

## RESEARCH ARTICLE

# Diverse migratory strategies for a hawksbill sea turtle population

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## Abstract

1. Outside of short, infrequent visits to reproductive habitats, sea turtle lifespans are largely spent in foraging areas. Supporting imperilled populations in an era of biodiversity declines and environmental change requires improvements in the understanding of foraging distributions, plus the migratory corridors that connect foraging and reproductive habitats.
2. This study evaluates the migratory strategies and foraging geography of hawksbill sea turtles (*Eretmochelys imbricata*) in the Western Atlantic. The post-nesting migrations of 22 females were tracked via satellite telemetry from Long Island, Antigua, during 2016–2019, and a state-space model was utilized to estimate true turtle locations from Argos satellite fixes. Model output was used to characterize migratory routes and home ranges occupied during non-migratory inter-nesting and foraging periods.
3. Hawksbill migrations ( $N = 19$ ) resulted in displacements to foraging areas ranging 7–2300 km. Foraging geography varied considerably—whereas eight turtles remained in the immediate vicinity of Antigua and Barbuda (<30 km), there were also longer-distance migrations (>470 km) to locations such as The Bahamas and Nicaragua. Inter-nesting core home ranges (50% utilization distributions) ranged from 7 to 72 km<sup>2</sup>, while foraging core areas ranged from 7 to 46 km<sup>2</sup>.
4. These results add to evidence suggesting that, broadly, post-nesting hawksbills forage in neritic habitats throughout the Wider Caribbean, including several high-use areas. Short displacements to foraging habitats relatively nearby to nesting beaches appear to be the most common migratory behaviour, but individuals in a single population may exhibit various migratory strategies, resulting in basin-wide connectivity between nesting and foraging sites. Given that a single individual or nesting population may inhabit several management jurisdictions, an idealized scenario for regional hawksbill conservation would entail data sharing between managers at linked nesting areas, foraging habitats and migratory corridors such that policies to protect key habitats and mitigate human impacts are designed and evaluated based on best-available science.

## KEYWORDS

Argos, Caribbean, *Eretmochelys imbricata*, home range, satellite tracking, switching state-space model, telemetry, utilization distribution

## 1 | INTRODUCTION

An understanding of the geographic distributions of wildlife is foundational for conservation. Such knowledge serves as a basis for actions to limit human impacts and protect key habitats. Yet, for highly mobile and migratory species, documenting distributions can be both logistically and conceptually challenging. Logistical difficulties arise from the complexities associated with observing or tracking animals across large distances, and this problem is compounded for species that occupy difficult-to-access habitats (e.g. marine environments). Conceptual challenges can result when animals occur in distinct habitats at different times or life history phases. In these cases, distributions may be assessed when observing animals is easiest, such as when populations form conspicuous breeding aggregations (e.g. Kendall et al., 2019; Koivuniemi et al., 2019). However, such observations often provide only a partial view of geographic distributions, and this ‘snapshot’ may not reflect where animals spend the majority of their time. Grappling with these logistical and conceptual challenges is crucial for the conservation of mobile, migratory species in the context of biodiversity declines.

Migratory marine megafauna like sea turtles exemplify the multifaceted issues that can emerge when assessing spatial distributions. Historically, the distribution of adult sea turtles was commonly characterized in terms of the distribution of nesting habitats. This ‘nesting-centric’ paradigm was established based on logical reasons—sea turtles are difficult to observe in marine habitats, especially with historically available tools, whereas nesting females are more readily encountered on nesting beaches. As a result, nesting beaches have been mapped in detail for many regions (e.g. Eckert & Eckert, 2019). The distribution of reproductive habitats is crucial information, as productive nesting beaches are a cornerstone for population viability. Moreover, sea turtle genetic stocks are delineated by source rookery (e.g. LeRoux et al., 2012), so understanding the location of rookeries is important for conservation and assessing population trends. However, despite these advantages, nesting beaches provide a limited picture of the overall geographic distribution of populations.

Sea turtles spend a large majority of their lifespans within marine foraging areas, making short, infrequent visits to breeding sites as adults (Miller, 1997). Furthermore, adults tend to occupy the same foraging home range between breeding migrations (Shimada et al., 2020), such that individual foraging ranges may be relatively static on decadal timescales. Thus, building a robust knowledge-base for lesser-known foraging distributions is crucial, as threats and environmental conditions in foraging habitats can affect survival, energetics and reproductive output (Baumbach et al., 2022; Calvert et al., 2009; Ceriani et al., 2017; Rushing et al., 2016; Stubbs et al., 2020). More data describing foraging locations would, among

other things, make for better-informed measures to limit human impacts, for example fisheries interactions that remain one of the top sources of sea turtle mortality globally (e.g. Putman et al., 2020). For adults, satellite telemetry is a leading tool for studying foraging space use (Hays & Hawkes, 2018), and much of what is known about adult foraging distributions comes from females. This is due to relative ease of access—an adult female sampled on a nesting beach can be fitted with a transmitter and remotely tracked to its foraging range. Importantly, data describing adult female foraging patterns are made more useful by the fact that they may reflect space use by other demographic segments such as males and juveniles (Beal et al., 2022; Limpus et al., 1992; Musick & Limpus, 1997; Schofield et al., 2010; Varo-Cruz et al., 2013). Thus, satellite tracking post-nesting migrations is a powerful starting point for understanding overall foraging distributions.

The present study used satellite telemetry to describe patterns in space use for hawksbill sea turtles (*Eretmochelys imbricata*) in the Caribbean Sea. Hawksbills are classified by the IUCN as Critically Endangered (Mortimer & Donnelly, 2008) and are one of the least studied of the seven sea turtle species in terms of number of satellite transmitters deployed (Hays & Hawkes, 2018). In the Atlantic, hawksbills primarily inhabit reef environments, where the bulk of their diet consists of sponges (León & Bjorndal, 2002; Meylan, 1988). As corals decline globally, it is unclear how coral-competing sponges, and by extension, foraging hawksbills, will respond (Bell et al., 2018), adding further uncertainty to future population dynamics in the context of climate change (Maurer, Seminoff, et al., 2021; Patrício et al., 2021). Bolstering the understanding of hawksbill foraging geography is important not only to support direct, habitat-based conservation but also to enable monitoring at key foraging areas in the context of ongoing declines in habitat quality.

