

RSC Chemical Biology

rsc.li/rsc-chembio



ISSN 2633-0679

REVIEW ARTICLE

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frontier of chemical synthesis



Cite this: *RSC Chem. Biol.*, 2025, 6, 1195

Exploring marine glycans: structure, function, and the frontier of chemical synthesis

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Marine glycans are structurally diverse biomolecules that play pivotal roles in oceanic carbon cycling by regulating microbial metabolism, accelerating organic matter turnover, and contribute to carbon sequestration. Glycans originating from marine organisms exhibit a wide range of bioactivities and applications in medicine, biotechnology, cosmetics, food and agriculture. The structural complexity of glycans poses significant challenges in understanding their functions, as traditional purification and characterization methods are often hindered by their inherent heterogeneity. To overcome these challenges, enzymatic extraction using glycoside hydrolases and carbohydrate-active enzymes (CAZymes) enables the selective recovery of native glycans, while automated glycan assembly (AGA) provides a robust approach for the rapid and reproducible synthesis of structurally defined glycans. Subjecting synthetic glycans to enzymatic degradation enables researchers to explore the inverse relationship between glycan complexity and microbial degradation, suggesting that algae can generate complex glycans at a rate exceeding bacterial decomposition, thereby reinforcing carbon storage. Here, we present a comprehensive overview of marine glycan sources and their structural diversity. We highlight the importance of employing two complementary methods, enzymatic extraction as a critical tool for glycan identification and AGA as an advanced synthetic platform, to build a refined framework for elucidating the ecological role and industrial potential of marine glycans.

Received 15th April 2025,
Accepted 4th June 2025

DOI: 10.1039/d5cb00090d

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1. Introduction

The ocean fixes approximately 50 gigatons of carbon each year, making it the Earth's most important carbon reservoir.¹ This immense carbon storage is regulated by the marine carbon cycle, a crucial process that maintains the global carbon balance. Central to this cycle are glycans, or complex polysaccharides that fuel carbon fixation and transfer. Microscopic planktonic algae, such as diatoms, capture carbon dioxide from

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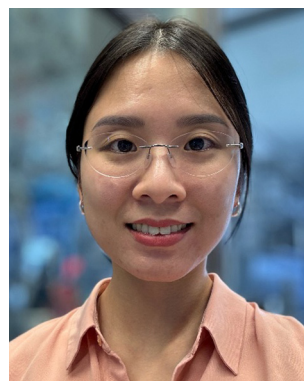
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the atmosphere at the ocean's surface and convert it into organic matter in the form of glycans.^{2,3} These glycans provide structural integrity to the algal cell walls^{4,5} and are subsequently circulated through the marine food web as organisms consume algae and other plankton. When marine organisms die, their remains form sinking particles that release glycans into the environment. While these glycans are typically degraded by deep-sea microbes, many are resistant to decomposition and remain sequestered in the ocean floor for up to centuries.^{6,7}

Beyond their ecological importance, marine glycans have diverse applications across various industries (Table 1). The therapeutic potential of marine glycans has been explored for anti-cancer⁸ and anti-microbial⁹ activity as well as for drug delivery enhancement.¹⁰ In biotechnology and bioengineering, marine glycans are utilized for bioprinting,¹¹ tissue engineering,¹² and other innovative technologies. In the cosmetics and food industries, these glycans serve as active ingredients in cosmetics¹³ and key components for food packaging¹⁴ and preservation.¹⁵ In agriculture and aquaculture, marine glycans have been employed to improve fertilization,¹⁶ plant growth,¹⁷ and animal health.¹⁸ The range of application for marine glycans continue to expand in numerous fields.

The primary challenge associated with marine glycans lies in their structural complexity. While their functional roles are well-established, the detailed molecular mechanisms by which their structures dictate these functions remain poorly understood. This knowledge gap arises largely because most studies have been conducted using isolated glycans or heterogeneous mixtures, which provide bioactivity information but lack the precision needed to elucidate structure–function relationships. Although a limited number of studies have investigated these glycans through defined structures, such studies are often resource-intensive, requiring expert chemists and complex synthetic methodologies. As a result, advancing research techniques is imperative to deepening our understanding of marine glycans.



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One approach to studying marine glycans is enzymatic extraction using CAZymes, enzymes that break down carbohydrates and provide insights into the building blocks of complex glycans.^{19–22} However, a limitation of this method is the lack of a full set of enzymes capable of degrading all glycans, highlighting their inherent complexity. This complexity likely explains their role in carbon sequestration, as some glycans resist microbial breakdown, contributing to long-term carbon storage in the ocean.^{23,24}

To address this challenge, AGA has emerged as a powerful tool. AGA allows for the efficient, reproducible, and controlled synthesis of marine glycans, bypassing the need for expert chemists.^{25,26} Using AGA, researchers can create pure, defined glycans, enabling detailed studies such as NMR spectroscopy to identify specific epitopes and examine the enzymatic processes of carbohydrate degradation. This strategy helps uncover glycans that are resistant to microbial breakdown and their role in carbon sequestration. In particular, algae produce complex glycans with modifications, such as sulfation, that protect them from degradation and enhance their contribution to carbon storage in the ocean.

Here, we review the structures and sources of marine glycans, while exploring the diverse bioactivities of glycans and their applications. We highlight two complementary approaches to gaining a deeper understanding of marine glycans, focusing on their role in the carbon cycle and their structure–function relationships. We emphasize the synergy between harnessing the industrial potential of marine glycans and advancing our molecular understanding of these complex molecules (Fig. 1).

2. Sources and structures of marine glycans

Marine organisms synthesize glycans that are vital for biological processes such as metabolism, cell signalling, immune modulation, and structural integrity.^{5,27} The structure and composition of these glycans vary significantly across classes of organisms and between species. In this section we categorize glycans from three major groups of marine organisms: macroalgae, invertebrates and vertebrates, and microbes (fungi, bacteria, and microalgae, including cyanobacteria and diatoms). The unique glycan structures within these groups will be explored in more detail to highlight their functional significance in the marine environment (see Fig. 2 and 3).

