

REVIEW

The underexplored potential of green macroalgae in aquaculture

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Abstract

Green macroalgae (Chlorophyta) currently represent a residual fraction (<1%) of global seaweed biomass production landings. In turn, red (Rhodophyta) and brown (Ochrophyta) macroalgae dominate the remaining percentage of aquaculture production, exceeding 32 million tonnes per annum. However, the industry relies on a relatively low number of species, in which as few as seven macroalgal genera collectively represent the bulk of global production metrics. At present, innovation and increased sustainability of the industry calls for diversification of macroalgal species/strains in aquaculture to counteract potential adverse effects ensuing from genetic impoverishment, decreased resilience to disease and climate change. Despite the dominance of red and brown seaweed regarding production figures, aquaculture of green macroalgae has witnessed an increasing trend in productivity and diversification over the last decades, particularly in Asia, where green seaweed taxa often occupy specific market niches in the food sector. Furthermore, growing interest in green seaweeds in aquaculture has been highlighted for different applications in emerging western markets (eg IMTA, biorefineries, food delicacies), owing to a unique diversity of cytomorphologies, ecophysiological traits, propagation capacities and bioactive compounds featured by this group of macroalgae. Cultivation technologies are relatively well developed, but sustainability assessments are scarce and required to unlock the potential of green seaweeds. Although it is likely that green macroalgae will remain occupying specialised market niches, in which high-value products are favoured, we argue that aquaculture of chlorophytan taxa presents itself as a compelling option under the current quest for commercial diversification of products and expansion of the sector.

KEYWORDS

bioactive compounds, cultivation techniques, integrated multitrophic aquaculture, life-cycle assessment, seaweeds, Ulvophyceae

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1 | INTRODUCTION

Macroalgae (or seaweeds) comprise a diverse group of photosynthetic, multicellular, eukaryotic organisms assigned to either the Plantae or Chromista kingdoms. Most are marine, where they play predominant roles as primary producers in coastal waters of the planet.¹ Despite being avascular and lacking true roots, stems, leaves and complex reproductive structures, some macroalgae display plant-like appearances, in that they present differentiated thalli with attachment organs (holdfasts), stem-like structures (stipes) and photosynthetic blades (fronds).² Marine macroalgae can be divided into three phyla: Chlorophyta (green), Rhodophyta (red) and Ochrophyta (brown), classified according to photosynthetic pigment content, carbohydrate reserves, cell wall components and flagella construction and orientation.¹ Collectively, the diversity of these groups exceeds 10,000 species, while new taxa are described every year. Currently, more than 1500 macroalgal species are assigned to Chlorophyta; approx. 2000 to Ochrophyta; and about 7300 to Rhodophyta.³ Together, macroalgae constitute an important biological resource, providing a variety of ecosystem services and socio-economic value.^{4,5}

Since prehistoric times, ca. 160 thousand years ago, early hominids have relied on intertidal habitats as foraging grounds for marine resources.^{6,7} Eventually, the inclusion of macroalgae in human diet is thought to have prompted profound impacts upon the evolution of human civilisation.^{8,9} The earliest evidence of the relationship between humans and marine macroalgae dates to the Neolithic (ca. 14,000 years ago) according to archaeological findings, when humans seemingly collected and transported a variety of seaweed species to be used as foodstuffs, trade items and ancient pharmacopeia.¹⁰ In addition, written records support that seaweed harvesting has been going on for centuries in virtually all shoreline areas where coastal communities have established, namely in Asia,¹¹ Europe,¹² Americas,¹⁰ Oceania^{13,14} and Africa.¹⁵ Such communities relied on marine macroalgae for a variety of different purposes including human and animal feed, soil fertilisation, medicinal, cultural activities and raw material for different applications.^{14,16}

Like other organisms included in human diet and well-being, some macroalgal species were domesticated and cultivated, once growing demand exceeded natural beds' holding capacities.^{17,18} Modern cultivation technologies first emerged in the 20th century in China and in Japan, after the description of the reproductive cycle of bladed Bangiales (*Pyropia* sp., Rhodophyta).¹¹ Soon after, the aquaculture of macroalgae rapidly expanded into what currently represents approximately half of global marine aquaculture production landings (51%), comparing to molluscs (27%), fish (13%) and crustaceans (9%); while exploitation of natural stocks represents a fraction (~2.8%) of total production of seaweeds.¹⁹ Macroalgal production is nowadays the fastest growing sector in global marine aquaculture generating an excess of US\$ 13 billion per annum,¹⁹ even though still holds a remarkable potential for innovation, particularly on the development of valuable products (eg functional foods, cosmeceuticals, nutraceuticals, pharmaceuticals)²⁰ and is expected to gain further

traction given the increasing perception of algae as healthy and sustainable foodstuffs, particularly in developing markets of western cultures.²¹⁻²³

The bulk of macroalgae aquaculture takes place in South-East Asian and Pacific countries, of which China, the Philippines, Indonesia, Republic of Korea and Japan contribute a staggering ~98% of global seaweed biomass production, while the same industry is sustained by as few as seven macroalgal genera, all of which assigned to either Rhodophyta or Ochrophyta.¹⁹ Some of these macroalgae are destined for the hydrocolloid industry, such as *Euclima* spp., *Kappaphycus alvarezii* and *Gracilaria* spp., whereas other taxa are used directly as human food, namely *Saccharina japonica*, *Undaria pinnatifida*, *Sargassum fusiform* and *Pyropia* spp.^{19,24} In turn, the output of green macroalgae (Chlorophyta) aquaculture currently represents only a fraction of global landings (<1%), lagging well behind the most relevant taxa in terms of production metrics. Despite presenting comparably lower production figures, the aquaculture of green seaweeds has witnessed an increasing trend in productivity and commercial diversification over the last decades (Figure 1).¹⁹ Nevertheless, asymmetries deriving from the dominance of few taxa in macroalgal aquaculture intensify the need for increased innovation and sustainability of the industry. Particularly, the commoditisation of the industry is thought to be inconsistent with future demand of high-value seaweed products, by failing to provide standardised, high quality, traceable products.²⁵ Advances are therefore required to meet the challenges of an evolving industry, through species and/or cultivar diversification, standardisation of cultivation techniques and increased awareness of local genetic and environmental variability.^{18,20,25,26}

In this context, expanding green macroalgae aquaculture emerges as a compelling solution towards the diversification and improvement of the sector, by providing a diverse pool of largely untapped biological resources, with intrinsic potential to unlock an array of different biotechnological applications. Indeed, due to the evolutionary divergence between the major macroalgae phyla, the Chlorophyta, Rhodophyta and Ochrophyta differ in their elemental composition,²⁷ metabolomic^{28,29} and fatty acid profiles,³⁰⁻³³ nutritional properties,^{34,35} polysaccharide types³⁶ and organoleptic properties.³⁷ Ultimately, distinctive features among macroalgal phyla will allow different applications, and therefore innovation in the industry. Accordingly, green macroalgae have been recently promoted for different applications, including biorefinery operations,³⁸ land-based integrated multitrophic aquaculture (IMTA) systems^{39,40} and high-value food products in modern cuisine.⁴¹ Examples of developing industrial applications using green macroalgae as raw material include the extraction of cellulose⁴² or sulphated polysaccharides⁴³ and the production of biochar,⁴⁴ bioethanol⁴⁵ and bioplastics,⁴⁶ while an indefinite number of bioactive molecules will keep emerging from green macroalgae metabolite screening studies.^{47,48}

The present review aims to provide a complete overview of the status, ongoing developments and future perspectives of green macroalgae in aquaculture. A detailed description of the diversity and potential of major taxa are given alongside known applications,

