Green seaweed *Ulva* spp. bioprocessing: Bioactive molecules, emerging extraction technologies, and industrial applications in the circular bioeconomy

Thomas Wichard [1,*,§], Paula Mapelli-Brahm[2,§], Francisco J. Barba[3], Rosario Domingues[4], Lior Guttman[5], Lenka Hutarova[6], Joana Loureiro[7], Dilek Unal[8], Pelin Koseoglu-Yilmaz[9], Gabrielle Zammit[10], Antonio Jesús Meléndez Martínez[2]

Affiliations

1. Friedrich Schiller University Jena, Institute for Inorganic and Analytical Chemistry, Lessingstr. 8, 07743 Jena, Germany
2. Food Colour and Quality Laboratory, Facultad de Farmacia, Universidad de Sevilla, 41012, Sevilla, Spain
3. Research group in Innovative Technologies for Sustainable Food (ALISOST), Department of Preventive Medicine and Public Health, Food Science, Toxicology and Forensic Medicine, Faculty of Pharmacy and Food Sciences, Universitat de València, Burjassot, 46100, València, Spain
4. CESAM – Centre for Environmental and Marine Studies; Mass Spectrometry Center, LAQV-REQUIMTE, Department of Chemistry, University of Aveiro, Campus Universitário de Santiago; 3810-193 Aveiro, Portugal
5. The Department of Blue Biotechnologies and Sustainable Mariculture, The Leon H. Charney School for Marine Science, University of Haifa, Israel.
6. Institute of Biology and Biotechnology, Faculty of Natural Sciences, University of Ss. Cyril and Methodius in Trnava, Trnava, Slovakia
7. LEPABE - Laboratory for Process Engineering, Environment, Biotechnology and Energy; ALiCE - Associate Laboratory in Chemical Engineering, Faculty of Engineering; Department of Metallurgical and Materials Engineering, Faculty of Engineering, University of Porto, 4200-465 Porto, Portugal
8. The Department of Molecular Biology and Genetic, Faculty of Science, University of Bilecik Seyh Edebali, 11230, Bilecik, Turkiye
9. Department of Analytical Chemistry, Faculty of Pharmacy, Istanbul University, 34116, Istanbul, Turkiye
10. Department of Biology, Faculty of Science, University of Malta, Msida, MSD2080, Malta.

* Corresponding author: thomas.wichard@uni-jena.de
§ Joint first authorship

OrcID

- Thomas Wichard: https://orcid.org/0000-0003-0061-4160
- Paula Mapelli-Brahm: https://orcid.org/0000-0003-1940-442X
- Francisco J. Barba: https://orcid.org/0000-0002-5630-3989
- Rosário Domingues.https://orcid.org/0000-0001-5357-3601
- Lior Guttman: https://orcid.org/0000-0002-7714-2643
- Lenka Hutarova: https://orcid.org/0000-0002-0131-1797
- Joana Loureiro: https://orcid.org/0000-0002-9841-3967
- Dilek Unal: https://orcid.org/0000-0002-6915-9699
- Pelin Koseoglu-Yilmaz: https://orcid.org/0000-0002-9871-1710
- Gabrielle Zammit: https://orcid.org/0000-0003-2890-5736
- Antonio Jesús Meléndez-Martínez: https://orcid.org/0000-0002-1553-2427

Abstract

Ulva, commonly known as "sea lettuce," is a resilient green macroalga and a promising sustainable source of bioactive compounds. Thriving in nutrient-rich waters and amenable to cultivation, *Ulva* is abundant in coastal ecosystems and well positioned to support marine circular economies. This review critically evaluates its chemical composition, bioactivities, extraction technologies, and industrial applications relevant to the food, pharmaceutical, cosmetic, and agricultural sectors. *Ulva* biomass contains polysaccharides (notably ulvan), proteins, essential amino acids, polyunsaturated fatty acids, polar lipids, vitamins, minerals, carotenoids, and phenolic compounds. These constituents are associated with diverse health-promoting properties, including antioxidant, anti-inflammatory, antimicrobial, neuroprotective, and antihyperlipidemic activities. Advances in extraction are expanding the potential for scalable, efficient recovery of high-value compounds. Emerging methods include ultrasound-assisted extraction, microwave-assisted extraction, enzyme-assisted extraction, pressurized liquid extraction, and supercritical fluid extraction. Complementary developments in green solvents, such as bio-based reagents, deep eutectic solvents, and ionic liquids, offer environmentally friendly alternatives to conventional solvents. The range of potential applications is broad, encompassing functional foods, dietary supplements, animal feed, bio-based packaging, cosmetics, and pharmaceuticals. Integrating *Ulva* into sustainable value chains directly supports the United Nations Sustainable Development Goals , particularly in relation to health, resource efficiency, and environmental protection. Despite significant progress, challenges remain in taxonomic resolution, biomass standardization, large-scale biorefinery implementation, and regulatory harmonization. We conclude that *Ulva* holds strong promise as a flagship marine bioresource, provided that advances in biotechnology, aquaculture engineering, and green chemistry are coupled with enabling policies that facilitate its full integration into the emerging blue bioeconomy.

Keywords

Ulva spp.; Ulvan; Bioactive compounds; Green extraction technologies; Biorefinery; Circular bioeconomy; Sustainable applications

1. Introduction

Ulva Linnaeus (Chlorophyta, Ulvales, Ulvaceae), commonly known as sea lettuce, is a green macroalga frequently associated with diverse microbial consortia. Seaweeds have long been exploited for food, medicine, construction materials, and livestock feed, and continue to play vital ecological and economic roles in coastal regions. Many *Ulva* species exhibit exceptionally rapid growth, often forming extensive blooms, or "green tides," in nutrient-rich coastal zones influenced by agricultural runoff and urban wastewater (Smetacek and Zingone, 2013; Areco et al., 2021). The high biomass productivity of *Ulva*, together with its rich repertoire of bioactive compounds and adaptability to diverse cultivation systems, positions it as an ideal candidate for sustainable bioprocessing (Fernand et al., 2017). As a potential source of valuable metabolites, *Ulva* has gained increasing attention for applications in the food, feed, pharmaceutical, and cosmetic industries (**Fig. 1, Table 1**). Within the framework of the circular bioeconomy, integrated biorefinery strategies allow for the efficient valorization of *Ulva* biomass through green extraction technologies, supporting zero-waste objectives and the development of high-value bioproducts (Ozogul et al., 2025).

This review provides a concise overview of *Ulva* biology and synthesizes recent advances in the extraction and application of its bioactive substances, with emphasis on sustainable and cost-effective methodologies. Key nutritional components—including lipids, sterols, oligosaccharides, polysaccharides, vitamins, minerals, carotenoids, and phenolic compounds—are examined alongside emerging extraction technologies and environmentally friendly solvents. Industrial applications in the food, pharmaceutical, cosmetic, and agricultural domains, as well as relevant regulatory considerations, are also critically evaluated.

1.1. *Ulva* in aquaculture

Due to its high areal productivity and broad environmental tolerance, *Ulva* is suitable for both wild harvesting and controlled cultivation. The genus comprises foliose and tubular species found in marine, estuarine, and freshwater environments, many of which hold substantial commercial relevance (Tran et al., 2022). Individual thalli range in size from a few millimeters to several meters and display significant morphological diversity. However, this simplicity and variability often complicate species identification, as many *Ulva* taxa share overlapping morphologies. Ongoing taxonomic and nomenclatural revisions reflect this complexity (Hughey et al., 2021), and species names cited in this review should be considered provisional.

Molecular tools, including sequencing of the plastid-encoded ribulose-1,5-bisphosphate carboxylase/oxygenase large subunit (*rbcL*) gene, elongation factor Tu (*tufA*), and the internal transcribed spacer (ITS) region, have revealed previously unrecognized *Ulva* species in the Mediterranean Sea (Bartolo et al., 2022; Wolf et al., 2012) and the Yellow Sea (Cai et al., 2021; Liu et al., 2016). These studies underscore the limitations of morphology-based taxonomy and highlight the importance of genetic identification for ensuring safety, reproducibility, and consistency in commercial *Ulva* products (Simon et al., 2022; Steinhagen et al., 2019, 2022).

Note: Because of unresolved taxonomy and historical mislabeling, *Ulva* species names should not be used for direct data pooling or quantitative comparison across studies.

Seaweed aquaculture is increasingly central to the sustainable Blue Economy, valued for its low environmental footprint and reservoir of compounds applicable in food, feed, and cosmetics (Jesús Alberto et al., 2016; Holdt and Kraan, 2011; Naylor et al., 2021). Large-scale *Ulva* cultivation has been successfully integrated with abalone farming in South Africa (Bolton et al., 2009) and Scandinavia (Steinhagen et al., 2022). Cultivation methods are diverse, ranging from recirculating aquaculture systems (Shpigel et al., 2019) to integrated multitrophic aquaculture (IMTA), where *Ulva* functions as a biofilter, to offshore seaweed farms (Fernand et al., 2017; Steinhagen et al., 2021) and highly controlled systems with defined microbiomes

(Wichard, 2023). The life cycle of *Ulva* is well characterized and manipulable, an essential feature for industrial cultivation. Most species exhibit isomorphic alternation between gametophytic and sporophytic stages, though parthenogenesis can also occur, producing clonal gametophytes without fertilization (Hoxmark and Nordby, 1974). For aquaculture, vegetative propagation is generally preferred to maintain yield, and sporulation is typically suppressed to prevent biomass loss (Vesty et al., 2015). Predictive models of biomass accumulation and sporulation events are under active development to optimize production in large-scale algal aquaculture (Obolski et al., 2022).

1.2. *Ulva* and associated bacteria

Ulva forms intimate associations with specific bacterial communities that are essential for normal morphogenesis and development (Singh and Reddy, 2014; Wichard et al., 2015; Saha et al., 2024). In the absence of key bacteria, *Ulva* fails to differentiate properly and develops into a callus-like morphology (Spoerner et al., 2012). Normal morphogenesis can be restored by introducing certain bacteria or their released signaling compounds, such as thallusin (Dhiman et al., 2022; Wichard, 2023). Recent studies show that bacterial families including Flavobacteriaceae and Roseobacteriaceae promote the growth and development of *U. compressa*, even under stress conditions (Ghaderiardakani et al., 2022). These microbial partners may also enhance the nutritional and commercial value of *Ulva* by influencing metabolite production (Polikovsky et al., 2020; Holbl et al., 2025).

1.3. Bioactive compounds in *Ulva*

Ulva is a natural reservoir of bioactive compounds, including polysaccharides, proteins, peptides, amino acids, polyphenols, lipids, and pigments, many of which display biological and therapeutic activities (**Table 1**). The abundance and composition of these constituents are influenced by genetic background (Steinhagen et al., 2022), life cycle stage, and environmental parameters such as temperature, salinity, irradiance, and nutrient availability (Simon et al., 2022). Interest in *Ulva* as a functional ingredient for food, nutraceutical, and cosmeceutical applications is driven by its documented health benefits. Epidemiological evidence indicates that populations with high seaweed consumption exhibit lower rates of diet-related illnesses and greater life expectancy (Pangestuti et al., 2021). However, because of ongoing taxonomic uncertainty, reported concentrations of bioactives should not be directly compared across studies, even when referring to the same nominal species (**Tables 2–6**).

1.4. Culinary and industrial applications

Historically, seaweed has been valued for its nutritional content and broad availability. *Ulva* has become increasingly popular as a sea vegetable, consumed in salads, soups, and as an alternative to nori in sushi (Hollants et al., 2013). It is also incorporated as a food additive in processed products. As an alternative protein and mineral source to conventional crops, *Ulva* holds considerable potential. Its nutritional composition should be assessed using standardized protocols, such as those recommended by the Association of Official Agricultural Chemists (AOAC) (Echave et al., 2021). Wild-harvested *Ulva* blooms are already processed into health and animal nutrition products worldwide (Dominguez and Loret, 2019). Beyond nutrition, recent studies have demonstrated antibacterial, antifungal, and anti-inflammatory properties, positioning *Ulva* as a promising candidate for novel therapeutic and industrial applications (Shobier and El Ashry, 2021).

