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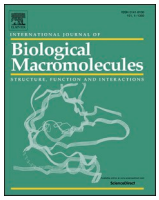

Review

Sustainable production of ulvan from green macroalgae and its potential in carbon sequestration: A critical review

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ABSTRACT

Ulvan, a sulfated polysaccharide abundant in green macroalgae, has emerged as a promising biopolymer due to its diverse biological activities. However, current understanding of its large-scale production pathways and ecological application potentials remains fragmented. This review synthesizes ulvan content in green seaweeds, revealing that it varies widely among species—ranging from very low to over 40 % of dry weight—and is significantly influenced by environmental factors such as temperature and light. We further analyze global biomass trends, noting a shift from wild harvest to aquaculture, alongside the immense and fluctuating biomass contributed by green tides, which represents a substantial yet underutilized source of ulvan. Crucially, we highlight ulvan's inherent resistance to bacterial degradation, which, combined with the massive biomass of green macroalgae in coastal ecosystems, underscores its significant but unexploited potential for long-term carbon sequestration. To balance economic feasibility and ecological sustainability, we propose an integrated framework for ulvan production and utilization. Offshore-grown macroalgae are prioritized for high-purity ulvan extraction to support the food and biomedical industries. Meanwhile, coastal algal biomass is leveraged for bioenergy production, with the resultant CO_2 sequestered in geological reservoirs. By synthesizing production dynamics and ecological synergies, this study provides novel insights into unlocking ulvan's potential as a sustainable biopolymer for blue bioeconomy and carbon-neutral initiatives.

1. Introduction

Ulvan is a major cell wall polysaccharide in the species of the genus *Ulva* (family: Ulvaceae), though smaller amounts are also present in certain other genera including *Cladophora* [1,2]. The term ulvan is derived from the original names ulvin and ulvacin, which were used to denote different fractions of water-soluble sulfated polysaccharides in *Ulva lactuca*. Currently, ulvan refers to sulfated polysaccharides derived from members of the order Ulvales, predominantly *Ulva* spp. Except for ulvan, there are three other cell wall polysaccharides including cellulose, xyloglucan and glucuronan, and the total cell wall polysaccharides account for 38–54 % of the dry algal matter [2,3]. In terms of ulvan, it contributes from 9 to 36 % of the dry weight biomass of *Ulva* depending on species and growth conditions, and it is the only one of the four cell wall polysaccharides to include both rhamnose and iduronic acid [2,4,5]. Cell wall polysaccharides play an important biological role in maintaining cell wall integrity, regulating osmotic pressure, serving as defense mechanism for organism, etc. [6].

Ulvan has shown various biological activities, including plant defense, antioxidant, anti-inflammatory, anticancer, antibacterial and antiviral activities, etc. [2,7–9]. Therefore, ulvan has potential applications in biomedicine, functional food, health products and cosmetics industries. Recent studies have indicated that ulvan has optimal physicochemical properties (water solubility, gelation ability, biodegradability, etc.) and bioactivity (antioxidant activity, anti-inflammatory and immunomodulatory, lipid-lowering effect, etc.) that can serve as therapeutic biological agents [10–12]. Furthermore, the biocompatibility of ulvan makes it a versatile candidate for biomaterial design [13]. Hence, there has been a surge in scientific investigations focusing on the structural properties, extraction techniques, functional applications, and production yield of ulvan polysaccharides. [14–17].

To figure out current status of ulvan study, a comprehensive literature search was performed in May 2025 using the Web of Science database with “ulvan” as the search term. The initial search yielded 614

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publications, including both research articles and books. To elucidate current research trends and identify potential knowledge gaps in ulvan studies, we conducted a bibliometric analysis using VOSviewer software (version 1.6.20). Keyword co-occurrence maps were generated with a minimum threshold of 20 occurrences per term, employing the binary counting method for analysis. Based on bibliometric analysis, the number of publications related to ulvan shows a notable rising trend during the past 20 years, and the research focus has been shifting from structure and extraction to its applications in food and biomaterials (Fig. 1A&B).

In addition to biological functions, there is rising concern about ecological functions of seaweed polysaccharides [18]. Due to higher biomass density and longer turnover time than microalgae, marine macroalgae owns more effective carbon sequestration capacity [19]. Most of the inorganic carbon fixed by algae is converted into polysaccharides, up to 80 %, and the polysaccharides that are not degraded by bacteria can sequester carbon in the ocean [20]. For instance, about 660 Gt dissolved organic carbon was injected to ocean by fucoidan [18]. Owing to the high growth rate and broad environmental tolerance, *Ulva* species are widely distributed in global coastal intertidal habitats, especially in eutrophic regions [21]. Furthermore, *Ulva* can cause large-scale algal blooms in many areas of the world. Therefore, the ecological functions of ulvan should be considered. However, our understanding in this topic remains limited and fragmented (Fig. 1B). Therefore, in this study, we focus on sustainable production and ecological functions (particularly carbon sequestration) of ulvan, with the goal to increase the understanding of its impacts on marine ecology and promote the research in this area.

2. Production of ulvan

2.1. Ulvan content in Ulva species

Crude ulvan content has a large variation, ranging from 2.67 to 41.96 % (Table 1). These variations can be species-dependent. *Ulva lactuca* has the highest crude ulvan content while *U. flexuosa* has the lowest content [1,30]. In addition, extraction methodologies and conditions can also affect the yield of crude ulvant. For instance, the ultrasonic-assisted extraction method increased the ulvan yield obtained from *U. pertusa* by 16 % compared to hot water extraction method. Moreover, when enzyme was added for ultrasonic-assisted, the ulvan content reached the highest value of 26.7 % for crude ulvan [14]. Furthermore, crude yield also varies with culture conditions. High irradiance and temperature enhanced rhamnose content in *U. fenestrata* [43]. Notably, Pankiewicz et al. (2016) found that ulvan also existed in *U. flexuosa* collected from the Nielba river of Poland, which is the first discovery of ulvan in freshwater macroalgae [1]. The obtained ulvan yield of 2.67 % from the freshwater *U. flexuosa* is lower than that (15.6–20.2 %) from the seawater *U. flexuosa.*

2.2. Ulvan content in non-Ulva species

Ulvan is a unique sulfated polysaccharide mainly derived from green seaweed of the *Ulva* genus, such as *U. lactuca, U. prolifera, U. fasciata, U. nematoidea, U. conglobata, U. linza, U. reticulata, U. papenfussii, U. pertusa, U. armoricana,* etc. However, ulvan or ulvan-like substances can also be extracted from other green seaweed species. For instance, Pankiewicz et al. (2016) isolated ulvan from *Cladophora glomerata* and the yield ranged between 4.8 and 16.2 % depending on different harvesting dates [1]. In addition, *Cladophora crispate* was also found to have ulvan and the contents of sulfate and uronic acids of purified ulvan were 10.0–12.2 % and 10.6–18.5 %, respectively [22]. There is high possibility that other seaweeds, particularly green seaweeds, contain ulvan with different structures. This hypothesis needs to be investigated in future to expand the ulvan sources and its applications.

