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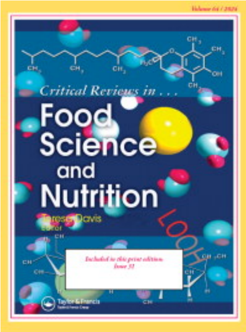

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REVIEW

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The green seaweed *Ulva*: tomorrow's "wheat of the sea" in foods, feeds, nutrition, and biomaterials

Laurie C. Hofmann[a,b], Sylvia Strauss[c], Muki Shpigel[d], Lior Guttman[e,f], Dagmar B. Stengel[g], Céline Rebours[h], Natasha Gjorgovska[i], Gamze Turan[j], Karina Balina[k,l], Gabrielle Zammit[m], Jessica M. M. Adams[n], Umair Ahsan[o,p], Angela G. Bartolo[q], John J. Bolton[r], Rosário Domingues[s,t], Ömerhan Dürrani[u], Orhan Tufan Eroldogan[v,w], Andreia Freitas[x,y], Alexander Golberg[z], Kira I. Kremer, Francisca Marques[s,t], Massimo Milia[ab], Sophie Steinhagen[ac], Ekin Sucu[ad], Liliana Vargas-Murga[ae], Shiri Zemah-Shamir[af], Ziv Zemah-Shamir[ag] and Antonio J. Meléndez-Martínez[ah*]

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ABSTRACT
Ulva, a genus of green macroalgae commonly known as sea lettuce, has long been recognized for its nutritional benefits for food and feed. As the demand for sustainable food and feed sources continues to grow, so does the interest in alternative, plant-based protein sources. With its abundance along coastal waters and high protein content, *Ulva* spp. have emerged as promising candidates. While the use of *Ulva* in food and feed has its challenges, the utilization of *Ulva* in other industries, including in biomaterials, biostimulants, and biorefineries, has been growing. This review aims to provide a comprehensive overview of the current status, challenges and opportunities associated with using *Ulva* in food, feed, and beyond. Drawing on the expertise of leading researchers and industry professionals, it explores the latest knowledge on *Ulva's* nutritional value, processing methods, and potential benefits for human nutrition, aquaculture feeds, terrestrial feeds, biomaterials, biostimulants and biorefineries. In addition, it examines the economic feasibility of incorporating *Ulva* into aquafeed. Through its comprehensive and insightful analysis, including a critical review of the challenges and future research needs, this review will be a valuable resource for anyone interested in sustainable aquaculture and *Ulva's* role in food, feed, biomaterials, biostimulants and beyond.

KEYWORDS
Ulva; food; feed; aquafeed; nutrition; biomaterials; biorefinery; seaweed

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1. Introduction

The world population is expected to reach 9.8 billion by 2050 (Population Reference Bureau, 2023). Accordingly, the agricultural food gap will increase due to climate change-induced constraints on natural resources, i.e., freshwater and farmland. Consequently, ensuring food security has become a global imperative. The oceans will play an increasingly important role in feeding the growing population with increasing demand for food and natural resources. Nevertheless, wild stocks cannot meet the increasing demand for fish or other biomass sources, including macroalgae. Therefore, seaweed cultivation may be essential for contributing to food security by provisioning food or feed ingredients (Araújo et al. 2022; Forster and Radulovich 2015; Radulovich et al. 2015).

Marine macroalgae, commonly known as seaweed, are considered the "promising plant of the millennium" (Dhargalkar and Neelam 2005) because of several advantages over land plants, such as no need for arable land, freshwater, fertilizer or pesticides to grow them, and the biomass can be utilized as food, feed, materials, gelling substances, and biofuels (e.g., Chapman and Chapman 1980). Furthermore, macroalgae grow more rapidly and occupy space more efficiently than terrestrial plants (Creed et al. 2019). In optimal conditions, macroalgae can produce higher dry biomass per unit area per year than fast-growing terrestrial crops such as sugar cane (Gao et al. 1994). Furthermore, macroalgae cultivation may help reduce greenhouse gas emissions in the food system by replacing food, feed, and materials with higher carbon footprints (Troell et al. 2022).

Seaweed production and processing can support the blue circular economy by contributing to the key drivers of the circular bio-based economy in the EU (Lange et al. 2021), namely bio-based products for health and new functionalities, primary production, land-use change, sustainable agriculture, biorefineries, and biomass supply for new biorefinery technologies. Further, many recent publications have promoted seaweed cultivation to meet many of the United Nations' global sustainable development goals (UNSDGs), including reducing hunger, improving good health and well-being, providing affordable and clean energy, and mitigating climate change (Duarte, Bruhn, and Krause-Jensen 2022). Despite these potential contributions to the circular economy, seaweed production in Europe is lagging (Araújo et al. 2021), and many risks and benefits must be assessed before upscaling macroalgal productions into sustainable seaweed aquaculture. These include (i) food safety considerations in integrated multi-trophic aquaculture (IMTA)/waste streams, (ii) genetic interactions of wild crops with cultivated crops, (iii) impacts of seaweed aquaculture on the surrounding ecosystems, (iv) diseases and epiphytes, (v) area utilization from a marine spatial planning perspective, (vi) threats associated with climate change, (vii) using a precautionary approach during carbon accounting and blue carbon financing, (viii) technological advancement for upscaling, and (ix) overcoming legal and economic constraints (Bermejo et al. 2022; Chopin, 2021; Cottier-Cook et al. 2016; Hasselström et al. 2022; Loureiro, Gachon, and Rebours 2015; Rosa et al. 2020, 2019; Stévant, Rebours, and Chapman 2017; Troell et al. 2022). Although algal cultivation technology has improved in the last decade, there is still a need to optimize production for energy efficiency, product quality, consumer safety, and biomass utilization (Stévant, Rebours, and Chapman 2017). Green algae in the genera *Ulva*, due to the characteristics described below, show high potential for becoming ideal model organisms for innovative mariculture.

In the last 30 years, *Ulva* spp. have been extensively analyzed for their value as food, feed, food ingredients (e.g., protein, carbohydrates, pigments, antioxidants), chemical constituents and medicinal properties, and the number of scientific publications involving *Ulva* has increased from 2130 in 2000 to 6724 in 2023 (Google Scholar). Major advancements have been made in cultivation methods, molecular identification techniques, and in the fields of aqufeed, terrestrial feed, biostimulants, biomaterials, and biorefinery strategies. From a food and feed perspective, green algae in the genus *Ulva* contain suitable levels of proteins, vitamins, trace minerals, and dietary fibers (Toth et al. 2020; Trigo et al. 2021; Stedt, Trigo, et al. 2022; Stedt, Toth, et al. 2022; Steinhagen, Larsson, et al. 2022; Steinhagen, Enge, et al. 2021; Steinhagen, Enge, et al. 2022; Taboada, MillÃ¡n, and MÃguez 2009) for human and animal consumption. The growing world population, environmental awareness and associated increased trends in vegetarianism and veganism, increasing demand for organic products, and global resource shortages are increasing the demand for sustainable marine crops and alternative proteins (Ismail et al. 2020; Faber et al. 2021; Yong et al. 2022; Duarte, Bruhn, and Krause-Jensen 2022). Furthermore, increasing environmental degradation and climate change awareness has actively encouraged health-promoting programs to link human diet and health with environmental sustainability (Patrick and Kingsley 2017). Considering that unhealthy diets primarily cause non-communicable diseases (NCDs), which are a leading cause of death (Lauber et al. 2020), health-promoting foods and lifestyles have attracted the world's attention. Indeed, the increase in the consumption of plant (and algae)-derived foods is recommended, as they are usually healthier and more sustainable (Willett et al. 2019) protein sources. Nevertheless, the much-cited EAT-Lancet Commission work discussing the need for identifying alternative sustainable food sources in the Anthropocene pays little attention to algae, although aquatic habitats (accounting for 70% of the Earth) will be critical in identifying novel sustainable and health-promoting foods such as seaweed. With an amino acid composition comparable to soy or egg protein, and including all essential amino acids (except tryptophan), selected strains of *Ulva* bearing high protein contents can partially substitute less sustainable protein sources (Dominguez and Loret 2019), and high contents of essential dietary fiber and other bioactive substances render it a beneficial food item providing health and functional advantages (Rajapakse and Kim 2011; Holdt and Kraan 2011; Lopes et al. 2019; Moreira et al. 2022; Qi et al. 2005). In particular, phytochemicals (e.g., carotenoids, phenolics) have health-benefiting characteristics and can be used in the cosmeceutical and pharmaceutical sectors and as functional foods (Abd El-Baky, El-Baz, and El-Baroty 2009; Khairy and El-Sheikh 2015; Lanfer-Marquez, Barros, and Sinnecker 2005; Mapelli-Brahm et al. 2020; Meléndez-Martínez et al. 2021; Steinhagen, Enge, et al. 2021; Steinhagen, Larsson, et al. 2022; Steinhagen, Enge, et al. 2022), increasing the economic value of *Ulva* biomass.

While *Ulva* spp., and seaweed in general, remains a niche product in Europe, the European market may play an important role in the future of seaweed production and consumption. Currently, the main importing countries of seaweed in Europe are the UK, France and Germany according to the Center for the Promotion of Imports from developing countries (CBI Ministry of Foreign Affairs). Therefore, the aim of this review is to improve awareness of the seaweed *Ulva* in food, feed, and beyond and to provide a critical review of the current status, challenges and opportunities of incorporating this genus into the mainstream so that it may become tomorrow's "wheat of the sea." To this end, *Ulva* spp. can play a pivotal role in the sustainable and health-promoting food era, and its consumption and applications are expected to increase in the future. The sustainable exploitation of *Ulva* as food and feed can contribute to the demand for renewable and novel nutritious food sources, especially with vegetarian and vegan protein, emphasized by the UNSDGs (United Nations, 2015). Because of its valuable constituent composition, *Ulva* can be biorefined to obtain and valorize products, including food ingredients, materials, chemicals, and fuels, consistent with the new circular economy paradigm. Of course, consumption of seaweeds in general and *Ulva* in particular also raises safety concerns as it may entail microbiological or chemical risks.

This review explores contemporary *Ulva* research through a comprehensive analysis of their distinct chemical composition, production, uses as food, feed, and biomaterials, and other important aspects, such as nutritional value, food safety, and emerging research needs. This review is targeted toward not only scientists and industry professionals working with seaweed-based foods, feeds and biomaterials, but also food scientists, nutritionists, feed manufacturers, dietitians, cooks, and pharmacists less familiar with *Ulva* as an ingredient or additive. We provide a critical review of the current status, challenges and future needs that are necessary to bring *Ulva* and *Ulva*-based products closer to the forefront of food science and nutrition research.

2. *Ulva* – tomorrow's "wheat of the sea"

Marine aquaculture is the fastest-growing component of food production (>7%/year) (Lomartire and Gonçalves 2022; Duarte, Bruhn, and Krause-Jensen 2022; Moreira et al. 2022). Green seaweeds account for <0.1% of the total seaweed production (Bolton et al. 2016). Nevertheless, the ubiquitously distributed genus *Ulva* (Ulvales, Chlorophyta), widely known as sea lettuce, has received increasing attention. The distinct characteristics of the representative species of this ecologically and economically important genus are summarized in Figure 1, which indicates the immense potential of *Ulva* species in playing a central role in the rapidly emerging European seaweed aquaculture industry as they can be cultivated in both on- and off-shore conditions (e.g., Bolton et al. 2009; Mata et al. 2016; Steinhagen, Enge, et al. 2021). The most notable characteristics include world-wide coastal distribution, fast growth rates, relatively simple life cycle, ease of culture, historical use in food and feed, documented bioactivity and efficiency as a biological filter (Figure 1). Furthermore, it is the only species of macroalgae with a sequenced genome, which facilitates genetic transformation and presents the genus as an ideal model organism (Wichard et al. 2015; de Clerck et al. 2018; Blomme et al. 2023; Wichard 2023).

2.1. *Ulva* taxonomy and identification

For most of taxonomic history, *Ulva* spp. have been discriminated using detailed morphological (blade shape or structure), anatomical (cell shape and size) and cellular (chloroplast position and appearance and the number of pyrenoids per cell) descriptions (Koeman and van den Hoek 1981). However, most species exhibit simple morphologies that are challenging to identify (Steinhagen et al. 2023; Hofmann et al. 2010; Kraft, Kraft, and Waller 2010), particularly due to phenotypic plasticity influenced by

Figure 1. Exceptional characteristics of the genus *Ulva*, demonstrating the reasons for its increased attention in diverse industries. High morphological plasticity: (Blomster, Maggs, and Stanhope (1999); Hayden et al. (2003); Wichard et al. 2015; Steinhagen, Weinberger, and Karez (2019); Steinhagen et al. (2023); massive proliferation: (Charlier et al. (2006); Charlier, Morand, and Finkl (2008); Smetacek and Zingone (2013); Gao et al. (2010); Steinhagen Weinberger, and Karez (2019)); high growth rates and ability to thrive at high stocking density: Mata, Schuenhoff, and Santos (2010); Lawton et al. (2013); Al-Hafedh, Alam, and Buschmann (2014); Sebök, Herppich, and Hanelt (2019); Stedt, Toth, et al. (2022); rapid nutrient uptake potential: Gao et al. (2013); Shahar et al. (2020); Stedt et al. (2022); wide environmental tolerance: Toth et al. (2020); Kirst (1990); Ghaderiardakani, Coates, and Wichard (2017); Bao et al. (2022); Thompson & Coates (2017); Ghaderiardakani et al. (2022); Steinhagen, Larsson, et al. (2022); Simon, McHale, and Sulpice (2022); Steinhagen, Enge et al. (2021); Kraft, Kraft, and Waller (2010).

environmental parameters (Wolf et al. 2012) and the microbiome (Wichard et al. 2015). To complicate matters, names initially used to describe European species are now used worldwide for species with different biogeographies, giving the impression that many *Ulva* species are cosmopolitan (Hughey et al. 2019 for the example of *U. lactuca* (Linnaeus, 1753)). In short, according to the 'International Code of Nomenclature for Algae, Fungi, and Plants' (Turland et al. 2018), the former *Ulva fasciata* is now correctly known as *Ulva lactuca*, and the former *Ulva lactuca* is now correctly known as *Ulva fenestrata* (Hughey et al. 2019).

