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Environmental drivers of diving behavior and space-use of juvenile endangered Caribbean hawksbill sea turtles identified using acoustic telemetry

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ABSTRACT: Space-use by aquatic ectotherms is closely linked to environmental factors such as temperature due to thermal-mediated metabolism and energy requirements. These factors are important, as they may alter an animal's exposure to food/predators, hinder physiological function, increase competitive interactions, or even prompt population or biodiversity loss. Using general linear mixed-effects models, we investigated the influence of medium-term (months–years) environmental (diel period, water temperature, season, wind speed, air pressure, habitat type) and biological (turtle size) variation on space-use metrics for the Critically Endangered hawksbill sea turtle *Eretmochelys imbricata*, including dive duration, activity space, and rate of movement. We tracked 17 resident juveniles between August 2015 and May 2018 with a compact acoustic telemetry array (35–41 receivers in ~1 km^2) in Brewers Bay, US Virgin Islands. Diel differences in space-use were significant and highlighted periods of relative inactivity (e.g. resting) during the night and activity (e.g. foraging) during the day. Water temperature was also an important covariate influencing behavior leading to shorter dive durations and higher rates of movement in warmer temperatures. High contribution of random effects (individual and year) to model variation was also apparent, suggesting that juvenile hawksbills can operate outside the relatively narrow environmental range experienced within the study area. Nevertheless, ongoing climate trends (e.g. warmer temperatures and more extreme weather events) pose a significant concern for hawksbill populations, as juveniles spend their developmental period in shallow nearshore areas where environmental impacts will likely be greatest.

KEY WORDS: Temperature · Thermal dependence · Q_{10} · Diving behavior · Aerobic dive limit · Climate change · Home range · Biotelemetry

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1. INTRODUCTION

Environmental conditions often influence the behavior of aquatic animals, modifying factors such as energetics, resource use, and habitat selection, among others (Schlaff et al. 2014, Scott et al. 2017, Brownscombe et al. 2019). The impacts of these environmentally mediated behavioral changes are complex and can directly or indirectly affect individuals and populations (Pörtner & Peck 2010). Furthermore, they can occur over small or large spatial and temporal scales, as part of routine daily or seasonal variation (e.g. Froeschke et al. 2010, Udyawer et al. 2015), or in response to pervasive (e.g. Johansen et al. 2015) or extreme climate events (e.g. Matley et al. 2019). The relative impact on animals can also vary, result-

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ing in positive outcomes in some scenarios (e.g. increase in nutrients, productive thermal shifts) and negative outcomes in others (e.g. reduced resource availability, habitat destruction, increased energetic demands; Magnuson et al. 1990, Sorte et al. 2013). For example, ocean warming and its multiplicative effects can re-shape species-specific ecological interactions and evolutionary outcomes by contributing to either the expansion or contraction of species' distributional ranges (Perry et al. 2005, Last et al. 2011).

The biology and physiology of most aquatic organisms are inherently linked to environmental variation because most fishes, amphibians, and reptiles cannot effectively thermoregulate internally (Avery 1982). As a result, daily and seasonal behavioral patterns are linked to environmental temperature because metabolism, oxygen uptake, and other physiological mechanisms are thermally coupled with the surrounding water (Seymour 1982). A typical product of this relationship is that animals are more active and mobile during warm periods or within warm areas. Warmer temperatures are typically beneficial for the survival of aquatic animals because they supplement energetic budgeting (e.g. increased food intake and locomotion) and support the development of offspring (Schofield et al. 2009, Fossette et al. 2012). However, the increasing temperature can reach a critical threshold, after which physiological functioning and energetic gain deteriorate (Spotila et al. 1997, Pörtner & Knust 2007, Johansen et al. 2015). For air-breathing aquatic animals such as sea turtles, an increase in metabolism, oxygen consumption, or activity due to a rise in water temperature could lead to decreased aerobic dive limit (ADL) and more time breathing at the surface (Kooyman 1989, Jackson 2007, Campbell et al. 2010), which may increase risk of predation (von Brandis et al. 2010) and vessel strikes (Hazel et al. 2007). Still, sea turtles appear to tolerate a wide thermal range (Mendonça 1983, Seminoff 2000) and some demonstrate low thermal dependence of metabolic rate, enabling consistent activity year-round (Southwood et al. 2003, Kinoshita et al. 2018). Other environmental factors may also affect energetics or access to resources. For example, green sea turtles *Chelonia mydas* appear to use wind-borne cues (at least in part) to travel between foraging grounds and nesting sites at large spatial scales (Hays et al. 2003, Painter & Plochocka 2019). At a smaller spatial scale, juvenile hawksbill sea turtles *Eretmochelys imbricata* increased their horizontal space-use and spent more time in deep water in response to environmental changes (e.g. increased wind and decreased air pressure) associated with Hurricanes Irma and Maria in the US Virgin Islands (Matley et al. 2019). However, the influence of medium-term (months–years) environmental fluctuations on behavior or energetics is not well studied, particularly for species inhabiting relatively small areas for extended periods such as juvenile hawksbill sea turtles.

Hawksbill sea turtles inhabit tropical and sub-tropical regions around the world (Witzell 1983). Despite their wide range, global hawksbill populations have declined 80% or more in the past 105 yr (Meylan & Donnelly 1999, McClenachan et al. 2006) and the species is listed as endangered under the US Endangered Species Act (https://www.fisheries.noaa.gov/species/hawksbill-turtle) and Critically Endangered on the IUCN Red List (https://www.iucnredlist.org/species/8005/12881238). A primary threat to this species is the destruction of foraging habitats, and one main global research priority for the conservation of sea turtles is to investigate the drivers of space-use, particularly within these foraging habitats (Hamann et al. 2010, Rees et al. 2016). Although hatchling and adult hawksbills make long-range movements (Meylan 1999), juvenile hawksbills (~20–65 cm carapace length) are typically resident in localized coastal areas at relatively small (<2 km^2) spatial scales for many years (Bolten 2003, Scales et al. 2011, Carrión-Cortez et al. 2013, Wood et al. 2017). This provides a unique opportunity to study how environmental factors influence space-use during a crucial developmental period of this Critically Endangered species.

Previous research has been conducted on juvenile hawksbill dive patterns (e.g. van Dam & Diez 1997, Blumenthal et al. 2009), and habitat/space-use (e.g. van Dam & Diez 1998, Chevis et al. 2017, Wood et al. 2017), as well as the influence of water temperature on diving behavior in adult females (e.g. Storch et al. 2005, Gaos et al. 2012). However, few studies have explored the diverse spatial patterns (diving, activity, and home range) of hawksbills in response to the multiple environmental factors they are exposed to throughout the year. This research, part of a 5 yr capture, tag, and release project in Brewers Bay, St. Thomas, US Virgin Islands, utilized a compact passive acoustic telemetry array and pressure-detecting transmitters to investigate environmental factors influencing diving and space-use patterns of a relatively abundant population of Critically Endangered juvenile hawksbill sea turtles. Three spatial metrics were investigated: dive duration, activity space, and rate of movement. The acoustic array used in this study enabled medium-term (months–years) and consistent tracking of animals at a small spatial scale,

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providing novel high-resolution information about behavioral responses to environmental variability. Furthermore, this research has relevance for future conservation and management efforts as ongoing climate trends alter access to resources and impose energetic consequences (Hawkes et al. 2009), both of which are intrinsically associated with diving and space-use patterns.

