Vol. 54: 245–259, 2024
https://doi.org/10.3354/esr01339

ENDANGERED SPECIES RESEARCH
Endang Species Res

Published June 27

Satellite telemetry reveals high-use internesting areas and international foraging extent for loggerhead turtles tagged in southeast Florida, USA

Glenn D. Goodwin[1,*], Kristen M. Hart[2], Abby C. Evans[1], Derek A. Burkholder[1]

[1]Halmos College of Arts and Sciences, Nova Southeastern University, Dania Beach, FL 33004, USA
[2]US Geological Survey, Wetland and Aquatic Research Center, Davie, FL 33314, USA

ABSTRACT: Developing conservation strategies for highly migratory marine species relies on understanding their spatial distributions. Nesting populations of female loggerhead (*Caretta caretta*) turtles typically travel from widely dispersed foraging areas and make use of common internesting areas between nesting events. Protection of these areas is essential to the conservation of this species. In this study, we used satellite tracking and behavioral switching state—space movement modeling to examine the internesting use-areas, migration patterns, and foraging area distribution of a previously uninvestigated nesting loggerhead population in southeast Florida. While these turtles spent much of their internesting period close to their nesting site, only 17.4% of the identified internesting area is within the boundaries currently designated under the US Endangered Species Act as critical loggerhead 'nearshore reproductive habitat'. Additionally, 72% of turtles in this study (17 of 21) that were tracked to foraging grounds have foraging home ranges outside of the USA, with 62% of turtles (n = 13) in The Bahamas. Considering the proximity of their internesting areas to a large human population center and their largely international foraging distribution, this population could benefit from expanding federally designated critical habitat, along with developing collaborative conservation strategies between the USA and The Bahamas.

KEY WORDS: *Caretta caretta* · Movement · Critical habitat · Home range · Satellite tracking

1. INTRODUCTION

Managing the recovery of wild populations relies on a fundamental understanding of species distributions. For highly migratory species, especially marine vertebrates, mapping these distributions can be difficult due to limited access to animals and habitats (Runge et al. 2014). However, animal-borne telemetry studies have revealed movements and habitat-use patterns for many marine species (e.g. seals, Thompson et al. 2003; sharks, Papastamatiou et al. 2013; green turtles *Chelonia mydas*, Sloan et al. 2022). By understanding the spatial and temporal distribution of species of conservation concern, researchers can investigate the anthropogenic threats faced by these populations (e.g. recreational boating, Welsh & Witherington 2023; commercial fisheries, Hardy et al. 2014).

Sea turtles are listed as Vulnerable to Critically Endangered by the International Union for the Conservation of Nature (IUCN; Casale & Tucker 2017), with loggerhead turtles *Caretta caretta* listed as Vulnerable. Additionally, the US Endangered Species Act lists all identified population segments of loggerhead turtles as threatened or endangered (NMFS & USFWS 2011). In response, the National Marine Fisheries Service and US Fish and Wildlife Service developed recovery plans, listing multiple tasks that require investigation of loggerhead movements and distribution (NMFS & USFWS 2008), along with designating areas with environmental features essential

*Corresponding author: gg558@nova.edu

Publisher: Inter-Research · www.int-res.com

to loggerhead conservation as critical habitat (e.g. 'nearshore reproductive habitat' for areas offshore of high-density nesting beaches for hatchling swim frenzy and female internesting habitat during nesting season, 'breeding habitat' for areas with high densities of reproductive male and female turtles during breeding season) under the US Endangered Species Act, providing loggerhead turtles special federal protections within these boundaries (NMFS 2014).

Management of this species is complicated, as they occupy broad geographic ranges, differing by life stage and population (Musick & Limpus 1997, Hamann et al. 2010, Wallace et al. 2010, 2011) and have highly varied foraging area dispersal from shared nesting areas (Schofield et al. 2010a, 2013, Evans et al. 2019), as well as the capacity to migrate great distances between nesting and foraging grounds (mean ± SD: 618 ± 445 km; Hays & Scott 2013). Thus, researchers have limited access to study individual turtles throughout most of their lifecycle, with the exception of adult females, which nest on tropical and sub-tropical sandy beaches throughout the world (Wallace et al. 2023). During their nesting season, female loggerheads will nest multiple times (Addison 1996, Sato et al. 1998) and typically remain in internesting habitats relatively close to their nesting area between nesting events (Schofield et al. 2010b, Phillips et al. 2021).

Florida hosts globally significant loggerhead nesting populations, representing 40% of the global and 90% of the Northwest Atlantic nesting populations (Florida Fish and Wildlife Conservation Commission 2016, Casale & Tucker 2017). As such, the post-nesting movements of nesting females have been investigated at many nesting sites throughout the state (e.g. southwest Florida, Hart et al. 2015; east Florida, Ceriani et al. 2017; west Florida; Hart et al. 2018a), identifying foraging areas in US waters, including the Gulf of Mexico (Hart et al. 2012, 2018b) and along the US Atlantic coast (Vander Zanden et al. 2015, Ceriani et al. 2017), as well as areas throughout The Bahamas (Hart et al. 2015, Vander Zanden et al. 2015) and southern Gulf of Mexico (e.g. Girard et al. 2009, Hart et al. 2012). Unlike the more well-studied nesting loggerhead populations in southwest Florida (e.g. Girard et al. 2009, Hart et al. 2012, Phillips et al. 2021) and central east Florida (see Evans et al. 2019), no satellite tracking studies of nesting females have occurred in southeast Florida.

Here, we used satellite telemetry to delineate the post-nesting movements of loggerheads nesting in southeast Florida. Our specific objectives were to identify the spatial extent and high-use areas occupied during the internesting period and examine the overlap between internesting movements and critical habitat as designated under the US Endangered Species Act, identify timing and location of migration paths, and identify the locations of foraging areas.

2. MATERIALS AND METHODS

2.1. Study site and sampling

From 2017 to 2021, we intercepted and tagged nesting female loggerheads encountered during nighttime surveys (21:00–05:00 h) occurring 2–4 times weekly during May to August on beaches in southeast Florida between 26.321° and 25.975° N (see Fig. 1), with the majority of the tagging efforts focused in areas with greater nesting density within the northern and central portions of the study site. Following established protocols (NMFS–SEFSC 2008), we captured turtles following their nesting attempt, using a corral to restrain them for workup (Hart et al. 2010). We outfitted all turtles with internal passive integrated transponder (PIT) and external Inconel flipper tags if none were detected and measured the curved carapace length from the nuchal notch to the tip of the longest supracaudal scute (CCL-tip). For satellite tracking, we outfitted each individual turtle with Argos platform transmitter terminals (PTTs, i.e. satellite tag; SPOT6; Wildlife Computers), following established protocols (NMFS–SEFSC 2008). All turtles were released at the point of capture within 2 h of capture time.

We programmed satellite tags to limit location uplink transmissions to 250 per day and to either report continuously for the entire deployment (i.e. daily; n = 20) or to switch to reporting every third day after a period of 90 d, allowing time to migrate to foraging areas (n = 4). As previous studies have suggested, battery life is not the dominant cause for tag failure but rather caused by transmitter loss or damage and/or biofouling (Hays et al. 2007, Hart et al. 2021), and thus we treated all tags with an antifouling coating (Lightspeed; Propspeed) prior to deployment.

2.2. Data processing

Satellite telemetry data were collected through the Argos satellite system, which uses Kalman filtering (Kalman 1960) to assign location classes (LC) based on accuracy estimates (CLS 2016). We excluded locations without error estimates (LC Z) from the analysis. We downloaded telemetry data from the Wildlife

Computers Data Portal (www.wildlifecomputers.com) and summarized until the date of last transmission.

We investigated the potential causes for tag failure (i.e. battery expired, fouling, unknown) by visually examining the battery voltage readings and wet–dry sensor values plotted over time (see Hart et al. 2021). If the reported voltage dropped and remained below 3.0 V, we inferred that the tag stopped reporting due to the battery expiring. If the MinWetDry and MaxWetDry values came within ~50–75 units of each other or these values converged near the end of reporting, the tag was classified as 'fouled.'

2.3. Switching state–space modeling

Argos location data commonly have wide-ranging error estimates with non-Gaussian distributions, as well as temporally irregular location fixes. To accommodate this uncertainty, we used a behavioral switching state–space model (SSM), allowing us to estimate locations at set intervals, as well as predict the behavioral movement states (i.e. area-restricted search [ARS; indicative of foraging behavior for locations away from internesting areas] or migration) associated with each location (Jonsen et al. 2003, Patterson et al. 2008).

We estimated the movement states (internesting, migration, and foraging) and daily locations using a Bayesian hierarchal double-correlated random walk model fitted to the satellite tracking data of each turtle. Following Roberts et al. (2021), we ran the model using the 'bsam' package (Jonsen et al. 2005, Jonsen 2016), which calls JAGS through the package 'rjags' (Plummer 2022) using R version 4.0.4 (R Core Team 2021). We ran the model using uninformative priors, with sampling from the posterior distribution based on 10 000 iterations after a burn-in of 7000, thinned by 5, and using a time step of 24 h (1 point d^{-1}). If tracks had model parameters that failed to converge on the initial run, we ran these again with an additional 10 000 iterations. To avoid poor location estimates commonly associated with multi-day gaps in tracking data, we removed temporal gaps of >20 d and tracking sections with <50 locations (Hart et al. 2020, Benscoter et al. 2022).

