



The Atlantic *Sargassum* invasion impedes beach access for nesting sea turtles

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ABSTRACT

One characteristic of global change is an increase in the frequency and magnitude of algae blooms. Although a large body of work has documented severe ecological impacts, such as mortality due to toxins or hypoxia, less research has described sublethal effects that may still affect population dynamics. Here, we focus on blooming *Sargassum* macroalgae in the North Atlantic and describe effects on nesting sea turtles. Since 2011, large masses of the algae have been inundating Atlantic nesting habitats. We documented the accumulation of *Sargassum* at Long Island, Antigua, and quantified effects on a rookery of hawksbill sea turtles (*Eretmochelys imbricata*). Using monitoring data from 2010 to 2019, we analyzed population- and individual-level patterns in nesting. Our results suggest that sea turtles respond to *Sargassum* at nesting beaches by shifting space use away from heavily impacted areas. We also tested for an effect on nesting success, but found no change in the years and areas most impacted by *Sargassum*. The algae may not increase the energetic costs of nesting after a turtle has emerged onto the beach, but we speculate that costs are imposed in algae-filled waters as turtles initially seek to emerge. As the *Sargassum* “invasion” continues, sea turtles at impacted sites will need to exhibit plasticity when choosing nesting sites, and nest densities may increase in areas with less *Sargassum* present. Individuals may also be required to expend more energy per nesting season. More broadly, this work demonstrates that algae blooms can have sublethal effects on fauna that affect population dynamics.

1. Introduction

The recent Anthropocene has featured increases in explosive algae growth that threaten human and natural systems. Blooming phenomena have been documented globally and across taxonomically diverse groups, from the phytoplanktonic species that drive harmful algal blooms (HABs) to free-floating *Sargassum* macroalgae [1–5]. A relatively large body of work has described the most evident and proximate ecological impacts from some algae blooms—eutrophication and harmful toxins can drive high mortality in resident aquatic species [6–9]. Although immediate mortality is a conspicuous impact, sublethal effects (e.g., on energetics or movement) can also have important impacts on populations via changes in survival rates and reproductive output.

Algae blooms in offshore habitats can generate huge quantities of algal biomass that are eventually intercepted by coastlines, resulting in widespread impacts on coastal species [3]. This phenomenon has been dubbed “green and golden tides” [3]. The recent surge of *Sargas-*

sum spp. in the North Atlantic presents a notable case study for golden tides [5,10–17]. After a substantial amount of *Sargassum* moved into the tropical Atlantic in 2010, the macroalgae established an apparently permanent population with spikes in biomass occurring seasonally when growing conditions peak [18]. Whereas patterns in the distribution and transport of *Sargassum* are well-described [e.g., 5,18–21], information on its ecological impacts is comparatively lacking [22].

In contrast to theoretical benefits from increased availability of native *Sargassum* spp. in pelagic habitats [e.g., 23–28], many negative impacts have been documented on coasts. Indeed, we suggest that a coastal-pelagic dichotomy (i.e., negative-positive) may exist for *Sargassum*'s ecological effects (although further research is needed to elucidate impacts more comprehensively). *Sargassum* can fill whole bays (Fig. 1), where it decomposes and gives rise to hypoxic conditions [29]. Die-offs in coastal marine communities have been referred to as “*Sargassum* brown tides” [8]. Short of broad mortality events, leachates from *Sargassum* can negatively affect nearshore and neritic communities (e.g.,

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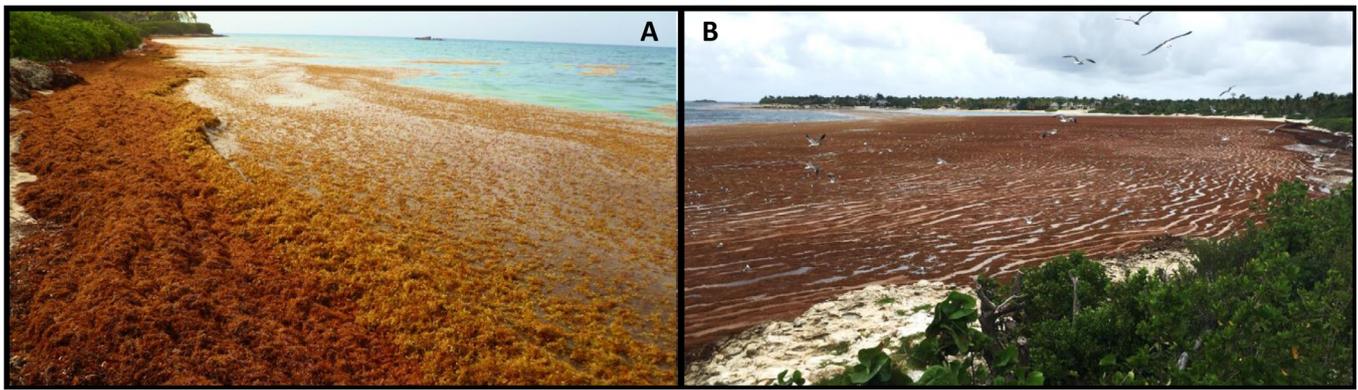


Fig. 1. *Sargassum* at a regionally important hawksbill sea turtle (*Eretmochelys imbricata*) nesting beach at Pasture Bay, Antigua. Arrivals of the seaweed were episodic but commonly amassed into a substantial “barrier” along the shoreline and saturated the nearshore water column. (A) Shoreline and nearshore abundance in the northwestern zones of Pasture Bay in 2015 (photo credit: Andrew Maurer). (B) The morning after a particularly massive arrival that nearly filled the whole bay in 2018, stretching > 50 m from the shore (photo credit: Alexandra Fireman).

reefs); leachates have been tied to declines in algae that cascade up to affect urchin trophic dynamics [30] and have been shown to impede coral dispersal [31]. These effects related to decomposition are accompanied by impacts from its sheer physical magnitude. For instance, we posit that *Sargassum* likely alters coastal erosion-accretion dynamics and impedes movement and habitat use by mobile animals.

In this article, we focus on how sea turtles are impacted by *Sargassum* blooms. The latitudinal distribution of sea turtles in the Western Atlantic—especially nesting habitats—has a major overlap with that of *Sargassum* [32]. We focus here on how nesting ecology is impacted, but postulate that broader effects (i.e., considering all life-history stages) are consistent with the coastal-pelagic dichotomy we suggest. More abundant macroalgae may benefit younger sea turtles in pelagic habitats by increasing the availability of habitat and shelter. Indeed, sea turtles in the North Atlantic exhibit an early pelagic stage during which many individuals may associate with floating seaweed [26–28,33]. By contrast, most studies documenting impacts of *Sargassum* inundation on coasts suggest negative impacts on nearshore foraging habitats and nesting beaches—accumulation of the macroalgae may alter littoral waters [8] and create a physical barrier to nesting adults and hatchlings [34,35,36,37, although see 38]. Biomass accumulation could therefore have consequences for population dynamics through effects on reproduction, space use, energetics, and neonate recruitment [34,37].

