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## A concise review of the highly diverse genus *Sargassum* C. Agardh with wide industrial potential

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### Abstract :

*Sargassum* C. Agardh is a highly diverse genus within the brown algae, with 615 currently recognized species, varieties and forms worldwide. This high level of species diversity led early taxonomists, using morphological-anatomical criteria only, to divide the genus into up to five sub-genera and several lower-ranking taxonomic units (e.g., sections, tribes). With the advent of molecular data, subsequent authors revised this complex and archaic classification, with the genus now comprising only two sub-genera: *Sargassum* and *Bactrophycus*. Whilst most *Sargassum* species are benthic, only two are known to be holopelagic and responsible for strandings along tropical Atlantic coasts. The rest of the genus is cosmopolitan, occurring from tropical to temperate regions. *Sargassum* has not yet been reported in polar regions. Where *Sargassum* is present, macroalgal populations can grow in large quantities, and the resulting biomass can be valuable to the local communities for a variety of uses. Here we review the genus *Sargassum* from a taxonomic, ecological and physiological perspectives, and explore the different ways of taking advantage of this extraordinary biomass, which while becoming an invasive pest in some countries, could represent opportunities for coastal populations worldwide.

**Keywords :** Fucales, Phaeophyceae, Taxonomy, Ecology, Invasive species, Chemical composition, Economical uses

## Introduction

### Nomenclature and taxonomy

Valid scientific name

*Sargassum* C. Agardh (1820) is a brown macroalgal genus of the family Sargassaceae (Fucales, Phaeophyceae). The first species was described from an English specimen under the name *Fucus bacciferus* Turner. **Since this description**, a very large number of species, varieties and forms, as well as infraspecific names, have been described (up to 973 are recorded by [Guiry and Guiry 2022](#)) as well as various sub-genera and sections. Most were established based on traditional morpho-anatomical characters, without prior knowledge of the significant polymorphic nature of the genus. At present, the genus *Sargassum* comprises 615 currently recognized species, varieties and forms ([Guiry and Guiry 2022](#)).

Nomenclatural synonyms

With the advent of molecular tools, particularly phylogenetic markers, and with larger geographical explorations, the genus *Sargassum* was considerably revised and presently accounts for 359 species and 256 infraspecific names that are currently accepted taxonomically ([Guiry and Guiry 2022](#); noted C - “accepted taxonomically” on the Algaebase website). As a result, a significant number of species, varieties and forms are considered synonyms. Significant examples include *S. ilicifolium* (Turner) C. Agardh with **11 synonyms**, or ***S. polycystum*** C. Agardh and *S. aquifolium* (Turner) C. Agardh, both with 13 synonyms.

Vernacular names

The common English name **of the genus is** *Sargassum*. It comes from the Portuguese *sargaço*. In Brittany (France), only one representative **of the genus *Sargassum*** is present, and is called ‘*sperrn-mor Japan*’, in reference to the Japanese species *S. muticum*. In Japan, members of the community working on *Sargassum* species commonly use the name ホンダワラ (hondawara), although it refers to the common name for *S. fulvellum*. Another common name for *Sargassum* is もく (moku) which is said for **mokuzu, meaning** debris of seaweeds. In China, the kanjis used for *Sargassum* are 马尾藻.

Taxonomy

*Sargassum* C. Agardh is a brown macroalgal genus of the phylum Ochrophyta, class Phaeophyceae in the order Fucales and family Sargassaceae. The genus is currently subdivided in two sub-genera, i.e., *Sargassum* and *Bactrophyucus* (Dixon et al. 2014, Liu et al. 2017). The first, sub-genus *Sargassum*, is further sub-divided into eight sections: *Sargassum*, *Binderiana* (Grunow) Mattio et al., *Ilicifolia* (J. Agardh) Mattio et al., *Polycystae* Mattio and Payri, *Zygocarpicae* (J. Agardh) Setchell, *Johnstonii* E.Y. Dawson ex J.N. Norris, *Lapazeanum* E.Y. Dawson ex J.N. Norris, *Sinicola* E.Y. Dawson ex J.N. Norris. The second, sub-genus *Bactrophyucus*, is divided into four sections: *Halochloa* (Kützing) Yoshida, *Hizikia* (Okamura) Yoshida, *Spongocarpus* (Kützing) Yoshida, *Teretia* Yoshida (Mattio and Payri 2011, Dixon et al. 2014).

Early workers on the genus *Sargassum* only had at their disposal fragments collected during multi-disciplinary voyages of discovery around the world, and without prior knowledge of the natural morphological variation in the field, numerous species, varieties and forms were described (about 1,000 according to Mattio et al. 2010). However, the advent of molecular taxonomy and more extensive collections throughout the geographic distribution of the genus shed new light on diversity and taxonomy, leading to a drastic reduction of taxa. A number of phylogenetic studies (e.g., Stiger et al. 2003, Mattio et al. 2009, Mattio and Payri 2010, Dixon et al. 2014, Camacho et al. 2015, Yip et al. 2018) produced significant taxonomic revisions and numerous species, varieties and forms are now considered synonyms (Guiry and Guiry, 2022), resulting in a total of 359 current epithets (Guiry and Guiry 2022). Notable examples include the works of Mattio et al. (2008) for French Polynesia, where only three species were retained out of 18 previously recorded taxa, Mattio and Payri (2009) for New Caledonia where only 12 taxa were considered current out of the 45 records, or Mattio et al. (2013) for Mauritius where seven remain out of 44 records.

### **Morphology and anatomy**

As for most genera of the family Sargassaceae, the traditional classification of the genus *Sargassum* relies mainly on external morphology (Fig. 1a,b) and the anatomy of reproductive organs (Fig. 1e). Macro-morphological characters include the shape and organization of the holdfast, axes, blades, vesicles and receptacles (Fig. 1a,b,c,d,e), while anatomical observations mainly focus on reproductive structures.

### **Figure 1**

*Sargassum* is usually tightly attached to the substratum (Fig. 1g) by a cone-shaped or discoidal holdfast (most species) or creeping axes (subgen. *Sargassum* sect. *Polycystae*). The only known exceptions are the two free living species in the tropical Atlantic Ocean: *S. natans* (Linnaeus) Gaillon and *S. fluitans* (Børgesen) Børgesen (Godínez-Ortega et al. 2021, Dibner et al. 2021, Fig. 1f). The overall shape of the thallus may be more or less linear (e.g., *S. muticum*, Arenas and Fernández 2000, Le Lann et al. 2012a, Engelen and Santos 2009 and *S. horneri*) or short and bushy (e.g., *S. aquifolium* in coral reef environments, Mattio et al. 2009), with one to several axes arising from the base and differentiating into branches of several orders. Stipes can be cylindrical, more or less flattened and three-sided (subgen. *Bactrophycus*). The surface can be smooth, wrinkled or bear spine-like appendages. Axes bear leaf-like appendages (blades), commonly referred to as ‘leaves’ although they are not functionally similar to higher plant leaves. Blade shape is highly diverse depending on species, and can be simple, bifid or divided several times, round, turbinate, spatulate, lanceolate, linear or any intermediate form. The shape of the base and the apical section of the blade, as well as its margins (entire or serrated, ...), presence and distribution of cryptostomata and midrib, as well as the length of the pedicel, are also of taxonomic importance. Vesicles (or aerocysts) may be spherical, ovoid, pyriform, or any intermediate shape. They are smooth or bear a mucron which may be simple or multiple, thin and spine-like, foliar, or forming a crown. For some species, the vesicle may develop in the middle of the leaf (phyllocyst). Receptacles (containing reproductive bodies) are either solitary or in tight to open clusters, simple, branched, bearing or not small vesicles and/or blades (mixed receptacles). Receptacle shape and aspect of the margins are also of taxonomic importance and can vary if they are male, female or dioecious. All morphological and anatomical characters of taxonomic importance are described and illustrated in detail by Mattio and Payri (2011). The high intraspecific morphological plasticity between populations and even within populations can be a source of considerable taxonomic confusion. For example, Kilar and Hanisak (1989) identified as many as 47 different morphotypes within the same *S. polyceratium* Montagne population in Florida. Morphological variability is also encountered depending on seasons, habitat type and exposure, e.g., exposed vs. sheltered, as reported in various regions (reviewed in Mattio and Payri 2011).

## Genetic data

A considerable number of molecular studies were dedicated to *Sargassum* since the earliest molecular analyses of Phillips (1998), which shed new light on the diversity and phylogenetic relationships between the various species, sections and sub-genera of the genus (e.g., Yoshida et al. 2000, Stiger et al. 2000, 2003, Mattio et al. 2010, Dixon et al. 2014, Camacho et al. 2015, Gonzalez-Nieto et al. 2020, Yip et al. 2020). As a result, the GenBank nucleotide database (searched on 15/09/2022) records a total of 5,386 *Sargassum* sequences for over 122 taxa and a number of unidentified specimens. They include sequences for markers of the three cellular compartments, mainly ITS2 (1,802 sequences, 139 different epithets), partial Rubisco (521 sequences, 92 different epithets), *cox3* (919 sequences, 71 different epithets), *cox1* (220 sequences, 53 different epithets), and to a lesser extent: 23S, *psaA* and *psba*, *tufA*, *trnWI*, *atp9*, *nad1*, an anonymous locus and various other loci. The most sequenced species are *S. natans*, *S. polycystum* and *S. ilicifolium*. The mitochondrial and/or chloroplast genomes of 27 species are also available on the Genbank (searched on 15/09/2022).

## Distribution, ecology and metabolism

### Geographical distribution

Specimens of the genus *Sargassum* are largely distributed in temperate and tropical areas and are absent from the two polar circles. Among the two sub-genera structuring the genus, species belonging to *Bactrophyucus* have a more restricted distribution and are observed in Europe (with *S. muticum* the only representative of the sub-genus in the area), in the North-West Pacific, Southern Australia and at the tip of South Africa (Dixon et al. 2014) while the rest of temperate and tropical regions is colonized by specimens belonging to the sub-genus *Sargassum* (Dixon et al. 2014, Yip et al. 2020). Some species present a restricted distribution, for example, *S. amaliae* is endemic to tropical and sub-tropical Australia (Phillips and Blackshaw 2011) or *S. quinhonense* occurs only along the Central and South West coasts of Vietnam (Nguyen and Boo 2020). Similarly, *S. fluitans* and *S. natans* are the only representatives of holopelagic *Sargassum* species and they are restricted to the Atlantic Ocean (Butler et al. 1984, Schell et al. 2015, Wang et al. 2019, Johns et al. 2020, Goodwin et al. 2022). Conversely, with its invasive status, *S. muticum* native from Asia, colonized various areas around the world and is now also largely distributed in the North Pacific, i.e. from Alaska to Mexico (Aguilar-Rosas et al. 2007), and the Eastern Atlantic Ocean, with populations present from Morocco (Sabour et al. 2013) to Norway (Tanniou et al. 2014, 2015).

## Ecology

*Sargassum* species are canopy-forming brown macroalgae distributed in sublittoral waters, and usually form mono- or plurispecific underwater ‘grasslands/bush or forest’ (depending on their size) along the coasts of all continents and islands as illustrated by Fig. 2, showing *S. coreanum* and *S. nigrifolium* forming grasslands in Japan (Fig. 2a,b), *S. macrocarpum* and *S. spinuligerum* forming small marine forests in Japan (Fig. 2c) and New Caledonia, respectively (Fig. 2d) and *S. polycystum* presenting thalli up to 2 m long and forming a true marine forest in Tuvalu (Fig. 2e).

## Figure 2

Species of *Sargassum* can settle in a wide range of habitats, including subtidal and intertidal zones in temperate areas and seagrass beds, mangroves and coral reefs in tropical areas. In the intertidal zone, since the species do not tolerate prolonged exposure, they favour foreshore rockpools, which allow them to be always submerged. This dense vegetation provides habitats for fish, shellfish, copepods, crustaceans and also other algae as epiphytes. Most of the *Sargassum* spp. are benthic, i.e., fixed to a hard substratum (rocks, rubbles, etc), with the exception of holopelagic species spending their entire life in a floating state. These holopelagic species form drifting rafts of *Sargassum* species and play important ecological roles in offshore waters, providing spawning grounds and nursery sites for juveniles of many fish species (Butler and Stoner 1984).

