



Simulating transport pathways of pelagic *Sargassum* from the Equatorial Atlantic into the Caribbean Sea

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ABSTRACT

Since 2011, beach inundation of massive amounts of pelagic *Sargassum* algae has occurred around the Caribbean nations and islands. Previous studies have applied satellite ocean color to determine the origins of this phenomenon. These techniques, combined with complementary approaches, suggest that, rather than blooms originating in the Caribbean, they arrive from the Equatorial Atlantic. However, oceanographic context for these occurrences remains limited. Here, we present results from synthetic particle tracking experiments that characterize the interannual and seasonal dynamics of ocean currents and winds likely to influence the transport of *Sargassum* from the Equatorial Atlantic into the Caribbean Sea. Our findings suggest that *Sargassum* present in the western Equatorial Atlantic (west of longitude 50°W) has a high probability of entering the Caribbean Sea within a year's time. Transport routes include the Guiana Current, North Brazil Current Rings, and the North Equatorial Current north of the North Brazil Current Retroflexion. The amount of *Sargassum* following each route varies seasonally. This has important implications for the amount of time it takes *Sargassum* to reach the Caribbean Sea. By weighting particle transport predictions with *Sargassum* concentrations at release sites in the western Equatorial Atlantic, our simulations explain close to 90% of the annual variation in observed *Sargassum* abundance entering the Caribbean Sea. Additionally, results from our numerical experiments are in good agreement with observations of variability in the timing of *Sargassum* movement from the Equatorial Atlantic to the Caribbean, and observations of the spatial extent of *Sargassum* occurrence throughout the Caribbean. However, this work also highlights some areas of uncertainty that should be examined, in particular the effect of “windage” and other surface transport processes on the movement of *Sargassum*. Our results provide a useful launching point to predict *Sargassum* beaching events along the Caribbean islands well in advance of their occurrence and, more generally, to understand the movement ecology of a floating ecosystem that is essential habitat to numerous marine species.

1. Introduction

Pelagic *Sargassum* spp. aggregates to form “Lagrangian ecosystems” that drift across the ocean surface. *Sargassum* provides important habitat for a diversity of invertebrates, fishes, turtles, and birds (Coston-Clements et al., 1991; Wells and Rooker, 2004; Witherington et al., 2012). However, when large accumulations of *Sargassum* enter coastal waters it may also act as marine debris, disrupting ship traffic, fishing, and tourism, which negatively impacts the economies of coastal communities. Major and unexpected accumulation of *Sargassum* occurred

near and along the islands of the eastern Caribbean starting in 2011 and continued through December of that year (Gower et al., 2013; Hu et al., 2016). A similar event occurred in 2012 (Marechal et al., 2017), followed by even greater *Sargassum* inundation events throughout the Caribbean in 2014 through 2015 (Hu et al., 2016; Wang and Hu, 2016, 2017). These anomalous events caused widespread negative impacts to the fishing and tourism economies throughout the region. These events have been the subject of considerable scientific investigation using remote-sensing observations from satellite (Gower et al., 2013; Hu et al., 2016; Wang and Hu, 2016, 2017) and morphological and genetic

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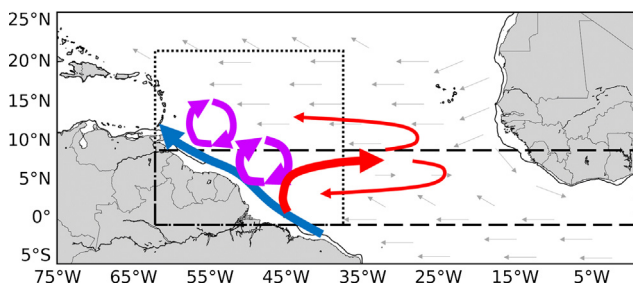


Fig. 1. Schematic of general surface circulation relevant to the transport of pelagic *Sargassum* from the Equatorial Atlantic into the Caribbean Sea. Grey arrows show typical surface current directions across the region, colored arrows represent the ocean circulation patterns of the North Brazil Current System (Lumpkin and Garzoli 2005). The blue arrow depicts the North Brazil/Guiana Current, the purple arrows show North Brazil Current Rings (which translate northward toward the Caribbean on the order of several times per year), the thick red arrow represents the North Brazil Current Retroflexion, and the thin red arrows indicate the potential westward return via the North and South Equatorial Currents (Kelly et al., 2000). The dashed lines indicate the Equatorial Atlantic (0–10°N) where extensive and anomalous *Sargassum* was detected by satellite from April through September 2011 (Gower et al., 2013). Ocean currents in this region are hypothesized to play an important role in the beaching events that occurred in the Caribbean that same year (Franks et al., 2016). The dotted lines represent the area of ocean where long-term, monthly measurements of *Sargassum* coverage have been obtained (2000–2015) (Wang and Hu 2016). (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

characterization of the *Sargassum* present (Schell et al., 2015; Amaral-Zettler et al., 2017). Satellite-based observations of large ($> 4000 \text{ m}^2$) *Sargassum* mats in the Equatorial Atlantic appear to coincide with the timing of inundation events (Gower et al., 2013; Hu et al., 2016; Wang and Hu 2016; 2017), from which a statistics-based prediction can be made on *Sargassum* blooms in the eastern Caribbean (Wang and Hu, 2017).

However, oceanographic context for the movement of *Sargassum* into the Caribbean Sea has received limited attention (Franks et al., 2016). Transport pathways between the Equatorial Atlantic and the Caribbean Sea are well-described, and the North Brazil Current System appears to play an important role (Kelly et al., 2000; Lumpkin and Garzoli, 2005; Johns et al., 2014). There are three main surface dynamical oceanographic features whereby *Sargassum* travel from the Equatorial Atlantic into the Caribbean Sea: (1) along the continental shelf break of South America via the Guiana Current, (2) across the deep ocean translated via North Brazil Current Rings, and (3) initially moving eastward with the North Brazil Current Retroflexion before being swept westward by the North Equatorial Current (Johns et al., 2014) (Fig. 1). With increased understanding of how these advection processes influence the distribution of *Sargassum*, it may be possible to better assess and predict the occurrence and timing of *Sargassum* accumulation in the Caribbean Sea, an important first step to assessing the potential for beaching (Marechal et al., 2017) as *Sargassum* abundance in the Caribbean appears to be directly related to beaching events (Wang and Hu, 2017).

Here, we present results from a series of numerical experiments examining surface transport pathways into the Caribbean Sea from the Equatorial Atlantic. We first assess spatial, seasonal, and annual variability in surface transport from the Equatorial Atlantic into the Caribbean Sea with synthetic particle tracking simulations using the Global Hybrid Coordinate Ocean Model surface currents (HYCOM) (Chassignet et al., 2007) and National Centers for Environmental Prediction Reanalysis (NCEP) winds (Kalnay et al., 1996; Kanamitsu et al., 2002) for the years 2000–2015. We explore the statistical relationships between surface currents and *Sargassum* coverage in the western Equatorial Atlantic and the occurrence of *Sargassum* in the eastern

Caribbean Sea. We then develop a simple mechanistic model to predict annual *Sargassum* coverage in the eastern Caribbean Sea by pairing particle transport predictions with remotely-sensed satellite data on *Sargassum* in the western Equatorial Atlantic. Finally, we assess the relative contributions of three main surface routes to the movement of *Sargassum* from the Equatorial Atlantic into the Caribbean Sea to provide recommendations for what aspects of ocean circulation could be monitored to serve as a potential tool to provide seasonal warnings to coastal communities that may be negatively affected by future *Sargassum* accumulation events.