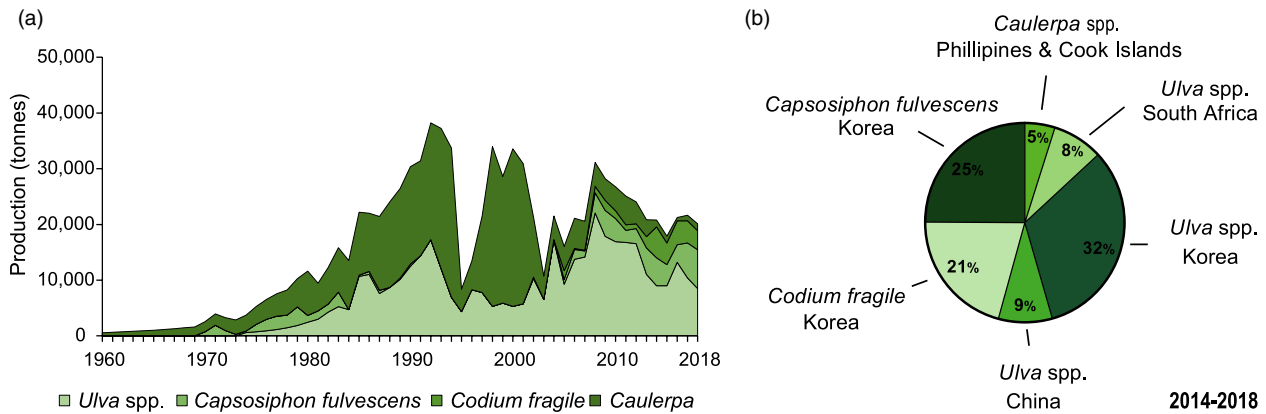


FIGURE 1 Global production of green macroalgae in marine aquaculture. (a) Production metrics are represented for the main taxa (tonnes fresh weight) from 1960–2018. (b) Five-year average relative percentage by weight of representative taxa by country (FAO, 2020). Note: aquaculture statistics for green macroalgal species in Japan are not listed separately in FAO databases and therefore not represented graphically. Production estimates of *Monostroma*, *Ulva* and *Caulerpa* in Japan can exceed 25,000 tonnes fresh weight annually, in which case global production figures are significantly underestimated (see text for references, Section 2)

regional importance and global production estimates, as well as existing cultivation techniques. We further analyse existing literature on the prospection of bioactive compounds and conclude by outlining future perspectives of this mostly underexplored group of macroalgae in aquaculture.

2 | DIVERSITY AND POTENTIAL OF GREEN SEAWEEDS IN AQUACULTURE

Most green seaweeds are currently assigned to Ulvophyceae, the most morphologically and ecologically diverse class of Chlorophyta, while few representatives occur in otherwise evolutionary distant groups, for example genus *Prasiola* (Trebouxiophyceae).⁴⁹ Although the phylogenetic relationships among Chlorophytan lineages have long been subject of controversy and debate, marine ulvophycean macroalgae are currently classified and distributed among distinct orders (Ulvales, Ulotrichales, Bryopsidales, Cladophorales and Dasycladales), each one presenting a distinct set of cytomorphological features.^{50,51}

Three major cytomorphological types can be distinguished among green seaweeds: (i) the uninucleate cell type, consisting of macroalgae composed of uninucleate cells arranged in multicellular filaments or sheet-like external morphologies, characteristic of most Ulvales and Ulotrichales, (ii) the siphonocladous type, composed of multinucleate cells with regularly spaced nucleocytoplasmic domains, characteristic of the Cladophorales and few genera of the Ulotrichales (eg *Urospora* and *Acrosiphonia*) and *Blastophysa* (enigmatic taxa), and (iii) the siphonous type, in which macroalgal bodies are composed of a single giant tubular cell containing thousands to millions of nuclei, typical of the Bryopsidales and Dasycladales.⁴⁹ The variety of cytological architectures found in green macroalgae is explained by the independent evolution of macroscopic growth that took place in several ulvophycean lineages that diverged from

ancestral unicelled green algae millions of years ago, following different evolutionary pathways.⁵²

The diversity of ulvophycean seaweeds presents itself in a pallet of organisms with different ecophysiological traits, various anatomical features, and unique secondary metabolites of interest for commercial exploitation in aquaculture. While a variety of representatives of the orders Ulvales, Ulotrichales and Bryopsidales have been traditionally cultivated in relatively small quantities in South-East Asian and Pacific countries for human consumption, the diversity of green seaweeds in aquaculture remains largely untapped. Furthermore, an increasing number of publications have evaluated the potential of several taxa in IMTA with emphasis on the Cladophorales,^{53,54} while members of the Dasycladales have been traditionally overlooked, despite of existing biotechnological potential.^{55,56}

2.1 | Ulvales and Ulotrichales

The Ulvales and Ulotrichales form an early branching clade among Ulvophyceae of predominantly marine macroalgae, presenting multicellular thalli that range from branched or unbranched filaments to blade or tubular morphologies.⁵⁰ The orders Ulvales and Ulotrichales are distinguished based on life history features. The Ulvales present diplohaplontic life cycles with alternating isomorphic generations. In turn, the Ulotrichales present diplohaplontic heteromorphic life cycles in which the sporophyte stage consists of a small, thick-walled unicell that attaches to the substrate by a stalk, the so-called Codiolum stage.⁵⁷ Representative taxa of both orders have been historically exploited in aquaculture and mostly represented by *Ulva* spp. (syn. *Enteromorpha* spp.) (Ulvales), *Monostroma* spp. and *Capsosiphon fulvescens* (Ulotrichales). Today, these taxa collectively represent more than two thirds of global green seaweed aquaculture biomass production¹⁹ (Figure 1).

Taxa affiliated to the genera *Ulva* (syn. *Enteromorpha*) and *Monostroma* are registered in FAO databases under common trade names, for example 'bright green nori' and 'green laver', reflecting a certain degree of taxonomic uncertainty in those algal products. According to existing literature, macroalgae commercialised under the trade name 'bright green nori' reportedly cultivated in China (3400 tonnes in 2017¹⁹) is often identified as *Ulva clathrata* in the literature,^{20,58} despite the lack of supporting molecular studies. It is possible that 'bright green nori' is composed of other *Ulva* species instead. For instance, some *Ulva prolifera* morphotypes present high similarity with *U. clathrata* and require molecular confirmation to discriminate between species.⁵⁹

On the other hand, 'green laver' or aonori in Japan, traditionally consisted of a mixture of members of the genera *Ulva* and *Monostroma*, in which some species originated from aquaculture (presumably *Ulva prolifera*, *Ulva intestinalis* and *Monostroma* spp.), while other wild collected *Ulva* species could be added to the mix.^{60,61} Today, 'green laver' aquaculture production reportedly originates entirely from the Republic of Korea (6800 tonnes in 2018).¹⁹ Molecular studies suggest that cultivated 'green laver' is composed exclusively of *Ulva prolifera*.⁶² In turn, 'green laver' associated genera (*Ulva* and *Monostroma*) are considered important components of the aquaculture industry in Japan,^{61,63,64} despite not showing in FAO statistics. A thorough revision of the taxonomic affinity of green seaweed products originating from aquaculture is therefore required, particularly those labelled under common trade names. Molecular studies are necessary towards higher product traceability, increased food safety and consumer confidence.⁶⁵

2.1.1 | *Ulva*, Linnaeus

The genus *Ulva* comprises about 305 recognised species, in which macroalgae present blade-like or filamentous morphologies. Several *Ulva* species are considered edible⁶⁶ and generally present interesting characteristics that make them highly compelling for aquaculture purposes, such as ubiquitous distribution, high growth rates, high environmental tolerance, low epiphytism susceptibility and high nutrient uptake capacities.⁶⁷⁻⁷⁰ These features make *Ulva* particularly interesting as integrated components in IMTA systems around the world.

Owing to extensive morphological plasticity and the existence of numerous subspecies and varieties, taxonomy based on morphological characters (eg thallus shape, cell size, number of pyrenoids) is particularly challenging in *Ulva* and often requires molecular studies for correct taxonomic assignment.^{59,71-73} While extensive research has been published on *Ulva* spp. in aquaculture, the species identity remains unresolved for most studies. For instance, based on morphological characters, species of *Ulva* have been identified as either *U. rigida*, *U. linza*, *U. capensis* or *U. lactuca* in different IMTA systems to feed abalone (*Haliotis midae*, Linnaeus 1758), although in some cases it is possible that more than one species were concurrently cultivated.³⁹

Irrespective of the underlying issues of *Ulva* (syn. *Enteromorpha*) taxonomy, examples of the use of *Ulva* species in IMTA systems include *Ulva clathrata* in effluent biofiltration, or in co-culture in shrimp aquaculture (*Litopenaeus vannamei*; *Farfantepenaeus californiensis*), functioning as biofilter and feed additive;⁷⁴⁻⁷⁶ *Ulva lactuca* as biofilter in semi-recirculating systems with abalone (*Haliotis discus hannai*, Ino 1953), sea urchin (*Paracentrotus lividus*, Lamarck 1916) and gilthead seabream (*Sparus aurata*, Linnaeus 1758);⁷⁷⁻⁷⁹ and as biofilter and feed additive for *L. vannamei* production;^{80,81} *Ulva rigida* and *Ulva flexuosa* as biofilters of fish aquaculture effluents.^{82,83} Overall, these studies showed promising results in using *Ulva* species in IMTA systems, by providing both increased water quality and added value when employed as feed for other trophic levels. However, commercial scale application of *Ulva* in such systems has rarely been adopted. The few published examples of commercial exploitation of *Ulva* species in IMTA systems, with established ongoing operations, are limited to South Africa, where *Ulva* spp. have been successfully grown to feed abalone (*Haliotis midae*) (*Ulva* annual biomass production estimated at 1100 tonnes).³⁹ On a smaller scale, examples of other countries producing *Ulva* in IMTA include Israel⁸⁴ and Portugal⁴⁰ (Figure 2).

