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Chapter

A Natural History of Floating
*Sargassum* Species (Sargasso) from Mexico

José Luis Godínez-Ortega, Juan V. Cuatlán-Cortés, Juan M. López-Bautista and Brigitta I. van Tussenbroek

Abstract

For at least several centuries, sargasso has inhabited the Atlantic Ocean, and there are historical records of these algae reaching the Mexican Veracruz State in the Gulf of Mexico. Blooming of sargasso in the southern tropical Atlantic is a current a global problem from Africa to the Greater Caribbean. Since 2015, exceptionally large quantities of sargasso have been arriving intermittently on the Mexican Caribbean coast, affecting coastal ecosystems and tourist beaches. Sargasso includes two holopelagic species, *Sargassum natans* and *S. fluitans*, with several varieties. There are no records of sexual reproduction in these species, and the algae are thought to spread exclusively by clonal reproduction by fragmentation. Although sargasso seaweeds have grown in the Sargasso Sea for centuries; they have not been well studied. This chapter deals with historical aspects of these algae, their taxonomic and morphological characteristics, distribution, ecology, and practical uses. Sargasso blooms in the central Atlantic started in 2011. In later years, the bloom developed to extend from West Africa, Brazil, and the Great Caribbean, including West-Indies, Mexico, and the Gulf of Mexico. The pelagic sargasso is a global phenomenon that must be understood by integrating natural history, modern biology, social and economic aspects.

Keywords: pelagic *Sargassum*, bloom, Sargasso Sea, Great Atlantic Sargasso Belt, uses, historical background, algal biology

1. Introduction

The Mexican beaches of the western Atlantic Sea, particularly those of the Mexican Caribbean in the state of Quintana Roo, are among the most visited by national and international tourists due to their beautiful turquoise waters and white calcareous sand. These beaches have recently been infested by huge drifting rafts of macroalgae the genus *Sargassum* (Phaeophyceae); i.e. *Sargassum fluitans* and *S. natans*. In the open ocean these rafts are refuge, substrate or nursery for many marine flora and fauna. However, the quantities reaching the Mexican beaches intermittently in recent year have been massive, covering vast coastal areas, causing severe problems to marine ecosystems and tourism [1–4]. The massive influxes and beaching of these seaweeds have become a persistent phenomenon, which has led to a series of investigations in Mexico and other parts of the world, that aim to understand this phenomenon and to develop adaptation strategies to mitigate its damage to the ecosystems and economy.
This problem has prompted us to ask ourselves various questions of a natural history nature: How long have these seaweed rafts been around? Have similar bloom events occurred in the past? What is the origin of the recent blooms? These are essential questions to understand the recent infestation and their answers may aid to further research into mitigation of its effects in the short, medium, and long term. We will do so from an historical and biological perspective, starting with the algal names, which today seems trivial but has a fascinating history beginning in the 15th century. We also recognize that it is crucial to know their correct scientific name as the first step to study their biology. Many herbarium specimens have been collected in the past and are awaiting to be investigated in terms of their macroscopic morphology, internal anatomy, molecular biology, reproduction, ecology, and geographical distribution. We will also provide information on past and present uses of sargasso.

1.1 Fossil and historical records of sargasso

The fossil record of sargasso species assemblages goes possibly back to the Tethys Sea. Jerzmańska and Kotlarczyk [5] described numerous brown algae (Phaeophyceae), together with fish skeletons from the Oligocene (33.9–23.03 mya) in the Polish Carpathians [5]. These authors pointed out that in this fossil record some algae were observed with air bladders inserted on branches, but without holdfasts or attachment structures, similar to modern “pelagic forms of the genus *Sargassum*” [5]. The authors hypothesize that the fish genera in this thanatocoenosis fossil assemblage, belonging to the upper part of the upper bathypelagic horizon (seabed at 1000 to 4000 m deep), might be formed at the bottom of a sargasso sea, with the presence of pelagic sargasso, bathypelagic and pelagic fishes comparable to those of recent marine biocenoses of the Sargasso Sea. They called this Oligocene assemblage “quasi-Sargasso”. Since there are no fossil records from the North Atlantic, the hypothesis presented in this work is that the “quasi-Sargasso” assemblage had its origin in the Tethys Sea and subsequently migrated towards the Atlantic Ocean before its original habitat was destroyed by alpine folding at the end of the Miocene [5]. Despite early fossil records of sargasso-like algae, extensive phylogenetic analysis indicates that the diversification of the genus *Sargassum* was likely relatively recent, not before the late Pliocene (5.3–2.6 mya), with its origin in the central Indo-Pacific, and diversification into the Atlantic 0.2 to 0.4 million years ago [6]. Following this hypothesis, the fossils found in the Oligocene Carpathians’ beds corroborate the existence of an ancestor of the genus *Sargassum* 36 million years ago, with diversification in the late Pliocene. From this, we can tentatively conclude that the pelagic species were probably present in the Atlantic long before the diversification of benthic species, which will need verification with further future studies. Børgesen [7] mentioned that the pelagic *Sargassum* species were of benthic origin, but Parr [8] pointed out that the lack of benthic species with comparable morphology to that of the pelagic ones in the western Atlantic, casts doubt on Børgesen’s hypothesis. The oldest written observation on sargasso are from Columbus; thus, there is a great time gap between fossil records and actual sightings.

