



Inferring vertical and horizontal movements of juvenile marine turtles from time-depth recorders

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ABSTRACT: Acquiring knowledge of the spatial ecology of many aquatic species, particularly their juvenile life stages, is challenging when they are small in size; this limits the attachment of tracking devices that routinely provide spatially explicit information on larger juveniles and adults. Using depth utilisation data gathered by time-depth recorders, we inferred patterns of habitat utilisation of juvenile hawksbill turtles *Eretmochelys imbricata* occupying a shallow reef system in the Caribbean. Hawksbill turtles ($n = 9$, curved carapace length = 42.3 ± 9.7 cm, range = 27.7 to 60.0 cm) demonstrated diel patterns of behaviour, with greater activity and shorter dives during the day (mean duration = 7.5 ± 5.0 min, range = 2.6 to 34.4 min) and longer, less active dives during the night (mean duration = 16.6 ± 12.0 min, range = 2.5 to 61.5 min). A level of fidelity to sites facilitated recaptures (mean minimum straight-line distance from release of TDR-equipped turtles to their subsequent recapture locations = 0.9 ± 0.9 km, range = 0.01 to 2.3 km), but recapture success after 130 h, over a 43 d period, was relatively low: of 19 individuals instrumented, 9 were recaptured. From depth records, i.e. maximum depths achieved, it was clear that some recaptured individuals moved considerably during the monitoring period; 3 individuals moved to deeper waters, with minimum possible straight-line movement distances from their capture sites of 3.7 to 9.2 km. These findings emphasize the likely influence of habitat structure on site fidelity and further highlight that data from traditional capture–mark–recapture studies could lead to an underestimation of home-range size.

KEY WORDS: Habitat utilisation · Spatial ecology · Coral reef · Hawksbill turtle · *Eretmochelys imbricata* · Telemetry · British Virgin Islands

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INTRODUCTION

While the horizontal and vertical movements of large marine vertebrates are being increasingly described (Priede 1984, Duron-Dufrenne 1987, Polovina et al. 2000, Block et al. 2005, Bonfil et al. 2005), remote recording of accurate spatial movements made by smaller species or early life stages has been slower, due to the challenges of miniaturising power sources, development of attachment techniques and hydrodynamic packaging of equipment (Watson & Granger 1998, Wilson & McMahon 2006, Pavlov et al. 2007, Godley et al. 2008).

For many species this problem has set limits on the size classes that can be tracked with the more sophisticated, power- and memory-demanding biologging technologies, such as satellite tracking units and dead-reckoning technologies. Many aspects of juvenile behaviour have, therefore, remained elusive to ecologists and conservation managers seeking to develop spatially explicit management plans.

The time-depth recorder (TDR) represents a useful and cost-effective technology for studying depth-utilisation in juvenile life stages, as units are typically small and comparatively inexpensive. TDRs, however,

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record only depth and, optionally, light and/or temperature. These data make it difficult to ascertain habitat use within a spatial context, particularly for species or life stages that have patterns of movement or habitat preferences not well suited for light geolocation techniques (i.e. crepuscular diving, preference for turbid water, or non-migratory behaviour). It has, however, been possible to use TDR data, alongside environmental data, to reconstruct the migratory routes of free-ranging fish species (Metcalf & Arnold 1997, Hunter et al. 2003, Hunter et al. 2006, Righton & Mills 2008).

Adult hawksbill turtles *Eretmochelys imbricata* undertake considerable migrations between breeding grounds and subsequent coral reef foraging habitats (van Dam et al. 2008, Cuevas et al. 2008), which are also the foraging habitats of juveniles recruiting from oceanic environments (Musick & Limpus 1997), a process that is accompanied by an ontogenetic dietary shift to predominant spongivory (Meylan 1988, Bjørndal 1997). Hawksbill turtles represent an important predator on sponges in reef systems (Hill 1998, Leon & Bjørndal 2002). Reef occupancy will be driven by several factors, including the spatial distribution of preferred dietary items (Meylan 1988), an individual's relative capacity to dive to exploit these items and predator avoidance tactics (van Dam & Diez 1996). As their mass and subsequent capacity to attain greater dive depths increases (Mori 2002, Hochscheid et al. 2007), larger juvenile turtles are able to transit to deeper habitats in search of food, most likely driving niche partitioning (Blumenthal et al. 2009b). Previous work has suggested that although juveniles make sequential moves between foraging grounds (Meylan 1999), home ranges are typically small (0.07 to 0.14 km², van Dam & Diez 1998; 545 ± 515 m capture to recapture, Blumenthal et al. 2009a).

Previous TDR studies on hawksbill turtles have been carried out in the vicinity of reef wall habitats in Puerto Rico (van Dam & Diez 1996, 1997) and the Cayman Islands (Blumenthal et al. 2009b). Here we assessed patterns of habitat utilisation in an extensive shallow reef system to ascertain whether there was any size-specific structuring and diel patterns. Additionally, we determined the degree of site fidelity.

