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Beached *Sargassum* alters sand thermal environments: Implications for incubating sea turtle eggs

Andrew S. Maurer[a,b,*,1], Kevin Gross[c], Seth P. Stapleton[b,d]

[a] *Department of Biological Sciences, North Carolina State University, Campus Box 7617, Raleigh, NC 27695, USA*
[b] *Jumby Bay Hawksbill Project, Antigua and Barbuda*
[c] *Department of Statistics, North Carolina State University, Campus Box 8203, Raleigh, NC 27695, USA*
[d] *Department of Fisheries, Wildlife and Conservation Biology, University of Minnesota, 2003 Upper Buford Circle, St. Paul, MN 55108, USA*

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ABSTRACT

Global environmental change has featured a rise in macroalgae blooms. These events generate immense amounts of biomass that can subsequently arrive on shorelines. Such a scenario has been playing out since 2011 in the tropical and subtropical Atlantic, where *Sargassum* spp. have been causing periodic ‘golden tides’ in coastal habitats. Here we describe impacts on sea turtle nesting ecology, with a focus on the below-ground thermal environment for incubating eggs. *Sargassum* may blanket the surface of beaches due to natural wave or wind energy and can be redistributed via anthropogenic beach cleaning. When it covers egg clutches, it may alter incubation temperatures and therefore affect both embryonic survival and primary sex ratios. To evaluate the thermal impacts of *Sargassum*, we measured sand temperatures with data loggers buried under *Sargassum* cover treatments on a beach in Antigua, West Indies. Our split-plot experiment also tested for effects from shade, season (summer versus autumn), and high rainfall events. We modeled temperatures with a mixed-effects model and, surprisingly, our most compelling finding suggested that *Sargassum*'s effects on below-ground temperatures were contingent on season. Greater *Sargassum* cover was associated with a cooling effect in the summer but warming in the autumn. We assume that the model term for season integrates several climate-related factors that vary seasonally in the Eastern Caribbean and modulate *Sargassum*'s impact, including windspeeds. Comparing estimated marginal means for the high-cover treatments versus the controls, *Sargassum* cover led to a 0.21 °C increase in the autumn and a 0.17 °C decrease in the summer; these thermal changes can significantly impact developmental outcomes for sea turtle embryos. Atlantic nesting beach managers should monitor this macroalgal phenomenon and can use these data to begin to infer impacts on sea turtle populations and develop potential management strategies.

1. Introduction

Anthropogenically induced changes in marine environments have broadly resulted in more favorable growing conditions for algae. Consequently, there has been a worldwide increase in rapid blooming phenomena with widespread economic and biological consequences (Fu et al., 2012; Smetacek and Zingone, 2013; Lapointe et al., 2021). For instance, macroalgae blooms from the globally distributed *Ulva* and *Sargassum* genera result in immense quantities of floating seaweed that are transported by currents and winds to inundate shorelines (Smetacek and Zingone, 2013). Beyond significant implications for coastal tourism and commerce, these ‘green and golden seaweed tides’ affect a multitude of nearshore and coastal species that did not evolve with such high quantities of seaweed. Characterizing ecological impacts on these species will be important for developing and evaluating potential management solutions.

Over the past decade, the explosion of *Sargassum* macroalgae in the tropical North Atlantic has generated golden tides on coasts that serve as essential nesting habitat for sea turtle populations (Eckert and Eckert, 2019; Johns et al., 2020). Floating windrows of algae are advected seasonally into the Caribbean from a transatlantic *Sargassum* ‘belt’ that spans the Gulf of Mexico to Western Africa (Putman et al., 2018; Wang et al., 2019). Evidence suggests that abundance has been increasing since the region was colonized out of the North Atlantic in 2010 (Schell

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[*] Corresponding author at: Department of Biological Sciences, North Carolina State University, Campus Box 7617, Raleigh, NC 27695, USA.
E-mail address: andrew.maurer@noaa.gov (A.S. Maurer).

[1] Present address: Southwest Fisheries Science Center, NOAA-National Marine Fisheries Service, La Jolla, CA 92037, USA.

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et al., 2015; Wang and Hu, 2016; Wang et al., 2019; Johns et al., 2020). Such an inflow of organic matter—e.g., a 20× increase when comparing 2015 to any year before 2011 (Wang and Hu, 2016)—presents major issues at sea turtle nesting habitats, especially considering that seasonal spikes in *Sargassum* biomass occur at the same time as peak nesting (Johns et al., 2020). However, the impacts of *Sargassum* on nesting remain mostly unstudied (though see Maurer et al., 2015, 2019, Maurer et al., 2021a; Ricardo and Martín, 2016; Gavio and Santos-Martínez, 2018; Rodríguez-Martínez et al., 2021).

