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Physiological Effects of *Sargassum* Beach Coverage on Three Species of Sea Turtle Hatchlings

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ABSTRACT

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Sea turtle hatchlings face a variety of obstacles as they crawl down the beach to the ocean after emergence. One of these obstacles is *Sargassum*, a floating brown macroalgae that may wash up in large quantities on beaches from Florida to South America. This study examined the physiological response and physical performance of three species of sea turtle hatchlings (*Dermochelys coriacea*, *Caretta caretta*, and *Chelonia mydas*) after crawling over a 13 m sand pathway and then 2 m of two different depths of *Sargassum*. In all three species, the addition of *Sargassum* significantly increased the amount of time it took to crawl the length of the pathway *vs*. a 15 m control with no *Sargassum*. After the crawl, righting response and blood glucose levels were tested. No significant differences were found in righting response times or blood glucose levels between different crawling treatments within species. During periods of high *Sargassum* accumulation, hatchlings will spend more time on the beach trying to navigate through the algae, leaving them vulnerable to predation for longer periods of time.

ADDITIONAL INDEX WORDS: *Algae, loggerhead, leatherback, green sea turtle, beach obstacle, frenzy crawl.*

INTRODUCTION

Florida has three species of sea turtles that commonly nest on local beaches, including leatherback (*Dermochelys coriacea*), loggerhead (*Caretta caretta*), and green turtles (*Chelonia mydas*). After nests are laid and incubation is complete, the fully developed turtles hatch and dig out from the nest, beginning the frenzy period. This stage is critical for survival and includes the hatchlings emerging from the egg chamber, crawling rapidly to the water, and then actively swimming offshore (Carr and Ogren, 1960). This high level of activity makes it possible for hatchlings to move quickly away from the beach and escape high-predator areas as fast as possible (Erb and Wyneken, 2019; Wyneken and Salmon, 1992). Hatchlings swim continuously for approximately 24 hours during the frenzy period, so any added fatigue can lead to a decrease in their swimming capabilities and hence their likelihood for survival (Booth, 2009; Salmon and Wyneken, 1987; Wyneken and Salmon, 1992).

During this energetically taxing period, hatchlings rely on both aerobic and anaerobic metabolism; hatchlings exceed their aerobic scope and use anaerobic metabolism during the digging, crawling, and swimming phases of the frenzy (Baldwin *et al.*, 1989; Dial, 1987; Pereira *et al.*, 2012). Glucose is the primary fuel source used during both aerobic and anaerobic metabolism and is released during high-activity levels. However, hatchlings have finite energy stores while moving offshore because they do not eat during the frenzy, instead relying on energy from their residual yolk (Kraemer and Bennett, 1981). Because of the potential energy limitations that occur during the crawling and swimming periods, a decrease in the amount of available fuel may affect their physical capabilities, and obstacles encountered during the frenzy stage could increase energy expenditure and result in lower energy stores.

Obstacles encountered while crawling to the water (*e.g.,* vehicle ruts, marine debris, misorientation due to artificial lighting) can slow hatchlings down and increase energy expenditure (Aguilera *et al.*, 2019; Aguilera *et al.*, 2018; Hosier, Kochhar, and Thayer, 1981; Pankaew and Milton, 2018; van de Merwe, West, and Ibrahim, 2012). Added time on the beach increases their exposure to potential terrestrial predators, such as ghost crabs, foxes, raccoons, and birds (Erb and Wyneken, 2019). Hatchlings would potentially be more vulnerable to predation in the water as well if higher energy expenditures slowed them while swimming or prevented them from swimming as far (Hamann, Jessop, and Schäuble, 2007).

One obstacle of increasing concern is *Sargassum*, a macroalgae that has been accumulating on beaches (Figure 1) more frequently in recent years, which hatchlings must therefore traverse on their way from the nest to the water (Maurer, De Neef, and Stapleton, 2015; Schell, Goodwin, and Siuda, 2015; Schiariti and Salmon, 2022). *Sargassum* is a genus of floating brown algae found mainly in the Atlantic Ocean and is an essential habitat for many marine organisms (Doyle and Franks, 2015). Located in the North Atlantic Subtropical Gyre, the Sargasso Sea serves as a valuable refuge for sea turtles in their post-hatchling and early juvenile years. As a floating seaweed, *Sargassum* is carried by currents and is known to wash up on shorelines, where it can help stabilize beaches and dunes and adds nutrients to the sand (Williams and Feagin, 2010). However, while there are benefits to *Sargassum* accumulation on beaches, in the last decade, *Sargassum* biomass

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Figure 1. Extensive Sargassum may accumulate on southeastern Florida beaches during the summer months. Juno Beach, Florida, July, 2021. (Photo credit: A. Appelt.)

has increased in oceans and on beaches, leading to some potential negative effects within the beach ecosystem (Schell, Goodwin, and Siuda, 2015; Wang and Hu, 2016).

Sargassum mats wash ashore from spring to fall in large amounts during bloom years (Oviatt *et al.*, 2019). This time period overlaps with sea turtle nesting season in Florida, which occurs on Florida's east coast from March to October. The accumulation of *Sargassum* could thus have an effect on the three sea turtle species that commonly nest in this location (Figure 2). For example, in Antigua, vast quantities of *Sargassum* washed ashore and prevented gravid hawksbill sea turtles from reaching suitable nesting habitat because they could not crawl over the piles of algae. This massive *Sargassum* accumulation reduced the amount of viable nesting area by 25% (Maurer, De Neef, and Stapleton, 2015). Significant accumulations of *Sargassum* are expected to continue in coastal areas and may be related to climate change as well as nutrient input (Louime, Fortune, and Gervais, 2017). Large amounts of nutrients are entering the ocean through the Amazon River, which coupled with warming water is most likely leading to this increase in *Sargassum* biomass (Wang *et al.*, 2019).

