Satellite tracking of hawksbill turtles nesting at Buck Island Reef National Monument, US Virgin Islands: Inter-nesting and foraging period movements and migrations

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ABSTRACT

To conserve imperiled marine species, an understanding of high-density use zones is necessary prior to designing and evaluating management strategies that improve their survival. We satellite-tracked turtles captured after nesting at Buck Island Reef National Monument (BIRNM), St. Croix, US Virgin Islands to determine habitat-use patterns of endangered adult female hawksbills (*Eretmochelys imbricata*). For 31 turtles captured between 2011 and 2014, switching state-space modeling and home range analyses showed that inter-nesting (IN) core-use areas (i.e., 50% kernel density estimates [KDEs]) were 9.6 to 77.7 km^2 in area, occupied for 21 to 85 days, and in shallow water (21 of 26 centroids > -10 m). The IN zones overlapped with areas both within the protected borders of BIRNM, and outside BIRNM (32% of turtle-tracking days outside during IN). Turtles migrated to their foraging grounds between July and October with path lengths ranging from 52 to 3524 km; foraging areas included 14 countries. Core-use foraging areas (50% KDEs) where turtles took up residence were 6.3 to 95.4 km^2, occupied for 22 to 490 days, with mean centroid depth -66 m. Our results show previously unknown habitat-use patterns and highlight concentrated areas of use both within and adjacent to a US protected area during the breeding season. Further, our results clearly demonstrate the need for international conservation to protect hawksbills, as migrating turtles crossed between two and eight different jurisdictions. Our results provide critical spatial and temporal information for managers charged with designing strategies to minimize human impact to and maximize survival for this globally imperiled species.

1. Introduction

Marine Protected Areas (MPAs) are important for managing and sustaining ocean biodiversity (Agardy, 1994), however < 3% of the world's oceans are within MPAs and < 1% are regulated as no-take (Costello and Ballantine, 2015). Further, global studies of MPA effectiveness indicate successful MPAs include four or five key features (no take, enforcement, old, large, and isolated), but most MPAs only have one or two of these features, making them indistinguishable from unprotected areas (Edgar et al., 2014).

Assessing the effectiveness of MPAs and implementing appropriate management strategies at a local level requires understanding the spatial ecology patterns for species of interest. However, with highly mobile species that travel globally across geopolitical boundaries, such as sea turtles, it can be difficult to assess these patterns. Remote tracking through satellite telemetry allows researchers to address increasingly complex questions on habitat-use and movement (Godley et al., 2008; Hart and Hyrenbach, 2009; Hazen et al., 2012) and gain understanding of spatial use during breeding, foraging, and migration for sea turtles (e.g. Hart et al., 2014; Fossette et al., 2010; Schofield et al., 2010; Shillinger et al., 2010).

Although global MPA coverage is small, studies indicate they are

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Fig. 1. Study Area. Buck Island Reef National Monument (BIRNM, US Virgin Islands), where adult female hawksbills (*Eretmochelys imbricata*) were satellite-tagged from 2011 to 2015. The black line around Buck Island indicates the current boundary of BIRNM; the prior BIRNM boundary is represented by the narrow black outline filled with diagonal lines. Dotted lines indicate 1000 m bathymetry depth contours.

important for sea turtles. Satellite-tracked green sea turtles (*Chelonia mydas*) aggregate in MPAs during foraging (Hart et al., 2013; Scott et al., 2012) and in some cases degrade seagrass habitat within them, owing to high turtle concentration (Christianen et al., 2014). Similarly, nine (83%) of the hawksbill sea turtles (*Eretmochelys imbricata*) tracked in the Dominican Republic were predominantly within the local MPA during inter-nesting (IN; Revuelta et al., 2015) and over half (55%) of post-nesting female hawksbills were tracked to foraging areas that overlapped with MPA locations in Brazil (Marcovaldi et al., 2012). Telemetry data can therefore be useful for evaluating the effectiveness of current MPA boundaries or creating new protected areas (Dawson et al., 2017; Maxwell et al., 2011).

Hawksbill sea turtles primarily inhabit coral reef habitats throughout the Caribbean (Carr et al., 1966; Mortimer and Donnelly, 2008), but are also recorded in mangrove estuaries in the eastern Pacific (Gaos et al., 2011). Endangered in all parts of their range (NMFS and USFWS, 1993, 1998), the International Union for Conservation of Nature (IUCN) Red List of Threatened Species listed hawksbills as critically endangered in 1996, owing to extensive population declines (Mortimer and Donnelly, 2008). Hawksbill nesting occurs in few places in the Caribbean (NMFS and USFWS, 1993), and is much reduced from historic numbers (McClenachan et al., 2006). However, recent increases in nesting numbers at monitored locations in Antigua (Richardson et al., 2006), Barbados (Beggs et al., 2007), Guadeloupe (Kamel and Delcroix, 2009) and Puerto Rico (Van Dam et al., 2008) are promising.

Previous studies on movement patterns of both sexes of adult hawksbills in the Caribbean were conducted in Puerto Rico (Van Dam et al., 2008), Barbados (Horrocks et al., 2001; Walcott et al., 2012), Lesser Antilles (Esteban et al., 2015), Cuba (Moncada et al., 2012), Costa Rica (Troëng et al., 2005), the Dominican Republic (Hawkes et al., 2012; Revuelta et al., 2015) and the US Virgin Islands (USVI; Starbird et al., 1999). Meylan (1999) summarized hawksbill flipper tag returns to infer foraging areas, and more recent satellite tracking (see studies cited above) has revealed both local and distant foraging sites in many countries including Nicaragua, Honduras, Venezuela, Bahamas, St. Eustatius, St. Maarten, British Virgin Islands, St. Barthélemy, Columbia, and Mexico, highlighting the importance of understanding the

broad scale spatial ecology of sea turtles during different movement stages (IN, migration, foraging) for adequate protection. Still, the spatial ecology and movements of hawksbills nesting in the USVI are not well understood, and there is a paucity of information available for managers on hawksbill distribution (see Godley et al., 2008 for review).

The habitat-use patterns of adults, including the space-use overlap between individuals, is useful for managers charged with protecting reproductively active individuals, which is necessary for population recovery. The US Hawksbill Recovery Plan calls for more demographic information on all life stages of hawksbills. This includes, but is not limited to, their distribution, abundance, and seasonal movements (NMFS and USFWS, 1993). Buck Island Reef National Monument (BIRNM) is a protected area in the USVI and the only fully protected area in the Caribbean where hawksbills both forage and nest (NMFS and USFWS, 1993). Although BIRNM is an important nesting and foraging area for hawksbills where a saturation tagging program has been ongoing for 30 years, little information is available on the spatial ecology of turtles in this protected area. Only one study has delineated IN habitat use of hawksbills at BIRNM, through radio-tagging seven females in 1991, which identified that all IN areas were within 3 km of Buck Island and in water depths from −9 to −20 m (Starbird et al., 1999). In addition, a case study by Sartain-Iverson et al. (2016) tracked one hawksbill turtle through IN, migration, and foraging. The long-term movement patterns during IN, migration, and foraging, with a greater number of individuals and more advanced telemetry will aid in clarifying the spatial distribution of breeding hawksbills at this important site.

In this study, we used satellite tracking to delineate IN habitats, migratory routes, and foraging areas for adult female hawksbills post-nesting at BIRNM. We assessed habitat-use both within and outside the protected area boundary and examined remotely sensed depth data to describe characteristics of selected habitat. As the protected waters within BIRNM are limited, we also determined the extent of habitat-use overlap between different hawksbill individuals. Further, we characterized timing of migration, and individual turtle site-loyalty and occupancy patterns. Finally, we determined protected status of waters containing foraging areas for conservation relevance.

Table 1
Size and satellite-tracking dates for hawksbill (*Eretmochelys imbricata*) nesters tagged at Buck Island, 2011–2014. N = neophyte, R = remigrant, EEZ = the number of exclusive economic zones the turtle traveled through (calculated over entire tracking period). Only the filtered migration points outside of Buck Island Reef National Monument area were used for whether the migratory path crossed a protected area.