Pérez-Rubín Feigl [9] cited sightings of sargasso by inhabitants of the American continent before Christopher Columbus’ voyage in 1492 and up to 1792 in his detailed study on “Las algas y los antiguos navegantes españoles (1492-1792)” [“Algae and ancient Spanish navigators (1492-1792)”]. In Mexico, there is a record of sargasso by the ancient Mayans. They call sargasso “U tail kaknab”, which means “is thrown by the lady of the sea”. Possibly, this is the reason for a present-day confusion in the Yucatan Peninsula about the term “sargazo” which is the local name for all types of plant material found on the beach and not only sargasso or
other Sargassum spp. [10]. But, it is very certain that they had seen sargasso among the other beach-cast specimen. Christobal Columbus, in his “Relaciones y Cartas,”
from his first trip, mentioned the following: “en amaneciendo hallaron tanta yerba que parecía ser la mar cuajada de ella, y venía del Oeste” (Viernes 21 septiembre 1492) [“at dawn, they found so much grass that it seemed to be the sea curdled with it, and it came from the West” (Friday, September 21, 1492)] [11].

Sargasso is a brown pelagic alga kept afloat by their small air-filled bladders (pneumatophores), that can form large entangled assemblages. The Portuguese ships were often entrapped in the algal masses due to the lack of wind, giving crews plenty of time to explore it. As these men came from a country where vines abound, the air bladder assemblages of the seaweeds seemed bunches of grapes to them, of a variety called “salgazo” . “Sargacinha” means grape, which comes from “sarga” (variety of grape) [12], and finally, it was derived in “sargaço” or “sargaçao” [13]. This may be how this alga acquired its name. In another letter dated October 3, 1492, Columbus commented on these algae and mentioned: “Aparecieron parcelas, yerba mucha, alguna muy vieja y otra muy fresca, y traía como fruta;” [“Plots appeared, a lot of herbs, some very old and some very fresh, and they brought like fruit,” [11]. It is probable that at this time, the Sargasso Sea was named.

The name sargasso may have yet another origin than the one described above. It is known that in Portugal, from the Middle Ages to the 20th century, the harvesting of algae was an economically and socially significant activity. In a letter dated March 9, 1308, D. Dinis orders that the “argaço” that came from the sea, belonged to the residents of the place, which they prepared and dried to fertilize the fields [14, 15].

Thus, the sailors on Columbus ships may have called them “argaço” or “salgazo.” In this case, the evolutionary line of the word alga> algaço> argaço and sargaço, is thought to derive from argaço under the influence of another word, probably salt [16, 17].

Between 1526 and 1590, Gonzalo Fernández de Oviedo (1478–1557) and José de Acosta (1540–1600) disseminated the natural sciences of America, and their texts had a worldwide distribution at that time. After the Columbian period, authors such as Juan López de Velasco (1530–1598), Bartolomé de Las Casas (1474 or 1484–1566), Gonzalo Fernández de Oviedo (1478–1557), José de Acosta (1540–1600), Pedro Martir de Angleria (1457–1526) in their Decades (1515) and Alexander von Humboldt (1769–1859) mentioned the “mar de hierbas” [sea of herbs] or Mare Herbidum [9].

The description by Fernández de Oviedo in 1535 [18] stands out because he mentioned “the great grassland” and named the algae on the surface of the sea “salgazos”. Acosta [19] wrote the following: “En la muy profunda y larga mar de la muy nombrada, y no menos temida Vuelta del Sargazo (que así se llama de los navegantes de las Indias de diez y ocho hasta treinta y cuatro grados de la línea equinoccial de la parte del Norte) aparece la mar llena de esta yerba, llamada sargazo. Es de un palmo: los ramillos delgados y sin raíz: véase toda el agua cubierta de esta yerba en montones pegada y liada una con otra y especulando bien le ve venir del profundo de la mar tan liada, y envuelta, que parece cada montón una grande mata.” [“In the very deep and long sea of the much named, and no less feared Vuelta del Sargazo (which is the name of the navigators of the Indies from eighteen to thirty-four degrees of the equinoctial line of the northern hemisphere) appears the sea full of this herb, called sargasso. It is of a hand span (20 cm): the thin and detached branchlets: see all the water covered with this herb in heaps stuck together and bundled with each other and, speculating well, you see it coming from the deep sea so bundled, and messy, that each heap seems one big clump.”].

Alexander von Humboldt (1769–1859) was the first scientist to study the Sargasso Sea in more detail, situating it in the eastern and American region, the latter with the highest concentration, placing it between Bermuda and the Bahamas. The area was well known to sailors: “An ancient tradition, which has been preserved among the pilots of Galicia, says that this large bank of “fucus” marks the middle
of the route they take through the “Golfo de las Yeguas” [“Gulf of Herbs”] the ships return to Spain from Cartagena de Indias, Veracruz or Havana, which are favored by the current of the Gulf Stream” [20]. Humboldt interpreted this Sargasso Sea as a community association, constituted by the algal species and an animal community [9, 20]. Hipólito Ruiz López (1754–1816), a Spanish botanist, published his study on sargasso and pointed out the distribution in the Atlantic Ocean between 22° to 38°N. In this study, he illustrated *Fucus natans* and confused its epibionts (hydrozoid) with anthers and pistils from vascular plants and the pneumatocysts with seeds (Figure 1) [21]. Sargasso was mentioned in 1799 by José de Viera y Clavijo.
(1731–1813), who presented morphological descriptions and characteristics of its habitat. Viera and Clavijo’s works were published in the 19th century [22, 23].