2.1. Glycans in marine macroalgae

Marine macroalgae, including brown, red, and green seaweeds, are vital components of the marine ecosystem. Each algal class produces unique glycans in their cell walls that contribute to structural integrity and facilitate cellular signalling.^{4,5} As crucial players in the marine carbon cycle, macroalgae generate diverse and complex glycans that resist microbial degradation, and enhance carbon sequestration in the ocean.⁶



**Table 1** Industrial applications of marine glycans

Glycan	Medicine and pharmaceutical	Biotechnology and bioengineering	Cosmetics and skincare	Food and nutrition	Agriculture and aquaculture
Alginate	Anti-microbial, ^{9,89–91} anti-cancer, ^{92,93} anti-fibrosis, ⁹⁴ drug delivery ¹⁰	Bioprinting, ^{11,95,96} tissue engineering, ^{12,97,98} fluorescent materials, ⁹⁹ hydrogels, ¹⁰⁰ bioplastic, ⁹⁹ air-filtration ¹⁰¹	Scrubbing additive, ¹⁰² exfoliating agent, ¹⁰³ active ingredient-carriers ^{13,104,105}	Edible films, ^{106,107} food packaging ^{14,108,109}	Irrigation, ¹¹⁰ fertilization, ¹⁶ desalination, ¹¹¹ herbicide control ^{113,114}
Fucoidan	Anti-cancer, ^{8,115,116} anti-diabetes, ^{117–119} neuroprotective, ¹²⁰ vaccination, ¹²¹ gut microbiota regulation ¹²²	Bioprinting, ¹²³ bone tissue engineering, ¹²⁴ endothelialization, ^{125–127} biomaterials ^{128,129}	Whitening, ¹³⁰ antioxidant, ^{131–133} skin protection, ¹³⁴ cosmetics formulation ¹³⁵	Food additive delivery, ¹³⁶ digestibility, ¹³⁷ starch quality ¹³⁸	Animal health, ^{18,139} pesticide toxicity reducing ¹⁴⁰
Laminarin	Anti-bacterial, ¹⁴¹ anti-cancer, ^{142,143} immunomodulatory, ^{144,145} gut microbiota regulation ^{146,147}	Membrane anti-fouling, ¹⁴⁸ bioplastic ¹⁴⁹	Anti-wrinkle, ⁸⁰ skin protection ^{150,151}	Shelf-life extension, ¹⁵ digestibility, ¹⁵² gelatinization ¹⁵³	Fish immunopotentiator ^{154,155}
Carrageenan	Anti-viral, ¹⁵⁶ anti-cancer, ¹⁵⁷ anti-inflammatory ¹⁵⁸	Bioprinting, ^{72,159} bone tissue engineering, ^{160–162} aerogel, ¹⁶³ hydrogels, ¹⁶⁴ biodegradable devices ¹⁶⁵	Skin hydration, ⁸¹ anti-photoaging ¹⁶⁶	Cold storage, ¹⁶⁷ meat quality, ^{168,169} anti-glycation ¹⁷⁰	Plant growth, ^{17,171} fertilization, ¹⁷² pest control, ¹⁷³ dye removal ¹⁷⁴
Agar	Drug delivery, ¹⁷⁵ nanomedicine ¹⁷⁶	Bioprinting, ¹⁷⁷ bio-cleaning, ¹⁷⁸ hydrofilms ¹⁷⁹	Wound healing, ¹⁸⁰ anti-aging facemasks ¹⁸¹	Emulsifier, ¹⁸² food jellies, ⁸⁷ packaging ^{183,184}	Harvesting, ¹⁸⁵ dye removal ¹⁸⁶
Mannan	Anti-viral, ⁶⁶ anti-cancer ¹⁸⁷				
Ulvan	Anti-viral, ¹⁸⁸ anti-inflammatory, ¹⁸⁹ anti-diabetes, ¹⁹⁰ immunomodulatory, ⁶⁷ drug delivery ^{191,192}	Skin tissue engineering, ¹⁹³ drug endothelialization, ¹⁹⁴ nanofibers, ^{195,196} hydrogels ^{97,198}	Antioxidant and whitening ⁸²	Edible films, ¹⁹⁹ healthy-aging nutraceuticals ²⁰⁰	Plant health, ^{201,202} fish immunopotentiator ²⁰³
Chitin	Anti-microbial, ²⁰⁴ anti-cancer, ^{68,205} inflammatory ²⁰⁶	Bioprinting, ⁷⁴ hydrogels, ^{207,208} nanomaterials ^{209,210}	Skin regeneration ^{211,212}	Emulsifier, ²¹³ packaging, ^{214,215} quality control ²¹⁶	Pest control, ²¹⁷ metal ²¹⁸ and microplastic ²¹⁹ removal
Chitosan	Anti-viral, ^{69,220} anti-bacterial, ^{221,222} anti-cancer, ²²³ anti-coagulant ²²⁴	Green nanotechnology, ⁷⁵ biosensor, ^{225,226} hydrogels ²²⁷	Anti-aging, ^{83,228} color cosmetics, ²²⁹ skin penetration, ²³⁰ acne removal ²³¹	Packaging, ^{232,233} quality control ²³⁴	Soil strength, ²³⁵ fertilization, ²³⁶ pest control, ^{237,238} wastewater filtration, ^{239,240} plant health ^{241,242}
GAGs	Anti-inflammatory, ^{243,244} cartilage repair, ^{245,246} bone regeneration, ²⁴⁷ neuroprotective ²⁴⁸	Brain tissue repair, ²⁴⁹ 3D biomimetics, ^{250,251} tissue engineering ²⁵²	Anti-aging and antioxidant, ⁸⁴ cosmetics formulation ²⁵³	Functional food ingredients ^{254–256}	
Glucan	Anti-cancer, ^{257,258} immunomodulatory, ⁵⁸ intestinal health ⁵⁷				Fish immunopotentiator ^{259,260}
EPS	Anti-bacterial, ⁷¹ anti-cancer, ^{261,262} anti-coagulant, ²⁶³ anti-inflammatory ²⁶⁴	Biodiesel, ²⁶⁵ biosurfactants, ²⁶⁶ bioremediation ⁷⁷	Anti-allergy, ⁸⁵ active ingredient formulation ⁸⁶	Emulsifier, ^{267,268} thermostable gelling agent ²⁶⁹	Aquatic infection control, ²⁷⁰ metal removal ²⁷¹



Fig. 1 Overview over marine glycans and methods to establish their structure–activity relationships. (A) Marine glycans, sources, and applications. (B) Glycans as central metabolic fuels in the marine carbon cycle. (C) Enzymatic extraction and automated glycan assembly as complementary methods to access marine glycans.

Brown algae contain three main classes of glycans: alginate, fucoidan, and laminarin. The structure and composition of these glycans are highly species-specific and reflect the glycan diversity within brown algae.