The correct identification of both parental wild stocks and cultivated *Ulva* spp. biomass is necessary, as the traits vary between the species (Fort et al. 2019; Olsson, Toth, et al. 2020; Olsson, Toth, et al. 2020; Cardoso et al. 2023), and is particularly important due to their prevalent application in commercial projects and industrial product labeling. In order to identify species and strains of particular commercial value, for example using species selection criteria, DNA barcoding, i.e., the amplification and sequencing of specific loci in the genome, must be used. With respect to EU legislation, the need for DNA barcoding to confirm the identity of commercially produced *Ulva* material is relevant, because only two species, *Ulva lactuca*, and the outdated genus "*Enteromorpha*" (Aonori), are is listed as acceptable non-novel food in the Novel Food catalogue of the Regulation (EU) 2017/2470 (Lähteenmäki-Uutela et al. 2021; Bolton, 2020; Barbier et al. 2019). Thus, several other *Ulva* species named differently may have been long used as foods and could also qualify for such status (Roleda et al. 2021; Barbier et al. 2019). Furthermore, several *Ulva* species are nuisance species in some coastal areas and negatively affect valuable coastal ecosystem functions when introduced to non-native areas (Charlier et al. 2006; Charlier, Morand, and Finkl 2008; Smetacek and Zingone 2013; Steinhagen, Weinberger, and Karez 2019; Fort, Mannion, et al. 2020). Therefore, correct species identification is critical to preventing invasive species propagation and introduction through aquaculture initiatives, and an integrative systematics approach is required to accurately identify *Ulva* spp., considering morphological characteristics, DNA sequencing of different markers, and species biogeography. However, due to a lack of algal barcode sequences from various geographical locations on public repositories (Bartolo et al. 2020) as well as sequence misidentifications in herbaria and online databases (Fort, McHale, et al. 2022), approximately 24–32% of foliose *Ulva* spp. in genetic databases are misidentified (Fort, McHale, et al. 2022). Thus, the taxonomy of *Ulva*, including identifying taxonomically valid names, species numbers and their circumscription, must be clarified using molecular methods with globally distributed specimens. Significant research has recently been conducted in Europe using foliose species, and currently both nomenclatural and taxonomic revisions of *Ulva* spp. are ongoing (Fort, McHale, et al. 2021; Fort et al. 2022; Hughey et al. 2019, 2020, 2021; Tran et al. 2022). Nevertheless, the names of *Ulva* species presented in this review should be taken with caution unless the authors have provided evidence of molecular identification confirmed by the type specimen. Possible alternatives to molecular approaches and their potential benefits and drawbacks, are comprehensively discussed by Tran et al. (2022). Future investigations would ideally facilitate molecular species identification without requiring sequencing, as proposed by Fort et al. (2021), who employed a restriction digest of the ITS1 PCR product to discriminate between the main foliose *Ulva* species.

2.2. *Ulva* production

The FAO database reports data on the production of green seaweed, such as sea lettuce, since 1979. Various denominations can be found, such as bright green nori (*Enteromorpha clathrata*), green laver (*Monostroma nitidum; Monostroma* is a green macroalgal genus similar in form to *Ulva*, but not closely related), lacy sea lettuce (*Ulva pertusa*), and sea lettuces nei (*Ulva* spp.). The FAO database records aquaculture of sea lettuce for *Ulva* spp. in South Africa (3715 t in 2020), *Monostroma nitidum* in South Korea (8286 t in 2020), and *Ulva prolifera* (as *Enteromorpha prolifera*) in China (200 t in 2020). The annual production rates of these taxa are shown in Figure 2. The Republic of Korea's 12,965 tonnes of green seaweed cultivation in 2019, including *M. nitidum*, *Capsosiphon fulvescens*, and *Codium fragile*, accounted for 78% of the global production. A recent report assessed that green macroalgae cultivation has recently decreased compared to the peak level of production, which occurred in the 1990s and early 2000s, depending on species (Cai 2021). This decrease can be seen in Figure 2, most notably for *M. nitidum* in South Korea and *U. prolifera* in China. The 16,696 tonnes of global green macroalgae production recorded in 2019 (approximately 0.05% of global macroalgae production) was less than half of the peak level in 1992 (38,556 tonnes), as opposed to the rapid growth in the production of brown macroalgae (3-fold) and red macroalgae (15-fold) between 1992 and 2019 (Cai 2021; FAO 2021). The reasoning behind this is unclear; however, recent statistics show that growth rates of total seaweed production in the leading Asian countries have slowed since 2015, potentially due to climate change, arrival at maximum carrying capacity, changes in marine spatial planning, and the aging seaweed farming workforce (Rieve, 2023). The 2,155 tonnes of *Ulva* produced globally in 2019 was also less than its peak production between 1950 and 2019, with 14,074 tonnes in 2008. The decline primarily reflects the decrease in *Ulva prolifera* (as *Enteromorpha prolifera*) production in China from 12,540 tonnes in 2008 to almost zero in 2019, whereas the global Ulva production in 2019 was 2,155 tonnes exclusively from South Africa (Table 1) (Cai, 2021; FAO, 2021). Nevertheless, the production numbers reported from South Africa may be overestimated, considering that only 2000 tons/year have been reported by Rothman et al. (2020). Because the *Ulva* is used as feed on farms rather than sold, production numbers are only estimates. Portugal has reported Ulvophyceae (the class of green algae that includes the genera *Ulva* and *Monostroma*) production in Europe since 2014; in 2019, this production reached 35 t (wet weight, FAO estimates). This IMTA-produced Portuguese alga has been identified as *Ulva*

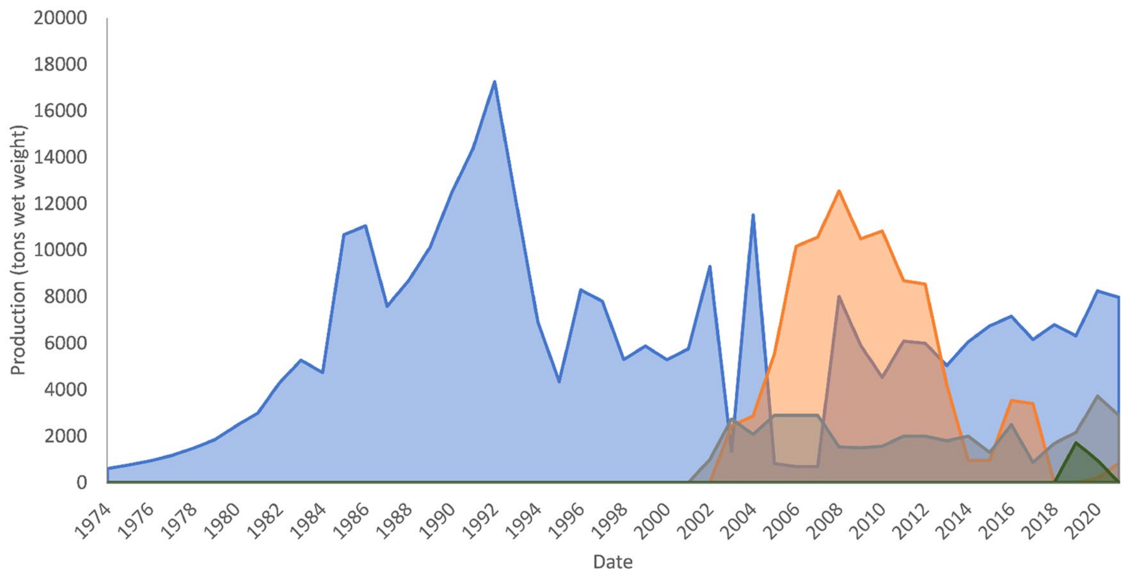

Figure 2. Global production of green seaweeds reported in the FAO database since the 1970s reported by country; grey, *Ulva* spp. in South Africa; green, *Ulva* spp. in Vietnam; blue, *M. nitidum* in South Korea; orange, *U. prolifera* in China; not visible due to insignificant amounts: *Ulva* spp. produced in Portugal and Spain.

Table 1. Average and maximum global production of green seaweeds by country, 1950–2019 (Cai 2021; FAO 2022).

Ulva species	Average annual production 1950–2019 (wet tonnes)	Maximum annual production 1950–2019 (wet tonnes)	Maximum annual production 1950–2019 (year)	Cultivation in 2019 (wet tonnes)	Cultivation in 2020 (wet tonnes)	Cultivation in 2021 (wet tonnes)	Country
Monostroma nitidum	3,991	17,248	1992	6,321	8,241	7,958	Republic of Korea
Enteromorpha (Ulva) prolifera	1,367	12,540	2008	–*	200	850	China
Ulva spp.	515	2,900	2005	–	3,715	2,882	South Africa
Green seaweeds nei	–	–	2019	1,717	952	0	Vietnam
Green seaweeds nei	17.56	35	2019	35	5	5	Portugal
Green seaweeds nei	0.35	0.87	2019	0.87	–	–	Spain

**Notes*: "–" indicates zero or no data.

lacinulata (formerly *U. rigida*), a non-sporulating species that grows well in floating culture and contributes to green tide formation in some regions. Surprisingly, the FAO database does not list any *Ulva* production from Israel, despite its largest company (Seakura, Israel) producing 50 tons FW/year. Within Europe, a recent assessment of the status of algal production in Europe reported 15 enterprises that cultivate *Ulva* spp. (Vazquez Calderon and Sanchez Lopez 2022). Nevertheless, not all European data are reported in the FAO database, which only includes data from Portugal and Spain. One of the leading European producers produced 150 tons of fresh weight in 2022, which is still only a fraction of the production rate (2000 tons/year) reported from abalone farms in South Africa (Bolton et al. 2016; Rothman et al. 2020). Considering that other countries may not be disclosing their production rates, the data currently available should be interpreted with caution and regarded as an underestimation.

2.3. Nutritional content

The keywords "nutrient composition," "*Ulva*," "fatty acids," "amino acids," and "minerals" were searched through Scopus and Google Scholar to conduct a review on the nutritional content of *Ulva* spp. Special care was taken to include the species diversity of *Ulva* in all available data. The concentration ranges of proteins, carbohydrates, ash, lipids, amino acids, fatty acids, and minerals are summarized in Tables 2 and 3 and Supplementary Tables 1 and 2. In some cases, concentration ranges are provided, as well as seasonal variations when available.

The biochemical profiles of different *Ulva* species are characterized by 13–50% ash, 5–27% protein, 0.5–4% lipids, and 53–78% total carbohydrates, of which 37–61% are fiber (data referring to dry weight (DW), Table 2). The protein content in sea lettuce is considered high among seaweeds; for instance, values >20% DW have been reported in *Ulva reticulata* and *U. lactuca* (Ortiz et al. 2006; Ratana-Arporn & Chirapart 2006) and can reach content >30%, more than double the natural content, when produced in nutrient-enriched environments (Viera et al. 2011). The levels found in high-protein terrestrial plants, such as soybeans, reach up to 40% DW ("USDA FoodData Central"). To measure the seaweed protein content, the nitrogen factor of 4.76 was used, which provides a lower nitrogen-to-protein ratio value (Angell et al. 2016). A conversion factor of 5 has been proposed to measure the nitrogen-to-protein ratio of seaweeds accurately.

Table 2. Nutritional composition of different species of *Ulva*.

Species	Season/Month	Protein %	Carbohydrate %	Lipid %	Ash%	Moisture	Reference
Ulva pertusa	April	ND	ND	2.15	ND	83.32	(Floreto, Teshima, and Ishikawa 1996)
U. reticulata	May	21.1	55.8	0.75	17.6	22.5	(Ratana-Arporn and Chirapart 2006)
U. clathrata		ND	ND	2.62	ND	92.00	(Kendel et al. 2015)
U. lactuca		27.2	61.5	0.3	11.0	12.6	(Ortiz et al. 2006)
U. clathrata	MSS	21.9	ND	2.5	49.6	ND	(Peña-Rodríguez et al. 2011)
	LSS	20.1	ND	2.2	27.5	ND	
U. expansa		4.12	ND	0.65	35.66	84.59	(Osuna-Ruíz et al. 2023)
U. prolifera		19.87	ND	6.06	17.50	ND	(Pirian et al. 2016)
U. flexuosa		10.55	ND	2.82	33.00	ND	
U. fasciata		14.06	ND	0.56	20.21	ND	
U. californica		15.20	ND	3.75	28.76	ND	
U. compressa		18.64	ND	0.90	22.30	ND	
U. lactuca		21.55	ND	0.75	12.18	ND	
U. linza		10.16	ND	3.70	24.62	ND	
U. rigida		16.6	56.4	3.7	25.2	82.09	(Viera et al. 2011)
U. rigida		33.8	40.5	4.4	21.5	82.0	(Viera et al. 2011)
U. rigida		ND	ND	0.8	ND	ND	(Ivanova, Stancheva, and Petrova 2013)
U. fenestrata		ND	ND	0.5	ND	ND	(Colombo et al. 2006)
U. fenestrata	Spring	20.79	32.21	3.2-3.55	16.6	82	(Steinhagen, Larsson, et al. 2022; Steinhagen, Enge et al. 2021)
	Summer	4.67	40.21	1.17	22.56	81	
U. fenestrata		17.8–23.2	ND	ND	ND	ND	(Stedt, Trigo, et al. 2022)
U. fenestrata (as *U. lactuca*)		15%–21%*	ND	ND	ND	ND	(Roleda et al. 2021)
U. linza		ND	ND	1.31	ND	ND	(Bakan et al. 2021)
U. lactuca	Spring	20.12	44.81	4.09	22.08	8.9	(Khairy and El-Shafay 2013)
	Summer	17.88	46.42	3.57	17.56	14.57	
	Autumn	16.78	42.09	3.14	23.19	14.8	
U. lacinulata[a]	Lab	11.08	32.66	7.00	17.08	83.57	Current authors
U. compressa[b]	Lab	26.19	20.66	8.13	12.52	90.59	Current authors
Ulva sp.[c]	Fall	23.87	9.36	3.12	20.06	83.75	Current authors

*Calculated from total nitrogen using the conversion factor 4.6.
MSS: medium scale system; LSS: large scale system; ND: not determined.
[a]From the North Atlantic (Portugal). See Cardoso et al. (2023) for information on the origin of this strain and the molecular identification.
[b]From the German Wadden Sea, Dorum Neufeld, (53.742433, 8.514724).
[c]From the North East Harbor of Helgoland, Germany (54.184237, 7.890829).

The amino acid profiles of *Ulva* species are characterized by the predominance of aspartic acid, glutamic acid, and alanine (Supplementary Table 3) (Ferreira et al. 2021; Maehre et al. 2014; Peña-Rodríguez et al. 2011; Shuuluka, Bolton, and Anderson 2013). The values presented are standardized to % of protein where possible, but, strong variability between studies and differences in the units reported (% of protein vs. dry weight) make comparisons difficult, suggesting the need for a more systematic, standardized analysis (see future research directions). A principal component analysis (PCA) of the amino acid content of various *Ulva* spp. from various geographic regions and cultivation conditions showed that the first two components accounted for 78% of the variability. The first principal component was primarily influenced by glycine, serine, leucine, and tyrosine, while the second component was notably affected by cysteine. Cysteine was detected in only some species, resulting in significant separations between them in the PCA. Notably, *U. capensis* exhibited an exceptionally high concentration of glycine, *U. fenestrata* showed a high concentration of histidine, and *U. clathrata* displayed elevated levels of both arginine and glycine (Figure 3). The analysis also revealed co-occurrence patterns: glycine/serine (positive), leucine/tyrosine (positive), and cysteine/glycine (negative).

In order to compare the nutritional quality of *Ulva* spp. to terrestrial plants, we conducted a PCA of the nutritional content of *Ulva* spp. presented in Table 2 and the nutritional content of soy, corn, rice and wheat from the USDA FoodData Central website. The results show that the *Ulva* spp. clustered more closely together than to the terrestrial plants, but all species clustered most closely to wheat, compared to corn, rice or soy (Figure 4). The protein and lipid content separated *Ulva* spp. most strongly from soy. The implications of these results are discussed in the section on future research directions below.

