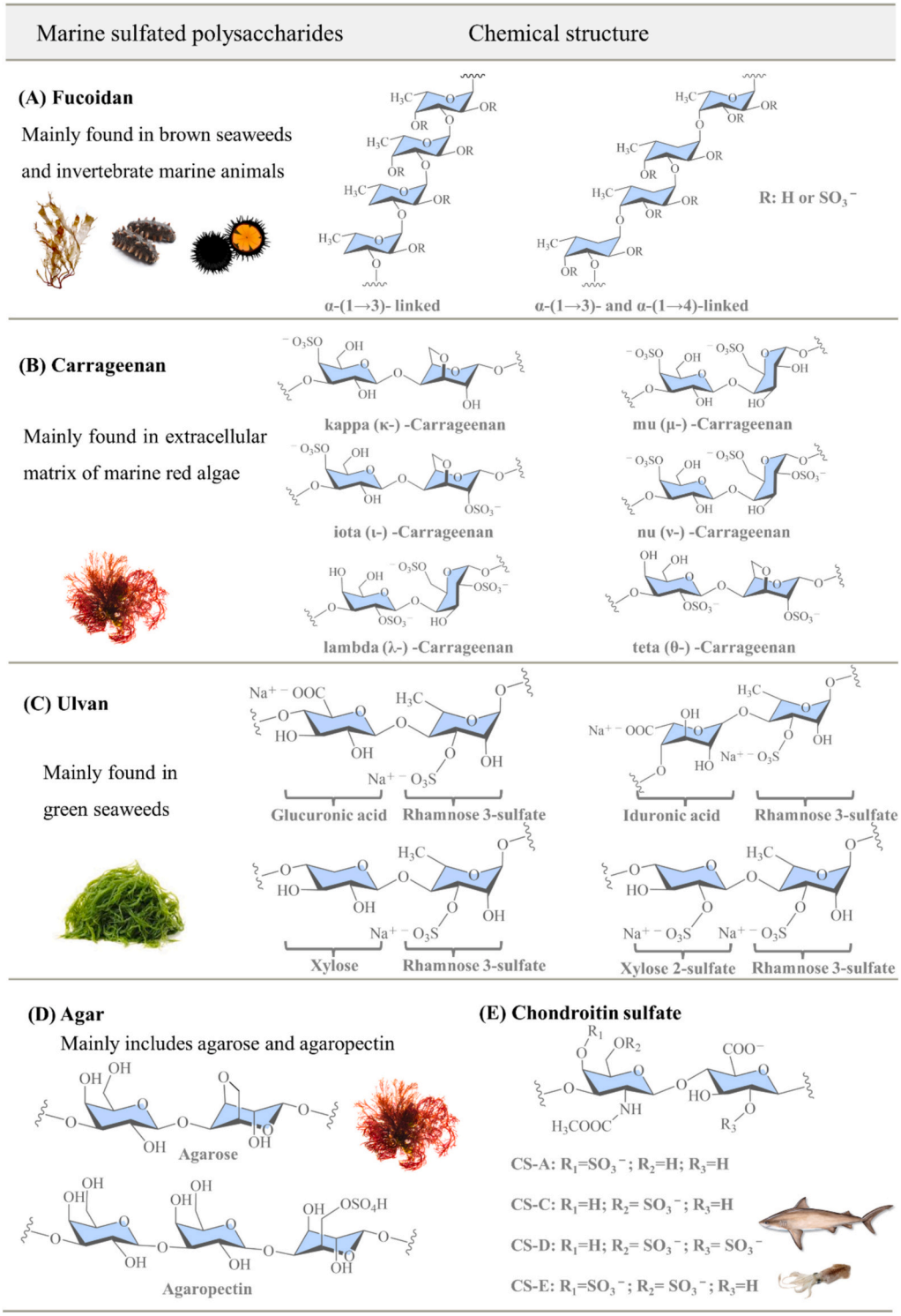

Fig. 1. The chemical structure of MSPs.

For fucoidans of various origins, the sulfate group content usually reaches 7.66 %–38.3 %, and the fucose content, monosaccharide composition, and others may also vary [8]. For instance, Yang, et al. [9] revealed that fucoidan isolated from *Durvillaea antarctica* had a sulfate content of 23.13 % and monosaccharides were composed of fucose (76.3 %), galactose (20.8 %) and glucose (2.9 %). Liyanage, et al. [10] demonstrated that fucoidan (24.01 % of sulfate content) obtained from Sargassum coreanum contained 54.46 % of fucose, 29.31 % of galactose, and 1.06 % of rhamnose. In addition, different extraction methods significantly affect the monosaccharide composition of fucoidan, albeit usually reflected in the proportions of each monosaccharide. Nevertheless, the effects of extraction methods on the molecular weight and sulfate content of fucoidans, which associated with their bioactivity and physicochemical properties are noteworthy. For instance, ultrasound-assisted extraction is conducive to achieving fucoidan with a lower molecular weight and more uniform distribution, whereas acid extraction seems to be more prone to obtain highly sulfated fucoidan [11]. Despite being highly hygroscopic, the difference is that fucoidan will not form a highly viscous solution. Thus, fucoidans are rarely used as thickener or gelling agents, and the rheological properties of fucoidans can be improved by regulating temperature and concentration or by adding metal cations (e.g., sodium and calcium) [12].

2.1.2. Carrageenan

Carrageenan is a vital component of the extracellular matrix of marine red algae and a group of naturally linear SPs. Currently, carrageenan has been approved by FDA as a GRAS (generally recognized as safe) food additive and widely used in the food industry. Intrinsically, carrageenans belong to the group of sulfated galactans with disaccharide repeating units presented as α-(1 → 4)-linked β-D-galactopyranose or 3,6-D-anhydrogalactopyranose, and β-(1 → 3)-linked 3,6-D-anhydrogalactopyranose (**Fig. 1B**). The sulfate group is covalently linked to C2, C4, or C6 of the galactose primarily through ether bonds [13,14]. On the basis of the structural characteristics of disaccharide units, carrageenans are further categorized into six groups: kappa (κ−), lambda (λ−), iota (ι−), nu (ν−), mu (μ−), and teta (θ−). Of these, κ, ι and λ, are the most commercially valuable, in which one, two, and three sulfate groups are contained, respectively. In addition, natural carrageenan tends to be a mixture of several conformations and not a homogeneous polysaccharide.

Gelling is a fundamental property of carrageenan. Carrageenan exists in solution as irregular coils when temperature increases above the melting point of carrageenan, and then transforms into a single- or double-helix structure with subsequent cooling below the critical temperature, resulting in the formation of gel [15]. Typically, the gelling properties of carrageenan tend to decrease as the amount of sulfate groups increases. Therefore, κ-carrageenan allows the formation of high-strength, hard, and brittle thermoreversible gels, ι-carrageenan forms soft and elastic thermoreversible gels, and λ-carrageenan commonly only exhibits viscous behavior [16]. Furthermore, the existence of sulfate groups allows carrageenan to carry a negative charge. Hence, ionic gelation may occur in the presence of metal cations through electrostatic interactions. The strength of gels may differ in response to metal cations. In addition, the presence of salt reduces the electrostatic repulsion among the sulfate groups, and the helix will further aggregate to form stronger gels. For instance, κ-carrageenan is extremely sensitive to K^+. Thus, higher gels will be obtained through K^+ – induced gelation of κ-carrageenan [17]. In addition, carrageenans with more sulfate groups tend to have a lower dissolution temperature. Hence, κ-carrageenan is only soluble in hot water, whereas λ-carrageenan is soluble in hot/cold water.

2.1.3. Ulvan

Ulvan is the main SP, which is primarily found in green seaweeds. Ulvan mainly consists of sulfated rhamnose, xylose, glucuronic acid, and iduronic acid, which are linked through α- and β-(1,4)-glycosidic bonds. Typically, the sulfation site of ulvan primarily involves C3 or C2 and C3 of rhamnose, whereas the backbone of ulvan mainly involves repeating units: β-D-glucuronic acid α-(1 → 4) L-rhamnose 3-sulfate, α-L-iduronic acid α-(1 → 4) L-rhamnose 3-sulfate, β-D-xylose α-(1 → 4) L-rhamnose 3-sulfate and β-D-xylose-2-sulfate (1 → 4)-α-L-rhamnose-3-sulfate (**Fig. 1C**) [18,19]. In addition, other monosaccharides, such as galactose, mannose, and glucose may be involved, varying depending on the species. Notably, ulvan can form thermoreversible gels under the presence of boric acid and Ca^{2+} when the pH is in the range of 7.5–8.0, but the formation mechanism remains controversial [20].

2.1.4. Agar

Agar is another polysaccharide found in red seaweeds (approximately 20 % of dry weight), with 3,6-anhydro-L-galactose and D-galactose as repeating units linked by α-(1,3) and β-(1,4)-glycosidic bonds [21]. The polysaccharide chain of agar primarily consists of two parts: agarose and agaropectin (**Fig. 1D**). Nevertheless, as 3,6-anhydro-L-galactose in agaropectin is partially or completely substituted by α-L-galactose-6-sulfate, the gelling properties of agar will be weakened. Hence, to obtain agar powder with high gel strength, agaropectin needs to be removed.