Turtle	Size (CCL-tip, cm)	Tracking start (days)	N/R	Migration				
				Migration Period (days)	Path Total Distance (km)	Mean Depth (m)	Cross protected area? (% of filtered points)	EEZ
1	82.4	8/23/11 (61)	R	9/19–9/26 (8)	282.9	−889.8	Y (5%)	2
2	84.5	8/25/11 (536)	N	10/6–10/9 (4)	NA	−1812.0	N	8
3	85.0	8/25/11 (71)	R	10/15–10/25 (11)	425.2	−501.4	Y (2%)	2
4	88.2	8/26/11 (382)	R	9/26–9/27 (2)	70.6	−420.9	Y (9%)	3
5	86.7	8/26/11 (600)	R	10/18–10/20 (3)	167.1	−484.3	N	3
6	83.5	8/27/11 (418)	R	9/11–9/15 (5)	221.1	−870.8	Y (2%)	7
7	83.6	8/27/11 (257)	R	10/5–10/8 (4)	255.6	−774.9	Y (24%)	6
8	84.9	8/28/11 (390)	R	10/5–10/11 (7)	200.9	−1007.8	Y (5%)	2
9	92.6	8/28/11 (582)	R	8/28–9/1 (4)	154.9	−1370.4	Y (3%)	3
10	90.5	7/30/12 (497)	R	9/13–9/13 (1)	51.9	−1938.7	N	3
11	95.0	7/30/12 (310)	R	9/14–10/26 (43)	2588.6	−1997.4	Y (3%)	7
12	87.3	8/1/12 (384)	N	9/8–9/21 (14)	589.6	−635.7	Y (22%)	8
13	84.7	8/1/12 (247)	R	10/11–10/21 (11)	602.2	−571.5	Y (12%)	7
14	86.4	8/2/12 (336)	R	9/14–9/21 (8)	173.4	−413.6	Y (2%)	2
15	88.6	8/2/12 (445)	R	10/3–10/8 (6)	199.9	−783.7	N	2
16	88.0	8/3/12 (96)	N	9/23–9/24 (2)	84.7	−530.8	N	2
17	89.9	8/3/12 (495)	R	8/4–8/8 (5)	197.0	−979.8	N	3
18	87.0	8/4/12 (120)	N	9/9–11/16 (69)	3523.8	−1280.4	Y (12%)	7
19	91.8	8/7/12 (480)	N	10/15–11/13 (27)	1658.7	−1871.6	Y (3%)	6
20	85.2	8/8/12 (91)	N	9/25–9/29 (5)	238.8	−1367.8	N	4
21	86.8	8/9/12 (269)	N	10/5–11/24 (40)	1533.8	−1585.5	Y (7%)	4
22	92.7	7/29/13 (135)	R	9/16–9/18 (3)	137.3	−834.0	Y (23%)	2
23	92.3	7/29/13 (135)	R	8/29–9/11 (14)	901.7	−1640.6	N	4
24	85.1	7/29/13 (109)	N	10/2–10/5 (4)	202.2	−590.8	Y (3%)	4
25	96.3	7/30/13 (134)	R	10/14–11/18 (33)	1991.7	−1307.2	Y (12%)	5
26	86.9	7/30/13 (134)	N	7/31–8/4 (5)	213.5	−961.9	Y (13%)	3
27	95.3	7/31/13 (133)	R	9/12–9/15 (4)	189.4	−738.7	N	2
28	83.1	8/2/13 (462)	R	none	NA	NA	NA	3
29	86.2	8/3/13 (129)	R	9/14–9/22 (9)	443.2	−284.0	Y (10%)	5
30	83.5	8/5/14 (106)	R	9/30–10/4 (5)	180.6	−481.8	Y (8%)	2
31	96.5	8/5/14 (162)	R	10/29–11/28 (31)	2432.7	−3006.6	N	8
32	87.7	8/7/14 (104)	R	8/7–8/9 (3)	95.2	−481.2	N	2

2. Materials & methods

2.1. Study site

Tagging and sampling occurred at BIRNM, which includes 76.3 km² of submerged lands and the 0.7 km² uninhabited Buck Island, located on the shallow St. Croix shelf (approx. −15 to −20 m depth), 2.4 km northeast of St. Croix island in the USVI (Fig. 1). BIRNM is a nesting and foraging area for loggerhead (*Caretta caretta*), green (*Chelonia mydas*), leatherback (*Dermochelys coriacea*), and hawksbill sea turtles. Approximately 50–80 individual hawksbill females lay nests annually at BIRNM.

2.2. Turtle capture and transmitter deployment

Nightly surveys were conducted from 19:00 to 05:00 h from 15 July through 30 September 2011–2015. Thirty-two satellite transmitters were used to monitor movements of 31 post-nesting hawksbill turtles over a 5 yr period from 2011 to 2015 (Table 1). Turtles were outfitted with transmitters using established protocols (NMFS-SEFSC, 2008), following methods in Hart et al. (2017). Briefly, we intercepted nesting hawksbill females after they finished egg-laying on the beach. We used PTTs from Wildlife Computers (Redmond, WA, USA; SPOT5 [n = 27] and SPLASH [n = 5] models; dimensions [length × width × height]: SPOT5–72 × 56 × 24 mm, SPLASH10–200–72 × 55 × 30 mm). We streamlined attachment materials to minimize buoyancy or drag effects on the turtle's swimming ability and limited the epoxy (two part Superbond™ epoxy) footprint. Each tag was set as active for 24 h d[1] with duty-cycling implemented in 2012–2014 December through May (every

3rd day) to conserve battery life.

2.3. Sea turtle tracking and switching state-space modeling

We used Satellite Tracking and Analysis Tool (STAT; Coyne and Godley, 2005) available on www.seaturtle.org to retrieve location data (see Appendix A for details on Location Class [LC] accuracy and Argos location processing); LCs 3, 2, 1, 0, A, and B were used to reconstruct routes.

We applied switching state-space modeling (SSM; Jonsen et al., 2003; Patterson et al., 2008) as described in Jonsen et al. (2005) to determine the beginning and end date of the IN period for each hawksbill. SSM methods follow our previous studies (see Hart et al., 2013, 2014, 2015; Shaver et al., 2013, 2016, and Appendix A for information on this technique). Earlier applications defined a binary behavioral mode with 'foraging' and 'migration' (Jonsen et al., 2005, 2007); however, since we tagged animals during the nesting season, our behavioral mode definitions were 'foraging and/or IN' and 'migration'. From the 'IN and/or foraging' mode, a period was defined as 'IN' if points occurred before migration away from the nesting beach. We summarized data until the transmitters stopped sending information or until the time of data synthesis: 13 January 2015.

2.4. Migration

We used the SSM approach to determine the beginning and end date of migration mode for each turtle following Hart et al. (2012). We present migration periods representing movement away from the IN area to the foraging grounds (i.e., brief [2–8 days] movements within IN

Table 2

Hawksbill (*Eretmochelys imbricata*) home range analysis details for individuals tagged at Buck Island Reef National Monument, St. Croix. Filt locs = filtered locations, KDE = kernel density estimate, MCP = minimum convex polygon, MDLs = mean daily locations, C. = centroid, Prot. Area = Protected Area. Inter-nesting Protected Areas include Buck Island Reef National Monument (BIRNM) and East End Marine Park (EEMP, in St. Croix). Foraging Protected Areas include Agoa Specially Protected Area (ASPA; Cartagena Convention, Regional), Arrecifes de Tourmaline Natural Reserve (ATNR; National), Arrecifes de la Cordillera Natural Reserve (ACNR; National), Cayos Miskitos y Franja Costera Inmediata Biological Reserve (CMFC; National), Cabezas de San Juan Natural Reserve (CSJNR; National), and Nelson's Dockyard National Park (NDNP). Foraging area country Exclusive Economic Zones (EEZs) include Puerto Rico (PR), US Virgin Islands (USVI), British Virgin Islands (BVI), Saint-Martin (SM), Saba (S), Sint Eustatius (SE), Nicaragua (Nic), Bahamas (Bah), Guadaloupe (Gua), Antigua and Barbuda (AB), Anguilla (Ang), St. Kitts and Nevis (KN), Venezuela (Ven) and Dominican Republic (DR). Italics means the centroid was within 4 km, but not within, the protected area. A cell with "." denotes there are no values available.