Describing impacts on nesting ecology is important given that *Sargassum* inundation appears to be the new normal for the region [18]. Herein, we address this research need by analyzing spatiotemporal patterns in nesting for a rookery of hawksbill sea turtles (*Eretmochelys imbricata*) in the Eastern Caribbean. We set out to evaluate two primary hypotheses. First, we hypothesized that *Sargassum* impedes beach access for turtles seeking to emerge from the ocean to nest. We assessed whether space use on nesting beaches (i.e., where sea turtles choose to emerge and lay nests) changes as a function of *Sargassum* presence and abundance on the shore. Second, we postulated that *Sargassum* increases the energetic demands of nesting by making it more difficult for a hawksbill to successfully deposit a clutch after emerging. We analyzed rates of nesting success to determine whether the probability that a sea turtle emergence results in a successful nest varies with *Sargassum* abundance.

2. Materials and methods

2.1. Study area

We conducted research on Long Island (Jumby Bay), Antigua, positioned in the Leeward Islands of the eastern Caribbean. Long Island is a 120-ha barrier island located northeast of mainland Antigua. Pasture

Bay is the primary nesting site on Long Island, and its crescent-shaped beach runs approximately 650 m along its northern coast. Smaller peripheral beaches that host variable amounts of seasonal nesting activity exist on either side of Pasture Bay; most were artificially constructed in front of private residences. Pasture Bay is windward-facing and oriented to the north and northeast. This windward orientation is somewhat rare for a hawksbill nesting site. The species often nests on lower energy leeward beaches, but a nearshore reef system reduces wave energy on Pasture Beach and makes it suitable for nesting. The windward orientation also means that Pasture Bay is effectively a *Sargassum* “trap.” Prevailing winds and currents can amass great quantities of the seaweed on the beach, particularly on its western end (Fig. 1). When last quantitatively assessed in 2010, total female abundance for the Long Island rookery was estimated at roughly 200–275 individuals [39]. Intensive and continuous monitoring (described below) for over three decades has resulted in its status as a regional index population [e.g., 40,41].

2.2. Data collection

2.2.1. Monitoring hawksbill sea turtle nesting activity

Personnel for the Jumby Bay Hawksbill Project (hereafter JBHP) have monitored Pasture Bay and its peripheral beaches since 1987. The JBHP implements saturation tagging protocols in which hourly foot patrols and metal flipper tags are used to track all nesting activity from 1 June to 15 November [40,41]. Herein, we consider and analyze adult female nesting activity in terms of nests, false crawls, total crawls, and nesting success, as defined below.

- (1) A **nest** is a beach emergence by a turtle that results in a successfully laid clutch of eggs. JBHP staff can check flipper tags during egg-laying without disturbing the nesting process and thus assign each nest to an individual turtle. Hawksbills typically lay 4–6 nests, with a mode of five, at intervals of roughly two weeks [40]. They will then migrate from the nesting site and return in two or more years to nest again.
- (2) A **false crawl** is an emergence onto the beach that does not result in the deposition of eggs, i.e., an unsuccessful nesting attempt. Sometimes turtles may make several false crawls over multiple nights before depositing their clutch. JBHP personnel catalog crawls to avoid double-counting, but false crawls are generally not assigned to individual turtles because they do not afford an opportunity to check flipper tags.
- (3) **Total crawls** refer to all nesting activity, summing nests and false crawls. We also refer to total crawls as crawl counts.

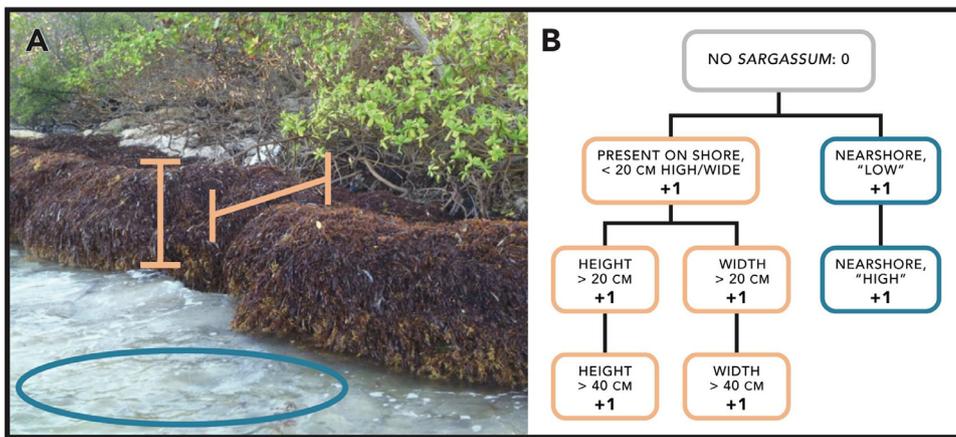


Fig. 2. The indexing system used to quantify the relative abundance of *Sargassum* in 2015. This additive index resulted in a nightly abundance score for each of 36 beach zones during the hawksbill (*Eretmochelys imbricata*) nesting season on Long Island, Antigua. (A) The dimensions used for the *Sargassum* index were height, width, and nearshore presence (photo credit: Andrew Maurer). (B) A flowchart shows the index calculation based on these three dimensions: height and width thresholds were set at 20 cm and 40 cm, with the score increasing as thresholds in abundance were crossed; nearshore density was estimated by a single observer as being either relatively low or high.

(4) **Nesting success** refers to the probability that a crawl results in a nest, and we represent this probability with the ratio of nests relative to total crawls in a given period and/or zone.

Every nest and false crawl at Pasture Bay is attributed to one of 36 beach zones (first outlined during monitoring in the 1980s and 90 s). These numbered zones were delineated perpendicular to the shoreline and increase from –5 to 30 as the shore runs from its southeast to its northwest end. Zones were originally designated based on notable landmarks like trees and large rocks. As a result, they are irregular in the length of shoreline, ranging from 12 to 28 m (mean = 18.2 ± 4.5 SD). Relatively low levels of nesting activity occur in a zoneless area in the northwesternmost portion of Pasture Bay in addition to on small beaches peripheral to the bay; we excluded these areas from analyses due to inconsistent monitoring. Occasionally, a nest or false crawl occurs in which a turtle emerges and crawls laterally into adjacent zones. In these cases, we assigned false crawls to the zone of emergence but, due to recordkeeping protocols, assigned nests to the zone in which eggs were deposited. Records do not offer an opportunity to quantify how often this occurs but, based on years of anecdotal observations on the nesting beach, we posit that this happens only rarely such that any resulting biases during analyses were negligible.