1.5. Sustainable exploitation of aquatic resources

The global transformation of production systems requires meeting growing food demand while reducing the prevalence of diet-related diseases and safeguarding resources for future generations. The landmark EAT–Lancet Commission report, developed by an international consortium of experts in health, agriculture, policy, and sustainability, sets scientific targets aligned with the United Nations Sustainable Development Goals (SDGs) and the Paris Agreement. According to the United Nations (2021), food production exerts the greatest anthropogenic pressure on the planet: agriculture occupies ~40% of global land, contributes ~30% of greenhouse gas emissions, and consumes ~70% of freshwater resources. At the same time, poor diets now pose a greater health risk than alcohol, tobacco, drug use, and unsafe sex combined. More than 820 million people face undernourishment, 151 million children experience stunting, and nearly 2 billion adults are overweight or obese. Furthermore, the global prevalence of diabetes has nearly doubled in the past three decades. To address these interconnected crises, the report highlights three strategies: reducing food loss and waste, shifting dietary patterns, and adopting sustainable production systems (Willett et al., 2019).

Overexploitation of terrestrial land for agriculture underscores the need to explore the potential of aquatic ecosystems and leverage their vast biodiversity. Seaweed aquaculture, which accounts for nearly 50% of global mariculture output, offers multiple advantages. Beyond serving as food and raw materials for various industries, seaweed cultivation provides key ecosystem services, including carbon sequestration and water quality improvement (Duarte et al., 2021). In addition, seaweeds represent promising feedstocks for biofuels, hydrogen, biochar, and other bioproducts, aligning with circular economy principles (del Río et al., 2020; Steinbruch et al., 2020).

2. *Ulva* nutrients and other dietary compounds

Marine macroalgae such as *Ulva spp.*, in close association with their microbiomes, produce a diverse array of bioactive compounds with ecological, nutritional, and industrial significance. The following subsections highlight major categories of these bioactive constituents.

2.1. Lipids

Lipids are a diverse class of hydrophobic organic molecules that include fatty acyls, sterols, triacylglycerols, hormones, and complex membrane lipids. The principal lipid constituents in *Ulva* are fatty acids (FAs), polar glycerolipids (e.g., phospholipids, glycolipids, and betaine lipids), and sterols. These compounds serve as structural elements of cellular membranes, energy reserves, and mediators of signaling pathways (Jouhet et al., 2024).

In *Ulva* species, total lipid content is generally modest, averaging ~2% of dry weight (dw) (Kendel et al., 2015; Moreira et al., 2021), although higher levels (up to 15% dw) have been reported in certain taxa (El-Sheekh et al., 2021). Despite their relatively low abundance, *Ulva* lipids contain nutritionally and pharmacologically valuable components. The FA profile includes both saturated fatty acids (SFAs) and unsaturated fatty acids (UFAs), the latter encompassing monounsaturated fatty acids (MUFAs) and polyunsaturated fatty acids (PUFAs). Common SFAs include myristic acid (C14:0), palmitic acid (C16:0), stearic acid (C18:0), and behenic acid (C22:0), with palmitic acid typically the most abundant, consistent with other macroalgae (McCauley et al., 2016; Moreira et al., 2020). UFAs often constitute ~60% of total FAs in *Ulva*. Reported MUFAs include myristoleic acid (C14:1), palmitoleic acid (C16:1), oleic acid (C18:1 n-9), and vaccenic acid (C18:1 n-7). The PUFA fraction is dominated by C16 and C18 chains, which together account for ~85% of total FAs, including hexadecatetraenoic acid (C16:4 n-3), stearidonic acid (C18:4 n-3), linoleic acid (C18:2 n-6), and α-linolenic acid (C18:3 n-3). These compounds exhibit algicidal properties that may confer ecological advantages (McCauley et al., 2016) and also represent nutritionally important essential FAs such as C18:2 n-6 and C18:3 n-3, as well as omega-3 (ω3) FAs. Longer-chain PUFAs, including arachidonic acid (C20:4 n-6), eicosapentaenoic acid (EPA; C20:5 n-3), and docosapentaenoic acid (DPA; C22:5 n-3), occur in smaller, species-dependent amounts (Alsufyani et al., 2014; Moreira, 2020). Several *Ulva* species—including *U. lobata*, *U. lactuca*, *U. rigida*, and *U. armoricana*—are particularly enriched in C18 PUFAs (Ivanova et al., 2013; Kendel et al., 2015; Nelson et al., 2002; Ortiz et al., 2006), with *U. lobata* also containing notable levels of C16 and C22 PUFAs (Nelson et al., 2002).

Notably, *Ulva spp.* possesses higher levels of essential PUFAs compared to most terrestrial plants (Ortiz et al., 2006). These include both omega-3 (ω-3) and omega-6 (ω-6) FAs, distinguished by the position of the first double bond from the methyl end. The lipidome of *U. rigida* includes ALA and DPA (Lopes et al., 2019). Reported FA profiles show high variability, influenced by species-specific genetics, environmental conditions, and differences in extraction and analytical methodologies (McCauley et al., 2016; Nelson et al., 2002; Zammit et al., 2023). Marine-derived ω-3 PUFAs from *Ulva* exhibit significant health-promoting properties; for example, higher ω-3 intake is associated with reduced heart failure risk (Sakamoto et al., 2019). The favorable ω-6/ω-3 ratio in *Ulva* is also considered beneficial for both human and animal health (Ivanova et al., 2013).

Polar lipids, including phospholipids, glycolipids, and betaine lipids, constitute a substantial proportion of the lipid fraction, typically ranging from ~20% to 60% of total lipids (Cardoso et al., 2017; Kumari et al., 2014). Their abundance and composition vary with environmental conditions, seasonal changes, geographic origin, and species (Cardoso et al., 2017; Kumari et al., 2014; Moreira et al., 2020, 2021). Glycolipids, localized mainly in plastidial and thylakoid membranes, are among the most prominent polar lipids. These include the neutral galactolipids monogalactosyldiacylglycerol (MGDG) and digalactosyldiacylglycerol (DGDG), as well as the acidic sulfolipid sulphoquinovosyldiacylglycerol (SQDG) (Lopes et al., 2019, 2021).

Phospholipids such as phosphatidylglycerol are also prevalent in *Ulva*, functioning in membrane architecture and photosynthetic complex assembly. Other classes include phosphatidylethanolamine, phosphatidylinositol, phosphatidylserine, and phosphatidic acid. Phosphatidylcholine, a major phospholipid in many other seaweeds, is present only in low amounts in *Ulva* (Kumari et al., 2014; Lopes et al., 2019, 2021). Betaine lipids, including diacylglycerol 3-O-4′-(N,N,N-trimethyl) homoserine, have been detected in extraplastidial membranes of *Ulva*. These zwitterionic, phosphorus-free lipids are structurally analogous to phosphatidylcholine and may be upregulated under phosphorus-deficient conditions (van Ginneken et al., 2017). Polar lipids act as key carriers of essential FAs such as LA (ω-6) and ALA (ω-3). Compared with triglycerols, phospholipids and glycolipids enhance the bioaccessibility and bioavailability of ω-3 FAs (Lordan et al., 2017). However, the FA composition of polar lipids is sensitive to environmental fluctuations. For example, warm acclimation has been shown to decrease the n-3/n-6 and UFA/SFA ratios, as well as the overall unsaturation index (Barkina et al., 2020; Monteiro et al. 2022; Gnayem et al. 2024).

Beyond their nutritional value, polar lipids from *Ulva* exhibit diverse bioactive properties. Marine-derived phospholipids and glycolipids have been linked to the prevention of chronic diseases such as cardiovascular disorders (Lordan et al., 2017). Lipid extracts from *U. lactuca* improved serum and hepatic lipid profiles in rats fed a high-fat, high-cholesterol diet by lowering total cholesterol and increasing high-density lipoprotein (HDL) levels (Kushnerova et al., 2022). Specific glycolipids, such as DGDG (14:0_18:3) from *U. armoricana*, display antiproliferative activity against non-small cell lung carcinoma (NSCLC-N6) cells (Kendel et al., 2015). Other lipid extracts from *Ulva* species demonstrate antioxidant (Lopes et al., 2019), antimicrobial (Moreira et al., 2021), and anti-inflammatory effects.

Given the combined nutritional and bioactive roles of ω-3, ω-6, and polar lipids in *Ulva spp.*, these seaweeds hold considerable potential for applications in the food, feed, cosmetic, pharmaceutical, and biotechnology sectors (Kumari et al., 2010; Moreira et al., 2021). However, careful selection of species and strains is critical, as variations in PUFA content influence both nutritional quality and sensory characteristics (Alsufyani et al., 2014; Moreira et al., 2021). Odor development often arises from the breakdown of unsaturated FAs into smaller aldehydes, alcohols, or ketones. The production of oxylipins varies significantly among *Ulva* species and morphotypes and should therefore be considered in strain selection for food applications (Alsufyani et al., 2014; Roleda and Heesch, 2021).

2.2. Steroids

Steroids are triterpenoid molecules composed of six isoprene units arranged into a core cyclopentane-perhydrophenanthrene ring system. In *Ulva*, they function as membrane constituents and hormonal precursors, contributing to reproduction, signaling, and stress adaptation (Berneira et al., 2021; Fomenko et al., 2019). Steroid profiles vary among macroalgal taxa and can serve as useful taxonomic markers. Green algae, including *Ulva*, typically contain a broad spectrum of sterol derivatives. Reported compounds include 28-isofucosterol, cholesterol, β-sitosterol, fucosterol, campesterol, brassicasterol, and several rare sterols (Al Khazan et al., 2016; Geng et al., 2017; Shah et al., 2020; Eltamany et al., 2021).

Steroids from *Ulva spp.* exhibit a range of bioactivities, including antioxidant, antitumor, antibacterial, antiviral, antifungal, and anti-ulcerative effects (Berneira et al., 2021; Vanbrabant et al., 2021). For example, 24(R,S)-saringosterol acts as a liver X receptor agonist and crosses the blood–brain barrier, suggesting therapeutic potential for neurological disorders such as Alzheimer’s disease. Cholest-4-en-3-one, a cholesterol derivative found in both plants and animals, is an intermediate in steroid biosynthesis and autoxidation, with additional anti-obesity effects mediated through intestinal cholesterol catabolism. Phytosterols such as campesterol, brassicasterol, and isofucosterol lower serum cholesterol by reducing its intestinal absorption (Kendel et al., 2015) (**Table 2**).

Other notable *Ulva* steroids include cholest-5-en-3-ol, which shows moderate antialgal activity against red tide microalgae (Sun et al., 2016), and several complex derivatives (e.g., stigmasta-5,22-dien-3β-ol acetate; pregn-5-en-20-one, 3-(acetyloxy)-17-hydroxy-(3β)-; allopregn-5,16-

diene-3β-ol-20-one acetate; 5,16,20-pregnatriene-3β,20-diol diacetate), which demonstrate antimicrobial, anti-inflammatory, anticancer, and antiasthmatic properties (Mickymaray and Alturaiki, 2018).

Additional compounds such as (24*R*)- and (24*S*)-5,28-stigmastadiene-3β,24-diol-7-one and vinylcholesta-3β,5α,6β,24-tetraol isomers inhibit human recombinant aldose reductase, an enzyme implicated in diabetic complications. Steroids isolated from *U. fasciata* display antibacterial activity against Gram-positive bacteria, likely due to structural similarity to cholesterol, which allows disruption of membrane receptor function and cellular integrity (Moghanjoughi et al., 2020).

Finally, several steroids have demonstrated antiviral activity. For example, stigmasterol inhibits tobamoviruses (Eltamany et al., 2021). Taken together, the primary sterols in macroalgae—including cholesterol, fucosterol, and isofucosterol—are promising candidates for nutraceutical and pharmaceutical development (Serviere-Zaragoza et al., 2021).

2.3. Oligosaccharides and polysaccharides

Oligosaccharides and polysaccharides are complex carbohydrates composed of repeating monosaccharide units linked by glycosidic bonds. Oligosaccharides typically contain 3–10 monomers, whereas polysaccharides comprise hundreds to thousands. In *Ulva*, polysaccharides form the predominant fraction of the cell wall, consisting mainly of water-soluble ulvan and insoluble cellulose, along with alkali-soluble fractions such as xyloglucan and glucuronan. Collectively, these polysaccharides may account for 38–54% of dry algal weight (dw) (Kidgell et al., 2019; Kim et al., 2011). Their abundance is influenced by geographic origin, seasonal fluctuations, and environmental growth conditions (Dave et al., 2021; Jansen et al., 2022; Sfriso et al., 2017). Moreover, *Ulva* species differ in their monosaccharide composition, relative ratios, and resulting structural sub-complexes (Dave et al., 2021; Kidgell et al., 2019; Ning et al., 2022).

