



Resident areas and migrations of female green turtles nesting at Buck Island Reef National Monument, St. Croix, US Virgin Islands

Kristen M. Hart^{1,*}, Autumn R. Iverson², Allison M. Benschoter¹, Ikuko Fujisaki³, Michael S. Cherkiss¹, Clayton Pollock⁴, Ian Lundgren⁴, Zandy Hillis-Starr⁴

¹US Geological Survey, Wetland and Aquatic Research Center, Davie, FL 33314, USA

²CNT, contracted to US Geological Survey, Wetland and Aquatic Research Center, Davie, FL 33314, USA

³University of Florida, Ft. Lauderdale Research and Education Center, Davie, FL 33314, USA

⁴National Park Service, Buck Island Reef National Monument, Christiansted, US Virgin Islands, USA

ABSTRACT: Satellite tracking studies can reveal much about turtles' spatial use of breeding areas, migration zones, and foraging sites. We assessed spatial habitat-use patterns of 10 adult female green turtles *Chelonia mydas* nesting at Buck Island Reef National Monument (BIRNM), US Virgin Islands (USVI; 17° 47.4' N, 64° 37.2' W) from 2011 to 2014. Turtles ranged in size from 89.0 to 115.9 cm curved carapace length (CCL) ($\bar{x} \pm SD$: 106.8 \pm 7.7 cm). The inter-nesting period for all turtles ranged from 31 July to 4 November, and sizes of the 50% core-use areas ranged from 4.2 to 19.0 km². We observed consistency of inter-nesting habitat-use patterns, with all turtles using near-shore (<1.5 km), shallow waters (<20 m depth) within approximately 10 km of Buck Island. Seven of the 10 turtles remained locally resident after the nesting season; 5 turtles (50%) established resident foraging areas around Buck Island, 2 established resident foraging areas around the island of St. Croix, and the other 3 (30%) made longer-distance migrations to Antigua, St. Kitts & Nevis, and Venezuela. This is the first empirical dataset showing limited migration and use of 'local' resources after the nesting season in the USVI by this unique management unit of green turtles. Five of the turtles had resident foraging area centroids within protected areas; thus, inter-nesting and foraging areas at BIRNM that overlap with human use zones present an important management concern. Delineating spatial areas and identifying temporal periods of near-shore habitat use can be useful for natural resource managers with responsibility for overseeing vulnerable habitats and protecting marine turtle populations.

KEY WORDS: *Chelonia mydas* · Green sea turtle · Inter-nesting · Foraging · Switching state-space model · Kernel density estimation · Migration · Minimum convex polygon

INTRODUCTION

Delineating high-use areas for marine species is critical for identifying essential habitat and times of the year when vulnerable species may warrant increased levels of protection. However, it is challenging to delineate such high-use areas for highly mobile marine species. Satellite telemetry affords the opportunity to reveal location-based habitat-use pat-

terns for these species (Godley et al. 2008, Hart & Hyrenbach 2009), and a growing body of literature indicates that this tool continues to evolve, allowing researchers to address increasingly complex questions for many cryptic vertebrates of conservation concern. To date, the global use of satellite tracking in marine turtle studies has revealed much about their spatial use of breeding areas, migration zones, and foraging sites (Schofield et al. 2009, Fossette et

*Corresponding author: kristen_hart@usgs.gov

al. 2010, Shillinger et al. 2010, Hart et al. 2014). Coupled with recent advances in analytical modeling techniques such as switching state-space modeling (SSM; see Jonsen et al. 2003, 2005, 2006, 2007, Patterson et al. 2008, Hoenner et al. 2012), tracking data can provide an unprecedented window into behavioral modes of marine turtles (i.e. directed movement or migration, area restricted search or foraging; see Bailey et al. 2008, 2009, Hart et al. 2015).

Green turtles *Chelonia mydas* (Linnaeus, 1758) use nesting and foraging sites throughout tropical and subtropical zones (Hirth 1997, Seminoff 2004). In the Caribbean, at approximately 2 yr intervals, mature female green turtles breed and lay eggs at natal beaches roughly every 2 wk from July through November (Carr et al. 1974, Allard et al. 1994, Broderick et al. 2002, 2007, Plotkin 2003), then return to distinct foraging areas (Limpus et al. 1992, Broderick et al. 2007). Although green turtles can migrate large distances (i.e. 1000s of km) between nesting beaches and foraging sites (Mortimer & Portier 1989, Plotkin 2003), recent evidence of non-migratory behavior has emerged through satellite-tracking studies (Whiting et al. 2007, Hart et al. 2013, Esteban et al. 2015). In their role as herbivores, green turtles consume seagrasses and algae, which consequently maintains the structure and productivity of seagrass pastures (Thayer et al. 1982, 1984, Zieman et al. 1984, Moran & Bjorndal 2005) and coral reefs (Goatley et al. 2012).

Listed as Endangered by the International Union for the Conservation of Nature (Groombridge 1982, Groombridge & Luxmoore 1989, Seminoff 2004), and threatened under the US Endangered Species Act, Caribbean green turtles are part of the North Atlantic distinct population segment (DPS), yet little is known about the species in the US Virgin Islands (USVI). Analysis of mitogenomic haplotype frequencies from rookeries within the southern Greater Caribbean region indicates that green turtles at Buck Island Reef National Monument (BIRNM) in St. Croix warrant recognition as a distinct management unit that is part of the larger USVI stock (Shamblin et al. 2012).

Much reduced from historic numbers (Jackson 1997, McClenachan et al. 2006), green turtle population numbers in Caribbean rookeries are low, but recovering. Three separate long-term saturation nesting programs in St. Croix (The Nature Conservancy [TNC] at East End Marine Park [EEMP], National Park Service at BIRNM, and US Fish and Wildlife Service [USFWS] at Sandy Point) have documented increases in nesting green turtle numbers since the 1990s, but annual numbers of nesting individuals at

each of these 3 main sites are only in the 20s (e.g. 26 in 2015 at BIRNM; C. Pollock pers. obs.). An increase in seagrass distribution at BIRNM (Kendall et al. 2004a,b), federal protection for green turtles in the 1970s (NMFS & USFWS 1991), a decrease in poaching, and the removal of mongoose from BIRNM nesting beaches in the 1980s all provided increased habitat security for green turtles at BIRNM. By 1995, the number of nesting green turtles at BIRNM had increased, followed by increased numbers at East End beaches (K. Lewis [TNC] pers. comm.).

Currently, critical habitat for green turtles is delineated in waters surrounding Culebra Island, Puerto Rico (NOAA 1998), and there is a pending proposal to list 11 DPSs of green turtles as endangered or threatened, with a revision of current listings (NMFS & USFWS 2015, March Federal Register). Understanding the specific movement ecology for different DPSs can help inform conservation efforts targeted towards those population segments. Further, understanding green turtle movement patterns in protected areas is considered a priority for ongoing conservation efforts and Federal recovery plans (NMFS & USFWS 1991, Hart et al. 2013). However, green turtle spatial habitat use within BIRNM waters has not been assessed.

To assess spatial habitat-use patterns of green turtles nesting at BIRNM, our goals were to delineate zones used during inter-nesting periods, define any migration paths after the nesting season, and identify foraging sites where turtles remain resident. Where possible, we quantified spatial overlap of habitat use for individuals at inter-nesting areas and foraging sites. To glean possible reasons behind spatial selection of habitats and whether resident areas were selected by turtles of a specific size or experience level, we quantified ecological and spatial correlates such as the relationship between turtle size and bathymetry values at inter-nesting areas, characterized the habitats associated with foraging areas, and determined whether habitat overlap varied depending on nesting 'experience' (i.e. 'neophyte' for first time nester vs. 're-migrant' status). Finally, we discuss green turtle habitat use in relation to nearby marine protected areas (MPAs).