In the 18th century, Martín de Sessé and José Mariano Mociño, members of the Royal Botanical Expedition of New Spain, recognized algae and particularly sargasso. In the “Catálogo de los animales y plantas que han reconocido y determinado según el sistema de Linneo los facultativos de mi expedición D. José Mociño y D. José Maldonado” [24]. This document was found in the Archivo General y Biblioteca del Ministerio de Asuntos Exteriores from Madrid as a manuscript: “Viaje a la
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Table 1. Records of floating Sargassum spp. in Mexico.
2. Biology of sargasso

2.1 Methodology of the study of herbarium specimen

The material deposited in the National Herbarium (MEXU) of the Institute of Biology, National Autonomous University of Mexico (UNAM) (Table 1) was reviewed. Herbarium samples were hydrated for 24 h with seawater and a liquid soap solution (5%). Once hydrated, they were fixed in a 4% formalin solution neutralized in seawater. For morpho-anatomical observations, 15 μm-thick sections were made with a microtome (Reichart Jung 820) and a Mectron cryostat with disposable blades. Sections were mounted in a 70:30 Karo® corn syrup/water solution with a trace of phenol to prevent fungal growth [51]. A Zeiss light microscope, model 1206 S09432, equipped with a Canon PowerShot G6 digital camera, was used to determine the alga’s morphological characteristics. For cell measurements AxioVision software (SE64, Rel. 4.9.1 Carl Zeiss) was used. The species descriptions below are based on this material.

2.2 Classification and species descriptions

The study of the genus Sargassum began with the work of C. Agardh in 1820 [52]. However, this name was born from the Fucus of Linnaeus [53]. The basionym Fucus natans was mainly applied to sargasso from the Atlantic Ocean or “Common Gulfweed,” while S. fluitans was named “Broad-toothed Gulfweed.”

The taxonomic and nomenclatural history of S. fluitans and S. natans is explained extensively by Silva et al. [54]. The genus Sargassum from the order Fucales is a diversified genus with almost 361 species [55]. Identification of the species may be problematic due to their polymorphic character and phenotypic plasticity [56]. Traditionally, classification was based on the blade morphology, the margins of the blades, blade midrib, the pneumatophores (air bladders), the branching, degree of branching, and morphology of the receptacles (reproductive organs) [57].
The genus *Sargassum* has received increasing attention since 1985 [57]. At first, four subgenera were recognized: *Sargassum*, *Arthrophycus*, *Bactrophycus*, and *Phyllotrichia*. The subgenus *Sargassum* is the most diverse one, and it is divided into three sections: Zygocarpicae, Malacocarpicae, and Acanthocarpicae [57]. Recently, the traditional classification has been put to the test using nuclear, chloroplast, and mitochondrial markers. One of the resulting outcomes was polyphyly of the section Acanthocarpicae, which was subsequently considered as a synonym of the section *Sargassum*. Also, based on molecular analysis, *S. natans* was placed in section *Sargassum*, because its receptacle morphology cannot be verified [57] since until date only its vegetative form is known. At present, the genus has only two recognized subgenera: i.e., *Sargassum* and *Bactrophycus*, with nine sections found in temperate and tropical latitudes [58].

In Mexico, both pelagic species, *S. fluitans* and *S. natans* have been recorded [50, 59]. According to Parr [8], there are three morphotypes or ecotypes for the Mexican region.

**Figure 3.** *Sargassum fluitans* type III. A: Stems of the branches with three spines (arrows), spineless pneumatophores with many more or less wide blades (NI-MEXU 2459); scale 2 cm. B: Cross section of the leaf shows the midrib and a cell layer in the cortex. C: Cross section of the stem. D: Cross section of the pneumatophore formed from a thick layer of cells. Scale bars: 200 μm.
It is essential to point out that Parr [8] did not follow the International Code of Botanical Nomenclature [60] while designating its types, so his designations are considered an artificial classification. However, due to the massive sargasso invasions on the western Atlantic Ocean, Parr’s classification of the morphotypes is useful.

Classification: Phylum Ochrophyta; Class Phaeophyceae; Subclass Fucophycidae; Order Fucales; Family Sargassaceae; Genus Sargassum; Subgenus Sargassum; Section Sargassum.

Descriptions from Mexican material:
Homotypic synonym:
*Sargassum hystrix* J. Agardh var. *fluitans* Børgesen, 1914a: 11 [61].

Figure 4.
*Sargassum fluitans* type III (Puerto Morelos). Scale bar: 1 cm.
Pelagic specimens (up to 1 m; usually 20–30 cm long) of yellowish-brown color are forming rafts of variable sizes. Cylindrical axis 0.4–1.8 mm thick, smooth or with few spines near the apex, with a well-formed midrib in the center surrounded by rounded cells and a single layer cortex of cells (Figure 3A,C). Blades with short pedicels of 1–5 cm long by 1–4 mm wide, 423 μm thick in the distinctive midrib; blades firm, lanceolate in shape and pointed apices, serrate margins with broadly flattened teeth at the base; in cross-section, a well-formed midrib is observed in the center surrounded by polygonal medullary cells protected with a cortex of a layer of quadrangular cells (Figure 3A,B). Cryptostomatas (sterile cavities with hairs) absent. Pneumatophores at the base of the blades 2–5 mm in diameter, with a pedicel of 3–4 mm without wings; in cross section with two cell layers, the outer cortex with smaller cells (Figure 3A, D). Unknown receptacles.

Figure 5.
Sargassum natans type I. A: Smooth branches with distal spine on pneumatophores (arrow) and narrow blades (NI-MEXU 2665). B: Cross section of the blade shows the midrib and a cell layer in the cortex. C: Cross section of the pneumatophore formed by a thick layer of cells. D: Cross section of the stem. Scale bars: 200 μm.
**Sargassum fluitans** Type III [8]. **Figures 3 and 4.**

Upon close examination, the main axis can be differentiated from the secondary ones with few branches with spines in distal areas. Pneumatophores (1.4–2.9 mm diam.) are more abundant than the oblong blades, without a spine. Always sterile, without receptacles.