Little investigation has occurred into the effect that crawling over *Sargassum* may have on sea turtle hatchlings. Schiariti and Salmon (2022), found that *Sargassum* became impassible by loggerhead hatchlings at a height of 30 cm, and another study found that crawling over wrack zone seagrass (*Cymodocea nodosa*) increased crawl time in loggerhead hatchlings in the Mediterranean (Triessnig, Roetzer, and Stachowitsch, 2012). An observational study of *Sargassum* in the Caribbean suggested that hatchlings will likely struggle crawling and swimming through dense mats of *Sargassum*; however, no quantitative data on this has been reported to date (Maurer, De Neef, and Stapleton, 2015; Maurer, Stapleton, and Layman, 2019). Additionally, published data are lacking on physiological responses of hatchlings to crawling over *Sargassum* on the beach, although increasing amounts of *Sargassum* on beaches may pose both physical and physiological threats to sea turtle hatchlings during the nesting season.

Figure 2. Sargassum accumulations greater than 30 cm in height are obstacles for sea turtle hatchlings crossing the beach, and may interfere with adult nesting as well. Juno Beach, Florida, July, 2021. (Photo credit: A. Appelt.)

This study examined the effect of *Sargassum* accumulation on hatchlings of the three sea turtle species (leatherback, loggerhead, and green turtles) that commonly nest in Florida to determine whether the algae is likely to affect hatchling energy and behavior during the frenzy period and thus affect the likelihood of survival.

METHODS

All research was permitted by the Florida Fish and Wildlife Conservation Commission permit MTP-21-053A and the Florida Atlantic University Institutional Animal Care and Use Committee protocol A21-26. Research methods complied with protocols in both permits.

Study Site and Species

This study was conducted on three beaches on the east coast of Florida: Juno Beach, Jupiter, and Boca Raton. Leatherback hatchlings were collected from nests in Juno Beach and Jupiter monitored by Sea Turtle Specialists at the Loggerhead Marinelife Center. Loggerhead and green turtle hatchlings were collected from nests located in Boca Raton monitored by the Gumbo Limbo Nature Center Sea Turtle Specialists. A total of 30 nests were used: 10 hatchlings were collected from each of 10 nests per species, of which 80 hatchlings total per species were used in experimental and control groups.

Hatchling Collection

Hatchings were collected during nighttime natural hatchling emergences (hatch outs). When a nest emergence was expected, a wire mesh cage was placed around the nest and monitored throughout the night. After emergence, 10 randomly selected hatchlings were placed in a bucket with warm, damp sand, which was then covered with a towel to keep the hatchlings quiescent until the crawling trial began. The first trials began within 10 minutes of emergence.

Crawl Pathway

Each hatchling crawled down a 15×1 m crawl pathway on the beach where they hatched. The pathway was raked and cleared of all debris, then previously collected *Sargassum* was added to the final 2 m of the pathway. The pathway was lined on both sides with black plastic sheeting 16 cm in height to prevent the hatchlings from navigating off course. A dim light placed several meters ahead of the hatchling was used to encourage it down the pathway. The observers remained several meters to the side of the runway and in front of the hatchling to avoid disturbing their natural crawling behavior. The pathway was designed to simulate how hatchlings would normally encounter washed up *Sargassum* on their crawl to the ocean: The first 13 m were only sand, and the last 2 m of the pathway had varying amounts of *Sargassum*. *Sargassum* heights were chosen based on Schiariti and Salmon (2022). The *Sargassum* was arranged so hatchlings had to crawl up a $\sim$70° angle. The *Sargassum* was placed loosely on the pathway to closely mimic how it is found naturally on the beach; it was not packed down or manipulated in any way.

Twenty hatchlings were included in each of four treatment groups for each species, totaling 80 hatchlings per species. Each hatchling went through only one trial; no hatchling was used for multiple treatments. All hatchlings were released into the ocean on the night they emerged after data collection was complete.

Treatments

The following treatments were used in this study.

No-Crawl Control

Hatchlings did not crawl down the beach path. All measurements were collected immediately after emergence and before crawling to the ocean.

Crawl Control

Hatchlings crawled 15 m down the beach pathway that was free of any *Sargassum* or other obstacles, crawling only on bare sand.

Light Coverage

Hatchlings crawled 15 m down the beach pathway with *Sargassum* at the end. The first 13 m of the crawl was on bare sand, and the last 2 m was on a continuous patch of *Sargassum* 7–9 cm high (Schiariti and Salmon, 2022).

Heavy Coverage

Hatchlings crawled 15 m down the beach pathway with *Sargassum* at the end. The first 13 m of the crawl was on bare sand, and the last 2 m was on a continuous patch of *Sargassum* 17–19 cm high (Schiariti and Salmon, 2022).

The order in which hatchlings were run through the different treatment groups was rotated each night so that the same treatment was not first nor last each time.

Times

As hatchlings crawled down the pathway, the time to crawl the length of each section of the pathway was recorded, including the following.

Sand Time

Sand time included the amount of time it took to crawl down the first 13 m of the crawl pathway on only sand.

