Industrial Bioresource Engineering
https://ojs.wiserpub.com/index.php/IBE/

Review

Red Algae Phycocolloids: Functional Properties and Emerging Applications

Leonel Pereira[1,2]

[1]Centre for Functional Ecology (CFE), Marine Resources, Conservation and Technology, Marine Algae Lab, Associate Laboratory TERRA, Department of Life Sciences, University of Coimbra, Coimbra, 3000-456, Portugal
[2]IATV—Institute of Environment, Technology and Life, Coimbra, 3030-790, Portugal
E-mail: leonel.pereira@uc.pt

Received: 14 November 2025; **Revised:** 23 January 2026; **Accepted:** 26 January 2026

Abstract: Phycocolloids obtained from red seaweeds, such as agar, carrageenan, and other sulphated polysaccharides, are increasingly valued for their diverse functionalities and broad industrial relevance. These ocean-derived biopolymers possess distinctive molecular structures and biological activities, making them suitable for applications across the food industry, medicine, cosmetics, and biomedical fields. This review provides a comprehensive synthesis of current knowledge on red algae phycocolloids, beginning with their biological origin, biosynthetic pathways, and ecological roles. It highlights recent advances in extraction and purification technologies, with a focus on improving yield, safety, and environmental sustainability. The review also explores emerging applications in drug delivery, tissue engineering, and green technologies, underscoring their potential in sustainable innovation. Key challenges, including regulatory constraints, scalability, and the need for interdisciplinary collaboration, are discussed, along with future directions for research and industrial development. This work aims to support the strategic integration of red algae phycocolloids into next-generation biotechnological solutions.

***Keywords*:** red algae, phycocolloids, agar, carrageenan, polysaccharides, industrial applications, seaweed biotechnology

Abbreviations

CO_2	Carbon dioxide
COVID-19	Corona Virus Disease-2019
EAE	Enzyme-Assisted Extraction
FDA	Food and Drug Administration
GDP	Gross Domestic Product
GRAS	Generally Recognized As Safe
HPAEC	High-Performance Anion Exchange Chromatography
IMTA	Integrated Multi-Trophic Aquaculture
MAE	Microwave-Assisted Extraction
mRNA	Messenger Ribonucleic Acid
PHA	Polyhydroxyalkanoates

Copyright ©2026 Leonel Pereira.
DOI:
This is an open-access article distributed under a CC BY license
(Creative Commons Attribution 4.0 International License)
https://creativecommons.org/licenses/by/4.0/

PLA	Polylactide
siRNA	Small interfering Ribonucleic Acid
SRC	Semi-Refined Carrageenan
UAE	Ultrasound-Assisted Extraction

1. Introduction

Beneath the sea's surface, seaweed flourishes, playing a crucial role in the production of oxygen and creating habitats rich in life. These photoautotrophic multicellular organisms, primarily marine with some freshwater species, belong to the domain Eukarya and are categorized into the kingdoms Plantae (green and red algae) and Chromista (brown algae) (Mendes et al., 2024). Macroalgae are classified into three phyla based on their pigment composition and chemical makeup: green (Chlorophyta), brown (Heterokontophyta, Phaeophyceae), and red (Rhodophyta) (Figure 1). They are widely distributed from tropical to polar regions, occupying ecoregions that range from intertidal to submerged zones still exposed to sunlight (Pereira, 2021; Freitas et al., 2022).

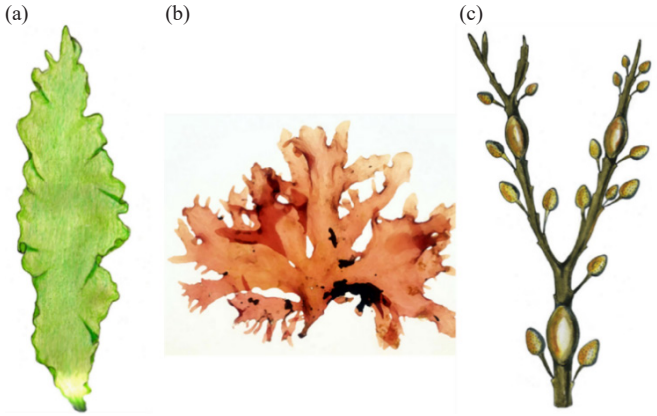


Figure 1. The three main taxonomic groups of macroalgae: (a) phylum Chlorophyta—green algae; (b) phylum Rhodophyta—red algae; (c) phylum Heterokontophyta, class Phaeophyceae—brown algae (Pereira, 2021)

The diversity of seaweed chemical content is a result of their widespread distribution, leading to a variety of environments. To withstand challenging environmental stresses, seaweeds synthesize distinctive polysaccharides, extended chains of simple sugars joined through glycosidic linkages. These polysaccharides serve multiple functions, including protection against waves and desiccation, maintenance of ionic equilibrium, structural support for cell walls, and food storage (Otero et al., 2023).

The quantity and characteristics of polysaccharides in seaweeds fluctuate considerably with the seasons and are shaped by a range of biological and environmental influences. Current research on these determining factors differs according to the specific polysaccharide under investigation; yet, even for those extensively examined, results frequently show discrepancies across various species and studies. Reviews on the responses of carrageenan and agar exist, but the considerable variation in recent study results underscores the need for a new review on the responses of these polysaccharides in seaweed (Kravchenko et al., 2018; Mendes et al., 2024).

Khalil et al. (2018) highlighted that one of the main challenges in current phycocolloid production (derived from red seaweed) is the difficulty in controlling and optimizing the yield of agar and carrageenan. Furthermore, large-scale production is more viable with standardized products, as suggested for high-value bioactive products derived from seaweed (Hafting et al., 2015). Cultivation methods can potentially be adjusted to improve polysaccharide content (Hafting et al., 2015), with environmental factors easily controlled in onshore aquaculture. Offshore and nearshore cultivation can be optimized by selecting locations with suitable environmental conditions (Hafting et al., 2015) and appropriate cultivation techniques (Friedlander, 2007). Moreover, recognizing the seasonal patterns of polysaccharide

production can help determine the most favourable period for harvesting. Beyond practical applications, knowledge of the various factors influencing polysaccharides in seaweed can enhance our scientific understanding of how seaweed responds to global warming (Kumar et al., 2020). Overall, further research is needed on the impact of nutrients, carbon metabolism (Roleda & Hurd, 2019), and other influential factors (Lee et al., 2017; Véliz et al., 2017).

Phycocolloids like agar and carrageenan, obtained from red algae, are essential biomaterials widely utilized across numerous industries. The production process of these polysaccharides involves several stages, each influenced by environmental conditions and genetic factors. Understanding these influences is key to optimizing yield and quality (Figure 2) (Pereira et al., 2009).

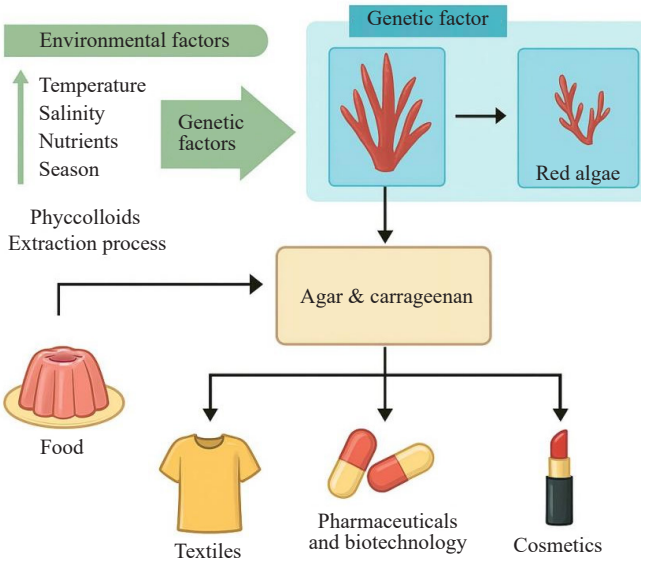


Figure 2. Schematic overview of agar and carrageenan extraction workflows, highlighting critical control points influenced by environmental and genetic factors

The composition and quality of phycocolloids can vary significantly due to seasonal changes. For example, agar content is often higher during summer when light and temperature conditions are optimal. This variability requires careful monitoring and adjustment of cultivation practices to ensure consistent production. Environmental factors such as light intensity, temperature, and nutrient availability directly impact the synthesis of polysaccharides, making it essential to select cultivation sites with favourable conditions (Afonso et al., 2021).

In onshore aquaculture, environmental conditions can be more easily controlled, allowing for the optimization of factors that affect phycocolloid production (García-Poza et al., 2020). Offshore and nearshore cultivation, on the other hand, can benefit from selecting locations that naturally provide suitable conditions for seaweed growth. The integration of advanced cultivation techniques can further enhance the efficiency and sustainability of phycocolloid production (Pereira & Cotas, 2024).

Understanding the seasonality of polysaccharides is also critical for determining the best harvest times. Seaweed often produces higher quantities of polysaccharides during certain seasons, and aligning harvesting schedules with these periods can maximize yield. Additionally, knowledge of the biotic and abiotic factors influencing polysaccharide production can provide insights into how seaweed may respond to environmental changes, such as global warming (Ptak et al., 2021). Additional studies are required to clarify how nutrient availability and carbon metabolic pathways influence the synthesis of phycocolloids. Studies on the responses of agar and carrageenan to different environmental conditions have shown considerable variation, highlighting the need for ongoing investigation. By expanding our understanding of these factors, we can develop more effective strategies for cultivating seaweed and producing high-quality phycocolloids (Pereira, 2025a).

The potential for optimizing cultivation methods to improve polysaccharide content is significant. By adjusting

environmental conditions and employing innovative techniques, the industry can enhance the production of standardized, high-value bioactive products. This approach not only supports large-scale production but also contributes to the sustainable use of marine resources (Otero et al., 2023).

Although several reviews published between 2017 and 2024 have addressed agar and carrageenan, none have integrated recent advances in biosynthetic regulation, sustainable extraction technologies, and emerging biomedical and green-technology applications. This review provides an updated synthesis that connects environmental drivers, molecular biosynthesis, industrial scalability, and regulatory constraints, an integration not yet addressed in the literature.

2. Drivers of polysaccharide production

Polysaccharides derived from macroalgae are increasingly acknowledged as a sustainable resource with strong potential for future applications. This recognition has fueled growing interest in their extraction and use, and the worldwide demand for large volumes of seaweed is projected to expand significantly in the years ahead. However, optimizing cultivation systems remains essential to meet this expanding demand and ensure sustainable seaweed production and processing (Zhang et al., 2022). To address the increased demand for seaweed and seaweed-based products, it is crucial to enhance both the growth and collection of seaweed. The scarcity of farmed seaweed poses a significant threat to wild seaweed populations due to commercial overexploitation, raising serious marine environmental concerns (García-Poza et al., 2020). Therefore, for the seaweed polysaccharide industry, it is imperative to maintain high quality while achieving higher yields of polysaccharides. This necessity studies seaweed metabolism and responses to abiotic and biotic factors, aiming to increase polysaccharide yield without compromising quality or incurring prohibitive economic costs (Mendes et al., 2024).

To further ensure the sustainability and efficiency of seaweed production, it is imperative to invest in advanced research and development initiatives. These should focus on innovative farming techniques, such as Integrated Multi-Trophic Aquaculture (IMTA) and offshore cultivation, which can help alleviate pressure on wild seaweed populations (Figure 3) (Ali et al., 2024).



Figure 3. Innovative farming techniques, such as Integrated Multi-Trophic Aquaculture (IMTA) and nearshore cultivation of *Kappaphycus alvarezii* (original illustration from Leonel Pereira)

Additionally, the development of biotechnological methods to enhance the growth rates and polysaccharide content of farmed seaweed is essential (Pereira, 2025a). Collaboration between researchers, industry stakeholders, and

policymakers is crucial to create supportive frameworks and incentives for sustainable practices. By adopting a holistic approach that includes environmental, economic, and social dimensions, the seaweed industry can achieve higher yields, maintain quality, and contribute to the global demand for sustainable resources while minimizing its ecological footprint (Samoraj et al., 2024).

2.1 *Abiotic factors*

Light is a fundamental driver of photosynthesis, enabling carbon fixation into energy-rich compounds and shaping seaweed growth and metabolic activity. Variations in light intensity and wavelength directly influence the biosynthesis of polysaccharides such as agar and carrageenan (Mendes et al., 2024). Because seaweeds inhabit different depths with unequal light penetration, the type and yield of polysaccharides produced are strongly depth-dependent (Zhong et al., 2020). Red algae are particularly adapted to thrive under low-light conditions, unlike green and brown species that require higher illumination. Temperature also plays a decisive role, regulating metabolic rates and polysaccharide accumulation. Although the optimal thermal range differs among species, elevated temperatures generally stimulate growth until stress thresholds are reached, at which point polysaccharide production declines. Seasonal temperature variations can lead to fluctuations in polysaccharide content, with certain species producing more during cooler seasons (Bastos, 2019).

Nutrient availability is a key factor in seaweed growth, as environments rich in nutrients generally accelerate development and can modify the composition of polysaccharides. However, excess nutrients can cause changes in the polysaccharide structure (Pereira, 2024). Elements like iron, magnesium, and potassium are necessary for the enzymatic activities involved in polysaccharide production (Leandro et al., 2020). Fluctuations in salinity can trigger osmotic stress in seaweeds, altering their metabolic processes and influencing polysaccharide synthesis. Elevated salt concentrations frequently stimulate the accumulation of specific polysaccharides, which serve as protective adaptations. The type and quantity of polysaccharides produced by different seaweed species depend on their salinity tolerance (Mendes et al., 2024).

The movement of water, or hydrodynamic flow, plays a key role in regulating nutrient supply and gas exchange, processes essential for seaweed growth and polysaccharide synthesis. While moderate circulation typically supports healthy development, excessive turbulence can cause physical stress and diminish polysaccharide yields. High turbidity can decrease light penetration, thereby affecting photosynthesis and polysaccharide formation (Hurd, 2017).

Moreover, the interaction between light and other environmental factors further complicates seaweed metabolism and polysaccharide production. For instance, while optimal light conditions can boost growth and polysaccharide synthesis, the combination with nutrient-rich waters can further enhance these effects (Singh & Singh, 2015). Conversely, suboptimal light conditions, combined with nutrient deficiencies, can result in stunted growth and lower polysaccharide yields. Therefore, managing light exposure along with other environmental variables is crucial for maximizing seaweed productivity (Mamede et al., 2023).

(a) (b)

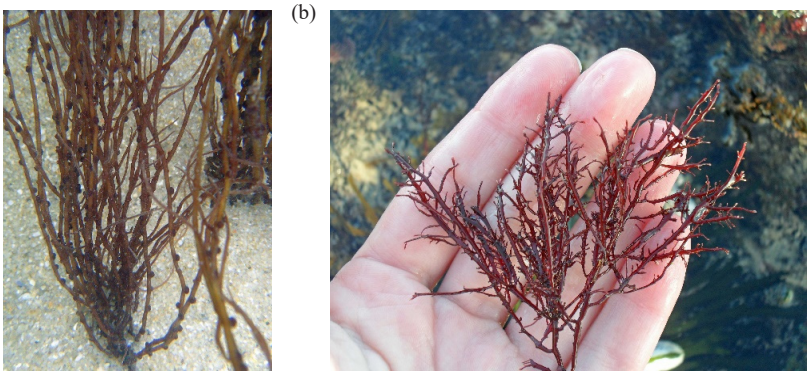


Figure 4. *Gracilaria gracilis* (a) and *Gelidium corneum* (b) (Rhodophyta)

Macroalgae cultivation techniques must also account for the specific needs of different species. For example, red seaweeds like *Gracilaria gracilis* (Figure 4a) and *Gelidium corneum* (Figure 4b) (Rhodophyta) require careful management of light and nutrient levels to optimize agar production (Farghali et al., 2023; Khan et al., 2024).

Research into the genetic factors influencing seaweed growth and polysaccharide production is also advancing. Genetic modifications and selective breeding programs hold potential for developing seaweed strains with enhanced polysaccharide content and resilience to environmental stress. Such advancements could significantly boost seaweed yields and ensure a more stable supply of high-quality polysaccharides for industrial applications (Charrier et al., 2015; Mendes et al., 2024).

Furthermore, the development of sustainable harvesting and post-harvest processing techniques is essential for maintaining the quality of seaweed polysaccharides. Traditional methods of harvesting and drying can sometimes result in degradation of polysaccharide quality. Innovations in these areas, such as the use of solar drying and controlled storage environments, can help preserve the integrity and functionality of seaweed polysaccharides, ensuring they meet the high standards required by various industries (Zhu et al., 2021; Lafeuille et al., 2023).

Understanding and optimizing the environmental and genetic factors that influence seaweed growth and polysaccharide production is crucial for meeting the rising demand for these valuable compounds (Table 1) (Akter et al., 2024). Through integrated cultivation strategies, advanced genetic research, and innovative processing techniques, the seaweed industry can sustainably expand its production while maintaining the high quality of its polysaccharides. This holistic approach not only supports the industry's growth but also contributes to environmental sustainability by reducing the pressure on wild seaweed populations and promoting the use of red macroalgae as a renewable resource (Pereira et al., 2009; Pereira & Cotas, 2024).

Table 1. Comparative influence of abiotic factors on agar vs. carrageenan production

Abiotic factor	Effect on agar (*Gracilaria*, *Gelidium*)	Effect on carrageenan (*Kappaphycus*, *Eucheuma*)	Species examples	Notes
Light intensity	Moderate light enhances agar content; low light tolerated; excessive light may reduce yield	Strongly light-dependent; high light increases κ-carrageenan; low light reduces 3,6-anhydrogalactose	*Gracilaria gracilis*, *Gelidium corneum*	Red algae adapted to low-light; carrageenophytes more sensitive
Temperature	Higher agar content in warm seasons; extreme heat reduces gel strength	Optimal 26-30 °C; heat stress reduces carrageenan quality and increases epiphytes	*Kappaphycus alvarezii*, *Eucheuma denticulatum*	Seasonal variability stronger in carrageenan species
Nutrients (N, P)	Nitrogen enrichment decreases agar yield (carbon diverted to proteins)	Moderate N increases growth but may reduce κ-carrageenan quality	*Gracilaria* spp.	Nutrient effects differ by species and life stage
Salinity	Hypo- and hyper-salinity can increase agar as a stress response	High salinity increases κ-carrageenan viscosity; low salinity reduces gel strength	*Kappaphycus* spp.	Carrageenan more sensitive to salinity shifts
Hydrodynamics	Moderate flow improves nutrient uptake; strong turbulence reduces agar	Strong currents reduce carrageenan deposition; sheltered sites preferred	*Eucheuma* spp.	Hydrodynamics critical for offshore farms
Seasonality	Summer peaks in agarose content	Dry season peaks in κ-carrageenan	All species	Seasonal harvesting essential for standardization

2.2 *Cultivation strategies to enhance phycocolloid production in red algae*

Optimizing the cultivation of red macroalgae requires a coordinated management of environmental variables that directly influence the biosynthesis, structure, and yield of phycocolloids such as agar and carrageenan. Several abiotic factors can be strategically manipulated in aquaculture systems to enhance polysaccharide accumulation and improve gel quality (García-Poza et al., 2020; Mendes et al., 2024).

2.2.1 *Light management*

Controlled light regimes are essential for maximizing carbon assimilation and galactan biosynthesis. Moderate irradiance (typically 50-150 µmol photons $m^{-2} \cdot s^{-1}$, species-dependent) promotes higher agar and carrageenan content, while excessive light induces photoinhibition and reduces polymer quality. Depth-adjusted cultivation lines, shading nets, and seasonal light modulation are commonly used to maintain optimal irradiance (Lee et al., 2021).

2.2.2 *Temperature optimization*

Temperature strongly regulates metabolic rates and the activity of key enzymes involved in 3,6-anhydrogalactose formation. Warm-temperate species such as *Gracilaria* often show higher agar yields at 20-28 °C, whereas carrageenophytes like *Kappaphycus alvarezii* perform best at 26-30 °C. Avoiding thermal stress is critical, as temperatures above species-specific thresholds reduce gel strength and increase susceptibility to epiphytes (Lee et al., 2021; Mendes et al., 2024).

2.2.3 *Nutrient regulation*

Nitrogen and phosphorus availability influence carbon allocation between proteins and polysaccharides. Mild nitrogen limitation often enhances agar and carrageenan content by diverting carbon toward structural galactans rather than growth. Conversely, excessive nitrogen reduces gel strength and increases sulphation. Controlled fertilization, pulse-feeding, and Integrated Multi-Trophic Aquaculture (IMTA) systems help maintain balanced nutrient levels (Troell et al., 2009).

2.2.4 *Salinity control*

Red algae exhibit species-specific salinity optima, and moderate osmotic stress can stimulate phycocolloid accumulation as a protective response. For example, *Kappaphycus* shows improved κ-carrageenan viscosity under stable high-salinity conditions (32-35 PSU), while *Gracilaria* tolerates wider fluctuations. Avoiding rapid salinity shifts is essential to prevent stress-induced degradation of polysaccharide quality (Araújo et al., 2014; Mendes et al., 2024).

2.2.5 *pH stability*

Although often overlooked, pH affects enzyme activity in the biosynthetic pathway and the ionic environment of the cell wall. Maintaining seawater pH between 7.8 and 8.3 supports optimal growth and polysaccharide deposition. In land-based systems, buffering and CO_2-stripping are used to stabilize pH and prevent acidification from respiration (Hsieh-Lo et al., 2019; Mendes et al., 2024).

2.2.6 *Hydrodynamic flow and water movement*

Moderate water flow enhances nutrient uptake, gas exchange, and removal of metabolic by-products, all of which support polysaccharide synthesis. Excessive turbulence, however, causes mechanical stress and reduces agar and carrageenan deposition. Farm design, rope spacing, orientation, and depth can be adjusted to maintain ideal flow conditions (Hurd, 2000; Hurd, 2017).

