Pelagic *Sargassum* as an emerging vector of high rate carbonate sediment import to tropical Atlantic coastlines

Michael A. Salter[1], Rosa E. Rodríguez-Martínez[2], Lorenzo Álvarez-Filip[3], Eric Jordán-Dahlgren[2], and Chris T. Perry[1]

[1]Department of Geography, College of Life and Environmental Sciences, University of Exeter, Exeter, UK

[2]Instituto de Ciencias del Mar y Limnología, Universidad Nacional Autónoma de México, Puerto Morelos, Quintana Roo, México

[3]Biodiversity and Reef Conservation Laboratory, Unidad Académica de Sistemas Arrecifales, Instituto de Ciencias del Mar y Limnología, Universidad Nacional Autónoma de México, Puerto Morelos, Quintana Roo, México

Corresponding author: Michael A Salter. Email: m.a.salter@exeter.ac.uk

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Abstract

Since 2011, pelagic *Sargassum* has inundated Caribbean, West African, and northern Brazilian shorelines in increasing volumes. These events are linked to the emergence of a major new *Sargassum* bloom region in the Atlantic Ocean, and annual high-volume *Sargassum* beachings are seemingly becoming an established norm. Resultant socio-economic and ecological implications are widespread and potentially serious, but an important question that has so far received no attention is whether these *Sargassum* inundations might represent a new source of carbonate sediment in affected coastal areas. This sediment derives from calcareous epiphyte communities that colonise *Sargassum* (e.g., bryozoans, serpulid worms, and red algae), and if volumetrically significant, may help to counteract aspects of *Sargassum* beachings thought to reduce sediment supply and decrease coastal stability. Here we determine the carbonate contents of *Sargassum* from coastal waters of the Mexican Caribbean. Integrating these with volumetric data on beached *Sargassum*, we then estimate total epiphytic carbonate import during 2018 at 11 sites along a 60 km section of the Quintana Roo coast, Mexico. Based on measured mean carbonate content of *Sargassum* (2.09% wet weight; 95% confidence interval [CI]: 1.83–2.32), and estimates of annual beached *Sargassum* (7.0×10^3 kg drained weight$\cdot m^{-1}$ of shoreline; 95% CI: 6.9–7.2), our findings indicate that *Sargassum* beachings in the Mexican Caribbean contributed an average of 179 kg $CaCO_3 \cdot m^{-1}$ of shoreline (95% CI: 173–185) in 2018: close to our upper estimate of seagrass epiphyte contributions (210 kg$\cdot m^{-1}$). Although quantitative data on *Sargassum* beachings from other locations are sparse, numerous media reports suggest the scale of these events is comparable for many exposed tropical Caribbean and Atlantic shorelines. This represents the first documentation of pelagic *Sargassum* as a major vector of coastal sediment import, the significance of which has likely only arisen since the onset of large-scale inundations in 2011.

1. Introduction

During the past decade, unprecedented volumes of the pelagic brown macroalgae *Sargassum* spp. (*S. natans* and *S. fluitans*) have inundated Caribbean, West African, and northern Brazilian coastlines (Gower et al, 2013; Smetacek & Zingone, 2013; Oyesiku & Egunyomi, 2014; Maréchal et al., 2017; Sissini et al., 2017; Wang et al., 2019; Rodríguez-Martínez et al., 2016; 2019; 2020). Reliable quantitative data on the scale of these beaching events is limited but reported amounts are huge: in the Mexican Caribbean a total of 522,226 t was reportedly removed from managed parts of its c450 km coastline in 2018 (Espinosa & Ng, 2020). Similarly, informal reports suggest up to 50,000 t of dry *Sargassum* arrived on the Guadeloupe coast each year between 2011 and 2015 (excluding 2013; ANSES report, 2017), and estimates from a single beach in northern Brazil suggest up to 1,843 t wet weight arrived per inundation even in 2015 (Sissini et al., 2017). Numerous research and media reports indicate the scale of inundations is similar throughout the Caribbean, and exceed anything in living memory (Gower et al., 2013; Smetacek & Zingone, 2013). The onset of these events in 2011 coincided with the formation of an exceptionally large accumulation of *Sargassum* in the Central Atlantic that generated a satellite signal 200 times larger than any previously recorded (Gower et al., 2013) and has since been termed the Great Atlantic *Sargassum* Belt (GASB; *sensu* Wang et al., 2019). Subsequent near-annual recurrences of this phenomenon, involving increasingly large volumes and to date peaking at >20 million t in June 2018 (Fig. 1A), suggest that the events of 2011 marked something of a regime shift in *Sargassum* bloom patterns, which could become an established norm in the long-term (Wang et al., 2019).

Historically, the most significant quantities of pelagic *Sargassum* have been largely confined to a ‘nursery area’ in the Gulf of Mexico and the ‘repository’ it supplies in the Sargasso Sea region of the North Atlantic Ocean, with an estimated two to eleven million tonnes of *Sargassum* produced annually in these areas (Parr, 1939; Gower & King, 2011). A proportion of this *Sargassum* drifts onto shorelines of the Caribbean, the Gulf of Mexico, and Bermuda (e.g., Butler et al., 1983; Pestana, 1985; Moreira et al., 2006; Gavio et al., 2015), but large volume beaching events have been sporadic and generally rare (van Tussenbroek et al., 2017). Although small quantities of beached *Sargassum* can play an important role in coastal ecosystems, such as by improving beach stability and acting as a natural fertiliser for coastal plants (Williams & Feagin, 2010), the impacts of these widespread and massive *Sargassum* beaching events are mainly considered deleterious. Significant socio-economic issues have arisen due to the impacts on tourism and fisheries, and on human health (Smetacek & Zingone, 2013; Oyesiku & Egunyomi, 2014; Doyle & Franks, 2015; Hu et al., 2016; Resiere et al., 2018), leading the Barbados government to declare a national emergency in 2018. Efforts to alleviate these effects, such as large-scale cleaning of tourist beaches along the Caribbean coastlines (van Tussenbroek et al., 2017), are a major management and economic burden (Webster & Linton, 2013). For example, the cost of *Sargassum* removal per km of Mexican Caribbean coast in 2018 was US$128,770 to US$284,830 for personnel and transport alone, and does not include loss of tourism revenue and the cost of equipment. In addition, these activities contribute to enhanced beach erosion (e.g., Bruun, 1983; Rodríguez-Martínez, 2016), and may potentially contaminate local aquifers following inland disposal (Rodríguez-Martínez et al., 2020). Furthermore, significant nearshore and coastal ecological impacts have been documented, including: i) eutrophication and reduced oxygen, pH and light, resulting in faunal mortalities and the loss of seagrass meadows—the latter potentially having longer-term consequences for coastal stability and other ecosystem services (Waycott et al., 2009; van Tussenbroek et al., 2017; Rodríguez-Martínez et al., 2019); ii) accumulation of physical barriers that interfere with turtle nesting (Maurer et al., 2015); and iii) alterations to *Diadema* urchin trophic structure, with potential consequences for nearshore coral reef health (Cabanillas-Terán et al., 2019).