The research presented herein focused on a hawksbill nesting population in Antigua, West Indies, situated in the Eastern Caribbean. This rookery is regionally important and has been intensively monitored since 1987, making it an ‘index’ population for the Western Atlantic. The Jumby Bay Hawksbill Project (hereafter JBHP) monitors annual nesting, employing rigorous sampling protocols that enable the documentation of virtually all nesting activities (Kendall et al., 2019; Richardson et al., 1999). Long-term data revealed a promising increase in nesting population size over the first ~28 years of monitoring (~1987–2014; Stapleton et al., 2010; Kendall et al., 2019; JBHP, unpubl. data). However, more recent data show a downward trend in nesting numbers over ~2014–2022 (JBHP, unpubl. data). Available evidence suggests that changes to transience and/or nesting beach carrying capacity cannot account for the magnitude of decrease (Kendall et al., 2019); therefore, key mechanisms driving the decline are presumably acting away from the nesting beach—within

foraging areas or migratory corridors. Gaining a better understanding of the distribution of migratory routes and foraging areas for this population is a top priority for local managers, as prior to the current study, only four turtles from the rookery had been sampled with satellite transmitters (over two decades ago; Maurer, Dawson, et al., 2022). Therefore, to address this research need, as well as the broader goal of building a better understanding of regional sea turtle distributions, a multi-year project was undertaken to track post-nesting hawksbills from Antigua to their foraging home ranges.

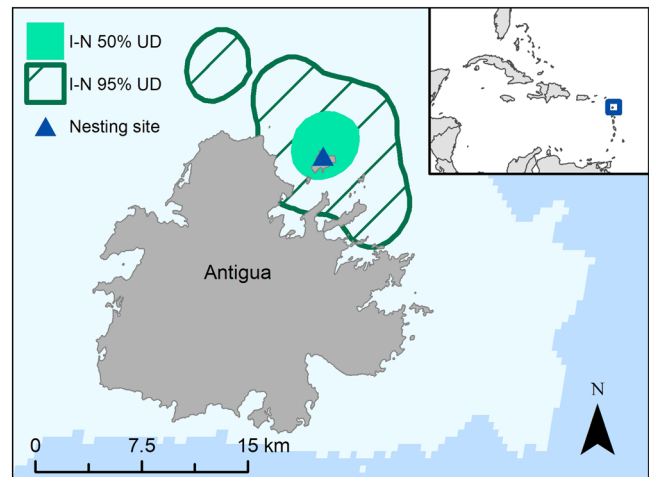
## 2 | METHODS

### 2.1 | Study area

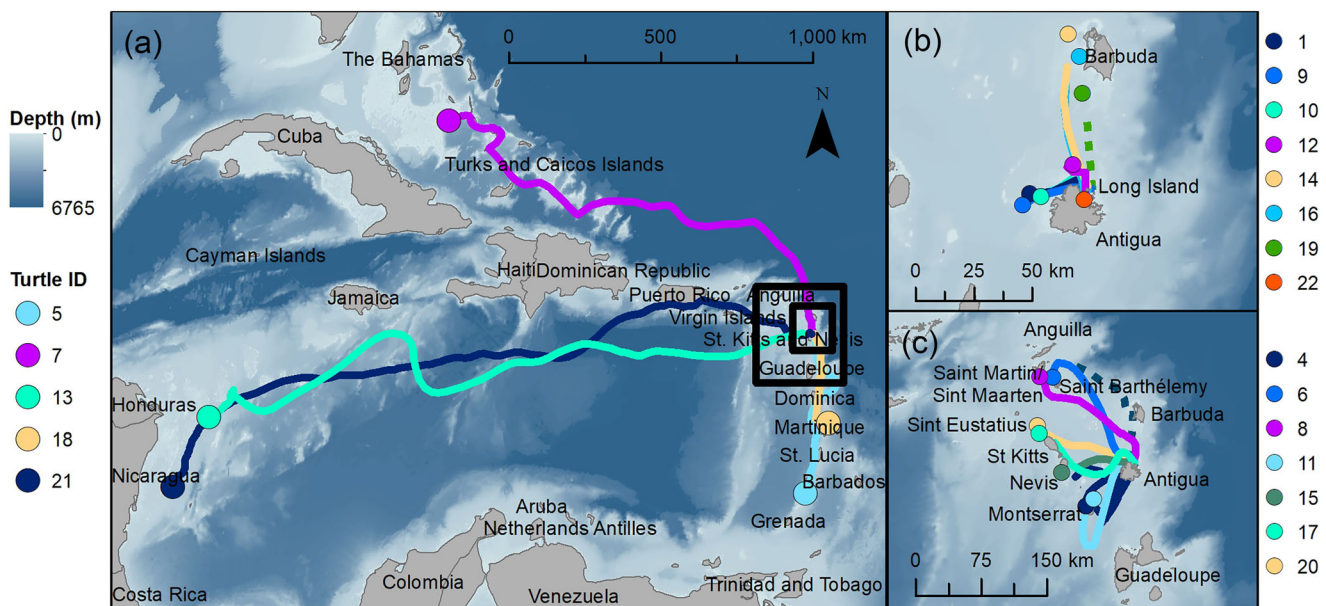
Fieldwork took place at Long Island (aka Jumby Bay), Antigua, a barrier island to the northeast of mainland Antigua (Figures 1b and 2). The primary nesting beach on the ~1.2 km<sup>2</sup> Long Island is Pasture Bay (17.159°N, 61.755°W), which is situated on the island's northern shoreline. Since the inception of monitoring in 1987, JBHP field teams have implemented 'saturation' mark-recapture protocols. Methods entail hourly foot patrols of Pasture Bay and small adjacent beaches to record nearly all nesting activities throughout monitoring seasons that run from 1 June to 15 November (Kendall et al., 2019; Richardson et al., 1999). Uniquely coded flipper tags are used to identify individuals, resulting in a dataset detailing the nesting behaviour of individual hawksbills within the population.