2. Methods

To simulate *Sargassum* transport we used output from Global HYCOM for ocean current data and output from the NCEP Reanalysis for wind data. Global HYCOM hindcasts are daily snapshots of ocean velocity at a spatial resolution of 0.08° . HYCOM is an eddy-resolving model that assimilates in situ and satellite observations to depict oceanic conditions that occurred at specific times in the past. The NCEP Reanalysis provides a historical depiction of global atmospheric conditions, including daily averaged surface wind velocity at a spatial resolution of 2.5° . For HYCOM ocean velocities (surface layer) and NCEP winds (10 m above sea level) we extracted daily output for 2000–2015. HYCOM outputs were obtained from the Global Reanalysis (expt. 19.1) for years 2000–2012 and from the Global Analysis (expts. 90.9, 91.0, and 91.1) for years 2013–2015.

Global HYCOM performs reasonably well at portraying the main ocean circulation features, such as fronts, filaments and mesoscale eddies, which are relevant to the transport of marine organisms (Chassignet et al., 2007; Putman and He 2013). Other physical processes occurring at the ocean surface may also play an important role in organismal movement, but are not accounted for in HYCOM (Putman et al., 2016). Such processes include direct forcing of near-surface currents by winds (e.g., the top of the Ekman surface spiral, described more precisely as Stommel shear (Rio et al., 2014; Bonjean and Lagerloef 2002)), direct momentum transfer to floating material from the wind (i.e., windage (Trinanes et al., 2016)) and residual transport due to waves (i.e., Stokes drift (Monismith and Fong 2004)). The influence of these processes on the trajectory of an object is dependent upon its shape, profile, buoyancy, etc. At present, such factors are not well-described for pelagic *Sargassum*. For instance, *Sargassum*'s buoyancy likely changes with time (age), the amount of biofouling, and ocean conditions (Johnson and Richardson 1977; Woodcock 1993; Zhong et al., 2012). Buoyancy can change the surface expression of *Sargassum* and thus the cross-sectional area it presents to surface winds; this in turn may change the drag coefficient appropriate to estimating momentum transfer from those winds.

As a first approximation to explore the sensitivity of transport predictions to such effects, we performed simulations using the Global HYCOM surface velocity and a simple “windage” factor of 1.0% of the 10 m wind speeds from the NCEP reanalysis that was applied in the same direction as the wind. This value falls within the range of possible windage factors that might be expected for *Sargassum*, or for a variety of floating objects, perhaps towards the lower end of what is likely (Breivik et al., 2011; Nero et al., 2013; Trinanes et al., 2016). Regardless, we reiterate the value was chosen as a simple test of the sensitivity of Global HYCOM predictions to aspects of particle transport not contained in that model. The NCEP data were interpolated to the 0.08° HYCOM grid to perform simulations that included windage. We used ICHTHYOP v.2 particle tracking software (Lett et al., 2008) to simulate the movement of *Sargassum* in the numerical experiments described below. ICHTHYOP used a Runge-Kutta 4th-order time-stepping method to compute trajectories at 30-minute intervals. Particle trajectories were simulated for up to one year, following the initial analyses of Franks et al. (2016), which suggested strong connectivity between the Equatorial Atlantic and Caribbean Sea on this time-scale.

2.1. Backtracking

To assess which areas in the Caribbean could be impacted by *Sargassum* originating in the Equatorial Atlantic, we released synthetic particles across the Caribbean Sea during the years 2003–2015 and backtracked them for up to one year. For the seasons in which *Sargassum* was reported as first entering the Caribbean during 2011 (Wang and Hu 2017; Franks et al., 2016), 2500 synthetic particles were released at randomly assigned locations at 5-day intervals across the Caribbean Sea, resulting in 30,000 synthetic particles backtracked each spring (April–June or AMJ), summer (July–September or JAS), and autumn (October–December or OND). Particles were then aggregated into $0.5^\circ \times 0.5^\circ$ release zones and the percentage of particles in each zone that were backtracked to the Equatorial Atlantic was computed. We defined backtracked particles that crossed east of 58°W and south of 10°N as having an Equatorial Atlantic origin (Fig. 1).

2.2. Forward tracking

To examine from which areas of the Equatorial Atlantic transport of *Sargassum* into the Caribbean is likely, we released synthetic particles between 0° – 10°N and bounded by the coasts of South America and Africa (Fig. 1). This region has been identified as the most likely source of *Sargassum* in the 2011 event (Gower et al., 2013; Franks et al., 2016). Particles were released at randomly assigned locations at 5-day intervals, 500 particles per release, and forward tracked for one year. This resulted in 9000 synthetic particles tracked during each winter (JFM), spring (AMJ), summer (JAS), and autumn (OND) for the years 2000 through 2014. For analysis, particles were aggregated into $1^\circ \times 1^\circ$ release zones and the percentage of particles in each that entered the Caribbean Sea (i.e., the same area from which synthetic particles were backtracked in the preceding section) within one year was determined.

2.3. Statistical exploration of annual variation in the role of ocean transport on *Sargassum* abundance

We used statistical models to explore the relationships between the results of synthetic forward-tracking experiments (described above) and annual variation in *Sargassum* abundance in the Equatorial Atlantic and the Caribbean Sea. Satellite-based *Sargassum* observations were provided in Wang and Hu (2016) for the region between 0 – 22°N and 63 – 38°W (Figs. 1 and 2). These data are reported as the percentage of *Sargassum* cover across a $0.5^\circ \times 0.5^\circ$ area for each month from 2000 to 2015. We obtained an annual value of *Sargassum* percent coverage (SPC) in the eastern Caribbean Sea (10 – 22°N , 58 – 63°W) and an annual value of SPC in the region where forward-tracking of synthetic particles and SPC data overlap (Equator– 10°N , 60 – 38°W ; Fig. 1). To assess variability in transport, we computed the annual percentage of synthetic particles released from this region of the western Equatorial Atlantic that entered the Caribbean Sea (see above).

We used Spearman correlation (non-parametric) tests (Spearman, 1904) to determine whether the relative annual variation in transport predictions into the Caribbean were related to relative annual variation in SPC values in the eastern Caribbean Sea (e.g., whether years of high transport probability were also years of high SPC values). For comparison, we performed the same tests to examine the relationship between western Equatorial Atlantic SPC values and eastern Caribbean Sea SPC values. Using multiple regression and variance partitioning procedures (Legendre and Legendre, 1998), we calculated the relative contributions ocean transport and western Equatorial Atlantic SPC values for predicting eastern Caribbean SPC values. For these analyses, SPC data were log-transformed.