MATERIALS AND METHODS

Study sites

Sampling and tagging of green turtles occurred from 15 July to 30 September annually from 2011 to

2014 in the USVI at BIRNM (17° 47.4' N, 64° 37.2' W), which includes a 0.71 km² uninhabited island (Buck Island) located on the shallow St. Croix shelf (depth range approx. -15 to -20 m), 2.4 km northeast of the island of St. Croix (see Fig. 1). Buck Island is 1.82 km long and 0.8 km wide, and rises 103 m above sea level at the highest peak. With the expansion of the monument boundaries in 2001, the amount of submerged lands around Buck Island now covers 76.3 km². BIRNM is a nesting and foraging area for loggerhead *Caretta caretta*, leatherback *Derموchelys coriacea*, hawksbill *Eretmochelys imbricata*, and green sea turtles.

Turtle capture and transmitter deployment

Nightly surveys were conducted from 19:00 to 05:00 h local time. Turtle interception and tagging followed methods similar to those of Hart et al. (2013); turtles were documented and fitted with transmitters using established protocols (NMFS-SEFSC 2008). Briefly, female green turtles were intercepted on the beach after nesting. Immediately after marking each turtle with Inconel and PIT tags, standard carapace measurements were recorded, including curved carapace length (CCL). We adhered platform transmitter terminals (PTTs; Wildlife Computers SPOT5s; length × width × height: 7.2 × 5.4 × 2.4 cm, mass: 119 g in air) using slow-curing epoxy. Attachment materials were streamlined to minimize the epoxy footprint and potential buoyancy and/or drag effects on turtle swimming ability. Each tag was programmed to transmit 24 h d⁻¹.

Sea turtle tracking and switching state-space modeling

Location data were retrieved using Satellite Tracking and Analysis Tool (STAT; Coyne & Godley 2005) available at www.seaturtle.org. Location classes (LCs) 3, 2, 1, 0, A, and B were used to assess the position of the turtles during the tracking period, and served as the location data to characterize inter-nesting, foraging, and migration behavior of each turtle. We used switching state-space modeling (SSM; Jonsen et al. 2003, Patterson et al. 2008) as described in Jonsen et al. (2005) to assess the fine-scale behavioral modes of individual green sea turtle tracks that originally nested in BIRNM. Switching SSM techniques followed our previous studies (see Hart et al. 2013, 2014, 2015, Shaver et al. 2013, 2016 and the

Supplement at www.int-res.com/articles/suppl/n032/p089_supp.pdf for general information on this technique). Earlier applications defined a binary behavioral mode, categorized as either 'foraging' or 'migration' (Jonsen et al. 2005, 2007, Breed et al. 2009); however, since we tagged animals during the nesting season, behavioral modes predicted by the SSM algorithm were defined as either 'inter-nesting or foraging' or 'migration'.

We summarized data acquired until the transmitters stopped sending information or until the time of data synthesis: 13 November 2014. We used the SSM approach to determine the beginning and end date of the inter-nesting, migration, and foraging behavioral periods for each turtle. After assigning the beginning and end dates of each behavioral mode for each turtle track, we used the original satellite locations within those time periods for all further analyses.

Inter-nesting and foraging periods

We verified SSM behavioral modes both spatially and temporally using the satellite data. Inter-nesting periods occurred before migration to foraging grounds. Some turtles exhibited local foraging behavior around Buck Island, and also did not show a distinct migration period. Nesting activity data for this species on Buck Island indicates that the end of October is the end of the inter-nesting season, based on the last beach encounters for 9 nesting green sea turtles from 1995 to 2013. Therefore, a temporal cutoff of 31 October was applied to differentiate between inter-nesting and foraging behavior for the turtles that did not migrate. From the satellite data during the inter-nesting and foraging periods, we filtered out locations that represented movement speeds >5 km h⁻¹, locations on land, and very distant spatial locations (>120 km from the nearest valid point). We also filtered out points associated with ocean water depths deeper than -200 m (neritic zone delineation). Green turtles have been found to stay in shallow waters during residency times (see Meylan 1995), remaining in mean depths shallower than -10 m in the Mediterranean (Hays et al. 2002) and the Gulf of Mexico (Hart et al. 2013), and shallower than -25 m in the Caribbean (Esteban et al. 2015). For all tracks in this study, the removed locations deeper than -200 m comprised less than 7.0% of available speed-filtered locations. For bathymetry, we used the ETOPO1 global relief model (bedrock, cell-registered, 1 arc-minute; Amante & Eakins 2009).

Characterization of inter-nesting and foraging areas

After assigning the tracking data to inter-nesting and foraging behavioral modes, we quantified inter-nesting and foraging home ranges using kernel density estimation (KDE) and minimum convex polygon (MCP) analyses. To minimize autocorrelation of points, we generated mean daily locations (MDL) within each inter-nesting and foraging period in the software program R version 3.1.2 (R Development Core Team 2014) from the filtered satellite locations. We used MDLs (when $n \geq 20$) for KDE analysis and filtered satellite locations (when MDLs < 20) for 95% MCPs.

Kernel density is a non-parametric method used to identify one or more areas of disproportionately heavy use (i.e. core areas) within a home-range boundary (Worton 1987, 1989, White & Garrott 1990), with appropriate weighting of outlying observations. We used the software program R and the package 'adehabitatHR' (Calenge 2006) to calculate home range analyses. We applied the fixed-kernel least-squares cross-validation smoothing factor (h_{cv}) for each KDE (Worton 1995, Seaman & Powell 1996). Following Walcott et al. (2012), we used 95% of points to create MCP polygons, as it is possible for a proportion of distant filtered locations to represent infrequent movements or explorations external to the home range (sensu Burt 1943, Rodgers & Kie 2011). When the standard deviations of the x and y coordinates were unequal (< 0.5 or > 1.5), data were re-scaled prior to home range calculations by dividing the coordinates by their standard deviation (following Seaman & Powell 1996). We used ArcGIS 10.2 (ESRI 2013) to plot the data and to calculate the area (km^2) within each kernel density contour (50 and 95%) and each MCP. The 95% KDEs were used to represent the overall home range, and the 50% KDEs represented the core area of activity (Hooge et al. 2001).

We tested location data for, and quantified site fidelity to, the in-water inter-nesting and foraging locations using the Animal Movement Analysis Extension for ArcView GIS 3.3 (ESRI 2002). Using Monte Carlo random walk simulations (100 replicates), we tested tracks during each inter-nesting and foraging period for spatial randomness against randomly generated walks (Hooge et al. 2001). We bounded the range for random walks from -200 to 0 m bathymetry to encompass all filtered locations, and smoothed the bounding polygon with a 250 m inland and 5 km seaward buffer to account for

numerous small bays, and allow for the generation of random walks with points in close proximity to land (the 5 km seaward border was extended an additional 5 km for one turtle track: Turtle ID 7 inter-nesting). Tracks exhibiting site fidelity indicate movements that are more spatially constrained rather than randomly dispersed (Hooge et al. 2001); any tracks that failed site fidelity were not analyzed in the home range analyses.

We also calculated the centroid of each 50% KDE and MCP; if a 50% KDE included multiple activity centers, we calculated the centroid for the largest activity center. We extracted bathymetry depths for all centroids and the distance from each centroid to the nearest land.

Turtle inter-nesting and foraging days per grid cell

To depict the inter-nesting and foraging locations used by the turtles over time, we calculated the number of turtle inter-nesting days and foraging days in grid cells (2×2 km). For each turtle track containing days in either inter-nesting or foraging mode (regardless of whether a KDE or MCP was calculated), we determined the number of days that each turtle was recorded in each grid cell (turtle days) using all filtered satellite locations, and summed the number of turtle days across all turtles for each grid cell. We derived mean bathymetry in each 2 km grid cell and examined associations between the turtle days and bathymetry for each inter-nesting and foraging period.

Core area space-use sharing

We calculated the amount of home range overlap for the core-use areas (50% KDEs) during inter-nesting and foraging using the 'adehabitatHR' package in R (Calenge 2006, R Development Core Team 2014) to quantify the extent to which green turtles share their home ranges. The utilization distribution overlap index (UDOI) is a non-directional joint measure that is a function of the product of the 2 utilization distributions (UDs), a modification of Hurlbert's (1978) E/E_{uniform} statistic to allow for continuous spatial UD, and is the most appropriate statistic for measuring space-use sharing between animals. The UDOI is zero for 2 UD without overlap, and 1 for uniformly distributed UD with complete overlap; however, UDOI can be > 1 for non-uniformly distributed UD with a high degree of overlap, indicative of

higher than normal overlap relative to uniform space use (Fieberg & Kochanny 2005).