Climb Time

Climb time included the amount of time it took to crawl from the sand to the top of the *Sargassum* pile. This time started when hatchlings touched the *Sargassum* and ended when the hatchling's entire body was on top of the *Sargassum* pile. The crawl-control group did not have this time category because they simply continued their crawl on sand only.

Sargassum Time

Sargassum time indicates the amount of time it took to crawl the final 2 m of the crawl pathway on top of the *Sargassum*. For the crawl control, these final 2 m were still on sand but are referred to as the *Sargassum* time for comparison to the other treatment groups.

Total Time

The total time includes the amount of time from the start to end of the crawl pathway (Sand Time + Climb Time + *Sargassum* Time).

Time Limits

Loggerhead and green turtle hatchlings were allowed to crawl down the pathway for a maximum of 30 total minutes; leatherbacks, which crawl more slowly, were allowed a maximum of 45 total minutes (Seaman, 2020).

Inversions

As hatchlings were crawling up onto or over the *Sargassum* pile, some flipped upside down onto their carapace; each event was recorded as an inversion.

Blood Samples

After each hatchling completed its crawl, $\leq$100 μL of blood was collected using a 1 cc syringe coated with Na-Heparin, and a 27-gauge needle, which was used to determine blood glucose levels. Blood was collected from the external jugular vein or sinus using safe practices with the skin sanitized before collection (NOAA United States Department of Commerce, 2008). Blood glucose was measured with a standard

Table 1. *Median and interquartile range of the different recorded crawl times in the pathway for each three sea turtle species.*

	Sand Time (s)	Climb Time (s)	*Sargassum* Time (s)	Total Time (s)
		Leatherback		
No crawl	NA	NA	NA	NA
Crawl	233 (198, 280)	NA	44 (41, 67)	279 (233, 336)
Light	222 (164, 299)	25 (15, 48)	132 (104, 151)†	430 (363, 509)†
Heavy	225 (182, 263)	312 (102, 770)†	123 (107, 171)†	720 (443,1246)††
		Loggerhead		
No crawl	NA	NA	NA	NA
Crawl	169 (127, 199)	NA	39 (28, 51))	201 (156, 249)
Light	161 (143, 178)	42 (19, 64)	162 (130, 217)†	383 (315, 470)†
Heavy	156 (101, 213)	142 (59, 928)†	146 (99, 218)†	552 (300, 1211)†
		Green		
No crawl	NA	NA	NA	NA
Crawl	80 (68, 89)	NA	24 (21, 29)	106 (92, 122)
Light	85 (73, 106)	17 (9, 26)	72 (64, 123)†	185 (154, 255)†
Heavy	85 (76, 106)	93 (25, 128)†	78 (64, 104)†	274 (204, 332)†

†*Indicates significance. Data with multiple indicators are significantly different from each other for the same measurement. Significance is shown only within species, not between species.*
NA = not available

blood glucose monitor (Easy Touch Blood Glucose Monitor, validated by Kunze *et al.* [2020] and Perrault *et al.* [2018]). The glucose monitor was checked for accuracy using standards on a weekly basis.

Righting Response

After the blood sample was collected, a righting response test was conducted in a 19 L bucket filled with ~10 L of seawater. Hatchlings were placed floating upside down on their carapace; the time it took them to right themselves back onto their plastron was recorded with a stopwatch (Fleming *et al.*, 2020). Each hatchling underwent three timed trials, and the average time was calculated.

Sand and *Sargassum* Temperatures

Environmental temperature can affect reptile metabolism and activity, and sand and *Sargassum* temperatures were recorded (Davenport, 1997; Triessnig, Roetzer, and Stachowitsch, 2012). Sand temperature was measured at the beginning, middle, and end of the crawl pathway before each crawl, and the average temperature was calculated. All temperatures were measured using a thermal gun (Fluke 62 Max Infrared Thermometer).

Statistical Analyses

All statistical analyses were conducted using R software (R Core Team, 2021). Significance was determined at a p value <0.05.

Data Analyses

To determine whether the data were normally distributed, QQ plots and Shapiro-Wilk's tests were used. All data were found to violate the assumptions of normality; therefore, Kruskal-Wallis tests were performed to determine significant differences for crawl times, glucose concentrations, righting response time, and temperatures between treatment groups and species. If statistically significant differences were found ($p < 0.05$), Dunn's nonparametric post-hoc comparisons were conducted.

RESULTS

The addition of *Sargassum* increased the total amount of time it took hatchlings to crawl down the pathway and increased the number of inversions, but it did not affect blood glucose levels or time to self-right in the sea turtle hatchlings.

Crawl Times

The total time it took for the hatchlings to crawl the entire length of the pathway increased with the addition of *Sargassum* in all three species when compared with the crawl-control treatment (Table 1, Figure 3). All species showed a significant difference in total crawl time between the *Sargassum* treatments and the crawl control. Based on the median value, total leatherback hatchling times increased by 54.1% in the light *Sargassum* treatment and 158.1% in the heavy *Sargassum* treatment, loggerhead hatchling times increased by 90.6% in the light *Sargassum* treatment and 174.6% in the heavy *Sargassum* treatment, and green sea turtle hatchling times increased by 74.5% in the light *Sargassum* treatment and 158.5% in the heavy *Sargassum* treatment. No significant difference occurred between treatment groups within species for the time it took to crawl the first 13 m (Sand time column, Table 1).

