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Satellite Telemetry Elucidates Migratory Pathways and Foraging Areas for Hawksbill Sea Turtles, *Eretmochelys imbricata*, in the Caribbean

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ABSTRACT—Adult female sea turtles are highly migratory, moving between foraging and nesting areas that can be thousands of kilometers apart. Conserving sea turtles and their habitats therefore depends on knowledge of space use across these migration-linked environments. Here, we describe migratory behavior of hawksbill sea turtles (*Eretmochelys imbricata*), a globally imperiled species. We used satellite telemetry to characterize the movements of females from nesting areas in Jamaica (n = 4) and Antigua (n = 4), West Indies, over 1998–2001. We mapped migrations and summarized space use during inter-nesting and foraging periods with kernel utilization distributions (UDs) and minimum convex polygons. Seven of eight turtles made post-nesting migrations, with paths ranging 56–1324 km in length, representing straight-line displacements of 68–1206 km. Two turtles sampled in southern Jamaica made short-range migrations within southern Jamaican waters, whereas two from northern Jamaica migrated further to foraging areas in the waters of Belize and Honduras. Three migrants sampled at Long Island, Antigua migrated to St. Eustatius, St. Kitts, and Redonda, respectively, with a fourth individual remaining resident in northeastern Antigua. Inter-nesting movements observed for three turtles produced 50% UD's ranging 12–44 km², with centroid depths between 4–13 m. Foraging UD's for seven turtles spanned 8–111 km² and 2–161 m in depth. Our results reveal variable migratory strategies, demonstrate international connectivity between hawksbill foraging and nesting habitats, and provide important information for Caribbean conservation efforts such as the design of protected areas or fisheries policies.

Adult sea turtles (Cheloniidae) spend the majority of their lives at sea in foraging habitats where they are often difficult to locate and observe. After accumulating sufficient energy reserves, females periodically migrate to their nesting beaches where observation is much easier. Studies based at nesting beaches form the foundation for most population monitoring programs, but these habitats are visited only briefly by adult females during the nesting season every ~2–4+ years (Lutz and Musick 1997). A better understanding of marine habitat use is essential for conservation strategies

such as protected area design and threat management (e.g., fisheries bycatch reduction), as well as research efforts, e.g., evaluating the relationship between foraging habitat quality and population dynamics (Ceriani et al. 2017; Hays and Hawkes 2018; Hart et al. 2019).

The advent and growth of satellite telemetry technology over the past several decades have helped to address knowledge gaps surrounding the movement ecology of sea turtles (Hays and Hawkes 2018). Adult females can be outfitted with satellite transmitters on nesting beaches and then tracked to foraging areas.

However, to date, satellite-tracking research has been disproportionately concentrated on certain populations, regional management units (RMUs; Wallace et al. 2010), and species. For example, Hays and Hawkes (2018) synthesized sea turtle satellite tracking research to find that almost half of all transmitters deployed have been placed on loggerhead sea turtles (*Caretta caretta* (Linnaeus, 1758)), with the other six species lagging well behind.

Hawksbill sea turtles (*Eretmochelys imbricata* (Linnaeus, 1766)) in the Caribbean present a clear situation in which more satellite tracking research would be beneficial. Hawksbills nest on nearly all land masses in the Caribbean Sea, often in low densities on relatively small beaches (Eckert and Eckert 2019). Yet, satellite-tracking records documenting post-nesting migrations from regional rookeries have been published for only 85 individual females from 12 nations or insular territories (Horrocks et al. 2001; Troëng et al. 2005; van Dam et al. 2008; Moncada et al. 2012; Esteban et al. 2015; Revuelta et al. 2015; Nivière et al. 2018; Hart et al. 2019; Uribe-Martínez et al. 2021; Soanes et al. 2022). As individuals are tracked from additional nesting locations, connectivity with new foraging areas is often revealed, underscoring the need for wider geographic representation in tracking research. Nonetheless, previous work has revealed a preliminary pattern in the distribution of regional foraging areas, and it is apparent that hawksbills can migrate thousands of kilometers and cross through multiple exclusive economic zones (EEZs). This combination of highly migratory behavior and a relatively large number of management authorities makes the management of sea turtles in the Caribbean particularly complex.

In the present article, we describe the movements of post-nesting hawksbills tracked from Antigua and Jamaica over 1998–2001. This work was coordinated by the United States National Oceanic and Atmospheric Administration (NOAA) and hinged on collaboration with several sea turtle monitoring programs in the Caribbean region. We revisit this project, part of the Caribbean Hawksbill Tracking Consortium, to disseminate key data and extract as much information as possible for the benefit of hawksbill conservation. The eight satellite tracks represent an important contribution to the regional knowledge base regarding hawksbill habitat use, providing a ~9% increase in the number of post-nesting females tracked from Caribbean nesting

beaches. Our goals were to model and map post-nesting movements, characterize habitat use during foraging periods and inter-nesting intervals (i.e., during a nesting season, before migrating), and put results in the context of related work in the region.

MATERIALS AND METHODS

Study areas and transmitter deployment

We deployed eight satellite transmitters (hereafter platform terminal transmitters; PTTs) during this study—four in Antigua and four in Jamaica. Antiguan hawksbills were outfitted with PTTs (Telonics ST-14 1.0 watt) at Pasture Bay on Long Island (17° 09' 31" N; 61° 45' 19" W), a barrier island to the northeast of mainland Antigua where the Jumby Bay Hawksbill Project (JBHP) has conducted yearly monitoring since 1987 (e.g., Richardson et al. 1999; Kendall et al. 2019). Transmission records for these four turtles began when PTTs were deployed in 1998, on 12 September (PTT 8455), 16 October (PTT 8456), 25 October (PTT 8552), and 12 November (PTT 8553). Two individuals had nested at Long Island several years previously and were therefore remigrants (Table 1). The other two turtles were observed for the first time in the year of PTT deployment.

Two of the Jamaican turtles were outfitted with PTTs in 1998 in the vicinity of Portland Bight (17° 43' 31" N; 77° 07' 42" W) in southern Jamaica. Both turtles were intercepted after nesting on the night of 19 September, one at Little Portland Cay (PTT 8442) and the other at Big Half Moon Cay (PTT 8443). Available transmission records for both began later, on 6 October (preceding data may have been lost during long-term storage, however, we still observed inter-nesting behavior for both turtles). The other two individuals were outfitted with PTTs in 2000 in St. Mary Parish on the northern coast of Jamaica, in the vicinity of Oracabessa and Port Maria. PTT 7677 was deployed on 19 July and PTT 7665 was deployed on 13 September.

Information on turtle Inconel flipper tag numbers and nesting histories, where available, is provided in Table 1, along with the number of raw and model-fit locations used in subsequent analyses. Methods for PTT attachment followed those outlined by Balazs and Parker (1998). Researchers waited for a turtle to finish laying eggs and covering its nest, then safely detained it in a wooden box or frame in order to affix the PTTs with polyester resin and fiberglass cloth.

TABLE 1. Summary of satellite transmitter deployments. A “•” denotes information was not available. Days tracked indicates the span of satellite transmissions rounded to the nearest whole day. Raw fixes refer to the number of ARGOS locations (post filtering) that were used to model movements. IN (inter-nesting), migration, and foraging points display the number of switching SSM model-estimated locations assigned to each period (three points estimated per day).

PTT ID	Days tracked	Raw fixes	IN points	Migration points	Foraging points	Flipper tag no.	Annual nesting history
7665 ^a	133	179	46	73	282	•	•
7677	288	300	0	106	759	•	•
8442	423	1211	131	7	1131	•	•
8443	404	930	176	13	1025	•	•
8455	438	1353	145	10	1160	PPN-011	1987, 1989, 1991, 1993, 1995, 1998, 2001, 2004, 2007
8456	413	843	0	10	1230	PPC-946	1998, 2000, 2002, 2004, 2006
8552	404	1140	0	19	1194	PPN-058	1988, 1990, 1992, 1994, 1996, 1998, 2003, 2005, 2007, 2010, 2012, 2015
8553 ^b	318	139	0	0	653	PPC-943	1998, 2002

^aThis turtle made an initial migration to forage for ~71 days before making a second migration to its final foraging destination; we summed migration and foraging points for the two migratory and two foraging periods.