We calculated UDOI space-use sharing for all turtles during inter-nesting ($n = 10$ turtles, 45 pairs), because KDEs were calculated for each turtle. Of the 5 turtles for which foraging KDEs were determined, we calculated UDOI space-use sharing for the 3 turtles that foraged in the same area around Buck Island ($n = 3$ pairs). Four turtles had foraging MCPs; one was located near Antigua, but for the others we calculated the distance between same-region centroids. This included 2 turtles foraging SW of St. Croix and 1 turtle foraging in the Buck Island area (we determined the mean distance from this MCP centroid to the 3 KDE centroids). We also determined the level of temporal overlap (days) that same-region turtle pairs had during foraging. For inter-nesting, we conducted a non-parametric Mann-Whitney rank sum test to determine whether there was a difference in space-use sharing between turtle pairs with and without neophytes in order to examine whether newly nesting turtles shared inter-nesting habitat with experienced nesters any differently than experienced pairs shared habitat. We classified any turtles that were 1st time nesters at BIRNM as neophytes.

Ecological and spatial correlates

For the inter-nesting periods, we conducted linear regression analyses to determine whether there was a relationship between turtle size (i.e. CCL) and the size of the 50% KDE, the bathymetry values at the 50% KDE, and the bathymetry values at the MDLs; additionally, we conducted linear regression analyses to examine whether there was a relationship between the number of tracking days and the size of the 50% KDE using SigmaPlot (Systat Software 2012). For turtles foraging around Buck Island and St. Croix ($n = 6$), we determined the benthic habitat type located at the foraging centroids using NOAA benthic habitat maps of Puerto Rico and the USVI (Kendall et al. 2001).

Migration periods

We summarized the primary migration periods that represented movement away from the inter-nesting area to the foraging grounds; these periods occurred after inter-nesting and directly before the foraging period. After the migration periods were assigned, they were verified both spatially and temporally

using the satellite location data. We filtered out satellite locations during the primary migration periods representing movement speeds $>5 \text{ km h}^{-1}$, locations on land, and very distant spatial locations ($>120 \text{ km}$ from the nearest valid point). We quantified the number of days in the primary migration period, the straight-line migration distance, the migration path distance (when applicable), and the depth along migration paths. Some turtles in our study did not exhibit a migration path (e.g. turtles that foraged locally near Buck Island), and therefore only the straight-line migration distance was quantified, calculated as the distance between inter-nesting and foraging centroids. For Turtle ID 8, the mean center of the filtered foraging satellite locations was quantified and used for the straight-line distance calculation, because this turtle did not exhibit site fidelity and therefore no centroid was calculated.

RESULTS

Turtle size and tracking duration

We tagged 10 adult female green turtles over a 4 yr period between 2011 and 2014 (Table 1). Turtles ranged in size from 89.0 to 115.9 cm CCL (Table 1). In a total of 1681 tracking days across all turtles, individual turtle tracking durations ranged from 100 to 372 d (Table 1). Turtles were a mix of neophytes ($n = 2$) and re-migrants ($n = 8$), with varied nesting histories since 1995 (see Table S1 in the Supplement at www.int-res.com/articles/suppl/n032p089_supp.pdf).

In-water inter-nesting areas

We obtained SSM results for all 10 turtles (see Fig. S1, Table S2 for example SSM prediction paths and model parameters). We tagged turtles early enough in each nesting season to track them through inter-nesting periods, and all showed site fidelity (proportion of tracks that were more constrained than random movement paths >99.0099 for all 10 turtles; Table 1) and comprised enough MDLs (≥ 20) to conduct KDE analyses (Table 1). One individual (Turtle ID 8) was also observed on 13 September 2013 nesting on property that TNC monitors at the East End of St. Croix (i.e. EEMP). The 10 inter-nesting periods totaled 760 d across all turtles, and ranged from 21 to 92 d (Table 1). The inter-nesting period across all turtles (regardless of year) ranged from 31 July ($\bar{x} \pm \text{SD}$

Table 1. Turtle identification, size (curved carapace length; CCL), and satellite-tracking dates for 10 female green sea turtle *Chelonia mydas* nesters tagged at Buck Islands in the US Virgin Islands from 2011 to 2014, including information on inter-nesting and migration. Inter-nesting areas presented here were comprised of at least 20 mean daily locations; variables include information regarding the timing, duration, area, depth, and distance to shoreline for each inter-nesting period. Periods are given as mm/dd/yy. FINLs: filtered inter-nesting locations; MDLs: mean daily locations; KDE: kernel density estimation; centroids were derived from 50% KDEs; na: not applicable. Site fidelity proportions (p) were all > 99.0099; turtle tracks with $p > 95.00$ indicate movement paths that are more constrained than random movement paths. NE: not estimated because centroid had positive value

Turtle ID	CCL (cm)	Tracking period (d)	Inter-nesting period (d)	FINLs	MDLs	50% KDE area (km ²)	95% KDE area (km ²)	Centroid distance to shore (km)	Depth at centroid (m)	Primary migration period (d)
1	89.0	08/24/11–03/04/12 (194)	08/25/11–09/14/11 (21)	135	21	4.2	22.9	0.3	NE	09/15/11–09/18/11 (4)
2	107.9	08/01/12–04/10/13 (253)	08/01/12–10/31/12 (92)	672	86	4.4	20.5	1.3	-1.0	na
3	108.1	08/07/12–12/28/12 (144)	08/08/12–10/12/12 (66)	188	40	5.3	23.8	0.0	NE	na
4	115.9	07/31/12–08/06/13 (372)	08/01/12–10/31/12 (92)	550	76	7.4	32.3	1.4	-1.0	na
5	109.8	07/30/12–12/22/12 (146)	07/31/12–10/08/12 (70)	118	23	7.2	45.3	0.3	NE	10/09/12–10/11/12 (3)
6	114.3	08/13/13–12/08/13 (118)	08/14/13–10/31/13 (79)	742	78	8.3	37.5	1.1	-17.0	na
7 ^a	101.4	08/14/13–12/09/13 (118)	08/15/13–10/21/13 (68)	603	67	19.0	91.3	1.3	-1.0	10/22/13–11/04/13 (14)
8	107.0	08/01/13–11/15/13 (107)	08/02/13–10/31/13 (91)	598	76	5.4	21.2	0.8	-1.0	na
9	111.1	08/01/13–12/07/13 (129)	08/02/13–10/30/13 (90)	439	66	6.3	33.8	0.0	NE	10/31/13–11/03/13 (4)
10	103.3	08/06/14–11/13/14 (100)	08/06/14–11/04/14 (91)	768	91	5.7	28.9	0.5	-16.0	na
Mean	106.8	168.1	76.0	481.3	62.4	7.3	35.8	0.7	-6.2	6.3
SD	7.7	85.3	22.1	249.3	25.4	4.3	21.1	0.6	8.0	5.2
Min.	89.0	100.0	21.0	118.0	21.0	4.2	20.5	0.0	-17.0	3.0
Max.	115.9	372.0	92.0	768.0	91.0	19.0	91.3	1.4	-1.0	14.0

^a13 Sept 2013, observed by The Nature Conservancy (TNC) at East End Marine Park (EEMP), mainland St. Croix

of first inter-nesting date: 7 August \pm 8.2 d, $n = 10$) to 4 November ($\bar{x} \pm$ SD of last inter-nesting date: 21 October \pm 16.0 d, $n = 10$). In total, we obtained 624 MDLs for inter-nesting KDE analyses (Table 1). Mean size of the 50% core-use areas during inter-nesting was 7.3 km² (range: 4.2 to 19.0 km²); mean size of the 95% KDE areas during inter-nesting was 35.8 km² (range: 20.5 to 91.3 km²); and distance to the nearest land from the 50% KDE centroids (Fig. 1) ranged from 0.0 to 1.4 km (Table 1). Bathymetry values (i.e. a proxy for water depth) at the 50% KDE centroid locations ranged from -17.0 to -1.0 m (Table 1).