The lipid content of *Ulva* is relatively low (0.5–4%). The predominant fatty acid is the saturated fatty acid (SFA) palmitic acid (16:0), making up an average of 27.8% in the species presented in this review. *Ulva* also contains monounsaturated and polyunsaturated (PUFA) fatty acids, particularly the essential linoleic acid (18:2 n-6) and linolenic acid (18:3 n-3) (Supplementary Table 2; Cardoso et al. 2017; Maehre et al. 2014; Neto et al. 2018; Lopes et al. 2019). The SFA/USFA ratio of all species presented is below 1 (0.15–0.90), with the exception of cultivated *U. clathrata* from a large-scale cultivated system, which had a ratio of 2.00. The MUFA/PUFA ratios ranged from 0.3 to 2.02 and the omega 6/omega 3 ratios ranged from 0.2 to 2.7. Wild collected *U. fenestrata*, *U. lactuca* and *U. rotundata* had the

Table 3. Mineral composition of different species of *Ulva*.

Elements	Wet				Dried							Dried		Dried
	Winter	Spring	Summer	Autumn	Winter	Spring	Summer	Autumn	June			Spring	Summer	
Macro elements (mg/g)														
	U. rigida									*U. clathrata*		*U. fenestrata*		*U. fenestrata*
Ca	0.69	3.23	0.46	1.11	2.11	12.73	1.56	2.23	ND	9.05	18.80	ND	ND	1.5–1.8
K	5.66	6.09	4.68	7.18	7.01	7.19	6.52	8.17	ND	ND	ND	ND	ND	16–18
Mg	5.97	8.41	5.69	8.92	10.55	8.91	6.13	10.22	ND	ND	ND	ND	ND	15–17
Na	5.19	5.74	4.44	4.62	6.27	6.31	5.83	5.21	ND	ND	ND	ND	ND	17–22
Micro elements (µg/g)														
Al	89.00	60.00	44.93	110.80	158.00	211.87	171.73	224.60	ND	ND	ND	27.446	36.727	ND
B	17.67	15.53	52.27	33.53	36.87	34.73	59.40	45.93	ND	ND	ND	ND	ND	ND
Ba	0.53	0.80	0.67	0.80	0.60	1.27	0.87	1.67	ND	ND	ND	ND	ND	ND
Co	<0.035	<0.035	<0.035	<0.035	<0.035	<0.035	<0.035	<0.035	ND	ND	ND	<0.035	0.039	ND
Cr	<0.010	0.20	0.60	0.20	<0.010	0.20	0.07	<0.010	ND	0.52	0.80	0.047	0.15	ND
Cu	3.27	3.00	2.00	1.33	6.33	4.13	1.00	1.93	1.6	54.17	13.80	0.482	0.74	11–26
Fe	227.87	188.20	124.60	225.07	293.93	461.47	574.53	399.87	130	340.1	41.72	25.89	35.56	30–60
Mn	3.00	3.07	4.60	5.40	5.47	10.07	10.27	6.93	8.4	ND	ND	1.29	4.77	5–14
Ni	<0.035	<0.035	<0.035	<0.035	<0.035	<0.035	<0.035	<0.035	ND	2.37	5.72	0.084	0.348	ND
Zn	13.20	8.47	2.00	4.40	20.13	17.60	13.80	14.40	1.0	188.91	16.66	1.59	1.52	5–14
Reference	(Beril and Çankırılıgil 2019)								(Queirós et al. 2021)	(Peña-Rodríguez et al. 2011)		(Steinhagen, Larsson, et al. 2022)		(Roleda et al. 2021)

ND: not determined.

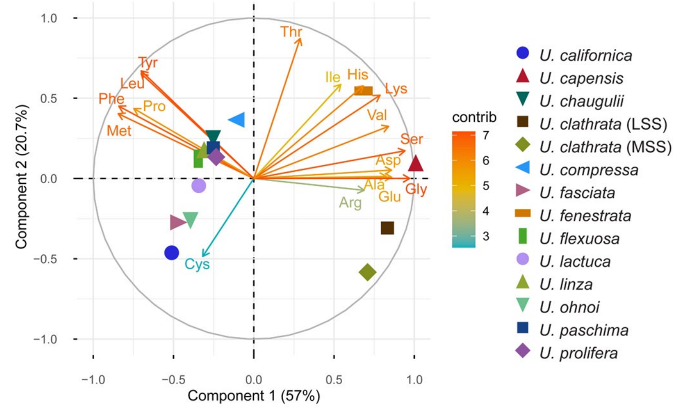

Figure 3. A principal component analysis of the amino acid profiles (% of protein) of various *Ulva* spp. from different geographic regions and cultivation conditions. Data are taken from Supplementary Table 3 and analyzed using JMP® pro v. 17 (SAS Institute Inc., Cary, NC, USA). Prior to analysis, data underwent a log + 0.1 transformation. The "contrib scale" indicates the contributions (in percentage) of the variables to the principal axes. LSS: large scale system; MSS: medium scale system (Peña-Rodríguez et al. 2011). Arg: arginine; ala: alanine; asp: aspartic acid; cys: cysteine; gly: glycine; glu: glutamic acid; his: histidine; ile: isoleucine; leu: leucine; lys: lysine; met: methionine; phe: phenylalanine; pro: proline; thr: threonine; tyr: tyrosine; ser: serine; val: valine.

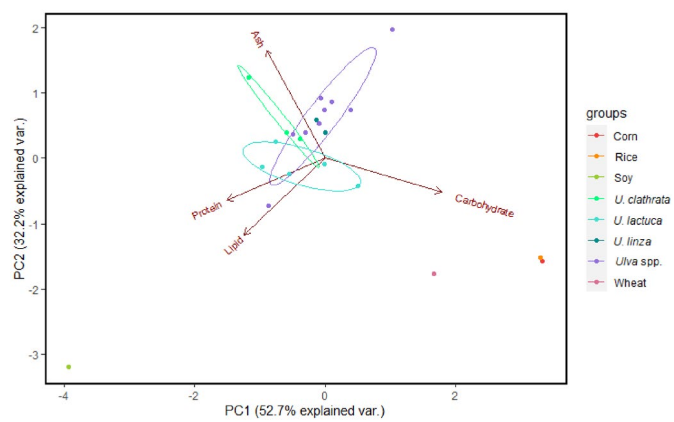

Figure 4. Principle component analysis (Martin and Maes 1979; Becker and Venkataraman 1984; Venables 1997) of the nutritional content (ash, protein, lipids, carbohydrates) of different *Ulva* spp. and soy, corn, rice and wheat. Data for *Ulva* were taken from Table 2 as percentages. When single values were missing, mean values were used. Data for soy, corn, rice and wheat were taken from the United States department of agriculture food data Central website (https://fdc.nal.usda.gov/index.html.) as percentages. The analysis was performed using the environment of R (version 4.02.), RStudio (version 2022.02.3). Data were not transformed prior to analysis. Percentages were transformed by arcsine-square-root transformation to correct for deficiencies of the proportions in normal distribution.

highest omega-3 fatty acid content and *U. fenestrata* and *U. rotundata* had the highest UFSA/FSFA ratios. A PCA of the fatty acid data, which grouped species by morphology (tubular, foliose, or both), indicated that many blade-forming species clustered together (Figure 5). On average, these foliose species (blades) exhibited higher total PUFA and SFA levels than the tubular species. *Ulva clathrata* was distinctive due to its particularly low MUFA content. *Ulva lactuca* demonstrated high variability, likely stemming from misidentification. Given that *U. lactuca* is not found in Europe, the data presented by van Ginneken et al. (2011) probably pertain to

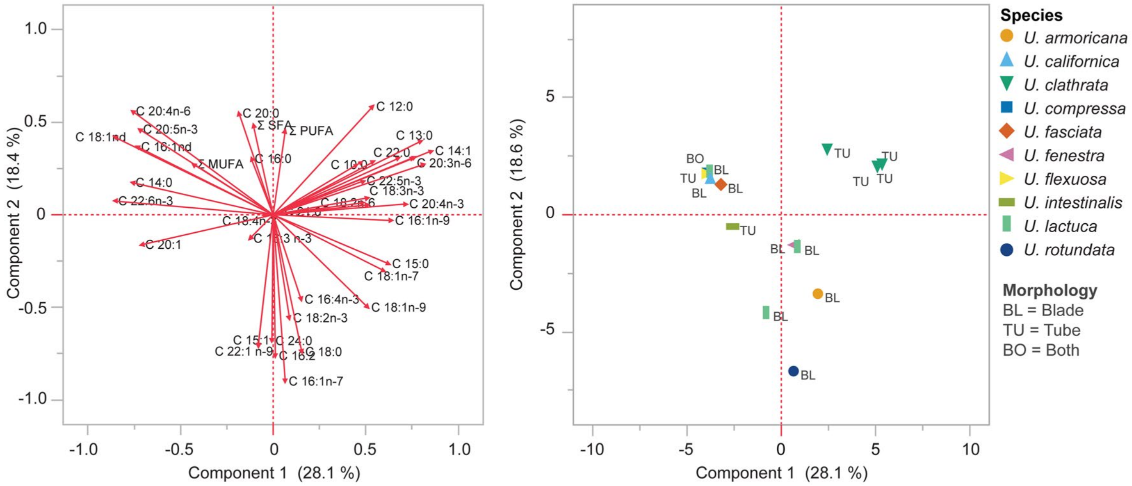

Figure 5. Principal component analysis (PCA) of the fatty acid profiles (left panel) of various *Ulva* spp. grouped by morphology (tubular or foliose/blade, right panel). Two species known to exhibit both morphologies were labeled as "both." data were sourced from Supplementary Table 2 and analyzed using JMP® pro v. 17 (SAS Institute Inc., Cary, NC, USA). Prior to analysis, data underwent a log + 0.1 transformation. Trace values (less than 0.1%) were substituted with 0.001%.

U. fenestrata, which, as indicated by other studies (Colombo et al. 2006; Steinhagen, Kramár, and Toth 2022), has notably high PUFA levels compared to other *Ulva* species.

The carbohydrate fraction characteristically contains sulfated polysaccharides, mainly ulvan, representing approximately 18–29% of the DW (Robic et al. 2009). Regarding micronutrients, *Ulva* species contain considerable amounts of potassium, magnesium, calcium, iron, and provitamin A (Table 3; Paiva et al. 2016). *Ulva* is also a rich source of bioactive compounds (Dominguez and Loret 2019). The large variations reported for different *Ulva* species and strains (Tables 2 and 3 and Supplementary Tables 1 and 2), even in samples with slight genetic variations (Fort et al. 2019; Ismail and Mohamed 2017; Roleda et al. 2021) are often due to different geographical locations (Tabarsa et al. 2012; Lee, Chang, and Lee 2014; Yaich et al. 2011; Mamede et al. 2021) characterized by different environmental conditions (temperature, irradiance, season, pH, salinity pCO_2; Olsson, Toth, et al. 2020; Olsson, Toth, et al. 2020; Toth et al. 2020; Fort et al. 2019; Jansen et al. 2022; Lawton et al. 2021; Queirós et al. 2021; Steinhagen, Enge, et al. 2022). In addition, differences in the analytical methods contribute to variability, and the need for standardized methods is discussed below. While these variations can be used to produce more homogenous or optimized biomass (e.g., higher protein) in land-based cultivation systems with a controlled nitrogen source, nutrient flux, aeration regime, and other variables (Ben-Ari et al. 2014; Diamahesa et al. 2017; Shahar et al. 2020; Zertuche-González et al. 2021), further advancements in strain selection and a better understanding of the genes that control different phenotypes are needed in order to advance and optimize the aquaculture of *Ulva* spp. (Simon, McHale, and Sulpice 2022). Furthermore, the *Ulva*-associated microbial community (i.e., holobiome) can influence algal growth performances and biochemical content; however, this finding warrants further research (Polikovsky et al. 2020).

Despite a plethora of data on nutritional content, identifying species selection criteria for different industries has proved challenging for *Ulva* spp., mainly because the nutritional content is species and site specific. In general, several foliose species like *U. fenestrata* (formerly *U. lactuca*), or *Ulva compressa* have shown high protein content compared to other species, but the protein levels of a species can be doubled by enriching the seaweed with an additional nitrogen source (e.g., Viera et al. 2011). In addition, selective pressure in regions where green tides occur result in fast-growing strains with high pigment and protein content, suggesting that these strains may be particularly useful for aquaculture (Fort et al. 2020). Therefore, by optimizing cultivation conditions, isolating fast growing strains and combining future improvements in strain selection and selective breeding, *Ulva* spp. with optimal characteristics for any industry of interest can be produced, as has already been pointed out by Toth et al. (2020). Nevertheless, it will be important to ensure that the highest quality biomass is reserved for food and feed, while lower quality biomass can be used in other industries, biomaterials and biostimulants, in order to avoid any competition between industries.

3. Ulva for human consumption: a candidate for the food industry and new cuisine

In South Asian regions (China, the Republic of Korea, Japan, and Vietnam), seaweeds have been consumed as foods or to alleviate diverse conditions (such as goiter), in some cases, since ancient times (Mouritsen, Rhatigan, and Pérez-Lloréns 2019; Blikra et al. 2021). The production and consumption of seaweed continues to be critical in the Southeast Asia (China, the Philippines, Indonesia, the Republic of Korea, and Japan), i.e., *aonori* in Japan or *gamtae* in Korea. However, commercial products containing *Ulva* are not commonly found in European supermarkets, except for regions with a tradition of seaweed consumption, for example in some coastal communities, particularly those with Celtic heritage. The interest in *Ulva* as food has only recently emerged among seaweed producers and the food industry. So far, many products contain dried or fresh whole algae for a small niche market. Fresh or dried *Ulva* can simply be used as the main ingredient from home cooking to high-end gastronomy, in dishes such as salads, tempura, or pesto, or can replace other green-leaved vegetables in traditional dishes (Turan and Cirik 2018). Furthermore, it can replace or reduce salt as seasoning in food preparations (Magnusson et al. 2016; Shannon and Abu-Ghannam 2019). However, *Ulva*'s most promising applications are as an enriching ingredient to profit from its versatile potential, better valorize raw biomass in food, and increase its sustainable impact.

Cereal-based products such as bread, pasta, or crackers are mainly produced from refined flour, being poor in fibers and micronutrients. The enrichment of bread with 1–4% *Ulva* powder or dried flakes can improve the dietary value without impairing the taste (Cofrades, Serdaroğlu, and Jiménez-Colmenero 2013; Kusumawati et al. 2022; Menezes et al. 2015; Shannon and Abu-Ghannam 2019). Incorporation of either 20% fresh (Debbarma et al. 2017; Ainsa et al. 2022) or 3% dried (Ainsa et al. 2022) *Ulva* in pasta formulations improves the products' nutritional profiles with higher fiber content while retaining or improving the taste. Furthermore, *Ulva* can serve as gluten-free ingredient in pasta or bread and and improves the quality when applied in concentrations up to 2%, (Turuk and Banerjee 2023; Yesuraj et al. 2022).

