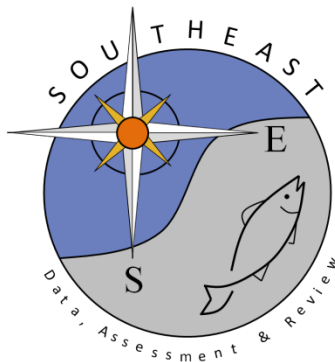


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MARINE ECOLOGY

The great Atlantic *Sargassum* belt

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Pelagic *Sargassum* is abundant in the Sargasso Sea, but a recurrent great Atlantic *Sargassum* belt (GASB) has been observed in satellite imagery since 2011, often extending from West Africa to the Gulf of Mexico. In June 2018, the 8850-kilometer GASB contained >20 million metric tons of *Sargassum* biomass. The spatial distribution of the GASB is mostly driven by ocean circulation. The bloom of 2011 might be a result of Amazon River discharge in previous years, but recent increases and interannual variability after 2011 appear to be driven by upwelling off West Africa during boreal winter and by Amazon River discharge during spring and summer, indicating a possible regime shift and raising the possibility that recurrent blooms in the tropical Atlantic and Caribbean Sea may become the new norm.

The Sargasso Sea is named after the floating mats of *Sargassum* seaweed, first reported by Christopher Columbus in the 15th century. These seaweed attract fish, shrimp, crabs, birds, and turtles (1–3), providing essential habitats and serving as hotspots for biodiversity and productivity. Two species of *Sargassum*, *S. fluitans* and *S. natans*, are the most abundant in the Sargasso Sea and the Gulf of Mexico (1, 4), which are notably connected by ocean currents.

Large quantities of *Sargassum* have recently been reported in the central Atlantic Ocean and the Caribbean Sea (5–14), accompanied by frequent beaching events that have caused serious environmental, ecological, and economic problems (15, 16). Numerous workshops have been held to develop strategies to respond to *Sargassum* inundations (17, 18). A critical question is whether a regime shift in the atmospheric and/or oceanic climatic conditions has led to the recent changes. Several hypotheses have been proposed concerning the relative roles of warming temperatures, climate change, and nutrient enrichment (19–23), but the lack of large-scale *Sargassum* data has prevented investigators from reaching a solid conclusion.

We attempt to address this question using long-term satellite data, numerical models, and field measurements. The 19-year record of observations from the Moderate Resolution Imaging Spectroradiometer (MODIS) satellite instrument reveals a recent, recurrent *Sargassum* belt extending across the Intra-Americas Sea and the tropical Atlantic (Fig. 1). The environmental and field data, along with numerical models, help us to understand the formation of this great Atlantic *Sargassum* belt (GASB), the connectivity between different regions, as well as the mechanisms behind the tipping point in 2011 and interannual variations in subsequent years.

The entire monthly sequence of *Sargassum* abundance distributions (movie S1) shows that from 2000 to 2010, the central Atlantic showed very low abundance (5, 6, 12, 13), with occasional small quantities near the Amazon River mouth from August to November. The first massive *Sargassum* bloom in the central Atlantic started in 2011 (6), and in later years the bloom developed to a GASB extending from West Africa to the Caribbean Sea and into the Gulf of Mexico (Fig. 1 and movie S1).

The GASB formed in the summer months (Northern Hemisphere in this paper) of 2011–2018 except in 2013 (Fig. 1C). In 2015 and 2018, the GASB showed the highest coverage, extending >8850 km and carrying a wet biomass of >9 million tons (>20 million tons in June 2018) (24). Once reaching the Gulf of Mexico, the belt followed the Loop Current and Gulf Stream to enter the North Atlantic Ocean. Some *Sargassum* were transported directly into the North Atlantic from the central west Atlantic following the Antilles Current (Fig. 1C).

Although multiple sources of *Sargassum* may exist, the shape of the GASB is consistent with advection by the ocean circulation patterns in the tropical Atlantic. Through particle-tracking numerical experiments that account for both physical transport and biological growth, the July GASB patterns were well reproduced by forward tracking of simulated *Sargassum* particles for 6 months (fig. S1). This holds true even when a uniform particle distribution is used to initialize the model, although a more realistic initialization using MODIS observations led to improved model performance in reproducing the GASB patterns in July (25, 26) (fig. S1, A and B). Furthermore, after accounting for biological factors under various scenarios, *Sargassum* density in the tropics could be captured even more accurately (fig. S1).