The grids of the turtle days showed that high-use areas during inter-nesting periods were concentrated around Buck Island (Fig. 2). There was a weak but significant association between turtle days and bathymetry in the grid cells (Spearman's rank correlation, $r_s = 0.34$, $n = 253$, $p < 0.0001$).

Core area space-use sharing

During inter-nesting, across all pairs of inter-nesting females, UDOI ranged from 0 to 0.18 ($\bar{x} \pm$ SD: 0.04 \pm 0.05, $n = 45$; Table S3 in the Supplement), where greater UDOI indicates greater space-use sharing between turtle pairs. Temporal overlap across all pairs of inter-nesting females ranged from 0 to 91 d ($\bar{x} \pm$ SD: 19.2 \pm 32.5, $n = 45$). Results of the non-parametric Mann-Whitney rank sum test indicated there was no difference in UDOI between turtle pairs with and without neophytes (Mann-Whitney U -test, $U = 182.5$, $n_1 = 22$, $n_2 = 23$, $p = 0.169$, where $n_1 =$ pairs with neophytes and $n_2 =$ pairs without neophytes).

Ecological and spatial correlates

We did not find any significant relationships between turtle CCL and either the size of the 50% KDE (linear regression, $r^2 = 0.01$, $F_{1,4} = 0.003$, $p = 0.87$) or the bathymetry values at the 50% KDE centroid (linear regression, $r^2 = 0.01$, $F_{1,8} = 0.11$, $p = 0.75$), or between the number of tracking days and the size of the 50% KDE (linear regression, $r^2 = 0.04$, $F_{1,8} = 0.30$, $p = 0.60$). Thus, turtle size was not predictive of inter-nesting habitat selection.

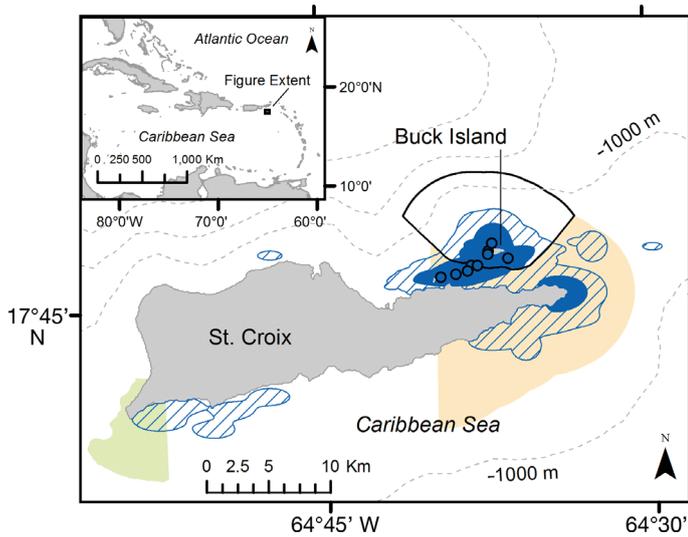


Fig. 1. Buck Island Reef National Monument (BIRNM; dark line represents Monument boundary) study site (small black square in the inset) where adult female green sea turtles *Chelonia mydas* were satellite-tagged from 2011 to 2014. Kernel density estimation (KDE) for 10 inter-nesting adult female green sea turtles are shown with hatched blue lines (95% KDE contours) and blue areas (50% KDE core-use contours; contour areas for all 10 turtles were merged for visualization purposes). Centroids of core-use area kernel density estimation (50% KDE) are shown as open circles. Orange shading indicates marine protected area at East End Marine Park and green shading indicates marine protected area at Sandy Point National Wildlife Refuge

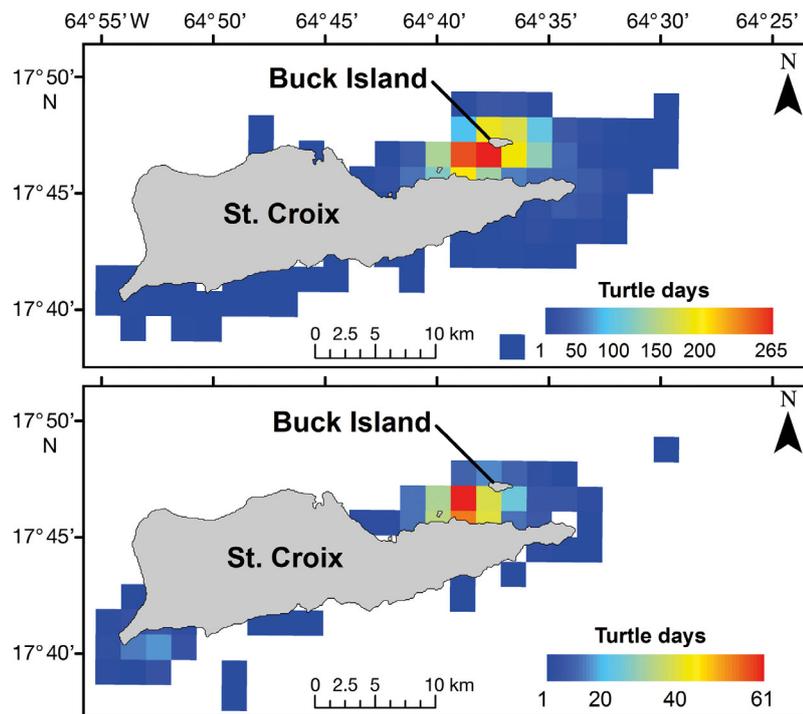


Fig. 2. Grids of inter-nesting days for 10 adult female green sea turtles *Chelonia mydas* (top panel) and foraging-days for 7 adult female green sea turtles (bottom panel). All turtles were satellite-tagged on Buck Island, US Virgin Islands

Migration

Four of the 10 turtles exhibited a migration period, as determined by SSM (Fig. 3). Three of these 4 turtles had migration points along their tracks after filtering (Turtle ID 5 had a single unfiltered point during her short 3 d migration, and zero points after filtering, therefore the migration path could not be delineated; Table 1). Migration periods lasted 3 to 14 d, and the distance along the migration path ranged from 84.4 to 906.0 km (Table 1). The straight-line migration distance for all 10 turtles ranged from 0.2 to 694.0 km (Table 1). Mean water depths associated with migration points across the 3 migration periods (Table 1) ranged from -3613.7 to -387.3 m.

In-water foraging areas

All 10 turtles were tracked past inter-nesting and migration to their respective foraging grounds. Five of these turtles (50%) settled around Buck Island, 2 settled around the island of St. Croix, and the other 3 (30%) made longer-distance migrations to Antigua, St. Kitts & Nevis, and Venezuela, where they took up residence (Fig. 3). Nine of the

10 turtle tracks passed site fidelity tests during the foraging period (proportion of tracks that were more constrained than random movement paths >96.0396 ; Table 2). Of the 9 foragers that passed site fidelity tests, 5 had enough MDLs to conduct KDE analyses; we conducted MCP analyses for the other 4 turtles. The 5 KDE foraging periods (Fig. 3) totaled 772 d across all turtles, and ranged from 35 to 372 d (Table 2). In total, we obtained 265 MDLs for KDE analyses (Table 2). Mean size of the 50% core-use areas during foraging was 5.6 km^2 (range: 2.0 to 11.9 km^2 ; Table 2). Mean size of the 95% KDE areas was 26.6 km^2 (range: 9.5 to 59.4 km^2 ; Table 2). The 4 MCP foraging periods (Fig. 3) totaled 172 d across all 4 turtles with 44 MDLs (Table 2). Mean size of the MCPs across the 4 turtles was 20.6 km^2 (range: 9.0 to 30.7 km^2 ; Table 2).