Ulva is also included in processed meats such as burgers and sausages and meat replacement products. Supplementation with 1–4% *Ulva* powder in pork patties produces juicier meat with less cooking loss (Jeon and Choi 2012). Similar results have been observed for fish burgers with 2% *Ulva* powder (Kumarathunge, Jayasinghe, and Abeyrathne 2016). Similar to other different seaweed species, substituting approximately 40% of meat content in burgers or sausages with whole seaweed can result in a tastier and healthier product with less fat, increased fibers, and reduced CO_2 footprint (Cofrades et al. 2017; Cox, Abu-Ghannam, and Gupta 2010; Mohammed et al. 2022; Peñalver et al. 2020; Shannon and Abu-Ghannam 2019). Additionally, the increasing demand for meat-free analogs opens further opportunities for *Ulva* (Yesuraj et al. 2022). Furthermore, *Ulva* enriches dairy products such as probiotic milk (del Olmo, Picon, and Nuñez 2019), cheese (del Olmo, Picon, and Nuñez 2018), seasoned butter and sauces, spreads, and mayonnaise (Yesuraj et al. 2022). Additionally, the addition of *Ulva* biomass or extracts to the manufacturing process can modify the products' technological properties. *Ulva*'s antioxidant capacity has been explored to increase the shelf life of processed meat products (Lorenzo et al. 2014; Roohinejad et al. 2017) or seafood (Jannat-Alipour et al. 2019). However, more research is required to develop products that meet customer acceptance. Finally, the characteristic sulfated polysaccharide ulvan has been explored in food processing for its gelling and water-binding properties similar to other known gelling agents, such as carrageenan and agar, rendering ulvan suitable as an alternative stabilizer replacing gelatin in vegan products (Kraan, 2012).

3.1. Food safety

The accumulation of contaminants can occur in seaweeds from the environment or during their production, processing and transformation. These elements may pose potential risks to human and animal health (Guo et al. 2023). The most common hazards of concern with respect to food safety are linked to chemical hazards, iodine and heavy metal content found in some seaweed species, based on Reports from the FAO/WHO expert meeting (FAO and WHO 2022), the Food Safety Authorities of Ireland (FSAI), the Nordic Council of Ministers (NCM – consisting of Norway, Denmark, Sweden, Iceland and The Faroe Island) and New Zealand (NZFS). Additional risks include pathogenic microorganisms (*Salmonella*, *Bacillus*, *Norovirus*), persistent organic pollutants, radionuclides, biotoxins, and microplastics and nanoplastics. Other chemical hazards include environmental pollutants such as PCBs, dioxins and pesticide residues, but these are not exclusive to food made with seaweed. While there is limited data on the occurrence of hazards in seaweed, with an attendant paucity of legislation on the hazards, there is also currently insufficient data available to suggest that physical hazards like microplastics and nanoplastics pose a significant risk to consumers in general through the consumption of seaweed or seaweed-based foods. In addition, there is currently no Codex standard or guidelines that specifically address food safety vis-à-vis seaweed production, processing and utilization. Both FAO and WHO believe that there is a significant global regulatory gap concerning food safety in seaweed (FAO and WHO, 2022; Food Safety Authority of Ireland, 2020; Nordic Council of Ministers, 2023; New Zealand Food Safety, 2023).

The maximum level (ML) for iodine varies significantly among countries. In China and the EU there are no established maximum levels (MLs) except in France (2000 mg/kg dry weight), Germany (20 mg/kg dry weight), and Nordic countries (115 mg/kg dry weight). A high intake of iodine in seaweed within a short period may temporarily induce the reversible Wolff-Chaikoff effect (Guo et al., 2023). Recently, Jacobsen et al. (2023) reviewed the mean content of iodine in *U. intestinalis,* which was higher than in *U. fenestrata*, 12.4 and 3.2 mg/100 g dried weight, respectively, but not detected in *U. rigida*. Therefore, iodine levels in *Ulva* spp. do not pose a relevant threat to human health.

Currently, there are no MLs established for heavy metals such as arsenic, cadmium, lead and mercury in food supplements made exclusively or mainly of seaweed. The EU MLs for lead (3.0 mg/kg wet weight) and mercury (0.1 mg/kg wet weight) are set under Regulation (EC) 1881/2006. The MLs for cadmium were recently lowered by Regulation (EU) 1323/2021 to 3 mg/kg wet weight for food supplements. Jacobsen et al. (2023) also found that theamin content of inorganic arsenic, lead, and cadmium may also constitute a risk for health if seaweed, especially *Ulva* species, were consumed frequently. On the other hand, in a survey of potentially toxic elements in seaweed in Ireland, Norway and Sweden, *Ulva fenestrata* (formerly *U. lactuca*) had the lowest levels of potentially toxic elements overall (Jönsson and Nordberg Karlsson 2023).

While data are lacking on the occurrence of hazards in seaweed, there are numerous articles in the literature reporting heavy metal concentrations in *Ulva* spp. In general, the levels are species and site specific, but a thorough review of the literature on this topic is currently in progress by the current authors. Most of the analyses deal with wild-collected seaweed. However, a few studies suggest that aquaculture-grown *Ulva* spp. may contain lower levels of heavy metals (Roleda et al. 2021) and microbial organisms, particularly if they are grown in land-based systems with artificial seawater (authors own unpublished data).

In conclusion, chemical and biological hazards in *Ulva spp*. may be present, but data occurrence is scarce and limited, especially for toxic forms of heavy metals. The harmonization of analytical methods to identify and quantify chemical hazards is important and crucial to further assess the risk of these contaminants. Standards and guidelines related to seaweed products can vary nationally, and should be unified at the European level. In addition, it is crucial to increase knowledge on how the processing methods may affect the content of hazards, including the possible and unintentional presence of products or substances with adverse health effects. The impacts of post-harvest processing on biomass quality within the context of food safety are discussed in the section below.

3.2. Post-harvest processing

Freshly harvested seaweed quickly deteriorates unless stabilizing processes are used to avoid rapid biodegradation. If the macroalgae are not immediately stabilized, spoilage bacterial counts rapidly exceed upper limits; molds and yeasts also become problematic. Hazard analysis and critical control points (HACCP) or other national guidelines should be used to identify the critical control points and reduce microbial loads at these points (Adams et al. 2021). Processing methods such as washing, blanching, drying, freezing, salting, brining, or fermentation, can be performed to ensure food quality and safety (Blikra et al. 2021) and are discussed below.

3.2.1. Washing

Harvested macroalgae should be washed to remove fouling, fauna, sand, and other impurities. This is particularly relevant for *Ulva* biomass harvested from shallow lagoons or at-sea cultivation, whereas for tank-cultivated *Ulva* grown under controlled conditions this might not be necessary. For practical reasons, seawater should be used for washing, followed by a brief, final rinsing with freshwater if residual sea salt needs to be removed (Zhu et al. 2021) which is essential for the use of *Ulva* as feedstock. However, extended freshwater washing reduces the ash content in *Ulva* (Stokvis et al. 2021) and remarkably influences the overall quality of *U. tepida* and *U. ohnoi* biomass (Magnusson et al. 2016). The removal of inorganic minerals in the washing process can be explained by leaching due to osmotic changes, which indirectly increase the organic matter proportion, protein content, and caloric energy by 11–24% and 20–50%, respectively, and can leach other valuable compounds from the biomass, such as ulvan (Magnusson et al. 2016).

3.2.2. Blanching

Blanching is commonly used in processing seaweed to (i) reduce microbiological hazards caused by harmful bacteria within the seawater or by post-harvest contamination (Quero et al. 2015; Blikra et al. 2019; Ho and Redan 2022; Løvdal et al. 2021) (ii) inactivate inherent enzymes that initiate seaweed tissue breakdown (iii) reduce excess iodine levels, mostly relevant for iodine-rich brown algae (FAO and WHO 2022; Nielsen et al. 2020; Bruhn et al. 2019; Stévant et al. 2018) but also in *Ulva intestinalis* (Nitschke and Stengel 2016) (iv) potentially improve the profile of beneficial compounds, including a higher ratio of essential amino acids and a higher proportion of omega-3 fatty acids (Nielsen et al. 2020) (v) increase value and consumer acceptability by improving seaweed's organoleptic quality (Akomea-Frempong et al. 2021), such as reducing unattractive fishy odors from *U. rigida* (Thunyawanichnondh et al. 2020) and improving seaweed color (Blikra et al. 2019).

3.2.3. Drying

Drying is the most applied method for preservation of seaweed ensuring a long shelf life and enabling the most economical solution for storage and transport. *Ulva* has the advantage of drying quickly due to its thin thallus structure. For large-scale seaweed harvests, either sun-drying or convective drying is usually applied. Although solar drying is the most sustainable solution, its application may be limited to warm and sunny climates. Furthermore, in its simplest form as unprotected open-air drying, the hygienic quality of the biomass for food might be impaired via exposure to possible airborne microbial and other contamination. Well-constructed solar dryers, however, that protect against contamination, e.g., on racks off the ground, with natural ventilation and roofing, can be suitable for food quality. In regions with insufficient solar exposure, convective oven drying is the method of choice for drying seaweed, although this technology requires certain investments and is associated with high energy costs (FAO and WHO 2022; Kadam et al. 2015; Santiago and Moreira 2020). Other drying methods, such as freeze-drying or microwave-assisted drying, better maintain the bioactivities of nutrients (Amorim, Nardelli, and Chow 2020) but they are expensive and technically only suitable for low-volume, high-value commercial applications (Badmus, Taggart, and Boyd 2019).

The choice of temperature in convective drying modifies the conservation of nutritional values, bioactive compounds, and antioxidant capacity (Rodríguez-Bernaldo de Quirós and López-Hernández 2021); it depends on the specific application of the commercial end-product. Rapid drying at higher temperatures can avoid contamination and oxidation, which may occur with prolonged drying at lower temperatures but might deteriorate heat-labile compounds, particularly certain polyphenols (Badmus, Taggart, and Boyd 2019). Silva et al. (2019) investigated different oven-drying temperatures (25, 40, and 60 °C) in *U. rigida, Gracilaria sp.*, and *Fucus vesiculosus*, suggesting 25 °C a favorable temperature for extracting pigments from *Ulva*, whereas higher temperatures increase ulvan yield. Interestingly, in contrast to *Gracilaria* and *Fucus*, higher drying temperatures (60 °C) did not alter the antioxidant activity in *Ulva* material. In a study with Chilean *Ulva* spp., Uribe et al. (2019) compared different drying methods (freeze-, vacuum-, solar-, and convective-drying) and showed the best retained physicochemical parameters and antioxidant capacity after convective drying with 70 °C for 120 min. Regarding the seaweed flavor after drying, semi-drying (using a solar-drying system) releases more flavor compounds, such as free amino acids and volatile compounds, resulting in a better taste than fully dried seaweed. Seaweed maturation, also termed curing or ripening, can also improve seaweed flavor and aroma (Stévant et al. 2020). Even before processing, the seawater type and quality significantly influence the seaweed flavor (personal observations by Jessica Adams and Laurie Hofmann), and further research is needed to investigate how seaweed can be grown and processed to optimize taste for the European market.

3.2.4. Salting, brining, and fermentation

A low-cost and low-tech stabilization alternative to thermal processing can be dry salting or brining in a salt solution. Compared to thermal drying, osmotic dehydration using salt allows to retain an almost fresh food matrix while maintaining the nutritional values. Pinheiro et al. (2019) investigated the quality and nutritional parameters of *Ulva rigida* over six months of storage after air drying, brining in salt solution (25%, *w/v*), and dry-salting (28 and 49%, *w/w*); the nutritional parameters remained stable in the salt-treated samples while only showing slight alterations in color and texture. Although this traditional preservation method is not common in the Western seaweed industry, this might be an advantage for certain applications and producers.

Fermentation is another traditional way of preserving crops and ensiling *Ulva* to simultaneously preserve fresh biomass and to improve the quality of feedstock for biorefinery has been demonstrated before (Wu, Li, and Cheng 2018). However, seaweed fermentation technology for food purposes is still an underdeveloped yet efficient method for adding nutritional value by enhancing its digestibility and the bioavailability of bioactive compounds (Wu, Li, and Cheng 2018; Campbell et al. 2020; Reboleira et al. 2021; Strauss 2023). In the past decade, seaweed lacto-fermentation has been proposed as a promising new sector in the food industry (Uchida and Miyoshi 2013), in which beneficial strains such as lactic acid bacteria (LAB) metabolize carbohydrates into lactic acid and CO_2. Consequently, the food is preserved by the acidic environment and simultaneously develops distinctive textures and flavors from other organic acids, flavonoids, and free amino acids (Gupta and Abu-Ghannam 2012). Importantly, seaweed fermentation improves organoleptic qualities, which has been shown in brown algae (Figueroa, Farfán, and Aguilera 2021), but also in *Ulva* (Hung et al. 2023). The unwanted sea smell that often impedes the culinary acceptance of seaweed can be reduced or omitted by lactofermentation (Hung et al. 2023; Bruhn et al. 2019; Duarte, Bruhn, and Krause-Jensen 2021).

However, despite the high total carbohydrate content of approximately 50% in *Ulva,* only small amounts of these sugars can be directly metabolized by LAB into lactic acid because the majority comprises uncommon, complex polysaccharides (Hwang et al. 2011). Therefore, to achieve successful seaweed fermentation, a pretreatment is required, such as heat treatment or biochemical treatment using saccharifying enzymes. This splits the cell wall structure, which otherwise holds valuable compounds for digestion (Gupta, Cox, and Abu-Ghannam 2011; Bruhn et al. 2019; Maneein et al. 2018; Akomea-Frempong et al. 2021). Furthermore, the choice of suitable LAB strains is essential for the success of large-scale fermentation. Currently, commercial applications of lactofermentation remain marginal, but these promising results may encourage further research with *Ulva* and inspire more food applications.

4. Ulva in aquafeed: status quo, challenges, and opportunities

4.1. Status quo

Aquaculture's further growth, like that of all livestock production industries, depends on the supply of sustainable feed protein and energy resources and optimizing aquafeed production and use will be crucial to support industry growth. Nutrition is the most expensive aspect of producing edible finfish (Naylor et al. 2009). The daily aquafeeds consumed account for approximately 75% of production costs (Lamm, 2003), mostly from fishmeal and fish oil, although there have been widespread efforts to reduce these costs in past years. However, due to the rapid growth of the entire aquaculture sector, the volumes of these resources must keep up with the demand for sustainability. Conventional feed resources, such as fishmeal, are expensive, and their future availability will be limited by an expected reduction in fisheries. Therefore, significant effort is being directed at reducing the content of the expensive and unsustainable fishmeal and fish oil in formulated feed, replacing them with other more sustainable nutritional ingredients.

Plant products have become common alternatives to replace fishmeal and fish oil in formulated aquafeeds. Increasing regulations on using animal-derived products in feed (e.g., bone meal) and the relatively low cost of plant production favor using plant meals and oils in aquafeeds (Wan et al. 2019; Gatlin et al. 2007) However, growing demands for land crops for aquafeed production will increase aquaculture's dependence on the two exhaustible core resources: land and water, both required for plant production, and will compete with the production of human food. For example, China and Norway have been experiencing a shortage of high-quality proteins from soybean (Nair et al. 2023; Kim et al. 2019; Lindberg et al. 2016), and a larger supply of protein crops is recently needed in Europe. The soy industry is associated with ecosystem degradation, resource depletion, and greenhouse gas emissions in some of the world's most biodiverse regions. Life cycle assessment studies underline that soy as an aquafeed ingredient is the main contributor to the environmental impacts of Norwegian salmon production (Hognes et al. 2012; Ólafsdóttir et al. 2013; Anmarkrud 2023). Furthermore, the high content of anti-nutritional factors (ANFs), low palatability, continued deforestation, and increasing use of nonrenewable fertilizers threaten the potential reliance on plants for aquafeeds. Thus, for more sustainable global aquaculture, alternative protein and lipid sources with lower costs and ecological footprints must be identified.