2.2.7 *Stress-induction strategies*

Mild, controlled stress (e.g., low-level salinity or nutrient stress) can upregulate protective polysaccharide pathways, increasing 3,6-anhydrogalactose content and improving gel strength. These strategies must be carefully timed, typically applied shortly before harvest to avoid compromising biomass yield (Tee et al., 2015; Mendes et al., 2024).

2.2.8 *Selective breeding and strain selection*

Cultivation success is strongly influenced by strain-level differences in polysaccharide biosynthesis. Selecting high-yielding strains of *Kappaphycus*, *Eucheuma*, or *Gracilaria* with stable phycocolloid profiles across seasons is a key strategy for industrial production. Hatchery-based propagation ensures genetic consistency and reduces variability (Bixler & Porse, 2011).

2.3 *Biotic factors*

Seaweed species, along with individual strains within a species, display distinct genetic profiles that determine both the type and concentration of polysaccharides they generate. As a result, identical environmental conditions may lead to different outcomes depending on the genetic background and geographic location of the algae. In addition, the developmental stage of the organism, whether in its juvenile phase or fully mature, plays a significant role, with certain life stages producing greater polysaccharide yields. Polysaccharide production relies on specialized enzymes, whose activities are modulated by both genetic and environmental factors, thereby affecting the quantity and structure of the polysaccharides produced (Mendes et al., 2024; Pereira, 2024).

Herbivory and pathogen attacks can trigger polysaccharide synthesis as a defensive mechanism, with variations in polysaccharide content enhancing their protective properties (El-Beltagi et al., 2022). Additionally, microbial populations on the seaweed's surface can impact polysaccharide synthesis, further influencing their composition and function (Akbar et al., 2024).

Understanding the interplay between genetic and environmental factors is crucial for optimizing seaweed cultivation and polysaccharide production. Advances in genetic research have the potential to identify specific genes responsible for polysaccharide synthesis, enabling selective breeding and genetic modification to enhance desired traits. By leveraging these genetic insights, it is possible to develop seaweed strains that are more resilient to environmental stressors and have higher polysaccharide yields (Charrier et al., 2015; Nagahawatta et al., 2023).

The conditions under which seaweed is cultivated strongly influence both the yield and composition of polysaccharides. In managed aquaculture settings, whether coastal or offshore, environmental variables such as illumination, temperature, nutrient supply, and salinity can be carefully regulated to optimize production. These systems can be tailored to meet the specific needs of different seaweed species, ensuring optimal growth conditions and maximizing polysaccharide production (Pasquini et al., 2024).

Another important aspect to consider is the impact of herbivory and pathogen pressure on seaweed health and polysaccharide synthesis. Macroalgae have evolved various defence mechanisms, including the production of bioactive compounds that deter herbivores and inhibit pathogen growth. Understanding these interactions can inform the development of integrated pest management strategies that minimize damage to seaweed crops while maintaining high polysaccharide yields (Lomartire & Gonçalves, 2022).

The role of microbial communities in seaweed cultivation is also gaining attention. Microbiomes associated with seaweed surfaces can influence nutrient uptake, growth rates, and polysaccharide synthesis. By studying these microbial interactions, researchers can develop probiotics or other microbial treatments that enhance seaweed health and productivity. This holistic approach to seaweed cultivation, considering both macro and microbiological factors, can lead to more sustainable and efficient production systems (Singh & Reddy, 2014; Macrae & Vickers, 2024). In addition, post-harvest processing techniques are critical for maintaining the quality of extracted polysaccharides. Innovative methods, such as cold extraction and enzymatic treatments, can improve the purity and functionality of polysaccharides, making them more suitable for various industrial applications. The development of eco-friendly extraction processes also aligns with the growing demand for sustainable and green technologies in the seaweed industry (Zhu et al., 2021; Otero et al., 2023).

Overall, the future of seaweed polysaccharide production lies in the integration of advanced genetic, environmental, and processing techniques. By adopting a multidisciplinary approach, the industry can achieve higher yields, better quality, and greater sustainability, contributing to the global demand for natural and renewable resources. This not only supports the economic growth of the seaweed sector but also promotes environmental conservation and the responsible use of marine ecosystems (Mamede et al., 2023; Samoraj et al., 2024).

2.4 *Biosynthesis of agar and carrageenan*

The biosynthesis of red algal phycocolloids is a tightly regulated process involving coordinated metabolic, enzymatic, and structural pathways that culminate in the deposition of complex galactans within the cell wall (Chevenier et al., 2023). Although agar and carrageenan share a common evolutionary origin as sulphated galactans, their biosynthetic routes diverge significantly, resulting in polymers with distinct structural features, degrees of sulfation, and physicochemical properties. Understanding these pathways is essential for interpreting how environmental and genetic factors influence polysaccharide yield and quality, and for developing strategies to enhance phycocolloid production in cultivated species (Ciancia et al., 2020).

2.4.1 *Precursor formation and nucleotide-sugar supply*

Both agar and carrageenan biosynthesis begin with the generation of activated nucleotide sugars, primarily Uridine Diphosphate (UDP)-galactose, derived from photosynthetically fixed carbon. The Leloir pathway plays a central role in converting glucose-1-phosphate into UDP-galactose, which serves as the immediate donor for galactosyl residues incorporated into the polymer backbone. The availability of UDP-galactose is influenced by light intensity, carbon assimilation rates, and nitrogen status, linking primary metabolism to cell-wall biogenesis.

In carrageenophytes, additional pools of 3′-phosphoadenosine-5′-phosphosulphate (PAPS) are required to support extensive sulfation. PAPS is synthesized in the plastid and cytosol and represents a major metabolic cost, explaining why carrageenan production is more sensitive to environmental stress than agar biosynthesis.

2.4.2 *Polymer backbone assembly*

The initial assembly of the galactan backbone occurs in the Golgi apparatus through the action of galactosyltransferases, which catalyse alternating β-1,4 and α-1,3 linkages between D-galactose and L-galactose residues. Although the general architecture is conserved across red algae, lineage-specific differences in enzyme families contribute to the structural divergence between agar and carrageenan.

In agar-producing species (e.g., *Gelidium*, *Gracilaria*), the backbone is only lightly sulphated, and the biosynthetic machinery favours the formation of agarose, a neutral polymer enriched in 3,6-Anhydro-L-Galactose (3,6-AG). In contrast, carrageenan-producing species (e.g., *Kappaphycus*, *Eucheuma*) synthesize highly sulphated precursors that are subsequently modified into κ-, ι-, or λ-carrageenan, depending on the pattern of sulfation and the presence or absence of 3,6-AG.

2.4.3 *Sulfation and de-sulphation reactions*

Sulfation is a defining step in carrageenan biosynthesis. Galactose-6-sulfotransferases and related enzymes transfer sulphate groups from PAPS to specific hydroxyl positions on the galactose residues. The degree and position of sulfation determine the type of carrageenan produced:

- κ-carrageenan: one sulphate group per disaccharide, with 3,6-AG on the α-linked residue.
- ι-carrageenan: two sulphate groups per disaccharide, also containing 3,6-AG.
- λ-carrageenan: three sulphate groups per disaccharide, lacking 3,6-AG and therefore non-gelling.

Agar biosynthesis involves minimal sulfation, and in many species, sulphated precursors undergo desulphation before or during the formation of 3,6-AG. This low sulfation level contributes to agar's high gel strength and thermal hysteresis.

2.4.4 *Formation of 3,6-anhydrogalactose*

The conversion of L-galactose-6-sulfate into 3,6-anhydro-L-galactose is catalysed by galactose-6-sulfurylases (also known as 3,6-AG cyclase's). This reaction is essential for the formation of the rigid, linear agarose chains characteristic of agar. In carrageenan biosynthesis, the same reaction distinguishes κ- and ι-carrageenan (which contain 3,6-AG) from λ-carrageenan (which does not).

Environmental factors such as temperature, salinity, and nutrient availability influence sulfurylase activity,

explaining seasonal fluctuations in gel strength and polymer composition.

2.4.5 *Transport and cell-wall deposition*

Once synthesized and modified in the Golgi, agar and carrageenan precursors are transported to the cell wall via secretory vesicles. Deposition occurs in the fibrillar matrix, where the polymers interact with cellulose microfibrils and other wall components. Agar typically forms a rigid, brittle matrix, whereas carrageenan contributes to a hydrated, flexible wall structure, reflecting their ecological roles in desiccation resistance and mechanical flexibility.

The final structure of the polysaccharide is influenced by:

- Ionic environment (e.g., K^+ promotes κ-carrageenan gelation).
- pH and redox conditions.
- Developmental stage of the thallus.
- Presence of epiphytes or pathogens.

These factors can alter polymer conformation, degree of aggregation, and extractability.

2.4.6 *Genetic regulation and species-specific pathways*

Recent genomic and transcriptomic studies have identified gene families associated with galactosyltransferases, sulfotransferases, sulfurylases, and Carbohydrate-Active EnZymes (CAZymes) involved in phycocolloid biosynthesis. Expression patterns vary across species, life-cycle stages, and environmental conditions, suggesting that polysaccharide production is under complex regulatory control.

Selective breeding and strain improvement programs increasingly target:

- Enhanced 3,6-AG content.
- Reduced unwanted sulfation.
- Improved stress tolerance.
- Stable polysaccharide profiles across seasons.

These advances hold promise for improving the consistency and quality of phycocolloid production in aquaculture systems (Table 2).

Table 2. Biosynthetic differences between agar and carrageenan pathways

Biosynthetic step	Agar (Gracilariales, Gelidiales)	Carrageenan (Gigartinales)	Key enzymes/Notes
Monosaccharide precursor	UDP-galactose	UDP-galactose	Shared precursor
Polymer backbone formation	β-1,4 and α-1,3 galactosyltransferases	Same general pathway	Enzyme families differ by lineage
Sulfation	Minimal sulfation	Extensive sulfation (κ, ι, λ patterns)	Galactose-6-sulfotransferases
3,6-anhydrogalactose formation	High proportion in agarose	κ and ι require conversion; λ lacks 3,6-AG	3,6-anhydrogalactose cyclases
Cell-wall deposition	Rigid, brittle matrix	Flexible, hydrated matrix	Determines ecological function
Environmental sensitivity	Moderate	High (light, salinity, temperature)	Explains variability in carrageenan farms

3. Applications of red algae phycocolloids

Red algae-derived phycocolloids, particularly agar, carrageenan, and other sulphated galactans, possess unique physicochemical and bio-functional properties that support a wide range of industrial applications. Their gelling capacity, viscosity modulation, biocompatibility, and structural versatility make them indispensable across the food, pharmaceutical, medical, cosmetic, agricultural, and livestock sectors. Recent technological advances and sustainability-

driven innovation have further expanded their relevance in emerging bio-based industries (Table 3).

Table 3. Recent studies on applications of red algae phycocolloids

Application area	Phycocolloid	Species source	Key findings	References
Food structuring and dairy stabilization	κ-carrageenan	*Kappaphycus alvarezii*	Improved gelation and stability in dairy matrices	Campo et al. (2009)
Plant-based meat and gel systems	Agar	*Gelidium corneum*	Strong thermoreversible gels for plant-based foods	Imeson (2010)
Drug delivery hydrogels	Carrageenan	*Eucheuma denticulatum*	Mucoadhesive and controlled-release properties	Necas and Bartosikova (2013)
Tissue engineering scaffolds	Agarose	*Gracilaria* spp.	Biocompatible scaffolds with tunable porosity	Sivashankari and Prabaharan (2020)
Cosmetic emulsions	Carrageenan	*Chondrus crispus*	Enhanced viscosity and sensory properties	Lourenço-Lopes et al. (2020)
Plant biostimulants	Sulphated galactans	*Gracilaria gracilis*	Improved germination and stress tolerance	Pacheco et al. (2021)
Aquaculture feed binders	Carrageenan	*Kappaphycus alvarezii*	Increased pellet stability and digestibility	Ruscoe et al. (2005)

3.1 *Food industry*

Agar and carrageenan are long-established hydrocolloids in food processing, where they function as gelling, thickening, stabilizing, and texturizing agents. κ-carrageenan is widely used in dairy systems to improve mouthfeel and prevent syneresis, while ι-carrageenan provides elastic gels suitable for low-fat formulations. Agar is valued for its strong, thermally stable gels in confectionery, bakery fillings, and plant-based alternatives. Increasing consumer demand for clean-label and vegan ingredients has strengthened the role of red-algal phycocolloids as natural, allergen-free stabilizers (Campo et al., 2009).

3.2 *Pharmaceutical and biomedical applications*

The biocompatibility, biodegradability, and tunable rheology of phycocolloids support their use in drug delivery, wound dressings, tissue engineering scaffolds, and controlled-release systems. Agarose hydrogels are widely used for cell encapsulation and electrophoresis, while carrageenan-based matrices have shown promise in mucoadhesive drug delivery and antiviral formulations. Sulphated galactans also exhibit immunomodulatory, anticoagulant, and antioxidant activities, positioning them as candidates for next-generation biomedical materials (Necas & Bartosikova, 2013).

3.3 *Medical and clinical uses*

Agar and agarose are essential in microbiology for culture media preparation due to their thermal hysteresis and inertness. Carrageenan has been explored for antiviral nasal sprays, hemostatic materials, and bio-adhesive medical gels. Their structural versatility enables the development of hydrogels with tailored porosity, mechanical strength, and degradation profiles for regenerative medicine.

3.4 *Cosmetic and personal-care applications*

Carrageenan is widely used in cosmetic formulations as a thickener, stabilizer, and sensory enhancer in lotions, creams, toothpaste, and hair-care products. Its ability to form smooth, elastic gels improves product texture and stability. Agar contributes to peel-off masks and moisturizing gels, while sulphated polysaccharides provide hydration and film-forming properties valued in skin-care formulations.

3.5 *Agriculture and plant bio-stimulation*

Red-algal polysaccharides have gained attention as sustainable agricultural inputs. Sulphated galactans can act as elicitors of plant defense responses, enhancing resistance to pathogens and abiotic stress. Extracts containing agar or carrageenan have been shown to promote seed germination, root development, and nutrient uptake. Their biodegradable nature aligns with the shift toward eco-friendly agricultural practices (Pacheco et al., 2021).

3.6 *Livestock and aquaculture feed applications*

Phycocolloids contribute to feed pellet stability, water retention, and nutrient delivery in aquaculture. Carrageenan improves pellet cohesion and digestibility, while agar enhances gel strength in formulated feeds. Bioactive sulphated polysaccharides may also support gut health and immune modulation in livestock, offering potential as natural feed additives (Ruscoe et al., 2005).

4. Red macroalgae polysaccharide studies in polysaccharide production

Red seaweeds are renowned for their ability to produce a variety of valuable polysaccharides, notably agar and carrageenan. These polysaccharides have attracted widespread interest because of their broad utility across the food, medical, cosmetic, and biotechnological sectors. The unique chemical properties of agar and carrageenan make them indispensable in various formulations, offering gelling, thickening, and stabilizing functionalities (Alba & Kontogiorgos, 2019; Mamede et al., 2024).

Polysaccharide synthesis in red algae is shaped by a multifaceted interaction of genetic traits, environmental conditions, and physiological processes. Understanding these factors is crucial for optimizing both the yield and quality of polysaccharides (Sudha et al., 2014). Research into the genetic makeup of red seaweed has revealed that different species, and even different strains within the same species, possess distinct genetic profiles that affect polysaccharide synthesis (Xie et al., 2024). Environmental factors such as light, temperature, nutrient availability, and salinity play pivotal roles in modulating the metabolic pathways involved in polysaccharide production (Lopes et al., 2024). Additionally, the stage of the seaweed's life cycle can significantly impact poly-saccharide content, with certain developmental stages producing higher quantities of these compounds (Pacheco et al., 2021). The enzymatic processes underlying polysaccharide synthesis are also subject to regulation by both internal and external cues, further adding to the complexity of production (Gomes-Dias et al., 2020).

Recent research emphasizes the critical role of abiotic elements, particularly light intensity and spectral quality, in regulating photosynthetic processes in seaweeds. These processes are central to carbon fixation and the generation of energy, directly influencing algal productivity. Temperature fluctuations, seasonal variations, and nutrient dynamics are also critical in shaping the polysaccharide profiles of red seaweed. Moreover, biotic interactions, including herbivory and microbial associations, can influence polysaccharide composition and abundance (Lalegerie et al., 2020). In this revision, we will delve into the various studies that have explored the production of polysaccharides in red seaweed (Qiu et al., 2022). We will examine the key factors that influence polysaccharide yield and quality and discuss the latest advancements in cultivation techniques aimed at enhancing polysaccharide production. By providing a comprehensive overview of the current state of research, this chapter aims to offer valuable insights for scientists, industry stakeholders, and policymakers interested in harnessing the potential of red seaweed polysaccharides for sustainable and innovative applications (Qiu et al., 2022).

4.1 *Agar*

Agar (Figure 5) is an important sulphated galactan primarily located within the cell walls of several red algal species, most notably those belonging to *Gracilaria* and *Gelidium*. Its significance lies in its ability to protect these organisms from desiccation, extreme temperatures, high salinity, pH variations, and pathogens, while also maintaining ionic equilibrium (Lee et al., 2017). Due to its unique gelling properties, agar has found extensive applications in food, pharmaceutical, and biotechnology industries (Rhein-Knudsen et al., 2017).

Agar is composed of two primary polysaccharides: agarose (Figure 5) and agaropectin. Agarose typically accounts for roughly 70% of the mixture, while agaropectin represents the remaining 30%.

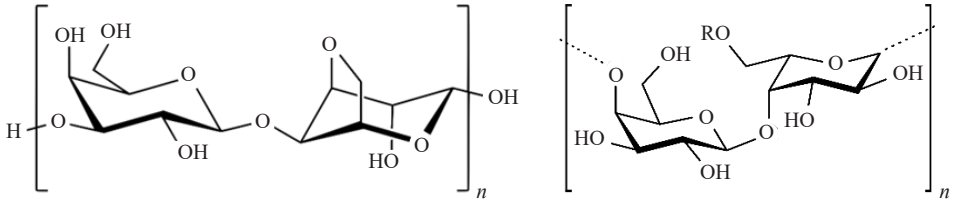


Figure 5. Chemical structure of agarose (a) and agaropectin (b)

Galactans, commonly found in the cell walls of various red algae, are believed to protect these organisms from desiccation, extreme temperatures, high salinity, pH variations, and pathogens, as well as maintain ionic balance (Pomin, 2010). A considerable portion of seaweed research on agar has concentrated on refining extraction techniques, as outlined in (Mendes et al. 2022). The effects of environmental conditions on agar yield have also been widely investigated. Findings indicate that agar levels tend to rise during summer and under both low- and high-salinity environments, as well as in reduced light exposure. Conversely, nitrogen enrichment and epiphyte colonization are typically associated with lower agar content. An earlier review by Lee et al. (2017) discussed the factors affecting agar yield and quality. However, several new studies have emerged since then, which will be examined here alongside the key points from Lee et al.'s review (2017).

Numerous studies have examined the environmental factors that influence agar content in red algae. Seasonal variations play a significant role, with research indicating that agar content is generally higher during the summer months. This increase is attributed to optimal light conditions and warmer temperatures, which enhance photosynthetic activity and polysaccharide synthesis. Light intensity and quality are crucial factors that affect agar production (Sánchez-Astráin et al., 2024). Red algae, adapted to dimmer light environments relative to green and brown species, exhibit differences in agar concentration depending on the surrounding light conditions. Hypo- and hyper-salinity conditions have also been found to influence agar production, with these stress conditions potentially triggering mechanisms that increase agar synthesis as a protective response. Conversely, factors such as nitrogen enrichment and the presence of epiphytes have been associated with a decrease in agar content. Nitrogen enrichment can alter the metabolic pathways, redirecting resources away from polysaccharide synthesis. The growth of epiphytes on the surface of red algae can impede light absorption and nutrient uptake, further affecting agar production (Lee et al., 2017).

The extraction of agar from red algae has been the focus of extensive research, aiming to optimize yield and quality. Traditional extraction methods involve hot water extraction, where the algae are boiled to release agar into the solution. This is followed by filtration and purification processes to obtain pure agar (Castejón et al., 2021). Recent progress in extraction methodologies has aimed at enhancing process efficiency while minimizing ecological consequences. Enzyme-assisted extraction methods, for example, use specific enzymes to break down cell walls, enhancing agar release while minimizing the use of harsh chemicals (Xiao et al., 2021). Microwave-assisted extraction is another innovative technique that uses microwave energy to rapidly heat the algae, resulting in faster extraction and higher yields. These modern methods not only improve the efficiency of agar extraction but also help in obtaining agar with better gelling properties, making it more suitable for various industrial applications. The ongoing research and development in this area are crucial for meeting the rising demand for high-quality agar while ensuring sustainable production practices (Morais, 2013).

Agar remains a vital polysaccharide with extensive applications across various industries. Continued research into optimizing its production and extraction will ensure that the benefits of this remarkable compound can be fully realized, supporting both economic growth and environmental sustainability. Understanding and optimizing the environmental and genetic factors that influence seaweed growth and polysaccharide production is crucial for meeting the rising demand for these valuable compounds. Through integrated cultivation strategies, advanced genetic research, and innovative processing techniques, the seaweed industry can sustainably expand its production while maintaining the

high quality of its polysaccharides (Table 4) (Mamede et al., 2023; Ali et al., 2024).

