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REVIEW PAPER

Harnessing green tide *Ulva* biomass for carbon dioxide sequestration

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Abstract Green tides, characterised by massive blooms of the seaweed *Ulva*, pose a significant threat to coastal economies and marine ecosystems. This review explores the potential repurposing of harmful *Ulva* blooms for carbon sequestration, addressing the critical global issue of CO_2 emission. We conducted a comprehensive literature review and examined the conversion of shoreline *Ulva* biomass into biochar through pyrolysis, a process that can be implemented directly at biorefineries. This approach not only facilitates carbon sequestration but also mitigates greenhouse gas emissions and enhances soil quality through soil amendments. Our review covers data from 2008 to 2022, focusing on the carbon sequestration potential of *Ulva* during green tide episodes in China and Korea. Our assessment indicates that *Ulva* biomass has the potential to sequester approximately 3.85 million tons of CO_2 equivalent (CO_2e), with about 1.93 million tons of CO_2e potentially stabilised through biochar conversion. Furthermore, we conducted a hypothetical techno-economic analysis

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assessing the sustainability and economic viability of *Ulva* cultivation and biochar production for CO_2 sequestration. These findings suggest that the combined biomass and biochar production could be financially viable and profitable. Despite the challenges posed by green tides, our review highlights their potential role in mitigating global climate change.

Keywords Green tide · *Ulva* bloom · Carbon sequestration · Biochar production · Pyrolysis · Techno-economic analysis

1 Introduction

Although the term 'green' is often associated with environmental sustainability, 'green tides' can lead to significant economic, social, and environmental disruptions. Green tides result from fast-growing macroalgal blooms, typically dominated by species of the ephemeral green seaweed genus *Ulva*, including *Ulva lactuca*, *Ulva linza*, *Ulva pertusa*, *Ulva prolifera*, and *Ulva rigida*. Green tides are increasingly frequent in coastal areas worldwide (Fig. 1). The first reported *Ulva* bloom occurred in Belfast, Northern Ireland, at the end of the nineteenth century (Letts and Richards 1911). Since 2007, the Yellow Sea, particularly along the coast of the Shandong peninsula, has experienced several green tide outbreaks since 2007 (Zhang et al. 2019).

The largest recorded green tide occurred in 2021, covering approximately 1975.89 km^2 of the Yellow Sea with *U. prolifera* when it peaked (Chen et al. 2022).

As a result, the city of Qingdao spent 350 million CNY (approx. \$49 million USD) to clean up the biomass, consuming 46.7 kt oil-equivalent of fossil fuels and emitting 331.0 kt CO_2-equivalent (Chen et al. 2022). Green tides off the coast of the Korean peninsula may originate from blooms near Shandong. However, it cannot be ruled out that they originated locally, as the patches in Korea are relatively small and difficult to track using satellite imagery (Harun-Al-Rashid and Yang 2018).

In addition to cleanup costs, green tides cause economic losses by impacting tourism, aquaculture, and traditional fisheries. The environmental consequences of *Ulva* blooms are significant and multifaceted, affecting marine ecosystems, water quality, and biodiversity. *Ulva* blooms are typically fuelled by excess nutrients, particularly nitrogen and phosphorus, which lead to eutrophication and promote rapid algal growth that disrupts the natural balance of marine ecosystems (Zhang et al. 2013). As *Ulva* blooms grow and decay, they consume large amounts of oxygen, creating hypoxic (low oxygen) or anoxic (no oxygen) conditions detrimental to marine life. Many aquatic organisms, including fish and invertebrates, require oxygen-rich environments to survive; thus, hypoxic conditions can lead to mass die-offs and decreased biodiversity (Zhang et al. 2019). During their growth phase, *Ulva* absorbs inorganic carbon from seawater, which increases the pH (alkalinity) of water. However, as blooms die and decompose, they release large amounts of CO_2, which can lower the pH and contribute to ocean acidification (Barakat et al. 2021). This shift in pH can harm marine organisms, particularly those with calcium carbonate shells or skeletons, such as corals and shellfish (Doney et al. 2020). The rapid growth of *Ulva* can overshadow and outcompete native marine plants and algae, disrupting local ecosystems. This competition can decrease biodiversity, as native species struggle to survive or are displaced (Xiao et al. 2019). The accumulation of decaying *Ulva* biomass on the seafloor can smother benthic habitats, affecting bottom-dwelling organisms and altering the physical structure of the ecosystem, with long-term consequences for marine habitat health and stability (Zhang et al. 2019). The presence of large quantities of *Ulva* can alter the composition and structure of microbial communities in the water, affecting nutrient cycling and other ecological processes, potentially leading to further ecosystem imbalances (Qu et al. 2020). *Ulva* blooms can disrupt local food webs by altering food resource availability and changing habitat structure. The loss of oxygen and changes in water chemistry can affect the populations of various marine species, from primary producers to top predators, causing cascading effects throughout the ecosystem (Green-Gavrielidis et al. 2018). Large mats of floating *Ulva* can create physical barriers that affect navigation, fishing, and other human activities (Rybak and Gąbka 2018). These

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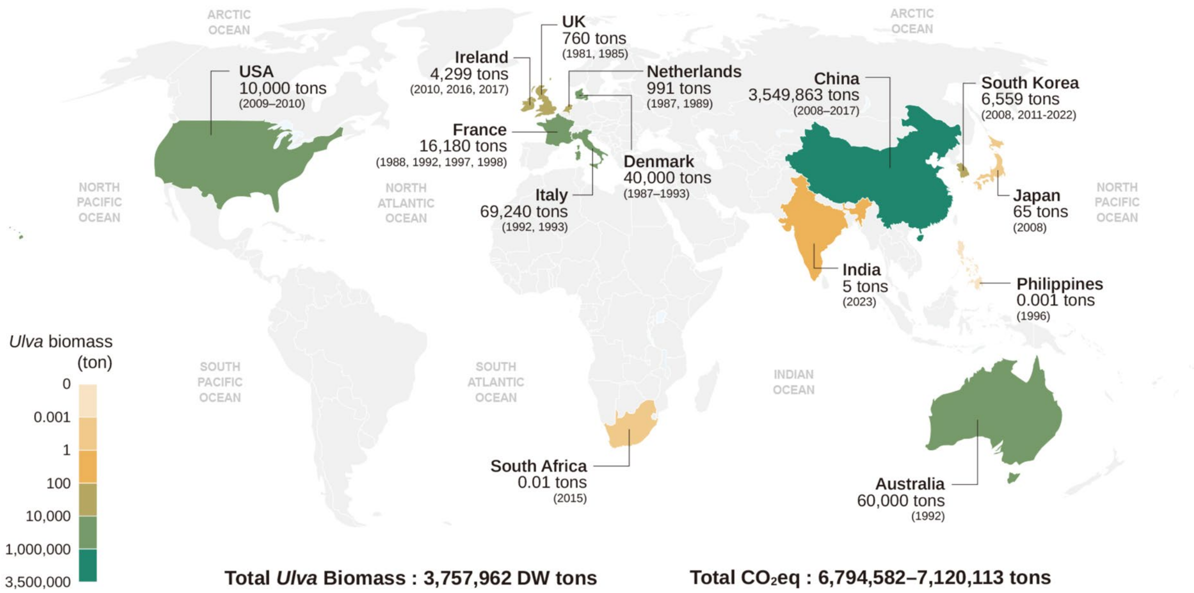

Fig. 1 Global distribution of *Ulva* blooms by country, year of occurrence, and amount of total biomass. The extent of the green coloration serves as an indicator of biomass, wherein a greater saturation of green corresponds to a higher biomass content. The quantification of biomass in relation to the coloration can be assessed by referring to the scale bar on the left

mats can also wash ashore, causing beach fouling and negatively impacting coastal tourism and recreational activities.

Given these significant ecological and economic consequences, urgent mitigation strategies are necessary. Some proposals include collecting and removing overwintering and germinating *Ulva* spp. prior to outbreaks by pumping *Ulva* masses onto the decks of harvesting boats and concentrating them using nets and filters (Smetacek and Zingone 2013). Implementing upstream reduction strategies for dual-nutrient (i.e., N and P) emissions in rivers and the sea can significantly impact the control of algal bloom events and their cascading effects; however, these approaches are expensive. Other suggestions involve applying chemicals, such as strong oxidants, metals, and synthetic biocides, to reduce green tides (Tang et al. 2021), which can lead to environmental pollution and cause significant ecological damage. Biocontrol methods, such as using (in)vertebrates or enzymatic degradation by viruses up to 1 µm in size, have also been proposed to limit *Ulva* biomass development (Geertz-Hansen and Sand-Jensen 1992; Abergel et al. 2015). Preventing the propagation of *Ulva* sp. in seaweed culture systems is another strategy to prevent outbreaks, with methods like the "freezing net" technique where *Neopyropia* spp. seeded on nets can tolerate extended periods at −20 °C, whereas *Ulva* spp cannot survive. Similarly, modified clays can be used in seaweed cultivation areas to remove micropropagules of *Ulva* spp. (Xia et al. 2022). Encouraging individuals, communities, and industries to adopt sustainable practices and reduce their nutrient footprints can mitigate overall nutrient loads and prevent algal blooms.

The practical use of seaweed as a raw material in industsrial processes could counterbalance the economic expenses of removing harmful seaweed (Milledge and Harvey 2016; Dominguez and Loret 2019; Prabhu et al. 2020a, b). *Ulva* spp. serve as natural sources of chemicals for a wide range of industrial applications, including food production, animal and fish meals, energy and biofuels, biomaterials, plant biostimulants, and bioelectric materials (Dominguez and Loret 2019; Zollmann et al. 2019; Mantri et al. 2020). *Ulva* contains high levels of crude proteins, including the major essential amino acids, cysteinolic acid, cysteic acid, proline, glutamic acid, and chondrine (Mantri et al. 2020), in addition to polysaccharides, such as ulvans, sulphated polysaccharides comprising rhamnose, uronic acids, xylose, and glucans (Holdt and Kraan 2011; Kraan 2013). *Ulva* also contains water- and fat-soluble vitamins, such as vitamins A, B, C, and E; valuable carotenoid and chlorophyll pigments; polyunsaturated fatty acids; and minerals, such as calcium and magnesium (Holdt and Kraan 2011; Mantri et al. 2020). Some studies have proposed that green tide *Ulva* spp. could be directly used for human consumption, although potential contamination issues depend on the collection location (Li et al. 2018).

The essential components for producing and commercialising biofuels and biomaterials from *Ulva* include costly processing chemicals, advanced equipment, high energy consumption, and labour-intensive tasks requiring a skilled workforce (Zollmann et al. 2019). Therefore, alternative methods to streamline biorefinery approaches and maximise the production of value-added products from *Ulva* biomass are necessary to achieve commercial viability in these processes. This review explores recent advancements in utilising the nuisance green tide alga *Ulva* from 'blue economy' perspective. Coined by Belgian Environmentalist Dr. Gunter Pauli in 2010, the 'blue economy' advocates for leveraging natural ecosystem principles to stimulate economic revitalisation. This review proposes strategies for utilising *Ulva* to sequester CO_2, thereby aiding in mitigating global warming attributed to excessive fossil fuel consumption.

2 A portrait of *Ulva*

Ulva is a cosmopolitan green macroalgae with global geographic distribution in fresh, brackish, and marine waters. Of the 594 *Ulva* species, 130 have been taxonomically identified (Guiry and Guiry 2013). Most *Ulva* thalli are morphologically similar, comprising one or two layers of cells with a diffuse growth habit, likely giving *Ulva* spp. little non-photosynthetic structural tissue and a net positive carbon uptake under optimal conditions (Beach et al. 1995; Park 2020). These algae tolerate various environmental conditions, including light, salinity, and temperature (Kim and Chojnacka 2015; Gao et al. 2017; Food Agriculture Organization of the United Nations 2018). *Ulva* spp. has a higher surface-area-to-volume ratio than those of other macroalgae, with thicker thalli facilitating nutrient uptake. *Ulva* species proliferate (9–37% day^{-1}) (Huntzinger et al. 2017; Wu et al. 2018) in a short generation time (31.3–35.5 days) (Cui et al. 2018), and produce abundant reproductive cells ($2.84\text{-}6.62 \times 10^6$ reproductive spores cm^{-2} thallus area) (Zhang et al. 2013). They are ruderal species; they can readily colonise open substrates and opportunistically disturb environments. Further, they grow exponentially under favourable conditions. Given that 1 cm^2 of *Ulva* thallus tissue yields 10^6 spores, with a germination rate of 91.6% (Cui et al. 2018), and subsequently, only 1% of these spores survive and mature within 35.5 days. Thus, the proliferation of *Ulva* plants from 1 cm^2 would match the human population within 4–5 weeks (Fig. 2).

