

Epiphytic macroalgae of maricultured *Sargassum* and their potential utilizations

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Abstract – Epiphytism commonly occurs in marine benthic macroalgae and seagrass communities under natural conditions and those of mariculture. This can greatly obstruct the cultivation of commercial seaweeds and ultimately impacts the seaweed aquaculture industry negatively. Against a background of climate change and a rapidly increasing market demand, the commercial *Sargassum* species is experiencing increasing challenges posed by epiphytic macroalgae. Severely reduced growth, lower quality, the emergence of diseases, and the ultimate death of the algae can lead to a commercial loss. Attempts to limit epiphytic macroalgae in aquaculture have so far been inefficient. However, epiphytic macroalgae are also rich in nutritional compounds and their relative biomass could be used as efficiently as the cultivated seaweed. As epiphytes cannot effectively be controlled by the current physical, chemical, and other methods in most cases, the perspective of comprehensive utilization could be an alternative over complete prevention and control by traditional methods. Compared to the existing strategies for controlling the growth and spread of epiphytes in seaweed aquaculture, the integrated and indiscriminate harvest and utilization of epiphytic macroalgae as fertilizer, animal food additive agents, as well as the development of biodegradable materials, might prove to be alternative valorization. However, the implementation of epiphytic macroalgae utilizations still needs to overcome the technical obstacles.

Keywords: Phaeophyta / brown algae / epibiosis / interspecific competition / control strategy

1 Introduction

Epiphytism is a typical form of invasive interspecific relationship that commonly occurs in marine benthic macroalgae and seagrass communities under natural and mariculture conditions. Epiphytes are an essential component of biological diversity in natural and farmed seaweed communities. Taking cultured *Sargassum fusiforme* as an example, as many as 28 kinds of epiphytic macroalgae had been identified (Li et al., 2009b; Tian et al., 2023). In addition, the fixed amount of C and N of *Ulva*, a representative epiphytic green alga, were 179.96 and 32.40 t, respectively, which accounted for nearly 6% of the output of cultured *S. fusiforme* (Tian et al., 2023). Unfortunately, under artificial cultivation conditions, commercial seaweeds are subjected to high incidences of epiphytism

(Williams and Smith, 2007; Ward et al., 2020). Cultivated seaweeds and other marine aquaculture facilities provide considerable surface area for the epiphytes to colonize.

Although the combination of epiphytes and the cultured seaweeds are important for the construction of the temporary raft/rope-dependent biome, the epiphytes are opportunistic space-grabbers (Xie et al., 2013; Nakajima et al., 2015; 2016; Gribben et al., 2019; Guy-Haim et al., 2020). This trait of the epiphyte has allowed them to spread rapidly around the farming areas. Epiphytic macroalgae (EpMA) associated with farmed seaweeds mainly include epiphytic algae attached to seaweeds and their farm-related facilities (i.e., species of *Ulva*, *Ectocarpus*, and *Polysiphonia*, as shown in Tabs. 1 and 3). These algae compete directly with the cultured thalli for living space on cultivation ropes and rafts, or they might invade the various cultivation systems (Ask and Azanza, 2002; Kerrison et al., 2016).

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Table 1. List of reported epiphytic macrophytes of maricultured *Sargassum* (S.).

Epiphytic species	Host	Country	References
Chlorophyta			
<i>Ulva lactuca</i>	<i>S. naozhouense</i>	China	Jia et al., 2012; Xie et al., 2013; Xu et al., 2022a; Tian et al., 2022
<i>Ulva fasciata</i>	<i>S. fusiforme</i>		Li et al., 2009b
<i>Ulva pertusa</i>			
<i>Ulva</i> spp.			Pang et al., 2007
<i>Ulva</i> spp.	<i>S. horneri</i>		Zhang et al., 2009
	<i>S. thunbergii</i>		Li et al., 2009a
	<i>Sargassum</i> sp. 1	Korea	Redmond et al., 2014
<i>Ulva prolifera</i>	<i>S. naozhouense</i>	China	Jia et al., 2012; Xie et al., 2013
<i>Ulva linza</i>	<i>S. fusiforme</i>		Li et al., 2009b
<i>Ulva clathrata</i> *			
<i>U. clathrata</i> *	<i>S. naozhouense</i>		Xie et al., 2013
<i>Chaetomorpha spiralis</i>	<i>S. fusiforme</i>		Li et al., 2009b
<i>Cladophora</i> spp.	<i>S. naozhouense</i>		Jia et al., 2012
<i>Cladophora glaucescens</i>	<i>S. fusiforme</i>		Li et al., 2009b
<i>Codium fragile</i>			
<i>Bryopsis</i> spp.			
Phaeophyta			
<i>Ectocarpus</i> spp.	<i>S. fusiformis</i>	China	Pang et al., 2007
	<i>S. horneri</i>		Zhang et al., 2009
	<i>S. thunbergii</i>		Liang et al., 2013
	<i>Sargassum</i> sp. 1	Korea	Redmond et al., 2014
<i>Ectocarpus confervoides</i>	<i>S. naozhouense</i>	China	Jia et al., 2012; Xie et al., 2013
	<i>S. fusiforme</i>		Li et al., 2009b
<i>Endarachne binghamiae</i>	<i>S. fusiforme</i>		
<i>Leathesia difformes</i>			
<i>Colpomenia sinuosa</i>			
Rhodophyta			
<i>Polysiphonia</i> spp.	<i>S. horneri</i>	China	Zhang et al., 2009
	<i>S. fusiformis</i>		Pang et al., 2007
	<i>S. thunbergii</i>		Li et al., 2009a
<i>Polysiphonia japonica</i>	<i>S. fusiforme</i>		Li et al., 2009b
<i>Hypnea boergesenii</i>	<i>S. naozhouense</i>		Jia et al., 2012; Xie et al., 2013
	<i>S. fusiforme</i>		Li et al., 2009b
<i>Chondrus ocellatus</i> *	<i>S. fusiforme</i>		Li et al., 2009b
<i>Ceramium kondoi</i>	<i>S. naozhouense</i>		Jia et al., 2012; Xie et al., 2013
	<i>S. thunbergii</i>		Li et al., 2009a
<i>Ceramium paniculatum</i>	<i>S. fusiforme</i>		Tian et al., 2022
<i>Gracilaria tenuistipitata</i> *	<i>S. naozhouense</i>		Jia et al., 2012; Xie et al., 2013
<i>Gracilaria</i> spp.*	<i>Sargassum</i> sp. 1	Korea	Redmond et al., 2014
<i>Gracilaria bursa-pastoris</i> *	<i>S. fusiforme</i>	China	Li et al., 2009b; Tian et al., 2022
<i>Grateloupia turuturu</i> *			
<i>Grateloupia filicina</i> *			
<i>Grateloupia livida</i> *			
<i>Pyropia haitanensis</i> *			
<i>Pyropia yezoensis</i> *			
<i>Corallina officinalis</i>			
<i>Amphiroa ephedraea</i>			
<i>Lomentaria catenata</i>			
<i>Antithamnion cruciatum</i>			
<i>Dasya villosa</i>			
<i>Acanthophora spicifera</i>	<i>S. naozhouense</i>		Xie et al., 2013