The model considers the mean turn angle and relative speed (and thus move persistence) between consecutive points to estimate behavioral states (ARS or migration) for each time step. Posterior means for behavioral state estimates range continuously between 1 and 2, with means <1.5 indicative of faster, more directionally persistent movements (i.e. migration) and means >1.5 indicative of slower movements with more acute turn angles (i.e. ARS; Jonsen 2016). All ARS locations prior to migration were classified as internesting (though these meandering movements are not necessarily indicative of searching for resources) and those after migration as foraging. We used SSM-estimated daily locations for all analyses, as location estimates produced from this approach account for location error, ultimately resulting in more accurate estimates of the true position of the animal over time. We filtered out all points on land, indicated as having a depth of >0 m as determined by the GEBCO_2023 grid, a global terrain model on a 15 arc-second interval grid global relief model (www.gebco.net, accessed 25 October 2023; used to obtain depth values for all analyses).

2.4. Internesting

We defined the internesting period as the period between tag deployment (or the tracked arrival to the nesting area) and the initiation of the post-nesting migration (Schofield et al. 2009, Hart et al. 2016, Phillips et al. 2021). We did not estimate internesting intervals (the period of time between one deposition and the next during a single reproductive season), as we rarely encountered turtles during subsequent nesting events, and we did not obtain a sufficient number of high-quality location estimates to accurately pinpoint individual nesting events.

To depict the spatial distribution of loggerhead turtles in the internesting period, we summed the number of tracking days during which each turtle was recorded within 2 × 2 km grid cells along southeast Florida. Grid cell size was chosen to incorporate the maximum error estimate for Argos tracking data using Kalman filtering (CLS 2016). We classified summed grid cells in ArcMap version 10.8.1 (ESRI 2020) using the Jenks natural breaks classification method, classifying cells with the highest counts as high-use cells. For high-use cells, we calculated the distance to shore using the Global Self-consistent Hierarchical High-resolution Geography database (Wessel & Smith 1996) and the 'rgeos' package (Bivand & Rundel 2020). We selected the location within each cell with the furthest distance to shore as the maximum distance to shore for each cell. To investigate the use of federally designated loggerhead turtle critical habitat by this nesting population, we quantified the number of internesting daily locations that fell within the designated 'nearshore reproductive' and 'breeding' critical habitats (NMFS 2014).

2.5. Migration

Using SSM migration locations, we determined the start and end dates of migration and calculated migration duration (d), cumulative migratory track length (km), water depth (m), and distance to shore (m) along each turtle's migratory route using the package 'adehabitatLT' (Calenge 2006). We applied a Welch 2-sample *t*-test to assess if there were significant differences in migration start dates between foraging regions. Due to small sample sizes, we pooled the data into 2 larger foraging regions (i.e. Atlantic and Gulf of Mexico). We determined the proportion of time each turtle spent migrating in waters along the continental shelf using the 200 m isobath as a cutoff (i.e. if depth was less than 200 m for a daily location, it was considered over the shelf; greater than 200 m, it was off the shelf).

2.6. Foraging

Using only the points that occurred after the end of the migratory period, we fit home ranges for each individual using kernel density estimation (KDE), a non-parametric method used to estimate an animal's relative frequency distribution over time (i.e. its utilization distribution), smoothed 2-dimensionally, from observed locations throughout the individual's home range (Worton 1987, 1989). This robust approach to the probability density function allows for spatial estimation of high-use areas by specifying a fixed percentage of the confidence region described by the utilization distribution (e.g. 95% confidence region represents the estimated spatial range where the animal spends 95% of its time; Kie et al. 2010). Following established methods (Shaver et al. 2017, Hart et al. 2020), we used SSM-estimated daily locations to generate individual 95 and 50% KDEs, using fixed-kernel least-squares cross-validation (h_{lscv}) as the smoothing factor.

To characterize foraging home range size, we calculated the area of the 95% KDE for each turtle. For other foraging area characteristics, we calculated the centroid of the 50% KDE and used these for depth and distance to shore characterization. We calculated the distance to shore of each centroid as the distance between the centroid and nearest intermediate-resolution shoreline polygon from the Global Self-consistent Hierarchical High-resolution Geography database (Wessel & Smith 1996) using the 'rgeos' package (Bivand & Rundel 2020).

For any turtles that migrated between seasonal foraging sites, we calculated separate KDEs and centroids for their summer and winter foraging areas. Similar to above, we used the predicted behavioral states and visual inspection to determine the departure and arrival dates for each turtle's seasonal foraging areas. Using these dates, we classified the predicted foraging locations as either summer or winter foraging. To ensure the home ranges were limited only to foraging areas, we filtered out all migration-classified locations and used the filtered ARS locations to generate 95 and 50% KDEs.

For turtles foraging in The Bahamas, we used ArcMap version 10.8.1 to plot 50% KDE foraging centroids together with foraging centroids from other foraging studies (Dodd & Byles 2003, Girard et al. 2009, Phillips 2011, Foley et al. 2014, Tucker et al. 2014, Hart et al. 2021, Uribe-Martínez et al. 2021, M. Cherkiss et al. unpubl. data), using published coordinates when available or otherwise visually estimated coordinates from published figures.

3. RESULTS

From 2017 to 2021, we deployed satellite tags on 24 nesting loggerhead turtles, with CCL-tip ranging from 87.1 to 110.7 cm (n = 24; Table 1). Tracking durations ranged from 31 to 1216 d, with each tag reporting between 223 and 8112 locations for a total of 67 535 locations over the entire study period (Table S1 in the Supplement at www.int-res.com/articles/suppl/n054p245_supp.pdf). There were 45 temporal data gaps of >3 d, with gap length ranging from 4 to 130 d (mean ± SD: 12.2 ± 20.6 d) occurring during internesting (n = 3 gaps) and foraging (n = 42 gaps; Table S2). We removed the 5 gaps (11.1%) that were >20 d, which occurred during foraging for Turtle 5 (n = 4) and Turtle 12 (n = 1).

After completing their respective nesting season, 21 of the 24 tagged loggerhead turtles were tracked along their post-nesting migration back to one of 4 foraging regions on the continental shelf: The Bahamas (n = 13); mid-Atlantic bight (MAB, between 33° and 41° N; n = 2); and 2 regions within the Gulf of Mexico: the eastern Gulf of Mexico (EGOM; along the west coast of Florida, n = 4); and southwestern Gulf of Mexico (SWGOM; along the west coast of the Yucatán peninsula, n = 2) (Table 1, Fig. 1, Fig. S1a).

Satellite tags reported longer on average in the Atlantic (i.e. MAB and The Bahamas, mean: 468.6 d, range: 107 to 1216 d) than in the Gulf of Mexico (mean: 191.0 d, range: 87 to 378 d). We inferred the potential causes for tag failure for 11 out of the 24 tags using battery voltage and wet–dry sensor data. At the end of

Table 1. Tracking details of nesting female loggerhead turtles tagged in southeast Florida. Turtles were tracked to 4 foraging regions: mid-Atlantic bight (MAB), Bahamas, eastern Gulf of Mexico (EGOM), and southwestern Gulf of Mexico (SWGOM). N/A: turtles not successfully tracked to foraging grounds. For Turtles 9 and 15, the final tracking date indicates the end of the first foraging period, and the deploy date for tracks for 9-2 and 15-2 indicates the beginning of their second nesting periods. CCL-tip: curved carapace length from the nuchal notch to the tip of the longest supracaudal scute. Dates are formatted as m/d/yyyy or m/d

Turtle	Size (CCL-tip, cm)	Deploy date	Migration period (d)	Final tracking date	Tracking duration (d)	Foraging region
1	96.5	6/8/2019	7/19–8/21 (34)	12/21/2020	563	MAB
2	95.3	6/4/2021	7/2–8/8 (38)	11/30/2021	180	MAB
Mean ± SD	95.9 ± 0.8		36.0 ± 2.8		371.5 ± 270.8	MAB
3	96.2	5/18/2018	7/23–8/5 (14)	9/1/2018	107	Bahamas
4	106.4	6/5/2018	7/15–8/2 (19)	6/11/2019	372	Bahamas
5	98.5	7/8/2018	7/21–8/2 (13)	11/4/2021	1216	Bahamas
6	93.6	8/12/2018	8/26–12/9 (106)	1/18/2020	525	Bahamas
7	110.7	8/13/2018	8/14–8/28 (15)	1/8/2019	149	Bahamas
8	102.0	8/15/2018	9/7–9/20 (14)	12/25/2019	498	Bahamas
9	99.1	6/7/2019	7/16–8/4 (20)	4/2/2021	768	Bahamas
9-2		4/18/2021	Incomplete	7/13/2021		
10	88.0	6/7/2019	8/20–9/9 (21)	1/26/2021	600	Bahamas
11	101.2	7/10/2019	7/28–8/10 (14)	5/27/2020	323	Bahamas
12	97.4	5/30/2020	7/22–8/6 (16)	4/23/2021	329	Bahamas
13	97.9	6/6/2020	6/30–7/11 (12)	4/30/2021	329	Bahamas
14	99.4	6/6/2020	6/29–7/31 (33)	3/20/2022	653	Bahamas
15	104.0	6/15/2021	8/5–8/16 (12)	4/7/2022	417	Bahamas
15-2		4/20/2022	7/22–8/5 (15)	8/5/2022		
Mean ± SD	99.6 ± 5.7		23.8 ± 25.3		483.5 ± 289.5	Bahamas
16	102.4	5/22/2018	8/3–8/15 (13)	11/5/2018	168	EGOM
17	88.6	6/8/2019	6/28–8/3 (37)	9/2/2019	87	EGOM
18	87.1	5/30/2020	7/14–7/18 (5)	10/13/2020	137	EGOM
19	104.0	5/29/2021	7/25–8/15 (22)	6/10/2022	378	EGOM
20	101.5	5/31/2018	7/27–8/28 (33)	10/15/2018	138	SWGOM
21	98.5	6/5/2020	8/11–9/11 (32)	1/28/2021	238	SWGOM
Mean ± SD	97.0 ± 7.3		23.7 ± 12.6		191.0 ± 104.2	Gulf of Mexico
22	104.3	5/22/2018	Incomplete	6/21/2018	31	N/A
23	96.2	5/23/2018	Incomplete	7/14/2018	53	N/A
24	101.0	5/28/2021	Incomplete	7/3/2021	37	N/A
Total			538		8296	
Mean ± SD	99.0 ± 5.6		24.5 ± 20.6		345.7 ± 280.2	All
Range	87.1–110.7		6/28–9/7 (5–106)		31–1216	