2.1.1 Alginate. Alginates are a major component of the extracellular matrix in brown algae. These linear polymers consist of three main units: β -(1 \rightarrow 4)-D-mannuronic acid (M block), α -(1 \rightarrow 4)-L-guluronic acid (G block), and the alternating β -(1 \rightarrow 4)-D-mannuronic acid- α -(1 \rightarrow 4)-L-guluronic acid (MG block) units. Alginates are typically found in calcium salt form, particularly in the G-rich regions²⁸ and extracted from various brown seaweeds, including *Laminaria hyperborea*, *Laminaria digitata*,²⁹ and *Macrocystis pyrifera*.³⁰ The proportion of M and G blocks can vary depending on the species, with the G block content ranging from 10% to 70%.³¹

2.1.2 Fucoidan. Fucose-containing sulfated polysaccharides, termed fucoidan, constitute a major component of the brown algal cell wall. These polysaccharides can be classified into two main types: homogeneous fucoidans, also known as fucans, which are primarily composed of highly sulfated L-fucose residues; and heterogeneous fucoidans that have more complex backbones incorporating monosaccharides other than fucose, such as D-galactose, D-xylose, D-mannose, and D-glucuronic acid.²⁸ Fucans typically have two major backbone structures: one consisting of pure α -(1 \rightarrow 3)-L-fucose and the other of alternating α -(1 \rightarrow 3)-L-fucose and α -(1 \rightarrow 4)-L-fucose linkages. The prevalence of these backbones varies by species, with Fucales (such as *Fucus* and *Sargassum*) being rich in the α -(1 \rightarrow 3)-L-fucose backbone,³² while Laminariales are more enriched in the alternating backbone.³³ Fucans are heavily sulfated on the L-fucose residues, with O-sulfate esters typically occupying the 2S, 3S, and 4S positions. In contrast,

heterogeneous fucoidans display greater diversity in their backbones and degree of sulfation, with no single common structure or trait defining them. The full characterization of fucoidans remains incomplete, and further research is necessary to better understand their structural diversity.²⁸

2.1.3 Laminarin. Laminarin is a major component found in the vacuoles of brown algae, serving as a food reserve.³⁴ Laminarin is typically characterized as a linear polymer of β -(1 \rightarrow 3)-D-glucose units, with fractional branches of β -(1 \rightarrow 6)-D-glucose residues. The ratio of (1 \rightarrow 3) and (1 \rightarrow 6) linkages varies between species. For instance, when extracted from *Dictyota dichotoma* and *Sargassum fusiforme*, the ratio is 3:1 for (1 \rightarrow 3) and (1 \rightarrow 6) linkages, while in *Sargassum duplicatum*, the ratio is 6:1.³⁵ Laminarin is further classified into two types based on the nature of the reducing ends: the G-chain, containing a terminal D-glucose unit, and the M-chain, containing O-substituted D-mannitol at the termini. The proportion of M versus G chains varies among species, and in some cases, the M-chain is completely absent.³⁵

The next class of macroalgae is red algae, which contains a variety of glycans. This section focuses on three primary types: carrageenan, agar, and mannan.

2.1.4 Carrageenan. Carrageenan is a class of sulfated polysaccharides primarily composed of D-galactose units, found predominantly in red algae. Carrageenan exists in three main types: κ -carrageenan, ι -carrageenan, and λ -carrageenan. All three types share a general backbone of alternating α -(1 \rightarrow 4)-D-galactose or 3,6-anhydro-D-galactose and β -(1 \rightarrow 3)-D-galactose, with varying positions containing sulfate esters and 3,6-anhydro bridges.³⁶ κ -Carrageenan consists of a disaccharide repeating unit of β -(1 \rightarrow 3)-D-galactose-4-O-sulfate linked to α -(1 \rightarrow 4)-3,6-anhydro-D-galactose. ι -Carrageenan contains a



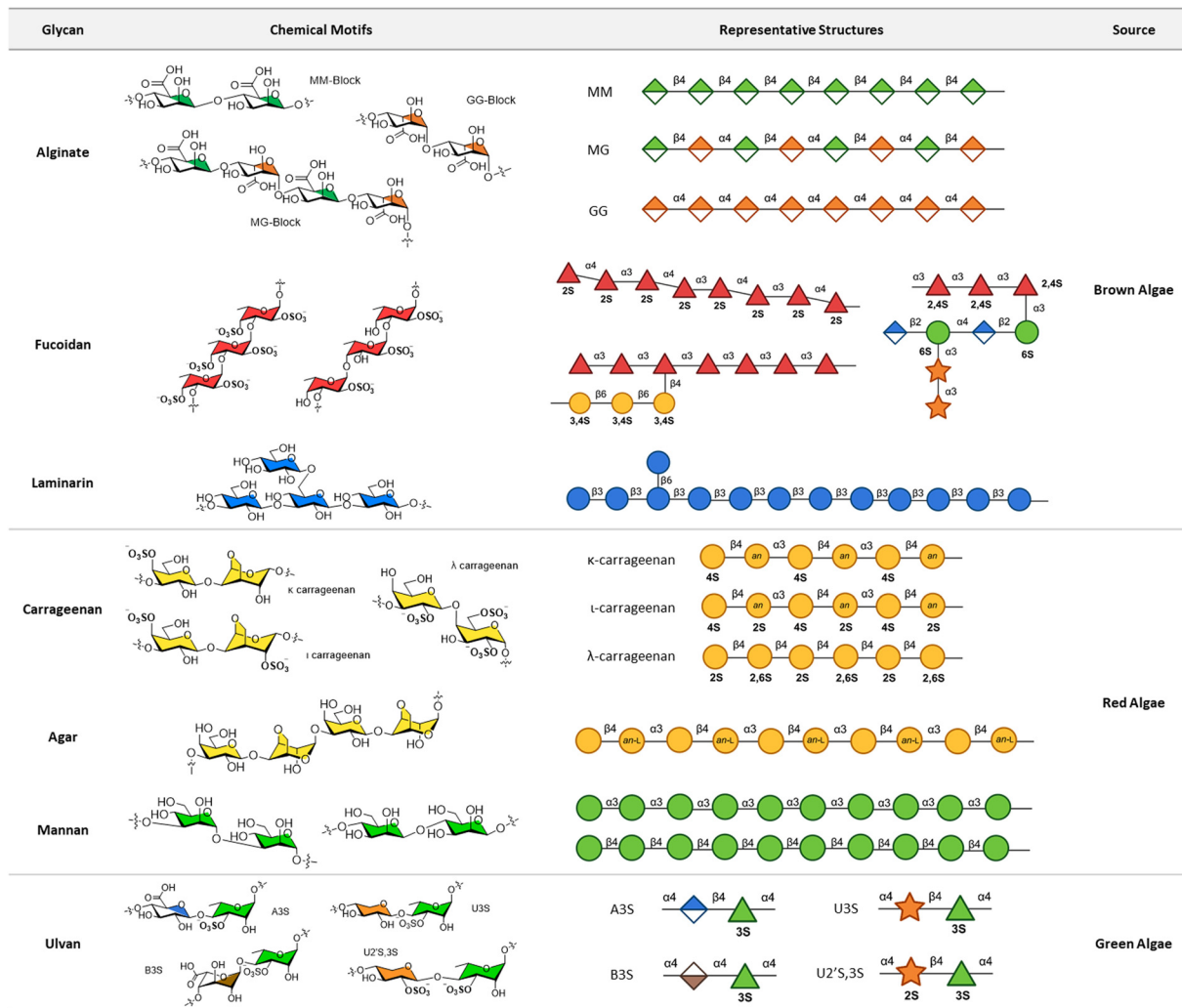


Fig. 2 Structures of marine glycans derived from macroalgae. Chemical motifs highlight core structural features specific to each glycan, while the representative structures illustrate the diversity of these glycans in nature. All glycan symbols follow the symbol nomenclature for glycans (SNFG) guidelines.