Sargassum poses a threat on nesting beaches through several mechanisms. The sheer amount of macroalgae represents a blockade for gravid females attempting to access sandy nesting substrate (Maurer et al., 2015; Ricardo and Martín, 2016), as well as for hatchlings seeking the sea after emerging from nests (Gavio and Santos-Martínez, 2018). When the macroalgae are relatively less abundant and turtles are not prevented from crossing the shoreline, more nuanced energy costs are likely imposed. *Sargassum* also may impact incubating eggs in cases where it is pushed atop nests buried in the sand. Our field observations suggest that natural wind and wave action can result in beaches being covered in a layer of *Sargassum* that stretches several meters from the water line, and human beach 'cleaning' in some contexts can redistribute wrack to areas with low foot traffic. A blanket of macroalgae atop nests may prevent hatchlings from leaving the nest chamber altogether. In other instances, *Sargassum* may cover nests only temporarily, or hatchlings may dig through or around the macroalgae to emerge to the sand's surface. In these cases, any effects from *Sargassum* on the egg incubation environment would have consequences for hatchling phenotype and survival. Our focus here is on evaluating the potential effects of *Sargassum* on incubation temperature.

Sea turtle eggs experience a fluctuating thermal environment over the course of an incubation period of roughly two months. Importantly, thermal conditions have direct implications for demographic dynamics because they affect embryonic survival, hatchling morphological phenotype, and primary sex ratios (Maurer et al., 2021b). Thus, potential changes to incubation temperatures from factors such as *Sargassum* cover are important to document and account for against a backdrop of ongoing global change. Primary sex ratios in particular are determined during the middle-third of embryonic development via temperature-dependent sex determination (Girondot et al., 2018), producing more females at warmer temperatures. Relatively short thermal impacts of a few days or less can occur during the middle-third of incubation and have an outsized effect on resulting hatchling sex ratios (e.g., Staines et al., 2020). Indeed, the transitional range of temperatures (TRT) between which sex ratios shift from ~95% male to 95% female is narrower than 1 °C for some populations (Hulin et al., 2009). Thus, even small thermal changes could have significant ramifications for sex ratios, depending on the starting or background sand temperatures relative to the extremes of the TRT.

In this study, we built on previous work (Maurer et al., 2019) to quantify how *Sargassum* alters the thermal conditions of sea turtle nests. Our working hypothesis was that *Sargassum* cools below-ground temperatures due to a shading effect, but it is also possible that it could have an insulating or negligible effect on belowground temperatures. To evaluate thermal effects, we implemented an experiment on a hawksbill sea turtle (*Eretmochelys imbricata*) nesting beach using temperature data loggers and *Sargassum* treatments. We quantified changes in sand temperatures as a proxy for effects on egg incubation temperatures, with results that are broadly applicable for thermally sensitive species that occur on beaches affected by algal inundation.

2. Materials and methods

2.1. Study area

We conducted research on Long Island (a.k.a. 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 (17° 09′ 31"N, 61° 45' 19"W) and its crescent-shaped beach is approximately 650 m in length, windward facing, and oriented to the north and northeast. Its beach consists of calcareous white sand with spatial variation in vegetative community composition and gradients in sedimentary organic matter (Maurer and Stapleton, 2021). The bay's windward orientation combined with the concave shape of the coastline result in Pasture Bay being an effective *Sargassum* 'trap.' Prevailing winds and currents can amass great quantities of the seaweed on the northwestern end of the nesting beach.

2.2. Data collection

To assess impacts on nest incubation temperatures, we implemented a two-way factorial experiment in which we used data loggers (HOBO Water Temperature Pro v2) to measure temperatures under varying *Sargassum* and shade conditions. Between June and November 2015, loggers were buried for either four or five days at a depth of 25 cm, approximating the depth of the center of an average hawksbill clutch at this site (Jumby Bay Hawksbill Project, unpubl. data). We sit the minimum duration to four days to integrate over the variation of several diel temperature cycles and extended to five days when logistically possible. We refer to this four- or five-day span as a deployment. Loggers recorded temperature every five minutes starting at midnight, and we used these measurements to compute mean temperatures for full deployments.