The application of *Ulva* in experimental diets for finfish has become an increasingly widespread method since the study by Nakagawa, Kasahara, and Sugiyama (1987) on *U. pertusa* in the diet of black sea bream (*Acanthopagrus schlegeli*). Various diets have been developed and tested on species from different nominal trophic levels, including the strict herbivore Nile tilapia (*Oreochromis niloticus*), omnivores such as the black, red, and gilthead seabream (*Acanthopagrus shlegeli*, *Pagrus major*, and *Sparus aurata*, respectively), and straight carnivores such as the European sea bass (*Dicentrarchus labrax*), rainbow trout (*Oncorhynchus mykiss*), and the Atlantic salmon (*Salmo salar*) (Table 4).

Many of these species are characterized by high production yields and relatively significant market share in terms of volume, value, or both (FAO Fisheries Division). Similarly, various experiments have been performed on the king prawn (*Litopenaeus vannamei*), one of the two most produced species by the shrimp aquaculture industry worldwide (Boyd and Jescovitch 2020). The examination of *Ulva*'s nutritional value expanded far beyond any market size or value threshold with trials on fish like goldfish (*Carassius auratus*), jewfish (*Argyrosomus japonicus*), croaker (*Larimichthys polyactis*), nibbler (*Girella laevifrons*), snapper (*Lutjanus stellatus*), sole (*Solea senegalensis*), and others (Table 4). Various studies on finfish have shown that regardless of the fish or *Ulva* species examined, an inclusion rate of 15–20% in the fish diet is not detrimental to fish growth, feed conversion ratio (FCR), or protein intake (Table 4). However, the biological trophic level of the fed fish may determine the nutrient utilization efficiency of *Ulva*. It is likely that aquafeeds with a lower inclusion rate of 5% is more suitable in nutrition of carnivorous fish (e.g., European seabass, rainbow trout). In contrary, a higher ratio of *Ulva* may be more beneficial for fish of low trophic level like tilapia, carps and catfish (Table 4). Moreover, in a trial with Nile tilapia (*O. niloticus*), 30% of *U. intestinalis* in the diet did not affect fish growth performances or feed conversion. Similar results were obtained in a 20-week trial with seabream, where 29.1% of *U. lactuca* in the aquafeed did not harm the fish's performance even when accompanied by the elimination of fishmeal from the diet and limitation of the fish oil content to only 0.9% (Shpigel et al. 2017). In studies of commercially valuable invertebrates, including shrimp, abalone, sea urchins, and sea cucumbers, the results confirmed the potential to increase *Ulva* content in aquafeeds by over 20% (Table 4). Moreover, commercial production of abalone in Europe (*Haliotis tuberculata*) and South Africa (*Haliotis midae*) relies on *Ulva* and other macroalgae or compound feed as a feeding source, contributing to satisfying growth rates. The significant results of the various trials with fish and invertebrates are promising, as the examined *Ulva* originated from various genotypes (at least eight species), geographical areas, seasons, and environmental conditions, encompassing wild and cultured *Ulva*. Moreover, they also provided evidence concerning the potential of dietary *Ulva* in the long-term nutrition of aquatic animals. For example, the positive impact of *U. ohnoi* in the diet of Senegalese sole (*S. senegalensis*) on fillet texture and color was evident six months after transferring fish to a commercial *Ulva*-free diet (Sáez et al. 2020).

4.2. Challenges

Large quantities of *Ulva* biomass are available worldwide, although their quality varies greatly, and biomass valorization is difficult. Natural stocks display a higher uncertainty of biomass yield and quality than cultivated biomass. The levels of protein and essential amino acids can be relatively low and variable depending on seasonal changes, strain variability, and habitat-related forces like the local salinity and depth, as mentioned above. Contrastingly, algaculture appears to be the future for developing *Ulva*-based products because of the possibility of controlling and optimizing factors related to yield and quality at different stages of production (Calheiros et al. 2021). For example, recent studies with large-scale *U. fenestrata* cultivation in Sweden showed that feasibility and sustainable potential for large-scale offshore cultivation can be achieved by increasing the seedling density in the hatchery, resulting in higher biomass yield (Steinhagen, Enge et al. 2021).

The presence of ANFs also presents a challenge to applying *Ulva* in aquafeeds. Studies that followed the results from trials with sole and Pacific white shrimp revealed that the observed growth deficits were due to the presence of ANFs in the dietary *Ulva* (Qiu, Neori, et al. 2017; Vizcaíno et al. 2020). ANFs in *Ulva* include alkaloids, tannins, saponins, lectins, polyphenolics, phytic acid, and other inhibitors that reduce the bioavailability and digestibility of algal nutrients (Aguilera-Morales et al. 2005). Several surveys have been conducted to analyze potential ANFs in wild *Ulva*, such as those in green tides (Wu et al. 2013; Li et al. 2018). Calheiros et al. (2021) concluded that the ANFs of *Ulva* were lower than that of soybean. However, in another study, high levels of trypsin and amylase inhibitors were observed in the winter *Ulva*-rich biomass beached at Baja California, Mexico (de Oliveira et al. 2009). In addition, anti-nutritional tannins, polyphenolics, and phytic acid were observed in the collected biomass. Although data on the harmless inclusion rate of *Ulva* in aquafeed can be gleaned from previous studies, the number of specific studies on ANFs in *Ulva* is negligible. Such studies may provide supportive and applicable information on the factors determining the presence and level of ANFs in the biomass, their active mechanism, the threshold level beyond which they become harmful, and methods to neutralize their activity.

4.3. Opportunities

More empirical knowledge on ANFs in *Ulva* biomass is expected to become available in the coming years due to the rapid increase in *Ulva* research and development in fish nutrition. The mechanisms by which *Ulva* ANFs harm fish can be concluded from studies on homologous compounds such as those derived from plants. For example, agglutinin is a common lectin in various plants, which is also found in *Ulva* (e.g., *U. curvata* collected in the US; (Bird et al. 1993)). Soybean agglutinin in the diet of Atlantic salmon was associated with high mucus secretion in the intestine, limiting the enzymatic and absorptive capacity (Hendriks et al. 1990). Few studies have successfully demonstrated the potential active mechanisms of *Ulva* ANFs in fish diets (Vizcaíno et al. 2020; Vizcaíno et al. 2019; Sáez et al. 2020; Martínez-Antequera et al. 2021). Among these, the bioactivity of protease inhibitors in *Ulva ohnoi* was confirmed in trials introducing digestive proteases from Senegalese sole, gilthead seabream, or European seabass with the *U. ohnoi* extract. The *U. ohnoi* extract inhibited fish digestive proteases at a rate of approximately 70% (Vizcaíno et al. 2020). However, the study also revealed that heat treatment of this alga significantly reduces the harmful inhibition to only 20%, but is accompanied by damage to amino acids and bioactive molecules (Vizcaíno et al. 2020). Another trial revealed that 5% of heat-treated *Ulva* sp. in the diet improved gilthead sea bream tolerance to hypoxia by enhancing the antioxidant properties of the heat-treated biomass (Magnoni et al. 2017). Post-harvest hydrolysis is also considered efficient in improving *Ulva*'s nutritional value and digestibility. An improved amino acid profile and higher *in vitro* nitrogen digestibility were observed in an *Ulva* extract heat-treated with enzymatic hydrolysis (Bikker et al. 2016). The inclusion of *Ulva* hydrolysate in the diet of European bass improved fish protein utilization without detrimentally affecting growth (Fernandes et al. 2022). Nevertheless, as in land crops, improving crude biomass often requires high energy investment, thus compromising the cost-effectiveness and sustainability of such processes.

The economic impact of including *Ulva* in fish diets has not yet been well documented. However, Shpigel et al. (2017) reported the first calculations of the achievable savings in feed, fish production, and operating costs when culturing seabream on a 14.6% protein-rich *Ulva* diet (30–36% DW protein). The total feed cost was reduced by $0.25 kg^{-1}. A feed conversion ratio of 1.7 resulted in a cost reduction of $0.45 kg^{-1} of fish produced. Because fish feed can account for more than 60% of the operating costs in intensive aquaculture, approximately 10% savings on feed costs are economically relevant.

In conclusion, *Ulva* is a new value-added dietary resource in aquafeed. However, seasonal and species-dependent variability in the nutritional content, ANFs and the lack of commercially sufficient quantities of *Ulva* biomass are limitations that the aquafeed production industry has yet to overcome (Wan et al. 2019). Furthermore, sustainable technologies (e.g., IMTA, integrated marine systems) still need to be improved to enable large-scale commercial production of such important aquafeed resources. However, as *Ulva* spp. can thrive under high stocking densities, they are exceptional candidates for large-scale production for future aquafeed formulations (Al-Hafedh, Alam, and Buschmann 2014; Steinhagen, Larsson, et al. 2022). Furthermore, before considering *Ulva* as a biocircular feed ingredient, further measures are needed to monitor their heavy metal content. Therefore, monitoring and selection programs for harvesting *Ulva* biomass will provide aquafeed manufacturers with high nutritional value and low content of undesired ingredients.

5. Ulva in terrestrial feed

Approximately 70% of protein, including fish meal, for animal feed is imported into Europe. Increasing food-feed-fuel competition for limited natural resources has threatened future economic and supply chain security. Therefore, developing emerging alternative ingredients for animal feed based on locally available resources is being emphasized to reduce feed costs, improve animal feed self-sufficiency, and maximize the land/water/energy space for agricultural production for human consumption across Europe and the world. The expanding global population and greater affluence are expected to increase global demand for animal-derived goods, which will substantially affect animal agribusiness due to the overuse of maize and soybean crops - the two most important traditional livestock feeds. Consequently, more affordable animal feed components are required. Recently, many studies have been conducted using seaweed as a protein source and nutraceuticals in terrestrial animal nutrition. Based on nutrition science, the nutritive value of seaweeds was too poor to be recommended for livestock during the early twentieth century (Evans and Critchley 2014). The prevalence of refractory polysaccharides in seaweed cell walls has anti-nutritional consequences in non-ruminants, such as chickens and pigs, and the digestibility of the proteins is inhibited owing to their entrapment in the cellular matrix. Thus, a corresponding reduction in feed breakdown and uptake by retaining vital nutrients (Øverland, Mydland, and Skrede 2019) advocates the use of specialized carbohydrate-active enzymes, widely used as feed additives, or fermentation to improve animal digestion and specific growth rate. For example, Bikker et al. (2016) showed that simulated *in vitro* ileal nitrogen digestibility was increased from 79.9% in intact *Ulva lactuca* to 84.7% in the extracted fraction, presumably through the release of cell wall-bound or encapsulated protein during pretreatment hydrolysis. Pretreatment hydrolysis and fermentation may also increase protein digestibility by degrading insoluble fiber (Marrion et al. 2003). In addition, different studies have highlighted the capacity of the ulvan to stimulate mucin secretion in the intestinal tract (Barcelo et al. 2000). The main findings from studies investigating the impact of *Ulva* as a feed supplement for poligastric and monogastric terrestrial animals and poultry are discussed below.

5.1. Polygastric terrestrial animals (cattle, sheep, and goats)

To date, studies on using marine algae in bovine, caprine, and other ruminant nutrition have mainly concentrated on adding small amounts of various marine algae species to the feed and then evaluating their prebiotic activity for improved animal

Table 4. Summary of the effect of *Ulva*-supplemented aquafeed on different cultivated seafood.

Examined organism	Species	Inclusion rate (% of DW)	Time (weeks)	Weight gain and growth rate	FCR	PER	PPV	Protein utilization	Other impacts	Ref.
African catfish (*Clarias gariepinus*)	*U. lactuca*	10, 20, 30	10	Decreased under diets of >10%	Impaired under diets of ≥20%	Decreased under diets of ≥20%	Decreased		Decreased diet palatability at high inclusion rate (≥20%)	1
Common Carp (*Cyprinus carpio*)	*U. rigida*	5, 10, 15, 20	16	Decreased only under diet of 20%	Impaired only under diet of 20%	N.s.				2
Nile tilapia (*Oreochromis niloticus*)	*U. lactuca*	5, 10	9	N.s.	N.s.	N.s.				3
Nile tilapia (*Oreochromis niloticus*)	*U. intestinalis*	10, 20, 30, 40, 50	6	N.s. under diet ≤30% but decreased at higher inclusion rates	N.s.	N.s.				4
Nile tilapia (*Oreochromis niloticus*)	*Ulva* spp. (IMTA- cultured)	10, 15, 20	9	N.s. under diet of 10% but decreased at higher inclusion rates	N.s. under diet of 10% but impaired ≥15%	Decreased under diets of ≥15%			Highest lipid content in fish flesh under diet with 20%; No apparent effect on diet palatability	5
Nile tilapia (*Oreochromis niloticus*)	*Ulva* sp.	5, 10, 15, 20, 25		Increased under diets of ≤15%, decreased under diet of 25%	Improved under diets of ≤15%; No change under other diets	Increased under diets of ≤20%	Increased under diets of 10–25%			6
Nile tilapia (*Oreochromis niloticus*)	*U.* spp.	10	12	N.s.	N.s.	N.s.				7
Nile tilapia (*Oreochromis niloticus*)	*U. rigida* and *U. lactuca 1:1*	10, 15, 20	9	Decreased under diets of >10%	Impaired under diets of ≥15%	Increased under diets of ≥15%				8
Nile tilapia (*Oreochromis niloticus*)	*U. rigida*	10, 20, 30	11	Decreased only under diet of 30%	N.s. but increased under diet of 30%	Decreased only under diet of 30%				9
Nile tilapia (*Oreochromis niloticus*)	*U. rigida*	5	16	Improved	Improved	Increased		Increased		10
Nile tilapia (*Oreochromis niloticus*)	*U. rigida*	5, 10, 15	12	Decreased only under diet of 15%	Impaired only under diet of 15%			Increased only under diet of 15%		11
Striped mullet (*Mugil cephalus*)	*U. lactuca*	10, 15, 20, 25	15	Improved with increasing inclusion rate	Improved with increasing inclusion rate	Increased with increasing inclusion rate				12
Gilthead seabream (*Sparus aurata*)	*U. lactuca*	5	8	N.s.	N.s.	N.s.				13
Gilthead seabream (*Sparus aurata*)	*U. lactuca* (IMTA-*Ulva*)	2.6, 7.8, 14.6, 29.1	16-20	Decreased only under diet of 29.1%	N.s. but impaired under diet of 29.1%	Decreased				14
Gilthead seabream (*Sparus aurata*)	*U. rigida*	5, 15, 25	10	N.s. but Improved under diet of 30%	N.s.					15

(*Continued*)

Table 4. Continued.

