PLOS CLIMATE

REVIEW

Climate-sargassum interactions across scales in the tropical Atlantic

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Citation: Marsh R, Skliris N, Tompkins EL, Dash J, Dominguez Almela V, Tonon T, et al. (2023) Climate-sargassum interactions across scales in the tropical Atlantic. PLOS Clim 2(7): e0000253. https://doi.org/10.1371/journal.pclm.0000253

Editor: Frédéric Cyr, Fisheries and Oceans Canada, CANADA

Published: July 19, 2023

Funding: This work was supported by the UK Economic and Social Research Council through the Global Challenges Research Fund (GCRF) project, Teleconnected sargassum risks across the Atlantic: building capacity for TRansformational Adaptation in the Caribbean and West Africa (SARTRAC), grant number ES/T002964/1 to ELT. The funders had no role in study design, data collection and analysis, decision to publish, or preparation of the manuscript.

Competing interests: The authors have declared that no competing interests exist.

Abstract

The impacts of climate change on ecosystems are highly uncertain but potentially profound. One such impact may be the emergence of extensive mats of seaweed (macroalgae), due to the extraordinary proliferation of pelagic sargassum species, in the tropical Atlantic since 2011. Sargassum blooms are now an annual event and reached record levels across what is now known as the 'Great Atlantic Sargassum Belt' (GASB) in summer 2022. Monitoring across scales, from satellite surveillance to in-situ beach surveys, is bringing step changes in process-level understanding of sargassum. Physical and biogeochemical drivers of sargassum act at basin scale to shape the GASB, highly variable from year to year. In the local environment, sargassum is sensitive to ambient conditions, with new findings confirming that growth rates are temperature dependent. Multidecadal ocean warming may therefore be detrimental to sargassum, although projected changes in other drivers are uncertain. Emerging options for climate change action around sargassum include valorisation and carbon sequestration, although uncertainties are again considerable. In conclusion, the emergence of sargassum across the tropical Atlantic highlights interconnected systems that embrace physical, biogeochemical, and socioeconomic dimensions, with considerable scope for improved monitoring, process-level understanding and prediction.

Introduction

'Sargassum' is becoming part of the vocabulary of tourists, fishers and the wider communities in the Caribbean, the Caribbean coast of Central America, and West Africa. Pelagic sargassum comprises two species and three dominant morphotypes, *Sargassum natans* (I and VIII) and *S. fluitans* III, which we here collectively refer to as 'sargassum'. These brown macroalgae, which have proliferated since 2011 [1,2], bring negative socioeconomic consequences for a variety of employment sectors [3], including environment, health, tourism, and fisheries [4–12]. The intensity of these events can be exacerbated in areas with capacity deficits (e.g., policy, people, or funds), impeding the effectiveness of response to manage the seaweed [13]. A range of valorisation options has meanwhile been explored, including bioenergy, agricultural applications, and other products [14–23]. With a view to long-term adaptation and appropriate capacity building, it is timely to undertake a review of this ecological 'new normal', in relation to ongoing and future climate and environmental change across the tropical Atlantic.

Despite valuable pioneering studies and a growing research community, the wide-ranging scales associated with sargassum distribution and management present a difficult challenge. While satellite remote sensing plays a vital role in large-scale surveillance in parts of the tropical Atlantic not regularly covered in cloud, a key limitation is the in-situ monitoring of sargassum at coastal locations, and the lack of long-term records of the frequency and magnitude of previous events. There has been a natural geographical focus around the main research organisations in affected areas, for example near two of the University of the West Indies campus locations in Jamaica and Barbados, in the French departments of Martinique and Guadeloupe, in South Florida, and at several locations along the Caribbean coast of Mexico [3]. As a result, there are significant geographical gaps in monitoring and hence limits to current understanding, particularly along the coasts of West Africa, and along much of the Caribbean coastline of Central America. Proliferation being so recent, there are also limits to the evidence for a climate influence on sargassum. Thus motivated, we review climate-sargassum interactions *across scales of time and space*. We specifically ask:

- How well do we currently monitor sargassum across scales, and what improvements are emerging?
- How do climate and environmental drivers shape the distribution and vitality of sargassum around the tropical Atlantic?
- How is regional climate change likely to impact sargassum in coming decades?
- How is sargassum implicated in a changing carbon cycle?

We first review the current capabilities for monitoring sargassum, from basin scale to coastal locations, considering the evolution of monitoring systems and prospects for future improvements. We then review the environmental drivers of sargassum, considering basin-scale environmental change and the dynamical drivers of sargassum drift, followed by the physiological response of sargassum to in-situ ambient conditions. We further consider sargassum in relation to regional climate change projected over coming decades, and as a part of the carbon cycle. In conclusion, we highlight four key points, regarding monitoring across scales, physical and biogeochemical drivers, projections under climate change, and prospects for adaptation and mitigation.

Monitoring sargassum across scales

At basin scale, satellite imagery reveals the 'Great Atlantic Sargassum Belt', or GASB, stretching from the Gulf of Mexico to west Africa [2]. Conveyed inshore from oceanic sources, sargassum may rapidly accumulate at the coast on successive tides. Throughout the summer in particular, accumulations of freshly-beached sargassum (typically beached for less than 6 hours) exceed 100 m^3 per km of beach at many locations (e.g., at Walker's beach, Barbados–see below), although this varies considerably over time. Monitoring the local arrival and accumulation of sargassum is a particular challenge. Given the central importance of observational datasets that reveal the evolving distribution of sargassum, we first review the various approaches to monitoring sargassum, from basin-scale to nearshore and coastal scales.

Basin scale

Since pioneering use of satellite imagery from the European Space Agency (ESA) Medium Resolution Imaging Spectrometer (MERIS) to infer seasonal movement of sargassum from the northeast Gulf of Mexico to the western subtropical North Atlantic [24], major progress has been achieved in the remote sensing of sargassum at basin scale [25–27]. In particular, the 'Alternative Floating Algae Index' (AFAI) has revealed very valuable information. It is an ocean colour index based on spectral reflectance in red, near infrared and shortwave infrared wavelengths obtained with the Moderate Resolution Imaging Spectroradiometer (MODIS) instrument onboard the Terra and Aqua satellites [25]. Based on AFAI, 'Floating Algae density' maps are provided by the Optical Oceanography Laboratory at the University of South Florida (https://optics.marine.usf.edu) for selected sub-regions of the tropical Atlantic. Composite images are presented daily as means of the preceding 7 days, from as early as 25 February 2000, and updated to the present time. Images may be downloaded and re-processed.

In Fig 1, we illustrate both the potential and limitations of such images, showing typical sargassum distributions across the 'Central Atlantic Region' at a standard spatial resolution of 1 km, in early July of years 2011 to 2022. Highest densities are typically detected in a southeast-northwest orientation along the axis of the North Brazil Current. Sargassum first appeared extensively in 2011 [1,26], returned in 2012, and was largely absent in 2013. Since 2014, sargassum has become a seasonal fixture across the tropics, with notable 'heavy' years in 2015 and since 2018, and even heavier conditions in 2021 and 2022. These images provide rich information on seasonal and interannual variability, and changes in distribution, that have motivated further studies of dynamics, prediction, and drivers [28–30]. Despite this wealth of data, the images must be considered with some caution, due to uncertainties in data processing, limitations near land, and the inevitable challenges of cloud cover. The maps in Fig 1 are obtained by selecting the maximum value of density per pixel, to increase the number of cloud-free pixels, given rapid changes of cloud cover on synoptic timescales. Nevertheless, many areas indicating no sargassum are adjacent to high index values, suggesting that clouds are still obscuring much of the sargassum distribution.