disaccharide repeating unit of β -(1 \rightarrow 3)-D-galactose-4-O-sulfate linked to α -(1 \rightarrow 4)-3,6-anhydro-D-galactose-2-O-sulfate. λ -Carrageenan is composed of a disaccharide repeating unit of β -(1 \rightarrow 3)-D-galactose-2-O-sulfate linked to α -(1 \rightarrow 4)-D-galactose-2,6-O-sulfate.³⁷ The highest global production of carrageenan comes from species of *Eucheuma* and *Kappaphycus*, with *Kappaphycus alvarezii* being the primary producer of κ -carrageenan.³⁸

2.1.5 Agar. Agar is composed of two main components, agarose and agarpectin, which are found in the cell walls of red algae, particularly in species of *Gracilaria* and *Gelidium*.^{39,40} Agarose consists of a disaccharide unit called agarobiose, composed of α -(1 \rightarrow 4)-3,6-anhydro-L-galactose and β -(1 \rightarrow 3)-D-galactose. Agarpectin makes up a smaller portion of agar, shares a similar backbone but also contains additional modifications, such as methoxyl, sulfate, and pyruvate groups at various positions along the chain.⁴¹ The amount of agarpectin varies across species; for example, *Gracilaria* species generally contain more agarpectin than *Gelidium* species.⁴² Unlike

carrageenan, agar contains 3,6-anhydro-L-galactose, whereas carrageenan contains 3,6-anhydro-D-galactose.

2.1.6 Mannan. Mannans are important polysaccharides found in red seaweeds, exhibiting considerable diversity, including both α - and β -mannan forms. One prominent variant found in *Nemalion vermiculare* is α -(1 \rightarrow 3)-D-mannan, often sulfated at the O-4 and O-6 positions, with a D-xylose residue branching from C-2.⁴³ Another form, β -(1 \rightarrow 4)-D-mannan, is found in the cuticle of *Porphyra umbilicalis*.⁴⁴ These mannans, particularly the sulfated varieties, are crucial for the structural integrity and functional properties of the red seaweed cell wall, helping the organism withstand environmental stresses.

The final class of macroalgae is green algae that are primarily recognized for producing ulvan.

2.1.7 Ulvan. Ulvan is a highly sulfated polysaccharide found in the extracellular matrices of green algae, particularly within *Ulva* species. Ulvan consists of two main types of repeating disaccharide units, type A and type B, commonly referred to as ulvanobiuronic acids. Type A is characterized by a





Fig. 3 Structures of marine glycans derived from marine invertebrates, vertebrates, and microorganisms. Chemical motifs highlight core structural features specific to each glycan, while the representative structures illustrate the diversity of these glycans in nature. All glycan symbols follow the symbol nomenclature for glycans (SNFG) guidelines.

repeating unit of β -(1 \rightarrow 4)-D-glucuronic acid linked to α -(1 \rightarrow 4)-L-rhamnose-3-O-sulfate (A3S), while type B consists of α -(1 \rightarrow 4)-L-iduronic acid linked to α -(1 \rightarrow 4)-L-rhamnose-3-O-sulfate (B3S). In some variants, the uronic acids are replaced by D-xylose, forming ulvanobioses, which include β -(1 \rightarrow 4)-D-xylose linked to α -(1 \rightarrow 4)-L-rhamnose-3-O-sulfate (U3S) or β -(1 \rightarrow 4)-D-xylose-2,3-O-sulfate linked to α -(1 \rightarrow 4)-L-rhamnose-3-O-sulfate (U2'S,3S).⁴⁵ The occurrence of these ulvan variants is highly species-dependent. For instance, ulvanobiuronic acids are more widely distributed across *Ulva* species, whereas ulvanobioses are primarily found in *Ulva rigida* from the Canary Islands and France.⁴⁵

2.2. Glycans in marine invertebrates and vertebrates

Marine invertebrates and vertebrates produce glycans of significant interest, such as chitin, chitosan, and glycosaminoglycans that have been studied extensively. Unlike glycans from macroalgae and other organisms discussed in this review, the structures of these glycans are generally well-preserved across species, making them valuable for scientific research and applications.

2.2.1 Chitin. Chitin is a linear polysaccharide composed of β -(1 \rightarrow 4)-N-acetyl-D-glucosamine residues. It is commonly

found in the exoskeletons of marine invertebrates, such as crustaceans (shellfish, crabs, shrimps),⁴⁶ as well as in the cell walls of terrestrial fungi and exoskeletons of insects.⁴⁷ The structure of chitin remains largely consistent across species, from terrestrial organisms to marine invertebrates, making it the second most abundant polysaccharide after cellulose.⁴⁸

2.2.2 Chitosan. Chitosan is formed through the deacetylation of chitin, resulting in repeating units of β -(1 \rightarrow 4)-D-glucosamine and β -(1 \rightarrow 4)-N-acetyl-D-glucosamine, with more than 50% deacetylation.⁴⁹ Chitosan is obtained by first extracting chitin and then subjecting it to deacetylation.⁵⁰

2.2.3 Glycosaminoglycans (GAGs). Glycosaminoglycans are linear, unbranched polysaccharides composed of disaccharide repeating units that carry a high negative charge. These polysaccharides are found in the extracellular matrices of mammalian cells, as well as those of marine invertebrates and vertebrates.⁵¹ GAGs are classified into four main groups based on their disaccharide repeating units: heparin/heparan sulfate (HS), chondroitin sulfate (CS)/dermatan sulfate (DS), keratan sulfate (KS), and hyaluronic acid (HA).

Heparin and heparan sulfate are composed of disaccharide units of (1 \rightarrow 4)- α -N-acetyl-D-glucosamine linked to α -(1 \rightarrow 4)-L-iduronic acid (heparin) or β -(1 \rightarrow 4)-D-glucuronic acid (heparan



sulfate).⁵² Heparin contains a high degree of sulfation, with modifications varying depending on the source. Sulfation commonly occurs on the amino group of the amino sugar and on O-6 of the glucosamine residue, while O-2 sulfonate groups are found on the uronic acids.⁵³ Chondroitin sulfate consists of β -(1 \rightarrow 4)-D-glucuronic acid linked to β -(1 \rightarrow 3)-N-acetyl-D-galactosamine, with frequent sulfation at O-6 of the galactosamine residue. Dermatan sulfate, similar to chondroitin sulfate in backbone structure, differs by having L-iduronic acid instead of D-glucuronic acid residues.⁵⁴ Keratan sulfate is composed of disaccharide repeating units of β -(1 \rightarrow 3)-D-galactose linked to β -(1 \rightarrow 4)-N-acetyl-D-glucosamine, with the sulfate group often present on O-6 of the glucosamine residue.⁵⁵ Finally, hyaluronic acid is the only non-sulfated GAG. HA consists of a disaccharide unit of β -(1 \rightarrow 4)-D-glucuronic acid linked to β -(1 \rightarrow 3)-N-acetyl-D-glucosamine, forming an alternating structure with respect to the (1 \rightarrow 4) and (1 \rightarrow 3) linkages.⁵²

2.3. Glycans in marine microorganisms

Marine microorganisms, namely fungi, bacteria, and microalgae, are key players in the oceanic carbon cycle. Marine fungi and bacteria, residing in the deep ocean, break down glycans into their chemical constituents.^{6,56} In contrast, microalgae, including diatoms and cyanobacteria, inhabit the ocean's surface where they fix carbon from the atmosphere and serve as a primary food source for marine organisms.³ These marine microbes contribute to the circulation of marine carbon by biosynthesizing and releasing glycans into the environment. This section provides an overview of the common types of glycans originating from these marine microorganisms.