Over the course of our experiment, we deployed 60 data loggers in groups (i.e., blocks) of six. These blocks of six measured temperatures synchronously and were split into unshaded and shaded groups of three. A group of three was buried in a line with loggers spaced apart by 0.5 m, and no more than 3 m from the other group of three within that block. Within these groups of three, each logger was buried and centered beneath one of three *Sargassum* treatments that covered a full 0.25 m^2 quadrat of sand but varied in height. We used a no *Sargassum* treatment (control), a 5-cm treatment (low), and a 15-cm treatment (high). We tested for an effect from shade to account for the fact that hawksbill sea turtle clutches are often laid under vegetative cover, which can affect egg thermal conditions (Kamel, 2013). Shaded treatments were placed underneath the canopy of seagrape (*Coccoloba uvifera*), the most common native species at Pasture Bay. All loggers were buried >5 m from the high-water mark.

Blocks ($n = 10$) were spread randomly throughout the beach and were split between the summer (June and July; $n = 4$) and autumn (October and November; $n = 6$). This schedule was a result of opportunistic field logistics (i.e., logger availability alongside other research projects), but reflect both the early part of annual hawksbill nesting season in the Caribbean, when nesting is beginning and activity is mounting toward an August peak, and the end of the nesting season after which most nests have been laid (Beggs et al., 2007; Kendall et al., 2019). In the Eastern Caribbean region there are seasonal differences in climate variables that may affect sand temperatures, including major changes in trade wind speeds (Chang and Oey, 2013). Thus, we accounted for season with a binary variable (summer or autumn). Further, the different timings for blocks subjected them to variable precipitation, a factor with direct effects on sand thermal environments. Rainfall over the four- or five-day deployments amounted to an approximately binary covariate—mean daily totals were between 0 and 1.1 mm for eight blocks, but 6.4 and 7.2 mm for the remaining two. Thus, we represented rainfall with a binary indicator denoting whether or not high rainfall occurred. Precipitation data were accessed via the National Climatic Data Center for the V.C. Bird Weather Station in Antigua, located approximately 4 km southwest of Pasture Bay.

2.3. Data analysis

We analyzed this experiment as a blocked, split-plot design. Each group of six loggers formed a block. Within each block, the subgroup of three loggers assigned to the same shade treatment (the ‘whole-plot’) was considered as a single replicate of the shade treatment, to account for possible correlations among nearby loggers. Each individual logger (the ‘split-plot’) was considered a replicate for the *Sargassum* treatment (control, low, or high). Additionally, we included two binary, block-level covariates: season (summer or autumn) and high rainfall (present or absent). Hereafter, we refer to these independent variables as ‘shade,’ ‘*Sargassum*,’ ‘season,’ and ‘rain.’

We analyzed these data with a linear mixed-effects model. The response variable was mean temperature computed over each full logger deployment ($n = 60$). Fixed effects were used to model the factorial effects of the two experimental treatments (shade and *Sargassum*) and the two block-level covariates (season and rain). Random effects were used to model the differences among the blocks ($n = 10$) and the residual differences among the whole-plots within each block ($n = 20$).

We used variable selection to find a parsimonious model for the block-level covariates. Given our experimental design, we only considered models that included full factorial effects for the two experimental treatments (shade and *Sargassum*) and both random effects. With these conditions, we entertained 25 models that had different structures for the block-level covariates (season and rainfall)—we considered: (i) not including them, or including them (ii) without any interaction, (iii) with an interaction with shade, (iv) with an interaction with *Sargassum*, or (v) with a three-way interaction with shade and *Sargassum*. We did not consider an interaction between season and rainfall because there were no high rainfall blocks in the summer. To determine the most parsimonious of the 25 possible models, we used backward elimination starting from the most parameter-rich model (i.e., including all terms and eligible interactions) and removing the block-level covariate term with the highest *P*-value in steps until all terms involving block-level covariates were significant ($P \leq 0.05$). Models were fit by maximum likelihood using the lme4 and lmerTest libraries (Bates et al., 2015; Kuznetsova et al., 2017) in program R (version 3.3.1; R Core Team, 2016) using RStudio (version 1.0.136; R Team, 2015). *P*-values at each step were computed using type III ANOVAs with Satterthwaite's approximation.