Many species of *Sargassum* have the potential to float on the surface of the ocean, but unlike holopelagic species, they only float for part of their life-cycle. The thallus, and more often the laterals, are torn from their substratum and drift to/under the water surface. Examples are *S. pacificum* and *S. polycystum* in South Pacific (Zubia et al. 2015, Andrefouët et al. 2017), *S. horneri* in Asia (Komatsu et al. 2014, Liu et al. 2021), or *S. muticum* in the Mediterranean Sea (Benali et al. 2019) for the most famous species. In the South Pacific and also the central Atlantic Ocean, rafts of *Sargassum* species are so large that they can be seen on satellite images (Andrefouët et al. 2004, Komatsu et al. 2007, Gower and King 2011, Ody et al. 2019). Benthic *Sargassum* species are able to survive as floating rafts due to the buoyancy provided by the air vesicles. After being detached from the substratum, they form rafts that drift on the surface and

constitute true oases in the middle of the ocean as described for *S. horneri* in the China Sea by Komatsu et al. (2007), or other species in the South Pacific Ocean (Stiger and Payri 1999a, Andrefouët et al. 2004, Zubia et al. 2015). The majority of *Sargassum* species live attached to diverse types of substrata such as rocks, patches or rubbles of various kinds.

Some *Sargassum* species are invasive. This is the case for example in the South Pacific atoll of Tuvalu, where *S. polycystum* (a species not previously reported in the literature from that locality) suddenly appeared and proliferated around the year 2010, with beds being found to occur predominantly on hard surfaces such as rocks, coral rubble and concrete/cement slabs and rubble in populated areas of the main atoll of Funafuti, subject to high anthropogenic nutrient inputs (N'Yeurt and Iese 2015b, Andrefouët et al. 2017). As the years progressed, an association was found between *S. polycystum* and *Padina boryana* Thivy, another possibly invasive brown macroalga, within 30 - 55 m from the shoreline (Iese and N'Yeurt 2018), indicating that over time, invasive populations of *Sargassum* are also subject to ecological competition and succession by other macroalgae. The abundance of *S. polycystum* decreased as the distance from the shore increased, with almost no *S. polycystum* occurring at 100 m from shore, possibly due to lesser influence from land-derived nutrient sources. In sandy bottom areas close to the shore, subject to transversal water currents creating concentric dunes, *S. polycystum* was found growing on the ridges only, creating a distinctive banded pattern of growth visible from the air. Since the genus *Sargassum* was assumed not to occur in the Central Pacific (Doty 1954) and *S. polycystum* had not been reported from a survey of Funafuti Atoll, Tuvalu by Chapman (1955) nor from neighbouring Kiribati (Tsuda 1964), there are strong suggestions that this species had recently spread from Fijian ports of entry to other islands via regional shipping routes, as it was observed in Wallis Island (N'Yeurt and Payri 2004) and in the Fiji Islands since the year 1970 or earlier (N'Yeurt et al. 1996). However, this has not yet been definitively resolved through population genetic studies of South Pacific species of *S. polycystum*.

In Indonesia, Setyawidati et al. (2018a) combined fieldwork and satellite images to follow populations of brown macroalgae occurring around Libukang Island (South Sulawesi). They found that species of *Sargassum*, i.e., *S. ilicifolium* and *S. polycystum*, were abundant throughout the studied seasons, with a maximal percentage of cover of 84% during the dry season and a minimum of 60% during the wet season. Both species settled on heterogeneous and soft substrata around Libukang Island (South Sulawesi) and never on sandy substrata.



This was not the case for other brown macroalgae such as *Turbinaria* spp. and *Padina* spp. which mainly settled on coral debris and sand respectively (Setyawidati et al. 2018a).

*Sargassum* species are known to have an impact on the surrounding marine communities. Salvaterra et al (2013) demonstrated the impacts of the introduced species *S. muticum* on the functioning of an Irish marine reserve, with important changes in native communities, including significant reduction of the primary production (by decreasing associated *Fucus* spp. biomass), a decrease of the native algal community and associated fauna in the shallow subtidal zone, and alteration of the structure of the faunal benthic community (including the arrival of several generalist species and a redistribution of top and intermediate predators). In various European coastal areas, many authors have demonstrated competition between the introduced and native species, as *S. muticum* reduced the abundance of the native canopy and understory algae, suggesting these effects were caused by competition for light (Britton-Simmons 2004, Sanchez et al. 2005, Olabarria et al. 2009, Baer and Stengel 2010).

### Metabolism

Due to the variety of environments (pelagic/benthic and temperate/tropical) in which *Sargassum* spp. live, their metabolism and response to any environmental change will vary strongly depending on the site. Indeed, their photosynthetic characteristics reflect both the adaptation of the species to the general environmental conditions, and their ability to acclimate to seasonal changes within their geographical range of distribution (Falkowski and Raven 2007, Hurd et al. 2014). For example, the light saturation point of *Sargassum horneri* ( $80 \mu\text{mol photons m}^{-2} \text{s}^{-1}$ ; Bao et al. 2022) and *S. macrocarpum* ( $105 \mu\text{mol photons m}^{-2} \text{s}^{-1}$ ; Terada et al. 2020) from deeper waters (3m) was lower than that of *S. fusiforme* ( $391 \mu\text{mol photons m}^{-2} \text{s}^{-1}$ ; Kokubu et al. 2015), *S. muticum* ( $300 \mu\text{mol photons m}^{-2} \text{s}^{-1}$ ; Yan et al. 2021) and *S. patens* ( $289 \mu\text{mol photons m}^{-2} \text{s}^{-1}$ ; Terada et al. 2018) from shallower waters (0.5–2 m). Within these species, *S. horneri* could also survive floating at the surface of the ocean for months when detached (Komatsu et al. 2007). When both populations (benthic and pelagic) of *S. horneri* were compared, relative growth rates were significantly lower in the pelagic population than that in the attached; and all thalli from the pelagic population died in culture within 20 days (Bao et al. 2022).

The growth of *Sargassum* spp. is also highly variable with 0.03 - 0.04 doublings  $\text{d}^{-1}$  for the two holopelagic species, *S. fluitans* and *S. natans*, which are considered as low productive (Lapointe



1986); and for benthic species, from 3-4% d<sup>-1</sup> for *S. cymosum* (Costa et al. 2017) to 8% d<sup>-1</sup> for *S. muticum* (Yan et al. 2021). There is however a strong temporal variation in biomass due to their marked seasonal growth (Plouguerné et al. 2006, Baer and Stengel 2010, Le Lann et al. 2012a). When exposed to nutrient-enriched seawater, *Sargassum* spp. also showed different responses: *S. natans* and *S. fluitans* increased their growth and photosynthesis with P, but not N, addition (Lapointe 1986), whereas *S. fusiforme* and *S. muticum* increased their photosynthetic rate and growth under N-enrichment (Hong et al. 2021, Yan et al. 2021). Most species within the genus exhibit broad salinity tolerances: *S. fulvellum* can survive in salinities from 15-35 (Dawes and Tomasko 1988); *Sargassum polycystum* optimal growth was in the range of 24-36 (Zou et al. 2018); *S. muticum* germlings were able to survive in salinities as low as 5 (Steen 2004); and *S. thunbergii* germlings exhibited a strong tolerance to fluctuating salinity (Chu et al. 2012). Moreover, strong tolerance to dehydration and salinity stress provides *S. fusiforme* an advantage to grow in the intertidal zone (Yonemori et al. 2022). Under a temperature increase, a strong modulation of various metabolic pathways (i.e., amino acids, sugars, esters, organic acids, etc.) was observed in *S. fusiforme* that may contribute to the tolerance and adaptability of this species to high-temperature stress (Liu and Lin 2020). Similarly, *S. muticum* in its native area showed a high adaptation to a broad temperature range (8-28°C) and to desiccation that may explain its potentially high invasive capacity (Ito et al. 2021). Ocean acidification was observed to have no negative effect on *S. fusiforme* (Wen and Zou 2021), nor *S. vulgare* (Kumar et al. 2017) and even in the latter an increase in photosynthesis and growth, as well as higher activities of oxidative metabolizing enzymes, were observed under acidified conditions, suggesting that these species could benefit from projected climate change impacts of increased atmospheric CO<sub>2</sub> concentrations (Kumar et al. 2017). Indeed, these seaweeds do not need carbon-concentration mechanisms (CCMs) under increased CO<sub>2</sub> levels allowing a reallocation of energy to growth which can also explain the dense populations of *S. vulgare* around volcanic vents in the Mediterranean Sea (Baggini et al. 2014). Due to their broad tolerance to many environmental parameters, many *Sargassum* species may have the ability to colonize and further spread in different environmental zones all around the world. This may occur naturally, or through anthropogenic vectors such as shipping and aquaculture activities.

## Life history

## Life cycle

The life cycle of *Sargassum* spp. is diplontic, where only the diploid generation is multicellular and dominant (Bringloe et al. 2020). The main phase in the life cycle of *Sargassum* species (Fig. 3a) is the diploid thallus, which produces haploid gametes, i.e., eggs within oogonia and antherozoids within antheridia, within conceptacles grouped together in receptacles.

## Figure 3

Following fertilization, which occurs at the surface of the receptacles, a diploid zygote is produced. The fertilized eggs appear on the outside of the receptacle (ostiole) for one to several days, a period described as incubation which may play a role in the success of establishment of multicellular propagules. Small germlings with already developing rhizoids are then released into the seawater and dispersed with currents until they settle on an appropriate substratum. The time between fertilization of the oogonium (containing only one egg) and the release of the embryo is estimated at 4-5 days for the tropical species *S. pacificum* (Stiger and Payri 1999a), and 4 days in the temperate species *S. vestitum* (May and Clayton 1991). In the case of *S. pacificum*, it takes about 2-3 months for a zygote to become a young plantlet with two basal fronds and 9-10 months for this juvenile to become an adult thallus (Fig. 3a). In cultivation conditions, Hales and Fletcher (1989) and Steen (2004) showed that *S. muticum* germlings take one month to reach a length of 3-5 mm; similar results were reported for other cultivated species such as *S. fulvellum* and *S. vacchellianum* (Hwang et al. 2006, Chai et al. 2014).

## Reproduction

Various *Sargassum* species reproduce via: (1) sexual and/or (2) asexual reproduction (Fig. 3). Sexual reproduction ensures genetic mixing that maintains genetic diversity within populations which gives a species adaptive potential. This type of reproduction is characterized by meiosis and fertilization, and then implies the production of gametes, i.e., eggs and antherozoids, and their fusion. A fertile thallus of *Sargassum* can bear many hundreds of small receptacles that liberate gametes. At maturity, gametes produced within conceptacles are emitted from the ostiole with the particularity for the oogonia to stay at the surface of the receptacle, fixed at the bottom of the conceptacle by an oogonial stalk, until the fertilization (May and Clayton 1991). Depending on the species, monoecy and dioecy exist within the genus.

In a monoecious species, only one type of individual is present which produces both female gametes (a single egg in an oogonium) and male gametes (64 antherozoids in an antheridium). As monoecious species, we can cite as examples *Sargassum filicinum* native from Japan and Korea and introduced in Mexico (Miller et al. 2007, Aguilar-Rosas et al. 2007), *S. muticum* native from Japan and invasive in many areas around the world (Critchley 1983, Loughnane et al. 2002, Plouguerné et al. 2006, Le Lann et al. 2012, Liu et al. 2013, Engelen et al. 2015), and *S. pacificum* (Stiger and Payri 1999b, Mattio et al. 2008).

In a dioecious species, the sexes are separated and two types of individuals are present in the population, a female individual that produces female gametes (a single egg in an oogonium) and a male individual that produces male gametes (64 antherozoids in an antheridium). As dioecious species, we can cite as examples *Sargassum horneri* (Uchida 1993), *S. fusiforme* (Pang et al. 2008), *S. ilicifolium* and *S. polycystum* from New Caledonia (Mattio and Payri 2009), *S. mathiesonii* from the Gulf of Mexico (Kilar 1992), and *S. vestitum* from Australia (May and Clayton 1991).