* Indicates that this EpMA is also a type of seaweed known to be cultivated in other countries or regions.

Table 2. Current strategies for epiphyte control that applied to *Sargassum* mariculture practice.

Strategies	Principles	References
Removed by hand	Physical processing	Xu et al., 2022a
Cultured with filtered water during indoor tank cultures		Xie et al., 2013
Strong water jet	Different tolerance to chemical reagent	Pang et al., 2007; Redmond et al., 2014
Chemical methods such as sodium hypochlorite or ammonium sulfate		Kerrison et al., 2016
Treated with organic acid (citric acid, acetic acid), or inorganic acid (phosphoric acid, hydrochloric acid)	Higher acid and alkalinity tolerance in host algae than epiphytes	Hwang et al., 2015
Growing plants at high densities in rope cultures	Minimizing underwater light availability to depress epiphytes growth	Pang et al., 2007

Table 3. Comparisons of chemical compositions of the main epiphytic macrophytes (g 100 g⁻¹ dw).

Epiphytic species	Protein	Lipid	Ash	Carbohydrate	Dietary fiber	Reference
Chlorophyta						
<i>Ulva lactuca</i>	8.46	7.87	19.59	–	–	Yaich et al., 2011
<i>Ulva pertusa</i>	14.6–16.1	2.1–7.4	25.9–28.6	–	52.2–59.0	Benjama and Masniyom, 2011
<i>Ulva</i> spp.	9.45–14.10	2.24–2.27	32.64–36.38	–	–	Aguilera-Morales et al., 2005
<i>Ulva prolifera</i>	24.9–27.40	1.09–1.49	10.93–14.15	50.67–51.14	36.66–45.94	Hwang et al., 2008
<i>Ulva linza</i>	10.69±0.67	0.99±0.00	18.03±2.37	–	5.6±1.69	Tabarsa et al., 2012a
<i>Codium fragile</i>	10.8±0.0	1.5±0.0	20.9±0.2	66.8±0.4	–	Ortiz et al., 2009
Phaeophyta						
<i>Ectocarpus</i> spp.	–	4–6	–	–	–	Müller and Eichenberger, 1994
<i>Endarachne binghamiae</i>	16.3	0.77	24.78	45.15	13.0	Huang and Lee, 2005
<i>Colpomenia sinuosa</i>	11.83±1.47	1.79±0.56	33.08±0.82	–	11.6±0.56	Tabarsa et al., 2012b
Rhodophyta						
<i>Hypnea boergesenii</i>	16.31–18.64	1.27–1.56	18.65–21.57	20.60–22.89	37.92–40.59	Siddique et al., 2013
<i>Gracilaria tenuistipitata</i>	11.6±1.1	2.7±0.6	22.9±2.2	–	64.0±0.2	Masniyom and Benjama, 2012
<i>Gracilaria bursa-pastoris</i>	2.3–12	–	–	–	25.6–39	Korzen et al., 2016
<i>Grateloupia turuturu</i>	22.9	2.6	18.5	–	60.4	Denis et al., 2010
<i>Grateloupia filicina</i>	9.50	1.35	14.95	68.25	–	Athukorala et al., 2007
<i>Pyropia haitanensis</i>	34.88–37.21	1.68–2.09	8.75–9.92	46.86–49.27	–	Xie et al., 2009
<i>Corallina officinalis</i>	5.91	1.37	–	27.98	–	Ismail, 2017

The genus *Sargassum* (Phaeophyceae) encompasses the largest number of species (350) among the brown algal lineage (Yip et al., 2020) and they are widely distributed from the temperate to tropical latitudes (Bringloe et al., 2020). *Sargassum* species, such as *S. fusiforme* (Xu et al., 2022b), is harvested and cultivated mainly in Southeast Asia for human consumption as sea vegetables, or used as medicinal “seaweed herbs” as other species such as *S. fulvellum* (Hwang et al., 2015), *S. horneri* (Pang et al., 2009), *S. naozhouense* (Xie et al., 2013), *S. thunbergii* (Zhao et al., 2008), *S. vachellianum* (Chai et al., 2014), and *S. muticum* (Le et al., 2018).