Turtle	Inter-nesting							Foraging							
	Inter-nesting period (days)	Filt locs	50% KDE or 95% MCP	Area, km² (MDLs)	C. depth, (m)	C. to shore, (km)	Prot. Area	Forging period (days)	Filt locs	50% KDE or 95% MCP	Area, km² (MDLs)	C. depth, (m)	C. to shore, (km)	Country (EEZ)	Prot. Area
1	8/27–9/18 (23)	42	MCP	525.7	−2523	8.7	No	9/27–10/22 (26)	13	MCP	898.66	−2495	22.4	PR	No
2	8/26–10/5 (41)	87	KDE	59.4 (40)	−3	1.3	BIRNM	10/10–2/10 (490)	1016	KDE	33.44 (319)	−18	2.9	SM	ASPA
3	8/25–10/14 (51)	258	KDE	17.4 (51)	−2	0.3	BIRNM	10/26–11/3 (9)	4	MCP	0.86	−15	6.7	PR	ATNR
4	8/27–9/25 (30)	131	KDE	24.9 (30)	−204	2.0	BIRNM	9/28–10/21 (24)	106	KDE	49.83 (24)	−24	1.3	USVI	No
4	.	.	.	.	.	.	.	10/25–9/10 (322)	1183	KDE	51.48 (243)	−32	2.7	USVI	No
5	8/26–10/17 (53)	246	KDE	77.7 (53)	−2	1.5	BIRNM	10/21–6/4 (228)	805	KDE	40.07 (169)	−42	2.4	USVI	No
5	.	.	.	.	.	.	.	6/28–4/15 (292)	1063	KDE	39.44 (220)	−42	2.2	USVI	No
6	8/28–9/10 (13)	85	MCP	392.4	−113	2.4	BIRNM	9/16–10/24 (39)	125	KDE	95.43 (32)	−24	3.0	SE	No
6	.	.	.	.	.	.	.	11/2–11/19 (18)	7	MCP	1082.42	−770	15.2	S	No
6	.	.	.	.	.	.	.	11/30–10/17 (323)	940	KDE	62.87 (231)	3	1.3	SE	No
7	8/28–10/4 (38)	213	KDE	14.4 (38)	−2	0.6	BIRNM	10/9–10/19 (11)	53	MCP	149.75	−60	6.6	SM	ASPA
7	.	.	.	.	.	.	.	10/23–5/9 (200)	524	KDE	13.58 (118)	−43	4.6	SM	ASPA
8	8/29–10/4 (37)	116	KDE	60.3 (35)	−15	0.9	EEMP	10/12–9/19 (344)	721	KDE	6.29 (201)	−5	0.0	PR	No
9	No IN period	.	.	.	.	.	.	9/2–9/4 (369)	1052	KDE	50.66 (272)	−23	2.1	PR	ACNR
9	.	.	.	.	.	.	.	9/8–9/10 (3)	11	MCP	44.59	−28	5.5	PR	ACNR
9	.	.	.	.	.	.	.	9/14–3/30 (198)	386	KDE	44.41 (114)	−22	1.7	PR	ACNR
10	7/31–9/12 (44)	305	KDE	31.1 (44)	−3	1.1	BIRNM	9/14–12/8 (451)	1440	KDE	26.53 (357)	−44	0.9	BVI	No
11	7/31–9/13 (45)	302	KDE	27.6 (45)	−6	0.9	EEMP	10/27–6/3 (220)	858	KDE	14.76 (150)	−19	20.0	Nic	CMFC
12	8/2–9/7 (37)	218	KDE	41.8 (37)	23	0.0	BIRNM	9/22–8/18 (331)	953	KDE	24.67 (185)	−263	2.5	Gua	ASPA
13	8/1–9/2 (33)	196	KDE	12.5 (33)	−3	0.6	BIRNM	10/22–4/3 (164)	370	KDE	15.11 (82)	−47	15.8	S	No
13	9/12–10/10 (29)	104	KDE	22.7 (27)	−3	0.7	BIRNM	.	.	.	.	.	.	.	.
14	8/3–9/13 (42)	177	KDE	9.6 (39)	−3	0.1	BIRNM	10/2–7/3 (275)	620	KDE	13.91 (137)	−30	3.3	PR	ACNR
15	8/3–10/2 (61)	310	KDE	18.6 (60)	−62	0.8	No	10/9–10/19 (19)	1248	KDE	9.19 (236)	−29	18.1	BVI	No
16	8/4–9/22 (50)	303	KDE	10.8 (50)	−3	0.7	BIRNM	9/25–11/6 (43)	183	KDE	14.38 (43)	−38	8.8	USVI	No
17	No IN period	.	.	.	.	.	NA	8/9–12/10 (489)	2681	KDE	10.11 (365)	−26	2.3	Ang	No

Table 2 (*continued*)

| Turtle | Inter-nesting | | | | | | | Foraging | | | | | | | |
	Inter-nesting period (days)	Filt locs	50% KDE or 95% MCP	Area, km² (MDLs)	C. depth, (m)	C. to shore, (km)	Prot. Area	Forging period (days)	Filt locs	50% KDE or 95% MCP	Area, km² (MDLs)	C. depth, (m)	C. to shore, (km)	Country (EEZ)	Prot. Area
18	8/5–9/8 (35)	179	KDE	62.7 (35)	−6	1.8	BIRNM	11/27–11/30 (4)	30	MCP	106.17	−11	6.1	Nic	CMFC
19	8/8–10/14 (68)	405	KDE	19.3 (64)	−2	0.6	BIRNM	11/14–12/1 (18)	100	MCP	248.13	−1	84.3	Bah	No
19	.	.	.	.	.	.	.	12/5–11/28 (359)	339	KDE	25.17 (65)	−1	86.6	Bah	No
20	8/9–9/24 (47)	185	KDE	31.6 (44)	−6	1.5	EEMP	9/30–11/5 (37)	83	KDE	44.24 (23)	−38	2.5	KN	No
21	8/9–10/4 (57)	377	KDE	14.1 (57)	−3	1.0	BIRNM	11/25–5/4 (161)	316	KDE	23.4 (61)	−71	9.2	DR	No
22	7/30–9/15 (48)	251	KDE	13.7 (48)	6	0.3	BIRNM	9/19–9/10 (22)	93	KDE	24.42 (22)	−25	1.7	PR	ACNR
22	.	.	.	.	.	.	.	10/14–12/10 (58)	268	KDE	22.33 (52)	−29	1.8	PR	ACNR
23	7/30–8/28 (30)	208	KDE	16.8 (30)	−8	2.5	BIRNM	9/12–12/10 (90)	399	KDE	18.1 (84)	−355	23.6	Ven	No
24	7/30–10/1 (64)	377	KDE	17.4 (51)	−3	0.5	BIRNM	10/6–11/13 (39)	198	KDE	29.59 (37)	−181	2.6	KN	No
25	7/31–10/13 (75)	399	KDE	20.5 (75)	−2	0.9	BIRNM	11/19–12/10 (22)	92	MCP	364.31	−1	39.5	Bah	No
26	No IN period	.	.	.	.	.	.	8/5–12/10 (128)	759	KDE	41.77 (122)	−39	2.5	PR	CSJNR
27	8/1–9/11 (42)	187	KDE	44.3 (42)	−3	1.4	BIRNM	9/16–12/10 (86)	340	KDE	23.32 (78)	−210	2.8	BVI	No
28	8/2–9/6 (36)	58	MCP	905.3	−9	0.9	BIRNM	2/22–9/7 (198)	175	KDE	45.69 (54)	−5	1.6	USVI	No
29	8/3–8/21 (19)	115	MCP	92.4	−3	1.6	BIRNM	9/23–12/9 (78)	205	KDE	19.2 (68)	−266	1.2	AB	NDNP
29	8/24–9/13 (21)	101	KDE	12 (20)	−41	1.4	BIRNM	.	.	.	.	.	.	.	.
30	8/6–9/29 (55)	340	KDE	19.2 (55)	−3	1.7	BIRNM	10/5–11/18 (45)	216	KDE	20.42 (44)	−25	3.0	PR	No
31	8/5–10/28 (85)	364	KDE	19 (82)	−2	0.4	BIRNM	11/29–1/13 (46)	191	KDE	21.82 (38)	−132	118.3	Nic	No
32	No IN period	.	.	.	.	.	.	8/10–11/18 (101)	495	KDE	36.27 (99)	−28	2.0	PR	No

or foraging periods were not included). From the raw satellite data, we filtered out locations that were on land, very distant (> 120 km from nearest valid point), or that represented straight-line movement speeds > 5 km h^{-1}. We selected the conservative 5 km h^{-1} speed filter based on Parker et al. (2009) who reported hawksbill travel speeds between 0.7 and 1.2 km h^{-1} during transit in a Hawaiian study site, and on previous application of this speed filter in other hawksbill tracking studies (Gaos et al., 2012; Luschi et al., 1998; Troëng et al., 2005; Van Dam et al., 2008).