In recent years, availability of data from other sensors, i.e., the Ocean and Land Colour Instrument (OLCI, 300 m) and the Visible Infrared Imaging Radiometer Suite (VIIRS, 750 m), complements the MODIS data coverage and has shown potential to reveal more detailed structure of sargassum rafts at finer scales, ranging from 'windrows' (extending up to many km in length) to quasi-circular patches [31]. In addition, several enhanced capabilities have been developed with the higher resolution satellite data. For a more complete inventory of sargassum, and fuller dynamical understanding, a semi-analytical approach has also been recently applied to Sentinel-3/OLCI data to detect immersed sargassum [32]. Processing of Sentinel-3/OLCI data has also been further improved to account for the impact of sargassum that may be mistaken for aerosols [33]. Detailed understanding of sub-mesoscale structure, a more complete detection of immersed sargassum, and improved atmospheric corrections are all essential refinements in basin-scale monitoring of sargassum to improve confidence in understanding variability and long-term change.

Nearshore and coastal scales

Of direct interest to island and coastal nations throughout the region, but also essential for evaluation of basin scale remote sensing and models of sargassum drift and growth, are observations of sargassum at nearshore and coastal scales. Drifting through the Caribbean, a substantial fraction of sargassum 'beaches' along exposed coastlines, as summarised on two scales in Fig 2. Using the SARTRAC-EFS forecast system [34], with 1% windage, we evaluate the

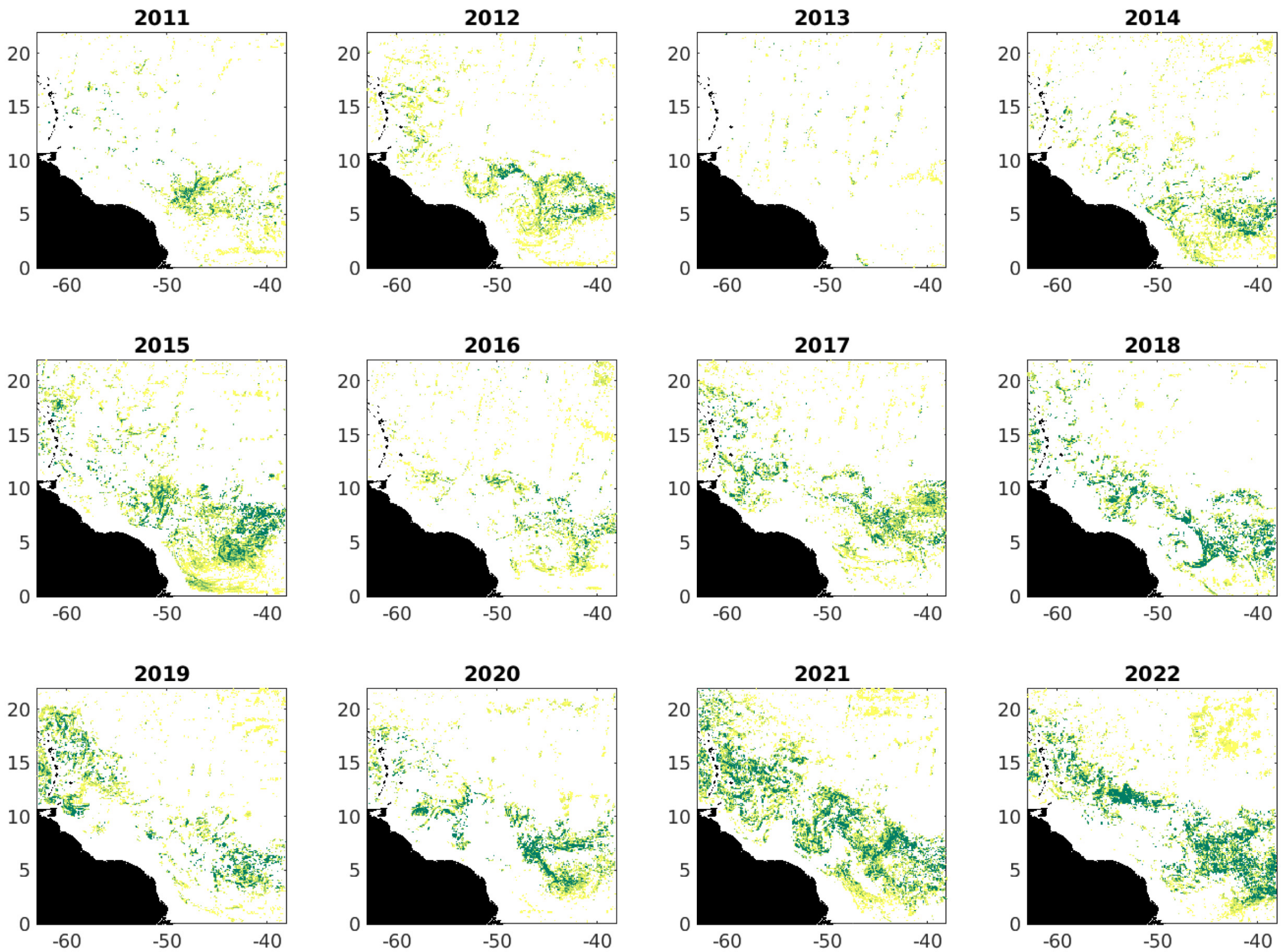

Fig 1. Sargassum in the 'Central Atlantic Region' (CAR, 38-63˚W, 0-22˚N). Floating Algae density satellite images are provided by the Optical Oceanography Laboratory at the University of South Florida (https://optics.marine.usf.edu); images are sampled for 1–5 July over 2011–2022; each image represents a mean of the 7 past days (including that day); we select the maximum FA_density value per pixel, from the 5 composite images (1–5 July), to minimize data loss due to day-to-day variations in cloud cover.

https://doi.org/10.1371/journal.pclm.0000253.g001

implicit beaching of 'particles' that each represents a fixed area of sargassum. On a 0.25˚ grid, we count particles at 'pre-beaching' locations over 180 days of simulated drift. Sampling particle locations at 5-day intervals, these locations are mostly within 100 km of the coast. In an example, we map this total count over days 90–270 of the year 2020, accounting for variable winds and currents by sampling an ocean model hindcast spanning 1988–2010. Ensemble-mean counts of pre-beached particles summarised in Fig 2A reveal that beaching is largely localised to windward (eastward) coasts of the Lesser and Greater Antilles. At 127 selected coastal and island locations, we specifically identify the implied quantities of beaching sargassum, emphasizing the highest values along the Lesser Antilles and the south coast of Hispaniola.