2.2. SPs in marine animals

Chondroitin sulfate (CS) is a glycosaminoglycan composed of glucuronic acid and 2-acetamido-2-deoxy-galactose (*N*-acetyl-galactosamine, GalNAc) alternately linked by β-(1,3) and β-(1,4)-glycosidic bonds [22]. Depending on the position of sulfation, CS is divided into four major types (**Fig. 1E**): chondroitin-4-sulfate (CS-A), chondroitin-6-sulfate (CS-C), chondroitin-2,6-sulfate (CS-D), and chondroitin-4,6-sulfate (CS-E). Of these, CS-A is the main component of tracheal cartilage, CS-C and CS-D are the main components of shark cartilage, and CS-E was isolated first from squid cartilage [23]. In addition, fucoidan glycosylated CS has been found in sea cucumbers, which has different biological activities due to its structural differences. For instance, sulfated polysaccharides in sea cucumbers with linear conformation exhibited higher hypolipidemic activity than spherical conformation [24].

3. Potential health benefits

The main health-promoting properties of MSPs are displayed in Fig. 2.

3.1. Antioxidant activity

In biological terms, redox reactions occur throughout almost the entire lifecycle, and the oxidative and antioxidant capability of biological systems is relatively homeostatic under normal physiological circumstances. However, external environmental triggers may disrupt this equilibrium in organisms and may induce oxidative stress, which in turn leads to an overproduction of ROS/RNS. In this case, free radicals with high oxidizing capacity (e.g., hydroxyl radicals and nitric oxide) will induce oxidation of biological macromolecules such as proteins, lipids, and nucleic acids in the body, leading to abnormal cellular functions and mortality. Such oxidative damage is typically associated with chronic diseases such as aging, cardiovascular disease, diabetes, and Alzheimer's disease [25].

Fortunately, the positive antioxidant effects of MSPs have been assessed using several chemical and biological methods. Currently, the antioxidant mechanism of polysaccharides mainly involves: scavenging free radicals, regulating antioxidant enzymes activities or signal pathways mediated by oxidative stress, and reducing the generation of ROS. For instance, ulvan (isolated from *Ulva intestinalis*) may terminate free radicals as hydrogen donors or electron donors. The scavenging abilities of DPPH and ABTS radicals reached 73.24 % and 94.94 % at a

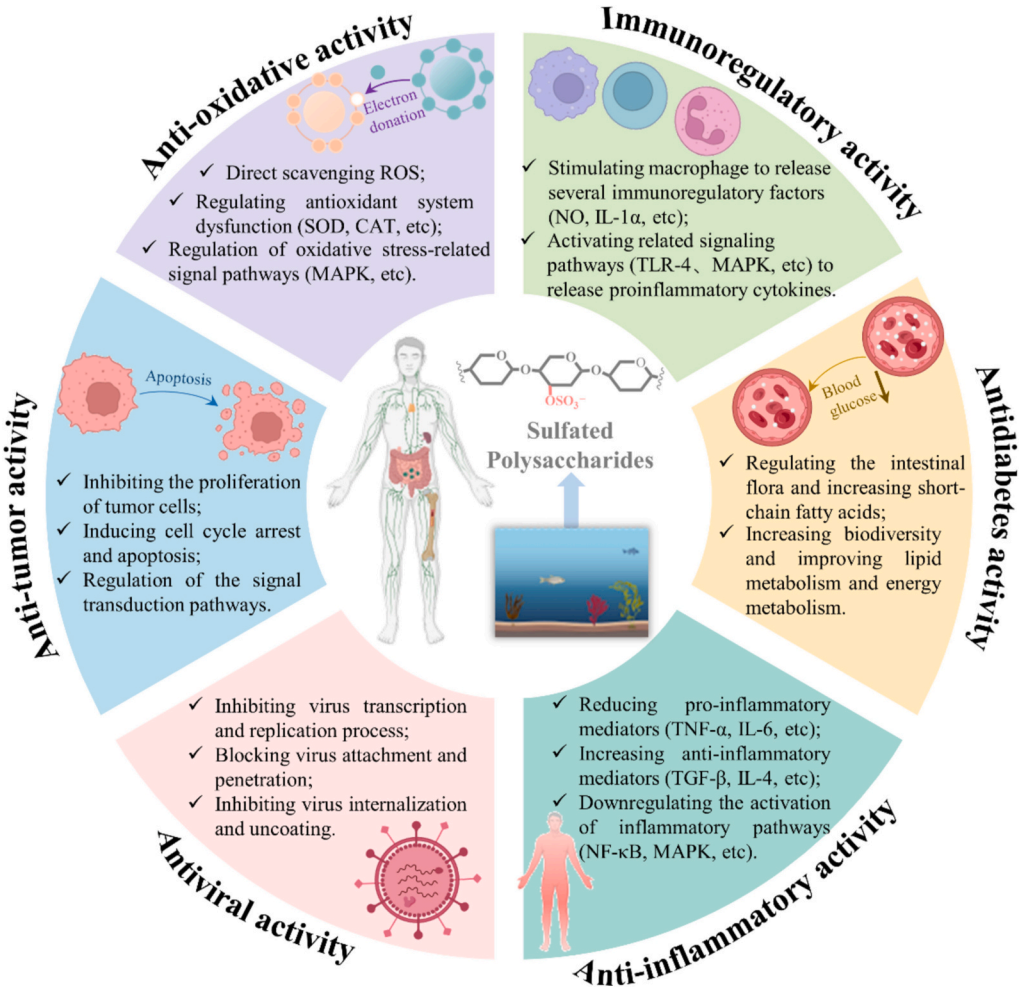

Fig. 2. The main biological activities and health-promoting properties of MSPs.

concentration of 6 mg/mL, respectively [26]. According to Wang, et al. [27], fucoidans isolated from *Turbinara ornata* have the potential to reduce apoptosis in a dose-dependent manner by reducing the level of ROS in APPH-induced oxidative stress in Vero cells.

It is noteworthy that the antioxidant activity of SPs is related to their structural characteristics. Sulfate position and content, molecular weight, monosaccharide composition, and branched chain distribution may affect the antioxidant potential of SPs. In particular, the presence of sulfate groups may increase the hydrogen supply capacity of polysaccharides by lowering the energy of the C − H bond near the glycosidic bond, thus suppressing the production of free radicals [28]. Therefore, it is generally accepted that the quantity of sulfate groups is positively correlated with the antioxidant capacity of polysaccharides. For molecular weight, SPs with lower molecular weights are prone to expose more active sites and penetrate more efficiently to the cell interior, thus exhibiting more effective antioxidant activities than high molecular-weight SPs (which are compact in structure) [29]. As reported by Geun Lee, et al. [30], a low-molecular-weight fucoidan (2.937×10^6 g/mol) isolated from *Sargassum autumnale* contributed to the reduction in hydrogen peroxide−induced apoptosis in Vero cells and oxidative damage in zebrafish. Moreover, the superior antioxidant activity may be highly correlated with the levels of fucose and galactose in fucoidans. The effect of monosaccharide composition on the antioxidant activity of SPs can be attributed to the large accumulation of uronic acid with an electrophilic ketone or aldehyde groups, which will facilitate the formation of hydrogen bonds [31]. For instance, a high rhamnose content (up to 33 %) had a positive effect on the capacity of hydrogen donation in ulvan isolated from *Ulva intestinalis* [26]. In addition, the degree of branching of SPs is positively correlated with their antioxidant activity within a certain range. Excessive branching hinders the interaction of polysaccharides with reactive oxygen species, and minimal branching reduces the exposure of active sites [32].

3.2. Immunoregulatory activity

Immunological responses are the defense of organisms against pathogens and various harmful foreign substances (e.g., bacteria and viruses), including specific immunity and nonspecific immunity. As the first line of defense, nonspecific immunity primarily involves macrophages, natural killer cells, and dendritic cells. Conversely, specific immunity is typically mediated by T and B lymphocytes. Recently, numerous naturally derived polysaccharides have been confirmed having the ability to enhance the immunological response of the host and serve as potential immunomodulators. Comparatively, the immune-potentiating effect of SPs is seemingly more prominent. This was greatly ascribed to the existence of sulfate groups that increased the flexion and water solubility of the polysaccharide chains. For example, Yang et al. [33] comparatively investigated the immunomodulatory activity of four polysaccharides isolated from *Sargassum thunbergii*, including water extract, crude polysaccharide, fucoidan, and sodium alginate. The results revealed that at the same concentration (5 μg/mL), fucoidan more effectively activated the NF-κB signaling pathway and induced the production of nitric oxide (a major mediator of immune and inflammatory responses) [33]. In addition, the immunomodulatory

activity of SPs is featured with multi-targets and multi-pathways. In particular, SPs may exert immunomodulatory effects by activating corresponding signaling pathways based on recognition of membrane receptors (e.g., TLRs) in cells. Typically, these include regulation of immune cell activity (macrophages, lymphocytes, natural killer cells, etc.) and modulation of cytokine levels (e.g., interleukins, interferons, and tumor necrosis factor) [34].