We quantified the mean bathymetry (m) across all filtered points in the migration track, the straight-line distance between IN and foraging centroids (km; see Migration to foraging areas), and actual distance along the migration path (km). For bathymetry, we used the ETOPO1 global relief model (bedrock, cell-registered, 1 arc-minute; Amante and Eakins, 2009). We also determined the number of exclusive economic zones (EEZ) crossed by each turtle during the entire tracking period using an EEZ map (Flanders Marine Institute, 2014).

2.5. High-use areas (IN and foraging)

We filtered home range analysis locations as above for migration, then quantified core-use areas for IN and foraging using 50% kernel density estimation (KDE); in the absence of 50% KDE, we calculated 95% minimum convex polygon analysis (MCP) to represent the habitat area used. To minimize autocorrelation of points, mean daily locations within each IN and foraging period were generated in the software program R (R Development Core Team, 2014) using filtered satellite locations, and the resulting coordinates (mean daily) provided raw data for 50% KDE analyses (applied to periods with > 20 mean daily locations); the filtered points were used to calculate 95% MCP analyses (applied to periods with < 20 mean daily locations).

Kernel density is a non-parametric method that uses appropriate weighting of outlying observations to identify areas of disproportionately heavy use within a home range (White and Garrott, 1990; Worton, 1987, 1989). To create KDEs, we used the Home Range Tools for ArcGIS extension (Rodgers and Kie, 2011) and fixed-kernel least-squares cross-validation smoothing factor (h$_{cv}$) (n = 23 turtles; Seaman and Powell, 1996; Worton, 1995) as well as a custom script in R using the package 'adehabitatHR' (Calenge, 2006; n = 2 turtles, see Appendix A). When x and y coordinates had unequal variances, data were rescaled to select the best bandwidth (Laver and Kelly, 2008; Seaman and Powell, 1996). We used ArcGIS 9.3 (ESRI, 2007) to calculate the in-water area (km^2) within each kernel density contour; the 50% KDEs represent core-use area of activity (Hooge et al., 2001).

Minimum convex polygons (MCPs) were created using ArcMap 9.3 (ESRI, 2007; n = 3 turtles) and a custom script in R using the package 'adehabitatHR' (Calenge, 2006; n = 1 turtle). Following Walcott et al. (2012), we created MCP polygons using 95% of filtered points, as it is possible for a proportion of distant filtered locations to represent only occasional movements outside the home range area (Burt, 1943; Rodgers and Kie, 2011).

We quantified site-fidelity to IN and foraging areas using the Animal Movement Analysis Extension for ArcView 3.2. Using Monte Carlo Random Walk simulations (100 and 200 replicates for IN and foraging, respectively), we tested for spatial randomness of tracks against randomly generated walks (Hooge et al., 2001). Random walks were bound from −4500 m to 0 m bathymetry to encompass all filtered locations during IN, and −5200 to 0 m to encompass all filtered locations during foraging. Tracks exhibiting site-fidelity signify movements that are spatially constrained and not randomly dispersed (Hooge et al., 2001). We did not use tracks failing site fidelity in home range analyses.

2.6. Characteristics of high-use areas

We calculated centroids for 50% KDEs and 95% MCPs (both IN and foraging) following Hart et al. (2017). For each centroid we determined

bathymetry, distance to nearest land, and the MPA status. For bathymetry in Caribbean waters, we used the GEBCO_2014 Grid (General Bathymetric Chart of the Oceans) a 30 arc-second continuous terrain model of both ocean and land (www.gebco.net; accessed 30 June 2016).

To depict IN locations for all turtles, we calculated the number of turtle-tracking days in grid cells (2 × 2 km) around BIRNM, using both "old" and "new" BIRNM boundaries. Specifically, we counted the number of days each turtle was observed in each grid cell using filtered IN points. With this grid, we determined the number of IN days inside and out of the BIRNM boundary. We also extracted bathymetry values for high-use cells using the GEBCO_2014 Grid. To ensure independence of the core-area size and tracking duration, we examined the association between the two variables for IN using Spearman's ρ. We also calculated Spearman's ρ between IN core-area size and turtle size (CCL).

2.7. Core area space-use sharing

We conducted a Kruskal-Wallis non-parametric one-way ANOVA to determine whether there was a difference in space-use sharing among turtles with different levels of nesting experience: neophyte-neophyte (NN), neophyte-remigrant (NR), and remigrant-remigrant (RR) turtle pairs; where neophytes are first-time nesters and remigrants are repeat nesters at BIRNM. We calculated the core-use area (50% KDEs) space-use sharing during IN and at common foraging grounds using the 'adehabitat' package in R (Calenge, 2006; R Development Core Team, 2014). We used the utilization distribution overlap index (UDOI) following our previous work (Hart et al., 2017), which is considered the most appropriate measure of animal space-use sharing (Fieberg and Kochanny, 2005). Two UDs with no overlap produce a UDOI value of zero, whereas uniformly distributed UDs have a UDOI value of 1. The UDOI value can also be > 1 for non-uniformly distributed UDs with a high degree of overlap, which indicates a higher than normal overlap relative to uniform space-use (Fieberg and Kochanny, 2005). The UDOI space-use sharing was calculated for the 25 turtles that had 50% KDEs during IN (n = 300 pairs), as well as the amount of temporal overlap (days) that turtle pairs were foraging in the same area.

2.8. Regional hawksbill foraging ranges

We mapped foraging locations of female hawksbills satellite-tagged on Buck Island, US Virgin Islands (n = 31 turtles) along with female hawksbills from other studies that were tagged in the Caribbean and satellite-tracked to foraging grounds (n = 33 turtles from other studies; Esteban et al., 2015 [n = 2 turtles], Horrocks et al., 2001 [n = 4 turtles], Moncada et al., 2012 [n = 9 turtles], Revuelta et al., 2015 [n = 9 turtles], Troëng et al., 2005 [n = 2 turtles], Van Dam et al., 2008 [n = 7 turtles]). Some studies provided foraging location XY coordinates (Horrocks et al., 2001; Van Dam et al., 2008); for the other studies, figure images were georeferenced in ArcGIS v10.2.2 (ESRI, 2014), and foraging locations were calculated using the center of post-nesting movement points (Troëng et al., 2005), the last migration or tracking point (Moncada et al., 2012; Esteban et al., 2015), or by determining the centroid of a 95% MCP or 50% KDE (Revuelta et al., 2015). In total we mapped 66 foraging locations (e.g., centroids) across seven studies (including this one). For each centroid, we calculated the number of centroids within 30.6 km, the average size of the core-use area (50% KDE) reported in this study.