2.4. A *Sargassum* transport index

We developed a simple mechanistic model of *Sargassum* transport by

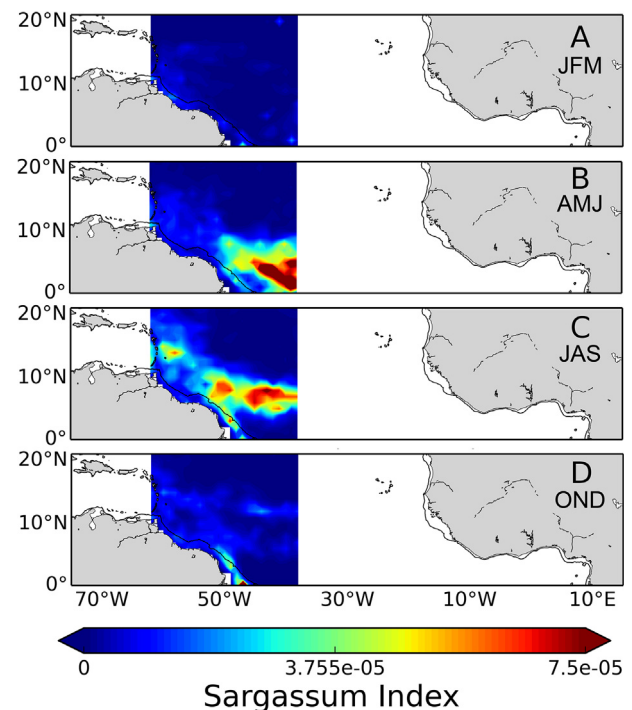


Fig. 2. Panels show the mean of *Sargassum* percent coverage (SPC) at 1-degree grid size for the years 2000–2014 by season (A) January–March, (B) April–June, (C) July–September, (D) October–December. Detections of *Sargassum* in this area were rare prior to 2011, after which such occurrences have become increasingly common. Satellite data east of 38°W is still being analyzed and thus was not available for these models. Data derived from (Wang and Hu 2016).

combining synthetic particle transport predictions from the western Equatorial Atlantic with SPC values across this region. We aggregated the synthetic particles released into $1^\circ \times 1^\circ$ bins for each winter (JFM), spring (AMJ), summer (JAS), and autumn (OND). For each seasonal bin, we multiplied the probability of transport into the Caribbean Sea within one year (derived from synthetic particle tracking experiments) by the seasonally aggregated percent coverage of *Sargassum* for the same period. This allowed us to scale our transport predictions relative to the amount of *Sargassum* present at a given location. Thus, if a $1^\circ \times 1^\circ$ bin was half covered with *Sargassum* ($\text{SPC} = 0.5$) and the probability of transport from that bin to the Caribbean was 10%, the index value associated with that bin would be 0.05. From these data we produced a seasonal index that indicates the amount of *Sargassum* likely to move into the Caribbean Sea from the western Equatorial Atlantic, where forward-tracking and SPC data overlap (Equator– 10°N , 60 – 38°W), which is also the region where the highest concentrations of *Sargassum* tended to initially occur (Figs. 1 and 2). It is important to note that this transport index makes no attempt to account for growth, sinking, grazing, physical aggregation or dispersion of mats, or other processes that may change the amount of *Sargassum* that enters the Caribbean Sea. Our focus is entirely on assessing the role of surface currents and winds on the movement of *Sargassum* between regions.

We assessed whether this *Sargassum* transport index from the western Equatorial Atlantic could predict SPC values in the eastern Caribbean for a given year. We used Spearman correlation (non-parametric) tests (Spearman, 1904) to determine whether the *Sargassum* transport predictions into the Caribbean were related to relative annual variation in SPC values in the eastern Caribbean Sea, i.e., whether years with a high *Sargassum* transport index were also years of high SPC values in the Caribbean or vice versa. Additionally, these data were log-transformed to perform linear regressions to assess what percent of variance in eastern Caribbean SPC values could be explained by the *Sargassum* transport index. Because this mechanistic model explicitly

links oceanic transport and *Sargassum*, variance partitioning analyses would not be meaningful to perform in this instance.

2.5. Oceanographic pathways

A key benefit of the mechanistic model we developed is the ability to assess the oceanographic pathways that *Sargassum* might take to reach the Caribbean Sea from the Equatorial Atlantic. There are three main routes available (Fig. 1): (1) along the continental shelf break of South America via the Guiana Current (Condie, 1991), (2) across the deep ocean translated via North Brazil Current Rings (Goni and Johns, 2001), and (3) initially moving eastward with the North Brazil Current Retroflexion before being swept westward by the North Equatorial Current (Johns et al., 2014). To infer the transport pathways of particles we first determined which particles entered the Caribbean Sea. Of these particles, we then determined the maximum eastward longitude the particle traveled and computed a “straightness index” for each particle (the straight-line distance between the start location and where it first entered the Caribbean Sea divided by the sum of length of 5-day track segments along the particle’s path). The following criteria were chosen after visually inspecting a subset of trajectories to identify values that would be conservative with respect to assigning false positives to each of the three categories. Particles traveling east of longitude 35°W were placed into the “retroflexion” category. Owing to the characteristic “looping” translation motion of objects traveling with rings (Richardson, 2005), particles with relatively low straightness index values are likely to be associated with North Brazil Current Rings whereas particles with high straightness index values are more likely to travel more directly to the Caribbean Sea via the Guiana Current. We assumed particles with a straightness index of less than 0.6 were associated with North Brazil Current Rings and assumed particles with a straightness index of greater than 0.8 traveled with the Guiana Current. Those particles that did not meet these criteria were excluded from the “oceanographic pathways” analysis (mean = 34% of trajectories). We then computed the percentage of particles released within the western Equatorial Atlantic (Equator–10°N, 60–38°W) that followed each of these three routes into the Caribbean Sea for each season, weighted by the seasonal SPC values at the start locations of the particles.

3. Results

3.1. Backtracking

Results obtained here indicate that *Sargassum* present in the eastern Caribbean has a high probability of originating proximately in the Equatorial Atlantic (Fig. 3). Including a 1% windage factor in the computation of trajectories tended to increase the probability of backtracked particles originating from the Equatorial Atlantic, particularly in the western Caribbean Sea. Simulations including windage also resulted in greater seasonal differences than those only using the original HYCOM velocity fields.

In recent years, there are stark differences in the probability of transport from the Equatorial Atlantic into and across the Caribbean Sea (Fig. 4). *Sargassum* beaching has been most pronounced July through September (Wang and Hu, 2017). Interannual differences in inputs from the Equatorial Atlantic predicted by Global HYCOM simulations (no-windage) appear consistent with observed regional patterns of *Sargassum* beaching. In 2011 *Sargassum* beaching was reported across the eastern Caribbean, and in 2012 beaching was more restricted to the southeastern Caribbean. For both of these years, HYCOM simulations suggest that transport from the Equatorial Atlantic to the western Caribbean would be unlikely (Fig. 4A and C), whereas simulations including windage predicted higher than usual inputs to the western Caribbean (Fig. 4B and D). In 2013 no major *Sargassum* beaching was reported, but in 2014 and 2015, widespread *Sargassum* beaching was reported throughout the entire Caribbean (Hu et al., 2016; Wang and

Hu, 2016). During the summer of 2014, much greater transport from the Equatorial Atlantic was predicted by HYCOM, especially into the western Caribbean.

3.2. Forward-tracking

Transport into the Caribbean from the western Equatorial Atlantic is highly likely (Fig. 5). Including a windage factor of 1% increased the probability of transport into the Caribbean, extending eastward the area where transport was most likely (Fig. 5). Seasonal variation in transport predictions was more apparent when not including windage: the area of the western Equatorial Atlantic with the highest probability (> 80%) of being a potential source for *Sargassum* in the Caribbean broadened to nearly the 30°W meridian in the winter and shrunk westward to the 55°W meridian in the summer.

Anomalies for the transport predictions into the Caribbean Sea for the spring months (AMJ) of 2011 through 2014 (the season with the greatest average *Sargassum* coverage in the western Equatorial Atlantic) suggest that ocean circulation processes were fairly similar in those years (Fig. 6) to the long-term mean for spring months in other years (Fig. 5). Albeit in 2011, the year when *Sargassum* beaching was first reported in the Caribbean, increased transport to the Caribbean from east of longitude 30°W was predicted (Fig. 6A and B).