2. MATERIALS AND METHODS

2.1. Study area

This study was conducted in Brewers Bay (18.3425° N, 64.9800° W; Fig. 1), a small bay ~1 km^2 located on the western side of St. Thomas, US Virgin Islands. Habitat and bottom structure in Brewers Bay consists of seagrass, sand, fringing coral and rocky reefs, patch reefs (corals and sponges), and large artificial concrete and rock structures forming the foundation for the airport runway. An acoustic receiver array, consisting of between 35 and 41 VR2W-69 kHz receivers (Vemco; Fig. 1), was deployed during the study period (August 2015 to May 2018). Detection range varied by habitat and tag type (see Matley et al. 2019), but a conservative estimate of receiver coverage in the study area (depth range: 1–27 m) was ~75–90% (100–200 m range at 75% detection efficiency). Water temperature was collected every 15 min within the bay via 13 sub-surface loggers (U22-001 HOBO® Water Temp Pro v2; Onset Computer Corporation; Fig. 1) deployed <5 m from the bottom. Additional environmental data were collected from Charlotte Amalie Airport adjacent to the study area (https://mesonet.agron.iastate.edu/request/download.phtml?network=VI__ASOS), including wind speed and air pressure.

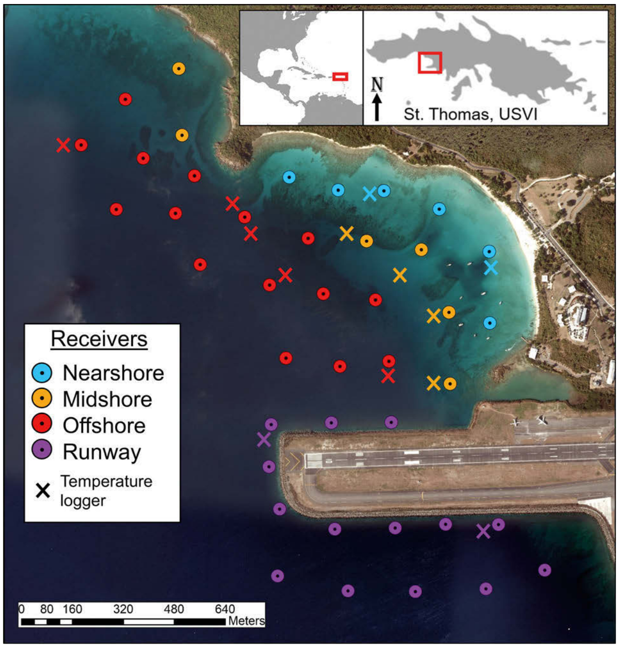

Fig. 1. Acoustic telemetry array located in Brewers Bay, St. Thomas, US Virgin Islands. Circles: receivers, color-coded based on the area within the bay; '×' temperature loggers deployed near the bottom

2.2. Animal tagging

A total of 17 juvenile hawksbill sea turtles were tagged between August 2015 and February 2018 in Brewers Bay with Vemco V13P or V16P transmitters equipped with pressure sensors (error: ±1.7 m). Pressure and detection data were transmitted at random intervals every 30–60 or 30–90 s depending on transmitter specifications. Using snorkeling equipment, we caught hawksbill sea turtles by hand and brought them back to the dock (<5 min trip), where transmitters were attached to 2 marginal scutes (adjacent to the postcentral scutes) via a plastic coated wire (2.5 mm) and marine epoxy (Marine-Tex®) (Fig. S1 in the Supplement at www.int-res.com/articles/suppl/m652p157_supp.pdf). A suite of biometric measurements including curved carapace length (CCL) were recorded for each individual at the same time as transmitter attachment. After tagging, individuals were released at the same location of capture (<2 h between capture and release). Tagging and all other procedures were carried out with the approval of the University of the Virgin Islands Animal Care and Use Committee (IRBNet ID: 1106790-2), and following the relevant guidelines and measures described in US National Marine Fisheries Service protected species permit no. 15809.

2.3. Dive duration

Prior to estimating dive duration, a zero-offset (linear) correction was applied to depth sensor data because exploratory date–depth plots demonstrated sensors gradually became uncalibrated. To address this issue, weekly minimum depth values were adjusted to 0 m (i.e. breathing at the surface), and detections were similarly adjusted based on these weekly corrections. Given the large volume of data each week and the need for turtles to breathe at the surface regularly, these corrections were reliable.

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Individual dives were identified by calculating the time between detections when the turtle moved deeper than 1 m (after breathing at the surface) and when it returned to the surface <1 m (to breathe again) (see Fig. S2 for example of diving profiles provided by pressure tags). To address the possibility that detections did not occur when the turtle was at the surface, thus leading to inaccurate dive segregation, only dive times that were between 5 and 120 min were included (3.5% of total dives removed) based on previous research nearby in Puerto Rico using time–depth recorders (TDRs) (van Dam & Diez 1996, 1997). Additionally, dives that did not reach a maximum depth >2 m were excluded because these instances incorporated surface resting or breathing events and also encompassed transmitter sensor error. Due to the designed variability of tag transmissions and range-limited detections, surface intervals may have occasionally been missed. Therefore consecutive (and independent) dives could have been combined resulting in longer dive duration estimates; however, in large part, singular dives appeared to be designated correctly and dive durations were within the range found in van Dam & Diez (1996, 1997; see Figs. 2 & S3). Additional steps taken to reduce the influence of potential dive segregation bias are described in Section 2.5. Further, the high detection rate of turtles (e.g. mean ± SD number of detections dive^{-1}: 20 ± 22 [day], 28 ± 31 [night]) provided a high level of confidence for detecting surface intervals. Individuals often used unique day and night locations with transitioning movements between these locations between sunrise and sunset. The focus of this study was strictly on diurnal (08:00–17:00 h) (i.e. feeding) and nocturnal (20:00–05:00 h) (i.e. resting) periods; therefore, crepuscular periods were not examined.

Considering that most sea turtle dives are within an animal's ADL, which relies explicitly on aerobic metabolism and the body's oxygen stores, estimates of thermal dependence, Q_{10} (the factor by which the rate of a reaction, such as metabolism, changes for every 10°C rise in temperature; Hochscheid et al. 2004), were made based on dive durations for each individual that experienced a thermal range >4°C (day: 12 of 17 turtles; night: 10 of 15 turtles) using the following equation:

$$Q_{10} = (M_1 / M_2)^{[10 / (T_2 - T_1)]} \quad (1)$$

where M_1 and M_2 represent dive durations (in min) calculated using the linear regression of dive durations across the range of temperatures (T_1 and T_2) (in °C) for each individual.

2.4. Horizontal space-use

Space-use by hawksbills was quantified within the acoustic telemetry array using 2 metrics: activity space (see Heupel et al. 2004; equivalent to home range within a limited sampling area — i.e. acoustic telemetry) and rate of movement. These metrics were explored to determine the influence of environmental variables on horizontal movement in addition to diving patterns. For both metrics, habitat-specific detection probability functions calculated from range testing in Brewers Bay were used to estimate adjusted locations of detections (instead of assuming all detections occurred at the location of the receiver) by randomly assigning a position within a receiver's detection range weighted by the detection probability (i.e. more detections closer to the receiver than further away; see Supplementary Materials in Matley et al. 2019). The maximum detection range was set to 400 m because detections did not regularly extend that far in the study area.