For example, rhamnose residues in *Ulva* occur in several configurations, including (1→)-Rha, (1→4)-Rha, (1→2,4)-Rha, [→2)-α-L-Rhap-(1→], and [→3)-α-L-Rhap-(1→]. Studies have also reported arabinose and galactose as dominant sugars in the polysaccharide profile of *U. clathrata*, while rhamnose predominates in *U. prolifera* and *U. linza* (Qi et al., 2005, 2012, 2013; Xu et al., 2015). In *U. fasciata*, polysaccharides contain up to 35% uronic acid, an unusually high level compared with other seaweeds (Shao et al., 2014).

Ulvan, the most extensively studied *Ulva* polysaccharide, typically consists of rhamnose (42.2–54.8 mol%), xylose (5.4–23.8 mol%), glucuronic acid (11.6–30.4 mol%), and iduronic acid (6.0–7.0 mol%) (Cosenza et al., 2017; Lahaye and Robic, 2007). Two principal ulvan backbones have been proposed, featuring repeating disaccharide units such as [→4)-α-D-Glcp-(1→4)-β-L-Rhap3S-(1→] and [→4)-α-L-Idop-(1→4)-α-L-Rhap3S-(1→]. Unique structural features have also been identified, including sulfated arabinose in *U. clathrata* (Qi et al., 2012). Several *Ulva* species—including *U. lactuca*, *U. linza*, *U. compressa*, *U. prolifera*, and *U. intestinalis*—biosynthesize sulfated glucuronorhamnans (Bikker et al., 2016; Lahaye and Robic, 2007; Li et al., 2018b; Wang et al., 2013) (**Table 3**).

Ulva polysaccharides are generally indigestible by humans, making them a valuable source of dietary fiber. The fiber profile of *U. lactuca* includes high levels of hemicellulose, cellulose, and lignin, often surpassing those of many fruits and vegetables (Misurcova, 2011; Yaich et al., 2011). Extraction conditions strongly influence the yield and bioavailability of ulvan and other saccharides. For instance, extraction at low pH and high temperatures (80–90 °C) yields 20–24% uronic acid and 20–29% sugars, while raising the extraction pH from 3 to 7 increases insoluble fiber content (Guidara et al., 2019; Yaich et al., 2017).

Ulvan has attracted attention for its diverse bioactivities, including antioxidant, anti-inflammatory, antihyperlipidemic, anticoagulant, antiviral, immunomodulatory, and anticancer effects. Polysaccharides and oligosaccharides from *U. pertusa* demonstrated lipid-lowering activity by reducing LDL cholesterol and triglycerides while increasing HDL cholesterol (Pengzhan et al., 2003). Low–molecular-weight ulvans exhibit superior cellular uptake and antioxidant activity compared with higher–molecular-weight forms (Qi et al., 2005; Abd El Hafez et al., 2020). Additional reported benefits include cholinesterase inhibition and neuroprotection (Olasehinde et al., 2019), as well as stimulation of antioxidant enzymes (Li et al., 2018b).

Anticoagulant activity has been confirmed in several *Ulva* species, including *U. lactuca*, *U. neumatoidea*, and *U. conglobata* (Guerra-Rivas et al., 2011; Mao et al., 2006). Immunomodulatory effects have been observed both *in vitro* and *in vivo* (Berri et al., 2017; Liu et al., 2019; Ponce et al., 2020).

Beyond healthcare, ulvan is under investigation in agriculture as a plant immune system elicitor to reduce pesticide dependence (Amin, 2019) and as a biogenic agent for nanoparticle synthesis (Amin, 2020). Its antibacterial, antifungal, and antiviral properties also suggest utility in agriculture and aquaculture (Anjali et al., 2019; Boisvert et al., 2015; de Borba et al., 2021; Deveau et al., 2016). In biomaterials science, ulvan is being explored for tissue engineering, scaffolds, wound dressings, and anti-biofilm coatings (Chandika and Jung, 2015). It functions as a hydrogel polymer and prebiotic and can be incorporated into edible films or emulsions for food and cosmetic applications (Barros et al., 2013; Popa et al., 2015; Ramu Ganesan et al., 2018; Morelli et al., 2016).

Continued research and development are essential to expand the industrial, biomedical, and applications of *Ulva*-derived polysaccharides and oligosaccharides.

2.4. Vitamins

Vitamins are essential organic micronutrients with diverse chemical structures and biological functions. They are broadly classified as fat-soluble (A, D, E, and K) or water-soluble (C and B group). Seaweeds, including *Ulva*, are valuable dietary sources of these compounds.

Ulva is particularly rich in vitamin A (up to 9,581 IU/kg in *U. rigida*), vitamin C (94 mg/kg, dw), vitamin E (20 mg/kg), and several B vitamins, including B1 (4.7–4.9 mg/kg), B2 (0.9–2.0 mg/kg), and B12 (0.1 g/kg) (Rasyid, 2017; Taboada et al., 2010). Notably, the concentrations of vitamins B1 and B2 in *U. rigida* exceed those in more commonly consumed seaweeds such as wakame (*Undaria pinnatifida*) and kombu (*Laminaria japonica*). In a comparative assessment of ten Chlorophyceae species, *U. reticulata* exhibited the highest vitamin C content (2.44 µg/g dw), although *U. rigida* contained comparatively low levels of vitamins B3 and B6 (Taboada et al., 2010). More recent studies reported vitamin B12 levels ranging from 462 to 709 ng/g dw in *U. intestinalis* and *U. fasciata*, respectively, with concentrations up to 22-fold higher than those found in the red alga *Palmaria palmata* (Trigo et al. 2025). According to European Regulations No. 1169/2011 and 1924/2006, *U. fenestrata* qualifies for the nutritional claim “High in Vitamin B12” (Trigo et al., 2025; Imchen et al., 2024) (**Table 4**).

Vitamins in *Ulva* contribute to diverse physiological functions. Vitamin C supports immune function and enhances iron absorption, while B vitamins are essential for energy metabolism. Despite their low daily requirements, these micronutrients are indispensable for growth, reproduction, and overall health (Riaz et al., 2009). Because humans cannot synthesize sufficient quantities of most vitamins, dietary intake is essential. It has been estimated that 43 g of *Ulva* can supply the recommended daily allowance of vitamin C, and just 1.4 g of *U. lactuca* can fulfill the daily requirement for vitamin B12 (García-Casal et al., 2007, **Table 4**).

Deficiencies in vitamins result in characteristic diseases such as pellagra (B3), beriberi (B1), blindness (A), anemia (B12), rickets (D), and scurvy (C) (Dhakal and He, 2020). In response, the food and pharmaceutical industries have developed multivitamin supplements and fortified foods, though their long-term efficacy remains debated. Given growing consumer interest in natural health-promoting compounds, *Ulva* offers a promising alternative for vitamin supplementation (Calheiros et al., 2021). *Ulva*-based vitamin products may be particularly beneficial for vegetarians, who are prone to vitamin B12 deficiency (Taboada et al., 2010). Nevertheless, limited data exist on the bioaccessibility and bioavailability of *Ulva*-derived vitamins. Preliminary evidence suggests a positive correlation between vitamin C and carbohydrate content in *Ulva*, which could guide the development of nutrient-dense algal food products (Taboada et al., 2010).

In summary, the vitamin profile of *Ulva* supports its role as a functional food ingredient, though further studies are required to evaluate absorption and health impacts within the algal matrix.

2.5. Carotenoids

Carotenoids are isoprenoid compounds characterized by a system of conjugated double bonds that confer their distinctive pigmentation and antioxidant properties. Structurally, they may be cyclic or acyclic and are classified into two major groups: carotenes (hydrocarbon carotenoids) and xanthophylls (oxygenated derivatives). Carotenoids can exist in various geometrical (cis/trans or Z/E) and optical isomeric forms and may undergo enzymatic cleavage (Rodriguez-Concepcion et al., 2018).

In plants, carotenoids are predominantly associated with chloroplasts, with violaxanthin, neoxanthin, lutein, and β-carotene being most common, along with minor quantities of others. Owing to their evolutionary proximity to terrestrial plants, green algae such as *Ulva* exhibit a comparable carotenoid profile (Eismann et al., 2020; Rodriguez-Concepcion et al., 2018). In addition to these major pigments, *Ulva* spp. contains α-carotene, antheraxanthin, zeaxanthin, and β-cryptoxanthin. Reported concentrations of total carotenoids in *Ulva* typically range from 0.05 to 0.20 mg/g fresh weight (fw) (Eismann et al., 2020) (**Table 5**).

Carotenoid accumulation in *Ulva* is strongly influenced by genotype and environmental conditions, including light intensity, nutrient availability, temperature, and salinity. Their levels are often positively correlated with algal biomass and can be modulated using external stimuli such as selenium or phytohormone supplementation, short-term ultraviolet exclusion, temperature shifts, CO_2 depletion, or transient hypersalinity stress. These responses are thought to enhance photosynthetic efficiency and mitigate oxidative stress by scavenging reactive oxygen species (Eismann et al., 2020).

Given the ecological significance of *U. prolifera*, particularly in large-scale "green tide" events, there is growing interest in its carotenoid biosynthesis and environmental regulation (He et al., 2022). Several carotenoids in *Ulva*, including β-carotene, α-carotene, and β-cryptoxanthin, function as precursors to vitamin A, which is essential for vision, immunity, and development. These provitamin A carotenoids are especially relevant for alleviating vitamin A deficiency, a widespread global nutritional problem. Beyond their role as nutrient precursors, carotenoids and their cleavage products have been associated with protective effects against certain cancers, cardiovascular and metabolic disorders, ocular degeneration, bone and skin conditions, cognitive decline, and complications in pregnancy and early development (Meléndez-Martínez, 2019).

Despite recognized health benefits, carotenoid intake in many populations falls below the levels recommended by the European Food Safety Authority (EFSA) (Meléndez-Martínez et al., 2021). Caution is advised in individuals at high risk of lung cancer, as daily β-carotene supplementation above 15 mg has been linked to increased cancer incidence in smokers and asbestos-exposed individuals, although such effects have not been observed in healthy cohorts (Blot et al., 1993; Heinonen, 1994; Hennekens et al., 1996; Omenn et al., 1996; Eggersdorfer and Wyss, 2018; Meléndez-Martínez, 2019).

Carotenoids have wide-ranging industrial applications. In the food sector, they are used as natural colorants, antioxidants, and functional ingredients. In cosmetics, they provide protective and aesthetic benefits, while in pharmaceuticals, specific carotenoids such as β-carotene and canthaxanthin have been investigated for skin disorders. Carotenoids are also widely used in animal feed formulations to enhance pigmentation and health. Overall, they represent multifunctional bioactive compounds with significant value for the agro-food, aquaculture, pharmaceutical, and cosmetic industries (Meléndez-Martínez et al., 2019; Meléndez-Martínez et al., 2021).

2.6. Phenolic compounds

Polyphenols are structurally diverse secondary metabolites characterized by multiple hydroxylated phenyl rings. Functional groups such as hydroxyl, methoxy, and carboxyl moieties contribute to their reactivity and biological activity, enabling chemical modifications including oxidation, glycosylation, and methylation. Polyphenols are broadly classified into flavonoids, phenolic acids, stilbenes, and lignans (Aneklaphakij et al., 2021; Ghani, 2020).

Although *Ulva* is not the richest source of polyphenols among seaweeds, it contains appreciable amounts of flavonoids, phenolic acids, and tannins (Cotas et al., 2020). Reported total phenolic content varies widely—from 0.8 to 583 mg gallic acid equivalents (GAE)/g (dw), depending on species and analytical methodology (Mezghani et al., 2015; Pappou et al., 2022) (**Table 6**).

Several flavonoids have been identified in *Ulva*, including apigenin (in *U. lactuca* and *U. rigida*), quercetin, kaempferol, and luteolin. These compounds exhibit antioxidant, anti-inflammatory, and cardiovascular-protective effects (Salehi et al., 2019; Dabeek and Marra, 2019; Wekre et al., 2019; Lin et al., 2008). Quercetin and kaempferol also demonstrate antimicrobial activity, suggesting potential applications as natural food preservatives or antimicrobial agents in clinical settings (Daglia 2012). Luteolin has been investigated for anticancer and neuroprotective effects, with evidence of benefits for cognitive function. Additionally, luteolin inhibits foodborne pathogens such as *Salmonella* and *Escherichia coli*, highlighting its potential as a natural preservative (Xi et al., 2022; El-Bilawy et al., 2022).

