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Factors regulating incubation temperature and thermal stress in hawksbills in St. Croix, USVI

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ABSTRACT: The hawksbill sea turtle is listed as Critically Endangered under the IUCN Red List and has been slow to recover in the Caribbean due to historical exploitation and ongoing anthropogenic threats. In turtles, sex and reproductive success are determined by incubation temperatures, whereby lower temperatures produce male hatchlings and higher temperatures produce female hatchlings. As incubation temperatures increase due to climate change, nests are predicted to produce predominantly female hatchlings, threatening sex ratios, reproductive success, and species persistence. One of the largest remaining nesting hawksbill populations within the USA nests on Buck Island. This study aimed to (1) assess the factors driving incubation temperatures and (2) identify the relationship between hatch success and the proportion of time exposed to increasing incubation temperatures. Nest incubation temperatures, beach sector, habitat type, deposition month, percent soil composition, hatch success, and emergence success data were collected from 2019 to 2021. Differences in incubation temperatures across these factors confirmed that the absence of vegetative cover is increasing incubation temperatures on Buck Island, leading to reduced hatchling survival. Results from this study indicate that declines in hatch success may be driven by long-term exposure to temperatures that were previously considered in the literature to be non-lethal to embryos. These findings emphasize the continued need for conservation interventions to protect the future of hawksbills.

KEY WORDS: Hawksbill · Thermal stress · Climate change · Embryonic mortality

1. INTRODUCTION

The hawksbill sea turtle *Eretmochelys imbricata* is a circumtropical marine reptile that relies on hard bottom and coral reef ecosystems for its predominantly sponge-based diet (Meylan 1988, León & Bjorndal 2002, Rincon-Diaz et al. 2011). As with other chelonians, hawksbills migrate varying distances between foraging grounds and mating or nesting grounds to lay eggs on or near the beach where they themselves hatched (Miller 1997). A variety of threats has contributed to the global decline of approximately 80–90% of hawksbills throughout the last few hundred years, including harvest for their eggs, meat, and carapaces, loss of nesting and foraging habitat, entanglement in fishing gear, ingestion of marine debris, oil

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spill pollution, and boat strikes (NMFS USFWS 1993, Meylan & Donnelly 1999, Fuentes et al. 2013). Collectively, these factors led the International Union for Conservation of Nature (IUCN) to list hawksbills as Critically Endangered (Appendix 1) in 1996 (IUCN 1996). The species has also been listed as endangered under the United States Endangered Species Act throughout its entire range since 1973 (NMFS USFWS 1993, Mortimer & Donnelly 2008). However, increasing local temperatures and inundated nesting habitats, both stemming from global climate change, may represent the greatest threat to the continued existence of these animals (Bellard et al. 2012, IPCC 2014). Climate change and associated sea level rise may disproportionately affect the egg phase, as embryos are immobile, susceptible to drowning by inundation, and highly sensitive to the ambient temperature inside the egg chamber (Hawkes et al. 2009, Pike 2014).

A hatchling's sex is determined by the incubation temperature inside the nest cavity (temperature-dependent sex determination, TSD) during the middle third of incubation (thermosensitive period) (Godfrey et al. 1999, Mrosovsky et al. 2009). Increased temperatures produce more females and cause higher embryonic mortality and decreased hatch success (Hawkes et al. 2007, Fuentes et al. 2009). Sustained variances from the pivotal temperature (T_{PIV}), at which 50% of hatchlings are male and 50% are female, during the thermosensitive period can result in skewed sex ratios among hatchlings (Mrosovsky et al. 1992, Godfrey et al. 1999, Mrosovsky et al. 2009, Laloë et al. 2014, 2016). T_{PIV} varies for different species, populations of the same species, and between clutches; 29°C is the estimated T_{PIV} for hawksbills in the Caribbean based on relevant literature (Mrosovsky et al. 1992, Wibbels 2003). Metabolic heat, or the heat produced by the process of converting yolk to embryonic cells, is estimated to increase incubation temperatures by 0.5°C throughout incubation (Laloë et al. 2014, 2016, Gammon et al. 2020). This increase in incubation temperature could potentially push embryos already close to their upper thermal maximum much closer to, or over, lethal temperatures as threats from climate change increase (Laloë et al. 2017). For hawksbills, thermally induced embryonic mortality is suspected to occur at approximately 35°C; however, the duration of exposure to near-lethal temperatures may be a larger driver of embryonic mortality and is also mediated by the individual size of the embryo (Valverde et al. 2010, Howard et al. 2014, Girondot et al. 2018). When incubation temperatures approach the upper lethal limit, available oxygen is reduced and phenotypic and locomotive abnormalities can cause embryonic mortality and reduce the emergence of live hatchlings (Matsuzawa et al. 2002, Du & Ji 2003, Segura & Cajade 2010, Howard et al. 2014). Higher incubation temperatures can also negatively impact hatchling fitness characteristics such as carapace size, crawling speed, and self-righting speed, increasing the risk of predation after emergence (Ischer et al. 2009, Read et al. 2012, Wood et al. 2014). Depth of the nest cavity, precipitation, air temperature, color of the sand, and tidal inundation all affect the overall temperature of the egg chamber (Laloë et al. 2014, 2016).

Air temperature models and other field studies estimate that hatchling sex ratios in the Caribbean have been historically female dominated and will continue to be so under future climate scenarios (Wibbels et al. 1999, Laloë et al. 2016). Evidence also suggests that naturally skewed female sex ratios are an adaptation to increase natural population growth rates and genetic diversity (Santidrián Tomillo et al. 2015). Larger populations of breeding females produce more clutches each nesting season than smaller populations of breeding females, increasing fecundity within the population and the number of viable hatchlings (Santidrián Tomillo et al. 2015). Studies on other species of sea turtle have found that males breed more frequently (annually) than females (bi- or tri-annually), and this balance of reproductive activity may potentially offset female-skewed hatchling sex ratios (Wright et al. 2012, Hays et al. 2014). Promiscuity among females that leads to multiple paternity (MP) within clutches may hypothetically increase genetic diversity and offset the decline of male hatchlings associated with increased incubation temperatures (Hillbrand 2018). Although these adaptations may have historically offset skewed female sex ratios, if there are too few males available to fertilize available eggs, hawksbill and other sea turtle populations may experience an Allee effect (Bell et al. 2010, Wright et al. 2012, Laloë et al. 2014). Models suggest that depensation may occur in marine turtles when populations drop below 5% of the historical population size; however, the above characteristics make this threshold highly complex, and depensation in marine turtles remains understudied in the literature due to its complicated nature (Bell et al. 2010). The evolutionary advantages provided by TSD may not persist under future climate models, and female-dominated operational sex ratios may lead to population declines, local extirpation, and extinction (Santidrián Tomillo et al. 2015).