However, a key feature of pelagic *Sargassum* that has received little attention during these recent inundation events, is their calcareous component. Calcareous epiphytes known to occur on various fixed and floating *Sargassum spp.* include foraminifera, bryozoans, polychaete worms, and Rhodophyta (Morris & Mogelberg, 1973; Ryland, 1974; Withers et al., 1975; Spindler, 1980; Niermann, 1986; Sterrer & Schoepfer-Sterrer, 1986; Langer, 1993). These carbonate epiphyte communities, which are visually evident on *Sargassum* samples collected from floating mats, are comparable to those that widely colonise the blades of tropical seagrasses (Corlett & Jones, 2007), and which are known to produce large quantities of carbonate sands and muds in coastal ecosystems (Land, 1970; Patriquin, 1972; Nelsen & Ginsburg, 1986; Perry et al., 2019). A key question that arises therefore is: has the rapid increase in pelagic *Sargassum* observed in the Caribbean region since 2011 also resulted in the emergence of a new source of carbonate sediment to its beaches and shallow nearshore environments? This idea was actually alluded to in a small scale study of beached *Sargassum* in Bermuda in the 1980s (Pestana, 1985), but it remains an unstudied aspect of the recent massive beaching events affecting Caribbean and West African coastlines. If significant in terms of carbonate volumes, this may have important implications for beach sand accumulation rates and coastal stability, potentially counteracting aspects of *Sargassum* beaching events that reduce sediment supply (e.g., degradation of seagrass meadows) and promote coastal erosion. Here we explore these emerging questions based on data collected from sites along a 60 km sector of the Mexican Caribbean coast during the 2018 beaching event—the most prolific *Sargassum* year in the Caribbean recorded to date (Rodríguez-Martínez et al., 2019; Wang et al., 2019). Specifically, we quantify the amounts of *Sargassum* arriving along this sector of coast on a monthly basis and then, based on empirical data on *Sargassum* carbonate epiphyte contents, estimate monthly and annual rates of epiphytic carbonate sediment supply.

2. Materials and Methods

2.1 Quantification of epiphytic carbonates

Samples of *S. fluitans* (variant III; *sensu* Parr, 1939) were collected for carbonate quantifications during September 2018 from multiple *Sargassum* rafts floating within 2 km of the eastern coastline of Quintana Roo, Mexico, at Puerto Morelos and Punta Allen (Fig. 1B). Individual thalli (n = 25) were collected at random and without prior examination of epiphytic content. A branch typically representing 5–20% of total thallus volume was then randomly isolated from each and examined in the field for carbonate epiphytes. Branches were retained for later analysis only if the degree of carbonate encrustation was judged to be similar to the remainder of the thallus, which was then discarded. The combined wet weight of these branches was approximately 400 g. Separately, five samples with little or no visible encrustation were collected as controls. Following collection, all samples were rinsed in deionised water to remove seawater salts, dried at 50 °C, and carefully transferred to individual sealed bags for storage.

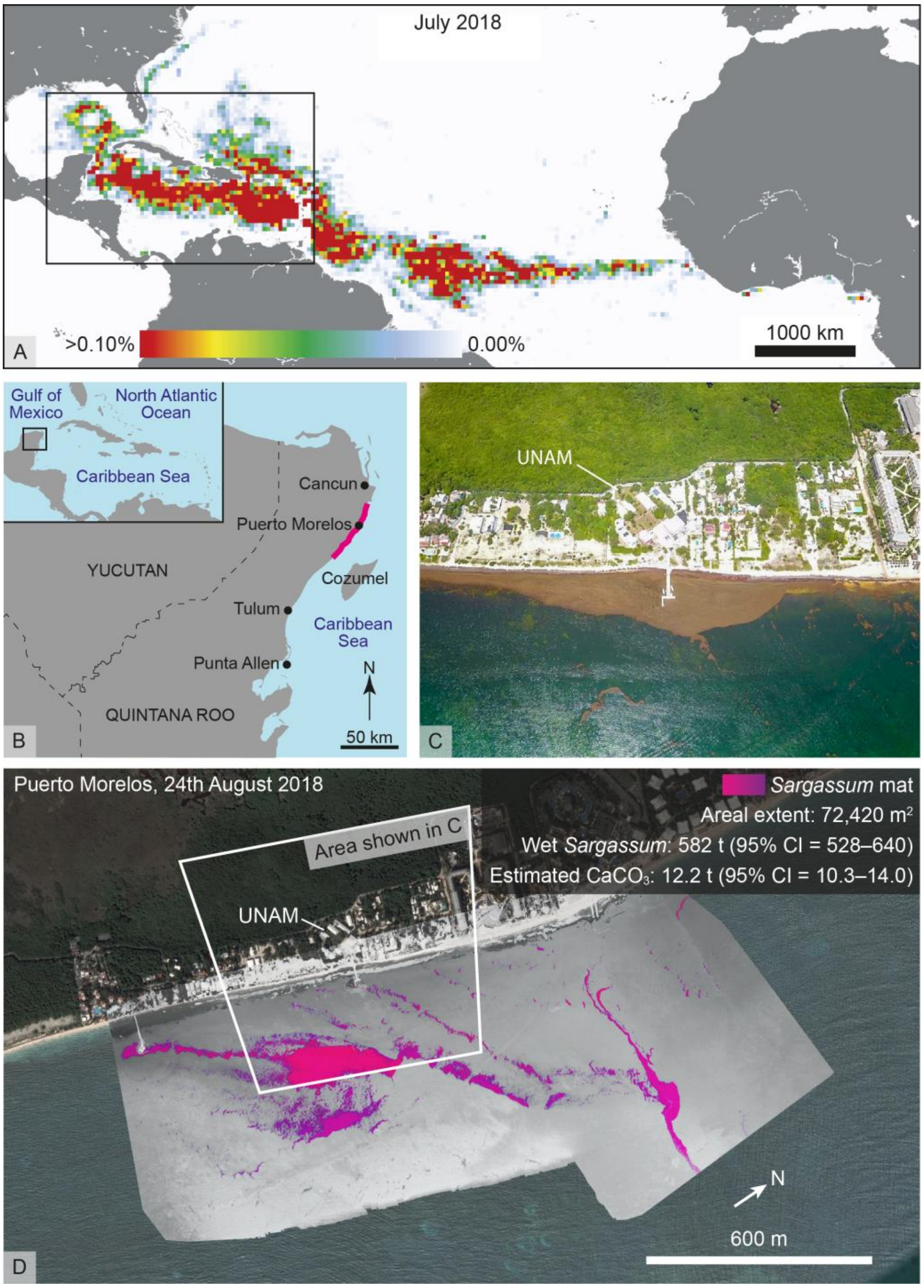

Figure 1 The 2018 *Sargassum* bloom at regional and local scales. A: *Sargassum* density (% cover) in the GASB in July 2018 (Reprinted after Wang et al., 2019, with permission from AAAS), showing its pervasiveness throughout the Caribbean (inset). B: Study area in the Mexican Caribbean. *Sargassum*

samples for $CaCO_3$ assessments were collected in September 2018 offshore from Puerto Morelos and Punta Allen. Beached *Sargassum* volume data for 2018 were obtained from 11 sites along a 60 km section of shoreline of Quintana Roo, highlighted magenta. C: Drone image of a *Sargassum* mat arriving on the Puerto Morelos shoreline at the National Autonomous University of Mexico (UNAM) campus (credit: Lorenzo Álvarez-Filip). Approximate width of view is 650 m. D: Geo-referenced orthomosaic of a large *Sargassum* mat arriving on the Puerto Morelos shoreline at UNAM (overlaid on base image using Google Earth Pro 7.3.2; base image created 10th January 2017, © 2020 Maxar Technologies). The image was processed to isolate areas of floating *Sargassum* and used to quantify its areal extent, thus facilitating an estimate of its epiphytic $CaCO_3$ content. Nearly all this *Sargassum* accumulated on the immediately adjacent shoreline shortly after the image was taken—as illustrated in panel C, which shows part of the same area two hours later.

Each branch was examined under light microscopy to identify encrusting organisms and to estimate their relative abundances in terms of surface cover. Two branches (one from each sampling location) were retained and further examined with scanning electron microscopy (JEOL JSM-6390LV) after application of a conductive Au/Pd (80:20) coating. Control samples were also examined under light microscopy and branches, leaf blades, and pneumatocysts with no visible epiphytes were isolated and used as carbonate-free controls.