Volumes of beached sargassum have been monitored in situ at only a few beaches in the region. One such location is Walker's Beach in northeast Barbados (arrowed in Fig 2A), a long stretch of open beach on the windward shore, directly exposed to sargassum arrivals. A desk study of Google Earth imagery from 2011 to 2021 indicated that this stretch of coastline is

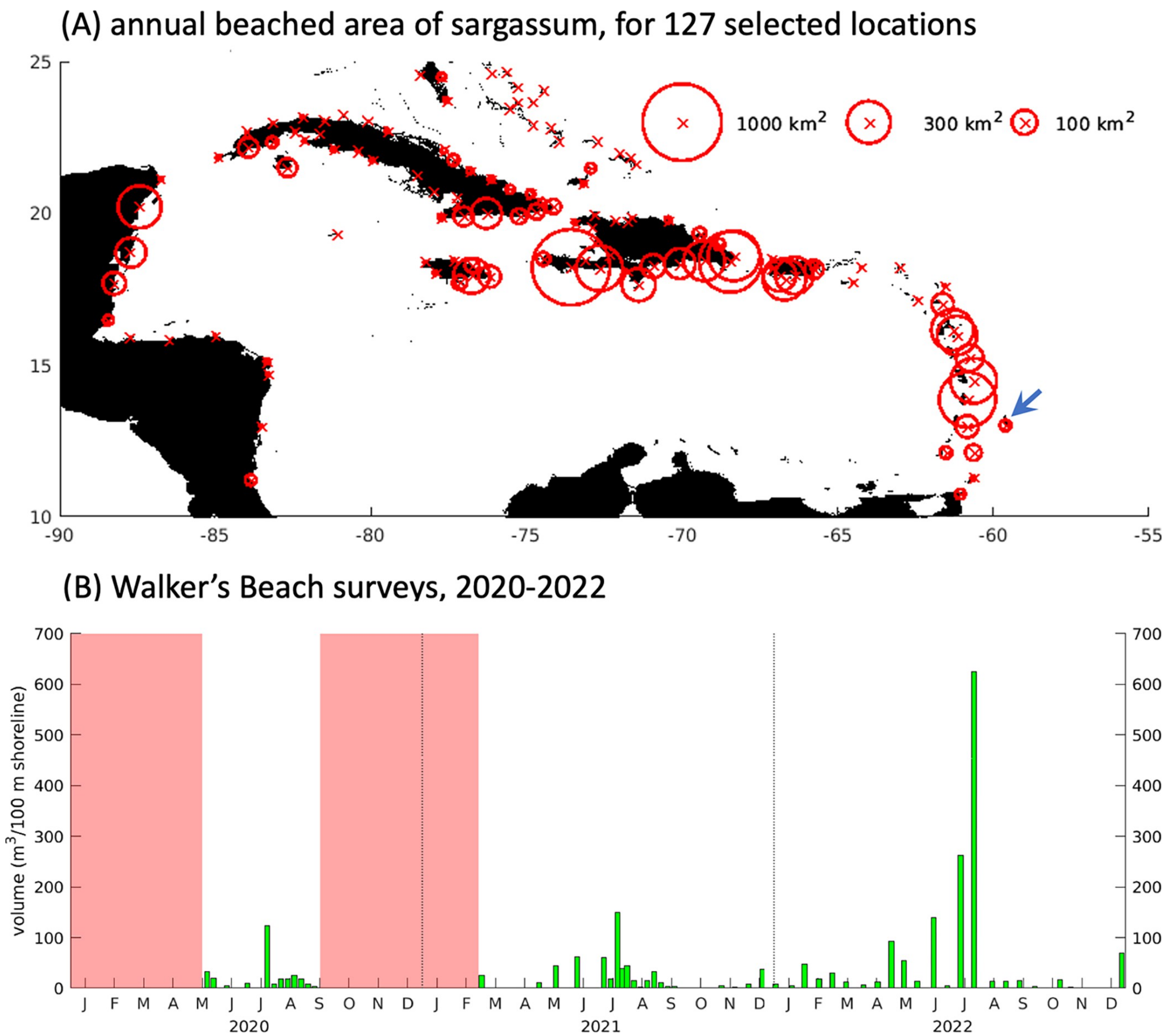

Fig 2. Sargassum landing at beaches throughout the Caribbean and at Walker's Beach in Barbados. (A) the quantity of sargassum evaluated at 127 coastal and island locations in the Caribbean region, for which associated circle area is proportional to the accumulated amount of beaching sargassum in 2020 (sampled in an adjacent 0.25˚ ocean grid-cell–see text for details); (B) weekly or bi-weekly survey data over 2020–2022 for Walker's Beach on the northeast coast of Barbados, indicated with the blue arrow in (A), recording the volume of 'fresh' golden brown sargassum per 100 m of shoreline; periods without regular surveys are red-shaded.

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exposed to sargassum inundations 90.4% of the time and that, 26% of the time, these are classified in the highest magnitude category, ranking this 9.8 km stretch of beach among the topmost exposed beaches to sargassum in Barbados [35]. In Fig 2B, we present estimates of the volume of beached sargassum at Walker's Beach, Barbados. Monitoring was carried out weekly over much of the summer of 2020 and 2021, and then fortnightly to December 2022. Regular monitoring was undertaken along a 100-m stretch of beach. An Unmanned Aircraft System (UAS) was deployed to map the surface area of freshly beached sargassum, whilst mean height of the sargassum was measured in situ at set intervals along a minimum of five line transects oriented perpendicular to the waterline. These observations are used in combination to estimate sargassum volume [36]. Survey data for 2020, 2021 and 2022 provide one of the first systematic time series of sargassum beaching in the region, alongside recently published time series from the Turks and Caicos Islands [11] and Mexico [37,38]. It is evident from these data that sargassum beaches throughout much of the year, but most notably during summer, with record quantities of beached sargassum recorded in summer of 2022.

Remote sensing is providing complementary information on the nearshore presence of sargassum [39]. The highest resolution satellite data–via the Multispectral Instrument (MSI, resolution 10–20 m) on board of Sentinel 2, Operational Land Imager (OLI, 30 m) on board of Landsat mission, WorldView-II (WV-2, 2 m), and PlanetScope/Dove (3 m)–have been combined, with deep learning methods, to fill previous gaps of monitoring in nearshore waters [40] and in some cases for automatic identification of Sargassum features [41]. By combining different sources of remote sensing data, it is further possible to detect both floating and beached sargassum with increased accuracy [3]. Furthermore, data from Sentinel-2 MSI could be used to distinguish different decomposition levels of sargassum and to map sargassum accumulation hotspots [39]. At very high spatial resolution, there are also prospects to better understand distribution of the three dominant sargassum morphotypes; by identifying the in-situ spectral signatures of different morphotypes using field spectrometers on the beach, these observations could potentially be scaled up through UAS with hyperspectral sensor and high spatial resolution satellite images. While satellite sensors such as the Sentinel programme provide ever enhanced detection capability both spatially and temporally, new sensors such as EnMAP [42] provide the hyperspectral capability that would enable detection of different species/morphotypes and decomposition level.