^bBecause of two large gaps in usable transmissions, this individual's track was split into three for modeling (and then combined); this resulted in < 3 model locations estimated per day of deployment.

State-space modeling

We performed all data analyses in program R version 3.5.2 (R Core Team 2018) using RStudio version 1.1.463 (R Team 2015). State-space movement models additionally used JAGS version 4.2.0 (Plummer 2003). Location data from satellite transmitters were provided by the ARGOS satellite system. ARGOS fixes result when turtles surface and expose a PTT's sensors and antenna to air, with longer periods at the surface generally corresponding to more signals sent to satellites and thus better location accuracy. Location fixes additionally depend upon satellites being in position overhead. As a result, transmitted locations are temporally irregular and are each assigned a class representing estimated spatial accuracy (from highest accuracy to lowest: class 3, 2, 1, 0, A, B, and Z; numbered classes range < 250 m to >1500 m in estimated accuracy and lettered classes have no associated estimate for spatial accuracy).

We used a Bayesian, hierarchical state-space model (SSM) to accommodate inaccuracy and irregularity in observations and estimate true locations at regular timesteps. Specifically, we fit a switching, first differ-

ence correlated random walk (DCRWS) model that uses Markov Chain Monte Carlo (MCMC) sampling to estimate locations and assign each location one of two behavioral states. This type of model focuses on the differences between consecutive locations (i.e., distance and turning angle) as described by Jonsen et al. (2005). The model assumes two distinct behavioral states, each with different movement parameters, and discriminates (i.e., switches) between the two states based largely on patterns in swimming speed and direction. This SSM approach is useful for quantitatively differentiating between migratory and non-migratory states—migrations are associated with straighter paths and higher swim speeds (state 1), whereas non-migratory behavior entails high turning angles and slower speeds (state 2). The switching SSM has been used extensively to model movement data for sea turtle migrations (e.g., Jonsen et al. 2007; Hart et al. 2019, 2020).

We first used the R package ‘argosfilter’ to filter raw location data by removing erroneous satellite fixes that would produce swimming speeds above a conservatively high velocity of 2.5 m s⁻¹ (Freitas 2012). We

then used the remaining data to implement the SSM with the R package 'bsam' (Jonsen et al. 2005; Jonsen 2016). The eight tracks were modeled in a single, hierarchical run. This joint approach entails the estimation of identical movement parameters for all individuals and can significantly improve state estimation by pooling statistical power (Jonsen 2016). We specified the model to estimate locations every eight hours. MCMC settings were designated for an adaptation and burn-in phase of 10,000 samples each followed by 10,000 posterior samples that were thinned by five. We evaluated model convergence by assessing stationarity in the posterior samples and monitoring for well-mixed MCMC chains, low within-chain sample autocorrelation, and sufficiently low Brooks–Gelman–Rubin shrink factors (below 1.1; Brooks and Gelman 1998).

Summarizing space use

We characterized patterns in movement during migratory and non-migratory periods based on the SSM-generated dataset of model-fit locations for the eight turtles. We first used the median behavioral state (either 1 or 2) from the model posterior samples to assign each location to a turtle's inter-nesting, migratory, or foraging period. To summarize movements during migratory periods, we calculated the distance each hawksbill traveled along its migratory path. Additionally, we computed the straight-line distance (i.e., displacement) between the centroids of each turtle's foraging and inter-nesting range; if no inter-nesting behavior was observed, we instead used the first location of the migratory path.

We characterized space use during inter-nesting and foraging periods with home range analyses from the R package 'adehabitatHR' (Calenge 2006). For all non-migratory periods, we computed 50% and 95% utilization distributions (UDs) with kernel density estimation, in addition to 95% minimum convex polygons (MCPs). Kernel UD uses a smoothing parameter to estimate the true area of use based on all observed locations (i.e., satellite fixes), accounting for where fixes are most concentrated (Worton 1989). Here, we used a 50% UD to represent the inner core area of use and the 95% UD for the full extent of home range movements (excluding 5% to reduce bias from outliers). In contrast, a MCP more simply bounds a polygon to the outermost locations, here after excluding the outer 5% to remove outliers. Thus, MCPs provide a less-manipulated (i.e.,

no smoothing function) representation of the full home range and are also useful for comparing results to previous studies utilizing this method. We did not delete model-fit locations on land before computing UD and MCPs to avoid introducing user bias, as these locations could be closer to true turtle positions than a given point in water. When generating maps, we excluded UD and MCP areas that overlapped land by placing home range polygons underneath land polygons. We computed centroids for the 50% UD (both inter-nesting and foraging) to measure straight-line migration distances. We also used these centroids to examine water depth, extracting depth data from the 2020 General Bathymetric Chart of the Oceans (15 arc-second resolution; GEBCO Compilation Group 2020). At this resolution, the depth data presented are a coarse representation of bathymetry in these areas. In one case, UD geometry resulted in an inter-nesting centroid located on land (PTT 7665); we assigned this centroid the value from the nearest raster cell containing a depth below sea level.

RESULTS

Transmitter deployments

Satellite transmissions for the eight hawksbills spanned a mean \pm SD of 353 ± 103 days per turtle (Table 1). Transmissions began on the start date of the inter-nesting period for turtles that exhibited this behavior, otherwise the start of the migration represents the beginning of transmissions (Table 2; Table 3). PTT 8553 is the exception, because we assigned all locations to the foraging period for this individual (Table 3). Three of the six PTTs deployed in 1998 ceased transmitting on 3 December 1999, when service was stopped due to financial considerations. All other PTTs, including the two from 2000, ceased transmitting on their own, likely due to loss of battery power, damage, or failure (although mortality cannot be ruled out).

PTT 8553 did not provide usable satellite location data over two stretches of >50 days (e.g., 1 July–28 August 1999). During these times it provided only locations of quality Z, the highest error designation, and no associated coordinates. Therefore, we split this track into three segments and modeled each separately so that the SSM would not estimate locations during long stretches with no raw data to inform the model. We then combined the three sets of model-estimated behavioral states and locations for further analysis.