3.3. Statistical relationships between transport predictions and *Sargassum* observations

As seen previously (Wang and Hu, 2017), SPC values in the western Equatorial Atlantic were positively correlated with those in the eastern Caribbean Sea (Spearman $r = 0.564$, $p = 0.028$, $n = 15$). In contrast, however, a strong negative relationship between transport predictions without windage and Caribbean SPC values was detected (Spearman $r = -0.796$, $p = 0.00038$, $n = 15$). Transport predictions assuming 1% windage did not correlate strongly with SPC values in the eastern Caribbean Sea (Spearman $r = -0.418$, $p = 0.121$, $n = 15$), though the relationship was also negative. Multiple regression and variance partitioning procedures indicated that 90.8% (89.1%) of the annual variation in eastern Caribbean SPC values could be accounted for by western Equatorial SPC values and no-windage (with windage) transport predictions from that region. Variance partitioning of the statistical models uniquely ascribed 48.9% (67.2%) of the variation in Caribbean SPC values to western Equatorial Atlantic SPC values and 1.8% (0.2%) to transport predictions; the remaining 40.1% (21.7%) of variation in Caribbean SPC values represents interactions between *Sargassum* occurrence and the no-windage (with windage) transport predictions.

Our initial expectation was that increased transport from the equatorial Atlantic into the Caribbean Sea would correlate with increased *Sargassum* in the eastern Caribbean Sea. Detecting the opposite relationship, however, may suggest a possible mechanism responsible for the increased concentration of *Sargassum* in the Equatorial Atlantic. One hypothesis is that when transport to the Caribbean Sea is reduced within the western Equatorial Atlantic, *Sargassum* and the nutrients that facilitate its growth might be allowed to concentrate in this region, eventually resulting in a major “bloom.” Given that oceanic transport from the western Equatorial Atlantic into the Caribbean Sea is, essentially, inevitable (e.g., synthetic particles (Fig. 5), drifters (Lumpkin and Garzoli, 2005), water masses (Kelly et al., 2000), nutrients and larval fish (Johns et al., 2014), and young sea turtles (Mansfield et al., 2017)), the initial reduction in transport would eventually result in an increase in *Sargassum* reaching the Caribbean Sea. Consistent with this possibility, we found a strong negative correlation between the annual percentage of synthetic particles transported into the Caribbean Sea and the SPC of the western Equatorial Atlantic in the following year (Spearman $r = -0.789$, $p = 0.0008$, $n = 14$). No such correlation was obtained when using transport predictions that included windage (Spearman $r = -0.345$, $p = 0.227$, $n = 14$).

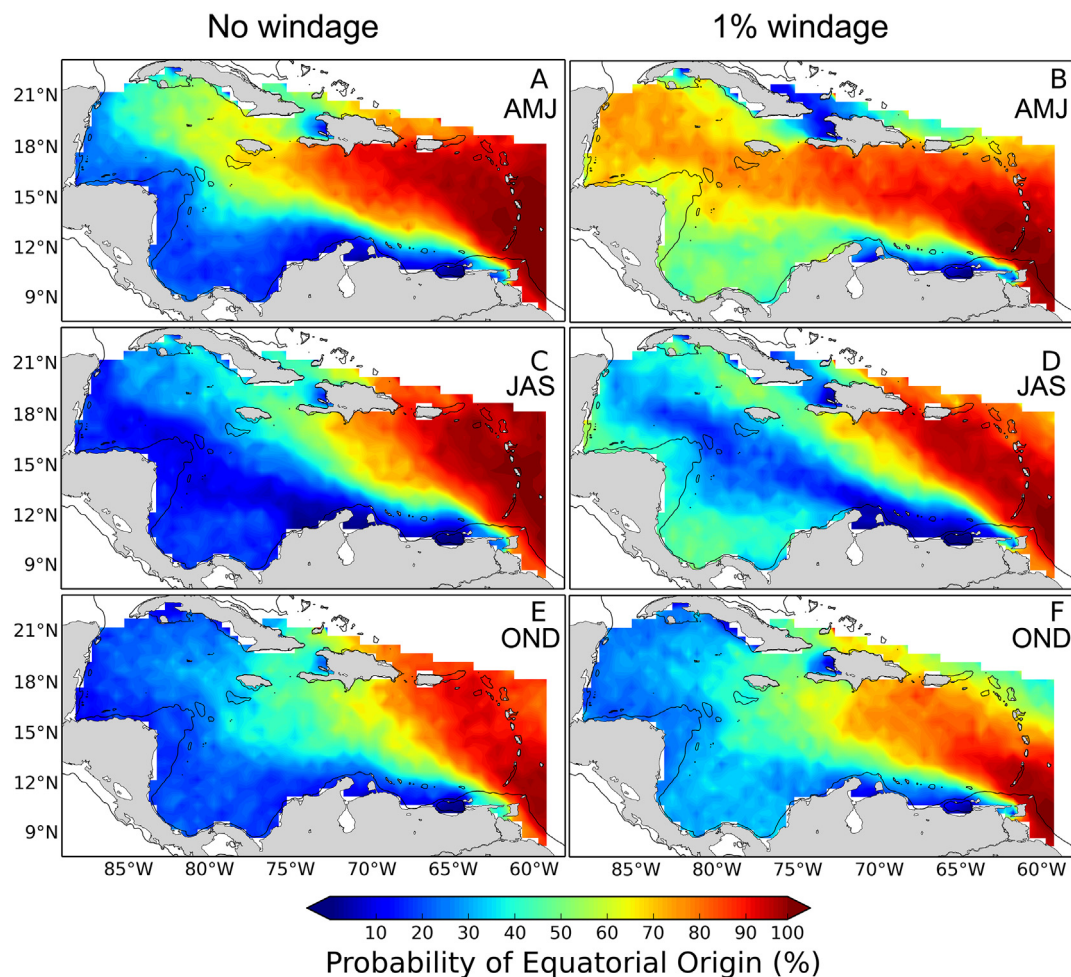


Fig. 3. Spatial distribution of the predicted origins of particles released across the Caribbean Sea and backtracked to the Equatorial Atlantic within one year of their release. Particles were released in 2003 through 2015 during (A, B) spring (April–June), (C, D) summer (July–September), and (E, F) fall (October–December), the seasons when *Sargassum* beaching has been most prevalent within the Caribbean Sea. Coloration indicates the mean percentage of particles within a $0.5^\circ \times 0.5^\circ$ bin that were backtracked to south of 10°N and east of 58°W (Fig. 1). Left hand columns (A, C, E) show results based on the surface layer of Global HYCOM, while right hand columns (B, D, F) show results based on HYCOM plus a windage factor of 1% using winds from the NCEP Reanalysis. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

3.4. A *Sargassum* transport index

The region of highest probability of transport into the Caribbean (Fig. 5) was also a region where *Sargassum* remote sensing observations were available (Figs. 1 and 2) (Wang and Hu 2016). Weighting transport predictions of particles released in the western tropical Atlantic by SPC values at their starting locations showed there was minimal input into the Caribbean between 2000 and 2010, followed by a dramatic increase in 2011, 2012, and 2014. A significant correlation with *Sargassum* observations in the eastern Caribbean was found when a windage factor of 1% was assumed (Spearman $r = 0.557$, $p = 0.031$, $n = 15$). However, this relationship was weaker without accounting for windage (Spearman $r = 0.421$, $p = 0.117$, $n = 15$). These mechanistic models show similar results to statistical models (Wang and Hu, 2017) that indicated SPC values in the western Equatorial Atlantic are positively correlated with those in the eastern Caribbean Sea (Spearman $r = 0.564$, $p = 0.028$, $n = 15$).