2.2.2. Characterizing *Sargassum* abundance

We intensively monitored *Sargassum* abundance at Pasture Bay during the 2015 nesting season (11 June to 15 November). On a nightly basis a single observer characterized abundance once in each of the 36 zones using an index that ranged from 0 to 7. The seaweed tended to accumulate in a pile along the shoreline, and index scores increased according to thresholds in the dimensions of this pile. Fig. 2 displays this indexing system; any amount of *Sargassum* resulted in a score of 1, but if the pile exceeded 20 or 40-cm thresholds in either height or width at any point in a zone, the score would increase by another 1 point (up to a maximum of 5). Nearshore *Sargassum* (i.e., floating in shallow waters along the shoreline, but not washed ashore) was also scored on a relative basis—as none, low, or high—and could account for another 2 points in the indexing system. We did not calculate absolute measures of biomass. We acknowledge that this index is coarse, and we scored zones based on maximum amounts which did not account for within-zone variation. However, the spatiotemporal resolution with which we estimated abundance provides a sound basis for evaluating effects on sea turtles.

In multiple subsequent analyses, we analyzed yearly data (i.e., for a full nesting season) for 2010–2019. Five of these years featured high *Sargassum* abundance (Table 1), when JBHP staff frequently observed turtles struggling through and interacting with the macroalgae. Moreover, personnel often had to adjust the routes of hourly foot patrols along

Table 1

Summary of annual nesting activity and *Sargassum* impact (i.e., designations for the yearly indicator term) at Pasture Bay, Long Island, Antigua (2010–2019).

Year	False crawls	Nests	Total crawls	Nesting success	<i>Sargassum</i>
2010	210	243	453	0.54	no
2011	145	202	347	0.58	no
2012	225	209	434	0.48	no
2013	229	212	441	0.48	no
2014	373	298	671	0.44	yes
2015	216	282	498	0.57	yes
2016	181	204	385	0.53	no
2017	298	284	582	0.49	yes
2018	132	144	276	0.52	yes
2019	152	183	335	0.55	yes

the shore to skirt areas where the mass of macroalgae was difficult to traverse. By contrast, the other five years featured only low amounts of *Sargassum*. In these low years, *Sargassum* was still present at Pasture Bay, but not at a level likely to affect the nesting behavior of hawksbills. We assigned each year one of these two conditions based on field observations, yielding a binary indicator variable (Table 1). These designations are largely corroborated by satellite-based estimates that show the highest *Sargassum* abundances in the years we designated as high-impact years [5]. Subsequently, we refer to these binary conditions as *Sargassum* versus non-*Sargassum* years (or years with high versus negligible algal biomass). We do not assume that the absolute amount of *Sargassum* was consistent among impacted years and account for this in statistical analyses.

2.3. Statistical analyses

2.3.1. Impacts on crawl counts and nesting success in the 2015 nesting season

Temporally intensive sampling during 2015 allowed us to evaluate *Sargassum*'s effects on hawksbill nesting throughout a nesting season. *Sargassum* abundance can vary through time as it episodically collects and recedes according to processes such as offshore transport, winds, currents, tides, and decomposition. We explored the hypotheses that crawl counts and nesting success would both change as a function of this temporal variation, and specifically that *Sargassum* would have a negative effect on these metrics. We used data for the bulk of the 2015 nesting season (11 June to 11 November) and divided this period into 11 secondary sampling periods of 14 days, which represents the approx-

imate interval between successive nests for hawksbills [39,42]. We then fit two linear mixed-effects models, one each to evaluate effects on crawl counts and nesting success. Predictor and response variables were summarized by zone per 14-day period. We conducted all analyses for this paper in program R (version 3.3.1 [43]) and RStudio (version 1.0.136 [44]). We did not conduct variable selection here or for other analyses because model structures were designated *a priori* to test specific hypotheses.

In the first model, the response variable was crawl counts ($n = 36$ zones \times 11 periods = 396 counts), and we used a negative binomial distribution to model dispersion in the count data (mean = 1.16; variance = 2.99). We chose this distribution over four others suitable for count data (e.g., Poisson) based on AICc scores and visual inspections of raw versus predicted values to verify that overfitting did not occur (see Table S1 in the supplement). We fit the model with the R package *glmmTMB* [45] using restricted maximum likelihood (REML) and a log link function. We included three fixed effects—our predictor of interest was the mean index of *Sargassum* abundance, and we also included fixed effects for the sampling period and its square. This quadratic effect modeled the strong unimodal peak in crawl counts in the middle of a nesting season [e.g., 42]. Finally, we included a random intercept term for zone to model variation in size and habitat suitability among zones.

The second mixed-effects model explained variation in nesting success. Many zone-period combinations had zero crawls, so we aggregated the 36 zones into six larger zones to minimize the incidence of zeroes while still preserving spatial variation. This resulted in $n = 66$ zone-period combinations, of which three were excluded due to an absence of crawls (and thus no ratio of nesting success for modeling). We modeled nesting success as a Bernoulli process, considering each crawl as a trial with two possible outcomes (i.e., nests represented Bernoulli successes and total crawls represented trials). Given this response, we used the *lme4* package [46] to fit a binomial mixed-effects model with a logit link function. We included a fixed effect for the mean *Sargassum* index and random effects for zone and sampling period. The random intercepts term for zone was included to model variation in habitat suitability. We estimated a random intercept for each sampling period to model effects from temporal variation in weather and individual behavior (e.g., some turtles are relatively poor nesters, with high rates of false crawls relative to total crawls, and thus may influence population nesting success during their residence times at the nesting site).

2.3.2. Impacts on crawl counts and nesting success over 10 years

Intensive sampling in 2015 allowed us to evaluate *Sargassum*'s impacts at a fine temporal resolution, but we also used longer-term data to frame similar questions at a coarser temporal scale, comparing nesting data among years with and without *Sargassum*. Similar to our analyses of 2015 data, we hypothesized that crawl counts and nesting success would decline as a function of *Sargassum* abundance, here focusing on 10 nesting seasons (1 June to 15 November) from 2010 to 2019.