Also noteworthy is the fact that the structural characteristics of SPs are related to their immunomodulatory activity. For instance, the immune-potentiating activity of SPs may not necessarily be positively correlated with the sulfate content but depends on other factors (e.g., molecular weight). According to Liu, et al. [35], low molecular-weight fucoidan (<10 kDa) may promote the maturation of dendritic cells and the secretion level of IL-6 by activating the TLR-4, MAPK, and NF-κB signaling pathways, thus achieving an immune-potentiating effect. Similarly, fucoidan glycosylated CS can significantly increase the level of NO, cell viability, and phagocytic activity of macrophage RAW264.7 by activating the TLR-4-NF-κB signaling pathway [36]. This immune-potentiating activity is more pronounced with a decreased molecular weight, because SPs with low molecular weights are more conducive to diffusion and transport to immune cells. However, an excessively lower molecular weight may induce changes in the conformation of the polysaccharide chain, which may reduce its immunoreactivity. For instance, polysaccharides with a triple-helix structure are more readily recognized by receptors on immune cells [37].

3.3. Antitumor activity

Cancer, also known as malignant tumors, is a disease caused by the excessive proliferation of cells in organisms out of normal modulation, and has emerged as one of the primary causes of mortality. Currently, SPs mainly achieve antitumor activity by inhibiting the proliferation of tumor cells. For instance, Luo, et al. [38]. investigated the potential antiproliferative activity of fucoidan and the degradation derivatives against MCF-7, HepG2, A549, and Hela by MTT assay. The results revealed that all fractions exhibited inhibitory effects on the proliferation of tumor cells in the concentration range of 0.5–8 mg/mL, and molecular weight was the dominant factor influencing the antiproliferative activity of fucoidan. According to Wu, et al. [39], depolymerized CS possessed more satisfactory bioaccessibility and anticancer activity. In particular, depolymerized CS inhibited the proliferation of colon cancer cells while activating the p53 signaling pathway and inhibiting TOPK, thereby inducing cell apoptosis. In another study, Qiu, et al. [40] demonstrated that ulvan suppressed tumor growth predominantly by facilitating the production of ROS. On one hand, ulvan modulated the composition of gut microbes that significantly increased the level of *D*-phenylalanine in H22-bearing mice, thereby facilitating the production of ROS. On the other hand, ulvan downregulated the expression of miR-98-5p in HepG2 cells and regulated the expression of reactive oxygen species-related genes, such as CDKN1A and JNK, which increased the level of ROS and thus inhibited the growth of HepG2 cells.

In addition, SPs can indirectly exert antitumor effects through the activation of the immune system in organisms. In particular, SPs can potentially regulate immune cells in the tumor immune microenvironment, reversing the immunosuppression state and enhancing the immune response, thereby inhibiting tumor growth and metastasis. For instance, *Undaria pinnatifida* – derived fucoidan can strengthen the first line of immunity by enhancing the phagocytosis of mononuclear phagocytes in tumor-bearing mice, thus achieving the antitumor effect [41]. Moreover, it can promote the proliferation and differentiation of T-lymphocytes and the maturation of dendritic cells, thus inhibiting the proliferation of tumor cells. Similarly, λ-carrageenan oligosaccharides enhance the phagocytic activity of BALB/c mice macrophages and attenuate 5-fluorouracil-induced immunosuppression [42]. Furthermore, it increases the secretion level of TNF-α and IFN-γ and activates the Par-4 signaling pathway, thereby inducing apoptosis in gastric cancer cells.

3.4. Anti-inflammatory activity

Inflammation is a biological process in response to harmful stimuli, such as physical trauma, chemical exposures, and viral infections. This process mainly involves immune cells (e.g., macrophages) and the sequential release of proinflammatory cytokines (e.g., NO and TNF-α) [43]. However, the excessive accumulation of proinflammatory cytokines causes various diseases, such as allergies, atherosclerosis, diabetes, and cancer. Therefore, SPs with anti-inflammatory properties are desirable as natural regulators of proinflammatory gene expression to counter the inflammatory response. According to Wang, et al. [44], fucoidan isolated from fermented Sargassum fusiforme reduced the lipopolysaccharide-induced production of NO and decreased the secretion levels of proinflammatory factors (e.g., prostaglandin 2) in RAW264.7 cells in a concentration-dependent manner. Furthermore, the initiation of inflammatory responses was suppressed by modulating the NF-κB signaling pathway, and the positive effects of fucoidan was verified with zebrafish as a model. Similarly, Pei, et al. [45] demonstrated that SPs (sulfate content of 16.5 %) extracted from the red algae (*Gelidium crinale*) reduced the secretion of proinflammatory factors (e.g., IL-6) by blocking the NF-κB and MAPK signaling pathways.

In another study, Obluchinskaya, et al. [46] comparatively assessed the anti-inflammatory activity of fucoidan from different sources of brown algae with regard to the inhibition of protein denaturation and the maintenance of human erythrocyte membrane integrity. The results revealed that fucoidan containing higher levels of sulfate and fucose exhibited superior anti-inflammatory activity, which also reflected the impact of the structural characteristics of SPs on their anti-inflammatory activity. According to Li, et al. [47], low molecular-weight ulvan (2.56 kDa) may attenuate the symptoms (e.g., mucosal necrosis) of DSS-induced colitis in mice by modulating the NLRP3 inflammasome. Nevertheless, not all SPs have anti-inflammatory activities. An increasing number of studies have found that carrageenan induces intestinal inflammation, but the specific mechanism remains controversial. Guo, et al. [48] summarized two possible pathways: 1) inducing changes in the intestinal microflora, which results in a decrease in anti-inflammatory bacteria, and 2) directly binding to epithelial cell receptors and activating inflammatory signaling pathways.

3.5. Others

With regard to antiviral, MSPs seem to act as inhibitors that target binding to proteases associated with viral transcription and replication [49]. In addition, on the basis of the polyanionic properties of SPs, viruses can be directly inactivated by interfering with viral adsorption and invasion on the cell surface or by acting on spiny glycoproteins [50]. Noticeably, high molecular-weight SPs seem to be more beneficial in blocking the adsorption and invasion of pathogenic bacteria. As mentioned by Sun, et al. [51], fucoidan was observed to be more effective than its photocatalytic degradation product in inhibiting pathogenic bacterial adhesion and in suppressing SARS-CoV-2 by blocking the binding of S proteins to the ACE2 receptor.

In addition, recent studies have confirmed the prebiotic activity of SPs and their potential role in regulating lipid metabolism. According to Chi, et al. [52], ulvan dietary intervention increased the content of short-chain fatty acids in the cecum of mice under a high fat diet, activated the AMPK signaling pathway, upregulated the expression of genes relevant to β-oxidation of fatty acids, and downregulated the expression of genes relevant to the synthesis of fatty acids, which in turn improved lipid metabolism. Further, ulvan promoted glycolysis and the pentose phosphate pathway by positively regulating the intestinal flora of mice. Of interest, diet-induced inflammatory and immune responses also affect the lipid and energy metabolism of the host. For instance, mitochondrial dysfunction interferes with energy metabolism and induces

inflammation, which results in obesity and related complications [53]. According to Qin, et al. [54], SPs isolated from *Chaetomorpha linum* appeared to serve as potential antidiabetic agents. In particular, the SPs could reduce mitochondrial aggregation damage caused by hIAPP-induced damage in a dose-dependent manner (0–200 μg/mL).

4. Interactions with food components

In mixed food systems, interactions between SPs and food components (e.g., proteins, polyphenols) are unavoidable. The interactions that occur contribute to the formation of different microstructures, thus exhibiting different impacts on matrix properties. For instance, the superior water holding capacity of SPs can attribute to the hydrogen bonds formed between functional groups on SPs (e.g., hydroxyl and carboxyl groups) and water molecules, thus allowing the free water being attracted to the sugar chains [55]. And the network structure of SPs crosslinked with other components can retain more free water and improve the water holding capacity of food matrix. Therefore, the non-covalent/covalent interactions of SPs with proteins, polysaccharides, and polyphenols are presented in the following sections.

4.1. Interactions with proteins

4.1.1. Noncovalent interaction

Noncovalent interactions represent the most prevalent binding mechanism between MSPs and proteins, and the common types are the following: electrostatic interactions, hydrogen bonding, hydrophobic interactions, and van der Waals forces. Of these, electrostatic interactions exert a dominant role in the noncovalent binding of SP-protein complexes. In an aqueous phase, SPs carry more negative charges than other polysaccharides on the surface over a wide pH range because of the presence of sulfate groups [56]. However, the surface charge and polarity of proteins depend on the pH of the dispersing medium. In particular, the protein surface is negatively charged at pH above the protein isoelectric point and positively charged at pH below the protein isoelectric point. Thus, such differences in charge polarity create the possibility for the binding of SPs to proteins.

Typically, four phenomena may be observed in the mixed solutions of SP-proteins: soluble complex, complex coacervation, *co*-soluble polymers, and phase separation. The formation of complexes is spontaneously driven by electrostatic attraction between oppositely-charged SPs and proteins. The formed complexes are either soluble or insoluble, which greatly depends on pH. When the pH of the protein−SPs mixed system is above the isoelectric point of the protein, both of them carry negative charges, in which case electrostatic attraction occurs less likely.