Activity space was quantified at weekly daytime (diurnal) and nighttime (nocturnal) intervals, due to the evident behavioral differences, using auto-correlated kernel density estimation as described by Fleming et al. (2015) from the R package 'ctmm' (Fleming & Calabrese 2020). This approach was selected because it accounts for non-independent movement data — inherent in small-scale acoustic telemetry studies — by incorporating an auto-correlation function associated with non-stationary continuous movement processes (Fleming et al. 2015). Activity space estimates were derived from location positions using 30 min centers of activity (COA, also known as position averaging; Simpfendorfer et al. 2002). Briefly, detections within a 30 min period were spatially weighted arithmetically based on the number of detections and their adjusted location (as described above). The 30 min period was selected because this was the time period that typically corresponded to one dive during diurnal periods (i.e. 1 position dive^{-1}). If, by this process, COA positions were placed on land (<1% of COAs), they were randomly reassigned to water within the area used by the individual during that week, as determined using a minimum convex polygon (R package 'adehabitatHR'; Calenge 2006).

Activity space for each turtle (presented as 50 and 95% utilization distributions [UDs]) were calculated weekly. The weekly interval was chosen to characterize relatively short-term changes in activity space (i.e. between weeks). The optimally weighted continuous-velocity Ornstein-Uhlenbeck-F model, which reduces position errors, incorporates finer resolution,

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and mitigates sampling bias compared to other methods (Fleming & Calabrese 2020), was selected to calculate UD estimates. If the UD output overlapped with land, that specific area was removed from the overall estimate. Only weekly UDs with 25 or more positions (for each individual) were used in the analysis because UD estimates derived from <25 positions were often biased (i.e. smaller UDs than similar detection data with more positions). This approach also ensured that estimates only incorporated weeks with numerous detections (e.g. 24 COA positions is equivalent to 12 h of detections). Preliminary investigations showed no discernible difference in space-use caused by the number of receivers used in the array, which varied from 35–41 over the 4 yr of monitoring. Two-dimensional UDs (i.e. horizontal space-use) were employed rather than 3-dimensional UDs because the latter approach incorporates a measure of volume instead of area, making it difficult to disentangle vertical movements from horizontal ones.

Rate of movement was defined as the distance moved during 2 h intervals for both day and night periods. To ensure time periods had uniform detection data, only 2 h intervals consisting of 12 consecutive 10 min COA estimates were incorporated. If, during a 2 h interval, there were no detections in one or more 10 min period, that 2 h interval was not included in further analysis. A 10 min COA period was used for this approach to increase the number of possible unique locations to estimate distances traveled. Similarly, a 2 h interval was selected because it was large enough to incorporate movements throughout several dives, but also small enough to ensure consecutive detection periods could be incorporated.

2.5. Statistical analysis

All analyses were conducted using R version 3.6.1 (R Core Team 2018). A residency index was calculated for each individual to evaluate the consistency in which hawksbills remained within the array area. It was calculated as the number of unique days detected divided by the number of days between the first and last detection. General linear mixed-effects models (R package 'nlme'; Pinheiro et al. 2013) assessed if dive duration, activity space, and rate of movement were influenced by the following explanatory variables: diel category (day or night), water temperature, dynamic size (CCL), season, wind speed, air pressure, mean depth of dive (for dive duration only), and habitat of dive (for dive duration only). The mean depth of dives was strongly correlated with the maximum depth of each dive, therefore only one variable was used in the analysis. As an additional precaution to reduce bias associated with the possibility of combining independent dives (i.e. due to surfacing period not being detected), dive durations were averaged each day and night period. This reduced within-day and within-night variation but we deemed this conservative approach necessary to alleviate these uncertainties.

Environmental variables were averaged daily/nightly, weekly, and bi-hourly to match dive duration, activity space, and rate of movement metrics, respectively. The dynamic size variable was used to account for growth over time by extrapolating weekly size estimates using growth curves from Hawkes et al. (2014). Habitat within Brewers Bay was designated relative to the depth of receivers and location from shore, including nearshore (<5 m bottom depth), midshore (5–15 m bottom depth), offshore (15–25 m bottom depth), and runway (11–28 m; Fig. 1). The water temperature values used in dive duration and rate of movement models were selected from the habitat each dive/movement began in for that sampling period (i.e. all HOBO values within that habitat were averaged together). Mean water temperature throughout the study area was used for each activity space period because space-use often incorporated several habitats. Continuous variables were scaled and centered to standardize comparisons. Exploratory analysis using variance inflation factors (VIFs; R package 'car'; Fox & Weisberg 2011) indicated there were no strong correlations among explanatory variables (VIF ≤3). Individual turtle identification was added to the model as a random factor nested within each year of detection because of repeated measures of individuals and the unbalanced sampling period, respectively. During the study period, Hurricanes Irma and Maria produced extreme wind speeds and air pressure, as well as reduced receiver detection efficiency (see Matley et al. 2019). Therefore, to avoid biasing models with these outliers and because behavioral responses to 'regular' trends were of interest in this study, data between 6 and 20 September 2017 were not incorporated. Over-dispersion and homogeneity of residuals met assumptions for Gaussian distribution within the models after log transformation. A first-order auto-correlation structure was incorporated in model designation after auto-correlation function plots indicated the data were serially auto-correlated. A model-averaging approach was used from the R package 'MuMIn' (Barton 2019) to test all combinations of explanatory variables and identify those that con-

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tributed to the most variation among the best models (based on Akaike's information criterion adjusted for small sample sizes; $\Delta AIC_C < 2$). Given the interest in examining differences between behavioral responses during the day and night, a diel category (day/night) was included in the main effects as well as an interaction term with all explanatory variables. Marginal R^2 (variation explained by fixed effects) and conditional R^2 (variation explained by both fixed and random effects) were calculated for the optimal model (i.e. lowest AIC_C).

3. RESULTS

A total of 17 individuals were incorporated in the analysis for this study including detections between August 2015 and May 2018 (Fig. S4, Table S1). The total number of days with detections ranged between 38 and 879, with 16 individuals detected on >95% of days during detection periods (i.e. residency index; Table S1).