In summary, advances in nearshore remote sensing and in-situ monitoring of beached sargassum provide the detailed spatial analysis and ground truth to underpin basin-scale satellite surveillance and modelling. With observations spanning these scales, we can more fully understand the drivers of variability and long-term change in sargassum, and attribute changing quantities of individual species/morphotypes to specific drivers, now considered in the following section.

Environmental drivers of sargassum

Changes across the tropical Atlantic associated with large-scale modes of natural variability in atmosphere-ocean processes appear to drive changes in sargassum quantity and drift. Drifting sargassum will also gain or lose biomass in response to local-scale environmental variation encountered along their transport pathways. We review in turn the drivers that act at basin scale and at local scales.

Basin scale

Following the first proliferation of sargassum in the Equatorial Atlantic in 2011, each year has brought variable amounts, distribution, and timing of sargassum blooms, forming the GASB that is associated with surface convergence under prevailing winds [2]. Several studies have explored the physical drivers of basin-scale sargassum proliferation and drift [29,30,34,43–47]. In Fig 3, we summarise a range of drivers that have been considered to explain the GASB.

With an initial focus on passive drift, high-fidelity ocean model currents and winds were used to obtain trajectories for ensembles of virtual particles released across the tropical Atlantic, in the zone 0–10˚N [43]; westward drift through the Caribbean is consistent with satellite evidence for the source of pelagic sargassum being the central tropical and equatorial Atlantic, often referred to as the North Equatorial Recirculation Region (NERR); interannual variability

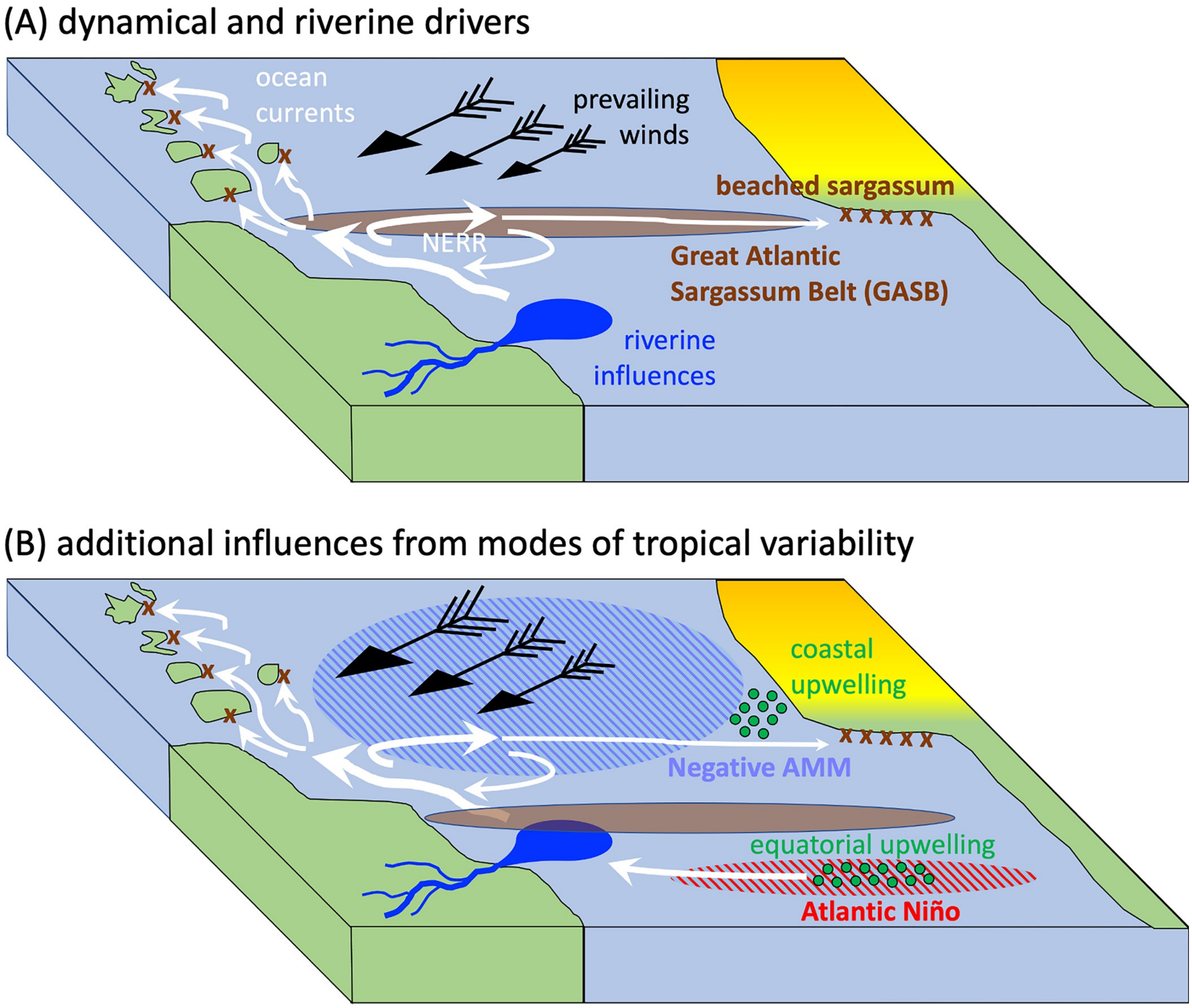

Fig 3. Schematic illustrations of various drivers of basin-scale environmental change that may explain recent influxes of sargassum in the Eastern Caribbean and off West Africa. (A) dynamical and riverine drivers, emphasising how sargassum recirculating in the North Equatorial Recirculation Region (NERR) since 2011 forms a belt across the northern tropical Atlantic that follows seasonal migration of the ITCZ [29], potentially subject to waters enriched by nutrient-laden riverine runoff; (B) additional influences from modes of tropical variability, specifically the strong influence of sea surface temperature (SST) anomalies, strengthened trades and associated enhanced upwelling of nutrients off West Africa and along the Equator (green dots), associated with the Atlantic Meridional Mode (in negative phase) and the Atlantic Niño, following [30]. Locations of sargassum beaching events are indicated with 'x' symbols.

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in sargassum drift, and shoreline beaching, may further be related in particular to dynamical changes in the complex North Brazil Current system. Further trajectory experiments confirmed a strong influence on sargassum drift of skin drag and form drag associated with prevailing winds, collectively known as 'windage' and typically applied to drifting particles as 1% of the local wind [48]. The variable winds and currents emphasized in Fig 3A were thus a focus of these early studies.

The GASB was further explained in terms of dynamical processes that shift sargassum–more in some years than others–towards the nutrient sources associated with equatorial upwelling and the Amazon outflow. Central to this explanation is a hypothesis for the emergence of sargassum in 2011, and subsequent persistence, that can be specifically attributed to physical mechanisms [29], as highlighted in Fig 3A; it is suggested that the trigger was an exceptionally negative phase of the North Atlantic Oscillation (weak Icelandic low and Azores high pressure centres) in the winter of 2010/11, which drove sargassum from the western subtropics (the Sargasso Sea) to the northeast, as far as Gibraltar. Conveyed southward in the Canary Current as far as the eastern central tropical Atlantic, subsequent spring growth led to the first Caribbean inundation of summer 2011. It is further hypothesized that this sargassum has subsequently recirculated in the NERR, forming the GASB across the northern tropical Atlantic that follows seasonal migration of the Intertropical Convergence Zone (ITCZ), subject to strong zonal flows that seasonally reverse direction.