As pH decreases, three critical pH values are observed in the system: pHc, pHφ1, and pHφ2, corresponding to the formation of the soluble complex, complex coacervation, and *co*-soluble polymers, respectively (Fig. 3) [57]. In general, the co-solubility complex occurs near the isoelectric point of the protein, where the positively charged surface patches of protein attaches to SPs by electrostatic attraction [58]. With a further decrease in pH (below the isoelectric point), the electrostatic attraction between the protein and SPs progressively increases, which in turn induces the formation of complex coacervation. Typically, the pH that allows the two polymers with maximum and equal opposite charges is referred to as the electrical equivalent pH, in which the positive charge on the surface of the protein is just neutralized by SPs, and the electrostatic interactions are the strongest, which contributes to obtaining higher yields of the composite coacervate [59]. In addition, other conditions of the system (e.g., temperature, polymer concentration, and ionic strength) can affect the noncovalent binding of protein−SPs. For instance, proteins may expose more cationic "patches" upon heat treatment, thereby facilitating the establishment of electrostatic interactions with SPs, which is desirable for obtaining emulsions with high stability and rheological properties [60].

4.1.2. Covalent interaction

Protein−SPs are predominantly covalently combined in two types: Maillard reaction and cross-linking (Fig. 3). For the former, protein−SP conjugates are obtained primarily by inducing a condensation reaction between the carbonyl group of reducing sugar in the polysaccharide backbone and the amino group of protein. For the latter, chemical cross-linking agents (e.g., genipin and glutaraldehyde) or enzymes (e.g., transglutaminase and laccase) are used to promote the formation of covalent bonds between proteins and SPs [57].

Compared with noncovalent binding, covalent binding is an

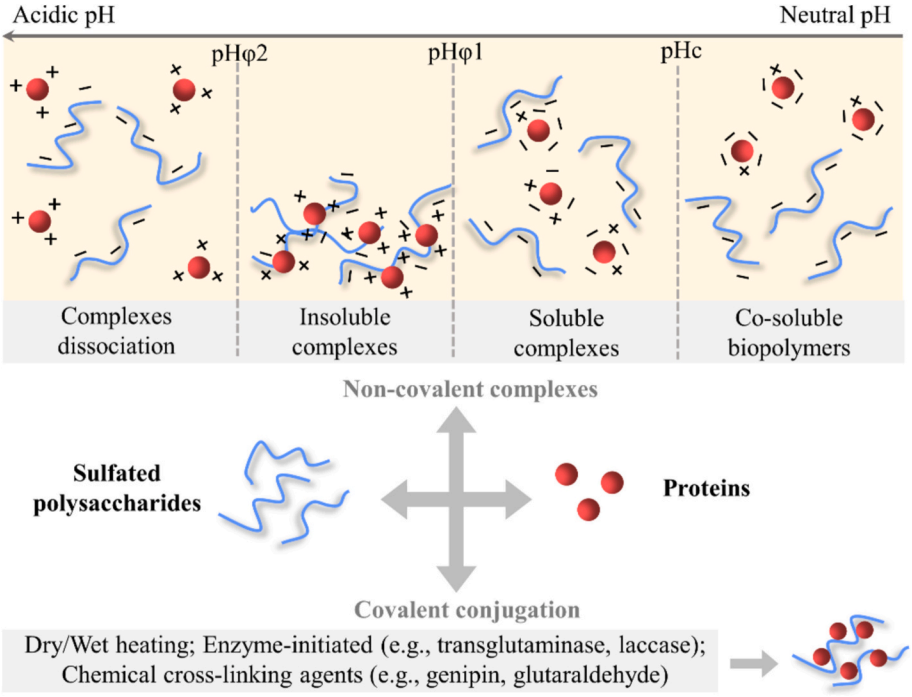

Fig. 3. The schematic diagram of the transitions of protein–polysaccharide complexes induced by pH changes.

irreversible process. As a common approach for obtaining protein–SP conjugates, the Maillard reaction has been widely reported in improving the functional properties and biological activities of proteins. For instance, the stability of coconut globulins was effectively improved by conjugating with fucoidan using the moist heat method [61]. In particular, a high degree of glycosylated coconut globulins (55.70 %) possessed enhanced electrostatic repulsion and formed a thicker elastic film on the surface of oil droplets, thus exhibiting higher emulsification stability. Similarly, the conjugates obtained by moist heating κ-carrageenan with milk isolate proteins for 12 h possessed better emulsification and stability [62]. Alternatively, emerging nonthermal processing techniques can also induce covalent binding of protein-SPs. For instance, cold plasma, ultrasound, and pulsed electric field treatments may promote changes in the secondary and tertiary structures of proteins to expose more active sites, thereby inducing protein glycosylation [63]. Notably, the functional properties of the conjugates obtained by glycosylation primarily depend on the molecular weight of the polysaccharide and the type of protein. Typically, high molecular–weight polysaccharides reduce the availability of free amino groups in the system because of higher spatial site resistance, resulting in lower protein glycosylation. For proteins, unfolded proteins (e.g., casein) tend to expose more free amino groups than other proteins under identical circumstances, which may facilitate the formation of covalent bonds [64].

4.2. Interactions with polysaccharides

Noncovalent interactions exert crucial roles in polysaccharide–SP complex systems (Fig. 4A) (e.g., hydrogels and edible films). The polyanionic nature of sulfated polysaccharides allows the establishment of electrostatic interactions with cationic polysaccharides, such as the electrostatic cross-linking of SPs with chitosan. According to Rabelo, et al. [65], the interaction of SPs with chitosan is stronger than that of carboxylated polysaccharides. Nevertheless, the electrostatic shielding effect of Na^+/Cl^- resulted in weakened electrostatic interactions among the polymers at higher salt concentrations. In the study by Davydova, et al. [66], κ-carrageenan and chitosan were selected for the preparation of polyelectrolyte complexes. In particular, the surface charge of κ-carrageenan was neutralized from −61.9 to −38.4 mV at a mass ratio of 10:1, sufficient electrostatic repulsion allowing the complex for superior colloidal stability. Notably, compact and smaller sized polyelectrolyte complexes exhibited enhanced antiviral activity by more readily interacting with viruses. Similarly, quaternary ammonium chitosan can be adsorbed on the surface of fucoidan through electrostatic interactions (Fig. 4B) for self-assembly to form nanoparticles for drug delivery [67]. Although electrostatic interactions dominate the formation of polysaccharide electrostatic complexes, hydrogen bonding and van der Waals forces may also be involved. According to Wang, et al. [68], fucoidan and κ-carrageenan were mixed at 95 °C with continuous stirring, following which κ-carrageenan formed a helical structure among the chains of fucoidan and tightly integrated through hydrogen bonding as the temperature decreased, thereby inducing gelation of the non-gelatinizing fucoidan. In addition, the improved water-holding properties and freeze–thaw stability of hybrid gels were observed because of the formation of the entanglement network.

Conversely, SPs can also be integrated with other polysaccharides by metal ions or cross-linking agents. In the study by Dou, et al. [69], the formation of alginate/fucoidan hydrogels was induced by Ca^{2+}, and a porous structure was constructed, which contributes to the maintenance of probiotic activity. Further, ionic cross-linking endowed the hydrogel with good physicochemical properties (e.g., tissue adhesion and solubility). Thus, the composite hydrogel exhibited a greater potential in promoting healing of oral ulcers. According to Mensah, et al. [70], fucoidan and chitosan were cross-linked through the formation of glycine derivatives using hexamethylene diisocyanide and formaldehyde as cross-linking agents. Such multicomponent-based cross-linking reactions contribute to achieving colloidal systems with favorable stability and stereoselectivity. In another study, citric acid was used as a