### 2.2 | Transmitter deployments

In this study, 21 satellite transmitters were deployed on 22 nesting females over the course of 4 years (2016–2019; Table 1). Individuals outnumbered transmitters because one transmitter was recovered



**FIGURE 2** The combined inter-nesting (IN) area for hawksbill sea turtles (*Eretmochelys imbricata*) nesting at Long Island, Antigua, over 2016–2019. Joint utilization distributions (UDs) were computed from the centroids of 19 individual 50% UD. The transition from light to dark blue backgrounds marks the 100-m depth contour. The blue square in the top-right inset shows the approximate extent of the map within the Wider Caribbean.



**FIGURE 1** Migratory paths and foraging area centroids for post-nesting hawksbills (*Eretmochelys imbricata*) tracked after nesting at Long Island, Antigua, during 2016–2019. The smaller and larger black squares within extent A show the extents of B and C, respectively. Turtle IDs match those used in Tables 1–3. (a) Five individuals made long-range migrations (290–2300 km displacements) to relatively distant foraging locations. (b) Eight turtles made short-range migrations (<65 km displacements) to remain within the exclusive economic zone of Antigua and Barbuda. (A dashed line is shown for Turtle 19, as its path and foraging centroid may not reflect true foraging behaviour. No path was observed for Turtle 22). (c) Eight individuals made mid-range migrations (59–163 km displacements) to neighbouring Leeward Islands. (The dashed line without a foraging centroid shows the partial migration of Turtle 2; its satellite transmitter ceased transmitting mid-migration).

Turtle	Days tracked	Raw fixes	IN locs	Migration locs	Foraging locs	CCL (cm)
1	337.5	2340	38	6	969	85.5
2	71.5	551	199	14	0	91.6
3	36	213	109	0	0	94.6
4	220.5	1298	113	36	514	83.5
5	251	1451	47	41	666	90.6
6	94.5	410	16	15	253	85.9
7	190	1158	44	108	419	95.7
8	190	603	0	18	553	93.5
9	215	1277	38	4	590	88.5
10	180.5	1124	52	8	482	86.0
11	202.5	912	133	13	462	85.1
12	179.5	848	90	8	441	89.4
13	166	820	0	113	386	98.7
14	179.5	894	51	6	482	91.6
15	111	671	40	9	285	86.3
16	169.5	1081	0	10	500	82.7
17	201.5	1068	83	15	507	93.9
18	61.5	266	47	27	111	86.9
19	27.5	155	50	6	27	91.2
20	102.5	571	121	11	177	82.7
21	118.5	796	87	162	107	84.5
22	400.5	2982	119	0	1202	82.5

**TABLE 1** Summary of satellite transmitter deployments for 22 post-nesting hawksbill sea turtles (*Eretmochelys imbricata*) tracked from Long Island, Antigua. Days tracked is the span of satellite transmissions rounded to the nearest half day. Raw fixes refer to the number of raw data points (post-filtering) that were used in modelling. IN (inter-nesting), migration and foraging 'locs' denote the number of model-estimated locations assigned to each period.

Abbreviations: CCL, curved carapace length; IN, inter-nesting.

and redeployed after an animal mortality post-migration. Three turtles were fitted with Sirtrack KiwiSat 202 platform terminal transmitters in 2016, and all later deployments featured Wildlife Computers SPOT-352B models (Table 1).

Deployments took place at Pasture Bay. Turtles were restrained in a collapsible plywood frame (1.5–3 h) for transmitter attachment after nesting females completed egg laying and finished scattering sand around (i.e. camouflaging) the nest site. Before attachment, acetone, sand paper and steel wool were used to clean and gently score the area of the carapace designated for the transmitter and epoxy footprint. The transmitter was then attached by applying quick-setting marine epoxy in several layers, placing the device on the spinal centre line of the carapace in a slightly anterior position with the antenna facing forward (SPOT-352B) or up (KiwiSat 202).

### 2.3 | State-space movement modelling

Location fixes were obtained via the Argos satellite system. Argos fixes are generated when turtles surface and expose transmitter saltwater sensors to air. Each location is assigned one of seven classes representing the estimated accuracy of the fix (i.e. the radius that contains the true location). Accuracy is affected by satellite positioning and the number of satellite uplinks per surfacing episode. Argos fixes can entail significant spatial error and are therefore best

suited to applications over broad spatial extents (Witt et al., 2010), such as tracking megafauna migrations, while providing weaker inference into finer scale elements of space use like movements within foraging home ranges.

Argos locations were used to evaluate hawksbill movement during three distinct periods: the inter-nesting period including movements during a turtle's nesting season, the migratory period during when turtles journey from nesting to foraging habitats, and lastly, the foraging period encapsulating post-migratory movements within a foraging home range. To characterize period-specific movements, a Bayesian state-space model (SSM) framework was implemented that addressed two issues: (1) accommodating variable accuracies associated with satellite fixes and (2) quantitatively differentiating between migratory and non-migratory behavioural states (Jonsen et al., 2005). Briefly, the first SSM component modelled the observation process, weighting high-accuracy satellite fixes to estimate true turtle locations at user-designated timesteps. The second component modelled the behavioural process, estimating one of two behavioural states for each location based on differences between consecutive locations (utilizing a first difference correlated random walk model). Migrating animals generally swim at faster speeds in straighter paths, while non-migratory behaviour entails slower speeds and variable turning angles. The SSM uses Markov Chain Monte Carlo (MCMC) sampling to estimate location and state parameters, generating posterior distributions from which to draw inference.

Model fitting and all other analyses were performed in programme R (version 3.5.2; R Core Team, 2018) using RStudio (version 1.1.463; R Team, 2015). The SSM functions were sourced from the R package *bsam* (Jonsen, 2016; Jonsen et al., 2005), which executed MCMC sampling in programme JAGS (version 4.2.0; Plummer, 2003). Before modelling, raw Argos data were filtered to remove satellite fixes that would produce swim speeds above  $2.5 \text{ m s}^{-1}$  using the R package *argosfilter* (Freitas, 2012). All 22 filtered tracks were then modelled jointly in a single hierarchical run; this assumed identical movement parameters for all individuals and pooled statistical power to improve estimation of behavioural states (Jonsen, 2016). The model was specified to estimate a location every 8 h during deployments. MCMC settings included an adaptation and burn-in phase of 5000 samples each, followed by 25,000 posterior samples that were thinned by five. Model convergence was deemed satisfactory given stationarity in the posterior samples, well-mixed MCMC chains, low within-chain sample autocorrelation, and Brooks–Gelman–Rubin shrink factors under 1.1 (Brooks & Gelman, 1998).