Acting as a seasonal source, sargassum from the NERR drifts westward in winter/spring to subsequently beach along the windward shores of the Lesser Antilles and throughout the Caribbean. With development of the North Equatorial Counter Current (NECC) in the approximate zone 5-10˚N during the second half of the year, the NERR also supplies the sargassum that beaches along West Africa, evident in drifter data [45]. Sargassum may thus be conveyed eastward, joining the Guinea Current to reach West African coastlines from Senegal to Nigeria. In summary, these basin-scale, tropical-extratropical dynamical perspectives have emphasized physical connectivity in understanding sargassum distributions and change.

Complicating hypotheses for the triggers and drivers that have established the GASB is the fact that sargassum distributions, drift and beaching events have been subject to considerable interannual variability since 2011 [30]. An identified southward shift of the ITCZ in years of most excessive sargassum, notably 2015 and 2018 (subsequently also 2021 and 2022), is consistent with the scenario outlined in Fig 3A and developed in Fig 3B. Furthermore, this shift is associated with two leading modes of natural variability in the tropical Atlantic, notably a negative phase of the Atlantic Meridional Mode (AMM) in all four years, and additionally the Atlantic Niño in 2018. The AMM is associated with anomalies in the cross-equatorial meridional gradient of SST in the Atlantic, which tend to peak in boreal spring [49]. A negative phase of the AMM is characterized by negative SST anomalies centred around 10˚N and anomalously strong trade winds centred around 5˚N, associated with the shifted ITCZ [50]. The Atlantic Niño is also associated with a southward shift of the ITCZ during boreal summer, but with a reduction of (westward) equatorial winds over the east equatorial upwelling zone. This results in strong surface warming along the Equator, with peak warming at around 10˚W [50,51].

In addition to physical drivers, evidence is emerging for biogeochemical drivers affecting sargassum proliferation [e.g., 52]. Various physical mechanisms may have raised levels of key macronutrients, of consequence for sargassum growth. A sequence of unusually large Amazon floods since 2011 have been highlighted as a possible source of elevated nutrient levels, along with enhanced nutrient sources to the eastern equatorial Atlantic in some years that may be associated with coastal upwelling off west Africa and Congo floods [53]. Increased nutrient supply has also been attributed to more active hurricane seasons in recent years [53,54]. In this case, an active June-November hurricane season is thought to broadly raise surface nutrient levels through stirring up deep nutrient-rich waters to the surface. Increasing nitrogen availability in the Atlantic Basin is also emerging since the 1980s, in seawater and in sargassum itself [55].

Of consequence for sargassum, a negative phase of the AMM is associated with both increasing trade winds in the equatorial and tropical North Atlantic–enhancing West African and equatorial upwelling–and a southward shift of the ITCZ; in contrast, the Atlantic Niño is only associated with the southward shift of the ITCZ–bringing sargassum closer to equatorial nutrient sources [30], as outlined in Fig 3B. The AMM and Atlantic Niño thus drive extensive interannual variability in both transport and nourishment of sargassum across the tropical Atlantic, compounding a simple explanation of the GASB in relation to anthropogenic climate change.

A recent refinement to our understanding of the drivers that explain variable sargassum strandings is provided through backtracking samples of the three morphotypes collected from east Barbados through 2021–22 [56]. This analysis suggests two district pathways and origins, with *S. fluitans* III-dominated mats arriving from March to early August via a southerly convoluted pathway from an equatorial source, including the Gulf of Guinea and passage close to the coast of South America–a nutrient-rich pathway. In contrast, significantly higher amounts of *S. natans* VIII arrived from late-August to March via a northerly and more zonal pathway–a nutrient-poor alternative. The distinct temperature and nutrient conditions along these two broadly defined pathways may explain some of the variability in beached sargassum, including amounts and morphotype composition.

In summary, proliferation of sargassum across the tropical Atlantic was most likely physically triggered, under anomalous Atlantic-wide atmospheric and oceanic conditions around 2011; high sargassum biomass has since been sustained under favourable, although variable, SST patterns and nutrient levels, with sargassum rafts subject to extensive dispersal under prevailing ocean currents and winds.

Local scale

Along a given drift pathway, sargassum will respond physiologically to the local physical and biogeochemical environment. In Fig 4, we summarise non-dimensional 'growth factors', scaling sargassum growth rates as functions of ambient temperature, solar radiation, and nitrogen and phosphorus quotas (in relation to carbon), as used in the sargassum-enabled ocean model NEMO-Sarg1.0 [57] and based in turn on earlier studies [55,58]. These growth factors are highly uncertain, for several reasons:

(1) previous studies were focused on sargassum from the subtropical North Atlantic [58–61] as opposed to the equatorial population;

(2) one previous study found no difference in growth rate between the two species under similar conditions [58], whereas [61–63] indicate that *S. fluitans* grows considerably faster than *S. natans*;

(3) there is wide variation (by an order of magnitude) in reported growth rates for the same species across growth trials, different locations and a range of abiotic conditions [58,60–64].

Despite uncertainties, some general dependencies are suggested in these functionalities:

- growth peaks at an optimal water temperature range of ~26–27˚C, while mortality only starts to increase above ~28˚C;
- growth increases steadily with light levels, by almost 5% per 100 W m^{-2} at lower levels of insolation;
- growth increases steadily with nitrogen quota, approximately doubling per 10% increase;
- growth increases more non-linearly with phosphorus quota, increasing by ~50% for ~25% increase in quota, at mid-range values.

Based on these generalisations, we may conclude that:

- sargassum biomass may be limited by high temperatures;
- increased light levels may lead to modest increases in growth;