The time it took hatchlings to climb up onto the heavy *Sargassum* treatment (17–19 cm high) was significantly greater for all species when compared with the climb time for the light (7–9 cm high) *Sargassum* treatment (Table 1). Based on the median value, leatherback hatchlings had a climb time that was 20.8 times longer, loggerhead hatchlings took 6.2 times longer, and green sea turtle hatchlings took 5.6 times longer.

The time it took the hatchlings to crawl down the path increased significantly in all three species when *Sargassum* was present, as compared with the crawl control; however, no significant difference occurred in *Sargassum* time between the light and heavy treatments for any species (Table 1). Based on the median value, leatherback hatchlings in *Sargassum* treatments took 179.5% longer (decreasing their

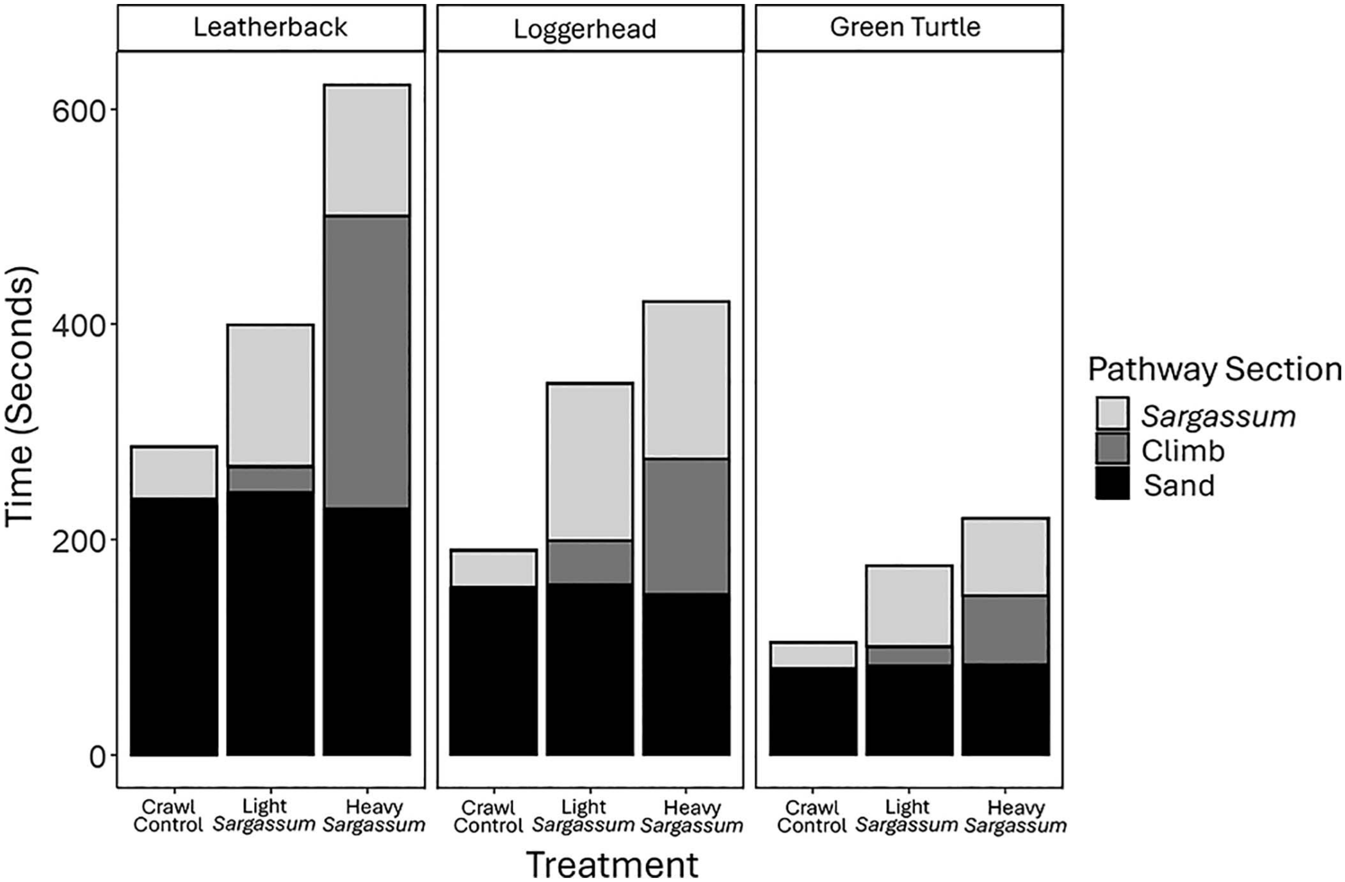

Figure 3. The median total time it took for leatherback, loggerhead and green turtle hatchlings to crawl the entire length of the pathway increased with the addition of *Sargassum* in all three species when compared to the crawl control treatments. Hatchlings took significantly more time to both climb up onto the *Sargassum* and to crawl across it than on the sand only control surface. Sand: time to crawl the first 13 meters on sand only. Climb: time to climb up to the top of the *Sargassum* pile. *Sargassum*: time to crawl the last 2 meters across varying heights of *Sargassum*, controls crawled across sand only for the final 2 meters.

speed from 0.045 m/s on sand to 0.016 m/s on *Sargassum*), loggerhead hatchlings in *Sargassum* treatments took 274.4% longer (decreasing their speed from 0.051 m/s on sand to 0.013 m/s on *Sargassum*), and green sea turtle hatchlings in *Sargassum* treatments took 200.0% longer (decreasing their speed from 0.083 m/s on sand to 0.027 m/s on *Sargassum*).