3. Results

3.1. Turtles

Turtles (n = 31 individuals, one tracked in two different years for 32 total tracks) ranged in size from 82.4–96.5 cm curved carapace length (CCL; mean ± SD = 88.1 ± 4.1 cm, Table 1). We tracked
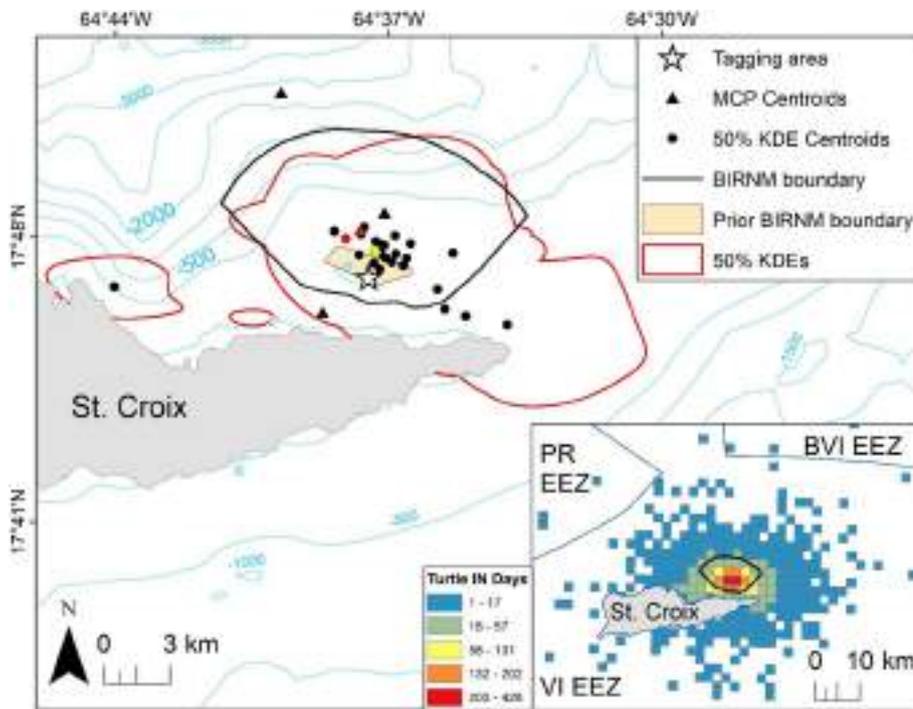
Fig. 2. Inter-nesting (IN) areas. Core-use IN areas (50% kernel density estimation [KDE] and 95% minimum convex polygon [MCP]) for 25 nesting female hawksbills (*Eretmochelys imbricata*) satellite-tagged on Buck Island (26 KDEs; red line). The red KDE line represents the outer boundary of all KDEs. The black line is the Buck Island Reef National Monument (BIRNM); the tan area shows the prior BIRNM boundary, before expansion. The KDE (circles) and minimum convex polygon (MCP; triangles) centroids are shown for 28 nesting female hawksbills (26 KDEs for 25 turtles and 4 MCPs for 4 turtles; one turtle had both KDE and MCP for 28 total turtles). The star indicates approximate tagging areas (beaches on south and west shores of Buck Island). Red and yellow centroids in main panel show centroids for turtles with more than one IN area (KDE and/or MCP). Inset: The IN days per 2 km grid cell for 28 nesting female hawksbills satellite-tagged post-nesting on Buck Island. World Exclusive Economic Zones (EEZs) are shown by the dark blue lines. Abbreviations for inset: VI = U.S Virgin Islands; BVI = British Virgin Islands; PR = Puerto Rico. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

turtles for a total of 8810 days, ranging from 61 to 600 days (mean ± SD = 275.3 ± 173.3 d).

Turtles were remigrants (n = 22) and neophytes (n = 9; see Table 1). Remigrant histories for two individuals date back to the beginning of the saturation-tagging program at Buck Island in 1989 (25 years, n = 1 turtle) and 1993 (21 years, n = 1 turtle). Most remigrants were first encountered at BIRNM between 2001 and 2005 (9–13 years, n = 12 turtles) and the remainder from 2007 to 2009 (5–7 years, n = 8 turtles; see Table A1). Remigration intervals varied between turtles with 15 (68%) having 2 yr, 3 yr, or 2–3 yr remigration intervals (see Table A1).

3.2. Inter-nesting

We obtained SSM results for all 31 turtles/32 tracks (Fig. A1 and Table A2 provide example SSM prediction paths and model parameters). Twenty-eight turtles had locations available during IN; several turtles departed the study area immediately after nesting so thus did not have IN data. Twenty-five of the 28 turtles had enough mean daily locations for KDE analysis, and all of these displayed site fidelity (p > 99.0099 for all turtles) for a total of 26 KDEs (Turtle 13 had two IN KDEs; Table 2). We obtained 1196 mean daily locations for KDE periods totaling 1218 days (Table 2). The overall size of core-use areas (50% KDEs) ranged from 9.6–77.7 km² (Table 2). Core-use area size (ρ = 0.29, p = 0.16) was not strongly associated with number of tracking days. Also, turtle size (CCL) was not associated with core-use area size (ρ = −0.02, p = 0.94).

When KDE analyses were not possible, we calculated 95% MCPs (Fig. A2); the four turtles showed site fidelity (p > 99.0099) and had a total of 300 filtered locations over 92 days for analysis. MCP areas ranged from 92.4–905.3 km² (Table 2). We calculated centroids for 50% KDEs and 95% MCPs (Fig. 2). The mean distances to the nearest land from core-use area centroids was 1.0 km (3.4 km for MCPs; Table 2). Mean bathymetry at these centroid locations was −16.2 m (−662.0 m for MCPs; Table 2). Two centroids had erroneous positive values and most of the remaining centroids were in shallow water (21 of 24 centroids > −10 m; Table 2).

For all turtles, the number of IN days in the current BIRNM boundary grid (including intersecting cells) was 3212 (68%; total of

4751 turtle days across all cells), with 1539 (32%) days outside the boundary (Fig. 2). For comparison, the number of IN days in the "old" BIRNM boundary (see Proclamation 7392, 2001) in place prior to 2001 was 1409 (30%). The mean bathymetry of grid cells with the highest number of IN turtle-days (203–428 days, red cells in Fig. 2 inset) was −4.9 m. The median bathymetry values for turtle-day grid cells (58–428 days) were between −3 and −37 m.

3.3. Core area space-use sharing during inter-nesting

We calculated UDOI space-use sharing for 300 turtle pairs during IN (n = 25 turtles). Across all pairs, UDOI ranged from 0 to 0.23 (mean ± SD = 0.08 ± 0.06; Table A3, Fig. A3), where greater UDOI indicates greater space-using sharing between turtle pairs. The mean (± SD) UDOI was 0.09 ± 0.05 for NN pairs (n = 28), 0.08 ± 0.06 for NR pairs (n = 136), and 0.07 ± 0.06 for RR pairs (n = 136). Temporal overlap across all pairs ranged from 0 to 62 days (mean ± SD = 10.5 ± 17.3). The non-parametric ANOVA (Kruskal-Wallis) comparing UDOI habitat overlap among NN, NR, and RR pairs was significant (H = 6.91, df = 2, p = 0.03). Although there was evidence for greater space-use sharing for NN turtle pairs compared to RR pairs, pairwise comparisons were not significant when the alpha value was corrected for the false discovery rate in conducting multiple comparisons (Benjamini and Hochberg, 1995; Garcia, 2004).