**Sargassum natans** (Linnaeus) Gaillon, 1828: 355 [63]. **Figures 5–8.**

Homotypic synonym:
**Fucus natans** Linnaeus, 1753: 1160 [53] (lectotype locality: “Indica”, probably Jamaica fide [54, 64].

Heterotypic synonym:
**Fucus baccifer** Turner, 1802: 55–60 (“bacciferus”) [65].
Pelagic species branching in several directions, of variable size up to up to 60 cm; usually 20–30 cm wide. Main axis absent, 0.5–2 mm thick, without spines, and with a wiry appearance; in cross-section, in the center, a midrib is observed, surrounded by subspherical cells and a cortex of a layer of quadrangular cells (Figures 5A, 6, 7A, B). Blades firm, linear, or lanceolate with the apices pointed, 1–4 cm long by 1–5 mm wide, serrated margin with elongated and acute teeth; in cross-section, a conspicuous midrib (329 μm thick) is observed in the center surrounded by few rounded cells and with a cortex of a layer of quadrangular cells (Figures 5A, B, 7A, B); cryptostomatas absent. Blades relatively sparse; generally, a gradual reduction in the secondary branches’ size is presented. Pneumatophores abundant, spherical in shape, 2–6 mm in diameter with a 2–5 mm pedicel, with or
without spine (Figures 5A, 6, 7A, 8) with branching alternate, or at the base and a small leaf-shaped projection; in cross-section, a thick layer of round cells with a hollow center and a cortex of a single layer of cells is observed (Figures 5C, 7C). Fertile specimens never found.

*Sargassum natans* Type I [8]. Figures 5 and 6.

The relative ratio of blades/pneumatophores is 2:1, pneumatophores 2.1–3.6 mm diameter with frequently a distal spine. Blades linear to narrowly lanceolate, 1–40 mm long, and 1–3 mm wide.

*Sargassum natans* Type VIII [8]. Figures 7 and 8.

Pneumatophores numerous, 2–5 mm in diameter and larger than Type I, with a pedicel (1–4 mm), spine absent and central axis evident. Lanceolate blades are wider than Type I.

Figure 8.
*Sargassum natans* type VIII (Puerto Morelos). Scale bar: 1 cm.

The features to identify *Sargassum fluitans* (including Type III) specimens correspond to a branched thallus, with lanceolate or linear blades, with an irregularly toothed margin, slightly oblong pneumatophores and an axis with mainly apical spines; this corresponds to Parr’s [8] description. There is an incongruity with Børgesen’s original description of material from the Sargasso Sea [7] with large and clearly visible cryptostomatas. Taylor [50] described, however, the absence or presence of only a few cryptostomatas and pneumatophores without a distal spine. Littler and Littler [59] also indicated few or no cryptostomatas. We did not observe cryptostomatas in Mexican material, as was also found in other studies of Caribbean material [66, 67]. Another characteristic that coincides with [50, 59] is the prominent midrib of the blades of the specimen in the MEXU herbarium (Figures 3A-C).

In the Mexican material, *S. natans* differ from *S. fluitans* by the absence of spines on the axis. The blades are linear or lanceolate, and the margin is serrated with elongated teeth, cryptostomatas absent, spherical pneumatophores with a pedicel, and often a thorn present depending on type I. Although Taylor [50] and Littler and Littler [59] agreed with almost all the characteristics of *S. natans*, they mentioned that the midrib is not prominent and the pneumatophores have a long spine, coinciding with the material of MEXU corresponding to *S. natans* type I together with the linear blades. *S. natans* type VIII has a thallus also free of spines on the axis and the pneumatophores. It has broader blades with a lanceolate shape, and it is consistent with Taylor [50], without a prominent midrib (Figures 7B, 8). In the MEXU material, the pneumatophores wall is slightly thinner in *S. fluitans* (231–318 μm, Figure 3D) than in *S. natans* (362–392 μm, Figures 5C, 7C). In both species, the receptacles are unknown.

2.3 Molecular biology

The identification of *Sargassum* species often requires both extensive morphological studies of specimens and molecular analyses. For molecular identification of *Sargassum* species, the use of genetic DNA markers such as nuclear ITS-2, a portion of the partial RubisCO operon or *rbcL* chloroplast, the variable intergenic mitochondrial spacer mtsp, and the universal mitochondrial markers COI and COX3, have been proposed. However, these barcode markers are less efficient when intraspecific variability and interspecific divergence overlap, as is often the case for *Sargassum* spp. [68]. So far, nuclear ITS-2 and partial plastid RubisCO have been ineffective to identify morphologically different species, but mitochondrial markers (mtsp, COI, and cox3) may have more potential for this purpose [69].

In the Mexican coasts of the Atlantic Ocean, 16 species of *Sargassum* [70] have been reported, and 24 species have been identified for the region from North Carolina to Brazil [62]. However, according to recent molecular studies on species diversity in Mexico, the number of species is lower than initially thought [70]. *Sargassum* species diversity is likely to be overestimated [56]. A recent phylogenetic analyses using three independent molecular markers (COI-5P, ITS-2, and *rbcL*) for Mexican species found that ten previously reported species (*S. bermudense*, *S. buxifolium*, *S. cymosum*, *S. filipendula*, *S. furcatum*, *S. hystrix*, *S. polyceratium*, and *S. vulgare*) were grouped into a single polytomy,
with low genetic diversity [29]. Surprisingly, the two pelagic species, *S. fluitans* and *S. natans*, were also included in this polytomy. However, further studies on authentic *Sargassum* materials (types), using higher resolution markers, are needed to validate such a taxonomic proposal. Species diversity has not yet been assessed using a multigene molecular approach, where a higher resolution would be expected using concatenated sequences [71]. Integrative investigations of morphology, life-cycle, and molecular analyses are essential to better understand the taxonomy of *Sargassum*.