The 2 hawksbill index nesting beaches in the USA occur exclusively in the Caribbean, on Mona Island, Puerto Rico, and on Buck Island in St. Croix, US Virgin Islands (Spotila 2004). Although historical population data are lacking for hawksbills, it is estimated that populations in the Caribbean have seen reductions of up to 75%; also, population estimates suggest that approximately 13 000 nesting females remain in the wider Caribbean (Beggs et al. 2007, Mortimer & Donnelly 2008, Leroux et al. 2012). Although hawksbill sea turtle management units in the Western Atlantic have been identified as more resilient to climate change compared to other management units (East Pacific, Southwest Atlantic, and East Atlantic), this population is still vulnerable to future anthropogenic stressors (Fuentes et al. 2013). Decreases in MP rates among clutches may indicate that populations are becoming male-limited and may prove to be problematic for future egg fertility levels (Hays et al. 2022). Hawksbills historically have some of the lowest levels of MP (10% for the nesting population at Buck Island) compared to other sea turtle species, putting them at a potentially higher risk of fertility issues in the face of increased climate change (Hillbrand 2018). This low percentage of MP could be due to the already small population of hawksbills at Buck Island Reef National Monument (BIRNM), where encountering multiple mates is difficult. If this is the case, decreases in genetic diversity could already be occurring for this nesting population. A recent study on Buck Island found declines in nest abundance, the occurrence of new nesting females, female body size, and clutch size (Gulick et al. 2022). This decline, coupled with high instances of feminization as indicated in a previous study, indicates that the overall productivity of this population may already be decreasing (Wibbels et al. 1999). This decline in productivity, in concurrence with increasing anthropogenic threats, highlights the urgent need for managers to evaluate the factors influencing incubation temperatures and implement management practices to reduce incubation temperatures on Buck Island.

This multi-year study assessed the relationship between incubation temperatures and the physical characteristics of Buck Island beaches to identify nesting areas at higher risk of thermal stress and factors affecting incubation temperatures. The physical characteristics examined were habitat type, beach sector, soil composition, and deposition month. Tropical storm activity and its potential impact on incubation temperatures was observed but not quantified. Furthermore, the relationships between hatch success, emergence success, temperature, and percentage of time spent above multiple critical temperature thresholds were also assessed. We hypothesize that the presence or absence of vegetation is the main factor driving incubation temperatures on Buck Island and that length of exposure to high temperatures is more detrimental to hatch success and emergence success than previously considered in the literature.

2. MATERIALS AND METHODS

Buck Island is a 176 acre (71 ha) forested tropical island within BIRNM in the US Virgin Islands and has been managed by the National Park Service since 1961 (NPS 2012). Buck Island has 4 beaches: North Shore (NS), West Beach (WB), South Shore (SS), and Turtle Bay (TB), totaling 1.5 km (Fig. 1). Each beach sector consists of 3 habitats from inland to shore: beach forest (BF), seaward vegetation (SV), and open beach (OB), respectively. Hawksbill turtles prefer nesting in areas with dense forested habitat, and on Buck Island, this habitat is more commonly found on NS and SS than on the other beaches (Kamel & Mrosovsky 2005). This habitat preference causes hawksbill nesting on Buck Island to be concentrated on these 2 beaches.

The National Park Service implemented the Buck Island Sea Turtle Research Program to monitor and conduct saturation tagging for hawksbill turtles in 1988. Since then, from July to October, researchers patrol Buck Island on a nightly basis to monitor nesting females during peak nesting season. During monitoring, nesting females are tagged, tissue is biopsied, and information is collected on nesting behavior, site selection, fecundity, and size. The information includes distance from the nest to SV, distance to high water mark, GPS location, soil composition, and distance to nearest vegetative cover species. Over the study period (July–November 2019, 2020, and 2021), soil composition data were recorded as a percentage of the amount of soil present (0% soil, 25% soil, etc.). Vegetative cover species were identified (using the Buck Island (BUIS) coastal vegetation handbook; Roberson et al. [date unknown]) and recorded for the vegetation that provided most of the shading for each nest.

Each nest was excavated and inventoried 72 h after the first signs of emergence or 70 d after deposition to ensure that all hatchlings had an opportunity to escape the nest on their own. These data were collected to calculate hatch and emergence success for each nest. Hatch and emergence success were determined using the following equations (Zárate et al. 2013):