MATERIALS AND METHODS

Study site. Anegada (18.7°N, 64.3°W) is a crescent-shaped island of the British Virgin Islands archipelago in the eastern Caribbean Sea (Fig. 1a). The southern nearshore region of Anegada hosts tidally dominated habitats, including patch reefs and mangroves. Sea surface areas circumscribed by water depths of 0–5, 5–10 and 10–20 m are 136, 87 and 567 km², respec-

tively. These habitats have been the focus of research investigating the composition and life history traits of juvenile hawksbill turtles (McGowan et al. 2008).

Turtle capture, instrumentation, release and recapture. Hawksbill turtles were caught using a rodeo style technique (Limpus & Reed 1985) by crew members surveying aboard a Boston whaler throughout July–September 2005. Captured hawksbill turtles were instrumented with TDRs (model LTD1110, Lotek, weight in air 5.4 g) and acoustic transmitters (models V13 and V16, Vemco, weight in air 11.4 and 24.9 g, respectively). Morphometric measurements were recorded for each captured turtle, including mass and curved carapace length (CCL), a common measure of body size in marine turtles (Bolten 1999). Seabed depth (m), measured using a hand-held depth echo-sounder, and a GPS-derived position were recorded for each capture, release and recapture location. TDRs recorded pressure (pounds per square inch, psi) and ambient temperature (°C) at a frequency of 10 s to a maximum of 7.6 d with a depth resolution of 0.05 m with ±1% accuracy. TDRs and acoustic transmitters were housed together in bespoke plastic units (Blumenthal et al. 2009b). The mean total package mass, including an estimated mass for epoxy, as a percentage of body mass (in air) was 0.95 ± 0.66% (range = 0.24 to 2.57%) and therefore negligible in water. Each unit was attached to the posterior left or right section of the carapace using 2-part epoxy resin (Power-Fast). All instrumented turtles were released as close as possible to the capture location, showing no apparent problems with diving or surfacing. Turtles instrumented with TDR-acoustic transmitter packages were held for no longer than 2 h between capture and release. Using an acoustic receiver (VR100, Vemco), the study area was surveyed to relocate instrumented turtles from 5 d following the deployment of the first TDR. All turtles sighted during surveying were, where possible, recaptured.

Mapping turtle captures and surveying effort. To construct a generalised pattern of hawksbill turtle capture locations, we applied a quartic kernelling technique, i.e. spatial point pattern smoothing, to all capture locations (n = 104 captures, gridding interval = 100 m, smoothing parameter = 750 m; Fig. 1b). To derive the spatial distribution of survey effort, we resampled the daily boat survey route, which was recorded continuously by a hand-held GPS receiver, to a 1 min time interval using linear interpolation. The spatial density of survey effort was then mapped using an equal-area grid where each cell represented 0.25 km². Recapture effort initially focused on the region where captures had occurred, but was subsequently extended. Approximately 130 h, over 43 d, were expended attempting to recapture study animals. When instrumented turtles were recaptured, housings

