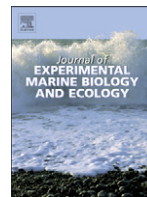




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## Diving behaviour of hawksbill turtles during the inter-nesting interval: Strategies to conserve energy

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## ABSTRACT

Hawksbill sea turtles (*Eretmochelys imbricata*) nesting in Barbados were outfitted with time-depth recorders (TDRs) with temperature sensors to investigate the form and patterns of diving behaviour during the inter-nesting interval (INI; average 14.7 days). All females, regardless of size, surfaced infrequently during dives of average 56 min duration, and the majority of dives (90%) were spent in the bottom phase at 15–25 m depths, which corresponded to the depth of benthic habitat at each location. Diving activity was highest while commuting to and from the nesting beach (about 1–2 days each way), with a level of quiescence during the intermediate period (i.e. the majority of the INI). Despite little thermal variation in seawater at this latitude (13.1°N), the length of the INI was influenced by ambient sea water temperature. Diving behaviour was consistent with females conserving energy reserves built up at foraging grounds prior to arrival at the nesting beach and minimising time spent in the water column away from safe refuge at night. The frequency of surfacing and the depths at which females spend most of their time varies between sites even within one species and may be crucial in managing the risks to animals temporarily residing offshore from important nesting beaches.

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## 1. Introduction

Limited accessibility historically posed a problem for researchers seeking to understand the movements and behaviours of sea turtles while at sea, and this led to fragmented data collection across much of their life cycle (Hays et al., 2000). In recent years, improved technologies have provided researchers with new tools to allow the tracking of horizontal movements by means of radio tags, GPS dataloggers and satellite transmitters, collecting much needed data on foraging, inter-nesting behaviour and migratory phases (e.g. Hays et al., 1999; Schofield et al., 2007a; Walcott et al., 2012; Whiting et al., 2007). In addition, researchers have also been able to begin tracking larger numbers of individuals, facilitating inferences at the population level (Hawkes et al., 2011; Polovina et al., 2006; Schofield et al., 2013a). These data can be greatly enhanced with the addition of dive data; dive profiles being used to add a vertical dimension to understanding the activity of submerged animals (e.g. Hochscheid et al., 1999; Houghton et al., 2002). To date, logging equipment, such as time depth recorders (TDRs) and satellite transmitters with depth recording capabilities, have been deployed quite widely (e.g. Houghton et al., 2002; Sakamoto et al., 1993), to collect dive data on juveniles (e.g. Blumenthal et al., 2009; van Dam et al., 2008), and on adults at foraging grounds (e.g.

Storch, 2003), breeding grounds (e.g. Bell and Parmenter, 2008) and while moving between the two (e.g. Godley et al., 2003; Hays et al., 1999). Such equipment has often also been designed to collect water temperature data, providing additional insights to understanding diving behaviour. Accelerometers are also being increasingly employed to provide additional data on activity levels and infer energy budgets (see Fossette et al., 2012).

Distinctive patterns of diving in juveniles and adults have been reported for several sea turtle species (Blumenthal et al., 2009; Fossette et al., 2008, 2012; Fuller et al., 2009; Storch, 2003; Witt et al., 2010), with dive duration and depth being correlated with size or weight (e.g. hawksbills: Blumenthal et al., 2009; van Dam and Diez, 1997; greens: Ballorain et al., 2011). Longer dives at night appeared to be a consistent pattern for both juveniles and adults of several species at foraging and breeding grounds (Bell and Parmenter, 2008; Blumenthal et al., 2009; Hays et al., 1999, 2000; Storch et al., 2005; van Dam and Diez, 1997). At their foraging grounds, adult females not only made longer dives at night, but used a relatively small range in bottom depth, during which time they were assumed to be resting, while shorter dives made during the day, to a variety of depths and with more depth variation within bottom phases, were interpreted to be times when they were actively feeding (Storch et al., 2005).

Most hawksbill turtles (*Eretmochelys imbricata*) reside in coral reef habitats (but see Bjorndal and Bolten, 2010; Gaos et al., 2012a), where they forage primarily on reef-associated sponges (León and Bjorndal, 2002; Meylan, 1988). Adult females occupy resident foraging grounds (Gaos et al., 2012a; Horrocks et al., 2001; van Dam et al., 2008) and

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every 2–3 years migrate to inter-nesting habitats near to nesting beaches, often hundreds or even thousands of kilometres away, where they take up residence for the breeding season (Blumenthal et al., 2006; Godley et al., 2002; Horrocks et al., 2001; Storch, 2003; Troëng et al., 2005). During the inter-nesting interval (INI), dives tended to be long with only marginal differences in diel dive duration (Bell and Parmenter, 2008; Storch, 2003), suggesting that hawksbill females spend more time resting during the energy demanding inter-nesting period. At higher latitudes, ambient water temperature has been shown to influence diving behaviour as well as the length of the INI in loggerhead and green turtles (Hays et al., 2002; Schofield et al., 2009) and Fossette et al. (2012) used accelerometers to confirm that activity of loggerheads to locate warm spots decreased as water temperature increased. However, the extent to which water temperature may influence diving behaviour and reproductive biology of the more tropical hawksbill turtle during the INI is unknown.