2.3. Effects of extraction methods on ulvan yield

Beyond biomass source, the extraction and purification of ulvan profoundly influence both quantitative yield and structural quality [13]. Method selection is guided by ulvan's physicochemical properties and its interactions with cell wall components, such as cellulose and proteins [5]. Broadly, ulvan extraction methodologies are categorized into physical, chemical, and enzymatic approaches, each yielding distinct outcomes in yield and purity due to divergent operational parameters reported in literature (Table 1).

2.3.1. Physical extraction

Physical methods, such as warming, microwave and ultrasonic-assisted techniques, improve extraction by disrupting cell walls through rapid heating or mechanical vibrations, and thus enhance ulvan yields. For instance, increased temperature (50–70 °C) and time (45–90 min) with deionized water as the solvent boosted ulvan yields in *U. lactuca* by 30–92 % [31]. In addition, microwave and ultrasonic assisted treatments increased ulvan yield in *U. intestinalis* from 17.76 % (control) to 20.41 % and 22.73 %, respectively [29].

2.3.2. Chemical extraction

Chemical solvents—acids, bases, organic reagents, or chelators—are employed to disrupt cell wall structures and enhance extraction efficiency. Acidic solvents generally outperform alkaline ones: Kazemi et al. (2023) reported 23.21 % ulvan yield from *U. intestinalis* using hot acidic extraction, versus 16.11 % with hot alkaline conditions [13,29]. This superiority is attributed to acid-mediated cleavage of ester linkages in the cell wall, though harsh conditions may risk ulvan degradation if not carefully controlled.

2.3.3. Enzymatic extraction

Enzymatic techniques offer a gentle, targeted alternative by hydrolyzing specific glycosidic linkages (e.g., cellulases, pectinases) to release ulvan with minimal structural damage and lower energy input. For instance, enzyme-assisted extraction of *U. pertusa* at 50 °C yielded 25.3 % crude ulvan—a 42 % increase over hot water extraction (17.8 %)—demonstrating both efficiency and mild processing advantages [14]. Such methods are particularly promising for preserving ulvan bioactivity, a critical factor for pharmaceutical or nutraceutical applications.

2.3.4. Methodological considerations

The choice of extraction method must balance yield, structural integrity, and operational feasibility. Physical methods enhance yield through energy input but risk thermal degradation; chemical approaches improve solubilization but may introduce contaminations or require extensive purification; enzymatic methods offer specificity and sustainability but depend on enzyme cost and substrate compatibility. These trade-offs highlight the need for context-driven optimization—aligning extraction parameters with downstream applications to maximize ulvan utility in research and industry.

2.4. Impacts of morphology on ulvan yield

Green seaweeds in the genus *Ulva* exhibit two distinct morphological forms: flat, leafy (foliose) thalli (sometimes appearing as thin ribbons) and tubular, filamentous structures [24]. Most studies on ulvan yield have focused on single species or a single morphological form, limiting comparative insights. Kidgell et al. (2021) were the first to directly compare ulvan yields between foliose and filamentous *Ulva* using optimized extraction protocols [24]. Their results demonstrated that foliose species (14.0–19.3 % ulvan) produced higher yields than filamentous counterparts (7.2–14.6 %), attributed to differences in cell wall architecture affecting extractability. Conversely, Manikand et al. (2022) reported contrasting findings: nine out of eleven extraction methods yielded lower ulvan from foliose vs. filamentous morphotypes [41]. This

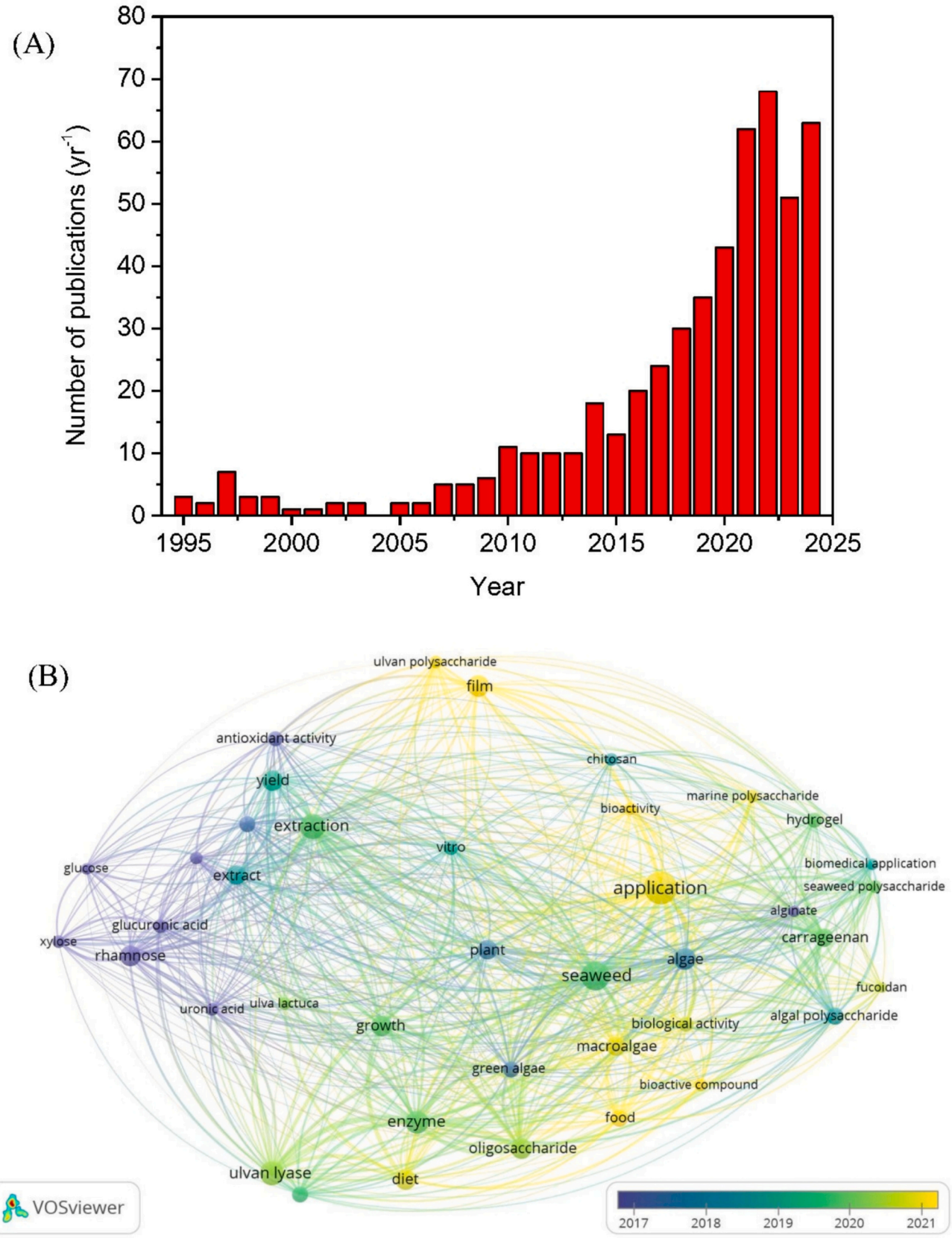

Fig. 1. Publication trends (A) and research hotspots (B) of ulvan. Bibliometric analysis was performed via Web of Science with the search topic "Ulvan" up to May 2025. In panel B, nodes represent keywords, with size proportional to their occurrence frequency in the corpus. Edges denote co-occurrence of keywords in the same publication, where edge thickness reflects the strength of association. Node color indicates the year when each keyword exhibited the highest publication frequency. Visualization was generated using VOSviewer.