Since 2010, global production has increased from 97,000 tons to more than 300,000 tons (FAO, 2021; Tian et al., 2023). This means the market demand for commercial *Sargassum* seaweed is expected to increase rapidly. This is due to the consumer’s need for new nutrition sources and healthy food supplements as well as the food industry’s interest in sustainable

textural additives and food safety (Tian et al., 2023). Therefore, there is a need to expand the cultivation of various *Sargassum*, and this will create opportunities for the proliferation of epiphytes. However, epiphyte species and abundance vary between cultivated species that is being colonized and the cultivation conditions. For the *Sargassum* species that are being cultivated, they are kept submerged in seawater during the cultivation to give them a more suitable growth condition. This tends to promote the diversity of epiphytes that attach to and colonize other seaweeds (Tian et al., 2022, 2023).

To optimize the commercial cultivation methods for *Sargassum*, many researchers have focused on the prevention and control of macroalgal epiphytes (Pang et al., 2007; Redmond et al., 2014; Kerrison et al., 2016; Han et al., 2021; Xu et al., 2022a). Fewer studies have explored the comprehensive utilization of these EpMA. This review discusses the detrimental effects of EpMA on the production

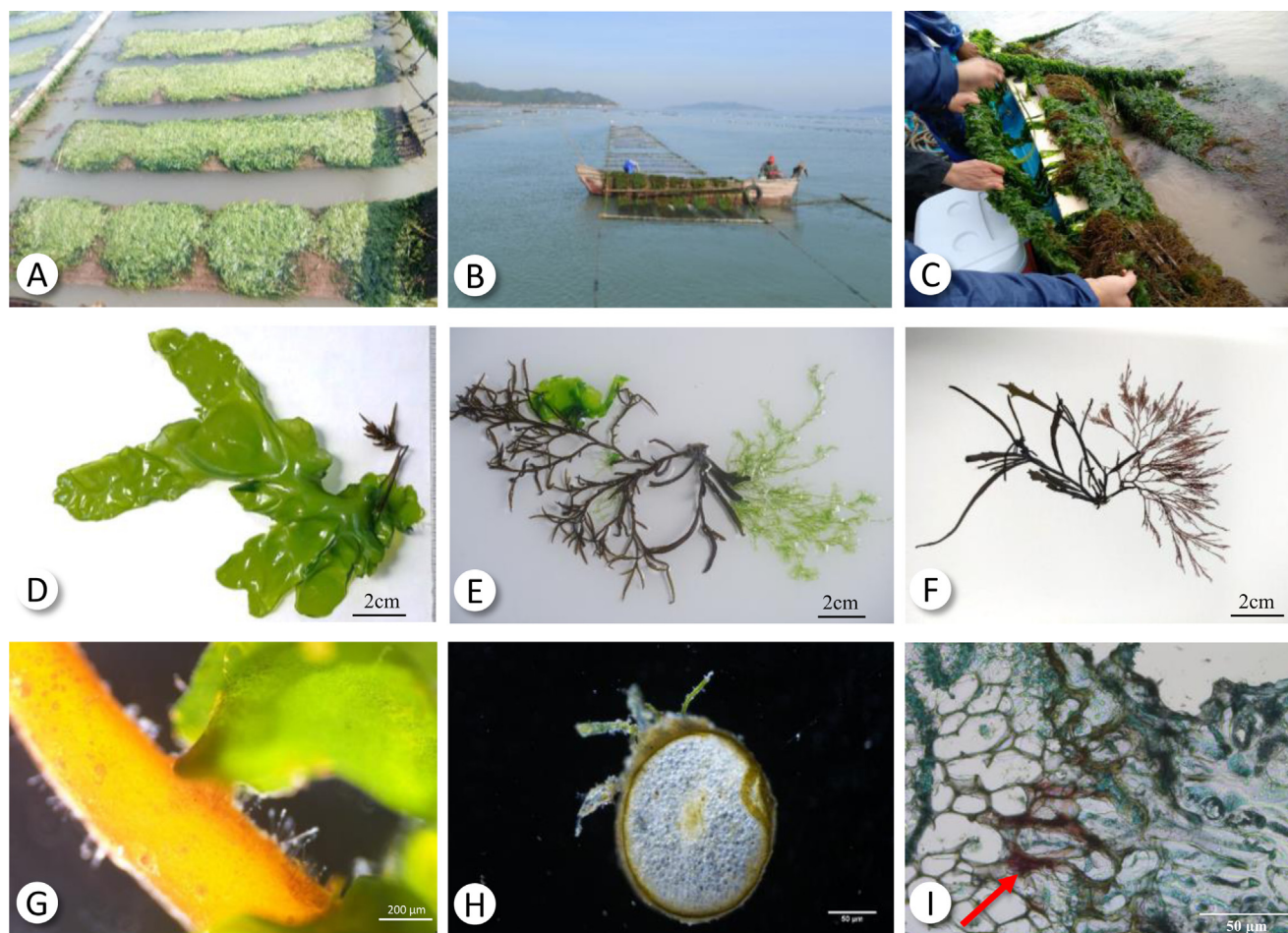


Fig. 1. Epiphytic macrophytes (EpMA) from seaweed mariculture (a case investigation of *Sargassum fusiforme*). A–C: EpMA attached to the juveniles and the ropes/rafts; D–F: species of *Ulva*, *Cladophora*, *Polysiphonia* attached to the juvenile; G–I: shows the microscopically amplified stem of juvenile with attached green algae (G–H) and the deformed superficial layer of the stems due to EpMA attachment (red arrow in I).

of commercial seaweeds in mariculture and their comprehensive utilizations as means of EpMA control method. The current challenges in epiphyte control will also be discussed.