**Asexual** reproduction produces one, or more, individuals genetically conforming to the parent(s). It often allows a production of offspring quantitatively larger than sexual reproduction, which brings to the population potentialities of colonization (Fig. 3b). **Asexual** reproduction was shown in some *Sargassum* species. In laboratory experiments, Uchida (1993) demonstrated that *S. horneri* was able to reproduce vegetatively with branches separated from a shoot that continue to grow. Also, regenerative ability of segments excised from thalli were demonstrated for *S. muticum* and *S. tortile* (Fletcher and Fletcher 1975, Tsukidate 1984). Regeneration of new shoots, which develop into primary axes, from a holdfast have been commonly observed in some temperate Asian *Bactrophyucus* species such as *S. miyabei*, *S. thunbergii* and *S. fusiforme* (Yoshida 1983), as well as two species from the Philippines (Ang Jr 1985). Yatsuya et al. (2012) reported experimental regeneration of erect axes from holdfast-excised, primary axis in 11 *Sargassum* species along the temperate coast of Japan. Moreover, *S. stolonifolium* produced axis equivalents to stolon/runners that allowed for the development of new thalli (Phang and Yoshida 1997), this phenomenon was also illustrated in *S. polycystum* on Fig. 3b. As another example, in *S. fusiforme*, primary axes are washed away after the reproductive season. Only filamentous holdfasts thrive following the high temperature season and regenerate new shoots when seawater temperature decreases. Such regeneration of erect axes from a filamentous holdfast has been utilized as a seedling method in mariculture (Hwang et al. 1999, Ito et al. 2009). Similarly, in *S. macrocarpum*, Yoshida et al. (2001) reported

spontaneous formation of adventive shoots on cauline leaves under culture condition and developed to utilize such adventive embryos as seedlings. Asexual reproduction is the main reproductive mode used by both holopelagic species *S. fluitans* and *S. natans*, as no receptacles have ever been observed on these two holopelagic species (Butler et al. 1984 and all the papers that have subsequently treated this topic in these species). In both species, vegetative multiplication through fragmentation is the only known reproductive mode (Kilar et al. 1992).

### **Dispersal and recruitment**

For habitat colonization, *Sargassum* species present two modes of dispersal: (1) short-distance of germlings released by attached parental thalli, and (2) long-distance dispersal of germlings (released by whole or partial thalli) or entire/part of thalli drifting over many kilometers (Norton 1992). Short-distance dispersal, also called marginal dispersal, gives rise to a contiguous distribution of individuals around parents without much genetic mixing and intraspecific competition between recruits (Stiger and Payri 1999a). Conversely, long-distance dispersal, also called remote dispersal, allows for greater dispersal of individuals but is often accompanied by risks, such as the lack of partners in the case of dioecious species, and the lack of substrata to settle on for benthic species. Nevertheless, this type of dispersal allows the species to colonize distant sites and to increase their genetic diversity.

In *Sargassum* species, the distances traveled by zygotes, after the incubation period on the surface of the parental thallus can be measured in the field by suctioning the substratum with a venturi suction pump (Kendrick and Walker 1991), or using fixed experimental plates (Stiger and Payri 1999a). Indeed, Kendrick and Walker (1991) estimated in *Sargassum spinuligerum* that the dispersal of propagules was highly localized (i.e., within 1 m) and declined exponentially with distance from parent thalli. Similar distances were obtained by Stiger and Payri (1999a) who estimated that the dispersal of germlings from *S. pacificum* was limited to within 90 cm of the parental thallus, with a sweep of germlings settling very close to the holdfast.

### **Phenology**

The Pacific Ocean represents an area of great specific diversity for *Sargassum* spp. Accompanying this specific richness, *Sargassum* species show variations in their growth, and reproductive periodicity (as examples of phenological variables) during a year. In temperate waters around Japan, some *Sargassum* spp. show clear seasonal changes in biomass. Most

species show maximum values in thallus length and number of lateral branches in spring to early summer (Yoshida 1983, Murase and Kito 1998, Yoshida G 2005 and references listed therein). For *S. horneri*, one of the major components of seaweed beds along Japanese coasts, thallus length reaches 1-2 m and 30-80 g DW in winter to early summer (Uchida 1993, Yoshida G 2005), just before they become fertile. However, larger values of more than 7 m have been also reported for populations of this species in deeper habitats. In the case of annual species such as *S. horneri*, entire thalli including the holdfast are detached from the substrata and drift for long distances by ocean currents or are cast ashore nearby (Komatsu et al. 2007, Su et al. 2018, Zhang et al. 2019). In case of perennial species, such as *S. macrocarpum* (Murase and Kito 1998) and *S. thunbergii* (Yoshida 1983), macroalgae form receptacles when the thallus length reaches its maximum and lateral branches begin to decay after maturation. The perennating holdfasts and primary axes remain and persist during the high temperature season and subsequently regenerate primary laterals.

Although detailed studies have been limited to a few select species, clear seasonality in growth and maturation of temperate *Sargassum* spp. are explained in relation to photo-periodicity (Hales and Fletcher 1990, Uchida 1993, Hwang and Dring 2002, Yoshikawa et al. 2014). In *S. horneri*, for example, elongation of laterals can be observed under short-day condition and their transfer to long-day conditions (i.e., more than 14 h light period/ day) induced formation of receptacles (Yoshikawa et al. 2014). Being either annual or perennial species, it is thought that each species of *Sargassum* has a limited/defined duration reproductive season (Yoshida 1983), hence photoperiodic control of growth and reproductive maturation would be more common amongst temperate members of the genus. Conversely, it is known that phenological shifts, i.e., differentiation in reproductive seasons, occur between sympatric, conspecific populations (Yoshida G et al. 2004, Yoshida G 2005, Homma et al. 2020).

## **Chemical composition**

The composition of *Sargassum* species can be influenced by abiotic factors, such as geographical location, season, water temperature and salinity, but is also related to growth and maturity of the algal thallus (Gorham and Lewey 1984, Plouguerné et al. 2006, Kamiya et al. 2010, Murakami et al. 2011, Le Lann et al. 2012a,b, Balboa et al. 2016, Zou et al. 2017) and importantly, to the method of extraction (Tanniou et al. 2013, Saldarriaga-Hernández et al. 2021). The effects of the seasonal and spatial variations in *S. muticum* can be found in numerous

publications on this introduced, invasive species (Gorham and Lewey 1984, Núñez-López and Casas Valdez 1998, Plouguerné et al. 2006, Le Lann et al. 2012a, Balboa et al. 2016). Table 1 summarizes the proximal composition of some *Sargassum* species reported in various studies.

## Table 1

**Inorganic constituents.** The ash content in seaweeds accounts for 30-40% DW (Leandro et al. 2020), but brown macroalgae show an affinity to accumulate metals (Patrón-Prado et al. 2011, Devault et al. 2021a). Seaweed can accumulate minerals and essential elements from the environment, and can be determined as ash content, particularly high for some *Sargassum* spp., with values between 24-60% (Machado et al. 2022, Damayanti et al. 2021, Saldarriaga-Hernández et al. 2021, Milledge et al. 2020). This was found to depend on the collection site. On the other hand, the ash content showed seasonal variations for some species (Murakami et al. 2011), yet remained relatively constant for others (Gorham and Lewey 1984), and even species growing in the same area showed a different accumulation pattern (Davis et al. 2021). These highly variable parameters have significance for food applications due to their key roles in human health (Circuncisão et al. 2018). The main trace elements found in these brown seaweeds are iron, manganese, copper, zinc, cobalt, molybdenum, selenium, and iodine. The latter being necessary for human health in order to maintain correct functioning of thyroid hormones (Sun et al. 2021). Potassium, sodium, calcium and magnesium have been reported as the major macro-minerals components in members of the genus *Sargassum* (Thadhani et al. 2019, Kumar et al. 2021). However, accumulation of some trace elements, i.e., arsenic or zinc in *S. fusiforme*, could represent a potential risk for human health (Zhu et al. 2022).

## Organic constituents

### Carbohydrates

Total dietary fiber content increases with seaweed growth and maturity (Murakami et al. 2011). The distribution of soluble and insoluble fractions differs according to the estimation procedures; however, the soluble fraction can be 40-75% (Gómez-Ordóñez et al. 2010, Kumar et al. 2021). Brown macroalgae also contain alginate, laminarin(an), mannitol and fucoidan or other sulphated polysaccharides, which have attracted attention based on their biological properties, including antioxidant, anti-tumoral, anti-inflammatory, anti-obesity, and anti-diabetic properties amongst others (Rushdi et al. 2020, Zhang et al. 2020). Mannitol was also



found in *Sargassum* species (Hernández-Bolio et al. 2021, Davis et al. 2021), accounting for 12% DW in tropical *S. mangarevense* (Zubia et al. 2008). The content of alginate has been reported as relatively constant (Zubia et al. 2008, Gorham and Lewey 1984, Davis et al. 2021), whereas mannitol and laminarin(an) contents were maximal during the growing period in many species (Gorham and Lewey 1984). Alginates, linear polysaccharides formed by mannuronate (M) and guluronate (G) acids with different ratios of M/G depending on the type of species, age, and location, are found in the cell walls of brown seaweeds, and in addition to their collative properties within the thallus, also provide protection from desiccation and flexibility (reviewed by Stiger-Pouvreau et al. 2016). According to its structure, different rheological properties of alginate, such as viscosity or elasticity, can be developed through chemical modification during the industrial extraction process. Alginates have been proposed in several biomedical applications, such as tissue engineering, encapsulation, hydrogels, wound-healing and drug delivery (Xie et al. 2022, Parente et al. 2022, Zamboulis et al. 2022). Fucoidans (fucose-containing polymers) are a group of polysaccharides mainly composed of fucose and sulphate groups, and other saccharides in minor content. The importance of the quantity and location of associated sulphate groups has been associated with the biological activity of this polymer (Shao-Hua et al. 2020, Hsiao et al. 2021). This is highly influenced by both composition and structure, and these characteristics are also defined by the techniques used for their extraction and depolymerization (Grosso et al. 2015, Flórez-Fernández et al. 2018). Laminarans(ins), neutral polysaccharides mainly comprising  $\beta$ -D-glucose, with  $\beta$ -(1 $\rightarrow$ 3) glycosidic bonds, are produced by photosynthesis (Zhang et al. 2020). These polymers have been demonstrated to have anti-viral and anti-tumoral properties (Jin et al. 2020, Cui et al. 2021, Claus-Desbonnet et al. 2022, Li et al. 2021). Additionally, the dietary inclusion of alginates can have a positive effect as a regulator of intestinal microbiota (Cui et al. 2021).

#### Protein and amino acids

Brown seaweeds contain lower levels of protein content than red and green seaweeds, ranging from 6-20 % (Matanjan et al. 2009, Murakami et al. 2011, Zheng et al. 2020, Machado et al. 2022). In various *Sargassum* species, maximum protein content occurs during winter (Gorham and Lewey 1984, Dewinta et al. 2020, Kumar et al. 2021). These seaweeds exhibit a balanced amino acid composition, the most abundant being glutamic and aspartic acids, leucine and glycine (Tonon et al. 2022) and the minor methionine and tyrosine (Nazarudin et al. 2021). In addition to their nutritional value, these amino acids are determinants of flavor properties,



particularly the *umami* taste later synthesized as monosodium glutamate or MSG commonly used as a food condiment in Asian cuisine (Moerdijk-Poortvliet et al. 2022). However, the protein digestibility of *Sargassum* spp. can be reduced due to the presence of phenolic compounds. Improved digestibility may be achieved by boiling and steaming (Sun et al. 2021).