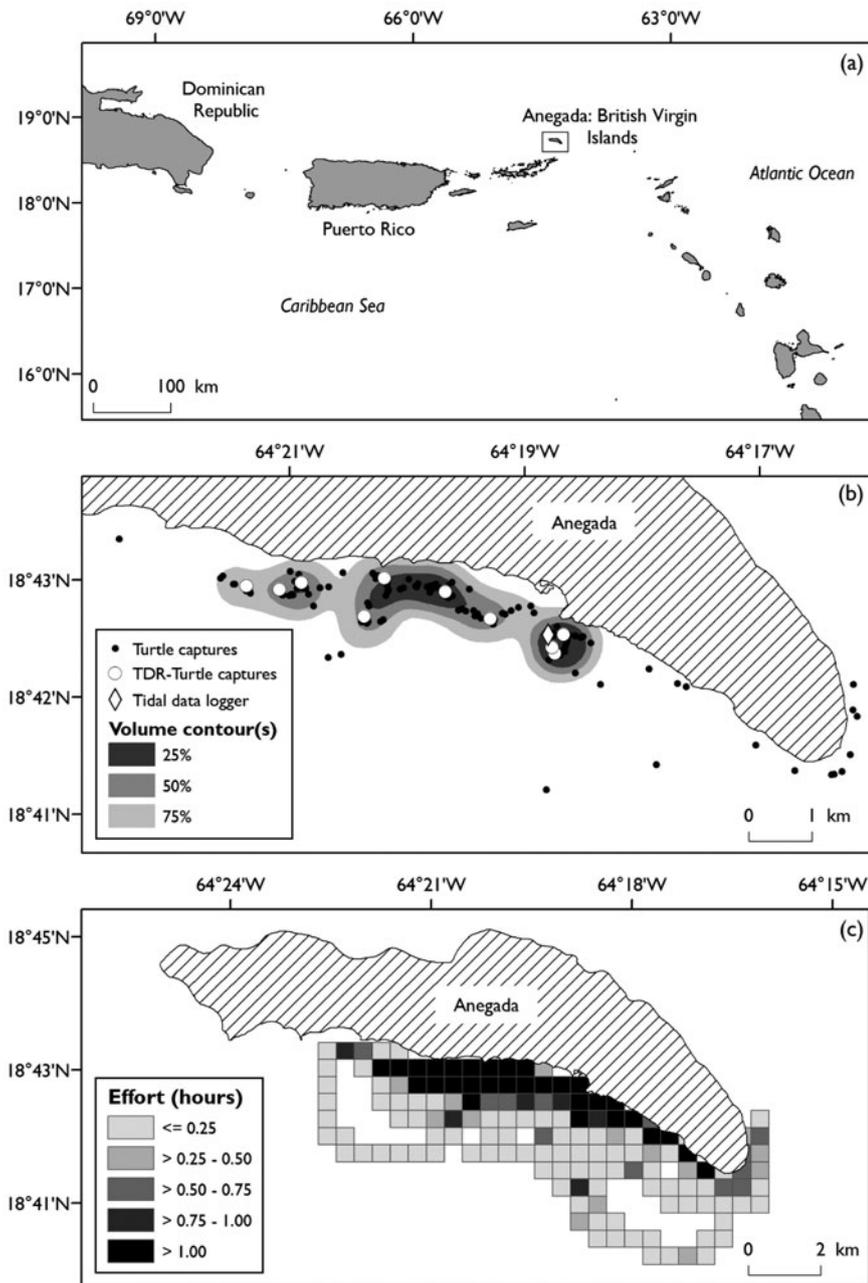


Fig. 1. Study site, turtle captures and survey effort. (a) British Virgin Islands. (b) Locations of all hawksbill turtle captures (●), capture locations of hawksbill turtles instrumented with time-depth recorders (TDRs) that were subsequently recaptured ($n = 10$, ○) and quartic kernelling indicating spatial density of all capture events (volume contours). (c) Survey effort (h) defined using an equal-area grid, where each cell represents 0.25 km^2

were removed without causing damage to the carapace and turtles were subsequently released in the vicinity of the recapture location.

Tidal data and digital elevation model. Data on the tidal movement of water in the study area, during TDR deployments, were recorded at a 10 min frequency using a pressure (depth) logger attached to the seabed

(Minilog, Vemco; Fig. 1b). A digital elevation model of the local seabed was constructed from navigation charts (Imray Lolaire, chart A232 and United Kingdom Hydrographic Office, chart 2006). These charts were georeferenced in ArcMap (ESRI) and the geographic position of depth soundings transcribed. In addition, measurements of seabed depth ($n = 248$, range = 0.1 to 4.6 m) were also taken using a hand-held echo-sounder at locations of turtle captures over a 2 yr period. Depth soundings from both sources were collectively used to form a continuous surface of depth at a $50 \times 50 \text{ m}$ horizontal resolution using cubic spline interpolation.

TDR data analysis. Pressure and temperature data were downloaded from each retrieved TDR. Pressure data were converted to depth using the relationship $1 \text{ m} = 1.45 \text{ psi}$. To ensure all surfacing events occurred at 0 m depth, a correction was applied to each TDR data set. On an hourly basis the difference between the minimum depth value and zero was ascertained. All depths recorded within that hour were subsequently corrected by this difference. We chose a 1 h correction frequency as dives during hours of darkness were typically extended with only 2 or 3 surfacing intervals per hour. Dives were considered to be periods of submergence greater than 0.3 m depth in excess of 1 min. For each TDR data set we determined the absolute maximum depth recorded and calculated individual dive summary metrics using custom written Matlab script (Version 7.8.0, MathWorks); these metrics included dive duration, maximum dive depth and coefficient of variation (CV) (Zar 1999). CV was calculated as an approximate measure of activity during dives based on the assumption that dives with greater activity, e.g. dives involving commuting and foraging, would demonstrate greater variability in depth than

less active dives, e.g. resting dives. These dive-based metrics were subsequently aggregated by time, i.e. day and night, to produce mean dive duration, mean maximum dive depth and mean CV for each day and night of deployment. Due to the shallow nature of the occupied habitat, we calculated CV for each dive using all depth data greater than the 0.3 m depth threshold. Periods of

day and night were defined by civil dawn and dusk times for each TDR data set using solar position equations available from NOAA (www.srrb.noaa.gov/highlights/sunrise/solareqns.PDF). Relationships between time of day and dive metrics were assessed using generalised linear mixed models (GLMM) in GenStat (12th edition, VSN International), controlling for the effect of individual and specifying either a Poisson error distribution with a logarithm link function, due to non-normal distributions of dive depth and duration data, or a normal distribution with a logit link function for dive CV. Relationship between body size and dive duration, while controlling for individual and time of day, was similarly assessed using GLMM utilising a Poisson distribution and a logarithm link function. The significance of statistical relationships was assessed using Wald statistics.