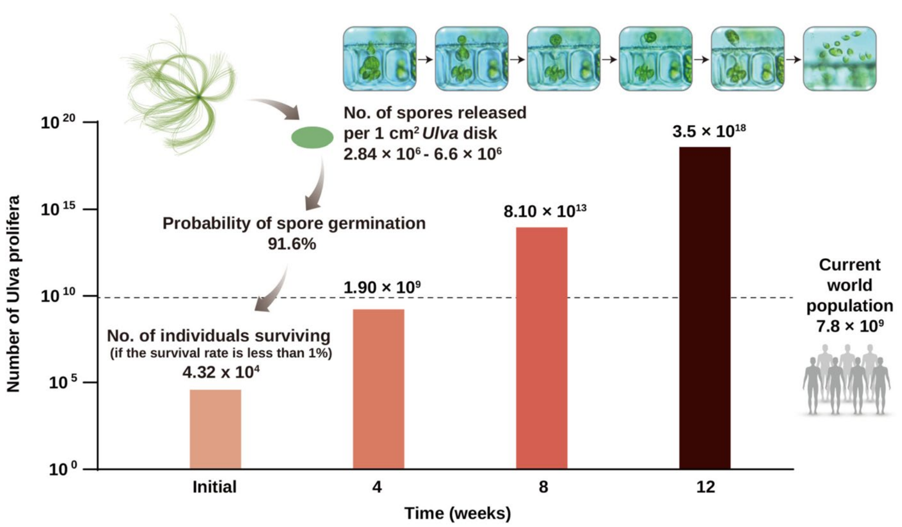

Fig. 2 Explosive growth of *Ulva*. The number of *Ulva* cells was expressed as an exponent of 10 at 4-week intervals for up to 12 weeks, assuming that 91.6% of the spores released from a 1 cm^2 area of *Ulva* will germinate and less than 1% of these will survive. The *Ulva* cells at the top of the graph show a cross-section of the thallus during sporulation and spore release

The exact mechanisms behind green tide formation remain elusive, but they are associated with several factors. These include heightened dissolved inorganic nitrogen concentrations and phosphorus from rapid industrialisation, urbanisation, and excessive fertiliser use in agriculture and horticulture. Changes in ocean nutrient levels contribute to nitric oxide production, a crucial factor in *Ulva* sporulation, which releases numerous spores. Furthermore, global climate change can influence the dynamics of green tides. Rising temperatures and increased atmospheric CO_2 concentrations, critical indicators of climate change, create conditions conducive to the growth and photosynthetic carbon fixation in seaweeds. This, in turn, facilitates more frequent green tides than the existing ones. Laboratory-based studies have shown that ocean warming and acidification can expedite gamete colonisation, promoting the proliferation of *U. rigida*, a common green tide species (Gao et al. 2017).

2.1 Uses of *Ulva*

Ulva biomass offers many options for valorisation, including salts, pigments (chlorophyll *a*/*b* and carotenoids), sulphated carbohydrate oligomers and monomers, ulvans (water-soluble carbohydrates), water-insoluble carbohydrates, proteins, and amino acids (Dominguez and Loret 2019; Sadhukhan et al. 2019; Zollmann et al. 2019). Chlorophylls, the predominant pigments in *Ulva* that support photosynthesis, have antioxidant properties (Ragonese et al. 2014). Tetrapyrroles extracted from chlorophyll can be used as food colourants and supplements (Solymosi et al. 2015). Carotenoids in *Ulva* are similar to those in higher plants and include β-carotene, lutein, violaxanthin, antheraxanthin, zeaxanthin, and neoxanthin. These compounds possess bioactive and therapeutic properties, making them potential alternatives to synthetic medicines and nutrients (Nabi et al. 2020). *Ulva* contains considerable quantities (15–65%) of polysaccharides, including ulvans and glucans such as starch (Kraan 2013; Bikker et al. 2016). Ulvans are composed of many sulphonic acids, sulphated l-rhamnose, xylose, and glucose compounds possessing antioxidant, antiviral, antitumor, anticoagulant, lipid-inhibitory, liver-protective, immunostimulant, antidepressant, and anxiolytic properties. Therefore, these compounds may be suitable for biomedical, pharmaceutical, and food applications (Cardoso et al. 2014; Sari-Chmayssem 2019).

Through the selective, sequential extraction of water-soluble polysaccharides (e.g. ulvans) from *Ulva*, followed by the enzymatic degradation of carbohydrates, proteins can be concentrated for use in high-value nutritional products. *Ulva* spp. contains substantial quantities of proteins (7–24% dry weight) (Gao et al. 2017) and essential amino acids (> 40%) (Korzen et al. 2016; Karray et al. 2017). These amino acids, including methionine and lysine, are potentially important sources of protein for humans and animals (Taboada et al. 2010; Shuuluka et al. 2013). The total amino acid composition of *Ulva* is very similar to that of egg ovalbumin (Shuuluka et al. 2013). However, further studies are needed to assess the feasibility of food-related applications because *Ulva* proteins contain allergens such as superoxide dismutase, thioredoxin-h, aldolase A, and troponin C (Polikovsky et al. 2019). *Ulva* spp. have unique fatty acid profiles characterised by high levels of alpha-linolenic acid and stearidonic acid, which may mitigate the adverse effects of fatty acids on cardiovascular and neurological functions, as demonstrated in a hypercaloric diet rat model (Cardoso et al. 2018).

Cellulose, a polymer of C_6 sugars linked by β-(1-4)-glucoside bonds, constitutes 38–52% of *Ulva* biomass. As cellulose from *Ulva* does not have lignin fractions, its extraction is more suitable for biomedical applications (Halib et al. 2017) and does not degrade easily (Wahlström et al. 2020). Therefore, it can serve as a feedstock for industrial applications, ranging from biofuels and foods to nanocomposites, micro- and nanocrystals, and bioplastics (Klemm et al. 2005; Sadhukhan et al. 2016; Sadhukhan and Martinez-Hernandez 2017).

2.2 *Ulva* as a feedstock for biorefineries

Biorefineries integrate biomass conversion and separation processes to generate a range of bioproducts (e.g. food, feed, and chemicals) and bioenergy (e.g. fuel, electricity, and heat) with minimal waste (Bastiaens et al. 2017). They contribute to sustainable industrial economies by creating value-added products that offer environmental benefits through reduced pollution and dependence on ecosystem services (Balina et al. 2017). Biorefineries based on seaweed feedstock have attracted increasing interest in recent years, and these mainly use ruderal seaweed species often associated with eutrophication, such as *Ulva* and *Sargassum*.

Ulva offers several advantages as a biorefinery feedstock compared to other photosynthetic organisms, such as microalgae and cyanobacteria. It produces a higher biomass yield per unit area compared to microalgae and cyanobacteria (Bikker et al. 2016; Dominguez and Loret 2019). Unlike microalgae, which require complex harvesting methods such as centrifugation and filtration, the larger size of *Ulva* makes it easier to harvest, reducing the energy and costs associated with the harvesting process and making *Ulva*-based biorefineries more economically viable (Bikker et al. 2016). *Ulva* is particularly noted for its high protein and amino acid content, making it a valuable nutritional source. Its cell walls contain polysaccharides with unique bioactive properties not commonly found in microalgae or cyanobacteria (Dominguez and Loret 2019). The conversion of *Ulva* biomass into biochar is a promising method of carbon sequestration. The structure of *Ulva* allows for a higher yield of biochar compared to microalgae and cyanobacteria, potentially providing better solutions for carbon capture and storage (Aravind et al. 2020). Additionally, *Ulva* can grow in a wide range of salinities and temperatures, making it more resilient and easier to cultivate in diverse environments compared to some microalgae and cyanobacteria, which may require specific conditions (Gao et al. 2017). These advantages make *Ulva* biorefineries a compelling option for sustainable development, with multiple applications and environmental benefits (Chen et al. 2022).

A considerable amount of research has been dedicated to the development of pilot-scale biorefining systems (Bikker et al. 2016; Cappello et al. 2016; Mata et al. 2016; Magnusson et al. 2016; Milledge and Harvey 2016; Gajaria et al. 2017; Glasson et al. 2017; Gao et al. 2018; Prabhu et al. 2020a, b).

Guidelines for using *Ulva* across different biorefinery platforms have been examined in detail in recent publications (Dominguez and Loret 2019; Sadhukhan et al. 2019; Torres et al. 2019; Zollmann et al. 2019; Filote et al. 2021); a schematic overview is shown in Fig. 3. However, only a few of these compounds are commercially available. Therefore, considerable research is required to develop commercially viable biorefineries.

Biochemical consistency is important for developing biorefineries that use *Ulva* blooms as feedstock. From an economic point of view, these resources are abundant but likely not reliable enough for a sustainable business model unless they are provided continuously over the long term through cultivation and harvesting, which are the most expensive and energy-consuming steps in biorefining (Bruton et al. 2009; Tedesco and Daniels 2018). Thus, challenges related to current technological inefficiencies and the variability in seaweed biomass quantity and quality must be addressed to fully utilise the potential of *Ulva* spp. in developing a sustainable bioeconomy.

3 Can *Ulva* fight climate change?

3.1 *Ulva* can capture huge amounts of CO_2

The 2018 Intergovernmental Panel on Climate Change (IPCC) Special Report asserted that CO_2 emissions must fall to zero between 2045 and 2080 to meet the Paris Climate Summit target of limiting global temperature increases to 1.5–2 °C (IPCC 2018). However, a recent IPCC Working Group 1 report titled ‘Code Red for Humanity’ indicated that warming has accelerated in recent decades and reached 1.2 °C, dangerously close to the threshold of 1.5 °C. At the same time, extreme weather events and climatic disasters are becoming more frequent and intense.

The role of photosynthetic organisms in mitigating CO_2 emissions has gained increasing attention, making them a potential sustainable solution to combat climate change. The Amazon rainforest exemplifies the ecological services provided by organisms that filter and reprocess harmful CO_2 emissions. Interest in using seaweed, known as blue carbon (BC) for the carbon stored in coastal and marine ecosystems, as a CO_2 sink is growing among photosynthetic organisms (Duarte et al. 2017; Sondak et al. 2017; McCoy et al. 2018). Early investigations into seaweed’s potential for CO_2 mitigation and energy production spurred initiatives such as the proposal by the Tokyo University of Marine Science and Technology. This initiative involves deploying giant nets filled with rapidly growing brown seaweed and seagrass covering an area of 2,012 km^2 off the northeast coast of Japan to capture CO_2. It is estimated that seaweeds along Japan’s