Examined organism	Species	Inclusion rate (% of DW)	Time (weeks)	Weight gain and growth rate	FCR	PER	PPV	Protein utilization	Other impacts	Ref.
Gilthead seabream (*Sparus aurata*)	*U. rigida*	5 (+incresing lipid content)	7	N.s. but improved under a high-lipid diet (22%)	N.s. but improved under a high-lipid diet (22%)	N.s.		N.s.		16
Red seabream (*Pagrus major*)	*U. pertusa*	5	6	N.s.	N.s.	N.s.				17
Black seabream (*Acanthopagrus shlegeli*)	*U. pertusa*	10	20.5	N.s.						18
Rainbow trout (*Oncorhynchus mykiss*)	*U. rigida*	10	12	Decrease (only after starvation)						19
Rainbow trout (*Oncorhynchus mykiss*)	*U. lactuca* or *U. linza*	10	8.5	Decreased						20
European seabass (*Dicentrarchus labrax*)	*U. lactuca*	5, 10, 15	8	Decreased when content in feed incresed	Impaired when content in feed incresed		Increased			21
European seabass (*Dicentrarchus labrax*)	*U. rigida*	5	10	Decreased when content in feed incresed	Impaired when content in feed incresed	N.s.				22
European seabass (*Dicentrarchus labrax*)	*U. lactuca*	5, 10, 15	8	Improved under diets of ≤10%; decreased at 15%	Improved under diets of ≤10%; impaired at 15%	Increased only under diet of 5%	Increased only under diet of 5%			23
European seabass (*Dicentrarchus labrax*)		10	4	Decreased	N.s.		Inhibitory of protein digestion			24
White-spotted snapper (*Lutjanus stellatus*)	*U. lactuca*	5, 10, 15, 20	8.5	N.s.	N.s.				Reduced pepsin and lipase activity in the gut under diets of >5%	25
Senegalese sole (*Solea senegalensis*)	*U. ohnoi*	5	13	Decreased	N.s.					26
Senegalese sole (*Solea senegalensis*)	*U. ohnoi*	6	13	N.s.				N.s.	Selective retention of n-3 PUFA, EPA & DHA; positive effect on fish fillet texture & color. Positive effects maintained over a long period after supplementation	27
Senegalese sole (*Solea senegalensis*)	*U. ohnoi*	5		Decreased						28
Large yellow corvina (*Larimichthys polyactis*)	*U. prolifera*	5, 10, 15	10	Improved when content in feed incresed	N.s.			Decreased when content in feed incresed		29
Goldfish (*Carassius auratus*)	*U. reticulata*	2, 4, 6, 8	6	Improved					Improved haematological parameters and fish color	30
sea chub (*Girella laevifrons; Kyphosidae)*	*U. lactuca*	15, 30, 45	4	N.s. under diet of 30%; decreased under other diets						31
dusky kob (*Argyrosomus japonicus;* Sciaenidae)	*Ulva. sp.*	5, 10, 15, 20	9	Decreased	Impaired					32
Pacific white shrimp (*Litopenaeus vannamei*)	*U. lactuca*	1, 2, 3	4	Improved	Improved				Higher content of lipid and carotenoid in shrimp flesh under 3% diet	33

(*Continued*)

Table 4. Continued.

Examined organism	Species	Inclusion rate (% of DW)	Time (weeks)	Weight gain and growth rate	FCR	PER	PPV	Protein utilization	Other impacts	Ref.
Pacific white shrimp (*Litopenaeus vannamei*)	*U. lactuca* (IMTA-*Ulva*)	25, 50 (fresh *Ulva* for replacing aquafeed)	7	N.s. under diet of 25%, decreased under the diet of 50%	Improved (due to the reduced aquafeed in the diets)				Low protein content in shrimps flesh (although *Ulva* contained 32% protein as in the aquafeed)	34
Pacific white shrimp (*Litopenaeus vannamei*)	*U. lactuca*	6.35, 12.7, 19.05, 25.4	6	Decreased under diets of >6.35%	Impaired under diets of ≥19.05%			Decreased under diets of >6.35%	Low energy, protein, and amino acid digestibility (compared with fishmeal or soybean meal)	35
Abalone (*Haliotis midae*)	*Ulva* sp. (IMTA-*Ulva*)	20, 30, 40, 60 (replaced commercial aquafeed)	52	N.s.					Unique associations in the gut microbiome and a lower abundance of *Vibrio sp.*	36
Abalone (*Haliotis asinina*)	*U. pertusa*	2.7, 5.4, 8.1	17.5	N.s.	N.s.	N.s.				37
Abalone (*Haliotis discus*)	*U. australis*	4, 8, 12, 16, 20 (replaced *Unidaria pinnatifida*)	2.5	Improved					Reduced mortality after exposure to air	38
Abalone (*Haliotis laevigata*)	*Ulva sp.*	fresh or enriched *Ulva* as sole feed compared to commercial aquafeed	13	Decreased	Impaired	Decreased			Enriched *Ulva* improved growth compared with non-enriched *Ulva*	39
Abalone (*Haliotis laevigata*)	*Ulva sp.*	5, 10, 20	13	Improved						39
Abalone (*Haliotis tuberculata*)	*Ulva rigida*	Enriched *Ulva*, non enriched macroalgae	12	Improved	Improved	Decreased			Enriched *Ulva* improved growth compared with non-enriched *Ulva*	40
Abalone (*Haliotis tuberculata*)	*U. rigida*	Young and old *U. rigida*'s effect on abalone post larval growth	4	Improved					Old and young *U. rigida* germlings with *U. lens* germlings improved postlarval growth	41
Purple sea urchin (*Arbacia punctulata)*	*U. lactuca*	Fresh *Ulva* and commercial fish diets	12	N.s.					Increased gonads mass and altered their color; reduced alimentary canal index (% of total mass)	42
Collector sea urchin (*Tripneustes gratilla elatensis*)	*U. fasciata* (IMTA-*Ulva*)	Fresh *Ulva* as sole feed and *Gracilaria sp.* or algal-free pellets	8	Improved					Positive effect on the gut microbial networks and occurrence of unique microbes related to metabolism of *Ulva* polysaccharides	43
Collector sea urchin (*Tripneustes gratilla*)	*U. rigida* (IMTA-*Ulva*)	5, 15, 20 in the pelleted diet	12	N.s.					Improved diet palatability, consumption, and digestibility (compared with algal-free pellets); increased gonads somatic index (compared with fresh *Ulva* diet)	44
Collector sea urchin (*Tripneustes gratilla*)	*U. pertusa*	Fresh *Ulva* as sole feed and *Undaria* or *Gloiopeltis*		Decreases compared with *Undaria* but better than *Gloiopeltis*	Improved					45
Collector sea urchin (*Tripneustes gratilla lineus*)	*U. armoricana*	Fresh *Ulva*, or in pelleted diet (20%)		improved					*Ulva* diets eliminated the need for a high-protein diet. *Ulva*-containing pellets during the 12 weeks prior harvesting is necessary for improving gonad size and color	46

(*Continued*)

Table 4. Continued.

Examined organism	Species	Inclusion rate (% of DW)	Time (weeks)	Weight gain and growth rate	FCR	PER	PPV	Protein utilization	Other impacts	Ref.
Purple sea urchin (*Paracentrotus lividus*)	*Ulva sp.*	50 (fresh *Ulva* for replacing pelleted feed)								46
Purple sea urchin (*Paracentrotus lividus*)	*U. lactuca* (IMTA-*Ulva*)	Fresh *Ulva* and *Gracillaria* compared to pelleted diet	13	N.s.					Improved gonads color but reduced gonad somatic index	47
Sea cucumber (*Holothuria scabra*)	*U. lactuca*	Raw vs. mechanically shredded *Ulva*	0.5	N.s.					Higher feed ingestion and fecal production rates under the shredded *Ulva* diet	48
Sea cucumber (*Apostichopus japonicus*)	*U. lactuca*	5, 10, 40 in pelleted diet	12	Improved with increasing feed content	Improved with increasing feed content				Higher attractiveness and intake of 40% *Ulva* diet. Lower performances compared with soybean-containing diet	49
Sea cucumber (*Apostichopus japonicus*)	*U. lactuca*	14, *Laminaria* at same rate or algal free pellets		Decreased compared with *Laminaria*					Lower content of n-3 PUFA in flesh than in *Laminaria* diet	50

N.s.: no significant change; DW: dry weight; FCR: food conversion ratio; PER: protein efficient ratio; PPV: protein productive value.
[1](Abdel-Warith, Younis, and Al-Asgah 2016); [2](Diler et al. 2007); [3](Natify et al. 2015); [4](Siddik and Anh 2015); [5](Marinho et al. 2013); [6](El-Tawil, 2010); [7](Silva et al. 2015); [8](Marinho et al. 2013); [9](Azaza et al. 2008); [10](Ergün et al. 2009); [11](Kut Güroy et al. 2007); [12](Wassef, El Masry, and Mikhail 2001); [13](Guerreiro et al. 2019); [14](Shpigel et al. 2018); [15] (Vizcaíno et al. 2016); [16](Emre et al. 2013); [17](Mustafa, 1995); [18](Nakagawa, Kasahara, and Sugiyama 1987); [19](Güroy et al. 2011); [20](Yildirim et al. 2009); [21](Wassef, El-Sayed, and Sakr 2013); [22](Valente et al. 2006); [23](Wassef, 2005); [24](Martínez-Antequera et al. 2021); [25](Dashi Zhu et al. 2016); [26](Cerezo et al. 2022); [27](Sáez et al. 2020); [28](Vizcaíno et al. 2019); [29](Asino, Ai, and Mai 2011); [30](Rama Nisha et al. 2014); [31](Cruz, 2019); [32](Madibana et al. 2017); [33](Elizondo-González et al. 2018); [34](Laramore et al. 2018); [35](Qiu, Neori, et al. 2017); [36](Macey, 2021); [37](Santizo-Taan, Bautista-Teruel, and Maquirang 2020); [38](Ansary et al. 2019); [39](Bansemer, Qin, Harris, Duong, Hoang, et al. 2016)[40] (Bansemer, Qin, Harris, Duong, Currie, et al. 2016); [41](De Viçose et al. 2012); [42](Suckling et al. 2022); [43](Masasa et al. 2021); [44](Cyrus et al. 2015); [45](Floreto, Teshima, and Ishikawa 1996); [46](Cyrus et al. 2015); [47](Prato et al. 2018); [48](Shpigel et al. 2018); [49](Irfan et al. 2022); [50](Joaquina Ibarra-Arana et al. 2018); [51](Anisuzzaman et al. 2018).

performance (Morais et al. (2020); the information is scarce). The main drawbacks to using *U. lactuca* in ruminant diets are frequently cited as their low dry matter and high ash content (Tayyab et al. 2016) and low effective degradability (41% for organic matter degradability) values (Arieli, Kissil, and Sklan 1993). The high mineral content of seaweeds restricts their net, digestible, and metabolizable energy values and gross energy content. *Ulva* has been regarded to be nearly equivalent to a low-to-moderate quality forage and ideal to be used with feeds that have a high energy/low protein content like cereal crops (Arieli, Kissil, and Sklan 1993).

Samara et al. (2013) reported that 3%–5% (DM) of *Ulva lactuca* could be safely supplemented to lambs without negatively affecting blood water balance, liver, or kidney functions. However, feeding rams a lamb diet supplemented with intact *Ulva lactuca* did not positively affect growth performance, thermoregulatory responses, or plasma oxidative status, whereas feeding lambs intact *Ulva lactuca* negatively affected rams' seminal and testicular characteristics, which were more pronounced at 5% than at 3%. Male lambs can consume up to 20% *U. lactuca* in a diet composed primarily of vetch hay or concentrate without negatively affecting the diet's flavor. It had a moderate energy digestibility (60%) and a low (40%) protein degradability (Arieli, Kissil, and Sklan 1993). El-Waziry et al. (2015) reported that *U. lactuca* supplementation did not affect sheep growth, *in vitro* gas production, potential degradability, estimated energy, organic matter digestibility, or microbial protein synthesis. Furthermore, Ventura and Castañón's (1998) concluded that *U. lactuca* is a high-protein, medium-quality forage for goats.

In a different study (Rey-Crespo, López-Alonso, and Miranda 2014), adding a seaweed blend (*Ulva rigida*, *Laminaria ochroleuca*, *Saccharina latissima*, *Saccorhiza polyschides*, *Mastocarpus stellatus*, and *Sargassum muticum*) to the diets of dairy cows at a rate of 100 g/cow/day increased the amount of iodine in the milk. This suggests that incorporating seaweed into the diet is a viable method of increasing iodine levels in milk.

Although various results have been reported with variable effects on rumen fermentation, *Ulva* has shown promising potential for reducing ruminal methane production *in vitro* (Dubois et al. 2013; Machado et al. 2014; Kinley et al. 2016). When incubated at 25%, *Ulva* sp. significantly decreased methanogenesis from 101 mL g^{-1} DM to 86.2 mL g^{-1} DM compared to the control; however, the effect on methane production depended on the substrate because all seaweeds decreased methane production when combined with hay, but only *Gigartina* sp. reduced methane production when incubated with corn silage (Maia et al. 2016). Recently, *Ulva* sp. was the only macroalgae species tested that did not reduce methane production (Mihaila et al. 2022), suggesting that more research is needed to reach a more conclusive result regarding the impact of *Ulva* spp. on methane production.

5.2. Monogastric terrestrial animals (swine, cuniculus)

Recently, seaweeds have been included in low amounts (1–2% for the potential benefits to pig health and meat quality (Mišurcová, 2011). A new feed supplement containing *Ulva* enriched with Zn (II) and Cu (II) as a dietary source of microminerals for pigs showed higher bioavailability than an inorganic salt control when fed to piegs (Michalak, Chojnacka, and Korniewicz 2015). Furthermore, an algae–clay-based complex made from *Ulva* sp., *Solieria chordalis*, and montmorillonite clay increased the ileal digestibility of energy and essential amino acids when added to the diets of growing pigs (Suarez and Gallissot 2016). A study using an *in vitro* system of porcine intestinal epithelial cells showed that ulvan from *Ulva armoricana* upregulated the gene expression of cytokines such as IL1, IL6, IL8, and TNF (Berri et al. 2017, Bikker et al. 2016). The immunomodulatory effect of *Ulva armoricana* was evaluated in sows by Bussy et al. (2019). The higher dietary level increased anti-Bordetella IgG in the sow's blood and colostrum, whereas with the middle dietary integration, IgA increased in milk. Thus, based on digestibility, *Ulva* may be a better feed ingredient for pigs than for poultry (see below), whereas the extracted fraction seems a promising ingredient for further evaluation in both organisms. Based on the essential amino acid content and *in vitro* nitrogen (85%) and organic matter (90%) digestibility, the extracted fraction seems a promising protein source in diets for monogastric animals with improved characteristics compared to intact *Ulva* (Bikker et al. 2016). Furthermore, a recent study has found that enzymatic supplementation with carbohydrase, such as the recombinant ulvan lyase, may exacerbate the indigestibility effects observed from feeding *U. lactuca* alone to piglets (Ribeiro et al. 2024).

Studies investigating the effect of *Ulva*-supplemented diets on other terrestrial animals are rare; however, meal supplemented with low amounts (1%) of *Ulva* have shown positive effects on the growth performance and diet digestibility in rabbits, with no negative hematological or biochemical effects on rabbit health (El-Banna et al. 2005).