2.3.1 Glucan. Glucans are present in marine fungi and diatoms in the forms of α - and β -glucans. α -Glucans, commonly found in marine fungi, typically feature a backbone of α -(1 \rightarrow 4)-D-glucose, with some fractions containing α -(1 \rightarrow 6)-D-glucuronic acid at the non-reducing end.⁵⁷ Meanwhile, β -glucans are predominantly composed of β -(1 \rightarrow 3)-D-glucan residues, with lower amounts of β -(1 \rightarrow 6)-D-glucan branching units. These β -glucans are frequently observed in marine diatoms.^{58,59}

2.3.2 Exopolysaccharides (EPS). Exopolysaccharides are glycans secreted by marine microbes into their environment, primarily serving as a defence mechanism against extracellular stress.⁶⁰ These glycans are composed of diverse monosaccharides, including common sugars like D-mannose, D-galactose, and D-glucuronic acid, and rare sugars such as 3-deoxy-D-manno-oct-2-ulosonic acid (Kdo) and deoxy sugars. EPS exhibit significant structural diversity, with modifications like acetylation, carboxymethylation, phosphorylation, and sulfation. They also feature a variety of glycosidic linkages, which can include branched, terminal, or linear motifs.⁶¹ EPS have been studied in a wide range of microbial species, including fungi, bacteria, and diatoms.⁶² For example, an EPS from the deep-sea bacterium *Vibrio alginolyticus* contains a tetrasaccharide unit with α -(1 \rightarrow 3)-D-galacturonic acid- α -(1 \rightarrow 4)-D-galacturonic acid- α -(1 \rightarrow 3)-D-galacturonic acid- β -(1 \rightarrow 3)-N-acetyl-D-glucosamine.⁶³ In contrast, an EPS from the seawater bacterium *Pseudoalteromonas flavipulchra* features a trisaccharide

unit composed of 4-O-acetylated-6-deoxy-L-talose, β -(1 \rightarrow 3)-D-galactose, and α -(1 \rightarrow 7)-Kdo.⁶⁴

3. Industrial applications of marine glycans

Marine glycans play a significant role across numerous industrial sectors. This section will explore five primary applications of marine glycans: (1) biomedicine and pharmaceutical, (2) biotechnology and bioengineering, (3) cosmetics and skincare, (4) food and nutrition, and (5) agriculture and aquaculture. Each application area will highlight select examples from the three main groups of marine organisms. A more comprehensive listing is provided in Table 1. As research progresses, the applications of marine glycans continue to expand, unveiling new opportunities across various fields.

3.1. Biomedicine and pharmaceuticals

The biomedical and pharmaceutical industries continuously seek to improve existing therapeutics and explore novel treatments, driving the investigation of marine-derived glycans for their diverse therapeutic properties and potential to advance medicine.

3.1.1 Marine glycans from macroalgae. Wang *et al.*⁸ demonstrated that fucoidan from brown algae alleviated chemotherapy-induced alopecia and enhanced chemotherapy efficacy. Jang *et al.*⁶⁵ reported that λ -carrageenan displayed antiviral activity against influenza viruses and SARS-CoV-2. Meanwhile, Recalde *et al.*⁶⁶ showed that over-sulfated mannans from the red alga *Nemalion helminthoides* had potent virucidal activity against herpetic and dengue viruses. Son *et al.*⁶⁷ found that ulvan from *Ulva pertusa* reduced weight loss, activated immune cells, and increased cytokine secretion in immunosuppressed mice.

3.1.2 Marine glycans from invertebrates and vertebrates. Solairaj *et al.*⁶⁸ reported the anticancer potential of chitin-copper/silver nanocomposites against human breast cancer cells. Loutfy *et al.*⁶⁹ demonstrated that chitosan nanoparticles incorporating silymarin were effective antiviral agents against SARS-CoV-2. In addition, Egea *et al.*⁷⁰ highlighted the antioxidant and neuroprotective activities of chondroitin sulfate (CS) in neuroblastoma cells, suggesting CS's potential for treating neurodegenerative diseases.

3.1.3 Marine glycans from microorganisms. Rizzi *et al.*⁵⁸ isolated a β -glucan from the marine diatom *Conticribra weissflogii*, which enhanced macrophage activity without cytotoxicity against glioblastoma cells. Ghareeb *et al.*⁷¹ studied EPS from the marine bacterium *Streptomyces vinaceusdrappus*, which exhibited antioxidant, anti-inflammatory, anti-diabetic, anti-Alzheimer, antibacterial, and antibiofilm properties.

3.2. Biotechnology and bioengineering

In biotechnology and bioengineering, growing interest in new bio-based technologies motivates the exploration of marine-derived glycans, whose unique properties enable innovations in bioprinting, tissue engineering, and biosynthetic materials.



3.2.1 Marine glycans from macroalgae. Norouzi *et al.*¹¹ identified that a 4% w/v alginate concentration in silk fibroin bioink provided optimal accuracy for 3D printing scaffolds in bone tissue engineering. Bitencourt *et al.*⁷² developed carrageenan-based gels for dysphagia patients, noting that κ -carrageenan concentration impacts gel texture and printing performance. Pari *et al.*⁷³ further reviewed the diverse applications of ulvan-based biomaterials in biotechnology.

3.2.2 Marine glycans from invertebrates and vertebrates. Zheng *et al.*⁷⁴ explored chitin's potential in 3D printing hydrogels for wound dressings, finding that β -chitin nanofiber concentration significantly influenced the quality of the printed scaffold, with 5–10 wt% yielding optimal performance. Ahmed *et al.*⁷⁵ developed chitosan–MgO nanocomposites with antibacterial properties for leather, improving durability and resistance to environmental degradation. Lou *et al.*⁷⁶ fabricated hyaluronic acid–collagen-based hydrogels to mimic the extracellular matrix in 3D cell cultures, enhancing cell spreading and fiber remodelling by adjusting HA concentration and crosslinking properties.