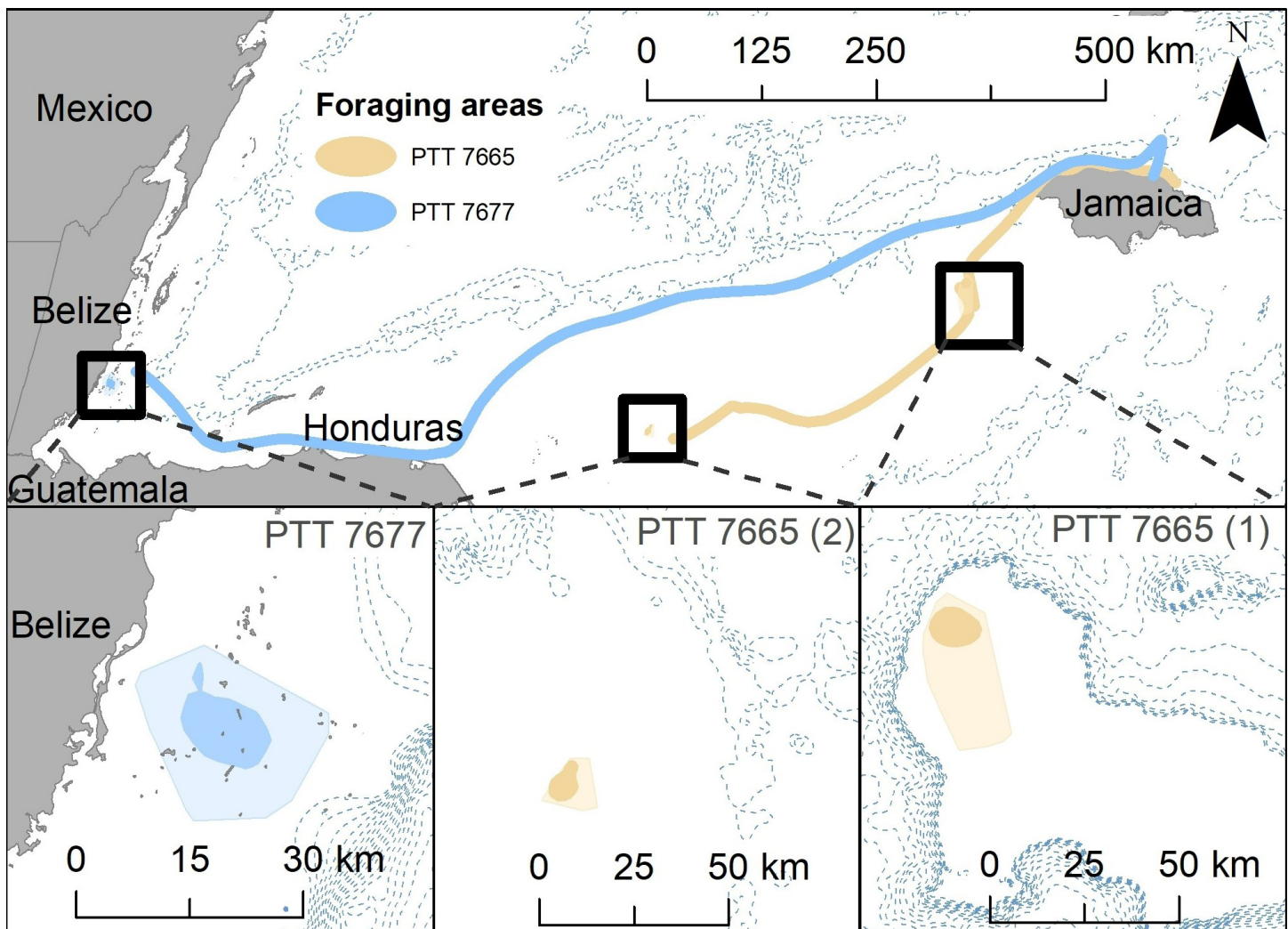


FIG. 1. Migrations and foraging home ranges for two hawksbill sea turtles (*Eretmochelys imbricata*) outfitted with satellite transmitters (PTTs) after nesting in St. Mary Parish, northern Jamaica in 2000. Darker polygons in the insets show 50% kernel utilization distributions and are paired with larger, lighter 95% minimum convex polygons. Dashed lines display 2000-m depth contours in the large map and 100 m contours in the insets.

Migrations

Seven of the eight hawksbills exhibited post-nesting migrations, with paths ranging 56–1324 km in length (mean \pm SD = 357 ± 488 km; Table 2). One turtle tagged in northern Jamaica exhibited two distinct migrations (PTT 7665), first traveling 321 km to forage in Jamaican waters for ~71 days and then migrating another 403 km to a destination in Honduras' EEZ (Fig. 1). For migratory summary statistics presented here, we summed the two resulting path lengths and computed an overall straight-line distance to its final foraging home range. Notably, the two individuals tagged in northern Jamaica had straight-line migration distances >600 km, whereas all other individuals had migratory distances <140 km (Table 2; Fig. 1; Fig. 2; Fig. 3). Of the seven migrants, three did not exhibit inter-nesting behavior

(detailed below), and therefore we calculated their straight-line migration distances using the first location of the migratory path (not the inter-nesting centroid); these three first locations were <200 m from shore and thus did not introduce appreciable bias as compared to using centroids to compute migration distances.

The two long-range migrants from northern Jamaica established foraging areas in southern Belizean and eastern Honduran waters (Fig. 1). The double migrant from northern Jamaica first foraged in an area in the northwestern portion of Pedro Bank, Jamaica, and made its second migration to an area approximately 200 km west of Serranilla Bank, Colombia. The other female from northern Jamaica foraged near Placencia, Belize, easternly adjacent to Lark Caye. The two individuals tagged in Portland Bight remained in southern

TABLE 2. Migration information for eight hawksbill sea turtles (*Eretmochelys imbricata*) tracked from Caribbean nesting beaches in 1998 and 2000. Migratory durations are rounded to the nearest half-day. A “•” denotes the parameter is not applicable due to no observed migration. Coordinates provide the location of the foraging centroid.

PTT ID	Nesting location	Start	Duration (days)	Path (km)	Straight-line distance (km)	Foraging location	Coordinates
7665 ^a	N Jamaica	28 Sep 00	13	320.5	235.7	Jamaica	78.8867° W, 17.4434° N
7665 ^a	N Jamaica	22 Dec 00	10.5	403.2	372.0	Honduras	82.0968° W, 16.1233° N
7677	N Jamaica	19 Jul 00	35	1323.7	1205.5	Belize	88.2168° W, 16.5465° N
8442	S Jamaica	19 Nov 98	2	55.7	100.9	Jamaica	77.7782° W, 17.0891° N
8443	S Jamaica	3 Dec 98	4	90.5	95.4	Jamaica	77.9641° W, 17.8888° N
8455	Antigua	30 Oct 98	3	120.6	139.3	St. Eustatius	62.9993° W, 17.5205° N
8456	Antigua	16 Oct 98	3	59.4	67.6	Redonda	62.3499° W, 16.9495° N
8552	Antigua	25 Oct 98	6	126.5	119.1	St. Kitts	62.8386° W, 17.4415° N
8553 ^b	Antigua	•	•	•	•	Antigua	61.7784° W, 17.1474° N

^aThis turtle made an initial migration to a foraging area, remaining for ~71 days before making a second migration to a final foraging destination; straight-line distance from IN centroid to final foraging area centroid was 607.3 km.

^bNo migration observed, individual remained local to NE Antigua.

Jamaican waters, migrating to the relatively shallow areas of Blossom Bank and northeastern Pedro Bank (Fig. 2). The migrations of all four Jamaican turtles were contained within the Nicaraguan Rise, an oceanic ridge that begins in eastern Honduras and northern Nicaragua and stretches northeast to Jamaica. The three hawksbills that migrated from Antigua traveled relatively short distances to coastal areas near St. Eustatius, St. Kitts, and Redonda, respectively (Fig. 3). Redonda is an uninhabited, small island (< 3 km²) located to the southwest of Antigua and is part of the nation of Antigua and Barbuda.

The fourth turtle tracked from Antigua remained resident in northeastern waters around Long Island (Fig. 4). The SSM did not detect any switches in behavior for this individual and therefore estimated a non-migratory state for all locations. Biologically speaking, over 318 days the turtle must have transitioned from a nesting state to a foraging state, as the nesting season for hawksbills does not exceed three months (Bjorndal et al. 1985; Kendall et al. 2019). Model-fit locations revealed that the turtle stayed around Long Island during the whole period of satellite transmissions. Thus, we infer that this was a resident turtle, and any small migra-

tion went unobserved, perhaps occurring during a gap in transmissions. We assigned all model-fit locations as the foraging period because the turtle was sampled on 14 November, which is at the end of the nesting season (Hart et al. 2019). However, it is likely that this period hosted both inter-nesting and foraging behavior (Table 3).