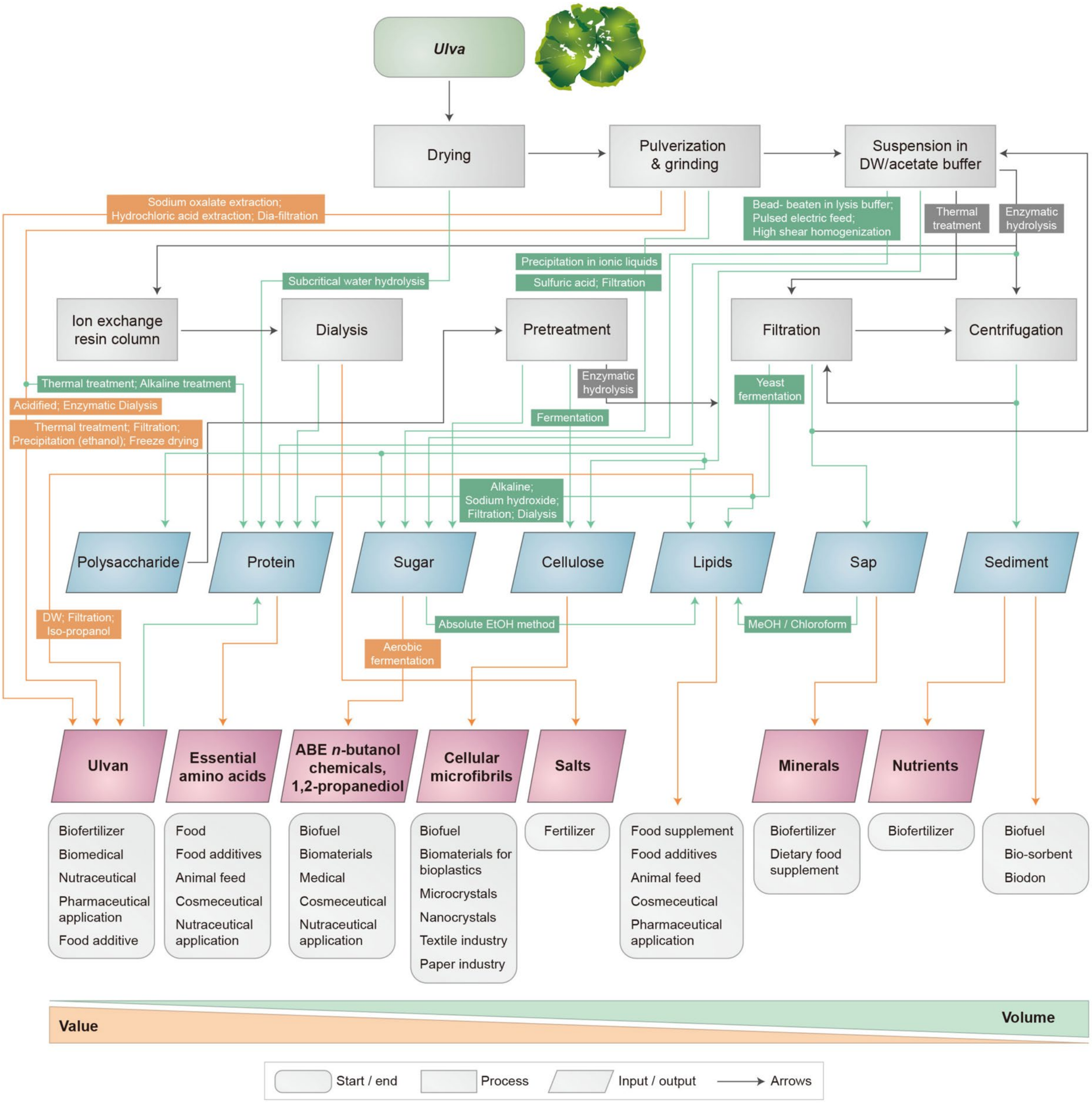

Fig. 3 Integrated biorefinery approach using *Ulva* for the production of valuable chemicals. Start/End (Brown Boxes): Indicate the beginning and end points of the process. Process (Green Boxes): Represent the various processing steps *Ulva* undergoes, including drying, extraction methods like sodium oxalate and hydrochloric acid extraction, diafiltration, and fermentation processes. Input/Output (Yellow Arrows): Show the flow of materials into and out of each process. Components (Orange Arrows): Extracted substances from *Ulva*, such as polysaccharides, proteins, sugars, cellulose, lipids, sap, and sediment. Final Products (Pink Boxes): Resultant materials ready for application, including ulvans, essential amino acids, ABE n-butanol chemicals, cellular microfibrils, salts, minerals, and nutrients. Application Areas (Gradient Boxes): Potential uses for each product are categorised by their economic value and volume, ranging from biofertilisers and biofuel to food additives and biomedical applications. Value and Volume (Gradient Scale): The gradient scale at the bottom indicates the relative economic value and production volume for each product

coast could absorb 2,700,000 tons of carbon annually. Therefore, the harvested material annually represents a substantial biomass energy source, roughly equivalent to 5.3 billion gallons of bioethanol or 16 billion gallons of gasoline.

In 2005, the Incheon National University and the Korean Phycological Society explored the use of seaweeds for CO_2 removal based on initial measurements of photosynthetic activity in the red seaweed *Pachymeniopsis* sp. and green seaweed *U. pertusa* collected from wild stocks. They found that the red and green seaweeds assimilate 0.20 and 9.49 kg CO_2 per ton of fresh weight per hour, respectively. Subsequently, the Korean Ministry of Oceans and Fisheries included CO_2 absorption by seaweed in its Technology Roadmap for 2005–2010 and funded projects to use seaweed as a CO_2 sink. However, scientific consensus on whether seaweed qualifies as a BC source remains unsettled (Fujita et al. 2023).

The higher photosynthetic rates observed in the green tide species *Ulva prolifera* may be attributed to its predominant use of the more efficient C4 photosynthetic pathway for carbon fixation, compared to the more common but less efficient C3 pathway.

This species primarily assimilates CO_2 through the C3 pathway using HCO_3^- via the carbonic anhydrase mechanism under low CO_2 levels. However, it switches to the more efficient C4 pathway under high irradiation levels. This dual carbon uptake strategy enables the formation of extensive blooms, with dense floating mats exposed to intense surface irradiation and CO_2 limitation (Liu et al. 2020).

From 1992 to 2022, global *Ulva* blooms accumulated a total dry-weight biomass of 3,757,962 tons (Fig. 1). Considering the average carbon content of *Ulva* species (29.5%), these blooms sequestered an estimated 1,108,602 tons of carbon over that period, equivalent to 4,068,573 tons of CO_2e. CO_2e is a standardised unit for comparing the global warming potential of different greenhouse gases, calculated by multiplying carbon stocks by 3.67, the molecular weight ratio of CO_2 to C.

To estimate the carbon sequestration and economic impact of *Ulva* blooms at these sites, we aggregated the dry weight biomass of *Ulva* blooms and the corresponding area of occurrence for each country (data lacking biomass or area information were excluded). Our calculations show that *Ulva* blooms sequestered 3,843,270 tCO_2e across 46,437 km^2 in China and 7101 tCO_2e across 19 km^2 in South Korea, respectively (Table S1). Unlike BC ecosystems such as mangroves, tidal and salt marshes, and seagrasses, which can store two to four times more carbon than terrestrial forests and are thus considered crucial components of nature-based solutions to climate change (IOC UNESCO 2023). Seaweeds are rarely categorised as BC sinks because the carbon they assimilate is quickly respired and released back into the atmosphere (Krause-Jensen and Duarte 2016). For seaweeds to significantly contribute to global carbon sequestration, several conditions must be met: the carbon they capture must be stored long-term within their habitats, they must be transported and buried where they are not subject to subsequent microbial breakdown (Hill et al. 2015; Krause-Jensen and Duarte 2016), or they must be utilised to replace fossil fuels (Kraan 2013). *Ulva* species are short-lived, which limits their potential in long-term greenhouse gas reduction and climate change mitigation programs. However, green tide *Ulva* stands apart from other natural and cultivated seaweeds by efficiently binding CO_2 and forming large floating biomasses carried by currents and concentrated along shorelines, where it can be harvested relatively easily. Therefore, collecting intact *Ulva* biomass from shorelines before it decomposes and releases carbon into the atmosphere, followed by its conversion into stable forms such as biochar, presents a promising approach for carbon sequestration, storage, and sustainable energy production. Importantly, the yield of biochar production depends significantly on the characteristics of the feedstock material and specific pyrolysis conditions, such as temperature, heating rate, and residence time (Fig. 4).

3.2 *Ulva* biochar can close the loop of carbon absorbed during photosynthesis

Biochar is a solid black carbonaceous material produced via pyrolysis, the thermal decomposition of organic components in dry biomass by heating in the absence of oxygen (McKendry 2002; Saidur et al. 2011). Pyrolysis produces a solid (biochar), a liquid (bio-oil), and a gas phase, of which the former (biochar) is resistant to microbial and chemical decomposition. The carbon atoms in biochar are strongly bonded to each other in large aliphatic and aromatic molecular structures, giving rise to highly stable char,

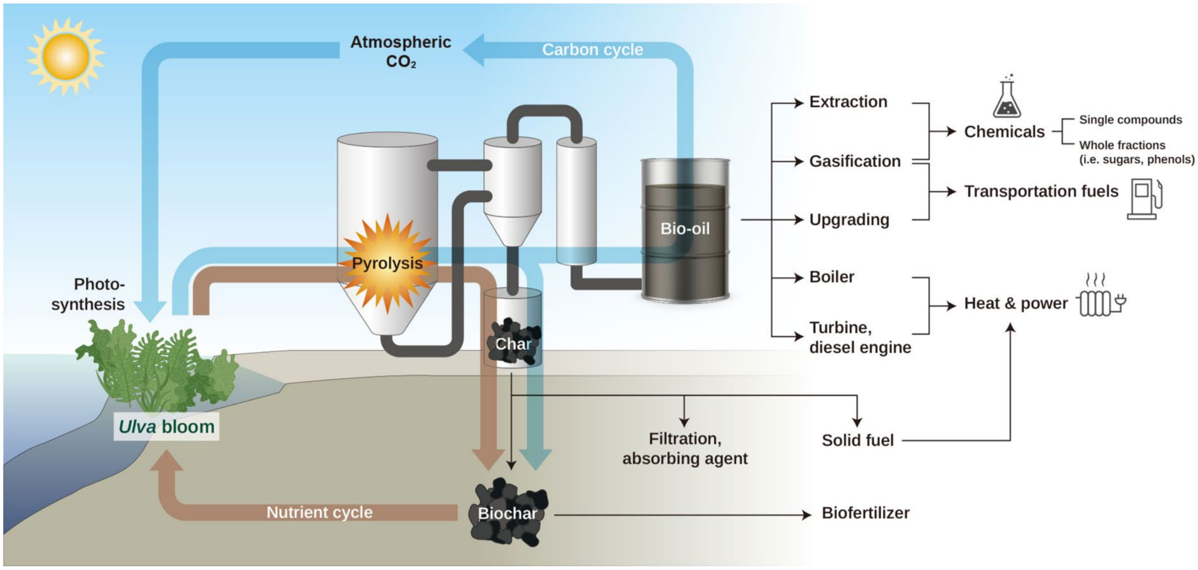

Fig. 4 The potential role of the pyrolysis process in valorising *Ulva* biomass. Pyrolysis yields various product fractions, including char and condensable gases (bio-oil). Roughly half of the feedstock C ends up in the char, which can subsequently be used in soil amendments, thereby sequestering C in soil. The remaining half of the feedstock C is converted into pyrolysis gas and bio-oil. The bio-oil can be used for heat and power generation, as well as for the production of fuels and chemicals

resulting in the sequestration and mitigation of CO_2 emissions (Yu et al. 2018).

In contrast, the carbon in most organic matter is quickly returned to the atmosphere as CO_2 through respiration, whereas the carbon in biochar is much more resistant to decomposition and remains sequestered for a longer period. Therefore, biomass conversion to biochar is a potentially valuable method for stabilising and storing carbon in soils for prolonged periods, making it a viable strategy for removing CO_2 from the atmosphere (Mulabagal et al. 2017). Hence, adding biochar to soil creates a stable carbon pool with an estimated residence time of hundreds to thousands of years (Marzeddu et al. 2021). The stability of biochar is supported by the discovery of dark Amazonian soils. These fertile soils, rich in charcoal organic carbon, are thought to have been intentionally introduced by pre-Columbian farmers 800–5000 years ago (Ronsse et al. 2015). The amount of carbon the soil can maintain is staggering: 1 ha of soil can store as much as 250 tons of carbon. Therefore, the potential impact of soil-based carbon sequestration on climate change mitigation cannot be overestimated. By the end of this century, soil-based sequestration combined with biofuel production could store up to an estimated 2.6 Gt CO_2e year^{-1} (i.e. 2.6 Gt or 2.6 Pg of carbon a year), more than what has been emitted by all fossil fuels to date (Keerthanan et al. 2023).

Biochar's porous nature contributes to its capacity to retain water and nutrients, thus serving as an efficient soil amendment that can reduce reliance on traditional fertilisers. Most feedstock's inorganic components, including P and K, remain in biochar after pyrolysis. Depending on the concentrations of these nutrients, biochar can at least partially replace artificial fertilisers. Numerous studies have assessed the effects of biochar application on soil productivity. A meta-analysis by Jeffery et al. (2011) found an average crop yield benefit ranging from 28 to 39%, with a mean of 10%. This study used biochar as a soil enhancer in agricultural systems to close nutrient loops.

In recent years, the potential of algae-derived biochar as a means to sequester atmospheric carbon has gained considerable attention in both academic and industrial spheres (Ji et al. 2021). This interest is mainly attributable to algae's comparative advantages that algae possess over traditional terrestrial biomass sources. Notably, algae cultivation demands significantly less land area and is characterised by a higher growth rate, ranging from 10 to 27 g per square metre per day (Bach and Chen 2017; Lee et al. 2020; Sekar et al. 2021). This results in higher biomass that can produce substantial biochar yields of 36 to 68 percent through pyrolysis. Additionally, algae are composed of high mineral content and devoid of lignin, an attribute that simplifies the pyrolysis process.

The conversion of *Ulva* into biochar requires substantial thermal energy, which can be self-supplied by combusting the syngas and bio-oil generated during the seaweed's pyrolysis (Zollmann et al. 2019). However, the efficacy of this process is contingent upon the dryness of the feedstock, as *Ulva* naturally has a high moisture content, which diminishes its inherent energy yield and renders it insufficient for self-sustained drying at an industrial scale. To overcome this hurdle, solar drying emerges as a viable solution capable of ensuring a net positive energy balance by harnessing solar energy to reduce the moisture content of *Ulva* prior to pyrolysis.

Alternative to traditional pyrolysis, hydrothermal carbonisation (HTC) presents an innovative approach for biochar production, utilising wet biomass under high pressure and temperature to yield 'hydrochar' (Fig. 5). This method is particularly advantageous for processing biomass with high moisture content, as it circumvents the need for preliminary drying. Unlike the solid state of conventional biochar, hydrochar is typically obtained as a slurry, comprising both solid and liquid phases.