Phenolic acids reported in *Ulva* include caffeic acid and chlorogenic acid, both associated with antioxidant and anti-inflammatory properties. These compounds reduce the risk of chronic and neurological diseases, such as Alzheimer’s disease and cancer (Zaatout et al., 2019; Alam et al., 2022; Tajik et al., 2017). Tannins present in *Ulva* also contribute antiviral, antibacterial, antioxidant, anti-inflammatory, and anticancer activities (Salehi et al., 2019). Despite this growing evidence, data on the bioavailability, metabolism, and in vivo efficacy of *Ulva*-derived polyphenols remain limited. More research is needed to validate their health benefits and to develop practical strategies for their incorporation into functional foods, pharmaceuticals, and nutraceuticals.

2.7. Minerals and Metals

In addition to vitamins, lipids, and proteins, the nutritional value of edible seaweeds such as *Ulva* is significantly influenced by their mineral composition. Like terrestrial plants, macroalgae require both macronutrients such as nitrogen, phosphorus, potassium, calcium, sulfur, and magnesium as well as trace elements like iron, boron, manganese, zinc, copper, molybdenum, nickel to support growth and development (Ho, 1981). Owing to their strong bioaccumulative capacity, seaweeds often contain mineral concentrations up to 100-fold greater than those of land vegetables, with some species reaching ash contents as high as 40% of their dry weight (Circuncisão et al., 2018; Vargas-Murga, 2025; Whelton, 2014).

Species, geographic origin, seasonality, and cultivation practices strongly influence mineral content. In *U. lactuca*, however, factors such as salinity, pH, and temperature appear to exert minimal effects on metal accumulation (Bonanno et al., 2020).

Ulva is also recognized for its ability to bioaccumulate heavy metals, making it a reliable biomonitor of coastal metal pollution. Metal uptake is influenced by algal physiology, cell age, and environmental conditions, including pH, temperature, and light intensity (Mourad and El-Azim, 2019). Some seaweeds can accumulate toxic elements such as arsenic, cadmium, copper, and mercury at concentrations 200–500 times higher than those in terrestrial plants (Circuncisão et al., 2018). This highlights the importance of monitoring, as excessive consumption of contaminated seaweed may pose significant health risks. Accordingly, regulatory authorities have established maximum permissible levels for heavy metals and iodine in edible macroalgae (European Food Safety Authority, 2023; Gallego et al., 2018; Stévant et al., 2018).

Compared with terrestrial vegetables, seaweeds generally contain higher concentrations of sodium and potassium. Importantly, their favorable Na/K ratios may contribute to cardiovascular health (Whelton, 2014). High sodium levels, however, may be a concern in regions with elevated dietary sodium intake. *Ulva* is also a good source of calcium, phosphorus, and magnesium, minerals essential for bone health and cellular function. Nevertheless, the presence of trace elements alone does not guarantee bioavailability; absorption depends on the physical and chemical properties of the food matrix and interactions with other dietary components (Domínguez-González et al., 2010). Polysaccharides such as ulvan, abundant in

Ulva cell walls, exhibit metal-binding properties that may influence mineral bioavailability (Chi et al., 2021; Olasehinde et al., 2019).

Additionally, soluble fibers enriched in ulvan can be processed to extract valuable sea salts within a cascading biorefinery framework. This approach not only yields food-grade salts but also enhances the utility of residual biomass for downstream applications such as fertilizers, animal feed, and biofuels (Magnusson et al., 2016).

2.8. Other secondary compounds

Marine green algae such as *Ulva* and their associated microbiomes produce a wide array of secondary metabolites, including alkaloids, cyclic peptides, diterpenoids, glycerol derivatives, phlorotannins, polyketides, quinones, and sterols (Blunt et al., 2008). Many of these bioactives mediate cross-kingdom interactions and enhance adaptability to environmental stressors, while also showing potential for pharmaceutical applications (Wichard and Beemelmanns, 2018).

Although *Ulva* is generally less chemically diverse than red or brown algae, it has yielded several notable secondary metabolites. The alkaloid pyrrolopiperazine-2,5-dione [cyclo-(Pro-Gly)], identified in *U. prolifera*, exhibits neuroprotective and anti-amnesic effects (Hayasaka et al., 2016). Terpenoids such as loliolide, isololiolide, and (+)-epiloliolide have been isolated from *U. prolifera* and *U. lactuca*, with (+)-epiloliolide demonstrating potential regulation of the p53 signaling pathway (Chung et al., 2021; Sun et al., 2016). To date, however, most research has been conducted on crude extracts, leaving many active constituents unidentified. The isolation, structural elucidation, and mechanistic characterization of *Ulva* metabolites remain promising avenues for medicinal chemistry (Shah et al., 2020).

2.9. Bioavailability of bioactives

The complex biochemical matrix of seaweeds, rich in fibers and polysaccharides, can limit the release and absorption of embedded bioactives. Encapsulation technologies and advanced formulations may enhance bioavailability by protecting compounds from gastrointestinal degradation and facilitating intestinal uptake. Some seaweed-derived compounds exert health benefits indirectly through modulation of the gut microbiota. For example, non-digestible polysaccharides such as alginate and fucoidan act as prebiotics, stimulating the production of short-chain fatty acids, which have systemic metabolic and immunological benefits. Bioactive interactions can also modulate absorption: lipids may enhance the uptake of fat-soluble compounds such as carotenoids, whereas polyphenols can shield other molecules from oxidative degradation. Optimizing processing methods, delivery systems, and synergistic formulations is therefore critical to maximize the nutritional and therapeutic potential of *Ulva*-derived bioactives.

3. Extraction methodologies

Extraction technologies and operating conditions critically influence the yield, purity, and biological activity of natural compounds. In most cases, a solvent extraction step is required to selectively separate target components from algal biomass. From a sustainability perspective, factors such as human and animal toxicity, photochemical oxidant formation, primary energy demands, and climate change impacts must be considered when selecting extraction methods (Zapata-Boada et al., 2022). Traditional extraction approaches often rely on toxic solvents, high energy inputs, and large solvent volumes, limiting their applicability in food- or pharmaceutical-grade production. Recent advances have focused on scalable, efficient, and environmentally friendly processes to overcome these drawbacks. The use of water as a solvent is particularly promising, as it prevents the formation of toxic by-products and undesirable residues in the final product (Díaz-Reinoso et al., 2017; Harrysson et al., 2018). However, extraction from *Ulva* remains technically challenging due to the presence of rigid cell walls, capsules, and a complex extracellular polymeric substance matrix, all of which hinder solvent penetration and compound release (Zammit and Agius, 2022). To enhance recovery, combinations of extraction techniques are often employed to increase yields while preserving the native structure of metabolites (Robin et al., 2018a). Sequential extraction strategies further improve biomass utilization and reduce waste generation, transforming residual material into feedstock for other applications (Mhatre et al., 2019). Thus, extraction efficiency is a key determinant of the economic and industrial value of *Ulva*-derived compounds.

This section first outlines the principles of emerging extraction methodologies (**Fig. 2**). Green solvents and sustainability considerations are then discussed in detail.

3.1. Ultrasound-assisted extraction (UAE)

UAE applies sound waves at frequencies above the audible range (>20 kHz) and below microwave frequencies (≤10 MHz). As ultrasound passes through the medium, alternating compression and rarefaction cycles induce cavitation. The collapse of cavitation bubbles near the cell surface generates localized mechanical energy that disrupts cell walls and membranes, enhancing solvent penetration and release of intracellular metabolites (Mason et al., 1996).

UAE is considered one of the most cost-effective extraction methods compared with alternatives such as supercritical fluid extraction (SFE), pressurized liquid extraction (PLE), or accelerated solvent extraction (Chemat et al., 2020; Tiwari, 2015). It enables efficient recovery of target compounds while reducing the use of organic solvents, thereby qualifying as a clean and environmentally friendly technology (Wang et al., 2019). Additional advantages include versatility, operational simplicity, and flexibility (Barba et al., 2020; Tiwari, 2015). However, several variables—such as frequency, power, duty cycle, extraction time, temperature, solvent type, and liquid–solid ratio—must be carefully optimized for consistent yields (Kumar et al., 2021).

In comparative studies, UAE outperformed conventional methods in extracting phenolic compounds and enhancing radical scavenging activity from *Sargassum wightii*, *U. rigida*, and *Gracilaria edulis*. For instance, 30 min of UAE from *U. rigida* yielded higher phenolic recovery than 120 min of conventional extraction (Kumar et al., 2020). Optimized UAE conditions (100% amplitude, 1300 W, pH 5.7) yielded 0.253 g GAE/100 g dw of phenolics (Cameselle et al., 2025). UAE has also been effective for polysaccharides: yields of ulvan ranged from ~9% to 23% depending on experimental conditions (Thanh et al., 2023; Cameselle et al., 2025), while sulfated polysaccharides reached 8.3% in *U. intestinalis* (Rahimi et al., 2016). Higher yields have been reported for *U. lactuca,* including 17.6% (Tian et al., 2015) () and 30.1% using UAE combined with enzymatic-assisted extraction (EAE; enzyme concentration 1.5%, 1.1 h, 60 °C, 90 min ultrasound) (Wang et al., 2025). UAE has also been applied to extract pigments and secondary metabolites. Ultrasound-assisted solid–liquid extraction with ethanol recovered high-purity chlorophylls and xanthophylls from *U. rigida* (Martins et al., 2021a). In *U. lactuca*, UAE with 50% ethanol achieved higher quercetin and antioxidant yields than 100% ethanol (Rashad et al., 2023). Compared with other techniques, including microwave-assisted extraction (MAE), ultrasound–microwave-assisted extraction (UMAE), hot aqueous extraction, and high-pressure-assisted extraction, UAE yielded the highest phytochemical concentrations in *Fucus vesiculosus* and *Pelvetia canaliculata* (Garcia-Vaquero et al., 2021). For oil extraction, ultrasound methods also outperformed pre-treatments such as deep freezing, lyophilization, and microwaving, which often induce partial hydrolysis and pre-esterification (Piccini et al., 2019).

Despite these promising results, most UAE studies remain limited to laboratory scale with probe-based systems. For industrial-scale application, challenges such as acoustic energy density optimization and reproducibility must be addressed. Continuous-flow UAE systems represent a promising direction for scale-up due to improved energy distribution and operational efficiency (Alexandre et al., 2018; McDonnell and Tiwari, 2017; Tiwari, 2015).

3.2. Microwave-assisted extraction

MAE is a widely applied technique for recovering bioactive compounds from plants and macroalgae (Wang and Weller, 2006). MAE employs electromagnetic waves in the 300 MHz–300 GHz range, which cause dipolar molecules and electrolytes to oscillate under an alternating field. This rapid oscillation generates internal heating, leading to cell rupture without significant external heat loss. MAE can be performed in either open-vessel systems at atmospheric pressure or in closed systems under elevated pressure. Open-vessel MAE is considered safer and better suited for large sample volumes, particularly when targeting heat-resistant compounds. MAE is recognized as an environmentally friendly technique, as it typically requires less solvent, shorter extraction times, and lower energy consumption compared with conventional methods. Equipment costs are relatively modest, and the process is scalable. However, high operating temperatures can degrade thermolabile compounds such as chlorophylls and carotenoids, and additional filtration or centrifugation steps are often necessary to remove solid residues (Gomez et al., 2020). Several examples illustrate the efficiency of MAE in *Ulva*. Polysaccharides were extracted from *U. pertusa* under optimized MAE conditions (43.6 min, 600 W, water-to-material ratio 55.5, pH 6.6), achieving a yield of 42% (Le et al., 2019). In *U. rigida*, chlorophyll recovery using MAE produced comparable yields to UAE and conventional methods but required only one minute of processing (Martins et al., 2021b). Similarly, MAE yielded higher concentrations of chlorophylls and carotenoids from *U. flexuosa* compared with Soxhlet extraction and SFE (Fabrowska et al., 2018).