Inferring habitat utilisation. TDR data from each turtle were resolved to hourly maximum depths; these depths were then tidally corrected using the temporally closest water-column depth recorded by the tidal logger. Maximum extents of movement were determined by interrogating the digital elevation model with respect to these calculated seabed depths from maximum dive depths.

RESULTS

Survey effort, captured turtles and instrumentation

A total of 19 hawksbill turtles (mean \pm SD CCL = 42.3 ± 9.7 cm, range = 27.7 to 60.0 cm) were fitted with TDRs and acoustic transmitters. Recaptured turtles were at liberty for 13.9 ± 12.2 d (range = 4.9 to 34.8 d; $n = 10$). Depth utilisation data from release to recapture were obtained from 4 of these turtles, and a further TDR dataset was found to be corrupt. For the remaining 5 turtles, 16.0 ± 11.2 d (range = 1.2 to 28.5 d) elapsed between TDR memory exhaustion and recapture. Mean CCL of the recaptured group ($n = 10$) was 41.4 ± 10.1 cm (range = 29.5 to 58.2 cm, median = 41.8 cm). Mean CCL of turtles not recaptured ($n = 9$) was 43.2 ± 9.9 cm (range = 27.7 to 60.0 cm, median = 41.5 cm). The median CCL of these 2 groups did not differ significantly (Wilcoxon rank sum test, signed rank = 95, $p = 0.72$).

The capture locations of hawksbill turtles selected for instrumentation occurred within the 0–25% ($n = 7$), 25–50% ($n = 5$), 50–75% ($n = 4$) and 75–95% ($n = 2$) kernelled regions of all turtle initial capture locations (Fig. 1b). The capture location of 1 instrumented individual could not be recorded due to a faulty GPS; this individual was not recaptured.

The mean minimum straight-line distance between the locations of capture and recapture was 0.9 ± 0.8 km (range = 0.1 to 2.3 km; Fig. 2). These distances did not