Regression analyses indicated that the *Sargassum* transport index can account for much of the variation in annual SPC values in the eastern Caribbean (no-windage scenario: $R^2 = 0.798$, $p < 0.00001$, $n = 15$; 1% windage scenario: $R^2 = 0.875$, $p < 0.000001$, $n = 15$) (Fig. 7). The variance explained by these mechanistic models was similar to the statistical model that considered only western Equatorial

Atlantic SPC values ($R^2 = 0.889$, $p < 0.000001$, $n = 15$). The general agreement between the *Sargassum* transport index, statistical models (see Section 3.3), and observations (Fig. 7) suggests that annual variation of *Sargassum* entering the eastern Caribbean Sea is closely related to surface transport processes from the tropical western Atlantic.

3.5. Oceanographic pathways

The movement of *Sargassum* from the Equatorial Atlantic into the Caribbean Sea is predicted to be strongly influenced by the dynamics of the North Brazil Current System (Figs. 1, 5 and 8). *Sargassum* is in greatest abundance in the western Equatorial Atlantic in spring and summer (Fig. 2). Transport of *Sargassum* in the spring is most likely associated with the Guiana Current, whereas in the summer, North Brazil Current Rings are the primary pathway. The relative contributions of both pathways, over the course of a year, are similar (Fig. 8). Movement of *Sargassum* into the Caribbean that was initially retroflected eastward is possible within one year but is relatively rare. Adding a windage factor of 1% increases the probability of particles following each of these three routes to the Caribbean, but the relative contributions are similar (Fig. 8). *Sargassum* traveling with the Guiana Current in the spring would, on average, arrive to the Caribbean in approximately 2 months. This predicted timing coincides well with the

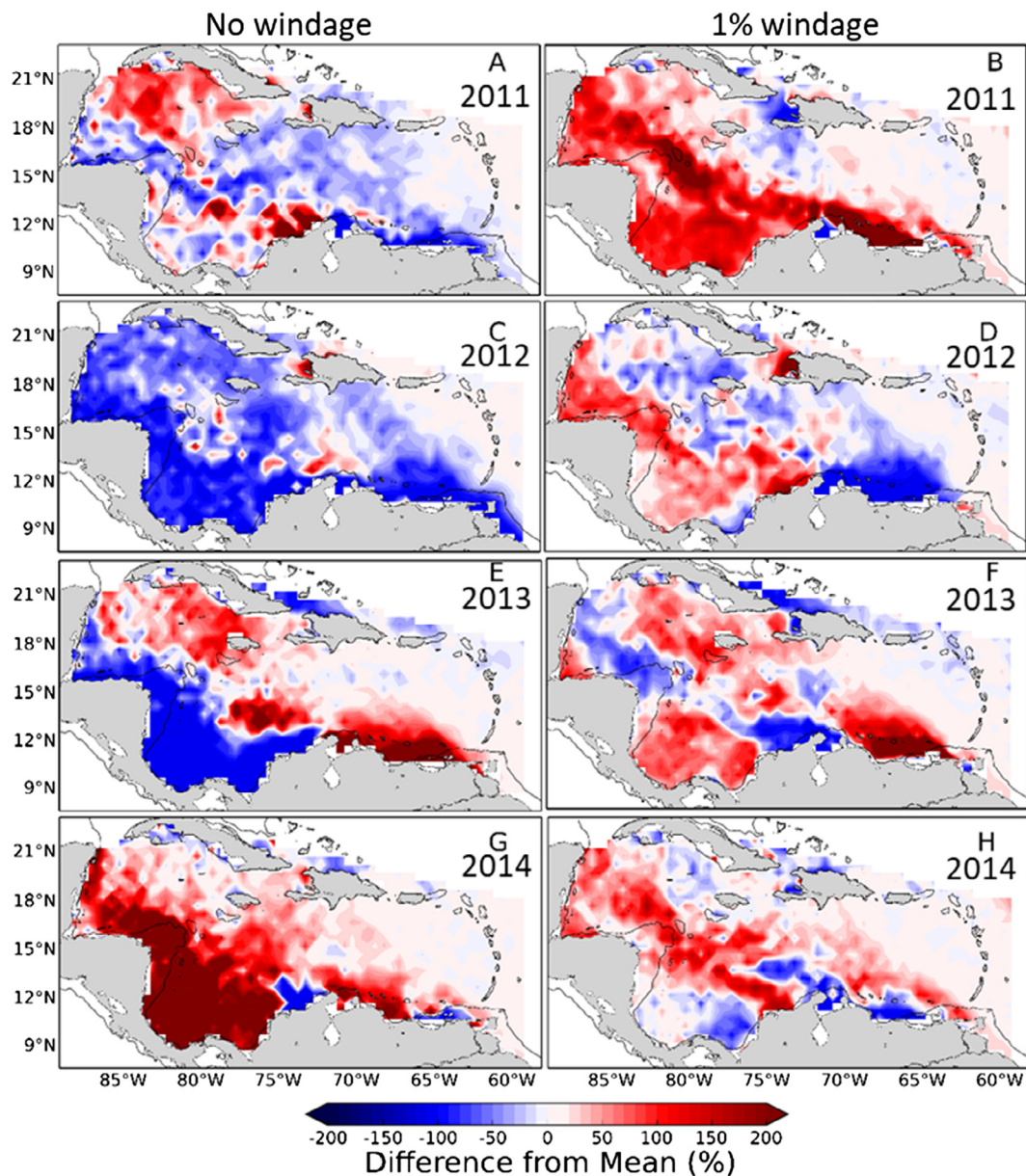


Fig. 4. Percent difference in Equatorial origins between the 2003 and 2015 mean values and those for (A, B) 2011, (C, D) 2012, (E, F) 2013, and (G, H) 2014. Left hand columns (A, C, E, G) are simulations performed with the surface layer of Global HYCOM and right hand columns (B, D, F, H) include 1% windage from the NCEP Reanalysis.

increase in *Sargassum* observed in the Caribbean in the summer months. In contrast, *Sargassum* associated with NBC Rings averages closer to a 6-month transit time, resulting in an influx of *Sargassum* that would occur in the fall. Transit times for the retroflection route average approximately 9 months, but this may be an underestimate given that we only tracked particles for one year. Depending on the seasonal timing, particles may go back and forth across the Atlantic between Brazil and Africa several times before either entering the Caribbean or passing north of the Antilles via the North Equatorial Current.

4. Discussion

Our simulations suggest that *Sargassum* in the western Equatorial Atlantic would consistently enter the Caribbean Sea. This finding is in agreement with remote sensing data that suggest the recent major *Sargassum* events likely result from inflow from the Equatorial Atlantic (Wang and Hu 2017). Additionally, our work builds upon and complements the study by Franks et al. (2016). They used Global HYCOM to

backtrack 5 particles from each *Sargassum* beaching site that was reported in 2011 and found all trajectories passed through the Equatorial Atlantic (south of 10°N). Likewise, their analysis of drifter data supports the conclusion that ocean circulation dynamics of the Equatorial Atlantic play a central role in the transport of *Sargassum* into the Caribbean Sea (Franks et al., 2016). Our work indicates that those conclusions are robust to annual and seasonal variability in ocean circulation. Likewise, the general patterns of transport from the Equatorial Atlantic into the Caribbean are observed irrespective of whether a windage factor of 1% is included in simulations.