Previous studies of sea turtles have categorised dives into different types, i.e. visual representations of dives on a time/depth scale, and then associated each type with a specific activity or activities (see Hays et al., 2000; Hochscheid et al., 1999; Houghton et al., 2002; Minamikawa et al., 1997). Dive depths have often been shown to correspond to water depth, substantiating a demersal life style of studied species. Variation in depth during the bottom phase of dives is related to differences in activity, as confirmed by ground-truthing (e.g. Fuller et al., 2009; Seminoff et al., 2006; Thompson et al., 2011). Dive profiles generated for inter-nesting females are usually populated with dives where females remain at a fixed depth for the majority of the submergence period (U-shaped dive [hereafter called U-dive] or Type 1 dive: Minamikawa et al., 1997; Type 1a dive: Houghton et al., 2002; see Sakamoto et al., 1993; Storch et al., 2002; Bell and Parmenter, 2008). Bell and Parmenter (2008) suggested that such dives, exhibited by hawksbills nesting on Milman Island Reef, could represent periods of inactivity within reefal structures or on the sea floor. Given that the bathymetry and temperature of neritic habitats near breeding grounds can potentially influence dive behaviour (Gaos et al., 2012b; Houghton et al., 2002), it may not be possible to generalise behaviour between locations. This highlights the need for diving data to be collected for breeding females temporarily residing in the vicinity of important nesting beaches, where the beaches themselves are often protected but crucial inter-nesting habitats may not be (Schofield et al., 2007a, 2013b; Zbinden et al., 2007). The frequency of surfacing and the depths at which females spend most of their time are important in managing risks to these animals, e.g. boat strikes, while they are in these nearshore habitats (Hazel et al., 2007), and can potentially be used to guide management of human activities in these important areas.

The spatial locations of areas occupied by female hawksbills (i.e. inter-nesting resident areas) nesting at Needham's Point beach, Barbados, during their INIs have already been mapped and the three stages of the INI identified (Walcott et al., 2012). In this paper, we investigated the diving behaviour of these gravid hawksbills during the INI. The breeding season is a time period that females spend in a relatively unknown environment, away from familiar foraging grounds (Horrocks et al., 2001) and where food sources may be unavailable (e.g. Hays et al., 2002; Krueger et al., 2011). Many females will be on only their first or second nesting season at a location where they stay for only a few months. Furthermore, the marine environment of a breeding ground can change significantly within a 2–3 year period due to natural events, such as hurricanes and storms which are common to this region, as well as events such as coral bleaching and anthropogenic impacts. We predicted that females would adopt energy conserving strategies while maturing eggs, i.e., dives would be to the depths of preferred resting and/or refuge sites and that diving behaviour would reflect overall lower levels of activity while in resident areas. We also predicted that the higher and less varied water temperatures experienced by this circumtropical species would be less likely to affect activity levels and reproductive biology compared to more sub-tropical nesting species.

## 2. Materials and methods

### 2.1. Study site

Barbados hosts an average of 450–500 nesting hawksbills along its south and west coasts yearly (Beggs et al., 2007), with females laying 4–5 clutches each separated by approximately two week INIs (Beggs et al., 2007). Needham's Point (13° 04' 41.33" N, 59° 36' 32.69" W) was used as the site for deployment and retrieval of equipment (see Walcott et al., 2012). Located to the southwest of the island, the 1.5 km stretch of beach provides nesting habitat for >25% of the island's nesting hawksbills annually (Beggs et al., 2007; Horrocks, 1992).

Barbados has a narrow insular shelf, with the 200 m isobath lying 2–3 km offshore (Lewis and Oxenford, 1996). This provides sea turtles access to a wide range of depths over only a short distance. Coral rubble, fringing and patch reefs, and a bank reef extending unbroken along much of the west and south coasts are major characteristics of the neritic habitats of Barbados. The patch reefs range in depth from 6 to 15 m, while the crest of the bank reef ranges from 15 to 25 m, dropping off on both sides to depths in excess of 40 m (Lewis and Oxenford, 1996). Depths between the patch reefs and the bank reef can reach as much as 40–55 m (Lewis and Oxenford, 1996).

### 2.2. Equipment

VEMCO (Nova Scotia, Canada) 8-bit Minilog TDRs with temperature sensors were used to collect dive data on study animals. TDRs had a memory capacity of 16K RAM (allowing for 8000 temperature and 8000 depth reads per deployment). TDRs had a depth range up to 68 m with  $\pm 2.0$  m accuracy and a 0.4 m resolution, and a temperature range of 0–40 °C with  $\pm 0.3$  °C accuracy and a 0.2 °C resolution.

Two stages of the inter-nesting interval (Stages 1 and 3) consisted of directed horizontal movement; the travel towards the resident area and the travel away from the resident area back to the nesting beach, each of which was approximately 1–2 day duration. Stage 2, refers to the time spent in the resident area (approximately 10 days; Walcott et al., 2012). TDRs were set to record at 53 s intervals to allow the continuous collection of dive and temperature data for approximately five days. Using the 'delayed start' function provided by VEMCO, TDRs were programmed to collect data during Period 1 – the initial five days of the INI which included the period of travel to the inter-nesting resident area (Stage 1) in addition to part of the time spent in the resident area (i.e. the first part of Stage 2), Period 2 – the intermediate five days while in the resident area (i.e. Stage 2 only), or Period 3 – the final five days which included time spent in the resident area, as well the time spent travelling back to the nesting beach at the end of the INI (the last part of Stage 2 and all of Stage 3).