Inversions

The addition of *Sargassum* increased the number of times hatchlings inverted while crawling in the crawl pathway; these occurred when hatchlings were attempting to climb onto the pile. Turtles crawling onto the heavy *Sargassum* treatment had significantly greater numbers of inversions when compared with both the crawl control and light *Sargassum* treatments for all three species (Table 2). A higher number of inversions resulted in a longer climb time and total time (Figure 4).

Time Limit

In all species, a few hatchlings were not able to successfully crawl the entire length of the crawl pathway because they were unable to climb over the *Sargassum*. Out of the 60 hatchlings of each species that crawled down the pathway, four were leatherback hatchlings, five were loggerhead hatchlings, and two were green hatchlings that timed out during their crawling trial. These data are not included in the calculations of crawl times.

Blood Glucose

No species showed a significant difference in blood glucose concentrations between the treatments within species, with one exception (Table 2). Glucose levels in leatherback hatchlings in the no crawl–control treatment were significantly higher than all other treatment groups for that species.

Righting Response

No significant difference in righting response within any species occurred between treatment groups (Table 2).

Environmental Temperature

No significant correlation occurred between crawl time and sand or *Sargassum* temperature in any species, with one exception (Figure 5). Warmer sand temperatures correlated with faster crawl times in the heavy *Sargassum* treatment in

Table 2. *Median and interquartile range for number of hatchling inversions while in the crawl pathway, blood glucose levels, and righting response times.*

Treatment	Inversions	Glucose (mg/dL)	Righting Response (s)
		Leatherback	
No crawl	NA	115.5 (105, 141)†	1.36 (1.14, 1.49)
Crawl	0 (0, 0)	87 (80.5, 101)	1.24 (1.27, 1.32)
Light	0 (0, 1)	93 (79, 104)	1.28 (1.16, 1.52)
Heavy	2 (1, 7)†	91.5 (73.2, 105)	1.50 (1.37, 1.68)
		Loggerhead	
No crawl	NA	132.5 (89.5, 174.8)	0.83 (0.71, 0.99)
Crawl	0 (0, 0)	111 (97, 152)	0.79 (0.67, 0.86)
Light	0 (0, 1.25)	116 (97.5, 131)	0.78 (0.70, 0.83)
Heavy	1 (0, 4)†	115 (101, 128)	0.81 (0.73, 1.04)
		Green	
No crawl	NA	140 (114, 154)	0.61 (0.50, 0.75)
Crawl	0 (0, 0)	123 (102, 146)	0.60 (0.54, 0.70)
Light	0 (0, 0.25)	112.5 (96.8, 136)	0.61 (0.56, 0.76)
Heavy	2 (0, 4)†	120.5 (93.5, 150.2)	0.68 (0.54, 0.75)

†*Indicates significance. Data with multiple indicators are significantly different from each other for the same measurement. Significance is shown only within species, not between species.*
NA = not available

loggerhead hatchlings. Although this was the only significant correlation, an overall general effect of warmer environmental temperatures leading to faster crawl times occurred.

Across Species Comparison

All species showed an increase in the total time it took hatchlings to crawl the entire pathway with the addition of *Sargassum*. In general, leatherbacks and loggerheads had similar total times, with leatherbacks being slightly slower in the crawl-control treatment. Green turtles were significantly faster than the other two species in every treatment group (**Figure 5**). In each species, the climb time was responsible for the majority of the additional time that thus also increased the total crawl time. The number of inversions increased as the amount of *Sargassum* increased in all species, and the median number of inversions was not significantly different between species.

Blood glucose concentrations remained the same between treatment groups within each species, except for the leatherback in the no-crawl control. No significant difference in glucose levels between species was found in the no-crawl control. However, in all of the crawling trials, loggerheads and green turtles had significantly higher glucose levels than leatherbacks but were not significantly different from each other.

No species showed a difference in righting response between treatment groups within the same species, although differences were found between species. Leatherbacks were significantly slower to right themselves than loggerheads and green turtles in all treatment groups. In the no-crawl control as well as the crawl control, green turtles were significantly faster to right themselves than loggerheads; however, in the light and heavy *Sargassum* treatment, green turtles and loggerheads were not significantly different.

DISCUSSION

With warming ocean waters and increased nutrient levels, the amount of *Sargassum* washing up on shorelines of the