transmission, 22 tags had sufficient battery voltage to remain operational. The 2 tags (8%) with batteries that expired were on Turtles 5 and 14, both with foraging areas in The Bahamas. The total tracking duration for each tag was 1216 and 653 d, respectively (Table 1). Overall, as indicated by the tags MinWetDry and MaxWetDry values, 13 tags (54%) became fouled, with 10 of 13 tags (77%) from The Bahamas becoming fouled. However, fouling was only the potential cause for tag failure for 9 tags overall (38%; Bahamas, n = 8; EGOM, n = 1). The cause of failure of the remaining 13 tags (MAB, n = 2; Bahamas, n = 3; EGOM, n = 3; SWGOM, n = 2) was unknown.

Two turtles (Turtles 9 and 15) were tracked for a subsequent nesting season following their initial encounter. We tagged Turtle 9 in 2019 and she returned in 2021, for a total of 768 tracking days. Turtle 15 was tagged in 2021 and returned in 2022, with a total of 417 tracking days (Table 1).

After nesting in the USA, the turtles we tracked traveled through and foraged within the exclusive economic zones (EEZs) of 3 countries: the USA, The Bahamas, and Mexico (Fig. 1, Fig. S1). Overall, post-nesting turtles spent 31% of total tracked days in the US EEZ, 66% in The Bahamas EEZ, and 3% in Mexico's EEZ (Figs. S1 & S2, Table S3). Turtles foraging in the MAB spent 100% of tracked days in the US EEZ. Turtles that foraged in The Bahamas spent 88% of tracked days in The Bahamas EEZ and 12% in the US EEZ. Turtles foraging in the EGOM spent 100% of

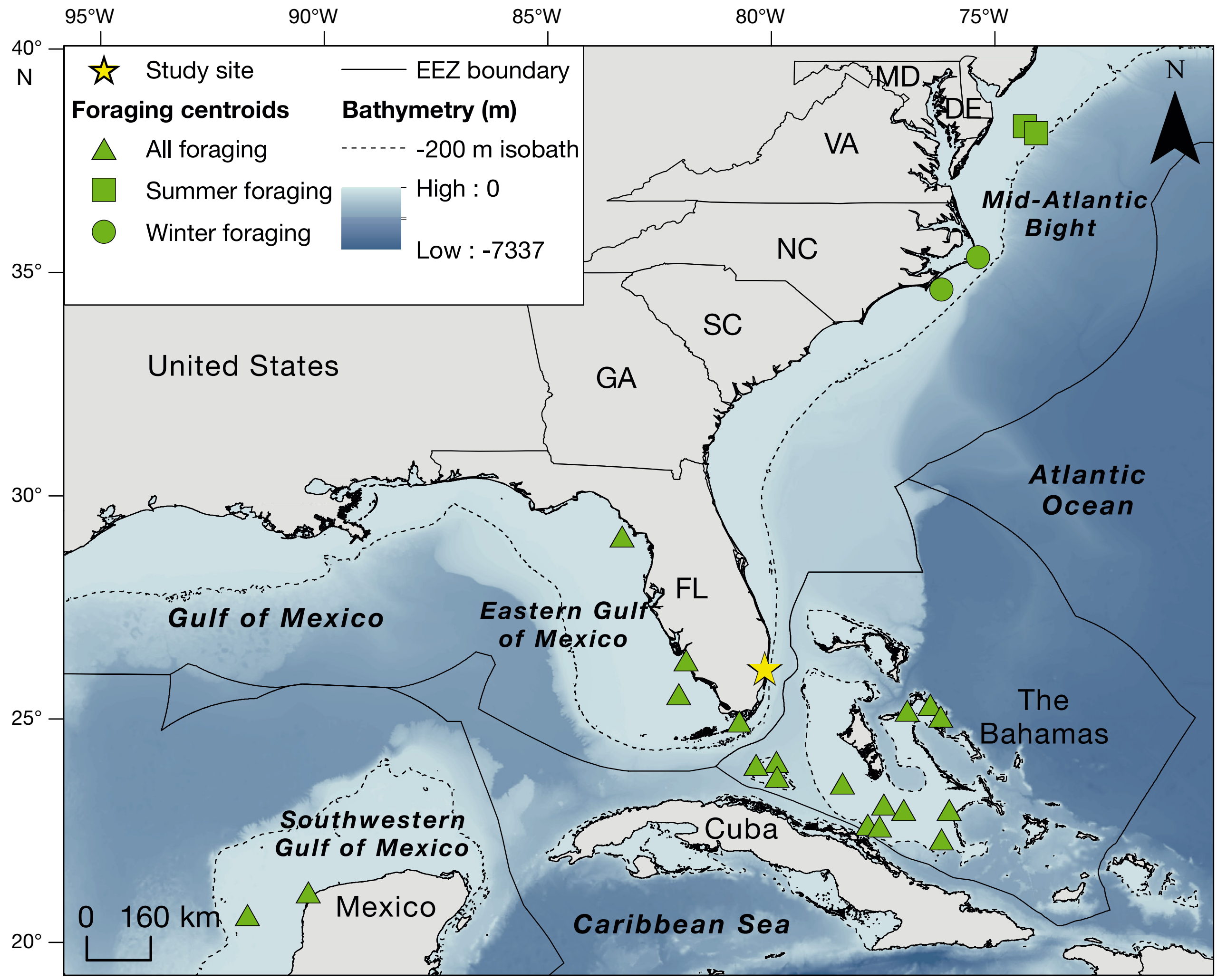

Fig. 1. Study site and foraging centroids of 21 female loggerhead turtles tagged after nesting in southeast Florida from 2017 to 2021, showing regional locations and exclusive economic zones (EEZs). Turtles nesting in the mid-Atlantic bight demonstrated seasonal movements between summer and winter foraging areas, while turtles nesting in other regions remained in the same area for the duration of their tracked foraging period

tracked days in the US EEZ, while turtles foraging in the SWGOM spent 57% of tracked days in Mexico's EEZ and 43% in the US EEZ (Figs. S1 & S2, Table S3).

3.1. Internesting

Of the 24 tagged individuals, 23 had internesting locations available, with the duration of available internesting tracking data ranging from 12 to 92 d (mean: 41.8 d) for a cumulative tracking duration of 1088 internesting days. Turtle 7 was tagged late in the nesting season and had no internesting data available as she began her post-nesting migration within 24 h of tag deployment. Turtle 9 and Turtle 15 provided 2 sets of internesting tracking data, returning for a second nesting season after initial tag deployment. These subsequent nesting seasons lasted for 84 d between 18 April and 11 July, and 92 d between 20 April and 21 July, respectively (Table 1). These are the only known complete internesting periods we recorded, as tags were deployed later than the start of the season and it is unknown how many nests each turtle laid prior to being tagged. The initial and subsequent internesting periods for these turtles were treated separately within the internesting grid, resulting in 25 separate turtle internesting periods for summary.

When summarizing the internesting area, we set the minimum days per cell to 2 d to exclude wandering movements from single individuals. The north-to-south extent of the internesting area was 27.145° to 25.725° N (Fig. 2), with a total area of 469.1 km^2, maximum distance to shore of 8.6 km (median: 1.8 km) and depth range of 1–214 m (median: 19 m; Table S4); 80% of gridded days were in waters ≤50 m deep.

During the 25 monitored turtle internesting periods, 23 turtles (92%) spent some of their internesting days in areas directly east of the study site, with 8 turtles (32%) using areas directly east of the study site for their entire internesting period. Thirteen turtles (52%) used areas up to 91 km north of the study site (Fig. 2, Table S5), and 6 turtles (24%) spent some of their internesting period up to 27 km south of the study site.