With the final model identified, we used type III ANOVA to determine whether the two experimental treatments and two covariates had statistically significant effects on sand temperatures. Because these tests were conducted after model selection on the covariates, significance tests of the covariate effects are best regarded as descriptive. We also used the emmeans library in R to compute model-based marginal means for various treatment combinations to illustrate interactions of interest (Russell, 2018). Marginal means are estimated over all the levels of a random effect and resulting error estimates are uniform within groupings with the same number of observations. Herein, we concentrated on the broader relationships between experimental treatments and the response (i.e., whether model terms received statistically significant support). We interpret effect sizes between *Sargassum* treatments, but do not explore pairwise contrasts because treatments were designated somewhat arbitrarily (i.e., 5 versus 15 cm of coverage).

Table 1
Mean sand temperatures (°C ± SD) measured by data loggers buried underneath *Sargassum* treatments and subjected to different seasonal and environmental conditions. Shade was an experimental treatment but is not shown because it was not a supported term in the final linear mixed effects model. Rain denotes whether replicates were subjected to high rainfall.

Sargassum	Rain	Summer T°	Autumn T°
Control	No	29.06 ± 0.912	27.69 ± 0.361
Low	No	28.96 ± 1.02	27.79 ± 0.381
High	No	28.77 ± 0.813	27.77 ± 0.413
Control	Yes	NA	29.70 ± 0.837
Low	Yes	NA	29.90 ± 1.03
High	Yes	NA	30.03 ± 1.01

$N = 8$ for each combination without high rainfall events, and $N = 4$ for combinations with high rain.

Table 2
ANOVA table for the fixed effects of a mixed model evaluating the impacts of *Sargassum* on below-ground sand temperatures. Numerator and denominator degrees of freedom are denoted by numDF and denDF, respectively, with denDF rounded to the nearest tenth.

Model term	Sum Sq	Mean Sq	numDF	denDF	F	*P*
Sargassum	0.0123	0.00614	2	40	0.542	0.59
Shade	0.0387	0.0387	2	10	3.42	0.094
Season	0.126	0.126	1	10	11.1	**0.0075**
Rain	0.271	0.271	1	10	24.0	**<0.001**
Sargassum:shade	0.0528	0.0264	2	40	2.34	0.11
Sargassum:season	0.281	0.141	2	40	12.4	**<0.001**
Sargassum:rain	0.0785	0.0393	2	40	3.47	**0.041**

Bolded *P*-values are statistically significant at α = 0.05.

Table 3
Parameter estimates from the final model for sand temperatures. Estimates for levels of the *Sargassum* treatment are shown relative to the control. Binary terms for shade, season, and rain are shown relative to unshaded, autumn, and no high rainfall event, respectively.

Fixed effect	Estimate	SE	*P*
Intercept	27.9	0.28	**<0.001**
Sargassum(low)	0.117	0.063	0.071
Sargassum(high)	0.0349	0.063	0.58
Shade(shaded)	−0.504	0.26	0.084
Season(summer)	1.37	0.36	**0.003**
Rain(yes)	2.01	0.44	**<0.001**
Sargassum(low):shade(shaded)	−0.0374	0.067	0.58
Sargassum(high):shade(shaded)	0.103	0.067	0.13
Sargassum(low):season(summer)	−0.201	0.075	**0.011**
Sargassum(high):season(summer)	−0.375	0.075	**<0.001**
Sargassum(low):highrain(yes)	0.100	0.092	0.28
Sargassum(high):highrain(yes)	0.242	0.092	**0.012**
Random effect	**Variance**	**SD**	
Block:shade	0.335	0.58	
Block	0.0813	0.29	
(residual variance)	0.0113	0.11	

Variance estimates for random effects are shown in the bottom portion. Bolded *P*-values are significant at α = 0.05.

3. Results

Overall mean ± SD sand temperature under the control *Sargassum* treatment was 28.63 ± 1.10 °C, for the low treatment was 28.68 ± 1.15 °C, and for the high treatment was 28.63 ± 1.11 °C ($n = 20$). However, results from model selection suggested that mean temperatures should be interpreted as a function of different combinations of the independent variables; relevant means are presented in Table 1. Indeed, after removing four terms with backwards elimination, we arrived at a final model that included fixed effects for *Sargassum*, shade, season, rain, and interactions between *Sargassum* and shade, *Sargassum* and season, and *Sargassum* and rain (Tables 2 and 3). The most notable result was a highly significant interaction between *Sargassum* and season ($P < 0.001$; Tables 2 and 3). We also observed a significant interaction between *Sargassum* and rain, although the *P*-value for this term was closer to 0.05 and should therefore be interpreted cautiously because of the variable selection approach we used. Neither the interaction between shade and *Sargassum* nor the main effect for shade was statistically significant (Table 2).