### 2.3. Study animals and deployment of TDRs

Deployments were conducted at night (18:00–04:00) during the peaks of the 2009 and 2010 nesting seasons, after females had nested successfully (see Walcott et al., 2012). Selection criteria, similar to those used by Bell and Parmenter (2008), were employed to maximize equipment retrieval. Females either on their first or second clutch of the season were selected based on nesting data from previous seasons (Barbados Sea Turtle Project, unpublished data) and/or the external appearance of ample neck fat (see Walcott et al., 2012). Females were gently restrained in a wooden enclosure for measurement and to allow TDRs to be attached to the highest part of the carapace, along with GPS dataloggers and VHF transmitters, all pre-mounted onto a piece of plywood. Foot patrols of the index beach using a VHF radio receiver allowed returning females to be located and equipment to be retrieved. Given that equipment was re-used throughout the study period, once the TDRs were retrieved, data were downloaded and

equipment readied for re-deployment. Full details of the attachment procedure and retrieval process are described in Walcott et al. (2012).

#### 2.4. Data analysis

The VEMCO Minilog PC interface V3.09 was used to download and view dive data. However, all dive data were analysed using MultiTrace Ver. 2012.1 (Jensen Software Systems, Germany). As noted by Hays et al. (2000) the depth at which descents are considered a dive is somewhat arbitrary. Therefore, records of depths greater than 2 m, similar to studies on hawksbill (Storch, 2003) and green turtles (Cheng, 2009), were considered in this study to constitute diving. Hawksbills in Barbados average 89 cm in length (CCL curved carapace length; Beggs et al., 2007). Thus a depth of 2 m should eliminate any time spent just below the surface and the effect of waves rolling over a turtle.

Dives were placed into five categories based on their profiles, three of which (i.e. U, V and W-dives; Fig. 2) were based on previous studies conducted by Minamikawa et al. (1997), Houghton et al. (2002) and Seminoff et al. (2006). The fourth category (U<sup>^</sup>-dives) represented a modified U-dive where the dive profile generally conformed to the U shape with the normally 'flat' shape of the bottom phase being interrupted by a depth change (Fig. 2). Dives which did not fit into one of the above mentioned categories were referred to as X-dives (i.e. other dive types, see Hochscheid et al., 1999; Fig. 2).

Days were divided into diurnal (06:00–17:59) and nocturnal (18:00–05:59) periods to investigate diel patterns in dive behaviour. Activity levels were approximated by reviewing the Coefficient of Variation of the depth during the bottom phase (i.e. portion of dive between the descent and ascent inflection points). The CV is a statistical measure of the dispersion around the mean; a larger CV indicates greater variation in the depth of the bottom phase of a dive and vice versa, thus a high CV serves as a proxy for greater activity (Blumenthal et al., 2009). Where data failed testing for normality and no significant difference was seen after data transformations, non-parametric test statistics were calculated using SPSS 11.0 for Windows. Correlation analysis was used to investigate relationships between turtle body size (cm CCL) and various dive parameters i.e., dive duration, bottom time (total time in bottom phase), maximum dive depth (deepest point recorded during a dive), mean bottom depth (average depth in the bottom phase) and CV, to determine whether diving capabilities of adult hawksbills were limited by size, as has been found with juveniles. Dive parameters were compared between Stages 1, 2 and 3 of the INI. Given the sampling interval of 53 s, surface intervals (SIs) (the length of time the animal was at the surface) were placed into the following categories: SI 1 ( $\leq 1$  min), SI 2 ( $>1$  min,  $\leq 2$  min), SI 3 ( $>2$  min,  $\leq 3$  min) up to SI 7 ( $>6$  min).

Means and standard deviations were provided to allow for direct comparison with previous studies, even if data were analysed with non-parametric tests.

### 3. Results

Of the 15 study animals equipped with TDRs during the two nesting seasons (turtles T09–T23), thirteen were re-sighted allowing for equipment retrieval (see Table 1). Study animals ( $n = 13$ ) ranged in size (CCL) from 85 to 100 cm with the majority (91.7%,  $n = 12$ ) being above 90 cm (Table 1). All animals provided dive data from Stage 2 (i.e., while in the resident area), five provided data from Stage 1 and four from Stage 3 (Table 1). Details on transition points between stages are provided in Walcott et al. (2012). The data collection period for turtle T22 spanned two INIs, providing data from Stage 3 in the first INI and Stages 1 and 2 in the second INI (Table 1). A total of 1540 dives were recorded over a total of 1471.1 h.

None of the dive parameters recorded (i.e. dive duration, bottom time, bottom depth, CV and maximum depth) were correlated with size (CCL) across the limited size range of our adult female study

**Table 1**

ID, curved carapace length, inter-nesting interval length and stage for which diving data were collected for each study animal.