Beach-wide responses. We initially evaluated hypotheses at the scale of the whole beach (i.e., summing crawls across all 36 zones). Because high interannual variation in crawl counts is typical for sea turtle rookeries and is driven primarily by the size of annual nesting cohorts (unrelated to *Sargassum*), we did not model crawl counts at this beach-wide spatial scale. However, we did test for an effect from the yearly *Sargassum* indicator (high or negligible) on beach-wide nesting success probabilities. We used a binomial model with nesting success as the response ($n = 10$), again considering this as a Bernoulli process. The model used a logit link function and included the *Sargassum* indicator as the lone predictor variable.

Zone-by-zone responses. Next, we focused on responses at the scale of individual beach zones. This approach allowed us to account for spatial variation in *Sargassum*, which may be necessary for observing its effects on crawl counts and nesting success. To represent spatial variation across all years, we first assumed that the pattern in the relative distribution of *Sargassum* by zone documented in 2015 was consistent among all

years (i.e., even in non-*Sargassum* years; Box 1). We hypothesized that those zones with the highest algal abundance would feature the greatest decreases in both crawl counts and nesting success in *Sargassum* years. Conversely, we anticipated that in non-*Sargassum* years, crawl counts would rebound in those same high-impact zones, and nesting success may rebound as well. This expectation equates to a hypothesized interaction effect between the yearly *Sargassum* indicator and the index of abundance.

We first modeled annual crawl counts by zone with a linear mixed-effects model ($n = 10$ years \times 36 zones = 360 counts). We again selected a negative binomial distribution to model dispersion in the count data (mean = 12.3; variance = 118) on the basis of AICc scores (Table S2). We fit the model using REML and a log link function with the R package *glmmTMB* [45], including fixed effects for the yearly *Sargassum* indicator, the index of abundance, and their interaction. (This interaction applies because we assumed that spatial distribution of *Sargassum*—the indices of abundance by zone—was consistent among all years, although the magnitude of abundance varied greatly; Box 1). We included two random intercepts terms, one each to model variation in crawl counts among zones and years. Variation among zones was expected due to differences in habitat suitability, and high variation among years was expected because of differences in annual nesting cohort size, differences in cohort composition (i.e., individual behavior), potential interannual changes in beach morphology, and finer-scale variation in *Sargassum* abundance (beyond the gross differences represented with the yearly indicator).

Second, we modeled annual nesting success by zone. We first generalized Pasture Bay's 36 zones into nine to minimize the incidence of zeroes; we were able to preserve more spatial variation by doing this with nine zones, as compared to six when analyzing 2015 data, because of a greater sample size. We then modeled nesting success ($n = 9$ zones \times 10 years = 90 samples) with a binomial mixed-effects model. We fit the model using a logit link function in the R package *lme4* [46]. We included fixed effects for the yearly *Sargassum* indicator, the index of abundance, and their interaction. Random intercepts terms for zone and year were included for the same reasons as in the model of crawl counts explained above.

2.3.3. Impacts on spatial patterns in nesting for individual turtles over 10 years

One limitation of comparing population-level nesting activities among years is that some differences may be driven by the individual behavior of turtles in a given year's nesting cohort. Therefore, in a final analytical approach, we leveraged the iteroparity of sea turtles and compared where individual turtles nested in years with and without *Sargassum*. We hypothesized that individual rates of space use throughout the nesting beach would decrease as a function of *Sargassum* abundance. To test this hypothesis, we derived an "intensity of use" metric to quantify how frequently individuals nested in zones with *Sargassum* present in high-impact years (with the metric receiving more weight from zones with more *Sargassum*; Box 1). If *Sargassum* changes individual space use, the intensity of use should be significantly lower in high-impact years.

We identified 114 individual turtles that laid ≥ 2 nests at Pasture Bay in both ≥ 1 *Sargassum* year and ≥ 1 non-*Sargassum* year. Next, for each nesting year of every individual, we calculated the intensity of use of *Sargassum*-impacted zones (ranging 0–1). We modeled this response variable with a linear mixed-effects model (fit with REML [46]) with a term for the yearly *Sargassum* indicator and random intercepts for each individual. This model included a weight term for the number of nests used to compute each response datum (i.e., each annual intensity of use for each individual). The random intercepts term modeled variation among individuals (i.e., individual behavior). We did not include a random effect for year in this model because the response variance is partitioned by year.

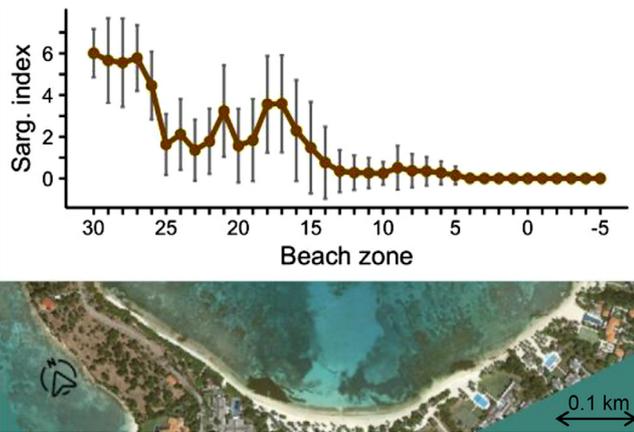


Fig. 3. *Sargassum* abundance by zone at Pasture Bay, Antigua during the 2015 hawksbill sea turtle (*Eretmochelys imbricata*) nesting season. Abundance was estimated nightly with an index ranging from 0 to 7. Error bars display one standard deviation. The bottom image shows an aerial photo of Pasture Bay, with beach zones roughly in line with corresponding zones displayed on the x-axis (source: Google Maps).

Box 1. Interannual modeling methods and assumptions

Assuming the distribution of Sargassum across years. We assumed that the relative distribution of *Sargassum* on Pasture Bay's shoreline was consistent from 2010 to 2019 because the factors that dictate the arrival of macroalgae within the bay exhibit little inter-annual variation. The nearshore reef that runs along the majority of the bay's shoreline is a primary determinant and has remained a fixed structural element over the study period. Patterns in winds and currents are also important in determining where algae collect. These factors are quite consistent in the region, coming predominantly out of the east. Winds and currents do shift seasonally, but in ways that are largely repeated across years [47]. As a result, the accumulation of *Sargassum* is generally much higher in the northwestern areas of Pasture Bay, with spatial variation at that western end largely driven by reef morphology. Arrivals of *Sargassum* can be episodic and variable, resulting in high variation in the absolute magnitude of biomass that accumulates within and among years; the extremes of annual variation are represented with the yearly *Sargassum* indicator term. Although the magnitude is variable, years of experience and observations at Pasture Bay lend support to the assumption that, for full nesting seasons, the distribution of this biomass is relatively consistent. In other words, the relative differences among zones are consistent despite major changes in absolute biomass. Nonetheless, because of uncertainty surrounding the applicability of the exact distribution from 2015 in other years, we suggest that inferences about multi-year trends are less robust than analyses of 2015 data alone.