## 2.4 | Quantifying migratory, inter-nesting and foraging movements

Turtle movements were characterized using each individual's dataset of model-fit locations—specifically the mean latitude, mean longitude and median behavioural state from the MCMC posterior distributions for each 8-h location. Estimated behavioural state was first used to assign locations to an individual's inter-nesting, migratory or foraging period. Inter-nesting and foraging periods had the same state designation but were distinguishable given that they were separated by a migration. When the SSM estimated non-migratory behaviour for short periods in the middle of migrations, these locations were included in the migratory path. Some individuals migrated away from the nesting site without a model-estimated switch in behaviour due to relatively subtle changes in swim speed and direction. In these instances ( $n = 5$ ), the start and end of the migration were manually designated based on the movement pattern revealed by examining the distance between an individual's first model location and each successive location. The migration's start and end corresponded with a pair of inflexion points, first when this distance began to rapidly increase as a turtle began migrating, and second when the distance plateaued as the turtle settled into a foraging area (Figure S1 in the Supporting Information). In one case, a turtle made an initial migration but then returned to the nesting beach to lay its final nest before making a final post-nesting migration (Turtle 9); in this instance, distances were reported for just the final migration, and inter-nesting and foraging locations were pooled across the staggered periods (Figure S2).

Movements during inter-nesting and foraging periods were summarized using home range analyses (Figure S3). Specifically, 50% and 95% utilization distributions (UDs) and 95% minimum convex polygons (MCPs) were computed for individual inter-nesting and foraging periods using the R package *adehabitatHR*, employing

a smoothing bandwidth selected via the ad hoc method for a bivariate kernel and the default extent parameter for UD (Calenge, 2006). Additionally, the centroids for inter-nesting UD were pooled across individuals to generate joint UD (50% and 95%) representing inter-nesting space use at the population level, as this information is particularly useful for informing local habitat management decisions. The 50% UD represented core areas of use and are presented herein as the primary result illustrating habitat use given limitations for Argos fix accuracy. In contrast, 95% UD are more reflective of the full extent of observed foraging or nesting movements, although these are more sensitive to satellite fix error. MCPs do not account for density as do UD (Worton, 1989), instead simply bounding a polygon to outermost points; MCPs were included primarily for mapping purposes, showing the full footprint of movement as estimated by the SSM. Telemetry locations for marine animals that fall on dry land are often deleted for spatial analyses; however, in the present work, locations on land were not deleted before computing home ranges because land-based points could be closer to 'true' turtle locations than a given point estimate in water. Features of habitat use were summarized by computing distance to land and bathymetric depth (GEBCO Compilation Group, 2020; 15 arc-second resolution) at the centroids for all 50% UD.

Migratory movements were characterized in terms of the distance each hawksbill travelled along its model-fit migratory path, in addition to the overall migratory displacement (i.e. straight-line distance between inter-nesting and foraging centroids). For migrants without inter-nesting behaviour, the first location of the migratory path was used to calculate displacement (rather than a centroid). Information on the number of maritime boundaries that turtles crossed or ended up inhabiting is additionally presented in the discussion; these boundaries included exclusive economic zones (EEZs) and territorial waters.

## 3 | RESULTS

### 3.1 | Transmitter deployments

Transmitters were deployed between 15 August and 23 November over the 4 years of the study (2016–2019; Table 2). Mean  $\pm$  SD tracking duration was  $168.5 \pm 90.4$  days, ranging 27.5–400.5 days (Table 1). Argos service was discontinued for 12 of 22 deployments after individuals had established clear residency patterns in their foraging area. For another nine deployments, transmissions likely ended because of damage to transmitters or epoxy, biofouling or electronic failure. Finally, Turtle 19's transmitter never stopped functioning, but this turtle was reported dead by fishers south of Barbuda after beginning a migration. The transmitter was subsequently recovered and redeployed onto Turtle 20.

Transmitters provided a total of 23,861 unique Argos locations during the 22 deployments. The location filter removed 2371 of these, resulting in a mean  $\pm$  SD of  $976.8 \pm 659$  locations per individual for the SSM. Modelling produced a mean per individual deployment



**TABLE 2** Migration summaries for 22 hawksbill sea turtles (*Eretmochelys imbricata*) satellite tracked after nesting at Long Island, Antigua, over 2016–2019. Migratory durations are rounded to the nearest half day. Migratory path provides the full distance travelled, whereas displacement is the straight-line distance between centroids of inter-nesting and foraging home ranges. Destination provides coordinates of the foraging area centroid. A ‘•’ denotes that no information was available, either because turtles did not exhibit associated behaviour or due to modelling constraints.

Turtle	Year	Start	Duration (days)	Path (km)	Displacement (km)	Destination
1	2016	28 August	1.5	24.4	25.4	17.14281, –62.0059
2 <sup>a</sup>	2016	20 October	4.5	157.1	150.0	•
3 <sup>b</sup>	2016	•	•	•	•	•
4	2017	11 September	11.5	312.6	68.1	16.75946, –62.2396
5	2017	19 August	13.5	560.6	479.0	12.86497, –61.2216
6	2017	10 August	4.5	152.7	139.5	17.97565, –62.8892
7	2017	18 October	35.5	1813.8	1611.4	23.00314, –75.7699
8	2017	2 October	5.5	166.6	163.2	17.98178, –63.0452
9	2018	28 July	1	31.7	28.3	17.10198, –62.0274
10	2018	20 August	2.5	25.5	20.6	17.13157, –61.953
11	2018	24 August	4	140.2	59.2	16.82235, –62.1655
12	2018	3 September	2.5	16.7	12.4	17.24389, –61.8366
13 <sup>c</sup>	2018	17 August	37.5	2444.5	2172.4	14.93019, –81.5906
14	2018	21 August	1.5	51.5	64.0	17.70787, –61.9552
15	2018	28 August	2.5	69.9	89.2	17.07585, –62.5937
16	2018	13 August	3	48.4	54.0	17.62748, –61.8865
17	2019	30 August	4.5	129.6	129.3	17.4429, –62.9323
18	2019	24 August	8.5	302.3	290.2	14.76636, –60.7682
19 <sup>d</sup>	2019	18 August	1.5	29.1	38.4	17.4972, –61.8469
20	2019	10 November	3.5	117.3	135.1	17.5154, –62.9664
21	2019	9 September	53.5	2486.2	2302.3	13.05273, –82.3934
22 <sup>e</sup>	2019	14 August	•	•	6.8	17.12148, –61.7623

<sup>a</sup>Turtle 2 ceased transmitting mid-migration; information presented pertains to a partial migration.