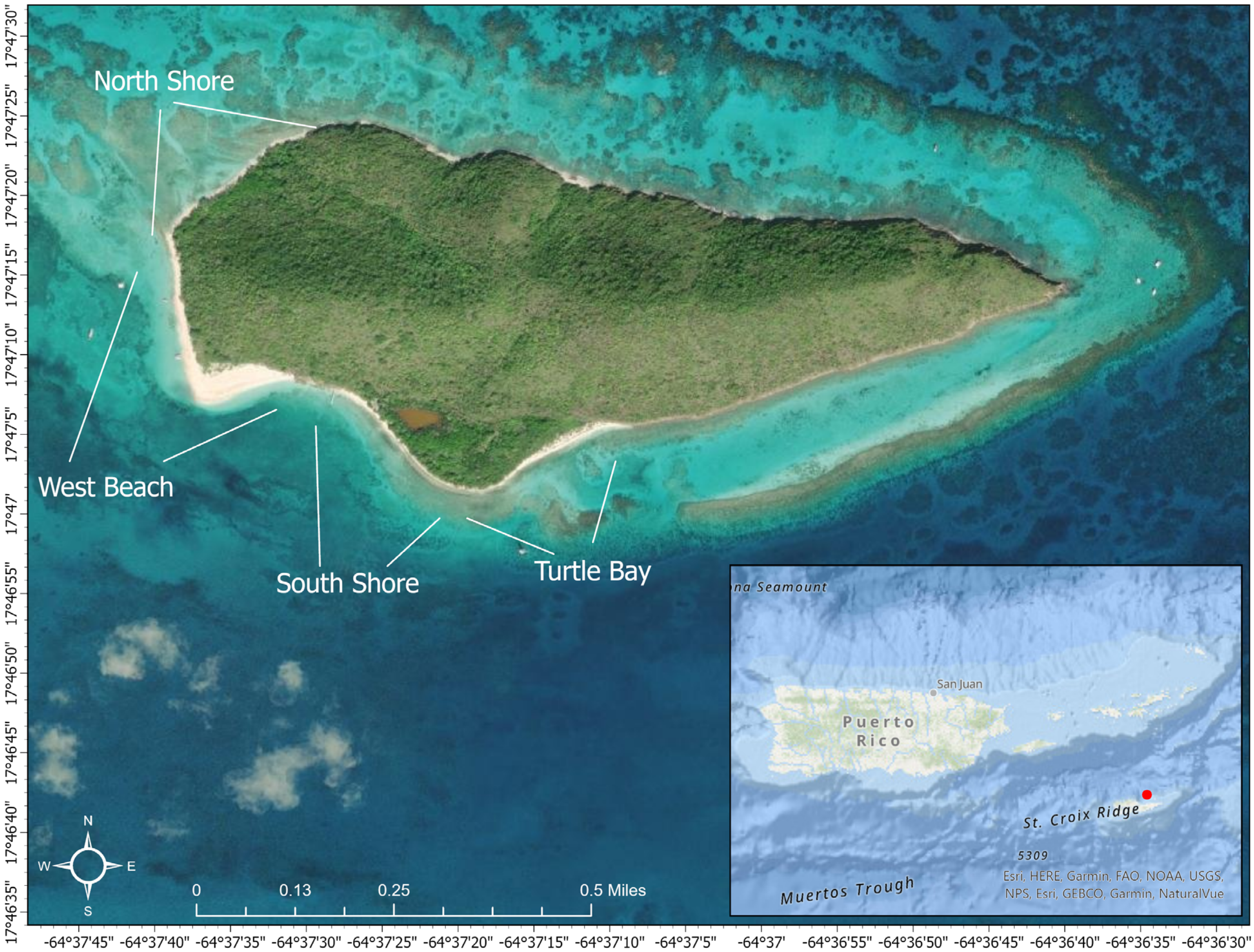

Fig. 1. The 4 survey beaches for hawksbill turtles on Buck Island in relation to the wider Caribbean region

$$\text{Hatch success} = \frac{\text{total eggs} - \text{unhatched eggs}}{\text{total eggs}} \times 100 \quad (1)$$

$$\text{Emergence success} = \frac{\text{total eggs} - \text{unhatched eggs} - \text{dead hatchlings}}{\text{total eggs}} \times 100 \quad (2)$$

Nests that were laid near or below the mean high tide water line and, in rare instances, in high-use recreation areas were deemed imperiled and were relocated within 1–2 h of egg deposition. Eggs were collected from the original egg chamber during or just after deposition and relocated to an artificial chamber at the same depth as the original egg chamber, approximately 51.5 cm deep for hawksbills on Buck Island. Artificial egg chambers were dug by technicians in a location away from the high tide line, where vegetation root systems were not too complex and some shade was likely to be provided. The eggs were covered with packed sand to imitate the covering process by the female.

2.1. HOBO temperature logger protocol

A total of 76 Onset HOBO temperature loggers (model: HOBO Pendant Temp/Light, 64K; temperature accuracy: ±0.53°C from 0°–50°C [±0.95°F from 32°–122°F]; temperature resolution: 0.14°C at 25°C [0.25°F at 77°F]) were deployed over all 3 yr of the study (2019, 2020, and 2021). On Buck Island, nests that contain 50% or greater soil content are sometimes treated with white sand to reduce incubation temperatures. This management technique was applied throughout the 2019, 2020, and 2021 seasons. Nests that are at risk of imperilment from a variety of mechanisms (tidal inundation, human disturbance, etc.) are relocated. This was considered a treatment during this study. A total of 71 loggers were deployed and successfully recovered during this study (2019: n = 23; 2020: n = 25; 2021: n = 23). Of those loggers, 29 were in untreated nests or nests that were not relocated and/or did not receive white-sand treatment (2019: n = 15; 2020: n = 7; 2021: n = 7). Loggers were distributed across each of the BUIS beaches (NS, WB, SS, and TB) and within all habitat types (BF, SV, and OB) in both *in situ* and relocated hawksbill turtle nests. All loggers were programmed to begin recording at 21:00 h AST and were set to take measurements at 1 h intervals. For *in situ* nests, each logger was deployed roughly halfway through egg deposition (after roughly 40–50 eggs had been deposited) and was placed in the center of the egg chamber so that the logger was surrounded by eggs and accurately recorded the temperature for the center of the clutch. For relocated nests, the logger was deployed roughly halfway through egg re-deposition following the same protocol outlined above. All loggers were left within nests until excavations occurred, approximately 72 h after emergence.

2.2. Hurricane impacts

Two tropical systems affected weather patterns within the region of Buck Island during each of the 3 study seasons. In the 2019 season, category 1 Hurricane Dorian suspended night patrols from 27–28 August, and Tropical Storm Karen suspended night patrols on 24–25 September. In the 2020 season, Tropical Storm Isaias suspended night patrols from 28–30 July and Tropical Storm Laura suspended night patrols from 20–22 August. In the 2021 season, Tropical Storm Fred suspended night patrols on 10 August and Tropical Storm Grace suspended night patrols on 15 August. The impacts and potential importance of these tropical systems in regulating incubation temperatures were noted but not quantified in this study.

2.3. Statistical analysis

Analyses were conducted using the R statistical language (version 4.3.1; R Core Team 2023) on macOS Ventura 13.4.1, using packages such as 'lubridate', 'report', and 'emmeans' (Grolemund & Wickham 2011, Wickham 2016, Lenth 2023, Makowski et al. 2023, Pinheiro et al. 2023). All statistical analysis was conducted using an alpha level of $\alpha = 0.5$. We fitted a linear mixed model (estimated using REML and 'nlminb' optimizer) to predict temperature with beach sector, habitat, percent soil, and deposition month (formula: Temp ~ BeachSector + Habitat + PercentSoil + DepMonth). The model included year as a random effect (formula: ~1 | Year). Standardized parameters were obtained by fitting the model on a standardized version of the data set. Confidence intervals (95% CIs) and p-values were computed using a Wald *t*-distribution approximation. The incubation temperature used in the analysis was the average temperature over the entire incubation period, which encompassed the time from when the HOBO loggers were deployed in the nest (as recorded in the field) until the nest began to cool, indicating hatching and emergence had occurred. This cooling was identified in the post-processing phase of data analysis by visual analysis of temperature curves since nests were not monitored for the exact time of emergence. Emergence was estimated from daytime monitoring and loggers were removed during excavation, approximately 72 h after first recorded signs of emergence.