The remaining branches (n = 23) and control samples (n = 5) were then processed to determine weight loss after acid digest following procedures adapted from previous studies of *Sargassum* epiphytes and more recently utilised to determine calcareous epiphyte content on seagrasses (Pestana, 1985; Perry *et al*., 2019). First, samples were dried at 50 °C for 112 hours and their dry weights recorded. They were then submerged in a 1M solution of HCl for one hour to dissolve epiphytic carbonates. The remaining organic material was then transferred to pre-weighed filters and rinsed with deionised water to remove residual salts from the dissolution reaction. Samples were then dried for a further 112 hours before carbonate-free dry weights were recorded. Carbonate content was calculated as the net weight differential before and after acid digests, after first correcting for weight loss due to decomposition of organic tissues—which averaged 20.1% of dry weight in control samples. Although this organic weight loss is higher than values reported in a previous study (Mean = 5.5%; Pestana, 1985)—probably on account of longer HCl soaking periods employed in this study—we found mass reductions to be reasonably consistent (range 17.6–23.1%) and independent of initial sample weight. Carbonate contents determined following this procedure are likely to be conservative owing to the possibility that control samples contained minor quantities of carbonate invisible under light microscopy.

2.2 Carbonate contents in nearshore floating Sargassum mats

To extrapolate the carbonate content determinations to larger scale estimates of epiphytic carbonate import, we followed two approaches. First, we estimated the wet mass of *Sargassum* present in a typically sized floating raft off the coast of Puerto Morelos. The surface area of the raft was determined from a geo-referenced orthomosaic produced using drone imagery collected during August 2018. The orthomosaic was processed using image analysis software (JMicroVision v1.3.3; Roduit, 2007) to extract pixels containing floating S*argassum* so as to determine their combined surface area. Total wet mass of the raft was estimated based on average wet mass data from three similar rafts sampled nearby. In each raft, wet mass of *Sargassum* collected from a 0.25 m^2 quadrat was recorded in three zones (central, outer, and an intermediate location) after being allowed to drip dry for one hour. The resultant data suggest the rafts had similar densities (one-way ANOVA: $F_{2,6}$ = 0.23, p = 0.80), with overall average wet mass of 8.03 $kg \cdot m^{-2}$ (95% confidence interval [CI]: 7.29–8.84). This value is considerably higher than other values reported from the Gulf of Mexico and Florida Straits (mean ± 1 SD: 3.34 $kg \cdot m^{-2}$ ± 1.34 ; Wang et al., 2018), likely due to a 'piling up' effect as *Sargassum* mats approach the shoreline. In addition, mats may have generally comprised greater densities in 2018 due to the especially prolific *Sargassum* bloom of that year (Wang et al., 2019).

Because our carbonate content determinations are based on dry weights, it was further necessary to construct a wet–dry weight *Sargassum* calibration to translate overall wet weight *Sargassum* to dry weight carbonate. Eight floating *Sargassum* thalli were collected from surface waters and weighed after being allowed to drip dry for one hour. Following a brief soak in deionised water they were dried at 50 °C for 112 hrs (following the carbonate content protocol) before being weighed again. Over a size range spanning wet weights of 3.4–83.8 g, this wet–dry calibration yielded a strong linear relationship (R^2 = 0.99) and a mean conversion factor of 8.49 (95% CI: 8.16–8.91).

2.3 Carbonate import rates associated with Sargassum beachings

We also estimated the total amount of carbonate imported during 2018 to eleven tourist beaches that collectively account for 11.15 km of sampling distance over a 60 km section of shoreline in the area between Cancun and Xcaret Park (Fig. 1B). Many tourist beaches in this area are subject to year-round monitoring to facilitate mechanical removal of beached *Sargassum* in order to maintain desired beach conditions. Monthly volumetric data on the amount of material removed from beaches were provided by ten hotels and the Municipal Service Direction of Puerto Morelos, and taken as an indirect measure of *Sargassum* import to these beaches. To convert these data to mass values, and thus facilitate estimates of carbonate import, we used the mean mass-to-volume value from data provided by several of these sources (276 $kg \cdot m^3$; 95% CI: 241–317). It is worth noting, however, that the values are somewhat variable (ranging from 200–420 $kg \cdot m^3$), primarily owing to differences in the timing and method of collections, and resultant differences in degree of compaction and amount of water and sand retention.

Although pelagic *Sargassum* typically accounted for a large proportion of the material removed in this manner, additional components commonly included various seagrasses, sand, and occasionally other macroalgae. To account for compositional heterogeneity, we assessed the compositions of twelve 1 kg samples of beached material collected from the Puerto Morelos shoreline adjacent to the National Autonomous University of Mexico (UNAM) campus (Fig. 1C) between February and April 2019. The average proportion of this material by weight that was *Sargassum* was then applied to the estimated monthly mass of material removed from each beach to correct overall values to *Sargassum*-only values.

These estimates of *Sargassum* import were used to calculate the associated monthly import of epiphytic carbonate using a similar approach to that described for nearshore floating rafts. However, because the subject material had typically been present on beaches for some hours prior to its removal, its estimated mass relates to partially drained and dried *Sargassum*. Consequently, application of our wet–dry conversion factor would tend to under-estimate the dry weight of beached *Sargassum* and its associated carbonate content. To overcome this issue, a separate conversion factor was generated for partially dried beached *Sargassum*. Using the protocol described above, but with *Sargassum* thalli collected from within beach piles, a size range spanning partially dried weights of 2.1–46.1 g yielded a strong linear calibration (R^2 = 0.95) and a mean conversion factor of 6.98 (95% CI: 6.21–7.80).

Confidence intervals reported in this study were obtained by non-parametric bootstrapping of the original sample data in R statistical software (R Development Core Team, 2008) using the *boot.ci* function in the *boot* package (Canty & Ripley, 2020). For each sample set, 10,000 bootstraps were performed and 95% CIs were obtained using the percentile method.

3. Results

3.1 Composition of Sargassum epiphyte communities

Microscopic examination of *Sargassum* branches revealed all samples collected in September 2018 (excluding controls) to be heavily encrusted with calcareous epiphytes. Older (basal) portions generally appeared more heavily encrusted than younger (distal) portions, but there was no obvious preference for anatomical position. Three main calcareous components were identified (Fig. 2): skeletal components of bryozoa (Membraniporidae; probably *Jellyella tuberculata*) and crustose red algae (Rhodophyta, probably *Fosliella* sp. and/or *Melobesia* sp.), and the tube casings of serpulid worms (Serpulidae; *Neodexiospira* sp.). Relative cover proportions were not individually quantified, but bryozoans were always the most visually abundant in terms of percent cover, in some cases accounting for up to an estimated 70% of sample surface area. Serpulid worm tubes were also readily visible on every sample examined and often abundant. However, crustose algae—although present on most samples—always accounted for a small proportion of calcareous encrustation and were not quantitatively important. The over-riding conclusion from these observations is that epiphytic encrustation is widespread on *Sargassum* fronds from the Caribbean Sea, and that the epiphytic community strongly resembles that observed on *Sargassum* from the Sargasso Sea (Ryland, 1974; Pestana, 1985; Niermann, 1986; Fabry & Deuser, 1991).