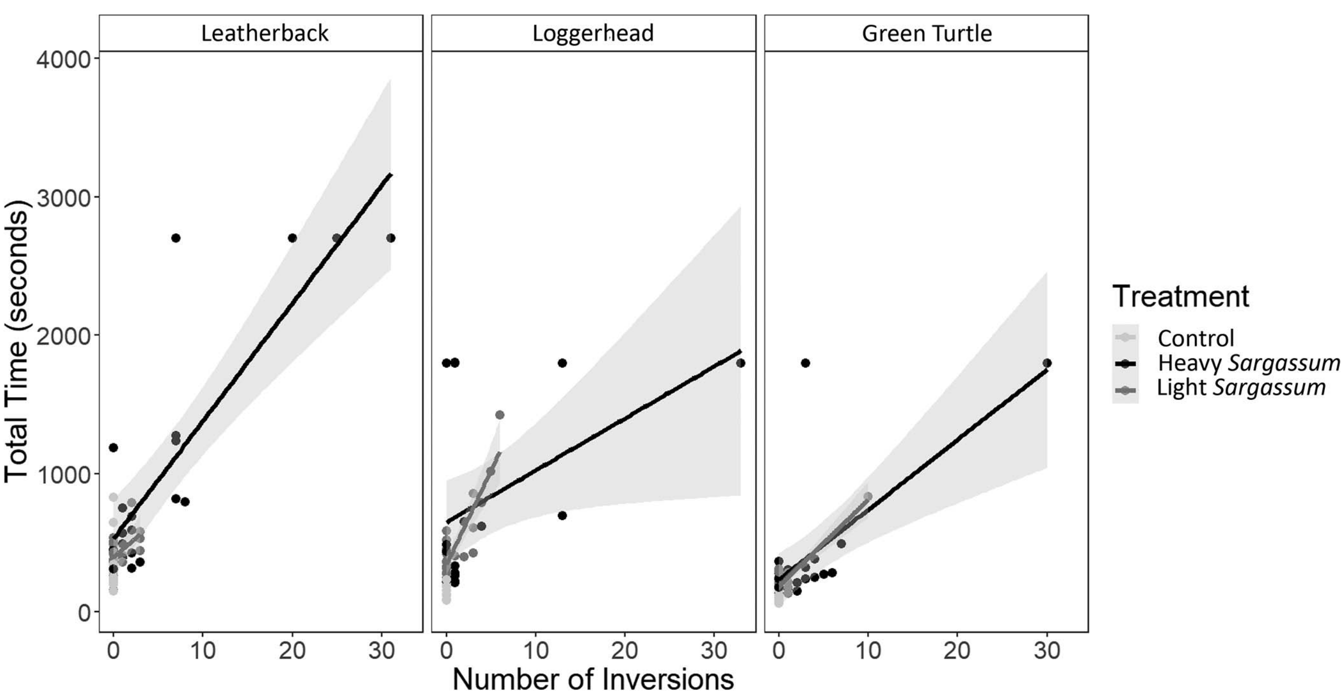

Figure 4. The number of hatchling inversions in all three hatchling species was positively correlated with total time to crawl the length of the entire pathway. Line shows the linear model, grey area is the 95% confidence interval.

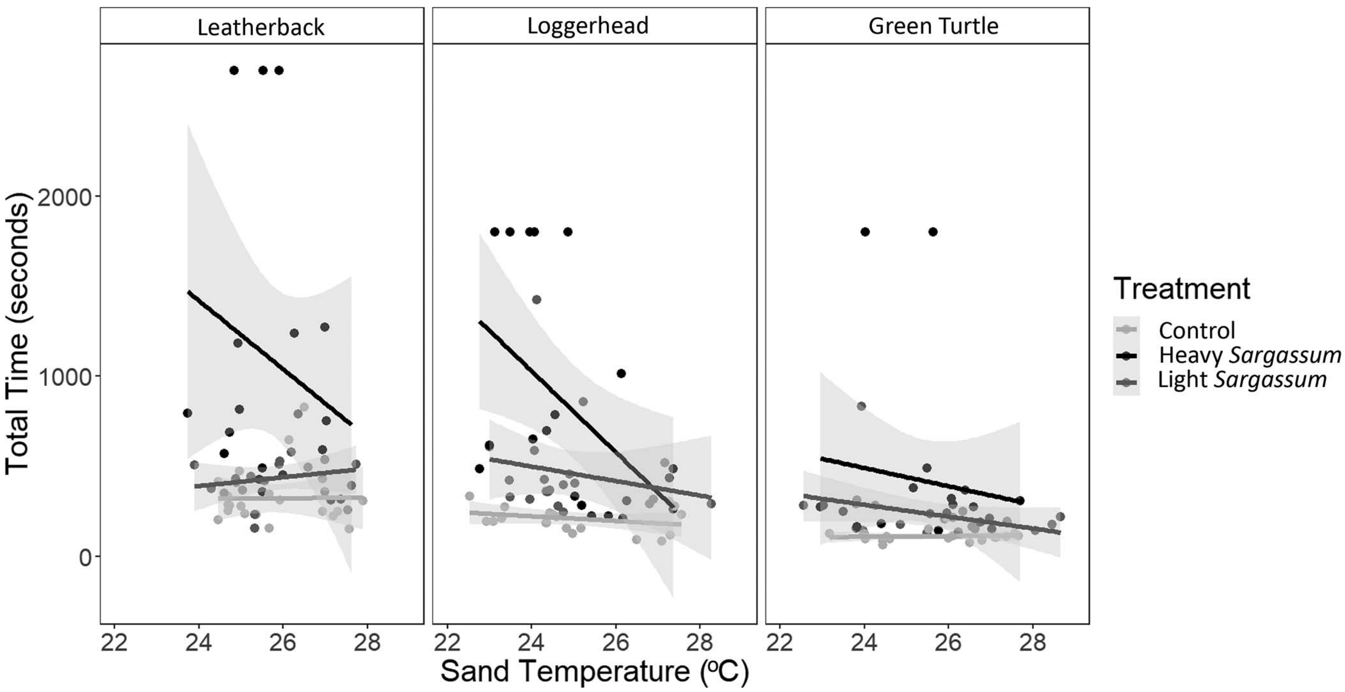

Figure 5. There is a general but not statistically significant correlation between warmer sand temperatures and lower total crawl time for each species in each treatment. Line shows the linear model, grey area is the 95% confidence interval.