Table 1. Mean (±SD) diurnal and nocturnal dive duration, horizontal space-use, and rate of movement metrics for juvenile hawksbill sea turtles in the US Virgin Islands. COAs: centers of activity; UD: utilization distribution. (*) sample size for the day or night period for rates of movement that were included in further analyses after removal of individuals with low sample size (i.e. <20 two h observations)

	Day	Night
Dive duration		
No. of individuals	17	15
No. of dives	2314 ± 1408	698 ± 674
Dive duration (min)	27.0 ± 7.3	46.0 ± 8.6
Dive max depth (m)	8.3 ± 2.3	5.6 ± 1.5
Q_{10}	1.83 ± 0.97	2.31 ± 1.53
Activity space		
No. of individuals	17	16
No. of weeks	37 ± 29	28 ± 12
No. of weekly COAs	108 ± 16	77 ± 28
50% UD (km^2)	0.064 ± 0.01	0.042 ± 0.03
95% UD (km^2)	0.270 ± 0.06	0.199 ± 0.11
Rate of movement		
No. of individuals	17 (*15)	14 (*8)
No. of 2 h intervals	497 ± 263	326 ± 362
2 h Distance moved (m)	1304 ± 227	1144 ± 223

3.1. Dive duration

During the study period, an average of 2314 and 698 dives were identified for each individual during the day and night, respectively (Table 1) Fig. 2 shows an example of diurnal and nocturnal dive profiles. All individuals made deeper maximum dives with shorter durations during the day compared to night (Table 1, Fig. 3a). Detections from individuals 1258 and 10651 were not included for the night analysis because they were not detected frequently at night within the array (Fig. S3). The significant variables that explained the most variance associated with dive duration (2 models with $\Delta AIC_C < 2$; Tables 2 & S2) were water temperature and interactions between diel category (i.e. day/night) and mean depth, CCL (size), season, habitat, and wind speed (Table 3). The fixed and random effects in the best model accounted for ~44 and ~24% of the variation in dive

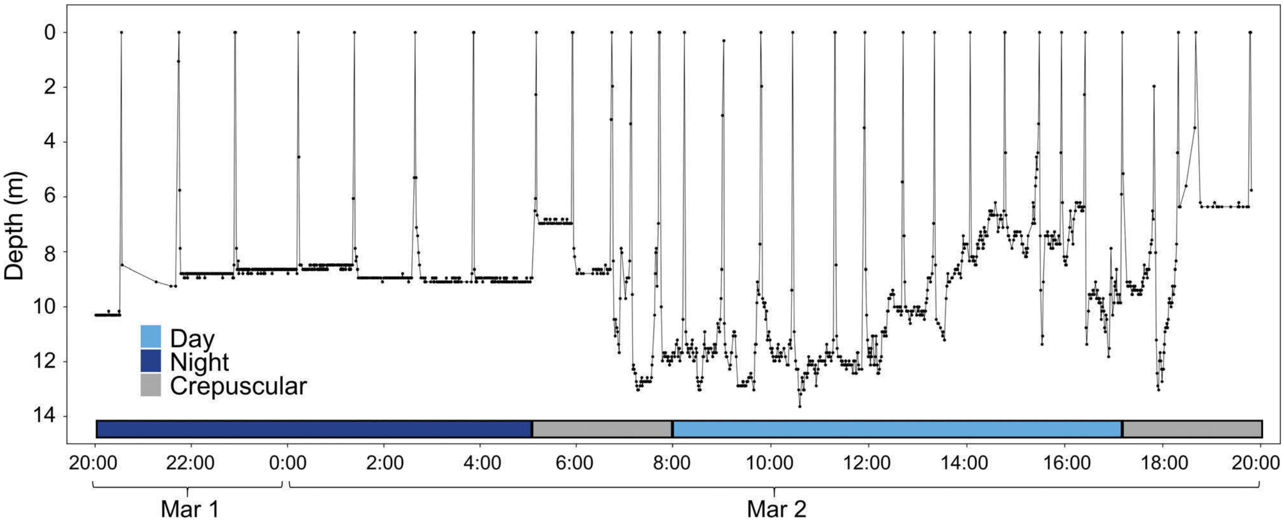

Fig. 2. Example of 24 h dive profile during nocturnal, crepuscular, and diurnal periods for tagged hawksbill sea turtle no. 1257 in 2017. Each point is a detection of a tag transmission detected on an acoustic receiver

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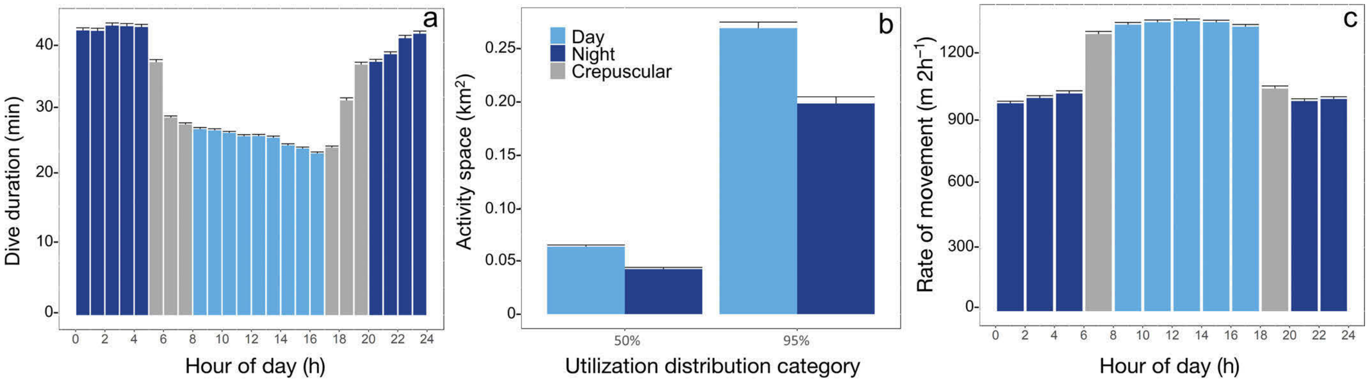

Fig. 3. Mean (±SE) (a) dive duration, (b) activity space, and (c) rate of movement for tagged hawksbill sea turtles grouped by day, night, and crepuscular (not included in b) time periods. For all 3 metrics, day and night periods differed significantly

Table 2. General linear mixed-effects sub-models based on model averaging, indicating the environmental variables that contribute most to the 3 response variables for juvenile hawksbill sea turtles. AIC_C: Akaike's information criterion adjusted for small sample sizes. All sub-models with $\Delta AIC_C < 2$ were incorporated in calculations of model averaging. UD: utilization distribution

Model no.	Model	df	logLik	AIC_C	ΔAIC_C	Weight
Dive duration (min; log transformed)						
1	Diel category + temperature + mean depth + size + season + habitat + wind speed + air pressure + mean depth×diel + size×diel + season×diel + habitat×diel + wind speed×diel + air pressure×diel	25	3946.8	−7843.33	0	0.72
2	Diel category + temperature + mean depth + size + season + habitat + wind speed + air pressure + mean depth×diel + size×diel + season×diel + habitat×diel + wind speed×diel + air pressure×diel + temperature×diel	26	3946.9	−7841.42	1.91	0.28
Activity space: 95% UD (km^2; log transformed)						
1	Diel category + air pressure + size + wind speed	9	27.8	−37.44	0	0.21
2	Diel category + air pressure + size + temperature + wind speed	10	28.7	−37.31	0.13	0.20
3	Diel category + air pressure + size + temperature	9	27.4	−36.74	0.71	0.15
4	Diel category + air pressure + size	8	26.2	−36.28	1.17	0.12
5	Diel category + air pressure + size + wind speed + size×diel	10	27.9	−35.56	1.88	0.08
6	Diel category + air pressure + size + wind speed + wind speed×diel	10	27.8	−35.51	1.93	0.08
7	Diel category + air pressure + size + temperature + wind speed + size×diel	11	28.8	−35.48	1.96	0.08
8	Diel category + air pressure + size + wind speed + air pressure×diel	10	27.8	−35.48	1.97	0.08
Rate of movement ($m\ 2h^{-1}$; log transformed)						
1	Diel category + temperature + size + season + air pressure + temperature×diel + size×diel + season×diel + air pressure×diel	18	6111.1	−12186.08	0	0.5
2	Diel category + temperature + size + season + air pressure + wind speed + temperature×diel + size×diel + season×diel + air pressure×diel	19	6111.5	−12184.92	1.16	0.28
3	Diel category + temperature + size + season + air pressure + size×diel + season×diel + air pressure×diel	17	6109.3	−12184.53	1.56	0.23

duration, respectively. Water temperature was negatively related to dive duration, where an increase of 4°C (26–30°C) resulted in shorter dives by ~6 min (Fig. 4). Mean depth and turtle size were positively associated with dive duration, and dives in the runway habitat were often ~5–10 min shorter than elsewhere during the day and night (Fig. 4). The mean (±SD) of Q_{10} of individuals during day and night periods was 1.8 ± 0.9 and 2.3 ± 1.5, respectively (Table 1).