3.3. Chemical extraction (CE)

A biorefinery approach can fractionate algal biomass into multiple products, including ulvan, proteins, lipids, pigments, animal feed, and biofuels (Bikker et al., 2016; Mhatre et al., 2018; Prabhu et al., 2020). Conventional CE typically involves acid or alkali treatments and solvents such as hexane, chloroform, or methanol (Gajaria et al., 2017; Zapata-Boada et al., 2022). For example, hydrochloric acid extraction of ulvan from *U. ohnoi* yielded purer extracts than sodium oxalate (Glasson et al., 2017). Lipid extraction is often performed using the Bligh and Dyer (1959) method with chloroform–methanol. Residual biomass can then undergo successive hydrolysis steps to isolate ulvan, proteins, and cellulose using NaOH, HCl, or NaOCl treatments (Gajaria et al., 2017). Although CE is effective and widely used, it raises significant environmental and safety concerns, including solvent toxicity, hazardous waste generation, and high energy demands. Furthermore, harsh chemical treatments can compromise the functional quality of extracted metabolites (Malik and Mandal, 2022). As a result, there is growing interest in chemical-free and green chemistry alternatives (Robin et al., 2018b; Prabhu et al., 2020). Nevertheless, most algal biorefinery studies remain at laboratory scale, with limited translation to industrial-scale operations (Zammit and Agius, 2022).

3.4. Enzyme-assisted extraction

is a sustainable alternative that employs enzymes to degrade algal cell walls and release intracellular metabolites. The efficiency of EAE depends on process parameters such as temperature, pH, extraction time, enzyme type and concentration, and substrate composition (Gagaoua, 2018). EAE is particularly valued for its specificity, mild reaction conditions, and compatibility with aqueous environments (Puri et al., 2012). However, the high cost of commercial enzymes remains a barrier, underscoring the need for low-cost crude enzyme preparations and tailor-made blends. EAE has industrial applications in the food, animal feed, and paper sectors, and has been used to recover oils, phenolics, pigments, and peptides (Ozkan et al., 2021). Applications to *Ulva* are relatively limited but promising. Endo-protease treatment has been used to produce crude ulvans followed by polysaccharide precipitation and to generate polysaccharide fractions with bioactivity on human dermal fibroblasts (Hardouin et al., 2016). In *U. armoricana*, EAE significantly improved extraction yields of organic matter, sugars, and proteins. Despite these encouraging results, further scale-up are required before EAE can be adopted for industrial *Ulva* biorefineries.

3.5. Pressurized liquid extraction

PLE employs elevated pressure and temperature to maintain solvents in liquid form, thereby improving mass transfer and compound solubility (de la Fuente et al., 2021). Typical operating conditions are up to 1,500 psi and temperatures ranging from 20 to 200 °C. PLE can also be applied under mild conditions (≤40 °C) to protect thermolabile compounds (Wang et al., 2023; Zhou et al., 2021b). PLE is considered a green extraction method, particularly when using food-grade solvents. However, preprocessing steps such as drying and homogenization increase energy consumption (Perez-Vazquez et al., 2023; Zhou et al., 2021a). Applications to *Ulva* have included the recovery of FAs (Otero et al., 2018), sugars (Greiserman et al., 2019), and glucose (Steinbruch et al., 2020). PLE has also been used to extract antioxidants and polyphenols from other algal taxa (Pangestuti et al., 2019; Bordoloi and Goosen, 2020). Although PLE has not yet been scaled for *Ulva*, successful scale-ups in other matrices, including plant materials and food residues (Ko et al., 2016; Cardenas-Toro et al., 2015), indicate its industrial feasibility. Potential technical issues include high-pressure requirements and clogging of equipment (Andrade et al., 2022).

3.6. Supercritical fluid extraction

SFE uses solvents above their critical temperature and pressure, where they exhibit properties of both gases and liquids, including high diffusivity and adjustable solvating power. Supercritical CO_2 is the most commonly used solvent due to its low toxicity, non-flammability, cost-effectiveness, and recyclability. Its tunable solvating power allows selective extraction of high-value compounds by adjusting temperature and pressure (Zhou et al., 2021). Importantly, CO_2 leaves no solvent residues, yielding high-purity extracts. SFE can also be coupled with analytical techniques such as chromatography, infrared spectroscopy, and nuclear magnetic resonance for in situ monitoring of compound quality. Despite these advantages, SFE has limitations, including the need for co-solvents to improve extraction of polar compounds, relatively long processing times, and high equipment costs.

SFE has been applied to extract oils, FAs, carotenoids, and polyphenols from *Ulva*. For example, Fabrowska et al. (2016) optimized SFE conditions for *Cladophora glomerata*, *U. flexuosa*, and *Chara fragilis*, reporting that *C. fragilis* produced the highest carotenoid and polyphenol yields, whereas *U. flexuosa* extracts had the strongest antioxidant activity. Veeranan et al. (2018) demonstrated that ultrasound-assisted SFE of *U. fasciata* enhanced combustion properties and improved acid and saponification values. Similarly, Messyasz et al. (2018) reported that SFE yielded more FAs, carotenoids, and chlorophylls from *U. clathrata* compared with conventional methods. Terme et al. (2017) compared SFE (with 2% ethanol as co-solvent) with the Bligh–Dyer method for lipid extraction from *Solieria chordalis* and *Sargassum muticum*, finding that although Bligh–Dyer yielded more total lipids, SFE produced higher proportions of neutral lipids.

While large-scale SFE of *Ulva* has not been demonstrated, successful scale-ups in other biomaterials—including *Phyllanthus niruri*, clove, sugarcane residues, and *Arthrospira* (*Spirulina*)—highlight its industrial potential (Hassim et al., 2021; Prado et al., 2011; Crampon et al., 2017).

3.7. Pulsed electric fields (PEF)

PEF extraction applies short bursts of high-intensity electric fields (0.1–40 kV/cm, <300 Hz) to permeabilize cell membranes via electroporation. This non-thermal technique minimizes solvent use and enables selective extraction with reduced risk of thermal degradation (Puértolas et al., 2016). Limitations include high capital investment and the need for low sample conductivity, which often necessitates pre-washing of algal biomass (Capodaglio, 2021; Zhang et al., 2023).

PEF shows particular promise for *Ulva* bioprocessing by enhancing extraction yields and reducing processing time through facilitated release of intracellular water and solutes. Studies have demonstrated its effectiveness for extracting proteins, starch, and minerals (Polikovsky et al., 2016, 2019; Robin et al., 2018; Postma et al., 2018; Steinbruch, 2024). Prabhu et al. (2019) reported efficient starch fractionation from *U. ohnoi* using a multistage PEF–mechanical pressing process. Similarly, Einarsdóttir et al. (2021) showed that PEF enhanced carbohydrate and polyphenol recovery from *L. digitata* without the need for heat or solvents. More recently, Efraim et al. (2022) combined PEF with enzymatic cell wall degradation to maximize water-soluble protein extraction from *Ulva*, underscoring the scalability of hybrid approaches.

3.8. Other innovative methods: hydrothermal treatments (HT) and diluted acid hydrolysis (DAH)

HT uses compressed liquid hot water for biomass fractionation. Autohydrolysis, a form of HT, employs water as both solvent and reagent, offering advantages such as chemical-free operation, low waste generation, and reduced energy demand (Carvalheiro et al., 2016; Gullón et al., 2012). For example, Bikker et al. (2016) combined HT with enzymatic hydrolysis and centrifugation to obtain sugar-rich hydrolysates and protein-enriched fractions from *Ulva*. Andrade et al. (2022) reported increased oligosaccharide yields and selective removal of rhamnan, mannan, and xylan at temperatures ≥150 °C.

DAH employs mineral acids (e.g., HCl, H_2SO_4) at 100–240 °C to depolymerize polysaccharides. DAH offers high selectivity and yields under relatively mild conditions but risks sugar degradation and equipment corrosion (Andrade et al., 2022). In *Ulva*, optimal sugar release occurred at 160 °C, while glucan solubilization peaked at 55.7% at 190 °C. Protein solubilization was lower (26.7%), but residual solids remained protein-rich and digestible.

Both HT and DAH are established in lignocellulosic biomass processing but remain underexplored and unscaled for algal biomass applications.

3.9. Sustainability aspects and future research

Innovative extraction methodologies contribute to several United Nations SDGs, including sustainable industry and innovation (SDG 9), climate action (SDG 13), and protection of marine and terrestrial ecosystems (SDGs 14, 15). They also support health and nutrition (SDG 3) and energy efficiency (SDG 7). Despite progress, significant gaps remain in standardization and industrial translation. A unified database supported by optimization tools such as response surface methodology and artificial neural networks could streamline process development and comparison. Future research should prioritize (i) hybrid extraction approaches (e.g., UAE+SFE, PEF+PLE), (ii) incorporation of green solvents such as natural deep eutectic solvents (NADES), and (iii) system-level life cycle assessments. These advances will be essential for scaling *Ulva* biorefineries in line with principles of the circular bioeconomy.

4. Extraction solvents: classical vs. emerging sustainable solvents

Extraction solvents used in the food, feed, pharmaceutical, and cosmetic industries are strictly regulated to safeguard human health. In the European Union, Directive 2009/32/EC governs the use of extraction solvents in the manufacture of foodstuffs and ingredients, applying equally to EU-produced and imported products. Permitted solvents include propane, butane, ethyl acetate, ethanol, carbon dioxide, acetone, and nitrous oxide, provided they are used in accordance with good manufacturing practices. Their use is acceptable only when technically unavoidable residues remain at levels that do not pose a health risk. Common solvents such as water, ethanol, and ethyl acetate are frequently employed for the extraction of carotenoids and phenolic compounds used in food colorants, dietary supplements, animal feed additives, and cosmetic formulations (Pappou et al., 2022). Additional authorized solvents include hexane, methyl acetate, ethylmethylketone, dichloromethane, diethyl ether, dimethyl ether, methanol, 1-propanol, 2-propanol, cyclohexane, butanols (1-butanol, 2-butanol), and 1,1,1,2-tetrafluoromethane, each subject to specific usage conditions and maximum residue limits.

Traditionally, organic solvents have been employed to maximize extraction efficiency. However, many pose health and environmental hazards, undermining sustainability goals (Chemat et al., 2020). Consequently, interest in greener and renewable alternatives has intensified. Beyond water—universally regarded as the safest solvent—emerging classes of "green solvents" include bio-based solvents, deep eutectic solvents (DES), and ionic liquids (ILs), which combine high extraction efficiency with reduced environmental impact (Janicka et al., 2022).

Bio-based are derived from renewable biomass through chemical or biochemical transformation and are typically biodegradable, low in toxicity, and renewable (Li et al., 2016). Examples include glycerol, 2-methyltetrahydrofuran (2-MeTHF), and ethyl lactate. Glycerol, a by-product of biodiesel production, has high polarity and solubilizing capacity for both organic and inorganic compounds. Mixtures of glycerol and hot water have successfully extracted polyphenols and antioxidants from plants, with the advantage that glycerol-extracted compounds can be used directly as food additives, eliminating the need for solvent removal and reducing processing time and cost (Apostolakis et al., 2014; El Kantar et al., 2019; Jabłonowska et al., 2021). 2-MeTHF, derived from lignocellulosic biomass, has been evaluated as a substitute for halogenated solvents in plant phenolic extraction (Cañadas et al., 2022), although applications in macroalgae remain limited. Ethyl lactate, with its high biodegradability and low toxicity, has been used effectively for selective fucoxanthin extraction from *Sargassum* *fusiforme* (Dandia et al., 2013; Nie et al., 2021). Other bio-based solvents include limonene and 2,3-butanediol. Despite their potential, bio-based solvents are still less widely applied to macroalgae compared with DES and ILs, which are currently receiving greater attention for *Ulva* and other seaweed extractions (Chemat et al., 2020; Lee et al., 2021).

4.1. Ionic liquids (ILs)

ILs are salts composed of bulky organic cations and organic or inorganic anions that remain liquid at or near room temperature. Common cations include cholinium, ethylpyridinium, and 1-butyl-1-methylpiperidinium, while typical anions include halides, fluorides, and nitrates (Lim et al., 2022; Raj et al., 2023). ILs are highly tunable, with physicochemical properties such as polarity, conductivity, and solubility tailored through specific ion combinations. Their ability to disrupt cell walls and membranes facilitates the release of intracellular metabolites (Sintra et al., 2018; Sneha et al., 2023). Aqueous IL solutions further improve biocompatibility and reduce viscosity, enhancing extraction performance.