<sup>b</sup>Turtle 3 yielded only inter-nesting information due to transmitter failure pre-migration.

<sup>c</sup>The first location for Turtle 13 was transmitted 4 days after its final nest, when it was already 40 km from the nesting site. We manually added 40 km to the migration path and displacement.

<sup>d</sup>Turtle 19 was found dead after migrating; reported information may reflect a partial migration.

<sup>e</sup>Turtle 22 did not display a clear migration but established residency in a distinct location approximately 1 week after laying a final nest. We designated foraging and inter-nesting areas, but no migratory path.

of  $67.13 \pm 50.3$  inter-nesting locations,  $28.64 \pm 42.6$  migratory locations and  $415.14 \pm 297.5$  foraging locations (Table 1).

### 3.2 | Migrations

Eighteen of the 22 hawksbills made clear migrations before establishing residency within foraging home ranges (Figure 1). The 18 migratory path lengths were quite variable, ranging from 17 to 2486 km in length (Table 2). Migratory displacements calculated for 19 individuals (including Turtle 22; see below) ranged from 7 to 2302 km. Migrations to foraging areas lasted from 1 to 53.5 days (mean =  $10.9 \pm 15$  days,  $n = 18$ ). The median behavioural states from SSM posteriors were used to identify the bounds of 13 migrations, and the other five migrations were manually delineated. In some instances when individuals exhibited a relatively straight migratory

path, the methods of computation produced path lengths that were shorter than the displacements because turtles stopped migrating before reaching the centroid of their foraging area (i.e. the distance between edges of inter-nesting and foraging areas was less than the distance between centroids).

The four individuals without clear migrations were Turtles 2, 3, 19 and 22; migratory information was reported for these individuals when available (Table 2) but excluded from the calculation of means and during model fitting. Turtle 2 exhibited migratory behaviour initially but stopped transmitting near Saint Martin without switching to foraging behaviour. Turtle 3 lost its transmitter during its inter-nesting period. Turtle 19 made an apparent migration to an area immediately south of Barbuda but did not establish a clear foraging area and was subsequently found dead. Finally, Turtle 22 never made an apparent switch to migratory behaviour but did exhibit two distinct periods of home range behaviour, one immediately adjacent to

the nesting beach and one close by to the south east (displacement = 7 km). Apparent residency in the second home range started after its last observed nesting event. Movement from the inter-nesting area to the putative foraging area entailed much backtracking, precluding demarcation of a migratory path. Rather, the inter-nesting versus foraging periods were conservatively delineated, and the transitional period was excluded.

### 3.3 | Inter-nesting movements

Data for 18 individuals provide information on inter-nesting home ranges (Table 3). Three turtles migrated immediately after tagging and thus did not exhibit observable inter-nesting behaviour (Turtles 8, 13 and 16). One individual (Turtle 6) exhibited non-migratory behaviour for 5 days after it was tagged, which provided an insufficient sample size for reliable home range estimation; available information was tabulated but excluded when calculating means. Observed inter-nesting periods (truncated by timing of transmitter deployment) spanned 12.5–66 days (mean  $\pm$  SD = 26.8  $\pm$  14 days). Mean area for 50% UD was 20.5  $\pm$  15 km<sup>2</sup>, and for 95% UD was 113.7  $\pm$  92 km<sup>2</sup>. The 18 centroids had a mean depth of 5.6  $\pm$  1 m and mean distance from land of 0.92  $\pm$  0.8 km. Maps of individual inter-nesting (and foraging) home ranges are provided in the Supporting Information (Figures S4–S7). The combined inter-nesting area computed for all individuals encapsulated a region encompassing Long Island and much of the north-eastern coast of Antigua, with a 50% core area directly surrounding Long Island and waters to its north (Figure 2). Area for the population-level joint-50% UD was 15.6 km<sup>2</sup> and for the joint-95% UD was 120.3 km<sup>2</sup>.

### 3.4 | Foraging movements

Post-migratory foraging behaviour was observed for 19 of the 22 individuals (all except Turtles 2, 3 and 19, explained above). Information for Turtle 19's observed foraging period was tabulated (Table 3) but excluded from summary statistics. Periods of observation of foraging movements (truncated by transmitter function) ranged from 35.5 to 353.5 days (mean = 156.3  $\pm$  82 days,  $n$  = 19). The mean 50% UD area was 19.4  $\pm$  11 km<sup>2</sup>, and the mean of 95% UD was 145.0  $\pm$  127 km<sup>2</sup>. Mean depth at foraging centroids was 32.2  $\pm$  20 m while mean distance from land was 12.0  $\pm$  22 km.

## 4 | DISCUSSION

### 4.1 | Variable migratory behaviour and foraging geography

Antiguan hawksbills demonstrated considerable diversity in foraging geography and migratory strategies. For example, whereas seven individuals migrated short distances to forage within Antiguan and

Barbudan waters (Figure 1b), two turtles crossed the Caribbean Sea to access shallow areas off the coast Nicaragua (Figure 1a). Overall, migratory displacements ranged from approximately 7 to 2300 km. Migrations ended at three new areas where, per published literature, post-nesting hawksbills have not been previously tracked—the islands of Barbuda ( $n$  = 2 individuals), Martinique ( $n$  = 1) and Montserrat ( $n$  = 2; Figure 1c). These areas have long been known to host foraging hawksbills (e.g. Fuller et al., 1992) and offer neritic habitats similar to those of other Eastern Caribbean islands for which post-nesting connectivity has already been documented.