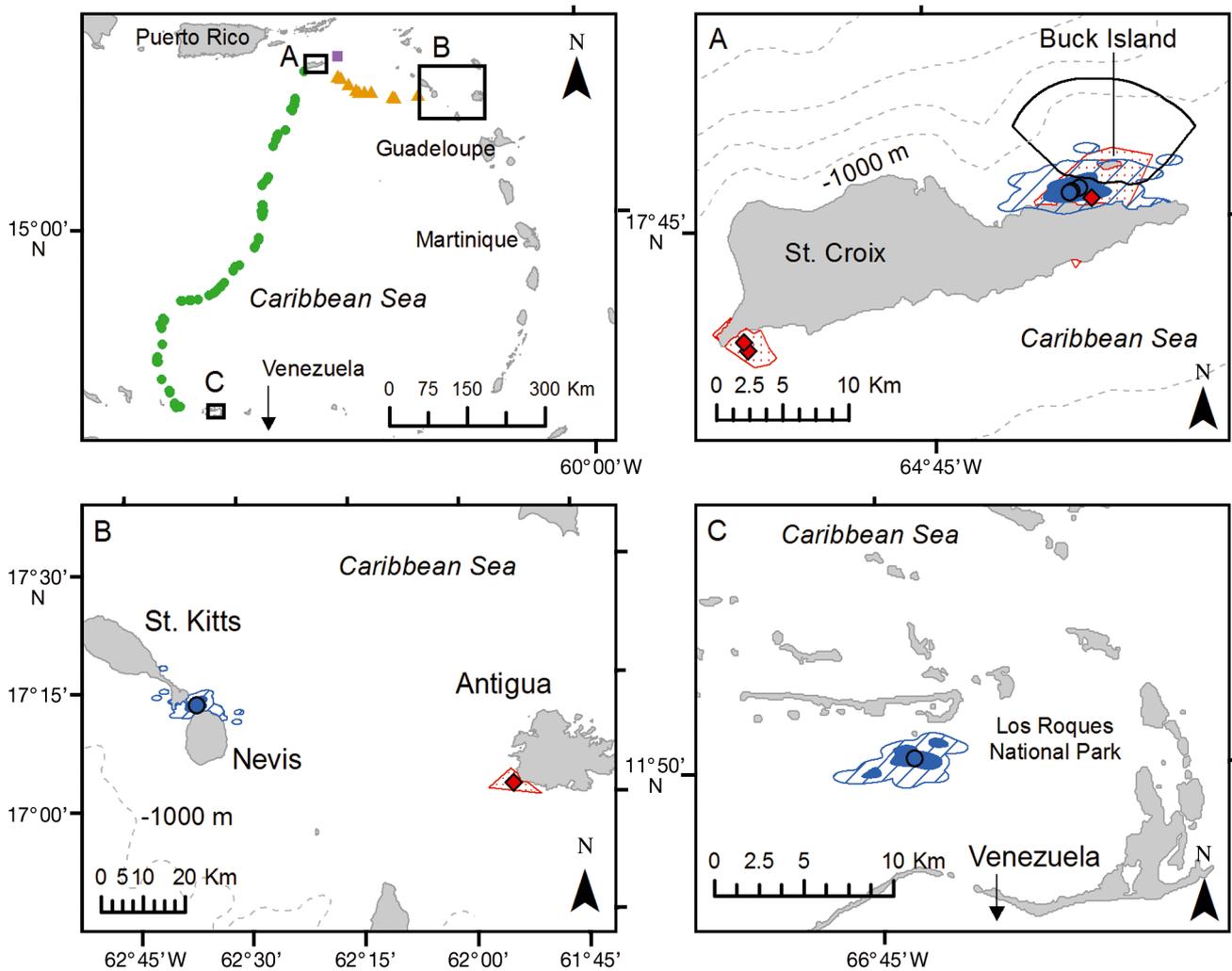


Fig. 3. Foraging and migration for adult female green sea turtles *Chelonia mydas* satellite-tagged on Buck Island, US Virgin Islands. Kernel density estimations (KDEs) for 5 turtles are shown with hatched blue lines (95% KDE) and blue areas (50% KDE); open circles represent 50% KDE centroids. Minimum convex polygons (95% MCPs) are shown by red polygons for 4 turtles; red diamonds represent 95% MCP foraging centroids. The rectangles labelled A, B, C, in the upper left panel show the figure extents for the other 3 panels: (A) 4 turtles foraging near Buck Island (Turtle IDs 2, 4, 6, and 9) and 2 turtles (Turtle IDs 3 and 10) foraging southwest of St. Croix; the boundary for Buck Island Reef National Monument is represented by the black line; (B) 1 turtle foraging near St. Kitts & Nevis Islands (Turtle ID 1) and 1 turtle (Turtle ID 5) foraging southwest of Antigua; and (C) 1 turtle foraging near Los Roques National Park (LRNP), Venezuela (Turtle ID 7). Both KDEs and MCPs were merged for visualization purposes. Migration paths from inter-nesting grounds to foraging grounds for 3 turtles are shown in the top left panel. Turtle ID 1 had a migration path to St. Kitts & Nevis (orange triangles), Turtle ID 7 had a migration path to LRNP (green circles), and Turtle ID 9 had a brief migration path to and from Buck Island, thereafter foraging locally (purple square)

Distances to the nearest land from the 50% KDE foraging centroids (Fig. 3) ranged from 0.7 to 1.6 km, and bathymetry values at the 50% KDE centroid locations ranged from -23.0 to -1.0 m (Table 2). Distances to the nearest land from the MCP foraging centroids ranged from 0.5 to 1.6 km, and the bathymetry values that corresponded to the foraging MCP centroids ranged from -13.0 to -6.0 m (Table 2).

Turtle foraging days per grid cell

In addition to the area around Buck Island, where we observed high use by turtles during the inter-nesting period, turtles were frequently located off the SW coast of St. Croix (Fig. 2). The number of turtle days per grid cell was weakly but significantly associated with bathymetry (Spearman's $\rho = 0.31$, $p < 0.0001$).

Table 2. Foraging area characteristics for 10 satellite-tracked female green sea turtles *Chelonia mydas* that originally nested on Buck Island, US Virgin Islands. Foraging kernel density estimation (KDE) areas presented here were comprised of at least 20 mean daily locations (MDLs), and minimum convex polygons (MCPs) were comprised of less than 20 MDLs; variables include information regarding the timing, duration, area, water depth, distance to shoreline, and foraging area characteristics for each foraging period. Centroids were derived from 50% KDEs or 95% MCPs. Foraging periods are given as mm/dd/yy. FFL: filtered foraging locations; EEMP: East End Marine Park; LRNP: Los Roques National Park; SVS: submerged vegetation (seagrass); CRCH: coral reef and colonized hardbottom; USS: unconsolidated sediments (sand); na: not applicable. Turtle ID 8 did not pass site fidelity, therefore no MCP was calculated. All proportions for KDE site fidelity were >99.0099; turtle tracks with values >95.00 indicate movement paths that are more constrained than random movement paths. Proportions for MCPs were >95.00 except for Turtle ID 8, which had value of 56.4356 and did not pass site fidelity. NE = not estimated because centroid depth had positive value