2 Epiphytic macroalgae – their abundance and phenological patterns

According to the results reported in the collected literatures for cultivated *Sargassum* species, epiphytic macroalgae comprise three main macroalgal groups: green (Chlorophyta), brown (Phaeophyta), and red algae (Rhodophyta), and these groups show different dominance among these categories (Pang et al., 2007; Redmond et al., 2014; Hwang et al., 2015; Kerrison et al., 2016). Among them, the Chlorophyta and Rhodophyta have the most EpMA species, which are represented by *Ulva* and *Polysiphonia* (Tab. 1). Of these epiphytic macroalgae, the most troublesome ‘filamentous weedy’ species *Ectocarpus* (Phaeophyta) and *Polysiphonia* (Rhodophyta) occur most frequently in seaweed farming and pose huge challenges to *Sargassum* cultivation (Fig. 1).

The horizontal surface area provided by seaweed and the cultivation facilities is quite different from the longitudinal habitats of intertidal zone because the cultured seaweed remains submerged in the water all the time. The growth and reproduction patterns of the epiphytes mostly follow the annual growth phase of their hosts, with the most rapid growth increase occurring during the early stages of the cultivation period. *Ulva* species have been found throughout the cultivation period of *Sargassum fusiforme* in the coast of Southeast China (Xu et al., 2022a; Tian et al., 2022). By synchronizing with the host, these epiphytes would enhance their survival and increase the probability of host-epiphyte association (Young and Gobler, 2021). For the epiphytes most found in maricultured *Sargassum* and other species, observed phenological patterns suggest that the marine cultivation period of seaweed is precisely the time of year when epiphytic macroalgae develop and reproduce best (Tian et al., 2022), but there are vertical differences in the distribution of these macroalgae and their epiphytes in the natural environment (Armitage et al., 2017).

3 Detrimental effects of EpMA on cultured *Sargassum* and seaweed industries

3.1 Resources competition in *Sargassum* cultivation

Most of the EpMA on the cultivated *Sargassum* spp. are opportunists that exhibit rapid growth. The propagules may settle on the nearest algae and rafts/ropes in dense aggregations, thereby occupying the space meant for the cultured *Sargassum* seaweeds and competing for dissolved gases (i.e., dissolved inorganic carbon, DIC, and oxygen) (Tian et al., 2022, 2023). Moreover, under low light stress which is induced by dense epiphytic layer, the uptake of DIC by the host and its growth are reduced (Buschmann and Gómez, 1993; Snoeijs, 1994; Baer and Stengel, 2014) due to suppressed photosynthesis (Chen et al., 2015; Gao et al., 2019).

Another important adverse effect of EpMA is probably linked to their competition for nutrients (Buschmann and Gómez, 1993; Chen et al., 2015, 2019). Most fast-spreading EpMA have good strategies for nutrient utilization, such as higher nutrient absorption capacity or rapid proliferation under high nutrient supply. For instance, our previous studies have shown that during the culture cycle, the nitrogen absorption rate of the typical epiphyte *Ulva* was more than 50–80% higher than that of the cultured *S. fusiforme* growing at the same time (Tian et al., 2022). In a benthic community, *Sargassum polycystum* and *S. sanyaense* that are covered by thick layers of epiphytic algae will have a reduced capacity to utilize nutrients (Titlyanov and Titlyanova, 2013). During cultivation, eutrophication and even short, sporadic nutrient pulses tend to increase the growth of the EpMA such as *Ectocarpales* (Strain et al., 2014; Armitage et al., 2017), while the dense layers of epiphytic thalli including *Ulva* spp. can lead to low availability of nutrients and decreased growth rates of 20–60% for the hosts (Chen et al., 2015, 2019; Tian et al., 2022), which include *S. fusiforme* in China (Tian et al., 2022) and other commercial seaweeds (Wedchaparn et al., 2017).

3.2 Breakage and allelopathy of EpMA on cultivated *Sargassum* seaweed

Epiphytic macroalgae may penetrate the host cell wall, disrupting the cortical tissue at the attachment site (Kim et al., 2017; Tian et al., 2022). The penetrating rhizoids of some epiphytes can reach the medullary tissue of the host, destroying the host cells around the penetration site (Garbary and Deckert, 2002; Leonardi et al., 2006; Kim et al., 2017). Fouling and damage to the cultured seaweeds could subsequently intensify bacterial- or fungal- infections, even if the EpMA are not the carriers of the diseases (Xiong et al., 2018). For example, shading by dense EpMA such as species of *Ulva* and *Ectocarpus* can weaken *S. fusiforme* and other *Sargassum* species, rendering them vulnerable to breakage or the detachment of the whole thallus from the substratum, especially during increased current or wave action (Buschmann and Gómez, 1993; Tian et al., 2022). Such losses can markedly reduce the biomass production of cultured *Sargassum*.

Another detrimental effect is related to the allelopathic interactions. Some epiphytic algae can introduce enzymes

upon penetration of the host tissue (Leonardi et al., 2006). These enzymes can hydrolyze the intercellular polysaccharide matrices of the hosts (Bouarab et al., 1999; Leonardi et al., 2006). Different hosts might employ different chemical defense mechanisms against the epiphytes. For example, cultured *Sargassum* may show different degrees of susceptibility to EpMA, due to the different cell wall structures of the host macroalgae (Dawes et al., 2000), or different chemical defense mechanisms of the host against epiphytes (Nakajima et al., 2015).

3.3 Effects of epiphytes on industry

EpMA are significantly more abundant at high water temperatures during the cultivation of *Sargassum* (Xie et al., 2013; Kim et al., 2017). The limited defense strategies currently used against epiphytes in seaweed mariculture (Sureda et al., 2008; Kim et al., 2017) require manual removal of the algae when attached to the host as well as the rafts/ropes, especially during the period of slow *Sargassum* seaweed growth, which is labor-intensive (Xie et al., 2013). In addition to the induction of host thallus damage (Siniscalchi et al., 2012; Gauna et al., 2019), these fouling macrophytes may also become entangled with the farmed seaweed, restricting the latter's movement.