### 2.4 Reproduction

As all species in the genus *Sargassum*, sargasso has a diploid thallus, and clonal reproduction is the only mechanism of propagation known for the sargasso species until today. Neither *S. fluitans* or *S. natans* have been seen to multiply sexually. Vegetative reproduction occurs by fragmentation of old thalli sections (with epibionts) that disintegrate breaking apart, and the newly formed fragments grow again [68]. Generally, no clearly obvious main axes are observed as is the case in benthic species attached to a substrate.

Moreira and Suárez [72] found beach-cast specimens of *Sargassum* spp. in Cuba having fertile receptacles with male or female sexual structures; however, they did not present photographs, and from the illustrations it may be deduced that the thalli were partly decayed, making difficult the identification of these specimens to species level or their habits (pelagic or benthic); however, it is worthwhile to follow up this observation and confirm the identity of the fertile specimens. Only *S. fluitans* presents occasional cryptostomatas; as Simons [73] indicated, cryptostomatas, although sterile, are homologous to conceptacles (reproductive structures).

In benthic sargasso species, female oogonia are exposed outside the conceptacle through the ostiole, remaining attached to the receptacle, which is a modified terminal structure of the thallus that contains the conceptacles, whose function is to produce reproductive cells. The conceptacle is a cavity (crypt) immersed in the surface of the thallus with an ostiole (opening) to the outside that contains the reproductive structures or gametangia retained by a mucilaginous stalk. Once the sperm is chemically attracted to the oogonium and fertilization occurs, the zygote is released from the receptacle driven by light and temperature cues [74]. The young thalli of benthic *Sargassum* species come into contact with a solid substrate, on which they will produce rhizoids and growing axes. Until now the absence of sexual reproduction in pelagic *Sargassum* species remains an enigma, but the drifting thalli are perfectly capable of growing vegetatively through fragmentation when they are transported by the marine currents and winds [75].

### 2.5 Distribution, ecology, and origin

The genus *Sargassum* is distributed in all the world's oceans, except for Antarctica [68]. The highest concentration of sargasso (pelagic *Sargassum* species) used to be in the Sargasso Sea, in the subtropical clockwise circulating gyre in the North Atlantic, delimited by the Gulf Stream on the western edge, the North Atlantic Current in the north, the Canary Current in the east and the North Atlantic Equatorial Current in the south. Satellite images have allowed for easier and more comprehensive ways to track the sargasso distribution (e.g. [76, 77]). The accumulations of the sargasso in the Sargasso Sea can be massive (hundreds square meters), completely segregated, distributed in small patches (several to tenths of square meters), or along lines due to the Langmuir circulation [78]. Small or occasionally
larger quantities of sargasso from the Sargasso Sea have always been arriving intermittently to the coasts of the Mexican Caribbean and the Gulf of Mexico when, due to high-pressure anomalies, the algae from this sea were transported southwards, and subsequently introduced into the Caribbean through the Windward, Mona and Anegada Passages, caught up by the Yucatan Current and then re-entering the Sargasso Sea directly through Florida Straits or after passing through a loop in the Gulf of Mexico (The Sargasso Loop System) [79]. Sargasso moves through this large area from spring and early summer, heading towards the Sargasso Sea during autumn and early winter just north of the Bahamas [80]. In certain years, massive quantities of sargasso have beached in the northern Gulf of Mexico, especially in Texas, during the summers [80]. But, in 2011, a new area of concentration was found in the southern tropical Atlantic near the Equator, i.e. Northern Equatorial Recirculation Region (NERR) [81]. Since then, sargasso has been introduced intermittently into the southern Caribbean, to be transported northwards by the Caribbean and Yucatan currents. This new area of concentration of sargasso in the NERR, from the eastern coast of Africa to Brazil, throughout the Caribbean, and into the Gulf of Mexico has been named the Great Atlantic Sargasso (Sargassum) Belt (GASB) by Wang and collaborators [77]. In the peak month of June 2018, the GASB covered 6000 km$^2$ with an estimated 20 million tons of algal mass, making this the largest macro-algal bloom ever recorded [77]. The algal masses in the GASB show large interannual variability, which to date has been difficult to predict [77]. The influx of sargasso into the Caribbean shows a seasonal pattern, as the North Equatorial Counter Current breaks down from January until May; thus, the generated westward surface flow transports sargasso into the Southern Caribbean Sea [77, 82]. Once released from the NERR and transported into the Caribbean, sargasso flows through the Caribbean and (possibly) the Gulf of Mexico to end its journey in the Sargasso Sea [83]. The pelagic masses of sargasso arrive on the Mexican coasts approximately 2–3 months after their introduction into the southern Caribbean. Southeastern trade winds transport the sargasso masses accumulated in the Yucatan current towards the Mexican coast inundating the beaches with algae at seasonal intervals from March/April until August/September (Figure 9) [37, 84].