Apart from its use in IMTA, aquaculture of *Ulva* for human consumption has been mostly assigned to a single species (*U. prolifera*). *Ulva prolifera* (syn. *Enteromorpha prolifera*⁷²) is globally distributed, notorious for its bloom forming nature, and principal causative agent of green tides in China.⁸⁵ Dried specimens of *U. prolifera* are particularly dark green, with strong flavour compared with other congeners (eg *U. linza* and *U. intestinalis*) that confers high commercial value as 'green laver'.⁸⁶ In Japan, commercial aquaculture of *U. prolifera* is focused on niche, high-value food products, where mass cultivation of the species has been going on since the early 1980 s and relies on artificial seed production.^{87,88} Today, *U. prolifera* aquaculture production in Japan turns out unnoticed in FAO aquaculture statistics, although annual production metrics have been reported elsewhere, despite with inconsistent values (eg 200, 1500, 3000 tonnes dry weight; equivalent to approximately ten times as much in fresh weight).^{63,89,90} The species is also cultivated in the southern coast of Korea, where it is valued as an ingredient in salads, soup and cookies^{62,91} and likely represents the bulk of 'green laver' production reported at 6800 tonnes in 2018 (as previously referred).

2.1.2 | *Monostroma*, Thuret

The genus *Monostroma* includes popular edible taxa consumed as food in various forms, used as an important ingredient in soup, salad, jam and spices in countries like Japan, China, Brazil and in the Pacific Coast of America.⁹² Commercial aquaculture activities for *Monostroma* production have been established in Japan at least since the 1960 s, with an estimated annual production in the range of 1400–2500 tonnes dry weight.^{90,93-95} At least three species (*M. latissimum*, *M. nitidum* and *M. kuroshiensis*)⁹⁶ have been reportedly cultivated in brackish waters and estuaries of central Japan and



FIGURE 2 *Ulva rigida* grown in an IMTA system operating in Aveiro (Portugal). *U. rigida* (left) grown in tanks receiving effluent water from adjacent fish farm ponds at ALGAplus Ltd. Dried seaweed (right) is one of several products sold by the company to grocery stores and restaurants. Photographs courtesy of ALGAplus Ltd

relies on artificial propagation techniques.⁹⁴ Other taxa within the *Monostroma* complex have been experimentally cultivated in different parts of the world, such as *Gayralia oxysperma* and *Monostroma* sp. in Brazil, although commercial aquaculture of these taxa is currently not operational.^{97,98}

2.1.3 | *Capsosiphon fulvescens*, (C. Agardh) Setchell and N. L. Gardner

Capsosiphon fulvescens is a filamentous macroalgae that inhabits the upper intertidal zone of North Atlantic and Northern Pacific coasts. This species has been traditionally used in Korea as food owing to its unique flavour and soft texture, and to treat stomach disorders and hangovers.⁹⁹ At the beginning of the 21st century, commercial interest in the species led to the development of artificial seed production and cultivation techniques that enabled the establishment of large-scale cultivation of *C. fulvescens*.¹⁰⁰ Nowadays, the species is produced from November to March in the south-western province of Korea. The trade price of *C. fulvescens* may range from US\$ 0.9 to 5.5 kg⁻¹ (wet weight), a value 2–4 times higher than that of other macroalgae species produced in Korea.¹⁰¹ In 2017, production figures were reported at 6280 tonnes fresh weight, valued at approximately US\$19 million, thus representing the highest value per unit wet weight among several macroalgal species.¹⁰²

2.2 | Bryopsidales

The Bryopsidales forms a diverse ulvophycean order that includes approx. 600 recognised species,³ important primary producers in coral reefs, rocky shores, lagoons and seagrass beds, with representative species found from tropical to Arctic waters.¹⁰³ With siphonous architecture, members of the Bryopsidales form thalli composed of

a single, giant cell, that contains millions of nuclei, chloroplasts and mitochondria that move about freely by cytoplasmic streaming.¹⁰⁴ Bryopsidalean morphologies vary from simple branched siphons (eg *Bryopsis*, *Caulerpa*, *Derbesia*), to complex multiaxial thalli (eg *Codium*, *Udotea*, *Halimeda*).¹⁰⁵

A variety of bryopsidalean algae have been traditionally valued as food items in the Indo-Pacific, and in some cases relevant taxa have been cultivated. According to FAO, important taxa with well-established aquaculture activities include *Codium fragile*; ‘coarse seagrape’—presumably represented by species from the *Caulerpa racemosa-peltata* complex, namely *Caulerpa chemnitzia* (formerly *C. racemosa* var. *turbinata*);¹⁰⁶ and ‘*Caulerpa* spp.’—likely represented by both *C. chemnitzia* and *C. lentillifera*.

2.2.1 | *Codium fragile*, Suringar

Codium fragile has been cultivated in the Republic of Korea since the late 1980 s, when small-scale cultivation practices depended on natural blooming zygotes, thereby highly dependent on environmental conditions.¹⁰⁷ Years later, artificial seed production methods and nursery culturing techniques were developed,¹⁰⁸ enabling increased productivity. Currently, annual production figures are around 4000 tonnes fresh weight, worth approximately US\$ 2 million.^{19,102} *Codium fragile* is widely consumed in Korea, China, Japan and the Philippines, in various forms: mixed in the traditional Korean dish Kimchi; as winter vegetable; dried or salt cured; in salads, soups and sweets.⁶⁶ Apart from its use as foodstuff, pharmacological interest in the species has been reinforced by several studies that demonstrated anti-inflammatory, antitumor and osteoarthritis alleviating properties from *C. fragile* extracts.^{109–111} Additionally, studies proposed the use of *C. fragile* as an alternative candidate in IMTA systems given its higher tolerance to warmer temperatures in comparison with kelp species.¹¹²

2.2.2 | *Codium tomentosum*, Stackhouse

Another congener, *Codium tomentosum*, whose natural distribution range is restricted to European and North African coastal waters¹¹³ is commercially cultivated in Portugal by a company (ALGApplus Ltd.) dedicated to seaweed production in a land-based IMTA (Figure 3). The company optimised artificial propagation methods for *C. tomentosum* production and grows juvenile thalli in outdoor tanks, fed by the effluent of a semi-intensive aquaculture system producing marine fish. Despite unreported annual production, *C. tomentosum* is sold to high-end restaurants, where it is highly appreciated as a gourmet ingredient for its flavour of barnacles with notes of peach,⁴¹ or as raw material for the cosmetic industry. For instance, products based on *C. tomentosum* extracts have been patented as CODIAVELANE-BG[®],¹¹⁴ used as the main moisturising agent in a variety of skin-care products produced in the United States and in Europe.^{115,116} A recent study showed that lipid extracts of cultivated *C. tomentosum* presented lower seasonal variability than wild harvested specimens;¹¹⁷ therefore, aquaculture specimens may possess more consistent qualities, an important feature for industrial applications. Due to the commercial interest in the species, growth conditions for *C. tomentosum* in IMTA are currently under optimisation towards reduced operational costs and scale-up.¹¹⁸

2.2.3 | *Caulerpa*, J.V. Lamouroux

Species within the *Caulerpa racemosa-peltata* complex, presumably *C. chemnitzia* (formerly *C. racemosa* var. *turbinata*) and *C. lentillifera*,

collectively known as 'sea grapes' or 'green caviar', have been reportedly cultured in the Philippines for decades, while recent aquaculture activity began in the Cook Islands for *C. chemnitzia*.¹⁹ Other countries like Japan, Vietnam and China are also known to culture *C. lentillifera*,¹¹⁹ although production figures are not separately listed in national aquaculture statistics and turn out unnoticed in FAO databases. Nevertheless, annual landings of cultivated *C. lentillifera* in 2016 were estimated in the ranges of 600, 300–400 and 1000 tonnes, in Japan, Vietnam and China respectively.¹²⁰ These are significant numbers considering *Caulerpa* spp. production in the Philippines and Cook Islands in the same year was estimated under 600 tonnes.¹⁹