3.2. Activity space

During the day and night, a mean of 108 and 77 weekly positions (each out of a possible 126 COA periods of 30 min) were used to estimate activity space, respectively (Table 1). Mean UDs were larger during diurnal periods (50%: 0.064 km^2; 95%: 0.270 km^2) compared to nocturnal periods (50%: 0.042 km^2; 95%: 0.199 km^2; Fig. 3b, Table 3),

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Table 3. General linear mixed-effects output from the best model (based on model averaging) of each 3 space-use metrics for juvenile hawksbill sea turtles. Marginal (variation accounted for by fixed effects) and conditional (variation accounted for by fixed and random effects) R^2 values are indicated for each metric. Variables with significant p-values are in **bold**. UD: utilization distribution

Variable	df (num)	df (den)	*F*	p
Dive duration ($R^2_{marginal} = 0.44$; $R^2_{conditional} = 0.68$)				
(Intercept)	1	4995	4772.1	<0.001
Diel category	1	4995	4820.8	**<0.001**
Temperature	1	4995	96.5	**<0.001**
Mean depth	1	4995	581.3	**<0.001**
Size	1	4995	4.3	**0.037**
Season	3	4995	3.6	**0.013**
Habitat	3	4995	3.5	**0.014**
Wind speed	1	4995	0.0	0.936
Air pressure	1	4995	0.0	0.941
Mean depth × diel	1	4995	67.9	**<0.001**
Size × diel	1	4995	12.9	**<0.001**
Season × diel	3	4995	12.5	**<0.001**
Habitat × diel	3	4995	10.7	**<0.001**
Wind speed × diel	1	4995	6.0	**0.014**
Air pressure × diel	1	4995	0.3	0.594
Activity space: 95% UD ($R^2_{marginal} = 0.11$; $R^2_{conditional} = 0.31$)				
(Intercept)	1	1518	704.1	<0.001
Diel category	3	1518	65.0	**<0.001**
Size	1	1518	3.1	0.078
Wind speed	1	1518	0.1	0.854
Air pressure	1	1518	15.2	**<0.001**
Rate of movement ($R^2_{marginal} = 0.11$; $R^2_{conditional} = 0.36$)				
(Intercept)	1	7727	31880.3	<0.001
Diel category	1	7727	306.6	**<0.001**
Temperature	1	7727	3.6	0.057
Size	1	7727	20.8	**<0.001**
Season	3	7727	10.8	**<0.001**
Air pressure	1	7727	0.3	0.616
Temperature × diel	1	7727	43.0	**<0.001**
Size × diel	1	7727	128.0	**<0.001**
Season × diel	3	7727	2.8	**0.040**
Air pressure × diel	1	7727	6.7	**0.010**

and similar areas were typically used during both periods (Fig. 5). Individual 2958 was removed from the night analysis because there were not enough detections to calculate weekly activity space estimates. Both 50 and 95% UDs were strongly correlated (i.e. Pearson correlation > 0.95); therefore, only one metric (i.e. 95% UDs) was used in further analysis. The best model (8 had $\Delta AIC_C < 2$; Tables 2 & S2) indicated a significant difference between day and night periods with smaller areas used at night (Fig. 6, Table 3). Also, air pressure was negatively associated with activity space (Fig. 6, Table 3). The fixed and random effects in the best model accounted for ~11 and ~20% of the variation in dive duration, respectively.

3.3. Rate of movement

Hawksbills traveled longer distances within 2 h periods during the day (mean ± SD: 1304 ± 227 m) compared to the night (1144 ± 223 m; Table 1, Fig. 3c). After removing individuals with a low sample size (i.e. <20 two h observations), analysis of rate of movement during day and night incorporated 15 and 8 individuals, respectively. The best model (3 had $\Delta AIC_C < 2$; Tables 2 & S2) identified significant interactions between diel category and temperature, turtle size, air pressure, and season (Table 3). The fixed and random effects accounted for ~11 and ~25% of the variation in rate of movement, respectively. Water temperature was positively associated with rate of movement in both day and night, while turtle size and air pressure showed opposite trends between diel categories (Fig. 7).

4. DISCUSSION

Three spatial metrics — dive duration, horizontal space-use, and rate of movement — were calculated in this study to explore biological and environmental drivers of juvenile hawksbill behavior. There were clear differences between day and night patterns of the 3 metrics, highlighting differences between periods of activity and relative inactivity (e.g. van Dam & Diez 1997, Blumenthal et al. 2009). Random effects (individual and year) often accounted for the majority of the variance explained by the models, indicating a weak influence of the tested covariates on space-use metrics. Nonetheless, high variation among animal behaviors in the wild is expected, and environmentally mediated trends, for example water temperature effects on dive duration, were still apparent. The comprehensive data set used in this study provides one of the first insights into medium-term (months–years) responses to environmental change of the Critically Endangered hawksbill sea turtle.

4.1. Effect of temperature

Water temperature was a relevant variable influencing the dive and movement patterns of hawksbill sea turtles. In ectotherms, temperature has a significant regulatory role in metabolic functioning, oxygen consumption, activity levels, breathing frequency, heart rate, and blood chemistry, among others (Williard 2013). Dive duration during both day and night were negatively associated with temperature across a ther-