3.4. Migration to foraging areas

Of the 31 satellite-tagged turtles, 30 turtles showed migration paths away from Buck Island to their foraging grounds between July and October. Some migrations to foraging grounds were split by brief foraging "stopover" periods along the route, which resulted in 37 migration paths across the 31 turtles (Fig. 3). The "final" hawksbill foraging grounds were in many geographic areas (Fig. 4, Table A4) including the Bahaman (Lucayan) Archipelago, east of Nicaragua, the Greater Antilles including the waters surrounding Puerto Rico and the Dominican Republic, the Leeward Islands of the Lesser Antilles (e.g., British Virgin Islands, US Virgin Islands, St. Kitts and Nevis, Anguilla), and one turtle that foraged in Venezuelan waters (see Table A4). Migration periods lasted 1–69 days (Table 1, Fig. 3). Average mean
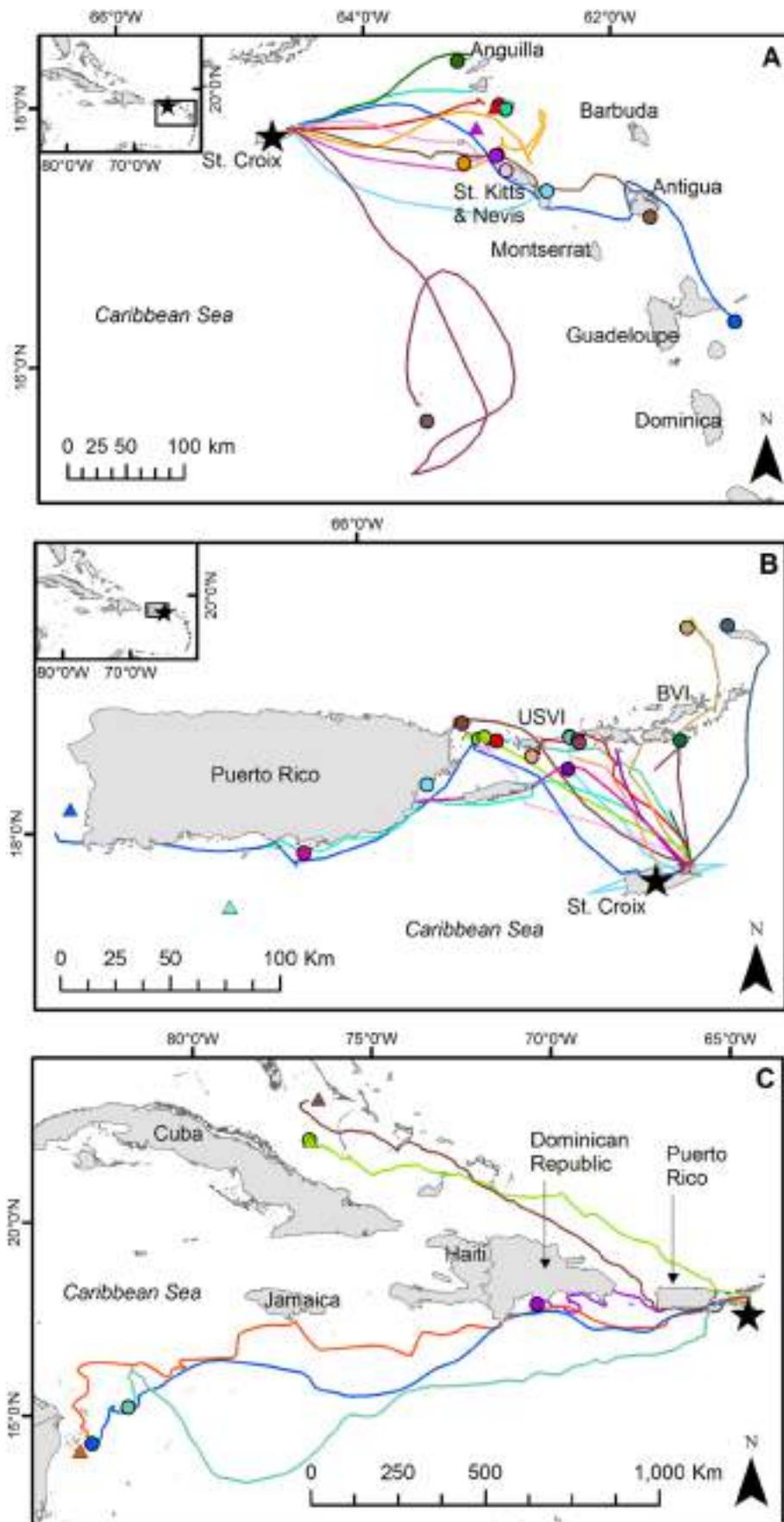
(caption on next page)

Fig. 3. Migration paths. Migration paths from IN grounds to foraging grounds of 31 adult female hawksbills (*Eretmochelys imbricata*) satellite-tagged on Buck Island, US Virgin Islands (USVI), and migrating to A. the Leeward Islands (n = 9 turtles) and Venezuela (n = 1 turtle), B. the Greater Antilles (n = 15 turtles; BVI = British Virgin Islands), and C. the Dominican Republic, the Bahamas, and Nicaragua. Circles represent centroids of 50% foraging kernel density estimation core-use areas (50% KDEs) and triangles represent centroids of 95% foraging minimum convex polygons (MCPs). Stars represent tagging location and the origin of migration.
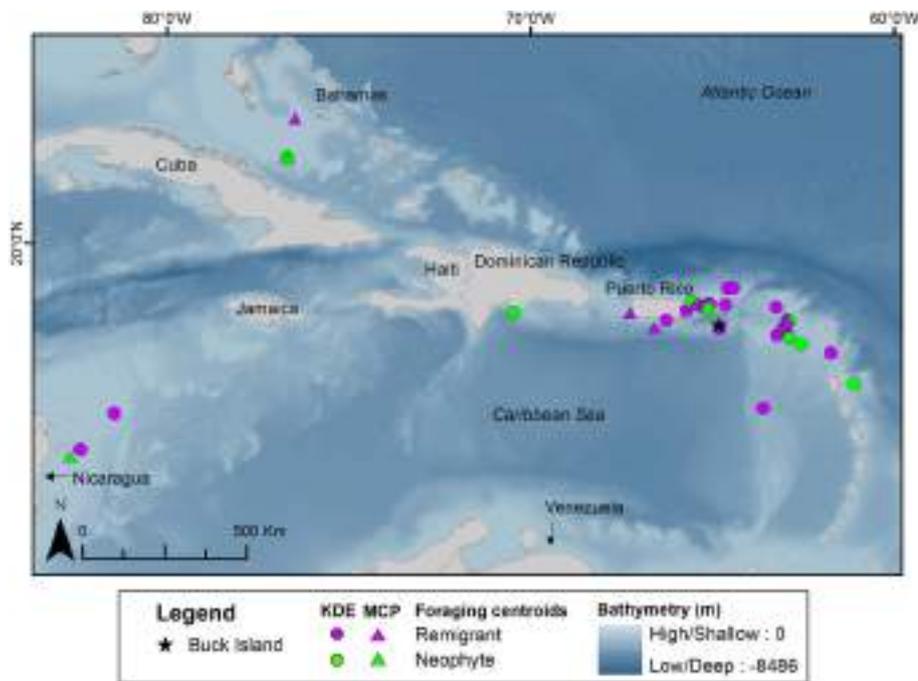
Fig. 4. Foraging Centroids. Foraging locations for female hawksbills (*Eretmochelys imbricata*) that were satellite-tagged in this study (nested on Buck Island [star], n = 31). Remigrant and neophyte foraging areas often occurred in similar areas/regions and foraging occurred in shallow waters (light blue). (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

bathymetry across all migration periods was −1045.7 m; Table 1). Straight-line migration distance ranged from 20.2–2370.0 km and the distance along the migration path ranged from 51.9–3523.8 km (Table 1, Fig. 3). During the entire tracking period, turtles crossed between two and eight different EEZ zones (Table 1).

3.5. Foraging areas

All 32 tracks had SSM results with time periods predicted as foraging. Across the 32 tracks, there were 41 distinct foraging periods (some turtles had multiple foraging periods that were interrupted by brief movements, as determined by SSM) that exhibited site fidelity. Of these 41 foraging periods, 33 had adequate sample size to conduct 50% KDE analyses (Table 2), and 95% MCPs were determined for the other 8 (Table 2). The 33 KDE foraging periods totaled 6626 days across all turtles, and ranged from 22 to 490 d. We obtained 4345 mean daily locations for KDE analyses and the range of core-use areas (50% KDEs) was 6.3–95.4 km^2 (Table 2). The eight 95% MCPs totaled 111 days across all eight turtles and 310 filtered locations. MCP area ranged from 0.9–1082.4 km^2 (Table 2, Fig. A2). Mean distance to the nearest land from centroids of 50% KDEs was 10.8 km (MCP mean = 23.3 m; Table 2) and mean bathymetry at the 50% KDE centroid locations was −65.8 m (MCP mean = −422.6 m; Table 2, Fig. 4).