Both species are highly valued as food items in the Indo-Pacific, while gaining increasing popularity in western countries and in modern cuisine.^{41,119} They are mainly served fresh, highly appreciated for the textural experience of bursting branchlets, palatable sea flavour and ornate structure with brilliant emerald colour¹²¹ (Figure 4). Other *Caulerpa* species may hold aquaculture potential given more than twenty *Caulerpa* species are considered edible in a range of different countries,⁶⁶ and at least fifteen different varieties are consumed in the Indo-Pacific alone.¹²² Some members of the genus are notorious for producing cytotoxic metabolites such as caulerpenyne,¹²³ despite presenting minimal toxicological risk to humans.¹²⁴ Diversification of aquaculture activities within *Caulerpa* seems promising but may require optimisation of culturing conditions for each species/variety. Such studies will enable the development of more uniform products and mitigate the impacts of over harvesting natural stocks.¹²¹ Accordingly, preliminary studies have assessed the potential of *Caulerpa okamurae* towards commercial cultivation in Korea.¹²⁵



FIGURE 3 *Codium tomentosum* grown in an IMTA system operating in Aveiro (Portugal). *C. tomentosum* is grown in tumble culture conditions in tanks receiving effluent water from adjacent fish farm ponds at ALGApplus Ltd. The thalli can develop 'pom-pom' shapes of potential appeal for high-end restaurants (left). Individual thalli can reach sizes up to 600 g fresh weight after several months in culture (right)



FIGURE 4 *Caulerpa* (seagrapes or green caviar) in a street market at Matnog, Luzon (Philippines). The local name for the seaweed is 'lato' presumably *Caulerpa chemnitzia ecad turbinata*. Photographs courtesy of Dr. Stefano Draisma

In addition, experimental studies have attempted to use *Caulerpa* species applied to the bioremediation of intensive tank-based aquaculture systems (eg *C. racemosa*, *C. serrulata*, *C. taxifolia*);¹²⁶ or integrated in co-culture with other species, as shown by studies on *Caulerpa lentillifera* in co-culture with sea cucumber (*Holothuria scabra*) and/or gastropod snails (*Babylonia areolata*);^{127,128} and *Caulerpa sertularioides* in co-culture with shrimp (*Farfantepenaeus californiensis*).¹²⁹

2.3 | Cladophorales

The order Cladophorales is species-rich, comprising about 485 recognised species,³ of mostly marine macroalgae representatives. The order evolved siphonocladous multicellular organisation, in which mitosis is uncoupled from cytokinesis, resulting in large multinucleate cells with nuclei organised in fixed cytoplasmic domains.⁵² Molecular data and morphological characters support the division of two main clades in the Cladophorales.^{130,131} The 'Cladophorales clade' characterised by branched (eg *Cladophora*) or unbranched filamentous morphologies (eg *Chaetomorpha* and *Rhizoclonium*); and the 'Siphonocladus clade', in which highly specialised forms of giant celled organisms develop more complex morphologies such as blade-like (eg *Anadyomene*) or balloon-shaped thalli (eg *Valonia*).^{49,130,132}

A variety of cladophoralean species are considered edible in different parts of the world, including several representatives of different genera (eg *Cladophora*, *Chaetomorpha*, *Valonia*, *Boodlea*, *Anadyomene* and *Aegagropila*).⁶⁶ However, no commercial cultivation of edible Cladophorales is currently reported for human consumption. Instead, some cladophoralean algae have been regarded as adequate biofilters to be incorporated in IMTA systems, especially representatives of the genera *Chaetomorpha* and *Cladophora*, as described in the following points.

2.3.1 | *Chaetomorpha*, Kützing

The genus *Chaetomorpha* includes about 73 recognised species³ that consist of attached or unattached unbranched filamentous thalli, mostly restricted to marine environments with few species occurring in brackish waters.¹³⁰ The genus is widely distributed in shallow coastal ecosystems worldwide, and particularly abundant in eutrophic estuaries and lagoons.¹³³ Species of *Chaetomorpha* are known to possess broad environmental tolerances (temperature, salinity, irradiance), high nutrient uptake capacities, high growth rates and perennial nature.¹³³⁻¹³⁷ Such features make *Chaetomorpha* species ideal candidates to be incorporated as biofilters in IMTA. In fact, the performance of *Chaetomorpha* species (eg *C. linum*) may well exceed that of *Ulva* spp. in IMTA systems, given comparatively higher nutrient uptake rates, higher tolerance to solar irradiance and lower propensity for seasonal changes in algal productivity.^{134,135}

Examples of studies that evaluated the usefulness of *Chaetomorpha* species towards integration in aquaculture include: *Chaetomorpha linum* in the bioremediation of nutrient-rich seawater;⁵³ as bioremediator and dietary component of fish feed formulations;¹³⁸ and as feed ingredient in sea cucumber (*Apostichopus japonicus*, Selenka 1867) aquaculture;¹³⁹ *Chaetomorpha linguistica* in co-culture as dietary supplement to juvenile tiger prawn shrimp (*Penaeus monodon*, Fabricius 1798),¹⁴⁰ and *Chaetomorpha indica* in tropical pond aquaculture systems.¹⁴¹

Development of mass scale aquaculture activities of members of this algal group may be expected in a near future given interesting industrial applications for biomass utilisation. For instance, the environmental tolerance and growth rate of *Chaetomorpha crassa* makes it more suitable than the other *Chaetomorpha* species naturally occurring in Japan, *C. moniligera* and *C. spiralis*, for mass cultivation towards bioethanol production.¹³³ Other studies have highlighted the potential of *Chaetomorpha* species (eg *C. linum*,

C. antennina, *C. aerea*, and *C. gracilis*) as feedstock for different biotechnological applications, namely from extracted compounds with pharmacological (eg heparin like sulphated polysaccharides; sulphated galactans), and industrial interest (eg cellulose; polyhydroxybutyrate).^{54,142,143}

2.3.2 | *Cladophora*, Kützing

The genus *Cladophora* is globally distributed and includes about 195 recognised species mostly inhabiting coastal marine waters.³ Members of *Cladophora* present distinctively branched thalli, perennial holdfasts, unusual cell dimensions and thick cell walls. Such structural features make *Cladophora* highly impactful in its environmental surroundings, namely in removing significant nutrient load from the water column.¹³² Like *Chaetomorpha*, some *Cladophora* species present high tolerance to a range of environmental conditions (temperature, salinity, nutrient availability) and are equally proposed as excellent biofilter agents in IMTA,¹⁴⁴ thereby potentially adding value by reducing the environmental impacts of aquaculture activities.¹⁴⁵

Examples of studies that evaluated the potential of *Cladophora* species integrated in aquaculture include: *Cladophora prolifera* as bioremediator in IMTA operating offshore¹⁴⁶ and as biofiltering agent of nutrient-rich seawater;⁵³ and *Cladophora coelothrix* as bioremediator in tropical land-based aquaculture systems.^{141,144}

3 | GREEN SEaweEDS CULTIVATION METHODS

A variety of technological approaches are currently employed in the commercial scale aquaculture of green macroalgae. Different phases of the production chain (propagule production, nursery, grow-out) require specific techniques depending on target species biology and ecophysiology, and the specificities of site location.

Primarily, the production chain largely depends on the ability to produce seed stock of the target species in sufficient quantity and quality to readily supply biomass production demand.¹⁴⁷ Different methods are currently employed to obtain viable propagules (often referred to as 'seedlings') in commercial scale aquaculture of green seaweeds including vegetative propagation; asexual propagation via parthenogenesis; or sexual reproduction via gamete conjugation (Figure 5). Vegetative propagation has proved successful in taxa with particularly high proliferation potentials of vegetative thalli, for example *Caulerpa*,^{122,125} *Chaetomorpha*¹⁴⁸ and *Codium*;¹⁰⁷ other taxa are preferentially propagated via manipulation of reproductive propagules (zoospores or gametes), thus requiring a greater knowledge on species life cycle patterns and developmental biology.¹⁴⁹ In such taxa, the industry has shifted from simple, natural seeding methods—placing artificial substrata (ropes, nets) in the vicinities of wild populations of the target species to serve as settling structures