Sargasso exhibits higher growth rates at higher temperatures (until 30°C) [85] and cannot survive in waters below 18°C [8, 86]. Sargasso in the Sargasso Sea usually has low productivity and a bright yellow color [8], typical of nutrient-depleted populations. Neritic populations (closer to the coast) have greater availability of nutrients (mainly N and P) and develop a deeper brown color, attaining higher photosynthetic capacity (Pmax) and productivity; alkaline phosphatase activity is lower in these nutrient-enriched algae compared to those from the Sargasso Sea, and their tissue

Figure 9. Biomass of beached fresh sargasso on a beach at Puerto Morelos in the north of the Mexican Caribbean between the summers of 2016 and 2020. The horizontal gray line indicates the minimal biomass when Sargasso-brown-tides (Sbt) are observed (modified from [37]).
concentrations of N and P are higher [87]. Sargasso in the Sargasso Loop System (from the Sargasso Sea to northern Caribbean, and back to the Sargasso Sea directly or through the Gulf of Mexico, see above) acquires nutrients when it passes through the nutrient-rich Gulf of Mexico; thus, there appears to be a neritic-oceanic coupling in this loop system that could have facilitated the adaptation of sargasso to large differences in nutrient availability, maintaining population in oligotrophic waters but rapidly responding to increasing nutrients when available. This capacity to rapidly respond to increasing nutrients may have contributed to the bloom of these algae once introduced into the more eutrophic NERR (than the Sargasso Sea) in 2010/2011.

The different conditions in the Sargasso Sea and NERR may also partially explain differences in specific composition of the sargasso masses in these regions. Studies from the 1990s to 2015 [73], found that *S. natans* I was the most important species in the Sargasso Sea (87%). However, sargasso in the Atlantic Ocean east of the Antilles and the Caribbean in 2014 and 2015 had different specific composition: *S. natans* VIII dominated the western tropical Atlantic (87.3% wet weight), the eastern Caribbean (95.3% wet weight), and the Antilles Current (92.0% wet weight) [88]. *Sargassum fluitans* III generally predominated with more than 60% of the total wet biomass; *S. natans* VIII decreased gradually from 2016 to 2019 but increased again in the beginning of 2020. *S. natans* I almost absent in 2015–2017, appeared in 2018 when it comprised on average 23% of the total sargasso in 2018, increasing in relative abundance from then onwards 2020 [37]. Garcia-Sanchez et al. [37] proposed that differences in abundance of species and their morphological forms could be explained multiple origins of the sargasso transported onshore, or may reflect variable environmental conditions in the seas where they passed through, since sargasso species have different thermal tolerances and growth rates.

In the open ocean, pelagic sargasso represents a diverse community, and it is a critical habitat recruitment area for macrofauna at various development stages, with a complex trophic network of energy flows among herbivores, predators, and detritivores [89]. Sargasso rafts providing breeding and development area for various fish of ecological and commercial interest [90]. For example, the larval fish of the European eel (*Anguilla anguilla*) and the American eel (*Anguilla rostrata*) hatch and grow in the Sargasso Sea to travel to respectively the European and American continent as juveniles, to return to the Sargasso Sea later in life as sexually mature adults to spawn [91]. Sea turtles are transported by ocean currents and eventually reach sargasso mats providing them with shelter and food [92]. The Sargasso Sea has at least ten species of invertebrates and two vertebrates that are endemic to the Sargasso Sea, including the sargasso fish (*Histrio histrio*), and the sargasso nudibranch (*Scyllaea pelagica*) [90, 93]. Floating masses of sargasso in the Gulf of Mexico are home to of 33 species of macrofauna, including *Callinectes sapidus, Latreutes fucorum, Portunus sayi, Portunus spinicarpus, Mugil sp.* and *Balistes capriscus*, and they are considered of importance for the fisheries in the Gulf region [94]. On the other hand, there is evidence that certain deep-sea fish and invertebrates consume the remains of sargasso and associated epibionts exported to the bottom; thereby contributing to the maintenance of deep-sea communities [95]. The superficial influence of the wind causing the Langmuir circulation leads to the formation of algal rafts in the form of rows. Langmuir circulation can sink the algae until a depth (up to 8-10 m), where the sargasso may maintain neutral buoyancy; as the algae age or accumulate epibionts these subsurface masses may sink following the benefits of sargasso, until reaching a depth with higher pressure that causes the implosion of the pneumatophores, resulting in total sinking to the deep-sea floor [95]. The sunken sargasso contains large amounts of carbon, and may thus be an important sink of organic carbon, helping to mitigate global climate change [96].
Beach-cast sargasso, in small quantities, provides food for various coastal species such as amphipods which in turn they are food for birds; it enhances stability to dunes, and it prevents beach erosion [89]. Massive obnoxious quantities of beach cast sargasso have been recorded intermittently in Texas since the 1890s [97]. Although the recent accumulation of sargasso in the Great Atlantic Sargasso Belt, since 2011, is a new phenomenon, these algae have been previously mentioned (since 1929) [98] in the floristic list from Brasil, the Caribbean islands, and mainland Caribbean [99]. Beach-cast macroalgae, including red, brown, and green algae, with species of the genus *Sargassum* often being the most frequent and abundant, have been frequently observed in the coastal areas of the Mexican Caribbean [100]; thus, beaching of sargasso are not of recent occurrence in this region (Table 1). However, the quantities of beach cast sargasso in the Caribbean used to be small or moderate; whereas since 2011 (and since 2015 in Mexico), they can be massive at times.

### 3. Golden and Sargasso Brown tides

Floating sargasso in the open ocean is considered a valuable habitat (see above), and has also been named “the golden floating rainforest of the Atlantic Ocean” by Lafolley and collaborators [101]. Smetacek and Zingone [96] used the name “Golden Tide” for sargasso; which reflects this value and the yellow brown color of the floating sargasso masses in the oligotrophic open ocean. As indicated above, the “golden forest” in the Sargasso Sea has likely existed for very long time; long enough for endemic species to evolve and species such as the European and American eels to adapt their life cycle to its persistence through time. Although large masses of sargasso from the Sargasso Sea has been arriving at intervals to the US coast of the Gulf of Mexico, in the 1990s, agricultural fertilizers and other pollutants in the USA were linked to unusual accumulations of sargasso biomass at the Mississippi River’s mouth between Florida and Texas [87].