Turtle ID	Foraging period (d)	FFLs	MDLs	50% KDE area (km ²)	95% KDE area (km ²)	Centroid distance to shore (km)	Depth at centroid (m)	Foraging location	Centroid in protected area?	Centroid habitat type for local foragers
KDEs										
1	09/19/11–03/03/12 (167)	481	82	11.9	59.4	1.6	–23.0	St. Kitts & Nevis	No	na
2	11/01/12–04/09/13 (160)	361	66	6.5	31.7	1.1	–1.0	Buck Island	Yes, EEMP	SVS
4	11/23/12–08/06/13 (372)	387	55	4.2	19.9	0.7	–1.0	Buck Island	Yes, EEMP	CRCH
6	11/01/13–12/08/13 (38)	325	33	2.0	9.5	0.8	–1.0	Buck Island	Yes, EEMP	SVS
7	11/05/13–12/09/13 (35)	338	29	3.2	12.3	1.2	–19.0	Venezuela	Yes, LRNP	na
Mean	154.0	378.4	53.0	5.6	26.6	1.1	–9.0			
SD	137.2	62.0	22.3	3.9	20.3	0.4	11.0			
Min.	35.0	325.0	29.0	2.0	9.5	0.7	–23.0			
Max.	372.0	481.0	82.0	11.9	59.4	1.6	–1.0			
Turtle ID	Foraging period (d)	FFLs	MDLs		95% MCP (km ²)	Centroid distance to shore (km)	Depth at centroid (m)	Foraging location	Centroid in protected area?	Centroid habitat type for local foragers
MCPs										
5	10/12/12–12/21/12 (71)	36	13		30.7	1.6	–13.0	Antigua	No	na
3	11/01/12–12/28/12 (58)	49	13		9.0	0.7	NE	St. Croix	No	SVS
9	11/04/13–12/07/13 (34)	33	9		23.2	0.5	NE	Buck Island	Yes, EEMP	USS
10	11/05/14–11/13/14 (9)	114	9		19.6	1.4	–6.0	St. Croix	No	SVS
8	11/01/13–11/15/13 (15)	7	4		na	na	na	Buck Island	na	na
Mean	37.4	47.8	9.6		20.6	1.1	–9.5			
SD	26.8	40.0	3.7		9.0	0.5	4.9			
Min.	9.0	7.0	4.0		9.0	0.5	–13.0			
Max.	71.0	114.0	13.0		30.7	1.6	–6.0			

Core area space-use sharing

There were 5 turtles for which foraging KDEs were calculated, 3 of which foraged in the same region (near Buck Island). These 3 turtle pairs were all re-migrants, and the amount of UDOI space-use

sharing for these turtle pairs ($n = 3$ turtles, $n = 3$ pairs) ranged from 0.09 to 0.14 ($\bar{x} \pm SD$: 0.12 ± 0.02 , $n = 3$; Table S3), where greater UDOI indicates greater space-use sharing between turtle pairs. Temporal overlap for these 3 pairs of foraging females near Buck Island ranged from 0 to 138 d

($\bar{x} \pm SD$: 46.00 ± 79.67 , $n = 3$). Of the 4 turtles with foraging MCPs, 2 (1 turtle pair) foraged in the same area, southwest of St. Croix; the distance between centroids for these 2 turtles was 0.69 km. For the turtle with a foraging MCP in the Buck Island area, the mean distance from the MCP centroid to the 3 KDE centroids was 1.47 km.

Ecological and spatial correlates

The benthic habitats associated with foraging centroids for turtles foraging near Buck Island and St. Croix consisted of submerged seagrass vegetation, coral reef and colonized hardbottom, and unconsolidated sand sediments (Table 2). Of the 9 turtles that had a foraging KDE or MCP ($n = 5$ KDEs, $n = 4$ MCPs), 5 turtles had foraging centroids located in protected or managed areas, including EEMP, USVI and Los Roques National Park (LRNP), Venezuela. The other 4 turtles had foraging centroids that were not located in protected areas (Table 2).

DISCUSSION

Through 4 yr of satellite tracking, we gained insight into the movement and habitat-use patterns of adult female green turtles nesting at BIRNM, which represents a unique management unit (see Shamblin et al. 2012), during breeding, migration, and foraging time periods. Our study presents key information on the BIRNM green turtle rookery, supports previous findings on spatial use from 3 other Caribbean studies (Blumenthal et al. 2006, Esteban et al. 2015, Becking et al. 2016), and our robust SSM approach accurately quantifies time periods of migration and residency at foraging and inter-nesting sites.

We observed consistency of inter-nesting habitat-use patterns over the 4 study years, with all turtles using near-shore, shallow waters (shallower than -20 m depth) within approximately 10 km of Buck Island. Green turtle inter-nesting habitat in Dry Tortugas National Park (Hart et al. 2013) and other Caribbean locations was also in near-shore, shallow waters (Lesser Antilles, Esteban et al. 2015; Cayman Islands, Blumenthal et al. 2006), although some exceptions have been found for turtles traveling between nesting sites and swimming through deep waters (e.g. mean depth -2940 m for 1 Cayman Islands turtle; Blumenthal et al. 2006, see also Becking et al. 2016).

Neophyte or first-time nesters may show different patterns during inter-nesting than established remigrants. For example, experienced re-migrant hawksbills were the only turtles to select distant resident areas during inter-nesting in Barbados (Walcott et al. 2012). However, we did not find differences in inter-nesting resident areas between green turtle neophytes and re-migrants; 2 of our tagged females (Turtle IDs 7 and 8) were neophytes, and their habitat-use patterns mirrored those of the other 8 turtles. One exception was that Turtle ID 7 showed variability in nesting beach selection and nested at a nearby TNC study site at EEMP (6.5 km straight-line distance away), whereas all other nesting events for tagged turtles occurred at BIRNM. This indicates that nesting site fidelity within a single nesting season may vary for some BIRNM green turtles. Flexibility in nesting-site use was also observed in the Cayman Islands, where 1 of 7 green turtles shifted her nesting site within a season (Blumenthal et al. 2006). Continued satellite-tracking and nest-monitoring at BIRNM and neighboring beaches could help determine if both neophytes and re-migrants share the same level of flexibility in site-use within a nesting season.

Ours is the first empirical dataset showing limited migration and use of 'local' resources in the USVI by green turtles. We found that 7 of 10 turtles did not migrate, supporting recent findings of plasticity in migration and selection of local foraging sites in Dry Tortugas National Park and the Florida Keys National Marine Sanctuary (Hart et al. 2013) where 9 of 11 turtles showed year-round residency, in the Indian Ocean (Whiting et al. 2007), where all 6 turtles migrated to shallow foraging grounds within 40 km of the nesting beach, and elsewhere in the Caribbean (Esteban et al. 2015) where 2 of 3 green turtles foraged within 50 km of their original nesting grounds. Not all turtles in our study remained near nesting grounds to forage, however; some migrated long distances (e.g. up to 694 km straight-line distance to Venezuela waters; Turtle ID 7). This was also the case for turtles studied in the Lesser Antilles, where 1 green turtle that did not forage locally migrated 607 km straight-line distance (Esteban et al. 2015) and 4 turtles studied in Bonaire migrated 198 to 3135 km away after nesting (Becking et al. 2016). In a study of green turtles in the Cayman Islands, all 7 tagged green turtles traveled 520 to 856 km straight-line distance to foraging locations (Blumenthal et al. 2006). Of all these studies, neither Bonaire nor the Cayman Islands had locally foraging post-nesting green turtles despite both areas supporting resident juvenile greens (Blumenthal et al. 2006, Stapleton et

al. 2014, Becking et al. 2016). Local habitat may not be particularly suitable for adults in these locations. In the Cayman Islands, legal and illegal sea turtle fisheries that mainly target larger turtles (Bell et al. 2006) could also play a role, potentially capturing resident turtles more often than those that migrate away. Fishing for turtles is not legal in US Gulf of Mexico waters, St. Eustatius and St. Maarten (Lesser Antilles) or the USVI (Bräutigam & Eckert 2006), where turtles were found to forage locally after nesting.

Similar to the inter-nesting period, foraging centroids for BIRNM nesters were also close to shore (at most 1.6 km away) and in relatively shallow waters (up to -23 m depth). This finding is similar to that of Esteban et al. (2015), where the 2 green turtles that migrated to the Lesser Antilles remained resident there in shallow nearshore foraging areas (within approximately 5 km of land).

The grid analysis revealed high-use zones for BIRNM green turtles to the northeast of St. Croix during inter-nesting, especially surrounding Buck Island. During foraging periods, high-use grid cells were to the northeast and southwest of St. Croix. Grid cells to the northeast of St. Croix lay directly in the path of commercial and recreational boats traveling to BIRNM. Inter-nesting and foraging areas at BIRNM that overlap with human use zones present an important management concern, especially because some individual adult female turtles are resident year-round in this relatively small area. The area from Green Key Marina (on the mainland of St. Croix) to Buck Island is a major human thoroughfare for boating, so boat strikes of turtles are a potential concern. Given that we found some overlap of satellite-tagged green turtle home ranges with human use areas at BIRNM, the density of turtles at these sites may be higher than we can demonstrate from satellite tracking alone. Investigation of these foraging sites to determine resource condition and to further quantify turtle numbers at these sites would be valuable for informing future management actions.