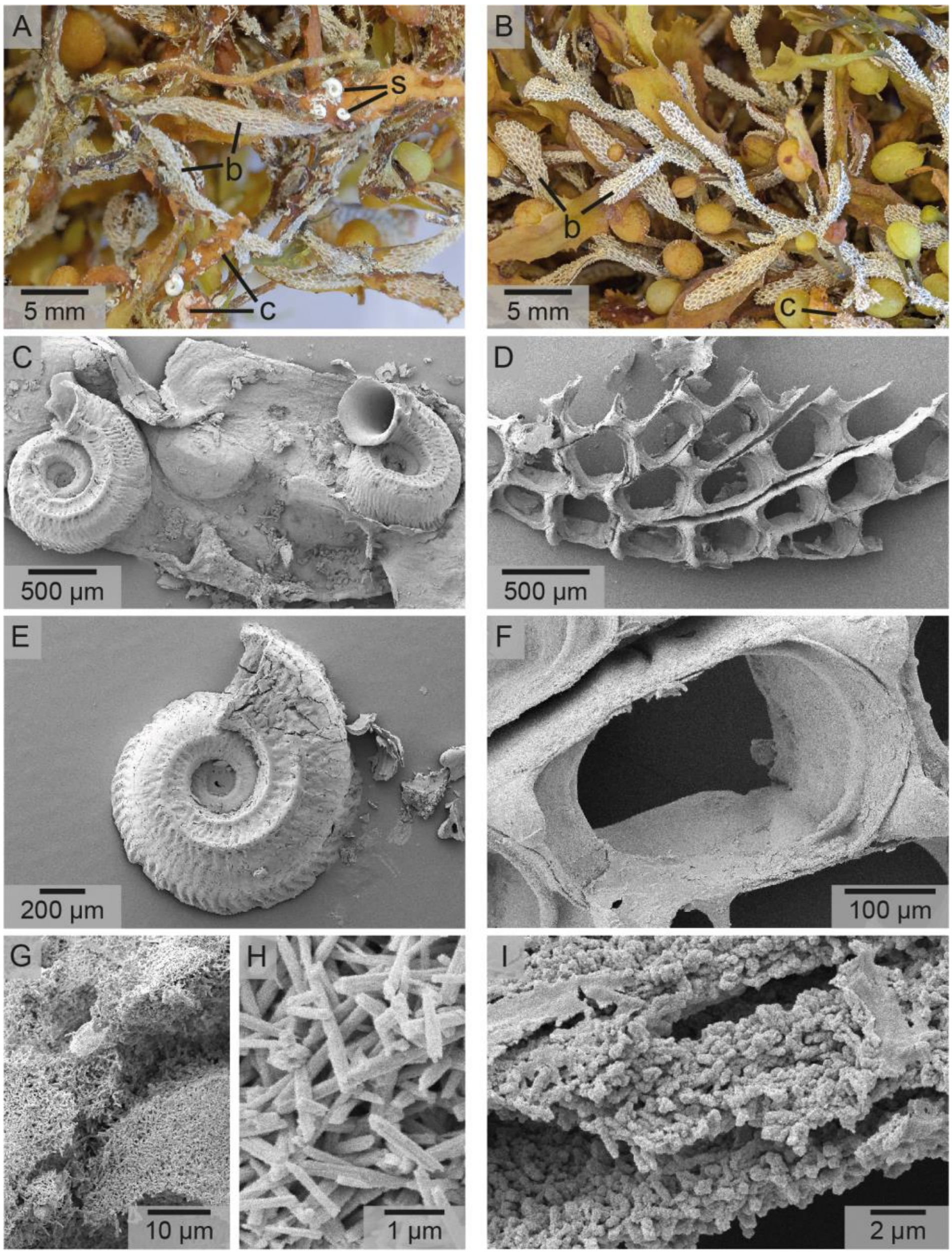

Figure 2 Light microscopy (A,B) and electron microscopy (C – I) images showing the main calcareous epiphytes on *Sargassum* collected from surface waters of the Mexican Caribbean in September 2018. A,B: Bryozoa (b) typically dominate surface area cover, with serpulid worm tubes (s) also common and often abundant, whereas crustose red algae (c) are common but sparse. C, E, G, H: Serpulid worm tubes typically have diameters in the range 0.3 – 1.5 mm, but their microstructure is comprised of loosely assembled acicular crystals with lengths in the range 1 – 3 µm. D,F,I: Bryozoan skeletons comprise a

regular calcareous framework around zooid cavities typically ~0.3 mm in length, and are composed of very fine subhedral rhombohedra typically <1 µm in length.

3.2 Epiphytic carbonate content of Sargassum mats

A total of 23 *Sargassum* samples with initial dry weights in the range 0.20 – 3.63 g (equivalent to wet weights of 1.70 [1.63–1.78] to 30.80 [29.60–32.32] g, and a combined total wet weight of 372 [357–390] g, using our conversion factor of 8.49 [8.16–8.91] – see Methods section 2.2) were analysed to determine carbonate content, which averaged 17.72% (95% CI: 15.74–19.54) of their dry weight (range: 8.02% to 25.49%). There was no significant difference between samples collected at Puerto Morelos and Punta Allen (mean = 18.07% vs. 17.06%; two-sample $t_{(21)} = 0.48$, two-tailed $p = 0.64$), suggesting our findings are relevant at least for the Mexican Caribbean coastline during September 2018. Application of our wet–dry conversion factor suggests calcareous epiphyte content averaged 2.09% (95% CI: 1.83–2.32) wet weight *Sargassum* (range: 0.94% to 3.00%). For partially dried *Sargassum*, carbonate content averaged 2.54% (95% CI: 2.13–2.92; range: 1.15% to 3.65%).

For the purposes of spatial upscaling we then considered data from a large *Sargassum* mat present in nearshore waters off Puerto Morelos on 24th August 2018, which had an areal extent of 72,420 m^2 and a shoreline-parallel width of approximately 1,600 m (Fig. 1D). Based on our average wet weight *Sargassum* density of 8.03 $kg \cdot m^{-2}$ (95% CI: 7.29–8.84) in similar mats, and by applying our mean wet *Sargassum* carbonate weight percent of 2.09% (95% CI: 1.83–2.32), we estimate that this mat alone contained 12,154 kg of $CaCO_3$ (95% CI: 10,272–13,968), or 0.17 kg $CaCO_3 \cdot m^{-2}$ (95% CI: 0.14–0.19). If, as seems reasonable (Fig. 1C), all of this mat drifted onto the adjacent 2 km stretch of shoreline (allowing for some shoreline-parallel spreading), it would have delivered an estimated 6.08 kg $CaCO_3 \cdot m^{-1}$ shoreline (95% CI: 5.14–6.98). Employing a lower *Sargassum* density value of 3.34 $kg \cdot m^{-2}$ assigned to oceanic *Sargassum* mats (Wang et al., 2018), even this very conservative approach suggests the mat contained about 5,000 kg of $CaCO_3$, potentially delivering about 2.5 kg $CaCO_3 \cdot m^{-1}$ shoreline. These numbers are clearly high on their own, but given that numerous such floating rafts drifted shoreward on a weekly to monthly basis during the summer months of 2018, the potential sediment delivery rates are exceptionally high. Indeed, only one day before this raft was imaged, a different raft arrived on the same shoreline which—using the same procedures—we estimate contained 6,830 kg of $CaCO_3$ (95% CI: 5,773–7,850) and potentially delivered 6.83 kg $CaCO_3 \cdot m^{-1}$ to the adjacent 1 km of shoreline (95% CI: 5.77–7.85).

3.3 Delivery of epiphytic carbonate to beaches and seasonal variability

To estimate the rate of this carbonate import to coastline between Puerto Morelos and Xcaret, we used measures of the volume of beached *Sargassum* material removed from 11 tourist beaches ranging in length from 0.37 to 2.20 km. Assessments of the mass of this material indicate that on average it weighed 276 $kg \cdot m^{-3}$ (95% CI: 241–317). This value is considerably higher than the mean value of 160 $kg \cdot m^{-3}$ reported for *Sargassum* collected from open water (data supplied by marine environment technology solutions company, DESMI), in part due to the presence of significant quantities of underlying beach sand in the removed material. However, application of the open water value in our calculations is problematic since it concerns only *Sargassum*, and in a different state to that removed from beaches. Instead, we corrected for compositional heterogeneity in beached material on the basis of mass-specific compositional data (Fig. 3). *Sargassum* dominated each sample, with *S. natans* (variants I and VIII) and *S. fluitans* (variant III) on average collectively accounting for 74% of total mass (95% CI: 68–80). Applying this percentage to our volume-to-mass conversion, we estimate the actual density of *Sargassum* removed from beaches to be 204 $kg \cdot m^{-3}$ (95% CI: 173–239). This corrected value is closer to the open water measurements; the slightly higher average likely being due to greater compaction of beached material.