Table 1
Overview of published ulvan yield, extraction method, composition and molecular weight (MW) in different green seaweed species. Slash means data unavailable, and %DW means %algal dry weight.

Species	Location	Morphology	Extraction method	Crude yield (%DW)	Purified yield (%DW)	Sulfate (% DW)	Rhamnose (mol%)	Glucuronic acid (mol%)	Iduronic acid (mol %)	Uronic acid (mol%)	Xylose (mol%)	MW (kDa)	Reference
Cladophor crispata	Syria, freshwater	Filamentous	Physical (ultrasonic-assisted)	/	/	10.0–12.2	/	/	/	10.6–18.5	/	/	[22]
Cladophor glomerata	Poland, freshwater	Filamentous	/	4.8–16.2	/	/	/	/	/	/	/	/	[1]
Ulva armoricana	France, seawater	Foliose	/	/	/	11.7–15.6	47.8–53.6	15.2–25.9	3.8–6.9	21.1–32.4	7.0–10.1	/	[23]
Ulva armoricana	France, seawater	Foliose	/	6.33–12.43	/	9.2–12.5	49.1–61.4	19.5–28.0	5.0–10.7	/	7.6–9.6	100–980	[5]
Ulva australis	New Zealand, seawater	Foliose	/	14.7	6.5	/	51	18	7	35	22	214	[24]
Ulva compress	New Zealand, seawater	Filamentous	/	7.2	3.3	/	47	24	7	31	17	346	[24]
Ulva conglobata	China, seawater	Foliose	/	/	/	23–35	64–72	/	/	11–15	1.0–2.0	/	[25]
Ulva fasciata	Egypt, seawater	Foliose	Chemical (HCl&NaOH)	/	/	14.9–15.0	/	/	/	/	/	/	[26]
Ulva fasciata	Egypt, seawater	Foliose	Chemical (HCl)	/	/	12.7–21.4	/	/	/	/	/	/	[26]
Ulva fasciata	Egypt, seawater	Foliose	Chemical (EDTA)	/	/	7.8–17.1	/	/	/	/	/	/	[26]
Ulva fenestrata	seawater	Foliose	Enzymatic (cellulases)	3.65–14.11	/	/	/	/	/	/	/	669–777	[27]
Ulva fenestrata	seawater	Foliose	Enzymatic (proteases)	3.01–13.21	/	/	/	/	/	/	/	672–892	[27]
Ulva flexuosa	Brazil, seawater	Filamentous	/	15.6–20.2	/	/	/	/	/	/	/	/	[28]
Ulva flexuosa	New Zealand, seawater	Filamentous	/	14.59	7.3	/	56	21	6	27	15	352	[24]
Ulva flexuosa	Poland, freshwater	Filamentous	/	2.67	/	/	/	/	/	/	/	/	[22]
Ulva intestinalis	Iran, seawater	Filamentous	Physical (ultrasonic-assisted)	17.76–23.21	/	/	/	/	/	/	/	/	[29]
Ulva intestinalis	Iran, seawater	Filamentous	Chemical (hot acidic)	23.21	/	/	/	/	/	/	/	/	[29]
Ulva intestinalis	Iran, seawater	Filamentous	Chemical (hot alkaline)	16.11	/	/	/	/	/	/	/	/	[29]
Ulva lactuca	Indonesia, seawater	Foliose	Chemical (DES ChCl-glycerol)	33.89	/	35.67	/	/	/	/	/	/	[30]
Ulva lactuca	Indonesia, seawater	Foliose	Chemical (DES ChCl-glycerol + peracetic acid)	31.21–41.96	/	23.20–33.39	/	/	/	/	/	/	[30]
Ulva lactuca	Indonesia, seawater	Foliose	Chemical (HCl)	16.72	/	58.15	/	/	/	/	/	/	[30]
Ulva lactuca	Indonesia, seawater	Foliose	Chemical (aquadest)	6.75–12.93	/	36.79–39.20	/	/	/	/	/	/	[31]
Ulva lactuca	Indonesia, seawater	Foliose	Chemical (HCl)	10.52–14.08	/	43.80–57.81	/	/	/	/	/	/	[31]

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Table 1 (*continued*)

Species	Location	Morphology	Extraction method	Crude yield (%DW)	Purified yield (%DW)	Sulfate (% DW)	Rhamnose (mol%)	Glucuronic acid (mol%)	Iduronic acid (mol %)	Uronic acid (mol%)	Xylose (mol%)	MW (kDa)	Reference
Ulva lactuca	Indonesia, seawater	Foliose	Chemical (NaOH)	10.79–16.96	/	49.71–52.99	/	/	/	/	/	/	[31]
Ulva lactuca	Tunisia, seawater	Foliose	Chemical (Alcohol)	21.68–32.67	/	13.35–15.59	/	/	/	/	/	/	[32]
Ulva lactuca	Italy, seawater	Foliose	/	7.27–15.76	3.86–10.78	11.45–21.36	20.88–28.25	/	/	/	/	/	[33]
Ulva linza L.	Egypt, seawater	Foliose	Chemical (acid)	19.53–29.33	/	2.77–22.98	/	/	/	/	/	3.95–218.48	[34]
Ulva ohnoi	Australia, seawater	Foliose	Chemical ($Na_2C_2O_4$)	3.7–4.3	/	7.1–11.5	33.2–41.1	23.6–29.4	5.5–7.4	29.1–36.8	5.6–7.3	/	[35]
Ulva ohnoi	Australia, seawater	Foliose	Chemical (HCl)	6.7–8.1	/	12.3–12.5	52.3–53.1	26.3–27.8	9.8–10.5	36.8–37.9	5.2–6.1	/	[35]
Ulva olivascens	France, seawater	Foliose	/	/	/	13.8	53.8	16.7	3.8	20.5	15.1	/	[23]
Ulva papenfussii	Peru, seawater	Foliose	Physical (hot water)	29	/	/	/	/	/	/	/	894	[36]
Ulva papenfussii	Peru, seawater	Foliose	Chemical (NaOH)	21	/	/	/	/	/	/	/	153–829	[36]
Ulva pertusa	South Korea, seawater	Foliose	/	20.2–25.1	/	11.5–15.7	51.2–71.6	/	/	22.7–23.8	1.1–3.1	/	[21]
Ulva pertusa	China, seawater	Foliose	Physical (hot water)	17.8	/	13.2	/	/	/	/	/	283	[14]
Ulva pertusa	China, seawater	Foliose	Physical (ultrasonic-assisted)	20.6	/	9.2	/	/	/	/	/	352	[14]
Ulva pertusa	China, seawater	Foliose	Enzymatic (cellulase)	25.3–26.7	/	3.9–6.8	/	/	/	/	/	300–404	[14]
Ulva pertusa	China, seawater	Foliose	Physical (hot water)	/	/	19.9	/	/	/	/	/	151.7	[37]
Ulva pertusa	China, seawater	Foliose	Chemical (H_2O_2)	/	/	19.1–20.4	/	/	/	/	/	28.2–64.5	[37]
Ulva prolifera	New Zealand, seawater	Filamentous	/	11.01	6.6	/	60	17	7	24	15	260	[24]
Ulva ralfsii (cult.)	New Zealand, seawater	Filamentous	/	8.59	4.1	/	38	24	4	28	16	406	[24]
Ulvar alfsii (wild)	New Zealand, seawater	Filamentous	/	7.38	4.3	/	43	26	6	32	14	328	[24]
Ulva rigida	France, seawater	Foliose	/	5	2	/	42.6	12.2	30.3	42.5	8	56.7	[38]
Ulva rigida	New Zealand, seawater	Foliose	/	14.01	5.7	/	49	26	18	44	6	190	[24]
Ulva rigida	seawater	Foliose	/	/	/	54.2–59.1	34.3–37.7	/	/	27.1–35.5	25.8–39.2	/	[39]
Ulva rigida	France, seawater	Foliose	/	/	/	14.3–19.8	50.9–58.3	19.0–30.4	2.5–4.7	23.0–35.1	6.3–12.0	/	[23]
Ulva rigida	Greece, seawater	Foliose	/	/	/	/	25.4	/	/	18.7	4.3		[40]
Ulva rotundata	France, seawater	Foliose	/	/	/	11.3–17.3	46.7–54.0	17.8–28.9	0.6–5.6	19.8–32.5	5.4–23.8	/	[23]