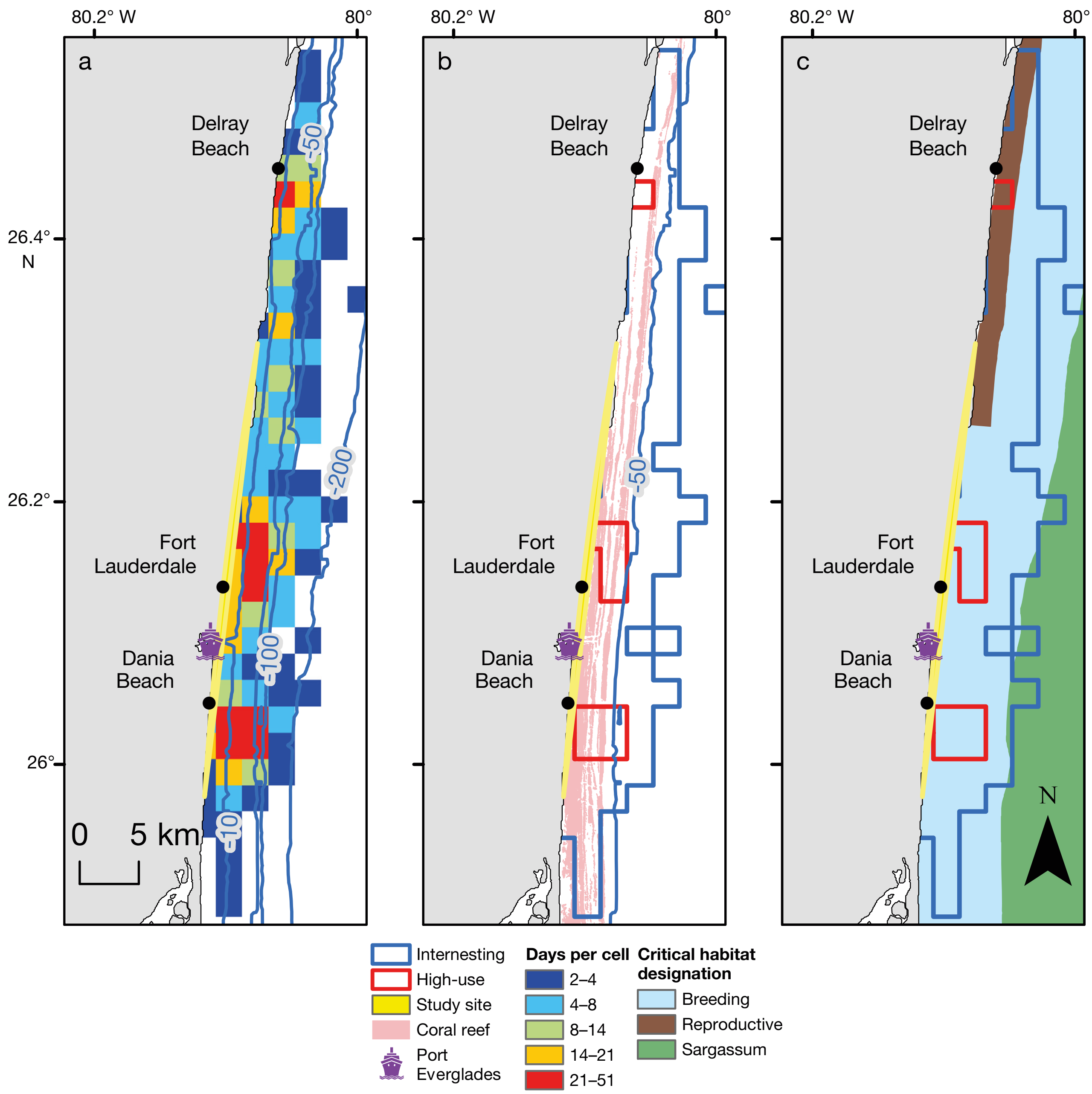

Fig. 2. (a) Grid of 2 × 2 km cells with summed internesting tracking days for 23 of the 24 female loggerheads tagged in this study, showing 2 high-use areas directly east of the study site and one northern high-use area. (b) Boundaries shown for the primary internesting area (cells with ≥2 d) and high-use areas (cells with ≥21 d) used by southeast Florida loggerheads overlayed onto benthic mapping data from the Unified Florida Coral Reef Tract Map v2.0 (Florida Fish and Wildlife Conservation Commission—Fish and Wildlife Research Institute 2016). (c) US federally designated loggerhead critical habitat areas (NMFS 2014) in relation to the primary and high-use internesting areas for southeast Florida loggerheads

We identified 3 high-use areas (cells with ⩾21 d) containing locations from 88% of turtles (n = 22) during internesting, with a maximum distance to shore of 4.6 km (median: 2.0 km) and a depth range of 4–63 m (median: 19 m; Fig. 2a, Tables S4 & S5). Two high-use areas were directly east of the study site and the third was located 12.5 km north of the study site (Fig. 2a). While turtles in the moderate and high-use cells adjacent to the nesting beaches remained within 5.1 km of shore, turtles that used the northern high-use area remained nearer to shore, with a maximum distance to shore of 2.0 km (Fig. 2a). The 2 southern high-use areas were located 3.8 and 5.5 km away from Port Everglades, a major cruise ship and container ship port, with nesting locations for each turtle located 5.0–22.4 km away from the port (Fig. 2a).

For the 2 turtles that were tracked for a second nesting season, the movements for each turtle's initial and subsequent internesting periods were notably similar. Turtle 9 spent 75 and 56% of tracked internesting days in the Dania Beach high-use cells during 2019 and 2021, respectively, and Turtle 15 spent 39 and 38% in the Fort Lauderdale high-use cells in 2021 and 2022, respectively.

We examined the extent of space use within 2 types of federally designated critical habitat: 'breeding habitat' and 'nearshore reproductive habitat' areas. All turtles (n = 25) used the 'breeding habitat,' which contained 97.6% of internesting days, while only 13 (52%) of turtles used the 'nearshore reproductive habitat,' which contained 17.4% of internesting days (Table 2). For turtles captured on beaches adjacent to the designated 'nearshore reproductive habitat', 9 out of 10 (90%) used the 'nearshore reproductive habitat' but were only within the designated boundary for 32.1% of their combined internesting days (Table 2).

3.2. Migration

We observed 22 post-nesting migrations for 21 turtles (Turtle 15 had 2 post-nesting migrations), for a total of 538 migratory tracked days (Table 1, Fig. S1). The tags on Turtles 22, 23, and 24 stopped reporting (tag failure cause unknown) either before they left the internesting area or partially through their post-nesting migration. We did not include incomplete migration data in the analyses. Turtles departed from internesting areas between 27 June and 6 September of each year, with a median departure date of 21 July, initiating their post-nesting migration to foraging grounds (Fig. S3). Migratory start dates did not differ significantly when compared by foraging area destination ($t = 0.40$, df = 11.86, p = 0.70), while migration durations and path lengths differed predictably, with longer duration and distances for foraging areas farther away from the study site.

Depending on the foraging destination, migratory durations ranged from 6 to 107 d (mean: 24.5 d), measuring 235.2–2712.9 km along the path length (median: 760.6 km; Table 3, Fig. S1a). Water depth along each migratory route ranged from 1 to 4675 m (median: 15 m), with turtles spending 80% of their migrations in waters less than 200 m deep within the continental shelf boundaries (Table 3, Table S6). While migrating, turtles stayed 0–372.8 km offshore (median: 18.5 km; Table 3).

We tracked 2 turtles to foraging grounds in the MAB, with migratory durations of 34 and 38 d, traveling 1339.0 and 1543.6 km, respectively (Table 3, Fig. S1b). Along the migratory routes, water depth ranged between 7 and 60 m (median: 27 m), and distance to shore varied between 1 and 101.9 km (median: 41.7 km), with 100% of their migrations over the continental shelf (Table 3, Table S6).

Turtles that migrated to The Bahamas (n = 14 migrations for 13 turtles) did so in 12–106 d (mean: 45.3 d), traveling between 436.5 and 2712.9 km (median: 795.0 km; Table 3, Fig. S1c). Along the migratory routes, water depth ranged from 1 to 4675 m (median: 9 m), and migratory distance to shore ranged from 0 to 180.7 km (median: 16.5 km), with 75% of their migratory locations over the continental shelf (Table 3, Table S6).

Turtles that migrated to the EGOM (n = 4) did so in 5 to 37 d (mean: 25.9 d), traveling 235.2–948.9 km

Table 2. Number of turtles and gridded internesting days loggerheads spent in 2 types of federally designated critical habitat during their internesting periods. Data were summarized for all internesting turtles and for only those that were tagged on beaches adjacent to the designated reproductive habitat

	All turtles			Capture location adjacent to reproductive habitat		
	Total count	Reproductive habitat	Breeding habitat	Total count	Reproductive habitat	Breeding habitat
Turtles	25	13 (52.0%)	25 (100%)	10	9 (90.0%)	10 (100%)
Internesting days	862	150 (17.4%)	841 (97.6%)	296	95 (32.1%)	292 (98.6%)

Table 3. Migration path characteristics for female loggerhead turtles tagged in southeast Florida, grouped by foraging region. Shelf: US continental shelf; NE: not estimated (means were not estimated for regions with only n = 2 individuals). Abbreviations as in Table 1

Foraging region (no. of individuals)	Migration duration (d)		Migration distance (km)		Migration depth (m)		Migration distance to shore (km)		Percent of migration days	
	Mean	Range	Median	Range	Median	Range	Median	Range	Over shelf	Off shelf
MAB (2)	NE	34–38	NE	1339.0–1543.6	27	7–60	41.7	1.0–101.9	100	0
Bahamas (14)	45.3	12–106	795.0	436.5–2712.9	9	1–4675	16.5	0–180.7	75	25
EGOM (4)	25.9	5–37	840.6	235.2–948.9	11	1–86	3.5	0.1–74.5	100	0
SWGOM (2)	NE	32–33	NE	1637.9–1802.4	69	2–3626	37.6	1.7–372.8	57	43
All (22)	24.5	5–106	760.6	235.2–2712.9	15	1–4675	18.5	0–372.8	80	20

(median: 840.6 km; Table 3). All 4 turtles traveled along the length of the Florida Keys, USA, before turning north into the Gulf of Mexico (Fig. S1d). Along the migratory route, water depth ranged from 1 to 86 m (median: 11 m) and distance to shore ranged between 0.1 and 74.5 km (median: 3.5 km), with 100% of migration days over the continental shelf (Table 3, Table S6).