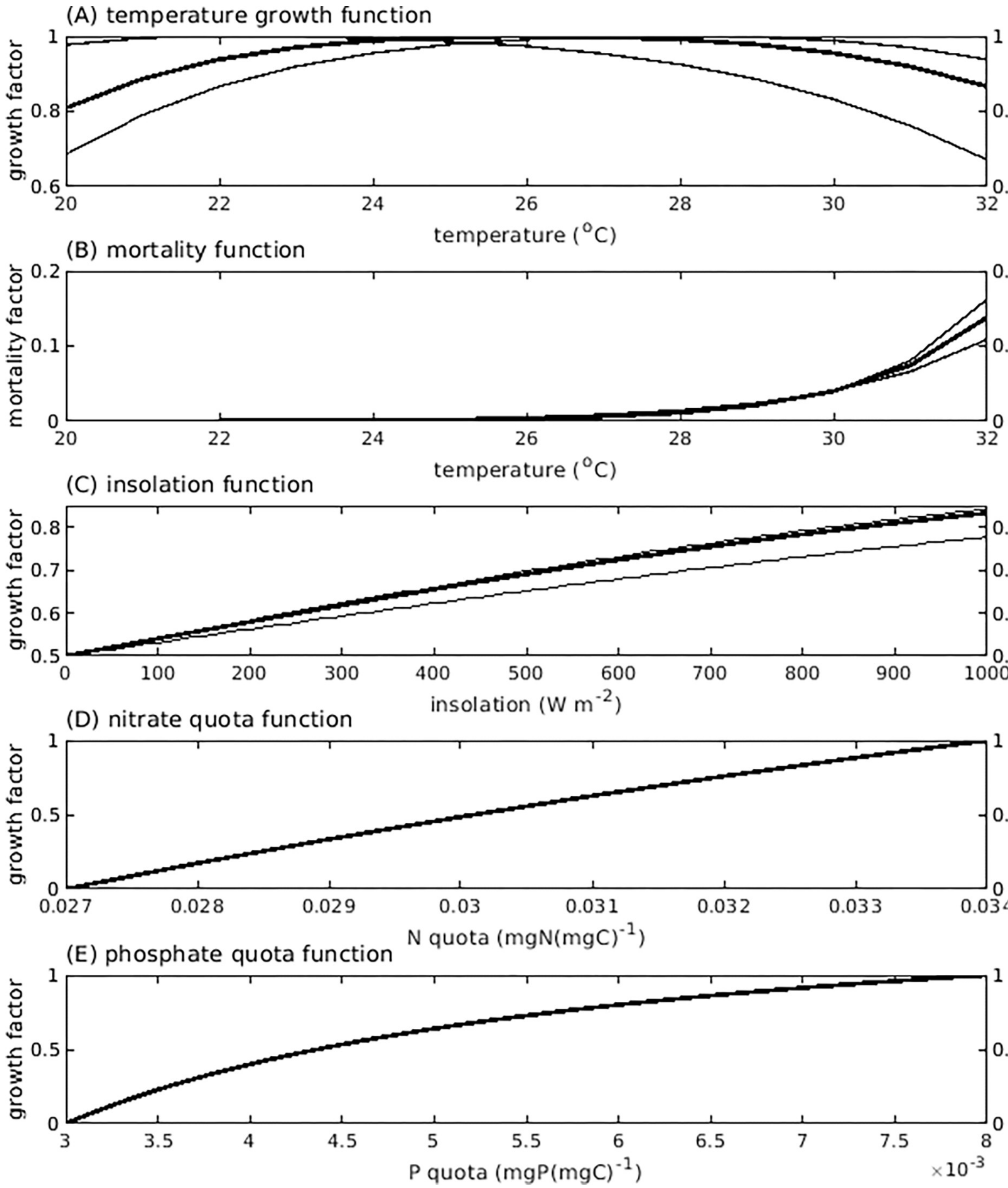

Fig 4. Growth and mortality factors for sargassum as functions of selected environmental variables, after [57]. (A), (B) growth and mortality factors as a function of temperature; (C) growth factor as a function of solar radiation; (D) growth factor as a function of nitrogen quota; (E) growth factor as a function of phosphorus quota. In (A), (B) and (C), thick curves are based on baseline parameter values, while thin curves are obtained by sampling the minima and maxima of parameter values; in (D) and (E), for which two parameters are necessary, only the baseline parameter values are used.

https://doi.org/10.1371/journal.pclm.0000253.g004

- increasing presence of nitrogen and/or phosphorus in oceanic waters will substantially stimulate growth, the latter influence being evident in phosphorus enrichment experiments [55,58,65].

The direct consequence of climate change is warming of the surface ocean. While changes in ambient temperature may be consequential for growth and mortality rates, these influences appear to vary between sargassum species and morphotypes. Previous findings based on the two sargassum species in the Sargasso Sea [59] may not extend to blooms in the tropics or to different species morphotypes.

Pioneering experiments with pelagic sargassum mesocosms in both coastal waters and in laboratory settings [62–64] are providing new insights into growth rates for tropical Atlantic populations, specifically on the temperature dependence. Cultivation of the three variants of sargassum in closed continuous motion systems, with temperature held constant at 22, 25, 28 and 31˚C, showed specific growth rates ranging from a maximum of 0.095 doublings day^{-1} for *S. fluitans* III at 28˚C to a minimum of 0.045 doublings day^{-1} for *S. natans* VIII at 31˚C [64]. The findings of [63] confirm that all three morphotypes have significantly different growth rates, with *S. fluitans* III being the fastest growing at ambient temperatures (27.6–29.6˚C), and that growth is reduced at the higher temperatures for all three morphotypes. These findings suggest a wider range of growth rates with temperature than is represented by the function in Fig 4A.

In summary, while recent and increasing proliferation of sargassum is clearly associated at basin scale with tropical modes of natural variability, it seems likely that sargassum now grows more vigorously in warmer tropical waters, subject to favourable nutrient levels that are in turn attributed to a range of drivers.

Sargassum under future climate change

We finally discuss the possible future of sargassum in a changing tropical climate. We first consider regional climate change of likely consequence for sargassum, with a focus on surface ocean warming over coming decades, before considering sargassum in various biogeochemical contexts that point to challenges and opportunities.

Regional climate change to 2050

Our ability to forecast sargassum on timescales from synoptic to seasonal has expanded substantially over the last decade, but useful evaluation of these forecasts is predicated on more complete monitoring [66]. Looking to longer (multi-annual) timescales, there is considerable uncertainty in the outlook for sargassum distribution. To further understand long-term changes in sargassum, we consider ongoing climate change in the region.

Over the satellite Earth Observation era of 1979–2018, an exception to widespread warming of the tropical Atlantic is a relative 'warming hole' over the equatorial zone, attributed to shoaling of the thermocline driven by anomalous winds [67]. Notwithstanding this recent hiatus, long-term warming of the region is evident in climate projections. With the time horizon of 2050, we examine SST across the western tropical Atlantic in a high-fidelity climate simulation, with ocean resolution of 1/12˚ and atmospheric resolution of 25 km [68], subject to historic forcing over 1950–2014 and greenhouse gas forcing associated with the 'Shared Socio-economic Pathway' of SSP5-8.5 over 2015–2050. While pessimistic, the SSP5-8.5 scenario of a 'Fossil-fuelled Development' pathway is the current best match for cumulative emissions over 2005–2020.