Beyond travelling to new post-nesting foraging areas, Antiguan hawksbills additionally migrated to two well-described foraging subregions. Two individuals migrated >2000 km to the Nicaraguan Rise, a large neritic shelf offshore from Honduras and Nicaragua, that appears to host an aggregation of turtles originating from several regional nesting sites (Nivière et al., 2018; Hart et al., 2019; Figure 1a). Another five hawksbills migrated shorter distances within the northern Leeward Islands: two to Sint Eustatius and one each to Nevis, Sint Maarten and Saint Barthélemy (Figure 1c). This island group within the northern Leeward Islands may represent another high-density foraging area, most notably for hawksbills from Saint Croix, USVI (Esteban et al., 2015; Hart et al., 2019; van Dam et al., 2008). Given current knowledge of adult hawksbill foraging distributions, these areas within the Nicaraguan Rise and Leeward Islands (Figure 1), albeit broad in extent, should be considered priorities for habitat protection and efforts to mitigate human interactions. Hawksbill telemetry data can guide measures such as protected area design and limitations on local fisheries. However, it is important to note that spatial sampling bias to nearby rookeries likely affects the perception of what constitutes a high-use area for hawksbills. Indeed, the Leeward Islands and neighbouring territories have served as the site of a large proportion of hawksbill transmitter deployments from Caribbean nesting beaches to date (e.g. Hart et al., 2019; Soanes et al., 2022), likely biasing observations of relatively high foraging use. Tracking individuals from additional rookeries will be necessary to refine the understanding of foraging distributions.

Several hawksbills migrated to previously documented, lower-density foraging areas. These individuals demonstrate migratory connectivity between Antigua and distant locations such as Saint Vincent and the Grenadines ( $n$  = 1 individual) and The Bahamas ( $n$  = 1; Figure 1a). Despite the noteworthy incidence of long-distance migrations, the modal migratory pattern observed was to remain within the immediate waters of Antigua ( $n$  = 5), particularly off the island's western shore (Figure 1b). A primary short-distance migratory strategy is corroborated by previous tracking of other regional populations (Hart et al., 2019), suggesting that the most probable scenario for foraging habitat selection entails turtles recruiting to sites near their nesting beaches at some point of ontogeny. However, drivers of fixation to home range areas for adults merit further study, as clearly other individuals occupy geographically distant sites. Factors such as current-aided dispersal by smaller size classes may play some role (Bowen et al., 2007).

**TABLE 3** Characteristics of inter-nesting and foraging home ranges for 22 hawksbill sea turtles (*Eretmochelys imbricata*) satellite tracked from a nesting area on Long Island, Antigua, Dominica. Durations, rounded to the nearest half day, show periods of observation (i.e. transmissions) and do not reflect full durations of turtle behaviour. Depths and distances from land are provided for UD centroids. A '•' denotes that no associated behaviour was observed.

Turtle	Inter-nesting period					Foraging period					
	Start	Duration (days)	50% UD (km <sup>2</sup> )	95% UD (km <sup>2</sup> )	Dist. to land (km)	Start	Duration (days)	50% UD (km <sup>2</sup> )	95% UD (km <sup>2</sup> )	Depth (m)	Distance to land (km)
1	15 August	12.5	27.8	203.3	6	30 August	322.5	11.9	73.0	21	11.62
2	14 August	66	71.8	358.8	4	•	•	•	•	•	•
3	13 August	36	9.0	44.2	5	•	•	•	•	•	•
4	4 August	37.5	13.3	68.6	6	23 September	171	7.1	52.2	53	1.12
5	3 August	15.5	10.9	56.6	5	1 September	221.5	16.1	102.0	25	3.06
6 <sup>a</sup>	5 August	5	89.1	323.8	10	15 August	84	36.1	594.3	33	2.14
7	3 October	14.5	13.2	52.5	5	23 November	139.5	45.8	340.3	34	1.77
8	•	•	•	•	•	8-October	184	25.0	143.9	15	2.63
9	29 June	12.5	7.8	34.6	6	29 July	185	17.4	99.3	27	12.99
10	3 August	17	16.1	63.3	6	23 August	160.5	20.9	119.9	16	5.95
11	11 July	44	13.6	67.8	4	29 August	153.5	16.2	92.6	34	1.78
12	4 August	29.5	23.6	124.3	6	5 September	146.5	38.1	226.9	30	7.8
13	•	•	•	•	•	24 September	128.5	7.3	60.5	81	83.51
14	4 August	16.5	10.7	48.8	5	23 August	160.5	9.8	79.5	17	7.35
15	15 August	13	24.7	104.3	6	31 August	94.5	22.7	130.0	19	2.11
16	•	•	•	•	•	17 August	166.5	19.8	113.0	6	3.76
17	3 August	27.5	14.0	77.3	6	4 September	168.5	12.1	72.3	62	3.55
18	9 August	15.5	39.0	165.7	8	2 September	36.5	8.5	38.7	60	11.26
19 <sup>b</sup>	1 August	16.5	17.2	88.4	5	20 August	8.5	47.2	207.4	22	9.25
20	30 September	40	23.6	106.9	5	13 November	58.5	27.5	145.2	32	1.39
21	11 August	28.5	6.9	34.3	6	2 November	35.5	8.7	56.6	45	63.31
22	5 August	39.5	27.4	136.1	6	20 September	353.5	16.8	151.5	2	0.09

Abbreviation: UD, utilization distribution.

<sup>a</sup>Inter-nesting home range information is provided for Turtle 6 but was excluded from summary statistics due to sample size constraints.

<sup>b</sup>Foraging home range information is provided for Turtle 19 but was excluded from summary statistics due to sample size.



Behavioural variation was also characteristic in the movement headings used by hawksbills transiting from Antigua, as migrants travelled to foraging areas to the north, west and south. The two southward long-distance migrations are of particular interest because they entailed movement against prevailing circulation patterns in the region. While an overall pattern of current-aided post-nesting movements from Eastern Caribbean beaches has been suggested previously (i.e. containing a strong westward vector; van Dam et al., 2008; Horrocks et al., 2011), findings from Antiguan migrants align with other studies showing that this is not a rule (Hart et al., 2019) and raise further questions about drivers of foraging site fixation, that is, specifically how and when turtles imprinted on these southerly habitats. Although seasonal variation in currents and westward water flow do exist (Johns et al., 2002), the region exhibits broadly consistent ocean circulation.