3.2.3 Marine glycans from microorganisms. Teixeira *et al.*⁷⁷ isolated an EPS from *Klebsiella oxytoca*, which effectively stabilized hydrophilic emulsions, displayed iron-chelating properties, improved viscosity, and was non-toxic to non-tumor cells. Gutiérrez *et al.*⁷⁸ investigated an EPS from *Antarctobacter* sp. TG 22, which formed highly stable emulsions, outperforming non-marine EPS like xanthan gum and gum Arabic in stabilizing ability.

3.3. Cosmetics and skincare

The cosmetics industry leverages marine glycans for their bioactive properties as active ingredients in cosmetic products. These glycans are valued for their therapeutic potential and sustainable sourcing.⁷⁹

3.3.1 Marine glycans from macroalgae. Cheong *et al.*⁸⁰ enhanced laminarin's bioactivity by introducing ester modifications, resulting in laminarin butyl esters with anti-glycation properties that prevent skin aging and promote skin whitening. Zhu *et al.*⁸¹ enzymatically degraded κ -carrageenan into tetrasaccharides, which maintained hydration in keratinocytes and reduced oxidative stress and inflammation. Don *et al.*⁸² developed a chitosan–ulvan film with enhanced tensile strength and bioactivities, including antioxidant effects, skin whitening, and selective toxicity to melanoma cells.

3.3.2 Marine glycans from invertebrates and vertebrates. A chitosan-based face mask with *Achyranthes aspera* leaf extracts exhibited antibacterial, antioxidant, and anti-aging properties, while being non-toxic to mouse embryonic fibroblasts.⁸³ Galvez-Martin *et al.*⁸⁴ investigated a hyaluronic acid matrix with dermatan sulfate, chondroitin sulfate, and collagen, demonstrating regenerative effects on fibroblasts and keratinocytes, alongside moisturizing, antioxidant, and anti-aging benefits for both oral and topical applications.

3.3.3 Marine glycans from microorganisms. Tseng *et al.*⁸⁵ found that polysaccharide extracts from the cyanobacterium *Nostoc commune* possessed anti-allergic and skin-protective

properties, improving skin elasticity and flexibility. Additionally, a wide range of marine EPS have been featured in several cosmeceutical patents,⁸⁶ showcasing anti-aging, anti-inflammatory, and wrinkle reducing activities.

3.4. Food and nutrition

Marine glycans are significant contributors to the food industry, utilized to elevate nutrient content and food preservation qualities.

3.4.1 Marine glycans from macroalgae. Moroney *et al.*¹⁵ observed that laminarin and fucoidan extracted from *Laminaria digitata* reduced iron-induced lipid oxidation in pork liver tissues, suggesting their antioxidant potential in high protein foods. Menaka and Wijesekara⁸⁷ explored agar from *Gracilaria longissimi* as a plant-based gelatin alternative for food jellies, highlighting its viability as a gelling agent. Morelli *et al.*⁸⁸ validated ulvan as an emulsifying agent in functional food formulations, particularly in sustainable oil and water emulsions for soft drinks.

3.4.2 Marine glycans from invertebrates and vertebrates. Yin *et al.*²¹³ investigated chitin's role in stabilizing Pickering emulsions, using chitin nanowhiskers to encapsulate flavor compounds in essential oils and reduce lipid oxidation. Paulose and Chakraborty²⁵⁴ extracted a sulfated glycosaminoglycan-like heteropolysaccharide from the octopus *Cistopus indicus*, which enhanced glucose uptake in adipocytes, suggesting its potential as a bioactive ingredient in functional foods for managing type-2 diabetes.

3.4.3 Marine glycans from microorganisms. Gan *et al.*²⁶⁷ identified a novel EPS from *Halomonas saliphila* strain LCG169T, which exhibited oil-capturing, foaming, and emulsifying properties, making it a potential bioemulsifier for oils like olive or sunflower oil. Sran *et al.*²⁶⁸ discovered an EPS from *Rhodobacter johrii* that formed a thermally stable bioemulsifier, ideal for improving texture and stability in food products.

3.5. Agriculture and aquaculture

Marine glycans are recognized for their efficacy in boosting productivity and promoting healthy ecosystems.

3.5.1 Marine glycans from macroalgae. Aboulella *et al.*¹¹¹ examined alginate's role in water management, synthesizing hydrogels that desalinated water and increased potassium concentrations for nutrient-rich irrigation. Thye *et al.*¹⁷¹ showed λ -Carrageenan improves nutrient uptake and cell homeostasis in banana plants to enhance growth. Velho *et al.*²⁰² observed that ulvan can boost plant resistance to pathogenic fungi by upregulating genes that strengthen cell walls.

3.5.2 Marine glycans from invertebrates and vertebrates. Liu *et al.*²³⁵ demonstrated chitosan, combined with enzyme-induced carbonate precipitation, protected red mud from wind erosion by enhancing carbonate production and formed a durable crust layer. Njimou *et al.*²¹⁹ synthesized chitin–MnO₂–alginate nanoparticles for wastewater treatment and achieved effective adsorption of Cd(II) and Pd(II) in a spontaneous and endothermic process.



3.5.3 Marine glycans from microorganisms. Reyes-Becceril *et al.*²⁶⁰ isolated a β -(1 \rightarrow 3)-glucan with (1 \rightarrow 6) branching from the marine yeast *Debaryomyces hansenii*; the glycan enhanced fish health by exhibiting antioxidant activities and promoting intestinal health without causing histopathological damage. Similarly, Perveen *et al.*²⁵⁹ studied β -(1 \rightarrow 3)-glucan from the microalga *Euglena gracilis* and reported that this glucan increased enzyme responses, upregulated innate immune genes, and exhibited dose-dependent antiparasitic activity in marine crabs against *Mesanothryx* spp.

4. Extraction of marine glycans

4.1. Enzymatic degradation of marine glycans

The enzymatic degradation of marine glycans is essential to global carbon cycling,²³ organic matter turnover, and biogeochemical processes, reinforcing ocean productivity and ecological balance.²⁷² Heterotrophic microorganisms biosynthesize a diverse array of specialized carbohydrate-active enzymes (CAZymes) that catalyze the hydrolysis of specific glycosidic bonds in polysaccharides. These enzymes include, but are not limited to, glycoside hydrolases (GHs), agarosases, sulfatases, carrageenases, alginate lyases, chitinases, amylases, lipases, phytases and proteases.²⁷³ They are systematically categorized into families based on their structures and functions, as detailed in the CAZymes database (<https://www.cazy.org>). This diverse array of CAZymes efficiently liberates valuable monosaccharides and bioactive molecules from marine biomass,^{274,275} including agarose, alginate and sulfated polysaccharides derived from seaweeds; chitin and chitosan from crustaceans; and collagen and glycosaminoglycans from fish. A deeper understanding of the enzymatic mechanisms unlocks significant potential for biotechnological and industrial applications (Table 1).^{46,276}

4.2. Enzymatic extraction of marine glycans

Different enzymatic methods have been explored to enhance the efficiency of marine polysaccharide degradation. Conventional extraction often employs harsh conditions that can diminish the target molecule's functional attributes. In contrast, enzymatic extraction with specific hydrolyses has emerged as a promising approach for augmenting product yield, preserving bioactive properties, and minimizing environmental impact.