The application of hydrochar for carbon sequestration is an emerging area of research (Galluci 2021; Masoumi et al. 2021). A notable study by Soroush et al. (2023) reported a yield of 44.0 ± 0.5% solid hydrochar from *Ulva pertusa*, utilising optimal HTC conditions including a temperature of 210 °C, a residence time of 4 h, and a water-to-biomass ratio of 5:1. This process resulted in a hydrochar with a specific surface area of 44.5 ± 0.3 m^2 g^{-1} and a maximum carbon content of 50.9 ± 0.5%. However, the stability of hydrochar in soil is comparatively lower than that of

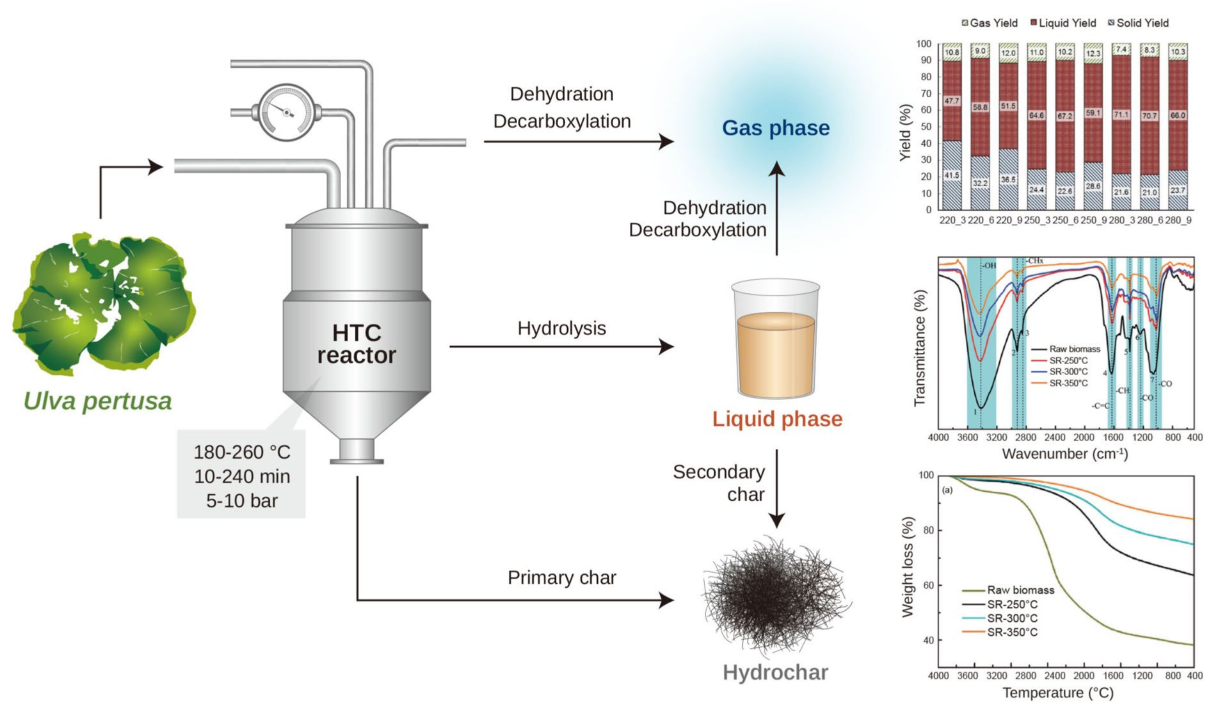

Fig. 5 Production of hydrochar from *Ulva pertusa*. Wet feedstocks, like *Ulva pertusa*, can be processed through hydrothermal carbonisation, which uses hot compressed water to convert the feedstock to three product fractions: non-condensable gases, a liquid phase and a carbonaceous solid residue known as hydrochar. The inserts (from top to bottom) demonstrate (i) the typical product distributions obtained in HTC of *Ulva pertusa* as a function of process conditions, (ii) identification of surface functional groups in *Ulva* hydrochar through FTIR and (iii) analysis of thermal stability of *Ulva* hydrochar using thermogravimetric analysis

traditional biochar, posing a challenge for long-term carbon sequestration.

Moreover, phytotoxic organic compounds and heavy metals within hydrochar raise concerns regarding soil health and productivity, potentially negating the benefits of HTC over slow pyrolysis. Given these factors, there is a critical need for comprehensive studies to assess and refine the carbon sequestration capacity of hydrochars. Such research should aim to optimise their use in soil systems, enhance stability, minimise the emission of greenhouse gases, and improve agricultural productivity (Kambo and Dutta 2015).

Ulva typically has a high mineral content, resulting in biochar with high mineral content. These minerals can benefit applications such as soil amendment or catalysts, catalyst supports, and electrodes for electrochemical applications (Sun et al. 2022). The high mineral content also gives biochar a high pH (typically pH ~ 10), which must be considered when deciding on suitable applications, such as treating acidic soils. Despite these desirable effects, certain inorganic compounds in biochar may serve as sources of contamination (such as heavy metals) or cause negative reactions in plants (e.g. high sodium content). Therefore, appropriate pretreatment steps, such as washing to remove salts or extraction of metals, may be required depending on the source of *Ulva* biomass. Such contamination issues are less likely to occur with *Ulva* residues already extracted and processed in biorefineries. Nevertheless, these steps would add to the cost of the process.

Ulva harvested from green tides will likely be contaminated with plastics and microplastics, making it unsuitable for many applications without further treatment. However, in most cases, this type of contamination does not pose a problem in biochar production. Biomass contamination with various plastics has no adverse effects on biochar quality, as plastic contaminants completely decompose during the pyrolysis step (Rathnayake et al. 2021). Halogenated plastics are an exception, as they tend to form various impurities during pyrolysis and must be handled carefully.

3.3 *Ulva* biochar may offer a good opportunity to draw down CO_2 from the atmosphere

The flux of carbon through green tide *Ulva* during the 2008–2022 blooms in China and South Korea was 1,049,147 tons. Considering that 50% of the carbon captured by photosynthesis is stabilised against short-term release back into the atmosphere (by burning syngas or bio-oil) after conversion of biomass to biochar (Lehmann et al. 2006), the hypothetical carbon stabilisation potential after conversion of *Ulva* biomass to biochar is estimated to be 524,580 tonnes of carbon (1,925,208 tCO_2e). The BC value of *Ulva* biochar is estimated to be US$38.72 million. The green tide phenomenon would thus generate US$116.15 million worth of BC from a 46,456 km^2 area in China and South Korea.

The pyrolysis of *Ulva* biomass also helps in reducing avoidable emissions (CO_2 sources). For example, the energy generated during pyrolysis replaces the energy that might otherwise be generated using fossil fuels. Carbon stabilised by biochar would otherwise be released as CO_2 or methane (an even more potent greenhouse gas) via combustion or decomposition. The application of biochar to agricultural soils can reduce the need for fertilisers and the corresponding emissions of nitrous oxide and methane. Processing 2 tons of dry matter from green waste, cattle manure, and wheat straw into biochar per hour, a single small-scale plant would store approximately 14,000–58,000 tCO_2e annually. Applying this biochar to agricultural land would further reduce avoidable emissions by 700–1700 tCO_2e (Sohi et al. 2009). If the same conversion ratio (34–50%) of avoidable emissions were applied to *Ulva* biochar from 3.56 million tons of green tide biomass in China and Korea, its application to agricultural land would result in a further reduction of 654,583–962,629 tCO_2e (Table S1). The additional economic value of BC from the *Ulva* biochar used in agriculture is estimated at US$13.16–19.36 million.

4 Land-based cultivation of *Ulva*

Drawbacks of the direct use of drifted and washed-ashore *Ulva* for CO_2 sequestration and valorisation result from contamination, decomposition, and, above all, from a variable and uncertain supply of biomass, which could severely hamper the long-term sustainability of a low-carbon bioeconomy based on *Ulva* biomass. Production in marine systems varies seasonally and annually according to environmental factors such as temperature, salinity, and nutrient availability. In temperate regions, ocean-based cultivation only occurs during cool winters and springs (Ohno 1993). Under warm conditions (> 20 °C), the reproductive maturity (sporulation) of *Ulva* usually leads to spore dispersal and a decrease in thallus biomass (Hiraoka et al. 1999). Furthermore, the fate of carbon in particulate and dissolved matter from farmed seaweed is not fully understood, particularly concerning the pathways and timescales relevant to carbon storage. Most of the carbon sequestered by seaweeds is stored as biomass for only a short period because seaweeds are subject to disturbances that can result in the immediate loss of biomass, leading to large landings of particulate and dissolved organic particles (Paine et al. 2021). Strong storm-induced water movement and pest infestation can also lead to large biomass loss (Pizarro and Santelices 1993). Most of the carbon in seaweed enters the fast carbon cycle and is not stored for the long term, unlike that in terrestrial plants, which is essential for mitigating global warming (Klinger 2021). Therefore, traditional net cultivation in the sea is not a suitable option for the mass production of *Ulva* as feedstock for biorefineries and carbon sequestration.

Cultivating *Ulva* under more controlled conditions may enable successful biorefining and valorisation of *Ulva* products for industrial applications and a blue bioeconomy. *Ulva* biomass can be produced in large onshore facilities (Bolton et al. 2009) or via tank or pond cultivation on land (Tsubaki et al. 2017), which offers many advantages for producing raw materials for functional products (Friedlander 2008). Land-based cultivation allows for improved seaweed management, efficient control of nutrient inputs and biotic factors, efficient use of available land, wastewater treatment, and maintenance of continuous or semi-continuous production (Sánchez-Barredo et al. 2020; Revilla-Lovano et al. 2021). The mass cultivation of *Ulva* from the spore to the adult stage is shown in Fig. 6.

A recent study demonstrated bimodal production of 3 kg m^{-2} *Ulva* in 100 m^3 ponds, with a strong peak in spring (258–290 g m^{-2} d^{-1}) and a smaller peak in autumn, alongside lower production in summer and much lower production in winter (40–85 g m^{-2} d^{-1}) (Zertuche-González et al. 2021). A similar study in Mexico grew *U. ohnoi* in a pond system, which produced about 178–214 g m^{-2} d^{-1} during the summer season. Bioreactor and tank systems have also been developed for *Ulva* cultivation. A recent design features a ring-shaped cultivation system, where *Ulva* moves in a circular pattern, simulating the movement pattern in a standard tank cultivation vessel. In this system, *U. lactuca* had a mean growth rate of 4.3% $day^{-1} \pm 0.83\%$ day^{-1} at ambient CO_2 concentrations (Sebök et al. 2019). Another approach utilised a bioreactor with a submersible LED light source for on-land cultivation. This system was operated away from seawater source to avoid competition with other activities such as recreation and fishing, to grow *U. intestinalis*. This system recorded growth rates of $7.72 \pm 0.04\%$ day^{-1} were recorded, with an estimated of 1.1 kg m^{-2} of biomass generation per year. However, this system was energy-intensive and significant design modifications are necessary make it sustainable (Schmitz and Kraft et al. 2022).

Land-based macroalgal cultivation systems face challenges because of the extensive use of seawater and high capital and operating costs (Milledge and Harvey 2016). Maintaining a constant water temperature to sustain optimal growth and inhibit spore formation requires high energy inputs for cooling in summer and heating in winter. To reduce costs, deep-sea water pumped from a depth of > 300 m is used in a land-based culture system that produces 3 tons of dried *Ulva* annually in Kochi, Japan (Tsubaki et al. 2017). The continuous supply of deep-sea water ensures a constant temperature throughout the year (Hiraoka and Oka 2008). Similarly, a continuous supply of saline groundwater pumped from the bottom of a nearby sea can ensure stable and effective *Ulva* production throughout the seasons. An important consideration is the land use changes when cultivating algae on land. If arable land is used, there is direct competition with food production, and changes in greenhouse gas emissions also need to be considered. Similarly, when other types of land are used, such as grassland or forested areas, the impact on the local ecology and greenhouse gas emissions should be considered (Handler et al. 2017).