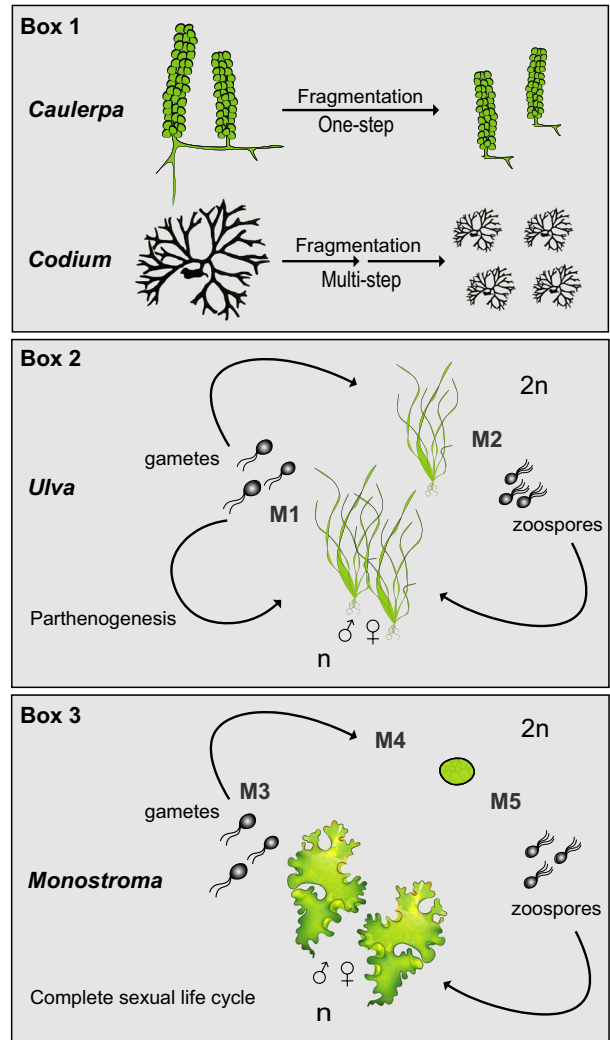


FIGURE 5 Main types of artificial seeding methods employed in green seaweed aquaculture. Box 1: In *Caulerpa*, fragmentation of vegetative thalli allows direct planting of rhizoidal fragments; in *Codium*, regeneration of small fragments requires a nursery phase prior to transplanting for grow-out, thus involving a multi-step technology. Box 2: In *Ulva*, the isomorphic diplohaplontic life cycle and macroscopic, exploitable thalli are formed in both the gametophyte (n) and sporophyte (2n) generations. Motile reproductive propagules (gametes and zoospores) develop directly into macroscopic thalli, after (i) gamete conjugation; (ii) unmated gametes through parthenogenesis; and/or (iii) direct development of zoospores. Manipulations to induce gametogenesis (M1) and zoosporogenesis (M2) may include fragmentation and washing for removal of 'sporulation inhibitors'. Box 3: In *Monostroma*, the heteromorphic diplohaplontic life cycle is dominated by the macroscopic gametophyte (n), and the sporophyte is represented by the microscopic Codiolum stage (2n). Artificial propagation involves several manipulation steps including: gamete release and conjugation (M3); zygote fixation/sporophyte maturation (M4); and zoospore release/seeding to artificial substrata (M5)

for naturally occurring seed; to more sophisticated artificial propagule production techniques taking place in land-based nursery facilities, for example *Ulva*,⁸⁸ *Monostroma*⁹³ and *Capsosiphon*.¹⁰⁰

Most artificial propagule production methods employed in commercial scale aquaculture of Ulvophyceae taxa are relatively well developed and mostly reliant on asexual propagation methods (vegetative propagation or parthenogenesis). Asexual propagation methods may confer relative advantages in cultivating green seaweeds (*Caulerpa*, *Codium*, *Ulva*, *Capsosiphon*) as opposed to other major taxa, for example kelps (Ochrophyta) and *Pyropia* spp. (Rhodophyta) that generally require manipulating the entire sexual life cycle. Accordingly, bypassing the manipulation of one of the sexual life history phases (sporophyte or gametophyte) via asexual looping allows for simpler cultivation technologies.¹⁴⁹ Despite unreported in green seaweeds, asexual reproduction through continuous vegetative propagation of macroalgae may result in reduced productivity and increased vulnerability to disease, as observed in red seaweeds (eg *Eucheuma*, *Kappaphycus* and *Gracilaria*).^{150,151}

Once propagules are obtained and present suitable size for transplantation, the grow-out phase occurs by transferring the propagules to open water cultivation grounds or to land-based systems. Traditionally, the main cultivation techniques involve the use of ropes or nets as artificial substrata (open sea), or in land-based tanks or ponds. These can be classified as follows: line or net cultivation methods—propagules are attached to ropes or nets at varying depths; floating raft cultivation methods—seeded ropes or nets are held within a rigid floating frame at the surface; tank or tumble culture cultivation methods—culture takes place in tanks under free-floating conditions; other methods include direct planting on the ocean floor or attached to artificial substrates close to the bottom.¹⁴⁷ All types of classical cultivation methods are well represented in Ulvophyceae macroalgae. In some cases, novel approaches and variations of such methods have been experimentally validated. The techniques involved in artificial propagation and grow-out phases in commercial cultivation of Ulvophyceae taxa, as well as the relevant innovation strategies depicted in the literature are described in the following sections (Table 1).

3.1 | Vegetative propagation

Caulerpa (sea grapes) represents the most distinct Ulvophyceae genus in which cultivation follows typical vegetative propagation methods, whereby seed stock is obtained by simple excision of vegetative thalli, which subsequently regenerate the entire plant, involving a 'one-step technology' *sensu* Santelices.¹⁵² Nonetheless, the survival and growth potential of excised fragments can be both organ and size specific. For instance, in *Caulerpa okamurae* excised erect fronds and stolons (horizontal runners) can regenerate from >3 cm and >5 cm fragments, respectively¹²⁵ (Figure 5, Box 1).

Cultivation of *Caulerpa* species (*C. lentillifera* and *C. chemnitzia*) began in the Philippines in the early 1950s in earthen fish ponds using bottom-planting methods, a simple technology still used to date in this South-East Asian country. Propagules (rhizoidal thalli) are buried on the surface sediment layer (2 cm) and left to grow allowing for multiple harvests.¹⁵³ However, a permanent ban on converting mangrove areas into earthen ponds constrained the expansion of this cultivation method in the Philippines, where more sustainable methods at open sea (cages or tubular nets placed off-bottom) have been attempted.¹⁵⁴

Other reported commercial scale operations for *Caulerpa* production include cultivation of *C. lentillifera* in land-based systems and in submerged cylindrical cages at sea (off-bottom). In Japan, *C. lentillifera* has been grown in concrete tanks (4 m³), in which the thalli are held between two plastic mesh grids fixed to a floating PVC frame. Unfiltered seawater flows through the tanks (volume turnover occurring 5 times per day), with strong aeration promoting water movement.¹²² In open water, *C. lentillifera* has been grown in cylindrical cages (60 cm in diameter and 100 cm long) made of net stretched on a metallic frame. The frames are tied to ropes and suspended by buoys at 0.5 m depth.¹⁵⁵ Several experimental approaches for the cultivation of *Caulerpa* species have been conducted worldwide, using a variety of different culture methods including in open

TABLE 1 Cultivation steps and major types of technologies employed for the commercial aquaculture of representative Ulvophyceae taxa

Species	Propagation	Nursery	Grow-out
<i>Caulerpa</i> spp.	Asexual—fragmentation	–	Pond; tanks; cages; nets in land/at sea
<i>Codium tomentosum</i>	Asexual—fragmentation	Flasks—tumble culture indoor	Tanks—tumble culture in land
<i>Codium fragile</i>	Asexual—fragmentation	Tanks—'seeding' ropes	Long line culture at sea
<i>Capsosiphon fulvescens</i>	Asexual—gametogenesis induction; parthenogenetic gametes attach directly to substrate	–	Bamboo nets at sea
<i>Ulva</i> spp.	Asexual—fragmentation Asexual—washing 'sporulation' inhibitors Sexual—gamete conjugation Propagules attach to ropes, 'bioballs', 'germling clusters' in tanks	–	Tanks—tumble culture; raceways; drip irrigation; Culture nets at sea
<i>Monostroma</i> spp.	Sexual—induced gamete release, in vitro fertilisation, zygote maturation, zoospore 'seeding' to ropes in tanks	–	Culture nets at sea

waters: attaching thalli to lines, ropes, nets (submerged at different water depths), cages and trays (off-bottom); and in earthen ponds using plastic trays held on top of bamboo frames (reviewed by de Gaillande et al.¹²²).