Table 4. Comparative properties of agar vs. carrageenan

Parameter	Agar	Carrageenan (κ, ι, λ)	Industrial implications
Primary structure	Alternating β-D-galactose and 3,6-anhydro-L-galactose	Sulfated galactans with varying sulfate positions	Structure determines gel type and rheology
Degree of sulfation	Low (≈ 0-5%)	κ: 20-25%; ι: 28-30%; λ: 32-39%	Higher sulfation → lower gel strength, higher solubility
Main functional fraction	Agarose (gelling) + agaropectin (nongelling)	κ (strong gel), ι (elastic gel), λ (thickener, no gel)	Determines application domain
Gel strength	Very high (600-1,200 $g \cdot cm^{-2}$)	κ: high; ι: elastic; λ: none	Agar preferred for microbiology and confectionery
Melting/setting point	Sets at 32-40 °C; melts at 80-90 °C	κ/ι set at 40-60 °C; melt at 60-70 °C	Agar's thermal hysteresis is unique
Solubility	Insoluble in cold water	Soluble only in hot water	Impacts extraction and formulation
Extraction difficulty	High for *Gelidium* (low yield, high quality)	Easier, high-volume cultivation	Carrageenan dominates global market
Main applications	Microbiology, food gels, pharmaceuticals	Dairy, meat, cosmetics, stabilizers	Complementary industrial roles

4.2 *Carrageenan*

Carrageenan (Figure 6) powder is typically a yellowish to colourless, coarse to fine powder that is practically odourless (Matos et al., 2024). For regulatory bodies across the globe to recognize a compound as carrageenan, it must include galactose, anhydro-galactose, and sulphate groups (Figure 6). The absence of any of these components means the substance cannot be classified as carrageenan. Carrageenan is only soluble in hot water and is not soluble in alcohol solutions above 1.5% (Younes et al., 2018).

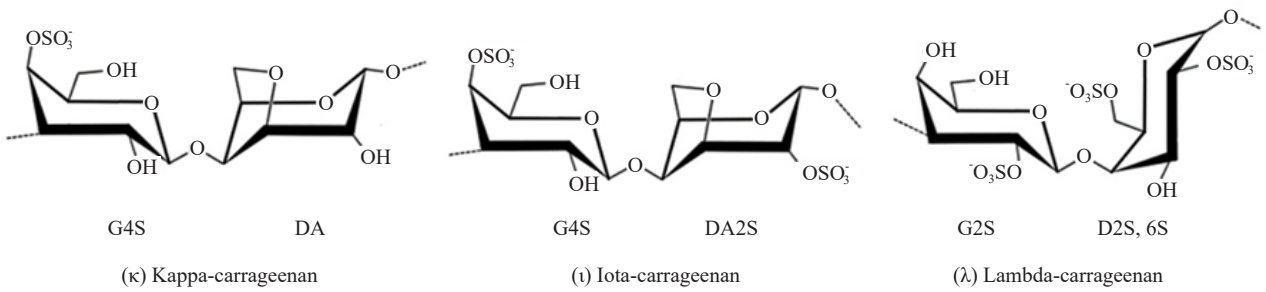


Figure 6. Idealized structure of carrageenan units

The purity of carrageenan intended for food applications is assessed through several key parameters. These include viscosity (5 mPa·s in a 1.5% solution at 75 °C), sulfation levels ranging from 15% to 40% of its dry weight, and ash content within the same range. Another critical factor is the proportion of low molecular-weight carrageenan: fractions below 50 kDa exceeding 5% are classified as poligeenan, which is not approved for food use. Additionally, acceptable samples must contain less than 5% combined starch, lipid, and protein residues. High water absorption capacity is

also an important criterion. These standards ensure that the carrageenan meets the biochemical and physical-chemical characterization methods similar to other polymers (Necas & Bartosikova, 2013).

The position and number of sulphate groups dramatically affect kappa (κ), iota (ι), and lambda (λ) carrageenan's gel strength, solubility, and rheology, with higher sulfate content generally reducing gelling power but increasing cold water solubility and flexibility, while κ-carrageenan's specific structure (lower sulphate, 3,6-anhydro galactose) yields rigid gels with K^+ ions, ι-carrageenan (higher sulphate at C4) forms elastic gels with Ca^{2+}, and λ-carrageenan (highest sulphate, no anhydro) doesn't gel but provides viscosity, all influencing network formation and interaction with cations (Table 2).

Research and development teams, along with industrial stakeholders, are actively pursuing innovative approaches to extract polysaccharides from red seaweeds using greener technologies and advanced purification strategies. Ongoing investigations must verify that these biopolymers consistently meet high-purity standards established by the Chemical Abstracts Service (CAS) and recognized international guidelines. This certification is essential to ensure the quality of the compound for further industrial exploitation (Mendes et al., 2024). Advancing sustainable extraction and purification methods for red seaweed polysaccharides, such as carrageenan, is essential for multiple reasons. Traditional extraction methods often involve the use of hot water and chemical solvents, which can be energy-intensive and environmentally damaging. By adopting greener methods, such as enzyme-assisted extraction and microwave-assisted extraction, the industry can reduce its environmental footprint while maintaining or even improving the yield and quality of carrageenan (Lomartire & Gonçalves, 2022).

Enzyme-assisted extraction employs targeted enzymes to degrade algal cell walls, enabling the release of carrageenan with greater efficiency while reducing reliance on aggressive chemical treatments. This method not only enhances the purity of the final product but also reduces the environmental impact of the extraction process (Tarma et al., 2020). Microwave-assisted extraction applies microwave energy to quickly heat algal material, enabling a more rapid and efficient release of target compounds. This technique has been shown to increase carrageenan yield and quality while conserving energy and reducing waste (Álvarez-Viñas et al., 2023).

To ensure that the extracted carrageenan meets the required standards for food and other industrial applications, rigorous testing and quality control measures are essential. This includes assessing the viscosity, sulfation content, ash yield, and molecular weight distribution, as well as detecting any impurities such as starch, lipid, and protein (Heriyanto et al., 2018). High water absorption capacity is also a key quality attribute, as it influences the functional properties of carrageenan in various applications (Heriyanto et al., 2018; Mendes et al., 2024). The pursuit of high-purity carrageenan is not only driven by regulatory requirements but also by the demand for high-quality products in food, pharmaceutical, and cosmetic industries (Ali et al., 2024). Carrageenan is widely used as a gelling, thickening, and stabilizing agent, and its performance is closely linked to its purity and molecular characteristics (Hale et al., 2024). By refining extraction and purification techniques, manufacturers can produce carrageenan that meets the stringent standards set by global regulatory agencies, ensuring its suitability for a wide range of applications (Pereira & Cotas, 2024).

Enhancing the methods used to extract and purify carrageenan from red algae is essential to satisfy the increasing global demand for this multifunctional polysaccharide. By adopting eco-friendly methods and maintaining high standards of purity, the industry can support sustainable production practices and deliver high-quality carrageenan for use in various sectors. Continued research and innovation in this field will be essential to achieving these goals and ensuring the long-term viability of the seaweed polysaccharide industry (Shafie et al., 2022). The assessment of carrageenan purity for food applications relies on several essential parameters. These include viscosity (5 mPa·s in a 1.5% solution at 75 °C), sulfation levels ranging from 15-40% of the dry weight, and ash content within the same range. Purity is also affected by the proportion of low molecular-weight carrageenan: fractions below 50 kDa exceeding 5% are classified as poligeenan, which is not permitted for food use. In addition, combined levels of starch, lipids, and proteins must remain below 5%. High water absorption capacity is also an important criterion. These standards ensure that the carrageenan meets the biochemical and physical-chemical characterization methods similar to other polymers (Necas & Bartosikova, 2013).

Research and development teams, alongside industrial partners, are actively exploring innovative approaches to extract polysaccharides from red seaweeds using environmentally sustainable methods and advanced purification technologies. Ongoing studies must confirm that these biopolymers meet strict purity standards set by the Chemical Abstracts Service (CAS) and international regulations. Such certification is vital to guarantee the compound's quality

for industrial applications (Mendes et al., 2024). Establishing greener extraction and purification strategies for polysaccharides like carrageenan is therefore of paramount importance for several key reasons. Traditional extraction methods often involve the use of hot water and chemical solvents, which can be energy-intensive and environmentally damaging. By adopting greener methods, such as enzyme-assisted extraction and microwave-assisted extraction, the industry can reduce its environmental footprint while maintaining or even improving the yield and quality of carrageenan (Lomartire & Gonçalves, 2022).

Enzyme-assisted extraction uses specific enzymes to break down cell walls, releasing carrageenan more efficiently and minimizing the need for harsh chemicals. This method not only enhances the purity of the final product but also reduces the environmental impact of the extraction process (Tarman et al., 2020). Microwave-assisted extraction harnesses microwave energy to quickly warm algal biomass, promoting a faster and more effective release of target compounds. This technique has been shown to increase carrageenan yield and quality while conserving energy and reducing waste (Álvarez-Viñas et al., 2023). To ensure that the extracted carrageenan meets the required standards for food and other industrial applications, rigorous testing and quality control measures are essential. This includes assessing the viscosity, sulfation content, ash yield, and molecular weight distribution, as well as detecting any impurities such as starch, lipid, and protein (Heriyanto et al., 2018). High water absorption capacity is also a key quality attribute, as it influences the functional properties of carrageenan in various applications (Heriyanto et al., 2018; Mendes et al., 2024).

The pursuit of high-purity carrageenan is not only driven by regulatory requirements but also by the demand for high-quality products in food, pharmaceutical, and cosmetic industries (Pereira & Cotas, 2024). Carrageenan is widely used as a gelling, thickening, and stabilizing agent, and its performance is closely linked to its purity and molecular characteristics (Hale et al., 2024). By refining extraction and purification techniques, manufacturers can produce carrageenan that meets the stringent standards set by global regulatory agencies, ensuring its suitability for a wide range of applications (Pereira & Cotas, 2024).

Improving the processes used to extract and refine carrageenan from red algae is vital to address the rising global demand for this highly adaptable polysaccharide. By adopting eco-friendly methods and maintaining high standards of purity, the industry can support sustainable production practices and deliver high-quality carrageenan for use in various sectors. Continued research and innovation in this field will be essential to achieving these goals and ensuring the long-term viability of the seaweed polysaccharide industry (Shafie et al., 2022).

5. Extraction technologies and safety in phycocolloid production

Phycocolloids, including agar and carrageenan, are obtained from seaweed through a range of extraction techniques. Safeguarding both workers and the environment during these processes is essential to ensure that the resulting products are of high quality and safe for use. When modern extraction methods are combined with rigorous safety protocols, phycocolloid production can be carried out effectively and responsibly. This approach ensures that the final products are of high quality and that both the workforce and the environment are safeguarded (Lomartire & Gonçalves, 2023).

5.1 *Industrial applications and challenges: Supply, processing, standardization, and regulatory constraints*

The expanding commercial relevance of red algal phycocolloids has intensified scrutiny of the industrial bottlenecks that constrain their large-scale deployment. Although agar and carrageenan remain indispensable across food, pharmaceutical, cosmetic, and biomedical sectors, the transition from traditional extraction to next-generation biorefinery models is hindered by several structural challenges. Addressing these constraints is essential for ensuring stable supply chains, improving product quality, and enabling the development of high-value applications (Pereira, 2025b).

Despite their long-standing importance in food, pharmaceutical, cosmetic, and biomedical sectors, agar and carrageenan production continues to face structural limitations that hinder scalability, consistency, and innovation. One

of the most pressing issues concerns biomass supply. The global industry remains heavily dependent on a narrow group of cultivated and wildharvested species, including *Kappaphycus alvarezii*, *Eucheuma denticulatum*, *Gracilaria* spp., and *Gelidium* spp. (Sugumaran et al., 2022). This dependence creates vulnerability to disease outbreaks, climatedriven stress, and market fluctuations. Declining wild stocks, particularly of *Gelidium*, further exacerbate supply instability, while seasonal and geographic variability complicates procurement and quality control. Limited aquaculture capacity, especially for species with complex life cycles or specific environmental requirements, underscores the need for expanded cultivation systems, improved strain selection, and diversification of phycocolloidproducing taxa (Liu et al., 2025).

Energy consumption represents another major challenge in phycocolloid extraction. Traditional processes rely on prolonged heating, alkaline treatments, and multiple purification steps, all of which demand substantial thermal energy (Torres et al., 2019). Rising energy prices have increased production costs, particularly in regions without access to low-cost renewable energy sources. Although energy-efficient technologies such as microwaveassisted extraction, ohmic heating, and enzymatic pre-treatments show promise, their industrial adoption remains limited due to high capital investment requirements and regulatory uncertainties. Reducing energy intensity is therefore essential for improving both the environmental footprint and the economic feasibility of phycocolloid production (Getachew et al., 2020).

Purification bottlenecks also constrain industrial performance. The complex architecture of red algal cell walls necessitates multi-step extraction and filtration to remove pigments, proteins, minerals, and other impurities (Hernández-Carmona et al., 2013). Variability in sulphation patterns and 3,6-anhydrogalactose content further complicates downstream refinement, often resulting in inconsistent functional properties (Ciancia et al., 2020). Membrane-based purification systems, while promising, are frequently hindered by fouling and low flux, and pre-treatment protocols remain insufficiently standardized across producers. These limitations highlight the need for improved clarification technologies, more robust membrane systems, and integrated biorefinery approaches capable of enhancing both purity and yield (Novoa et al., 2021).

Standardization issues remain a persistent concern for industrial users who require phycocolloids with predictable rheological and functional characteristics. Natural variability in biomass composition, driven by environmental and genetic factors, leads to fluctuations in gel strength, viscosity, and sulphation profiles (Rhein-Knudsen et al., 2017). Processing conditions also vary widely among producers, contributing to batch-to-batch inconsistency. The absence of harmonized global standards, particularly for emerging biomedical and pharmaceutical applications, creates additional barriers (Cotas et al., 2025). Defining molecular-level specifications, such as precise sulphation patterns or molecular weight distributions, is increasingly important for advanced applications but remains technically challenging (Beaumont et al., 2021).

Regulatory barriers further complicate the commercialization landscape. In the European Union (EU), agar (E406) and carrageenan (E407) must comply with stringent food-additive specifications, including limits on contaminants, heavy metals, and microbiological safety (Younes et al., 2018). In the United States, the Food and Drug Administration (FDA) requires Generally Recognized As Safe (GRAS) status for food applications and imposes more rigorous requirements for medical and pharmaceutical uses (FDA 2024). Novel applications in tissue engineering, drug delivery, and regenerative medicine face additional hurdles related to biocompatibility, sterility, and traceability. Sustainability and traceability requirements, particularly under the EU Green Deal and circular-economy frameworks, are becoming increasingly influential, adding new layers of compliance for producers (Calderon et al., 2025).

Techno-economic considerations reveal that the competitiveness of phycocolloid production is shaped by feedstock availability, energy and labor costs, capital investment needs, and market segmentation (Mendes et al., 2024). Feedstock cost remains the largest operational expense, while energy intensity significantly affects profitability (Sugumaran et al., 2022). High-purity biomedical-grade products offer greater market value but require more stringent processing and quality control. Co-product valorization, including pigments, proteins, and bioactive compounds, is increasingly recognized as essential for improving overall economic performance. Transitioning toward circular, multiproduct biorefinery models is therefore viewed as a key strategy for achieving longterm sustainability and competitiveness (Naghera et al., 2025).

5.2 *Industrial extraction methods*

The industry's traditional method of phycocolloid production involves a multistage processing procedure that

includes key phases such as cleaning/washing, pre-treatment, solid/liquid separation (extraction), precipitation, filtration, drying, and milling (Arvizu-Higuera et al., 2008; Khalil et al., 2018). These existing methods require high levels of chemical, water, and energy consumption, as well as meticulous control of waste generated throughout the process, making them less environmentally friendly and cost ineffective (Khalil et al., 2018). Considering these challenges, green extraction methods such as Ultrasound-Assisted Extraction (UAE), Microwave-Assisted Extraction (MAE), Enzyme-Assisted Extraction (EAE), Supercritical Fluid Extraction (SFE), Pressurized Solvent Extraction (PSE), reactive extrusion, and photo-bleaching are being explored to reduce chemical usage and improve the extraction yield and quality of seaweed-derived polymers (Gomez et al., 2020).

5.2.1 *Agar*

The industrial extraction of agar requires large volumes of solvent and produces considerable waste, making it a lengthy process that typically depends on prolonged heating in hot water. Acid pre-hydrolysis is frequently applied to chemically liquefy agarose (Villanueva et al., 2010). However, alkali treatment presents a significant drawback, as it generates effluents that may cause environmental harm if not adequately managed. An eco-friendly alternative to enhance the gel strength of agar could be enzymatic treatment, though its cost may not make it commercially competitive compared to alkaline treatment (Cardozo et al., 2007). Combining heat and ultrasound treatments can reduce the time and energy required for the process. Microwave-Assisted Extraction (MAE) significantly shortens the time needed for agar extraction compared to conventional methods, consuming less energy and solvent volume, and reducing waste disposal requirements (Hernández-Carmona et al., 2013).

5.2.2 *Carrageenan*

The conventional production of commercial carrageenans begins with washing to eliminate contaminants such as sand, epiphytes, and salt. Extraction is then carried out in a heated aqueous medium, which may be neutral or alkaline. The process proceeds with filtration, precipitation of carrageenan from the solution using alcohol, followed by drying and milling. Based on the extraction approach, carrageenan is categorized into two grades: Semi-Refined Carrageenan (SRC) and Refined Carrageenan (RC) (Rupert et al., 2022). Historically, in the late 1970s and early 1980s, carrageenan was obtained from seaweed by dissolving it directly into an aqueous solution. At this stage, when carrageenan is extracted by alkali treatment, it is referred to as SRC. Additional treatments, such as filtering and purifying, are required to eliminate residual components like cellulosic materials, resulting in RC (Moses et al., 2015).

To minimize resource use, including time, energy, water, chemicals, and solvents, new extraction strategies have been introduced. These approaches encompass pressurized solvent extraction as well as microwave-, ultrasonic-, and enzyme-assisted methods. Microwave-Assisted Extraction (MAE) improves efficiency by reducing both processing time and energy requirements. Likewise, ultrasound-assisted techniques, whether alkaline or aqueous, accelerate extraction compared to traditional methods, helping preserve sensitive compounds and causing only minor changes in sulphate levels and viscosity. These innovative techniques improve the extraction efficiency and sustainability of carrageenan production (Hernández-Carmona et al., 2013).

5.3 *Industrial safety measures*

Because polysaccharides vary in composition depending on extraction methods and environmental influences, it is crucial to apply chemical and biochemical techniques to verify their quality. Chromatography serves as a physical separation process in which mixture components are partitioned between two phases. The stationary phase, often a porous bed, liquid layer, or film, remains fixed, while the mobile phase, a fluid, passes through or across it. Multiple chromatographic approaches can be combined to achieve precise isolation and detailed characterization of seaweed-derived polysaccharides, although these procedures are often expensive. High-Performance Anion Exchange Chromatography (HPAEC) is a cost-effective alternative that quantifies and characterizes seaweed polysaccharide fractions, despite the challenging viscosity of liquid extracts. HPAEC employs a strong anion exchange to separate fractions based on pH and the acidic nature of seaweed polysaccharides (Shi, 2016).

Fourier Transform Infrared (FTIR) spectroscopy employs infrared frequencies to measure absorbance and

detect molecular bond vibrations in samples. Compared to methods such as Nuclear Magnetic Resonance (NMR), X-ray analysis, or chromatography, FTIR provides a more affordable option for examining chemical bonds in dried materials, eliminating the need for liquid extracts (Mohamed et al., 2017). This technique can be applied to identify polysaccharides, pigments, phenolic compounds, oxidation states, and even microplastic contamination in seaweed prior to commercialization. Despite its lower cost and ease of use, FTIR delivers less comprehensive biochemical quantification and quality assessment than chromatography. However, combined techniques can enhance seaweed quality (Monteiro et al., 2022). Pereira and his team employed Fourier Transform Infrared-Attenuated Total Reflectance (FTIR-ATR) spectroscopy to determine the composition of different phycocolloids by analysing dried ground seaweed, eliminating the need for KBr tablets (Pereira et al., 2009). In the seaweed polysaccharide industry, FTIR-ATR is employed to distinguish the quality of agar and carrageenan. It is regarded as one of the most efficient and environmentally friendly techniques for biomass characterization. The method is primarily used for identification, quality assurance, and structural analysis. Industrial applications rely on FTIR for the rapid evaluation of key properties, supporting the approval of phycocolloids and bioactive compounds for pharmaceutical use. In this context, FTIR spectra differentiate between agar- and carrageenan-producing seaweed (Mohamed et al., 2017; Cherniienko et al., 2024).

Every analytical method used to certify seaweed quality presents both strengths and limitations. Many current approaches are adapted from plant analysis, which means they may not fully address seaweed-specific requirements, particularly the mandatory testing for heavy metals. Because seaweed composition is highly complex, advancing and refining these analytical techniques is essential. At the same time, it is important to ensure that improvements remain cost-effective so that seaweed producers can adopt them sustainably. Legislative efforts are needed to establish comprehensive seaweed food quality control checks due to the chemical variability and compound complexity in seaweed (Gómez-Ordóñez et al., 2011; Hong et al., 2021; Vandanjon et al., 2023).

5.4 *Technical characteristics of agar and carrageenan*

Agar and carrageenan are extensively applied in the food, pharmaceutical, and biotechnology sectors because of their distinctive abilities to gel, thicken, and stabilize formulations. For their safe and reliable use in industry, these polysaccharides must undergo thorough technical evaluation and be formally recognized by the CAS as well as other national and international regulatory bodies.

5.4.1 *Agar*

Agar powder generally has no noticeable smell or only a faint odour. In its unprocessed form, it is sold as thin, membranous strands that are agglutinated together, or in sliced, flaked, and granular varieties. Its colour may vary from pale yellowish-orange to yellowish-grey, light yellow, or even transparent. When hydrated, agar becomes firmer and develops a jelly-like consistency, whereas in its dry state, it is brittle and easily broken. The powdered form is typically white, off-white, or light golden in appearance. Under microscopic observation in water, agar powder displays greater transparency. In a chloral hydrate solution, it is even more transparent than in water, showing a more granular, striated, and angular structure, occasionally containing diatom frustules (Matos et al., 2024; Mendes et al., 2024).