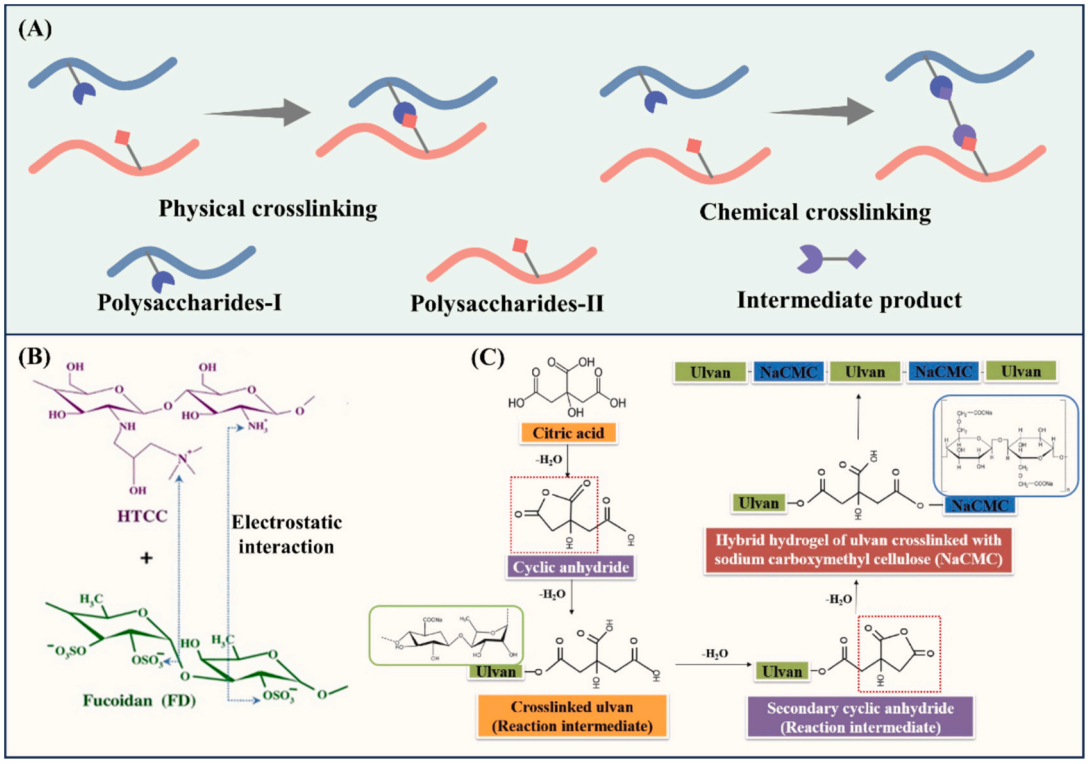

Fig. 4. Schematic diagram of (A) interactions among MSPs and polysaccharides; (B) Electrostatic interactions between quaternary ammonium chitosan and fucoidan [67]; (C) cross-linking mechanism of ulvan with sodium carboxymethyl cellulose using citric acid as cross-linking agent [71].

green cross-linking agent to fabricate ulvan-carboxymethylcellulose sodium hydrogels in conjunction with the extraction of ulvan (Fig. 4C) [71]. In particular, the cyclic anhydride formed when citric acid loses water during heating can esterify with the hydroxyl groups of polysaccharides, thereby inducing cross-linking among components.

4.3. Interactions with polyphenols

Polyphenols can also be bound to SPs through covalent or noncovalent interactions. Current investigations are primarily focused on noncovalent interactions, such as hydrogen bonding, hydrophobic interactions, and ionic bonding. Of interest, the physicochemical and functional properties of polyphenols were improved to some extent based on the interaction of polyphenols with SPs (e.g., higher stability and better dispersion). According to [72], intermolecular stacking induced the generation of hydrophobic cores during the formation of CS − anthocyanin nanocomplexes. The sulfate group of CS tightly bonded to the flavonoid cation of anthocyanins through electrostatic interactions. Furthermore, embedding CS-anthocyanin nanocomplexes into κ-carrageenan can endow anthocyanins with greater environmental stability. In another study, ferulic acid bonded to fucoidan through electrostatic interactions and hydrogen bonding and attenuated CDDP-induced acute kidney injury through the suppression of the cGAS-STING signaling pathway [73]. On one hand, the dispersion and bioaccessibility of ferulic acid were improved through noncovalent binding to fucoidan. On the other hand, nanoparticles fabricated by antisolvent precipitation were allowed to targeted deliver more ferulic acid than simple physical mixing, thus exerting an enhanced nephroprotective effect. Similarly, fucoidan−anthocyanin nanocomplexes (190.79 nm) that formed through ionic bonding and π − π stacking interactions were reported to possess superior stability and cell permeability [74]. Moreover, fucoidan−anthocyanin nanocomplexes exhibited more positive anticancer effects by inhibiting the IκBα/NF-κB signaling pathway and reduced the secretion of proinflammatory factors.

Typically, highly polymerized polyphenols are preferentially interacting with SPs [75]. In addition, environmental factors (e.g., pH, ionic strength, and temperature) are equally involved in polyphenol−SP interactions. Recently, attempts in promoting covalent binding of polyphenols with SPs have also been performed by aiming to obtain covalent conjugates with desirable physicochemical properties or biological activities. In general, the conjugates can be induced by enzymes (e.g., laccase) and cross-linking agents (e.g., EDC or free radicals) [76]. According to de Melo, et al. [77], gallic acid−fucoidan conjugates were synthesized using the redox method with ascorbic acid−hydrogen peroxide as a free radical initiator. The results revealed that fucoidan−gallic acid conjugates exhibited superior antioxidant activity and had the potential to mitigate oxidative damage caused by free radicals.

5. Application in the food industry

5.1. Improvement of textural and sensory properties

Natural MSPs are considered candidates for processing additives in the food industry owing to their excellent properties. They may serve as thickeners, emulsifiers, moisture retaining agents and stabilizers, exerting a positive effect on the sensory, textural, and nutritional properties of foods (Table 1). For instance, electrostatic interactions between the positively charged amino residues of casein and the negatively charged sulfate groups of carrageenan result in a more compact gel structure, which leads to an increase in hardness. Therefore, the addition of κ-carrageenan can significantly improve the hardness and water-holding properties of milk/starch-based gels, thereby obtaining higher-quality 3D-printed products for dysphagia people [78]. Moreover, the covalent combination of κ-carrageenan and milk protein can significantly increase the adsorption of κ-carrageenan on the surface of milk fat droplets. The formation of a thick interfacial film and the electrostatic repulsion between κ-carrageenan molecules can effectively improve the freeze-thaw stability of ice cream [79].

In addition, MSPs can also serve as fillers in protein matrix to enhance gelling properties. Specifically, the incorporation of MSPs may promote protein unfolding, thus exposing more sulfhydryl and hydrophobic groups and increasing the disulfide bonds and hydrophobic interactions among proteins [80]. As investigated by Zheng, et al. [81], low-concentration fucoidan (0.125 %) was beneficial in promoting the cross-linking of proteins in surimi, which resulted in the improved gel strength and water-holding properties of surimi. Notably, the presence of fucoidan sulfate groups enhanced the antimicrobial activity and antioxidant activity of surimi. Similarly, Zhao, et al. [82] confirmed the

Table 1
The application of marine sulfated polysaccharides in the improvement of food texture.

Sulfated polysaccharides	Targeted application	Involved interactions	Main descriptions	References
Fucoidan	Multilayer emulsion	Electrostatic interactions	1. Fucoidan could electrostatically deposit on the surface of caseinate-coated droplets under pH 3.0–5.0; 2. The stability of the emulsion was improved due to the presence of branching structure that increased the steric hindrance among droplets.	[100]
κ-carrageenan	Cakes	Covalent bond by Maillard reaction; electrostatic interactions	1. Reduced the production of glycation end products in baked cakes; 2. Delayed moisture loss and starch aging.	[111]
κ-carrageenan	Meat batters	Covalent bond by transglutaminase; electrostatic interactions; hydrogen bonds	1. The addition of transglutaminase (0.1 %) andκ-carrageenan (0.2 %) resulted in the superior gel properties	[112]
κ-carrageenan, λ-carrageenan, ι-carrageenan	Partially crystalline emulsions	Electrostatic interactions; hydrogen bonds; hydrophobic interactions; disulfide bonds	1. Prevented the watering-off and agglomeration during storage; 2. High sulphate contents (λ-carrageenan, ι-carrageenan) stabilized emulsions exhibited superior storage stability.	[113]

Sulfated polysaccharides	Targeted application	Involved interactions	Main descriptions	References
κ-carrageenan; ι-carrageenan	Cream desserts	Electrostatic interactions	1. κ-carrageenan was more effective than ι-carrageenan in thickening; 2. κ- and ι-carrageenan ≤0.050 g/100 g were recommended to produce cream desserts with softer consistency; 3. κ-carrageenan (≥0.100 g/100 g) and ι-carrageenan (≥0.125 g/100 g) was recommended for firmer cream desserts.	[114]
Agar	Hydrogels	–	1. The presence of semi-crystalline agaropectin in agar fractions contributed to the hydrogels with superior mechanical properties.	[115]

potentiating of fucoidan for the gel properties of surimi. This effect can be explained by the ionic and hydrogen bonds formed among fucoidan and surimi proteins inducing the unfolding of the protein structure, which in turn prompted the formation of more disulfide bonds. In addition, fucoidan and oligochitosan exhibited superior synergy in inducing gelatinization of surimi.

Overall, MSPs create the possibility to develop innovative foods with improved textural and sensory properties. Compared to single MSPs, composite systems (especially MSPs-protein complexes) are more favorable for controlling the microstructure of foods. However, research on the effects of MSPs type, structure, ratio, and external system conditions (e.g., temperature, pH, and ionic strength) on the physical properties of foods is currently limited. Understanding the phase behavior of various MSPs-protein complex systems will contribute to controlling the structural details of foods and producing food products with more desirable texture and mouthfeel.

5.2. Applied in functional foods

5.2.1. Low glycemic index foods

Glycemic Index (GI) reflects the glycemic effect of digestible carbohydrates (mainly starch) in food, and a high-GI diet will lead to a rapid rise in blood glucose levels and an increased risk of chronic diseases (e.g., type II diabetes and cardiovascular disease). Thus, the development of low-GI foods by inhibiting starch digestibility is more favorable to meet the consumer demand for healthy foods.