Integrated multi-trophic aquaculture (IMTA) practices may be useful for cultivating seaweeds and reducing costs. IMTA involves the co-cultivation of foraged species (such as finfish or shrimp) with

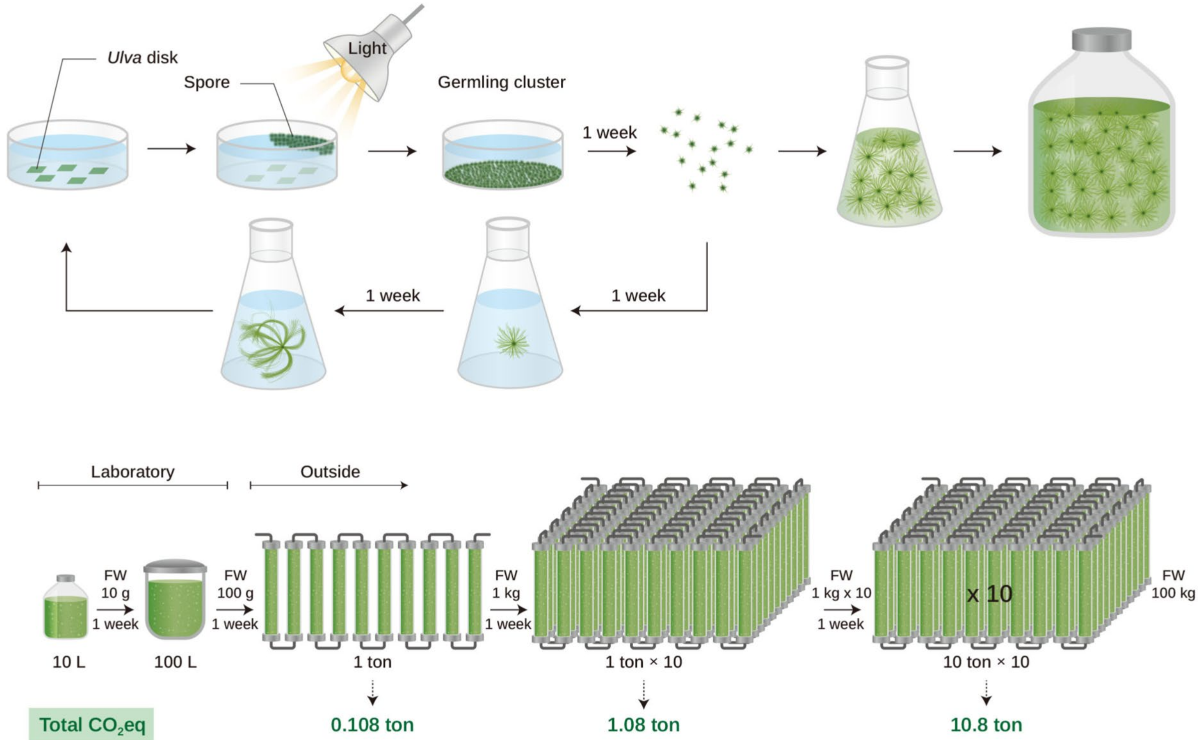

Fig. 6 Mass cultivation of *Ulva* from spore to the adult stage. The schematic illustrates *Ulva*'s cultivation, scaling process, and associated CO_2 sequestration. The process commences in the laboratory, where *Ulva* disks are prepared, and spores are induced and released. Subsequently, the spores undergo germination under light, forming clusters over the course of approximately one week. Next, the germling clusters are transferred to a flask and allowed to grow for a further week. The successive one-week growth periods in increasingly larger flasks facilitate the scale-up of *Ulva* cultivation. The diagram then proceeds to a large-scale outdoor cultivation process. Initially, cultivation in a 10-L container yields 10 g of fresh weight (FW) *Ulva* in one week. This is then scaled to a 100-L container, yielding 100 g of FW *Ulva* in another week. The process continues in outdoor photobioreactors, where one ton of *Ulva* sequesters 0.108 tons of CO_2e in one week. This can be scaled up further to 10 tons, sequestering 1.08 tons of CO_2e, and finally to 100 tons, sequestering 10.8 tons of CO_2e in one week. The figure illustrates the cumulative CO_2 sequestration achieved at each stage of the *Ulva* cultivation process, thereby emphasising the process's scalability and environmental benefits

extractive species, such as suspension feeders (e.g. mussels and oysters), deposit feeders (e.g. sea cucumbers and sea urchins), invertebrates, and macroalgae, which feed on the organic and inorganic effluents of foraged species (Buck et al. 2018). IMTA can reduce ecological impacts near aquaculture farms, improve social perceptions of aquaculture, and provide financial benefits to aquaculture producers through product diversification, faster production cycles, and price premiums for IMTA products (Knowler et al. 2020). An IMTA pilot system using *Ulva* has been successfully implemented (Ben-Ari et al. 2014; Shpigel et al. 2017). Such a system has also been used to remove excess nutrients from N- and P-rich wastewater in land-based aquaculture (Lawton et al. 2013). A recent study on an IMTA system using *U. rigida* found visible improvements in the beneficial prokaryotic community, which positively impacted *Ulva* development and could thus be important for improving biomass yields (Califano et al. 2020).

Ulva strain selection is essential for the success or failure of production systems. Natural populations of *U. prolifera* normally disappear in summer (Hiraoka and Higa 2016) as they sporulate and shed their reproductive cells at temperatures > 20 °C (Hiraoka et al. 1999). However, floating *Ulva* spp. that causes green tides have little or almost no sporulation activity (Hiraoka et al. 2004a, b). For example, representative green tide species, such as *U. prolifera* subsp. *qingdaoensis*, grow well vegetatively, even at high temperatures, and form large blooms in summer (Hiraoka et al. 2004a, b; Cui et al. 2018). Using green tidal species or strains for cultivation eliminates the risk of sudden decay due to sporulation and makes biomass production more stable. Selection of fast-growing strains may also be necessary for successful production. For example, a strain of *U. meridionalis* has a daily growth rate that is elevated more than two-fold under temperatures > 25 °C (Tsubaki et al. 2017). Thus, cultivating fast-growing species could be an effective option for CO_2 fixation and biomass production for biorefineries.

Other characteristics of *Ulva* species that are important for their cultivation are the amount and stability of the target biomolecules produced. Biomolecule quality and quantity differ between *Ulva* specimens found in the wild (Filote et al. 2021) and those grown under optimal light, nutrients, water depth, turbidity, and temperature cultivation conditions (Aravind et al. 2020). A biorefinery concept based on *Ulva* biomass collected from shorelines was recently tested in Europe as part of EU projects to produce an alternative feed additive for farmed fish feedstocks. Extensive research is required to assess this system's economic and environmental viability, whose revenues are closely related to the end product's operational costs, yields, and market values (Bastiaens and Postnikov 2017). In sustainable biorefineries, maximising biomass conversion and reducing residual waste is important for sustainable economic development and market growth.

5 Feasibility of *Ulva* cultivation

To expand the cultivation of *Ulva* on land for carbon sequestration and thus contribute to climate change mitigation, the economic feasibility of carbon dioxide reduction through *Ulva* aquaculture systems needs to be assessed (DeAngelo et al. 2023; Hurd et al. 2022; Troell et al. 2023). While some publications underestimate the costs of seaweed production, uncertainty regarding the exact production costs and potential revenues exists, particularly in land-based seaweed farming systems (van den Burg et al. 2016; Greene et al. 2020; Nazemi et al. 2021; Sultana et al. 2023).

Techno-economic models can be used to estimate the costs of *Ulva* production and the associated climate benefits and test the relative importance of model parameters systematically. Techno-economic assessment (TEA) is a sophisticated tool for evaluating the technical and economic viability of a process/system used for the strategic planning and management of research and development to achieve economically feasible and sustainable results (Borowitzka and Moheimani 2013). TEA can be used to evaluate the economic viability of the entire process pipeline, including cultivation, harvesting, biomass dewatering, drying, and biomass conversion into the desired products and product purification (Bhatt et al. 2022). TEA can also help define the scope of a macroalgal project/process and quantify the associated financial and technical risks (Bhatt et al. 2022). The built-in sensitivity analysis tool can help determine the effect of changes in the input variables (process or environmental conditions) on the outcome. The results of TEA can inform an appropriate strategy for meaningful decision-making, future research and development, and improving the economic viability of each macroalgae process.

Figure 7 shows the application of the proposed TEA framework for evaluating the economic feasibility of *Ulva* cultivation systems for CO_2 sequestration. TEA studies on microalgae and kelp cultivation have identified gaps that can be exploited to improve *Ulva* cultivation and biochar production for CO_2 sequestration. Recommendations include simplifying and optimising cultivation systems, automating processes, selecting sustainable materials, developing low-cost feedstock substitutes, improving flue gases and effluents/wastewater, and carefully selecting TEA parameters. Implementing these recommendations will improve the sustainability and economics of *Ulva* cultivation and biochar production for carbon sequestration.

Figure S1 shows an example of a hypothetical TEA for *Ulva* biomass and biochar production with the addition of carbon trading revenues using a land-based aquaculture system based on values from the literature (Nikolaisen et al. 2011; Korzen et al. 2015; van den Burg 2016; Soleymani and Rosentrater 2017; Greene et al. 2020; Prabhu et al. 2020a, b). The TEA results for combined biomass and biochar production suggest that this project has the potential to be financially feasible and profitable.

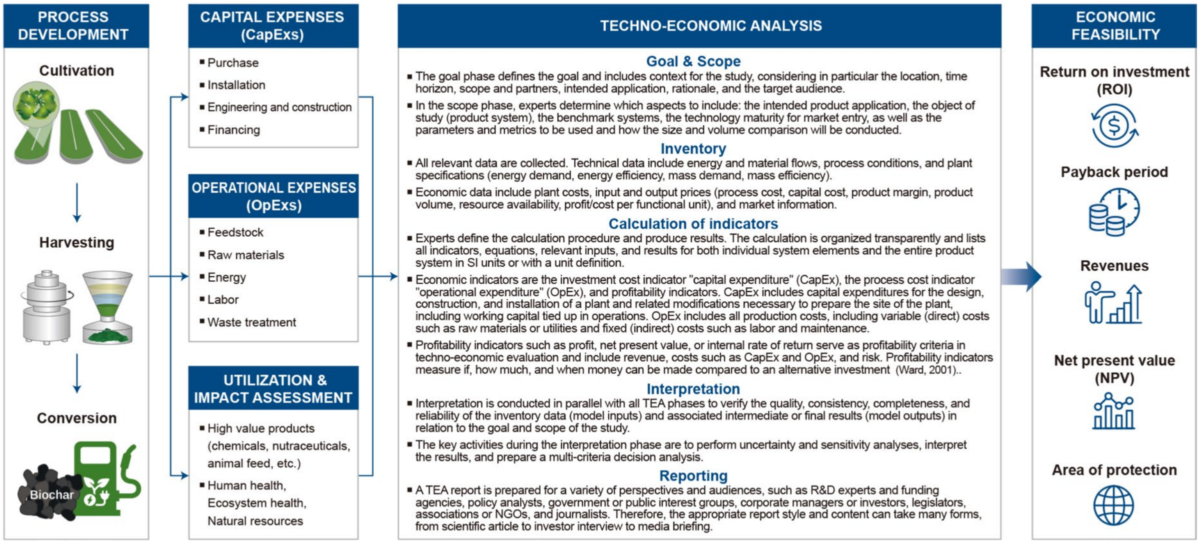

Fig. 7 Techno-economic analysis of the closed-loop system for *Ulva* cultivation and biochar production

6 Summary and future perspectives

Ulva spp. plays a crucial role in marine food chains and can contribute to the sequestration of atmospheric CO_2 through biological pumping. Additionally, they serve as carbon donors by providing organic carbon to BC ecosystems, thereby enabling effective carbon sequestration.

However, several significant challenges must be addressed to incorporate *Ulva* into the BC paradigm. These challenges include accurately quantifying organic matter inputs, identifying allochthonous (external) and autochthonous (internal) sources of organic carbon, and determining the specific contributions of *Ulva* to carbon storage and export. To address these obstacles, experts have proposed the forensic carbon accounting (FAC) approach (Hurd et al. 2022). This approach encompasses a wide range of physical, biogeochemical, biological, ecological, and mathematical techniques applied at both the local and global scales to forecast the fate and function of *Ulva*. A comprehensive understanding of the challenges and opportunities associated with integrating *Ulva* into the BC system is crucial for developing effective management strategies for carbon sequestration and greenhouse gas mitigation. The FAC approach enables the assessment of the extent of CO_2 removal and the distribution of carbon sequestered by *Ulva*. This knowledge will lead to developing efficient and sustainable approaches for addressing the pressing issues of carbon sequestration and greenhouse gas reduction.

The Kyoto Protocol, part of the United Nations Framework Convention on Climate Change, allows carbon sequestration exclusively through afforestation and reforestation in the trading programme established under the Clean Development Mechanism, excluding seaweed. However, macroalgal biomass is a promising feedstock for biochar production. Further work is needed to address challenges such as cost efficiency, productivity optimisation, and supply continuity (Yu et al. 2017). If biochar is a viable carbon offset option, feedstock and pyrolysis processes must be configured to achieve significant and scalable offset potentials quickly and effectively. This unique challenge presents opportunities for interdisciplinary research. Additionally, if carbon credits could be sold on carbon exchange, farmers applying *Ulva* biochar to their land could earn additional income, incentivising the large-scale adoption of this system.