In both July and January, most of the simulated *Sargassum* particles in the central Atlantic are traced back to the same region, with a very weak connection to West Africa and almost no connection to the North Atlantic or Caribbean Sea (fig. S2) (25). This suggests that the major blooms in the central Atlantic likely developed

locally rather than from seed populations in the Sargasso Sea. The weak connection between West Africa and the central Atlantic (fig. S2B) indicates that some *Sargassum* may enter the central Atlantic from West Africa and bloom there. These observations match well with previous modeling work emphasizing the role of North Equatorial Recirculation Region (NERR) as a potential source region (19–21, 27) and other modeling efforts on the regional connections (28, 29). Field measurements of species compositions (30) also suggest that the Sargasso Sea is unlikely to be the main source of the blooms in the central Atlantic.

It is natural to ask, then, what conditions in the central Atlantic triggered the first *Sargassum* bloom in 2011? Small amounts of *Sargassum* existed in the central Atlantic in previous years (movie S1), representing the seed populations. In 2009, higher-than-usual nutrients from the Amazon River discharge (31) (Fig. 2B and figs. S3A and S4C), as well as from upwelling in the eastern Atlantic (Fig. 2D, fig. S4D, and table S2), could stimulate *Sargassum* growth (32, 33), allowing massive blooms to occur. A related question is, why did a massive bloom not occur in 2010? We suggest that this was due to higher-than-usual sea surface temperatures (hereafter, SSTs) in 2010 (Fig. 2D), which, according to laboratory experiments (34) (fig. S5) and our analyses of satellite-derived *Sargassum* change rates (26), would suppress *Sargassum* growth. In 2011, the SSTs were more suitable for *Sargassum* growth and the recycled nutrients from previous years and new nutrients from the current year would have created the correct conditions to initiate a massive bloom. Also, the low salinity induced by a large freshwater input from 2009 and 2010 would likely hinder *Sargassum* growth (34). A reasonable scenario of the 2011 bloom is therefore that nutrient accumulations from 2009 due to stronger upwelling in the eastern Atlantic and excessive Amazon River discharge in the western Atlantic provided the initial conditions, whereas high temperature and low salinity in 2010 delayed the bloom until 2011.

After 2011, the *Sargassum* abundance in the central Atlantic showed similar seasonality as in the Gulf of Mexico, with increased abundance from January to June and decreased abundance from July to December (Fig. 3B and fig. S6). Considering the weak seasonality in insolation in the tropics, this seasonality might be the result of an innate biological clock (circannual rhythm), as exists in other brown seaweeds (35), combined with the seasonal nutrient supply (26). Such a mechanism is discussed further in the supplementary materials.

In 2012, a *Sargassum* bloom first developed in spring and summer, but decreased rapidly from August to December. The earlier growth could have been a result of higher nutrient supply from upwelling processes and lower SSTs in the central east Atlantic from winter 2011 to spring 2012, whereas the rapid decrease after August could have been due to the overall lower nutrient supply from the Amazon River during 2010–2011 and the relatively higher SSTs after late summer. By January 2013, most *Sargassum* disappeared