Year	I.D.	CCL (cm)	INI (day)	Stage	
2009	T09	93.0	16	1, 2	
	T10	92.8	15	2	
	T11	93.7	14	2	
	T12	93.1	15	1, 2	
	T13	90.2	17	1, 2	
	T14	90.8	16	2	
	T15	90.6	15	2, 3	
	T16	92.5	13	2, 3	
	2010	T17	85.0	15	1, 2
		T18	93.1	14	2
T19		100.0	15	2, 3	
T21		92.0	13	2	
T22		–	13	1, 2, 3	

animals (Spearman rank correlation,  $p > 0.05$  in all cases). Overall means (i.e. across all three Stages) for dive parameters are provided in Table 2. The majority of dives lasted longer than 56.1 min (54%,  $n = 1540$ ), had bottom times comprising  $>90.4\%$  of the dive time (76.3%,  $n = 1495$ ) and a CV throughout the bottom phase  $<4.4\%$  (76.9%,  $n = 1495$ ). In most dives recorded ( $>90\%$ ), females dived to the deepest point of the dive at first descent or soon thereafter. Over 70% of surface intervals observed were of duration SI 1, with 21.3% being SI 2 and only 8.6% SI 3 or longer, i.e., more than 2 min, but equal to or less than 3 min.

The majority of dives (about 65%) across all three Stages were to depths of less than 25 m (Fig. 1). Dividing the data into depth bins corresponding to habitat types most likely encountered along individual travel paths or while in the resident areas (i.e.  $<15$  m: patch reefs, 15–25 m: crest of bank reef, 25–40 m: sides of bank reef,  $>40$  m: non-living coral habitats), the most frequently utilised depth ranges were 15–25 m (42.3%) and 25–40 m (28.6%), while the  $>40$  m depth was the least utilised (5.8% of dives; Fig. 1). With increasing depth, the CV throughout the bottom phase halved from 6.7 to 3.1%, and dive duration doubled; increasing from 38.7 to 72.2 min (Fig. 1). There was a positive correlation of dive duration with bottom depth (Pearson correlation  $r_s = 0.51$ ,  $N = 1540$ ,  $p < 0.05$ ) and a negative correlation of CV with bottom depth (Pearson correlation  $r_s = -0.35$ ,  $N = 1495$ ,  $p < 0.05$ ).

#### 3.1. Dive types

U and U<sup>^</sup>-dives were the most frequent dive types utilised by study animals, accounting for 87.5% (73.7 and 13.8% respectively) of all dives, while V-dives accounted for only 2.9% (Table 3). Dive duration was significantly longer for U and U<sup>^</sup>-dives and shortest for V-dives (Kruskal–Wallis,  $p < 0.05$ ; Table 3). There was no bottom phase for V-dives, with females abruptly reversing direction and ascending, while during a U-dive a female dived to a depth, and remained at that depth throughout the bottom phase of the dive until returning to the surface. The mean percentage of dive time spent in the bottom phase of a dive was lower for W and X-dives than U and U<sup>^</sup>-dives (Table 3), suggesting that more time was spent in the water column ascending and/or descending during these dive types. W and X-dives also had the highest

**Table 2**

Summary of overall diving performance and water temperature.

Dive parameter	Mean (SD)	Range	N
Duration (min)	56.1 (23.4)	1.8–121.9	1540
Bottom time (%)	90.4 (10.9)	7.1–98.1	1495
Bottom depth (m)	23.1 (10.1)	2.1–64.3	1495
CV (%)	4.4 (7.8)	0.1–96.4	1495
Bottom temperature (°C)	28.8 (0.7)	26.3–30.3	1495

N.B. V shaped dives ( $n = 45$ ) did not have a bottom phase, thus leading to a reduction in N for some of the dive parameters. Bottom time refers to the percentage of the dive spent in the bottom phase (i.e. portion of dive between the descent and ascent inflection points).

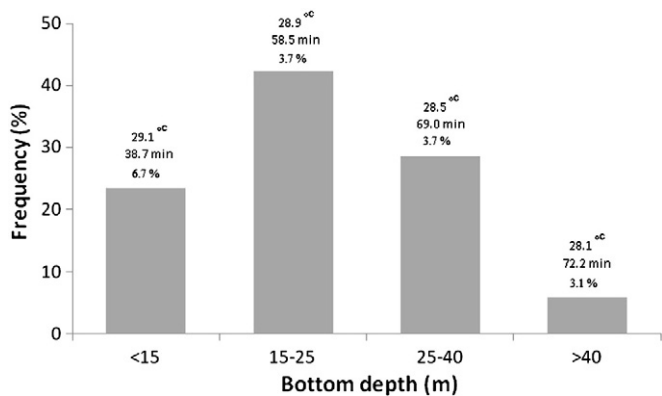


Fig. 1. Mean dive parameters (from top down: bottom temperature, dive duration and CV) for bottom depths (habitat defined) utilised.

CV in the bottom phase (Table 3), indicative of greater activity, while U and U<sup>^</sup>-dives had significantly lower CV in their bottom phases (1.8 and 7.2% respectively; Kruskal–Wallis,  $p < 0.05$ ; Table 3). The mean maximum dive depth reached during V-dives (8.9 m) was significantly shallower than the other four dive types which ranged from 23.7 to 30.6 m (Kruskal–Wallis,  $p < 0.05$ ; Table 3). Regardless of dive type and their respective dive variables (dive duration, bottom time, bottom depth, CV and maximum depth), surface intervals of  $\leq 1$  min (category SI 1) predominated.

Table 3  
Dive characteristics, presented as mean (SD), for each dive type ( $n = 1540$ ).