Massive infestations of EpMA can cause softening and bleaching of the host tissue. As reported on *S. fusiforme* in Eastern coast of China, EpMA infestation associated with diseases can also cause a severe reduction in the biomass production and low product quality for the cultivated *Sargassum* (Tian et al., 2022). Moreover, some species of EpMA, for instance, filamentous algae, are the preferred food for some groups of animals (Bittick et al., 2019). Once the cultured *Sargassum* coated with these EpMA, more grazers including *Gammarus* and *Siganus*, are attracted to graze on both host seaweeds and the EpMA (Strong et al., 2009). These rapidly growing EpMA severely hamper the growth of the hosts, and when harvested and dried under the sun, the *Sargassum* are tainted by the epiphytes. These lead lowered commodity value and yield for the cultured seaweed.

4 Current strategies for epiphyte controlling and the inadequacy thereof in *Sargassum*

Technological and experimental strategies have been developed to control the EpMA associated with cultured seaweeds (Tab. 2). The most straightforward method is to manually remove the epiphytes from the algal hosts, which is proved to be labor-intensive and impractical for large culture units (Huo et al., 2015). Excessive manipulation of the thalli can cause the fragmentation and rupture of the cultured seaweed, thereby reducing seaweed growth (Xu et al., 2022a). Moreover, after manual removal, the basal parts of the EpMA, such as *Ulva* sp. fronds, remain viable (Xu et al., 2022a) and may subsequently regenerate the thalli to re-occupy the space, including accessory structures and cultured *Sargassum* species. Other physical methods include the deployment of filtered water (Xie et al., 2013) or strong water jets for pressure washing (Pang et al., 2007; Redmond et al., 2014). However, it is very difficult to filter out the spores of the EpMA such as

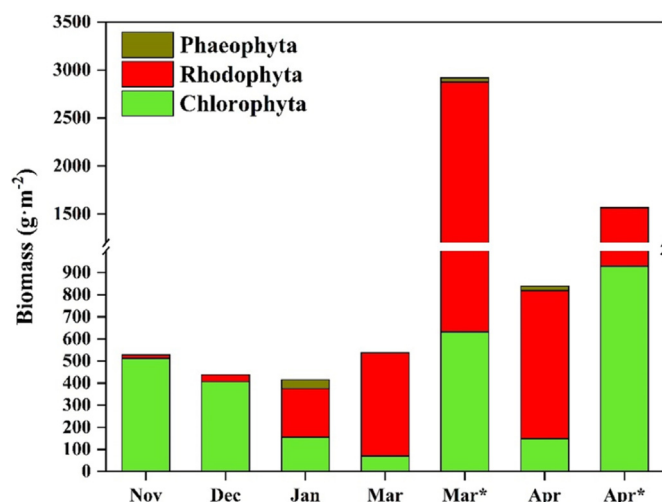


Fig. 2. Changes of epiphytic macroalgae biomass during *Sargassum fusiforme* culture. *: represents the algae attached to the host and the main rope.

Ulva, *Ecotocarpus*, *Polysiphonia* during the indoor seedling process, and others on a commercial scale of *Sargassum* cultivation in China and Korea, even with the use of sand-filter water treatment systems (Pang et al., 2007; Redmond et al., 2014). Some epiphytes are sensitive to osmotic changes and can be removed by means of creating salinity gradients in water during the indoor seedling stage. Desiccation of culture rope has also been proven efficient, especially in tank cultures (Pang et al., 2007; Xie et al., 2013; Chen and Zou, 2015), but it is impractical for large-scale cultivation in the open sea (Redmond et al., 2014).

Epiphytic macroalgae and cultured seaweeds generally have different tolerances to chemical reagents. Chemicals such as sodium hypochlorite or ammonium sulfate can be applied to eliminate EpMA and other epiphytic organisms such as *Ecotocarpus*, *Ulva*, and other species (Pang et al., 2007; Kerrison et al., 2016). However, treatment with a high concentration of the above-mentioned chemical reagents may also inhibit the growth of cultured *Sargassum* (Xu et al., 2022a). For differences in tolerance to pH, treatments with organic (citric acid, acetic acid) or inorganic acids (phosphoric acid, hydrochloric acid) have proven efficient for *Sargassum* species (Xie et al., 2013; Hwang et al., 2015; Xu et al., 2022a). However, if the reagent concentration is low, the elimination of EpMA may be incomplete (Xu et al., 2022a). Applicable methods for treating EpMA should consider the appropriate concentrations and treatment times for interspecific differences.

Studies on the interaction between the cultured *Sargassum* species of seaweeds and EpMA are important for developing potential control strategies. Despite the various methods for controlling EpMA, other aspects should be considered to limit the negative effects of EpMA. For example, high-quality seawater, suitable seawater currents, and appropriate temperatures are beneficial for the juvenile growth of some commercial seaweeds and the control of diseases in these seaweeds (Xie et al., 2013). Although some control methods

are indistinctively applied, seaweed in mariculture may require customized strategies based on the cultivation method for the cultured species. These methods are generally based on the differences in resource utilization capacity, stress tolerance of EpMA and the specific cultured seaweed (Pang et al., 2007; Wu et al., 2017). Until now, attempts at EpMA eradication are generally inefficient for large scale operations. The epiphytes are removed almost during the entire duration of the cultivation process, except at certain stages when a small amount of certain species of EpMA might be retained to prevent the juvenile from damage inflicted by high light intensity (personal investigation). In turn, the abandoned algae become a source of EpMA outbursts, such as the green tide (Wang et al., 2015). Therefore, it is necessary to develop more effective technologies and strategies to control the EpMA of *Sargassum* and other commercial seaweeds. However, no specific harvesting techniques for EpMA have been developed, and traditional harvesting methods includes manual collection by farmers, which takes some time and effort. Part of them can be carried out by the existing ways of economic seaweed cleaning and screening process. But there are still bottlenecks in the technology to carry out mechanized operations.