We performed 3 independent Welch's 2-sample *t*-tests in order to test the differences in incubation temperature between nests treated and not treated with white sand, the differences in hatch success between nests that were and were not relocated, and the differences in incubation temperature between nests that were and were not relocated. Effect sizes were labeled following Cohen's (1988) recommendations. We fitted multiple linear models (estimated using ordinary least squares, OLS) to make predictions about the relationships between hatch success and average incubation temperature and hatch success with the proportion of time spent above 33°C (Prop33), 34°C (Prop34), and 35°C (Prop35), respectively. Standardized parameters were obtained by fitting the model on a standardized version of the data set. The 95% CIs and p-values were computed using a Wald *t*-distribution approximation. The proportion of time spent above 33°C, 34°C, and 35°C was calculated using the equation below, where measures were recorded every hour:

$$\frac{\text{total \# of measures} > 33°\text{C}}{\text{total \# of measures during incubation period}} \times 100 \quad (3)$$

3. RESULTS

The average incubation period across the 3 yr of study was approximately 53 d. Three independent *t*-tests were conducted to determine differences between 2 groups. The incubation temperature of nests treated with white sand (n = 32 954; mean: 32.2°C) was significantly higher than that of nests not treated with white sand (n = 60 934: mean: 32.0°C) based on a 2-sample *t*-test (Table 1). The incubation temperature of *in situ* nests (n= 63 293; mean: 32.0°C) was significantly lower than relocated nests (n = 30 595; mean: 32.1°C) based on a 2-sample *t*-test (Table 1). The hatch success of *in situ* nests (n = 46; mean: 64.5%)

Table 1. Results from all *t*-test analyses identifying differences between 2 groups. Results include: incubation temperature between nests treated with and without white sand, incubation temperature between relocated and *in situ* nests, and hatch success between relocated and *in situ* nests

Variable	Difference	95% CI	*t*	p
White sand by temp	−0.23	[−0.25, −0.21]	$t_{67475.18} = -19.74$	<0.001
Relocation by temp	−0.09	[−0.11, −0.07]	$t_{63440.61} = -7.75$	<0.001
Relocation by hatch success	−2.29	[−2.61, −1.97]	$t_{55821.77} = -13.91$	<0.001

was significantly lower than relocated nests (n = 24; mean: 66.8%) based on a 2-sample *t*-test (Table 1). Because of these results, nests treated with white sand and nests that had been relocated were removed from analysis to reduce the introduction of confounding variables, leaving 22 nests for analysis.

For the 2019 season, incubation temperatures across all remaining nests averaged 31.6°C and ranged from 27.0° to 35.9°C. For the 2020 season, incubation temperatures averaged 32.5°C and ranged from 29.2° to 36.2°C. Finally, for the 2021 season, incubation temperatures averaged 31.8°C and ranged from 28.7° to 35.9°C. Incubation temperatures in nests on Buck Island increased from the beginning of incubation to the end of incubation (Fig. 2). There was also a visually steeper increase in incubation temperature during the last third of incubation and an obvious decrease associated with the passage of tropical storms.

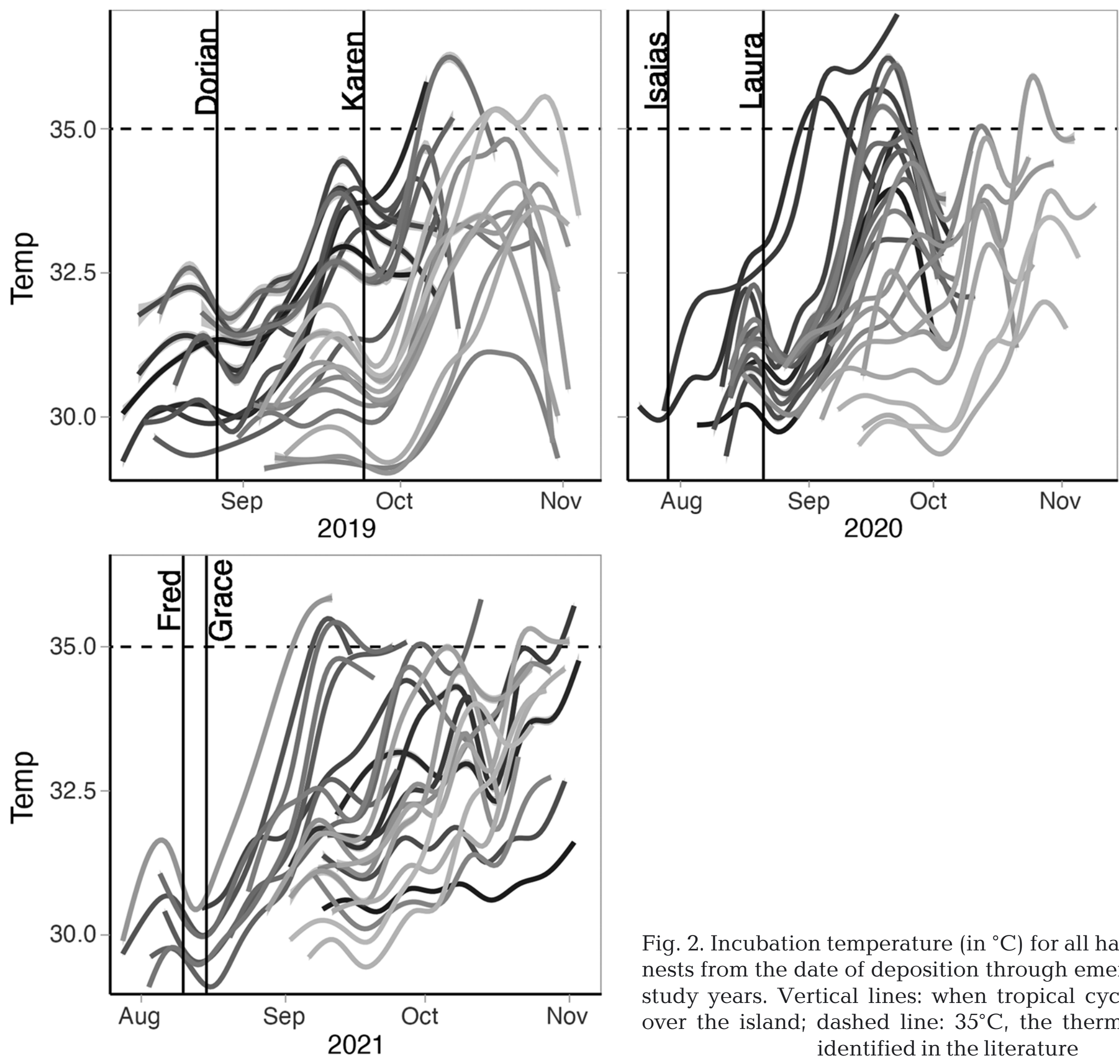

Fig. 2. Incubation temperature (in °C) for all hawksbill turtle nests from the date of deposition through emergence for all study years. Vertical lines: when tropical cyclones passed over the island; dashed line: 35°C, the thermal maximum identified in the literature