In *Codium* (green sponge fingers, velvet horn), different approaches have been developed for the vegetative propagation of two different species (*C. fragile* and *C. tomentosum*). In Korea, propagules of *Codium fragile* are obtained via regeneration of isolated utricles and medullary filaments.^{107,108} These structures are obtained from chopping adult vegetative spongy thalli into small fragments (<5 mm) with a hand blender. The resulting fragments are left to attach directly to a framed seed fibre (100 m) and follow regeneration from a filamentous morphology to juvenile spongy thalli during a nursery cultivation stage (1–3 months) in land-based culture tanks. Seeded fibre is subsequently coiled on culture ropes (100 m) and transplanted offshore to a long-line horizontal cultivation system. During the grow-out phase, propagules first endure a pre-main cultivation stage of stationary growth at 2 m depth (5 months), followed by a fast growth, main cultivation stage at 1 m depth (3 months) before harvest.¹⁰⁷

In Portugal, propagules of *Codium tomentosum* are obtained by cutting vegetative spongy thalli into ~2 cm fragments. The resulting fragments are subsequently maintained and grown in culture flasks with controlled temperature and lighting conditions, under sufficient aeration to move the fragments inside the culture vessels during the nursery phase. Once fully regenerated, juvenile thalli are transferred to outdoor tanks and grown in free-floating (tumble culture) conditions in a land-based IMTA operation.¹¹⁸ The company ALGApus Ltd. is dedicated to the aquaculture of organic certified fish (European sea bass and gilthead sea bream) and marine macroalgae native to the NW Atlantic coastal waters. In this system, nutrient-rich effluent derived from semi-intensive fish farming is continuously pumped through macroalgae growing tanks (max. 20,000 L) in an open-flow regime, after passing through a sedimentation pond and a mechanical filtration unit (>40 µm).⁴⁰

3.2 | Manipulation of reproductive structures

Among all macroalgae, the genus *Ulva* (sea lettuce) includes some of the best-known species regarding developmental biology. The genus presents isomorphic diplohaplontic life cycle patterns, in which species can naturally propagate through a variety of different modes including sexual and asexual reproduction.¹⁵⁶ Artificial propagation methods for *Ulva* are mainly achieved by inducing the release and germination of swarmers from vegetative thalli. The term swarmer collectively refers to motile reproductive propagules that differ according to the life stage from which they originate. These can be quadriflagellate zoospores (or zoids) when sourced from the sporophyte; or biflagellate male or female gametes when sourced from the gametophyte.⁸⁹ The sexual life cycle involves the alternation between isomorphic sporophytic and gametophytic generations. The gametophyte produces haploid biflagellate gametes that conjugate and form the sporophyte. The sporophyte produces quadriflagellate

zoospores that develop into male or female gametophytes, thereby closing the life cycle¹⁵⁷ (Figure 5, Box 2). In most *Ulva* species, asexual reproduction can occur from unfertilised gametes parthenogenetically,^{158,159} or from vegetative propagation through regeneration of fragmented tissue.⁸⁸ However, some species or subpopulations reproduce exclusively through asexual propagation, via direct germination of biflagellate gametes or quadriflagellate zoospores.^{160,161}

Extensive research on *Ulva* has allowed the development of laboratorial propagation methods, including classic genetic crosses by gamete conjugation as well as via parthenogenesis.¹⁵⁷ In some species, for example *U. mutabilis*, *U. lactuca* and *U. linza*, gametogenesis can be induced by removal of 'sporulation inhibitors' by cutting vegetative thalli, washing the fragments and transfer to fresh culture media.^{162–164} Further, gamete release can be induced and synchronised by dilution or removal of 'swarming inhibitors' from the culture media.¹⁶⁴

In aquaculture, artificial propagation of foliose *Ulva* species ('sea lettuce' type) may follow typical clonal fragmentation methods in which excised tissue fragments regenerate into adult thalli.¹⁶⁵ In filamentous species ('*Enteromorpha*' type), propagation is mainly achieved by inducing motile reproductive propagules release via fragmentation of vegetative thalli. According to early records on *Ulva prolifera* (syn. *Enteromorpha prolifera*) artificial propagation in Japan, propagules were obtained by mincing vegetative thalli in a rotary blender; the resulting fragments would release swarmers, which would be directly dispersed in 'seeding tanks' holding culture nets for attachment.¹⁶⁶ Optimisations to the same method attempted to promote synchronous gamete/spore release by cutting thalli into 1.2 mm diameter discs and studying optimum salinity and irradiance conditions.⁸⁸

Using the same principles, variations to the same techniques have been developed to allow for tank cultivation under free-floating conditions of *Ulva* species that require a fixed substrate. For instance, Hiraoka & Oka⁸⁶ developed a 'germling cluster method', in which motile reproductive propagules (gametes/spores) sourced from fragmented vegetative thalli are concentrated at high densities (10⁴ per mL) forming large propagule aggregations. These aggregations can then be split into 'germling clusters' containing 10–100 germlings each. Clusters are then transplanted to outdoor cultivation tanks under free-floating conditions.⁸⁶ More recently, another approach included the use of 'bioballs' as free-floating substrate for *Ulva tepida* cultivation in tumble culture. Briefly, gametes/spores obtained after thermal shock and fragmentation of vegetative thalli adhere to polyethylene wheel-shaped 'bioballs'.¹⁶⁷

Traditionally, the grow-out phase in commercial scale aquaculture of *Ulva* takes place in open waters, where seeded nets are cultivated on poles fixed in shallow, calm oceanic or estuarine waters with periodical exposure to air at low tide.⁸⁸ Tank-based cultivation methods have been established or experimentally validated for several *Ulva* species using a variety of different methods including: *U. prolifera* using the 'germling cluster method';⁸⁶ *U. tepida* in outdoor tanks attached to ropes at 10 cm depth^{89,168} or free floating attached to free-floating 'bioballs';¹⁶⁷ *Ulva* spp. in large-scale raceways using paddle-wheels for water recirculation;³⁹ *U. ohnoi* in free-floating in fibre-glass parabolic

tanks (10,000 L) receiving nutrient-rich water from barramundi (*Lates calcarifer*, Bloch 1790) hatchery,¹⁶⁹ *U. compressa* using a drip-irrigation system;¹⁷⁰ *U. rigida* in concrete tanks (20,000 L) in free-floating conditions using nutrient-rich effluent from fish farm in IMTA;⁴⁰ *U. lactuca* free floating in tumble culture,¹⁷¹ or in pilot scale photobioreactors.¹⁷²

Unlike *Ulva*, the aquaculture of commercially exploited *Monostroma* species in Japan (*M. nitidum*, *M. latissimum* and/or *M. kuroshiensis*) involves the manipulation of the sexual life cycle. Therefore, *Monostroma* cultivation involves alternating heteromorphic generations of macroscopic dioecious gametophytes and microscopic sporophytes, each generation produces biflagellate gametes and quadriflagellate zoospores, respectively.^{94,96} Although asexual propagation methods are currently unexplored in this genus, asexual reproduction via biflagellate gametes germination has been described in one strain of *M. kuroshiensis*.^{96,173}

Artificial propagation of *Monostroma nitidum* involves several steps including induction of gamete release; zygote conjugation; zygote maturation; and zoospore seeding to artificial substrata (Figure 5, Box 3). Each step is artificially induced by manipulating osmotic, thermal and irradiance conditions.⁹⁴ Traditionally, propagule production starts with the collection of mature gametophyte fronds from the environment. Gamete liberation is induced by drying fronds overnight in the dark, prior to placing them in warmer water (plus 2–3°C) and exposing to bright light. After in vitro fertilisation, zygotes are led to adhere to plastic settlement boards (20 × 10 cm) for 30 min and subsequently grown in culture tanks under natural light until they mature into zoosporangia (4–5 months). Zoospores are liberated by the zoosporangia and directly seeded on culture nets. The grow-out phase takes place after transplanting seeded nets to open water cultivation grounds. Nets are installed horizontally to wooden poles at appropriate height to provide adequate exposure to air during low tide.⁹⁴

Artificial propagation method for the production for *Capsosiphon fulvescens* has been developed in Korea and relies on asexual propagation via germination of parthenogenetic gametes.¹⁰⁰ To obtain germings, vegetative thalli are collected from the environment and fragmented into 1 cm sections. The fragments are incubated in controlled conditions until the formation of gametangia is observed (approx. 15 days). Then, gametangia liberate parthenogenetic gametes that can readily attach to adequate substrates (eg bamboo or nylon nets). Substrates are subsequently transferred to open water growing grounds, where they are fixed to poles in the intertidal zone. The best production rates have been achieved when germings are attached to bamboo nets (600 parallel bamboo sticks, 1.8 m long × 1.0 cm wide × 0.5 cm thick, that compose 40 m long units), placed in a high tide environment (5 h air exposure per day) allowing to produce a maximum of 7 kg wet weight per m² in two months.¹⁰⁰