Turtles with foraging areas in the SWGOM (n = 2) migrated for 32 and 33 d, traveling 1637.9 and 1802.4 km, respectively (Table 3, Fig. S1d). Along the migratory routes, water depth ranged from 2 to 3626 m (median: 69 m), and distance to shore ranged from 1.7 to 372.8 km (median: 37.6 km), with 57% of combined migration tracking days over the continental shelf (Table 3, Table S6).

Two turtles took indirect routes to their foraging grounds. Turtle 6 began by swimming about 150 km offshore and doing a roughly 700 km loop north of The Bahamas before swimming 350 km north of the original study site and then finally turning south to complete her 2712.8 km and 108 d migration to the Cay Sal Bank in The Bahamas (Fig. S1c). The other Bahamas turtles accomplished their migrations in an average of 26 d, with a median migration length of 802.4 km. Turtle 17, whose foraging grounds were in the EGOM, initiated her return migration by swimming 175 km north before turning back south to swim around peninsular Florida and arrive at her foraging area off southwest Florida (Fig. S1d), traveling a total of 948.9 km over 38 d, compared to the other turtles foraging in the EGOM with a median migration length of 489.0 km completed over an average of 14.3 d.

Turtles 9 and 15 returned for a second nesting season, providing pre-breeding tracking data, with Turtle 15 also providing a second post-nesting migration (Fig. S1e, Table S7). Both turtles took distinctly different paths for their respective pre-breeding and post-nesting migrations. When returning, each took a more direct path initially and then continued well north of the nesting area before turning back south and arriving at the nesting area (Fig. S1e). Aside from this brief summary, we did not include these migrations in any analyses as they were not post-nesting migrations.

3.3. Foraging

We tracked 21 turtles within their foraging areas for a combined total of 6222 d, ranging from 27 to 983 d per turtle (Table 4). We generated total foraging 95% KDEs for 19 of the 21 turtles (Bahamas, n = 13;

Table 4. Foraging area characteristics for female loggerhead turtles tracked from southeast Florida, summarized by foraging region. We did not estimate the means for foraging areas with n ≤ 2 turtles. Abbreviations as in Table 3; KDE: kernel density estimation. Seasonal foraging areas are indicated with an 'S' and 'W' for summer and winter, respectively

Foraging region (no. of individuals)	Total tracked foraging days			95% KDE area (km^2)		50% KDE centroids			
						Depth (m)		Distance to shore (km)	
	Total	Mean	Range	Mean	Range	Mean	Range	Mean	Range
MAB-S (2)	249	NE	76–173	NE	1546.3–12564.5	NE	45–74	NE	65.4–91.2
MAB-W (2)	242	NE	20–222	NE	386.3–2988.8	NE	24–34	NE	11.8–25.5
Bahamas (13)	5046	388	27–983	230.8	22.5–707.5	8.4	4–11	26.8	0.7–77.3
EGOM (4)	498	124	30–299	1690.7	22.5–4128.8	9.2	2–18	20.8	2.9–49.8
SWGOM (2)	187	NE	48–139	NE	55.6–395.8	NE	9–64	NE	11.4–51.3
All (23)	6222	270.5	27–983	1204.4	22.5–12564.5	17.2	2–74	29.9	0.7–91.2

EGOM, n = 4; SWGOM = 2) and seasonal 95% KDEs for the 2 turtles that foraged in the MAB. For foraging areas with n = 2 individuals (i.e. MAB and SWGOM), we did not estimate means for foraging area characteristics and instead report the values for each individual.

Overall, the 95% KDE foraging home range areas varied from 22.5 to 12 564.5 km^2 (mean: 1204.4 km^2; Table 4). Foraging centroids for the 50% KDEs had water depths ranging from 2 to 74 m (mean: 17.2 m), with centroid distance to shore ranging from 0.7 to 91.2 km (mean: 29.9 km; Table 4).

For both turtles that foraged in the MAB, we calculated 95% KDEs for summer and winter foraging areas, as both turtles exhibited seasonal foraging movements (Fig. S4a). Both turtles initially migrated to more northern summer foraging areas before moving to the southern winter foraging areas. Turtle 1 was tracked for 395 d at her foraging areas, providing tracking data throughout one full winter (2 October 2019 to 9 April 2020) and summer season (14 April 2020 to 11 October 2020) and an additional partial winter season (26 October 2020 to 21 December 2020; Fig. S4a–c). Turtle 2 was tracked for far less time on her foraging grounds (96 d), with tracking data for her summer foraging area limited to her initial arrival after nesting season on 9 August 2021 until departing on 26 October 2021 for her winter foraging area, where she was tracked until 30 November 2021 (Fig. S4a–c). The 95% KDE areas for the summer and winter home ranges used by Turtle 1 (12 564.5 and 2988.8 km^2, respectively) were an order of magnitude larger than the corresponding summer and winter home ranges for Turtle 2 (1546.3 and 386.3 km^2; Fig. 2) and 1–2 orders of magnitude larger than the home range areas in the other foraging regions (Table S8). Summer and winter centroid depths for Turtle 1 were 74 and 34 m, with centroid distances to shore of 91.2 and 25.5 km, respectively, while centroid depths for Turtle 2 were 45 and 24 m, with centroid distances to shore of 65.4 and 11.8 km, respectively (Table S8). The summer and winter centroids were 432.4 and 338.1 km apart for Turtle 1 and Turtle 2, respectively (Fig. S4a). Both turtles remained on the continental shelf for the entirety of their tracked foraging durations, remaining at shallower depths during the winter, with daily foraging locations largely bounded by the 50 m depth contour, spending 90 and 84% (Turtle 1 and Turtle 2, respectively) of their foraging locations at <50 m depth.

We calculated 95% KDEs for all turtles that foraged in The Bahamas (n = 13), which ranged in area from 22.5 to 707.5 km^2 (mean: 230.8 km^2; Table 4). Foraging centroid depths in The Bahamas were the shallowest, ranging from 4 to 11 m (mean: 8.4 m), with centroid distance to shore varying between 0.7 and 77.3 km (mean: 26.8 km; Table 4). Within The Bahamas, turtles settled in foraging areas on the Cay Sal Bank (n = 3), Great Bahama Bank (n = 7), and Eleuthera (n = 3; Fig. 3, Fig. S1c). Centroids closer to shore tended to have smaller home ranges (Table 4), with turtles in Eleuthera tending to have smaller home ranges and turtles on Grand Bahamas Bank tending to have larger home ranges.

For turtles foraging in the EGOM (n = 4), 95% KDE areas had the widest size range, from 22.5 to 4128.8 km^2 (mean: 1690.7 km^2; Table 4). Centroid depths were similar to The Bahamas, ranging from 2 to 18 m (mean: 9.2 m), with centroid distance to shore ranging from 2.9 to 49.8 km (mean: 20.8 km) and turtles with centroids closer to shore tending to have smaller home ranges (Table 4). Turtles foraging in the SWGOM (n = 2) had 95% KDE areas of 55.6 and 395.8 km^2, with centroid depths of 64 and 9 m, and centroid distances to shore of 51.3 and 11.4 km, respectively (Table 4). Within the EGOM, one turtle each settled in Florida Bay, a large open area in the southeastern Gulf of Mexico 100 km northwest of Cape Sable, FL; in San Carlos Bay, ~15 km southeast of Sanibel, FL; and in the Florida Big Bend, ~25 km southwest of Suwanee, FL. In the SWGOM, both turtles settled on the Campeche Bank (Fig. S1d).

4. DISCUSSION

This study provides the first characterization of movements for loggerhead turtles nesting in southeast Florida and identifies common areas used for internesting, migration, and foraging. Many of these areas have been identified in previous studies as important habitats for other loggerhead nesting populations, including the east-central Florida rookery (Ceriani et al. 2017), the Dry Tortugas National Park, USA, subpopulation (Hart et al. 2015), and Georgia, USA, nesting population (Griffin et al. 2013). As a significant number of these turtles divide their lives between habitats in multiple countries, a cohesive and multi-faceted regional approach to conservation is necessary to ensure effective management and recovery of this imperiled species.