Dive type:	U	U <sup>^</sup>	V	W	X
Frequency (%)	73.7	13.8	2.9	3.4	6.2
Duration <sup>a</sup> (min)	60.7 (20.0)	58.0 (23.0)	5.5 (3.8)	28.8 (13.8)	36.2 (22.9)
Max. depth <sup>a</sup> (m)	23.7 (10.1)	30.6 (12.4)	9.0 (10.4)	29.0 (15.9)	26.0 (16.0)
Bottom depth (m)	23.0 (9.8)	25.9 (9.6)	n/a	20.5 (11.0)	19.1 (12.1)
Bottom time (%)	92.8 (5.7)	88.5 (11.8)	n/a	77.3 (17.1)	73.8 (24.0)
CV <sup>a</sup> (%)	1.8 (1.9)	7.2 (5.4)	n/a	22.0 (12.8)	19.4 (16.5)

<sup>a</sup> Dive characteristics which differed significantly (Kruskal–Wallis,  $P < 0.05$ ).

### 3.2. Diving behaviour during the three stages of the inter-nesting interval

Dive parameters differed significantly among the three stages (Kruskal–Wallis,  $p < 0.05$  in all cases; Table 4). Non-parametric Tukey-type multiple comparisons (Dunn, 1964) indicated dive duration was significantly longer and CV was significantly lower when females were in their resident areas (i.e. Stage 2; Table 4). A diel difference was also detected in dive duration, with increased dive duration at night (Wilcoxon Signed Ranks Test,  $p < 0.05$ ). Maximum depth and mean bottom depths were significantly shallower during Stage 1 than Stages 2 and 3, and the percentage of time spent in the bottom phase of dives differed among all stages with Stage 2 showing the longest and Stage 1 the shortest bottom times (Table 4). For all three Stages, the mean bottom depths utilised coincided with the depth range at which the crest of the bank reef occurred (i.e. 15–25 m; see Walcott et al., 2012), while the surface intervals between dives were all of duration one minute or less (SI 1). Three of the 1539 surface intervals that were unusually

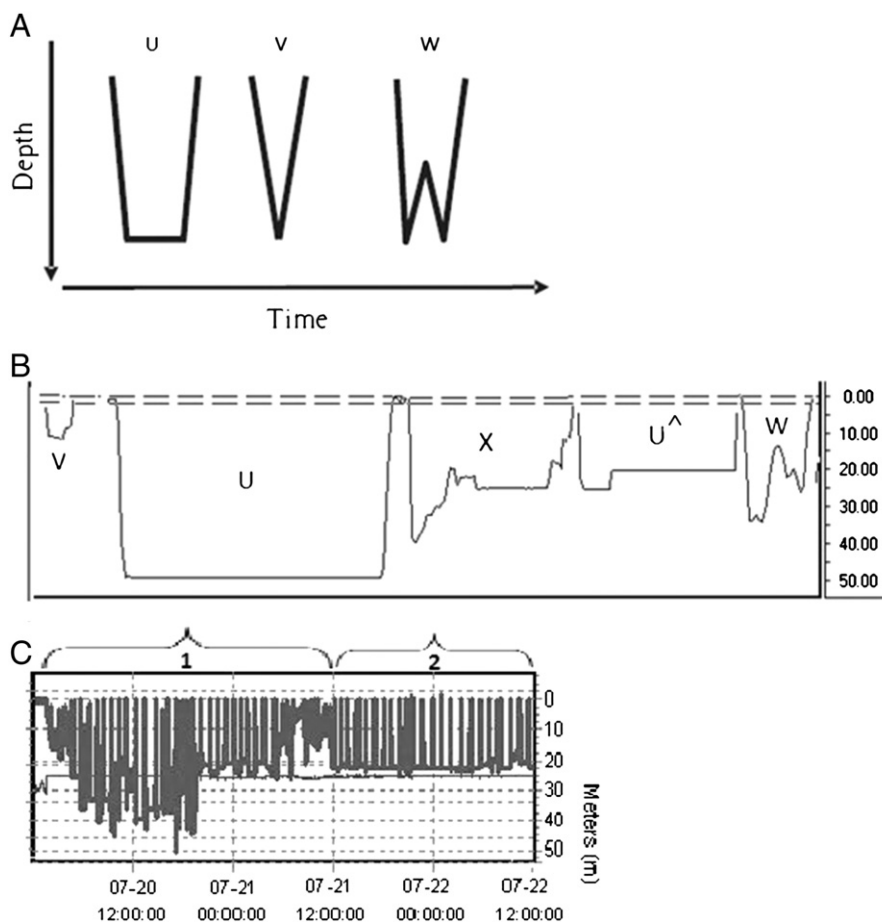


Fig. 2. A) Generalised dive profile of U, V and W-dives. B) Example of the five dive categories exhibited by study animals (adapted from Seminoff et al. (2006)). C) Section of actual dive data from T12 showing dive profiles while 1 – moving away from the nesting beach after nesting and 2 – once the resident area is reached.



**Table 4**

Dive characteristics, presented as mean (SD), for each stage of the inter-nesting interval (n = 1540).