Results from the present study fit into a rich body of global research documenting diversity in foraging and migratory space use by post-nesting hawksbills. Observed migratory displacements span several orders of magnitude, even within a single population, although patterns vary significantly with geographic context. For example, Gaos et al. (2012) documented relatively short-distance migrations (<300 km) from nesting beaches in El Salvador and Nicaragua; however, hawksbills in this region uniquely utilize estuarine and mangrove foraging areas, creating a distinct dispersal environment relative to other locations. Parker et al. (2009) likewise documented mid- to short-distance hawksbill migrations (< 350 km) but in a remote island setting (Hawaii, USA) where dispersal options are necessarily limited. Indeed, in most cases, migrations appear to follow neritic shelves, which likely dictates context-specific dispersal possibilities. Although absolute migratory distances vary with local and regional context, within-population variation is very common, as is variation in compass heading away from nesting beaches (Barr et al., 2021; Hart et al., 2019; Hoenner et al., 2016; Marcovaldi et al., 2012; Pilcher et al., 2014; Rees et al., 2018). The existence of highly variable migratory strategies in a capital-breeding animal (Bonnet et al., 1998) poses fundamental questions regarding energetic tradeoffs between migration and reproductive output. Such questions are further explored in the [Supporting Information](#) via preliminary analyses within the context of the long-term nesting dataset of the JBHP (Figure S8; Tables S1–S2).

## 4.2 | Characteristics of inter-nesting and foraging home ranges

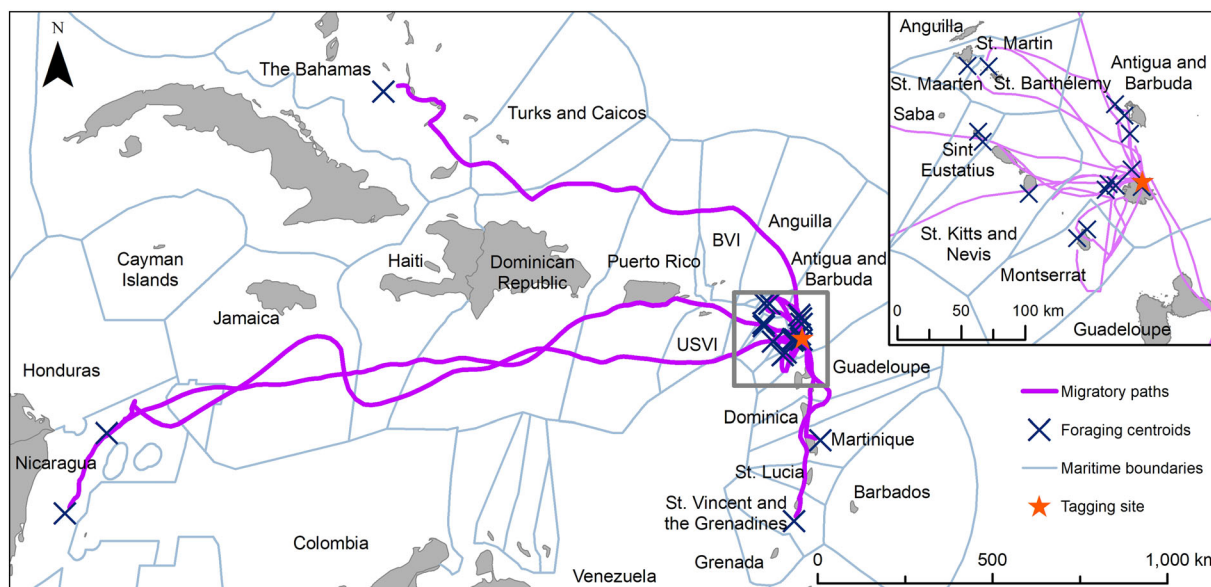
The core areas (50% UD) documented for both inter-nesting and foraging areas were of similar mean size (~20 km<sup>2</sup>), although inter-nesting UD showed more variation. However, 95% UD, representing the full extent of space used, were larger and more variable for foraging areas as compared to inter-nesting areas. This reflects more variable space-use outside the inner core of foraging home ranges, likely in addition to a greater influence from Argos satellite fix error associated with 95% UD. It is logical that space-use

patterns would entail less variation during nesting seasons, a shorter life-history phase when turtles are assumed to forego foraging (Bonnet et al., 1998) and have a relatively singular focus on reproduction. In contrast, habitat structure and prey availability/distribution should vary significantly by foraging location, introducing more variation in home range size. Foraging areas were also generally deeper and further from land than inter-nesting areas, a pattern consistent with previous research in the region (Hart et al., 2019). Relatively shallow bathymetry surrounds Long Island and many other nesting sites, so a shallow depth is unsurprising. Foraging areas were characterized by a range of depths (2–81 m), suggesting that suitable habitats exist across a variety of depths within neritic areas.

Overall, the variation in size and depth documented for both inter-nesting and foraging home ranges was fairly consistent with previous research in the region. Hart et al. (2019) tracked 31 post-nesting hawksbills from Saint Croix and modelled their movements with the same SSM approach, thus allowing for direct comparison. Inter-nesting 50% UD documented in their study ranged from approximately 9 to 77 km<sup>2</sup>, compared to 7–72 km<sup>2</sup> in this study, and foraging UD spanned 6–95 km<sup>2</sup> compared to 7–45 km<sup>2</sup> in this study. Despite limits to Argos-based inference, two primary observations arise from these consistencies. First, these ranges are reasonably similar, and remarkably so for inter-nesting areas, a trend corroborated by Argos-based research on other regional populations (Revuelta et al., 2015). Second, within the bounds of observed ranges, variation is abundant. Variation in foraging area size is to be expected, as noted above, given differences in individual behaviour combined with differences in prey density, prey quality and habitat structure among sites (e.g. Loarie et al., 2009). In contrast, inter-nesting areas for an insular population are clustered around the same nesting site, and hawksbills are thought to be capital breeders such that foraging during nesting seasons is uncommon (e.g. Goldberg et al., 2013). Thus, variation in inter-nesting areas is more likely driven by individual behaviour and habitat preferences unrelated to foraging.