Inter-nesting and foraging areas

Three turtles were outfitted with transmitters at the end of their nesting season and SSM results suggested that they immediately migrated, so no information on their inter-nesting movements was available (Table 3). Given modeling results, we did not observe inter-nesting movements for a fourth, nonmigratory individual from Antigua (PTT 8553). The four individuals with inter-nesting data—three from Jamaica and one from Antigua—exhibited inter-nesting behavior for a mean of 41 ± 19 days (Table 3; Fig. 4; Fig. 5). Hawksbills deposit clutches approximately every two weeks within a nesting season (Bjorndal et al. 1985; Kendall et al. 2019), so these turtles likely transmitted over periods spanning 1–4 clutches before migrating. Inferences into the inter-nesting home range of the single northern

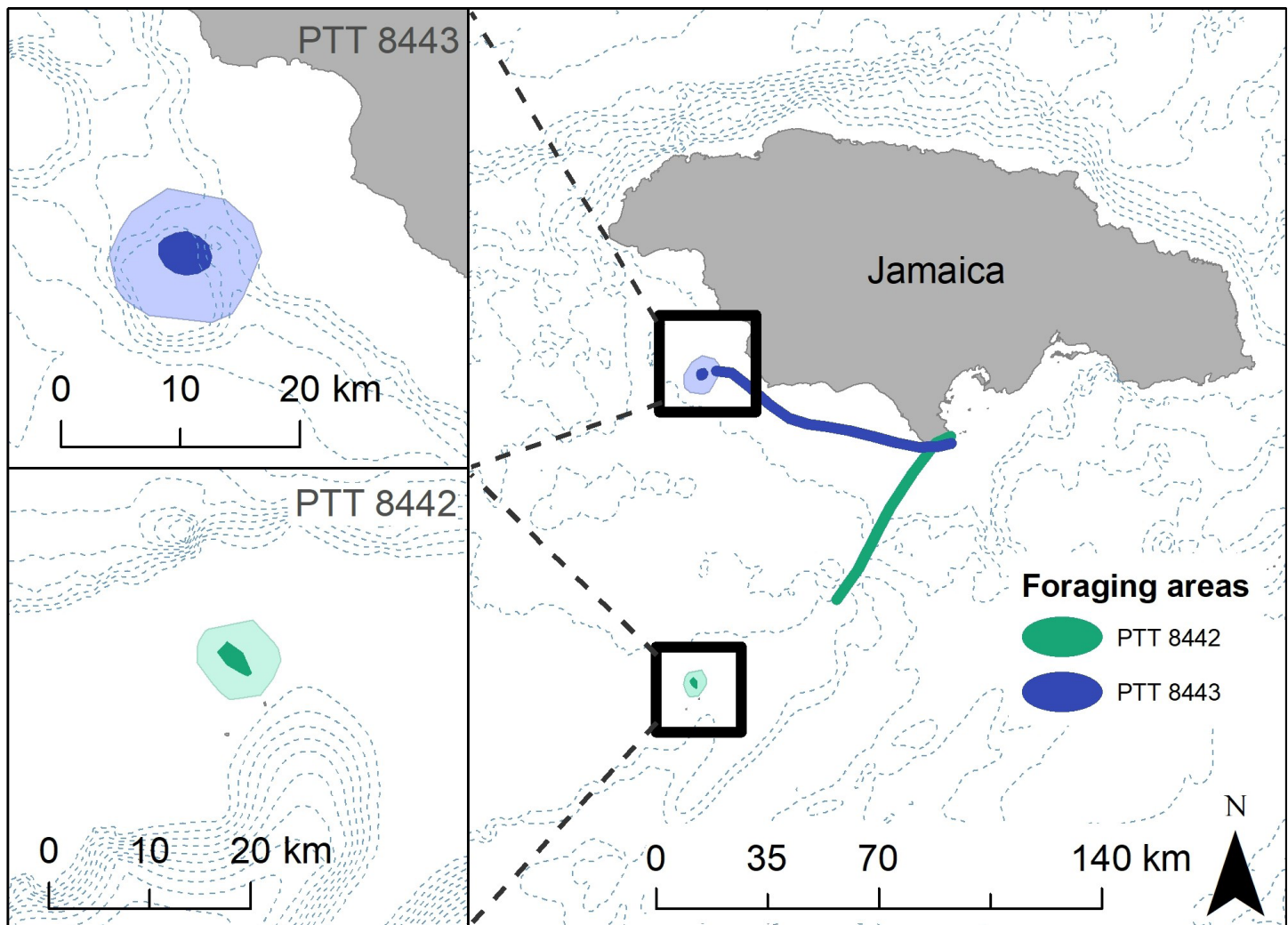


FIG. 2. Foraging home ranges for two adult female hawksbill sea turtles (*Eretmochelys imbricata*) outfitted with satellite transmitters (PTTs) after nesting in Portland Bight, Jamaica in 1998. Lines show post-nesting migrations and polygons display foraging home ranges, with darker polygons providing 50% kernel utilization distributions paired with larger, lighter 95% minimum convex polygons. Dashed lines display 500-m depth contours in the large map and 100-m contours in the two insets.

Jamaican individual with inter-nesting behavior (PTT 7665) were limited by sample size. This turtle's 50% UD was larger than its 95% MCP, potentially indicating an insufficient sample size for reliable home range estimation; we present these inter-nesting data but excluded them from summary statistics reported here. For the three other turtles with inter-nesting information, we observed considerable variation in home range sizes; 50% kernel UDs averaged $27.1 \pm 16 \text{ km}^2$, while 95% UDs covered a mean of $133 \pm 69 \text{ km}^2$ and 95% MCPs had a mean area of $90.9 \pm 49 \text{ km}^2$. Mean depth at the three inter-nesting UD centroids was $7.33 \pm 4.9 \text{ m}$.

We documented nine foraging periods for the eight hawksbill females, with one individual from northern Jamaica exhibiting two distinct foraging phases. For-

aging periods, including that of the non-migratory Antigua individual, spanned a mean of 286 ± 144 days. We note that observed foraging and inter-nesting durations were constrained by transmitter function, and not necessarily turtle behavior (i.e., true foraging durations before a subsequent migration would be much longer). The nine foraging areas that we documented had a mean 50% UD area of $39.2 \pm 38.5 \text{ km}^2$ (Table 3). Much of the variation in 50% UD area was driven by three individuals with exceptionally large UD sizes: the two long-range migrants from northern Jamaica and the non-migratory individual from Antigua. When excluding these three turtles, 50% UDs averaged $11.5 \pm 3.4 \text{ km}^2$. The nine foraging 95% UDs averaged $272 \pm 260 \text{ km}^2$, while 95% MCPs covered a mean of $210 \pm$

TABLE 3. Summary of inter-nesting and foraging home ranges for eight hawksbill sea turtles (*Eretmochelys imbricata*) tracked from Caribbean nesting beaches in 1998 and 2000. Durations of observation (i.e., satellite transmissions) are rounded to the nearest half-day. UD denotes utilization distribution as computed with kernel density estimation, and MCP denotes minimum convex polygon. Depths are provided for the centroid of 50% UDs. A “•” notes that we did not observe that behavior.

PTT ID	Inter-nesting period						Foraging Period					
	Start	Duration (days)	50% UD (km ²)	95% UD (km ²)	95% MCP (km ²)	Depth (m)	Start	Duration (days)	50% UD (km ²)	95% UD (km ²)	95% MCP (km ²)	Depth (m)
7665 ^a	13 Sep 00	15	41.7	207.3	31.0	5	11 Oct 00	71	110.5	861.0	618.7	31
7665 ^a	•	•	•	•	•	•	2 Jan 01	22.5	56.8	284.2	127.1	32
7677	•	•	•	•	•	•	23 Aug 00	252.5	90.2	466.0	384.2	3
8442	6 Oct 98	43.5	12.1	54.8	35.6	5	21 Nov 98	376.5	8.1	56.7	45.1	10
8443	6 Oct 98	58.5	44.3	158.7	110.3	13	8 Dec 98	341.5	12.0	109.0	100.4	19
8455	12 Sep 98	48	25.0	185.2	126.9	4	2 Nov 98	386.5	16.9	135.0	76.5	2
8456	•	•	•	•	•	•	19 Oct 98	409.5	11.4	108.3	107.1	161
8552	•	•	•	•	•	•	31 Oct 98	397.5	9.3	59.7	54.0	24
8553 ^b	•	•	•	•	•	•	12 Nov 98	317.5	37.8	367.9	377.2	4

^aAfter migrating away from the nesting beach, this turtle stopped to forage for ~71 days before making a second migration to its final foraging destination; information is shown for both foraging periods. Sample size limited inference into IN home range behavior; atypically, 50% UD area > 95% MCP, so these data were excluded from summary statistics.