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Table 1 (*continued*)

Species	Location	Morphology	Extraction method	Crude yield (%DW)	Purified yield (%DW)	Sulfate (% DW)	Rhamnose (mol%)	Glucuronic acid (mol%)	Iduronic acid (mol %)	Uronic acid (mol%)	Xylose (mol%)	MW (kDa)	Reference
Ulva rotundata	France, seawater	Foliose	/	6.06–11.10	/	10.3–13.8	41.9–55.6	14.8–27.9	2.5–8.8	/	7.0–25.1	630–1200	[5]
Ulva scandinavica	France, seawater	Foliose	/	/	/	13.1	42.2	11.6	4	15.6	9.6	/	[23]
Ulva sp.	New Zealand, seawater	Foliose	/	16.72	6.3	/	47	20	10	30	19	245	[24]
Ulva sp.	Ireland, seawater	Foliose	Chemical (citric acid)	17.9–41.0	/	16–22	/	/	/	/	/	/	[41]
Ulva sp.	Ireland, seawater	Foliose	Chemical (HCl)	38.6	/	16	/	/	/	/	/	/	[41]
Ulva sp.	Ireland, seawater	Foliose	Physical (H_2O)	10.9	/	22	/	/	/	/	/	/	[41]
Ulva sp.	Ireland, seawater	Filamentous	Chemical (citric acid)	25.4–39.0	/	21–29.5	/	/	/	/	/	/	[41]
Ulva sp.	Ireland, seawater	Filamentous	Chemical (HCl)	38.8	/	20	/	/	/	/	/	/	[41]
Ulva sp.	Ireland, seawater	Filamentous	Physical (H_2O)	7.7	/	29	/	/	/	/	/	/	[41]
Ulva sp. B (cult.A)	New Zealand, seawater	Foliose	/	17.75	9.5	/	51	22	15	37	11	218	[24]
Ulva sp. B (cult.B)	New Zealand, seawater	Foliose	/	16.3	8.3	/	48	31	11	42	7	254	[24]
Ulva sp. B (wild)	New Zealand, seawater	Foliose	/	19.33	8	/	48	26	13	39	11	229	[24]
Ulva spp.	Spain, seawater	/	Chemical (acid)	30.36	/	9.63	15.16	4.36	6.04	10.4	5.56	/	[42]
Ulva spp.	Spain, seawater	/	Physical (microwave assisted)	23.74–32.52	/	3.37–5.96						/	[42]

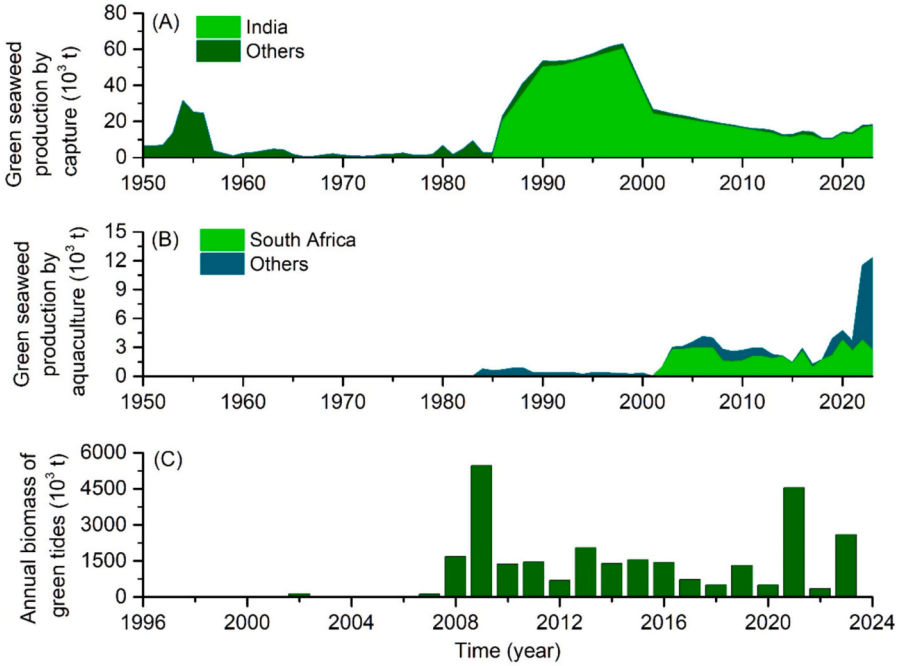

Fig. 2. Global green seaweed production (fresh weight) by wild harvesting (A) and aquaculture (B) and biomass of *Ulva*-driven green tides (C) in China. Data sources are FAO database (FishStatJ) and Feng et al. (2024). Biomass density of 2.6 kg/m^2 according to Xing et al. (2018), was used to convert coverage data in Feng et al. (2024) to biomass [46,47].

discrepancy highlights the critical role of extraction methodology in mediating morphological effects—harsh chemical treatments, for example, may disrupt filamentous cell walls more effectively, whereas gentle enzymatic approaches might favor foliose structures.

Thus, the influence of morphology on ulvan yield is not universal but contingent on extraction parameters, species-specific traits, and cell wall composition. These interactions underscore the need for standardized comparative studies across morphologies and methodologies to clarify how thallus structure influences ulvan biosynthesis and extractability. Such insights are essential for optimizing biomass selection and processing strategies in ulvan-based industries.