### Lipids and fatty acids

Lipids are relatively minor components in brown macroalgae, with values as low as 1%, reaching a maxima of 4-6 % (Terasaki et al. 2009, Balboa et al. 2016, Matanjun et al. 2009, Murakami et al. 2011, Lee et al. 2022, Kumar et al. 2021, Munsu et al. 2021, Yang et al. 2021). Known seasonal variations occur (except in tropical areas), where neither the content nor the fatty acid profiles showed significant variations throughout the year (Santos et al. 2019). It has been suggested that the low lipid content of *Sargassum* spp. could be due to the relatively higher light intensity requirements of this seaweed in order to carry out photosynthesis (Dewinta et al. 2020). Despite a low lipid content, *Sargassum* spp. may contain higher levels of essential polyunsaturated fatty acids than terrestrial **al plants**. The balanced  $\omega$ -3: $\omega$ -6 ratio was also observed for *Sargassum* spp. (Terasaki et al. 2009, Balboa et al. 2016) which confers beneficial effects on health. In addition to dietary interest, these fatty acids have been reported as having functionality on anti-microfouling activity (Plouguerné et al. 2010). The degree of unsaturation depends mainly on seawater temperature; *Sargassum* spp. harvested in colder regions present a higher PUFA content and degree of unsaturation than those from tropical waters. Amongst the saturated fatty acids, palmitic acid is predominant, accounting for 35-39% in different species (Matanjun et al. 2009, Terasaki et al. 2009, Noviendri et al. 2011); a high content in oleic acid (18:1 $\omega$ 9) was also found, in *S. polycystum*, *S. fusiforme/horneri/thunbergii*, and *S. binderi/duplicatum* respectively. Amongst the  $\omega$ -6 fatty acids, arachidonic and linoleic acids are the most abundant (Matanjun et al., 2009, Terasaki et al. 2009) and among the  $\omega$ -3 fatty acids, are  $\alpha$ -linolenic, eicosapentaenoic and eicosatrienoic acids (Terasaki et al. 2009, Matanjun et al. 2009).

### Vitamins

Vitamins are essential micronutrients involved **in biological activities** of humans and other organisms, and they are also associated with defenses against oxidative processes (e.g., ascorbic acid, vitamin E). Their relative content is related to sunlight, the content of vitamin C in *S. thunbergii* (Luo et al. 2019) showed promising levels **for utilization**. Tonon et al. (2022)

reported that vitamin E and vitamin B3 were the most abundant in pelagic *Sargassum* spp. biomass.

### Secondary metabolites

Seaweeds represent a potential source of bioactives and contain secondary metabolites, phenolic compounds and terpenoids (Nie et al. 2021, Jayawardena et al. 2021). The production of phenolic compounds in marine brown macroalgae is generally assumed to be a chemical defense against grazers and bacterial colonization. The phenolic content of selected *Sargassum* spp. has been reported to vary by season, environment and geography, as well as species and distribution within the thalli (Gorham and Lewey 1984, Connan et al. 2006, Stiger et al. 2004, Plouguerné et al. 2006, Kamiya et al. 2010, Le Lann et al. 2012a,b, Davis et al. 2021, Urrea-Victoria et al. 2022). Phenolics have been shown to increase in response to increased UV-B radiation (Plouguerné et al. 2006, Le Lann et al. 2012b) and their higher content at the beginning of growth maturation (ageing) and then decline could suggest their synthesis early in the growth cycle as a protection mechanism against grazers. *Sargassum muticum* contains high phenolic levels (6%), a value dependent on the conditioning of the raw material (Le Lann et al. 2008), the method and solvent used for extraction (Tanniou et al. 2013, Balboa et al. 2016), which usually correlated with an antioxidant activity (Connan et al. 2006, Stiger-Pouvreau et al. 2014). The xanthophyll fucoxanthin from *Sargassum* exhibits relevant biological activities (Kalasariya et al. 2021, Karpiński et al. 2022), which makes it interesting for cosmetics, functional food and pharmaceutical applications (Praiboon et al. 2018, Morais et al. 2021, Hosokawa 2021).

### **Inorganic constituents**

Another issue is the contamination of harvested raw material by various inorganic compounds.

High levels of arsenic and other toxic elements, such as cadmium, make it difficult to straightforwardly use *Sargassum* biomass as a bio-fertilizer, compost or animal feed in produce or livestock meant for human consumption. It was shown that *Sargassum* is able to concentrate chlordecone and arsenic (Devault et al. 2022, 2021a,b, Ortega-Flores et al. 2022). Marine algae are known to concentrate the arsenate ion ( $\text{AsO}_4^{3-}$ ), the major chemical form of arsenic in seawater, probably because of its chemical similarity to the phosphate nutrient ion ( $\text{PO}_4^{3-}$ ) (Sanders 1979, Taylor and Jackson 2016, Gobert et al. 2022). Total arsenic concentrations in

marine algae are therefore high and generally range from 10 - 100 mg/kg, and reach up to 200 mg/kg in *Sargassum*. While most algae convert inorganic arsenic from seawater into arsenic sugars or other low toxic organic forms, *Sargassum* can accumulate large amounts of inorganic arsenic, constituting up to 80% of the total arsenic (Milledge et al. 2018, Yokoi and Konomi 2012). There is also relatively little published information on the speciation of arsenic in holopelagic *Sargassum*, in particular on the proportion of the most toxic inorganic forms of this element, i.e., As(III) and As(V). For the Mexican-Caribbean coast, a comprehensive study by Rodríguez-Martínez et al. (2020) reported up to 28 elements found in both holopelagic *Sargassum fluitans* and *S. natans*, with spatial and temporal variations in concentrations. These authors also reported that about 86% of the samples they analyzed had total As concentrations above the maximum allowable level (i.e., 40 ppm DW) for use as animal feed under European regulations. Moreover, a report by ANSES (2017) mentioned analyses carried out by CEVA revealing levels of 40-70 mg/kg of inorganic arsenic in *Sargassum* from Martinique and Guadeloupe. However, no information is known about the geographic area where loading of arsenic occurred and the conditions which favor its concentration in *Sargassum* tissues.

## **Harvesting, production and markets**

### **Harvesting of *Sargassum* species for their consumption/uses in Japan**

*Sargassum fusiforme* is one of the traditional seafood used in Japan, and its consumption has increased from the 1970's due to growing health awareness in Asia, although the levels of arsenic and iodine are too high for this biomass to be exported to Western countries given the stricter regulations. In Japan, domestic production of *S. fusiforme* is made up from harvesting of wild populations in spring (Ito et al. 2008) and until now, its cultivation is not common. More than 90% of the total consumption of this alga in Japan (e.g., ca. 12,000 tons DW in 2009; Ofusa 2011) are imported from China and Korea (Ofusa 2011), and most of this biomass is made up by mariculture. In this case, young thalli growing naturally are collected from winter to spring and clasped between culture ropes (Hwang et al. 1999, Ito et al. 2008). This seedling method, however, results in considerable damage to wild populations (Hwang et al. 1999, Pang et al. 2008), and therefore there has been a move to produce seedlings by regeneration from the filamentous holdfast (Hwang et al. 1999, Ito et al. 2009), as well as zygotes (Pang et al. 2008).

### Total annual yields in some specific areas (selected examples)

Additional biomass requirements of macroalgae can be obtained either by aquaculture (sustainable and scalable), or by harvesting from wild populations (finite resources requiring careful management). The current worldwide production of *Sargassum* spp. (mainly *S. fusiforme*) under cultivation is 304,000 tonnes (Cai et al. 2021) with two main producers: China (270,000 tonnes) and the Republic of Korea (34,000 tonnes).

In the South Pacific Islands, people harvest macroalgae from wild populations. In French Polynesia, in order to valorise *S. pacificum* for applications in cosmetics and agriculture, biomass was estimated at between  $0.133 \pm 0.046$  and  $0.193 \pm 0.067$  kg DW m<sup>-2</sup>, on Tahitian reefs using satellite data (Andréfouët et al. 2004). In the atoll nation of Tuvalu in the Central Pacific, wet *S. polycystum* biomass was estimated at between 0.45-3.56 kg m<sup>-2</sup>, with an average of 1.68 kg m<sup>-2</sup> in Funafuti Lagoon (N'Yeurt and Iese 2015b). In Indonesia, which is the world's leading producer of red macroalgae for industrial purposes, an awareness of the risks to *Kappaphycus* seaweed cultivation, due to an increasing number of diseases, led the government to take an interest in diversification amongst brown seaweeds, which are abundant on the country's numerous coasts (Setyawidati et al. 2018). A vast program was developed in order to estimate the potential of some Indonesian bays to produce some brown macroalgae of commercial interest. Setyawidati et al. (2018a) demonstrated the potential of Malasoro Bay (South Sulawesi, Indonesia), to provide significant biomass of *Sargassum* species during the dry season, i.e., 1.19 kg DW. m<sup>-2</sup>. Interestingly, Setyawidati et al. (2018b) estimated the potential of alginate produced by both *Sargassum* and *Turbinaria* spp. within Ekas Bay (Lombok, Indonesia), averaging approximately  $207.61 \pm 0.42$  t DW for the Bay.

In the Tropical Atlantic Ocean, large amounts of beached *S. natans* and *S. fluitans* have been observed since 2011. Along many Caribbean coasts, massive beach-cast holopelagic *Sargassum* biomasses occur from April to August. These have forced human populations to either suffer the inundation or make use of this enormous biomass, which represents an opportunistic harvest, as it is highly dependent on the random/stochastic arrival of rafting thalli (Stiger-Pouvreau and Zubia 2020). In the same region, García-Sánchez et al. (2020) estimated the maximum mean daily arrival of biomass in 2018 for the Mexican Caribbean area, at  $17.3 \pm 1.8$  FW kg m<sup>-2</sup> and at  $3.1 \pm 0.7$  FW kg m<sup>-2</sup> as a minimum in 2017.

The beached biomass varied considerably amongst and between the various years and seasons, with maximal biomasses in summer.

In Europe, after the growth period of *Sargassum muticum* occurring in spring, a large biomass of lateral branches is present during the summertime. Seasonal harvesting of thalli (mainly for clearance and reduction of invasive biomass), mainly laterals, occurs from April - August all along the European coasts, from Portugal to Norway (Plouguerné et al. 2006, Engelen and Santos 2009, Le Lann et al. 2012a). During a three-year project named SNOTRA and co-funded by the Normandy Region (France), the potential for using the summer biomass of the temperate *S. muticum* was also estimated at an annual average quantity of 12,000 tons  $\approx$  24,000 m<sup>3</sup> of fresh biomass (Bouasria et al. 2021, Pien et al. 2016), which could be used in sectors such as agriculture and cosmetics.

## Utilization of biomass

This section summarizes the biological properties that could be the basis for several applications of *Sargassum* spp. biomass in relation to several domains, such as health and wellness, biostimulants, adsorbents, soil and energy. Based on the commercial uses of other brown seaweeds, different applications could be considered for a sustainable valorisation of the biomass of various species of *Sargassum* (Stiger-Pouvreau and Zubia 2020, Saldarriaga-Hernández et al. 2021). In 2018, the largest single global algal bloom biomass of over 20 million tonnes was produced by *Sargassum* spp. (Joniver et al. 2021). However, the high content of arsenic, particularly in pelagic *Sargassum* spp. limited the feed/food uses and a general lack of viability of biomass due to the low yields when compared to other brown algae (Davis et al. 2021), promoting the quest for non-food applications based on valorization of the biomass for its unique, bioactive compounds (Milledge et al. 2016, Pinteus et al. 2018, Pérez-Larrán et al. 2019, Barbosa et al. 2021), as well as other non-health related applications. In the case of the invasive behavior of *S. muticum* in certain areas of Europe and of holopelagic *Sargassum* on Caribbean and African coastal areas, sustainable use of the available biomass is crucial in order to mitigate negative impacts of beached algae (López-Miranda et al. 2021, Yan et al. 2021). Drying could allow the seaweed biomass to be further processed, i.e., by air drying (Le Loeuff et al. 2021), or by processing in microwave hydro-diffusion and gravity equipment (Pérez et al. 2014). Alternatively, frozen storage has been proposed (Pérez-Larrán et al. 2019). The economic feasibility of these strategies remains to be analyzed. It has recently

been strongly suggested that Techno-Economic Analyses (TEAs) and Life Cycle Assessments (LCAs) need to be carried out worldwide on blooming algal species for their effective conversion into economically viable products (Joniver et al. 2021).