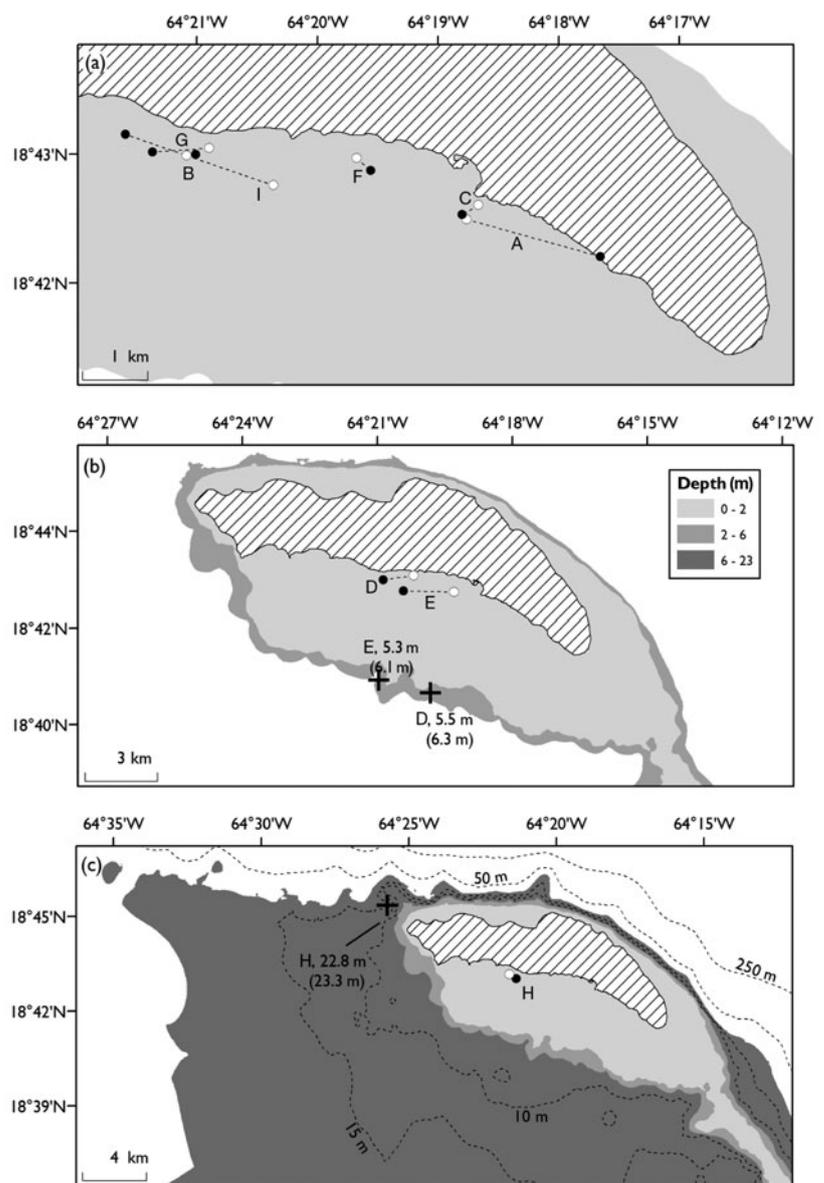


Fig. 2. *Eretmochelys imbricata*. (a) Capture (○) and recapture (●) locations of 6 hawksbill turtles (A–C, F, G and I) whose maximum depths were limited to <3 m. Dashed lines are minimum straight-line connections between capture and recapture locations. (b) As for (a) but for Turtles D and E, with location (+) and seabed depth for location of maximum dive depths (in parentheses). (c) As for (b), but for Turtle H; distance between release and recapture of Turtle H = 10 km

correlate with respective at-liberty durations (Spearman rank correlation, $r_s = -0.18$, $p = 0.64$) or CCL ($r_s = 0.10$, $p = 0.80$).

Diving behaviour

Turtles with usable TDR data sets ($n = 9$) are referred to here as turtles A to I based on increasing CCL. Data recorded by TDRs prior to the first midnight of deployment were withheld from statistical analysis. Instrumented turtles provided 5.7 ± 1.4 d of depth utilisation data (range = 3.3 to 7.1 d), and the mean maximum

dive depth was 5.1 ± 7.4 m (range = 1.0 to 23.3 m). The absolute maximum depth recorded for each turtle did not correlate with CCL (Spearman rank correlation, $r_s = 0.32$, $p = 0.40$) or time at liberty ($r_s = 0.54$, $p = 0.14$). Turtle H (54 cm CCL) achieved the maximum depth recorded among the study group, reaching 23.3 m at 21:35 h on Day 7 of TDR deployment.

Daylight maximum dive depths (mean of means = 1.7 ± 3.1 m, range = 0.4 to 18.1 m) did not differ significantly from night-time dive depths (mean of means = 1.8 ± 3.7 m, range = 0.4 to 19.5 m; GLMM, Wald = 0.05, $p = 0.83$; Fig. 3). Dives undertaken during the hours of darkness (16.0 ± 12.0 min, range = 2.5 to 61.5 min)