In conclusion, we propose that *Ulva* waste can be sustainably repurposed to promote the circular economy. By harnessing the biomass from green tides and cultivating *Ulva* as feedstock for biochar production, we can shift our perception of *Ulva* blooms from harmful weeds to valuable crops, transforming our outlook on green tides.

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Author's contribution JP and HL contributed equally to the study design, literature search, graph and table design, data analysis, TEA calculations, and drafting of the initial manuscript. HL secured funding for the project. JD, SD, JA, CJ, MH, and LKP collectively enriched the content related to land-based cultivation systems; PMH, FR, and OM enriched the section on carbon sequestration and biochar, with a particular contribution to Fig. 5 by PMH, DW, and FMGT played an important role by providing critical revisions to improve the overall quality of the manuscript. YH contributed to the calculations of the TEA analysis. TH designed the study, supervised the entire project, and made an invaluable contribution to the revision of the manuscript. All authors participated in the discussion of the results and contributed to the final version of the manuscript. Their dedication and expertise were essential to the completion of this review.

Declarations

Conflict of interest The authors declare no competing interests.

Consent for publication All authors gave informed consent to this publication and its content.

References

Abergel C, Legendre M, Claverie J-M (2015) The rapidly expanding universe of giant viruses: mimivirus, pandoravirus, pithovirus and mollivirus. FEMS Microbiol Rev 39:779–796. https://doi.org/10.1093/femsre/fuv037

Aravind S, Kumar PS, Kumar NS, Siddarth N (2020) Conversion of green algal biomass into bioenergy by pyrolysis. A review. Environ Chem Lett 18:829–849. https://doi.org/10.1007/s10311-020-00990-2

Bach Q-V, Chen W-H (2017) A comprehensive study on pyrolysis kinetics of microalgal biomass. Energy Convers Manag 131:109–116. https://doi.org/10.1016/j.enconman.2016.10.077

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

Barakat KM, El-Sayed HS, Khairy HM, El-Sheikh MA, Al-Rashed SA, Arif IA, Elshobary ME (2021) Effects of ocean acidification on the growth and biochemical composition of a green alga (*Ulva fasciata*) and its associated microbiota. Saudi J Biol Sci 28:5106–5114. https://doi.org/10.1016/j.sjbs.2021.05.029

Bastiaens I, Postnikov E (2017) Greening up: the effects of environmental standards in EU and US trade agreements. Environ Polit 26:847–869. https://doi.org/10.1080/09644016.2017.1338213

Bastiaens L, Van Roy S, Thomassen G, Elst K (2017) Biorefinery of algae: technical and economic considerations. In: Gonzalez-Fernandez C, Muñoz R (eds) Microalgae-Based Biofuels and Bioproducts, 1st edn. Woodhead Publishing, Cambridge, pp 27–345

Beach KS, Smith CM, Michael T, Shin HW (1995) Photosynthesis in reproductive unicells of *Ulva fasciata* and *Enteromorpha flexuosa*: implications for ecological success. Mar Ecol Prog Ser 125:229–237

Ben-Ari T, Neori A, Ben-Ezra D, Shauli L, Odintsov V, Shpigel M (2014) Management of *Ulva lactuca* as a biofilter of mariculture effluents in IMTA system. Aquaculture 434:493–498. https://doi.org/10.1016/j.aquaculture.2014.08.034

Bhatt A, Khanchandani M, Rana MS, Prajapati SK (2022) Techno-economic analysis of microalgae cultivation for commercial sustainability: a state-of-the-art review. J Clean Prod 370:133456. https://doi.org/10.1016/j.jclepro.2022.133456

Bikker P, van Krimpen MM, van Wikselaar P, Houweling-Tan B, Scaccia N, van Hal JW, Huijgen WJJ, Cone JW, López-Contreras AM (2016) Biorefinery of the green seaweed *Ulva lactuca* to produce animal feed, chemicals and biofuels. J Appl Phycol 28:3511–3525. https://doi.org/10.1007/s10811-016-0842-3

Bolton JJ, Robertson-Andersson DV, Shuuluka D, Kandjengo L (2009) Growing *Ulva* (Chlorophyta) in integrated systems as a commercial crop for abalone feed in South Africa: a SWOT analysis. J Appl Phycol 21:575–583. https://doi.org/10.1007/s10811-008-9385-6

Borowitzka MA, Moheimani NR (2013) Algae for Biofuels and Energy. Springer, Netherlands, Dordrecht

Bruton T, Lyons H, Lerat Y, Stanley M, Rasmussen M (2009) A review of the potential of marine algae as a source of biofuel in Ireland, Report prepared for Sustainable Energy Ireland. Sustainable Energy Ireland – SEI, Dublin

Buck BH, Troell MF, Krause G, Angel DL, Grote B, Chopin T (2018) State of the art and challenges for offshore integrated multi-trophic aquaculture (IMTA). Front Mar Sci 5:165. https://doi.org/10.3389/fmars.2018.00165

Califano G, Kwantes M, Abreu MH, Costa R, Wichard T (2020) Cultivating the macroalgal holobiont: effects of

integrated multi-trophic aquaculture on the microbiome of *Ulva rigida* (Chlorophyta). Front Mar Sci 7:52. https://doi.org/10.3389/fmars.2020.00052
Cappello V, Marchetti L, Parlanti P, Landi S, Tonazzini I, Cecchini M, Piazza V, Gemmi M (2016) Ultrastructural characterization of the lower motor system in a mouse model of Krabbe disease. Sci Rep 6:1. https://doi.org/10.1038/s41598-016-0001-8
Cardoso C, Martinho JP, Lopes PA, Martins S, Correia J, Afonso C, Alarcón FJ, González-Fernández MJ, Pinto RM, Prates JA, Bandarra NM, Guil-Guerrero JL (2018) Stearidonic acid combined with alpha-linolenic acid improves lipemic and neurological markers in a rat model subject to a hypercaloric diet. Prostaglandins Leukot Essent Fatty Acids 135:137–146. https://doi.org/10.1016/j.plefa.2018.07.010
Cardoso SM, Carvalho LG, Silva PJ, Rodrigues MS, Pereira OR, Pereira L (2014) Bioproducts from seaweeds: a review with special focus on the Iberian Peninsula. Curr Org Chem 18:896–917. https://doi.org/10.2174/138527281807140515154116
Chen Z, Liu M, Yang Y, Bi M, Li M, Liu W (2022) Environmental and economic impacts of different disposal options for *Ulva prolifera* green tide in the yellow Sea, China. ACS Sustain Chem Eng 10:11483–11492. https://doi.org/10.1021/acssuschemeng.2c02638
Cui J, Monotilla AP, Zhu W, Takano Y, Shimada S, Ichihara K, Matsui T, He P, Hiraoka M (2018) Taxonomic reassessment of *Ulva prolifera* (Ulvophyceae, Chlorophyta) based on specimens from the type locality and Yellow Sea green tides. Phycologia 57:692–704. https://doi.org/10.2216/17-139.1
DeAngelo J, Saenz BT, Arzeno-Soltero IB, Frieder CA, Long MC, Hamman J, Davis KA, Davis SJ (2023) Economic and biophysical limits to seaweed farming for climate change mitigation. Nat Plants 9:45–57. https://doi.org/10.1038/s41477-022-01305-9
Dominguez H, Loret EP (2019) *Ulva lactuca*, a source of troubles and potential riches. Mar Drugs 17:357. https://doi.org/10.3390/md17060357
Doney SC, Busch DS, Cooley SR, Kroeker KJ (2020) The impacts of ocean acidification on marine ecosystems and reliant human communities. Annu Rev Environ Resour 45:83–112. https://doi.org/10.1146/annurev-environ-012320-083019
Duarte CM, Wu J, Xiao X, Bruhn A, Krause-Jensen D (2017) Can seaweed farming play a role in climate change mitigation and adaptation? Front Mar Sci 4:100. https://doi.org/10.3389/fmars.2017.00100
Filote C, Santos SCR, Popa VI, Botelho CMS, Volf I (2021) Biorefinery of marine macroalgae into high-tech bioproducts: a review. Environ Chem Lett 19:969–1000. https://doi.org/10.1007/s10311-020-01124-4
Food Agriculture Organization of the United Nations (2018) Meeting the sustainable development goals. State World Fish Aquacult. Food and Agriculture Organization of the United Nations, Rome: 227
Friedlander M (2008) Israeli R & D activities in seaweed cultivation. Isr J Plant Sci 56:15–28. https://doi.org/10.1560/IJPS.56.1-2.15
Fujita R, Augyte S, Bender J, Brittingham P, Buschmann AH, Chalfin M, Collins J, Davis KA, Gallagher JB, Gentry R, Gruby RL, Kleisner K, Moritsch M, Price N, Roberson L, Taylor J, Yarish C (2023) Seaweed blue carbon: ready or not? Mar Policy 155:105747. https://doi.org/10.1016/j.marpol.2023.105747
Gajaria TK, Suthar P, Baghel RS, Balar NB, Sharnagat P, Mantri VA, Reddy CRK (2017) Integration of protein extraction with a stream of byproducts from marine macroalgae: a model forms the basis for marine bioeconomy. Bioresour Technol 243:867–873. https://doi.org/10.1016/j.biortech.2017.06.149
Gallucci M (2021) The ammonia solution: ammonia engines and fuel cells in cargo ships could slash their carbon emissions. IEEE Spectr 58:44–50. https://doi.org/10.1109/MSPEC.2021.9370109
Gao G, Clare AS, Rose C, Caldwell GS (2017) Eutrophication and warming-driven green tides (*Ulva rigida*) are predicted to increase under future climate change scenarios. Mar Pollut Bull 114:439–447. https://doi.org/10.1016/j.marpolbul.2016.10.003
Gao G, Clare AS, Rose C, Caldwell GS (2018) *Ulva rigida* in the future ocean: potential for carbon capture, bioremediation and biomethane production. GCB Bioenergy 10:39–51. https://doi.org/10.1111/gcbb.12465
Geertz-Hansen O, Sand-Jensen K (1992) Growth rates and photon yield of growth in natural populations of a marine macroalga *Ulva lactuca*. Mar Ecol Prog Ser 81:179–183
Glasson CRK, Sims IM, Carnachan SM, de Nys R, Magnusson M (2017) A cascading biorefinery process targeting sulfated polysaccharides (ulvan) from *Ulva ohnoi*. Algal Res 27:383–391. https://doi.org/10.1016/j.algal.2017.07.001
Green-Gavrielidis LA, MacKechnie F, Thornber CS, Gomez-Chiarri M (2018) Bloom-forming macroalgae (*Ulva* spp.) inhibit the growth of co-occurring macroalgae and decrease eastern oyster larval survival. Mar Ecol Prog Ser 595:27–37. https://doi.org/10.3354/meps12556
Greene JM, Gulden J, Wood G, Huesemann M, Quinn JC (2020) Techno-economic analysis and global warming potential of a novel offshore macroalgae biorefinery. Algal Res 51:102032. https://doi.org/10.1016/j.algal.2020.102032
Guiry M, Guiry G (2013) AlgaeBase. Worldwide Electronic Publication. National University of Ireland, Galway. http://www.algaebase.org
Halib N, Perrone F, Cemazar M, Dapas B, Farra R, Abrami M, Chiarappa G, Forte G, Zanconati F, Pozzato G, Murena L, Fiotti N, Lapasin R, Cansolino L, Grassi G, Grassi M (2017) Potential applications of nanocellulose-containing materials in the biomedical field. Materials (Basel) 10:977. https://doi.org/10.3390/ma10080977
Handler RM, Shi R, Shonnard DR (2017) Land use change implications for large-scale cultivation of algae feedstocks in the United States Gulf Coast. J Clean Prod 153:15–25. https://doi.org/10.1016/j.jclepro.2017.03.149
Harun-Al-Rashid A, Yang C-S (2018) Hourly variation of green tide in the Yellow Sea during summer 2015 and 2016 using Geostationary Ocean Color Imager data. Int J Remote Sens 39:4402–4415. https://doi.org/10.1080/01431161.2018.1457228

Hill R, Bellgrove A, Macreadie PI, Petrou K, Beardall J, Steven A, Ralph PJ (2015) Can macroalgae contribute to blue carbon? An Australian perspective. Limnol Oceanogr 60:1689–1706. https://doi.org/10.1002/lno.10128

Hiraoka M, Dan A, Hagihira M, Ohno M (1999) Growth and maturity of clonal thalli in *Enteromorpha prolifera* under different temperature conditions. Nippon Suisan Gakkaishi 65:302–303. https://doi.org/10.2331/SUISAN.65.302

Hiraoka M, Higa M (2016) Novel distribution pattern between coexisting sexual and obligate asexual variants of the true estuarine macroalga *Ulva prolifera*. Ecol Evol 6:3658–3671. https://doi.org/10.1002/ece3.2149