	Stage 1	Stage 2	Stage 3
Surfacing frequency (hr <sup>-1</sup> )	2.1	1.0	1.3
Duration (min)	29.7 (20.4)	60.0 <sup>a</sup> (21.2)	45.2 (25.8)
Bottom time (%)	78.3 <sup>a</sup> (17.6)	92.3 <sup>a</sup> (7.5)	82.7 <sup>a</sup> (19.2)
Max. depth (m)	20.4 <sup>a</sup> (13.4)	24.6 (11.1)	26.6 (14.2)
Bottom depth (m)	18.3 <sup>a</sup> (10.9)	23.5 (9.7)	23.6 (11.8)
CV (%)	10.5 (11.2)	3.1 <sup>a</sup> (4.9)	11.0 (15.6)

<sup>a</sup> Significantly different dive characteristics determined using non-parametric Tukey-type multiple comparisons (Dunn, 1964).

long (13, 19 and 20 min in duration) occurred during Stage 3, and may have been associated with searching for the nesting beach or for an emergence spot on the beach.

U-dives predominated throughout each of the three stages, but were utilised much more frequently during Stage 2, where they accounted for 80.9% of all recorded dives (Fig. 3). U-dives during Stage 1 were significantly shorter, utilised shallower bottom depths and had a relatively high CV in the bottom phase when compared to those of Stages 2 and 3 (Kruskal–Wallis,  $p < 0.05$ ; Table 5). In Stage 2, the mean bottom depths during U-dives utilised by different females ranged widely, from 15.5 to 39.1 m. By contrast to U-dives, V, W and X-dives occurred at low frequencies, particularly during Stage 2 (Fig. 3). Stages 1 and 3, the horizontal travelling phases of the INI, were therefore characterised by more variable forms of dives than Stage 2 when the females were in their resident areas.

### 3.3. Thermal influences on diving behaviour while in the resident areas

Being ectothermic animals, water temperature may also be a factor influencing diving activity and reproductive biology of the study animals. Temperature data (diurnal temperatures taken at depths of 5–30 m with a temperature probe) collected annually on selected reefs on the south coast of the island during the months of the breeding season over the years 2007–2012 averaged  $28.5 \pm 0.4$  °C (R. Suckoo, pers. comm., Coastal Zone Management Unit, Government of Barbados), suggesting little variation in sea water temperature, but temperatures experienced by females, as recorded by TDRs, were typically warmer at shallower depths (Spearman rank correlation  $r_s = -0.40$ ,  $N = 1495$ ,  $p < 0.05$ ; Fig. 1). Females experienced little diurnal variation in bottom temperatures during U-dives in Stage 2 (day time mean:  $28.7 \pm 0.7$  °C,  $N = 526$ ; night time mean:  $28.9 \pm 0.6$  °C,  $N = 497$ ) and no significant difference was observed in the CV between day and night periods for study animals (Wilcoxon Signed Ranks Test,  $p > 0.05$ ). However, despite the small range in temperature recorded, the overall length of the INI was negatively correlated with water temperature (Spearman rank correlation  $r_s = -0.68$ ,  $N = 13$ ,  $p < 0.05$ ; Table 1).

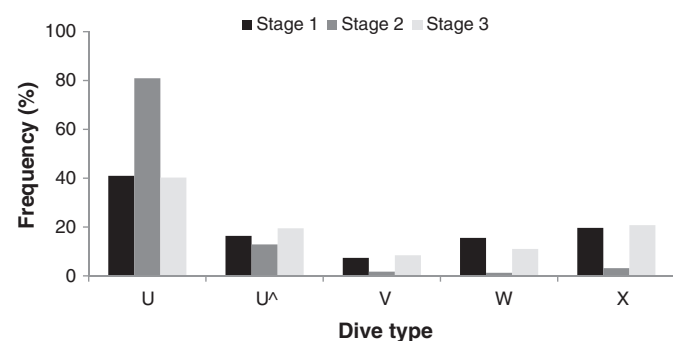


Fig. 3. Variation in dive types among the three stages of the inter-nesting interval.

**Table 5**

Dive characteristics, presented as mean (SD), for U dives across the three stages of the inter-nesting interval.

	Stage 1	Stage 2	Stage 3
Frequency (%)	41.0	80.9	40.3
Duration (min)	33.2 <sup>a</sup> (21.8)	62.0 (18.9)	62.4 (20.9)
Bottom depth (m)	18.2 <sup>a</sup> (10.8)	23.1 (9.6)	26.5 (11.5)
CV (%)	4.1 <sup>a</sup> (4.7)	1.7 (1.5)	1.9 (1.7)

<sup>a</sup> Significantly different dive characteristics determined using non-parametric Tukey-type multiple comparisons (Dunn, 1964).

## 4. Discussion

Sea turtles spend most of their lives under the ocean's surface where they are adapted to move efficiently. The minimal time spent at the surface by study animals, regardless of dive depth and level of activity, reinforces the point that these animals are surfacers rather than divers (Kooyman, 1989). While use of surface waters provides easy access for gaseous exchange, it is further from food sources, most of which are benthic for adult hawksbills (Houghton et al., 2003; Meylan, 1988; Stimmelmayer et al., 2010; van Dam and Diez, 1997). Efficiency of vertical movement in the water column by sea turtles moving between the air and their benthic habitats is therefore crucial, particularly for inter-nesting females who are using energy to prepare clutches of eggs (Fossette et al., 2012; Wallace et al., 2005).