2.5. Environmental factors affecting ulvan composition

While anthropogenic environmental changes—including ocean acidification, warming, and eutrophication—are widely recognized to impact the physiological and biochemical characteristics of green macroalgae, relatively few studies have investigated their effects on polysaccharide content, particularly ulvan [35]. To date, no direct research has explicitly examined environmental influences on ulvan content. The closest relevant investigation by Olsson et al. (2020) analyzed how irradiance, temperature, nitrate, phosphate, and CO_2 affect the monosaccharide composition of *U. fenestrata* [43]. Based on our recalculation of the original data from Olsson et al. (2020), we found that increased temperature (13 °C to 18 °C) and higher irradiance (50 to 100 μE) enhanced monosaccharide levels (rhamnose, glucuronic acid, iduronic acid, xylose) by 5.8–31.7 %, while elevated phosphorus (1 to 50 μM) decreased these components by 3.0–11.7 %. Elevated CO_2 (400 to 2500 ppm) slightly reduced monosaccharides by 4.9–7.7 %, except for iduronic acid, which was unaffected. Conversely, increased nitrogen (150 to 500 μM) boosted iduronic acid by 13.6–15.0 % without altering other monosaccharides. Similarly, our recalculation of the data from Lahaye et al. (1995) [44], indicated that in *U. rigida*, normal seawater caused a 7.2–9.0 % decrease in rhamnose, 22.5–23.7 % reduction in uronic acid, and a 38.8–52.0 % increase in xylose compared with nitrogen enriched seawater, indicating that monosaccharide profiles are both environmentally sensitive and species-specific.

Lahaye et al. (1999) cautioned that pronounced variations in ulvan sugar composition and repeating structure proportions could not be definitively attributed to seasonal/ecophysiological fluctuations or species traits due to limited sample sizes [23]. However, *U. rotundata* exhibited clear seasonal ulvan variations, with summer extraction yields (6.1–9.5 %) lower than spring/autumn levels (7.7–10.4 %), a pattern absent in *U. armoricana* [5]. Light quality also impacts ulvan yield: *U. pertusa* showed maximum (25.1 %) and minimum (20.2 %) yields under 100 % blue LED and fluorescent light, respectively [21].

Collectively, current understanding of environmental effects on ulvan yield and composition remains highly limited. These scattered findings highlight the need for systematic investigations to clarify how specific abiotic factors influence ulvan biosynthesis across different green algal species, which will inform both ecological modeling and biotechnological applications of these valuable polysaccharides.

2.6. Ulvan production trends

Ulvan production is not only influenced by ulvan content in biomass but also fundamentally determined by the biomass of *Ulva* species, which originates from three primary sources: wild harvesting, aquaculture, and floating green tides.

2.6.1. Wild harvesting dynamics

Wild *Ulva* includes both attached and floating forms. Commercial capture of green seaweeds began in 1950, reaching a peak of 31.5 × 10^3 t fresh weight (FW) in 1954 before declining sharply due to overharvesting, stabilizing at 0.5–9.2 × 10^3 t FW between 1957 and 1985 (Fig. 2A). A subsequent rapid increase driven by large-scale harvesting in India—contributing over 85 % of global production—peaked at 63.0 × 10^3 t FW in 1998. However, production dropped to 10.5 × 10^3 t by 2019, likely due to resource depletion, followed by a gradual recovery to 18.1 × 10^3 t FW in 2023 (Fig. 2A).

2.6.2. Aquaculture development

Green seaweed aquaculture emerged significantly later than wild harvesting, with the first recorded efforts in Japan in 1984 (Fig. 2B).

Production remained negligible (0.2–1.0 × 10^3 t FW) from 1983 to 2002, solely supported by Japanese practices. Post-2003, driven by demand for abalone feed in South Africa, aquaculture output surged, reaching a historic high of 12.3 × 10^3 t FW in 2023 (Fig. 2B). This regional dominance highlights the industry's reliance on niche markets rather than broad commercial applications [45].

2.6.3. Green tides as a resource

Floating green tides represent an underutilized but massive biomass source. The largest documented event, recurring in China's Yellow Sea, first emerged in 1999 with a coverage of 1.83 km^2 and 4.8 × 10^3 t FW of biomass (Fig. 2C). After peaking in 2009, biomass fluctuated between 499.2 and 2054.0 × 10^3 t FW from 2010 to 2020 due to government intervention strategies. However, extreme weather in 2021 triggered a resurgence, yielding 4539.6 × 10^3 t FW—the second-highest recorded—overriding earlier mitigation efforts (Fig. 2C).

2.6.4. Comparative biomass analysis

Biomass scales differ starkly across sources: wild harvesting yields an order of magnitude higher than aquaculture, while green tides exceed wild harvests by another order of magnitude. For instance, this hierarchy underscores the untapped potential of green tides, though their sporadic nature complicates industrial utilization. In contrast to brown or red seaweeds—whose aquaculture production far surpasses that of green seaweeds—the limited commercial demand for green seaweeds likely discourages investment in large-scale cultivation, despite abundant wild and tidal resources.

These trends highlight the need for integrated strategies to leverage green tide biomass sustainably, improve aquaculture efficiency, and balance wild harvesting practices—critical for unlocking the full potential of ulvan production amid evolving environmental and market dynamics.

2.7. Ulvan production in future

Ulvan production is fundamentally governed by two key parameters: ulvan content within seaweed biomass and the total biomass of *Ulva* species. As anthropogenic pressures like eutrophication, ocean warming, and acidification persist, their direct impacts on ulvan content remain poorly understood due to limited empirical data. Current insights rely on surrogate metrics, such as carbohydrate content, which Gao et al. (2017) used to infer ulvan-related changes: combined stressors reduced total carbohydrates in *U. rigida* by 21 % compared to controls [35]. However, this approach estimates carbohydrates as the residual fraction of unmeasured biochemicals, introducing potential inaccuracies compared to direct ulvan quantification.

While global environmental changes may alter ulvan biosynthesis, shifts in *Ulva* productivity and biomass are likely to have a more profound effect on ulvan production, given their potential for drastic fluctuations. For example, green tide biomass in China has varied over 1148-fold in the past 25 years, reflecting *Ulva*'s exceptional capacity to capitalize on favorable conditions. Mechanistically, *Ulva* species exhibit competitive advantages in eutrophic waters, including allelopathic suppression of red tide microalgae [46,48], adaptive life history shifts during marine heatwaves [49,50], and shortened generation times under warming and acidification [51]. These traits portend more intense green tide events in future oceans [46], with experimental evidence showing *U. rigida* biomass increasing 100-fold under projected climate conditions after 60 days [51].

Given that green tide biomass can exceed wild harvest and aquaculture yields by orders of magnitude (Section 2.6), the escalating availability of *Ulva* biomass—driven by both environmental adaptation and eutrophication—represents a critical opportunity for ulvan production. While uncertainties remain regarding ulvan content under stress, the amplifying effect of biomass growth is likely to outweigh moderate changes in ulvan concentration, positioning *Ulva* as a resilient feedstock for future ulvan extraction. Strategic management of green tides and optimization of extraction technologies will be essential to harness this potential sustainably.