While some turtles remained resident, 3 of our turtles migrated to other countries, supporting the need for international cooperation in conservation of these turtles (e.g. Blumenthal et al. 2006, Becking et al. 2016). We tracked BIRNM nesting green turtles on their migrations to Antigua, St. Kitts & Nevis, and Venezuela, and only one of these ended up in a protected area (Venezuela's LRNP). Exploitation of sea turtles in Antigua and St. Kitts & Nevis is not completely prohibited, although it is restricted (Bräutigam & Eckert 2006). Given the genetic distinctness of

BIRNM green turtles, continued long-term protection of the nesting beach and protection of the in-water inter-nesting and foraging sites delineated here may improve the likelihood of population recovery.

Acknowledgements. We thank NPS interns and USGS employees J. Beauchamp, M. Denton, A. Daniels, B. Smith, H. Crowell, and A. Crowder for assistance deploying satellite tags in the field, and E. Connolly-Randazzo for help with an earlier draft of the manuscript. Permission to tag and sample turtles was given under BUIS permit BUIS-2012-SCI-0002 and USGS-SESC-IACUC 2011-05, and USFWS permits issued to K.M.H. Funding was provided by the USGS Natural Resources Protection Program, National Park Service and USGS Ecosystems Program. Any use of trade, product, or firm names is for descriptive purposes only and does not imply endorsement by the US Government.

LITERATURE CITED

- ✦ Allard MW, Miyamoto MM, Bjørndal KA, Bolten AB, Bowen BW (1994) Support for natal homing in green turtles from mitochondrial DNA sequences. *Copeia* 1994:34–41
- Amante C, Eakins BW (2009) ETOPO1 1 arc-minute global relief model: procedures, data sources and analysis. National Geophysical Data Center, NOAA. <https://www.ngdc.noaa.gov/mgg/global/global.html> (accessed 8 April 2014)
- ✦ Bailey H, Shillinger G, Palacios D, Bograd S, Spotila J, Paladino F, Block C (2008) Identifying and comparing phases of movement by leatherback turtles using state-space models. *J Exp Mar Biol Ecol* 356:128–135
- ✦ Bailey H, Mate BR, Palacios DM, Irvine L, Bograd SJ, Costa DP (2009) Behavioural estimation of blue whale movements in the Northeast Pacific from state-space model analysis of satellite tracks. *Endang Species Res* 10: 93–106
- ✦ Becking LE, Christianen MJA, Nava MI, Miller N, Willis S, van Dam RP (2016) Post-breeding migration routes of marine turtles from Bonaire and Klein Bonaire, Caribbean Netherlands. *Endang Species Res* 30:117–124
- ✦ Bell CD, Blumenthal JM, Austin TJ, Solomon JL, Ebanks-Petrie G, Broderick AC, Godley BJ (2006) Traditional Caymanian fishery may impede local marine turtle population recovery. *Endang Species Res* 2:63–69
- ✦ Blumenthal JM, Solomon JL, Bell CD, Austin TJ and others (2006) Satellite tracking highlights the need for international cooperation in marine turtle management. *Endang Species Res* 2:51–61
- Bräutigam A, Eckert KL (2006) Turning the tide: exploitation, trade and management of marine turtles in the Lesser Antilles, Central America, Colombia and Venezuela. TRAFFIC International, Cambridge
- ✦ Breed GA, Jonsen ID, Myers RA, Bowen WD, Leonard ML (2009) Sex-specific, seasonal foraging tactics of adult grey seals (*Halichoerus grypus*) revealed by state-space analysis. *Ecology* 90:3209–3221
- ✦ Broderick AC, Glen F, Godley BJ, Hays GC (2002) Estimating the number of green and loggerhead turtles nesting annually in the Mediterranean. *Oryx* 36:1–9
- ✦ Broderick AC, Coyne MS, Fuller WJ, Glen F, Godley BJ (2007) Fidelity and over-wintering of sea turtles. *Proc R Soc B* 274:1533–1538

- Burt WH (1943) Territoriality and home range concepts as applied to mammals. *J Mammal* 24:346–352
- Calenge C (2006) The package 'adehabitat' for the R software: a tool for the analysis of space and habitat use by animals. *Ecol Modell* 197:516–519
- Carr A, Ross P, Carr S (1974) Internesting behavior of the green turtle, *Chelonia mydas*, at a mid-ocean island breeding ground. *Copeia* 1974:703–706
- Coyne MS, Godley BJ (2005) Satellite Tracking and Analysis Tool (STAT): an integrated system for archiving, analyzing and mapping animal tracking data. *Mar Ecol Prog Ser* 301:1–7
- ESRI (2002) ArcView GIS 3.3. Environmental Systems Research Institute, Redlands, CA
- ESRI (2013) ArcGIS Desktop 10.2. Environmental Systems Research Institute, Redlands, CA
- Esteban N, Van Dam RP, Harrison E, Herrera A, Berkel J (2015) Green and hawksbill turtles in the Lesser Antilles demonstrate behavioural plasticity in inter-nesting behaviour and post-nesting migration. *Mar Biol* 162: 1153–1163
- Fieberg J, Kochanny CO (2005) Quantifying home-range overlap: the importance of the utilization distribution. *J Wildl Manag* 69:1346–1359
- Fossette S, Hobson VJ, Girard C, Calmettes B, Gaspar P, Georges J, Hays GC (2010) Spatio-temporal foraging patterns of a giant zooplanktivore, the leatherback turtle. *J Mar Syst* 81:225–234
- Goatley CHR, Hoey AS, Bellwood DR (2012) The role of turtles as coral reef macroherbivores. *PLOS ONE* 7:e39979
- Godley BJ, Blumenthal JM, Broderick AC, Coyne MS, Godfrey MH, Hawkes LA, Witt MJ (2008) Satellite tracking of sea turtles: Where have we been and where do we go next? *Endang Species Res* 4:3–22
- Groombridge B (1982) The IUCN Amphibia-Reptilia red data book, Part 1: Testudines, Crocodylia, Rhynchocephalia. IUCN, Gland
- Groombridge B, Luxmoore R (1989) The green turtle and hawksbill (Reptilia: Cheloniidae): world status, exploitation and trade. CITES, Cambridge
- Hart K, Hyrenbach K (2009) Satellite telemetry of marine megavertebrates: the coming of age of an experimental science. *Endang Species Res* 10:9–20
- Hart KM, Zawada DG, Fujisaki I, Lidz BH (2013) Habitat use of breeding green turtles *Chelonia mydas* tagged in Dry Tortugas National Park: making use of local and regional MPAs. *Biol Conserv* 161:142–154
- Hart KM, Lamont MM, Sartain AR, Fujisaki I (2014) Migration, foraging, and residency patterns for northern Gulf loggerheads: implications of local threats and international movements. *PLOS ONE* 9:e103453
- Hart KM, Sartain AR, Fujisaki I (2015) Bahamas connection: residence areas selected by breeding female loggerheads tagged in Dry Tortugas National Park, USA. *Anim Biotelem* 3:3
- Hays GC, Glen F, Broderick AC, Godley BJ, Metcalfe JD (2002) Behavioural plasticity in a large marine herbivore: contrasting patterns of depth utilisation between two green turtle (*Chelonia mydas*) populations. *Mar Biol* 141: 985–990
- Hirth HF (1997) Synopsis of the biological data on the green turtle *Chelonia mydas* (Linnaeus 1758). *Biol Rep* 97(1):1–129. US Department of Interior, Washington, DC
- Hoenner X, Whiting SD, Hindell MA, McMahon CR (2012) Enhancing the use of Argos satellite data for home range and long distance migration studies of marine animals. *PLOS ONE* 7:e40713
- Hooge PN, Eichenlaub W, Hooge ER (2001) Animal movement extension to ArcView, version 2.5. Alaska Biological Science Center, US Geological Survey, Anchorage, AK
- Hurlbert SH (1978) The measurement of niche overlap and some relatives. *Ecology* 59:67–77
- Jackson JBC (1997) Reefs since Columbus. *Coral Reefs* 16: S23–S32
- Jonsen ID, Myers RA, Flemming JM (2003) Meta-analysis of animal movement using state-space models. *Ecology* 84: 3055–3063
- Jonsen ID, Flemming JM, Myers RA (2005) Robust state-space modeling of animal movement data. *Ecology* 86: 2874–2880
- Jonsen ID, Myers RA, James MC (2006) Robust hierarchical state-space models reveal diel variation in travel rates of migrating leatherback turtles. *J Anim Ecol* 75:1046–1057
- Jonsen ID, Myers RA, James MC (2007) Identifying leatherback turtle foraging behaviour from satellite telemetry using a switching state-space model. *Mar Ecol Prog Ser* 337:255–264
- Kendall MS, Monaco ME, Buja KR, Christensen JD, Kruer CR, Finkbeiner M, Warner RA (2001) Methods used to map the benthic habitats of Puerto Rico and the US Virgin Islands. NOAA Tech Memo NOAA NCCOS CCMA 152, Silver Spring, MD
- Kendall MS, Battista T, Hillis-Starr Z (2004a) Long term expansion of a deep *Syringodium filiforme* meadow in St. Croix, US Virgin Islands: the potential role of hurricanes in the dispersal of seeds. *Aquat Bot* 78:15–25
- Kendall MS, Christensen JD, Caldwell C, Coyne M and others (2004b) The influence of bottom type and shelf position on biodiversity of tropical fish inside a recently enlarged marine reserve. *Aquat Conserv* 14:113–132
- Limpus CJ, Miller JD, Paramenter CJ, Reimer D, McLachlan N, Webb R (1992) Migration of green (*Chelonia mydas*) and loggerhead (*Caretta caretta*) turtles to and from eastern Australian rookeries. *Wildl Res* 19:347–357
- McClenachan L, Jackson JBC, Newman MJH (2006) Conservation implications of historic sea turtle nesting beach loss. *Front Ecol Environ* 4:290–296
- Meylan AB (1995) Behavioral ecology of the west Caribbean green turtle (*Chelonia mydas*) in the interesting habitat. In: Bjorndal KA (ed) *Biology and conservation of sea turtles*, 2nd edn (revised). Smithsonian Institution Press, Washington, DC, p 67–80
- Moran KL, Bjorndal KA (2005) Simulated green turtle grazing affects structure and productivity of seagrass pastures. *Mar Ecol Prog Ser* 305:235–247
- Mortimer JA, Portier KM (1989) Reproductive homing and internesting behavior of the green turtle (*Chelonia mydas*) at Ascension Island, south Atlantic Ocean. *Copeia* 1989: 962–977
- NMFS (National Marine Fisheries Service) & USFWS (US Fish and Wildlife Service) (1991) Recovery plan for US population of Atlantic green turtle (*Chelonia mydas*). National Marine Fisheries Service, Washington, DC
- NMFS-SEFSC (National Marine Fisheries Service-Southeast Fisheries Science Center) (2008) Sea turtle research techniques manual. NOAA Tech Memo NMFS-SEFSC-579. NOAA, Miami, FL
- NOAA (1998) Designated critical habitat; green and hawksbill sea turtles. *Fed Regist* 63:46693–46701