Individual intensity of use of Sargassum-impacted zones. To test the hypothesis that *Sargassum* affects where individual turtles nest at Pasture Bay, we first had to derive a suitable response variable. Although there is a coarse northwest-southeast gradient in *Sargassum* abundance at Pasture Bay in impacted years, we did not test a directional hypothesis (i.e., turtles shift southeast) because in some cases turtles can shift northwest and encounter less *Sargassum* (Fig. 3). Therefore, we tested our hypothesis by focusing on rates (i.e., intensity) of use of the zones affected by *Sargassum*, regardless of spatial positioning. We quantified this intensity of use by focusing on turtles that remigrated to nest in both *Sargassum* and non-*Sargassum* years. We cataloged the zones in which these turtles laid nests each year, calculating the mean index of *Sargassum* abundance for those zones (as documented in 2015). For example, consider an individual that nested 10 times during the study period by laying five nests in each of two years—we would derive two response data points from this turtle, computing the

Table 2

Parameter estimates from a negative binomial mixed-effects model for hawksbill sea turtle (*Eretmochelys imbricata*) crawl counts on Long Island, Antigua, throughout 11 sampling periods in the 2015 nesting season. The estimate for the negative binomial parameter used to model dispersion, theta, was 6.85.

Fixed effect	Estimate	SE	p
intercept	-0.340	0.25	0.21
<i>Sargassum</i> index	-0.166	0.051	0.0011
period	0.355	0.080	<0.001
period ²	-0.0387	0.0068	<0.001
Random effect	Variance	SD	
zone	0.663	0.81	

mean index of *Sargassum* abundance for the five nests laid in each year. The resulting values provide a representation of “individual intensity of use of *Sargassum*-impacted zones” per year (with this metric receiving more weight from those zones with the highest abundance). Because zones vary in length, we computed intensities of use by using a weighted mean with weights proportional to each zone's shoreline length. We then divided all means by the maximum possible index value of seven to transform the metric to a 0–1 scale.

3. Results

3.1. Impacts on crawl counts and nesting success in the 2015 nesting season

We documented 458 total hawksbill crawls at Pasture Bay over the 11 sampling periods in 2015, including 265 nests and 193 false crawls. Total crawls per sampling period over the 36 zones averaged 1.16 ± 1.7 SD, ranging from 0 to 11. Activity peaked in the middle of the season as expected, reaching a maximum during the fifth sampling period (19 August–1 September; $n = 75$ crawls). The *Sargassum* index (ranging from 0 to 7) also varied through space and time. The mean index per sampling period per zone was 1.54 ± 2.2 (min = 0, max = 7.0). Overall nesting success (i.e., beach-wide nests/total crawls for the whole season) was 0.579, i.e., 58% of emergences resulted in a nest. Mean nesting success for the 63 period-zone combinations that we analyzed was 0.605 ± 0.27 (max = 1.0, min = 0).

In the negative binomial mixed-effects model for crawl counts, all fixed effects received statistically significant support ($p \leq \alpha = 0.05$; Table 2). After controlling for variation among sampling periods and beach zones, we documented a negative relationship between the *Sargassum* index and hawksbill crawl counts (Fig. 4), i.e., fewer crawls occurred in areas with more *Sargassum* on the shoreline. Parameter estimates from the second, binomial mixed-effects model demonstrated that, after controlling for variation among zones and periods, *Sargassum* did not have a statistically significant impact on nesting success ($p = 0.10$; Table S3).

3.2. Impacts on crawl counts and nesting success over 10 years

Beach-wide responses. We used a total of 2261 nests and 2161 false crawls at Pasture Bay over the 10 sampling years to derive crawl counts and nesting success (Table 1). Beach-wide rates of annual nesting success had a mean of 0.518 ± 0.043 SD, ranging from 0.444 to 0.582. The binomial model of nesting success did not provide evidence for an effect from the yearly *Sargassum* indicator ($p = 0.31$; Table S4).

Zone-by-zone responses. The mean for the 360 crawl counts (per year by zone) was 12.3 ± 11 . In Fig. 5 we summarize crawl frequencies (i.e., the proportion of total crawls in each zone by year), comparing the mean for all *Sargassum* years versus non-*Sargassum* years. With the

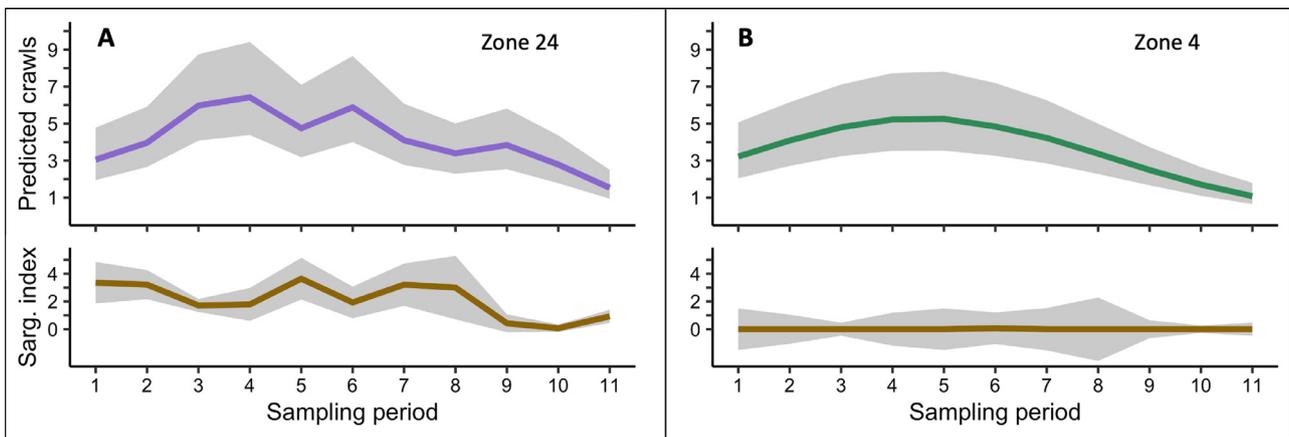


Fig. 4. Model-predicted crawl counts (top axes) show how spatiotemporal variation in shoreline *Sargassum* (bottom axes) affected hawksbill sea turtle space use at Pasture Bay, Antigua, in 2015. Top axes show predicted crawl counts per sampling period (of 14 days each) with a 95% confidence interval. The bottom axes show the observed mean index of *Sargassum* abundance over the same periods, plus or minus one standard deviation. In (A), a beach zone with relatively abundant and variable *Sargassum* is shown. In (B), a zone with consistently negligible *Sargassum* is shown. Predictions were made using a negative binomial mixed-effects model with fixed terms for the *Sargassum* index and a quadratic term for the sampling period, as well as a random intercepts term for beach zone.