The linear mixed model for predicting incubation temperature across beach sector, habitat, percent soil, and deposition month had weak total explanatory power (conditional $R^2 = 0.12$); the part related to the fixed effects alone (marginal R^2) was 0.07. The model's intercept, corresponding to beach sector = NS, habitat = BF, percent soil = 0%, and deposition month = August, was 31.68 (95% CI = [31.22, 32.13], $t_{37851} = 135.88$, $p < 0.001$). Within this model, the effect of the SS beach sector, OB habitat, SW habitat, 100% soil composition, 75% soil composition, 25% soil composition, 0% soil composition, and the deposition month of July were all statistically significant and positive (Table 2). Within this model, the effects of the TB and WB sectors were statistically significant and negative (Table 2). Overall, for the beach sector, incubation temperatures were generally higher on the southern side of the island and cooler on the northern side. For the different habitat types, BF habitat was the coolest, followed by SV and OB. For percent soil, the trend was less clear, but in general, the lower the percent soil content, the higher the incubation temperatures. Finally, for deposition month, incubation temperatures tended to be higher in July and cooled through September (Fig. 3).

The linear model shows a significant negative relationship between hatch success and incubation temperature and explains 24% of the variance in hatch success (Table 3, Fig. 4). Current literature indicates that 35°C is the upper thermal maximum for successful incubation, and additional linear models were used to predict if the proportion of time spent above 33°C (Prop33), 34°C (Prop34), and 35°C (Prop35) may also be significantly impacting hatch success. These linear models showed a significant negative relationship between hatch success and the proportion of time spent above 33°C, 34°C, and 35°C (Fig. 5), and the models explain 17%, 21%, and 21% of the variance in hatch success, respectively (Table 3). Results summarizing the linear model intercepts and effect for each of the relationships between hatch success and the proportion of time spent above 33°C, 34°C, and 35°C can be found in Tables S1 & S2 in the Supplement at www.int-res.com/articles/suppl/n053p247_supp.pdf.

4. DISCUSSION

From 1880 to 2012, combined sea surface and air temperatures have increased globally by 1.1°C, and future mean surface temperature models predict an increase of 2.5–4.0°C by the end of the 21st century (IPCC 2021). These trends highlight an unknown future for hawksbill populations, especially in the Caribbean. Our study determined the physical drivers of incubation temperatures on Buck Island and affirmed the negative relationship between hatch success and incubation temperature. Our study also draws on the importance that the proportion of time spent near lethal temperatures has on hatch success and calls for this situation to be further studied in the literature to better understand thermally induced mortality in sea turtles. We highlight an array of management practices that might be practical on Buck Island for reducing incubation temperatures in hawksbill nests.

4.1. Impacts of vegetative cover, soil composition, and nest location on nest temperatures

The relationship between incubation temperatures and habitat characteristics highlights the role that vegetative cover and shading play in reducing incu-

Table 2. Results from the linear mixed effect model on the relationship between incubation temperature for hawksbill turtle nests and the variables of habitat, beach sector, percent soil, and deposition month. SS: South Shore; TB: Turtle Bay; WB: West Beach; OB: open beach; SV: seaward vegetation

Variable	Level	β	95% CI	t	p
Beach sector	SS	0.29	[0.25, 0.34]	$t_{37851} = 12.54$	<0.001
Beach sector	TB	−0.40	[−0.48, −0.32]	$t_{37851} = -9.73$	<0.001
Beach sector	WB	−0.54	[−0.69, 0.39]	$t_{37851} = -6.98$	<0.001
Habitat	OB	0.81	[0.72, 0.89]	$t_{37851} = 19.05$	<0.001
Habitat	SV	0.64	[0.58, 0.69]	$t_{37851} = 23.35$	<0.001
Percent soil	100	0.45	[0.35, 0.56]	$t_{37851} = 8.54$	<0.001
Percent soil	75	−0.28	[−0.33, −0.24]	$t_{37851} = -11.52$	<0.001
Percent soil	25	0.17	[0.12, 0.22]	$t_{37851} = 6.40$	<0.001
Percent soil	0	0.71	[0.65, 0.78]	$t_{37851} = 20.49$	<0.001
Deposition month	July	0.54	[0.44, 0.64]	$t_{37851} = 10.19$	<0.001