3.6. Core area space-use sharing during foraging

We calculated the amount of UDOI space-use sharing for 66 turtle pairs foraging near two common foraging areas in Puerto Rico and the British Virgin Islands (n = 12 turtles). Across all 66 pairs, UDOI ranged from 0 to 0.17 (mean ± SD = 0.003 ± 0.02; Table A5), where greater UDOI indicates greater space-using sharing between turtle pairs. Temporal overlap across all pairs ranged from 0 to 494 days (mean ± SD = 74.2 ± 119.8).

3.7. Regional foraging areas

Hawksbills forage in numerous areas across the Caribbean Sea (Figs. 4 and 5). Furthermore, multiple areas provide foraging sites for breeding turtles that nest in different locations (Fig. 6); foraging areas include the waters east of Nicaragua and Honduras, the waters east of Puerto Rico in the Greater Antilles, and the Leeward Islands of the Lesser Antilles. Of the 66 foraging locations across the seven studies (including this one), there were 32 turtles (i.e., centroids) that had at least one other centroid within 30.6 km, the average size of the core-use area (50% KDE) in this study. Of these 32 total tracks, 13 had one centroid within 30.6 km, and the other 19 had 2–12 centroids within 30.6 km.

4. Discussion

By using satellite tracking technologies alongside advanced spatial modeling approaches, we delineated important in-water habitats used by hawksbills during inter-nesting periods, through migration, and at foraging areas. All turtles were tagged after nesting at BIRNM, a Caribbean MPA that supports breeding hawksbills that migrate and forage through waters of multiple countries (Sartain-Iverson et al., 2016). Migration paths crossed through multiple EEZs as turtles traveled to foraging sites in 14 different countries; these results underscore the importance of international conservation initiatives for the recovery of depleted hawksbill populations in the Caribbean basin. Using the robust method of SSM, we determined not only the size and location of intensely used areas, but also the time periods when turtles moved through international waters and arrived at their respective foraging areas. We also further characterized 'overlap' of individual space-use at foraging sites, which underscores the importance of these supporting resources that are critical for turtle survival. This is the first study to delineate high-use habitats throughout IN, foraging, and migration, for multiple critically endangered hawksbills nesting at BIRNM.
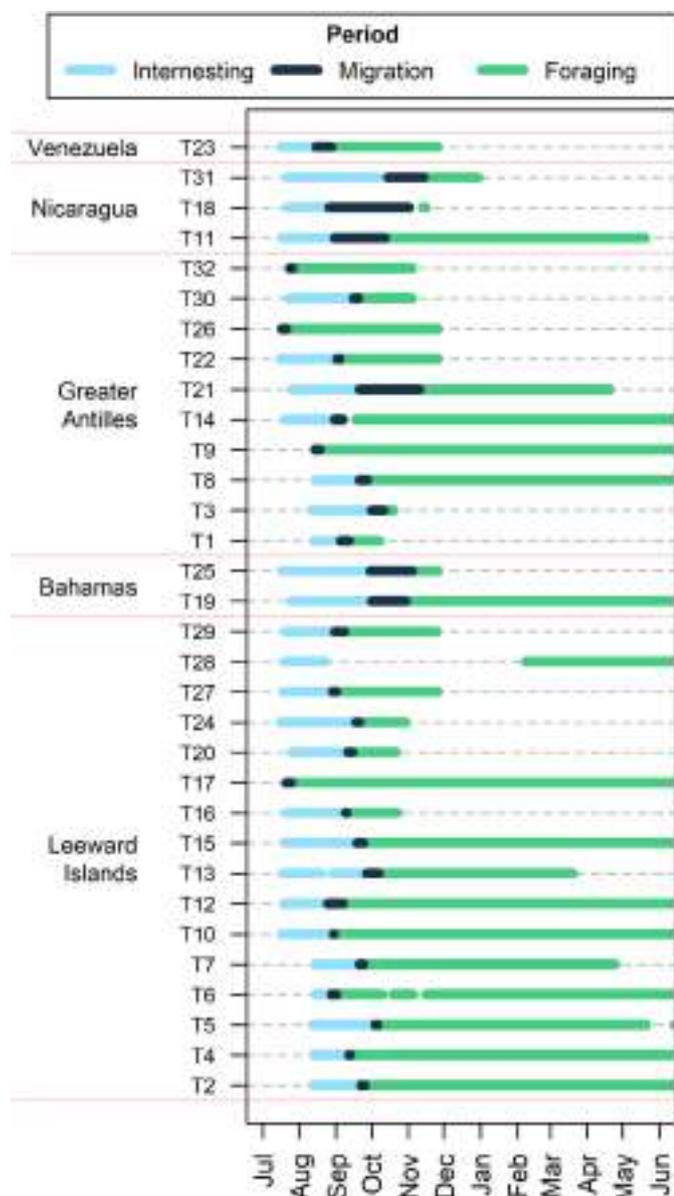
Fig. 5. Inter-nesting, foraging, and movement timeline for hawksbill turtles tagged after nesting at on Buck Island, US Virgin Islands. Turtles are organized by their foraging destinations. Breaks in the timeline indicate modes other than inter-nesting, migration or foraging, such as short movements between residency periods.

4.1. Inter-nesting (IN)

We found that IN core-use areas (mean 28.1 km^2) were larger than previously found in this area through radio telemetry (resident areas within 1.5 km^2; Starbird et al., 1999). Satellite telemetry may have a larger spatial error than radio-telemetry resulting in larger home range analysis estimates, but satellite tracking has advantages including a more robust representation of the IN duration. The previous study tracked 7 turtles for up to 45 days, whereas IN periods defined here for 28 turtles by SSM were up to 85 days; this longer tracking period may have resulted in more widespread locations. In the Dominican Republic, mean IN residence areas delineated by satellite tracking were 37.1 km^2 (90% KDEs) and 13.2 km^2 for core-use areas (50% KDEs; Revuelta et al., 2015). In Barbados, 23 hawksbill IN residence areas for 17 individual turtles generated using GPS satellite tags ranged from 0.01 to 0.40 km^2 (Walcott et al., 2012). Home range sizes are likely influenced by local resources as well as analytical methodology. For example, the location

accuracy as well as the number of locations used in analyses can greatly influence home range area estimates (Thomson et al., 2017). Combining locations received from an existing acoustic array (1st author, unpublished results) at BIRNM with satellite locations could help clarify finer-scale IN habitat use patterns for hawksbills in this area. Further, Fastloc-GPS technology provides locations with high accuracy and could be used to refine home range analysis estimates and uncover details on patch-use within core-use areas (Thomson et al., 2017).

We found that both neophytes and remigrants (with nesting records up to 24 years) used habitat close to the nesting beach in and around Buck Island during IN (up to 2.5 km [core-use areas] and 8.7 km [MCPs]). This finding is in line with Starbird et al. (1999) who showed seven adult females stayed within 3 km of the nesting beach during IN. These distances are similar to other sites in the Caribbean such as Barbados (mean 6.1 km; range: 0.7–21.2 km; Walcott et al., 2012), the Dominican Republic (mean maximum distance of 39 km, but usually from 1.4 to 4.3 km; Revuelta et al., 2015), and Costa Rica where one hawksbill stayed within 30 km of the nesting beach (Troëng et al., 2005). A recent study on the diving behavior of gravid hawksbills from a nearby site in USVI (on St. Croix) found that turtles rested on the seafloor and spent most of the IN time at a single depth range, which could indicate staying within a restricted area (Hill et al., 2017). Remaining near the nesting beach during IN may help females conserve energy as they transit to or from nesting sites.

In addition to being close to shore, IN habitat was also in shallow water (median bathymetry values in high-use grid were −3 to −37 m). This finding is similar to results from tracked hawksbills in the Dominican Republic (50% KDEs over water > −100 m; Revuelta et al., 2015) and Barbados (−18 to −41.5 m; Walcott et al., 2012) as well as for hawksbills tracked at nearby St. Croix (most of time spent at −20 to −30 m or less; Hill et al., 2017) and in BIRNM with radio-telemetry (−9 to −20 m; Starbird et al., 1999). The grid cells with the highest IN turtle-days, while in shallow water, were north of Buck Island which offers closer access to the deep-water shelf to the north. Hill et al. (2017) found that some St. Croix nesting hawksbills traveled to deeper depths (up to −95 m) during IN. Obtaining breeding season dive information for hawksbills nesting at BIRNM could help discern whether these turtles occasionally travel to nearby deep waters during their reproductive phase.