5.3. Poultry

Several studies have investigated the influence of *Ulva* spp. as a feed additive on chicken development and/or carcass characteristics (Matshogo, Mnisi, and Mlambo 2020; Abudabos et al. 2013; Nhlane et al. 2021; Thavasi Alagan et al. 2020; Ventura, Castañon, and McNab 1994). Most studies have shown that *Ulva* spp. can be used at low inclusion levels (<10%) without any suppression in the growth performance of chickens. Green seaweed meal derived from *U. lactuca* at 0, 2, 2.5, 3, and 3.5% had no adverse effect on the growth performance, visceral organ size, carcass characteristics, and meat quality of indigenous Boschveld chicken (Nhlane et al. 2021). Similarly, the addition of *Ulva*-based green seaweed meal (0, 20, 25, 30, and 35 g kg^{-1}) had no significant effect on the growth performance of broiler chickens; however, increases in various meat shelf-life indices were observed (Matshogo, Mnisi, and Mlambo 2020). Furthermore, corn can be replaced with 3% *U. lactuca* without affecting growth performance while improving the dressing percentage and breast muscle yield (Abudabos et al. 2013). In addition, broiler diets can be supplemented with *U. lactuca* without affecting health and growth performance (Nhlane et al. 2021). Ventura, Castañon, and McNab (1994) concluded that feeding *U. rigida* beyond 10% in the diet reduces the feed intake and suppresses the growth performance of broiler chickens, suggesting that *Ulva* supplementation levels should remain below 10%.

Using *Ulva* spp. in chicken feed at high concentrations is likely restricted because fiber fractions of indigestible algal cellulose and hemicelluloses (Øverland, Mydland, and Skrede 2019), which primarily consist of gel-forming ulvan and insoluble cellulose, as well as trace amounts of glucuronans and xyloglucan (Lahaye and Robic 2007), may impair nutrient digestibility, suppressing growth performance (Kraan, 2012). Enriched ash content can also make seaweeds inappropriate for animal diets, especially monogastric animals, at higher concentrations. In contrast, microalgae have been suggested to be a promising alternative feedstock for livestock and poultry (Saadaoui et al. 2021). Nevertheless, the scale and cost of production needed and potential competition with human consumption present limitations for microalgae in feed as well. The major benefit of using macroalgae for feed is that biomass from algal blooms which is unsuitable for human consumption could be valorized for feed. Therefore, advanced procedures, which can decrease ash content and improve digestibility are needed to improve the acceptable feed components from *Ulva* spp.

Digestibility can be improved by enzymatic hydrolysis with appropriate agents for seaweed species since the chemical makeup of seaweeds is different from that of terrestrial plants. Carbohydrate-active enzymes (CAZymes) have emerged as a promising alternative to destroy the *Ulva* spp. cell wall due to the efficacy of these enzymes in hydrolyzing *Ulva* spp. material for protein and carbohydrate extractions (Batista et al. 2020; Postma et al. 2018). Moreover, CAZymes have demonstrated carbohydrate action in microalgae cell walls (Coelho et al. 2020). Thus, the degradation of seaweed biomass with feed enzymes would optimize their utilization as feedstuffs to partially replace unsustainable and conventional sources, such as maize and soybean meal (Costa et al. 2021). Costa et al. (2022) conducted a trial on broiler chickens to study the influence of *U. lactuca* (15%) with and without enzyme addition (carbohydrase), indicating that 15% *U. lactuca* resulted in no harmful effects on growth performance and improved meat quality because of antioxidant influence, mineral, and PUFA (n-3) accumulation. Another study assessed the pretreatment of edible seaweed (*Ulva* spp.) with a mixture of proteolytic and fibrolytic enzymes on the physical and meat quality characteristics of broiler chickens (Matshogo, Mnisi, and Mlambo 2021), demonstrating that seaweed pretreatment with the enzyme mixture did not affect feed consumption, physiological responses, and carcass characteristics of broiler chickens.

In contrast, a co-product of *Ulva laetevirens* (synonomous with *U. australis*) exposed to a wide endo-protease supplementation in a broiler's diet showed no distinct effect on their growth performance, whereas protease pretreatment masked or suppressed the health-promoting bioactive substance of *U. laetevirens* (Stokvis et al. 2022). *Ulva laetevirens* improved the feed conversion rate of broiler chickens and reduced the digestibility and villus height, whereas protease pretreatment failed to improve growth performance and other health-related traits. It is critical to obtain a better knowledge of how the nutritional components of *Ulva* spp. behave in *in vitro* digestibility tests and the digestive tract of broiler chickens to explore the impacts of *Ulva* inclusion in poultry diets.

Given the protein content of wild *Ulva*, it can be concluded that wild *Ulva* is not a good source of protein (compared to any major vegetable protein source used in animal diets) and the presence of structural carbohydrates (usually referred to as fiber) limits the use of *Ulva* in diets for monogastric animals (poultry and pigs). Nevertheless, *Ulva* can be used in ruminant (cow, sheep, and goat) diets, however, studies are still underway since the fate of sulfonated carbohydrates is not yet known.

6. Beyond food and feed – *Ulva* in biomaterials

In 2019, the seaweed hydrocolloid industry was valued at 1.74 billion USD. Nearly 50 years of seaweed bioprospecting have resulted in over 3,000 marine natural products or bioactive molecules from seaweeds (Ferdouse et al. 2018). While green seaweeds do not contribute to the hydrocolloid industry and only approximately 8% of the marine natural products or bioactive molecules come from green seaweeds (Ferdouse et al. 2018), they still demonstrate significant potential in biomaterials industries, particularly due to the presence of ulvan. Ulvan has attracted increasing attention in the last decade, considering that less than five papers on ulvan were published annually during 2000–2009, but more than 35 papers were published in 2019 (Cindana Mo'o et al. 2020). The benefits and potential of ulvan in diverse biotechnical applications have already been thoroughly reviewed by several authors (Kidgell et al. (2019) for review); therefore, ulvan was not the focus of this section. However, we provide insights into the potential use of *Ulva* in other biomaterials, including packaging, which is comprehensively discussed below.

6.1. Packaging (packaging films and packaging materials)

The new circular economy plan, which is pivotal in the European Green Deal, EC's agenda, and UNSDGs for sustainable growth, includes designing sustainable products, empowering consumers, and improving reuse in production processes. Some key product value chains include packaging, plastics, textiles, construction, food, water, and nutrients. Thus, to meet these initiatives and those for protecting and restoring the marine environment, new production concepts are required to address the growing demand and provide sufficient quantities of high-quality materials and food in the future (Eroldoğan et al. 2022). Over half of the plastics made are only used once (Gross, 2017), and over 99% of plastic packaging is produced from petroleum-based sources (Arrieta et al. 2017). Rethinking and redesigning sustainable packaging materials using natural resources to replace single-use plastics will be essential to achieving the new circular economy action plan (European Commission 2022). Marine resources, including seaweed, provide an enormous pool of yet unexplored and potentially valuable resources for producing diverse biomaterials, including packaging, and interest is growing in the use of macroalgae in the packaging industry. The global seaweed-based packaging market is expected to account for $613.42 million USD by 2029 (Data Bridge Market Research). Diverse types of films for food packaging have recently been developed (Abdul Khalil et al. 2017; Amin 2021; Gomaa et al. 2022; Ganesan, Shanmugam, Palaniappan, et al. 2018) from macroalgae-derived sources. Considering *Ulva*, most packaging biofilms are produced by extracting ulvan and combining it with a plasticizer, such as polyethylene glycol (PEG), sorbitol, or glycerol (Davoodi, Milani, and Farahmandfar 2021; Guidara et al. 2019, 2020). In some cases, ulvan is combined with another natural material, such as cellulose extracted from the same species (Gomaa et al. 2022) or red algal polysaccharides (Ganesan, Shanmugam, and Bhat 2018; Ganesan et al. 2018). In many cases, ulvan addition to the packaging film increased the film's antioxidant activity (Amin 2021; Gomaa et al. 2022; Ganesan et al. 2018), suggesting that such seaweed-based packaging films may increase the shelf-life of certain packaged products.

Currently, most packaging products are produced from brown or red algae (e.g., products from Evoware (biodegradable, edible seaweed-based packaging), AMAM (agar plasticity), Ooho (edible water packets from seaweed extracts), Loliware (seaweed-based cups and straws), Algopack (brown-algae based bioplastics), Kelpn (kelp-based bioplastic), and Janoodam (seaweed-based bowls and lids)). To our knowledge, the only known *Ulva*-based packaging products are produced by the company Eranova (https://eranovabioplastics.com/technology/?lang=en), by enriching the content of starch, which is then extracted using an enzymatic cracking technique and then processed into biodegradable or durable bioplastic. However, some of the authors of the current work are presently conducting research to develop a sustainably produced, biodegradable, edible seaweed-based packaging material for the fast-food industry using mixtures of macroalgae biomass. This process requires no extraction, and is essentially waste-free. An initial screening of local seaweed species for packaging functionality led to testing and cultivating several species for seaweed-based packaging. Depending on the type and mixture of seaweed used and the applied preparation technologies (e.g., grinding), different material properties of the produced macroalgal-based packaging can be achieved. For example, the particle size distribution and film-forming abilities of the packaging material vary and have different material characteristics, such as lower or higher porosity, thicker and stronger films, or different material strengths. In external beta testing of the prototype with food products (baked fish and potato salad), 79–91% of customers rated the edible macroalgae packaging as good to very good (Bosse and Hofmann 2020). Based on these results, different types of packaging material can be developed for different functional uses, including in industries outside of food, by altering the seaweed species and their respective combinations. To our knowledge, this is the only seaweed-based packaging that uses 100% of the seaweed biomass and requires no extraction method. Further trials are currently underway to test different methods of packaging production from seaweeds (e.g., fiber casting or natural fiber injection molding). Nevertheless, one of the biggest hurdles, as in other industries, remains to be the processing and transport step from raw biomass to packaging production. The properties of *Ulva* that are conducive to packaging production (e.g., high cellulose and starch content) also make the seaweed a potential candidate for paper production. A recent study has shown that *Ulva* biomass can be successfully incorporated into filter paper at a concentration up to 4% without weakening the strength of the fiber network, and successfully removed pollutants (Cr, Cu, total Fe and Zn) due to its adsorbant properties (Caprita, Ene, and Cantaragiu Ceoromila 2021).

6.2. Plant biostimulants

Biostimulants promote plant processes, including nutrient uptake efficiency, stress tolerance, and crop quality (Regulation (EU) 2019/1009 of the European Parliament), and reduce the demand for inorganic inputs (Shukla et al. 2019). Currently, macroalgae are involved in 37% of the biostimulant market (Rouphael and Colla 2018) and contain classes of compounds, such as betaines, phenols, and polysaccharides, which are biostimulants (Stengel, Connan, and Popper 2011). The main temperate macroalgae-sourced biostimulant products (e.g., Maxicrop) are almost exclusively produced from the brown wild-harvested species *Ascophyllum nodosum* (www.solabiol.com/en/principles-maxicrop). In addition, *Ecklonia maxima* is used to produce the biostimulant Kelpak (https://www.kelpak.com/eckloniamaxima.html), which is exported globally. The red, tropical macroalgae *Kappaphycus alvarezii* has also been extensively studied (Kumar et al. 2020; Sahana et al. 2022; van Tol de Castro et al. 2023; de Araújo Amatuzzi et al. 2020) and is also commercially available as a biostimulant (e.g., www.prospersea.com).

Ulva spp. also have biostimulant properties, although there are little studies to date for green macroalgae compared to brown and red macroalgae. *Ulva* extracts improve salinity stress response (El Boukhari et al. 2021; Hussein et al. 2021; Latique et al. 2021), drought tolerance (Li et al. 2020), growth (Castellanos-Barriga et al. 2017; Hassan et al. 2021; Hussein et al. 2021; Mendoza-Morales et al. 2019; Michalak et al. 2016; Osuna-Ruíz et al. 2023), antioxidant activity (Osuna-Ruíz et al. 2023; Ennoury et al. 2022; Latique et al. 2021), and plant flavors (Paulert et al. 2021). Using *Ulva* spp. extracts as a biostimulant source increases crop yield and contributes to global food security while also creating another product route for some biomass produced during green tides (Shefer et al. 2022). While first plant trials using biochar produced from *Ulva* spp. have shown variable effects on plant growth (Kenneth et al. 2022; Roberts and de Nys 2016), this research field is still in its infancy, and finding solutions to reduce the sodium content in seaweed-based biochar will be a challenge for the future.

6.3. Biorefinery

Biorefineries use a biomass processing approach that facilitates the production of several value-added products from a given biomass feedstock (crops, lignocellulosic biomass, seaweed, microalgae, and insects) and ensure the full usage of resources, leading to zero waste and minimal greenhouse gas emissions (Barragán-Ocaña et al. 2023). By producing multiple products from the same raw materials, biorefineries increase the revenue per mass of feedstock, and diversify applications, making the whole system economically resilient (Golberg et al. 2020). The co-production of multiple products usually requires multiple subsequent processing steps produces one or several different products (Golberg et al. 2020). In an *Ulva* biorefinery, the separation of salt, cellulose, ulvan, starch, proteins, lipids, simple monosaccharides, and peptides has been reported in various process configurations (Table 5). High protein yields from *Ulva* can be obtained after extracting salt and ulvan from the seaweed (Magnusson et al. 2019), and extracting protein and water-soluble molecules in the first step increases the content and purity of residual water-soluble polysaccharides such as ulvan (Golberg et al. 2020). This is critical because achieving a certain level of concentration and purity is a major economic and technological hurdle for biorefineries. In addition, certain processes, such as crushing, milling, and other cell and tissue disruptions, usually benefit most subsequent processes by improving the biomass contact surface and the accessibility of intracellular components without intermediate drying. Therefore, the energy and cost of such processes benefit the entire processing chain rather than a single product (Zollmann et al. 2019). Although thermochemical approaches using high temperatures and solvents continue to be used at industrial scales to obtain different seaweed-derived products, more environment-friendly techniques to better preserve the product's quality and functionality are emerging, including enzyme-, microwave-, or ultrasound-assisted extraction, supercritical fluid extraction, pressurized solvent extraction, pulsed electric fields, or ohmic heating (Matos et al. 2021).

6.4. Knowledge gaps and future challenges

Currently, biorefinery design is a major challenge, i.e., choosing the processes and equipment and integrating them into one optimized process flow (Golberg et al. 2020) because biomass processes and equipment are usually designed to solely produce one product and not preserve the byproducts for subsequent processing targeting zero waste. Currently, there is no widespread and successful standard for industrial seaweed biorefinery design. Polysaccharides have been identified as the most common potential product from Chlorophyta (mainly *Ulva* spp.), accounting for 40% of the applications. Protein was second (21%), with lipids and pigments considered less frequently (Joniver et al. 2021). Future steps for the development of an *Ulva* biorefinery should include the demonstration of using common food and chemical industry methods for processing and equipment that can be scaled. These efforts will require mass and energy balances for each step. The subsequent steps should include process simulation using common industry tools, such as AspenPlus (https://www.aspentech.com/en/products/engineering/aspen-plus) or SuperPro (https://www.intelligen.com/) process design software, enabling economic and life cycle analysis of processes and plants. Further steps should include an integrated process demonstration for assessing product safety, stability, final applications, and complete economic and environmental analysis. This step will require the collaboration of biomass producers, process engineers, and environmental economists.