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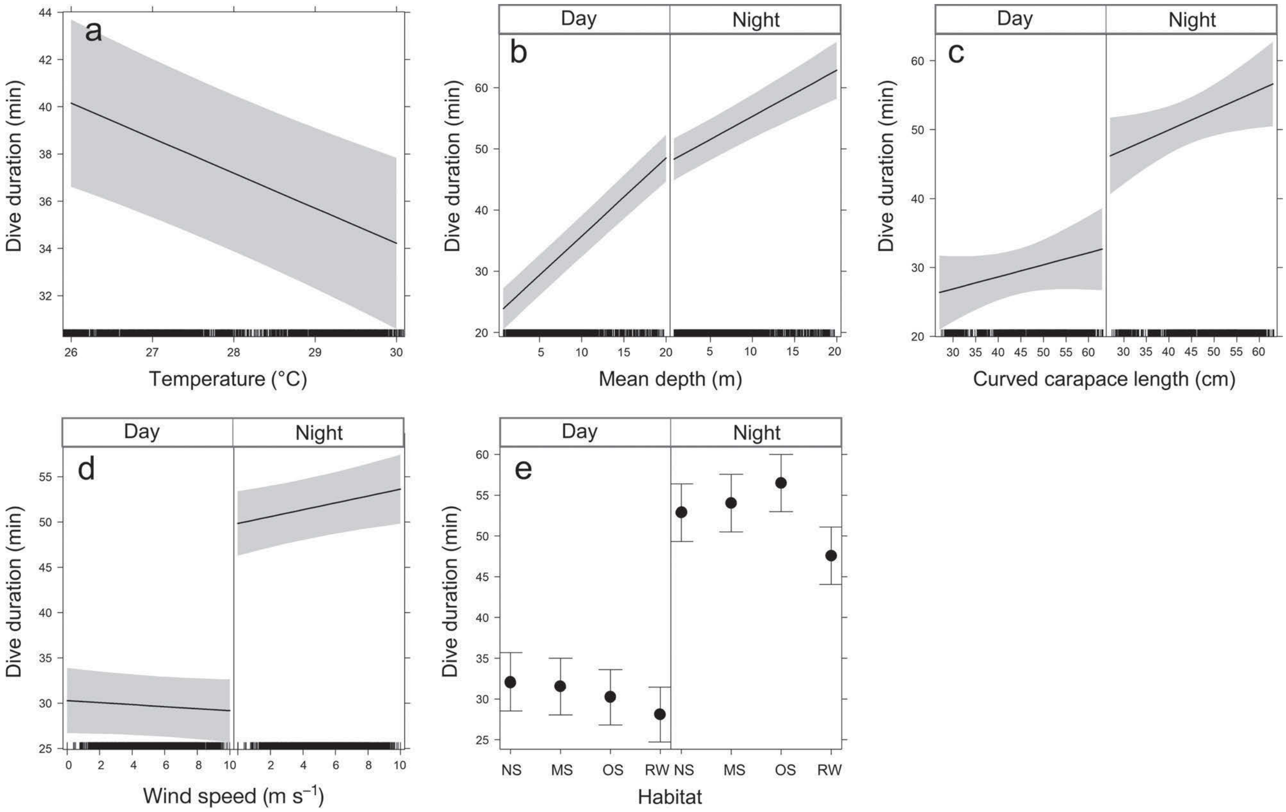

Fig. 4. Effects plots for each significant term in best candidate linear mixed-effects model (based on model averaging and $\Delta AIC_C < 2$): (a) temperature, (b) mean depth, (c) curved carapace length, (d) wind speed, and (e) habitat, with dive duration as the response variable (diel interactions included when significant). Habitats included nearshore (NS), midshore (MS), offshore (OS), and runway (RW). Shaded areas (continuous variables) and error bars (discrete variables) represent the pointwise 95% confidence band of fitted values based on standard errors

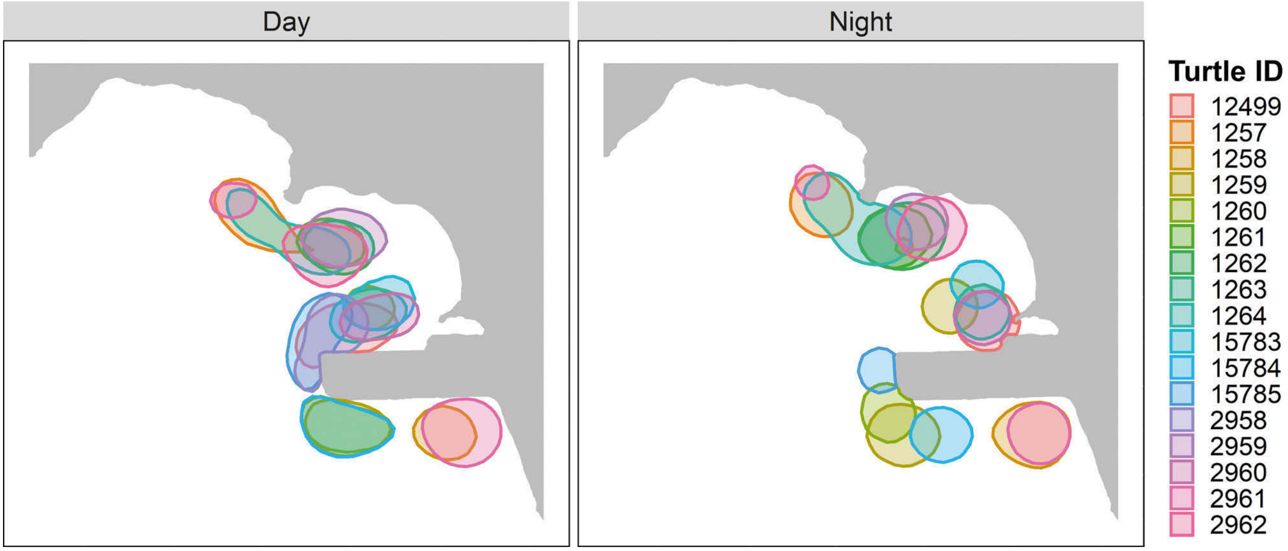

Fig. 5. Activity spaces (50% utilization distributions) for each tagged hawksbill sea turtle summarized for all detections during the study period (as opposed to weekly) to demonstrate general areas of use between day and night

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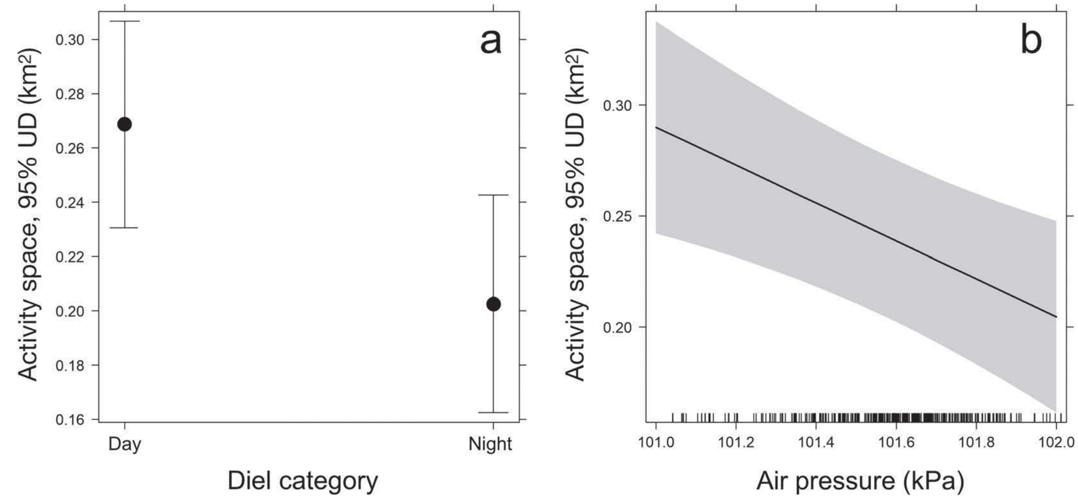

Fig. 6. Effects plots for each significant term in best candidate linear mixed-effects model (based on model averaging and $\Delta AIC_C < 2$): (a) diel category and (b) air pressure, with hawksbill turtle activity space (95% utilization distribution, UD) as the response variable. Shaded areas (continuous variables) and error bars (discrete variables) represent the pointwise 95% confidence band of fitted values based on standard errors