The IN core-use areas were all in the same general area NE of St. Croix and surrounding BIRNM, and we found spatial overlap for almost all of the 300 turtle pairs (n = 25 turtles) with temporal overlap from 0 to 62 days. Neophyte pairs had slightly higher mean space-use sharing than neophyte-remigrant pairs, with remigrant pairs having the lowest mean space-use sharing. It is possible that the small sample size of neophytes contributed to the non-significant statistical result (after the false discovery rate correction). Space-use sharing was also seen in the Dominican Republic, with hawksbills having large overlaps of IN and common-use areas (37.9 km^2 for 50% KDEs and 212.2 km^2 for 90% KDEs; Revuelta et al., 2015). While the much smaller IN areas of hawksbills tagged in Barbados with GPS tags did not show overlap within years (Walcott et al., 2012) these authors did find overlap in residence areas from females tracked in different years. That remigrant pairs at BIRNM had lower overlap indicates that they may use their experience to benefit from sites unoccupied by other nesters.

While in-water habitat-use was very similar across turtles, we did observe some plasticity in nesting behavior. Two turtles (one neophyte [turtle 26], one remigrant [turtle 32]) left the area immediately after tagging. Leaving the nesting beach early could represent either migration to foraging grounds or movement to a different nesting beach (e.g., Revuelta et al., 2015; Esteban et al., 2015). One of our tracked neophyte turtles (turtle 19) showed nesting variation when after her 2–year remigration, we received high-quality locations at a beach about 12 km distant on St. Croix (Sartain-Iverson et al., 2016). Turtles tagged in another study in the Lesser Antilles showed nesting site-selection plasticity as well: one hawksbill traveled in a circular pattern over
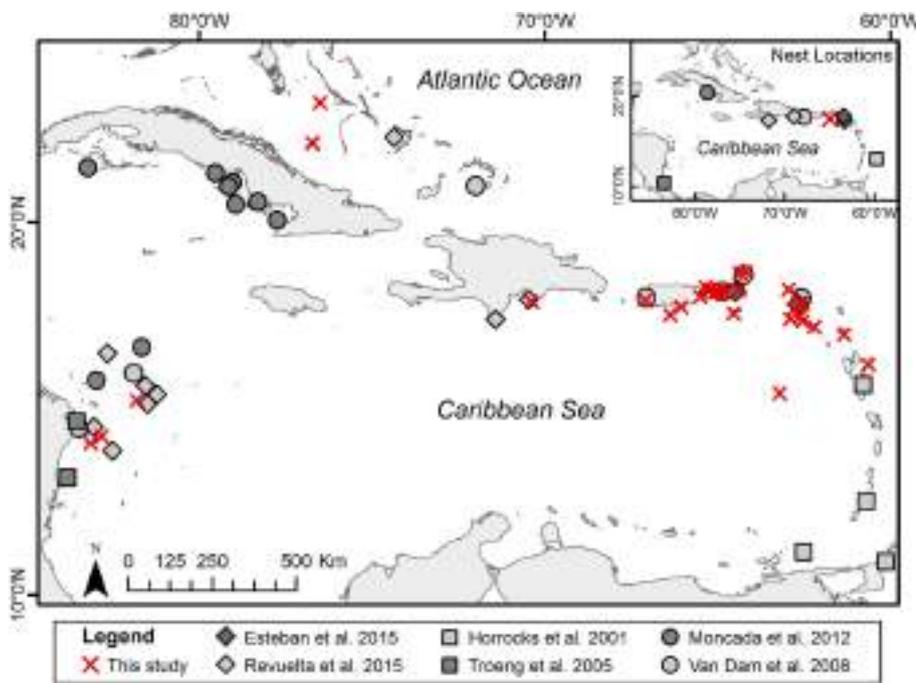
Fig. 6. Caribbean hawksbill foraging areas. Foraging locations of female hawksbills (*Eretmochelys imbricata*) that were satellite-tagged in this study (nested on Buck Island, n = 31), compared to other studies that tagged female hawksbills in the Caribbean and satellite-tracked them to foraging grounds (Esteban et al., 2015 [n = 2 turtles], Horrocks et al., 2001 [n = 4 turtles], Moncada et al., 2012 [n = 9 turtles], Revuelta et al., 2015 [n = 9 turtles], Troëng et al., 2005 [n = 2 turtles], Van Dam et al., 2008 [n = 7 turtles]). Inset shows the nest/tagging locations for each study.

200 km from the original nesting site, likely nesting in two other places (Anguilla and St Croix) before returning to forage within 50 km of the original site (Esteban et al., 2015). Similarly, hawksbills in the Dominican Republic nested at beaches up to 190 km apart (n = 2; Esteban et al., 2015). Characteristics of the nesting beach can influence the proportion of hatchlings to survive (Lee and Hays, 2004), so nesting at multiple beaches may provide an evolutionary advantage.

Most turtle-tracking-days during IN (68%) were inside the currently protected area of BIRNM which has reduced human impacts (fishing restrictions, no light and no point-source pollution from Buck Island, minimal boat traffic on north side due to shallow complex reef areas). This is an improvement in comparison to the 30% observed turtle-tracking days in the previous BIRNM boundary (Fig. 2); the current boundary of BIRNM was expanded in 2001 from the original 1961 designation, adding 73.4 km^2 of submerged lands (Proclamation 7392, 2001). In addition, most human recreation around Buck Island takes place to the south and is limited to daytime. Future habitat assessments of the reefs in this area along with fine-scale activity data could help point to important habitat features such as preferable reef structures for resting as well as help determine how females allocate their activity budgets during this energetically expensive time.

4.2. Migration periods

Timing of migration varied by individual and year, but most turtles traveled through multiple EEZs (range 2–8, mean = 4, mode = 2) between July and October. Turtles began migration periods in July (n = 1), August (n = 4), September (n = 14) and October (n = 12), and individual migration periods ranged from 2 to 69 days, with longer migrations for those that traveled across the Caribbean or to the Bahamas (Fig. 4). These results highlight the late summer and early fall as a critical time period to protect migrating females. However, few of these paths passed through other protected areas, indicating vulnerability to anthropogenic threats such as major shipping lanes during the migration periods. Depths on migration routes varied and reached up to approximately −3000 m.

4.3. Foraging areas

Turtles arrived at foraging areas in August (n = 3), September

(n = 12), October (n = 11), and November (n = 5); one turtle (turtle 28) had unclear arrival time owing to a time lapse in transmissions (Fig. 5). Locations and sizes of foraging areas in our study were similar to those in previous tracking studies (Fig. 6) but we did not track any turtles to Cuba (see Moncada et al., 2012) or as far south as Trinidad and Tobago (see Horrocks et al., 2001). However, additional tracking efforts may reveal use of those foraging areas and others by BIRNM nesting hawksbills. The common foraging areas used in Puerto Rico and off the coast of Nicaragua represent hotspots where multiple turtles took up residence; such information can be used to prioritize these areas for conservation. As several of the foraging areas delineated here are within or adjacent to current MPA boundaries, a fine-scale examination of habitat-use and movement patterns at those sites is warranted to assess how well current boundaries encompass required core-use areas.

5. Conclusions

Our results show previously unknown habitat-use patterns and highlight concentrated areas of use by hawksbills both within and adjacent to a US protected area during the inter-nesting season. Individuals used areas within the recently expanded boundary, highlighting that this additional protected area is beneficial for this imperiled species. However, our results also clearly demonstrate the need for international conservation to protect hawksbills, as migrating turtles crossed between two and eight different national jurisdictions. These results provide critical spatial and temporal information for managers charged with designing strategies to minimize human impact to this globally imperiled species. Although protecting migratory corridors would be challenging due to the international jurisdictions and remote nature of open ocean locations used during migration between breeding and foraging areas, protection of distinct foraging areas designated here may be possible. As adult female survival rates have an especially strong effect on population recovery (NMFS and USFWS, 1993), management strategies could beneficially focus on protecting adult females.

Acknowledgements

Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.biocon.2018.11.011.

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