The interactions between non-starch polysaccharides and starch have been reported to reduce starch digestibility and increase resistant starch content (digested in >120 min) [83]. For instance, fucoidan increased the content of resistant and slow-digesting starch by interfering with the molecular rearrangement of wheat starch [84]. Likewise, the integration of κ-carrageenan has been confirmed to inhibit water chestnut starch digestion [85]. However, the low concentrations of κ-carrageenan (below 0.3 %) may increase the exposure of starch to digestive enzymes by disrupting the crystalline regions. Therefore, the decrease in starch digestibility is also associated with following mechanisms: (1) MSPs interact with starch through hydrogen bonds, resulting in a reduction of the amylase-starch binding sites; (2) Increased viscosity of the system can affect enzyme diffusion and reduce substrate accessibility via barrier effects [86]. On the other hand, the incorporation of MPs into starch systems can also contribute to regulate the retrogradation of starch-based foods. Meng, et al. [87] confirmed the formation of a dense network structure among fucoidan and potato starch through hydrogen bonds, which limited the contact of starch with water molecules and inhibited the retrogradation of starch.

Although the integration of MSPs into starch matrix can serve as a potential strategy for the development of low-GI foods, the impact of MPs on the sensory quality and consumer acceptance of foods is also worth being considered. In addition, the interaction of MPs with digestive enzymes and the effect of processing conditions on the digestibility of resistant starch are also essential for the design of low-GI foods.

5.2.2. Fat substitutes

The development of fat substitutes can lower the fat content in food and reduce the total calorie intake, thus reducing the incidence of obesity and cardiovascular disease caused by excessive fat intake. In addition, a variety of functions are performed for these fat substitutes in foods, such as stabilizers, emulsifiers, thickeners and gelling agents [88]. Currently, the fat substitutes are classified into two types: those that directly replace fat with hydrocolloids and those that replace fat with emulsions, emulsion gels or oleogels. And these fat substitutes are usually assembled from polysaccharides and/or proteins and may also be used in combination with other food ingredients (e.g., polyphenols).

In the study by Su, et al. [89], ovalbumin–ferulic acid–κ-carrageenan complex–stabilized Pickering emulsions were used as a substitute for butter in breads. The results revealed that the incorporation of the emulsion increased the continuity of the gluten network structure and exhibited a higher overall acceptability level, which can be explained by the fact that κ-carrageenan enhanced the stability of the ovalbumin–ferulic acid complex–stabilized Pickering emulsion through electrostatic interactions [90]. Similarly, a better fatty acid profile can be obtained through partially replace lard in semidry sausages with olive oil gel/κ-carrageenan or olive oil gel/κ-carrageenan/gelatin bigels [91]. Although the presence of bigels increases moisture in semidry sausages, it can be ameliorated by properly adjusting the fermentation conditions. Moreover, carrageenan can be used to compensate for the texture deterioration of meat products caused by the reduction in salt content in the context of "reducing salt without reducing quality" [92].

Even though partial or complete replacing fat in food with fat substitutes can improve the nutritional properties, designing low-fat foods without losing the texture, flavor, and appearance of the food is still the main challenge. Maintaining the distinctive flavor of dairy and meat products containing fat substitutes will also increase consumer acceptability. In addition, the interaction of fat substitutes with other formulation components in foods and the effectiveness of fat substitutes under various processing conditions also need to be thoroughly analyzed to assess their applicability.

5.3. Delivery of bioactive ingredients

Recently, the inherent bioactivities (e.g., anti-inflammatory and antioxidant activities) of food-derived bioactive ingredients effectively mitigate the risk of various diseases such as cardiovascular disease, cancer, and diabetes. In addition, as the perspective of food changes from "full" to "well," the nutritional properties of food have gained greater attention. Of these, functional foods reinforced with bioactive ingredients in compliance with food safety-related regulations seem to be an effective strategy. However, a majority of bioactive ingredients are prone to oxidative degradation and inactivity caused by environmental stresses (e.g., light, heat, and oxygen). In addition, the poor water solubility of hydrophobic ingredients, such as curcumin, hinders dissolution and absorption [93]. These challenges may prevent the bioactive ingredients from reaching an effective dosage in target organs to realize the health benefits.

In this context, the construction of delivery systems for active substances based on natural macromolecules seems desirable to improve their stability and bioaccessibility (e.g., nanocomplexes, oral membranes, and emulsions) (Table.2). As reported by Bao, et al. [94], three SPs (CS, λ-carrageenan, and fucoidan) with different contents of sulfate groups were selected to construct HPMC-based oral films loaded with blueberry anthocyanins. The results revealed that CS significantly improved the stability of blueberry anthocyanins upon light stress within the system, and the retention of blueberry anthocyanins increased 5.5-fold compared with the control group after 8 d. This can be explained by more binding forms among the sulfate groups, carboxyl groups, and amino groups in CS and the hydroxyl groups and flavonoid cations of BAs. Furthermore, the SPs combined with HPMC through hydrogen bonding into more compact ternary complexes, which contributes to the sustained release of the bioactive ingredients and thereby guarantees effective absorption.

In addition, SPs are prevalently used for complexation with food proteins, which may contribute to improving the aggregation and precipitation of proteins and may provide better protection for bioactive ingredients. For instance, electrostatic complexation of SPs with ovalbumin contributes to the weakening of the hydrophobic interactions among nonpolar residues of ovalbumin, thus preventing precipitation. Likewise, noncovalent binding of SPs to ovalbumin effectively increases the digestive and environmental stability (heat and light) of anthocyanins [95]. This is ascribed to stronger electrostatic interactions among proteins and SPs with high charge densities. Similarly, electrostatic

Table 2
The application of marine sulfated polysaccharides for delivering bioactive ingredients.

Types of delivery system	Fabrication method	Encapsulation materials	Bioactive ingredients	Involved interactions	Changes in properties	References
Particles	Ugi crosslinking	Fucoidan, chitosan; hexamethylene diisocyanide, formaldehyde	Piperine	–	1. Improved bioavailability of piperine; 2. Higher antioxidant activity	[70]
Nanocomplexes	Heating-induced electrostatic self-assembly	Ovalbumin, carrageenan	Anthocyanins	Hydrogen bonds, hydrophobic and electrostatic interactions	1. Improved environmental and digestive stability; 2. Higher antioxidant activity	[95]
Nanoliposomes	Thin-film hydration	Fucoidan, chitosan, lecithin, cholesterol	Catechin, juglone	Hydrogen bonds, electrostatic interactions	1. Increased in pH, ionic, thermal and oxidative stability; 2. Improved sustained release in vitro digestion	[98]
Nanoparticles	Antisolvent precipitation	Fucoidan, zein	Curcumin	Hydrogen bonds, electrostatic interactions	1. Increased in thermal and storage stability; 2. Controlled release and improved antioxidant activity	[116]
Nanoparticles	Electrostatic self-assembly	Fucoidan, ovalbumin	Nicotinamide mononucleotide	Hydrogen bonds, hydrophobic and electrostatic interactions	1. Increased antioxidant activity and thermal stability; 2. Improved anti-aging ability	[117]
Nanoparticles	Antisolvent precipitation	Chondroitin sulfate, zein	Quercetagetin	Electrostatic interactions, hydrogen bonds, and hydrophobic interactions	1. Increased in photo and thermal stability; 2. Controlled release in simulated gastrointestinal digestion	[118]
Particles	Complexation	Ulvan	Nisin	Hydrophobic and electrostatic interactions	1. Long-term antibacterial activity against *L. innocua* and *B. subtilis*	[119]
Nanoemulsions	High-speed shear emulsification	κ-carrageenan, glycation of soybean oil body with soy soluble polysaccharide	Myricitrin		1. Higher bioavailability and storage stabilities of myricitrin	[120]
Nanoliposomes	Layer-by-layer electrostatic interaction	Chondroitin sulfate, chitosan; lecithin; cholesterol	Betanin	Electrostatic interactions	1. Increased in ionic, pH stabilities; 2. Improved bioavailability of betanin	[121]
Microcapsules	Ionic crosslink	Agar, sodium alginate, tween 80, soybean oil, $CaCl_2$;	*Lactobacillus plantarum* MB001	–	1. Remained viable for long-term storage; 2. Sustained release in the targeted intestine	[122]

complexation of CS with zein notably improves the encapsulation efficiency of curcumin (from 69.1 % to 94.7 %) and correspondingly enhances the tolerance of curcumin to light and heat [96]. In addition, SPs with a high charge density are also promising candidates for stabilizing emulsions or liposomes, which in turn improve the functional properties of the delivery system through the formation of charged interfacial layers on the droplet surface. For instance, the incorporation of κ-carrageenan results in a high net negative charge (−54.7 mV) of pea protein/κ-carrageenan complexes near the isoelectric point, which contributes a uniform emulsion with small droplet sizes [97]. Similarly, fucoidan can be adsorbed on the surface of chitosan through electrostatic interactions, which increases the surface charge of catechin/juglone-loaded liposomes (from −18.73 to −48.07 mV) to obtain smaller nanoliposomes [98]. Moreover, the polyelectrolyte layer contributes to the rigid structure of the liposome bilayer and regulates the fluidity of the membrane, which further improves the stability of the bilayer as well as the encapsulation efficiency of the bioactive ingredients.