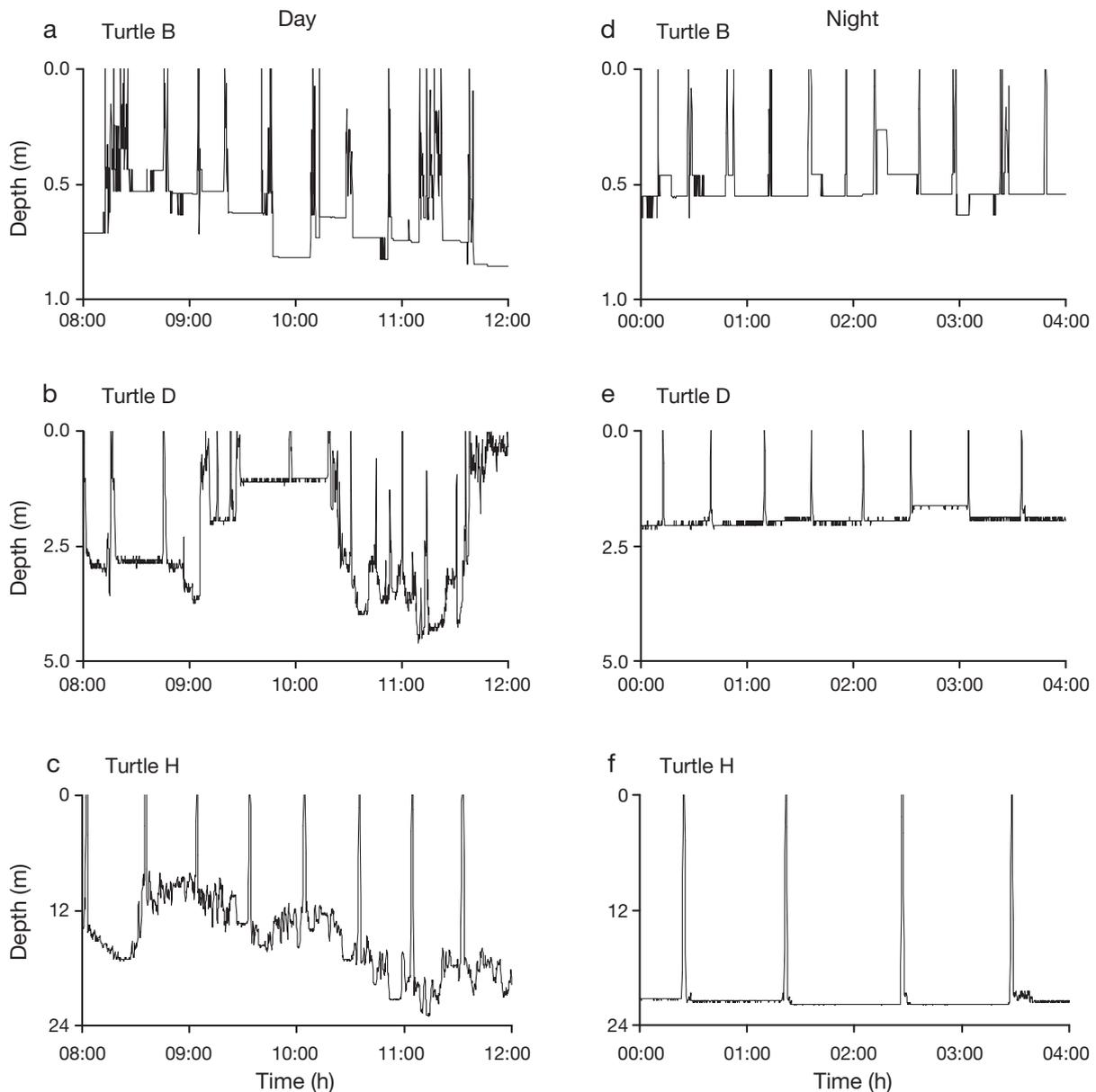


Fig. 3. *Eretmochelys imbricata*. Temporal pattern of depth utilisation behaviour from Turtles (a) B, (b) D and (c) H during selected periods of day and night

were significantly longer than those occurring during daylight hours (7.5 ± 5.0 min, range = 2.6 to 34.4 min; Wald = 69.46, $p < 0.001$; Fig. 3). Turtles demonstrated greater mean CV for dives made during daylight hours (0.2 ± 0.06 , range = 0.06 to 0.34) than those made during the hours of darkness (0.13 ± 0.03 , range = 0.07 to 0.2; Wald = 116.54, $p < 0.001$; Fig. 4). There was no relationship between body size (CCL) and dive duration when controlling for the effects of individual and time of day (Wald = 0.34, $p = 0.58$).

Inferred habitat utilisation

Habitat occupation for 6 individuals (A–C, F, G and I), whose maximum tidally corrected depths were < 3 m, appears to be limited to the inshore reef (Fig. 2a). For Turtles D, E and H, depth utilisation behaviour suggested movement away from the confines of the study area. The minimum straight-line distance between the seabed locations of these turtles' maximum tidally corrected dive depths, 5.5, 5.3 and 22.8 m, respectively, and their recapture locations were 4.8, 3.7 and 9.2 km, respectively (Fig. 2b), at locations outside the study area. Turtle H attained the greatest depth, 23.3 m, and was at liberty for 32 d. Seabed depths matching to this dive depth, once corrected for tidal pattern (22.8 m), suggest movement northwest of the study site to the reef wall on the Atlantic Ocean-facing coast of Ane-gada prior to returning to the site (Fig. 2c). The daily maximum depth of this individual increased in a step-wise fashion (Fig. 5c).

DISCUSSION

Determining patterns of habitat utilisation remains challenging for many juvenile life stages and smaller species, whose movements cannot be tracked with larger satellite-communicating and dead-reckoning devices; VHF methodologies can be used in these situations, as equipment is typically small, relative to body size. However, in most situations, acoustic or VHF tracking requires researchers to follow equipped individuals. Visual surveying efforts have provided considerable knowledge on the behaviour of marine turtles in foraging habitats (Houghton et al. 2003, Schofield et al. 2006), yet the presence of researchers could represent a disturbing force, and some areas may be inaccessible. Static acoustic monitoring arrays can be used to track the movements of individuals fitted with acoustic transmitters (Blumenthal et al. 2009b); however, this commonly requires a large financial investment to resolve movement at fine scales. These fiscal and logistical obstacles should not, however, detract from gath-