Agar does not dissolve in cold water but readily dissolves when exposed to hot water. The assessment of its purity is based on several parameters, including ash content (which must remain below 6.5% for food-grade quality), the presence of insoluble residues, and the detection of starch, fats, and proteins. Additional characteristics such as water absorption ability and viscosity also play a role in determining its overall quality. Therefore, several techniques like those used for other polymers' biochemical and physicochemical characterization and certification methods, such as glucans and xanthan gums, are applied (Mendes et al., 2024).

5.4.2 *Carrageenan*

Carrageenan powder generally ranges in appearance from pale yellow to nearly colourless and can vary in texture from coarse to fine. It is almost entirely free of odor. For global food agencies to classify a substance as carrageenan, it must contain galactose, anhydro-galactose, and sulphate groups. If any of these essential components are absent, the material cannot be identified as carrageenan. Carrageenan is only soluble in hot water and not in alcohol solutions above

1.5% (Matos et al., 2021).

The evaluation of carrageenan purity for food use depends on several critical parameters. These include viscosity (5 mPa·s in a 1.5% solution at 75 °C), sulfation levels ranging from 15-40% of the dry weight, and ash content within the same range. Purity is also influenced by the proportion of low molecular-weight fractions: if more than 5% of the material is below 50 kDa, it is classified as poligeenan, which is not approved for food applications. In addition, combined levels of starch, fats, and proteins must remain under 5%, while a strong water absorption capacity is also required. Several methods, similar to those used for other polymers' biochemical and physicochemical characterization, are applied (Rashedy et al., 2021).

Industrial and research groups are increasingly focused on developing sustainable methods for extracting polysaccharides from red seaweeds. The aim is to introduce greener extraction and purification technologies that reduce environmental impact while maintaining efficiency and product quality. Continuous research must demonstrate that polymers have high purity according to CAS and international conventions, which is essential to certify the quality of the compound for further exploitation (Pereira & Cotas, 2024).

5.5 *Research and development in polysaccharide extraction*

Although certified methods are already in use within the phycocolloid industry, they remain highly labour-intensive, deliver moderate to low yields, and demand large inputs of chemicals, water, and energy—while also producing significant waste. These limitations reduce both environmental and economic efficiency. In response, a range of eco-friendly extraction technologies is being developed to lower chemical consumption while improving the yield and quality of polymers derived from seaweed. Nevertheless, before such innovations can be adopted commercially, they must undergo rigorous testing and meet industrial standards for polysaccharide products. Furthermore, most studies are not designed for industrial scale, making the economic feasibility of the extraction process another important factor to consider (Cotas et al., 2024; Mendes et al., 2024; Pereira & Cotas, 2024).

Table 5. Extraction yields of phycocolloids obtained using green extraction technologies (Kadam et al., 2015; Herrero et al., 2006)

Green extraction method	Typical extraction yield (% dry weight)	Phycocolloid type	Representative red algae species	Key notes/Advantages
Ultrasound-Assisted Extraction (UAE)	20-45% agar; 25-55% carrageenan	Agar, Carrageenan	*Gracilaria gracilis*, *Kappaphycus alvarezii*	Cavitation enhances cell disruption; reduced extraction time and solvent use
Microwave-Assisted Extraction (MAE)	30-60% agar; 35-65% carrageenan	Agar, Carrageenan	*Gelidium corneum*, *Eucheuma denticulatum*	Rapid heating improves polysaccharide solubilization; high energy efficiency
Enzyme-Assisted Extraction (EAE)	25-50% agar; 30-70% carrageenan	Agar, Carrageenan	*Gracilaria* spp., *Kappaphycus* spp.	Enzymes (cellulases, proteases) improve purity and reduce harsh chemicals
Supercritical Fluid Extraction (SFE)	10-25% (mainly sulphated polysaccharides)	Sulphated galactans	*Porphyra* spp., *Gracilaria* spp.	Uses CO_2; excellent for bioactive fractions; mild temperatures preserve structure
Pressurized Solvent Extraction (PSE) (also called Pressurized Liquid Extraction (PLE))	35-70% carrageenan; 25-55% agar	Agar, Carrageenan	*Kappaphycus alvarezii*, *Gracilaria* spp.	High pressure improves solvent penetration; reduced extraction time
Reactive Extrusion (REX)	40-75% carrageenan; 30-60% agar	Agar, Carrageenan	*Eucheuma denticulatum*, *Gracilaria* spp.	Continuous, scalable, solvent-reduced process; suitable for industrial production
Ohmic Heating Extraction (OHE)	30-55% carrageenan	Carrageenan	*Kappaphycus alvarezii*	Uniform heating; reduced thermal degradation; energy-efficient
Subcritical Water Extraction (SWE)	40-80% polysaccharides (species-dependent)	Mixed sulphated polysaccharides	*Gracilaria* spp., *Palmaria palmata*	Water as green solvent; tunable temperature enhances selectivity

Yields are expressed as % of dry algal biomass, consistent with phycocolloid literature; Values represent ranges reported across multiple studies

Recent innovations in polysaccharide extraction include MAE, UAE, EAE, and a range of green solvent-based approaches. These eco-friendly methods cover processes such as Subcritical Water Extraction (SWE), ionic liquid extraction, and Supercritical Fluid Extraction (SFE), along with techniques like reactive extrusion and photo-bleaching. However, because of the diversity and specificity of these approaches, publicly available information remains limited. However, MAE and UAE procedures are low-cost and have been effectively utilized in large-scale commercial chemical extractions (Table 5) (Usman et al., 2023; Khalid et al., 2024).

The composition of polysaccharides can vary significantly, influenced not only by the extraction method but also by environmental and biological factors. As a result, multiple analytical procedures are required to properly characterize them and confirm their quality. For large-scale applications, it is essential to develop extraction technologies that are both efficient and environmentally sustainable, ensuring reliable production at a commercial level. Hydrocolloids, like carrageenan and agar, are often processed inefficiently using significant amounts of chemicals; nevertheless, there are innovative and equally acceptable alternatives to meet industrial productivity demands (Noelia et al., 2017).

When exploring new seaweed species and developing cultivation or extraction methods for carrageenan and agar intended for industrial approval, it is essential to thoroughly assess both identification and purity. These evaluations are critical to guarantee product safety and to ensure compliance with established regulatory standards. Mendes et al. (2023) demonstrated that different species strains (*Kappaphycus alvarezii*) (see Figure 3) can influence the appropriate method to extract carrageenan, which can be approved for food applications. Thus, the effect of different extraction procedures on the type of extracted carrageenan was very clear (Mendes et al., 2024).

6. Seaweed polysaccharides' current industrial applications

Expanding at around 6% annually, the phycocolloid sector is outpacing global Gross Domestic Product (GDP) growth. Traditionally, these compounds have served as food additives, with the food and beverage industry representing more than 70% of their worldwide market share. However, their use in personal care, cosmetics, and the medical and pharmaceutical industries is expected to grow the fastest (Pangestuti & Kim, 2015).

As scientific understanding and technology advance, the uses of algal polysaccharides are extending well beyond their conventional roles. Current research is investigating novel applications that remain under development or are just beginning to enter the industry. One area of particular interest is their antiviral potential: several seaweed-derived polysaccharides have shown promise in helping to inhibit viral processes, including the attachment, adsorption, and replication of pathogens such as the virus responsible for Corona Virus Disease-2019 (COVID-19). Furthermore, their safety, biodegradability, and biocompatibility, along with low production costs, may offer advantages over plant-based compounds (Holdt & Kraan, 2011; Pereira & Critchley, 2020). A further benefit of polysaccharides derived from red seaweeds lies in their natural bioactive properties. These compounds exhibit inherent biological activity, which enhances their value for applications in health, nutrition, and biotechnology. Certain polysaccharides, such as agar and carrageenan, exhibit various biological activities, which differ based on their molecular weight, sulphation level, and the number of sulphate ester groups present in the polymer (Carina et al., 2021). Antiviral activity has been demonstrated primarily *in vitro*; no clinical trials have validated these effects.

Seaweed species generate polysaccharides with distinct chemical profiles, which can be further shaped by the extraction technique applied. Carrageenophytes generally contain more sulphate groups compared to agarophytes. At the same time, carrageenan itself exhibits considerable structural variation, with the iota, lambda, and kappa forms representing the most commercially significant types. What distinguishes these forms of carrageenan is primarily their sulphate ester concentration and their location in the molecule (Zhong et al., 2020).

6.1 *Food industry*

Agar was the first hydrocolloid to receive the European registration number E406 and was approved as GRAS by the FDA for use as an additive in the food industry (Babich et al., 2022). Approximately 80% of the agar produced globally is used for food applications (Pereira, 2018a). Across many Asian regions, agar is widely used in the preparation of jellies. The process typically involves boiling macroalgae, adding flavouring, and then cooling the mixture to set into a jelly. The versatility of agar in these applications is primarily linked to its functional properties,

particularly its strong gelling capacity. Low-quality agar is primarily used in food products, while some may extend to industrial applications, such as paper sizing, coating, adhesives, textile printing/dyeing, casting, and impressions (Khalil et al., 2018). Despite being listed as a permitted food additive, agar (E406) is only used in a limited number of food items. It is estimated that around 90% of marketed agar is intended for the food sector (McHugh, 2003).

Carrageenan finds extensive use in both dairy processing and the baking sector because of its remarkable functional qualities, particularly its ability to thicken, stabilize, and improve texture. It binds milk molecules and retains water, which helps stabilize processed meat products (Hernández-Carmona et al., 2013). Additionally, carrageenan is commonly used as a gelling agent. However, its gel-forming abilities depend on the type of carrageenan used, with iota and kappa carrageenan forming a gel in the presence of potassium or calcium (Udo et al., 2023).

Carrageenans are incorporated into a wide range of food and beverage formulations to enhance texture, stability, and gel formation. Beyond culinary uses, these phycocolloids serve roles such as immobilizing biocatalysts, acting as stabilizers in toothpaste, and forming gels in air fresheners. They are also added to pet foods and processed meat products. More recently, innovative applications in the food sector include using carrageenan as an edible protective coating for freshly cut and packaged produce. Here, carrageenan acts as a gas barrier, altering the cut surfaces of the fruit, reducing respiration, and consequently slowing down discoloration while maintaining texture throughout the shelf life (Necas & Bartosikova, 2013).

6.2 *Pharmaceutical and medical industry*

Outside of food production, algal polysaccharides play an important role in pharmaceutical and medical contexts. Their natural gelling, stabilizing, and thickening abilities, combined with bioactive properties, make them highly useful in these sectors. In addition, phycocolloids can function as functional foods, delivering health-promoting benefits and contributing to the prevention of chronic illnesses. The bio-nanostructures of algal polysaccharides have become an important addition to the food industry, primarily focusing on health applications, including supplements and prebiotics (Lomartire & Gonçalves, 2023).

Polysaccharides derived from algae exhibit notable antibacterial, antimicrobial, and antiviral activities. Their therapeutic applications are wide-ranging, including roles in cancer and tumour prevention, as well as providing anti-inflammatory and antioxidant benefits. They are frequently employed in drug delivery systems and disinfectants, while more specialized uses involve dissolvable bandages and applications in tissue engineering. Additionally, various polysaccharides have specific uses, further highlighting their versatility and importance in different industries (Nigam et al., 2022). Antiviral activity has been demonstrated primarily *in vitro*; no clinical trials have validated these effects.

Agar has been reported to lower blood sugar levels, making it beneficial for individuals with hyperglycaemia, and it also helps inhibit red blood cell clumping. Research suggests that agar may absorb ultraviolet radiation (Tanna & Mishra, 2019). Beyond these health-related properties, agar is widely utilized in laboratories as a base for pharmaceutical-grade culture media. It is commonly used in culture mediums because it is not easily metabolized, is non-digestible, and has good gel firmness, elasticity, clarity, and stability (Khalil et al., 2018).

Agar of medium quality can serve multiple roles in pharmaceutical and medical applications. It is utilized in the production of monoclonal antibodies, interferons, steroids, and alkaloids. Additionally, it functions as a bulking agent, laxative, and base material for suppositories, capsules, and tablets, while also being applied as an anticoagulant. On the other hand, the most highly purified agar, obtained from a fraction of agar called agarose, is used for separation in molecular biology processes such as electrophoresis, immune diffusion, and gel chromatography (Pereira, 2011; Khalil et al., 2018).

Carrageenan demonstrates a wide range of medicinal benefits. It exhibits anticoagulant and antithrombotic effects, shows antiviral and antitumor potential, and contributes to lowering cholesterol levels. Antiviral activity has been demonstrated primarily *in vitro*; no clinical trials have validated these effects.

In addition, carrageenan is recognized for its immunomodulatory functions and antioxidant activity, making it valuable in pharmaceutical applications. These pharmaceutical aspects form the basis for carrageenan's application in the pharmaceutical field (Pereira, 2011; Khalil et al., 2018). Immunomodulatory responses reported in murine models cannot be extrapolated to human therapeutic use.

Carrageenan is used in the production of tetracyclines, a significant group of antibiotics (Necas & Bartosikova, 2013). Thanks to its gelling capacity, carrageenan is applied as a matrix to immobilize *Streptomyces aureofaciens*,

the microorganism responsible for producing certain antibiotics. Beyond this role, carrageenan also contributes to the synthesis of D-aspartic acid, which serves as a precursor in the development of semi-synthetic antibiotics. Moreover, carrageenan has been proven to inhibit the attachment of viruses such as the human papillomavirus, dengue virus, influenza A, and herpes virus (Pereira, 2011; Liu et al., 2015; Khalil et al., 2018).

6.3 *Industry of cosmetics*

There is a growing preference among consumers for cosmetics formulated with seaweed-derived ingredients rather than synthetic alternatives. These products typically feature purified compounds or extracts obtained from different seaweed species. The bioactive substances present in seaweed are particularly suitable for cosmetic applications, offering advantages such as low toxicity to cells and reduced allergenic potential. However, the biochemical profiles of seaweed can vary, and the extraction processes might lead to the loss of certain biomolecules (López-Hortas et al., 2021). Macroalgal hydrocolloids, commonly referred to as phycocolloids, represent the most significant polysaccharides for industrial use. These structural compounds, derived from seaweeds, are notable for their ability to form colloidal systems—intermediate states that lie between true solutions and suspensions. As a result, polysaccharides can be employed in various sectors, including cosmetics, where they serve as thickening, gelling, and stabilizing agents for suspensions and emulsions (Pereira, 2023).

Around one-fifth of global carrageenan production is directed toward pharmaceutical and cosmetic applications. It is a common ingredient in numerous everyday products, appearing in formulations such as toothpaste, shampoos, lotions, medicinal preparations, sunscreens, shaving creams, deodorant sticks, sprays, and foams. Its ability to form hydrogels allows it to be employed in various applications, including antiviral, antibacterial, and pathophysiological processes such as hyperlipidaemia management (Pereira, 2018b). Antiviral activity has been demonstrated primarily *in vitro*; no clinical trials have validated these effects.

Agar serves as both an emulsifying and stabilizing agent in cream formulations, while also helping regulate moisture levels in a variety of cosmetic products. It is commonly incorporated into items such as hand lotions, liquid soaps, deodorants, foundations, exfoliants, cleansers, shaving creams, facial moisturizers, and treatments targeting acne and skin aging. Agar can endure high temperatures (up to 250 °C) and preserve its properties even near boiling point temperatures, making it ideal for use in jellied confections where the components may be treated at high temperatures and subsequently cooled down (Balboa et al., 2015; Pereira, 2018b).

6.4 *Agriculture and industrial applications*

Seaweed-derived polysaccharides are incorporated into conventional fertilizers to improve soil quality by enhancing water and nutrient retention. Functioning mainly as soil conditioners, these natural compounds exhibit exceptional absorbency, capable of holding water volumes many times greater than their own weight. In agriculture, these polysaccharides are often referred to as moisture-holding hydrogels, which enhance soil water retention, a critical characteristic of healthy soil (Mamede et al., 2023). To enhance soil quality, agricultural scientists have created super-absorbent materials that improve abiotic properties. These compounds boost water retention and efficiency, increase soil permeability and infiltration, and support better plant growth and aeration. Additionally, they can reduce irrigation frequency, limit compaction shift, prevent erosion and water drainage, and decrease fertilizer solubility rates (Malik et al., 2023).

Carrageenans and their oligomers, obtained from red seaweeds, are abundant in bioactive molecules that stimulate plant defence mechanisms, enhancing resilience against both environmental and biological stress factors. Their effects are mediated through the regulation of diverse physiological and biochemical pathways. In addition, carrageenans influence several metabolic activities in plants, such as cell division, the synthesis of purines and pyrimidines, nutrient uptake of nitrogen and sulfur, and the process of photosynthesis. On the other hand, while numerous studies have been conducted on the bioactivities of agarophytes, there has been little research on the bioactivities of agar, particularly its influence on plants (Shukla et al., 2016).

Polysaccharides extracted from red seaweeds are currently applied across numerous industrial sectors (Table 6). However, expanding their use into new areas requires increasing seaweed production with consistently high polysaccharide yields while maintaining product quality. To achieve this, it is vital to identify and understand the key

factors that influence polysaccharide synthesis in seaweeds. New uses are being developed and applied in various fields, such as paper sizing, coating, adhesives, textile printing/dyeing, casting, and impressions (Jönsson et al., 2020).

Table 6. Summary of industrial applications of red seed polysaccharides (Mamede et al., 2023; Mendes et al., 2024; Cotas et al., 2025)

Industry	Polysaccharide	Main applications	Specific uses
Food industry	Agar	- Food additive (E406, GRAS approved). - Popular in jellies.	- Low-quality agar in food products. - High-quality agar in limited food items. - Common use as a jellifying agent.
	Carrageenan	- Food additive (E407, GRAS approved). - Processed meat products. Stabilization - Protective coating on fresh-cut packaged food.	- Binds milk molecules, retains water. - Gas barrier, reduces respiration, slows discoloration, and maintains texture in packaged foods.
Pharmaceutical	Agar	- Pharmaceutical grade growth media. - Drug delivery systems. - Functional foods with health. Benefits - Medical analysis.	- Decreases blood glucose, prevents red blood cell aggregation. - Acts as bulking agents in laxatives, suppositories, capsules, tablets, and anticoagulants. - Production and encapsulation of monoclonal antibodies, interferons, steroids, and alkaloids.
	Carrageenan	- Pharmaceutical drugs and agents. - Functional foods with health benefits.	- Decreases blood glucose, prevents red blood cell aggregation. - Highly purified agar (agarose) used in molecular biology (electrophoresis, immune diffusion, gel chromatography).
Cosmetic	Agar	Structural ingredients.	- Used in creams, hand lotions, liquid soap, deodorants, foundation, exfoliant, cleanser, shaving cream, face moisturizer/lotion, acne and anti-aging treatments.
	Carrageenan	Structural ingredient.	- Applications include toothpaste, hair wash products, lotions, medications, sun blocks, shaving creams, deodorant sticks, sprays, and foams.
Agriculture	Agar	Structural ingredients.	- Acts as moisture-holding hydrogel, reducing irrigation frequency, improving soil aeration, and limiting erosion. - Soil conditioner, improves water retention, soil permeability, and plant performance.
	Carrageenan	Functional ingredients. Regulates physiological and biochemical processes in plants (e.g., cell division, photosynthesis).	- Regulates plant metabolic processes, including purine and pyrimidine synthesis, nitrogen and sulphur absorption. - Activates plant defence systems, provides resistance to abiotic and biotic stressors.

The output of polysaccharides from red seaweeds is shaped by multiple influences, including economic conditions, environmental factors, technological capabilities, and market expectations. Rising consumer interest in natural, clean-label products has further accelerated demand for seaweed-derived polysaccharides, particularly agar and carrageenan. These polysaccharides are valuable for controlled drug delivery systems, wound dressings, and tissue engineering due to their biocompatibility, non-toxicity, and gel-forming properties (Otero et al., 2023).

Food and drug authorities, including the Food and Drug Administration (FDA), have classified polysaccharides as Generally Recognized As Safe (GRAS) (Younes, 2024), which has encouraged their adoption across multiple industries and stimulated greater production. Nations with abundant seaweed reserves are increasing output to satisfy rising international demand, especially in markets that prioritize natural and health-enhancing products. Moreover, seaweed cultivation is viewed as a more sustainable alternative to traditional agriculture, as it requires fewer inputs and resources. This sustainability factor is driving increased investment in seaweed polysaccharide synthesis (Ahmed et al., 2024; Matos et al., 2024).

6.5 *Livestock industry*

Macroalgae consumption extends beyond humankind, benefiting various animal species as well. European use of seaweed in animal husbandry dates back to the Roman era (Sultana et al., 2023). Countries like Iceland, France, and Norway commonly incorporate seaweed into domestic animal nutrition (Dhakal et al., 2024). Notably, the first seaweed meal for animal feed was produced in Norway, using brown seaweed that was collected, dried, and milled (Makkar et al., 2016).

Beyond their direct use as feed, macroalgae are incorporated into other feed formulations as both nutritional enhancers and nutraceutical ingredients. At present, algae-based supplements are employed to correct mineral deficiencies in livestock pastures, particularly in regions such as the United States, Australia, and New Zealand. Seaweed meals, primarily used as a vitamin and mineral supplement, are produced mainly from kelps like *Palmaria palmata* (Figure 7a), *Grateloupia filicina* (Figure 7b), *Neopyropia tenera*, and *Chondrus crispus* (Leandro et al., 2020; Min et al., 2021).