4 | GREEN MACROALGAE AS SOURCES OF BIOACTIVE COMPOUNDS

A survey of the published literature on natural compounds extracted from macroalgae reveals biased screening and bioprospecting

efforts in the major groups of seaweeds. Leal et al.¹⁷⁴ reported that only 8% of marine natural products isolated from macroalgae from 1965 to 2012 in the MarinLit database originated from green macroalgae, while red and brown macroalgae accounted for 53 and 39%, respectively. Within green macroalgae, the order Bryopsidales accounted for approx. 2/3 of these compounds.¹⁷⁴ Natural compounds extracted from green macroalgae identified with strong bioactive properties are highly diverse and include sulphated polysaccharides, lipids, photosynthetic pigments and various secondary metabolites.^{175–178}

4.1 | Sulphated polysaccharides

Macroalgae have been recognised as potential sources of sulphated polysaccharides, important components of cell walls.¹⁷⁷ Main types of macroalgal sulphated polysaccharides are fucans, carrageenans and ulvans extracted from brown, red and green seaweeds, respectively. Ulvans are water-soluble sulphated polysaccharides composed of disaccharide repetition moieties made up of sulphated rhamnose linked to either glucuronic acid, iduronic acid or xylose and represent about 8–29% of the algal dry weight.¹⁷⁹ Ulvans are not exclusive to *Ulva* species and are present in other ulvophycean genera such as *Monostroma*, *Caulerpa*, *Codium* or *Gayralia*.¹⁷⁷ Antioxidant, anti-inflammatory, antitumoral, immunomodulatory, anticoagulant and antiviral activities have been reported for green macroalgal sulphated polysaccharides (Table 2). Desulphation significantly decreases bioactivity of ulvans, indicating that the sulphate residues are important for the stimulatory capacity of these molecules.^{180–182} The presence of glucuronic acid in green macroalgae extracts has been related to skin hydration and protection capacities. Extracts from the green macroalgae *Codium tomentosum* are currently used as a moisturising agent in the cosmetic industry.^{183,184}

In addition, the bioactive properties displayed by sulphated polysaccharides extracted from Ulvophycean taxa are highly regarded for different biomedical applications. For instance, sulphated polysaccharides extracted from several green macroalgae in the genera *Codium* and *Monostroma* exhibited strong blood anticoagulant activity.^{182,185–187} Qi et al.¹⁸⁰ observed high scavenging activity of superoxide and hydroxyl radicals by ulvans extracted from *Ulva australis*. Ulvan polysaccharides extracted from *Ulva lactuca* were shown to induce apoptosis and suppression of cell division, providing antitumoral activity against cancer cell lines.¹⁸⁸ Antiviral and immunostimulatory activities were identified for sulphated polysaccharides extracted from several green macroalgal species^{181,189–193} (Table 2).

4.2 | Lipids

Lipids are molecules soluble in nonpolar solvents that act as main structural components of cell membranes but are also involved in energy storage and cell signalling pathways. Mass spectrometry

TABLE 2 Examples of natural compounds extracted from marine green macroalgae and reported bioactivity

Compound(s)	Bioactivity	Green macroalgal source	References
Sulphated polysaccharides	Anticoagulant	<i>Codium dwarkense</i>	185
		<i>Codium vermilara</i>	182
		<i>Monostroma latissimum</i>	186
		<i>Monostroma angicava</i>	187
	Antioxidant	<i>Ulva australis</i>	180
	Anti-inflammatory	<i>Ulva rigida</i>	181
	Antiviral	<i>Gayralia oxysperma</i>	190
		<i>Monostroma nitidum</i>	192
		<i>Ulva lactuta</i>	189
	Antitumoral	<i>Codium fragile</i>	193
		<i>Ulva lactuta</i>	188
<i>Ulva prolifera</i>		191	
Immunomodulatory	<i>Ulva rigida</i>	181	
Lipids	Antioxidant	<i>Codium tomentosum</i>	117
Sulfolipids	Antiviral	<i>Ulva fasciata</i>	197
	Antitumoral		
	Antibacterial		
Glycolipids	Antitumoral	<i>Ulva armoricana</i>	196
Clerosterol	Anti-inflammatory	<i>Codium fragile</i>	199
	Antitumoral		198
Squalene	Antioxidant	<i>Caulerpa racemosa</i>	200
	Anti-inflammatory		
Siphonaxanthin	Antiangiogenic	<i>Codium fragile</i>	201
	Antitumoral		202
Pheophytin <i>a</i>	Anti-inflammatory	<i>Ulva prolifera</i>	205
	Antitumoral		206
Pheophorbide <i>a</i>	Antioxidant		207
Terpenoids	Neuroprotective	<i>Caulerpa racemosa</i>	210
Racemosin A (alkaloid)	Neuroprotective		211
Caulerprenylols (<i>para</i> -xylene)	Antifungal		212
Caulerpin (alkaloid)	Anti-inflammatory		175
	Antitumoral	<i>Caulerpa cylindracea</i>	213
Sesquiterpenes	Antitumoral	<i>Ulva fasciata</i>	214
Cladophorols (phenol)	Antibacterial	<i>Cladophora socialis</i>	215
Kahalalide F (depsipeptide)	Antitumoral	<i>Bryopsis</i> sp.	217
	Antiviral		
	Antimalarial		

has allowed detailed characterisation of the polar lipid profile of macroalgae (glycolipids, phospholipids and betaine lipids), some of which with proven nutritional and health benefits.¹⁹⁴ Of particular relevance for lipid bioactivity is the high content of polyunsaturated fatty acids (PUFA), considered as essential components in human and animal health and nutrition.¹⁹⁵ Macroalgae are a potential source for large-scale production of essential PUFA with wide applications in the nutraceutical and pharmacological industries.¹⁷⁸ High relative abundance of long-chain PUFA, namely *n*-3 fatty acids,

was observed in *Codium galeatum*, *Codium tomentosum* and *Ulva armoricana*.^{32,117,196}

The biological activities of Ulvophyceae-derived lipids have been studied in some representative taxa, showing interesting biomedical potential. For instance, the sulfolipids of different algal species, including *Ulva fasciata*, exhibited strong antiviral, antitumoral and antibacterial activities.¹⁹⁷ Glycolipids from *Ulva armoricana* showed promising antiproliferative activities on cancer cell lines.¹⁹⁶ Clerosterol extracted from *Codium fragile* was shown to cause

apoptosis of human melanoma cells.¹⁹⁸ This sterol was also shown to reduce expression of pro-inflammatory proteins and could be used as a therapeutic agent against UVB-induced inflammatory and oxidative skin damage.¹⁹⁹ Prominent antioxidant and anti-inflammatory activities were observed for squalene extracted from *Caulerpa racemosa*.²⁰⁰

4.3 | Photosynthetic pigments

Photosynthetic pigments are light harvesting compounds present in the chloroplasts of plants and algae. Their main function is to absorb light energy within the visible spectrum (400–700 nm) that is converted to chemical energy in the process of photosynthesis. However, some pigments have strong antioxidant properties and their main function in the cell is to avoid light damage by heat dissipation or as part of reactive oxygen species scavenging mechanisms. Green macroalgae possess two main types of photosynthetic pigments: chlorophylls and carotenoids (carotenes and xanthophylls).

Photosynthetic pigments of green macroalgae have been reported to provide several health benefits that include antioxidant, anti-inflammatory, antitumoral and antiangiogenic activities (Table 2). Ganesan et al.²⁰¹ identified strong antiangiogenic properties of the xanthophyll siphonaxanthin extracted from *Codium fragile*. This keto-carotenoid specific to green algae was also shown to be effective in inducing apoptosis in human leukaemia cells.²⁰² Siphonaxanthin is a more potent antitumoral agent than fucoxanthin, a carotenoid that was previously shown to inhibit the proliferation of cancer cells through the induction of apoptosis.^{203,204} Chlorophyll *a*-derived pigments such as pheophytin and pheophorbide *a* have also been shown to possess bioactive properties. Pheophytin *a* derived from *Ulva prolifera* has been reported to have strong anti-inflammatory and anticarcinogenic activities,^{205,206} while antioxidant properties have been observed for pheophorbide *a*.²⁰⁷ Although natural pigments have the technological disadvantage of having lower stability compared with their synthetic counterparts, different methods and compounds have been successfully used to improve stabilisation of pigment properties and bioactivities.²⁰⁸ The development of efficient delivery systems is also an effective way to enhance pigment stability and bioavailability.²⁰⁹