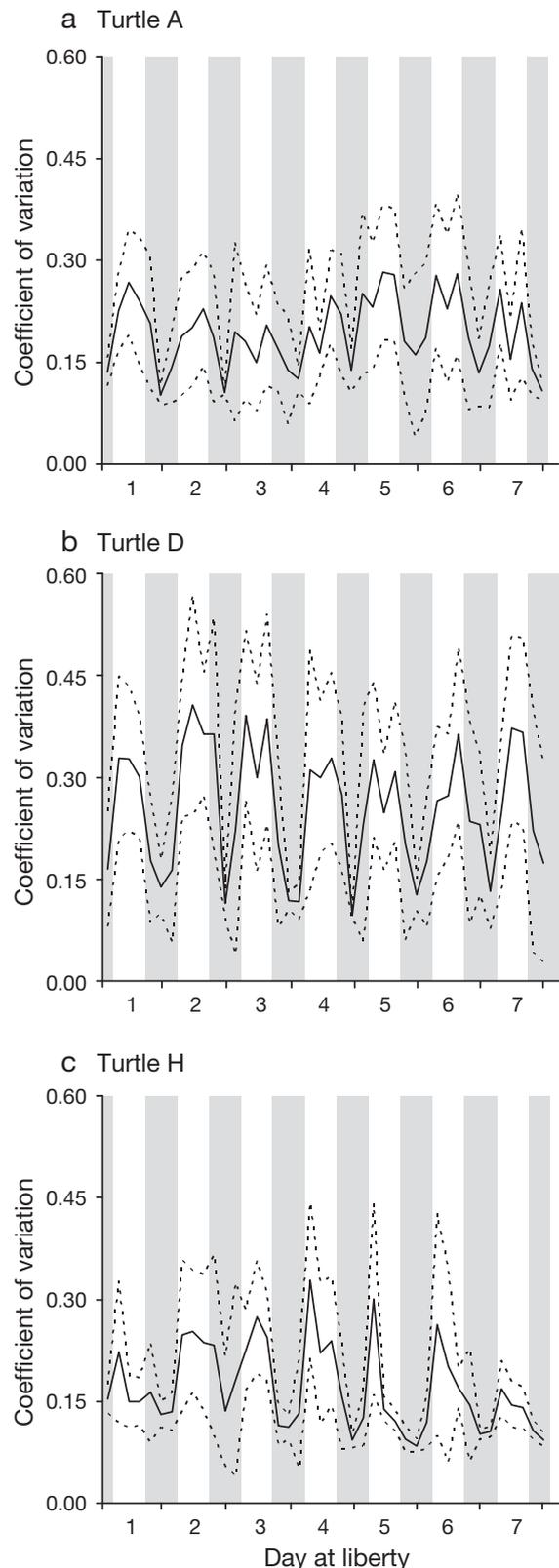


Fig. 4. *Eretmochelys imbricata*. Mean 4-hourly pattern (solid line) of dive coefficient of variation for Turtles A, D and H. Dashed lines are \pm SD. Periods of night, approximating to 18:00 to 06:00 h, are indicated by shaded bars