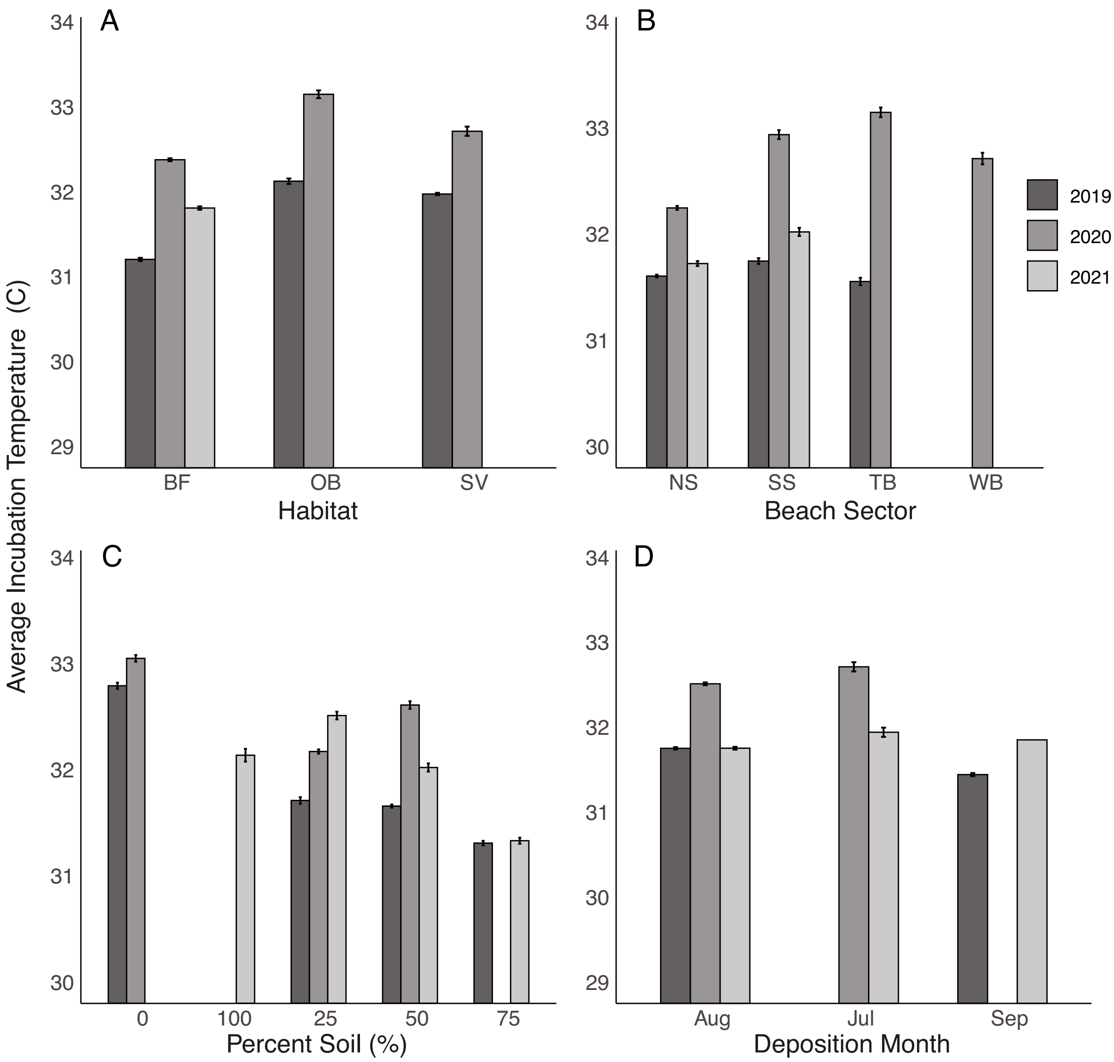

Fig. 3. Average incubation temperatures (°C) for hawksbill turtles as it relates to (A) habitat type (BF: beach forest; OP: open beach; SV: seaward vegetation), (B) beach sector (NS: North Shore; SS: South Shore; TB: Turtle Bay; WB: West Beach), (C) percent soil on Buck Island for all years (0%, 100%, 25%, 50%, and 75%), and (D) deposition month. Error bars: ±SE

bation temperatures on Buck Island. Similar findings concerning hatchling sex ratios, hatch success, and vegetative cover have been reported for other hawksbill nesting sites in the Caribbean (Mrosovsky et al. 1992, Kamel 2013). Here, the study results suggest that almost 1°C of warming can be negated by relocating hawksbill nests from OB areas to areas shaded by vegetative cover. An analysis of historical nesting data collected on Buck Island showed that relocated nests experienced an average reduction in hatch success of 13% compared to nests that were not relocated by monitoring staff (Gulick et al. 2022, National Park Service unpubl. data). Nests on Buck Island are permitted to be relocated only in situations in which the nest is otherwise mostly or completely likely to be imperiled by factors including, but not limited to, tidal inundation, beach erosion, and park visitor disturbance. Although relocating nests is

Table 3. Statistical values from the linear model analyzing the relationships between hatch success and incubation temperature and hatch success and the proportion of time spent above 33°C, 34°C, and 35°C

Variable	R^2	F	p	R^2_{adj}
Hatch success by AvgTemp	0.24	$F_{1,27} = 8.56$	0.007	0.21
Hatch success by Prop33	0.17	$F_{1,44} = 8.80$	0.005	0.15
Hatch success by Prop34	0.21	$F_{1,44} = 11.71$	0.001	0.19
Hatch success by Prop35	0.21	$F_{1,44} = 11.98$	0.001	0.20

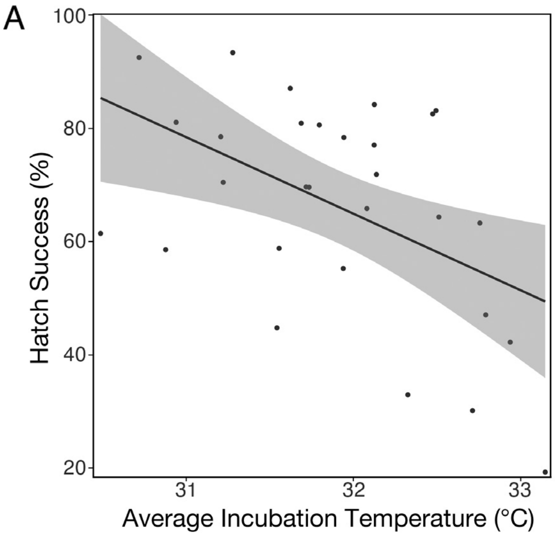

Fig. 4. Relationship between average incubation temperature and hawksbill turtle hatch success across all study years. p = 0.007

proven to reduce hatch success, leaving nests in areas with known high thermal stress will also reduce hatch success. Further study is needed to determine whether hatch success is higher in relocated nests or in nests that experience high thermal stress. If relocating nests decreases hatch success less than thermal stress, then relocating nests may be a feasible management option if allowed by permitting entities. However, the use of cooling techniques such as shading nests, revegetation of native species, and nest watering to reduce incubation temperatures should be considered before relocations are used for nests at risk of thermally induced mortality. Increasing vegetation in SV and OB habitats may also reduce incubation temperatures and offer a viable management option to reduce thermal stress.

Beach sector and habitat type also played a significant role in determining incubation temperature. Fig. 6 illustrates where nesting was predominantly concentrated during the study. Hawksbill nests were most concentrated on the NS and SS, indicating that the higher concentration of BF habitat could be driving nest site selection. TB and WB have limited amounts of vegetation to provide shade for nests, as these beaches consist of OB and shrubby vegetated habitats. This indicates that habitat is driving incubation temperatures on Buck Island. However, it is important to highlight the role that the interaction of a variety of factors, including but not limited to percent soil composition, beach sector, and habitat, are collectively having on incubation temperatures on Buck Island. It may be necessary for managers to assess each nest on