^bNo migration observed, information listed likely spans both inter-nesting and foraging movements.

200 km². Mean depth at the nine foraging centroids was 31.8 ± 50 m. Eight of the nine foraging UDs had centroids with a depth of <35 m, but one individual (PTT 8456) foraged near Redonda with a centroid depth of 161 m. The bathymetry around Redonda features a rapid drop-off running north-south on the island's western side, and the centroid was located in this steep area (Fig. 3).

DISCUSSION

Migratory behavior

Our results provide the first published information for hawksbill sea turtles making post-nesting migrations from Jamaica and Antigua. We tracked eight turtles, of which four remained to forage within the EEZ in which they nested, two crossed a single international boundary, and two crossed two boundaries (Fig. 6; Fig. 7). These data inform management efforts along migratory corridors and at nesting or foraging locations, especially in the context of previously published satellite tracking data for the region (discussed below). For example,

identifying home ranges can facilitate investigation of overlap with regional fishing effort (Dunn et al. 2010), which may inform the design of fisheries policies and marine protected areas. The migratory behavior we documented also was characterized by considerable variation. Whereas five of seven migrants made relatively short-range migrations (path lengths <130 km), two exhibited substantially longer movements (>700 km), with one turtle traveling >1300 km. Interestingly, all seven migrations featured a strong westward heading (with variation on the north-south axis), adding support to the idea that post-nesting females make use of prevailing currents when returning to foraging habitats (van Dam et al. 2008; Horrocks et al. 2011).

The two long-range migrants were both tagged in northern Jamaica. One stopped to forage for over two months in Pedro Bank, within Jamaica's EEZ, before migrating to a final destination in the EEZ of Honduras (Fig. 1). This site lies within a large area of the Nicaraguan Rise that may represent a regional foraging

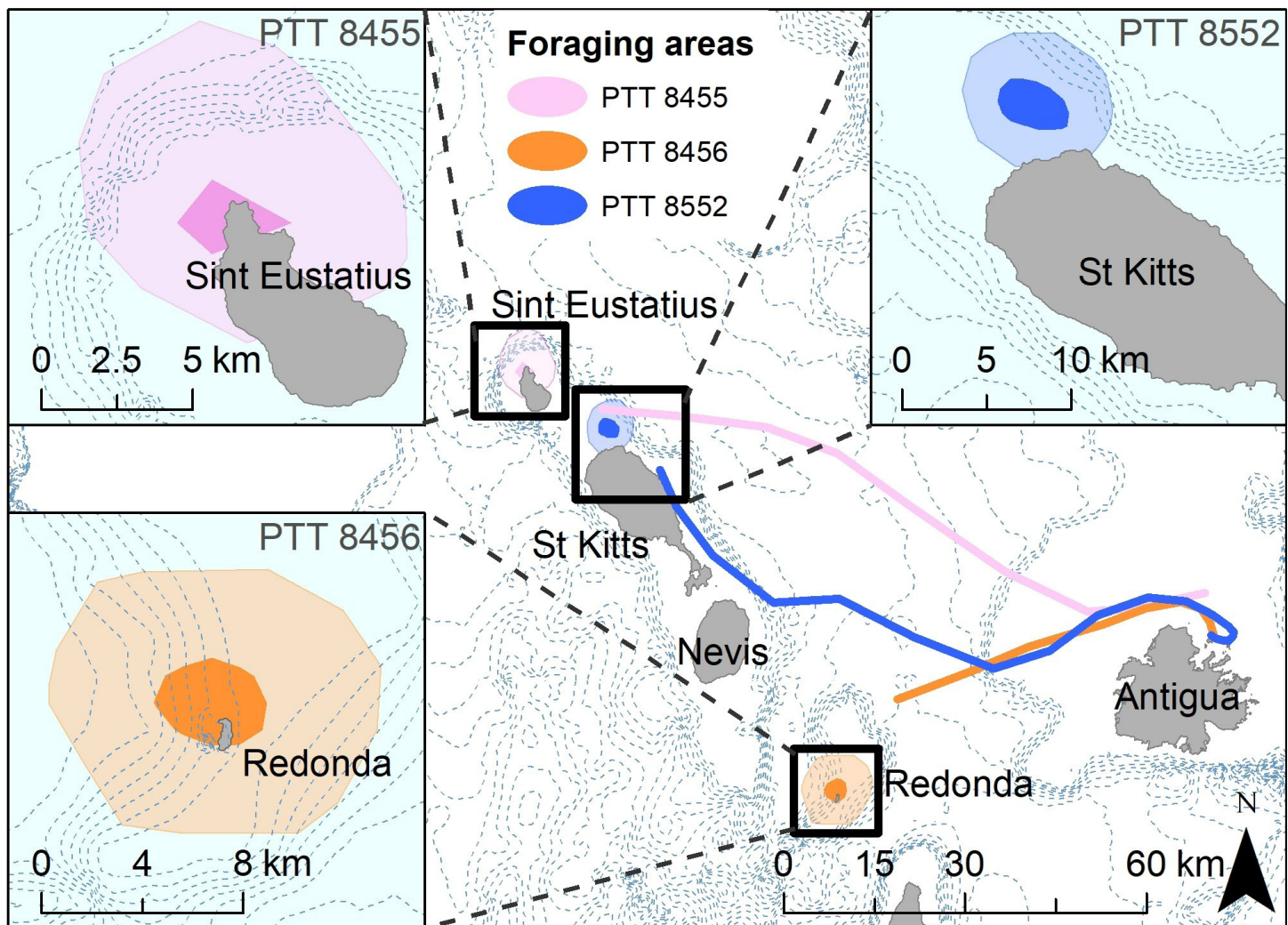


FIG. 3. Migratory movements and foraging home ranges for three adult female hawksbill sea turtles (*Eretmochelys imbricata*) outfitted with satellite transmitters (PTTs) after nesting at Long Island, Antigua in 1998. Lines show post-nesting migrations and polygons display foraging areas, with darker polygons providing 50% kernel utilization distributions paired with larger, lighter 95% minimum convex polygons. Dashed lines display 100-m depth contours.

ing hotspot given the significant proportion of female hawksbills tracked to date that have migrated there (Nivière et al. 2018; Hart et al. 2019; Uribe-Martínez et al. 2021). The other long-range Jamaican migrant traveled to southern Belize, where individuals of multiple sea turtle species are known to forage, including hawksbills (Uribe-Martínez et al. 2021). It is interesting that both long-distance migrants from our study were tagged in the same area of northern Jamaica and represent all individuals sampled from that site. Future satellite tracking efforts may be merited in this location to determine whether this reflects a more general trend or is an artifact of small sample size. In contrast, short-range migrants tracked from southern Jamaica remained in the national EEZ. While hawksbills of varying sizes have long been known to forage in Ja-

maican waters (Haynes-Sutton et al. 2011), these satellite tracks provide the first evidence of post-nesting hawksbills remaining to forage as national residents. The three turtles completing migrations from Antigua also exhibited relatively short-range movements—two migrated to another potential foraging hotspot in the Leeward Islands, spanning Anguilla to Nevis (Hart et al. 2019; Soanes et al. 2022), and the third established migratory connectivity between Antigua and the island of Redonda (still within Antigua and Barbuda's EEZ), where hawksbill foraging has long been known to occur (Fuller et al. 1992).