Beyond finding agreement in basin-scale patterns of connectivity, including a windage factor of just 1% to surface velocity fields results in considerable changes to transport predictions. When the influence of windage is simulated the mean probability of movement into the western Caribbean is increased (Fig. 3), as is the area in the Equatorial Atlantic over which transport into the Caribbean is most likely (Fig. 5). This effect can be attributed to the strong and consistently westward component of surface winds in the tropical Atlantic (between latitudes

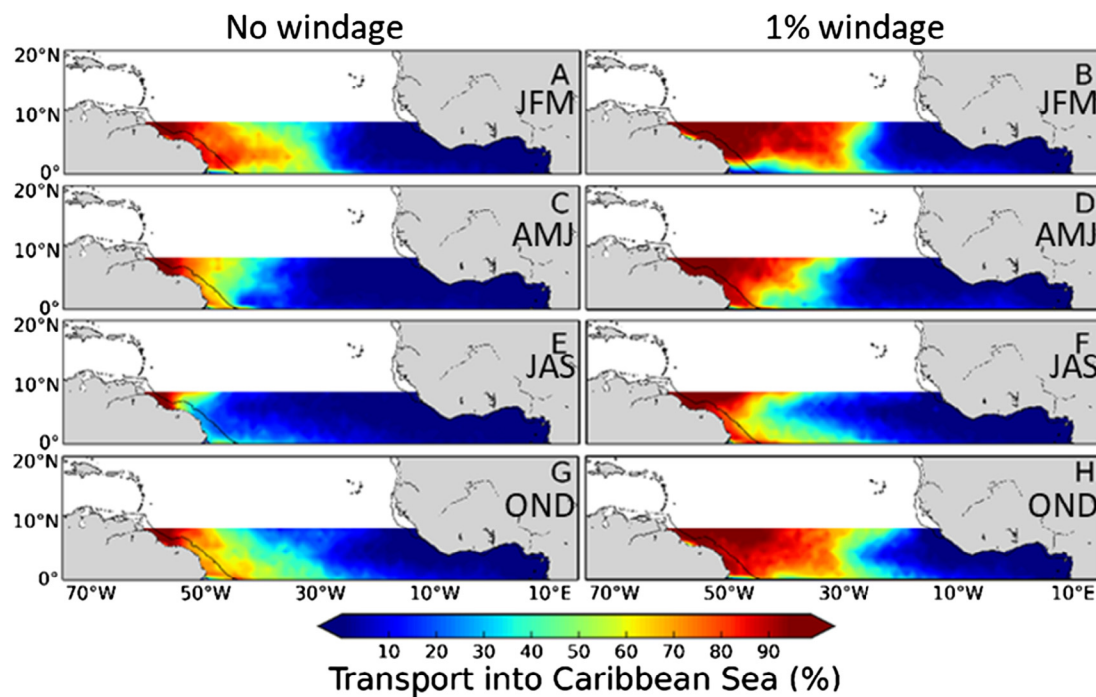


Fig. 5. Mean probability of transport from the Equatorial Atlantic into the Caribbean Sea. 36,500 synthetic particles were released annually between 2000 and 2014 and tracked for one year when released in (A, B) January–March, (C, D) April–June, (E, F) July–August, and (G, H) October–December. Left hand columns (A, C, E, G) are simulations performed with the surface layer of Global HYCOM and right hand columns (B, D, F, H) include 1% windage from the NCEP Reanalysis.

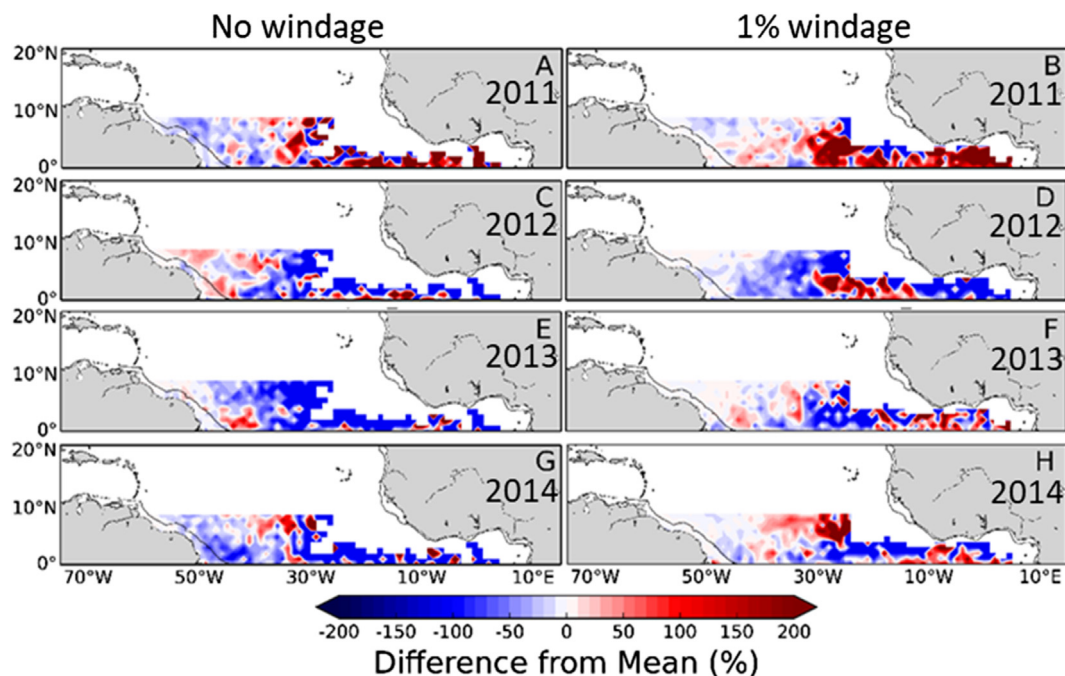


Fig. 6. Percent difference from mean transport into the Caribbean Sea (Fig. 5) and those for April–June in (A, B) 2011, (C, D) 2012, (E, F) 2013, and (G, H) 2014. In 2011 *Sargassum* beaching was reported across the eastern Caribbean, in 2012 beaching was also reported but primarily in the southeast Caribbean. In 2013 no major *Sargassum* beaching was reported, but in 2014 (through 2015) widespread *Sargassum* beaching was reported across the entire Caribbean (Hu et al., 2016; Wang and Hu 2017). Left hand columns (A, C, E, G) are simulations performed with the surface layer of Global HYCOM and right hand columns (B, D, F, H) include 1% windage from the NCEP Reanalysis.

20°S–20°N and longitudes 90°W–10°W) and the northward component of surface winds in the southern half of the equatorial Atlantic (between the equator and 5°N) (Atlas et al., 1996).

Comparisons of our simulations' predictions of transport from the western Equatorial Atlantic to SPC values in the eastern Caribbean suggest that including windage results in better agreement (Fig. 7).