ILs have been extensively studied for microalgal extraction, with increasing application to macroalgae. For instance, $[C_2C_1im][(C_4)_2PO_4]$ enabled 80.6% protein recovery from *U. lactuca* under alkaline conditions (Miranda, 2017). Similarly, Pezoa-Conte et al. (2015) reported that 1,1,3,3-tetramethylguanidine propionate ($[TMGH^+][CO_2Et^-]$) dissolved up to 67% of carbohydrates from *U. rigida*. Martins et al. (2021a) demonstrated efficient chlorophyll extraction using 250 mM tributyltetradecylphosphonium chloride ($[P_{4,4,4,14}]Cl$), which was both cost-effective and scalable. In addition, ILs have shown promise for lipid and carotenoid recovery from algal biomass (Vieira et al., 2018; Sneha et al., 2023).

4.2. Deep eutectic solvents

DES are formed by combining hydrogen bond donors and acceptors—typically a quaternary ammonium salt with a metal salt or an organic acid—resulting in a eutectic mixture with a melting point lower than that of its components. First introduced as alternatives to ILs in 2003, DES are valued for their ease of preparation, low cost, biodegradability, and reduced toxicity (Abbott et al., 2002; Kaoui et al., 2023; Raj et al., 2023). In algal bioprocessing, DES effectively disrupt biomass structure, enhancing solubility and mass transfer, and thereby improving recovery of proteins, lipids, phenolics, and other bioactives.

Xu et al. (2020) employed a DES-based aqueous two-phase system (choline chloride–urea) with ammonium sulfate precipitation to purify phycoerythrin from *Porphyra yezoensis*, achieving 69.9% recovery and a purity index of 3.825 (A_{565}/A_{280}). Saravana et al. (2018) combined DES with subcritical water extraction to obtain alginate and fucoidan from brown algae, achieving extraction rates of 28.1% and 14.9%, respectively, under optimized conditions (150 °C, 19.9 bar, 36.8 mL/g liquid–solid ratio).

Although applications of DES to *Ulva* remain limited, the diversity of potential hydrogen bond donors and acceptors suggests significant scope for tailoring DES systems to extract high-value metabolites in a sustainable manner.

5. Applications

Each class of bioactive compounds in *Ulva* spp. contributes to the macroalga's industrial relevance, with applications spanning pharmaceuticals, nutraceuticals, cosmetics, and aquaculture (Graphical abstract).

Health-promoting product categories:

- **Dietary supplements**: Concentrated sources of nutrients or bioactive compounds delivered in small-dose formats (e.g., capsules, drops), designed to support nutritional or physiological health (European Parliament, 2002).
- **Functional foods**: Conventional foods that provide additional health benefits beyond basic nutrition when consumed regularly (Binns and Howlett, 2009).
- **Nutraceuticals**: Foods or food components that deliver medical or health benefits, including disease prevention or treatment (DeFelice, 1995).
- **Nutricosmetics**: Ingestible products aimed at improving cosmetic appearance and skin health (Meléndez-Martínez, 2019).

5.1. Foods, feeds, safety, and regulation

Ulva spp. have long been consumed in Asian diets and are gaining popularity in Western markets. They can be eaten fresh, dried, or cooked, and are increasingly incorporated into dairy products and plant-based meat alternatives (Fleurence et al., 1999; del Olmo et al., 2019; Yesuraj et al., 2022). Ulvan's gelling properties also make it a valuable functional ingredient in vegan foods (Cindana Mo'o et al., 2020).

Nutritionally, *Ulva* spp. are rich in high-quality proteins, essential amino acids, vitamins, polyunsaturated FAs, and antioxidants. Their inclusion in animal feed has been shown to enhance growth performance and nutrient assimilation in livestock such as carp, shrimp, and chickens (Abudabos et al., 2012; Diler et al., 2007; Pallaoro et al., 2016). Furthermore, *Ulva*-based supplements improve the bioavailability of trace minerals in pigs compared to inorganic additives (Michalak et al., 2015). Safety remains a critical consideration. Potential risks include contamination with pathogenic microorganisms such as *Salmonella*, heavy metals (e.g., lead), and other pollutants. Rigorous safety assessments and adherence to regulatory framework are therefore essential to ensure for safe consumption of *Ulva*-derived food and feed products (Li et al., 2018a; Hofmann et al., 2024).

5.2. Pharmaceutical applications

Polysaccharides such as ulvan have attracted attention in pharmaceutical research due to their bioactivity and biocompatibility, with applications in wound healing and drug delivery. Components of *Ulva* spp. exhibit anti-inflammatory, antioxidant, immunostimulatory, antitumor, and antiviral properties (Barzkar et al., 2019; Salehi et al., 2019a; Sulastri et al., 2021). Extracts from *U. australis* and *U. lactuca* have demonstrated antidiabetic and antimicrobial activities, respectively (Trentin et al., 2020; Anjali et al., 2019). These findings underscore the potential of *Ulva* as a source of novel therapeutic agents.

5.3. Cosmetic applications

Ulva spp. contain multiple compounds of cosmetic interest, including unsaturated FAs, vitamins, phenolic compounds, and carotenoids, the latter being particularly relevant for skin health and protection against photoaging (Kalasariya et al., 2021; Lourenço-Lopes et al., 2020; Meléndez-Martínez et al., 2019; Salehi et al., 2019a). Among these, ulvan has gained prominence due to its ability to retain moisture and modulate extracellular matrix metabolism in fibroblasts, which may mitigate signs of skin aging (Fournière et al., 2019). Both native and chemically modified ulvans (e.g., conjugated with FA moieties) have been employed as stabilizing and emulsifying agents in colloidal systems for food and cosmetic applications. Such multifunctional formulations are proposed for use as clouding and flavoring agents in beverages, and as stabilizing or perfuming agents in creams and lotions (Morelli et al., 2019).

Commercial interest is reflected in the development of patented formulations such as Chlorofiltrat® Ulva HG, derived from *U. lactuca*, which is marketed for its moisturizing and anti-inflammatory benefits (Pimentel et al., 2018).

6. Future considerations in biotechnological and bioprocessing advancements

The biotechnological potential of *Ulva* is increasingly recognized, with advances in sustainable cultivation, biorefinery processes, multi-product development, and renewable biomass utilization supporting its integration into the circular bioeconomy (**Fig. 3**).

Contemporary "omics" methodologies, including genomics, transcriptomics, metabolomics, and synthetic biology, are providing deeper insights into *Ulva* metabolism and its interactions with associated microbiota (Blomme et al., 2023). These tools are essential for strain improvement, yield optimization of target metabolites, and tailoring of cultivation conditions to enrich specific bioactive profiles.

An important development in this context is the design of defined microbial consortia that enhance *Ulva* growth and morphogenesis. Such bacterial partners not only boost biomass productivity but also increase concentrations of valuable bioactive compounds (Wichard, 2023). In parallel, controlled stress strategies such as modulating light, salinity, or nutrient regimes are being used to stimulate metabolite accumulation, including polyphenols, carotenoids, ulvan, and FAs.

Innovations in aquaculture engineering, such as photobioreactors and IMTA, are enabling precise environmental control, nutrient recycling, and waste minimization, thereby supporting sustainable large-scale cultivation of *Ulva* (Shpigel and Buck, 2023). Emerging applications of synthetic biology and genome editing, although still nascent in green macroalgae, offer significant potential for targeted metabolic engineering and pathway optimization (Blomme et al., 2023).

Despite this promising foundation, major challenges remain in scaling production and processing. Most extraction technologies and biorefinery concepts have been validated only at laboratory or pilot scales. Industrial translation requires addressing technological, logistical, and economic bottlenecks, including securing a reliable year-round biomass supply, improving extraction efficiency, reducing energy and solvent use, and developing cost-effective cascade biorefineries that maximize value recovery from each biomass component. Technologies such as PEF, UAE, and enzyme-assisted extraction show considerable promise but require further validation for commercial feasibility.

Equally critical is the standardization of extraction methodologies to ensure reproducibility and comparability across studies (Vargas-Murga; Holdt and Kraan, 2011). Reported concentrations of bioactives in *Ulva* vary widely, even within the same species name, due to differences in taxonomy, developmental stage, environmental factors, seasonality, and microbial interactions. For example, cholesterol content has been reported between 2.0 and 12 mg/kg dw (**Table 2**), while gallic acid levels range from 0.01 to 10 mg/kg dw (**Table 6**). These discrepancies highlight the urgent need for publicly available *Ulva* reference materials to support quality control and inter-laboratory calibration, thereby strengthening confidence in bioactive quantification and facilitating regulatory approval.

7. Market development and regulatory outlook

Market development is a critical component of commercialization. As *Ulva*-based products gain traction in Asia and expand into Europe and North America, consumer awareness, transparent product labeling, and confidence in product safety and efficacy must be prioritized (Hofmann et al., 2024). Functional components of *Ulva*—including ulvan, proteins, and pigments—are increasingly incorporated into dietary supplements, vegan and clean-label foods, natural cosmetics, and medical formulations. This expanding market requires robust quality assurance, transparent sourcing, and comprehensive safety data to maintain credibility.

From a regulatory perspective, the integration of *Ulva*-derived products into mainstream markets depends on standardized rules and compliance protocols. Within the European Union, extraction solvents, contaminants, and novel food applications must conform to strict safety standards. Directive 2009/32/EC regulates solvent use in food production, while additional frameworks govern permissible pollutant levels, allergen control, and health claims. Genetic barcoding (e.g., *rbcL*, *tufA*, and ITS regions) is increasingly essential for species authentication, ensuring traceability and regulatory compliance in food and nutraceutical sectors (Roleda and Heesch, 2021).

International food safety authorities are also establishing maximum allowable concentrations for heavy metals (e.g., arsenic, cadmium, lead), iodine, and other potentially hazardous substances in edible seaweeds (Vargas-Murga et al., 2025). Continuous monitoring and certification, potentially supported by eco-labels or third-party sustainability standards, will be essential for regulatory approval and consumer trust.

The industrial utilization of *Ulva* aligns with several United Nations SDGs, including SDG 2 (Zero Hunger), SDG 3 (Good Health and Well-Being), SDG 7 (Affordable and Clean Energy), SDG 9 (Industry, Innovation, and Infrastructure), SDG 12 (Responsible Consumption and Production), and SDG 14 (Life Below Water). Seaweed-based biorefineries represent sustainable alternatives to terrestrial biomass, offering reduced freshwater and land requirements, higher productivity per unit area, and ecosystem services such as carbon sequestration and nutrient bioextraction.

To transition *Ulva* from promising research subject to a cornerstone of the blue bioeconomy, legislative incentives, public–private partnerships, and industry–academia collaborations are required. Investment in pilot-scale demonstration facilities, standardized life cycle assessments, and techno-economic feasibility studies will accelerate industrial adoption (Nillson, 2022). The creation of a unified knowledge repository, or "white book", documenting optimal extraction conditions could further streamline development and expedite commercialization.

8. Conclusion

In order to make Ulva use both economically feasible and environmentally conscious, it will be crucial to incorporate sustainable solvents, cutting-edge extraction technologies, and precision aquaculture techniques. *Ulva*'s potential as a flagship species for sustainable marine biotechnology has been strengthened by recent research that has discovered new functional compounds within the species. *Ulva*'s potential as a vital resource in the developing blue bioeconomy is highlighted by its wide range of uses in the food, pharmaceutical, cosmetic, agricultural, and energy sectors.

Abbreviations

ALA, α-linolenic acid; B12, vitamin B12 (cobalamin); CE, chemical extraction; DES, deep eutectic solvents; DGDG, digalactosyldiacylglycerol; DHA, docosahexaenoic acid; DPA, docosapentaenoic acid; dw, dry weight; EAE, enzyme-assisted extraction; EFSA, European Food Safety Authority; FA, fatty acid; FW, fresh weight; GAE, gallic acid equivalents; HDL, high-density lipoprotein; HPLC, high-performance liquid chromatography; HT, hydrothermal treatment; IL, ionic liquid; IMTA, integrated multitrophic aquaculture; IU, international unit; LA, linoleic acid; LDL, low-density lipoprotein; MAE, microwave-assisted extraction;

MGDG, monogalactosyldiacylglycerol; MUFA, monounsaturated fatty acid; NADES, natural deep eutectic solvents; NSCLC, non-small cell lung cancer; PEF, pulsed electric fields; PLE, pressurized liquid extraction; PUFA, polyunsaturated fatty acid; SFA, saturated fatty acid; SFE, supercritical fluid extraction; SDG, Sustainable Development Goal; SQDG, sulphoquinovosyldiacylglycerol; UAE, ultrasound-assisted extraction; UFA, unsaturated fatty acid.