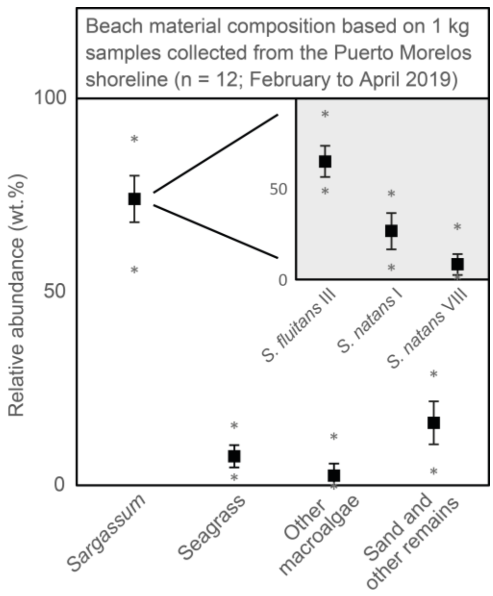

Figure 3 Mean weight percent of the primary components of material stranded on the Puerto Morelos shoreline. Error bars indicate 95% confidence intervals and asterisks indicate maxima and minima. Inset: relative abundances of species and variants that make up the *Sargassum* component.

On the basis of these density values, we then estimated the combined monthly totals of *Sargassum* removed from study beaches to range from 1,923 t in January (95% CI: 1,789–2,074) to 12,541 t in June (95% CI: 11,539–13,673). Averaged across the entire shoreline of the study area, this is equivalent to 172 kg·m^{-1} (95% CI: 160–186) to 1,124 kg·m^{-1} (95% CI: 1,035–1,226). Not surprisingly, these results show a clear seasonality consistent with broader regional patterns of *Sargassum* blooms detected in satellite observations spanning the same period (Wang et al., 2019), with the highest volumes being removed between March and September (Fig. 4). Although some study beaches removed an order of magnitude more *Sargassum* per metre than others (Table 1), this seasonal pattern was evident at all sites. Clear reasons for such large variability among beaches are not readily apparent, although coastal morphology is likely a factor, with beaches on shallow headlands returning the smallest quantities. Other geomorphological features (e.g., lagoon width and position relative to reef crest) were seemingly insignificant, but anthropogenic factors may have exerted some control: *Sargassum* removal boats were active during 2018 in some areas and several hotels installed *Sargassum* barriers (Table 1).

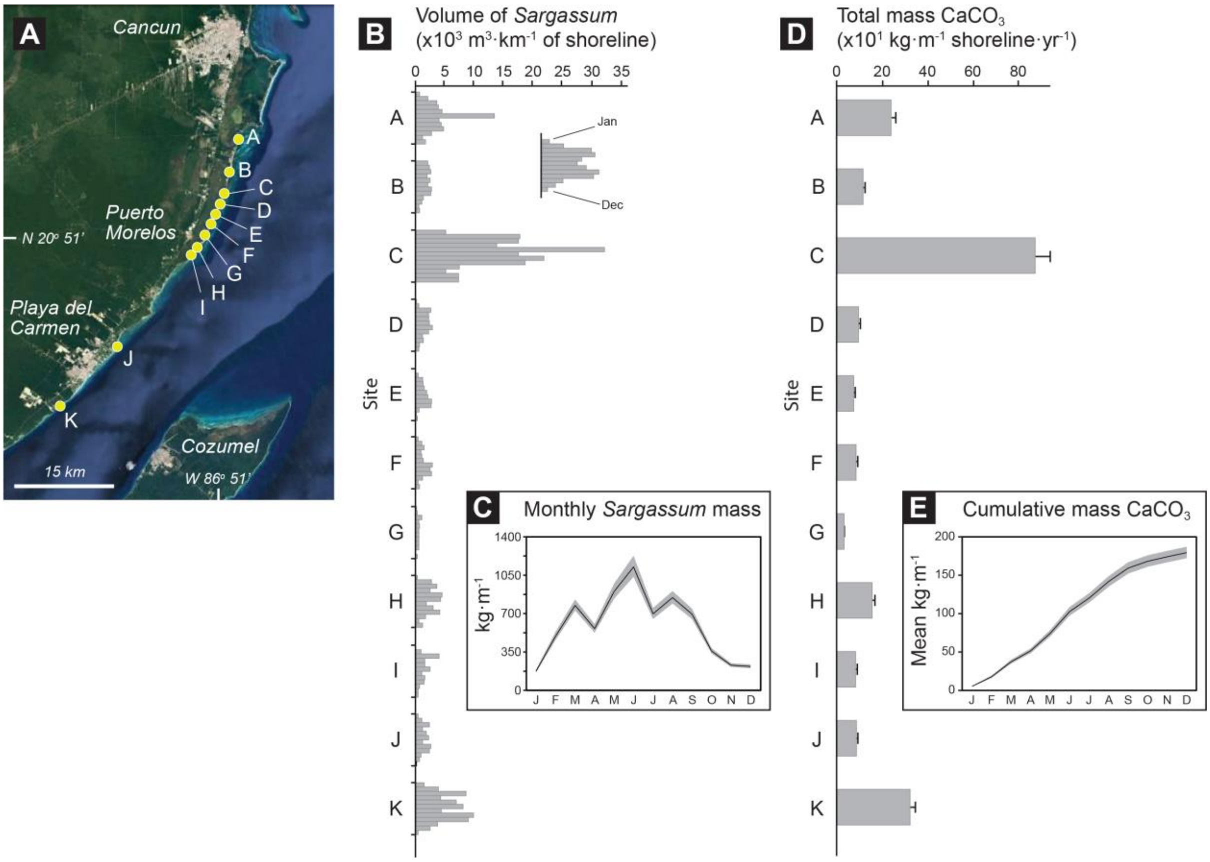

Figure 4 Estimated Sargassum and carbonate epiphyte delivery to the northern part of the Mexican Caribbean during 2018. A: Map showing the locations of sites where volumes of Sargassum removal each month were recorded (base image from Google Earth Pro 7.3.2 created 14th December 2015; Data SIO, NOAA, U.S. Navy, NGA, GEBCO; Image Landsat / Copernicus). B: Total volume of Sargassum removed by site and month. Inset (C) shows monthly mass of Sargassum removed per metre of shoreline (averaged across all sites; ± 95% CI). D) Total mass of $CaCO_3$ delivered per metre of shoreline by site. Inset (E) shows cumulative $CaCO_3$ delivered per metre of shoreline (averaged across all sites; ± 95% CI).

Application of our carbonate content data to these estimates (2.54 ± 0.47% of drained and partially dried beach *Sargassum* weight) yields a similar seasonal pattern of carbonate import, with collective monthly totals for all study sites ranging from 4.38 $kg \cdot m^{-1}$ of beach (95% CI: 3.95–4.84) in January to 28.57 $kg \cdot m^{-1}$ (95% CI: 25.36–32.00) in June. The total amount of carbonate estimated to have been imported to the entire study area during 2018 was 1,996 t (95% CI: 1,933–2,063), equivalent to 179 $kg \cdot m^{-1}$ of beach (95% CI: 173–185; Table 1).

Table 1 Summary of the amounts of pelagic *Sargassum* and associated epiphytic carbonate estimated to have arrived at 11 Mexican Caribbean study sites during 2018. Note that for commercial reasons actual hotel beach front sites cannot be named.