7. Patents of *Ulva*-based products and technologies

The diversification of macroalgal applications, including *Ulva* species, in increasingly sophisticated products, is accelerating the emerging macroalgal biotechnology patent market. The rate of patent registrations for seaweed-related products has been steadily increasing annually by approximately 11% (Mazarrasa et al. 2014). Similarly, increased *Ulva* production and demand for natural products have promoted research and development in *Ulva* biotechnology. Consequently, patents for processes and applications of *Ulva* have rapidly grown. Since 2014, 405 *Ulva*-related patents have been registered, representing 5.4% of seaweed-related registered patents (Mazarrasa et al. 2014). A more recent search using the keyword "*Ulva*" on the European Patent Office (EPO) website (https://www.epo.org/searching-for-patents.html) resulted in 2,954 patents related to *Ulva*-based products, which are classified under nine different codes according to the International Patent Classification (IPC) System (Supplementary Table 2). Of the classified patents, *Ulva*-related patents are distributed into categories relating to medicine (31%), cosmetics (31%), feed (19%) and modifications of nutritive qualities of food and dietic products (10%), revealing that *Ulva*-related patents in the food industry are lagging behind the medicine, cosmetics and feed industries.

8. Future research directions

Several technical and environmental challenges must be overcome to fully capture and realize the potential of *Ulva* biomass in the European circular economy. In fact, this is one of the main goals of the recently established COST Action CA20106 SeaWheat, which has resulted in the establishment of the network of authors who have collaborated on this manuscript. For successful large-scale production of *Ulva* spp. for the food, feed, and biomaterials industry, several challenges must be overcome through research, innovation, knowledge transfer and collaboration.

Green seaweed species misidentification inhibits production data analysis, making a thorough overview of national and global productions difficult. *Ulva* species must be correctly identified owing to their popular application in commercial projects and industrial product labeling. Consequently, an integrative systematics approach is required to accurately identify *Ulva* spp., considering morphological characters, DNA sequencing of different markers, and species biogeography. Such scientific advances will contribute to a better understanding of the *Ulva* biomass produced, allowing the development of a management plan and policy framework adapted to the specificity of this species' clades. Nevertheless, it is unrealistic to expect that existing and future producers of *Ulva* biomass will have the time and resources to double-check the identity of their product using genetic sequencing methods. In order for the *Ulva*-based industry in Europe to grow, new methods need to be developed that simplify this task, such as the sequencing-free assay for foliose *Ulva* species identification developed by Fort et al. (2021). Such technological advances will provide quicker and cheaper tools that will enable producers to guarantee the identity of the products they are selling.

Likewise, not all *Ulva* strains and species with economic potential have been identified, and further research into fine-tuned selection for specific applications is required. Additionally, population, strain, and environment-induced chemical variations complicate the development of chemically consistent biomass, which is key for developing an industry striving for nutritionally valuable ingredients or bioactive components for high-end uses. Correct identification of *Ulva* spp. would also contribute to a better understanding of the effect of genetic and environmental parameters on their composition, growth, and reproduction in their natural and controlled environment. Future research must therefore focus on harnessing the benefits of both genetic and environmental factors in order to support growth of the *Ulva* cultivation industry. This includes identifying robust strains (e.g., green tide strains Fort, et al. (2020)) with exceptional growth rates and/or high temperature tolerance, and optimizing the cultivation conditions in order to produce biomass with the desired traits (e.g., high proteins or high lipids). Future monitoring and selection programs are necessary to support these efforts and provide food and feed manufacturers with high quality biomass. As a first step toward closing these knowledge gaps, the SeaWheat COST Action has initiated a European-wide collection campaign to measure the nutritional content and microbiome of genetically barcoded *Ulva* species throughout Europe using standardized methods. These data will provide the first coordinated, European-wide effort to assess the species diversity and the assosiated biochemical and nutritional profiles and epibiontic microbial interactions of *Ulva* spp. throughout Europe.

Additionally, the effect of associated microbiota on *Ulva* must be further investigated. The close association between bacteria and the development and morphology of *Ulva* biomass has been demonstrated; however, further interactions within the seaweed holobiont could provide clues for manipulating desired traits in the seaweed. For example, current research by the authors is showing that protoplast development in *Ulva* spp. can occur naturally. While we do not yet know what triggers the natural production of protoplasts, if we could induce the production by manipulating the microbiome or other environmental factors, then this would provide a cheap and simple method to vegetatively produce large amounts of biomass, without relying on the expensive

Table 5. *Ulva* biorefinery. Co-production of various ingredients from *Ulva* and their transformation to additional products.

Species	Directly co-extracted products	Products produced by transformation of *Ulva*-derived ingredients	Reference
U. lactuca	Water-soluble proteins and carbohydrates		(Postma et al. 2018)
U. lactuca	Protein and carbohydrates	Glucose, rhamnose and xylose, acetone, butanol, ethanol, and 1,2-propanediol	(Bikker et al. 2016)
U. fasciata	Mineral rich liquid extract, lipid, ulvan, and cellulose	Ethanol	(Trivedi et al., 2015)
U. lactuca	Mineral rich liquid, lipid, ulvan, protein, and cellulose		(Gajaria et al., 2017)
U. lactuca	Water-soluble carbohydrates	Acetone, butanol, and ethanol (ABE)	(van der Wal et al., 2013)
U. rigida	Carbohydrate, salt, concentrated protein		(Pezoa-Conte et al., 2015)
U. ohnoi	Salt, pigment, ulvan, and protein		(Glasson et al., 2017)
U. lactuca	Mineral rich liquid extract, ulvan, protein	Methane	(Mhatre et al., 2019)
U. ohnoi	Salts, starch, lipids, ulvan, proteins, and cellulose.		(Prabhu et al., 2019)
Mix of U. rigida and *U. fascia*	Hydrochar, 5-HMF, monosaccharides, proteins, peptides.	Ethanol	(Polikovsky et al. 2020)
U. ohnoi	Mixture of monosaccharides	Ethanol	(Jiang et al., 2016)
U. ohnoi	Starch, proteins, and minerals		(Prabhu et al., 2019)
U. ohnoi	Hydrochar	Polyhydroxyalkanoates	(Ghosh et al., 2021)
U. lactuca	Polysaccharides, proteins		(Andrade et al. 2022)
Mix of Ulva species	Monosaccharides		(Robin et al., 2017)
Ulva sp. not defined	Polysaccharides	Biodiesel	(Ruangrit et al., 2023)
U. ohnoi	Hydrochar, monosaccharides	Polyhydroxyalkanoates	(Steinbruch et al., 2020)
U. lactuca	Antioxidants and phenolic compounds		(Rashad et al. 2023)
Ulva sp. not defined	Ulvan	Biogas, polyhydroxyalkanoates	(Arul Manikandan and Lens 2023)
Ulva rigida and *Ulva ohnoi*	Water-soluble and -insoluble protein		(Robin et al., 2018)
U. lactuca	Bio-oil, hydrochar	Bioethanol	(Sharmiladevi, Swetha, and Gopinath 2023)

enzymes that are currently required to induce protoplast development in *Ulva* spp.

Sustainable algal biomass production should include safe approaches, ensuring no harm to natural environments and ecosystems, including wild seaweed populations. Recently, three major challenges were identified for the expansion of seaweed cultivation in temperate environments: global climate change, limited carrying capacity in areas where large-scale cultivation already occurs, and the increasing cost and age of the seaweed labor force (Rieve, 2023). In order to overcome these challenges, the availability and suitability of areas for sea-based cultivation must be accounted for in marine spatial planning and form a beneficial component in coastal conservation, though restrictions on infrastructure may occur. The land-based cultivation approaches must be energy- and cost-efficient, based on full life-cycle assessment and implementation. Furthermore, significant investments must be made in the preservation of seaweed strains for preserving biodiversity, strain selection and selective breeding campaigns for the development of robust strains. Several initiatives have begun to support these efforts among European (SeaStrains), American (SugarKelpBase) global (Global Seaweed Coalition), and Asian networks.

The general principles and requirements of seaweed food safety in the EU are subject to the EU-enforced Regulation (EC) number 852/2004 on food hygiene. In many countries, the food manufacturing process is subject to the HACCP assessment, a system adopted by the WHO and the Codex Alimentarius Commission as recommended international code of practice for general principles of food hygiene. The regulation (EC) 68/2013 defines the use of algae as accepted feed materials. Green seaweeds are solely mentioned in the case of seaweed meals. No specific mentions are made for *Ulva* species. Whether offered live or processed (chilled, frozen, or dried), the compulsory declarations are the contents of crude protein, crude fat, crude ash, and iodine, which should be <100 ppm. However, considering the new market trends and processing technologies of seaweed feed and food products, guidelines and legislation on specific seaweed feed and food products remain lacking. Furthermore, whether legislation from one part of the world can be transferred to other areas without considering the biological (seaweed and microbial flora) and environmental (climatic) factors is doubtful.

Although societal acceptance of algal products has increased in Europe recently, further progress is needed to replace conventional biomass or nutritional constituent sources with plant and algae-based ingredients. Clear regulations on quality control relating to environmental contaminants, such as heavy metals and potential pathogens, must be implemented while ensuring the satisfaction of regulatory bodies, consumer safety, and medium- and large-scale practicability for industries. Quality control of strain/biomass origin and chemical composition must be assured based on standardized methodologies. Currently, the European Committee for Electrotechnical Standardization (CEN) is developing standards for algae and algae-based products, representing a major step toward realizing this potential. EU regulatory bodies, including EFSA, must review current restrictions on algae-derived products to support the effective integration of *Ulva* (or other seaweed) utilization in the European circular economy. Therefore, the risks related to feed and food safety and the possible environmental contamination from aquaculture, among other potential sources of pollution, represent important issues that require special attention from scientists and policymakers concerning the safe use of *Ulva* spp. in food and feed products.

Ulva species produced in land-based systems under a controlled environment would present easily manageable food and feed safety risks. The EU has also listed organic regulations (Council Regulation 834/2007) that classify farmed or wild-collected seaweeds, including *Ulva* species, as organic. However, when produced under IMTA, more data and scientific-based evidence would be needed relating to the risk posed by the production of low-level trophic organisms using different waste streams and processes. Such information would also help in developing the lacking regulations appropriate for IMTA products. Further, the wild-harvested biomass should be closely monitored because heavy metals, associated pathogens, and other persistent environmental or anthropogenic pollutants can pose risks stemming from seaweed consumption.

Using *Ulva* spp. and its derivative bioactive compounds in feed and food can be challenging as many of the compound's bioactivity remains unrecognized. Furthermore, high polysaccharide content and non-protein nitrogen are problematic and reduce digestibility. Non-starch polysaccharides (e.g., ulvan) also trap about 5% of the amino acid in the biomass. Solutions such as fermentation to improve digestibility, extended fresh water washing to reduce ash content, and biorefinery approaches for producing bioactive extracts for feed additives have all shown promising results. Nevertheless, further research is required to provide supportive and applicable information regarding the factors determining the presence and level of ANFs in the biomass, their active mechanism, the threshold level at which they are harmful, and methods for neutralizing their activity. Such research will contribute to defining the safe yet bioactive level of inclusion of *Ulva* ingredients in feed and food formulation. Further, when used as food or feed ingredients, the interactions between *Ulva* or its derivative ingredients with the matrix should be researched to ensure its safe utilization or conservation of the bioactive characteristics in the formulated feed or food. Furthermore, studies addressing the effect of culinary treatments on the levels of contaminants and bioavailability of health-promoting compounds are also needed.

The major challenge that currently hinders the widespread integration of *Ulva* into feed and food is competition with soybean. As presented above, differences in lipid and protein content separate the nutritional profile of *Ulva* most strongly from soy. Soybean has about 36.5% protein (USDA FoodData Central), compared to harvested *Ulva*, which ranges from about 4–27%. Only enriched *Ulva* grown with supplemental nitrogen can reach protein levels comparable to soybean. Additionally, the cost of *Ulva* production cannot currently compete with the cheap production of soybean. According to the US Department of Agriculture, soybean production costs about $162/acre. Assuming an average yield of 50 bushels/acre and a conversion rate of 40 bushels/ton, soybean production on a weight basis is approximately $130/ton. In comparison, estimates of production costs for seaweed farms range from $225 – $10,000/dry ton, depending on scale (Kite-Powell et al. 2022). Therefore, even the largest seaweed farm with the lowest production costs is still 1.7 times more expensive to produce than soybean, and most seaweed farms have even higher production costs. Unfortunately, there are no known published production costs for *Ulva* cultivation, but life cycle assessments of land-based production are currently underway. Another major limitation for integrating *Ulva* into the feed industry, both terrestrial and aquafeed, is the scale of production. Currently, the scale of *Ulva* production is catering mainly to human consumption, while biomass from green tides is used for animal feed research. Clearly it is important to save high quality biomass from aquaculture for human food, and the feed and biomaterials industries should not compete with human food for *Ulva* biomass, but the unpredictability of the availability of biomass from year to year continues to be a difficult challenge for industries relying on wild biomass. In both the food and feed industries, digestibility, taste, palatability, and flavors must be investigated further to better understand the potential attractiveness of *Ulva* products to animals or consumers. Customer acceptance and willingness to pay must be examined to determine the marketability and price of *Ulva*-based products. Currently, some producers are approaching well-known chefs to include seaweeds in their recipes, or to provide cooking courses. Such activities will help raise awareness about how to use seaweeds in general and *Ulva* specifically in food, and make European consumers more comfortable with incorporating *Ulva* into their diet.

Although *Ulva* is naturally available and culture techniques exist, several key issues exist regarding the market, technology, and product development (i.e., increased supply of *Ulva* biomass, product innovation, and processing). The effects of processing on chemical composition and potential modifications in bioactive profiles must be identified by companies and adjusted for end-user applications. To capitalize on the potential for increased profitability, the existing *Ulva* sector must migrate into the identified opportunity areas. The nutraceutical, pharmaceutical, and cosmetics industries represent greater profit opportunities than the agri-products and horticultural products sector alone (Barbier et al. 2019). To achieve this, the sector must identify specific market opportunities, innovate, and introduce greater automation, including new processing and packaging technology.

Effective *Ulva* biomass utilization in a cascading biorefinery concept will still need to demonstrate its potential to avoid compound loss and waste. Because improving crude biomass often requires high energy investments, the cost-effectiveness and environmental sustainability of such processes must be investigated. Life cycle assessment of current production systems will provide key insights into the sustainability and cost-effectiveness of *Ulva* production.

Therefore, the *Ulva* industry has been assigned an ambitious target. Greater value in the *Ulva* sector can only be achieved by industry activities in association with funding agencies and research providers.

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Author contributions

The author order reflects the first, second, third, and last (senior) authors. Authors four through nine contributed significantly to the writing as section leaders. All other authors are in alphabetical order and the order does not reflect their contribution. The author contributions are summarized as follows: LCH: conceptualization, writing of the original draft, visualization, review & editing, supervision, resources, investigation, methodology, project administration; SS, AJM-M: conceptualization, writing of the original draft, review & editing, methodology, project administration, supervision; JMMA, UA, KB, AGB, JJB, RD, ÖD, OTE, AF, NG, AG, LG, FM, SS, DBS, ES, GT, SZ-S, ZZ-S: writing of the original draft, review & editing. CR: writing of the original draft, review and editing, conceptualization; MS: funding acquisition, conceptualization, review & editing, project administration, supervision. ÖD, LCH, KIK: data visualization, MM: sample analysis. The following authors made major contributions to the writing as section leaders: LCH, AJM-M, KB, GZ, SS, LG, NG, GT, CR.

Disclosure statement

Antonio Jesús Meléndez-Martínez carries out consultancy work for diverse companies. Alexander Golberg has interests in Genesea Advansed Technologies which commercializes *Ulva* protein process.

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