### ***Sargassum* for human consumption**

In several parts of Asia, Japan and the Pacific Islands, species of brown macroalgae including *Sargassum* are commonly consumed as part of the traditional diet (Chapman and Chapman 1980, Abbott 1991, Nisizawa et al. 1987, Novaczek 2001, Novaczek and Athy 2001, Singh 2018). Trays of *Sargassum horneri*, sold fresh, can be found on the Japanese market (Fig. 4a). The most commonly known edible *Sargassum* species is *S. fusiforme*, previously known as *Hizikia fusiformis* (Harvey) Okamura or more commonly as Hijiki (ひじき). It is a common part of the daily diet in Japan. *Sargassum fusiforme* is sold either cooked as a supplement, as a ready-made dish in supermarkets (Fig. 4b) or freeze-dried (Fig. 4c). The thalli of *S. fusiforme* have a naturally bitter taste, and are therefore usually processed by boiling or steaming before being eaten. In addition to *S. fusiforme*, which has become popular throughout Japan, *S. horneri* and *S. fulvellum* have been utilized as a direct food along the coasts of the Japan Sea, China and Korea (Ikehara 1987, Hwang et al. 2007). For example, wild populations of *S. horneri* are collected in winter (i.e., end of January - early April), and the receptacles are eaten after a short period of boiling and chopping into small pieces. Recently, *S. horneri* has been recognized as a healthy food in all regions of Japan and in order to meet increased demand, mariculture of the species has started in various Prefectures of Honshu Island (Japan, Uwai S, com. pers.).

### **Figure 4**

Of particular concern for uses related to human consumption, several studies have shown that *S. fusiforme* contains high levels of inorganic arsenic (Yokoi and Konomi 2012), with thallus levels of arsenate, arsenite, monomethylarsonic acid and dimethylarsinic acid comparable to that of arsenic poisoning following the intake of a single serving of Hijiki (Nakajima et al. 2006). The highest levels of urinary arsenic from Hijiki consumption in Japan were in the form of dimethylarsinic acid (DMA) and arsenobetaine (AsBe) (Hata et al. 2007). While much of the inorganic arsenic was found to be excreted in urine (up to 38%), repeated intake of *S. fusiforme* could result in arsenic poisoning. It was reported that a pre-cooking treatment of the seaweed



through soaking in fresh water between one to six hours reduced the arsenic content by 36 and 50%, respectively (Sugawa-Katayama et al. 2005) while soaking in warm water above 30° and up to 75°C reduced the inorganic arsenic content further by 70-80% (Ichikawa et al. 2006, Katayama and Sugawa-Katayama 2007, Katayama et al. 2008b, 2015). Boiling *S. fusiforme* in seawater (Yamashita 2014) or a combination treatment of heating in water to 90°C followed by soaking in 2% NaCl solution (Park et al. 2018) removed up to 92% of the inorganic arsenic, making it safer for human consumption (in Japan, hijiki is sold in freeze-dried form, requiring the seaweed to be boiled before consumption). A sequential processing consisting of hot water, citric acid, and fermentation by the bacteria *Lactobacillus rhamnosus* was also proposed to lower the arsenic content in *S. fusiforme* (Wang et al. 2022). Moreover, research using simulated digestion of pre-soaked Hijiki using peptide and pancreatin enzymes, suggested that very little, if any, of the remaining arsenic in the seaweed actually entered the digestive tract (Sugawa-Katayama et al. 2010). Higher than average content of arsenic than even Hijiki were found in branches of *S. horneri* (Akamoku) in Japan (Suzuki and Iwata 1990, Katayama et al. 2008a). Using thermal neutron activation analysis of freeze-dried internal organs and the blood of rats fed on a *S. horneri*-rich diet, Katayama et al. (2019) found that the highest amounts of arsenic were transferred to the blood, spleen and lungs.

While pre-consumption processing methods traditionally used in Japan reduce to a greater or lesser extent the arsenic content of *S. horneri*, there could possibly exist in the Japanese population some genetic variations or selection processes that impart immunity to higher levels of arsenic in food due to long-term exposure to this element (Hata et al. 2007). Outside of Japan, only a few localities report using *Sargassum* as part of the human diet. This could largely be due to the fact that unlike *S. fusiforme*, other species are usually leathery and fibrous, and as such not so palatable. Imaginative ways to consume some species of *Sargassum* as part of household meals have been developed in the Pacific Islands, including deep-frying entire algae in batter, making crispy chips from young leaves, used in curry mixed with pumpkin, a thick vegetable or miso soup and a slimming tea (Novaczek and Athy 2001).

### **Animal feeds**

The earliest recorded use of algae in animal feeds dates back to 45 BC in Europe, when Greek cattle herders fed washed drift seaweeds to their animals in times of drought (Newton 1951). In the 1970s, research led to the discovery of beneficial chelated microminerals in seaweeds (Lunde 1970), opening the way for the use of marine algae as a source of complementary



minerals, iodine and vitamins in animal husbandry, but not as a source of energy replacing traditional fodders due to the indigestibility of complex carbohydrates found in algae. It was not until the early 2000s that it was shown that in low amounts of inclusion (<2%) the complex carbohydrates in seaweeds have a prebiotic effect promoting gut health, leading to improved immune response and higher productivity in farmed animals (Evans and Critchley 2013, Choi et al. 2020). For the brown macroalgae, *Sargassum flavicans* and *Padina australis* showed an *in-vitro* methane mitigation potential of 34 and 51%, respectively (Machado et al. 2014). The bioactive compounds known as phlorotannins (PTs) are marine phenolic compounds, only found in brown macroalgae, and have effective antimicrobial activities on rumen cellulolytic bacterium responsible for methane production (Abbott et al. 2020). The common tropical species *S. polycystum* has a high nutritional value and contains substantial amounts of protein (14.2%) and lipids (7.6%) (Perumal et al. 2019). The high inorganic arsenic content of some species of *Sargassum* (Milledge and Harvey 2016, Yokoi and Konomi 2012) poses a challenge when considering feed supplements for animals intended for human consumption, as the correct, well-defined dosage needs to be followed in order for the meat to stay within acceptable safety norms, which (of course) vary between countries and regions of the world. Nevertheless, several companies have developed portfolios of seaweed-based animal feeds, including *Sargassum* spp. which are marketed as nature-based (or nature-positive) solutions for farmers.

### **Active ingredients (human health, well-being, cosmetic sectors)**

One of the most studied properties of *Sargassum* extracts is antioxidant activity, determined as reducing, chelating, radical scavenging capacity in chemical assays, as the ability to protect against oxidation in different emulsion systems (Balboa et al. 2014), also in cell assays (Wen et al. 2014, Balboa et al. 2015, Sobhani et al. 2015) and in *in vivo* studies (Balboa et al. 2019). This action can be mainly due to the phenolic or phlorotannin compounds, but also to fucoidans, lipids and carotenoids (Balboa et al. 2013, Terme et al. 2018, Yu et al. 2019, Manggau et al. 2022). These bioactives are found in the extracts obtained by conventional solvent extraction (Terme et al. 2018), pressurized liquid extraction (Tanniou et al. 2013, Montero et al. 2016), supercritical carbon dioxide (Conde et al. 2015, Terme et al. 2018), or with assistance by ultrasound (Yu et al. 2019), microwave (Flórez-Fernández et al. 2019) or enzymes (Hardouin et al. 2014, Del Pilar Sánchez-Camargo et al. 2016). Abundant studies reported the potential for skin care and protection, including the potentiation of hair growth (Kang et al. 2016), skin-lightening action to prevent hyper-pigmentation-related diseases (Kim et al. 2007), protection

against ultraviolet B-induced oxidative stress in human HaCaT keratinocytes (Piao et al. 2011, 2014), UVA light photodamage attenuation and protection against intracellular ROS generation (Balboa et al. 2015), and protection against UVB radiation with anti-photoaging properties (Song et al. 2016, Ye et al. 2018, Fernando et al. 2020).

The anti-inflammatory properties of several *Sargassum* spp. compounds and fractions have also attracted attention (Yoon et al. 2010, Kim et al. 2013, Manzoor et al. 2014, Jeon et al. 2019, Saraswati et al. 2019), the most active components being terpenoids, phlorotannins, fucoxanthin and fucoidans (Park et al. 2010, Chae et al. 2013, Yang et al. 2013, Casas et al. 2016, Hwang et al. 2016, Sanjeeva et al. 2018, Yu et al. 2019). Other minor compounds have shown good anti-inflammatory properties, such as the norisoprenoid apo-9'-fucoxanthinone (Chae et al. 2013, Yang et al. 2013), or loliolide from *S. horneri* (Jayawardena et al. 2021). Anti-allergic properties have been described both for the alginate fraction, which protected against inflammation caused by fine dust in keratinocytes (Fernando et al. 2018), and for ethanolic extracts (Kim et al. 2020), which also showed *in vivo* protection, in mice, against ovalbumin and shrimp allergens as effectively as the anti-allergic drug disodium cromoglycate (Haider et al. 2009). **Figure 4d** presents **an example of a moisturizing cream based on the use of extracts from *Sargassum* from Brittany (France).**

A relatively large body of information exists on bioactive and antiviral/cytotoxic activities from algal extracts, including *Sargassum* spp. (Hossain et al. 2003, Peng et al. 2012, Perumal et al. 2019). Cytotoxic activity on human cancer cell lines has been observed for solvent extracts (Kim et al. 2009) and for fucoidans (Thin et al. 2013, Usol'tseva et al. 2017, Fernando et al. 2020, Torres et al. 2020). Further depolymerization of the fucoidan fraction was suggested to enhance the anti-proliferative potential (Flórez-Fernández et al. 2017), since the lower molecular weight fractions proved to be the most active (Álvarez-Viñas et al. 2019). Mannitol was found as the main constituent of *S. micracanthum* methanol extracts, which proved to be active against human head and neck squamous cell carcinoma (Ahn et al. 2022). Meroterpenoids from *S. siliquastrum* were found to be effective against human cancer cells (Lee et al. 2013) while the Asian species *S. fulvellum* was reported to have antioxidant, anti-coagulant, anti-inflammatory, neuro-protective, immunomodulatory, anti-diabetic, and anti-cancer effects (Liu et al. 2020). Ethanol-based extracts of *S. fluitans* demonstrated hepato-

protective activities in rats against inflammation and fibrosis of the liver (Quintal-Novelo et al. 2018).

Anti-microbial activities of *Sargassum* spp. extracts have been ascribed to phenolics, fatty acids and sulphated polysaccharides (Kim et al. 2007, Setyati et al. 2018, Sudaryono et al. 2018, Arguelles et al. 2019; Herawati and Sumanik 2019), but also crude extracts showed *in vitro* antibacterial activity against *Vibrio parahaemolyticus* (Félix et al. 2020). However, when incorporated in the diet of the shrimp, *Penaeus vannamei*, for eight weeks, a post-challenge infection did not impact survival. The antiviral activity of sulphated polysaccharides could be dependent on the sulphate content and molecular weight (Dinesh et al. 2016), and this action was reported by Nakamura et al. (1994), who described the anti-HIV action of the 50 kDa fraction of *S. muticum* extracts made in boiling water. The natural defenses against fouling may contribute to the invasion success of *S. muticum* (Schwartz et al. 2017) and could be an alternative to toxic, heavy metal-based paints currently used as anti-fouling agents. High activities have been reported for lipophilic fractions, against a number of marine fouling bacteria, fungi and biofilm-associated microorganisms (Plouguerné et al. 2008, 2010, Bazes et al. 2009), or for the control of harmful cyanobacteria, mainly due to the abundance of palmitic acid (Amrani Zerrifi et al. 2020).