Hiraoka M, Ohno M, Kawaguchi S, Yoshida G (2004a) Crossing test among floating *Ulva* thalli forming green tide in Japan. Hydrobiologia 512:239–245. https://doi.org/10.1023/B:HYDR.0000020332.12641.a2

Hiraoka M, Oka N (2008) Tank cultivation of *Ulva prolifera* in deep seawater using a new 'germling cluster'. method. J Appl Phycol 20:97–102. https://doi.org/10.1007/s10811-007-9186-3

Hiraoka M, Shimada S, Uenosono M, Masuda M (2004b) A new green-tide-forming alga, *Ulva ohnoi* Hiraoka et Shimada sp. nov. (Ulvales, Ulvophyceae) from Japan. Phycol Res 52:17–29. https://doi.org/10.1111/j.1440-1835.2003.00321.x

Holdt SL, Kraan SJ (2011) Bioactive compounds in seaweed: functional food applications and legislation. J Appl Phycol 23:543–597. https://doi.org/10.1007/s10811-010-9632-5

Huntzinger DN, Michalak AM, Schwalm C, Ciais P, King AW, Fang Y, Schaefer K, Wei Y, Cook RB, Fisher JB, Hayes D, Huang M, Ito A, Jain AK, Lei H, Lu C, Maignan F, Mao J, Parazoo N, Peng S, Poulter B, Ricciuto D, Shi X, Tian H, Wang W, Zeng N, Zhao F (2017) Uncertainty in the response of terrestrial carbon sink to environmental drivers undermines carbon-climate feedback predictions. Sci Rep 7:4765. https://doi.org/10.1038/s41598-017-03818-2

Hurd CL, Law CS, Bach LT, Britton D, Hovenden M, Paine ER, Raven JA, Tamsitt V, Boyd PW (2022) Forensic carbon accounting: assessing the role of seaweeds for carbon sequestration. J Phycol 58:347–363. https://doi.org/10.1111/jpy.13249

IOC, UNESCO (2023) Blue carbon. UNESCO Intergovernmental Oceanographic Commission. https://www.ioc.unesco.org/en/blue-carbon. Accessed 12 Jun 2024

IPCC (2018) Global Warming of 1.5 °C. Intergovernmental Panel on Climate Change, Geneva, Switzerland

Jeffery S, Verheijen FGA, van der Velde M, Bastos AC (2011) A quantitative review of the effects of biochar application to soils on crop productivity using meta-analysis. Agric Ecosyst Environ 144:175–187. https://doi.org/10.1016/j.agee.2011.08.015

Ji R, Wu Y, Bian Y, Song Y, Sun Q, Jiang X, Zhang L, Han J, Cheng H (2021) Nitrogen-doped porous biochar derived from marine algae for efficient solid-phase microextraction of chlorobenzenes from aqueous solution. J Hazard Mater 407:124785. https://doi.org/10.1016/j.jhazmat.2020.124785

Kambo HS, Dutta A (2015) A comparative review of biochar and hydrochar in terms of production, physico-chemical properties and applications. Renew Sustain Energy Rev 45:359–378. https://doi.org/10.1016/j.rser.2015.01.050

Karray R, Karray F, Loukil S, Mhiri N, Sayadi S (2017) Anaerobic co-digestion of Tunisian green macroalgae *Ulva rigida* with sugar industry wastewater for biogas and methane production enhancement. Waste Manag 61:171–178. https://doi.org/10.1016/j.wasman.2016.11.042

Keerthanan S, Rajapaksha AU, Mašek O, Vithanage M (2023) Plant uptake of personal care products and biochar-assisted immobilization in soil: an appraisal. J Soils Sediments 23:2669–2684. https://doi.org/10.1007/s11368-022-03400-y

Kim SK, Chojnacka K (2015) Marine algae extracts: processes, products, and applications. John Wiley & Sons, Hoboken, New Jersey

Klemm D, Heublein B, Fink H-P, Bohn A (2005) Cellulose: fascinating biopolymer and sustainable raw material. Angew Chem Int Ed Engl 44:3358–3393. https://doi.org/10.1002/anie.200460587

Klinger T (2021) Optimizing seaweed futures under climate change. Bot Marina 64:439–443. https://doi.org/10.1515/bot-2021-0036

Knowler D, Chopin T, Martínez-Espiñeira R, Neori A, Nobre A, Noce A, Reid G (2020) The economics of Integrated Multi-Trophic Aquaculture: Where are we now and where do we need to go? Rev Aquacul 12:1579–1594. https://doi.org/10.1111/raq.12399

Korzen L, Abelson A, Israel A (2016) Growth, protein and carbohydrate contents in *Ulva rigida* and *Gracilaria bursa-pastoris* integrated with an offshore fish farm. J Appl Phycol 28:1835–1845. https://doi.org/10.1007/s10811-015-0691-5

Korzen L, Peled Y, Shamir SZ, Shechter M, Gedanken A, Abelson A, Israel A (2015) An economic analysis of bioethanol production from the marine macroalga *Ulva* (Chlorophyta). Technology 03:114–118. https://doi.org/10.1142/S2339547815400105

Kraan S (2013) Mass-cultivation of carbohydrate rich macroalgae, a possible solution for sustainable biofuel production. Mitig Adapt Strateg Glob Change 18:27–46. https://doi.org/10.1007/s11027-010-9275-5

Krause-Jensen D, Duarte CM (2016) Substantial role of macroalgae in marine carbon sequestration. Nat Geosci 9:737–742. https://doi.org/10.1038/ngeo2790

Lawton RJ, Mata L, de Nys R, Paul NA (2013) Algal bioremediation of waste waters from land-based aquaculture using *Ulva*: selecting target species and strains. PLoS ONE 8:e77344. https://doi.org/10.1371/journal.pone.0077344

Lee XJ, Ong HC, Gan YY, Chen W-H, Mahlia TMI (2020) State of art review on conventional and advanced pyrolysis of macroalgae and microalgae for biochar, bio-oil and bio-syngas production. Energy Convers Manag 210:112707. https://doi.org/10.1016/j.enconman.2020.112707

Lehmann J, Gaunt J, Rondon M (2006) Bio-char sequestration in terrestrial ecosystems – a review. Mitig Adapt Strat Glob Change 11:403–427. https://doi.org/10.1007/s11027-005-9006-5

Letts E, Richards EH (1911) The chemical changes occurring in sewage-polluted seawater with one per cent. Sewage J R Inst Public Health 19:257–263

Li J-Y, Yang F, Jin L, Wang Q, Yin J, He P, Chen Y (2018) Safety and quality of the green tide algal species *Ulva prolifera* for option of human consumption: a nutrition and contamination study. Chemosphere 210:1021–1028. https://doi.org/10.1016/j.chemosphere.2018.07.076

Liu D, Ma Q, Valiela I, Anderson DM, Keesing JK, Gao K, Zhen Y, Sun X, Wang Y (2020) Role of C_4 carbon fixation in *Ulva prolifera*, the macroalga responsible for the world's largest green tides. Commun Biol 3:494. https://doi.org/10.1038/s42003-020-01225-4

Magnusson M, Carl C, Mata L, de Nys R, Paul NA (2016) Seaweed salt from *Ulva*: a novel first step in a cascading biorefinery model. Algal Res 16:308–316. https://doi.org/10.1016/j.algal.2016.03.018

Mantri VA, Kazi MA, Balar NB, Gupta V, Gajaria T (2020) Concise review of green algal genus *Ulva* Linnaeus. J Appl Phycol 32:2725–2741. https://doi.org/10.1007/s10811-020-02148-7

Marzeddu S, Cappelli A, Ambrosio A, Décima MA, Viotti P, Boni MR (2021) A life cycle assessment of an energy-biochar chain involving a gasification plant in Italy. Land 10:1256. https://doi.org/10.3390/land10111256

Masoumi S, Borugadda VB, Nanda S, Dalai AK (2021) Hydrochar: a review on its production technologies and applications. Catalysts 11:939. https://doi.org/10.3390/catal11080939

Mata L, Magnusson M, Paul NA, de Nys R (2016) The intensive land-based production of the green seaweeds *Derbesia tenuissima* and *Ulva ohnoi*: biomass and bioproducts. J Appl Phycol 28:365–375. https://doi.org/10.1007/s10811-015-0561-1

McCoy DE, Feo T, Harvey TA, Prum RO (2018) Structural absorption by barbule microstructures of super black bird of paradise feathers. Nat Commun 9:1. https://doi.org/10.1038/s41467-017-02088-w

McKendry P (2002) Energy production from biomass (part 2): conversion technologies. Bioresour Technol 83:47–54. https://doi.org/10.1016/S0960-8524(01)00119-5

Milledge JJ, Harvey PJ (2016) Potential process 'hurdles' in the use of macroalgae as feedstock for biofuel production in the British Isles. J Chem Technol Biotechnol 91:2221–2234. https://doi.org/10.1002/jctb.5003

Mulabagal V, Baah DA, Egiebor NO, Chen W-Y (2017) Biochar from biomass: a strategy for carbon dioxide sequestration, soil amendment, power generation, and CO_2 utilization. In: Chen W-Y, Suzuki T, Lackner M (eds) Handbook of Climate Change Mitigation and Adaptation, 2nd edn. Springer, Cham, Cham, pp 1937–1974

Nabi F, Arain MA, Rajput N, Alagawany M, Soomro J, Umer M, Soomro F, Wang Z, Ye R, Liu J (2020) Health benefits of carotenoids and potential application in poultry industry: a review. J Anim Physiol Anim Nutr (Berl) 104:1809–1818. https://doi.org/10.1111/jpn.13375

Nazemi F, Karimi K, Denayer JFM, Shafiei M (2021) Techno-economic aspects of different process approaches based on brown macroalgae feedstock: a step toward commercialization of seaweed-based biorefineries. Algal Res 58:102366. https://doi.org/10.1016/j.algal.2021.102366

Nikolaisen L, Daugbjerg Jensen P, Svane Bech K, Dahl J, Busk J, Brødsgaard T, Rasmussen MB, Bruhn A, Bjerre A-B, Bangsø Nielsen H, Albert KR, Ambus P, Kádár Z, Heiske S, Sander B, Schmidt ER (2011) Energy Production from Marine Biomass (*Ulva lactuca*). Danish Technological Institute

Ohno M (1993) Cultivation of the green algae, *Monostroma* and *Enteromorpha* 'Aonori'. In: Ohno M, Critchley AT (eds) Seaweed Cultivation and Marine Ranching. Jokosuka. Japan International Cooperation Agency, Tokyo, pp 7–16

Paine ER, Schmid M, Boyd PW, Diaz-Pulido G, Hurd CL (2021) Rate and fate of dissolved organic carbon release by seaweeds: a missing link in the coastal ocean carbon cycle. J Phycol 57:1375–1391. https://doi.org/10.1111/jpy.13198

Park J (2020) Photosynthetic and biochemical traits change in the green-tide-forming macroalga *Ulva pertusa* during sporulation. J Phycol 56:549–557. https://doi.org/10.1111/jpy.12969

Pizarro A, Santelices B (1993) Environmental variation and large-scale *Gracilaria* production. In: Chapman ARO, Brown MT, Lahaye M (eds) Proceedings of the fourteenth international seaweed symposium held in Brest, France, August 16–21, 1992 Fourteenth International Seaweed Symposium. Springer Netherlands, Dordrecht, pp 357–363

Polikovsky M, Fernand F, Sack M, Frey W, Müller G, Golberg A (2019) In silico food allergenic risk evaluation of proteins extracted from macroalgae *Ulva* sp. with pulsed electric fields. Food Chem 276:735–744. https://doi.org/10.1016/j.foodchem.2018.09.134

Prabhu M, Levkov K, Levin O, Vitkin E, Israel A, Chemodanov A, Golberg A (2020a) Energy efficient dewatering of far offshore grown green macroalgae *Ulva* sp. biomass with pulsed electric fields and mechanical press. Bioresour Technol 295:122229. https://doi.org/10.1016/j.biortech.2019.122229

Prabhu MS, Israel A, Palatnik RR, Zilberman D, Golberg A (2020b) Integrated biorefinery process for sustainable fractionation of *Ulva ohnoi* (Chlorophyta): process optimization and revenue analysis. J Appl Phycol 32:2271–2282. https://doi.org/10.1007/s10811-020-02044-0

Qu T, Zhao X, Hao Y, Zhong Y, Guan C, Hou C, Tang X, Wang Y (2020) Ecological effects of *Ulva prolifera* green tide on bacterial community structure in Qingdao offshore environment. Chemosphere 244:125477. https://doi.org/10.1016/j.chemosphere.2019.125477