However, it is premature to conclude that this windage factor better accounts for *Sargassum* movement than the surface layer of HYCOM alone. Examination of transport prediction anomalies across the Caribbean (Fig. 4) suggest that the windage scenario modeled may overestimate *Sargassum* transport into the western Caribbean. In 2011, *Sargassum* beaching was only reported east of 71°W (Franks et al.,

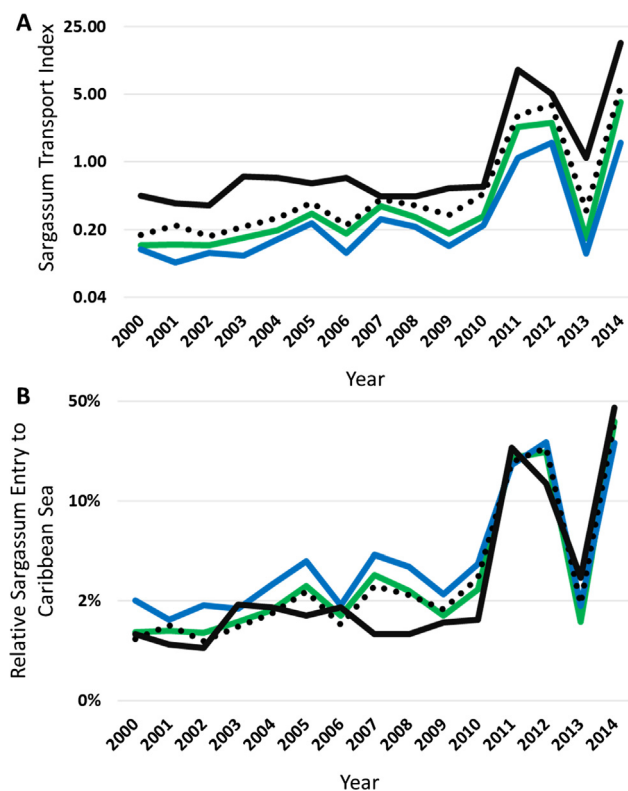


Fig. 7. (A) Predicted percent coverage of *Sargassum* moving into the eastern Caribbean from the western Equatorial Atlantic based on particle tracking experiments using Global HYCOM output and NCEP winds, scaled relative to the percent coverage of *Sargassum* from satellite observations. Colored lines are a *Sargassum* transport index based on particle transport weighted by *Sargassum* percent coverage (SPC) values. Blue indicates predictions from HYCOM surface currents, and green indicates predictions from HYCOM surface currents with a 1% windage factor added from NCEP winds. For comparison the solid black line indicates the annual sum of SPC values across the eastern Caribbean Sea (10–22°N, 58–63°W). For further context, the dotted black line indicates the annual sum of monthly averaged SPC across the western Equatorial Atlantic (Equator–10°N, 60–38°W), where particle tracking simulations were initiated. The y-axis is log₅-scaled to aid visual comparison of differences among metrics across years. (B) Relative transport of *Sargassum* from the western equatorial Atlantic into the Caribbean Sea. Of all *Sargassum* predicted to enter the eastern Caribbean Sea during the 2000–2014 study period, the percentage that occurred in a given year is plotted. Coloration and scaling of the y-axis follows conventions in panel (A). (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

2016), yet including 1% windage greatly increased the probability of transport west of this longitude (Fig. 4A and B). In 2012, *Sargassum* beaching was restricted to areas in the Caribbean even further to the east (Marechal et al., 2017). The scenario without windage is consistent with this observation, predicting much less transport from the Equatorial Atlantic into the Caribbean than usual (Fig. 4C). In contrast, the scenario including windage predicts greater transport into the western Caribbean than average (Fig. 4D). The 2014 *Sargassum* beach inundation events occurred throughout the Caribbean – as far west as Mexico (Hu et al., 2016; Wang and Hu 2017). For that year, the no-windage scenario predicts much greater inputs into the western Caribbean than is typical (Fig. 4G), whereas the windage scenario predicts lower probabilities of transport into the western Caribbean in 2014 than in 2011 (Fig. 4H).

At present, we only speculate as to why including windage brings forward-tracking simulations of *Sargassum* transport into better agreement with SPC values in the eastern Caribbean (Fig. 7), but the no-windage scenario of backtracking appears to better account for

variation in beaching events in the western Caribbean (Fig. 4). Perhaps *Sargassum* becomes less buoyant as it ages and moves east to west across the Atlantic and into the Caribbean and is less influenced by wind. The discrepancy between SPC values and transport predictions may be subject to other biological processes (e.g., growth) and biological – physical interactions that we do not model here. Nonetheless, the sensitivity of our predictions to a windage factor of just 1% shows that further research to understand the movement of *Sargassum* at and near the ocean surface is needed. We anticipate that numerical and in situ experiments to improve estimates of windage and other forcing terms acting on *Sargassum* mats will greatly increase the ability to simulate its movement and predict its distribution (Breivik et al., 2011).

Indeed, resolving the effect of processes at the air-sea boundary, which are not accounted for in most ocean circulation models, is an important area of investigation in marine ecology (Monismith and Fong, 2004; Werner et al., 2007). Such efforts may yield important insight into a number of ecological and evolutionary processes, including rare occurrences of transoceanic colonization of marine plants (Smith et al., 2018), meteorological and oceanographic drivers of population connectivity (Monzón-Argüello et al., 2012), the role of swimming behavior on the movements of small marine animals (Putman et al., 2016; Mansfield et al., 2017), and the distribution of anthropogenic debris in the ocean (van Sebille et al., 2015). Our results represent an initial test of the sensitivity of transport estimates to one such process, windage – direct, linear transfer of momentum from the wind to *Sargassum*. We anticipate that studies that test the sensitivity of transport estimates to other processes, including the Stommel shear (the upper part of the “Ekman spiral”, which is latitude dependent), residual transport due to waves (Stokes drift), and possible variations in the appropriate drag coefficient will help guide and prioritize empirical research on the life cycle, buoyancy characteristics, and aggregation patterns of *Sargassum*.

Regardless of differences in transport predictions between windage scenarios, however, our simulations imply that *Sargassum* transport into the Caribbean Sea is closely tied to the North Brazil Current System (Fig. 8). Further examination of the circulation processes associated with this region (Fig. 1) may yield increased predictive power regarding the timing of *Sargassum* entry into the Caribbean Sea. Variability in beach inundation events are likely primarily the result of high variability in *Sargassum* occurrence (Figs. 2 and 7), but variability in ocean circulation appears to also play a role. Indeed, statistical analyses indicate that *Sargassum* abundance in the Caribbean Sea may be linked to surface transport processes in complex ways. Our results suggest that reduced transport to the Caribbean Sea correlates with increased *Sargassum* coverage in the Equatorial Atlantic, resulting in an eventual increase in *Sargassum* coverage within the Caribbean Sea. For instance, in 2011 there was 180% greater *Sargassum* coverage in the western Equatorial Atlantic, south of latitude 10°N, than the 15-year average. This translated into 255% greater *Sargassum* coverage observed in the eastern Caribbean west of 60°W relative to previously measured years. In 2012, there was even more *Sargassum* in the western Equatorial Atlantic, 255% greater coverage than average. Yet, this only translated into a 100% increase in *Sargassum* coverage in the eastern Caribbean relative to the average. A likely cause for this difference is the different states of the North Brazil Current (Fig. 9). In 2011, annual eastward flow of the NBC retroflection was 10% lower than average (12.6 Sverdrups, $Sv = 10^6 m^3/s$), whereas in 2012 eastward flow increased by 24% (17.4 Sv). Thus, oceanic conditions in 2011 likely favored northwestward transport of *Sargassum* into the Caribbean, but in 2012 much of the *Sargassum* was likely carried eastward toward the central Equatorial Atlantic. This may also explain the hiatus in *Sargassum* entry into the Caribbean in 2013, its limited presence in the western Equatorial Atlantic, and its eventual return in 2014, as *Sargassum* was advected back into this region via the North and South Equatorial Currents.