Sea turtles have been shown to rest at the maximum depth at which they can still attain close to neutral buoyancy (e.g. 17–20 m in adult green turtles; Hays et al., 2004), and may not rest at shallower depths because they cannot inspire enough air to maximize diving efficiency. Whether inter-nesting females select resting depths to maximize diving efficiency or to utilise suitable benthic habitat or some combination is still unclear. In our study the mean dive depths of females tended to correspond to the varying depths of the crest of the bank reef, across both the travelling and resident stages of the INI. Although the size range of our study animals was relatively small, the mean bottom depths they utilised ranged from 16.3 to 37.2 m. It was expected that the range in bottom depths of resting dives would have been smaller had the attainment of neutral buoyancy been the only consideration, although the buoyancy of females likely changes both within each inter-nesting interval as eggs are matured and laid, as well as over the course of the nesting season as body fat is lost (Santos et al., 2010). Despite this, our study animals returned to the same depths in the same resident areas after each nesting emergence (see Walcott et al., 2012). This suggests that, at least during Stage 2, females are likely utilising depths at which preferred habitats are found; habitats which may provide assisted resting sites that allow females the opportunity to rest at depths which may be outside of the range over which neutral buoyancy could be achieved with a lung full of air.

The reef system may also be used in orientation, and perhaps because it offers refuge from predators, as females cyclically commute between inter-nesting habitats and the nesting beach. This result contrasted with studies on other turtle species in non-reefal habitats that have reported the use of shallow subsurface dives while actively travelling to and from inter-nesting sites (Hochscheid et al., 1999; Houghton et al., 2002). The reef crest is structurally and biologically complex; its greater rugosity compared to the reef slope not only provides ledges and overhangs for rest and possibly refuge (Walcott et al., 2012), but more opportunities for biological interactions such as cleaning stations (Sazima et al., 2004) as well as other interactions, both intra and inter-specific, that are rarely documented (see Heithaus et al., 2002; Schofield et al., 2006). At the same time, the energy expenditure required for repeat visits to the surface for gaseous exchange is minimised, as distance travelled is shortest from the crest as compared to the rest of the reef, and preferred resting ledges for which females may compete can be quickly relocated (see Walcott et al., 2012). The

minimal use of depths greater than 40 m (Fig. 1), i.e., depths where the abundance of sponges tends to increase while that of live corals decreases (Bellairs Research Institute, 1984), supports the suggestion that inter-nesting females do not dive to depths where they could potentially forage. Given that Barbados has previously been reported as a suboptimal adult foraging habitat (Krueger et al., 2011), a strategy of energy conservation over energy utilisation would not be surprising, as has been documented at suboptimal sites in more temperate locations (Fossette et al., 2012; Schofield et al., 2009).

Apart from differences in energy expenditure associated with diving to different depths, diving and surfacing also differ in energetic expenditure, perhaps explaining why females in this study dived to the deepest point early in each dive. In order to overcome the positive buoyancy following gaseous exchange at the surface (Minamikawa et al., 1997), on their initial descent turtles use powerful flipper strokes (Van Dam and Diez, 1997) with high flipper beat frequency and amplitude (Hays et al., 2007). Indeed hawksbills, loggerheads, greens and leatherbacks have all been reported to exhibit greater vertical velocities upon descent than on ascent (Eckert, 2002; Hochscheid et al., 1999; Houghton et al., 2002; van Dam and Diez, 1997), with ascents utilising very little swimming and more buoyancy control using lung gases. van Dam and Diez (1997) also partly attributed the slower ascent as a means of carefully surveying the surface zone for potential hazards and predators.

Dive durations were on average longer than 50 min, supporting the observation that hawksbills, at least during the INI, make some of the longest routine dives of all sea turtles (see also Starbird et al., 1999; Gaos et al., 2012b). The predominance of short surface intervals (i.e. SI 1: <1 min) seen in this study has also been reported for hawksbills nesting at Buck Island, where a median surface interval of 1.2 min was exhibited (Storch, 2003). By contrast, other species have been reported to spend considerable amounts of time at the surface (e.g. Hochscheid et al., 2010; Standora et al., 1984). Regardless of previous or subsequent dive type, time of day, or Stage of the INI, short intervals at the surface were most prevalent for Barbados hawksbills (see also Starbird et al., 1999) suggesting that time at the water surface during the breeding season functioned primarily for gaseous exchange, rather than thermoregulation or the control of ecto-parasites or infections that have been suggested for other species (see Hochscheid et al., 2010). Given that the study animals were tagged on their first or second nesting emergence, the lack of time at the surface also supports the generally accepted view that mating (much time of which is believed to occur at the surface) does not tend to occur after the first batch of eggs is laid (Miller, 1997; Schofield et al., 2013b).

The shorter dive durations recorded during Stage 1 when females were travelling away from the nesting beach indicated that females were surfacing more frequently while swimming against the westerly currents towards their resident areas (see Walcott et al., 2012), suggesting that dive duration decreased with increased metabolic rates (see also Hays et al., 2000). The high frequency of short, shallow V-dives while travelling both away from and towards the nesting beach suggests that these dives may be used for brief underwater surveys of benthic habitats and orientation (Fossette et al., 2008; Hochscheid et al., 1999; Thompson et al., 2011). W and X-dives were also most prevalent during the travelling phases; their short dive durations, decreased bottom time and significantly increased levels of CV in the bottom phase clearly indicated high activity levels. Seminoff et al. (2006) has already associated W-dives with exploratory behaviour of benthic habitats. X-dives similarly may function as exploratory, orientation and navigational dives, which have been influenced or interrupted by other random factors (e.g. boat traffic, conspecific interactions, weather conditions inter alia) leading to the dive profile differing from previously recognised dive types.