Significant interactions suggest that the relationship between *Sargassum* and sand temperatures should be interpreted in the context of season, and potentially precipitation. The *Sargassum* treatment effect varied with season—increasing *Sargassum* coverage was associated with warming in the autumn and cooling in the summer (Fig. 1). Marginal mean sand temperatures for autumn replicates for the control, low, and high *Sargassum* treatments were 28.69 °C, 28.84 °C, and 28.90 °C, respectively (SE = 0.261 °C, df = 14.7 in each case). In contrast, for summer replicates, the means for the same treatments were 30.07 °C, 30.01 °C, and 29.90 °C (SE = 0.399 °C, df = 14.7). Therefore, comparing the high *Sargassum* treatment to the control, we observed a marginal mean temperature increase of 0.21 °C in the autumn, and a decrease of 0.17 °C in the summer.

High rainfall was associated with an increase in sand temperatures (Fig. 2). Inferences into this rain effect were limited to the autumn season because of dry conditions across all summer replicates. Moreover, this effect was observed with only two high rainfall blocks. Nonetheless, when rainfall was high, increasing *Sargassum* cover was associated with warmer sand temperatures, consistent with the general autumn trend (Fig. 1). However, in the absence of high rainfall, the *Sargassum* treatment effect was nearly negligible (Fig. 2). Marginal mean sand temperatures for rainy replicates for the control, low, and high *Sargassum* treatments were 29.70 °C, 29.90 °C, and 30.03 °C, respectively (SE = 0.301 °C, df = 14.7). For dry replicates, the means for these same treatments were 27.69 °C, 27.79 °C, and 27.77 °C (SE = 0.426 °C, df = 14.7). The average marginal mean temperature (computed over the three *Sargassum* treatments) for high rain replicates was 1.9 °C warmer than for low rain replicates.

4. Discussion

We initially hypothesized that *Sargassum* coverage would have a cooling effect on sand thermal environments at the depth of sea turtle clutches, but we found that it had a more nuanced impact. Our experimental replicates were distributed across the summer and autumn seasons and were coincidentally subjected to one of two precipitation scenarios (high or low rainfall). Unexpectedly, the *Sargassum* treatment had a statistically significant interaction with each of these covariates (Figs. 1, 2). Whereas increasing *Sargassum* had a cooling effect in summer, this relationship was reversed to a warming effect in the autumn (Fig. 1). Further, high rainfall scenarios were associated with overall warmer sand temperatures and a warming effect with increasing *Sargassum* coverage, while drier conditions resulted in little to no treatment effect (Fig. 2). We did not observe a statistically significant effect from shade, which was surprising as it is well-established that shade cools sand temperatures (Kamel, 2013; Patrício et al., 2017; Staines et al., 2020). However, we note that the model term for shade had a *P*-value of 0.09, and its parameter estimate was negative as would be expected (i.e., shade may provide a cooling effect even if *Sargassum* is present); with increased replication, we may have documented a significant effect of shade.

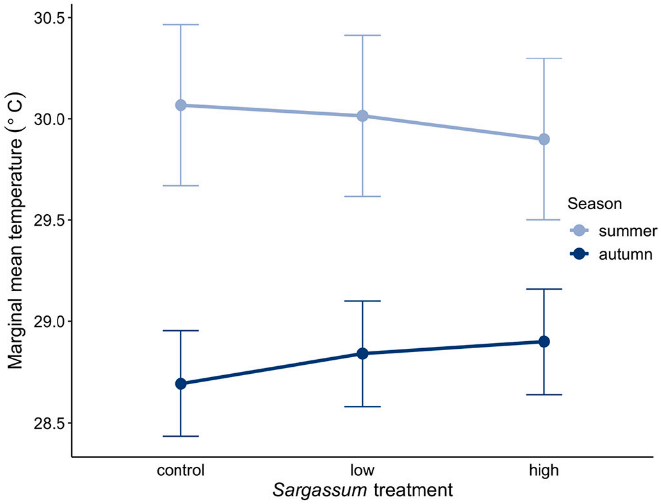

Fig. 1. Increasing *Sargassum* coverage decreased below-ground sand temperatures in the summer and increased below-ground sand temperatures in the autumn. This significant interaction ($P < 0.001$) suggests divergent effects on the thermal environment of incubating sea turtle eggs. Marginal means are displayed with bars representing one standard error. Data were collected using a blocked, split-plot experiment with temperature data loggers in Long Island, Antigua, West Indies.