Beach ID	Beach length *km*	Volume of beach material removed *10^3 $m^3 \cdot km^{-1} \cdot yr^{-1}$*	*Sargassum* mass *10^3 $kg \cdot m^{-1} \cdot yr^{-1}$ (95% CI)*		$CaCO_3$ mass *$kg \cdot m^{-1} \cdot yr^{-1}$ (95% CI)*	
A	2.20	46.0	9.4	(8.9–10.0)	240	(221–260)
B	1.00	22.2	4.5	(4.3–4.8)	115	(108–123)
C[1]	0.60	168.3	34.5	(32.8–36.4)	876	(815–942)
D[2]	0.48	18.4	3.8	(3.6–4.0)	95	(89–103)
E*	0.86	14.2	2.9	(2.7–3.1)	74	(69–80)
F	0.44	16.3	3.3	(3.2–3.5)	85	(79–91)
G**	1.80	5.9	1.2	(1.1–1.3)	31	(29–33)
H[3]	0.60	30.0	6.1	(5.8–6.5)	156	(145–168)
I	0.37	15.9	3.3	(3.1–3.5)	83	(77–90)
J	1.70	16.5	3.4	(3.2–3.6)	86	(80–93)
K	1.10	62.0	12.7	(12.1–13.4)	323	(300–347)
All sites	**11.15**	**34.4**	**7.0**	**(6.9–7.2)**	**179**	**(173–185)**

**No January data; **no November data; [1–3]Sargassum barriers installed at these sites in [1]August, [2]November, and [3]January.*

To our knowledge, the only previous assessment of carbonate beach sediment import from *Sargassum* epiphytes was the mid-1980s Bermuda study (Pestana, 1985). That study was of limited resolution (beached *Sargassum* was quantified over five sets of five-day intervals between June 1982 and March 1983), but the data indicated carbonate import rates per unit beach area of 0 to 93 g $CaCO_3 \cdot m^{-2} \cdot d^{-1}$, averaging 22.5 g $CaCO_3 \cdot m^{-2} \cdot d^{-1}$. These values are equivalent to shoreline import rates of 0 to 409 kg $CaCO_3 \cdot m^{-1} \cdot yr^{-1}$, averaging 116 kg $CaCO_3 \cdot m^{-1} \cdot yr^{-1}$, and are thus of the same order as our estimated rates for the Mexican Caribbean shoreline (31 to 876 kg $CaCO_3 \cdot m^{-1} \cdot yr^{-1}$, averaging 179 kg $CaCO_3 \cdot m^{-1} \cdot yr^{-1}$).

4. Discussion

Our findings indicate that *Sargassum* inundations along the Puerto Morelos shoreline were potentially a major source of new carbonate beach sediment during 2018. This represents the first documentation of pelagic *Sargassum* as a major vector of sediment import to Caribbean shorelines, the significance of which has likely only arisen since the onset of large-scale inundations in 2011 (or 2014 in the Mexican Caribbean; van Tussenbroek et al., 2017). The study period throughout 2018 coincided with the largest *Sargassum* bloom yet recorded in the Central Atlantic Ocean (Wang et al., 2019), and correspondingly the largest volumes of *Sargassum* arriving on Mexican Caribbean beaches (Rodríguez-Martínez et al., 2020), suggesting that our estimated average carbonate import rate of 179 $kg\cdot m^{-1}\cdot yr^{-1}$ of beach length is the highest associated with this mechanism in recent times.

Significantly, we note that increasingly large blooms in the GASB were recorded in nine out of the ten years up to and including 2020 (Wang et al., 2019; SaWS 2020), meaning *Sargassum* inundations in the Caribbean are likely to have become progressively important sources of new sediment throughout this period. For example, site-specific monthly *Sargassum* removals from beaches around Puerto Morelos peaked at 12,800 $m^3\cdot km^{-1}$ during the height of the 2015 influx (Rodríguez-Martínez et al., 2016). Applying the same metrics employed here to calculate carbonate import, this suggests monthly rates up to 67 kg $CaCO_3\cdot m^{-1}$ have occurred locally prior to 2018, compared with local monthly maxima up to 164 $kg\cdot m^{-1}$ at the height of the 2018 influx. Direct comparison of a section of shoreline between Cancun and Puerto Morelos (sites A–G in Table 1) indicates that average monthly *Sargassum* volumes peaked at 2,360 $m^3\cdot km^{-1}$ in 2015 and 6,242 $m^3\cdot km^{-1}$ in 2018, equating to monthly carbonate import of 12 versus 33 $kg\cdot m^{-1}$, respectively.

As standalone values, our estimates of *Sargassum* carbonate epiphyte import seem impressive. However, to better understand the significance of these findings it is useful to compare them with other epiphytic carbonate sediment sources. The most ubiquitous of these derive from the epiphytic communities that colonise the seagrass *Thalassia testudinum*, and which are acknowledged as an important source of carbonate sediment in many tropical coastal settings. It is especially relevant as a comparison here because of its high abundance in Mexican Caribbean coastal waters. Seagrass epiphyte production rates have not been determined for the Mexican Caribbean, but several studies have reported rates at other sites in the wider Caribbean region (Land, 1970; Patriquin, 1972; Nelsen & Ginsburg, 1986; Bosence, 1989; Frankovich & Zieman, 1994; Perry et al., 2019), and we refer to these to compare seagrass epiphyte carbonate production against our estimates of *Sargassum* epiphyte carbonate import. Relevant published rates differ by an order of magnitude, but we employ the those of Nelsen & Ginsburg (1986) on the basis that these represent the approximate median among published rates, and that they relate to maximum seagrass blade densities that are comparable to maxima reported from Puerto Morelos (Enríquez & Pantoja-Reyes, 2005). Benthic habitat data for the Mesoamerican Barrier Reef System (Cerdeira-Estrada et al., 2018) provides estimates of the areal extent of seagrass meadows (317.3 km^2) and mixed seagrass and macroalgal meadows (28.8 km^2) in lagoonal waters of the Caribbean coastline of Quintana Roo. To estimate total seagrass epiphyte production in these habitats, we make the following assumptions: i) seagrass meadows comprise dense seagrass cover (>1,500 $blades \cdot m^{-2}$); ii) mixed seagrass and macroalgal meadows comprise sparse seagrass cover (<500 $blades \cdot m^{-2}$); and iii) *Thalassia testudinum* is the dominant seagrass species. In reality, seagrass meadows in this area are of variable and often lower density than that of our first assumption (Enríquez & Pantoja-Reyes, 2005; Rodríguez-Martínez et al., 2010), but we use this high density value in order to estimate an upper limit for production. Thus, applying rates of 30.4 and 303.4 g $CaCO_3 \cdot m^{-2} \cdot yr^{-1}$ for sparse and dense seagrass respectively, we estimate an upper limit for total seagrass epiphyte carbonate production in Mexican Caribbean coastal waters at 0.97 x 10^8 $kg \cdot yr^{-1}$. Dividing by the length of adjacent 463 km shoreline, this is equivalent to 210 kg $CaCO_3 \cdot m^{-1}$ $shoreline \cdot yr^{-1}$, which is very close to our 2018 mean for *Sargassum* epiphytes of 179 $kg \cdot m^{-1} \cdot yr^{-1}$.

Although our findings provide clear evidence that *Sargassum* inundations can import large quantities of new carbonate sediment, we emphasise the need for further research to help refine estimates and more clearly understand annual and seasonal variations in these inputs. First, in our calculations we assume that our September carbonate contents are relevant throughout the year. However, the degree of carbonate encrustation on *Sargassum* can vary seasonally, with new *Sargassum* growths in the

Sargasso Sea being free of encrustations in spring but heavily encrusted by winter (Butler et al., 1983; Pestana, 1985). Given that the GASB tends to develop in spring and wane in autumn (Wang et al., 2019), it is possible that *Sargassum* arriving on the Mexican coastline in September is older—and thus more heavily encrusted—than that arriving earlier in the year. However, carbonate contents of *S. fluitans* collected in the nearshore environments of Puerto Morelos in July 2019 were not significantly different to those from the same area in September 2018: mean 16.27% of dry weight (95% CI: 12.12–20.51; n = 10) versus 18.09% (95% CI: 15.17–20.63; n = 15); two-sample $t_{(23)} = 0.70$, one-tailed $p = 0.24$. This suggests that use of the September value is reasonable, at least during the summer months when *Sargassum* arrival peaks. A more conservative approach using only July 2019 carbonate content data still yields a very high carbonate import estimate of 164 $kg \cdot m^{-1}$ (95% CI: 156–172) for 2018; only slightly lower than the 179 $kg \cdot m^{-1}$ (95% CI: 173–185) using the September data.