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Author contributions

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Declaration of Competing Interests

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

Figures

Figure 1

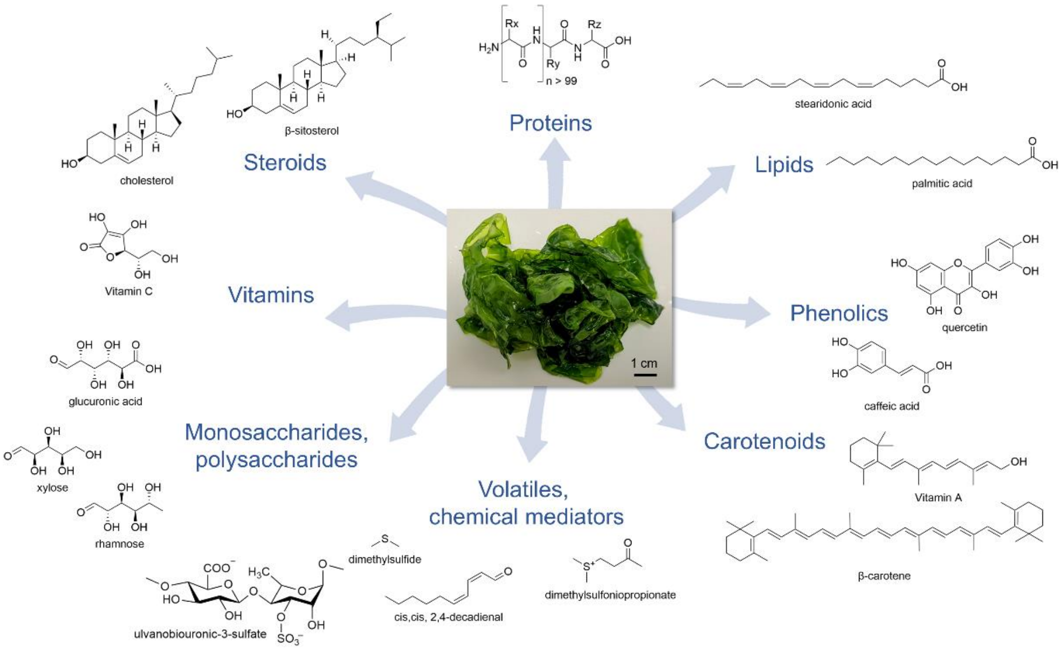

Fig. 1. Main nutrients and dietary compounds in the green macroalga *Ulva* (Chlorophyta) and its associated bacteria. *Ulva* produces diverse classes of compounds, including phenolics, steroids, fatty acids, and the unique sulfated polysaccharide ulvan. In addition to bioactives of for industrial interest, chemical exchanges occur between *Ulva* and its bacterial partners. Disentangling the specific contributions of these interactions to bioactive production remains an important future challenge.

Figure 2

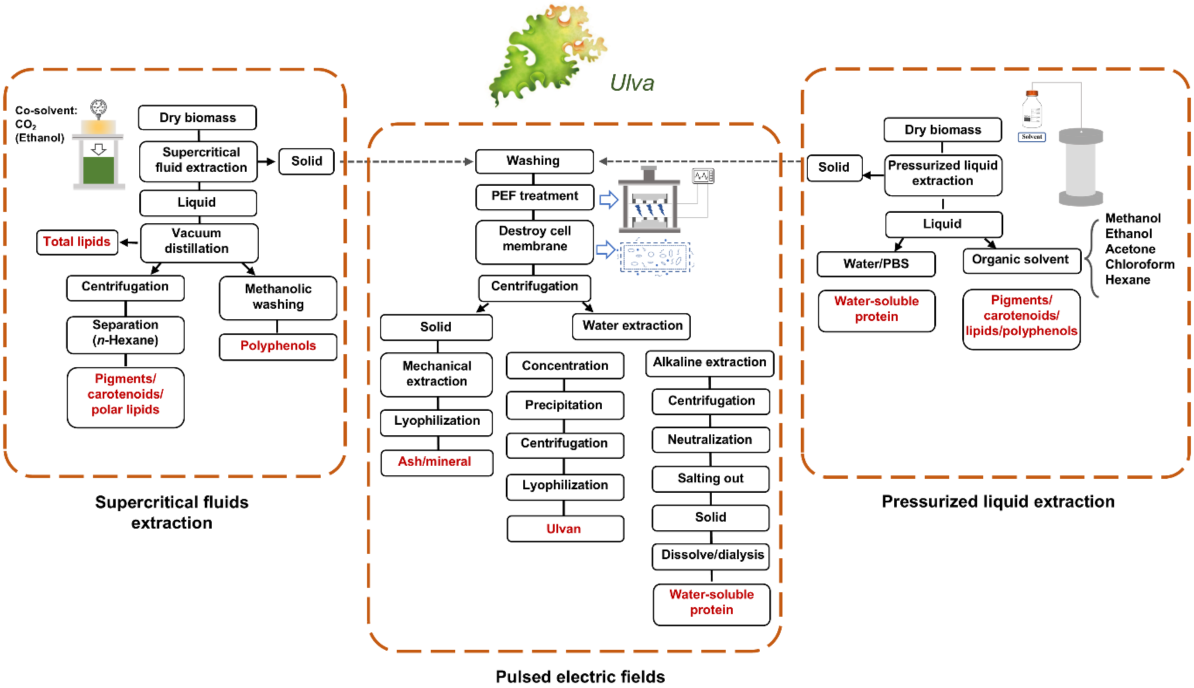

Fig. 2. Extraction methodologies. Schematic representation of supercritical fluid extraction (SFE) pulsed electric fields (PEF), and pressurized liquid extraction (PLE) processes for the recovery of high-value compounds from *Ulva* biomass.

Figure 3

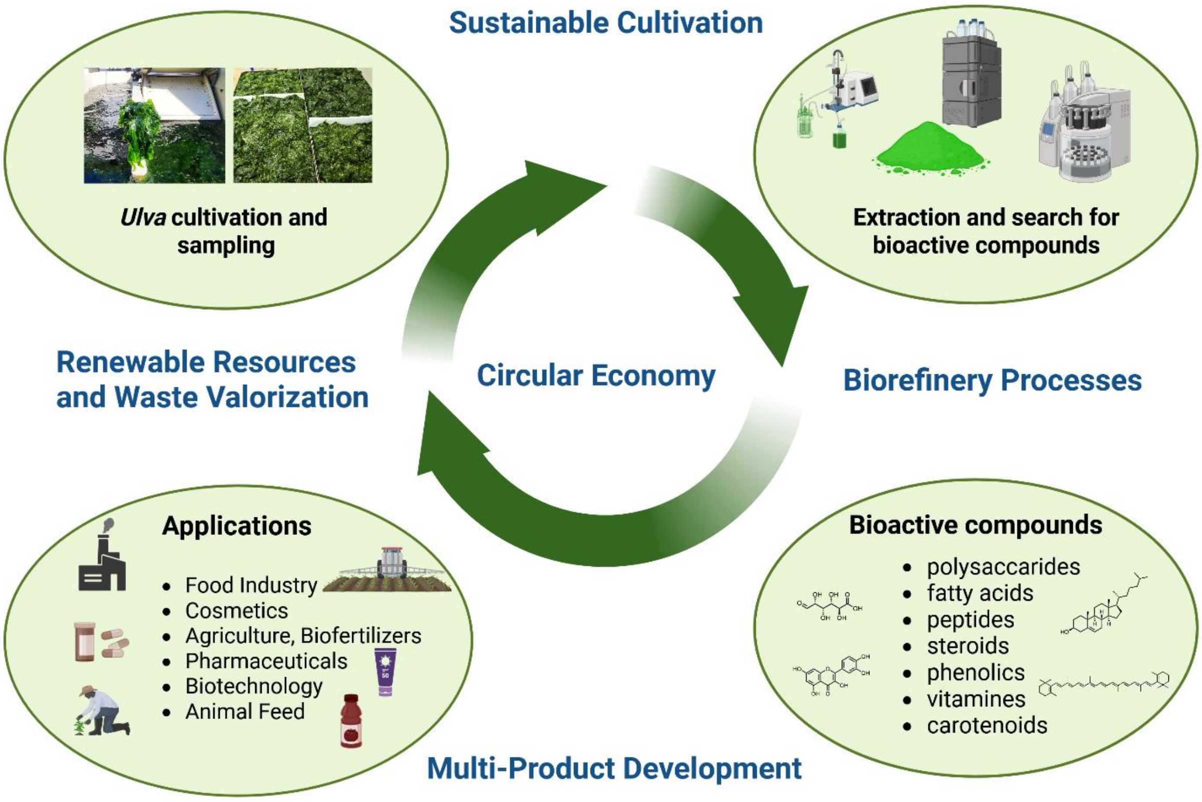

Fig. 3. Bioactives and *Ulva* in a circular economic framework. Images of aquaculture are courtesy of Muki Shpigel. Figure was created in BioRender. Wichard, T. (2025) https://BioRender.com/eln937t

Tables

Table 1. Major bioactive compounds in *Ulva* and their associated health benefits

Compound Group	Examples	Bioactives
Polysaccharides	Ulvan	Antioxidant, antiviral, anticoagulant
Phenolics	Flavonoids, phenolic acids	Antioxidant, anti-inflammatory
Proteins/peptides	ACE-inhibitory peptides	Antihypertensive, antimicrobial
Fatty acids	αLEA	Anti-inflammatory, cardioprotective
Pigments	carotenoids	Antioxidant, anticancer
Vitamins	vitamins A, C, E	General health, metabolism support
Sterols	stigmasterol	anticancer
Minerals	Ca, Fe	General health

Table 2. Selected steroidal compounds extracted from *Ulva* species (n.d. = not determined or mentioned in the study).

Taxon	Origin	Treatments	Extraction procedure		Steroids						References
				Units	**Fuco-sterol/ Unit**	**Isofuco-sterol**	**Chol-esterol**	**β-Sito-sterol**	**Campe-sterol**	**Brassica-sterol**	
Ulva lactuca	SeaConomy Belgium, Netherland	Dried (70°C). grounded	Extracted twice with cyclohexane after saponification; solvent evaporated at 65 °C under N_2	mg/g dw	0.21 - 0.38	n.d.	0.002 - 0,004	n.d.	n.d.	n.d.	Vanbrabant et al. 2021
Ulva lactuca	ALGAplus Ltd, Ria de Aveiro, Portugal	Washed with seawater, dried (20°C)	Lyophilized sample Soxhlet-extracted with dichloromethane (9 h), solvent evaporated to dryness	mg/kg dw	n.d.	n.d.	12.4	3.1	n.d.	n.d.	Santos et al. 2015
Ulva armoricana	Plestin-les-Grèves, Brittany, France	Rinsed with distilled water, grounded	Extracted with chloroform/methanol (1:1, v/v) for 2 days at RT with 5 h agitation	% dw ± SD	1.4 ± 0.1	25.0 ± 0.2	35.2 ± 0.3	n.d.	1.3 ± 0.1	3.0 ± 0.2	Kendel et al. 2015
Ulva prolifera	Coast of Lianyungang, China	Washed with water and dried (60°C, 48 h), milled and, sieved	Extracted with methanol (25 °C, 48 h, dark); residue (pH 11) re-extracted with ethyl acetate; ethyl acetate phase concentrated under reduced pressure	mg/kg dw	n.d.	n.d.	9.0	n.d.	n.d.	n.d.	Sun et al. 2016
Ulva prolifera	Coastal waters of China.	Lyophilized, grounded	Extracted with dichloromethane/methanol (2:1, v/v) in ultrasonic bath; supernatant evaporated at 40 °C under reduced pressure; residue saponified with 6% KOH/methanol (80 °C, 1 h), extracted with hexane;	% of sterols	90.8	n.d.	9.20	n.d.	n.d.	n.d.	Geng et al. 2017

			mixture evaporated to dryness under N_2								
Ulva expansa	Mazatlan Bay, Mexico	Rinsed with distilled water, lyophilize, grounded.	Extracted with chloroform/methanol (2:1, v/v), evaporated to dryness under N_2, sterols transesterified with sodium methoxide at RT (90 min)	% dw ± SD	Fucosterol + isofucosterol 78.8%±4.5 (fw)		7.15±0.42 (Chol + dehydrochol.)	4.34±1.10	4.53±0.80	1.68±0.70	Osuna-Ruiz et al., 2019
Ulva reticulata	Ervadi, India	Washed with water, dried in shade, and powdered.	Powder macerated in methanol (2 weeks), solvent removed under reduced pressure	mg/g dw	n.d.	7.0	n.d.	n.d.	n.d.	n.d.	Siddhanta et al. 2002