To obtain superior delivery carriers, clarification of the impact of the structure of SPs on the functional properties of the system is crucial. As mentioned by Shi, et al. [99], the minimum polysaccharide concentration required to stabilize the emulsion was negatively correlated with the molecular weight of sulfated fucose, which could be explained by the high affinity of large molecular−weight SPs to droplets. Furthermore, for sulfated fucose with similar molecular weights, the existence of branched chains allowed emulsions with better stability by increasing the steric hindrance among droplets [100]. Nevertheless, several issues related to the delivery systems still exist: (1) To further investigate whether the encapsulated bioactive ingredients can achieve the desired effect after integration into the food matrix to evaluate the suitability of MSPs as delivery carriers; (2) Based on the interaction of MSPs with other components (e.g., proteins, polysaccharides), it is desirable to design delivery carriers to deliver multiple bioactive ingredients simultaneously to achieve synergistic health-promoting effects; (3) Allowing MSPs-based delivery systems to responsively release in response to specific environmental factors (e.g., pH, temperature) will contribute to improve the effectiveness of the active ingredients.

5.4. Applied in food packaging

The food packaging industry embarked on a new green revolution in the context of “carbon neutrality”. This has sparked a passionate desire to find environmentally friendly, sustainable, biodegradable polymer materials to substitute the controversial, nonbiodegradable

petroleum−based plastics. Among various substitutes, polysaccharides are considered promising candidates for food packaging. The excellent film-forming, modifying and gelling properties of natural polysaccharides lead to widespread application and development in food coating and packaging. Currently, the development of SPs in food packaging mainly includes the following: 1) blending with additives (e.g., bioactive compounds, polymers, and delivery carriers) and plasticizers to prepare film-forming solutions, and 2) converting film-forming solutions into films. It is worth noting that using multi-polymers as the film-forming matrix is desirable to enhance the physicochemical properties of polysaccharide-based films, which will contribute to improving the shelf-life of targeted products (Table 3).

In terms of intermolecular interactions, the formation of hydrogen bonds can limit the film matrix-water interactions, and electrostatic interactions can prevent water molecules from entering the film matrix, which will contribute to increase the hydrophobicity of the film. As reported by Samani, et al. [101], the incorporation of fucoidan into agar/chitosan film−forming solutions resulted in a more structurally compact film, thereby reducing permeability to water vapor. In addition, the antioxidant activity of the composite film was significantly enhanced because of the existence of fucoidan, which is favorable for the maintenance of food quality. Similarly, for chitosan-fucoidan composite films, the hydrogen bonds formed by the hydrophilic groups, as well as the electrostatic interactions between the sulfate groups and the amino groups, significantly enhance the water barrier properties of the film. Further, with the addition of antioxidants (anthocyanins), the composite film can effectively delay the water loss and spoilage of salmon during storage [102].

5.4.1. Active food packaging

According to the Food and Agriculture Organization of the United Nations (FAO), approximately one-third of food is lost or wasted in the supply chain each year [103]. To avoid the economic losses caused by food spoilage to the greatest extent, food packaging has also been progressively diversified. For instance, fortifying the food packaging with natural active ingredients (e.g. polyphenols and essential oils) that endow the packaging with enhanced biological activity (e.g. antioxidant and antibacterial activities), which will be more favorable to prolonging the shelf life of foods and maintaining the original quality. According to Ning, et al. [104], the blending of phytic acid into the κ-carrageenan/carboxymethylcellulose nanofiber composite matrix can effectively slow down the rate of lipid oxidation of pork and can inhibit the proliferation of bacteria. On one hand, the formation of a complex cross-linked network reduces the transfer of water and oxygen on both sides of the film. On the other hand, the incorporation of phytic acid effectively improved the antimicrobial properties of the film (antibacterial rate against *S. aureus* and *E. coli* reached 100 % at 18 % and 9 % phytic acid content, respectively).

Recently, multilayer active packaging films were developed to overcome the deficiencies in the performance of single-layer biopolymer films, such as mechanical and barrier properties. Notably, the combination of different layers may provide better control of the release of active ingredients [105]. For instance, the multilayer films (inner layer consisted of sodium alginate, outer layer consisted of κ-carrageenan and gelatin) containing ZnO nanoparticles and oregano essential oil were prepared based on layer-by-layer assemble method [106]. The formation of network interwoven structure allows multilayer film to retain more oregano essential oil than monolayer film, thus exhibiting superior antioxidant and antimicrobial activities. However, a thorough assessment of the release rate of the active ingredients from packaging to the food is essential, too fast may migrate to the interior of the food, and too slow meaning not achieve the effective concentration. This requires more effective studies in food systems and combining release kinetics to elucidate the controlled release mechanisms of active ingredients.

5.4.2. Smart food packaging

As we all know, microenvironmental changes caused by chemical (e.g., fat oxidation), physiological (respiration and transpiration of fruits and vegetables), and microbial effects are often accompanied during food storage [107]. Smart food packaging can deliver real-time information to consumers about the changes in food quality via response to the packaging environment. Currently, natural pigments (e.g., anthocyanins, curcumin) are widely used as sensing materials in food packaging due to their color response to changes in food quality. In general, anthocyanins are mainly present as flavylium cation (red) under strongly acidic conditions (pH 2–3), and as pH increases, carbinol pseudobase (colorless) and quinonoid bases (blue) are formed and mediated by acid−base equilibrium and hydration equilibrium, respectively [108].

Notably, the interactions between polysaccharides and natural pigments (e.g., hydrogen bonding and electrostatic interactions) contribute to enhance the stability of pigments. As reported by Huang, et al. [109], smart packaging was prepared by integrating purple cauliflower extracts into the carboxymethyl chitosan, alginate, and fucoidan composite matrix. The results revealed that fucoidan formed more stable complexes with the anthocyanins extracts through electrostatic attraction and π-π stacking. Furthermore, the composite film crosslinked with calcium ions exhibited better functional properties and visualized the freshness of shrimps through color transformation from royal blue to brown (Fig. 5). However, as mentioned in Section 5.3, natural bioactive ingredients are unstable and highly susceptible to oxidative degradation. Thus, it seems desirable to enhance the functional properties of films with encapsulated forms. As reported by Zhou, et al. [110], the core−shell structure developed by anthocyanin/zein/cinnamaldehyde/κ-carrageenan nanoparticles achieved the co-encapsulation of two bioactive ingredients and incorporated as fillers into κ-carrageenan films. The results revealed that the formation of hydrogen bonds among the nanoparticles and film matrix resulted in improved mechanical properties and thermal stability of the composite film. Interestingly, the pH-responsive behavior of anthocyanins and the bioactivity of cinnamaldehyde provided the composite film with retarded quality deterioration of Mandarin fish while responding in real time to volatile nitrogenous compounds from the environment, thus visualizing the freshness of Mandarin fish.

Overall, active additives and natural pigments exhibit great promise in fabricating functional SP-based food packaging, which can contribute to the design of multifunctional food packaging, i.e., visualizing freshness while maintaining quality of targeted products. However, smart packaging for monitoring food freshness is currently focused on meat and seafood, and the studies on products such as fruits and vegetables are relatively limited. Moreover, smart food packaging at present mainly visualizes freshness in response to pH changes, and the design of smart packaging with other triggers (e.g., temperature and humidity) is equally worth to explore. As well, investigating the release of active ingredients and the sensitivity and reversibility of smart packaging in response to environmental changes is necessary to ensure food safety.

6. Conclusions and future perspectives

As one of the major resources of marine organisms, SPs have several advantages such as multiple bioactivities, sustainability, superior biodegradability, and biocompatibility. Compared with polysaccharides derived from terrestrial plants and animals, MSPs are characterized by a higher sulfate cotent (partial replacement of the hydroxyl group of the monosaccharide by sulfate). Notably, MSPs can be combined with food components to prepare complexes with desirable physicochemical and functional properties mediated by covalent or noncovalent interactions for applications in food nutritional fortification, food quality improvement, active ingredient targeted delivery, and food packaging. However, several prospects that need to be resolved may create opportunities for future research, including the following:

Table 3
The application of marine sulfated polysaccharides in food packaging.