Ragonese C, Tedone L, Beccaria M, Torre G, Cichello F, Cacciola F, Dugo P, Mondello L (2014) Characterisation of lipid fraction of marine macroalgae by means of chromatography techniques coupled to mass spectrometry. Food Chem 145:932–940. https://doi.org/10.1016/j.foodchem.2013.08.130

Rathnayake D, Ehidiamhen PO, Egene CE, Stevens CV, Meers E, Mašek O, Ronsse F (2021) Investigation of biomass and agricultural plastic co-pyrolysis: effect on biochar yield and properties. J Anal Appl Pyrol 155:105029. https://doi.org/10.1016/j.jaap.2021.105029

Revilla-Lovano S, Sandoval-Gil JM, Zertuche-González JA, Belando-Torrentes MD, Bernardeau-Esteller J, Rangel-Mendoza LK, Ferreira-Arrieta A, Guzmán-Calderón JM, Camacho-Ibar VF, Muñiz-Salazar R, Ávila-López MC (2021) Physiological responses and productivity of the seaweed *Ulva ohnoi* (Chlorophyta) under changing cultivation conditions in pilot large land-based ponds. Algal Res 56:102316. https://doi.org/10.1016/j.algal.2021.102316

Ronsse F, Nachenius RW, Prins W (2015) Carbonization of biomass. In: Pandey A, Bhaskar T, Stöcker M, Sukumaran RK (eds) Recent Advances in Thermo-chemical Conversion of Biomass. Elsevier, Amsterdam, pp 293–324

Rybak AS, Gąbka M (2018) The influence of abiotic factors on the bloom-forming alga *Ulva flexuosa* (Ulvaceae, Chlorophyta): possibilities for the control of the green tides in freshwater ecosystems. J Appl Phycol 30:1405–1416. https://doi.org/10.1007/s10811-017-1301-5

Sadhukhan J, Gadkari S, Martinez-Hernandez E, Ng KS, Shemfe M, Torres-Garcia E, Lynch J (2019) Novel macroalgae (seaweed) biorefinery systems for integrated chemical, protein, salt, nutrient and mineral extractions and environmental protection by green synthesis and life cycle sustainability assessments. Green Chem 21:2635–2655. https://doi.org/10.1039/C9GC00607A

Sadhukhan J, Martinez-Hernandez E (2017) Material flow and sustainability analyses of biorefining of municipal solid waste. Bioresour Technol 243:135–146. https://doi.org/10.1016/j.biortech.2017.06.078

Sadhukhan J, Ng KS, Martinez-Hernandez E (2016) Novel integrated mechanical biological chemical treatment (MBCT) systems for the production of levulinic acid from fraction of municipal solid waste: a comprehensive techno-economic analysis. Bioresour Technol 215:131–143. https://doi.org/10.1016/j.biortech.2016.04.030

Saidur R, Abdelaziz EA, Demirbas A, Hossain MS, Mekhilef S (2011) A review on biomass as a fuel for boilers. Renew Sustain Energy Rev 15:2262–2289. https://doi.org/10.1016/j.rser.2011.02.015

Sánchez-Barredo M, Sandoval-Gil JM, Zertuche-González JA, Ladah LB, Belando-Torrentes MD, Beas-Luna R, Cabello-Pasini A (2020) Effects of heat waves and light deprivation on Giant kelp juveniles (*Macrocystis pyrifera*, Laminariales, Phaeophyceae). J Phycol 56:880–894. https://doi.org/10.1111/jpy.13000

Sari-Chmayssem N, Taha S, Mawlawi H, Guégan J-P, Jeftić J, Benvegnu T (2019) Extracted ulvans from green algae *Ulva linza* of Lebanese origin and amphiphilic derivatives: evaluation of their physico-chemical and rheological properties. J Appl Phycol 31:1931–1946. https://doi.org/10.1007/s10811-018-1668-y

Schmitz TA, Kraft E (2022) Pilot scale photobioreactor system for land-based macroalgae cultivation. J Appl Phycol 34:507–516. https://doi.org/10.1007/s10811-021-02617-7

Sebök S, Herppich WB, Hanelt D (2019) Outdoor cultivation of *Ulva lactuca* in a recently developed ring-shaped photobioreactor: effects of elevated CO_2 concentration on growth and photosynthetic performance. Bot Mar 62:179–190. https://doi.org/10.1515/bot-2018-0016

Sekar M, Mathimani T, Alagumalai A, Chi NTL, Duc PA, Bhatia SK, Brindhadevi K, Pugazhendhi A (2021) A review on the pyrolysis of algal biomass for biochar and bio-oil–bottlenecks and scope. Fuel 283:119190. https://doi.org/10.1016/j.fuel.2020.119190

Shpigel M, Guttman L, Shauli L, Odintsov V, Ben-Ezra D, Harpaz S (2017) *Ulva lactuca* from an integrated multi-trophic aquaculture (IMTA) biofilter system as a protein supplement in gilthead seabream (*Sparus aurata*) diet. Aquaculture 481:112–118. https://doi.org/10.1016/j.aquaculture.2017.08.006

Shuuluka D, Bolton JJ, Anderson RJ (2013) Protein content, amino acid composition and nitrogen-to-protein conversion factors of *Ulva rigida* and *Ulva capensis* from natural populations and *Ulva lactuca* from an aquaculture system, in South Africa. J Appl Phycol 25:677–685. https://doi.org/10.1007/s10811-012-9902-5

Smetacek V, Zingone A (2013) Green and golden seaweed tides on the rise. Nature 504:84–88. https://doi.org/10.1038/nature12860

Sohi S, Shackley S, Meikel M, Pratt K, Lopez-Capel E, Haszeldine S, Gaunt J, Mašek O, Manning D, Carter S (2009) Biochar: An emerging technology for climate change mitigation? UK Biochar Research Centre Workshop proceedings, UKBRC Working Paper 1, 1st Apr 2009. University of Edinburgh. https://www.biochar.ac.uk/abstract.php?id=12

Soleymani M, Rosentrater KA (2017) Techno-economic analysis of biofuel production from macroalgae (seaweed). Bioengineering (Basel) 4:1–10. https://doi.org/10.3390/bioengineering4040092

Solymosi K, Latruffe N, Morant-Manceau A, Schoefs B (2015) Food colour additives of natural origin. In: Scooter M (ed) Colour Additives for Foods and Beverages, 1st edn. Woodhead Publishing, Cambridge, pp 3–34

Sondak CFA, Ang PO Jr, Beardall J, Bellgrove A, Boo SM, Gerung GS, Hepburn CD, Hong DD, Hu Z, Kawai H, Largo D, Lee JA, Lim P-E, Mayakun J, Nelson WA, Oak JH, Phang S-M, Sahoo D, Peerapornpis Y, Yang Y, Chung IK (2017) Carbon dioxide mitigation potential of seaweed aquaculture beds (SABs). J Appl Phycol 29:2363–2373. https://doi.org/10.1007/s10811-016-1022-1

Soroush S, Ronsse F, Park J, Ghysels S, Wu D, Kim K-W, Heynderickx PM (2023) Microwave assisted and conventional hydrothermal treatment of waste seaweed: comparison of hydrochar properties and energy efficiency. Sci Total Environ 878:163193. https://doi.org/10.1016/j.scitotenv.2023.163193

Sultana F, Wahab MA, Nahiduzzaman M, Mohiuddin M, Iqbal MZ, Shakil A, Mamun A-A, Khan MSR, Wong L, Asaduzzaman M (2023) Seaweed farming for food and nutritional security, climate change mitigation and adaptation, and women empowerment: a review. Aquac Fish 8:463–480. https://doi.org/10.1016/j.aaf.2022.09.001

Sun J, Norouzi O, Mašek O (2022) A state-of-the-art review on algae pyrolysis for bioenergy and biochar production. Bioresour Technol 346:126258. https://doi.org/10.1016/j.biortech.2021.126258

Taboada C, Millán R, Míguez I (2010) Composition, nutritional aspects and effect on serum parameters of marine algae *Ulva rigida*. J Sci Food Agric 90:445–449. https://doi.org/10.1002/jsfa.3836

Tang T, Effiong K, Hu J, Li C, Xiao X (2021) Chemical prevention and control of the green tide and fouling organism *Ulva*: key chemicals, mechanisms, and applications. Front Mar Sci 8:618950

Tedesco S, Daniels S (2018) Optimisation of biogas generation from brown seaweed residues: compositional and geographical parameters affecting the viability of a biorefinery concept. Appl Energy 228:712–723. https://doi.org/10.1016/j.apenergy.2018.06.120

Torres MD, Kraan S, Domínguez H (2019) Seaweed biorefinery. Rev Environ Sci Biotechnol 18:335–388. https://doi.org/10.1007/s11157-019-09496-y

Troell M, Henriksson PJG, Buschmann AH, Chopin T, Quahe S (2023) Farming the ocean–seaweeds as a quick fix for the climate? Rev Fish Sci Aquac 31:285–295. https://doi.org/10.1080/23308249.2022.2048792

Tsubaki S, Zhu W, Hiraoka M (2017) Production and conversion of green macroalgae (*Ulva* spp.). In: Kerton FM, Yan N (eds) Fuels, Chemicals and Materials from the Oceans and Aquatic Sources. John Wiley & Sons, Hoboken, New Jersey, pp 19–41

van den Burg SWK, van Duijn AP, Bartelings H, van Krimpen MM, Poelman M (2016) The economic feasibility of seaweed production in the North Sea. Aquac Econ Manag 20:235–252. https://doi.org/10.1080/13657305.2016.1177859

Wahlström N, Edlund U, Pavia H, Toth G, Jaworski A, Pell AJ, Choong FX, Shirani H, Nilsson KPR, Richter-Dahlfors A (2020) Cellulose from the green macroalgae *Ulva lactuca*: isolation, characterization, optotracing, and production of cellulose nanofibrils. Cellulose 27:3707–3725. https://doi.org/10.1007/s10570-020-03029-5

Wu H, Zhang J, Yarish C, He P, Kim JK (2018) Bioremediation and nutrient migration during blooms of *Ulva* in the Yellow Sea, China. Phycologia 57:223–231. https://doi.org/10.2216/17-32.1

Xia Z, Yuan H, Liu J, Sun Y, Tong Y, Zhao S, Xia J, Li S, Hu M, Cao J, Zhang J, He P (2022) A review of physical, chemical, and biological green tide prevention methods in the southern Yellow Sea. Mar Pollut Bull 180:113772. https://doi.org/10.1016/j.marpolbul.2022.113772

Xiao Y, Zhang J, Cui T, Gong J, Liu R, Chen X, Liang X (2019) Remote sensing estimation of the biomass of floating *Ulva prolifera* and analysis of the main factors driving the interannual variability of the biomass in the Yellow Sea. Mar Poll Bull 140:330–340. https://doi.org/10.1016/j.marpolbul.2019.01.037

Yu KL, Lau BF, Show PL, Ong HC, Ling TC, Chen W-H, Ng EP, Chang J-S (2017) Recent developments on algal biochar production and characterization. Bioresour Technol 246:2–11. https://doi.org/10.1016/j.biortech.2017.08.009

Yu KL, Show PL, Ong HC, Ling TC, Chen W-H, Salleh MAM (2018) Biochar production from microalgae cultivation through pyrolysis as a sustainable carbon sequestration and biorefinery approach. Clean Technol Environ Policy 20:2047–2055. https://doi.org/10.1007/s10098-018-1521-7

Zertuche-González JA, Sandoval-Gil JM, Rangel-Mendoza LK, Gálvez-Palazuelos AI, Guzmán-Calderón JM, Yarish C (2021) Seasonal and interannual production of sea lettuce (*Ulva* sp.) in outdoor cultures based on commercial size ponds. J World Aquac Soc 52:1047–1058. https://doi.org/10.1111/jwas.12773

Zhang JH, Huo YZ, Zhang ZL, Yu KF, He Q, Zhang LH, Yang LL, Xu R, He PM (2013) Variations of morphology and photosynthetic performances of *Ulva prolifera* during the whole green tide blooming process in the Yellow Sea. Mar Environ Res 92:35–42. https://doi.org/10.1016/j.marenvres.2013.08.009

Zhang Y, He P, Li H, Li G, Liu J, Jiao F, Zhang J, Huo Y, Shi X, Su R, Ye N, Liu D, Yu R, Wang Z, Zhou M, Jiao N (2019) *Ulva prolifera* green-tide outbreaks and their environmental impact in the Yellow Sea, China. Natl Sci Rev 6:825–838. https://doi.org/10.1093/nsr/nwz026

Zollmann M, Traugott H, Chemodanov A, Liberzon A, Golberg A (2019) Deep Water nutrient supply for an offshore *Ulva* sp. cultivation project in the eastern Mediterranean Sea: experimental simulation and modeling. Bioenergy Res 12:1113–1126. https://doi.org/10.1007/s12155-019-10036-3