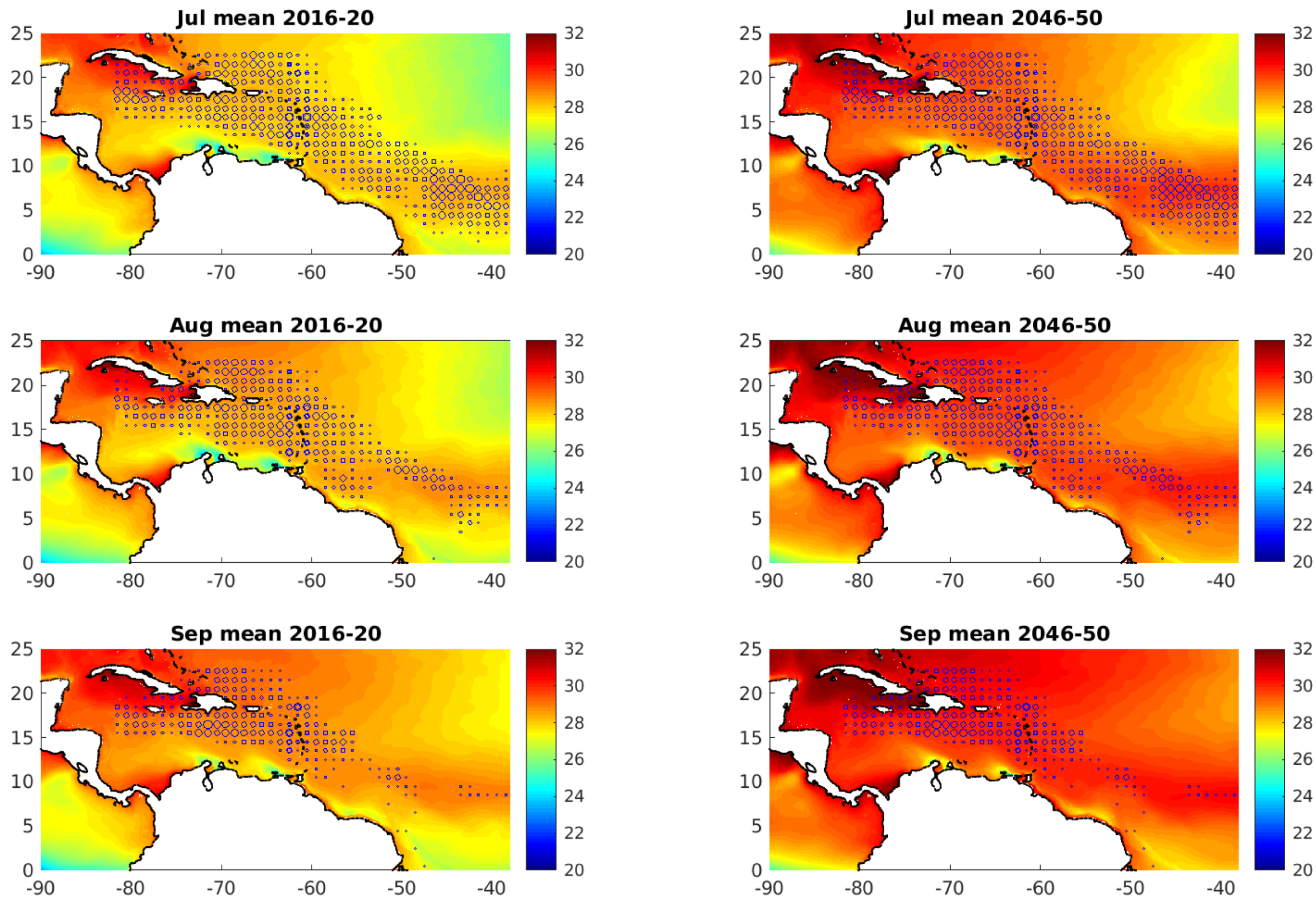

Fig 5. Summer sea surface temperature (SST) averaged over present and future pentads, overlaid with sargassum abundance as observed in 2021. July-September SST (˚C) averaged over 2016–2020 and 2046–2050 across the western tropical Atlantic. Data are extracted from the N512-ORCA12 configuration of the HadGEM3-GC3 climate model [68], subject to SSP5-8.5 forcing over 2015–50. Satellite-detected sargassum for the corresponding months of 2021, for the Central Atlantic, East Caribbean and Jamaica regions of the Satellite-based Sargassum Watch System (maintained by the Optical Oceanography Laboratory at the University of South Florida), is averaged on a 1˚ grid; blue circles are proportional in size to the quantity of sargassum above a threshold (25 units). We use the same temperature range as in Fig 4, emphasising SST above 30˚C that is both detrimental to sargassum growth and increases mortality.

https://doi.org/10.1371/journal.pclm.0000253.g005

In Fig 5, we show SST averaged over the pentads 2016–2020 and 2046–2050 for the months of July, August and September, when sargassum is subject to highest temperatures that may substantially influence growth and mortality rates. Superimposed on these temperature fields are typical Floating Algae density fields (here for 2021), emphasising the coincidence of the GASB with relatively high SST in summer. Over much of the region, SST increases over 2015–2050 are around 1.5˚C. Specific to the GASB, SST increases from around 28–29˚C to 30–31˚C over these months. Given the latest evidence for temperature-sensitive growth rates for sargassum from the tropical Atlantic, specifically significant declines in growth rate above 28˚C [62,63], this may be of consequence for sustaining the sargassum population.

Similar warming trends are evident in other climate projections. In the most recent report of Working Group 1 of the IPCC [69], decadal trends of annual-mean SST over 2005–2050 are averaged across the CMIP6 ensemble of 22 models and across a smaller HighResMIP ensemble of five high-resolution models, all subject to the SSP5-8.5 scenario [69]. These trends compare well with the SST increases in Fig 5. Elsewhere in the tropics, the CMIP6 ensemble shows maximum SST increase in the Atlantic Niño region of around 0.4˚C decade^{-1}, while the

HighResMIP models show stronger equatorial warming of up to 0.5˚C decade^{-1}, with both ensembles projecting minimum warming of 0.15–0.3˚C decade^{-1} in the southeast subtropics. In summary, warming across the wider tropics could limit growth rates and increase mortality rates of sargassum in future decades, more extensively and for most of the season. The basin-scale and annual-timescale consequences of these temperature-induced changes warrant further investigation.

With climate change, there are other possible influences on sargassum. A warming sea surface should reduce mixed layer depth, strengthen stratification, and inhibit the vertical mixing of nutrients (upwards) and sargassum (downwards). More extreme rainfall events in a warmer climate may increase runoff and associated nutrient fluxes. Systematic changes in wind stress may alter the long-range seasonal drift of sargassum. Trends in these variables are less pronounced in the analysed climate simulation [68], suggesting that SST may be a key variable in determination of ongoing change in sargassum biomass, although future changes in biogeochemical cycles may yet prove dominant.

Based on what is currently known about sargassum growth and mortality rates in response to temperature alone, and projected ocean warming in the tropical Atlantic under SSP5-8.5 forcing, sargassum by 2050 might be expected to:

- survive, grow and proliferate further poleward, increasing Sargasso Sea populations;
- change the relative species morphotype composition of populations, given their different growth responses to changes in temperature (62–64);
- arrive earlier in the year from equatorial source regions;
- potentially die off during the hottest months, across the extent of the GASB;
- persist later into the autumn, where surviving summer heat.

As already emphasised, we stress that these hypothesised changes are further subject to highly uncertain nutrient levels that are important in sustaining growth in oligotrophic ocean areas.