Such an influence of ocean circulation processes on the entry of

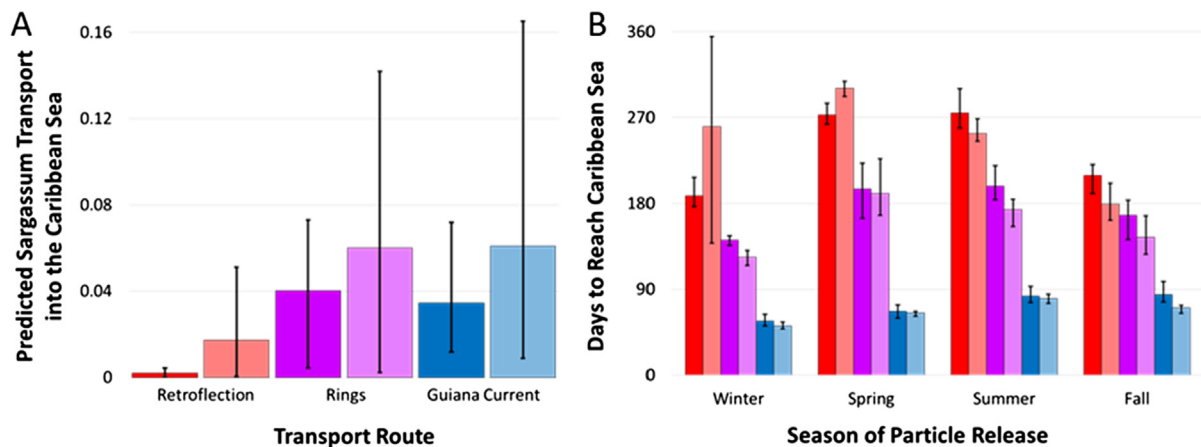


Fig. 8. (A) Predicted *Sargassum* transport into the Caribbean via the North Brazil Current Retroflexion (red), North Brazil Current Rings (purple), and the Guiana Current (blue) (Fig. 1). Darker bars show results using the surface layer of HYCOM, lighter bars show results that include 1% windage from the NCEP Reanalysis. Error bars indicate the range (maximum and minimum) of average seasonal values. The large error bars reflect the strong seasonal change in circulation patterns in this region, where the Guiana Current is the predominant pathway during January–June and NBC Rings are the predominant pathway during July–December (Supplemental Fig. 2). (B) For 2011–2014 (years when substantial *Sargassum* was observed (Fig. 7)), we computed the mean number of days to reach the Caribbean for particles released east of 50°W (the region where *Sargassum* is greatest (Fig. 2)) by each transport route and season. Error bars represent the 95% confidence interval of the mean. Other conventions and color scheme as in (A). (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

Sargassum into the Caribbean suggests that pairing remote sensing data with particle tracking simulations within ocean circulation models could become an effective means to predict future inundations. Indeed, our analyses indicate that much of the annual variation in *Sargassum* abundance (as observed from satellites) in the eastern Caribbean can be accounted for by scaling particle transport predictions to *Sargassum* coverage in the western Equatorial Atlantic. That better than 79% of the annual variation in *Sargassum* abundance in the eastern Caribbean Sea can be accounted for by *Sargassum* coverage and particle tracking simulations in the western Equatorial Atlantic, suggests that further refining this paired approach may allow for predictions and forecasts of *Sargassum* beaching events. Moreover, assessing the differences in the transport time for specific oceanic pathways from the Equatorial Atlantic into the Caribbean (Fig. 8b) suggests that timing of *Sargassum* beaching might be predictable well in advance of its occurrence. These results show the importance of monitoring North Brazil Current System dynamics in relation to *Sargassum* distribution (e.g., Figs. 2 and 8), which could allow the development of an early-warning system that

estimates the probability of *Sargassum* reaching specific areas of the Caribbean Sea within a certain time (e.g., Fig. 3).

Of course, *Sargassum* entering the eastern Caribbean might not be exclusively of western Equatorial Atlantic origin. The floating algae may grow as it moves towards the Caribbean and inputs from other oceanic regions may add to it. Expanding the analyses pairing remote-sensing and particle-tracking eastward into the Equatorial Atlantic, as well as into the Gulf of Mexico and Sargasso Sea (other areas of known *Sargassum* accumulation (Gower et al., 2013)) will provide a more comprehensive understanding of the dynamics of *Sargassum* throughout the Atlantic. Likewise, field campaigns are needed to obtain data on the biophysical properties of *Sargassum* (e.g., depth, buoyancy, growth rates, sinking rates) to parameterize numerical experiments and validate remote-sensing observations. Such work will provide a launching point to understand the ecosystem-level impacts of pelagic *Sargassum* as its movements may play an important role in the population dynamics of numerous species that depend upon it as habitat (Coston-Clements et al., 1991; Wells and Rooker 2004; Mansfield and Putman 2013).

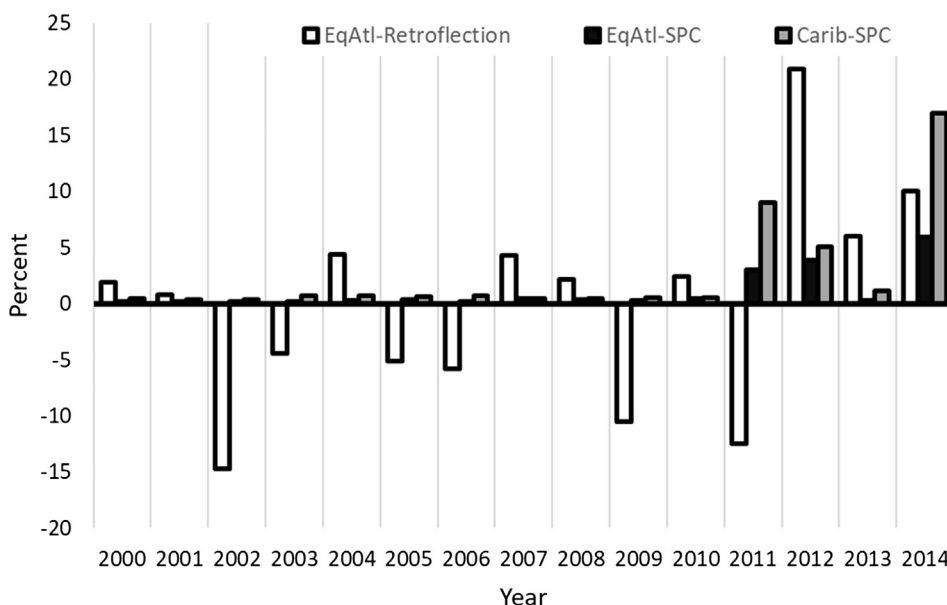


Fig. 9. Percent difference from annual mean values of monthly averaged *Sargassum* percent coverage across the eastern Caribbean Sea (10–22°N, 58–63°W) (gray), monthly averaged *Sargassum* percent coverage across the western Equatorial Atlantic (Equator–10°N, 60–38°W) (black), and retroflected flow (in Sv) from the North Brazil Current (white), based on sea height anomaly fields from satellite altimetry and climatological data (www.aoml.noaa.gov/phod/altimetry/cvar/nbc/transport.php). For retroflected flow, positive values indicate an increase in eastward transport.

Author contributions

NFP and GJG developed the initial conceptualization of research. CH and MW provided *Sargassum* coverage data. GJG, LJG, EJ, JT provided input on pairing ocean dynamics data with *Sargassum* fields. NFP performed simulations/analyses and wrote the initial draft. All authors contributed to interpretation of results and editing the manuscript.

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Appendix A. Supplementary material

Supplementary data associated with this article can be found, in the online version, at <https://doi.org/10.1016/j.pocean.2018.06.009>.

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