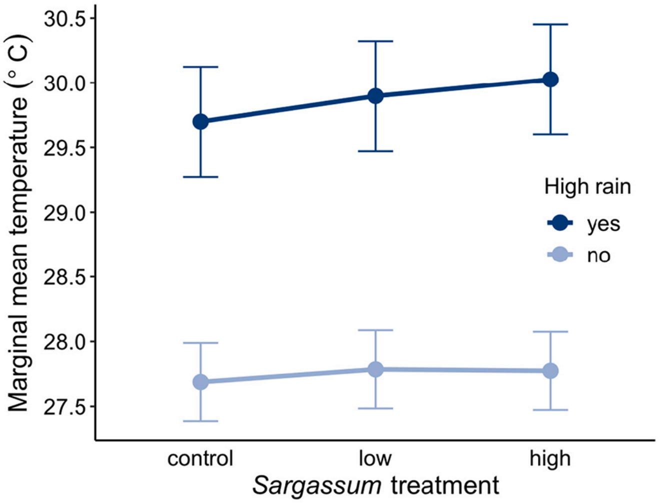

Fig. 2. High rainfall was associated with an increase in sand temperatures underneath *Sargassum* treatments. High rainfall events were only observed in the autumn, so summer replicates were excluded when estimating the marginal means shown. Marginal means computed from a mixed-effects model are displayed to illustrate this interaction ($P = 0.04$), with bars representing one standard error. Data were collected using a blocked, split-plot experiment with temperature data loggers in Long Island, Antigua, West Indies.

We offer more detailed interpretation below but, taken together, our results suggest that that *Sargassum*'s impacts on the incubation temperatures of sea turtle eggs may vary with spatiotemporal context. More broadly, our results indicate that beached *Sargassum* may have thermal impacts on numerous species whose physiologies have evolved on beaches without massive amounts of algae present. For example, ghost crabs (*Ocypode cordimanus*) use sandy substrate at varying depths to thermoregulate (Watson et al., 2018), and seasonal *Sargassum* episodes may necessitate changes to behavior to maintain thermal optima. Some beaches offer less-affected areas such that species can simply shift space use, but other sites have relatively narrow swaths of open sand that may be completely covered by peak *Sargassum* arrivals. Beyond thermal effects, other impacts such as hypoxia will presumably affect coastal species such as birds and invertebrates (e.g., Prins et al., 2009), but are beyond the scope of our study.

4.1. Covariate interactions

Divergent effects by season might be explained by season-specific patterns in climate and moisture. We speculate about possible explanations here, but further work is needed to definitively identify the mechanisms explaining the role of season. A binary model term for season likely integrates several climate variables that vary seasonally in this region. For example, trade wind speeds are higher in the summer (Chang and Oey, 2013; Fig. S1 in the supplementary materials). Summer *Sargassum* cover may have prevented evaporation due to solar radiation, leaving more moisture (as compared to the no *Sargassum* control) to interact with prevailing winds and generate evaporative cooling. The autumn season featured much more precipitation overall, both during and between the deployments of temperature loggers. This likely led to consistently wetter *Sargassum* material, which should be less porous and therefore a more effective above-ground 'shield' against wind and gas exchange, and thus evaporative cooling. Wetter *Sargassum* also presumably decomposes faster and generates more heat. By contrast, the Antiguan summer in 2015 featured drought-like conditions. This could have resulted in a more porous, desiccated, and stable *Sargassum* material that may have acted as a shade while allowing more gas exchange. Different moisture conditions by season also may have affected the properties of the sand itself. As water fills the pores of sediment, it may become more compact and lose less heat, especially if evaporative cooling is impeded (i.e., by a blanket of macroalgae).