5 Potential utilization of epiphytic macroalgae and obstacles encountered

EpMA are as rich in nutritional compounds as cultured seaweed. These nutritional compounds include carbohydrates, proteins, lipids, ash, and dietary fiber (Tab. 3). Comparatively, the content of each profitable component in EpMA are like that found in the commercial species (Fig. 3).

Algae belonging to Chlorophyta and Rhodophyta account most of the EpMA species in *Sargassum* cultures. Some of EpMA are in fact cultivated species/genus in different countries. Among these EpMA species, those from the Chlorophyta phylum are dominant in biomass. For example, EpMA species such as *Ulva linza*, *Ulva prolifera*, *Ulva lactuca* and *Cladophora* spp. are often found in *Sargassum* mariculture (Tab. 3). In the case of *S. fusiforme* cultured in the East China Sea (Fig. 2), *Ulva* was the main EpMA and was present throughout the culture cycle, especially in the early stage of culture, with a biomass ranging from 156.00 to 512.33 g·m⁻². In the late culture period of March and April, the biomass of Rhodophyta represented by genus *Ceramium* and *Grateloupia* was the largest at the late stage of culture in March and April, with the total biomass approaching 3000 g·m⁻².

Moreover, many Rhodophyta epiphytes have a greater protein content than some commercial *Sargassum* seaweeds, whereas species of Chlorophyta epiphytes have high ash and soluble carbohydrate contents. Most EpMA are rich in amino acids and polyunsaturated fats (Tiware and Troy, 2015; Pikosz et al., 2019), which represent high nutritional values, indicating large development potential. However, at the end of the harvest season for *Sargassum* and other commercial seaweeds, the EpMA are either removed, or they simply float away when the rafts are retrieved, resulting in the waste of biomass (Yu et al., 2016; Wu et al., 2017). Farmers should collect and dry the EpMA after its removal during the culture management stage, and the uses are not specific to any epiphytic species. The extraction technology of EpMA for

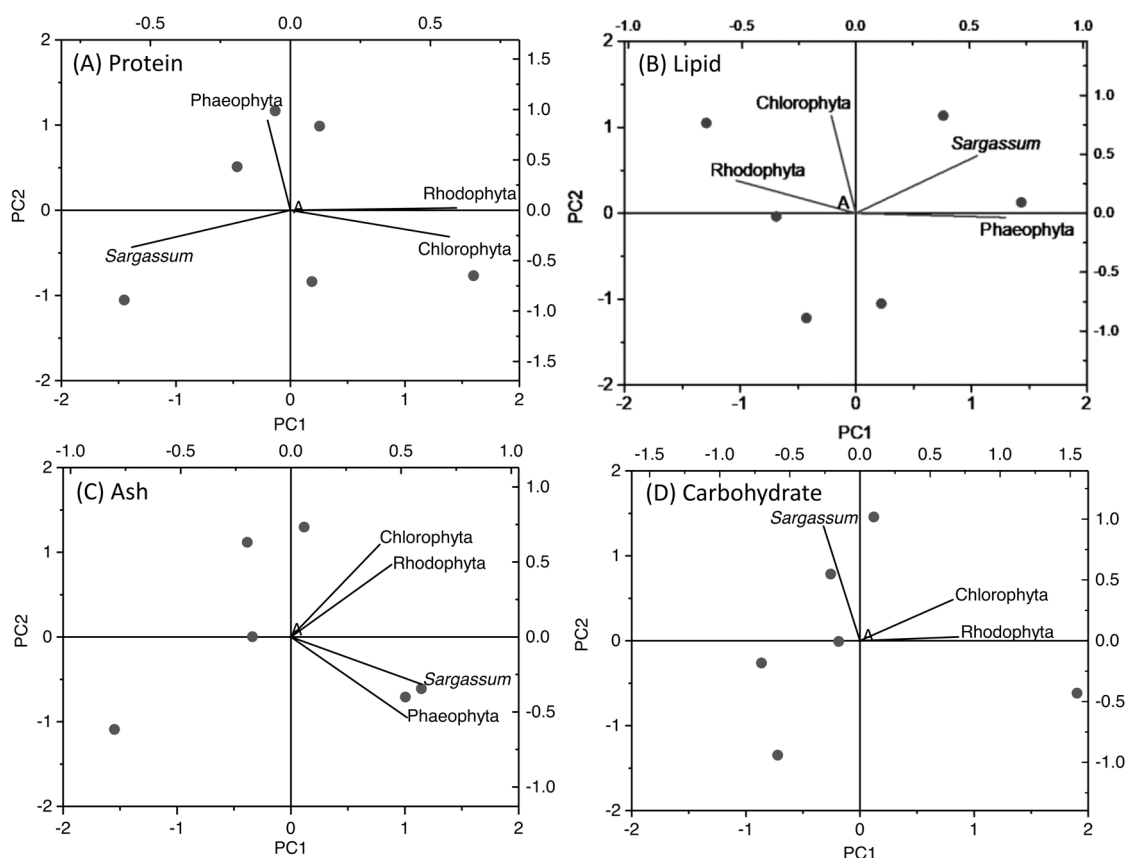


Fig. 3. Principal component analysis (PCA) of the reported contents of protein, lipid, ash, and carbohydrate in the commercial seaweeds as an example of commercial *Sargassum*. Their epiphytic macrophytes belonging to Chlorophyta, Phaeophyta and Rhodophyta, respectively. The data were derived from Table 3 and analyzed in Origin Pro 9 (OriginLab, USA).

seaweed extracts also needs to be further improved, as this practice can provide an additional income for the farmers.