In the context of previous satellite-tracking work, our study adds resolution to a spatial pattern emerging for foraging post-nesting females in the Caribbean, which may reflect patterns of adults more broadly. Hart

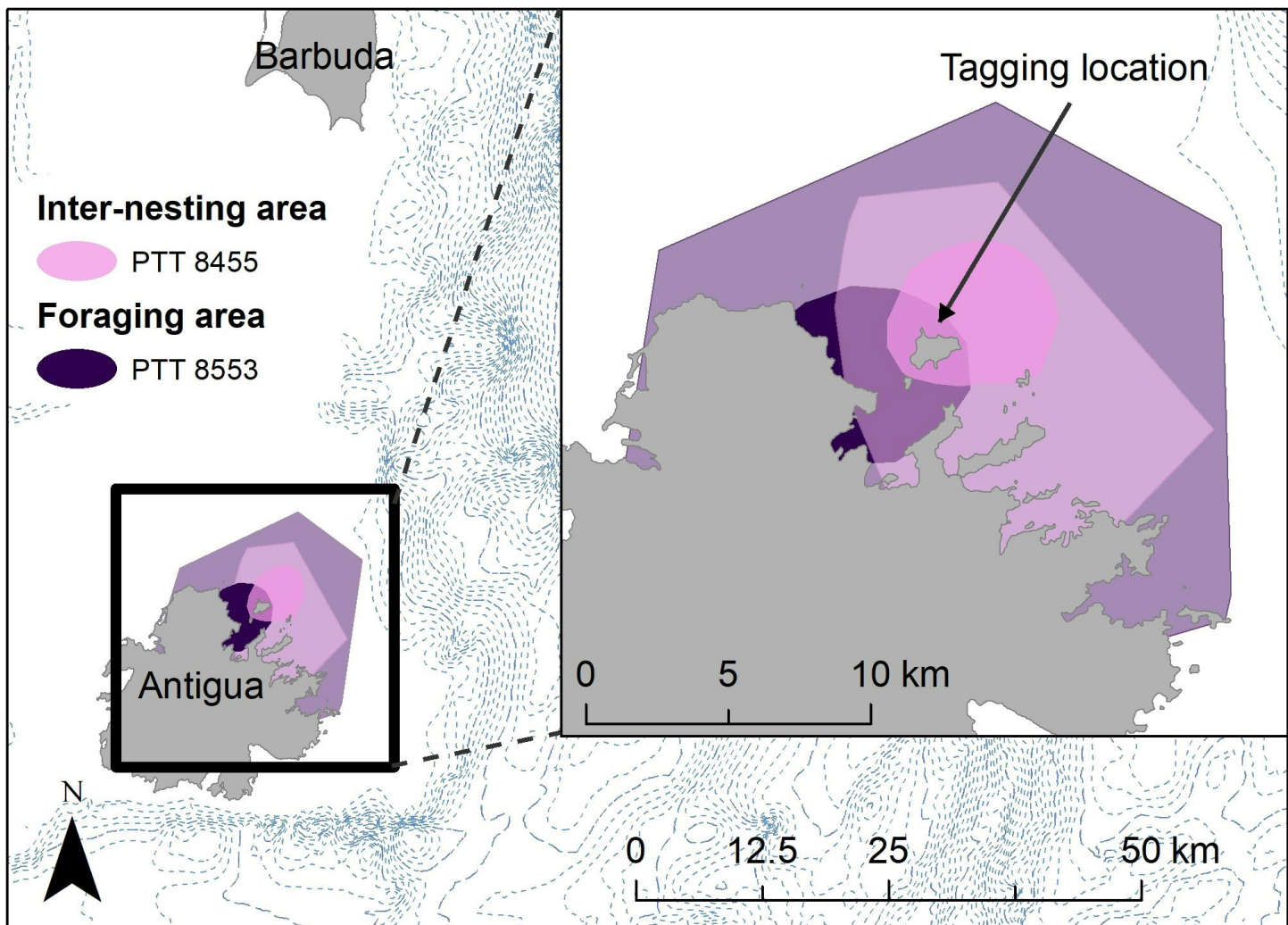


FIG. 4. Resident and inter-nesting Space use of two adult female hawksbill sea turtles (*Eretmochelys imbricata*) outfitted with satellite transmitters (PTTs) in northeastern Antigua in 1998. Dark polygons provide 50% kernel utilization distributions and are paired with larger, lighter 95% minimum convex polygons. Dashed lines show 100-m depth contours. For PTT 8455 the inter-nesting home range is shown. For PTT 8553, a home range is shown for all movements observed; we expect this turtle was resident and that this area may encompass both inter-nesting and foraging behaviors.

et al. (2019) described the movements of 31 nesting females tracked from St. Croix, U.S. Virgin Islands and summarized foraging destinations for 33 other females across six studies (see Figure 6 in Hart et al. 2019). Nivière et al. (2018) contributed information for another 11 adult females tracked from Martinique, French West Indies, Uribe-Martínez et al. (2021) tracked three individuals from Quintana Roo, Mexico, and Soanes et al. (2022) tracked seven from Anguilla. Satellite-tracking research is complemented by studies analyzing flipper tag returns, where tag numbers are physically observed and movements inferred based on where turtles were originally tagged (Meylan 1999; Horrocks et al. 2011; Barrios-Garrido et al. 2020). Combined, these

studies establish a pattern of adult female hawksbills inhabiting neritic areas that fringe the deeper waters of the Caribbean Basin to the west, north, and east (Hart et al. 2019). Moreover, they suggest highly variable migratory patterns. Many hawksbills migrate >2,000 km between nesting and foraging habitats, crossing through several EEZs. For instance, three hawksbills from St. Croix migrated west across the Caribbean Sea to an apparent foraging hotspot in the Nicaraguan Rise (Hart et al. 2019), and tags from females nesting in Barbados have been returned from Nicaragua and Honduras (Horrocks et al. 2011). In contrast, many other individuals have been recorded making shorter migrations in the range of hundreds of kilometers or less