## 4.3 | Conservation implications

The international migrations made by Antiguan hawksbills illustrate how highly migratory species connect conservation interests among disparate management authorities. Migrations passed through a total of 21 maritime jurisdictions, with one turtle traversing 11 boundaries on its own, and foraging areas were located in 10 distinct jurisdictions (Figure 3). This scenario means that the conservation of the Long Island rookery is dependent on marine management in multiple countries or territories, including several distant nations (e.g. Nicaragua, The Bahamas, St. Vincent and the Grenadines). The fact that both migratory paths and foraging home ranges were generally located within neritic habitats (with notable exceptions for migratory paths; Figure 1) matches previous work and is noteworthy for regional management, as relatively shallow coastal areas are also where potential anthropogenic impacts are most concentrated, such



**FIGURE 3** Hawksbill sea turtle (*Eretmochelys imbricata*) migrations passed through 21 distinct maritime boundaries, ending at foraging areas inside 10 different jurisdictions. Migratory paths ( $n = 19$ ) and foraging area centroids ( $n = 20$ ) were documented with satellite transmitters deployed after turtles nested at Long Island, Antigua, over 2016–2019.

as vessel traffic, habitat disturbance and fishing pressure (Dunn et al., 2010). Therefore, data describing distributions and movement corridors of Critically Endangered hawksbills should be made available to coastal managers to inform measures to limit anthropogenic impacts.

This study represents a pivotal first step toward investigating possible drivers of recent nesting declines on Long Island (JBHP, unpubl. data). Observed decreases in annual abundance of nesting turtles could be realized through changes to survival and/or nesting frequency (i.e. annual breeding probability). It is unlikely that changes to transience have played a major role (Kendall et al., 2019; Levasseur et al., 2019; 2020), and although changes to nesting habitat have occurred (Maurer et al., 2015; Maurer, Gross & Stapleton, 2022; Maurer, Stapleton, et al., 2021), we do not believe that any such changes or related effects on beach carrying capacity can account for the extent of decline. Thus, the mechanisms driving changes in survival or breeding probability likely include factors located within foraging areas (or migratory corridors). A better understanding of movements away from the nesting beach is a first step toward future work assessing potential drivers like habitat quality and anthropogenic threats, and given the amount of within-population variation observed herein, further deployments of satellite transmitters would be useful.

More broadly, this study adds to a growing body of telemetry research on hawksbills in the Caribbean Region (Becking et al., 2016; Esteban et al., 2015; Hart et al., 2019; Horrocks et al., 2001; Maurer, Dawson, et al., 2022; Moncada et al., 2012; Nivière et al., 2018; Revuelta et al., 2015; Soanes et al., 2022; Troëng et al., 2005; van Dam et al., 2008). Tracking work, combined with studies using other methodologies, such as flipper tag returns (Horrocks et al., 2011;

Moncada et al., 2012), may represent a basis for developing a ‘foraging-centric’ view of geographic distributions that would build upon seminal ‘nesting-centric’ concepts (see point 3 below for more). While an in-depth regional synthesis is merited, some initial Caribbean-wide patterns are coming into focus. Briefly, post-nesting migrations have revealed that hawksbills forage in neritic habitats that encircle the Caribbean Basin (Hart et al., 2019; Maurer, Dawson, et al., 2022). Relatively few migrations to habitats along the southern edge of the basin have been observed (Becking et al., 2016), although this is likely a product of sampling bias, underscoring a need for telemetry research from Caribbean South American nesting populations (Eckert & Eckert, 2019).

To conclude, the knowledge gained about the foraging distributions of Caribbean hawksbills via satellite tracking post-nesting migrations can be synthesized in the form of three takeaways that are highly relevant to conservation. A key qualifying note for these conclusions is that focusing on integrating data for males will be necessary moving forward (e.g. Cuevas et al., 2020).

1. Relatively short post-nesting migrations to foraging habitats are the most prevalent strategy overall, including those that do not cross maritime boundaries. Thus, many management entities (e.g. governments) with nesting beaches under their jurisdiction have the ability to implement policies within marine habitats that may directly affect population dynamics for resident rookeries.
2. Despite a modal behaviour of short range-migrations, trans-Caribbean movements are not uncommon. This basin-scale connectivity means that, although locally focused management can have a significant impact, supporting the recovery of Critically Endangered hawksbills is nonetheless inherently international. An

idealized scenario for conservation in the Wider Caribbean would entail data sharing and close coordination, for instance, via management working groups, throughout the region. For example, trends at nesting beaches are perhaps the most used indicator of populations status (Mazaris et al., 2017), and thus, managers of foraging habitats can exchange information with managers of migration-linked nesting habitats to determine the efficacy of conservation measures.

- Variation in foraging geography within populations abounds. Therefore, in contrast to reproductive phases when hawksbill females sort neatly by genetic stock, during foraging periods, populations are intermixed and dispersed throughout the region. This behaviour (occupying an assortment of geographically disparate habitats) buffers a population against impacts of environmental perturbation in any one habitat. However, it also makes management more complicated.

A theoretical, highly resolved version of a 'foraging-centric' distributional paradigm for adult sea turtles would entail a mixed-stock approach, where turtle densities are mapped to marine habitats in continuous space with representation of the relative contributions of different rookeries (consistent with approaches already applied to various aggregations of turtles of mixed size classes; e.g. Bowen et al., 2007). In tandem with better-described distributions for nesting habitats, this approach to exploring foraging area-derived population connectivity would be a powerful tool for conservation by giving practitioners a better sense of the necessary spatial and geopolitical scales of their efforts. However, practitioners will inevitably need to make decisions in the near term, before such tools are available. The data on hawksbill space use presented here add to the knowledge-base that can guide managers when making policies designed to protect habitats (e.g. marine protected areas) or mitigate human interactions (e.g. coastal zoning or fisheries limitations).

#### AUTHOR CONTRIBUTIONS

**Andrew S. Maurer:** Conceptualization; formal analysis; funding acquisition; writing—review and editing; writing—original draft. **Jeffrey A. Seminoff:** Funding acquisition; writing—original draft; writing—review and editing. **Martha O. Burford Reiskind:** Project administration; writing—review and editing; writing—original draft. **Seth P. Stapleton:** Conceptualization; funding acquisition; project administration; writing—original draft; writing—review and editing.

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#### CONFLICT OF INTEREST STATEMENT

The authors declare no conflict of interest.

#### DATA AVAILABILITY STATEMENT

The data that support the findings of this study are available from the corresponding author upon reasonable request.

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## SUPPORTING INFORMATION

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