Types of packaging	Film-forming materials	Manufacture technology	Involved interactions	Changes in properties	Application	References
Active packaging	Polycaprolactone, fucoidan, 2-Hydroxypropyl-β-cyclodextrin/ epigallocatechin inclusion complexes	Electrospinning	Hydrogen bonds	1. Increased in elastic modulus, thermal stability, and surface roughness; 2. Decreased in tensile strength, elongation at break; 3. Slow-release of epigallocatechin; 4. Higher antibacterial activity against *S. aureus* and *Botrytis cinerea*.	Retarded the lesion of cherry tomatoes caused by bacterial infection.	[123]
Active packaging	Fucoidan, gelatin; glycerol	Solution casting	Electrostatic interactions; hydrogen bonds	1. Increased in elongation at break, decreased in tensile strength and water solubility; 2. Enhanced thermal stability and antioxidant activity, 3. Higher antibacterial activity against *S. aureus* and *E. coli*.	–	[124]
Controlled-release packaging	Chitosan, fucoidan, cinnamaldehyde, glycerol	Dip-coating	Electrostatic interactions; hydrogen bonds	1. Decreased in water vapor permeability, increased in mechanical properties; 2. Higer release of cinnamaldehyde, higher antibacterial activity against *S. aureus* and *E. coli* in mildly acidic environments.	Prolonged the shelf life of litchi fruits (> 8 d)	[125]
Barrier packaging	Egg white protein, κ-carrageenan, glycerol	Solution casting	Hydrogen bonds; disulfide bonds	1. Decreased in tensile strength and water vapor permeability; 2. Increased in oxygen permeability and thermal stability.	Delayed the rancidity of soybean oil during storage	[126]
Coating packaging	Konjac glucomannan, κ-carrageenan, camellia oil	Immerse-coating	–	–	Extended the shelf-life of chicken meat to 10 d at 4 °C	[127]
Active packaging	Konjac glucomannan, carrageenan, peppermint essential oil, thymol, glycerol	Solution casting	Hydrogen bonds	1. Increased in elongation at break and UV-blocking activity, decreased in water vapor permeability and tensile strength 3. Improved antioxidant activity, higher antibacterial activity against *E. coli*, *Listeria monocytogenes* and *S. aureus*.	Extended the shelf life of strawberry to 16 d at 4 °C	[128]
Active packaging	Ulvan, gelatin, beeswax, tween80, glycerol	Solution casting	Hydrogen bonds	1. Increased in tensile strength and hydrophobicity; 2. Higher antibacterial activity against *E. coli*.	–	[129]
Smart packaging	Potato starch, chondroitin sulfate, blueberry anthocyanins, glycerol	Solution casting	Hydrogen bonds; electrostatic interactions	1. Decreased in elongation at break; 2. Higher colorimetric response to volatile ammonia	Monitored the freshness of shrimp at 4 °C (from pink to blue-green)	[130]
Active packaging	Chitosan, chondroitin sulfate, zein, curcumin, quercetin, glycerol	Solution casting	Hydrogen bonds; electrostatic interactions	1. Increased in tensile strength and elongation at break, decreased in water vapor and oxygen permeability; 2. Improved antioxidant activity, higher antibacterial activity against *S. aureus* and *E. coli*.	Reflected the fillets freshness through color changes (from light yellow to brownish yellow)	[131]
Smart packaging	Agar, anthocyanin extract	Solution casting	–	Decreased in thermal stability	The color change from blue/Gy to red with decreasing pH reflected the freshness of milk	[132]

Types of packaging	Film-forming materials	Manufacture technology	Involved interactions	Changes in properties	Application	References

(*continued on next page*)

Table 3 (*continued*)

Types of packaging	Film-forming materials	Manufacture technology	Involved interactions	Changes in properties	Application	References
Active packaging	Agar, konjac glucomannan, carvacrol, glycerol	Solution casting	Hydrogen bonds	1. Increased in elongation at break, tensile strength, and hydrophobicity; 2. Higher antibacterial activity against *S. aureus* and *E. coli*.	Retarded the shelf life of refrigerated chicken breast from 5 d to 9 d.	[133]

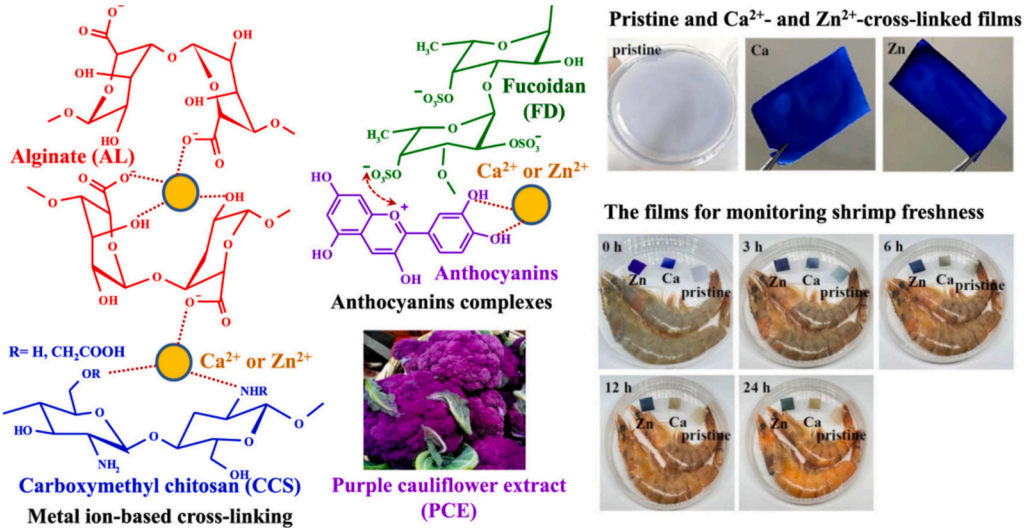

Fig. 5. Schematic diagram of the interactions for Ca^{2+}- and Zn^{2+}-cross-linked purple cauliflower extract-alginate/carboxymethyl-chitosan/fucoidan films and the color change during monitoring the freshness of shrimp maintained at 28 °C [109].

(1) In the food industry, MSPs can be used as natural food additives to improve the nutritional value and texture of food, as well as the film-forming matrix of food packaging films. However, because of the destruction of marine ecosystems, marine organisms (especially algae) can enrich pollutants, such as heavy metals and polycyclic aromatic hydrocarbons. Consequently, it is necessary to conduct more in vivo, in vitro and clinical studies to determine the toxic effects of MSPs on human health. Also, in vitro and in vivo studies are necessary to demonstrate the potential delivery efficacy of bioactive ingredients in functional foods and to determine their pharmacokinetics and bioavailability. In addition, with regard to MSP-based food packaging, it is critical for the design of sustainable food packaging to improve the performance of existing packaging by blending with more types of additives, such as lipids and carbon quantum dots.

(2) Currently, studies on the interaction of MSPs with food components are increasing. However, the unclear structure of SPs and the complexity of their interactions restrict the elucidation of their interaction mechanisms. Most of the studies have focused on the noncovalent interactions (e.g., hydrogen bonding and electrostatic interactions) between MSPs and common food components. Further studies on the preparation of covalent complexes and the regulation of the interactions are still required. In addition, according to the different application objectives and market demands, comparing the differences in the physicochemical and functional properties of different food ingredients with MSP complexes will facilitate the selection of optimal interaction complexes applied in the food industry.

(3) Compared with other natural components (e.g., proteins and polyphenols), the industrial application of MSPs in biomedicine and food is insufficient, which is largely attributed to the structural complexity of SPs and the ambiguity of structure–bioactivity relationships. Therefore, the structural characteristics of MSPs need to be systematically elucidated to make the application in food more industrialized and commercialized, and structure–bioactivity relationships require further clarification. In addition, multi-omics techniques (e.g., proteomics, metabolomics, and genomics) are imperative to reveal the connections between structure and biological activities at molecular levels, which will facilitate delving into the underlying molecular mechanisms.

(4) From what has been discussed, the biological activity of MSPs is closely related to their structure and molecular weight. Therefore, structural modification of MSPs is a useful process to improve their properties, which will contribute to broadening the development and application of MSPs in the food industry. For example, the degradation products of MSPs obtained by ultrasonication, and acid or enzymatic hydrolysis can expose more active sites for the purpose of enhancing bioactivity. Certainly, the relationship between modified MSPs and bioactivities remains speculative, and the structure–activity relationship still needs to be investigated in depth.

Overall, MSPs have great potential as natural active ingredients in modern food.

Abbreviations

APPH	2,2'-Azodiisobutyramidine dihydrochloride
A549	Lung cancer cells
BAs	Blueberry anthocyanins
CS	Chondroitin sulfate
CDKN1A	Cyclin-dependent kinase inhibitor 1A
CDDP	cis-Diamminedichloroplatinum (II)
DSS	Dextran sulfate sodium
EDC	1-Ethyl-3-(3-dimethylaminopropyl) carbodiimide
HepG2	Liver cancer cells
Hela	Cervical cancer cells
hIAPP	Human islet amyloid polypeptide

(*continued on next page*)

(*continued*)

HPMC	hydroxypropyl methylcellulose
HP-β-CD	2-Hydroxypropyl-β-cyclodextrin
JNK	Mitogen-activated protein kinase 8
MCF-7	Human breast cancer cells
MSPs	Marine sulfated polysaccharides
ROS	Reactive oxygen species
RNS	Reactive nitrogen species
SPs	Sulfated polysaccharides
TOPK	T-LAK cell-derived protein kinase

CRediT authorship contribution statement

Xiquan Li: Writing – review & editing, Writing – original draft, Visualization. **Ao Shen:** Software, Investigation. **Miaorong Xiao:** Software, Investigation. **Shuzhen Li:** Project administration, Funding acquisition, Conceptualization. **Weiwei Yang:** Supervision, Project administration, Funding acquisition.

Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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