Other activities **pertinent for health** have been reported for multiple species of *Sargassum*. Anticoagulant action initially studied in fucoidans, was reported as a property that could be enhanced by fermentation of the whole thallus with marine, lactic acid-producing bacteria (Shobharani et al. 2013). Hepato-protective activity has been reported for fucoidan (Chale-Dzul et al. 2017), and also for *S. polycystum* alcoholic extracts, which improved antioxidant levels and prevented depletion of liver mitochondrial enzymes in rats (Raghavendran et al. 2005). Safhi et al. (2019) observed the hepato-protective role of methanolic extracts from *S. muticum* in streptozotocin-induced hepatic injury, and also on the minimized glucose levels. Solvent extracts from some *Sargassum* spp. showed neuro-protective effects on Alzheimer's (Syad et al. 2013) and Parkinson's (Silva et al. 2018) diseases. Immunomodulatory effects have been observed for the sulphated polysaccharides (Chen et al. 2012, Wang et al. 2013), for ethyl acetate fractions (Chandraraj et al. 2010) and for supercritical fluid extracts (Kim et al. 2019) from members of this genus. Anti-hypertensive activities, measured as angiotensin converting enzyme inhibitory potential, were reported for phlorotannins (Vijayan et al. 2018), for o-heterocyclic analogues, isolated from the ethylacetate:methanol fraction of *S. wightii* (Maneesh and Chakraborty 2018), and for purified protein hydrolysates from *S. mcclurei* protein (Zheng

et al. 2020). Anti-glycative effects were described (Ismail et al. 2020), particularly in phlorotannin-rich *S. muticum* extracts (Barbosa et al. 2021). Anti-diabetic activity of 80% ethanol extracts (Lee and Han 2018) were published for plastoquinones (sargahydroquinonic acid, sargachromenol and sargaquinonic acid) (Ali et al. 2017) and fucoidan (Kwon et al. 2019). Polysaccharides show prebiotic actions, with potential for the formulation of functional food with beneficial effects on gut health (Chamidah 2018, Fu et al. 2018). Different metabolites were responsible for the anti-obesity action by reducing lipid accumulation and adipogenic differentiation, amongst them indole derivatives (Kang et al. 2017), meroterpenoids (Kwon et al. 2018), saringosterol (Lee et al. 2017), sargaquinonic and sargahydroquinonic acid and fucoxanthin (Kim et al. 2016). Fucoxanthin-rich extracts (Koyama 2011) and sargaquinonic and sargahydroquinonic acids (Kim et al. 2016) also showed anti-osteoporosis activity.

Many of the above reported activities were enhanced when the extracted compounds were incorporated in nanoparticles. *Sargassum muticum* extracts have been successfully used as reducing and stabilizing agents allowing lower use of toxic reagents. Azizi et al. (2014) prepared zinc oxide hexagonal nanoparticles (30-57 nm) using aqueous extracts. González-Ballesteros et al. (2021) also used water for the synthesis of homogeneous gold nanoparticles (15 nm). Madhiyazhagan et al. (2015) and Trivedi et al. (2021) proposed *S. muticum* extract as a capping agent for the formulation of bio-compatible, stable silver nanoparticles, which produced mosquito larvicidal and adult-icidal activities whilst inhibiting several bacterial strains of *Bacillus subtilis*, *Escherichia coli*, *Klebsiella pneumoniae* and *Salmonella typhi*. Sanaeimehr et al. (2018) used *S. muticum* extracts to produce zinc oxide nanoparticles and reported cytotoxic effects through induction of apoptosis in human liver cancer cell line (HepG2), as well as inhibition of angiogenesis. Using aqueous extract of *S. muticum*, Supraja et al. (2018) synthesized spherical, hexagonal silver nanoparticles (40-65 nm) with anti-cancer activity against a breast cancer cell line. Harinee et al. (2019) used *S. muticum* as a reducing agent during the green synthesis of silver nanoparticles to improve the photocatalytic efficacy of methylene blue dye and anti-micro-fouling performance against Gram Positive and Gram-Negative bacteria strains.

The cosmetic industry is also commonly using extracts from selected *Sargassum* species, which are formulated in several galenic forms. In French Polynesia, extracts of *S. pacificum* are used in a number of cosmetic products (e.g., monoi, cream, shampoo, shower gel, Stiger-Pouvreau and Zubia 2020). In Spain, Balboa et al. (2017) demonstrated the potential of an extract of *S. muticum* combined with thermal spring waters as good ingredients for the preparation of

a sunscreen which was well accepted by consumers. A *Sargassum filipendula* extract is used in several cosmetic formulations (Michalak et al. 2020), as skin protection agent, which prevents the harmful effects of external factors on the skin.

## **Agriculture**

Adding various seaweed biomass to the soil has been traditionally used as a conditioner and aqueous extracts can be effective as beneficial plant biostimulatory applications. In particular, those *Sargassum* extracts prepared in acidic media (hydrolysis) enhanced mung bean root formation (Sharma et al. 2012). Acid extracts of *Sargassum muticum* used as foliar feeds for Chinese cabbage (pak-choi) using a hydroponic system also had positive effects on rice and lettuce seed germination, general vegetative plant development and production. Other effects of *Sargassum* spp. extracts such as stress reduction at high salinity improved chickpea growth by providing enhanced activities of superoxide dismutase and peroxidase (Abdel Latef et al. 2017). In general, seaweed fertilizers not only improve plant growth and vigor but also soil health by increasing moisture content, growth, and health of soil microbes (Mageswaran and Sivasubramaniam 1984, Begum et al. 2018). Fertilizers made from brown seaweeds contain alginates and fucoidans which are known to have extensive chelating properties, combined with the metallic ions present in the soil and form the chelates that absorb moisture and swell, and in so doing improve the growth of soil bacteria (Khan et al. 2009). However, further research is required in this area to ensure that safe levels of inorganic arsenic and heavy metals are present in food for human and animal use, including other seafood such as clams that come into contact with *Sargassum* spp. (Tremearne and Jacob 1941, Modestin et al. 2022). In Asian countries, applications of bio-fertilizers specifically made from *Sargassum* spp. have proven to be beneficial to staple food crops such as green gram (Kumar et al. 2012). In French Polynesia and Fiji, agronomical enrichment trials were conducted using mixed biomass from members of the Sargassaceae collected drifting algae then used as organic additives and good candidates to generate bio-pesticides. Zubia et al. (2015) demonstrated that low supplements of drifting tropical brown algae (at 1 and 3%) added to plant compost significantly improved the growth of maize. These authors noted significant increases of stem length, aerial portions of plants and root dry masses. In Fiji and Tuvalu, large amounts of *Sargassum* spp. biomass, due to coastal anthropogenic nutrient pollution, made them good candidates as fertilizer additives for agricultural practices (N'Yeurt and Iese 2015a). Working with common Pacific food crops, Soreh (2019) showed that liquid seaweed extracts made from *S. polycystum* contained

macronutrients useful for plant growth, namely potassium and phosphorus which promoted vegetative plant growth in terms of leaf count, fresh plant weight, height, root mass and the sugar content of leaves. Nitrogen content, however, was relatively low in *S. polycystum*. Recently, assays were carried out in order to make use of drift and floating *Sargassum* spp. in the Caribbean. This topic was recently extensively reviewed by [Thompson et al. \(2020\)](#). As an example, the project ECOSAR3, examined the use of stranded biomass of *Sargassum* spp. to make compost for the agricultural sector. Also, the company Holdex Environment is making use of *Sargassum* spp. beachings as biomass for compost. Other examples of use exist, such as a small company on St Lucia, Algas Organics, awarded by the Commonwealth and now producing a liquid fertilizer/biostimulant product ([Fig. 4e](#)). As an alternative to traditional agrochemical fertilizers, seaweeds, having beneficial amounts of micro-, macronutrients vitamins and amino acids, with a multitude of applications, and can be used as biofertilizers, soil conditioners and enhancers of crop gain and resistance to stresses and diseases in the future ([Kumar and Sahoo 2011](#), [Arioli et al. 2015](#)). The phyto-elicitor activity of three Caribbean species of seaweeds from Trinidad was demonstrated by [Ramkissoon et al. \(2017\)](#), who showed a suppression of infections in cultivated tomato plants. Enhanced resistance to fungal, bacterial and insect attack has been also observed with selected seaweed preparations ([Arioli et al. 2015](#)). Hydrolyzed algal extract, oligo- and polysaccharides can act as signals in eliciting plant defenses ([Laporte et al. 2007](#)) and several brown macroalgal molecules, i.e., terpenes and phenolic compounds, have been demonstrated to possess strong anti-microbial, anti-helminthic, and nematicidal activities (as reviewed by [Sharma et al. 2014](#)). It should be noted, however, that some species of *Sargassum* have been also reported to contain certain cytotoxic compounds that inhibit seed germination ([Kuniyoshi 1985](#)). It is hence prudent to carefully assess at which stage of plant growth algal fertilizers derived from *Sargassum* spp. are applied.

### **Biomass for the biomaterial sector (bioplastics and cardboard)**

Components of *Sargassum* spp. can be good feedstock for the preparation of biomaterials. [Davis et al. \(2021\)](#) proposed the use of alginates in combination with arabic gum for riboflavin entrapment in gel beads for prolonged release in simulated gastric fluid. In other very different approaches, the pelagic *Sargassum* spp. biomass (i.e., *S. fluitans* and *S. natans*) has been assayed for civil construction materials (i.e., adobe and pavement) with potentially good results ([Rossignolo et al. 2022](#)). Also, [Nadi et al. \(2019\)](#) reported on the inhibition of *S. muticum* crude extracts, rich in alginate, against the corrosion of carbon steel. [Azeem et al. \(2019\)](#) proposed the utilization of *S. muticum*-based pigments in the textile industry, to provide



natural environmentally friendly dyes, e.g., phenolics being the dominant coloring agents which produced light brown shades of colour.

Plastics are undeniably part of our daily lives. Their low price/cost and weight are the main attractions behind their universal use. Unfortunately, oceans and animals in the world suffer from huge quantities of waste plastics (Lavers et al. 2019). The most notable macroalgal-derived bioplastic agents are starch and cellulose derivatives, as well as alginates from brown algae. Jantasrirad et al. (2021) prepared an alternative material to synthetic plastic, consisting of a biocomposite with a mixture of pregelatinized cassava starch and *S. plagiophyllum*, previously dispersed with the aid of ultrasound and prepared using compression molding. The material showed improved photo- and thermal-stability. Similar advantages were observed using wheat gluten for the preparation of a reinforced material with increased tensile strength and delayed degradation (Kachaanun et al. 2022). Algopack, based at Saint Malo (France), tested bioplastic formulae using Caribbean *Sargassum*, the resulting bioplastic is darker and slightly more brittle than conventional plastics (<https://www.algopack.com/nos-algues/> accessed August, 2022).

Another sector which needs innovation is that of paper and cardboards based on non-woody plants and agricultural residues and have attracted renewed, recent interest (Ververis et al. 2004). The strength of the conventional products (i.e., paper, cardboard, etc.) depends on the cellulose content of raw materials. Alginates from holopelagic *Sargassum* species, as shown in Fig. 4f, produce fibres, which in combination with other types of plant fibres allow the design of interesting cardboards. For example, the Siniamin Funeral Center in Martinique (French overseas territory) developed and patented cardboard coffins for cremation made from holopelagic *Sargassum* species (Siniamin 2019).