3. Carbon sequestration of ulvan

Carbon sequestration refers to the long-term storage of carbon dioxide (CO_2) or other forms of carbon to mitigate climate change by reducing atmospheric greenhouse gas concentrations [52]. This process is critical for achieving global carbon neutrality goals. Oceans, covering over 70 % of the Earth's surface, play a pivotal role in carbon cycling, with marine ecosystems acting as natural carbon sinks. Within this framework, the degradation of organic matter, including polysaccharides like ulvan, influences carbon storage efficiency by regulating the release and recycling of carbon in marine environments. Ulvan contributes to the marine carbon cycle through its structural complexity and recalcitrance to degradation. Unlike simpler storage polysaccharides (e.g., starch), ulvan's heterogeneous composition with intricate sulfation patterns—demands specialized enzymatic pathways for complete breakdown. This degradation process is biologically mediated by marine microorganisms, which secrete tailored enzymes to cleave ulvan's distinct glycosidic bonds [53].

3.1. Degradation of ulvan

To completely degrade a polysaccharide, bacteria must possess at least one specialized enzyme for each distinct chemical bond linking its monosaccharide building blocks. This biochemical requirement drives the evolution of elaborate polysaccharide-degrading cascades, where the repertoire of enzymes scales directly with the structural complexity of the target glycan. Compared to energy-storage polysaccharides, structural polysaccharides like fucoidan and xylans demand a more extensive enzymatic arsenal [20]. Given ulvan's diverse monosaccharide composition and branched architecture, its complete degradation presents a significant biochemical challenge.

To date, two classes of enzymes from distinct carbohydrate-active enzyme (CAZyme) families have been identified as critical for ulvan breakdown. Polysaccharide lyases (PLs) belonging to the PL24, PL25, and PL28 families catalyze the initial cleavage of glycosidic linkages between sulfated rhamnose (Rha3S) and uronic acid residues (GlcA or IdoA), generating oligosaccharides terminated with unsaturated uronic acids [54]. These reactive terminal residues are subsequently processed by glycoside hydrolases (GHs) from the GH105 family, which hydrolyze the modified linkages [55]. Genomic analyses reveal that bacteria such as *Formosa agariphila* encode ulvan-specific polysaccharide utilization loci (PULs), such as PULH, which cluster PL28, GH105, and over a dozen putative accessory enzymes predicted to facilitate ulvan catabolism. However, heterologous expression in *Escherichia coli* showed that only PL28 and GH105 exhibited direct ulvan-degrading activity, while other encoded enzymes remained inactive [55]. This suggests that complete ulvan degradation requires a coordinated, sequential enzymatic cascade rather than isolated enzyme actions.

Experimental validation by Reisky et al. (2019) further delineated the degradation pathway in *Formosa agariphila*, identifying a complex network of 12 biochemically characterized CAZymes—including two PLs, three sulfatases, and seven GHs—that act in concert to break down ulvan into fermentable monosaccharides [54]. These enzymes are encoded within a single genomic locus, highlighting the evolutionary adaptation of bacteria to assemble specialized enzymatic modules for degrading structurally complex polysaccharides. The interplay between these enzymes—each targeting specific glycosidic bonds and modifications—underscores the necessity of integrated, multi-enzyme systems to overcome the structural heterogeneity of ulvan, a paradigm consistent with the biochemical demands of degrading complex marine glycans.

The structural diversity and complexity of ulvan pose significant

challenges to its degradation by marine bacteria. While laboratory studies have identified bacteria capable of complete ulvan degradation, these investigations typically use extracted, purified ulvan and employ concentrated, isolated degradation enzymes. Such controlled conditions starkly contrast with natural environments, where ulvan occurs in complex matrices: it is tightly associated with cell wall proteins and metals, and living algal cells secrete compounds that actively inhibit bacterial degradation.

Additionally, resource and energy limitations profoundly constrain the capacity of heterotrophic microorganisms to degrade ulvan in situ. The genomes of these bacteria encode a limited repertoire of CAZymes due to evolutionary trade-offs, and the expression of these enzymes is tightly regulated. CAZyme synthesis and secretion demand substantial energy and nitrogen; for example, baseline expression is required even in the absence of ulvan to enable glycan detection [56], while constitutive secretion in nutrient-limited environments can reduce bacterial growth rates [57]. To balance these costs, bacteria have evolved adaptive strategies: some tether CAZymes to their cell surfaces or internalize digestion to minimize energy expenditure [58], whereas others enhance secretion of free enzymes to exploit transient glycan availability [59]. These ecological constraints—shaped by nutrient availability, energy budgets, and yet-unknown factors—ultimately dictate the repertoire, subcellular localization, and expression levels of CAZymes, exacerbating the intrinsic difficulty of ulvan degradation in natural systems. Further complicating this process, field-derived ulvan can undergo microbial transformation into more refractory compounds [60], which resist further decomposition.

3.2. Carbon sequestration potential by ulvan

Collectively, the factors—structural complexity, inhibitory cellular interactions, and microbial energetic trade-offs—highlight the limited efficiency of bacterial ulvan degradation in nature. This inefficiency, paradoxically, positions ulvan as a critical component of carbon sequestration by *Ulva* species, as its slow turnover contributes to long-term carbon retention in marine ecosystems. *Ulva* is a cosmopolitan genus of green macroalgae with a global distribution across freshwater, brackish, and marine ecosystems. Among the 594 recognized taxa in the genus, 130 have been formally taxonomically described [61]. Most *Ulva* thalli exhibit uniform morphological features, consisting of one or two layers of cells with a diffuse growth habit. This structural simplicity likely minimizes non-photosynthetic tissue, enabling net carbon uptake under optimal conditions [62]. Compared to other macroalgae, *Ulva* species possess a higher surface-area-to-volume ratio, with thicker thalli that enhance nutrient absorption efficiency. The genus demonstrates remarkable tolerance to dynamic environmental parameters, including fluctuations in light intensity, salinity, and temperature [63,64]. These traits collectively render *Ulva* an opportunistic taxon capable of rapid proliferation and bloom formation under favorable conditions.

A notable example is the massive green tide in China's Yellow Sea caused by *Ulva prolifera*, which reached a peak daily coverage of 1350 km^2 and accumulated 2.3 million tonnes (fresh weight, FW) of biomass in 2016 [65]. Assuming ulvan constitutes 11 % of cellular dry weight (Table 1), this bloom would have produced 278 × 10^3 t of ulvan given dry/fresh weight is 0.11 [66]. Beyond China, *Ulva* blooms occur globally in regions such as South Korea, Japan, Australia, the USA, the UK, France, and Denmark. The incidence of such green tides is escalating due to synergistic pressures from eutrophication and climate change [46,51], suggesting increased ulvan production during future blooms. Ulvan functions not only as a structural component of the cell wall but can also be excreted into seawater as dissolved organic carbon (DOC). For instance, *Ulva pertusa* releases approximately 8 mg DOC per gram of fresh weight (FW) during a 4-h light period [67]. Assuming DOC is released exclusively during a 12-h light period, the daily DOC release rate totals 24 $mg \cdot g^{-1}$ $FW \cdot d^{-1}$. If half of this DOC is ulvan, the 2016 *Ulva prolifera* bloom—with a biomass of 2.3 million tonnes FW would have generated 0.83 million tonnes of ulvan-derived carbon over 30 days.