5.1 Potential utilizations of EpMA

EpMA in nearshore cultivation may also sequester phosphates and nitrates in run-off, as macroalgae have high uptake rates for both elements (Fei, 2004; Kraan, 2013). The high ash content of EpMA can also provide minerals and trace elements beneficial as both fertilizer and animal feed. The first rationale behind the use of EpMA as biofertilizers is the high ash content since agricultural soils often do not have a rich source of mineral nutrients (Tab. 3). The ash can be obtained directly from the residues produced by energy gas fermentation and seaweed processing to make full use of EpMA (Fig. 4). Moreover, EpMA contain many growth-promoting hormone, making them potential candidates for developing effective bio-stimulants that can improve the growth of crops (Sridhar and Rengasamy, 2011; Latique et al., 2014; Latique et al., 2021). Alginate, for example, is a polysaccharide derived from marine brown algae and is widely found in algae such as *Ectocarpus*, *Sargassum*, *Laminaria*, *Colpomenia*, *Dictyota*, *Fucales*, and others (Liu et al., 2019; Zhang et al., 2020). These are kind of rich marine resources endowed with a variety of

biological activities. The research and development of alginate has been widely used in many fields, and its application in agricultural production is a typical representative. Alginate is a degradation product of a natural substance that has been shown to have no significant toxic side effects. It can promote plant growth, relieve growth inhibition under abiotic stress, induce plant defense response, and extend fruit shelf life, which gives it good agricultural application potential. In recent years, with the development of efficient preparation technology of alginate, its action and mechanism on plants have been widely studied (Li et al., 2018; Liu et al., 2019; Zhang et al., 2020). These developments provide a sufficient and effective way for the development and utilization of EpMA.

Other potential usages of EpMA include ethanol or water extracts as foliar sprays or soil drench, and granular/powder forms as soil conditioners and fertilizers (Lingakumar et al., 2004; Thirumaran et al., 2009; Pereira, 2011; Latique et al., 2021). Many studies have documented the effectiveness of seaweed extracts in increasing germination rate and greater seedling vigor, vegetative growth, reproduction, biochemical constituents, and chlorophyll synthesis in some vegetables and crops (Lingakumar et al., 2004; Kumari et al., 2011; Latique et al., 2014). Up to 2013, the market value of industrial seaweed applications for soil additives and fertilizer (seaweed

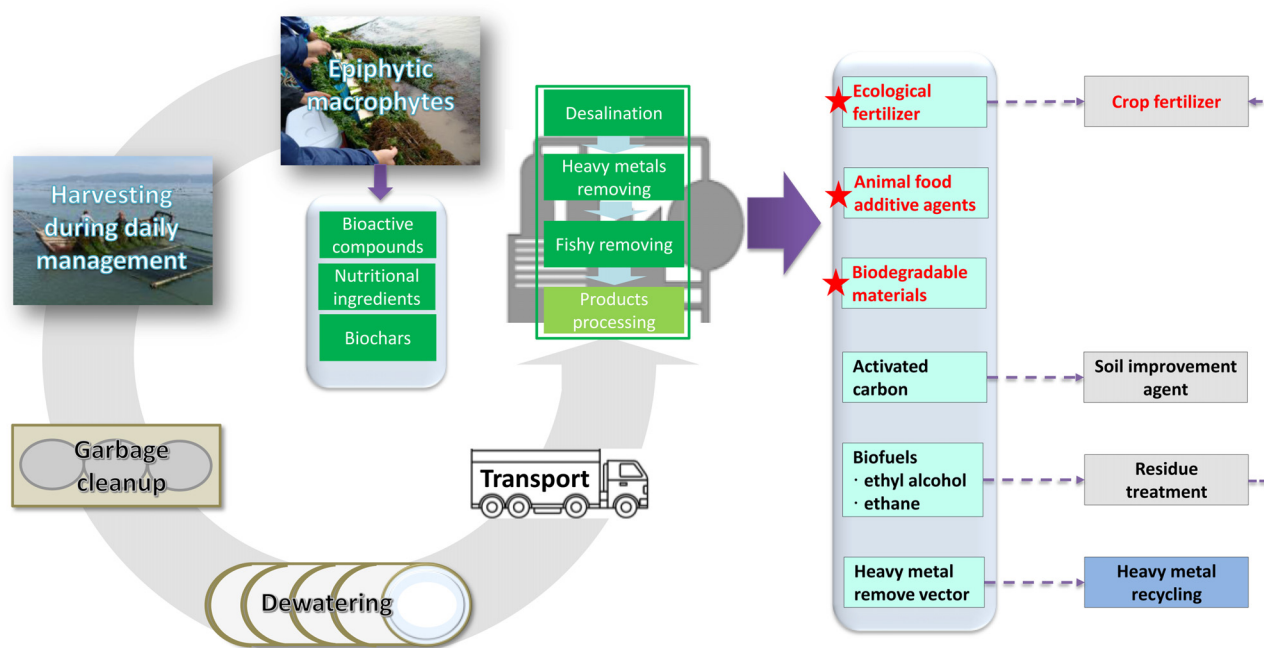


Fig. 4. Potential utilization patterns of epiphytic macroalgae (EpMA) that grow on cultivated seaweeds.

extract) were ~30 and ~10 million US\$, respectively (Nayar and Bott, 2014).

EpMA are rich in various nutrients and have potential as food agents. For example, as one of the main epiphytes for most cultured seaweeds, species of the genus *Ulva*, some of which are even being farmed in other countries or regions, have been used for food and feed purposes for decades because of their high contents of vitamins, trace metal, and dietary fiber (Bolton et al., 2009; Radulovich et al., 2015; Roleda et al., 2021). Compared with vegetable proteins, an imbalance of amino acids may limit the applicability of many EpMA as foodstuffs, they remain an alternative additive agent for livestock and aquatic animal feeds. However, agricultural sale volumes of seaweed-derived animal feed and fertilizer are low, which are almost exclusively derived from commercially cultured seaweeds.