western north Atlantic and Caribbean Sea has increased greatly in recent years, which may have significant effects on coastal species. In this study, the effect of *Sargassum* piles on sea turtle hatchling crawling ability down a 15 m path was examined. For 2 m long *Sargassum* piles either 7–9 cm or 17–19 cm high, the largest effect on leatherback, loggerhead, and green hatchlings crawling was a significant increase in the time they took to complete the total crawl. A significant increase in time spent crawling on the beach from the nest to the water would likely increase their risk of predation (Erb and Wyneken, 2019; Tomillo *et al.*, 2010). This finding is similar to an earlier study that found that crawling over seaweed on the beach decreased loggerhead hatchling crawl speed (Triessnig, Roetzer, and Stachowitsch, 2012). Another study found that a small number of loggerhead and green turtle hatchlings struggled to crawl through *Sargassum* while crawling to the water (Rodríguez-Martínez *et al.*, 2021). The current study examined only *Sargassum* heights up to 19 cm. So in areas in which *Sargassum* accumulation is even higher, it can be expected that the amount of time hatchlings will take to navigate this obstacle will increase even further, with the possibility of hatchlings not being able to climb over the pile at all, as reported by Schiariti and Salmon (2022).

In this study, multiple hatchlings were not able to climb up the pile (within the time limit), so as the height of *Sargassum* increases, the number of hatchlings failing to make it over the *Sargassum* will also likely increase. During the summer this study was conducted, *Sargassum* piles were more than 1 m high in some areas of South Florida beaches and could extend for hundreds of meters along the shoreline (Figures 1–2). In addition, hatchlings had to crawl over only one pile of *Sargassum* for this study; however, on some beaches hatchlings may encounter multiple bands of *Sargassum*. Climbing up the *Sargassum* created the largest increase in time spent on the beach, so climbing over multiple piles will further increase time spent crawling down the beach to the water. It was also found that crawling across the *Sargassum* patch increased time spent crawling when compared with bare sand regardless of *Sargassum* height, so even very light but widespread beach coverage would increase the amount of time spent crawling to the ocean.

During the heavy *Sargassum* trials, the number of times hatchlings inverted also significantly increased, with five hatchlings inverting more than 20 times while trying to navigate up the *Sargassum*. This increase in inversions is significantly correlated with an increase in total time as well as *Sargassum* climb time. Spending time upside down on the beach makes hatchlings more vulnerable to predation, and if they fail to right themselves, this alone can also increase mortality (Tomillo *et al.*, 2010). Hatchlings try to move as quickly as possible down the beach to avoid predators, so any added time spent on the beach when encountering *Sargassum* increases the time they are exposed to potential predators, as well the potential for overheating and desiccation after dawn (Burger and Gochfeld, 2014; Spencer and Janzen, 2011).

Despite the varying lengths of time it took hatchlings to crawl up and over the *Sargassum* piles, glucose concentrations post-crawl did not differ significantly by treatment group. Glucose levels observed in this study for all species were similar to previously reported values (Fleming *et al.*, 2020; Hamann, Jessop, and Schäuble, 2007; Pereira *et al.*, 2012; Perrault *et al.*, 2022). Only leatherback hatchlings in the no-crawl control had significantly higher glucose concentrations when compared with the other groups within the species. This suggests that crawling down the beach can have an effect on blood analytes, at least in leatherbacks, but the addition of *Sargassum* did not have an added influence.

A reduction in glucose levels can have an effect on hatchling locomotion because it acts as a fuel source (Hamann, Jessop, and Schäuble, 2007); however, this does not appear to be a large concern while crawling over *Sargassum* because neither a drastic drop in glucose nor an increase suggestive of glycogen breakdown due to a stress response was seen. Studies observing hatchlings crawling up to 500 m and then swimming for 2 hours did not see significant changes in plasma glucose when compared with hatchlings that did not crawl or swim (Hamann, Jessop, and Schäuble, 2007; Pankaew and Milton, 2018; Pereira *et al.*, 2012), so the fact that no difference was observed in hatchlings crawling only 15 m with a 30- or 45-minute time limit is not surprising. If hatchlings were to face multiple or higher piles of *Sargassum* that they struggled to climb over for an extended period of time, then a difference in blood glucose might be observed, which would affect the energy reserves required to swim up to 24 hours during the frenzy period. No difference in righting response was noted when hatchlings were tested in water after the crawl trial.

To measure a physical response in the hatchlings, a righting response was used as a proxy for physical aptitude, with longer righting response times correlating with lower physical abilities (Delmas *et al.*, 2007; Dial, 1987). Conducting the righting response in water mimics hatchlings becoming overturned by waves in the ocean during the frenzy swim (Fleming *et al.*, 2020). No significant difference between righting response times within species was found for the various treatment groups, so crawling over various amounts of *Sargassum* does not appear to have an effect on the immediate physical ability of hatchlings in water.

All species followed similar patterns across the different treatment groups in that as *Sargassum* cover increased, total time required to crawl the 15 m increased. Overall, green turtles crawled much faster than leatherback and loggerhead hatchlings and were able to more quickly climb the *Sargassum* piles (Figure 6). This suggests that with more *Sargassum*, leatherbacks and loggerheads would be more vulnerable to predation and possible exhaustion than green turtles when navigating *Sargassum* because they would spend more time on the beach. Green turtles' ability to navigate down the beach and over *Sargassum* more quickly than the other two species may be because they emerge from nests laid closer to the dunes, because green females in general nest higher up the beach than loggerhead or leatherback turtles (Wetterer *et al.*, 2007; Mrosovsky, 1983).