### **Environmental management and others uses**

Since seaweeds selectively absorb and assimilate minerals from the surrounding water their selection, domestication and future cultivation can be proposed to reduce water pollution (Saldarriaga-Hernández et al. 2020). The potential to lower the nitrate content in particular was reported for *Sargassum myriocystum* (Sweetly et al. 2021) and for other algae (Sharmila et al. 2019). However, most studies evaluated the use of the collected dead biomass as a low cost biosorbent for metal removal. Lodeiro et al. (2004) reported the cadmium binding of *Sargassum muticum* biomass, after different treatments to enhance stability for industrial uses; formaldehyde cross-linking increased the uptake to 99 mg/g and protonation to 95 mg/g. Enhanced biosorption of phenol and derivatives (Rubín et al. 2006) and cadmium, lead and



mercury (Carro et al. 2015) on *S. muticum* columns loaded with calcium were reported. Carro et al. (2013) reported high mercury removal capacities with native and treated *Sargassum* material without a competition effect, with methylene blue. Simultaneous uptake of methylene blue and lead (II) ions were also feasible and column operation allowed up to five adsorption–desorption cycles (Hannachi and Hafidh 2020). Biosorption of chromium(VI) (González-Bermúdez et al. 2012), antimony(III) (Ungureanu et al. 2015), and antimony(V) (Ungureanu et al. 2017) was reported as possible. The adsorptive ability has been ascribed to the alginate extracted from *Sargassum* species (Azcorra-May et al. 2022), but also the residual biomass after alginate extraction from *S. muticum* could be an appropriate, low-cost biosourced, material for removing hexavalent chromium from aqueous solutions, with a maximum uptake capacity of 35 mg/g (Belattmania et al. 2017). Alternatively, the biomass of invasive *S. muticum* was used as a precursor for producing porous carbon with KOH and H<sub>3</sub>PO<sub>4</sub> activation (Li et al. 2018). Combination of bioremediation and energy production has been proposed by Piccini et al. (2019), who treated metal-contaminated water, i.e., (nickel(II), zinc(II), cadmium(II) and copper(II)) and the metal contaminated biomass by hydrothermal liquefaction in order to yield a bio-crude oil, an aqueous phase, a solid residue and gas. The energetic power for the dried *S. muticum*, was quantified and was shown to have a 2.7–2.9 kcal/g calorific value (Saldarriaga-Hernández et al. 2021) and for the solid residue, remaining after autohydrolysis, 3.6 kcal/g, i.e., lower than that of wood (4.0–4.5 kcal/g). Anaerobic digestion could be an alternative use (Soto et al. 2015), but the harvesting of *S. muticum* is seasonal and in order to use it for anaerobic digestion, silage was effective for preserving biomass with less than 8% energy loss of the higher heating value. This treatment resulted in losses of salt from the biomass of *Sargassum* and the virtual total loss of organic sulphur, but had no effect on methane yield (Milledge and Harvey 2016). The low methane yields from *S. muticum* could be overcome by co-digestion with a low nitrogen content substrate such as crude glycerol (Milledge and Harvey 2016), by pre-treatment by washing in freshwater to reduce ash and salt content, although the methane production was delayed (Milledge et al. 2018), and by a hydrothermal pre-treatment (Flórez-Fernández et al. 2021). Another interesting management of high biomass of *Sargassum* species is their use as a natural solution to enhance dune plant growth as demonstrated by Williams and Feagin (2010) using *S. fluitans* and *S. natans* in Texas, as a natural solution to increase soil nutrients and then enhance the growth of some plants such as *Panicum amarum*. As the addition of *Sargassum* did not impair other halophytes, the authors concluded that *Sargassum* wracks, as cast onto sandy beaches, boosts dune plant growth.

Finally, artisans are using the morphology of *Sargassum* seaweed to create jewelry, with the “Sargasso” collection by the jeweler Alexandra Mosher (Studio jewelry, Bermuda) and by the seaweed-based jewellery shop Canaille et Bidule, with a pair of earrings made from *S. muticum* (Fig. 4g).

## **Perspectives of study about the genus – latest advances**

### ***Sargassum muticum*, a worldwide species**

Being a well-studied Japanese native species, *S. muticum* is known for its waves of introduction in various places around the world (reviewed by Engelen et al. 2015). It is now present from Alaska to Mexico and from North Japan to China in the Pacific Ocean. From Norway to Morocco in the Atlantic Ocean (Le Cam et al. 2019). Using restriction-site associated DNA (RAD) sequencing, no genetic variation was detected in introduced areas, with these authors who demonstrated that *S. muticum* represented “a unique example of a successful non-clonal (i.e., sexually reproducing) marine introduced species, which exhibits almost no genome-wide genetic variation over most of its circum-global introduction range”. Despite the lack of genetic polymorphism, Tanniou et al. (2015) were able to differentiate *S. muticum* populations present on the eastern Atlantic coast from Norway to Portugal using HR-MAS NMR and FT-IR fingerprintings, re-grouping Norwegian and Portuguese and French and Spanish populations and separated Irish populations from both groups. Based on a two-year research study, Pien et al. (2016) concluded that the invasive seaweed *S. muticum*, considered today as a nuisance, could be the raw material for an innovative and sustainable economy, and could represent a new economic resource for the Normandy region, France in the future.

### **Holopelagic *Sargassum* species, an opportunity to be seized for the countries of the tropical Atlantic Ocean (Caribbean, Mexican and African coasts)?**

Since 2011, many Atlantic coasts have suffered recurrent, massive strandings of pelagic *Sargassum* species, with no apparent solution soon (Fidai et al. 2020). Huge amounts of biomass have been washed ashore, with a negative socio-economic impact on tourism, fishing, and health (Smetacek and Zingone 2013). Numerous remote sensing observations around 7°N, might indicate the presence of new “Sargasso Seas” in the Tropical North Atlantic, a small one in the Gulf of Mexico and a larger one in Northern Brazil (Gower et al. 2013). Carbon derived from blooming *Sargassum* can account for up to 18% of the total particulate organic carbon present in the top layers of the ocean (Wang et al. 2018). In 2015, the *Sargassum* summer

coverage was estimated to be 20 times higher than that observed for summers between 2000 and 2010 (Wang and Hu 2016), and the risk of *Sargassum* washing up on the shore has increased in the Lesser Antilles between 2011 and 2015 (Maréchal et al. 2017). The factors leading to the *Sargassum* blooms for a time remained hypothetical, with regards to both the dynamics and the source regions of these rafts (Oyesiku and Egunyomi 2014, Schell et al. 2015). However, recently they were attributed to increased inputs of nutrients from runoffs due to the deforestation of the Amazon waters, followed by dispersal of algal biomass by oceanic currents to the Lesser Antilles and to western Africa, with an 111% increase in the N:P tissue ratio of holopelagic *Sargassum* since the 1980s (Lapointe et al. 2021). Interestingly, the Expedition Sargasses (Thibaut 2017) confirmed the presence of three distinct morphotypes of *Sargassum* within the rafts, as previously demonstrated by Schell et al. (2015). The huge amount of *Sargassum* that washes up on the coasts of Africa, the Caribbean and Mexico can represent a significant socio-economic opportunity for the production of various low and high value-added industrial products, as first proposed by Milledge and Harvey (2016). Already, many companies have emerged to produce materials for civil construction (Rossignolo et al. 2022), biocarton coffins for cremation (Siniamin 2019) as examples. Oxenford et al. (2021) present a state of the art of holopelagic *Sargassum* recovery with various industrial sectors being cited, in order to develop effective and sustainable solutions to the sargassum crisis. Given the many constraints identified for each application, Amador-Castro et al. (2021) conclude that a biorefinery approach is the most efficient way to valorise this huge biomass of holopelagic species.

## **Industrial challenges linked with the use of *Sargassum* biomass**

### **The biorefinery concept**

The more parsimonious approach to use *Sargassum* biomass as a raw material for industrial uses is to propose an integral valorization following the philosophy of biorefineries, thereby recovering the different components and fractions in a sequential, multi-stage and multi-product process (Pérez-Larrán et al. 2019). This biorefinery approach has been addressed to obtain alginates, antioxidants and energy (González-López et al. 2012), fucoxanthin, alginates, fucoidans and phlorotannins (Balboa et al. 2015), plant biostimulants, alginates, fucoidans, phlorotannins and biogas (Flórez-Fernández et al. 2021). A minimum selling price for fucoidan confirmed the economy-of-scale for both a process considering anaerobic digestion steps for producing biogas and generating electricity and an alternative with residual seaweed solids sold

as fertilizer (Caxiano et al. 2022). The economics of biorefinery processes can be favored by the incorporation of bio-fertilizer sales to the energetic valorization and the major challenges for scale-up and commercialization remain the seasonality and variability of seaweed composition (Thompson et al. 2021).

### **Degradation of the biomass and arsenic concentration**

The main concern with the use of *Sargassum* biomass is its rapid degradation with a decrease in its quality, especially true for Caribbean *Sargassum* spp. (ANSES 2017). Many works demonstrated the interest of freeze-drying as an efficient process to keep the biochemical composition of brown macroalgae (e.g., Chan et al. 1997). Moreover, as traditional extractive processes degrade the quality of raw material, innovative processes are favored (Tanniou et al. 2013). Recently, a pre-treatment by Pulsed Electric Fields (PEF) was developed which allows retention of the seaweeds' optimal biochemical composition (Robin et al. 2018). The use of pelagic *Sargassum* from Barbados in anaerobic digestion for energy production is of low bioconversion efficiency, and co-digestion with other forms of biomass would be necessary (Thompson et al. 2020).

### **Ecological challenges linked to *Sargassum* species**

#### **Bioremediation of Climate Change**

Recent studies estimated that coastal marine macroalgae could sequester up to 173 Tg of atmospheric CO<sub>2</sub> per year, mostly through export of dead material to deep-sea sediments (Krause-Jense and Duarte 2016, Duarte et al. 2017). Further theoretical calculations proposed that growing seaweeds over 9% of the world's oceans, through algal afforestation could remove 53 billion tons of atmospheric carbon annually, effectively offsetting global emissions and even offering climate mitigation if carbon-negative processes are used to make sustainable use of algal biomass (N'Yeurt et al. 2012, Capron et al. 2020). For holopelagic *Sargassum* in the Caribbean, about 5% of the atmospheric carbon intake was reported to be converted into inert calcite, which is eventually sequestered into marine sediments (Paraguay-Delgado et al. 2020).

### **Conclusion**

The genus *Sargassum* is characterized by a high diversity which has led to the interest of a large and worldwide number of researchers, resulting in thousands of studies carried out in temperate and tropical environments globally. In areas where the genus is present, the various species

constitute meadows hosting a large number of associated species and can be considered as the pioneer and dominant species in colonized areas, in temperate and tropical environments. Of the high species diversity, only one species, i.e., *S. muticum*, has a worldwide distribution with an associated lack of genetic variation. The majority of the species are benthic and only two species live in a floating state throughout their life cycle, i.e., *S. fluitans* and *S. natans*. Given the large number of *Sargassum* species and known morphological plasticity, the taxonomy of the genus is not straightforward; with the existence of two sub-genera, *Sargassum* and *Bactrophycus*. The large biomass of *Sargassum* species around the world have led people to exploit *Sargassum* fields in various industries. In Asia, two species are known to be edible and used in aquaculture, i.e., *S. fusiforme* and *S. horneri*. *Sargassum* species are used in various industrial sectors, from food, feed, human and plant health, to cosmetics as examples. The enormous quantities of *Sargassum* in some regions make it a raw material of interest for the extraction of various metabolites, highly represented as alginates, or weakly represented as certain lipids, or polyphenols as examples, with however an arsenic and heavy metal contamination that could be high in some areas. In areas where algal populations are disappearing, it is therefore crucial to develop programs to restore *Sargassum* meadows and in areas where large biomass strandings occur, it is crucial to develop recovery routes before the biomass degrades.

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• **The Authors' Contribution is as follows:**

**V. S.-P.:** Conceptualization, Methodology, Investigation, Writing - Original draft preparation and Writing - Review & Editing. **L.M., ADR.N'Y., S.U., H.D., N.F.-F., S.C., AT.C.:** Conceptualization, Writing - Review & Editing.