4.1. Internesting

We tagged turtles throughout each nesting season, resulting in a wide range of tracking durations during the internesting period. The only known complete

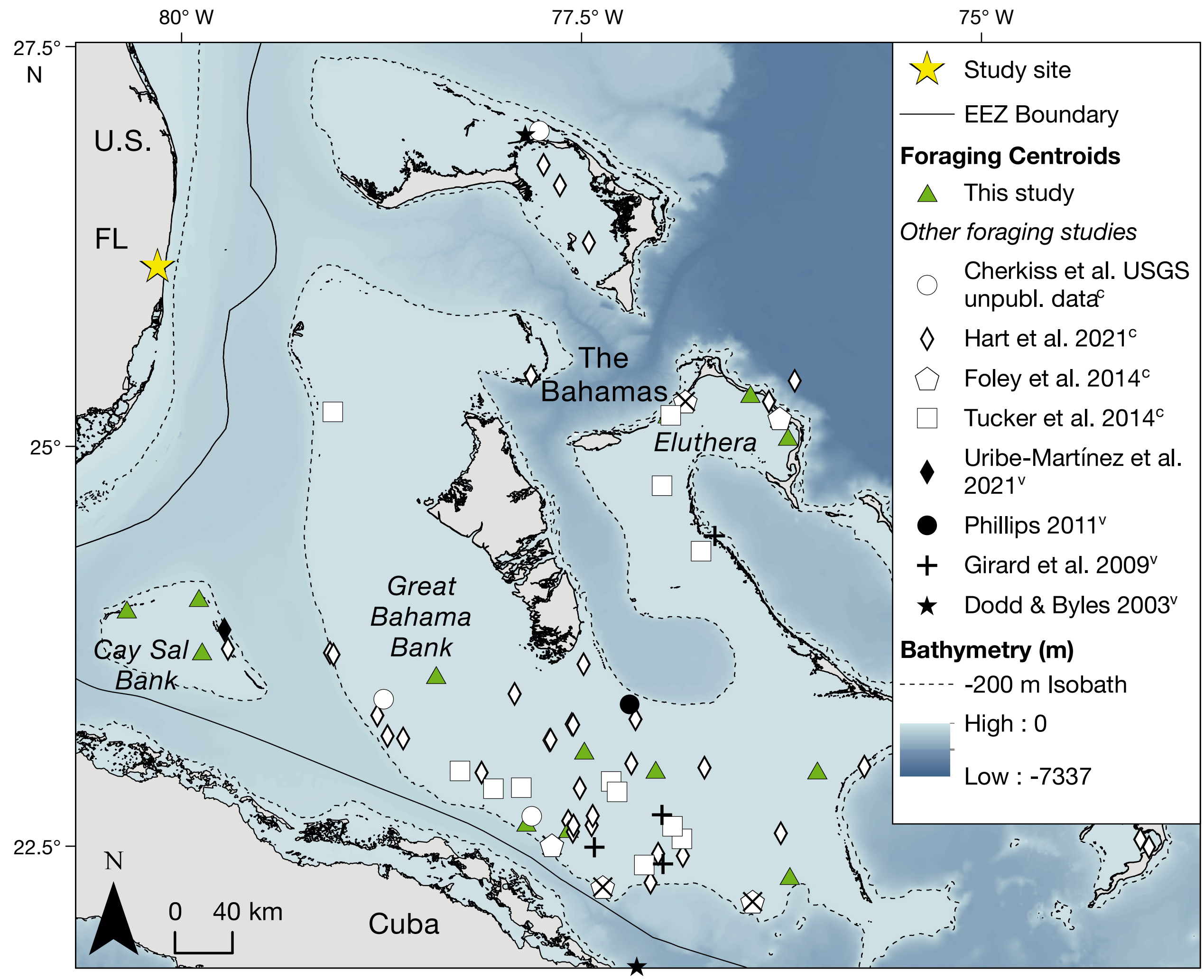

Fig. 3. Adult female loggerhead turtle foraging areas in The Bahamas. The locations of foraging centroids from this study are plotted alongside centroids from other foraging studies; superscript letters next to the study references indicate centroid locations from published or shared coordinates ([c]) or visually estimated centroid locations ([v])

internesting tracks are the second periods for Turtle 9 and Turtle 15 (84 and 92 d, respectively), with both arriving at the nesting area for their second nesting season in mid-April and departing in mid-July. Future studies that work early season tagging into the study design would be valuable to obtain a clearer picture of internesting movements throughout the full nesting season.

Twenty-two of 23 turtles utilized the nearshore waters directly east of the study site, where 2 of the 3 high-use areas were present, with Turtle 9 and Turtle 15 using this area during each of their subsequent tracked nesting periods. However, many turtles also utilized internesting areas markedly north of their observed nesting locations. These northern cells were consistently used by different turtles each year, indicating the value of the area as an important internesting area for this population. Additionally, 3 of the turtles initially tagged in this project were encountered by another team of researchers 60 km north of our study site (S. Hirsch pers. comm.).

Turtles in the moderate and high-use cells adjacent to the nesting beaches remained nearer to shore than those that used the northern high-use area (Fig. 2a). This tapering in east-to-west distribution roughly along the 50 m depth contour follows the longitudinal extent of the Florida Reef tract throughout the internesting area (Fig. 2b), suggesting that female loggerhead turtles prefer to use the habitat types present in this system during their internesting periods rather than choosing to travel elsewhere. Making use of these preferred habitat areas exposes the turtles to the increased threat risks associated with proximity to a major human-populated area, including boat strikes and entanglement (Witherington 1999, Smallwood et al. 2012, Welsh & Witherington 2023), as this area also hosts a high density of recreational boating, fishing, and cargo and cruise ship traffic. Port Everglades, located within the study site, is ranked as a top 3 busiest cruise port and 89th busiest container port globally, with 4048 ship calls in 2023 (www.porteverglades.net, accessed 14 December 2023). The close proximity of the port to the nesting locations and 2 southern high-use internesting areas creates the potential for frequent ship interactions for these nesting females.

The extensive use of these nearshore areas, and their associated threats, highlights the value of nearshore waters adjacent to nesting beaches as an important internesting area for loggerhead turtles (Hart et al. 2016, Phillips et al. 2021) and supports the designation of these areas as critical habitat under the US Endangered Species Act. For loggerheads, the US federal rule identifies 'nearshore reproductive habitat' as nearshore waters adjacent to designated high-density nesting beaches, used by hatchlings during their swim frenzy and by nesting females during internesting, while 'breeding habitat' includes areas of concentrated breeding during the 6 wk or so prior to the nesting season (NMFS 2014). However, while nearly all internesting locations fell within the federally designated 'breeding habitat', relatively few internesting days were within the designated 'nearshore reproductive habitat', which only included the northernmost high-use area (Fig. 2b). Even for turtles with nesting sites on beaches adjacent to the 'nearshore reproductive habitat' (those in the northern portion of the study site), only about one-third of their internesting days fell within the boundaries of the designated 'nearshore reproductive habitat' (Table 2). While these 2 federally designated habitat types provide good coverage of the identified internesting area for this population, the associated temporal limits within the rule are concerning for any future conservation strategies that are developed based on the currently set boundaries. Additional local conservation strategies (e.g. boating speed restriction zones in critical internesting habitat during nesting season) may be beneficial, as the protections imparted by the critical habitat designations only pertain to federal operations in these areas and do little to mitigate other potential risks. Based on our results, expansion of the current federally designated critical habitat areas could be beneficial for this imperiled turtle population.

4.2. Migration

Tracked loggerheads departed from the nesting area between 27 June and 6 September, with a mean internesting departure date of 25 July. Migratory movements were constrained to the continental shelf unless individual foraging areas required turtles to cross deeper waters, exhibiting common migratory behavior documented for multiple other loggerhead rookeries (Griffin et al. 2013, Foley et al. 2014, Evans et al. 2019; Fig. S1a).

While most turtles headed directly back to their foraging grounds after nesting was completed, 2 turtles took indirect, looping routes to their foraging grounds. Though this migration strategy is not common, other authors have documented similar looping movements during migrations for both loggerheads (e.g. Evans et al. 2019) and green turtles (Lamont et al. 2023).

4.3. Foraging

Previous studies on loggerhead post-nesting movements have demonstrated that a wide range of foraging areas from a single nesting rookery is common (Hardy et al. 2014, Evans et al. 2019, Phillips et al. 2021, Cerritelli et al. 2022). Southeast Florida loggerheads similarly returned to distinct foraging areas within 3 of the 4 larger foraging regions, all of which are common foraging grounds for multiple nesting populations. These areas in The Bahamas have been documented as important foraging areas for nearly every Florida rookery (Foley et al. 2014, Hart et al. 2015, Ceriani et al. 2017, Evans et al. 2019; Fig. 3), although prior to this study, Cay Sal Bank had only been documented for 2 individual turtles (nesting sites: southwest Florida, Phillips 2011; northwest Yucatan Peninsula, Mexico, Uribe-Martínez et al. 2021).

In the EGOM, turtles from this study used areas previously identified as foraging hotspots not just for loggerheads (Evans et al. 2019, Hart et al. 2020, Pfaller et al. 2020) but for Kemp's ridley *Lepidochelys kempii* and green turtles as well (Wildermann et al. 2019, Sloan et al. 2022, Lamont et al. 2023). Similarly, in the SWGOM, both turtles shared foraging areas with loggerheads from nesting sites along the northwest Yucatan Peninsula (Uribe-Martínez et al. 2021) and southwest Florida (Girard et al. 2009).

In the MAB, both turtles displayed seasonal migrations between winter and summer foraging grounds commonly seen for adult loggerheads in this higher latitude area (Hawkes et al. 2011, Griffin et al. 2013), remaining in areas of the continental shelf bounded by the 50 m depth contour, similar to the high-use areas selected during internesting. These areas overlap with major foraging areas for loggerheads nesting along eastern central Florida (Hawkes et al. 2011, Ceriani et al. 2017, Evans et al. 2019) and Georgia, USA (Griffin et al. 2013).