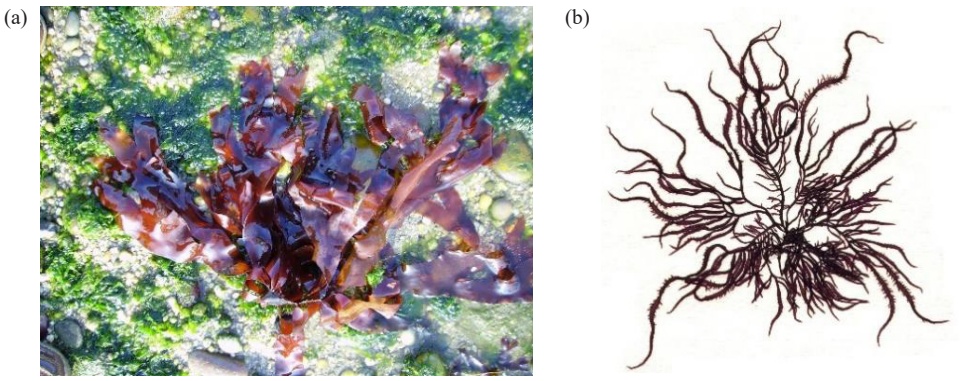


Figure 7. *Palmaria palmata* (a) and *Grateloupia filicina* (b)

In addition to direct feeding applications, animal diets are often supplemented with extracts such as sulphated polysaccharides derived from macroalgae. These compounds function as nutraceutical additives, enhancing the nutritional profile of feed and supporting animal health. These meals have been proven to enhance animal intestinal integrity and improve immune response efficiency (González-Meza et al., 2023).

The livestock industry and red seaweed (Rhodophyta) phycocolloids may seem like dis-tinct domains at first glance, but they intersect in intriguing and beneficial ways. Red seaweed, known for its high phycocolloid content, such as agar and carrageenan, has significant potential applications within the livestock industry. The integration of red seaweed into live-stock farming presents opportunities to address some of the industry's pressing challenges, such as environmental sustainability, animal health, and economic efficiency (Pereira, 2023).

A notable emerging use of red seaweed in animal husbandry is its ability to lower methane emissions from ruminants. Methane, a powerful greenhouse gas, plays a significant role in driving climate change, and animals such as cattle, sheep, and goats release large amounts of it through their digestive activity. Incorporating red seaweed into feed has shown promise in mitigating this environmental impact. Studies have shown that incorporating certain species of red seaweed, particularly *Asparagopsis*, into the diet of ruminants can significantly reduce methane production. This not only helps mitigate the environmental impact of livestock farming but also enhances the overall sustainability of the industry (Min et al., 2021).

Additionally, red seaweed phycocolloids can improve animal health and nutrition. Carrageenan, for example, has been found to possess antiviral and immunomodulatory properties, which can support the health and resilience of livestock. These properties can help reduce the reliance on antibiotics, addressing concerns about antibiotic resistance and improving the overall health management of livestock populations (Pereira & Cotas, 2024). Immunomodulatory responses reported in murine models cannot be extrapolated to human therapeutic use.

Moreover, red seaweed is a rich source of essential nutrients, including vitamins, minerals, and antioxidants, which

can enhance the nutritional profile of animal feed and contribute to better growth and productivity (Morais et al., 2020). Antiviral activity has been demonstrated primarily *in vitro*; no clinical trials have validated these effects.

Economically, the integration of red seaweed into the livestock industry can create new value chains and opportunities for coastal communities involved in seaweed farming. By promoting the cultivation and utilization of red seaweed, the livestock industry can support sustainable aquaculture practices and contribute to the economic development of regions where seaweed is an abundant and renewable resource (Rebours et al., 2014). The intersection of the livestock industry and red seaweed phycocolloids offers a promising pathway towards greater sustainability, improved animal health, and economic benefits. By leveraging the unique properties of red seaweed, the livestock industry can address some of its most pressing challenges and contribute to a more sustainable and resilient food system (Gadzama, 2024).

The livestock industry and red seaweed (Rhodophyta) phycocolloids may seem like distinct domains at first glance, but they intersect in intriguing and beneficial ways. Red seaweed, known for its high phycocolloid content, such as agar and carrageenan, has significant potential applications within the livestock industry. The integration of red seaweed into livestock farming presents opportunities to address some of the industry's pressing challenges, such as environmental sustainability, animal health, and economic efficiency (Pereira, 2023; Mendes et al., 2024).

A key emerging use of red seaweed in animal agriculture is its ability to curb methane release from ruminants. As a powerful greenhouse gas, methane plays a major role in driving climate change, and animals such as cattle, sheep, and goats generate substantial amounts of it through their digestive systems. Incorporating red seaweed into feed has shown strong potential to lessen this environmental burden. Studies have shown that incorporating certain species of red seaweed, particularly *Asparagopsis taxiformis* (Figure 8), into the diet of ruminants can significantly reduce methane production. This not only helps mitigate the environmental impact of livestock farming but also enhances the overall sustainability of the industry (Min et al., 2021; Wanapat et al., 2024).



Figure 8. Asparagopsis taxiformis (Scale = 1 cm)

Additionally, red seaweed phycocolloids can improve animal health and nutrition. Carrageenan, for example, has been found to possess antiviral and immunomodulatory properties, which can support the health and resilience of livestock. These properties can help reduce the reliance on antibiotics, addressing concerns about antibiotic resistance and improving the overall health management of livestock populations. Immunomodulatory responses reported in murine models cannot be extrapolated to human therapeutic use.

Moreover, red seaweed is a rich source of essential nutrients, including vitamins, minerals, and antioxidants, which can enhance the nutritional profile of animal feed and contribute to better growth and productivity (Álvarez-Viñas et al., 2021). Antiviral activity has been demonstrated primarily *in vitro*; no clinical trials have validated these effects.

Among the red seaweed species, *K. alvarezii* is another important example, as it serves as a primary source of

carrageenan. Besides its gelling, thickening, and stabilizing properties, carrageenan extracted from *K. alvarezii* has been studied for its antiviral and immunomodulatory effects on animals. Incorporating this alga into animal feed can help boost animal health, increase disease resistance, and reduce the need for antibiotics, thereby combating antibiotic resistance, a growing concern in modern livestock farming. Immunomodulatory responses reported in murine models cannot be extrapolated to human therapeutic use. Additionally, *K. alvarezii* enhances the nutritional quality of the diet, promoting healthier and more productive animal growth (Rupert et al., 2022; Shafie et al., 2022). Antiviral activity has been demonstrated primarily *in vitro*; no clinical trials have validated these effects.

Economically, the integration of red seaweed into the livestock industry can create new value chains and opportunities for coastal communities involved in seaweed farming. By promoting the cultivation and utilization of red seaweed, the livestock industry can support sustainable aquaculture practices and contribute to the economic development of regions where seaweed is an abundant and renewable resource (Ahmed et al., 2022). The intersection of the livestock industry and red seaweed phycocolloids offers a promising pathway towards greater sustainability, improved animal health, and economic benefits. By leveraging the unique properties of red seaweed, the livestock industry can address some of its most pressing challenges and contribute to a more sustainable and resilient food system (Pereira & Cotas, 2024).

7. Industrial innovation: Emerging applications of seaweed polysaccharides

The phycocolloid sector is experiencing rapid expansion, currently outpacing global GDP with an annual growth rate of about 6%. Traditionally, these seaweed-derived polysaccharides have been most widely applied as additives in food and beverage products, representing over 70% of their worldwide market share. Looking ahead, the fastest growth is anticipated in personal care, cosmetic, medical, and pharmaceutical applications (Pangestuti & Kim, 2015).

As scientific understanding deepens and technology advances, the range of uses for algal polysaccharides is broadening beyond their conventional roles. These compounds are increasingly being explored for innovative applications across diverse industries, highlighting their versatility and growing importance. This includes exploring new and emerging uses that are still under study. For instance, the antiviral properties of several seaweed polysaccharides have inspired research into their potential to combat the global COVID-19 pandemic (Pereira & Critchley, 2020). Polysaccharides derived from algae are thought to play a role in hindering viral activity. They may interfere with key stages of infection by blocking viral attachment to host cells, reducing adsorption, and limiting replication processes. Additionally, their safety, biodegradability, and biocompatibility, along with their low production costs, potentially offer advantages over plant-based compounds (Venkatesan et al., 2015). Antiviral activity has been demonstrated primarily *in vitro*; no clinical trials have validated these effects.

Moreover, red seaweed polysaccharides have inherent bioactivity potential that sets them apart from plant-based compounds. Polysaccharides like agar and carrageenan display diverse biological properties, which vary according to factors such as their molecular size, degree of sulphation, and the quantity of sulphate ester groups they contain. These structural differences influence how the compounds interact biologically, leading to distinct functional outcomes. Furthermore, different seaweed species produce chemically diverse polysaccharides, which may be influenced by the extraction process used (Lomartire & Gonçalves, 2022). Carrageenophytes typically contain more sulphate groups than agarophytes. Despite this, carrageenan exhibits considerable structural variation. Among its many forms, the three most commercially significant are iota, lambda, and kappa carrageenan, each valued for distinct functional properties. These forms are primarily distinguished by their sulphate ester concentration and their specific location within the molecule (Falshaw et al., 2003).

7.1 *Pharmaceutical applications*

The phycocolloid market is expanding more rapidly than the global economy, showing an annual growth rate of about 6%. Traditionally, these seaweed-derived polysaccharides have been most widely utilized as food additives, with the food and beverage industry representing over 70% of their worldwide market share. However, their application in personal care, cosmetics, and the medical and pharmaceutical industries is expected to expand the quickest (Liu et al., 2023).

As research deepens and technology evolves, algal polysaccharides are finding new roles that go beyond their conventional applications. These versatile compounds are increasingly being explored for innovative uses across diverse scientific and industrial fields. This includes exploring new and emerging uses that are still under study. For instance, the antiviral properties of several seaweed polysaccharides have inspired research into their potential to combat the global COVID-19 pandemic (Pereira & Critchley, 2020; Nigam et al., 2022). Algal-derived polysaccharides are thought to interfere with viral infection pathways. They may act by blocking the virus from attaching to host cells, reducing adsorption efficiency, and hindering replication, thereby limiting the spread of infection. Additionally, their safety, biodegradability, and biocompatibility, along with their low production costs, potentially offer advantages over plant-based compounds (Alfinaikh et al., 2025). Antiviral activity has been demonstrated primarily *in vitro*; no clinical trials have validated these effects.

Nanoparticles derived from seaweed polysaccharides are increasingly being explored for a variety of therapeutic purposes. Their unique structural and functional properties have attracted significant interest, opening new possibilities for medical and pharmaceutical applications beyond traditional uses. Drug delivery, insulin delivery, and bioactivities against fungal infections, tuberculosis, and cancer are some of the applications being explored (Ahmad et al., 2022). Carrageenan has attracted significant attention in recent years, with its incorporation into pharmaceutical products steadily increasing. Its unique properties make it a valuable ingredient for various medical formulations, driving growing interest in its therapeutic potential. It has been included in respected pharmacopoeias such as the United States Pharmacopeia 35-National Formulary, the British Pharmacopoeia, and the European Pharmacopoeia, suggesting its potential as a pharmaceutical excipient and a bright future (Mendes et al., 2024).

Carrageenan has been shown to have antiviral and antibacterial characteristics, as well as anticoagulant, anti-diabetic, and antioxidant properties (Pacheco-Quito et al., 2020). Researchers are increasingly exploring the blending of carrageenan with natural polymers like chitosan, starch, cellulose, and chitin. These combinations aim to create biodegradable materials with enhanced functional properties, making them particularly suitable for biomedical applications. These combinations have demonstrated tremendous potential in a variety of biological applications, including drug delivery and tissue engineering (Kokkuvayil et al., 2024). Carrageenan's outstanding bio-functionality and rheological properties, including cost-effectiveness, biological compatibility, biodegradability, and flexibility, make it an ideal functional compound for a wide range of biomedical applications, from developing nanostructure-based intelligent drug delivery systems to 3D bioprinting in tissue engineering and wound healing (Aga et al., 2021). Antiviral activity has been demonstrated primarily *in vitro*; no clinical trials have validated these effects.

Agar, an important phycocolloid, is gaining preference compared to synthetic polymers. Researchers are actively examining its potential as a sustainable raw material for therapeutic applications, highlighting its promise in biomedical innovation. It is highly desirable in the pharmaceutical industry due to its remarkable intrinsic properties, notably the strong gel it produces (Lomartire & Gonçalves, 2023). Agar has been exploited in the creation of injectable and phase-changeable composite hydrogels for cancer treatment using chemotherapy and photothermal therapy. Composite hydrogels incorporating agar have demonstrated strong potential for controlled delivery of chemotherapeutic agents and antibiotics (Wu et al., 2018). Likewise, agar-based nanocomposite films have been reported to inhibit the growth of Listeria monocytogenes (Alboofetileh et al., 2016). The blending of agar with other polysaccharides is becoming increasingly widespread. Within the pharmaceutical field, agar is mainly employed as a gelling, stabilizing, and thickening agent, while it also finds use in purgative treatments and as a supportive material in surgical procedures. Researchers have worked diligently to develop agar-based products such as composite hydrogels, nanocomposite films, and other materials with specialized applications in pharmacology (Pandya et al., 2022).

7.2 *Food packaging*

Additionally, food packaging is important for the preservation, protection, and convenience of food products, but is often not sustainable (Onyeaka et al., 2022). However, polysaccharide membranes can work as a barrier against oxygen and carbon dioxide, making them a promising candidate for food packaging (Ferreira et al., 2016). In addition, these materials are both safe to consume and biodegradable, meaning they pose no environmental burden regardless of whether the packaging is eaten or discarded. However, they do not work as a barrier for water or water vapor due to their hydrophilic properties, which can become a problem for durability and change the organoleptic characteristics of the product (Gupta et al., 2024). One effective approach to reducing the risk of food spoilage is the use of smart

packaging systems. These technologies monitor and respond to changes in food quality, helping to ensure freshness and safety throughout storage and distribution. This concept focuses on the observance and control of changes in the food or in the food packaging. It is done using biosensors made from polysaccharide hydrogels to measure those parameters (Chiu et al., 2024).

For example, it has been demonstrated that the spoilage of fish could be slowed by using a partly agarose-based hydrogel (Sumana et al., 2026). Polysaccharides also serve an important role in agriculture, where they are utilized to produce biostimulants that enhance plant growth. These natural compounds can improve nutrient uptake, boost resilience against stress, and promote healthier crop development. In a study where polysaccharide extract was given to growing plants, all the evaluated parameters (total plant size, leaf growth, and weight) showed further development in plants with the treatment (Mzibra et al., 2018). The versatility of seaweed-derived polysaccharides enables their application across numerous industries. With ongoing research and technological progress, these sustainable and bioactive compounds are expected to contribute to innovative solutions in areas such as healthcare and environmental protection. Still, many of these emerging uses remain at an early stage, with research and development facing notable limitations and challenges that must be addressed before widespread adoption. Furthermore, a cost-effective analysis of scaling-up still needs to be applied to determine if it is possible to be applied at an industrial scale (Mendes et al., 2024).

Nanotechnology in drug delivery has revolutionized the way treatments are administered, enabling the development of nanoparticles that can target specific cells or tissues. These nanoparticles can encapsulate drugs, enhance their stability and allow for controlled release, which improves the efficacy and safety of treatments. Examples include liposomes, dendrimers, and polymeric nanoparticles, all of which are used in targeted cancer therapy, gene delivery, and the treatment of various infectious diseases. This precise targeting reduces side effects and increases the therapeutic impact of drugs (Patra et al., 2018; Abotaleb et al., 2024).

Pharmacogenomics explores the influence of genetic variation on how people respond to medications. By analysing an individual's genetic profile, this field seeks to customize drug therapies, improving effectiveness and reducing adverse reactions through more precise treatment strategies. This personalized medicine approach optimizes drug efficacy and minimizes adverse effects by understanding genetic variations that influence drug metabolism and response. By developing treatments specifically suited to an individual's genetic makeup, pharmacogenomics offers more effective solutions for conditions such as cardiovascular diseases, cancer, and psychiatric disorders, leading to improved patient outcomes.

Biopharmaceuticals, often referred to as biologics, are therapeutic agents produced from living organisms. They are typically derived from biological materials such as proteins, nucleic acids, or even whole cells, and are widely used in modern medicine for treating complex diseases. These drugs offer targeted and highly specific treatments for various diseases. Examples of biopharmaceuticals include monoclonal anti-bodies, therapeutic proteins, and vaccines, which have shown great promise in treating autoimmune diseases, cancers, and infectious diseases. The precision and specificity of biopharmaceuticals contribute to advances in precision medicine, providing patients with tailored and effective treatments (Rang et al., 2013).

Regenerative medicine is centred on restoring or substituting damaged tissues and organs through advanced approaches such as stem cell therapy, tissue engineering, and gene-based treatments. Stem cells are particularly valuable because of their ability to transform into multiple cell types, enabling the repair and renewal of injured tissues. For example, *Gelidium amansii* extract, a red alga, has been studied for its potential to promote wound healing due to its bioactive compounds. Tissue engineering in-volves creating bioengineered scaffolds that support cell growth and tissue formation. These approaches offer innovative solutions for conditions like spinal cord injuries, heart disease, and neurodegenerative disorders, paving the way for breakthroughs in medical treatment and patient care (Rajabzadeh et al., 2019).

Antibody-Drug Conjugates (ADCs) represent a specialized form of cancer treatment that links monoclonal antibodies to potent cytotoxic agents. The antibodies act as precise guides, directing the drug payload to cancer cells while sparing healthy tissues. This selective targeting improves the effectiveness of chemotherapy and lowers adverse effects, offering patients a safer and more efficient therapeutic option. ADCs have shown promising results in treating various types of cancer, including breast cancer, lymphoma, and leukaemia (Fu et al., 2022).

Therapies built on RNA molecules, such as messenger Ribonucleic Acid (mRNA) and small interfering RNA (siRNA), are increasingly recognized for their capacity to influence gene activity. By modulating gene expression, these

approaches hold promise for addressing a range of genetic diseases and advancing precision medicine. mRNA vaccines, such as those developed for COVID-19, have demonstrated rapid development and high efficacy (Wang et al., 2025). Carrageenan derived from *K. alvarezii* has been explored for its potential to inhibit viral replication, offering a natural approach to combating viral infections. siRNA can silence specific genes, offering potential treatments for diseases like Huntington's disease and amyloidosis. These RNA-based therapies represent a new frontier in medical treatment, providing innovative approaches to combat genetic diseases (Rupert et al., 2022).

Drug repurposing refers to the strategy of finding new applications for drugs that are already approved or under investigation. By building on established safety and efficacy data, this method can accelerate the development of therapies, reduce costs, and bring treatments to patients more quickly. Drug repurposing has been explored for various diseases, including COVID-19, cancer, and neurodegenerative disorders. It offers a cost-effective and efficient strategy for expanding treatment options, providing patients with access to new therapies more quickly (Rauf et al., 2024). These themes represent some of the cutting-edge advancements and innovative approaches within the field of pharmaceutical applications. Each area has the potential to significantly impact healthcare, improve patient outcomes, and address unmet medical needs, pushing the boundaries of modern medicine and offering hope for a healthier future (Chintalapati et al., 2025).

8. Future directions for red seaweed polysaccharides

Within the framework of today's blue and circular economy, industries focused on agar and carrageenan are shifting toward a new objective: expanding production while advancing eco-friendly extraction and recovery methods. This transition emphasizes sustainability and innovation, aiming to align resource use with environmental responsibility. This circular economy concept, as discussed in Mendes et al. (2024), emphasizes the biorefinery approach, which integrates biomass into the production of various value-added products and compounds based on biomass quality, thereby reducing industrial waste (Balina et al., 2017; Pardilhó et al., 2023). The biorefinery model is built on a diversified approach, generating both small-scale, high-value products as well as large-scale, lower-value outputs. This dual strategy ensures resource efficiency and closes the production loop, aligning with sustainable development goals. The cascade valorisation strategy, which includes selective, sequential extraction of value-added chemicals, along with the generation of biofuels or soil amendments, is also part of the biorefinery concept (Pardilhó et al., 2022).

Red seaweed offers a range of bioactive substances that can be harnessed prior to the extraction of its polysaccharides. These compounds provide additional opportunities for utilization, enhancing the overall value of the biomass before the main polysaccharide recovery process. Once safety requirements are met, several high-value pigments and bioactive compounds can be used in the biomedical and food industries (Pardilhó et al., 2022). Although commercial extraction methods for some pigments, such as fucoxanthin and phycoerythrin, have been developed, industrial extraction methods are still in progress (Leandro et al., 2020). By implementing biorefinery from the beginning, seaweed biomass can be utilized more effectively, reducing the need for pre-treatments (currently used to clean polysaccharides at the industrial level) and lowering manufacturing costs (Pardilhó et al., 2023). The final waste from the biorefinery process primarily consists of ashes and minerals, which can be used to enrich agricultural soil (Pardilhó et al., 2022), contributing to a near zero-waste industry. Although this approach is still in its early stages, promising results have already been demonstrated on a small scale (Pardilhó et al., 2023).

Although our understanding of the biochemical diversity of polysaccharides from cultivated seaweeds remains limited, maximizing both yield and quality is crucial. The functional mechanisms of these compounds can differ depending on geographic and environmental conditions. Current studies fall short in clarifying how seaweed polysaccharides interact with specific abiotic and biotic factors, as well as in detailing the yield, molecular structure, and chain length of agar and carrageenan monomers. Given the industry's needs, the quality of polysaccharides is crucial (Buschmann et al., 2017). The implementation of green extraction and recovery techniques not only benefits the environment but also can increase the efficiency and sustainability of the agar and carrageenan industries. Adopting biorefinery methods allows for the full utilization of red seaweed biomass, transforming waste into valuable products and minimizing waste. This circular economy model is essential for addressing current environmental challenges and promoting a more responsible and innovative industry (Arias et al., 2023).

Beyond polysaccharide extraction, red seaweed can also serve as a source of bioactive compounds. These substances exhibit antioxidant, anti-inflammatory, and antimicrobial activities, opening opportunities for their use in pharmaceuticals, nutraceuticals, and functional foods. These compounds have significant potential for applications in the pharmaceutical and cosmetic industries, offering new market opportunities and contributing to the diversification of seaweed-derived products (El-Beltagi et al., 2022).