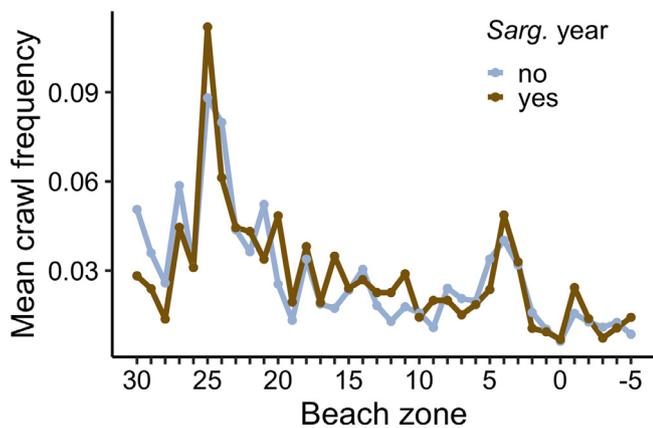


Fig. 5. Mean crawl frequencies (i.e., the average proportion of total crawls per year in each zone) illustrate the differences in nesting beach space use by hawksbill sea turtles (*Eretmochelys imbricata*) in *Sargassum* compared to non-*Sargassum* years. Non-*Sargassum* years ($n = 5$) represent the baseline nesting preferences of hawksbills at Pasture Bay, Antigua, whereas the trend from *Sargassum* years ($n = 5$) show how that baseline shifted. For example, zone 25 featured less *Sargassum* than zones 26–30 (refer to Fig. 3), and the spike in crawls in that zone in *Sargassum* years may be from crawls being displaced.

negative binomial mixed-effects model of annual crawl counts by zone, we documented a significant interaction between the *Sargassum* indicator and the index of abundance ($p = 0.01$; Table 3). Visualizing this interaction showed that, as predicted, crawls were displaced from high-impact zones during *Sargassum* years but then returned to those zones in non-*Sargassum* years (Fig. 6). We displayed this interaction effect using marginal means from the mixed model, estimating a marginal mean for each annual *Sargassum* scenario (low or high) at each of 15 values of the *Sargassum* index (0–7 at increments of 0.5) with the R package emmeans [48].

Dividing the beach into nine zones exposed more spatial variation in annual nesting success; mean nesting success per zone per year was 0.525 ± 0.16 (min = 0.14, max = 0.89, $n = 90$). Similar to the simpler model of beach-wide nesting success, the mixed-effects model of nesting success by zone did not indicate a significant effect from the yearly *Sargassum* indicator; none of the fixed effects received statistically significant support (Table S5).

Table 3

Parameter estimates from a negative binomial mixed-effects model for annual hawksbill sea turtle (*Eretmochelys imbricata*) crawl counts in each of 36 beach zones over 2010–2019. The estimate for the negative binomial parameter used to model dispersion, theta, was 8.3.

Fixed effect	Estimate	SE	<i>p</i>
Intercept	1.97	0.17	<0.001
<i>Sargassum</i> yearly indicator	0.216	0.17	0.21
<i>Sargassum</i> index	0.181	0.050	<0.001
<i>Sarg. year</i> * <i>Sarg. index</i>	-0.0685	0.026	0.0076
Random effect		Variance	SD
Year		0.0619	0.25
Zone		0.281	0.53

3.3. Impacts on spatial patterns in nesting for individual turtles over 10 years

We compared individual patterns in nesting in years with and without *Sargassum* (2010–2019) using data for 1363 nests laid by 114 turtles. Within this subset, turtles laid a mean of 11.9 ± 4.3 SD total nests (min = 5, max = 25). This included 734 nests in *Sargassum* years and 629 nests in non-*Sargassum* years. These data produced a response variable consisting of an individual intensity of use (of *Sargassum*-impacted zones) for each of 345 nesting seasons.

The mixed-effects model of these intensities of use did not provide evidence for a statistically significant effect from *Sargassum* ($p = 0.10$; Table 4), however, the result approached statistical significance and was consistent with our hypothesis (Fig. 7). The parameter estimate for the *Sargassum* indicator term was negative, and we discuss possible biological significance below. We illustrated the effect in Fig. 7 by estimating one marginal mean from the mixed model for each *Sargassum* scenario (low or high) with the R package emmeans [48].

4. Discussion

We set out to test two primary hypotheses about the effects of *Sargassum* on sea turtle nesting ecology. First, we postulated that *Sargassum* impedes nesting beach access and therefore drives changes in space use. Second, we expected that the presence of macroalgae would lead to decreases in nesting success, thereby increasing the energetic costs of nesting. We fit a series of six models to evaluate these hypotheses at different spatiotemporal scales (i.e., within and among nesting seasons) and

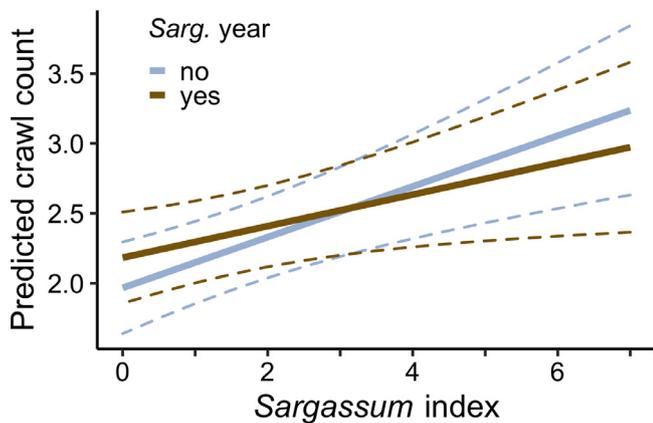


Fig. 6. A significant interaction between the index of *Sargassum* abundance in each beach zone and the yearly *Sargassum* indicator suggests that nesting hawksbill sea turtles (*Eretmochelys imbricata*) were displaced by the macroalgae. The interaction effect shows that turtles preferred the same zones where *Sargassum* collects most densely (i.e., zones with a greater index on the x-axis) and that they were displaced out of those zones in years when *Sargassum* was abundant. Dashed lines display 95% confidence intervals. We plotted this effect using estimated marginal means from a negative binomial mixed-effects model of hawksbill crawl counts on Long Island, Antigua, over 2010–2019.