Sargassum and carbon

Several reports have suggested that macroalgae play a significant role in marine carbon sequestration [70,71], and that seaweed offsetting could mitigate carbon emissions attributed to global aquaculture. Full carbon neutrality of the global aquaculture sector would require a substantial (and unrealistic) increase of the current area farmed for seaweed from 1.9 x 10^3 km^2 to 7.3 x 10^6 km^2, an estimated 15% of ocean area suitable for coastal seaweed farming [72]. In line with this, it has been advocated for macroalgae to be included into blue carbon assessments [73,74]. However, a divergent opinion has emerged, suggesting that seaweed ecosystems may not be significant sequesters of global carbon, as previously thought [75]. Furthermore though, the role of seaweeds for climate change adaptation and mitigation strategies is not limited to carbon capture and sequestration. As widely described [76–78], macroalgae can contribute to several of the United Nations Sustainable Development Goals. Seaweed-based regenerative ocean farming can efficiently restore marine ecosystems. Seaweeds also represent an interesting source of energy and renewable compounds for many industries to alleviate dependence on petroleum-based refining and to develop alternative supply and value chains.

In this context of marine climate change action, [79] used machine learning algorithms to model the distribution and biomass of floating (pelagic) Atlantic sargassum, with an estimated carbon stock of 7.52 Pg C. In a global coastal context, this estimate is comparable to those for salt marshes (10.36 Pg C), mangroves (6.2 Pg C) and seagrasses (8.5 Pg C) [79]. Compared to annual emissions for 2020 of 9.5 ± 0.5 Gt C (these units being equivalently Pg C) and a decadal (2011–2020) average ocean carbon sink of 2.8 ± 0.4 Gt C year^{-1} [80], annual sinking (export) of even modest fraction of this estimated biomass of floating sargassum would substantially contribute to the oceanic sink. Correcting this estimate, [81] use an alternative stepwise approach and refined treatment of satellite data to find that the carbon stock of floating sargassum across the Atlantic is unlikely to exceed 3.61 x 10^{-3} Pg C, and that carbon fixation cannot exceed 6.0 million tons C month^{-1}, $< 0.2\%$ of carbon fixation by phytoplankton in the region; the carbon stock estimate of [81] is noted to be 2000 times lower than predicted by [79]. While pelagic sargassum was found to play a key role in the cycling and sequestration of carbon at a local scale in the GASB, [81] emphasize the importance of relative areas at basin scale for understanding the wide disagreement; when aggregated together, sargassum covers at most 18,000 km^2 of the surface ocean, while phytoplankton (and associated carbon stock) is ubiquitous across an Atlantic area of ~100 million km^2. Notwithstanding the apparent uncertainty in this carbon stock, [82] developed a strategy to collect and sink pelagic sargassum that could help the Caribbean by establishing a negative emissions industry that builds resilience against blooming pelagic sargassum.

Several other directions for valorisation of bulk and processed biomass of bloom-forming pelagic sargassum have been investigated [83] and a comprehensive overview is given in [84]. Despite the wide potential of the pelagic sargassum biomass for re-uses, many constraints and challenges are faced by researchers, entrepreneurs, and established businesses [85,86]. Nevertheless, and in line with counteracting effects of climate change, the use of pelagic sargassum for the restoration of mangroves in Jamaica has been investigated [22], considering the key roles of mangrove ecosystems in carbon sequestration and in providing important ecosystem services, including shoreline protection during storms. Sargassum has also been tested for production of bioenergy through anaerobic digestion with food waste to produce biogas, and with rum distillery waste to produce transportation fuel [87]. Moreover, [87] opined that sargassum biofuel could contribute significantly to the national objective of Barbados becoming fossil fuel free by 2030. These projections, coupled with the anaerobic digestion by-product used as fertilisers in Barbados, could have significant positive impact in one of the countries most affected by pelagic sargassum events [88,89].

In summary, collective approaches to adaptation and mitigation are informed by the natural and anthropogenic drivers of sargassum. Considering the GASB as a natural analogue for the 'ocean afforestation' that has been proposed to offset CO_2 emissions, various physical and biogeochemical feedbacks (changes in ocean albedo, nutrient reallocation, associated calcification) may offset any carbon sequestration, substantially reducing any intended CO_2 removal [90]. From a holistic perspective, the scientific and ethical basis for sinking sargassum to sequester carbon is currently very limited [91], while rising ocean temperatures may accelerate decomposition of sargassum and release CO_2, as recently established for the kelp in extratropical coastal waters [92]. Conversely, with increased temperature and mortality rates, dying sargassum may sink fast and without decomposition; in this scenario, sargassum may effectively sequester carbon in deep ocean sediments.

Conclusion

The emergence of the Great Atlantic Sargassum Belt (GASB) in the tropical Atlantic parallels increasing incidences of macroalgae blooms that have inundated shorelines worldwide in recent years [93–98], alongside the increasing prevalence of harmful microalgae blooms that may be attributed to climate change [99]. The impacts of pelagic sargassum are, however, particularly widespread, persistent, and severe. Effects are particularly consequential for low-income households, such as in the Western Region Ghana, where fishing activities are disrupted [100–102]; with a limited evidence base for regional drivers of sargassum, this has raised tensions with oil companies [103]. Wealthier countries are better prepared to allocate management costs, with the Mexican government spending around USD 17 million in the removal of 522,226 tons of sargassum in just one year [9]. Advanced uses of sargassum are also difficult to replicate in poorer communities, where simpler valorisation options may be more sustainable [15].

These socio-economic perspectives and contexts serve to emphasize the importance of better understanding the underlying natural processes and likely future trajectory for the GASB. Four key points specifically align the emergence and evolution of sargassum with ongoing climate change:

- Establishing links between sargassum and climate must rely on sufficiently extensive, frequent, and quantitative monitoring across a wide range of scales in time and space, with opportunities to *better link basin-scale satellite surveillance with nearshore and in situ monitoring at selected locations*.
- Proposed physical and biogeochemical drivers suggest that sargassum movement and dispersal may be attributed to large-scale and long-term environmental and climatic changes, specifically *that sargassum is growing more vigorously in warm tropical waters*, *subject to favourable nutrient levels and modes of natural variability across the tropical Atlantic*.
- Sargassum prevalence over coming decades is highly uncertain, although *anticipated levels of tropical warming may prove detrimental to variants that are currently prevalent in the region during hottest months*, *while favouring an extended season and some poleward expansion beyond affected coastlines*, with a major caveat regarding future biogeochemical change.
- Sargassum could potentially deliver blue carbon mitigation benefits that could increase income for states affected by the GASB, and their influence within international climate change negotiations, although *the utility of sargassum as a carbon sink now and into the future is highly uncertain*.

In an overarching conclusion, we identify considerable scope for further research to better monitor, understand and predict sargassum, and this should be aligned with capacity building throughout maritime nations across the tropical Atlantic.

Acknowledgments

We acknowledge the ground survey teams in Barbados, from the Centre for Resource Management and Environmental Studies (CERMES). Core team members include Joseph Weekes and Micaela Small. Further significant contributions to data collection in 2020, 2021 and 2022 are attributed to Kim Baldwin, Kristie Alleyne, Makeda Corbin, Dale Benskin, Mia Clarke, Amina Desai, Annabel Cox, Carla Daniel, and Chad Barrow. The 127 locations identified in Fig 2A to evaluate beaching sargassum were originally selected by Finian Moore, as part of a final year undergraduate project at the University of Southampton. We thank three anonymous reviewers for a range of insightful comments that helped us to substantially improve the manuscript on revision.

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