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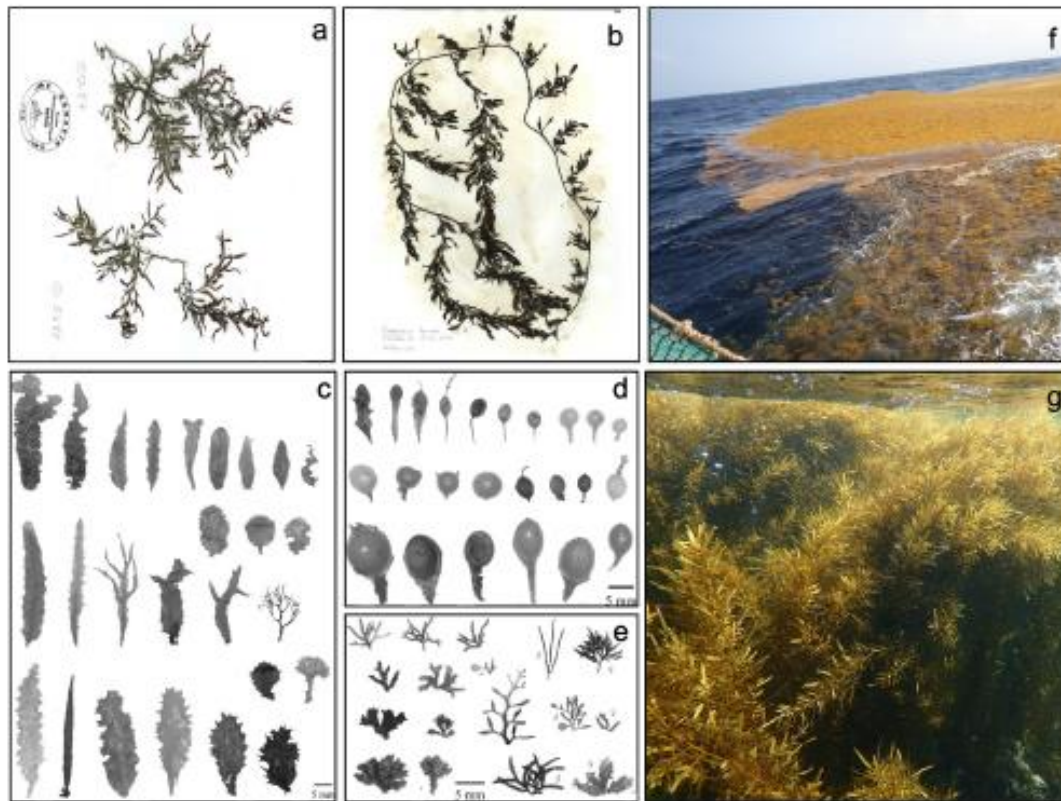
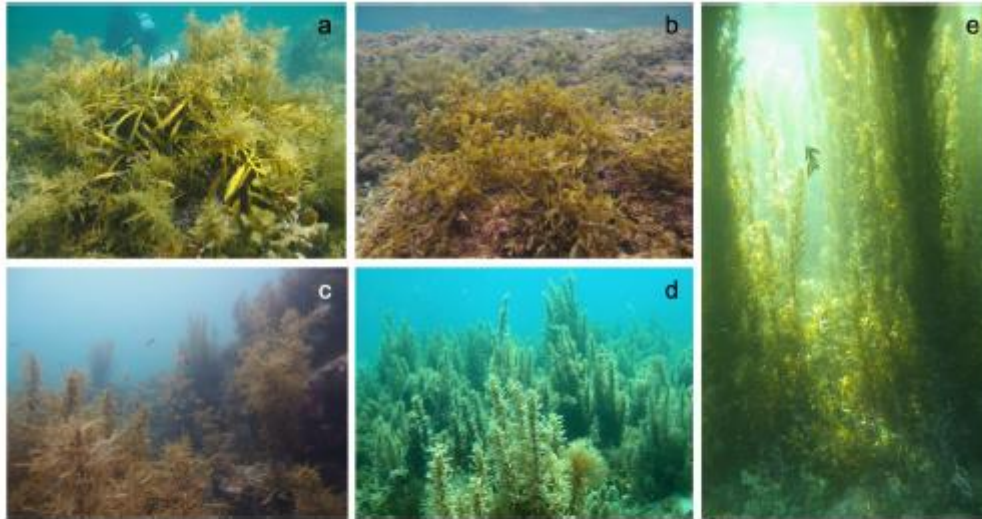


Fig. 1 General morphology of *Sargassum*, showing a) the general aspect of the thallus of the subgenus *Sargassum* with the type species *S. natans*, b) the general aspect of the thallus of the subgenus *Bactrophyucus* with the type species *S. horneri*, c) detail of blades, d) detail of floating vesicles and e) detail of receptacles within the genus, f)

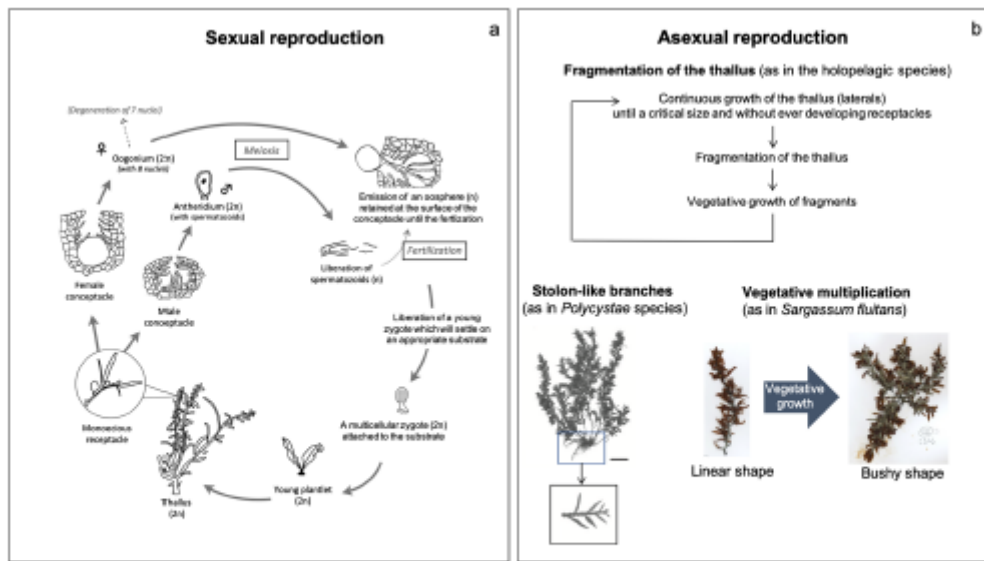
fragments of holopelagic *Sargassum* species structuring rafts in the central Atlantic Ocean, and g) individuals of *S. horneri* forming macroalgal beds from Japan, Pacific Ocean. Photos a,b,f: V. Stiger-Pouvreau (LEMAR-IUEM-UBO, France), Photo c,d,e from Mattio and Payri (2011), Photo g: S. Uwai (Kobe University, Japan)





**Fig. 2** Examples of subtidal *Sargassum* species forming plant formations, like lawns as a) *S. nigrifolium* and b) *S. patens* in Japan, forming marine meadows/bushes such as c) *S. macrocarpum* in Japan, d) *S. spinuligerum* from New Caledonia, and true submarine forests

such as e) *S. polycystum* in Tuvalu, where thalli reaching up to 2 m in height. Credit of Photos a,b,c: S. Uwai (Kobe University, Japan); d: C. Geoffray (New Caledonia), e: A.D.R. N'Yeurt (The University of the South Pacific, Fiji)



**Fig. 3** Sexual and asexual reproduction in the genus *Sargassum*. a) an example of the life-cycle of the monoecious *S. muticum* from Europe (left side, cycle produced by F. Lalegerie @iuem-ubo) showing the production of gametes (sexual reproduction). b) examples of asexual

reproductions with the fragmentation known in holoplagic species, the production of stolons as described in *S. polycystum* by Mattio et al. (2009) (scale bars for the thallus = 3 cm), and vegetative reproduction of *S. fluitans* in the central Atlantic Ocean





**Fig. 4** Examples of manufactured products based on the use of *Sargassum* species, extracts, morphology. **a)** Fresh specimens of *S. horneri* sold in Japanese markets, **b)** Cooked meal sold in Japanese supermarkets and including Hijiki (*S. fusciforme*), **c)** Dry specimens of *S. fusciforme* used as a vegetable. **d)** Moisturising cream made from *Sargassum muticum* from Brittany. **e)** A *Sargassum*-derived commercial product from Algas Organics, St Lucia, Caribbean. The raw materials used for the extraction are derived from beach washups and

Algas Organics holds a patent for the extraction process used to make a plant growth stimulant. **f)** Alginates fibers obtained from holopelagic *Sargassum*. **g)** An earring jewellery using *Sargassum muticum* fragments. Photos a,b: S. Uwai (Kobe University, Japan). c: V. Stiger-Pouvreau (LEMAR-IUEM-UBO, France). d: E. Deslandes (LEMAR-IUEM-UBO, France). e: A.T. Critchley (VCSEE, Nova Scotia, Canada). f: V. Stiger-Pouvreau (LEMAR-IUEM-UBO, France). g: P. Garnier (Camille et Bidak, France)

**Table 1** Proximal chemical composition of *Sargassum* spp. from different temperate and tropical regions

Species	Ash (%)	Protein (amino acids) (%)	Lipids (%)	Carbohydrates (fucoidan) (%)	Sulphate (%)	Fiber (%)	Alginate (%)	References
<i>Sargassum</i> sp.	24–31	2.5–11.1	2.6–3.8	1.8–7.0				Saldarriaga-Hernández et al. (2021)
<i>Sargassum</i> sp.	21.1	6.2		24.6			25	Azcorra-May et al. (2022)
<i>S. aquifolium</i>				29.0–41.7	13.7–60.6			Hsiao et al. (2021)
<i>S. crassifolium</i>	41.5	6.2	0.3	3.8		24.5		Dewinta et al. (2020)
<i>S. crassifolium</i>	25.0			1.2–5.9			16–33	Thadhani et al. (2019)
<i>S. cristaeifolium</i>	41.3	8.5	0.3	7.3		22.1		Dewinta et al. (2020)
<i>S. fluitans</i>	33.6	3.25	4.6	27.4		31.2		Milledge et al. (2020)
<i>S. fluitans</i>	33.7–55.7	2.3–3.5	0.6–1	43.1–65.8	4.0–20.0		5.1–16.3	Machado et al. (2022)
<i>S. fluitans III</i>				4.0			9.4	Davis et al. (2021)
<i>S. fusiforme</i>	8.5	9.1		29.1		19.6		Choi et al. (2020)
<i>S. henslowianum</i>	23.3	12.4	4.9			66.8		Wong and Cheung (2001)
<i>S. hemiphyllosum</i>	25.5	5.8	3.3	19.6		55.1		Wong and Cheung (2001)
<i>S. horneri</i>	27.8	7.6	0.8			47.2		Murakami et al. (2011)
<i>S. ilicifolium</i>		9.7	0.4	38.7				Ganapathi et al. (2013)
<i>S. muticum</i>	26.0	6.92	1.6	13.5		60		Balboa et al. (2016)
<i>S. muticum</i>		6.0–3.1		25.0–27.0	12.9–11.0			
<i>S. myriocystum</i>		13.2	0.2	40.2				Ganapathi et al. (2013)
<i>S. natans I</i>	35.7	3.81	4.5	19.0		31.2		Milledge et al. (2020)
<i>S. natans I</i>				4.4			11.1	Davis et al. (2021)
<i>S. natans VIII</i>	35.3	2.99	3.6	21.8		37.0		Milledge et al. (2020)
<i>S. natans VIII</i>				4.6			12.2	Davis et al. (2021)
<i>S. latifolium</i>		4.6	1.1	41.1	0.09		17.5	Dalal et al. (2021)
<i>S. oligocystum</i>	21.3–22.5	7.1–9.3	3.5–5.7	52.1–58.0		7.4–12.6		Praiboon et al. (2018)
<i>S. patens</i>	18.1–31.5	8.3–21.6	0.6–6.7	51.4–59.9		56.2	32.4	Wong and Cheung (2001), Løe et al. (2022)
<i>S. plagiophyllum</i>		12.3	0.16	33.4				Ganapathi et al. (2013)
<i>S. polycystum</i>	21.4	8.7 (37.3)	3.4	36.6		2.8		Nazarudin et al. (2021)
<i>S. polycystum</i>	25.0			(1.8–5.6)			18–30	Thadhani et al. (2019)
<i>S. polycystum</i>	29.0–34.1	5.2–14.2	0.24–7.6	25.0		21.3–38.0		Perumal et al. (2019), Munsu et al. (2021)
<i>S. subrepandum</i>	29.5	3.2	3.6			7.0		Abou-El-Wafa et al. (2011)
<i>S. thunbergii</i>	20.8	7.1	7.9	37				Yang et al. (2021)
<i>S. vulgare</i>	29.4	8.4	0.6	34.2		24.5		Arguelles et al. (2019)
<i>S. wightii</i>	25.0			(1.8–4.6)			22–29	Thadhani et al. (2019)
<i>S. wightii</i>	19.9		3.1	45.7		25.0		Kumar et al. (2021)