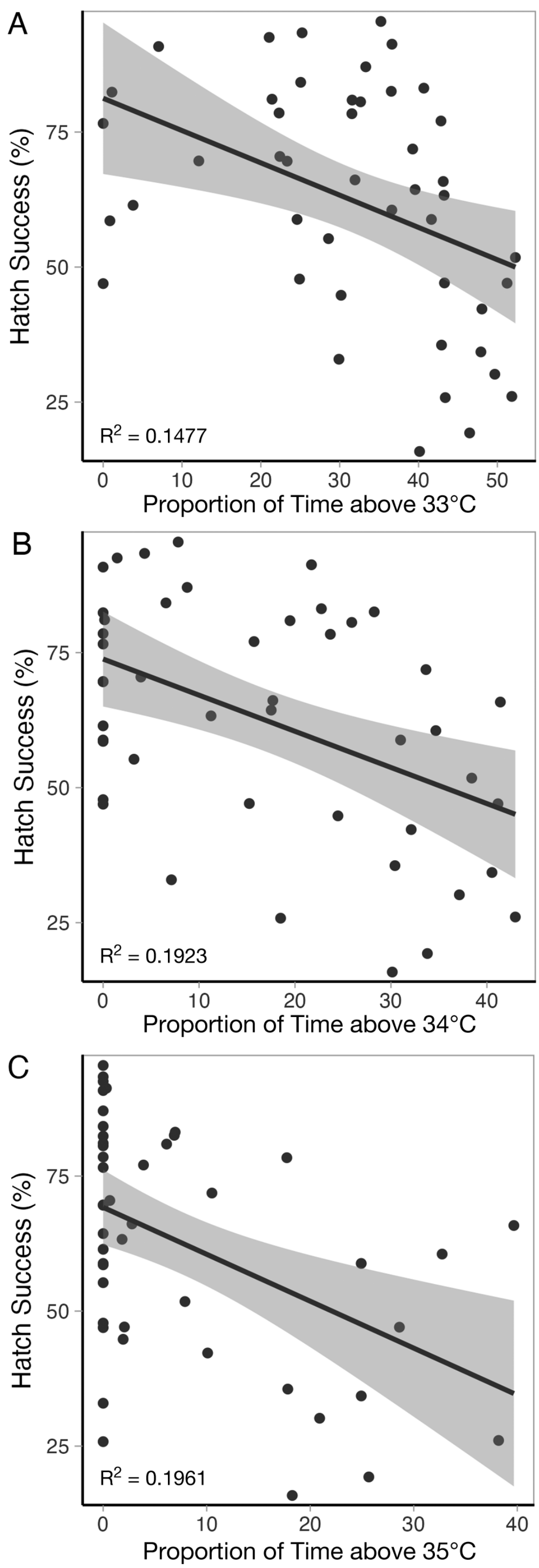

Fig. 5. Regression analysis for percentage of time hawksbill turtle nest temperatures were above (A) 33°C, (B) 34°C, and (C) 35°C for data from all years of the study. $p > 0.005$

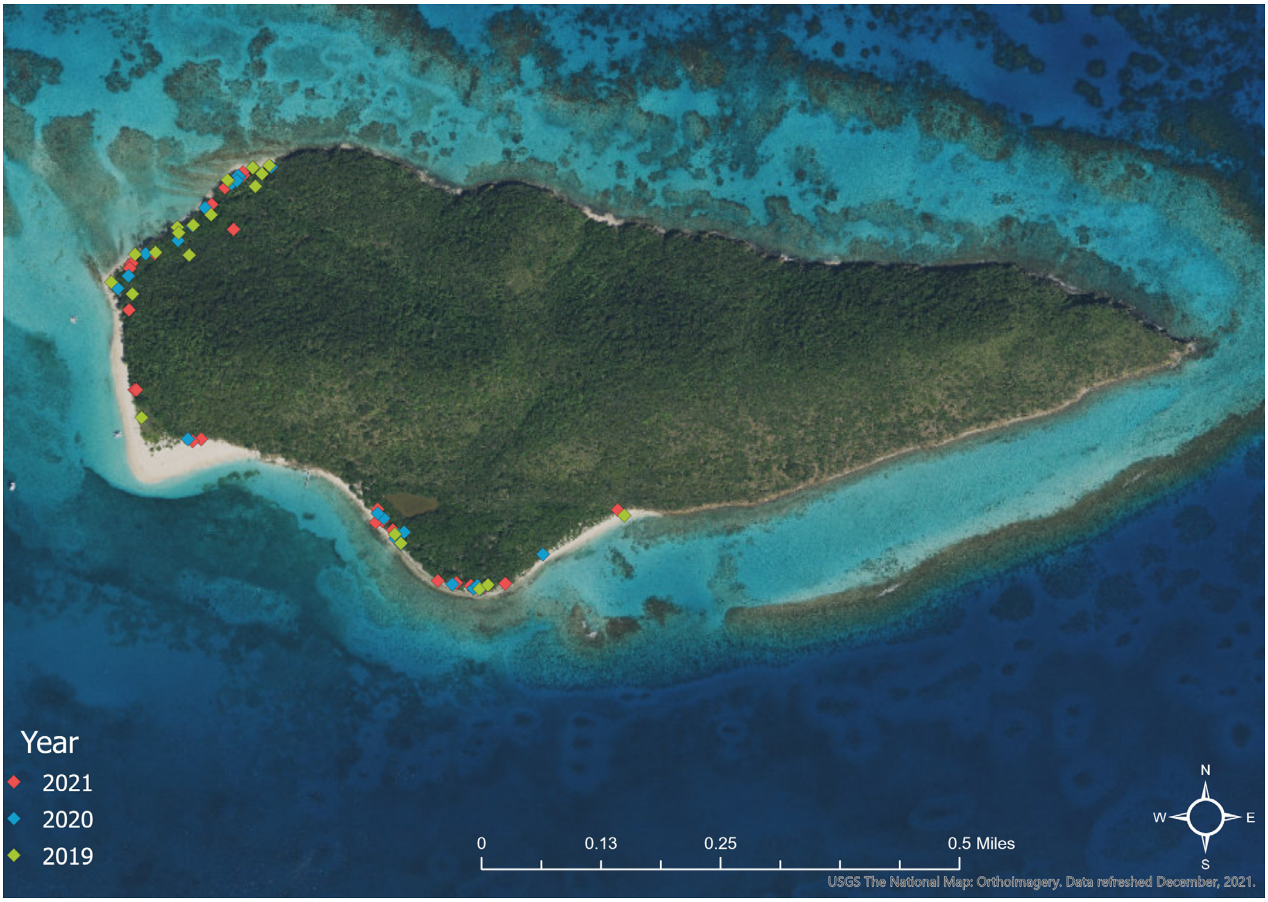

Fig. 6. Geographic nesting trends for hawksbill turtles on Buck Island for the 2019, 2020, and 2021 seasons

a case-by-case basis for thermal stress before implementing a management plan for any individual nest.

The significant differences in incubation temperatures for varying percent soil compositions again highlight the importance of vegetative shading as a regulator of incubation temperatures on Buck Island. Percent soil composition, or the darkness of the soil, can logically be both a cooling and warming factor. Lighter colored soils could be cooler in temperature due to their higher albedo or ability to reflect insolation from the sun, but lighter colored soils are also associated with less vegetation and shading. Darker nests, or those with a higher percent soil composition, could be warmer due to albedo; however, higher organic content in darker soils better supports the growth of vegetation that provides shade (which we have found correlates with cooler incubation temperatures). Abundant vegetation creates a positive growth feedback in which decomposing leaf litter causes the surrounding soil to have higher organic content, and more organic content spurs more vegetative growth. The significant differences in mean incubation temperature for the different habitat types found on Buck Island underscores the importance of vegetative cover for moderating temperature in hawksbill nests. Managers can use these data to predict hatch success, incubation temperatures, and feminization and identify habitat types that are more at risk from these lethal threats.