In addition to floating *Ulva* blooms, *Ulva* species usually dominant intertidal zones worldwide in the form of attaching hard substances, particularly in the upper part of the intertidal zone. For instance, the

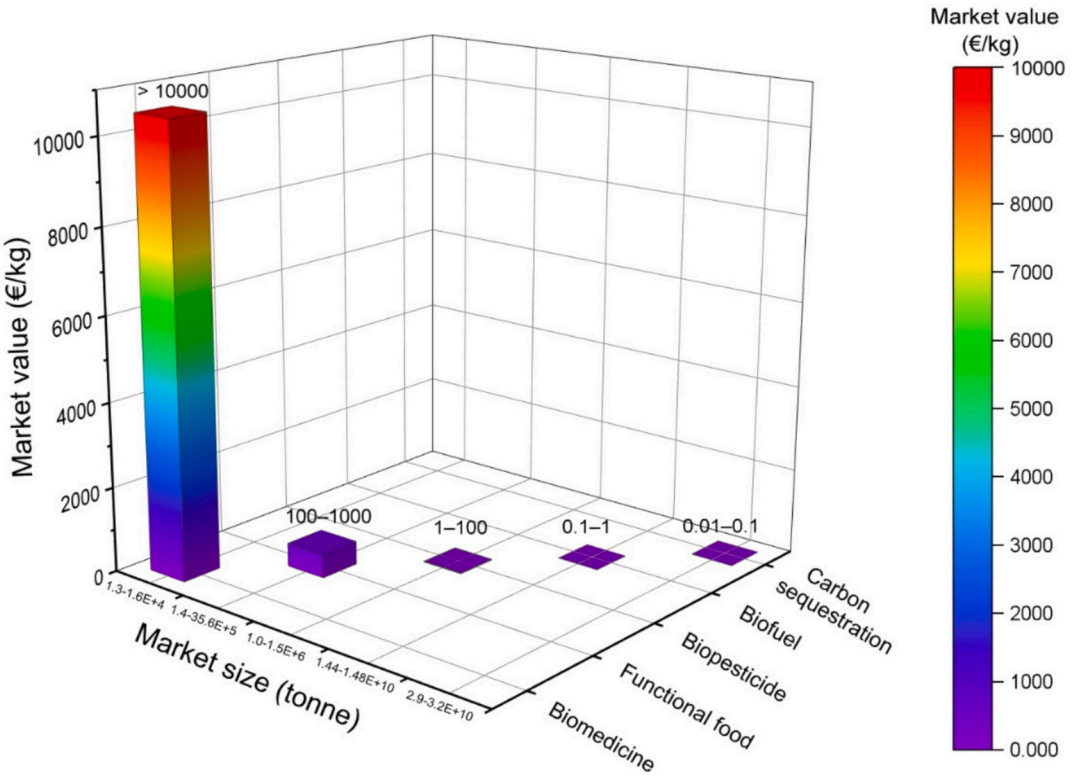

Fig. 3. Market value and size of various ulvan applications. The data are based on Prabhu et al. (2020), Hofmann et al. (2024) and authors' product inquiry [70,71].

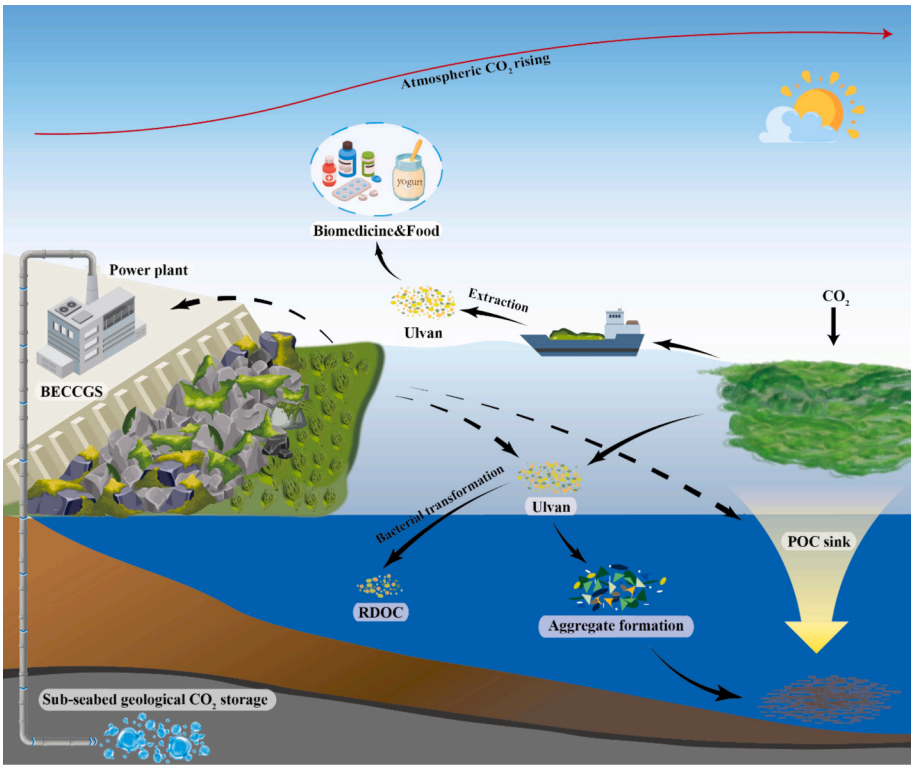

Fig. 4. Nature-based ulvan production and utilization. Coastal attached *Ulva* is collected and used for biofuel combined with carbon capture and geological storage (BECCGS). Offshore floating *Ulva* is harvested and ulvan is extracted for food and biomedicine. Both pathways can contribute to carbon sequestration by POC (particle organic carbon) sinking and RDOC (refractory dissolved organic carbon) formation.

biomass of *Ulva* at six coastal sites of Ireland reaches up to 9.15 million tonnes (dry weight) [68] and attached *Ulva* bloom could reach a biomass of 60,000 t (dry weight) in Australia [69]. Considering that wide distribution of *Ulva* in coastal areas of the world, attached *Ulva* can also make a substantial contribution to ulvan production in the forms of both POC and DOC.

4. Integrated utilization of ulvan: market analysis and nature-based strategies

4.1. Market value and size of ulvan applications

Market values (€/kg) and sizes (tonnes) for various ulvan applications vary significantly. Biomedicine commands the highest market value, exceeding 10,000 €/kg, while having the smallest market size (Fig. 3). This high-value segment likely reflects specialized biomedical uses—such as pharmaceutical or research applications—where premium pricing justifies smaller-scale production. In contrast, functional food applications exhibit a significantly larger market size, spanning 1.4 $\times$ 10^5 to 35.6 $\times$ 10^5 t, yet with a lower market value (100–1000 €/kg), indicating broader adoption in consumer-facing products. Biopesticide, biofuel, and carbon sequestration applications display progressively larger market sizes but lower market values. These trends underscore the diverse economic landscapes of ulvan applications, guiding strategic investments toward high-value biomedical uses or scalable functional food markets. On the other hand, biomedicine and food applications have high requirements for *Ulva* sources and ulvan purity, increasing production costs. In contrast, biofuel and carbon sequestration applications have lower requirements for *Ulva* sources and ulvan purity, making them suitable for utilizing high-volume, lower-quality *Ulva* biomass [70,71].