The warming effect of high rainfall during two of the autumn blocks supports the idea that *Sargassum*'s impacts on sand temperatures are contingent on spatiotemporal variation in climate and moisture. High rainfall had a significant warming effect overall, which was counterintuitive in light of previous work documenting the cooling effect of moisture (Houghton et al., 2007; Lolavar and Wyneken, 2015). The observed trend may be best explained by a correlation with higher atmospheric temperatures that we could not control for with a random effect for block. Weather station data suggest that the two high rainfall blocks experienced the warmest mean temperatures of any blocks (Fig. S1), so the rain may have resulted from warm fronts. For blocks that received high rainfall, increasing *Sargassum* coverage had a warming effect consistent with autumn blocks in general. However, for autumn blocks with low rainfall, the difference between the treatments and control was reduced. These drier autumn replicates may represent an intermediate condition between wet autumn replicates and summer replicates, and thus a flatter trendline would make sense. Taken together, our results showing significant interactions between *Sargassum* treatment and each of season and rain suggest that climate and moisture may modulate effects on egg incubation conditions. Future studies would benefit from controlling for the moisture conditions of both the sand and the *Sargassum* material used.

4.2. *Implications for incubating sea turtle eggs*

Comparing estimated marginal mean temperatures for the high treatments relative to the controls, we observed an increase of 0.21 °C in the autumn and a decrease of 0.17 °C in the summer (Fig. 1). The maximum raw difference in mean sand temperature that we observed between a control and high treatment within a single whole-plot was a 0.6 °C increase (the minimum was a 0.02 °C decrease). When translating these differences to hypothetical effects on sea turtle embryos, we note that the magnitudes of treatment effects are associated with experimentally designated amounts of *Sargassum*. Based on our field observations throughout Antigua (Long Island and beaches in southern and northeastern mainland Antigua) these amounts are realistic and relevant, but abundance will vary at different nesting beaches and on different sections within a beach (Maurer et al., 2019). Nonetheless, the differences in temperature that we documented offer an opportunity to explore implications for the developmental outcomes of sea turtle embryos.

The extent of impacts on embryos depends on the thermal reaction norms for the population or individual turtle in question. Thermal reaction norms for embryonic survival are characterized by temperature thresholds at which hatching success starts to (rapidly) decline at hot and cold extremes, and these reaction norms can vary among populations (Howard et al., 2014). Reaction norms for sex determination in sea turtles also vary and are typically characterized by a pivotal temperature around 29 °C (resulting in a balanced sex ratio) and the aforementioned TRT (transitional range of temperatures; Mrosovsky and Pieau, 1991; Hulin et al., 2009). If background sand temperatures are already close to levels that would cause increases in hatchling mortality or significant shifts in sex ratios, just a small change due to *Sargassum* may be problematic. We observed a 0.6 °C difference in temperature in one whole-plot—for some populations with a relatively narrow TRT, this thermal difference over the middle third of embryonic development could cause a complete shift from ~95% male to ~95% female hatchling production (Hulin et al., 2009). By contrast, a cooling effect from *Sargassum*, such as we documented in the summer, could buffer eggs against harmful or feminizing temperatures.

Sea turtle nesting populations throughout the North Atlantic are affected by *Sargassum* arrivals. Yet, it is mostly unclear exactly how sensitive specific populations are to impacts on embryo mortality and primary sex ratios, as thermal reaction norms can vary by species and population and remain unquantified for most rookeries (Hulin et al., 2009; Howard et al., 2014). Mrosovsky et al. (1992) documented a pivotal temperature of 29.2 °C for the Long Island hawksbill population from four clutches over 1989–90. Although the authors did not estimate a TRT from these data, it appears that an increase in temperature in the range of 0.2 °C during the middle third of embryonic development could greatly increase rates of feminization. This is especially true from a starting incubation temperature between 29 °C and 29.5 °C, an increment over which the percentage of female offspring increased from 17% to 85% (Mrosovsky et al., 1992). These temperatures are within the range of those measured under our *Sargassum* treatments, even after adding ~1.1 °C to correct for metabolic heating (i.e., where eggs are warmer than adjacent sand) documented during the middle third of incubation for hawksbill nests on Long Island (using a sand depth of 30 cm; Glen and Mrosovsky, 2004). In contrast to concerns of warming, a cooling effect from *Sargassum* would aid in male hatchling production. A thermal reaction norm for embryonic survival (i.e., egg hatching success) remains undescribed for the study population, but norms documented for other species generally suggest that survival starts to decline at constant or mean incubation temperatures between ~30–32 °C and reaches a lethal extreme around ~34 °C (with notable inter- and intra-specific variation; Howard et al., 2014). Thus, given the sand temperatures we observed, and especially after correcting for metabolic heating (Glen and Mrosovsky, 2004), *Sargassum* cover could modulate hatching success at Long Island by altering egg temperatures within this range (i.e., ~30–34 °C). Positive or negative effects are both possible depending on season and precipitation.