The large accumulation of sargasso in the Great Atlantic Sargasso Belt, first reported in 2011, is only a decade old [96]. Sargasso is not new for the southern tropical Atlantic as indicated by the above-mentioned historical reports, but its sudden increase or bloom is a new phenomenon. It is thought that this may have been caused by a combination of various events, all related to human interference with the plant’s biogeochemical cycles. It has been attributed to climatological changes related to the sea surface temperature (SST) and an anomaly in North Atlantic Oscillation (NAO) during 2009–2010, which may have introduced large “seed populations” of sargasso into the African side of the NERR [89]. The NERR naturally has more nutrients and is warmer than the Sargasso Sea, providing a more favorable environment for algal growth. Similar to the blooms of other algal species occurring in other parts of the world [102], the current reasoning is that these blooms are associated with an increase in nutrients input into the sea. Upwelling patterns along the African coast have been changing, bringing more nutrients into this oceanic region [77]. Also, increasing Sahara dust storms may have increased nutrients in the NERR [103], as well as increasing nutrient load from river discharges, such as the Congo in Africa or the Amazon in Brazil [77]. Sargasso has higher productivity in neritic waters, rich in nutrients, than, in oceanic waters, deficient in nutrients [88]; in neritic waters, sargasso doubled its biomass in 11 days in contrast to the 50 days in oceanic waters [104]. In addition, sargasso has no physical barriers for expansion, no competitors, and no large herbivores.

Mexico started to receive unusual quantities of sargasso late 2014, and the first massive beachings were reported in 2015 [4]. A general overview of the massive influx of sargasso into Mexico has been presented recently by Chavez and collaborators [84]. The first significant influx of sargasso was in the summer of 2015,
when on average 319 m$^3$ of sargasso were removed per km of beach per day in the northern part of the Mexican Caribbean [4]. Satellite images of sargasso in front of the Mexican coast revealed large interannual fluctuations in abundance, reaching a maximum cover of 22,900 ha in September 2018 [84]. Generally, large abundance in the ocean corresponded with larger quantities on the beaches, although not all coasts were equally impacted. During the peak years of 2018 and 2019, on average $3.2 \times 10^3$ and $1.7 \times 10^3$ m$^3$ were collected per month, per km of beach in the Northern Mexican Caribbean, respectively [84].

The excessive amount of sargasso on the beaches generates problems for productive sectors such as tourism. Decaying sargasso covers the beaches with a brown mud; its decomposition emits an unpleasant smell that attracts insects and can cause serious health problems. The business sector and the local, state, and federal governments are concerned about the consequences of the damage the emblematic image of these pristine turquoise beaches would bring to the tourist activity in the region [2]. Economic parameters such as the billing rate, jobs, and the hotel activity in this region, did not detect a discernible impact on the state’s economies during 2018 and 2019 [2]. However, hotel occupancy has declined and some hotels have invested major efforts in maintaining their beach fronts free from sargasso [84].

Massive beaching of sargasso are creating havoc to Caribbean coastal ecosystems as leachates and particulate organic matter from the stranded decaying algal masses deplete oxygen, reduce light and deteriorate water quality, which leads to the mortality of nearshore seagrasses and fauna, interference with seaward journeys of juvenile turtles, enhance beach erosion, and changes in trophic dynamics of benthic organisms. Excessive nutrient concentrations caused by sargasso leachates have been measured until the reefs, and release of heavy metals sequestered by sargasso (such as arsenic) are also of concern (summarized in [84]). This is why van Tussenbroek and collaborators [99] suggested the term Sargasso (Sargassum) Brown Tide instead of Golden Tide; to refer to the decaying algal masses washed ashore, coloring the near-shore waters with a dark, murky brown color.

4. Uses of sargasso and perspectives

The oldest known record of the use of sargasso was that of the Portuguese physician and naturalist Cristóbal de Acosta (1515–1594). Acosta, in his “Treatise on drugs and medicine of the East Indies” of 1578, described the sargasso located between 18 and 30° N, that is, in the eastern part of America. He noted that this hearty herb was pickled and flavored with fennel. He claims that he fed it raw and cooked to a sailor with “bad urine” [urinary tract infections] and claimed that he did it well and the sailor took it to his house when they disembarked [19]. In 1750, Georg Eberhard Rumphius (1627–1702), a Dutch naturalist famous for his “Herbarium amboinense”, described sargasso with narrow and long leaves, without roots, which are boiled and drunk with great success against the water accumulated in the kidneys. [105]. In his “Dictionnaire raisonné d’histoire naturelle”, Jacques Christophe Valmont de Bomare (1731–1807) described sargasso from the west coast of Africa in 1764 and identified it as Fucus natans, which is eaten in salads, he also uses it to facilitate delivery, it is used against urine retention and against scurvy [106]. In 1771, Dr. Vicente de Lardizábal Dubois (1746–1814) in his treatise on sargasso “The consolation of the navigators”, called it sea lentil or watercress that served as food for birds and cattle on boats and as beneficial medicine against scurvy [107]. Years later, Dr. Antonio Corbella published a dissertation where he did not recommend sargasso for scurvy, which could be better cured with a traditional vegetarian diet and lemon juice [14]. Sargasso was mentioned in 1799 by José de
Viera y Clavijo (1731–1813), who presented morphological descriptions and characteristics of its habitat; he cited the uses published by Lardizábal. The works of Viera and Clavijo were published in the 19th century [22, 23].