4.2. Nature-based ulvan production and integrated utilization strategy

Given the diverse biological and ecological functions of ulvan, we propose an integrated utilization strategy. As discussed earlier, future oceans are likely to experience more green tides, both in floating and attached forms. Thus, this strategy fully leverages wild *Ulva*, a nature-based solution (Fig. 4).

Floating *Ulva* can be harvested to extract ulvan for biomedicine and functional food applications. Being farther from coastlines, floating *Ulva* typically contains fewer pollutants (e.g., heavy metals, antibiotics, persistent organic pollutants), making it more suitable for biomedicine, food, and feed products that have strict contamination standards. The profitability would be substantial, considering the low raw material costs (from wild harvesting) and high product values (Fig. 3).

Meanwhile, coastal-attached *Ulva* can be utilized for bioenergy production. Bioenergy applications have lower requirements for heavy metals and other pollutants, which is advantageous as coastal-growing *Ulva* may contain such contaminants. Reducing *Ulva* biomass in coastal areas can also promote seaweed biodiversity [72]. Moreover, *Ulva* exhibits a high biomethane yield; for example, the biochemical methane potential of *U. rigida* can reach up to 286 mL CH_4 g^{-1} VS [73]. CO_2 emitted from biomethane-powered plants can be captured, transported, and stored in sub-seabed geological reservoirs (such as saline aquifers and depleted oil and gas reservoirs), integrating bioenergy with carbon capture and offshore storage (BECCOS). Compared to onshore CO_2 storage, offshore storage avoids issues like CO_2 contamination of drinking water and potential disruptions to agricultural and industrial activities [74]. Additionally, considering that coastal areas are major CO_2 emission sources, offshore CO_2 storage offers transport cost advantages over onshore storage [74].

Beyond artificial CO_2 storage, particulate organic carbon (POC) and dissolved organic carbon (DOC) released during *Ulva* growth and decay

(in both attached and floating forms) significantly contribute to CO_2 sequestration, especially given the resistance of ulvan to degradation and its transformation into more refractory compounds. Moreover, the transport of POC from coastal waters to the deep ocean can further reduce carbon remineralization, aiding carbon sequestration [19]. In summary, the integrated utilization of ulvan from natural *Ulva* biomass not only generates high-value products but also provides essential ecological services, such as mitigating green tides, enhancing seaweed biodiversity, and combating climate change (Fig. 4).

5. Conclusions and future research needs

5.1. Conclusions

This review systematically synthesizes the distribution patterns of ulvan in green macroalgae, with a critical analysis of factors governing its extraction yield—from species-specific variations to environmental drivers like temperature and light. Unlike conventional studies focusing primarily on ulvan's biomedical properties, this work breaks new ground by integrating its ecological significance into the research framework. We reveal ulvan's dual roles in marine ecosystems: as a bioactive polysaccharide with industrial utility and as a recalcitrant carbon reservoir due to its resistance to microbial degradation, particularly relevant amid escalating green tide biomass driven by eutrophication. Building on this, we propose a novel nature-based utilization model that differentiates ulvan extraction strategies: high-purity ulvan derived from offshore macroalgae supports food and biomedical industries, while coastal algal biomass is channeled into bioenergy production, with captured CO_2 sequestered in geological reservoirs. This framework establishes a circular "biorefinery-ecosequestration" system, bridging ulvan's biotechnological potential with global carbon neutrality objectives—a conceptual advance that addresses both ecological problems and planetary sustainability. Looking forward, future research should prioritize the following directions.

5.2. Future research needs

5.2.1. Strain engineering and production

Efforts must focus on developing genetic engineering tools, such as CRISPR-Cas9 systems, to modify algal strains for producing ulvan with tailored structural features—for example, increased sulfation to enhance antiviral activity—or to boost production yields. Additionally, research is necessary to investigate how growth conditions, including temperature, light intensity, and nutrient availability, influence ulvan's molecular structure, enabling precise control over biosynthesis to meet the requirements of specific applications.

5.2.2. Sustainable extraction and processing

Optimization of green extraction methods, such as enzymatic hydrolysis and microwave-assisted extraction, is essential to preserve the structural integrity of ulvan while improving extraction efficiency. Concurrently, the development of scalable purification techniques—including membrane filtration and chromatography—should be prioritized, accompanied by the establishment of standardized quality control metrics for key parameters like molecular weight and sulfation degree. Furthermore, initiatives to integrate byproducts from ulvan extraction into value-added outputs, such as biofertilizers and animal feed, will enhance the circularity of the production process and reduce waste.

5.2.3. Applied research

To align different ulvan variants—differentiated by their structural characteristics (e.g., sulfation patterns, monosaccharide composition)—with specific applications in pharmaceuticals, cosmetics, food science, and materials engineering, rigorous research is required to characterize the relationship between ulvan's structural features and its functional properties, including biological activities and material performance. Moreover, future studies should aim to refine and integrate ulvan's use across diverse sectors, such as advancing its role in biotechnological applications (e.g., drug delivery systems, prebiotic formulations) and ecological services (e.g., enhancing carbon sequestration and improving water quality).

5.2.4. Ecological effects of ulvan

Quantification of ulvan excretion rates by green seaweeds in both natural and cultivated environments, along with investigations into how these rates fluctuate under varying environmental conditions (e.g., salinity, nutrient levels), is critical to understanding its ecological role. Additionally, research must clarify the microbial transformation and decomposition processes of ulvan by bacterial communities, as well as the associated ecological impacts, such as effects on nutrient cycling, microbial diversity, and ecosystem dynamics. Investigations should also assess the potential of ulvan—both as intact biomass and through its degradation products—to contribute to climate change mitigation, including its role in marine carbon sequestration and oceanic carbon cycling.

5.2.5. Sustainability and regulation

Comprehensive life cycle assessments (LCAs) are necessary to evaluate the environmental footprint of ulvan production, from cultivation and extraction to processing and end-of-life disposal, identifying opportunities to enhance sustainability through process optimization. Efforts must also focus on establishing regulatory guidelines for ulvan purity, safety (including standardized toxicity testing), and labeling requirements, particularly for food and medical applications, to facilitate commercial adoption and ensure consumer confidence. Finally, promoting sustainable cultivation practices, such as integrated multi-trophic aquaculture, will be vital to minimizing ecological impacts—such as habitat disruption or nutrient runoff—associated with large-scale ulvan production systems.

CRediT authorship contribution statement

Xin Zhao: Writing – review & editing, Writing – original draft, Visualization, Validation, Methodology, Investigation. **Xiaoyu Wang:** Writing – review & editing, Visualization, Methodology. **Junxiao Zhang:** Writing – review & editing, Methodology. **Lan Feng:** Writing – review & editing, Methodology. **Guang Gao:** Writing – review & editing, Writing – original draft, Validation, Supervision, Methodology, Investigation, Funding acquisition, Conceptualization.

Declaration of competing interest

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

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Data availability

All data are included in this article.

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