Table 3. Selected oligosaccharide and monosaccharides extracted from *Ulva* species (n.d. = not determined or mentioned in the study)

Taxon	Origin	Treatments	Extraction procedure	Oligosaccharides (various targeted analysis)						References
Ulva clathrata	Fujian coast, China	Rinsed and dried	hot water, ion-exchange, SEC	10.3% of FEP in dry biomass; sulfated polysaccharide with high (1→4)-β-L-arabinopyranose; 31.0% sulfate ester in the polysaccharide						Qi et al., 2012
Ulva pertusa	Qingdao coast, China	Rinsed and dried	sulfur trioxide/*N*,*N*-dimethylformamide (SO3–DMF) in formamide	Sulfated ulvans						Qi et al., 2005
Ulva prolifera	Zhoushan, Zhejiang, China	Rinsed and air-dried	DEAE cellulose-52 and SEC	Polysaccharides hyrolysate; mainly composed of mannose, xylose, and glucose.						Xu et al., 2015
Ulva lactuca	Monastir, Tunisia)	Rinsed and dried	enzymatic and chemical extraction with cellulase and protease	UroA: 18-23%	Rha: 15-21.5%	Ara: 0.3-0.55%	Xyl: 2.7-3.3%	Glu: 1.4-7.5%	Gal:1.3-1.8%	Guidara et al., 2019
Ulva linza	Qingdao coast, China	Rinsed and dried	Hot water extraction and SEC	(1→4)-Rha	(1→3)- and (1→2)-Rha	(1→4)-GluA	(1→3)-Gal	(1→4)-Xyl		Qi et al., 2013
Ulva lactuca, linza, compressa, prolifera, intestinalis				sulfated glucuronorhamnans (Multiple references, e.g., Bikker et al., 2016; Lahaye & Robic, 2007; Li et al., 2018b; Wang et al., 2013)						
Ulva pertusa	Qingdao coast, China	Rinsed and dried	Hot water, precipitation by ethanol	UroA: 23.2%	Sulfate groups 17%	Rha, Man, Gal Ara	(-D-GlcpA-(1-> 4)--L-Rhap 3S)	(-L-IdopA-(1-> 4)--L-Rhap 3S)		Pengzhan et al., 2003
Ulva conglobata	Qingdao coast, China	Dried	Hot water, precipitation with ethanol,	sulfate ester 23.04 -	UroA 10.8-14.9%	Rha 63-72% mol	Glu 13-21%mol	Xyl, Glc, Man 1-3.3%mol		Mao et al., 2006

			purification by ion-exchange, SEC	35.20 %	
Ulva neumatoidea, fasciata, lactuca,	Northwest Mexican Pacific coast	Dried	Hot and cold water	n.d.	Guerra-Rivas et al., 2011;

Note: SEC = Size exclusion chromatography

Table 4 Selected vitamins extracted from *Ulva* Species

Taxon	Origin	Treatments	Extraction procedure	Vitamins						References
				A	B2	B9	B1	C	E	
Ulva rigida	Northwest Iberian coast, Spain	Dried	Vitamins were analysed by HPLC	9581 UI/kg dw	1.99 mg/kg dw	1.08 g/kg dw	4.70 mg/kg dw	94.20 mg/kg	19.70 mg/kg	Taboada et al., 2010
Ulva lactuca	Coasts, Northern Chile	Dried (sun), milled (flour)	α-Tocopherols and tocotrienols in lipid extracts analyzed by HPLC						1071.4 ± 9.2 mg/kg dw	Ortiz et al., 2006
***Ulva* sp.**	Margarita Island, Venezuela	Dried (sun), freeze-dried	Ferrozine method					37.8 mg/g dw		García-Casal et al., 2007
Ulva lactuca	Pameungpeuk Indonesia	Dried (sun, 5d), grounded	Vitamin A analyzed by HPLC; Vitamins B1 and B2 analyzed by UPLC	< 0.5 UI/100 g dw	0.86 mg/kg dw		4.87 mg/kg dw			Rasyid, 2017
Ulva intestinalis	Shallow waters, Corniche Bay Abu Dhabi.	Washed (20–25 °C)	Vitamin B complex clarified with Carrez solutions; Vitamin C treated with zinc acetate dihydrate and potassium ferrocyanide trihydrate; both analyzed by HPLC		<3.0 ppm fw		<3.0 ppm	<10.0 ppm fw		Farzanah et al., 2022
Ulva spp.	Upper infralittoral, Black Sea, Turkey	Dried (60ºC, 3 h)	Analysed by HPLC. (α-tocopherol only)						9.10 ± 0.50 µg/g dw	Durmaz et al., 2008
Ulva spp.	Serangan Beach, Bali, Indonesia	Dried (50°C, 0.5 h), blended	α-tocopherol by acetonic Soxhlet extract, colorimetry,						19.29 mg/100 g dw	Wrasiati et al., 2019
Ulva spp.	Mandapam, Tamil Nadu, India.	Dried (shade, 3d) powdered	Lipids extracted by Folch method, samples saponified, vitamins extracted with petroleum ether	n.d.					0.06 mg/100 g dw	Debbarma et al., 2016

Ulva rigida	South shore Marmara in Turkey	Dried (RT, 3d)	α-tocopherol extracted with phosphomolybdenum reagent (37 °C); Vitamin C titrated with 2,6-dichlorophenol indophenol	2.05 ± 0.33 mg/g dw	3.27 ± 0.22 mg/g dw	Yildiz et al., 2014

Table 5. Selected carotenoids extracted from *Ulva* species (n.d. = not determined or mentioned in the study).

Taxon	Origin	Treatments	Extraction procedure	Carotenoids							References
				Units	Total	Violaxanthin	Zeaxanthin	Lutein	Neoxanthin	β-carotene	
Ulva compressa	Coasts Mangaluru India	Dried overnight at 40 °C	Macerated, extracted in ice-cold acetone, analyzed by HPLC	µg/g dw	16.49	4.14 ± 0.06	3.95 ± 0.18	4.68 ± 0.51	3.81 ± 0.08	n.d.	Bhat et al. 2021
Ulva lactuca	Coasts Mangaluru India	Dried overnight at 40 °C	Macerated, extracted in ice-cold acetone, analyzed by HPLC	µg/g dw	32.87	0.02 ± 0.01	11.26 ± 0.12	21.13 ± 0.07	0.47 ± 0.11	n.d.	Bhat et al. 2021
Ulva fasciata	Coasts Mangaluru India	Dried overnight at 40 °C	Macerated, extracted in ice-cold acetone, analyzed by HPLC	µg/g dw	1.41	n.d.	0.25 ± 0.04	0.9 ± 0.12	0.26 ± 0.00	n.d.	Bhat et al. 2021
Ulva prolifera	Coasts Mangaluru (India)	Dried overnight at 40 ◦C	Macerated, extracted in ice-cold acetone, analyzed by HPLC	µg/g dw	43.75	3.66 ± 0.1	9.47 ± 0.07	10.23 ± 0.12	8.84 ± 0.12	10.85 ± 0.11	Bhat et al. 2021
Ulva linza	Intertidal zone Qingdao, China.	Enriched seawater, frozen in liquid N_2	Pulverized in liquid nitrogen, pigments extracted with cold 85% aqueous acetone	Chl a^{-1}	n.d.	6.64	n.d.	32.7	7.98	7.52	Zhang et al. 2015
Ulva rotundata	North River near Baufort, N.C, USA. .	Seawater, frozen in liquid N_2	Frozen samples extracted with 100% acetone, pigments analyzed by HPLC	µmol/ m^{-2}	n.d.	26.4	1.7	44.2	11.2	n.d.	Franklin et al. 1992, Eismann et al. 2020

Ulva rotundata	North River near Baufort, N.C, USA.	Seawater, lyophil.	Extracted with 100% acetone, pigments analyzed by HPLC	µmol/ m^{-2}	n.d.	12	4.0	33.6	4.07	n.d.	Franklin et al. 1994, Eismann et al. 2020
Ulva pertusa	Owase, Mie Prefecture, Japan.	Seawater, dried	Extracted with 100% methanol, analyzed by HPLC	mg/g dw	n.d.	2.1 ± 0.5	n.d.	7.5 ± 0.7	2.2 ± 0.4	6.0 ± 0.5	Eismann et et al. 2020
Ulva pertusa	Japan	PES medium dried	Extracted with 100% methanol, analyzed by HPLC	mg/ 100 g dw	n.d.	8.5 ± 0.36	n.d.	27.8 ± 1.01	6.9 ± 0.74	19.7 ± 1.09	Kakinuma et al. 2001
Ulva pertusa	Japan	PES medium dried	Extracted with 100% methanol, analyzed by HPLC.	mg/ 100g dw	n.d.	14.0 ± 1.72	n.d.	37.6 ± 2.9	9.5 ± 0.42	46.5 ± 10.3	Kakinuma et al. 2001

Table 6. Selected phenolic compounds extracted from *Ulva* species (n.d. = not determined or mentioned in the study).

Taxon	Origin	Treatments	Extraction procedure		Phenolics						References
				Units	Apigenin/ Unit	Quercetin	Kaempferol	Luteolin	Caffeic Acid	Gallic Acid	References
Ulva fasciata	Gulf of Mannar coast, India	Dried	Phenols were extracted with methanol and were analysed by HPLC	mg/kg dw	n.d.	n.d.	n.d.	n.d.	0.44	10.2	Abirami and Kowsalya 2016
Ulva fasciata	Ras El Bar coast	Dried	Alga biomass was extracted using the Soxhlet extraction method using a mixture of methanol and hexane and were analysed by HPLC	mg/kg dw	n.d.	0.84	0.39	n.d.	0.067	n.d.	El-Bilawy et al. 2022
Ulva fasciata	Saurashtra coast, India	Dried	Phenols were extracted with aqueous methanol and were analysed by HPLC	mg/kg dw	n.d.	10	n.d.	n.d.	n.d.	n.d.	Tanna, Brahmbhatt, and Mishra 2019
Ulva lactuca	Egyptian marine environment	Dried	Phenols were extracted with methanol/water and were analysed by HPLC	g/kg dw	n.d.	n.d.	62	n.d.	n.d.	n.d.	El-Gammal et al. 2024
Ulva lactuca	Nuniarchara sea beach in Cox's Bazar, Bangladesh	Dried	Phenols were extracted with ethanol/water and were analysed by HPLC	mg/kg dw	n.d.	2.6	6.6	n.d.	2.8	n.d.	Bokhtiar et al. 2024
Ulva lactuca	Saurashtra coast, India	Dried	Phenols were extracted with aqueous methanol and were analysed by HPLC	mg/kg dw	n.d.	n.d.	n.d.	n.d.	n.d.	n.d.	Tanna, Brahmbhatt, and Mishra 2019
Ulva lactuca	İskenderun, Turkey	Dried	Phenols were extracted with ethanol/water and were analysed by LC-MS/MS	g/kg dw	n.d	10.93	7.33	n.d	14.56	2.85	Korkmaz 2025
Ulva lactuca	Lara coast Antalya, Turkey	Dried	Phenols were extracted with hexaneisopropanol and were analysed by HPLC	mg/kg dw	n.d	0.011	0.012	n.d	n.d	n.d	Fatma et al. 2015

Ulva rigida	Gulf of Mannar, Mandapam	Dried	Phenols were extracted with methanol and were analysed by LC-MS/MS	mg/kg dw	n.d.	0.07	n.d.	n.d.	n.d.	0.01	Kumar et al. 2020
Ulva sp.	Mediterranean Sea at Abu Qir, Alexandria	Dried	Phenols were extracted with an ethanolic solvent and were analysed by GC/MS	mg/kg dw	294	n.d	n.d	25.9	n.d	n.d	Abdel-Razek et al. 2024

Declaration of generative AI and AI-assisted technologies in the manuscript preparation process

During the preparation of this work, the authors used ChatGTP/OPENAI to improve readability and language. After using this tool/service, the authors reviewed and edited the content as needed and take full responsibility for the content of the published article.

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