Overall, the most commonly recorded dives were U-dives (73.7% of all dives). This type of dive is frequently utilised at breeding grounds and has been reported to function either solely or partially for resting (e.g. Fossette et al., 2012; Fuller et al., 2009; Hays et al., 2000; Hochscheid et al., 1999; Houghton et al., 2002, 2008; Minamikawa

et al., 1997; Seminoff et al., 2006; Starbird et al., 1999; Storch et al., 1999, 2002; Thompson et al., 2011). The long duration, large percentage of dive time spent in the bottom phase, and the relatively small CV while in the bottom phase, particularly during Stage 2 of the INI, all suggested that the hawksbills in this study also reduced activity and established a level of quiescence, as observed at the temperate breeding area of Zakynthos (Fossette et al., 2012). Apart from resting, U-dives have also been linked to benthic activities such as foraging and horizontal movements (Fuller et al., 2009; Hochscheid et al., 1999; Seminoff et al., 2006; Thompson et al., 2011), and the modified U-dives (i.e. U<sup>+</sup>-dives) of this study could possibly indicate periods of horizontal movement. Second in frequency only to U-dives, the relatively long dive duration and high percentage in bottom time of U<sup>+</sup>-dives (though lower in both parameters than U-dives) supports an overall low activity level. However, the increase in mean CV in the bottom phase when compared to U-dives suggested a higher activity level than U-dives. U<sup>+</sup>-dives therefore possibly function as exploratory and orientation dives along the bottom, thus explaining their relatively high frequencies while travelling to and away from the nesting beach. At this time, females may be searching for previously used resident areas or looking for new or better resident areas. An alternative explanation is that U<sup>+</sup>-dives represented resting dives that were interrupted, either by other turtles (e.g. males looking to mate, females contesting suitable resting ledges and overhangs) or even humans (e.g. SCUBA divers), causing the animal to relocate before resuming resting (see Schofield et al., 2007b).

Active dives are characterised by greater movements, shorter durations and greater depth variation in the bottom phase (Cheng, 2009; Starbird et al., 1999; Witt et al., 2010). Overall means for surfacing frequency, dive duration and CV in the bottom phase in our study (1.1 per hr,  $56.1 \pm 23.4$  min,  $4.4 \pm 7.8\%$ ) would therefore suggest that animals maintained a relatively low level of diving activity while in the inter-nesting habitat at this rookery, as has been observed at other rookeries (see Fossette et al., 2012). The vertical movements exhibited by females in this study therefore supported previous findings derived from the spatial tracking of horizontal movements using GPS dataloggers of the study animals (Walcott et al., 2012). Together, the two datasets support a lack of foraging activity throughout the nesting season, and a reliance on fat reserves built up while at foraging grounds (see Hays et al., 2000, 2002; Santos et al., 2010; van Dam et al., 2008). The lack of diel variation in bottom depths utilised and CV during the bottom phase would suggest that activity levels during the day and night periods were equally low (see Hochscheid et al., 1999; Storch, 2003). However, dive duration and the time spent in the bottom phase of the dive increased at night in our study. Such behaviours may represent a strategy to minimise time spent in the water column and away from safe refuge (Blumenthal et al., 2009), with the lower visibility and increased risk of predation, particularly by tiger and bull sharks, at night.

The small variation in mean water temperatures in the Caribbean Sea around Barbados during the breeding season, as compared to more temperate locations (see Schofield et al., 2009) suggested that there was less potential for behavioural thermoregulation. However, even the relatively small temperature range (i.e. 4 °C) experienced by study animals may still have influenced diving behaviour exhibited due to changes in metabolic rates. Green turtles were shown to increase their oxygen consumption rate (proxy for metabolic rate) when resting by 52% due to an increase in temperature of 4.1 °C from winter to summer (Enstipp et al., 2011). The fact that the length of the INI was shorter at warmer water temperatures for females in our study, even though there is only a slight variation in temperature range around Barbados' latitude (13.1°N), suggested that ambient water temperatures may still play an influential role in female reproductive biology (see also Sato et al., 1998). Loggerheads nesting at higher latitudes around Zakynthos, Greece, experienced temperatures ranging between 13 and 26 °C and were found to actively select areas of warm water (Fossette et al., 2012; Schofield et al., 2009). Since water temperature decreased with depth in Barbados, shallower habitats on the reef that provided

optimal overhangs and ledges for buoyancy control and refuge, may also have been preferred for the opportunities for thermoregulation they provided.

Finally, diving behaviour exhibited by hawksbills at the Barbados rookery not only differed in some important respects from that of other species during their inter-nesting intervals (e.g. Hays et al., 2002; Minamikawa et al., 1997; Schofield et al., 2009), but also from that of hawksbills at other rookeries (see Bell and Parmenter, 2008; Gaos et al., 2012b; Starbird et al., 1999; Storch et al., 2002). Given this, behavioural and ecological data may need to be collected at a rookery level to better understand habitat use by endangered sea turtle populations and implement conservation and management strategies that will adequately protect reproductive females between nesting emergences.

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