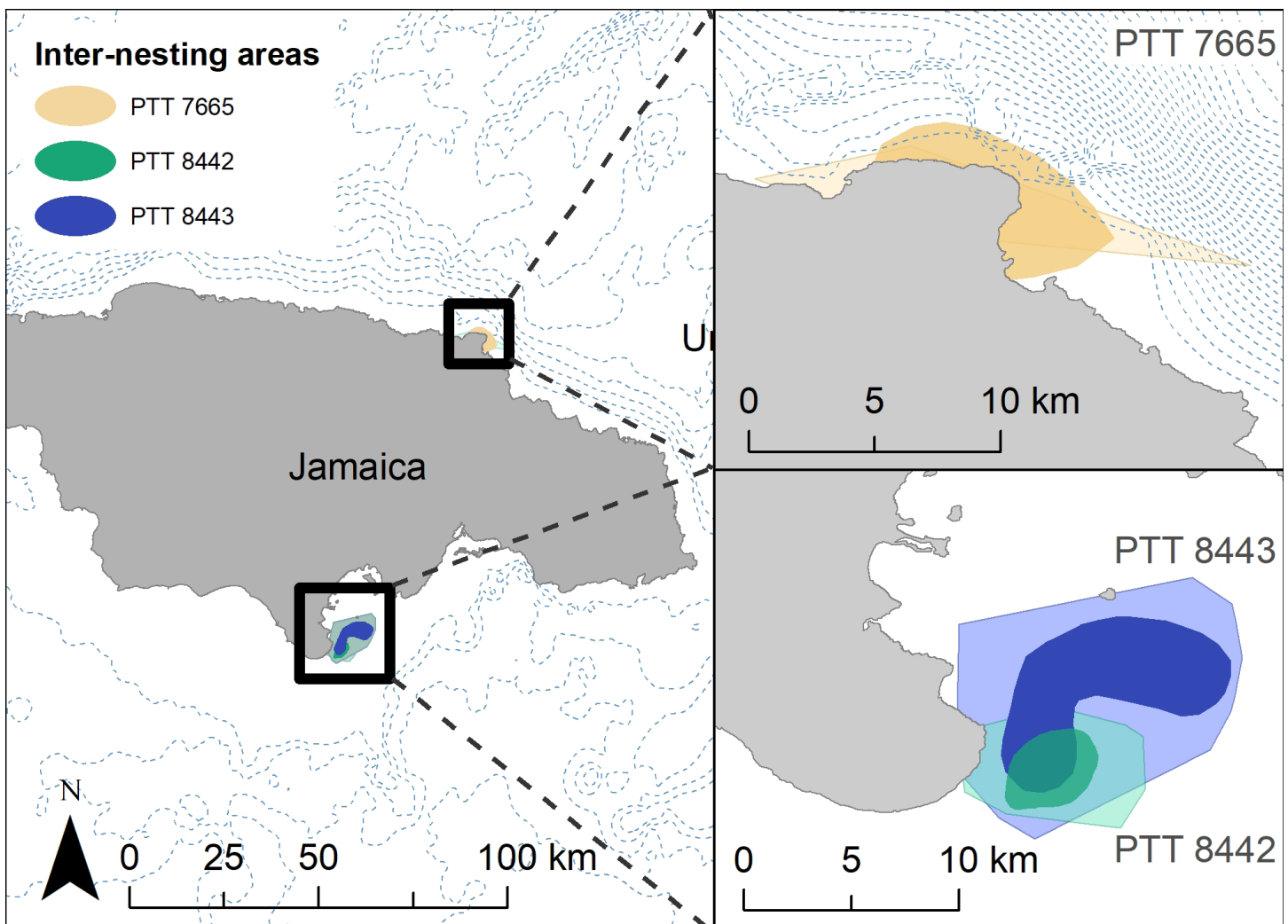


FIG. 5. Inter-nesting home ranges for three adult female hawksbill sea turtles (*Eretmochelys imbricata*) outfitted with transmitters (PTTs) in Jamaica over 1998–2000. Dark polygons provide 50% kernel utilization distributions (UDs) and are paired with lighter 95% minimum convex polygons (MCPs). Dashed lines display 500 m depth contours in the large map and 100 m contours in the two insets. Inferences into the home range for the individual with PTT 7665 were limited by sample size, with a 95% MCP smaller than the corresponding 50% UD.

(e.g., Horrocks et al. 2001) and/or remain resident near the island where they nest (e.g., Hart et al. 2019; Moncada et al. 2012). Similar short-range migrations have been documented in areas of the Pacific (Mortimer and Balazs 2000; Parker et al. 2009). In the present study, we observed migratory behavior that spanned this continuum.

Inter-nesting and foraging home ranges

The characteristics of the inter-nesting and foraging home ranges that we described for eight individuals provide useful insight into patterns in habitat use for adult female hawksbills in the Western Atlantic. Here we focus discussion on 50% UD, as these should be less sensitive to outlier behavior than 95% MCPs or

UDs. We documented inter-nesting 50% UD for three turtles, one from southern Jamaica and two from Antigua. UD sizes ranged 12–44 km², with a mean of 27 km². Mean depth at the centroids of the three UD was seven m, with a maximum of 13 m. These home range sizes fall squarely within the range of two previous studies that provide a basis for comparison. Using the same modeling methods (i.e., a switching SSM), Hart et al. (2019) documented inter-nesting 50% UD between 9.6 and 77.7 km² for 25 turtles from St. Croix, with a mean depth of 16.2 m. Revuelta et al. (2015) did not employ comparable SSM methods, but used ARGOS data to describe inter-nesting 50% UD for seven individuals from the Dominican Republic with a mean area of 13.2 km².

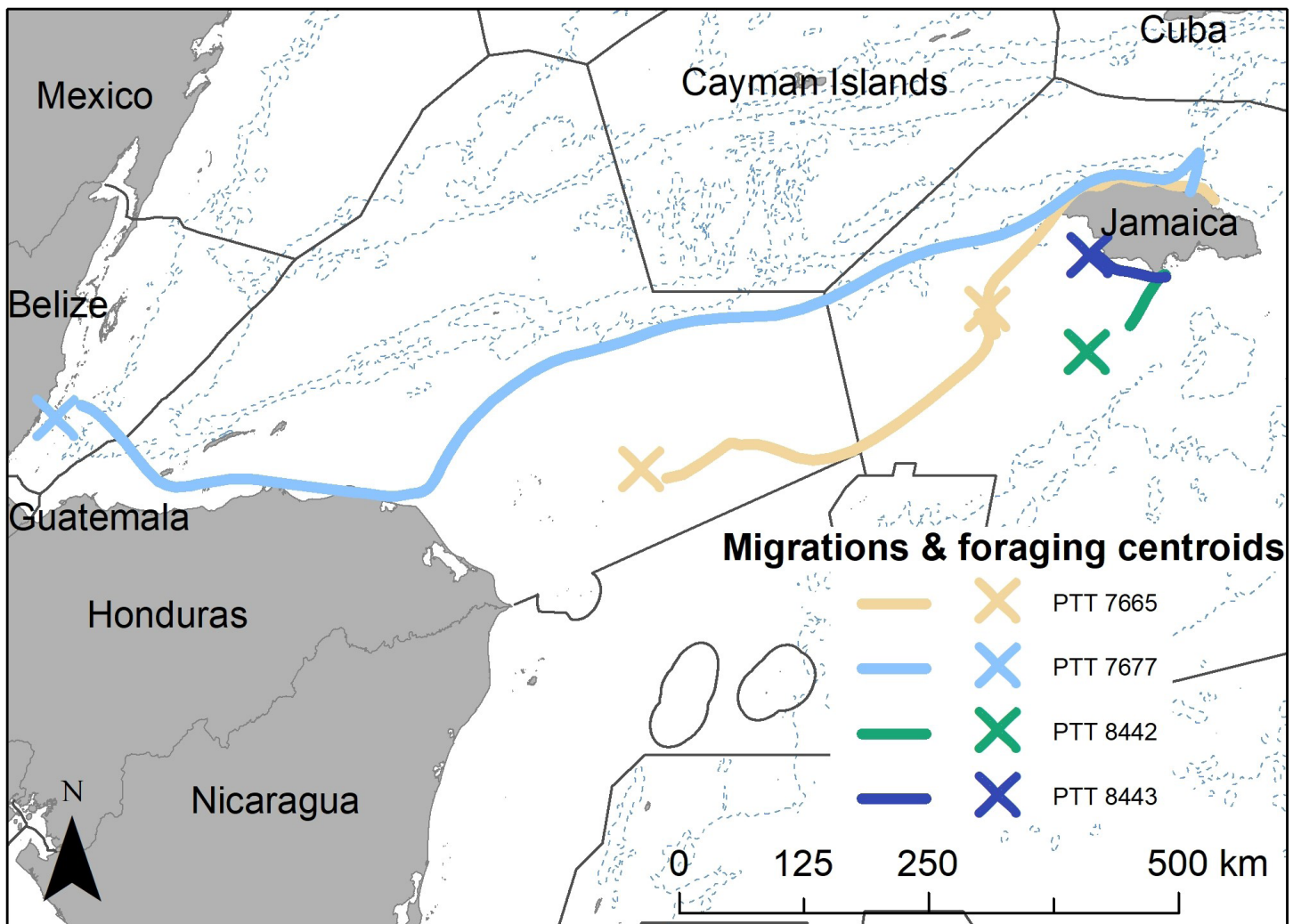


FIG. 6. Migrations and foraging area centroids for four adult female hawksbill sea turtles (*Eretmochelys imbricata*) outfitted with satellite transmitters (PTTs) after nesting in Jamaica. Black lines display national exclusive economic zones. Dashed lines show 2000 m depth contours and indicate that all individuals generally moved over the relatively shallow Nicaraguan Rise (an area extending from northern Nicaragua and eastern Honduras northeast to Jamaica). Solid black lines display national exclusive economic zones.