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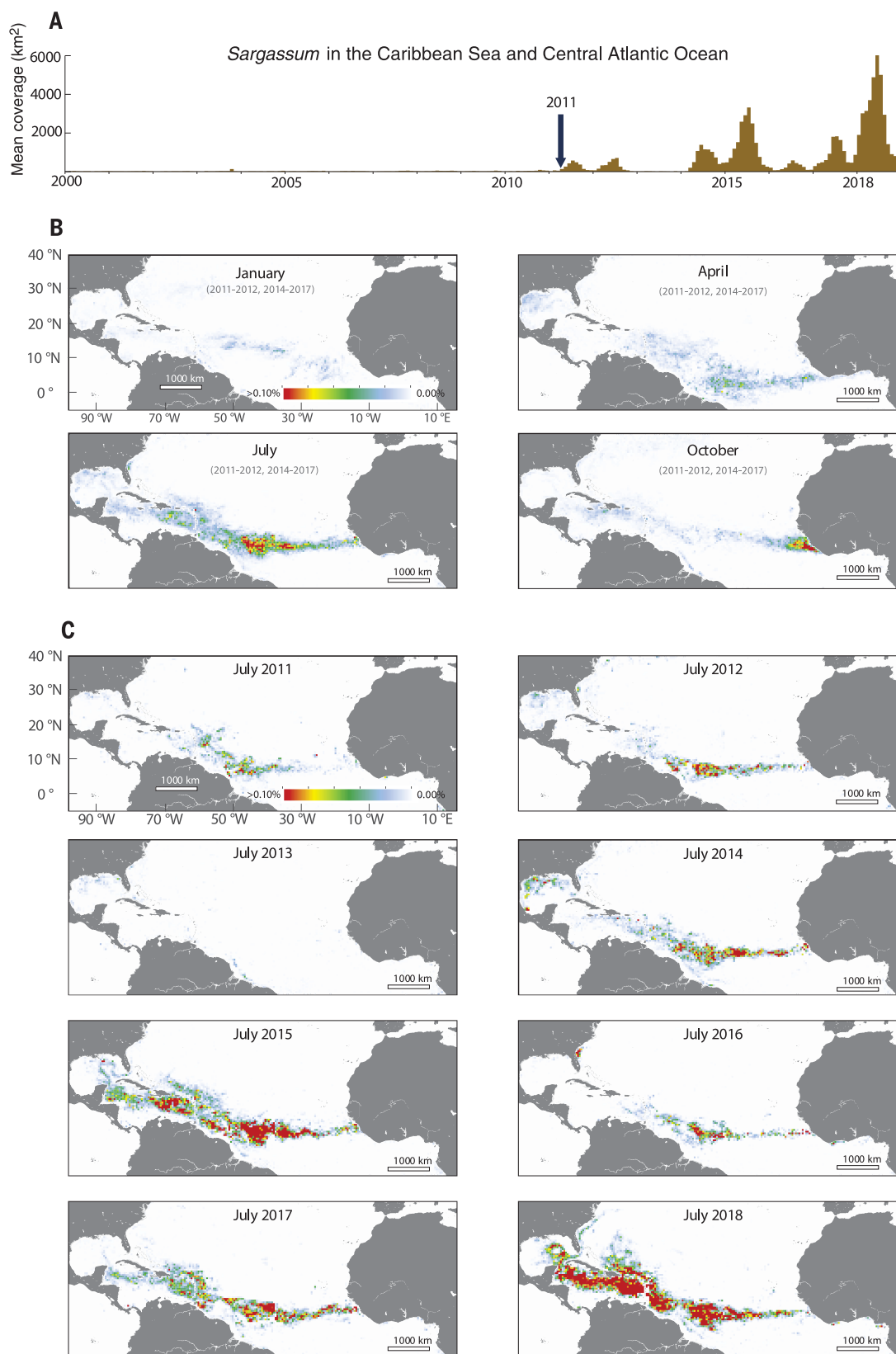


Fig. 1. *Sargassum* distributions in the Gulf of Mexico and the Atlantic Ocean. (A) Monthly mean *Sargassum* areal coverage in the Caribbean Sea and the central Atlantic Ocean, with a maximum of ~ 6000 km² or >20 million tons in June 2018. The year mark starts from January. (B) Monthly mean *Sargassum* density (% cover) in January, April, July, and October of 2011–2017 after excluding the nonbloom year of 2013. (C) Monthly mean *Sargassum* density for the month of July from 2011 to 2018. The GASB is observed in all years except 2013.