In The Bahamas and EGOM, turtles with centroids closer to shore tended to have smaller home ranges. This pattern of larger home ranges in deeper waters further from shore has been observed in multiple loggerhead populations, including the Mediterranean (Schofield et al. 2010a) and the northeastern Gulf of Mexico (Hart et al. 2020).

In this study, 72% of female loggerheads tracked to foraging grounds after nesting in the USA used foraging areas in an international EEZ, with 62% of turtles foraging in The Bahamas. Florida invests heavily in many aspects of sea turtle conservation, such as research, the development and enforcement of lighting ordinances (Witherington et al. 2014), nesting beach monitoring (Burkholder et al. 2024), and sea turtle rehabilitation centers. Yet, as turtles nest infrequently compared to the portion of their lives spent on foraging grounds, the majority of the tracked loggerheads spent relatively few days in Florida waters and the majority of their time outside of any state or federal protected areas. Our results point toward the increased need to design conservation strategies collaboratively with partnering nations in whose waters these turtles reside.

5. CONCLUSION

This study provides previously missing information on the movements of southeast Florida loggerhead nesting females, revealing the limited impact of current conservation measures within their internesting and foraging areas. By delineating the spatial distribution and associated high-use internesting areas, we identified important nearshore areas that would benefit from inclusion as 'nearshore reproductive habitat' within the designated loggerhead critical habitat. Identifying these critical internesting habitat zones provides important information to managers at the county, state, and federal levels for local conservation policy decisions. For example, our results can be used to enact seasonal slow boating zones within high-use internesting areas, similar to protections currently in place for manatees along intracoastal waterways. With such a large proportion of Florida loggerhead nesting females spending the majority of their lifetime in international habitats, it is imperative to investigate the potential for increased threat exposure in these areas to understand the regional conservation challenges for this population. Identifying conservation gaps such as these can better inform policymakers, helping them to craft new conservation strategies that cover the full spatial extent of individuals in this population and allowing for the continued recovery of this imperiled species.

Acknowledgements. We thank Joscelyn Phillips, Marinelle Villanueva, Humberto Gurrola, Colleen McMaken, Kelly Detmer, Sierra Ciciarelli, Caitlin Shanahan, Miranda Fuller, Jacob Larson, Katherine Meurer, Kimberly Schmutz, Briana Coulter, Sarah Gumbleton, Samantha King, Laura Dell, and other Nova Southeastern University (NSU) volunteers for assistance with fieldwork. We also thank Andrew Crowder, Allison Benscoter, Brian Smith, Michael Cherkiss, Jacquelyn Guzy, David Roche, Megan Arias, and other US Geological Survey (USGS) volunteers for assistance with fieldwork and guidance on data analysis. We thank Ryan Logan and the anonymous editors and reviewers who provided valuable feedback to improve the manuscript. Turtle tagging and handling was permitted under MTP-255. Methods were approved by the NSU Institutional Animal Care and Use Committee (IACUC) Protocols NSU IACUC 2020.12.DB2-BBC and the USGS (USGS/WARC/GNV 2017-04 and 2023-01). The present work was part of G.G.'s PhD dissertation. Any use of trade, firm, or product names is for descriptive purposes only and does not imply endorsement by the US Government. Funding for this project was provided by the Community Foundation of Broward, Rock the Ocean, the National Save the Sea Turtle Foundation, the US Animal Telemetry Network, the NSU Presidential Faculty Research and Development Grant, and the USGS Priority Ecosystem Science Program.

LITERATURE CITED

Addison DS (1996) *Caretta caretta* (loggerhead sea turtle) nesting frequency. Herpetol Rev 27:76

Benscoter AM, Smith BJ, Hart KM (2022) Loggerhead marine turtles (*Caretta caretta*) nesting at smaller sizes than expected in the Gulf of Mexico: implications for turtle behavior, population dynamics, and conservation. Conserv Sci Pract 4:e581

Bivand R, Rundel C (2020) rgeos: interface to geometry engine—open source ('GEOS'). R package version 0.5-5. https://CRAN.R-project.org/package=rgeos

Burkholder DA, Evans A, Ciciarelli S, Twiss M (2024) Broward County sea turtle conservation program 2023 technical report. Nova Southeastern University, Dania Beach, FL. https://hcas.nova.edu/seaturtles/data.html

Calenge C (2006) The package 'adehabitat' for the R software: a tool for the analysis of space and habitat use by animals. Ecol Model 197:516–519

Casale P, Tucker AD (2017) *Caretta caretta* (amended version of 2015 assessment). IUCN Red List of Threatened Species 2017: eT3897A119333622. https://dx.doi.org/10.2305/IUCN.UK.2017-2.RLTS.T3897A119333622.en (accessed 13 Dec 2023)

Ceriani SA, Weishampel JF, Ehrhart LM, Mansfield KL, Wunder MB (2017) Foraging and recruitment hotspot dynamics for the largest Atlantic loggerhead turtle rookery. Sci Rep 7:16894

Cerritelli G, Casale P, Sozbilen D, Hochscheid S, Luschi P, Kaska Y (2022) Multidirectional migrations from a major nesting area in Turkey support the widespread distribu-

tion of foraging sites for loggerhead turtles in the Mediterranean. Mar Ecol Prog Ser 683:169–177
CLS (Collecte Localisation Satellite) (2016) Argos user's manual. CLS, Toulouse
Dodd C Jr, Byles R (2003) Post-nesting movements and behavior of loggerhead sea turtles (*Caretta caretta*) departing from east-central Florida nesting beaches. Chelonian Conserv Biol 4:530–536
ESRI (Environmental Systems Research Institute) (2020) ArcGIS Desktop 10.8.1. Environmental Systems Research Institute, Redlands, CA. https://www.esri.com/en-us/arcgis/products/arcgis-desktop/overview
Evans DR, Carthy RR, Ceriani SA (2019) Migration routes, foraging behavior, and site fidelity of loggerhead sea turtles (*Caretta caretta*) satellite tracked from a globally important rookery. Mar Biol 166:134
Florida Fish and Wildlife Conservation Commission (2016) Marine turtle conservation handbook. Florida Fish and Wildlife Conservation Commission, Tallahassee, FL
Florida Fish and Wildlife Conservation Commission—Fish and Wildlife Research Institute (2016) Unified Florida coral reef tract map v2.0. https://ocean.floridamarine.org/IntegratedReefMap/Docs/Metadata_UnifiedFloridaCoralReefMap_v20.html
Foley AM, Schroeder BA, Hardy R, MacPherson SL, Nicholas M (2014) Long-term behavior at foraging sites of adult female loggerhead sea turtles (*Caretta caretta*) from three Florida rookeries. Mar Biol 161:1251–1262
Girard C, Tucker AD, Calmettes B (2009) Post-nesting migrations of loggerhead sea turtles in the Gulf of Mexico: dispersal in highly dynamic conditions. Mar Biol 156:1827–1839
Griffin DB, Murphy SR, Frick MG, Broderick AC and others (2013) Foraging habitats and migration corridors utilized by a recovering subpopulation of adult female loggerhead sea turtles: implications for conservation. Mar Biol 160:3071–3086
Hamann M, Godfrey MH, Seminoff JA, Arthur K and others (2010) Global research priorities for sea turtles: informing management and conservation in the 21st century. Endang Species Res 11:245–269
Hardy RF, Tucker AD, Foley AM, Schroeder BA, Giove RJ, Meylan AB (2014) Spatiotemporal occurrence of loggerhead turtles (*Caretta caretta*) on the west Florida shelf and apparent overlap with a commercial fishery. Can J Fish Aquat Sci 71:1924–1933
Hart KM, Zawada DG, Fujisaki I, Lidz BH (2010) Inter-nesting habitat-use patterns of loggerhead sea turtles: enhancing satellite tracking with benthic mapping. Aquat Biol 11:77–90
Hart KM, Lamont MM, Fujisaki I, Tucker AD, Carthy RR (2012) Common coastal foraging areas for loggerheads in the Gulf of Mexico: opportunities for marine conservation. Biol Conserv 145:185–194
Hart KM, Sartain AR, Fujisaki I (2015) Bahamas connection: residence areas selected by breeding female loggerheads tagged in Dry Tortugas National Park, USA. Anim Biotelem 3:3
Hart KM, Zawada DG, Sartain AR, Fujisaki I (2016) Breeding loggerhead marine turtles *Caretta caretta* in Dry Tortugas National Park, USA, show high fidelity to diverse habitats near nesting beaches. Oryx 50:283–288
Hart KM, Iverson AR, Fujisaki I, Lamont MM, Bucklin D, Shaver DJ (2018a) Marine threats overlap key foraging habitat for two imperiled sea turtle species in the Gulf of Mexico. Front Mar Sci 5:336
Hart KM, Iverson AR, Fujisaki I, Lamont MM, Bucklin D, Shaver DJ (2018b) Sympatry or syntopy? Investigating drivers of distribution and co-occurrence for two imperiled sea turtle species in Gulf of Mexico neritic waters. Ecol Evol 8:12656–12669
Hart KM, Lamont MM, Iverson AR, Smith BJ (2020) The importance of the northeastern Gulf of Mexico to foraging loggerhead sea turtles. Front Mar Sci 7:330
Hart KM, Guzy JC, Smith BJ (2021) Drivers of realized satellite tracking duration in marine turtles. Mov Ecol 9:1
Hawkes LA, Witt MJ, Broderick AC, Coker JW and others (2011) Home on the range: spatial ecology of loggerhead turtles in Atlantic waters of the USA. Divers Distrib 17:624–640
Hays GC, Scott R (2013) Global patterns for upper ceilings on migration distance in sea turtles and comparisons with fish, birds and mammals. Funct Ecol 27:748–756
Hays GC, Bradshaw CJA, James MC, Lovell P, Sims DW (2007) Why do Argos satellite tags deployed on marine animals stop transmitting? J Exp Mar Biol Ecol 349:52–60
Jonsen I (2016) Joint estimation over multiple individuals improves behavioural state inference from animal movement data. Sci Rep 6:20625
Jonsen ID, Myers RA, Flemming JM (2003) Meta-analysis of animal movement using state–space models. Ecology 84:3055–3063
Jonsen ID, Flemming JM, Myers RA (2005) Robust state–space modeling of animal movement data. Ecology 86:2874–2880
Kalman RE (1960) A new approach to linear filtering and prediction problems. J Basic Eng 82:35–45
Kie JG, Matthiopoulos J, Fieberg J, Powell RA and others (2010) The home-range concept: Are traditional estimators still relevant with modern telemetry technology? Philos Trans R Soc B 365:2221–2231
Lamont MM, Benscoter AM, Hart KM (2023) Green turtle movements in the Gulf of Mexico: tracking reveals new migration corridor and habitat use suggestive of MPA expansion. Glob Ecol Conserv 42:e02380
Musick JA, Limpus CJ (1997) Habitat utilization and migration in juvenile sea turtles. In: Lutz PL, Musick JA (eds) The biology of sea turtles, Vol 1. CRC Press, Boca Raton, FL, p 137–163
NMFS (National Marine Fisheries Service), USFWS (US Fish and Wildlife Service) (2008) Recovery plan for the northwest Atlantic population of the loggerhead sea turtle (*Caretta caretta*), second revision. National Marine Fisheries Service, Silver Spring, MD
NMFS, USFWS (2011) Endangered and threatened species; determination of nine distinct population segments of loggerhead sea turtles as endangered or threatened. Fed Regist 76:58868–58952
NMFS (2014) Endangered and threatened species: critical habitat for the northwest Atlantic Ocean loggerhead sea turtle distinct population segment (DPS) and determination regarding critical habitat for the North Pacific Ocean loggerhead DPS. Fed Regist 79:39856–39912
NMFS–SEFSC (Southeast Fisheries Science Center) (2008) Sea turtle research techniques manual. NOAA Tech Memo NMFS-SEFSC-579
Papastamatiou YP, Meyer CG, Carvalho F, Dale JJ, Hutchinson MR, Holland KN (2013) Telemetry and random-walk models reveal complex patterns of partial migration in a large marine predator. Ecology 94:2595–2606