Similarly, our calculations are based on an assumption that carbonate encrustation is comparable among *Sargassum* species and their variants. Our compositional data from spring 2019 indicate that *S. fluitans* III—for which our carbonate data are relevant—accounted for 65 ± 8.8% of beached *Sargassum* at Puerto Morelos, with the remainder comprising *S. natans* I and VIII (Fig. 3). These relative abundances are comparable to those reported from the same area throughout 2018 (Monroy-Velázquez et al., 2019; García-Sánchez et al., 2020), suggesting our *S. fluitans* carbonate data are at least relevant to the majority of beached *Sargassum* in the study area for that year. However, relative abundances of *Sargassum* species and variants inundating the Mexican Caribbean since 2014 have been somewhat variable, to the extent that the dominant variant in both the GASB and Mexican Caribbean shorelines in 2015 was *S. natans* VIII (reported at >75%; Schell et al., 2015; García-Sánchez et al., 2020). Although we did not quantify carbonate contents of *S. natans*, we did observe that floating specimens of both variants also host abundant carbonate epiphytes. Nevertheless, morphological differences among species and variants (e.g., *S. fluitans* III typically has intermediate blade breadth; Parr, 1939) could have implications for their capacity to host epiphytic communities. Epiphyte composition can reportedly differ among *Sargassum* species (Niermann, 1986), but previous quantitative assessments of carbonate content do not discriminate between species (Pestana, 1985;

Fabry & Deuser, 1991). Consequently, there is currently no basis on which to treat the species separately in this regard, but it is an obvious area for future research.

It is relevant here to point out that, prior to this study, the only other epiphytic carbonate content data for *Sargassum* that we are aware of derives from two studies in Bermuda, which reported average values equivalent to 3.0 and 9.4% of wet weight (Pestana, 1985; Fabry & Deuser, 1991). These values are considerably higher than our Mexican Caribbean average of 2.09%, for which there are several possible explanations. As discussed above, a species effect could explain this disparity, although the lack of species level reporting in previous studies means it is impossible to speculate further. Another possibility is the contrast in sea surface temperatures, with comparatively lower temperatures in Bermuda having been linked with increased epiphytic cover on pelagic *Sargassum* (Niermann, 1986). Alternatively, since the Sargasso Sea gyre is a sink for *Sargassum*, it is possible that the previous data relate to older and more heavily encrusted *Sargassum* than that arriving on the Mexican Caribbean shoreline.

Aside from carbonate content data, the challenge of constructing accurate budgets of *Sargassum* arriving on study beaches also merits wider consideration. Site-specific removal methods and reporting accuracy are important sources of uncertainty in overall volume, mass, and composition of removed beach material that are currently impossible to constrain. In addition, composition is subject to natural temporal and spatial variations resulting from: i) differences in the compositions of adjacent nearshore benthic communities (i.e., seagrass supply); and ii) the seasonality of *Sargassum* influxes (and thus seasonality in the proportion of beached material that is *Sargassum*). In these respects, the *Sargassum* content of beach material used in our calculations (74 wt.%) is probably conservative in relation to the peak of the 2018 influx. In part, this is because seagrass contents in our compositional analyses are likely to be relatively high owing to the position of our sampling station adjacent to a 1.2 km wide lagoon characterised by dense seagrass cover. In addition, at the time of our compositional assessments (spring 2019), the amount of *Sargassum* in the Caribbean Sea was comparable to the same months in 2018, and considerably lower than the peak months of May to August 2018 (SaWS, 2020). It is thus likely there would have been proportionately less *Sargassum* arriving at our sampling station than during the height of the 2018 influx.

A further issue is the possibility that active beach cleaning effectively increases accommodation space for beached *Sargassum*, potentially resulting in misleadingly high volumetric data. Whilst this may be true to some extent, it is important to realise that where there is no accommodation space *Sargassum* will typically accumulate in nearshore waters until it dies and sinks. In this case, our carbonate estimates per metre of shoreline still apply, but are relevant to larger shoreline-perpendicular areas that incorporate both beach and nearshore lagoon environments.

Accepting our estimated rates for 2018, they suggest that approximately 1,996 t of new carbonate sediment was delivered to the combined 11.15 km of study beaches. Assuming newly deposited carbonate sediment porosities of 40–70% (Choquette and Pray, 1970), and a mineral density of 2.82 $g \cdot cm^{-3}$ (i.e., intermediate between calcite and aragonite), this is equivalent to a total volume in the range 1,180–2,359 m^3, or 0.11–0.21 $m^3 \cdot m^{-1}$ of shoreline. If *Sargassum* beachings were broadly uniform throughout the 440 km of exposed Mexican Caribbean coastline between Cancun and Xcalak (including the east coast of Cozumel; Fig. 1), this equates to approximately 79,000 t of new sediment in this area, or 47,000–93,000 m^3 depending on porosity. Data to corroborate such extrapolations are not presently available, but visual observations of extensive *Sargassum* accumulations at many locations along this coastline—including Puerto Morelos, Playa del Carmen, Akumal, Tulum, Punta Allen, Mahahual, and Xahuayxol (Fig. 5)—suggest it is not unreasonable. Furthermore, *Sargassum* volumes removed from beaches along this coastline during August 2015 were broadly comparable, ranging from 132 to 262 $m^3 \cdot km^{-1} \cdot day^{-1}$ in the vicinities of Cancun, Tulum, Cozumel (east coast), and Playa del Carmen (Rodríguez-Martínez, et al. 2016).

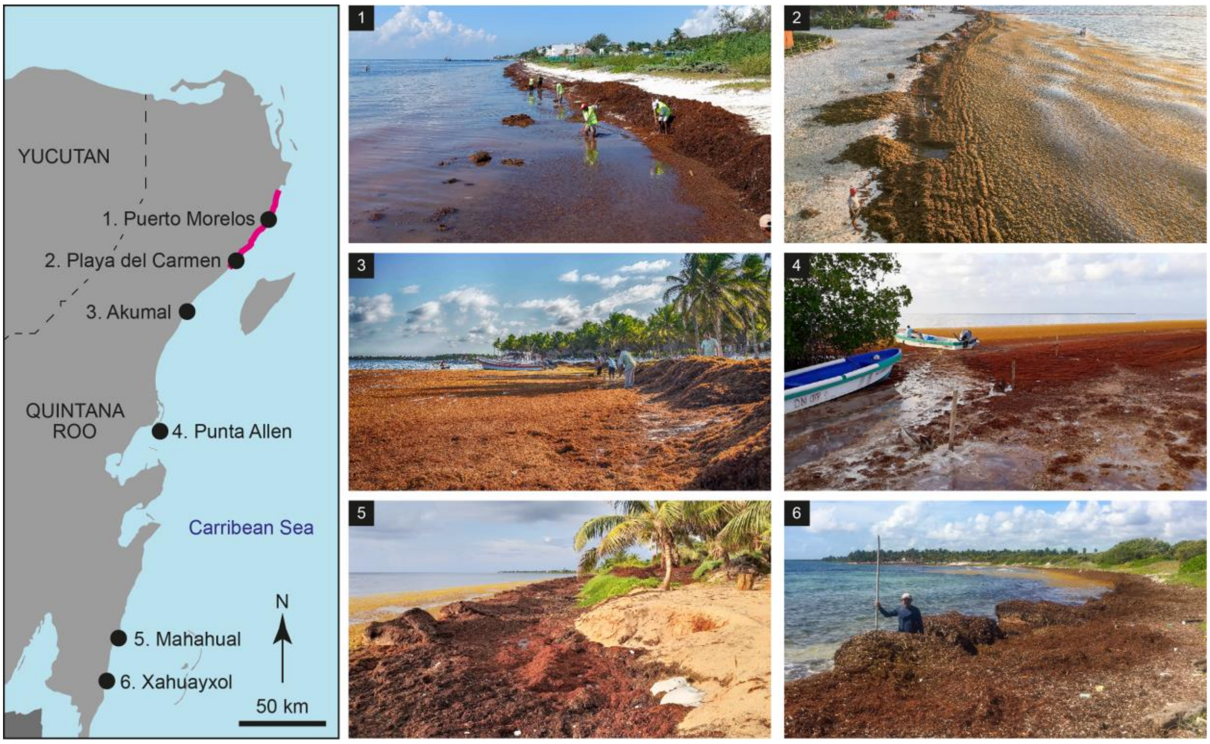

Figure 5 Examples of beached *Sargassum* at six locations spanning a 400 km extent of Mexican Caribbean coastline in 2018. These images illustrate the widespread nature of the 2018 *Sargassum* inundation event outside of our study area (highlighted magenta in the map panel). Coupled with numerous media reports of massive *Sargassum* beachings throughout the Caribbean in 2018, these observations suggest our findings are widely relevant. Photo credits: 1) Rosa Rodríguez Martínez; 2) Chris Perry; 3) Miguel A. Maldonado; 4) Alejandro Bravo Quezada; 5) Marcia Bales; 6) Nancy Cabanillas-Terán.