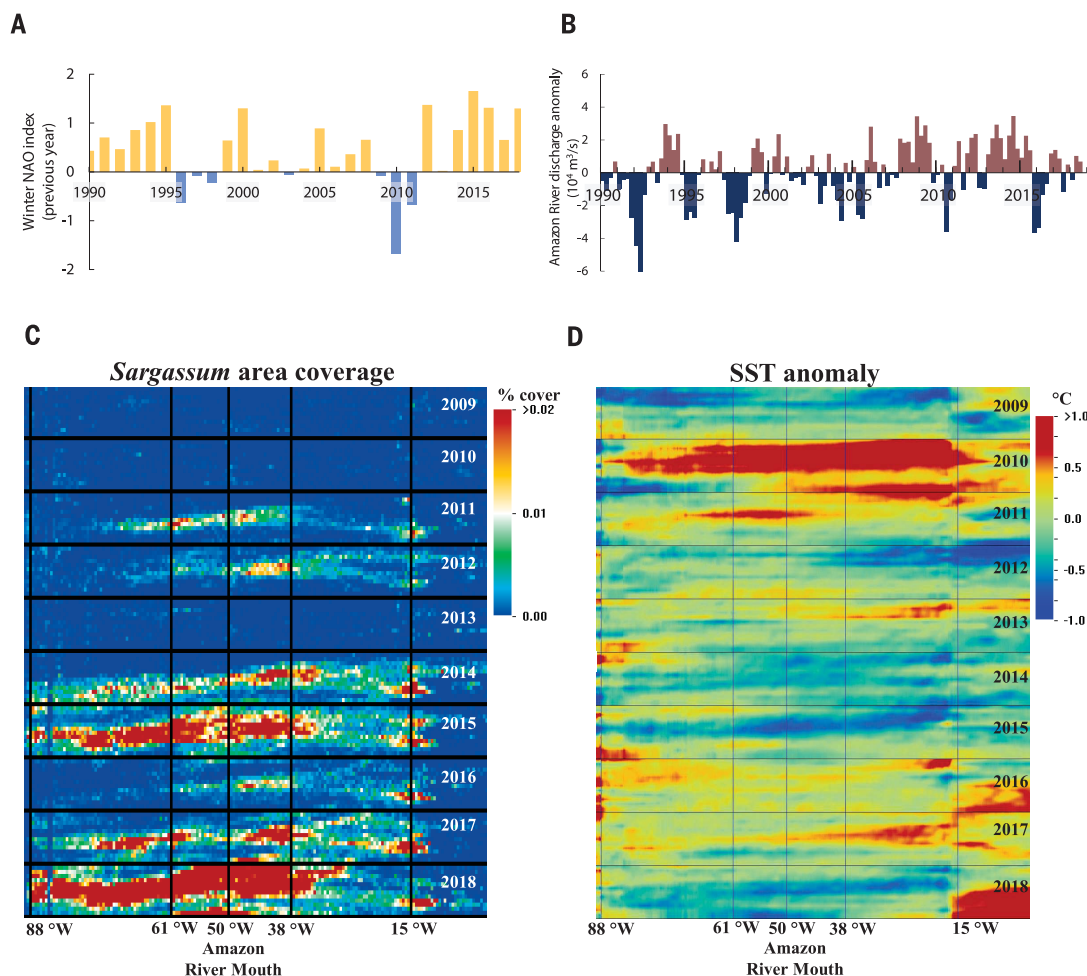


Fig. 2. Environmental conditions and climate indices used to explain interannual changes of GASB. (A) Mean NAO index averaged from December to February (winter NAO) for 1990–2018. (B) Seasonal mean discharge anomaly of the Amazon River from 1990 to 2018 measured at the Obidos station. (C) Latitude-averaged (from 5°S to 23°N) *Sargassum* monthly areal coverage density from 2009 to 2018. (D) Latitude-averaged monthly mean SST anomaly from 2009 to 2018. In (C) and (D), the vertical lines mark the locations of 88°W, 61°W, 50°W, 38°W, and 15°W, representing the Yucatan peninsula coast, Barbados coast, the Amazon River mouth, the middle of the central Atlantic, and the West Africa coast, respectively.

across the central Atlantic (movie S1). The reduced seed populations from 2012, higher SSTs in the growth phase, and limited nutrients together appeared to lead to a nonbloom year in 2013 (table S2 and movie S1).

In 2014, *Sargassum* grew rapidly during spring and summer. Unlike 2011, the first *Sargassum* aggregation was identified in early January in the central east Atlantic. This rapid growth can likely be attributed to the nutrient enrichment from the West Africa upwelling from winter 2013 to spring 2014 (table S2). The bloom continued to develop when reaching the central west Atlantic, where the *Sargassum* was nourished by high riverine nutrients accumulated in 2013–2014 (table S2 and Fig. 2B). The favorable growth conditions (higher nutrients and lower SSTs) in the central east Atlantic and central west Atlantic would also have sustained the winter bloom, providing higher-than-usual seed populations to initiate the massive bloom in 2015 (table S2).