Table 4

Parameter estimates from a mixed-effects model for individual intensities of use of beach zones impacted by *Sargassum* (see Box 1). Intensities of use were computed on a 0–1 scale for 114 hawksbill turtles (*Eretmochelys imbricata*) over a total of 345 individual nesting seasons (2010–2019). The estimated variance is shown in the bottom portion for the random intercepts term for individual turtle.

Fixed effect	Estimate	SE	<i>p</i>
intercept	0.268	0.014	<0.001
<i>Sargassum</i> yearly indicator	−0.0273	0.017	0.10
Random effect		Variance	SD
individual turtle (residual)	0.00673	0.082	0.30

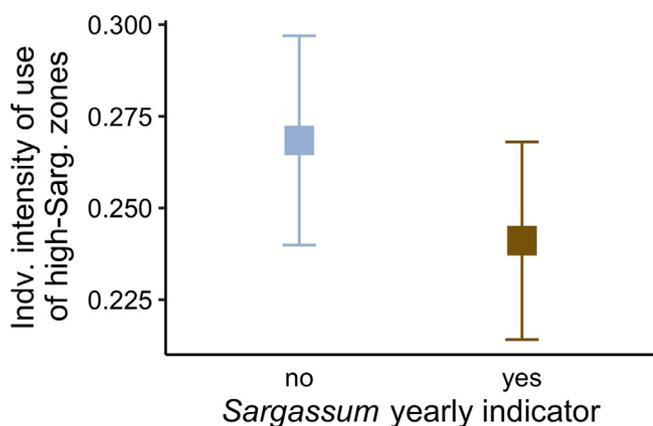


Fig. 7. Patterns in the individual behavior of hawksbills (*Eretmochelys imbricata*) nesting at Pasture Bay, Antigua, show differences in nesting beach space use between *Sargassum* and non-*Sargassum* years. We estimated an intensity of use of *Sargassum*-impacted zones for the nesting seasons of 114 individuals from 2010 to 2019 (explained in Box 1). A mixed-effects model provided evidence for a marginally significant effect from *Sargassum* ($p = 0.1$), providing some evidence that *Sargassum* displaces nesting when present and thus alters the nesting patterns for individual turtles. The estimated marginal mean for each *Sargassum* scenario is shown with a 95% confidence interval.

at different levels of biological organization (i.e., both population- and individual-level behavior). Because we monitored *Sargassum* abundance on a nightly basis during the 2015 nesting season, we could make robust inferences about effects on nesting within this period. We also made assumptions about *Sargassum*'s abundance while analyzing longer-term data over 2010–2019, and the results largely corroborated our findings from 2015. Combined, our analyses consistently suggested that *Sargassum* impedes nesting beach access and causes crawls to be shifted to low-impact areas of the beach. However, *Sargassum* does not strongly affect the probability of nesting successfully once turtles cross the shoreline and access nesting habitats. These findings have important implications for the ability of Atlantic sea turtles to maintain access to nesting habitats in the context of other impacts associated with global change, such as coastal squeeze [49,50].

4.1. Impacts on sea turtle nesting ecology

Although we hypothesized that *Sargassum* would cause decreases in nesting success, our finding that nesting success was not affected might be viewed as logical given the type of data that we used. Specifically, we derived rates of nesting success from crawls that were documented after hawksbills had crossed shoreline mounds of *Sargassum*, i.e., it was generally not possible to document false crawls that ended before or in the algal barrier. Within these constraints, it is reasonable that the relative proportions of nests and false crawls would not change. Indeed, much of the energetic costs from *Sargassum* are probably imposed below the high tide line and in littoral waters, before turtles emerge. However, we note that in the two models of nesting success in which we controlled for variation among zones with a random effect (one model using 2015 data, and one 2010–2019), all *Sargassum* terms had negative parameter estimates with $p \leq 0.15$ (Table S3; Table S5). Although not significant at $\alpha = 0.05$, the consistently negative effects and relatively low *p*-values may represent a biologically significant finding. This result, coupled with the reality that *Sargassum* likely blocks many nesting attempts through its presence in the water column (pre-emergence), may suggest that *Sargassum* increases the energy costs associated with nesting in high-impact years. When considering all regional nesting, increased energy expenditures may over time have the effect of decreasing per capita reproductive output as finite energy is reallocated away from offspring production.

Our results more clearly exemplify the impacts of *Sargassum* on space use. We documented a displacement of crawls from areas with relatively high amounts of *Sargassum*, as demonstrated by models of population-level crawl counts in 2015 and over 2010–2019, and we posit that the model of individual nesting patterns (i.e., intensities of use of *Sargassum*-impacted zones) offered some corroboration. Although the *Sargassum* indicator term did not have a statistically significant effect on individual intensity of use, we suggest that the relatively low *p*-value (i.e., within 0.05 of α) may be indicative of a biologically relevant effect, especially given an inability to control for other factors that may have affected individual nesting patterns (e.g., changes to beach morphology) and considering that a significant effect from *Sargassum* would have had to overpower the high individual fidelity of hawksbills to specific nesting sites [51].

At sea turtle nesting beaches, there are two possible outcomes from this displacement of crawls. Turtles may be completely blocked from the nesting beach and forced to search for a nearby nesting beach that remains more accessible. Alternatively, turtles may be displaced to less-impacted areas within the same nesting beach. If the latter occurs, nests may be concentrated within smaller portions of a nesting beach, thereby increasing the potential for density-dependent effects on nesting and hatching success (the former scenario could also lead to density dependence if nearby beaches already host nesting near carrying capacity).

At Pasture Bay, the geographical layout is such that potential nesting “refugia” exist that intercept little to no macroalgae (i.e., the latter scenario). Having refugia nearby reduces the distance that turtles

must travel to find accessible nesting habitat, however, as suggested, it concentrates nest densities in those low-impact areas. This concentrating effect was also observed for green (*Chelonia mydas*) and loggerhead (*Caretta caretta*) sea turtles in Cuba [35]. In some contexts, the concentration of nests may lead to density-dependent effects such as turtles digging into previously laid nests, thereby affecting offspring production [49]. Anecdotal evidence suggests that such density-dependent interactions occur at Pasture Bay, especially in hotspots of activity that feature concentrated nesting because of factors like vegetation and suitability of substrate (Fig. 5, blue line). A reduction in available nesting habitat caused by *Sargassum* will likely further concentrate nests and yield more density-dependent interactions.