A comprehensive analysis of the extraction, modification, degradation, and bioactivity of pivotal marine polysaccharides, encompassing agar, fucoidan,²⁸ ulvan,^{274,277} carrageenan,¹⁶¹ alginate, chitin^{278,279} and chitosan focused on elucidating the underlying enzymatic mechanisms.^{24,280–282} The biodiversity of CAZymes involved in marine polysaccharide degradation and their ecological roles have been studied.^{24,283} Liu *et al.*²⁸⁴ highlighted recent advancements in enzymatic, chemical, and physical methodologies for the depolymerization of fucoidan into low-molecular weight fucoidan and fuco-oligosaccharides. Wu *et al.*²⁸⁵ identified a broad-specificity, high-thermostability chitinase (AfChi28) from the marine fungus *Aspergillus fumigatus* df347, positioning AfChi28 as a potential biocatalyst for

chitin oligosaccharide production. Additionally, highly specific glycoside hydrolases derived from marine flavobacteria were characterized and demonstrated their efficacy in analysing laminarin from diatoms and seawater samples.²⁰ Challenges associated with the standardization of fucoidan preparations and the potential applications of fucoidanases in pharmaceutical and nutraceutical sectors have been explored.²⁸⁶ Analytical methodologies are key to the elucidation of structural features and molecular composition of compounds post-extraction, particularly in the characterization of complex marine polysaccharides.^{19,22}

4.3. Challenges in marine glycans biodegradation by enzymes

The intricate structural modifications of marine polysaccharides confer significant resistance to enzymatic degradation, presenting a major challenge for developing a comprehensive marine glycomic workflow.^{24,287} Structural complexity, unique monosaccharide compositions, distinct glycosidic linkages, heterogeneous molecular weights, diverse conformational architectures, intricate sulfation patterns, and limited enzymatic efficiency are challenging. The high variability of marine polysaccharides across species further complicates the establishment of standardized degradation and characterization methods. Understanding these complexities is essential for effectively harnessing the potential of marine polysaccharides (Fig. 4).

4.3.1 Structural complexity of marine glycans. Marine glycans exhibit remarkable structural complexity and monosaccharide variability, demanding a wide range of CAZymes for enzymatic degradation.²⁷²

A single CAZyme targets specific linkages, but complex polysaccharides necessitate a corresponding set of enzymes, each specialized for a particular linkage. Fucoidan, a highly heterogeneous sulfated polysaccharide derived from brown algae, features complex branching, diverse linkages, and variable sulfation patterns. As a result, fucoidan degradation requires 284 putative fucoidanases, glycoside hydrolases (GHs), sulfatases, and carbohydrate esterases, as shown in *Verrucomicrobium* bacteria.²⁸⁸ In *Lentimonas* sp. CC4, 100 enzymes are utilized to break down fucoidan,²⁸⁹ emphasizing the extensive enzymatic machinery needed to address its structural heterogeneity. In contrast, less complex β -glucans like laminarin are degraded rapidly by just two to three enzymes.²⁹⁰

The breakdown of carrageenan is a complex process, requiring the coordinated action of multiple enzymes to overcome the structural intricacies of sulfated galactan from red algae.²⁹¹ Side chains limit the activity of endo-acting enzymes due to steric hindrance, hindering the complete hydrolysis of polysaccharides like laminarin.^{21,292} Specifically, GH16 and GH17 enzymes exhibit different specificities towards laminarin, with GH17 enzymes showing narrow specificity for non-decorated β -(1 \rightarrow 3)-glucan stretches, suggesting that the presence of β -(1 \rightarrow 6) side chains impede their activity.²⁰ To fully degrade polysaccharides, bacteria require a unique enzyme for each distinct chemical bond between the building blocks, underscoring the need for a robust enzymatic repertoire to address the diversity of glycosidic linkages.²³



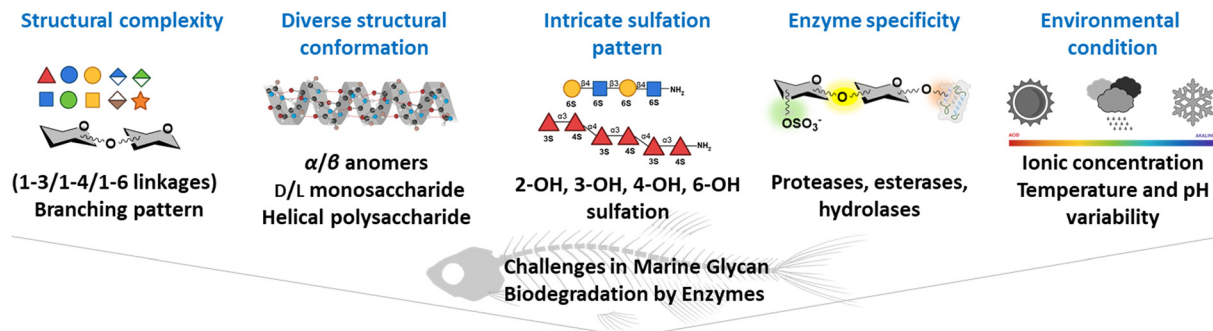


Fig. 4 Challenges in marine glycan biodegradation by enzymes.

4.3.2 Intricate sulfation patterns. Many marine polysaccharides are sulfated, and their sulfation levels and patterns can significantly influence their biological activities and interactions with cell receptors (Table 1). Desulfation of marine sulfated galactofucans resulted in lower anti-thrombin binding compared to their sulfated counterparts.²⁹³ On other hand sulfate groups attached at various positions on monosaccharides (O-2, O-3, or O-4) increase negative charge and steric hindrance, hindering enzyme access. Consequently, the removal of sulfate groups by sulfatases is often necessary before glycoside hydrolases can effectively act on the glycan backbone.²³ Sulfate groups are essential for the activity of the fucoidanase FFA, likely due to specific binding interactions with the enzyme, whereas for the fucoidanase from *Lambis* sp., sulfate groups interfered with enzyme hydrolysis.²⁸⁶ Thus, the presence or absence of sulfate groups, depending on the enzyme, can either promote or hinder activity, potentially by affecting the enzyme's ability to approach and bind the substrate.