In 2015, although the initial *Sargassum* growth rate was not as high as that in 2014, the seed

population was much larger than it was in previous years. This, along with higher nutrients from the central east Atlantic in spring and early summer as well as from the Amazon River from 2014 to 2015, led to a massive *Sargassum* bloom in 2015 (table S2). The higher concentrations of *Sargassum* required more nutrients to sustain, which would also explain the lower change rate in spring 2015 (Fig. 3, A and B). From fall to winter, *Sargassum* decreased faster than in 2014 under comparatively warmer waters and reduced nutrients (table S2). This significant decrease continued until February 2016.

In 2016, only a small amount of *Sargassum* survived from 2015 and it was located in the central east Atlantic. The early growth was limited by the lower nutrient supply from West African upwelling from winter 2015 to spring 2016 (table S2). When the *Sargassum* was transported eastward to the central east Atlantic after December 2016, however, it grew faster because of local nutrient enrichments (table S2), providing seed populations for the 2017 bloom.

In 2017, the bloom generally developed faster than in 2016 possibly as a result of higher nutrient supplies from the Amazon River and the West Africa upwelling since winter 2016 (table S2). During winter 2017, the *Sargassum* change rate was much higher than it was in 2016, which would also have benefited from the lower SSTs and the higher availability of nutrients. The large amount of *Sargassum* that developed in the winter months helped to form the bloom in 2018.

Overall, the recent bloom events show connections to nutrient enrichment and climatic variations. Higher wintertime North Atlantic Oscillation (NAO) values in the bloom years correlated well with lower SSTs and stronger upwelling (Fig. 2) (36, 37). Evidence for nutrient enrichment is also found in the *Sargassum* nutrient compositions. Specifically, the N:P ratios of the recent neritic samples show an increasingly P-limited growth compared with the historical baselines, which would be a result of long-term nutrient enrichment, especially N enrichment, in recent years (24). Other evidence to support recent nutrient