Patterson TA, Thomas L, Wilcox C, Ovaskainen O, Matthiopoulos J (2008) State—space models of individual animal movement. Trends Ecol Evol 23:87—94

Pfaller JB, Pajuelo M, Vander Zanden HB, Andrews KM and others (2020) Identifying patterns in foraging-area origins in breeding aggregations of migratory species: loggerhead turtles in the northwest Atlantic. PLOS ONE 15: e0231325

Phillips KF (2011) Beyond the beach: population trends and foraging site selection of a Florida loggerhead nesting assemblage. MSc thesis, University of Miami, FL

Phillips KF, Addison DS, Sasso CR, Mansfield KL (2021) Postnesting migration routes and fidelity to foraging sites among loggerhead turtles in the western North Atlantic. Bull Mar Sci 97:1—18

Plummer M (2022) rjags: Bayesian graphical models using MCMC. R package version 4-13. https://CRAN.R-project.org/package=rjags

R Core Team (2021) R: a language and environment for statistical computing. R Foundation for Statistical Computing, Vienna

Roberts KE, Smith BJ, Burkholder D, Hart KM (2021) Evaluating the use of marine protected areas by endangered species: a habitat selection approach. Ecol Solut Evid 2: e12035

Runge CA, Martin TG, Possingham HP, Willis SG, Fuller RA (2014) Conserving mobile species. Front Ecol Environ 12: 395—402

Sato K, Matsuzawa Y, Tanaka H, Bando T, Minamikawa S, Sakamoto W, Naito Y (1998) Internesting intervals for loggerhead turtles, *Caretta caretta*, and green turtles, *Chelonia mydas*, are affected by temperature. Can J Zool 76:1651—1662

Schofield G, Lilley MKS, Bishop CM, Brown P and others (2009) Conservation hotspots: implications of intense spatial area use by breeding male and female loggerheads at the Mediterranean's largest rookery. Endang Species Res 10:191—202

Schofield G, Hobson VJ, Fossette S, Lilley MKS, Katselidis KA, Hays GC (2010a) Fidelity to foraging sites, consistency of migration routes and habitat modulation of home range by sea turtles. Divers Distrib 16:840—853

Schofield G, Hobson VJ, Lilley MKS, Katselidis KA, Bishop CM, Brown P, Hays GC (2010b) Inter-annual variability in the home range of breeding turtles: implications for current and future conservation management. Biol Conserv 143:722—730

Schofield G, Dimadi A, Fossette S, Katselidis KA and others (2013) Satellite tracking large numbers of individuals to infer population level dispersal and core areas for the protection of an endangered species. Divers Distrib 19: 834—844

Shaver DJ, Hart KM, Fujisaki I, Bucklin D and others (2017) Inter-nesting movements and habitat-use of adult female Kemp's ridley turtles in the Gulf of Mexico. PLOS ONE 12:e0174248

Sloan KA, Addison DS, Glinsky AT, Benscoter AM, Hart KM (2022) Inter-nesting movements, migratory pathways, and resident foraging areas of green sea turtles (*Chelonia mydas*) satellite-tagged in southwest Florida. Front Mar Sci 8:775367

Smallwood CB, Beckley LE, Moore SA (2012) Influence of zoning and habitats on the spatial distribution of recreational activities in a multiple-use marine park. Coast Manage 40:381—400

Thompson D, Moss SEW, Lovell P (2003) Foraging behaviour of South American fur seals *Arctocephalus australis*: extracting fine scale foraging behaviour from satellite tracks. Mar Ecol Prog Ser 260:285—296

Tucker AD, MacDonald BD, Seminoff JA (2014) Foraging site fidelity and stable isotope values of loggerhead turtles tracked in the Gulf of Mexico and northwest Caribbean. Mar Ecol Prog Ser 502:267—279

Uribe-Martínez A, de los Angeles Liceaga-Correa M, Cuevas E (2021) Critical in-water habitats for post-nesting sea turtles from the southern Gulf of Mexico. J Mar Sci Eng 9:793

Vander Zanden HB, Tucker AD, Hart KM, Lamont MM and others (2015) Determining origin in a migratory marine vertebrate: a novel method to integrate stable isotopes and satellite tracking. Ecol Appl 25:320—335

Wallace BP, DiMatteo AD, Hurley BJ, Finkbeiner EM and others (2010) Regional management units for marine turtles: a novel framework for prioritizing conservation and research across multiple scales. PLOS ONE 5:e15465

Wallace BP, DiMatteo AD, Bolten AB, Chaloupka MY and others (2011) Global conservation priorities for marine turtles. PLoS One 6:e24510

Wallace BP, Posnik ZA, Hurley BJ, DiMatteo AD and others (2023) Marine turtle regional management units 2.0: an updated framework for conservation and research of wide-ranging megafauna species. Endang Species Res 52:209—223

Welsh RC, Witherington BE (2023) Spatial mapping of vulnerability hotspots: information for mitigating vessel-strike risks to sea turtles. Glob Ecol Conserv 46:e02592

Wessel P, Smith WHF (1996) A global, self-consistent, hierarchical, high-resolution shoreline database. J Geophys Res 101:8741—8743

Wildermann NE, Sasso CR, Stokes LW, Snodgrass D, Fuentes MMPB (2019) Habitat use and behavior of multiple species of marine turtles at a foraging area in the Northeastern Gulf of Mexico. Front Mar Sci 6:155

Witherington BE (1999) Reducing threats to nesting habitat. In: Eckert KL, Bjorndal KA, Abreu-Grobois FA, Donnelly M (eds) Research and management techniques for the conservation of sea turtles. Publication No. 4. SSC/IUCN Marine Turtle Specialist Group, Washington, DC, p 179—183

Witherington B, Martin R, Trindell R (2014) Understanding, assessing, and resolving light-pollution problems on sea turtle nesting beaches. FWRI Tech Rep TR-2, version 2. Florida Fish and Wildlife Conservation Commission, St. Petersburg, FL

Worton BJ (1987) A review of models of home range for animal movement. Ecol Model 38:277—298

Worton BJ (1989) Kernel methods for estimating the utilization distribution in home-range studies. Ecology 70: 164—168

Editorial responsibility: Paolo Casale, Pisa, Italy
Reviewed by: 2 anonymous referees

Submitted: December 23, 2023
Accepted: May 13, 2024
Proofs received from author(s): June 18, 2024