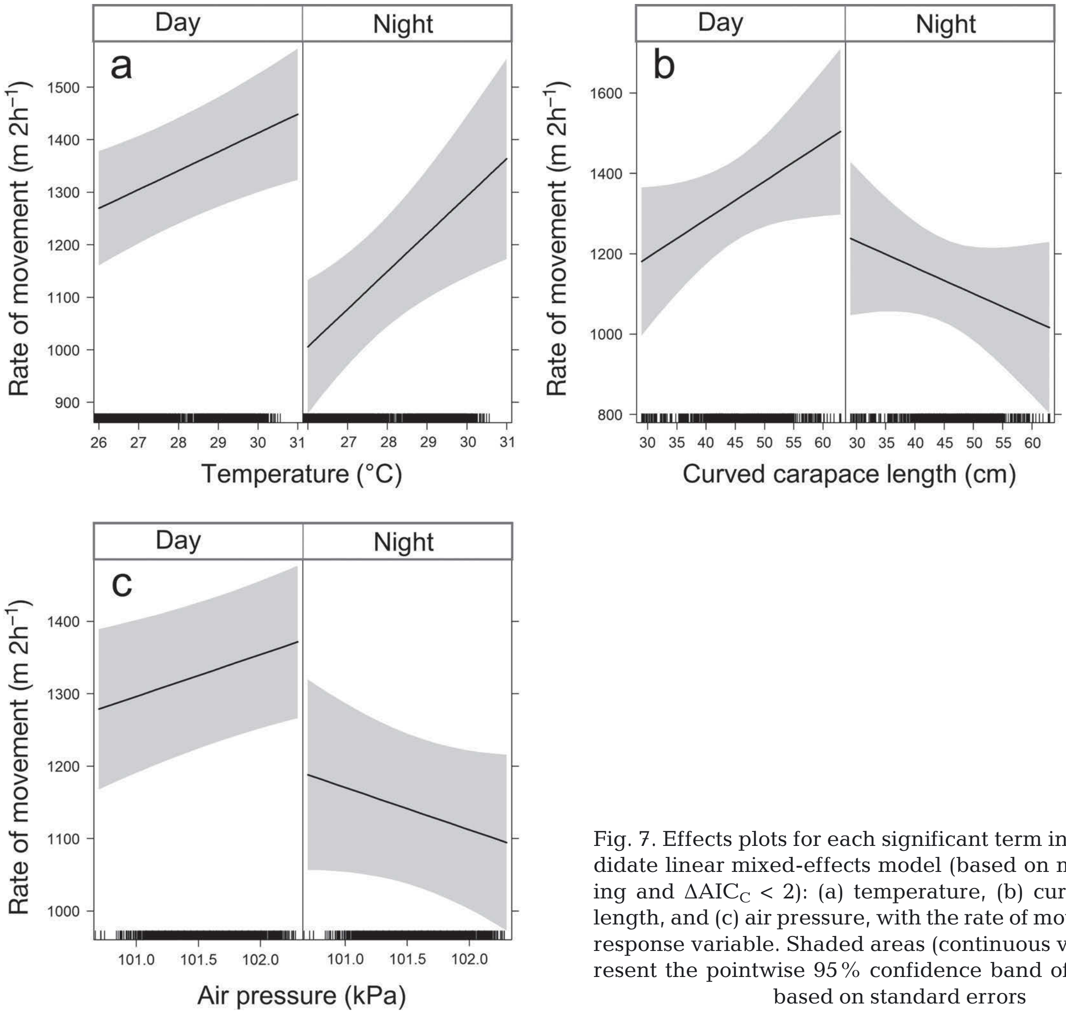

Fig. 7. Effects plots for each significant term in the best candidate linear mixed-effects model (based on model averaging and $\Delta AIC_C < 2$): (a) temperature, (b) curved carapace length, and (c) air pressure, with the rate of movement as the response variable. Shaded areas (continuous variables) represent the pointwise 95% confidence band of fitted values based on standard errors

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mal spectrum of ~25–31°C. The increase in dive duration as temperature decreased likely occurred as a result of predictable reduced metabolic activity in colder waters (Southwood et al. 2003). This has been demonstrated in sea turtles and other ectotherms (Bentivegna et al. 2003, Hochscheid et al. 2007, Campbell et al. 2010). Furthermore, when green turtles were exposed to winter conditions in a laboratory experiment, there was a ~25% decrease in oxygen consumption (Southwood et al. 2003). Reductions in oxygen consumption due to cold temperatures resulted in Q_{10} values as high as 5.4 in loggerhead turtles (Hochscheid et al. 2004). Similarly, TDRs were used to show 3 adult hawksbills monitored for 22 mo during inter-nesting periods had a strong temperature dependence, with longer dive durations in cooler water while at foraging grounds (Storch et al. 2005) resulting in similar daytime Q_{10} values as found in this study. Therefore, the approximate decrease in dive duration of ~6 min shown during the 4°C increase in water temperature in Brewers Bay follows expected increased metabolic rate effects on the ADL and provides new information to quantify the potential impacts future changes in the marine environment may have on these and other endangered sea turtles (see also Section 4.5). Unlike juvenile hawksbills that departed foraging grounds for several months when temperatures averaged 33.5°C in the Persian/Arabian Gulf (Pilcher et al. 2014), hawksbills from this study remained in the study area, suggesting water temperatures were within acceptable limits. In addition, we did not observe an inflection point in the effect of water temperature on dive duration at 27.8°C, or any temperature, as observed by Storch et al. (2005) in adult hawksbills resting at night. These differing preliminary results highlight the need for more research addressing how thermal extremes influence physiological functioning and resulting behavior in hawksbill sea turtles.

4.2. Effect of air pressure and wind speed

Air pressure and wind speed were environmental variables that also influenced dive behavior and space-use of juvenile hawksbills. Larger areas were used in weeks when air pressure decreased throughout diurnal and nocturnal periods. Similarly, greater distances were traveled in 2 h intervals at night when air pressure decreased. In the marine environment, air pressure has been demonstrated to alter the spatial patterns of animals. For example, Udyawer et al. (2015) found that increased movements of the spine-bellied sea snake *Hydrophis curtus* were associated with decreases in air pressure in Cleveland Bay, Australia. Similarly, the reef fish *Lethrinus miniatus* was more likely to be detected on the reef slope at Heron Island in the Great Barrier Reef with increasing air pressure (Currey et al. 2015). In both cases, the purported mechanisms that drive such behavioral changes are unknown, although water temperature could also be contributory. The particular influence of air pressure is more evident under extreme conditions, especially hurricanes (or typhoons/cyclones). Fishes (Sackett et al. 2007, Bacheler et al. 2019), sharks (Heupel et al. 2003), sea snakes (Liu et al. 2010, Udyawer et al. 2013), and sea turtles (Matley et al. 2019) appear to use air pressure, at least to some extent, as a cue to identify incoming storm events. Air pressure appears to be contributory to changes in juvenile hawksbill space-use independent of these extreme events (which were not included in this study) and may similarly be an inherent response to approaching storms, although notably there was a large amount of variation which requires discretion with interpretation.