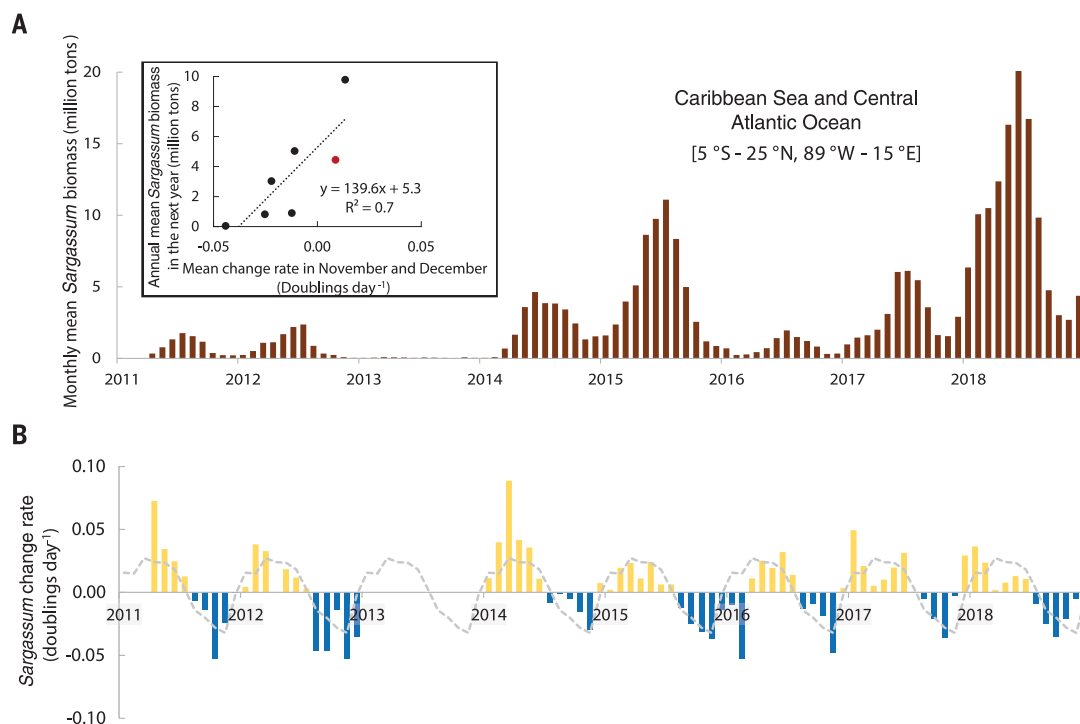


Fig. 3. *Sargassum* biomass and change rate from April 2011 to December 2018. (A) Monthly mean *Sargassum* biomass in the Caribbean Sea and central Atlantic. These estimates represent lower bounds because satellite measurements are insensitive to *Sargassum* accumulations in the vertical direction. The inset shows the correlation between the mean change rate in November and December (derived from the mean biomass change from October to December) with the annual mean *Sargassum* biomass in the next year. The red dot marks the data from 2019 (biomass averaged between January and April 2019). **(B)** *Sargassum* monthly change rate since 2011. The gray dashed line marks the climatological change rate between 2011 and 2018 except for 2013.

enrichment in the central west Atlantic comes from increased deforestation and fertilizer use in Brazil and increased water-column nitrogen from 2010 to 2018 (fig. S4).

The interannual changes in *Sargassum* blooms could be accounted for by changes in seed populations and oceanographic conditions, but a critical question remains: Can we predict future blooms based on these hindcast analyses? The following conditions appear to be associated with massive *Sargassum* blooms at magnitudes comparable to those in 2015 and 2018: (i) large seed populations during winter as a result of the previous year's bloom; (ii) higher nutrient supply from the West Africa upwelling in winter months, which can be inferred from higher chlorophyll levels and lower SSTs in satellite imagery; and (iii) higher nutrient supply from the Amazon River input but normal or lower SSTs during the current year. If these conditions are met, then a massive bloom is likely to occur in the central Atlantic, followed by severe beaching events in the Caribbean Sea in later months. Furthermore, during November to December, the *Sargassum* change rates showed negative correlations with SSTs (fig. S7, A and B), suggesting that the former might serve as an indicator for possible blooms in the following year (Fig. 3A, inset), with a lead time of at least 3 to 4 months.

Finally, we recognize that there are active discussions within the research community on

the mechanisms driving the recent trends of *Sargassum* blooms. The explanation presented here is based on the physical connectivity across several regions, on the analysis of several environmental factors, on limited field studies, and on the satellite-based *Sargassum* observations. These modeling and observationally based analyses, although reasonable to the best of our knowledge, still require validation in the future and admittedly may not rule out other explanations. Conversely, the recurrent GASB clearly shows a regime shift after 2011 in bloom patterns and possibly in oceanographic conditions as well. A critical question is whether we have reached the point where recurrent GASB and beaching events may become the new norm. Under continued nutrient enrichment due to deforestation and fertilizer use in agriculture (fig. S4), along with the substantial mass of *Sargassum* seed populations lingering in the tropics (movie S1), the answer is likely positive, and more recent satellite observations between January and April 2019 also support this interpretation. However, the considerable *Sargassum* accumulations along the pathway of the GASB underline the need for multidisciplinary research to better understand their ecological and biogeochemical impacts (24, 38), as well as their impacts on coastal environments, tourism, economies, and human health (39), especially if the role of *Sargassum* changes from

that of an essential habitat to that of a severe and perpetual nuisance.

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SUPPLEMENTARY MATERIALS

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Materials and Methods
Supplementary Text
Figs. S1 to S7
Tables S1 and S2
References (40–50)
Movie S1

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The biggest bloom

Floating mats of *Sargassum* seaweed in the center of the North Atlantic were first reported by Christopher Columbus in the 15th century. These mats, although abundant, have until recently been limited and discontinuous. However, Wang *et al.* report that, since 2011, the mats have increased in density and aerial extent to generate a 8850-kilometer-long belt that extends from West Africa to the Caribbean Sea and Gulf of Mexico (see the Perspective by Gower and King). This represents the world's largest macroalgal bloom. Such recurrent blooms may become the new normal.

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