Seaweed extracts and their derived polymers can be used as an effective source of biodegradable materials. Natural biomass-derived polymers have attracted great interest due to their abundant availability, ecological friendliness, and sustainability. Among them, seaweed is a sustainable, green, abundant, and cheap source of polysaccharide biomass. Algae-derived polymers such as agar, alginate and carrageenan have been widely used in biofilm formation and their mechanical properties have been extensively studied (Abdul Khalil et al., 2017; Wang et al., 2017; Hasan et al., 2019). Biofilms can be formed directly from raw algae alone or mixed with fibers, with remarkable effects comparable to those formed by algin-derived polymers (Abdul Khalil et al., 2017b; Hasan et al., 2019). However, seaweed has hydrophilic properties, and its water vapor barrier and mechanical properties are poor, which seriously limits their application in packaging materials. The mixing and enhancement of seaweed or algae-derived polymers with other hydrophobic or less hydrophilic organic and inorganic fillers provides a clever solution to this problem.

This also provides strategies for the research and application of biodegradable green materials (Abdul Khalil et al., 2017a, 2017b; Hasan et al., 2019). For example, the use of bamboo as raw material to extract microcrystalline cellulose as reinforcement material in algin-based composite membranes provides a biodegradable packaging material production technology and shows broad application prospects (Hasan et al., 2019).

EpMA can also be used as vectors for the removal of heavy metals and nutrients. EpMA grown on aquaculture rafts/ropes can remove a large quantity of the nitrogen and phosphorus from the seawater during one cultivation season. For example, during one cultivation period of *Neopyropia yezoensis* in China, epiphytic *Ulva* species present in the culture were able to remove approximately 77 tons of nitrogen and 3 tons of phosphorus (Wu et al., 2017). EpMA have a considerable ability for nutrient and heavy metal uptake and accumulation. This is associated with their higher ash content (Tab. 3). Many macroalgae can bio-concentrate heavy metals (Costa et al., 2017; Ma et al., 2018; Bahaa et al., 2019; Lin et al., 2020; Madkour and Dar, 2021). Thus, EpMA, especially the *Ulva* spp., can be used as a natural agent for the removal of nutrient from eutrophic water or used in transient culture in nutrient-rich polluted water (Costa et al., 2017; Ma et al., 2018). This approach has been applied to remove phosphate from effluent water via a novel adsorbent, such as algae-Mo in synthetic and real wastewaters (Sarvestani et al., 2016). However, the technology for heavy metal recycling requires further in-depth research.

Many species of EpMA (such as *Ulva* and *Gracilaria*) contain number of carbohydrates and essential minerals (Poo et al., 2018) (Tab. 3; Fig. 3). Biochars generated from wasted marine macro-algae (MMAB) can be obtained during the processes of cultivation, harvesting and processing, all of which have been shown to exhibit efficient performance in the removal of heavy metals such as copper, cadmium, and zinc

(Poo et al., 2018; Katiyar et al., 2021; Chen et al., 2022). Additionally, macroalgae have been identified as a third-generation carbon source for bioethanol, biohythane, and methane production as they have several advantages over terrestrial biomass (Bikker et al., 2016; Tan et al., 2020). Many epiphytic species in the phyla of Chlorophyta and Rhodophyta have a higher carbohydrate content than some commercial seaweeds (Tab. 3) and thus, they could be good alternative substitutes for energy production. However, due to the instability of the species and biomass of EpMA in the process of economic seaweed farming, the yield of bioactive carbon produced by EpMA may also be unpredictable. In any case, for the use of EpMA as raw materials to produce biofuel would require the screening and cultivation of microorganisms that are used in the fermentation of EpMA biomass is needed.

5.2 Traits and application status of EpMA

Commercial exploration of the biomass from EpMA for integrated utilization, including ecological fertilizer, activated carbon, and fuel should encourage its harvest and control. Thus, effective utilization of EpMA would be preferable, which may be partially instead of the raw seaweed materials for biochars, pharmaceutical developments, and even aquatic wastewater treatments that are harvested from the cultivated seaweeds or naturally growing populations (Holdt and Kraan, 2011; Kang et al., 2016; Sarvestani et al., 2016; Ma et al., 2018; Gokulan et al., 2019; Ji et al., 2021).

Due to the non-homogeneity of epiphytic species, a feasible method should consider the types and availability of the main biomass that can be used without much screening. One primary strategy that has emerged from the cultivation of algae is the use of EpMA as an ecological fertilizer, livestock, aquatic animal feed additive, cosmetic ingredients, as well as in the production of activated carbon. From the perspective of production and processing, massive amounts of EpMA can be collected through seaweed cultivation, which can then be included in the process of commercial seaweeds and facilities of commercial seaweed production. Economically, this can compensate expensive investment in production facilities and lower production cost.

6 Conclusion

The *Sargassum* aquaculture industry is experiencing increasing challenges from EpMA due to the expansion of cultivation scales. In most cases, available physical, chemical, and other control methods cannot effectively control EpMA. The integrated and indiscriminate collection and utilization of EpMA as ecological fertilizer and animal food additive agents is likely to be better options than traditional epiphyte control. This is preferred to pure prevention and control, but it requires a detailed study in terms of resource recycling and energy efficiency. Based on the current seaweed industry background, the use of epiphytic biomass to produce water extracts for the agricultural markets, as well as the development of biodegradable materials that can provide packaging or other uses, is potentially a most available strategy. However, in the actual production, there are still some problems that need to be verified or difficulties that must be overcome to implement the

utilization of EpMA. The differences in the effectiveness of the feed additive derived from a single EpMA species versus that from a mixed EpMA species also need to be validated. In addition, the implementation of various EpMA utilization needs to overcome the corresponding technical obstacles, but also to establish new harvesting and processing channels, thereby encouraging farmers to adopt this new approach.

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Conflicts of interest

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

Data availability statement

Data will be available from the corresponding author on reasonable request.

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