- Patterson TA, Thomas L, Wilcox C, Ovaskainen O, Matthiopoulos J (2008) State-space models of individual animal movement. *Trends Ecol Evol* 23:87–94
- Plotkin P (2003) Adult migrations and habitat use. In: Lutz PL, Musick JA, Wyneken J (eds) *The biology of sea turtles, Vol II*. CRC Press, Boca Raton, FL, p 225–241
- R Development Core Team (2014) R: a language and environment for statistical computing. R Foundation for Statistical Computing, Vienna
- Rodgers AR, Kie JG (2011) HRT: home range tools for ArcGIS – draft August 10, 2011. Centre for Northern Forest Ecosystem Research, Ontario Ministry of Natural Resources, Thunder Bay. <http://flash.lakeheadu.ca/~arodgers/hre/HRT%20Users%20Manual%20Draft%20August%2010%202011.pdf> (accessed 8 April 2015)
- Schofield G, Lilley MKS, Bishop CM, Brown P and others (2009) Conservation hotspots: implications of intense spatial area use by breeding male and female loggerheads at the Mediterranean's largest rookery. *Endang Species Res* 10:191–202
- Seaman DE, Powell RA (1996) An evaluation of the accuracy of kernel density estimators for home range analysis. *Ecology* 77:2075–2085
- Seminoff JA (Southwest Fisheries Science Center, US) (2004) *Chelonia mydas*. The IUCN Red List of Threatened Species 2004: e.T4615A11037468. <http://dx.doi.org/10.2305/IUCN.UK.2004.RLTS.T4615A11037468.en> (accessed 15 June 2016)
- Shamblin BM, Bjørndal KA, Bolten AB, Hillis-Starr ZM, Lundgren I, Naro-Maciel E, Nairn CJ (2012) Mitogenomic sequences better resolve stock structure of southern Greater Caribbean green turtle rookeries. *Mol Ecol* 21:2330–2340
- Shaver DJ, Hart KM, Fujisaki I, Rubio C and others (2013) Foraging area fidelity for Kemp's ridleys in the Gulf of Mexico. *Ecol Evol* 3:2002–2012
- Shaver DJ, Hart KM, Fujisaki I, Rubio C and others (2016) Migratory corridors of adult female Kemp's ridley turtles in the Gulf of Mexico. *Biol Conserv* 194:158–167
- Shillinger GL, Swithenbank AM, Bograd SJ, Bailey H and others (2010) Identification of high-use interesting habitats for eastern Pacific leatherback turtles: role of the environment and implications for conservation. *Endang Species Res* 10:215–232
- Stapleton S, Nava M, Willis S, Brabec B (2014) Sea turtle conservation Bonaire: research and monitoring of Bonaire's sea turtles. 2014 Technical Report, Sea Turtle Conservation Bonaire, Bonaire
- Systat Software (2012) SigmaPlot. Systat Software, San Jose, CA
- Thayer GW, Engel DW, Bjørndal KA (1982) Evidence for short-circuiting of the detritus cycle of seagrass beds by the green turtle, *Chelonia mydas* L. *J Exp Mar Biol Ecol* 62:173–183
- Thayer GW, Bjørndal KA, Ogden JC, Williams SL, Ziemann JC (1984) Role of larger herbivores in seagrass communities. *Estuaries* 7:351–376
- Walcott J, Eckert S, Horrocks JA (2012) Tracking hawksbill sea turtles (*Eretmochelys imbricata*) during inter-nesting intervals around Barbados. *Mar Biol* 159:927–938
- White G, Garrott R (1990) Analysis of wildlife radio-tracking data. Academic Press, New York, NY
- Whiting SD, Long JL, Coyne M (2007) Migration routes and foraging behaviour of olive ridley turtles *Lepidochelys olivacea* in northern Australia. *Endang Species Res* 3:1–9
- Worton BJ (1987) A review of models of home range for animal movement. *Ecol Modell* 38:277–298
- Worton BJ (1989) Kernel methods for estimating the utilization distribution in home-range studies. *Ecology* 70:164–168
- Worton BJ (1995) Using Monte Carlo simulation to evaluate kernel-based home range estimators. *J Wildl Manag* 59:794–800
- Ziemann JC, Iverson RL, Ogden JC (1984) Herbivory effects on *Thalassia testudinum* leaf growth and nitrogen content. *Mar Ecol Prog Ser* 15:151–158

Editorial responsibility: Brendan Godley,
University of Exeter, Cornwall Campus, UK

Submitted: June 29, 2016; Accepted: Nov 21, 2016
Proofs received from author(s): January 20, 2017