4.4 | Secondary metabolites

A diversity of other bioactive compounds have been described in green macroalgae, mainly secondary metabolites often playing important roles in defence against herbivory (Table 2). Secondary metabolites extracted from species of the genus *Caulerpa* are particularly diverse, with described neuroprotective, anti-inflammatory, antitumoral and antifungal effects.^{175,210–213} Among these metabolites, the alkaloid caulerpin has potential for therapeutical applications in the treatment of colorectal carcinoma.²¹³ Selective

cytotoxicity towards breast cancer cells was found for a novel sesquiterpene derivative extracted from *Ulva fasciata*.²¹⁴ Potent and selective antibacterial activity was shown for cladophorols extracted from *Cladophora socialis*.²¹⁵

Kahalalide F is a potent cytotoxic compound extracted from *Bryopsis* sp. with described antitumoral, antiviral and antimalarial activity.^{216,217} Zan et al.²¹⁸ recently showed that kahalalides, including kahalalide F, are indeed produced by an obligate bacterial symbiont of the marine alga as defensive molecules that protect the host from herbivory. The mollusc *Elysia rufescens* that feeds on *Bryopsis* is tolerant to kahalalides and hijacks these molecules using them for its own defence against predation.²¹⁸

5 | FUTURE PERSPECTIVES

The present review outlines the potential of further exploring green macroalgae in aquaculture and argues that this group of macroalgae presents itself as a compelling option under the current quest for commercial diversification of products and expansion of the sector. With a remarkable diversity of morphological forms, eco-physiological traits, bioactive molecules and propagation potentials, green macroalgae constitute an important, yet underexplored aquaculture resource. Despite presenting comparably lower production volumes compared with red and brown seaweeds, global green macroalgae aquaculture reportedly accounts for approx. 20,000 tonnes fresh weight annually.¹⁹ The present review indicates this value is significantly underestimated, particularly considering the absence of production data from Japan, where commercial cultivation of *Monostroma*, *Ulva* and *Caulerpa* species is a long standing and ongoing activity.⁶³ In addition, emerging ulvophyceyan taxa in aquaculture remain unaccounted for in international databases (eg *Codium tomentosum*), while taxonomic uncertainty of species and/or seaweed-derived products creates additional challenges to the academic, public and industrial players. These issues call for more detailed molecular surveys and transparent data communication of green macroalgae aquaculture goods to provide more standardised, higher quality, traceable products, important requisites to increase consumer and industrial confidence.^{25,65}

Nonetheless, several general advantages of cultivating green macroalgal taxa can be highlighted, such as: unique diversity; high tolerance to extreme abiotic conditions; high potential for biofiltration; easiness in obtaining quality seed; exclusive bioactive compounds; and high market value. Cultivation technologies are relatively well developed for representatives of the major ulvophyceyan lineages. This may form important baseline knowledge to support further domestication of local species or varieties. Additionally, green macroalgae aquaculture is expected to benefit from the implementation of nursery facilities dedicated to producing high-quality propagules of defined desirable strains, ready to supply farmers upon demand. For instance, commercial nursery facilities are now established in Europe (eg Hortimare). Furthermore, improvements to conventional propagule production methods are expected from advances in the

manipulation of protoplasts (somatic cells devoid of cell walls able to regenerate into *de novo* plants) to produce protoplast-derived propagules in aquaculture. Compelling arguments on the use of protoplast-derived propagules in aquaculture include the potential for genetic engineering, genetic transformation and somatic hybridisation processes that will facilitate the development of improved strains in aquaculture.^{219,220} Green macroalgae may be in the forefront of protoplast mediated propagation technologies. Protoplast isolation and regeneration protocols are well established for several ulvophyccean taxa (*Ulva*, *Monostroma*, *Chaetomorpha* and *Bryopsis*);^{219,221-223} while a detailed model system for high-throughput macroalgal nursery, based on protoplast-derived propagation technologies for large-scale aquaculture of *Ulva* species has been recently proposed.²²⁴

Macroalgal aquaculture is expected to gain traction in emerging markets, particularly in Europe where large-scale consortium projects/networks have been joining efforts to boost macroalgae aquaculture (eg GENIALG; PHYCOMORPH), also aiding in the development and publication of guidelines towards macroalgae aquaculture sustainability.²²⁵ Some of the major drivers impelling the movement include the following: (i) increased perception of macroalgae as sustainable healthy foods; (ii) the quest for alternative sustainable protein sources; and (iii) rising industrial interest. While changing western cultures dietary regimes to include macroalgae in the menu is an ongoing process,²² positive signs are emerging in the field of 'phycogastronomy',²²⁶ taken the example of high-end restaurants that currently offer a variety of dishes featuring green macroalgae as the main delicacy ingredient (eg *Codium tomentosum*, *Caulerpa lentillifera*).⁴¹ On the other hand, implementation of industrial operations using green seaweeds as raw material is expected to increase demand, given the growing interest in implementing biorefineries to produce various products (reviewed by Zollmann et al.³⁸). Ultimately, sustainability of the entire production chain will define the viability of each operation.

Today, sustainability assessments are scarce but required to unlock green macroalgae (and other seaweeds) potentials. Sustainability of products comprises three components: environment, economy and social aspects.²²⁷ These three components must be properly assessed and balanced when products are designed or improved. Life-cycle assessment (LCA) is a structured, comprehensive and internationally standardised method to evaluate environmental impacts of the bioeconomy.²²⁸ The LCA aims to assess the potential environmental impacts associated with a product, a process or a system throughout its life cycle. With sustainability and green markets becoming more popular around the globe, the concept of life cycle sustainability assessment (LCSA) has been introduced.^{227,229} The novelty of LCSA is the inclusion of equity in the environmental costs. Conclusions are withdrawn from a set of weighting indicators such as financial profitability, market demand, social acceptability, willingness to pay and bioeconomic modelling, to obtain a single common life cycle sustainability result. Although directly applicable methods for LCSA applied to macroalgae aquaculture are currently under

development,²² emerging LCSA case-studies highlight the potential benefits of performing such analysis. By allowing to identify impacting hotspots within the aquaculture value chain, improvements can be implemented towards increased sustainability. For instance, LCA studies applied to large-scale cultivation of the brown algae *Saccharina latissima*, suggested that seaweed farming has the potential of becoming a profitable industry in North West Europe,^{230,231} with great promise to reduce the resource footprint of seaweed cultivation once energetic efficiency is improved (electricity and transport) and biomass productivity increases;^{230,232} and/or improvements on infrastructural component materials (eg stainless steel chains, polypropylene ropes) and system design (eg number of cultivation strips in the water column) are employed.²³³ Similarly, an explorative LCA study performed to evaluate the environmental impacts of producing bioplastics from green macroalgae (*Ulva* spp.) allowed to identify the main impacting hotspots in the production chain, those related to high energetic costs of cultivation in land-based systems and material efficiency.⁴⁶ In this context, performing LCAs at the initial stage of implementing green macroalgal aquaculture and conversion will become advantageous, as the recommended design improvements can be implemented without significant economic investments.²³⁴ Overall, these studies suggest that an effective transition to renewable energies, and to more eco-friendly materials will greatly increase macroalgae aquaculture sustainability. Synergies between the academic and private sectors will further allow developing multidisciplinary methodologies assessing macroalgal aquaculture activity to gain market and social trust.

Despite the existing opportunities for green macroalgae in aquaculture, it is not expectable that production of this select group of seaweeds reaches the order of magnitude of their red and brown macroalgal counterparts. Instead, it is likely that green macroalgae will remain to occupy specialised market niches, in which high-value products are favoured as opposed to large quantity production rendering low price biomass. This has been the case in the Asia-Pacific region, where green macroalgae have been cultivated to produce speciality food products, constituting relatively small, localised market niches, within specific cultural backgrounds. In turn, the aquaculture of hydrocolloid-bearing macroalgal species (red and brown) supplies a growing, mass scale production and increasingly commoditised industry.²³⁵ To circumvent the competitive advantages of the seaweed-hydrocolloid industry thriving in Asia, the future of seaweed aquaculture in emerging markets (eg Europe) may not necessarily depend on producing large amounts of biomass, but rather focus on adding value to the seaweed production chain, through by-product development (eg fodder, fertilisers, bioactive compounds) and capitalising on societal benefits (eg economic, environmental).²² The unique features presented by Ulvophyccean macroalgae (eg distinct biochemical profiles and organoleptic properties, high nutrient uptake and propagation capacity, diverse cultivation technologies, tolerance to extreme conditions) represent a remarkable potential for innovation in macroalgal aquaculture.

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DATA AVAILABILITY STATEMENT

Data sharing not applicable – no new data generated.

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