4.3. *Considerations and limitations*

While we conducted this experiment at a hawksbill nesting beach, our results have relevance for any marine turtle species that nest at sites that intercept floating *Sargassum* mats. In fact, our findings may have more pertinence for turtle species that exhibit different nesting tendencies than hawksbills. Beach management activities (e.g., raking seaweed) and extreme tide events have the potential to move *Sargassum* throughout any beach, but in general, hawksbill nests should be relatively less impacted because they tend to seek out vegetated areas for their nests (Kamel and Mrosovsky, 2006; Kamel and Delcroix, 2009; Ditmer and Stapleton, 2012). This serves to draw them away from the shoreline where *Sargassum* accumulates. Hawksbills' propensity to nest on leeward beaches should further insulate them from windward arrivals of macroalgae. By contrast, species like leatherback (*Dermochelys coriacea*) and green turtles (*Chelonia mydas*) nest more frequently on windward beaches and in open sites close to the water (e.g., Kamel and Mrosovsky, 2004). Consequently, their nests would likely be blanketed by *Sargassum* more often. We also note that our temperature probe sampling depth was determined based on the center of hawksbill clutches. We therefore caution direct application to other species. For larger species such as leatherback or green turtles (Hirth, 1980), this sampling depth may represent the top rather than the middle of an egg clutch and effects may dampen with increased depth (Tomillo et al., 2017). In contrast, for smaller species, e.g., Kemp's Ridleys (*Lepidochelys kempi*, Hirth, 1980), this depth may translate to a deeper location within the clutch and thermal effects from *Sargassum* may be amplified overall.

Our experiment only tested for thermal effects from *Sargassum*, but the macroalgae likely has additional impacts on egg incubation environments. For instance, *Sargassum* cover may impede gas exchange, thereby affecting embryonic development (Ackerman, 1981; Phillott and Parmenter, 2001). Decaying *Sargassum* also may induce hypoxic conditions (van Tussenbroek et al., 2017). Moreover, impacts on incubation environments represent only a fraction of the multifaceted issues that *Sargassum* poses to sea turtle nesting ecology. Changes in access to nesting beaches can occur when the macroalgae becomes impassable (e.g., Maurer et al., 2015, 2019, Maurer et al., 2021a, but see Rodríguez-Martínez et al., 2021). Decreases in nesting beach access would be especially problematic for insular populations with high natal homing precision that may leave them less able to find passable beaches (Levasseur et al., 2019, 2020). Additionally, *Sargassum* may affect the geomorphological dynamics of beaches. Research is warranted to explore effects on rates of erosion and accretion. Any resulting changes to beach slope would be especially relevant to nesting beach managers, as this is an important cue for nesting turtles (Horrocks and Scott, 1991; Maurer and Johnson, 2017).

4.4. Conclusions

Our data illuminate the potential effects of *Sargassum* on beach thermal environments. The nature of thermal impacts appears to be contingent on seasonal aspects of climate: we documented a cooling effect in the summer but warming in the autumn. This has broad implications for species with thermally sensitive aspects of life history that have evolved in the absence of consistent and massive arrivals of algae. Sea turtles present a particularly compelling case study, as their reproduction is dependent on beach habitats. In some cases, *Sargassum* arrivals are so voluminous that whole beaches may be blanketed for periods that exceed the incubation duration of sea turtle nests. In these instances, hatchling hypoxia or entrapment (i.e., the inability to dig to the sand's surface) are likely more important considerations than changes to the nest thermal environment. Yet, in many cases such as at our study site in Antigua, *Sargassum* abundance exhibits dynamic temporal variation due to episodic arrival, decomposition, wave action, tidal variation, and anthropogenic beach management (Maurer et al., 2021a). If the *Sargassum* ‘invasion’ continues to increase in magnitude, the macroalgae will affect more nesting sites and managers will be faced with decisions in the face of additional impacts from ongoing climate change. Rising temperatures are an especially pertinent component of environmental change given effects on both embryonic mortality and sex determination for sea turtles, and *Sargassum* inundation adds to the numerous factors that can affect nest thermal conditions. Developing management solutions to address the impacts of the growing *Sargassum* problem will be necessary in many locations.

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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Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.jembe.2021.151650.

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