Perhaps green turtle hatchlings are more suited to climb over vegetation because they are more likely to encounter beach plants in the dunes than the other two species and have greater distances to crawl to the surf line. Green turtles also have a larger aerobic scope, which may help them move more quickly (Lutcavage and Lutz, 1986). Leatherbacks may have the slowest times because their elongated flippers and body shape are adaptations for deep diving and a more pelagic existence compared with other sea turtle species (Wyneken, 2015). Because of morphology needed to perform these activities in the ocean, they may not be able to navigate on land and over vegetation as easily as loggerhead and green turtle hatchlings. Leatherback hatchlings also lack claws on their flippers (Figure 7), which may help loggerhead and green turtle hatchlings grip onto the *Sargassum* more easily. In addition to physical aptitude, *Sargassum* may affect species differently because of differences in their nesting season.

Figure 6. Green turtle hatchlings are best able to crawl over Sargassum mats. Juno Beach, Florida, July, 2021. (Photo credit: A. Appelt.)

Based on observations during the study, *Sargassum* washed up on the beach from March until September 2021 with a peak from May to July, which was similar to other years (Appelt, *personal observation*). This seasonal change in *Sargassum* makes leatherback and loggerhead hatchlings (and nesting females) more likely to encounter *Sargassum* based on their nesting season in south Florida. Leatherbacks generally nest between March and June, with hatchlings emerging in May through August, whereas loggerheads primarily nest in May and June, with far fewer females coming ashore in July and later (Bjorndal, Meylan, and Turner, 1983; Stewart *et al.*, 2011). Green turtle peak nesting occurs

Figure 7. Leatherback hatchlings, which lack claws on the front flippers and are larger with longer flippers than either green or loggerhead sea turtle hatchlings, have the most difficulty navigating over Sargassum mats. Juno Beach, Florida, July, 2021. (Photo credit: A. Appelt.)

from June to August, thus the eggs hatch out later in the season, after the main peak of *Sargassum* accumulation has occurred. Green turtles were the fastest at navigating through the *Sargassum*, and they are the species that this macroalgae will likely affect the least. However, on beaches in Florida, some green turtle hatch outs begin in July, so *Sargassum* may have a greater effect in these areas.

As reptiles, sea turtle metabolism and performance are greatly influenced by environmental temperatures; in this case, sand temperatures could affect metabolic rate and speed. Moving more quickly over warmer sand has been documented in different species, such as olive ridley sea turtle hatchlings (Burger and Gochfeld, 2014). Although sand temperature only had a significant effect on loggerhead hatchlings in one treatment group, all species showed a general trend of faster crawl times when the sand was warmer. Higher *Sargassum* temperature also showed the same general trend of faster crawl times; however, it was not significant, which may be because a relatively narrow range of temperatures occurred.

Sand temperatures were all within 6°C of each other, *Sargassum* temperatures were within 8°C of each other, and, of course, air temperatures would not vary significantly from one end of the crawl path to the other. Thus, there may not have been a large enough range of sand temperatures to observe an effect on locomotion. Although the *Sargassum* temperature range was larger, it may have been that the temperatures were not warm enough that a further change in performance would occur or that sand temperature made more of an effect because hatchlings typically were in contact with *Sargassum* for the shortest amount of time in the crawl pathway.

CONCLUSIONS

The key finding of this study is that as the amount of washed up *Sargassum* increases, hatchlings will spend more time on the beach crawling to the water (Figure 1). A large effect does not appear to occur on hatchling energetics with *Sargassum* pile heights up to 19 cm because no significant changes in glucose or righting ability were noted. With increasing *Sargassum* abundance, exposure to potential predators for longer periods of time will likely have the largest influence. However, when *Sargassum* accumulates to a height in which hatchlings can no longer crawl over it (~30 cm), increased physical and physiological effects may occur as hatchlings spend more time and energy trying to climb over or around obstacles (Schiariti and Salmon, 2022).

This study did not account for hatchlings trying to navigate around the *Sargassum* because they were in an enclosed pathway, although a few crawled along the edge of the pile as though attempting to go around it. So, when *Sargassum* is too high for hatchlings to crawl over, they may expend time and energy trying to circumvent the *Sargassum*; however, when *Sargassum* washes up, it can cover kilometers of the beach (Figures 1–2) and hatchlings being able to circumvent such piles is unlikely.

The *Sargassum* phenomenon continues to increase and will have a larger effect on sea turtles as more mats wash onto the beach. Along with the effect on hatchlings observed in this study, *Sargassum* has been observed to have a negative influence on the amount of available nesting beach as well as altering incubating nest temperatures (Maurer, Gross, and Stapleton, 2022; Maurer, Stapleton, and Layman, 2019; Maurer *et al.* 2021). Although the complete removal of *Sargassum* from the beach is not necessarily the best option for the ecosystem, the amount of *Sargassum* accumulating has an effect on sea turtles and should be considered when creating management plans (Williams and Feagin, 2010; Williams, Feagin, and Stafford, 2008). Possible considerations include removing or burying *Sargassum* when heights reach more than 30 cm or to taking special care to thoroughly check the *Sargassum* for hatchlings during morning sea turtle nesting surveys. Large amounts of *Sargassum* would reduce the number of hatchlings that make it to the water and should be accounted for in end-of-year hatchling estimates; these numbers estimate the number of hatchlings that were produced during the nesting season and are a valuable part of population modeling, as well as species recovery plans.

Further research would be beneficial to better understand how many hatchlings are negatively affected by *Sargassum* and its effects on the likelihood of hatchling survival.

Updates may be needed to recovery plans, as well as beach management plans, to account for the effect of *Sargassum* on sea turtle hatchlings.

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