4.3.3 Diverse structural conformations. Glycosidic linkages buried within the three-dimensional network of marine polysaccharides due to folding, hydrogen bonding, or interaction with water and ions can influence their functionality, including interactions with complement enzymes.^{272,294} The polysaccharide conformation affects the accessibility of glycosidic bonds to hydrolyzing enzymes that are typically stereospecific and linkage-specific.²² Hence, variations in configurations require enzymes with corresponding specificities.²⁰ Compact three-dimensional arrangements, resulting from extensive inter- and intramolecular interactions, can render polysaccharides highly resistant to enzymatic degradation.²⁹⁴ The endo- α -1,6-mannanase (ShGH76) from *Salegentibacter* sp. HeI_I_6, interacts with kinked oligomannan conformations, a structural feature specific to fungal α -1,6-mannans.²⁹⁵ This study highlights how the complexity and conformational flexibility of glycans challenge enzymatic breakdown efficiency.

4.3.4 Enzyme specificity. The efficiency of CAZymes is constrained by their specificity for particular glycan structures.²³ GH enzymes, including porphyranases and agarases that target sulfated galactans, possess highly substrate-specific active sites.²³ The enzymatic degradation of microalgal cell walls also requires enzymes that are highly specific and versatile for effective bioconversion.²⁹⁶ Thus, finding the exact enzyme with the required specificity for a particular marine glycan is challenging,

given the underexplored nature of marine environments and their microbial enzyme diversity.²⁷²

4.3.5 Environmental conditions. As algal blooms mature, more complex polysaccharides become available, requiring enzymes with greater specificity and efficiency for their degradation.²⁹⁷ Seasonal shifts in CAZyme expression underscore this constraint: in spring, elevated β -(1 \rightarrow 3)-glucosidase activity targets laminarin, while in winter, α -glucan-degrading enzymes dominate.²⁹⁸ Enzymatic degradation is also dependent on environmental factors such as pH. Fucoidanases isolated from marine invertebrates, including the molluscs *Haliotus* sp., *Mizuhopecten yessoensis*, and the sea urchin *Strongylocentrotus nudus*, showed peak activity in the pH range of 3.5–5. In contrast, fucoidanase from the marine bacterium *Formosa algae* KMM 3553T exhibited maximal activity over a wide pH range from 6.5 to 9.²⁸⁶ Another factor influencing enzymatic degradation is optimal temperature. For κ -carrageenase OUC-FaKC16A, the optimal temperature ranges from 30 to 100 °C; ι -carrageenases function best between 30 to 65 °C; and alginate lyases from *Pseudoalteromonas* species shows optimal activity at 25 °C to 55 °C.²⁸² Ionic strength is also critical; κ -carrageenases require specific ionic conditions such as the presence of Na⁺ or Ca²⁺ for peak activity, and variations in these conditions significantly impact degradation rate and efficiency.²⁹⁹

4.4. Advances in enzyme engineering

Recent advancements in recombinant enzyme technologies have enabled the production of enzymes with enhanced specificity and catalytic efficiency, leading to improved precision in degradation, enhanced capability for detailed structural analysis, and increased yield of bioactive oligosaccharides from marine biomass.²⁷⁶ For instance, the use of recombinant cCgkA and cCgIA enzymes for carrageenan hydrolysis demonstrated a 3.1-fold increase in efficiency compared to individual enzymes.³⁰⁰ These innovations support the extraction of bioactive compounds from marine polysaccharides, such as YCP, a mitogenic polysaccharide that enhances phagocytic activity,³⁰¹ and fucoidan, which shows promise as a therapeutic agent for Alzheimer's disease.³⁰²

Combining enzyme-assisted extraction with ultrasound treatment has significantly boosted ulvan recovery from *Ulva fenestrata*, yielding up to 18% compared to enzymatic extraction alone.²⁷⁴ Ultrasound-assisted enzymatic extraction enhances polysaccharide



precisely construct GAGs with controlled sulfation patterns, offering a robust platform for investigating the structure–function relationships of marine GAGs. Automated solid-phase synthesis has been successfully employed for the synthesis of β -mannuronic acid alginates, major components of the cell walls of algae, demonstrating the feasibility of constructing structurally defined marine glycans with challenging (1 \rightarrow 2)-*cis*-mannosidic linkages.³¹⁸

The stereo controlled formation of (1 \rightarrow 2)-*cis*-glycosidic bonds is a general difficulty in oligosaccharide synthesis, particularly for fucoidan, which contains these challenging linkages. Additionally, the introduction of multiple sulfate groups at specific positions on the growing glycan chain adds considerable complexity. Careful design of protecting groups and compatible sulfation strategies that can be integrated into the automated process are required. The synthesis of algal fucoidan oligosaccharides, reaching lengths of up to 20-mers with diverse branching patterns and sulfate esters, reinforces AGA's capacity to handle the complexities of major marine polysaccharides.³⁰⁵

6. Future perspectives

AGA offers a powerful and versatile platform for synthesizing a diverse range of structurally defined marine glycans in a controlled laboratory setting. Marine glycans, such as heavily sulfated fucans and mannans, pose significant chemical challenges due to their complex structures. AGA platforms are continuously evolving to facilitate the rapid and reproducible synthesis of these glycans. Future advancements in AGA will focus on optimizing monosaccharide building blocks, glycan back-bone assembly, solid-phase chemistry, and sulfation methods to further expand the library of accessible glycans.

Synthetic glycans act as crucial tools for discovering new enzymes capable of degrading specific algal glycans like fucoidan and mannans. These enzyme cascades can then become tools for environmental detection and quantification of algal glycans, both in the laboratory and the ocean. By exposing microbes to this synthetic diversity, researchers can directly monitor microbe–glycan interactions, providing crucial insights into whether glycan diversity acts as a chemical barrier against degradation.

Synthetic glycans are essential for understanding their fundamental roles in ecological processes like carbon cycling, characterizing enzyme activities, developing new biocatalytic tools, and exploring their vast potential in industrial applications. Continued advancements in AGA methodologies will further enhance these capabilities, paving the way for groundbreaking discoveries in marine glycobiology.

7. Conclusions

Marine glycans are pivotal biomolecules in the oceanic carbon cycle, driving the sequestration of carbon in the deep ocean and contributing to the Earth's largest carbon sink. In addition to

their ecological importance, marine glycans exhibit potent bioactivities leveraged by several industries, from medicine to agriculture. Nevertheless, the complexity of glycan structures hinders a fundamental understanding of their functions. Enzymatic extraction methods have made significant advancements in decoding these intricate glycans, yet they face inherent challenges due to incomplete knowledge of glycan structures and the enzymes involved in their biosynthesis and degradation. AGA has emerged as a promising solution, providing a platform for achieving structurally defined glycans that inform enzymatic studies on the molecular constituents responsible for their diverse bioactivities. Together, these complimentary approaches facilitate a synergistic investigation into this essential class of biomolecules, uncovering their ecological and biological roles in the coming decades.

Conflicts of interest

The authors declare no conflicts of interest.

Data availability

No primary research results, software or code have been included and no new data were generated or analysed as part of this review.

Acknowledgements

Funding, including open access funding from the Max Planck Society, is gratefully acknowledged.

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