Continuous research on the biochemical diversity of cultivated seaweeds is essential to optimize extraction processes and ensure the quality of polysaccharides. Investigations into how seaweed polysaccharides interact with particular abiotic and biotic factors may uncover innovative approaches to enhance both the yield and the molecular characteristics of the resulting products. Such studies could provide valuable insights for optimizing extraction processes and improving structural quality. Collaboration between scientists, engineers, and industry is crucial to advance this field and develop innovative solutions that meet market needs (Wijesinghe & Jeon, 2012).

8.1 *Seaweed-derived biodegradable packaging*

Packaging materials made from seaweed have gained attention as a sustainable and eco-friendly substitute for conventional plastics. Using seaweed as a feedstock provides several benefits (Waseem et al., 2023). As a renewable resource, seaweed can be cultivated in abundance without competing for arable land or freshwater, unlike fossil fuel-based plastics. This makes it a more responsible option, helping to alleviate concerns about resource depletion and land-use pressures. Another key advantage is biodegradability: seaweed-based packaging naturally decomposes into harmless components through biological processes, in contrast to plastics that persist for centuries and contribute heavily to environmental pollution (Nesic et al., 2024).

Seaweed also contains polysaccharides and proteins that impart valuable barrier properties, including resistance to moisture, oxygen, and Ultraviolet (UV) radiation. These features are particularly useful for food packaging, as they help preserve freshness, extend shelf life, and reduce spoilage. Moreover, seaweed-based materials can be engineered to achieve the necessary mechanical strength and flexibility, making them versatile for diverse packaging applications (Carina et al., 2021).

A key benefit of seaweed-derived packaging is its ability to fit seamlessly into current manufacturing systems. Industries can transition from conventional plastics to seaweed-based alternatives without requiring major equipment changes or costly adjustments, making adoption more practical and widespread (Pereira & Valado, 2023). Beyond this ease of integration, seaweed cultivation itself supports carbon sequestration, as the algae absorb atmospheric CO_2 during growth, thereby contributing to climate change mitigation (Eswar et al., 2025).

Although research and commercialization are still developing, ongoing innovation aims to improve the efficiency, affordability, and scalability of these materials. Efforts are also underway to establish standardized processing methods and regulatory frameworks to ensure proper disposal and integration into waste management systems. Overall, seaweed-based biodegradable packaging represents a sustainable pathway to reducing plastic pollution. By leveraging seaweed's renewability, biodegradability, and natural barrier properties, these materials provide an eco-friendly alternative to fossil fuel-derived plastics, helping pave the way toward a cleaner and more sustainable future (Pereira & Cotas, 2024).

8.2 *Seaweed as a sustainable energy source in pharmaceuticals*

Seaweed presents considerable potential as a renewable energy resource for pharmaceutical production. Its diverse applications make it a promising candidate to support drug manufacturing processes in a more sustainable and environmentally responsible way. Harnessing the energy potential of seaweed reduces reliance on fossil fuels and contributes to a more environmentally friendly approach to pharmaceutical production (Sharma et al., 2025).

Seaweed biomass can be converted into renewable fuels such as bioethanol and biodiesel using methods like fermentation and thermochemical processing. These biofuels provide a sustainable substitute for conventional fossil fuels, supplying energy for machinery and equipment in drug production. By utilizing seaweed-based energy, industries can lower greenhouse gas emissions and contribute to climate change mitigation. Additionally, these compounds can be applied in drug manufacturing processes, directly replacing synthetic ingredients, such as using seaweed-based Polylactide (PLA) to substitute Polyhydroxyalkanoates (PHA) (Zhao et al., 2022) (Figure 9).

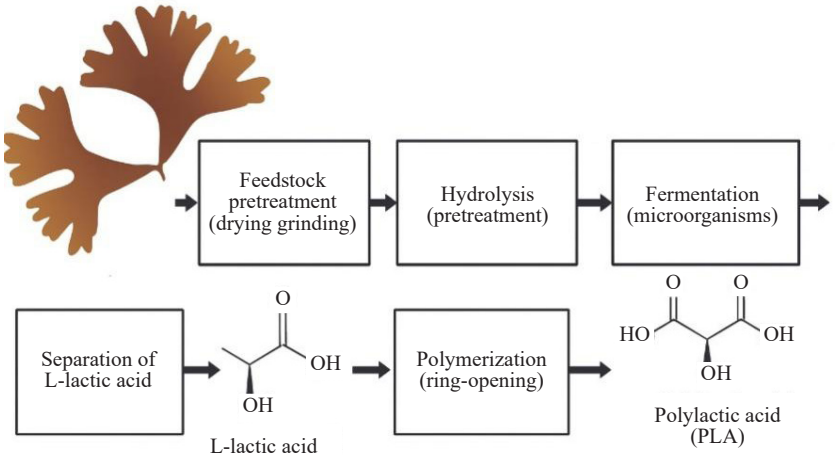


Figure 9. Transformation of seaweed into biodegradable PLA (Lee et al., 2011)

Seaweed can be processed through anaerobic digestion to generate biogas, a renewable fuel composed mainly of methane and carbon dioxide. This biogas can be harnessed for both heat and electricity, offering a sustainable energy source for pharmaceutical manufacturing operations. By replacing fossil fuels with biogas, industries can cut carbon emissions and lessen dependence on non-renewable energy (Faisal et al., 2022).

In addition, seaweed biomass, rich in polysaccharides, can be harvested and converted into energy through techniques such as combustion or gasification. These methods further expand the potential of seaweed as a versatile renewable energy resource. The energy generated can be used to meet the energy demands of drug manufacturing processes, contributing to a more sustainable and self-sufficient manufacturing ecosystem (Zhao et al., 2022).

Seaweed can serve as a direct fuel source, where burning the biomass generates heat or steam that can be applied in pharmaceutical manufacturing processes requiring thermal energy. This approach reduces dependence on fossil fuels, thereby lowering environmental impact and supporting sustainability (Wyper et al., 2024).

In addition, macroalgae can be converted into bioethanol, a renewable energy option suitable for powering drug production systems. The process involves several stages: harvesting, cleaning, drying, hydrolysis, and fermentation. During this conversion, seaweed carbohydrates are broken down into sugars, which are subsequently fermented to yield bioethanol. This pathway not only provides a sustainable energy supply but also contributes to reducing greenhouse gas emissions (Figure 10). This bioethanol can be used as a sustainable energy source for various pharmaceutical manufacturing applications, contributing to a more eco-friendly and efficient production process (Ramachandra & Hebbale, 2020).

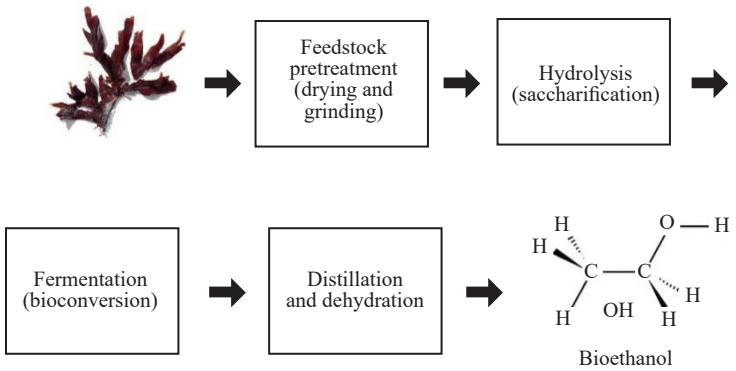


Figure 10. Production process of seaweed bioethanol (Lee et al., 2011)

Although seaweed shows strong potential as a renewable energy resource, ongoing research and technological innovation are essential to improve the efficiency of its energy conversion processes. At the same time, sustainable cultivation practices must be prioritized to safeguard marine ecosystems and ensure that large-scale harvesting does not create ecological imbalances. Integrating seaweed-based energy into a broader renewable energy portfolio, in conjunction with sources like solar, wind, and geothermal power, can help achieve a comprehensive and resilient energy supply for drug manufacturing processes (Harichandan, 2025).

Embedding biorefinery principles early in seaweed cultivation can lower production expenses and enhance the economic sustainability of industrial applications. A cascade valorization approach, where valuable compounds are extracted in a stepwise and selective manner, followed by the production of biofuels or soil enhancers, offers a comprehensive strategy for maximizing the utility of seaweed biomass. This strategy not only maximizes the value of natural resources but also contributes to the environmental and economic sustainability of the red seaweed industry (Trif et al., 2024).

9. Conclusions

This work provides a comprehensive overview of red algae-derived phycocolloids, emphasizing their structural diversity, ecological relevance, and industrial potential. The synthesis of key findings across chapters highlights the multifaceted nature of these biopolymers and their growing importance in sustainable development.

Red algae phycocolloids exhibit significant variability in composition and functionality, influenced by genetic, environmental, and technological factors. Advances in extraction technologies have improved the efficiency and safety of production, supporting broader industrial adoption.

Current applications span food, pharmaceutical, and cosmetic sectors, with emerging innovations in bioplastics and nanotechnology suggesting new frontiers. However, challenges persist, including sustainability concerns, economic barriers, and regulatory constraints. Addressing these issues requires coordinated efforts across research, industry, and policy.

Advancing the use of red algae phycocolloids will require collaboration across disciplines, strong regulatory support, and responsible harvesting methods. These measures are key to fully harnessing their potential in driving global sustainability initiatives.

Red algae phycocolloids stand out as a promising group of marine biopolymers with the capacity to transform multiple industries. Ongoing commitment to research and innovation is vital to address current challenges and establish their role in sustainable industrial growth.

Acknowledgments

Leonel Pereira thanks the FCT—Foundation for Science and Technology, I.P., in the structure of Project UIDB/04004/2025—Centre for Functional Ecology—Science for the People & the Planet.

Conflict of interest

The author declares no conflict of interest.

References

Abotaleb, S. I., Gheda, S. F., Allam, N. G., El-Shatoury, E. H., Cotas, J., Pereira, L., & Saeed, A. M. (2024). Biosynthesis of zinc oxide nanoparticles using seaweed: Exploring their therapeutic potentials. *Applied Sciences, 14*(16), 7069. https://doi.org/10.3390/app14167069

Afonso, C., Correia, A. P., Freitas, M. V., Baptista, T., Neves, M., & Mouga, T. (2021). Seasonal changes in the

nutritional composition of *Agarophyton vermiculophyllum* (Rhodophyta, Gracilariales) from the center of Portugal. *Foods, 10*(5), 1145. https://doi.org/10.3390/foods10051145

Aga, M. B., Dar, A. H., Nayik, G. A., Panesar, P. S., Allai, F., Khan, S. A., Shams, R., Kennedy, J. F., & Altaf, A. (2021). Recent insights into carrageenan-based bio-nanocomposite polymers in food applications: A review. *International Journal of Biological Macromolecules, 192*, 197-209. https://doi.org/10.1016/j.ijbiomac.2021.09.212

Ahmad, A., Gulraiz, Y., Ilyas, S., & Bashir, S. (2022). Polysaccharide-based nanomaterials: Health implications. *Food Hydrocolloids for Health, 2*, 100075. https://doi.org/10.1016/j.fhfh.2022.100075

Ahmed, N., Sheikh, M. A., Ubaid, M., Chauhan, P., Kumar, K., & Choudhary, S. (2024). Comprehensive exploration of marine algae diversity, bioactive compounds, health benefits, regulatory issues, and food and drug applications. *Measurement: Food, 14*, 100163. https://doi.org/10.1016/j.meafoo.2024.100163

Ahmed, Z. U., Hasan, O., Rahman, M. M., Akter, M., Rahman, M. S., & Sarker, S. (2022). Seaweeds for the sustainable blue economy development: A study from the southeast coast of Bangladesh. *Heliyon, 8*(3), e09079. https://doi.org/10.1016/j.heliyon.2022.e09079

Akbar, W. A., Rahim, H. U., & Rutigliano, F. A. (2024). Microbial- and seaweed-based biopolymers: Sources, extractions and implications for soil quality improvement and environmental sustainability—A review. *Journal of Environmental Management, 359*, 120964. https://doi.org/10.1016/j.jenvman.2024.120964

Akter, A., Sobuj, M. K. A., Islam, M. S., Chakroborty, K., Tasnim, N., Ayon, M. H., Hossain, M. F., & Rafiquzzaman, S. M. (2024). Seaweed polysaccharides: Sources, structure and biomedical applications with special emphasis on antiviral potentials. *Future Foods, 10*, 100440. https://doi.org/10.1016/j.fufo.2024.100440

Alba, K., & Kontogiorgos, V. (2019). Seaweed polysaccharides (agar, alginate, carrageenan). In L. Melton, F. Shahidi, & P. Varelis (Eds.), *Encyclopedia of food chemistry* (pp. 240-250). Academic Press.

Alboofetileh, M., Rezaei, M., Hosseini, H., & Abdollahi, M. (2016). Efficacy of activated alginate-based nanocomposite films to control *Listeria monocytogenes* and spoilage flora in rainbow trout slice. *Journal of Food Science and Technology, 53*(1), 521-530. https://doi.org/10.1007/s13197-015-2015-9

Alfinaikh, R. S., Alamry, K. A., & Hussein, M. A. (2025). Sustainable and biocompatible hybrid materials-based sulfated polysaccharides for biomedical applications: A review. *RSC Advances, 15*(6), 4708-4767. https://doi.org/10.1039/d4ra07277d

Ali, M. Q., Azhar, M. A., Munaim, M. S. A., Ruslan, N. F., Alsubhi, L. M., Ahmad, N., & Noman, A. E. (2024). Seaweed organic compounds source of hydrocolloids and sustainable food packaging: Properties, application, and future direction. *Discover Food, 4*(1), 101. https://doi.org/10.1007/s44187-024-00173-w

Álvarez-Viñas, M., Rivas, S., Torres, M. D., & Domínguez, H. (2023). Microwave-assisted extraction of carrageenan from *Sarcopeltis skottsbergii*. *Marine Drugs, 21*(2), 83. https://doi.org/10.3390/md21020083

Álvarez-Viñas, M., Souto, S., Flórez-Fernández, N., Torres, M. D., Bandín, I., & Domínguez, H. (2021). Antiviral activity of carrageenans and processing implications. *Marine Drugs, 19*(8), 437. https://doi.org/10.3390/md19080437

Araújo, P. G., Ribeiro, A. L. N. L., Yokoya, N. S., & Fujii, M. T. (2014). Temperature and salinity responses of drifting specimens of *Kappaphycus alvarezii* (Gigartinales, Rhodophyta) farmed on the Brazilian tropical coast. *Journal of Applied Phycology, 26*(5), 1979-1988. https://doi.org/10.1007/s10811-014-0303-9

Arias, A., Feijoo, G., & Moreira, M. T. (2023). Macroalgae biorefineries as a sustainable resource in the extraction of value-added compounds. *Algal Research, 69*, 102954. https://doi.org/10.1016/j.algal.2022.102954

Arvizu-Higuera, D. L., Rodríguez-Montesinos, Y. E., Murillo-Álvarez, J. I., Muñoz-Ochoa, M., & Hernández-Carmona, G. (2008). Effect of alkali treatment time and extraction time on agar from *Gracilaria vermiculophylla*. *Journal of Applied Phycology, 20*, 515-519. https://doi.org/10.1007/s10811-007-9258-4

Babich, O., Sukhikh, S., Larina, V., Kalashnikova, O., Kashirskikh, E., Prosekov, A., Noskova, S., Ivanova, S., Fendri, I., Smaoui, S., Abdelkafi, S., Michaud, P., & Dolganyuk, V. (2022). Algae: Study of edible and biologically active fractions, their properties and applications. *Plants, 11*(6), 780. https://doi.org/10.3390/plants11060780

Balboa, E. M., Conde, E., Soto, M. L., Pérez-Armada, L., & Domínguez, H. (2015). Cosmetics from marine sources. In S.-K. Kim (Ed.), *Springer handbook of marine biotechnology* (pp. 1015-1042). Springer.

Balina, K., Romagnoli, F., & Blumberga, D. (2017). Seaweed biorefinery concept for sustainable use of marine resources. *Energy Procedia, 128*, 504-511. https://doi.org/10.1016/j.egypro.2017.09.067

Bastos, G. A. P. (2019). *Cultivation of the wild seaweed Gracilaria gracilis under laboratory scale: The effect of light intensity and nutrients on growth, pigment and total soluble protein content* [Master's thesis, Polytechnic Institute of Leiria]. https://files01.core.ac.uk/download/pdf/286562861.pdf

Beaumont, M., Tran, R., Vera, G., Niedrist, D., Rousset, A., Pierre, R., Shastri, V. P., & Forget, A. (2021). Hydrogel-

forming algae polysaccharides: From seaweed to biomedical applications. *Biomacromolecules, 22*(3), 1027-1052. https://doi.org/10.1021/acs.biomac.0c01406

Bixler, H. J., & Porse, H. (2011). A decade of change in the seaweed hydrocolloids industry. *Journal of Applied Phycology, 23*(3), 321-335. https://doi.org/10.1007/s10811-010-9529-3

Buschmann, A. H., Camus, C., Infante, J., Neori, A., Israel, Á., Hernández-González, M. C., Pereda, S. V., Gomez-Pinchetti, J. L., Golberg, A., Tadmor-Shalev, N., & Critchley, A. T. (2017). Seaweed production: Overview of the global state of exploitation, farming and emerging research activity. *European Journal of Phycology, 52*(4), 391-406. https://doi.org/10.1080/09670262.2017.1365175

Calderon Moreno, J. M., Chelu, M., & Popa, M. (2025). Biocompatible stimuli-sensitive natural hydrogels: Recent advances in biomedical applications. *Gels, 11*(12), 993. https://doi.org/10.3390/gels11120993

Campo, V. L., Kawano, D. F., da Silva, D. B., & Carvalho, I. (2009). Carrageenans: Biological properties, chemical modifications and structural analysis. *Carbohydrate Polymers, 77*(2), 167-180. https://doi.org/10.1016/j.carbpol.2009.01.020

Cardozo, K. H. M., Guaratini, T., Barros, M. P., Falcão, V. R., Tonon, A. P., Lopes, N. P., Campos, S., Torres, M. A., Souza, A. O., Colepicolo, P., & Pinto, E. (2007). Metabolites from algae with economical impact. *Comparative Biochemistry and Physiology Part C: Toxicology & Pharmacology, 146*(1-2), 60-78. https://doi.org/10.1016/j.cbpc.2006.05.007

Carina, D., Sharma, S., Jaiswal, A. K., & Jaiswal, S. (2021). Seaweed polysaccharides in active food packaging: A review of recent progress. *Trends in Food Science & Technology, 110*, 559-572. https://doi.org/10.1016/j.tifs.2021.02.022

Castejón, N., Parailloux, M., Izdebska, A., Lobinski, R., & Fernandes, S. C. M. (2021). Valorization of the red algae *Gelidium sesquipedale* by extracting a broad spectrum of minor compounds using green approaches. *Marine Drugs, 19*(10), 574. https://doi.org/10.3390/md19100574

Charrier, B., Rolland, E., Gupta, V., & Reddy, C. R. K. (2015). Production of genetically and developmentally modified seaweeds: Exploiting the potential of artificial selection techniques. *Frontiers in Plant Science, 6*, 27. https://doi.org/10.3389/fpls.2015.00127

Cherniienko, A., Lesyk, R., Zaprutko, L., & Pawełczyk, A. (2024). IR-EcoSpectra: Exploring sustainable *ex situ* and *in situ* FTIR applications for green chemical and pharmaceutical analysis. *Journal of Pharmaceutical Analysis, 14*(9), 100951. https://doi.org/10.1016/j.jpha.2024.02.005

Chevenier, A., Jouanneau, D., & Ficko-Blean, E. (2023). Carrageenan biosynthesis in red algae: A review. *The Cell Surface, 9*, 100097. https://doi.org/10.1016/j.tcsw.2023.100097

Chintalapati, S., Sang, N., Miyahara, M., Iwata, S., Nishida, K., & Miyako, E. (2025). Living drugs: A wonderful evolution for therapeutic applications. *Cell Biomaterials, 1*(10), 100193. https://doi.org/10.1016/j.celbio.2025.100193

Chiu, I., Ye, H., Aayush, K., & Yang, T. (2024). Intelligent food packaging for smart sensing of food safety. In X. Lu (Ed.), *Advances in food and nutrition research* (Vol. 111, pp. 215-259). Academic Press.

Ciancia, M., Matulewicz, M. C., & Tuvikene, R. (2020). Structural diversity in galactans from red seaweeds and its influence on rheological properties. *Frontiers in Plant Science, 11*, 559986. https://doi.org/10.3389/fpls.2020.559986

Cotas, J., Lourenço, M., Figueirinha, A., Valado, A., & Pereira, L. (2025). Seaweed polysaccharides: A rational approach for food safety studies. *Marine Drugs, 23*(11), 412. https://doi.org/10.3390/md23110412

Cotas, J., Tavares, J. O., Silva, R., & Pereira, L. (2024). Seaweed as a safe nutraceutical food: How to increase human welfare? *Nutraceuticals, 4*(3), 323-362. https://doi.org/10.3390/nutraceuticals4030020

Dhakal, S., Jüterbock, A. O., Lei, X., & Khanal, P. (2024). Application of the brown macroalga *Saccharina latissima* (Laminariales, Phaeophyceae) as a feed ingredient for livestock: A review. *Animal Nutrition, 19*, 153-165. https://doi.org/10.1016/j.aninu.2024.07.001

El-Beltagi, H. S., Mohamed, A. A., Mohamed, H. I., Ramadan, K. M. A., Barqawi, A. A., & Mansour, A. T. (2022). Phytochemical and potential properties of seaweeds and their recent applications: A review. *Marine Drugs, 20*(6), 342. https://doi.org/10.3390/md20060342

Eswar, I., Majumder, A., Raja Mohamed, S. H., Logesh, K., Shek Alavudeen, S. M. I., Hariprakash, M., & Sundarraj, D. K. (2025). Seaweed responses to ocean acidification: Global impacts on growth, biochemical composition, and CO_2 mitigation potential. *Discover Ocean, 2*(1), 19. https://doi.org/10.1007/s44289-025-00060-x

Faisal, S., Zaky, A., Wang, Q., Huang, J., & Abomohra, A. (2022). Integrated marine biogas: A promising approach towards sustainability. *Fermentation, 8*(10), 520. https://doi.org/10.3390/fermentation8100520

Falshaw, R., Bixler, H. J., & Johndro, K. (2003). Structure and performance of commercial κ-2 carrageenan extracts.