In the 20th century and the beginning of the 21st, many research efforts and technological developments of sargasso have been developed. Sargasso can provide sustainable alternative routes based on renewable raw materials that can provide biofuels (biofuels, biomethane, nanocarbon), obtaining chemicals such as sugars, proteins, and alginates and fucoidans. Also purchase pharmaceutical products (antiproliferative, antiprotozoal, antioxidant, hepaprotective, antileishmanial), fertilizers, cosmetics (for hair treatments), bioplastics, biopolymers, cellulose, and other products such as materials to make shoes, bricks, varnishes, paper, cardboard, as well as services on environmental impacts (leachates) and on bioremediation.

Table 2 summarizes the uses that have been implemented in contemporary Mexico. Sargasso is not feasible for the production of biodiesel due to low concentrations of lipids and fatty acids, so other biofuels have been explored through the fermentation and anaerobic digestion of sargasso biomass to obtain liquid fuels such as ethanol or biogas such as biomethane [109]. The Renewable Energy Unit, Centro de Investigaciones Científicas de Yucatán AC (CICY), investigates sargasso with a fungal pretreatment that produced a 20% increase in methane yield [113].

Alginates are phycocolloids present in all brown algae, including sargasso. *S. fluitans* from the Caribbean, particularly in Cuba and Puerto Rico, with alginate yields of 16–19% [112, 123]. Sargasso yields are lower than those of other brown algae such as *Macrocystis pyrifera*, yielding 26.5 to 35.9% [124]. In Mexico, the Alquimar industry has two patents on alginate extraction technologies from sargasso (Table 2).

Some bioactive molecules to combat diseases caused by protozoa or substances that have a hepaprotective or antioxidant nature are under investigation, but with good results for the near future [120–122].

The Salgax company, among other companies, already has sargasso based fertilizers for sale with a sale price of $24 US for a 5-liter jug, in addition to other cosmetic products [111]. Other companies manufacture footwear and bricks with a majority percentage of sargasso [109, 116], among other products (Table 2).

Some research centers focus on bioremediation and leachate control processes such as the Center for Applied Physics and Advanced Technology (CFATA) and Autonomous National University of Mexico (UNAM) [109] or, in the case of biopolymer development, the Open and Distance University of Mexico of Quintana Roo [115].

However, despite the effort that has been achieved in the region of Mexico there are still some characteristics of sargasso that can hinder or interfere with some uses. Algae are known to be excellent at absorbing heavy metals and other pollutants, particularly arsenic [38]. Sargasso from the Mexican Caribbean has high arsenic concentrations (24–172 ppm), depending on the region. *Sargassum natans* VIII showed the highest concentration (123 ppm) and in the lowest concentration *S. fluitans* III (59 ppm) and *S. natans* I (55 ppm); however, in all morphotypes, arsenic exceeded the allowed limits (40 ppm DW). Arsenic concentrations are a concern both for environmental and aquifer contamination and for its use as food or biofertilizer [38]. Further studies are required to find out which arsenic speciation is more toxic (inorganic or organic arsenic such as arsenate and arsenite) and to investigate which parts of sargasso are more likely to absorb arsenic (stems, pneumatophores) [125]. Apart from arsenic, sargasso is high in salt and ash. Salt removal is expensive as it requires the use of large amounts of fresh water.

Sargasso is free, but it is expensive to collect and often requires specialized machinery depending on whether it is harvested from the ocean or from the beach. It is also necessary to take into account its storage due to the toxic gases it gives off, such as hydrogen sulfide and ammonia, together with the leachate generated,
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which can contaminate groundwater. As we can see, there are still enormous challenges to overcome. However, developing an ecological pretreatment method by incorporating the use of low-cost ionic resins to remove contaminants and promote cell fracture by solubilizing the polymers contained in sargasso would be methods that could be explored in the future and also the biorefineries concept; based on sargasso in Mexico, which would produce a feasible techno-economic model for the region (Paula Sánchez. Com. per.).

Creating a political or governance framework to manage the influx of sargasso and standards for the comprehensive management of sargasso and the availability of funds will be challenged to achieve in the future. It is our duty to encourage entrepreneurship, incorporating the newest scientific and technological advancements..

5. Conclusions

- Historical records of sargasso go back to centuries XV to XXI, not only in the Sargasso Sea but also throughout the Caribbean. Although there is also a pre-Hispanic record.
• The taxonomy of the genus *Sargassum* and the position of the pelagic *Sargassum* species (sargasso) still require further research.

• The absence of sexual reproduction is an enigma; further life-cycle studies and population genetic studies may shed further light on it.

• In the past sargasso has been used to treat urinary tract problems, to facilitate delivery, and also as food; it may be worthwhile to follow this up with further research.

• Sargasso in the open ocean is a Golden Tide, sustaining and providing energy for a diverse community, and serving as a nursery or refuge for commercially important or iconic species.

• Sargasso may be an important sink of organic carbon, helping to mitigate global climate change.

• The sargasso blooms in the NERR (North Equatorial Recirculation Region) since 2011, creating the Great Atlantic Sargasso Belt, are likely the new normal condition for the region.

• Likely causes of this bloom are thought to be (a combination of) changes in prevailing winds and currents due to Climate Change and increasing nutrient into the NERR from changes in upwelling and land-runoff.

• Sargasso, although capable to persist in the oligotrophic Sargasso Sea, also has the capacity to rapidly respond to increasing nutrients that may have contributed to the bloom of these algae in the NERR

• Massive quantities of beached sargasso create the Sargasso Brown Tides causing major havoc to ecosystems and local economies.

• Better understanding of the species, the movements of the rafts in the ocean, and new research into valorization, are necessary to create novel strategies of adaptation to the recent blooms of sargasso.

• Mexico has been working on the following mitigation actions: strengthening of monitoring programs, removal of oceanic and coastal sargasso, regulation plan for the deposit of sargasso, creation of a monetary fund, and increasing integration of national knowledge and capacities.

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