Acknowledging that *Sargassum* beaching events can deliver significant quantities of carbonate sediment, its fate should also be considered. Since our estimates are based on *Sargassum* removed from beaches, much of the imported carbonate along this highly urbanised sector of coastline will also have been removed, ultimately being disposed of inland along with the *Sargassum* as waste (Rodríguez-Martínez et al., 2016). However, calcareous epiphytes on beached *Sargassum* often appear damaged and are seemingly sparse compared to those on floating *Sargassum*—especially evident for delicate byrozoan skeletons. This observation is consistent with carbonate content data from Bermuda indicating that beached *Sargassum* on average contained 3% by wet weight less than floating *Sargassum* (Pestana, 1985), likely as a result of epiphyte displacement as the *Sargassum* washed ashore. Thus, at least some of the carbonate imported to our study beaches was probably dislodged and retained in the nearshore-beach face zone. However, managed tourist beaches represent only a small proportion of the Mexican Caribbean shoreline. During 2015, efforts to remove *Sargassum* concentrated on 71.1 km coastline between Cancun and Punta Allen (Rodriguez-Martinez et al., 2016)—approximately 25% of its eastern exposure. Consequently, most carbonate imported to the remaining ~75% of coastline will have remained on the beaches and in adjacent nearshore environments, at least in the short-term. If beach cleaning effort was similar in 2018, this could equate to approximately 34,000 t of new carbonate sediment input to coastal areas between Cancun and Punta Allen.

Regional studies indicate that, prior to the onset of massive *Sargassum* beaching events in 2014, the most abundant epiphytic carbonates on *Sargassum* thalli (serpulid tube casings and bryozoan skeletons) were typically rare or absent in the coral- and ooid-dominated coastal sands of the Mexican Caribbean (Aguayo et al., 1980; Carranza-Edwards et al., 2015). Despite subsequent import of evidently large quantities, our own analysis of beach sediment from three sites (n = 3 samples per site) along a 100 m section of shoreline adjacent to the UNAM campus (Puerto Morelos) interestingly showed no elevation in the abundance of epiphytic carbonates beneath the accumulating (~0.5 m thick) *Sargassum* mats. Specifically, identifiable fragments of bryozoan skeletons were absent, whilst serpulid tubes (both intact and fragmented) consistently accounted for <1% of grains. Given that *Sargassum* is not removed from this section of shoreline, it might be expected to be among the sites at which epiphytic carbonates are most likely to accumulate. However, the paucity of these grain types leads us to hypothesise that they must instead either be accumulating in nearshore or lagoonal waters, or are subject to physical reworking or chemical degradation following the beaching of *Sargassum*.

The first scenario could arise through mechanisms discussed above, such as epiphyte displacement in the swash zone, or because large volumes of *Sargassum* die and sink in nearshore waters having never washed ashore. These carbonates, as well as those delivered to beaches, will be subject to further physical processes that promote their fragmentation. This is likely to occur both during the desiccation of aerially-exposed *Sargassum* (as observed by Pestana, 1985), and as a result of aerial and sub-aqueous attrition. When handling serpulid tubes and bryozoan skeletons we noted that they would readily fragment under minimal force applied with fine tweezers, whereas the dominant grain types in beach sediments (corals, forams and molluscs) were generally resistant to breakage. This suggests that epiphytic carbonates are likely to be especially susceptible to rapid physical breakdown. Given they comprise micron-sized crystals (Fig. 2), they could ultimately disintegrate to mud-sized particles (<64 µm) that are unlikely to be retained in high energy nearshore or beach face settings.

Alternatively, degradation of epiphytic carbonates could arise as a result of exposure to the chemical environment regulated by *Sargassum* decomposition, which is often anaerobic in massive accumulations of beached *Sargassum* (as evidenced by very strong odours of hydrogen sulphide in affected areas; Smetacek & Zingone, 2013). Initially this will lower pH and may promote carbonate dissolution, but associated production of HCO_3^-, PO_4^{3-}, and NH_3 will simultaneously increase alkalinity and if sustained may ultimately result in carbonate supersaturation—and thus preservation (Morse & Mackenzie, 1990). *Sargassum* decomposition can also affect nearshore water chemistry, where it can result in pH values as low as 6.9 (van Tussenbroek et al., 2017) and will potentially influence the preservation potential of carbonates that accumulate there. The fate of epiphytic carbonates clearly requires further investigation, but collectively these scenarios highlight the potential for multiple depositional and post-depositional pathways that might explain the disconnect between demonstrably large quantities being imported and their apparent scarcity within beach sediments.

5. Conclusions

Large-scale *Sargassum* inundations that have been affecting exposed Caribbean coastlines since 2011 host an assemblage of epiphytic carbonates dominated by bryozoan skeletons but also including abundant serpulid worm tubes and smaller quantities of crustose red algae. These carbonates averaged 2.09% of the wet weight of *Sargassum* floating in nearshore areas of the Mexican Caribbean. Combined with very high rates of *Sargassum* import throughout 2018 (averaging 7,000 $kg \cdot m^{-1}$ of shoreline along a 60 km stretch of coast between Cancun and Playa del Carmen), this suggests total carbonate import for that year averaged 179 $kgCaCO_3 \cdot m^{-1}$ of shoreline. Thus, epiphytic carbonates associated with *Sargassum* inundations represent a new and potentially highly significant source of carbonate sediment in the region, with import rates similar to estimated production rates from other important regional sources such as *Thalassia* seagrass epiphytes. These 2018 rates are likely to be the highest yet to have occurred, but annual bloom patterns suggest *Sargassum* has emerged as a recurrent and increasingly important vector of sediment import since 2011.

Important questions arise about the rate and extent to which these epiphytic carbonates break down and their ultimate depositional fate. Some will inevitably contribute to beach accumulation but other portions may be flushed offshore and contribute to lagoon sediment accumulation. In any case, this material could make very significant contributions to coastal and nearshore sediment budgets in the wider Caribbean region and along tropical Atlantic shorelines, potentially buffering possible declines in sediment supply resulting from coastal habitat degradation (e.g., nearshore reefs and seagrass meadows) caused by the massive *Sargassum* inundations. However, this does not lead us to advocate leaving *Sargassum* on the beaches as a sediment supply source—the wider socio-economic and ecological impacts of *Sargassum* beachings will outweigh any sediment gains from a coastal zone management perspective—but it is important that the magnitudes of this new source of sediment input are acknowledged and quantified.

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Author Contributions

M.A.S. and C.T.P. conceived the idea for study, collected *Sargassum* samples, and performed the carbonate analyses; R.E.R.-M. and E.J.-D. obtained the beached *Sargassum* volume data; L.A.-F. produced the orthomosaics of floating *Sargassum* rafts and analysed them with M.A.S.; M.A.S. performed the carbonate upscaling calculations; M.A.S., C.T.P., R.E.R.-M., .L.A.-F., and E.J.-D. wrote the manuscript.

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