Our sample size for foraging UD was larger because we observed this behavior in all eight turtles. The nine foraging 50% UD we documented spanned from 8 to 111 km², with a mean of 39 km². With the exception of one turtle whose foraging centroid had a depth of 161 m, all centroids were shallower than 35 m. It is interesting that the three largest foraging UD were produced by the two longest-distance migrants (from northern Jamaica), including both UD exhibited by the turtle exhibiting two migrations. It is possible that longer-ranging migrants require more time to locate their preferred home range after switching to nonmigratory behavior in the vicinity of their foraging area, which could result in an expanded home range estimate. This potential association between long migrations and large

foraging home ranges may merit further investigation. Our results were largely consistent with the previous studies by Hart et al. (2019) and Revuelta et al. (2015), although the largest foraging 50% UD that we documented fell outside the range of the cited work. Hart et al. (2019) described foraging 50% UD for 31 individuals, ranging in area from 6.3 to 95.4 km² and with a mean depth of 65.8 m. Revuelta et al. (2015) described eight foraging UD with a mean area of 16.2 km².

Our results from home range analyses add to a body of evidence suggesting that variation in both inter-nesting and foraging area sizes is common. Future work elucidating the drivers of this variation would be valuable to the management of hawksbill habitat in the region, as clearly some hawksbills occupy much larger

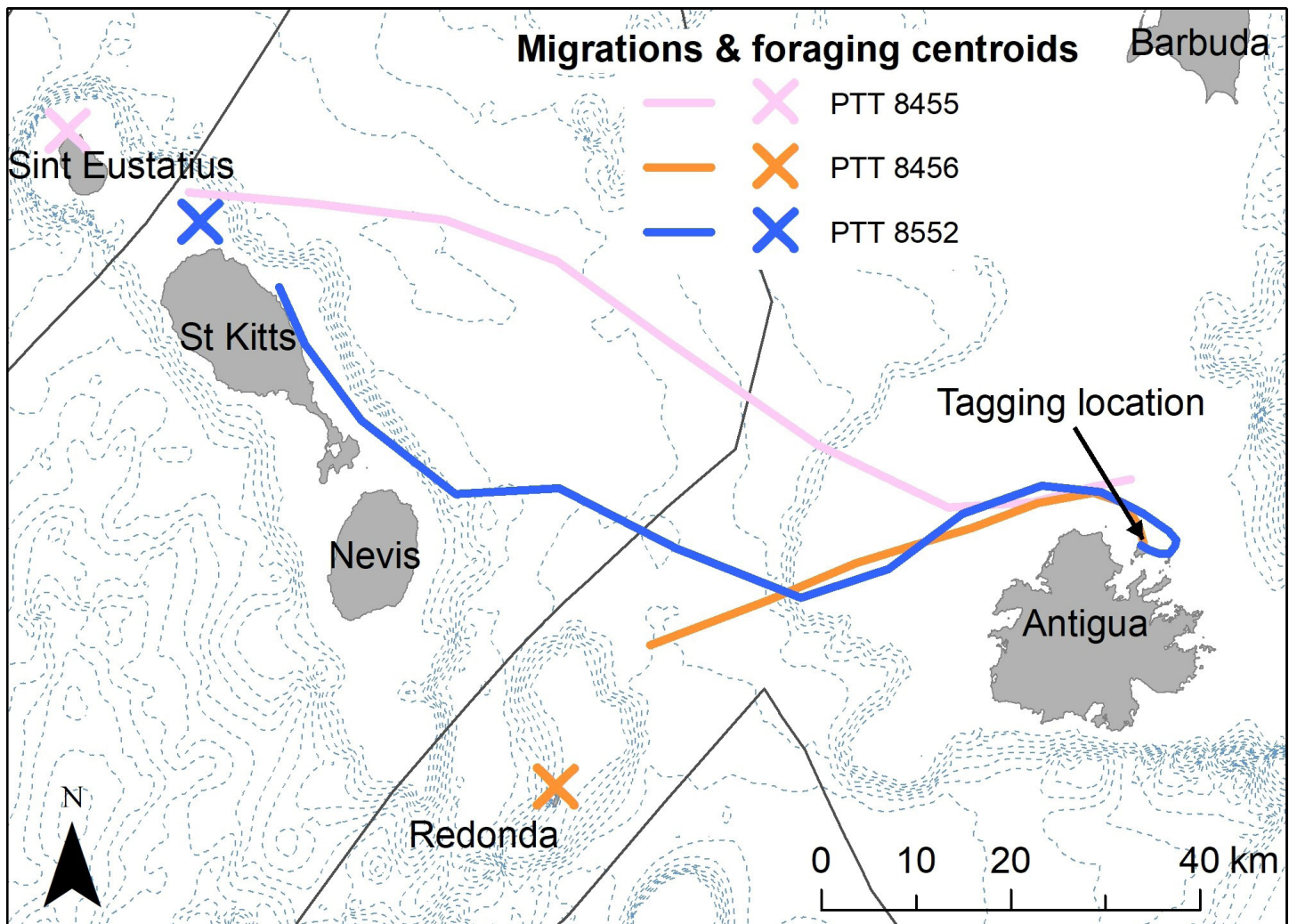


FIG. 7. Migrations and foraging area centroids for three adult female hawksbill sea turtles (*Eretmochelys imbricata*) outfitted with satellite transmitters (PTTs) after nesting at Long Island, Antigua. Migratory tracks do not intersect with centroids because turtles ceased migrating at the edge of their foraging home ranges. Solid black lines display national exclusive economic zones, and dashed lines show 100 m depth contours. A fourth individual tracked from Long Island did not migrate.

areas while nesting or foraging and thus would benefit from expanded habitat protection measures compared to turtles with smaller ranges. Drivers of home range variation could include factors such as site-specific availability and distribution of food sources and shelter areas, as well as potential competitive interactions with other turtles and marine fauna. Individual behavior (i.e., movement tendencies and habitat preferences) likely also plays a role in documented variation. Building on ARGOS datasets with higher accuracy, GPS-enabled transmitters would help to refine our understanding of home range behavior (Dujon et al. 2012). For instance, Walcott et al. (2012) used GPS data to examine fine-scale movement patterns of hawksbills in Barbados

during intervals between successive nests, identifying distinct phases of movement during which nesting females moved to and from small residency areas that ranged only 0.01–0.40 km². Expanding knowledge of these finer scale movement patterns, including within foraging areas, would be highly useful to site-specific management and lend insight into drivers of behavioral variation.

Conclusions

Our findings from satellite tracking eight individuals are consistent with an emerging spatial pattern for the migratory and foraging behavior of adult female hawksbills in the Caribbean. We also described post-nesting migratory connectivity to three foraging

locations to which hawksbill had not been tracked in previous literature (Blossom Bank, Jamaica; Pedro Bank, Jamaica; Redonda, Antigua and Barbuda). This result highlights the need for tracking from additional nesting areas to better characterize connectivity between hawksbill nesting and foraging areas in the Caribbean. Extremely little is known about the distribution of adult males in this region due to the difficulty of accessing this population sector, but we speculate that the foraging distribution of adult females may serve as a useful proxy for adult males given similar habitat preferences. Whether males exhibit similar migratory patterns merits further study. Hawksbills are highly imperiled in this region (Mortimer and Donnelly 2008) and face threats from human activities and global environmental change (Hamann et al. 2013; Maurer et al. 2015, 2021a, 2021b, 2022). Because the recovery of the Caribbean population will depend in part upon survival of adults, especially considering their high reproductive value (Crouse et al. 1987), identifying and protecting adult migratory and foraging habitats should be among our top priorities for conserving this species.

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