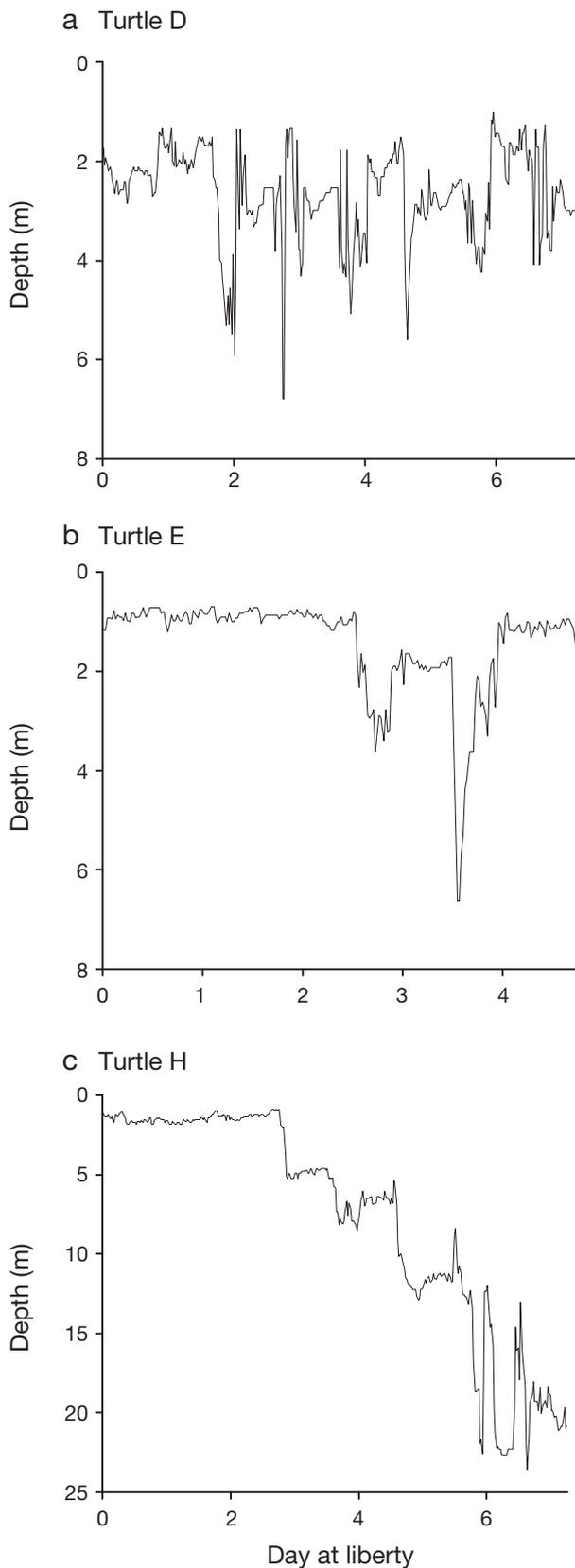


Fig. 5. *Eretmochelys imbricata*. Tidally corrected 30 min maximum depth profiles during at-liberty time for Turtles D, E and H

ering movement data, particularly for species of conservation concern, where bio-logged data are of increasing utility (Cooke 2008).

In the present study the recaptured group of hawksbill turtles provided depth utilisation data from across the size classes of turtles commonly encountered in the inshore reef. There was no apparent scaling of dive metrics (i.e. maximum dive depth, dive duration) with body size, although this may be a reflection of the study site as well as the number and recording duration of the TDRs. This lack of scaling contrasts to that found in similar-sized juvenile hawksbill turtles occupying deeper reef and reef wall habitats, which no doubt provide a greater choice of depths at which to rest and forage (van Dam & Diez 1996, Blumenthal et al. 2009b). However, the larger individuals in the present study seemed to undertake short-term movements to deeper habitats.

Although turtles were captured and recaptured in shallow-water habitats, the movement of some individuals to deeper water gave preliminary insights into horizontal movements and highlights the possibility of developing inferential geolocation procedures based on TDR data, where movement may be potentially constrained by bathymetry and perhaps habitat preference. Numerous modeling approaches exist which could integrate such constraints, e.g. Bayesian state-state switching models (Haydon et al. 2008), correlated random walk models (Morales et al. 2004, Sims et al. 2006) or models employing levy walk dynamics (Sims et al. 2008). Despite extensive attempts, we were, however, in this case frustrated by the short duration of the TDR data and the lack of a sufficiently high resolution bathymetric model which would have required additional surveying (e.g. side-scan sonar survey data).

The shallow nature of the Anegada inshore reef and the tendency for the instrumented turtles to remain within this region prevented behavioural categories (e.g. foraging, resting) from being consistently assigned to individual dives based on dive profile shape (see Houghton et al. 2002). We could, however, identify a strong diel signal in dive behaviour. Dives made during the hours of darkness were longer and less variable than those undertaken during daylight. Taken together, these observations suggest periods of decreased activity at night, which has been reported for other juvenile and adult hawksbill turtles (Van Dam & Diez 1996, 1997, Storch et al. 2005, Houghton et al. 2008, Blumenthal et al. 2009b). However, there was no diel difference in dive depths, highlighting the influence of a depth-limited environment on habitat utilisation behaviour.

Fidelity of juvenile hawksbill turtles to the inshore reef observed in the present study and from recapture data collected during long-term monitoring at the site (2003–2006, McGowan et al. 2008) suggest that home

ranges are small. Yet temporally and spatially limited recapture efforts likely systematically bias home range estimates as small. For the majority of instrumented turtles, depth recordings similarly indicated that movements were most likely constrained to the inshore reef. For 3 individuals, however, the depth utilisation history is suggestive of movement away from the immediate vicinity of the study site. When identifying the tidally corrected maximum depth recorded by turtles on the digital elevation model we see that home ranges may be on the order of several square kilometres or more, somewhat larger than that reported for hawksbill turtles at Mona Island, Puerto Rico (0.07 to 0.14 km², van Dam & Diez 1998), approximately 400 km west of Anegada.

Although utilisation of TDRs on this species is not new, significant additional insights are possible as a result of deployments at new sites, especially with longer-term data sets within habitats with enhanced bathymetry. Although we failed to obtain more than the most basic insights using inferential geolocation techniques, these have utility in the study of the spatial ecology of other predominantly benthic foraging or resting marine taxa, including crustaceans, molluscs and fishes, but also larger species, including walrus (Bornhold et al. 2005). These approaches will become particularly likely as bio-logged data are becoming increasingly prevalent (Ropert-Coudert et al. 2009), with even further utility when they are interfaced with multi-channel logging technologies currently under development (Wilson et al. 2008). These geolocation techniques could be validated with the advent of newly emerging miniaturised archival GPS technologies (Schofield et al. 2007).

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