Although *Sargassum*-free refugia exist at Pasture Bay, we caution that this may not be the case in other geographical contexts where sea turtles nest. For instance, for a windward shoreline that is relatively straight and oriented perpendicular to the paths of large *Sargassum* windrows, the aforementioned scenario may take place in which nesting turtles are completely displaced to differently oriented shores and at greater distances (provided that accessible nesting substrates are available nearby). Sea turtles, and especially insular hawksbills, have evolved fine-scale homing and fidelity to natal nesting beaches [e.g., 52], and research is warranted to determine whether populations that interact with large amounts of *Sargassum* can exhibit sufficient plasticity in space use to find nesting habitat with passable shorelines. Such plasticity has been previously described for individuals in some regional populations [e.g., 53]. Managers at particularly vulnerable nesting sites should closely monitor spatial changes in nesting activity.

While we observed clear impacts on hawksbills, the extent of *Sargassum*'s effects on the nesting of other sea turtle species remains somewhat uncertain. First, species may be differentially exposed to shoreline *Sargassum* because of differences in nesting beach characteristics. Algal arrivals are dictated primarily by prevailing currents and winds, leaving windward beaches the most vulnerable. Therefore, species such as leatherback turtles (*Dermochelys coriacea*) that nest frequently at windward sites may encounter *Sargassum* more than hawksbills (that nest more often on leeward coasts). Second, larger sea turtle species like leatherback, green, and loggerhead turtles may be better equipped to cope with the physical barrier of *Sargassum* [38]. Nonetheless, we suggest that the sheer scale of many *Sargassum* arrivals will impede any marine species, as the algae can accumulate in massive piles and completely saturate the nearshore water column. Impacts on space use similar to those we documented were described for nesting green and loggerhead turtles in Cuba [35]. Finally, sea turtle populations and species differ in their levels of fine-scale homing and fidelity to nesting sites [52,54,55]. Populations that exhibit more plasticity in the selection of nesting sites should have an advantage for coping with *Sargassum*. In sum, although *Sargassum*'s impacts on sea turtles will vary by population and geographical context, the magnitude of algae arriving on many coasts has clear potential to drive regionwide changes in space use and energetics.

We acknowledge that a variety of factors that we could not account for might have affected nesting, and in particular nesting success, during the study period. Occasional disruptions from observers on the beach can increase the likelihood of a false crawl, and thus annual differences in observers may have affected false crawl rates and locations. Interannual changes in beach morphology (e.g., erosion) and vegetation have also occurred at Pasture Bay, and any effects on nesting may confound inferences into the effects of *Sargassum*. Erosion-accretion cycles exist naturally, but these dynamics have recently been linked to *Sargassum* because the macroalgae alters nearshore hydrology and prompts the use of heavy equipment for removal by beach proprietors. We selected only the most recent 10 years of nesting data for analysis (including five *Sargassum* and five non-*Sargassum* years) in order to minimize the amount of morphological or vegetational change on the beach. Moreover, where possible, we controlled for these interannual changes in modeling with a random effect for year.

Finally, we note that in the present article we focus solely on the effects of *Sargassum* on adult females. We do not investigate impacts on other key life stages present at nesting beaches, namely eggs and hatchlings. Macroalgal biomass may impede hatchlings as they attempt to exit nest chambers and access ocean habitats and may cause changes to egg incubation environments when it collects atop nests [34–37]. Possible effects on egg thermal conditions are noteworthy given that incubation temperatures affect embryo survival, morphological development, and sex ratios [56]. We also note that, in the context of the proposed coastal-pelagic dichotomy for the ecological effects of the Atlantic *Sargassum* bloom, there is potential for offshore *Sargassum* mats to shelter hatchlings and improve survival. Given these hypothetical scenarios—and considering the importance of offspring production for population recovery—more research is warranted to evaluate the effects of *Sargassum* on these stages.

4.2. Conclusions

As global change continues to give rise to altered environmental conditions in marine habitats, the frequency and intensity of algae blooms will presumably increase [2,3]. Macroalgal species are responsible for some algae blooms and can produce immense amounts of biomass that subsequently inundate coastlines. We hypothesize that in the case of blooming *Sargassum* spp. in the tropical and subtropical North Atlantic, ecological impacts in pelagic waters may be largely beneficial, but in coastal areas appear to be broadly negative. The effects we documented on nesting sea turtles are consistent with the coastal aspect of this dichotomy. We found that *Sargassum* drives changes in space use for adult females at nesting sites. Our results suggest that sea turtles must have access to—and be able to find—passable nesting habitats if *Sargassum* abundance is high at their first choice for a nesting site. At Pasture Bay, Antigua, hawksbills were able to shift nests into proximal areas with low *Sargassum* abundance. However, such refugia may not exist at all sites. This reality, coupled with the fact that *Sargassum* inundation has increased through time [5], suggests broad and continuing impacts on sea turtle space use and energetics. This idea is corroborated by other previous work [35].

Sea turtles may also be viewed as a model species from which to draw parallel inferences for other fauna. For example, land crabs (*Cardisoma guanhumii*) are commercially and ecologically important throughout the Caribbean and, much like sea turtles, must cross the shoreline to lay eggs [57,58]. They do so in the reverse direction, leaving terrestrial habitats to release eggs in the ocean. For land crabs and other species that require access to coastal habitats, peak *Sargassum* densities pose a major issue and may reduce reproductive success, increase energy expenditures, and necessitate changes in space use. These sublethal effects, coupled with lethal impacts from hypoxia in some instances [8], suggest that coastal species would likely benefit from management measures that prevent the accumulation of *Sargassum* on shorelines. Strategies range from removing *Sargassum* after it arrives on coasts [e.g., 59], to the use of floating booms to divert it, and possibly harvesting it offshore [60]. For such an immense and diffuse problem, regionwide collaboration among management and ecological monitoring entities will be important.

Broadly, our findings exemplify the diverse impacts that algae blooms can have on ecological communities. While lethal effects are dire and more straightforward to understand, numerous sublethal impacts will still affect populations and are relatively poorly understood. Continuing to develop a comprehensive understanding of the ecological impacts from *Sargassum* and other algae blooms will aid the conservation of marine biodiversity in the Anthropocene.

Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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Supplementary materials

Supplementary material associated with this article can be found, in the online version, at doi:10.1016/j.ecochg.2021.100034.

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