4.2. Relationship between hatch success and incubation temperature

This study identified a negative relationship between hatch success and incubation temperature. While hatch success is highly controlled by temperature, other confounding variables such as soil moisture, predators, depth of the nest, etc. influence emergence success. Previous studies have shown that the duration of time that embryos spend at or above 35°C has a larger negative impact on hatch success than does a single threshold episode (Howard et al. 2014, Butt et al. 2016). Our results reaffirm these studies and indicate that the proportion of time spent above 33°C, 34°C, and 35°C may be a more critical driver of hatch success. This phenomenon has been seen in loggerhead and green turtles but is understudied in the sea turtle literature, especially as it pertains to hawksbills (Bladow & Milton, 2019). This highlights that long-term exposure to higher temperatures that are below lethal limits may be more detrimental to hatch success than acute exposure to extreme temperatures above the lethal limit, making the identification of lethal temperatures more complex than initially thought (Howard et al. 2014). More mortality may be occurring at sublethal incubation temperatures than previously believed. Qualitatively, most of the time spent above 35°C was in the third trimester, indicating that the increased heat was likely due to endogenous heat from organ differentiation and not adverse environmental conditions. This observation highlights the complexity of incubation in sea turtles and the need for further study to understand the complicated drivers of embryonic mortality in hawksbills.

4.3. Tropical cyclones

All nests included in this study showed signs of tropical cyclone-induced cooling. Each data set showed a visually significant decline in incubation temperature during the end of August and September. Although temperature reductions were observed, it is not known whether reductions were due to heavy rainfall, increased cloud cover, ambient temperature decline, wash-over from storm surge, or a combination of all these factors. However, increased global storm activity is likely to increase the number of nests that are imperiled by tidal inundation and beach erosion, even if temporary over-wash, increased rainfall, and cloud cover can lead to temperature decreases that may increase male hatchlings and hatch success in surviving nests (Staines et al. 2020). These observations were not validated quantitatively but should be an area of future study for managers on Buck Island.

4.4. Management actions

Management actions such as the identification and protection of male-producing beaches, relocating nests to cooler areas, white sand treatment, revegetation, water sprinkling, and artificial shading of nests have been found to be successful at reducing incubation temperatures (Fuentes et al. 2012, Patino-Martinez et al. 2012, dei Marcovaldi et al. 2014, Wood et al. 2014, Hill et al. 2015). Not all these management actions may be realistic or effective on Buck Island. Each nest environment is unique, and managers will need to consider a combination of factors in each situation before deciding what management tool will be most successful. Thermal management in the form of white sand treatment has been utilized in the past on Buck Island; however, the effectiveness of this management technique needs further study. Initial temperature data and findings from the 2019 season led managers on Buck Island to begin studying the effects of thermal management techniques on incubation temperatures in hawksbill nests. This study is ongoing.

Recent studies have found that shading, followed by watering and depth of the nest are effective management techniques for reducing sand temperature in sea turtle nests (Hill et al. 2015, Jourdan & Fuentes 2015). For watering to be an effective tool, water levels need to equal those of medium to high regional rainfall averages (Hill et al. 2015). The results of this study show that vegetative shading is an effective tool for controlling incubation temperatures. It is important to note that roots from vegetation may negatively impact the nest environment by desiccating the egg chamber, piercing eggs, entrapping hatchlings, and impeding gas exchange (Conrad et al. 2011). However, the benefits gained from shading may outweigh the negative impacts of roots. Vegetative shading should be investigated as a management tool on Buck Island for future nesting seasons.

Although artificial shading appears to be one of the most successful tools for the management of high thermal conditions, there are issues associated with this management approach. Installing artificial shades would make nests identifiable to the public, increasing the chances of nest tampering or poaching. Shades can also obstruct nesting turtles by causing entanglement and encourage the female to exit the beach without laying; therefore, expending unnecessary energy and potentially reducing the total number of nests. The installation of artificial shades is likely not an effective and feasible management technique on Buck Island. Watering nests also has its drawbacks for use on Buck Island. Watering requires excessive labor throughout the season to consistently water all nests and may not be feasible due to the limited number of staff and access to fresh water. Rather than relying on any one approach, a combination of these management techniques may be most successful for Buck Island. This study identified the important role that the proportion of time spent above 33°C, 34°C, and 35°C played on hatch success. Future studies can use this metric to determine and refine when and for how long management practices must be implemented to see increases in hatch success. Managers will be able to optimize resource use to increase hatch success, increasing overall management efficiency.

This study highlights how the unvegetated microhabitat on Buck Island is contributing to increased incubation temperatures and decreased hatch success in hawksbills. This thermal stress has the potential to impact future population success by increasing feminization and mortality of hatchlings, causing overall population decline. Decreases in hawksbill populations may eventually lead to losses in genetic diversity, genetic bottlenecks, and losses in individual fitness due to low population densities and increased difficulty in finding mates, eventually leading to population collapse and extinction, making conservation of this species ecologically paramount (Courchamp et al. 2008, Leroux et al. 2012). Continued loss of hawksbill populations could be detrimental to coral reef ecosystems because of the role hawksbills play by feeding on sponges (Meylan 1988, León & Bjorndal 2002, Spotila 2004, Carrión-Cortez et al. 2013).

4.5. Conclusions

Conservation of marine turtles globally is a major management concern under current climate change models because contemporary climate change is likely occurring faster than sea turtles can adapt (Hamann et al. 2013). This study on hawksbills shows that increased incubation temperatures and longer exposure to lethal temperatures led to significantly decreased hatch success and identified areas at high risk from this effect. OB habitat was significantly warmer than both SV and BF habitats. Vegetative cover is an important factor for reducing incubation temperatures in hawksbill nests.

For hawksbill populations to be resilient in the face of climate change, maintenance of genetic diversity, a large breeding population, and a wide geographic distribution are critical (Fuentes et al. 2013). To achieve this goal, similar studies are needed on other important regional hawksbill nesting beaches to understand the scope of thermal stress on hawksbill hatchlings (e.g. such as those conducted by Kamel 2013) and to determine which practices can provide the most effective and long-lasting benefits. As anthropogenic-induced climate change accelerates, managers will require additional information to create best management practices for hawksbill population recovery.

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