Part III. Structure analysis and performance in two dairy applications of extracts from the New Zealand red seaweed, *Gigartina atropurpurea*. *Food Hydrocolloids, 17*(2), 129-139. https://doi.org/10.1016/S0268-005X(02)00045-0

Farghali, M., Mohamed, I. M. A., Osman, A. I., & Rooney, D. W. (2023). Seaweed for climate mitigation, wastewater treatment, bioenergy, bioplastic, biochar, food, pharmaceuticals, and cosmetics: A review. *Environmental Chemistry Letters, 21*(1), 97-152. https://doi.org/10.1007/s10311-022-01520-y

Ferreira, A. R. V., Alves, V. D., & Coelhoso, I. M. (2016). Polysaccharide-based membranes in food packaging applications. *Membranes, 6*(2), 22. https://doi.org/10.3390/membranes6020022

Freitas, M. V., Pacheco, D., Cotas, J., Mouga, T., Afonso, C., & Pereira, L. (2022). Red seaweed pigments from a biotechnological perspective. *Phycology, 2*(1), 1-29. https://doi.org/10.3390/phycology2010001

Friedlander, M. (2007). Advances in cultivation of gelidiales. *Journal of Applied Phycology, 20*, 451-456. https://doi.org/10.1007/s10811-007-9285-1

Fu, Z., Li, S., Han, S., Shi, C., & Zhang, Y. (2022). Antibody drug conjugate: The "biological missile" for targeted cancer therapy. *Signal Transduction and Targeted Therapy, 7*(1), 93. https://doi.org/10.1038/s41392-022-00947-7

Gadzama, I. (2024). Red seaweed: A promising solution for sustainable ruminant production. *Medicon Agriculture & Environmental Sciences, 7*(6), 1-2.

García-Poza, S., Leandro, A., Cotas, C., Cotas, J., Marques, J. C., Pereira, L., & Gonçalves, A. M. M. (2020). The evolution road of seaweed aquaculture: Cultivation technologies and the Industry 4.0. *International Journal of Environmental Research and Public Health, 17*(18), 6528. https://doi.org/10.3390/ijerph17186528

Gomes-Dias, J. S., Romaní, A., Teixeira, J. A., & Rocha, C. M. R. (2020). Valorization of seaweed carbohydrates: Autohydrolysis as a selective and sustainable pretreatment. *ACS Sustainable Chemistry & Engineering, 8*(46), 17143-17153. https://doi.org/10.1021/acssuschemeng.0c05396

Gomez, L., Tiwari, B., & Garcia-Vaquero, M. (2020). Emerging extraction techniques: Microwave-assisted extraction. In M. D. Torres, S. Kraan, & H. Dominguez (Eds.), *Sustainable seaweed technologies* (pp. 207-224). Elsevier.

Gómez-Ordóñez, E., & Rupérez, P. (2011). FTIR-ATR spectroscopy as a tool for polysaccharide identification in edible brown and red seaweeds. *Food Hydrocolloids, 25*(6), 1514-1520. https://doi.org/10.1016/j.foodhyd.2011.02.009

González-Meza, G. M., Elizondo-Luevano, J. H., Cuellar-Bermudez, S. P., Sosa-Hernández, J. E., Iqbal, H. M. N., Melchor-Martínez, E. M., & Parra-Saldívar, R. (2023). New perspective for macroalgae-based animal feeding in the context of challenging sustainable food production. *Plants, 12*(20), 3609. https://doi.org/10.3390/plants12203609

Gupta, D., Lall, A., Kumar, S., Patil, T. D., & Gaikwad, K. K. (2024). Plant-based edible films and coatings for food-packaging applications: Recent advances, applications, and trends. *Sustainable Food Technology, 2*(5), 1428-1455. https://doi.org/10.1039/d4fb00110a

Hafting, J. T., Craigie, J. S., Stengel, D. B., Loureiro, R. R., Buschmann, A. H., Yarish, C., Edwards, M. D., & Critchley, A. T. (2015). Prospects and challenges for industrial production of seaweed bioactives. *Journal of Phycology, 51*(5), 821-837. https://doi.org/10.1111/jpy.12326

Hale, J., Gerhäuser, J., Gaukel, V., & Wefers, D. (2024). Commercially available carrageenans show broad variation in their structure, composition, and functionality. *European Food Research and Technology, 250*(12), 2989-3003. https://doi.org/10.1007/s00217-024-04605-w

Harichandan, S. (2025). Harnessing seaweed for biohydrogen production: An integrated ecological and energy framework. *International Journal of Hydrogen Energy, 136*, 1-10. https://doi.org/10.1016/j.ijhydene.2025.05.067

Heriyanto, H., Kustiningsih, I., & Sari, D. (2018). The effect of temperature and time of extraction on the quality of semi-refined carrageenan (SRC). *MATEC Web of Conferences, 154*, 01034. https://doi.org/10.1051/matecconf/201815401034

Hernández-Carmona, G., Freile-Pelegrín, Y., & Hernández-Garibay, E. (2013). Conventional and alternative technologies for the extraction of algal polysaccharides. In H. Dominguez (Ed.), *Functional ingredients from algae for foods and nutraceuticals* (pp. 475-516). Woodhead Publishing.

Herrero, M., Cifuentes, A., & Ibáñez, E. (2006). Sub- and supercritical fluid extraction of functional ingredients from natural sources: plants, food-by-products, algae and microalgae. *Food Chemistry, 98*(1), 136-148. https://doi.org/10.1016/j.foodchem.2005.05.058

Hsieh-Lo, M., Castillo, G., Ochoa-Becerra, M. A., & Mojica, L. (2019). Phycocyanin and phycoerythrin: Strategies to improve production yield and chemical stability. *Algal Research, 42*, 101600. https://doi.org/10.1016/j.algal.2019.101600

Holdt, S. L., & Kraan, S. (2011). Bioactive compounds in seaweed: Functional food applications and legislation.

Journal of Applied Phycology, 23(3), 543-597. https://doi.org/10.1007/s10811-010-9632-5
Hong, T., Yin, J.-Y., Nie, S.-P., & Xie, M.-Y. (2021). Applications of infrared spectroscopy in polysaccharide structural analysis: Progress, challenge and perspective. *Food Chemistry: X, 12*, 100168. https://doi.org/10.1016/j.fochx.2021.100168
Hurd, C. L. (2000). Water motion, marine macroalgal physiology, and production. *Journal of Phycology, 36*(3), 453-472. https://doi.org/10.1046/j.1529-8817.2000.99139.x
Hurd, C. (2017). Shaken and stirred: The fundamental role of water motion in resource acquisition and seaweed productivity. *Progress in Phycological Research, 4*(2), 73-81. http://dx.doi.org/10.1127/pip/2017/0072
Imeson, A. (2010). *Handbook of hydrocolloids* (2nd ed.). Woodhead Publishing.
Jönsson, M., Allahgholi, L., Sardari, R. R. R., Hreggviðsson, G. O., & Nordberg Karlsson, E. (2020). Extraction and modification of macroalgal polysaccharides for current and next-generation applications. *Molecules, 25*(4), 930. https://doi.org/10.3390/molecules25040930
Kadam, S. U., Tiwari, B. K., & O'Donnell, C. P. (2015). Extraction, structure and biofunctional activities of laminarin from brown algae. *International Journal of Food Science & Technology, 50*(1), 24-31. https://doi.org/10.1111/ijfs.12692
Khalid, S., Chaudhary, K., Amin, S., Raana, S., Zahid, M., Naeem, M., Mousavi Khaneghah, A., & Aadil, R. M. (2024). Recent advances in the implementation of ultrasound technology for the extraction of essential oils from terrestrial plant materials: A comprehensive review. *Ultrasonics Sonochemistry, 107*, 106914. https://doi.org/10.1016/j.ultsonch.2024.106914
Khalil, H. P. S. A., Lai, T. K., Tye, Y. Y., Rizal, S., Chong, E. W. N., Yap, S. W., Hamzah, A. A., Fazita, M. R. N., & Paridah, M. T. (2018). A review of extractions of seaweed hydrocolloids: Properties and applications. *Express Polymer Letters, 12*, 296-317. http://dx.doi.org/10.3144/expresspolymlett.2018.27
Khan, N., Sudhakar, K., & Mamat, R. (2024). Macroalgae farming for sustainable future: Navigating opportunities and driving innovation. *Heliyon, 10*(7), e28208. https://doi.org/10.1016/j.heliyon.2024.e28208
Kokkuvayil, R. B., Rhim, J.-W., & Roy, S. (2024). Recent progress of carrageenan-based composite films in active and intelligent food packaging applications. *Polymers, 16*(7), 1001. https://doi.org/10.3390/polym16071001
Kravchenko, A. O., Byankina Barabanova, A. O., Glazunov, V. P., Yakovleva, I. M., & Yermak, I. M. (2018). Seasonal variations in a polysaccharide composition of Far Eastern red seaweed *Ahnfeltiopsis flabelliformis* (Phyllophoraceae). *Journal of Applied Phycology, 30*(1), 535-545. https://doi.org/10.1007/s10811-017-1262-8
Kumar, A., Buia, M. C., Palumbo, A., Mohany, M., Wadaan, M. A. M., Hozzein, W. N., Beemster, G. T. S., & Abdelgawad, H. (2020). Ocean acidification affects biological activities of seaweeds: A case study of *Sargassum vulgare* from Ischia volcanic CO_2 vents. *Environmental Pollution, 259*, 113765. https://doi.org/10.1016/j.envpol.2019.113765
Lafeuille, B., Tamigneaux, É., Berger, K., Provencher, V., & Beaulieu, L. (2023). Impact of harvest month and drying process on the nutritional and bioactive properties of wild Palmaria palmata from Atlantic Canada. *Marine Drugs, 21*(7), 392. https://doi.org/10.3390/md21070392
Lalegerie, F., Gager, L., Stiger-Pouvreau, V., & Connan, S. (2020). The stressful life of red and brown seaweeds on the temperate intertidal zone: Effect of abiotic and biotic parameters on the physiology of macroalgae and content variability of particular metabolites. In N. Bourgougnon (Ed.), *Advances in botanical research* (Vol. 95, pp. 247-287). Academic Press.
Leandro, A., Pacheco, D., Cotas, J., Marques, J. C., Pereira, L., & Gonçalves, A. M. M. (2020). Seaweed's bioactive candidate compounds to food industry and global food security. *Life, 10*(8), 140. https://doi.org/10.3390/life10080140
Lee, S.-Y., Ahn, J. W., Hwang, H., & Lee, S.-B. (2011). Seaweed biomass resources in Korea. *KSBB Journal, 26*(4), 267-276. https://doi.org/10.7841/ksbbj.2011.26.4.267
Lee, W.-K., Lim, Y.-Y., Leow, A. T.-C., Namasivayam, P., Abdullah, J. O., & Ho, C.-L. (2017). Factors affecting yield and gelling properties of agar. *Journal of Applied Phycology, 29*(3), 1527-1540. https://doi.org/10.1007/s10811-016-1009-y
Lee, M.-C., Yeh, H.-Y., Jhang, F.-J., Lee, P.-T., Lin, Y.-K., & Nan, F.-H. (2021). Enhancing growth, phycoerythrin production, and pigment composition in the red alga *Colaconema* sp. through optimal environmental conditions in an indoor system. *Bioresource Technology, 333*, 125199. https://doi.org/10.1016/j.biortech.2021.125199
Liu, F., Duan, G., & Yang, H. (2023). Recent advances in exploiting carrageenans as a versatile functional material for promising biomedical applications. *International Journal of Biological Macromolecules, 235*, 123787. https://doi.org/10.1016/j.ijbiomac.2023.123787

Liu, J., Zhan, X., Wan, J., Wang, Y., & Wang, C. (2015). Review for carrageenan-based pharmaceutical biomaterials: Favourable physical features *versus* adverse biological effects. *Carbohydrate Polymers, 121*, 27-36. https://doi.org/10.1016/j.carbpol.2014.11.063

Liu, Y., Jiang, Z., Cottrell, R. S., Tlusty, M. F., Fitzsimmons, K., & Cao, L. (2025). Unstable supply and future shortages of wild forage fish heighten risks to global fed aquaculture production. *Nature Food, 6*(11), 1068-1078. https://doi.org/10.1038/s43016-025-01254-4

Lomartire, S., & Gonçalves, A. M. M. (2022a). An overview of potential seaweed-derived bioactive compounds for pharmaceutical applications. *Marine Drugs, 20*(2), 141. https://doi.org/10.3390/md20020141

Lomartire, S., & Gonçalves, A. M. M. (2022b). Novel technologies for seaweed polysaccharides extraction and their use in food with therapeutically applications—A review. *Foods, 11*(17), 2654. https://doi.org/10.3390/foods11172654

Lomartire, S., & Gonçalves, A. M. M. (2023). Algal phycocolloids: Bioactivities and pharmaceutical applications. *Marine Drugs, 21*(7), 384. https://doi.org/10.3390/md21070384

Lopes, C., Obando, J. M. C., Santos, T. C. d., Cavalcanti, D. N., & Teixeira, V. L. (2024). Abiotic factors modulating metabolite composition in brown algae (Phaeophyceae): Ecological impacts and opportunities for bioprospecting of bioactive compounds. *Marine Drugs, 22*(12), 544. https://doi.org/10.3390/md22120544

López-Hortas, L., Flórez-Fernández, N., Torres, M. D., Ferreira-Anta, T., Casas, M. P., Balboa, E. M., Falque, E., & Domínguez, H. (2021). Applying seaweed compounds in cosmetics, cosmeceuticals and nutricosmetics. *Marine Drugs, 19*(10), 552. https://doi.org/10.3390/md19100552

Lourenço-Lopes, C., Garcia-Oliveira, P., Carpena, M., Fraga-Corral, M., Jimenez-Lopez, C., Pereira, A. G., Prieto, M. A., & Simal-Gandara, J. (2020). Scientific approaches on extraction, purification and stability for the commercialization of fucoxanthin recovered from brown algae. *Foods, 9*(8), 1113. https://doi.org/10.3390/foods9081113

Macrae, O. C., & Vickers, C. J. (2024). The significance of microbiota in New Zealand seaweed aquaculture. *New Zealand Journal of Marine and Freshwater Research, 59*(3), 509-536. https://doi.org/10.1080/00288330.2024.2373881

Makkar, H. P. S., Tran, G., Heuzé, V., Giger-Reverdin, S., Lessire, M., Lebas, F., & Ankers, P. (2016). Seaweeds for livestock diets: A review. *Animal Feed Science and Technology, 212*, 1-17. https://doi.org/10.1016/j.anifeedsci.2015.09.018

Malik, S., Chaudhary, K., Malik, A., Punia, H., Sewhag, M., Berkesia, N., Nagora, M., Kalia, S., Malik, K., Kumar, D., Kumar, P., Kamboj, E., Ahlawat, V., Kumar, A., & Boora, K. (2023). Superabsorbent polymers as a soil amendment for increasing agriculture production with reducing water losses under water stress condition. *Polymers, 15*(1), 161. https://doi.org/10.3390/polym15010161

Mamede, M., Cotas, J., Bahcevandziev, K., & Pereira, L. (2023). Seaweed polysaccharides in agriculture: A next step towards sustainability. *Applied Sciences, 13*(11), 6594. https://doi.org/10.3390/app13116594

Matos, C., Moreira, M. M., Loureiro, H., & Gomes, L. R. (2024). Demystifying E407 and E407a additives (carrageenans) through their gastronomic alchemy: A contribution to increase consumer sovereignty. *Gastronomy, 2*(4), 191-214. https://doi.org/10.3390/gastronomy2040014

Matos, G. S., Pereira, S. G., Genisheva, Z. A., Gomes, A. M., Teixeira, J. A., & Rocha, C. M. R. (2021). Advances in extraction methods to recover added-value compounds from seaweeds: Sustainability and functionality. *Foods, 10*(3), 516. https://doi.org/10.3390/foods10030516

McHugh, D. J. (2003). *A guide to the seaweed industry*. FAO.

Mendes, M. (2023). *Novel extraction methods, yield, structural and rheological properties of carrageenan from novel Kappaphycus alvarezii strains from the Philippines* [Master's thesis, Universidade de Coimbra]. https://estudogeral.uc.pt/handle/10316/110322?locale=en

Mendes, M., Fortunato, D., Cotas, J., Pacheco, D., Morais, T., & Pereira, L. (2022). Agar content of estuarine seaweed *Gracilaria* using different cultivation methods. *Applied Food Research, 2*(2), 100209. https://doi.org/10.1016/j.afres.2022.100209

Mendes, M., Cotas, J., Gutiérrez, I. B., Gonçalves, A. M. M., Critchley, A. T., Hinaloc, L. A. R., Roleda, M. Y., & Pereira, L. (2024). Advanced extraction techniques and physicochemical properties of carrageenan from a novel *Kappaphycus alvarezii* cultivar. *Marine Drugs, 22*(11), 491. https://doi.org/10.3390/md22110491

Mendes, M., Cotas, J., Pacheco, D., Ihle, K., Hillinger, A., Cascais, M., Marques, J. C., Pereira, L., & Gonçalves, A. M. M. (2024). Red seaweed (Rhodophyta) phycocolloids: A road from the species to the industry application. *Marine Drugs, 22*(10), 432. https://doi.org/10.3390/md22100432

Min, B. R., Parker, D., Brauer, D., Waldrip, H., Lockard, C., Hales, K., Akbay, A., & Augyte, S. (2021). The role of seaweed as a potential dietary supplementation for enteric methane mitigation in ruminants: Challenges and opportunities. *Animal Nutrition, 7*(4), 1371-1387. https://doi.org/10.1016/j.aninu.2021.10.003

Mohamed, M. A., Jaafar, J., Ismail, A. F., Othman, M. H. D., & Rahman, M. A. (2017). Fourier transform infrared (FTIR) spectroscopy. In N. Hilal, A. F. Ismail, T. Matsuura, & D. Oatley-Radcliffe (Eds.), *Membrane characterization* (pp. 3-29). Elsevier.

Monteiro, P., Cotas, J., Pacheco, D., Figueirinha, A., da Silva, G. J., Pereira, L., & Gonçalves, A. M. M. (2022). Seaweed as food: How to guarantee their quality? In A. Ranga Rao & G. A. Ravishankar (Eds.), *Sustainable global resources of seaweeds volume 2: Food, pharmaceutical and health applications* (pp. 309-321). Springer.

Morais, S. (2013). Ultrasonic- and microwave-assisted extraction and modification of algal components. In H. Domínguez (Ed.), *Functional ingredients from algae for foods and nutraceuticals* (pp. 585-605). Woodhead Publishing.

Morais, T., Inácio, A., Coutinho, T., Ministro, M., Cotas, J., Pereira, L., & Bahcevandziev, K. (2020). Seaweed potential in the animal feed: A review. *Journal of Marine Science and Engineering, 8*(8), 559. https://doi.org/10.3390/jmse8080559

Moses, J., Anandhakumar, R., & Shanmugam, M. (2015). Effect of alkaline treatment on the sulfate content and quality of semi-refined carrageenan prepared from seaweed *Kappaphycus alvarezii* Doty (Doty) farmed in Indian waters. *African Journal of Biotechnology, 14*(18), 1584-1589. https://doi.org/10.5897/AJB2014.14203

Mzibra, A., Aasfar, A., El Arroussi, H., Khouloud, M., Dhiba, D., Kadmiri, I. M., & Bamouh, A. (2018). Polysaccharides extracted from Moroccan seaweed: A promising source of tomato plant growth promoters. *Journal of Applied Phycology, 30*(5), 2953-2962. https://doi.org/10.1007/s10811-018-1421-6

Nagahawatta, D. P., Liyanage, N. M., Jayawardena, T. U., Yang, F., Jayawardena, H. H. A. C. K., Kurera, M. J. M. S., Wang, F., Fu, X., & Jeon, Y.-J. (2023). Functions and values of sulfated polysaccharides from seaweed. *Algae, 38*(4), 217-240. https://doi.org/10.4490/algae.2023.38.12.1

Naghera, N., Parmar, R., Dudhagara, D., Gamit, S., Nandaniya, N., Chaun, D., Kothari, R., N, H., & Vyas, S. (2026). Colloidal and structural perspectives on seaweed-derived bioactives: Extraction techniques and emerging applications. *Food Hydrocolloids for Health, 9*, 100260. https://doi.org/10.1016/j.fhfh.2025.100260

Necas, J., & Bartosikova, L. (2013). Carrageenan: A review. *Veterinarni Medicina, 58*(4), 187-205. https://doi.org/10.17221/6758-VETMED

Nesic, A., Meseldzija, S., Benavides, S., Figueroa, F. A., & Cabrera-Barjas, G. (2024). Seaweed as a valuable and sustainable resource for food packaging materials. *Foods, 13*(19), 3212. https://doi.org/10.3390/foods13193212

Nigam, S., Singh, R., Bhardwaj, S. K., Sami, R., Nikolova, M. P., Chavali, M., & Sinha, S. (2022). Perspective on the therapeutic applications of algal polysaccharides. *Journal of Polymers and the Environment, 30*(3), 785-809. https://doi.org/10.1007/s10924-021-02231-1

Noelia, F., García-Mendoza, M. J., Rodríguez, D., Ferreira, E., Domínguez, H., & Fernández, M. (2017). Algae polysaccharides' chemical characterization and their role in the inflammatory process. *Current Medicinal Chemistry, 24*(2), 149-175. http://dx.doi.org/10.2174/0929867323666161028160416

Novoa, A. F., Vrouwenvelder, J. S., & Fortunato, L. (2021). Membrane fouling in algal separation processes: A review of influencing factors and mechanisms. *Frontiers in Chemical Engineering, 3*, 687422. https://doi.org/10.3389/fceng.2021.687422

Onyeaka, H. N., & Nwabor, O. F. (2022). Natural active components in smart food packaging system. In H. N. Onyeaka & O. F. Nwabor (Eds.), *Food preservation and safety of natural products* (pp. 119-131). Academic Press.