Wind speed during the night when hawksbills are primarily resting also appeared to influence behavior throughout the mean hourly range observed during the study (0–24 km h^{-1}), leading to longer dives. Increased wind-driven wave action at the water's surface may hinder breathing efficiency, reduce visibility to escape predators or find shelter/food, or increase energy expenditure returning to resting/foraging sites; however, these hypotheses need to be tested. High winds may also increase environmental noise and impact detectivity of transmitters, particularly when at the surface (Stocks et al. 2014), but the impact in this study are likely limited given the different trends in dive duration between day and night.

4.3. Effect of depth and habitat

Based on exploration of dive profiles in this study and previous research (e.g. van Dam & Diez 1997, Blumenthal et al. 2009), we expected most diurnal dives to be associated with foraging and nocturnal dives to be associated with resting (but see Gaos et al. 2012). The relatively shallow maximum depth of Brewers Bay (27 m) eliminated the possibility of deeper dives observed in juvenile hawksbills elsewhere (van Dam & Diez 1996, 1997, Blumenthal et al. 2009). Theoretically, diving in these shallow waters could be energetically inefficient because hawksbills, like other sea turtles, rely on lung capacity to control the buoyancy of dives and oxygen stores

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(Minamikawa et al. 1997, Houghton et al. 2000). Therefore, to be able to forage at shallow depths, the lungs need to be filled at reduced capacity, resulting in reduced oxygen stores and shorter dives. Van dam & Diez (1996) and Houghton et al. (2003) detected this pattern for juvenile hawksbills in a shallow reef habitat (<10 m), and further observed deeper resting dives following shallower foraging dives as a method of recovery. Consequently, deeper dives observed during the day compared to night may reflect optimization of this balance between buoyancy and foraging in the benthic environment (e.g. McMahon et al. 2007). The use of shallower waters during the night is in contrast to the buoyancy paradigm described above, indicating they likely use other techniques such as using habitat structure to assist with buoyancy control during resting (Houghton et al. 2003). Despite the deeper habitat available to turtles near the airport runway, diurnal and nocturnal dive durations were shorter there compared to other areas. The driver behind this pattern is unclear but may be related to the specific habitat of the runway, in which the top ~10–15 m is composed of large concrete dolosse that offers extremely high rugosity, providing many large crevices for protection from predators such as sharks, as well as overhanging shelter providing 'assisted' resting locations.

4.4. Effect of size and individual variation

Oxygen stores and metabolism of sea turtles increase proportionally, but not at the same rate, with body mass (Hochscheid et al. 2007, Blumenthal et al. 2009) providing larger turtles with relatively larger oxygen stores and therefore a longer ADL. This was evidenced, at least in part, by results that showed larger individuals often made longer dives during both day and night. This is analogous to deeper and longer dives made by larger juvenile hawksbills in the Cayman Islands, where dives as deep as 91 m were observed (Blumenthal et al. 2009) — much deeper than the depths available in Brewers Bay. Similarly, larger hawksbills showed higher rates of movement during the day, likely corresponding to increased foraging requirements. However, horizontal space-use did not increase with turtle size nor was it affected by water temperature, supporting that the size of areas used for feeding and resting sites are relatively consistent (see also van Dam & Diez 1998, Chevis et al. 2017, Wood et al. 2017).

Individual variation in spatial patterns is common for many aquatic animals because decision making is influenced by a variety of external and internal forces (Spiegel et al. 2017). These can lead to alternate behaviors partially or fully independent of environmental, physiological, or biological factors. In this study, a high amount of variation was displayed among individuals and sampling years, particularly for the activity space and rate of movement metrics. These results suggest that environmental variables such as temperature influence these behaviors less strictly than dive duration, which is likely closely linked to metabolism and oxygen consumption, and that other unidentified cues are more relevant to space use and rate of movement (e.g. competition, predation risk). It may also be that higher resolution spatial sampling is required to elucidate more discrete patterns. In addition, other constraints or characteristics of the habitat influence behavior and show a level of plasticity in hawksbill sea turtle responses. For example, the extremely rugose top 10–15 m provided by the construction of the runway may provide ideal resting habitat in shallow water and protection from environmental perturbation. Nevertheless, the unequal sampling periods also need to be considered; for example, not every individual was detected throughout all seasons or the full annual range of temperatures that occur in Brewers Bay (n = 7 of 17 detected in all seasons). Similarly, some individuals were only detected in the runway habitat (n = 3 of 17) and others were detected in every habitat except the runway (n = 6 of 17). These types of differences can contribute to individual- and main-effects patterns, particularly if different habitats provide unique resources or advantages (e.g. Christiansen et al. 2017). Although the data was treated to reduce the impacts of combining independent dives, future studies should combine high-resolution TDRs and fine-scale acoustic telemetry with additional sensors (e.g. accelerometry and temperature) to further explore energetic costs or behavioral responses to environmental variation or human activity (e.g. boating, SCUBA diving, snorkeling).

4.5. Conclusions

This study provided higher detection rates, greater longevity of detection periods, and increased spatial resolution compared to previous acoustic tracking research on hawksbill sea turtles. The information obtained provides fundamental knowledge concerning dive and space-use behavior of juvenile hawksbills over periods of months to years to help develop adequate spatial management in the face of ongoing

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environmental fluctuations and increasing human activity. Diving, activity, and horizontal space-use patterns of juvenile hawksbill sea turtles showed distinct diurnal and nocturnal patterns and were influenced by water temperature and other environmental and biological factors. Nevertheless, in several cases, particularly rate of movement and activity space, high variation among explanatory variables (low marginal R^2) and contributory random effects (i.e. individual and yearly variation) existed, suggesting that either physiological or behavioral responses are flexible to annual and individual variations within the specific environment. This adaptability, at least in juveniles, bodes well for resource managers in similar areas, who may be able to rely on consistent space-use patterns throughout monthly–yearly periods.

Water temperature was a dominant driver of diving patterns (e.g. 14 individuals had negative regression slopes for temperature and dive duration relationship) and allowed estimates of Q_{10} values during natural seasonal variations of 1.9 and 2.3 for diel and nocturnal periods, respectively. Although some authors have reported Q_{10} values as high as 4.5 and 5.4 (Hochscheid et al. 2004, Storch et al. 2005 [during night]), the estimates found here are well within the range reported for sea turtles and other reptiles, which commonly have Q_{10} values between 2 and 3, identifying a relatively normal thermal dependence (Davenport et al. 1982, Glass & Wood 1983, Lutz et al. 1989, Storch et al. 2005 [during day]) for juvenile hawksbills. More research is needed to understand the full extent that temperature directly influences behavior, but based on this study a rise in water temperature of 5°C decreases dive durations by ~25%. If greater changes in water temperature (i.e. outside annual variation) occur, it may be that more energetically costly adaptations will be required (e.g. increased activity space). Similarly, as sea surface temperatures rise, previously suitable protected areas consisting of shallow warm water may become less effective if the population shifts to cooler areas. Although it is difficult to predict how behavioral responses to environmental variation will change in the future (see also Storch et al. 2005, Blumenthal et al. 2009, Campbell et al. 2010, Gaos et al. 2012, Hawkes et al. 2014), temperature effects (in conjunction with other environmental factors) on diving, energetics, and space-use should be considered in future conservation and management efforts of sea turtles.

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