Otero, P., Carpena, M., Garcia-Oliveira, P., Echave, J., Soria-Lopez, A., Garcia-Perez, P., Fraga-Corral, M., Cao, H., Nie, S., Xiao, J., Simal-Gandara, J., & Prieto, M. A. (2023). Seaweed polysaccharides: Emerging extraction technologies, chemical modifications and bioactive properties. *Critical Reviews in Food Science and Nutrition, 63*(13), 1901-1929. https://doi.org/10.1080/10408398.2021.1969534

Pacheco, D., Cotas, J., Rocha, C. P., Araújo, G. S., Figueirinha, A., Gonçalves, A. M. M., Bahcevandziev, K., & Pereira, L. (2021). Seaweeds' carbohydrate polymers as plant growth promoters. *Carbohydrate Polymers: Technology and Applications, 2*, 100097. https://doi.org/10.1016/j.carpta.2021.100097

Pacheco-Quito, E.-M., Ruiz-Caro, R., & Veiga, M.-D. (2020). Carrageenan: Drug delivery systems and other biomedical applications. *Marine Drugs, 18*(11), 583. https://doi.org/10.3390/md18110583

Pandya, Y., Bakshi, M., & Sharma, A. (2022). Agar-agar extraction, structural properties and applications: A review. *The Pharma Journal, 11*(6S), 1151-1157.

Pangestuti, R., & Kim, S.-K. (2015). An overview of phycocolloids: The principal commercial seaweed extracts. In S.-K. Kim & K. Chojnacka (Eds.), *Marine algae extracts* (pp. 319-330). Wiley.

Pardilhó, S., Cotas, J., Pacheco, D., Gonçalves, A. M. M., Bahcevandziev, K., Pereira, L., Figueirinha, A., & Dias, J. M. (2023). Valorisation of marine macroalgae waste using a cascade biorefinery approach: Exploratory study. *Journal*

of Cleaner Production, 385, 135672. https://doi.org/10.1016/j.jclepro.2022.135672
Pardilhó, S., Cotas, J., Pereira, L., Oliveira, M. B., & Dias, J. M. (2022). Marine macroalgae in a circular economy context: A comprehensive analysis focused on residual biomass. *Biotechnology Advances, 60*, 107987. https://doi.org/10.1016/j.biotechadv.2022.107987
Patra, J. K., Das, G., Fraceto, L. F., Campos, E. V. R., Rodriguez-Torres, M. d. P., Acosta-Torres, L. S., Diaz-Torres, L. A., Grillo, R., Swamy, M. K., Sharma, S., Habtemariam, S., & Shin, H.-S. (2018). Nano based drug delivery systems: Recent developments and future prospects. *Journal of Nanobiotechnology, 16*(1), 71. https://doi.org/10.1186/s12951-018-0392-8
Pasquini, V., Biancacci, C., Milia, M., Moccia, D., Solari, P., Angioni, A., & Addis, P. (2024). Effects of different culture media on growth, composition, quality and palatability of the green algae *Ulva* sp. cultivated in cylindrical photobioreactors. *Algal Research, 84*, 103749. https://doi.org/10.1016/j.algal.2024.103749
Pereira, L. (2021). Macroalgae. *Encyclopedia, 1*(1), 177-188. https://doi.org/10.3390/encyclopedia1010017
Pereira, L. (2011). A review of the nutrient composition of selected edible seaweeds. In V. H. Pomin (Ed.), *Seaweed: Ecology, nutrient composition and medicinal uses* (pp. 15-47). Nova Science Publishers.
Pereira, L. (2018a). *Therapeutic and nutritional uses of algae*. CRC Press. https://doi.org/10.1201/9781315152844
Pereira, L. (2018b). Seaweeds as source of bioactive substances and skin care therapy—Cosmeceuticals, algotherapy, and thalassotherapy. *Cosmetics, 5*(4), 68. https://doi.org/10.3390/cosmetics5040068
Pereira, L. (2023). Atlantic algae as food and their extracts. *Exploratory Foods and Foodomics, 1*(1), 15-31. https://doi.org/10.37349/eff.2023.00003
Pereira, L. (2024). Non-indigenous seaweeds in the Iberian Peninsula, Macaronesia Islands (Madeira, Azores, Canary Islands) and Balearic Islands: Biodiversity, ecological impact, invasion dynamics, and potential industrial applications. *Algal Research, 78*, 103407. https://doi.org/10.1016/j.algal.2024.103407
Pereira, L. (2025a). *Industrial applications of red macroalgae phycocolloids*. Preprints. https://doi.org/10.20944/preprints202510.2134.v1
Pereira, L. (2025b). Illustrated guide to the main macroalgae of the Portuguese continental Atlantic coast. *Encyclopedia, 5*(4), 176. https://doi.org/10.3390/encyclopedia5040176
Pereira, L., & Critchley, A. T. (2020). The COVID-19 novel coronavirus pandemic 2020: Seaweeds to the rescue? Why does substantial, supporting research about the antiviral properties of seaweed polysaccharides seem to go unrecognized by the pharmaceutical community in these desperate times? *Journal of Applied Phycology, 32*(3), 1875-1877. https://doi.org/10.1007/s10811-020-02143-y
Pereira, L., & Valado, A. (2023). Harnessing the power of seaweed: Unveiling the potential of marine algae in drug discovery. *Exploratory Drug Science, 1*, 475-496. https://doi.org/10.37349/eds.2023.00032
Pereira, L., & Cotas, J. (2024). Seaweed: A sustainable solution for greening drug manufacturing in the pursuit of sustainable healthcare. *Exploratory Drug Science, 2*(1), 50-84. https://doi.org/10.37349/eds.2024.00036
Pereira, L., Amado, A. M., Critchley, A. T., van de Velde, F., & Ribeiro-Claro, P. J. A. (2009). Identification of selected seaweed polysaccharides (phycocolloids) by vibrational spectroscopy (FTIR-ATR and FT-Raman). *Food Hydrocolloids, 23*(7), 1903-1909. https://doi.org/10.1016/j.foodhyd.2008.11.014
Pomin, V. H. (2010). Structural and functional insights into sulfated galactans: A systematic review. *Glycoconjugate Journal, 27*(1), 1-12. https://doi.org/10.1007/s10719-009-9251-z
Ptak, S. H., Hjuler, A. L., Ditlevsen, S. I., Fretté, X., Errico, M., & Christensen, K. V. (2021). The effect of seasonality and geographic location on sulphated polysaccharides from brown algae. *Aquaculture Research, 52*(12), 6235-6243. https://doi.org/10.1111/are.15485
Qiu, S.-M., Aweya, J. J., Liu, X., Liu, Y., Tang, S., Zhang, W., & Cheong, K.-L. (2022). Bioactive polysaccharides from red seaweed as potent food supplements: A systematic review of their extraction, purification, and biological activities. *Carbohydrate Polymers, 275*, 118696. https://doi.org/10.1016/j.carbpol.2021.118696
Rajabzadeh, N., Fathi, E., & Farahzadi, R. (2019). Stem cell-based regenerative medicine. *Stem Cell Investigation, 6*, 19. https://doi.org/10.21037/sci.2019.06.04
Ramachandra, T. V., & Hebbale, D. (2020). Bioethanol from macroalgae: Prospects and challenges. *Renewable and Sustainable Energy Reviews, 117*, 109479. https://doi.org/10.1016/j.rser.2019.109479
Rang, H. P., LeVine, H., & Hill, R. (2013). Therapeutic modalities. In R. G. Hill & H. P. Rang (Eds.), *Drug discovery and development* (2nd ed., pp. 33-40). Churchill Livingstone.
Rashedy, S. H., Abd El Hafez, M. S. M., Dar, M. A., Cotas, J., & Pereira, L. (2021). Evaluation and characterization of alginate extracted from brown seaweed collected in the Red Sea. *Applied Sciences, 11*(14), 6290. https://doi.org/10.3390/app11146290

Rauf, A., Ahmad, Z., Naz, S., & Hemeg, H. A. (2024). Introduction to drug repurposing: Exploring new applications for existing drugs. In A. Rauf (Ed.), *Drug development and safety*. IntechOpen.

Rebours, C., Marinho-Soriano, E., Zertuche-González, J. A., Hayashi, L., Vásquez, J. A., Kradolfer, P., Soriano, G., Ugarte, R., Abreu, M. H., Bay-Larsen, I., Hovelsrud, G., Rødven, R., & Robledo, D. (2014). Seaweeds: An opportunity for wealth and sustainable livelihood for coastal communities. *Journal of Applied Phycology, 26*(5), 1939-1951. https://doi.org/10.1007/s10811-014-0304-8

Rhein-Knudsen, N., Ale, M. T., Ajalloueian, F., Yu, L., & Meyer, A. S. (2017). Rheological properties of agar and carrageenan from Ghanaian red seaweeds. *Food Hydrocolloids, 63*, 50-58. https://doi.org/10.1016/j.foodhyd.2016.08.023

Roleda, M. J., & Hurd, C. L. (2019). Seaweed nutrient physiology: Application of concepts to aquaculture and bioremediation. *Phycologia, 58*, 552-562. https://doi.org/10.1080/00318884.2019.1622920

Rupert, R., Rodrigues, K. F., Thien, V. Y., & Yong, W. T. L. (2022). Carrageenan from *Kappaphycus alvarezii* (Rhodophyta, Solieriaceae): Metabolism, structure, production, and application. *Frontiers in Plant Science, 13*, 859635. https://doi.org/10.3389/fpls.2022.859635

Ruscoe, I. M., Jones, C. M., Jones, P. L., & Caley, P. (2005). The effects of various binders and moisture content on pellet stability of research diets for freshwater crayfish. *Aquaculture Nutrition, 11*(2), 87-93. https://doi.org/10.1111/j.1365-2095.2004.00324.x

Samoraj, M., Çalış, D., Trzaska, K., Mironiuk, M., & Chojnacka, K. (2024). Advancements in algal biorefineries for sustainable agriculture: Biofuels, high-value products, and environmental solutions. *Biocatalysis and Agricultural Biotechnology, 58*, 103224. https://doi.org/10.1016/j.bcab.2024.103224

Sánchez-Astráin, B., Sainz-Villegas, S., Guinda, X., Fernández de la Hoz, C., & Juanes, J. A. (2024). Assessment of the growth capacity of newly sprouted shoots of *Gelidium corneum* (Florideophyceae, Rhodophyta) through field-based experiments. *Marine Environmental Research, 202*, 106781. https://doi.org/10.1016/j.marenvres.2024.106781

Shafie, M. H., Kamal, M. L., Zulkiflee, F. F., Hasan, S., Uyup, N. H., Abdullah, S., Mohamed Hussin, N. A., Tan, Y. C., & Zafarina, Z. (2022). Application of carrageenan extract from red seaweed (Rhodophyta) in cosmetic products: A review. *Journal of the Indian Chemical Society, 99*(9), 100613. https://doi.org/10.1016/j.jics.2022.100613

Sharma, A., Dubey, S., Singh, K., Mittal, R., Quille, P., & Rajauria, G. (2025). Innovative processing and industrial applications of seaweed. *Phycology, 5*(1), 10. https://doi.org/10.3390/phycology5010010

Shi, L. (2016). Bioactivities, isolation and purification methods of polysaccharides from natural products: A review. *International Journal of Biological Macromolecules, 92*, 37-48. https://doi.org/10.1016/j.ijbiomac.2016.06.100

Shukla, P. S., Borza, T., Critchley, A. T., & Prithiviraj, B. (2016). Carrageenans from red seaweeds as promoters of growth and elicitors of defense response in plants. *Frontiers in Marine Science, 3*, 81. https://doi.org/10.3389/fmars.2016.00081

Singh, R. P., & Reddy, C. R. K. (2014). Seaweed-microbial interactions: Key functions of seaweed-associated bacteria. *FEMS Microbiology Ecology, 88*(2), 213-230. https://doi.org/10.1111/1574-6941.12297

Singh, S. P., & Singh, P. (2015). Effect of temperature and light on the growth of algae species: A review. *Renewable and Sustainable Energy Reviews, 50*, 431-444. https://doi.org/10.1016/j.rser.2015.05.024

Sivashankari, P. R., & Prabaharan, M. (2020). Three-dimensional porous scaffolds based on agarose/chitosan/graphene oxide composite for tissue engineering. *International Journal of Biological Macromolecules, 146*, 222-231. https://doi.org/10.1016/j.ijbiomac.2019.12.219

Sudha, P. N., Aisverya, S., Nithya, R., & Vijayalakshmi, K. (2014). Industrial applications of marine carbohydrates. In S.-K. Kim (Ed.), *Advances in food and nutrition research* (Vol. 73, pp. 145-181). Academic Press. https://doi.org/10.1016/B978-0-12-800268-1.00008-1

Sugumaran, R., Padam, B. S., Yong, W. T. L., Saallah, S., Ahmed, K., & Yusof, N. A. (2022). A retrospective review of global commercial seaweed production—Current challenges, biosecurity and mitigation measures and prospects. *International Journal of Environmental Research and Public Health, 19*(12), 7087. https://doi.org/10.3390/ijerph19127087

Sultana, F., Wahab, M. A., Nahiduzzaman, M., Mohiuddin, M., Iqbal, M. Z., Shakil, A., Mamun, A.-A., Khan, M. S. R., Wong, L., & Asaduzzaman, M. (2023). Seaweed farming for food and nutritional security, climate change mitigation and adaptation, and women empowerment: A review. *Aquaculture and Fisheries, 8*(5), 463-480. https://doi.org/10.1016/j.aaf.2022.09.001

Sumana, S. L., Sidibe, G., Elshafey, A. E., Habinshuti, D., Mattia, A., Massaquoi, J., Tarawallie, S., Abdullateef, M. M., Shuaibu, A., Mabey, P. T., Mansaray, A., Yang, X., Jiang, R., Meinday, A. K., Osei, S. A., Sankoh, J. S., Conteh, A. B., Bah, A. S., Islam, M. M., ... Zhang, J. (2026). Seaweed as a functional feed additive in aquaculture: Efficacy, safety,

and fish species-specific optimization. *Algal Research, 94*, 104525. https://doi.org/10.1016/j.algal.2026.104525
Tanna, B., & Mishra, A. (2019). Nutraceutical potential of seaweed polysaccharides: Structure, bioactivity, safety, and toxicity. *Comprehensive Reviews in Food Science and Food Safety, 18*(3), 817-831. https://doi.org/10.1111/1541-4337.12441
Tarman, K., Sadi, U., Santoso, J., & Hardjito, L. (2020). Carrageenan and its enzymatic extraction. In S.-K. Kim (Ed.), *Encyclopedia of marine biotechnology* (pp. 147-159). Wiley.
Tee, M. Z., Yong, Y. S., Rodrigues, K. F., & Yong, W. T. L. (2015). Growth rate analysis and protein identification of *Kappaphycus alvarezii* (Rhodophyta, Gigartinales) under pH induced stress culture. *Aquaculture Reports, 2*, 112-116. https://doi.org/10.1016/j.aqrep.2015.09.001
Torres, M. D., Flórez-Fernández, N., & Domínguez, H. (2019). Integral utilization of red seaweed for bioactive production. *Marine Drugs, 17*(6), 314. https://doi.org/10.3390/md17060314
Troell, M., Joyce, A., Chopin, T., Neori, A., Buschmann, A. H., & Fang, J.-G. (2009). Ecological engineering in aquaculture: Potential for integrated multi-trophic aquaculture (IMTA) in marine offshore systems. *Aquaculture, 297*(1-4), 1-9. https://doi.org/10.1016/j.aquaculture.2009.09.010
Udo, T., Mummaleti, G., Mohan, A., Singh, R. K., & Kong, F. (2023). Current and emerging applications of carrageenan in the food industry. *Food Research International, 173*, 113369. https://doi.org/10.1016/j.foodres.2023.113369
Usman, M., Nakagawa, M., & Cheng, S. (2023). Emerging trends in green extraction techniques for bioactive natural products. *Processes, 11*(12), 3444. https://doi.org/10.3390/pr11123444
Vandanjon, L., Burlot, A.-S., Zamanileha, E. F., Douzenel, P., Ravelonandro, P. H., Bourgougnon, N., & Bedoux, G. (2023). The use of FTIR spectroscopy as a tool for the seasonal variation analysis and for the quality control of polysaccharides from seaweeds. *Marine Drugs, 21*(9), 482. https://doi.org/10.3390/md21090482
Véliz, K., Chandía, N., Rivadeneira, M., & Thiel, M. (2017). Seasonal variation of carrageenans from *Chondracanthus chamissoi* with a review of variation in the carrageenan contents produced by Gigartinales. *Journal of Applied Phycology, 29*, 3139-3150. https://doi.org/10.1007/s10811-017-1203-6
Venkatesan, J., Lowe, B., Anil, S., Manivasagan, P., Kheraif, A. A. A., Kang, K.-H., & Kim, S.-K. (2015). Seaweed polysaccharides and their potential biomedical applications. *Starch-Stärke, 67*(5-6), 381-390. https://doi.org/10.1002/star.201400127
Wanapat, M., Prachumchai, R., Dagaew, G., Matra, M., Phupaboon, S., Sommai, S., & Suriyapha, C. (2024). Potential use of seaweed as a dietary supplement to mitigate enteric methane emission in ruminants. *Science of the Total Environment, 931*, 173015. https://doi.org/10.1016/j.scitotenv.2024.173015
Wang, T., Shi, W., Mao, Z., Xie, W., & Wan, G. (2025). Neuroprotective mechanisms of red algae-derived bioactive compounds in Alzheimer's disease: An overview of novel insights. *Marine Drugs, 23*(7), 274. https://doi.org/10.3390/md23070274
Waseem, M., Khan, M. U., Majeed, Y., Ntsefong, G. N., Kirichenko, I., Klopova, A., Trushov, P., & Lodygin, A. (2023). Seaweed-based films for sustainable food packaging: Properties, incorporation of essential oils, applications, and future directions. *Potravinarstvo Slovak Journal of Food Sciences, 17*, 899-917. https://doi.org/10.5219/1908
Wijesinghe, W. A. J. P., & Jeon, Y.-J. (2012). Enzyme-assistant extraction (EAE) of bioactive components: A useful approach for recovery of industrially important metabolites from seaweeds: A review. *Fitoterapia, 83*(1), 6-12. https://doi.org/10.1016/j.fitote.2011.10.016
Wu, C., Zhao, J., Hu, F., Zheng, Y., Yang, H., Pan, S., Shi, S., Chen, X., & Wang, S. (2018). Design of injectable agar-based composite hydrogel for multi-mode tumor therapy. *Carbohydrate Polymers, 180*, 112-121. https://doi.org/10.1016/j.carbpol.2017.10.024
Xiao, Q., Wang, X., Zhang, J., Zhang, Y., Chen, J., Chen, F., & Xiao, A. (2021). Pretreatment techniques and green extraction technologies for agar from *Gracilaria lemaneiformis*. *Marine Drugs, 19*(11), 617. https://doi.org/10.3390/md19110617
Xie, C., Lee, Z. J., Ye, S., Barrow, C. J., Dunshea, F. R., & Suleria, H. A. R. (2024). A review on seaweeds and seaweed-derived polysaccharides: Nutrition, chemistry, bioactivities, and applications. *Food Reviews International, 40*(5), 1312-1347. https://doi.org/10.1080/87559129.2023.2212055
Younes, M., Aggett, P., Aguilar, F., Crebelli, R., Filipič, M., Frutos, M. J., Galtier, P., Gott, D., Gundert-Remy, U., Lambré, C., Leblanc, J.-C., Lillegaard, I. T., Moldeus, P., Mortensen, A., Oskarsson, A., Stankovic, I., Tobback, P., Waalkens-Berendsen, I., Wright, M., … Wolfle, D. (2018). Re-evaluation of carrageenan (E 407) and processed *Eucheuma* seaweed (E 407a) as food additives. *EFSA Journal, 16*(4), e05238. https://doi.org/10.2903/j.efsa.2018.5238
Zhang, L., Liao, W., Huang, Y., Wen, Y., Chu, Y., & Zhao, C. (2022). Global seaweed farming and processing in the past

20 years. *Food Production, Processing and Nutrition, 4*(1), 23. https://doi.org/10.1186/s43014-022-00103-2
Zhao, Y., Bourgougnon, N., Lanoisellé, J.-L., & Lendormi, T. (2022). Biofuel production from seaweeds: A comprehensive review. *Energies, 15*(24), 9395. https://doi.org/10.3390/en15249395
Zhong, H., Gao, X., Cheng, C., Liu, C., Wang, Q., & Han, X. (2020). The structural characteristics of seaweed polysaccharides and their application in gel drug delivery systems. *Marine Drugs, 18*(12), 658. https://doi.org/10.3390/md18120658
Zhu, X., Healy, L., Zhang, Z., Maguire, J., Sun, D.-W., & Tiwari, B. K. (2021). Novel postharvest processing strategies for value-added applications of marine algae. *Journal of the Science of Food and Agriculture, 101*(11), 4444-4455. https://doi.org/10.1002/jsfa.11166