

Migratory Routes and Foraging Areas of Post-Nesting Hawksbill Turtles, *Eretmochelys imbricata*, from the Pearl Cays Rookery, Caribbean Nicaragua

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ABSTRACT. – To aid in the conservation of sea turtle populations, it is important to learn about their migratory routes and foraging habitat use when females are away from nesting sites. In this study, 5 post-nesting hawksbill turtles (*Eretmochelys imbricata*) were satellite tracked between 2000 and 2004 from the Pearl Cays, located off the central Caribbean coast of Nicaragua. The 5 females were tracked northeastward to 3 separate resident foraging areas on the continental shelf of Nicaragua, with displacements from the rookery ranging from 140.8 km to 411.2 km. Fifty percent utilization distributions (UDs) computed from Argos locations reflected core inter-nesting home ranges for 2 females of 6.8 km² and 7.7 km² and 50% foraging UD ($n=5$) ranged from 12.5 km² to 62.7 km². Our results add to others suggesting that Caribbean Nicaragua, from the Pearl Cays northward and including the western portion of the Nicaragua Rise, is an epicenter of foraging and migratory habitat for marine turtles. We place our findings in the context of a regional synthesis to suggest that 18.9% ($n=40$) of post-nesting hawksbills satellite tracked from 13 nations or territories in the Caribbean, southern Gulf of Mexico, and Lucayan archipelago forage on the western Nicaragua Rise. Given this growing body of evidence, conservation measures targeted at addressing priority threats to hawksbills and their habitats within the western Nicaragua Rise would undoubtedly have positive impacts on Caribbean hawksbill populations. To this end, the establishment of a bilateral agreement between Nicaragua and Honduras to jointly manage use of marine resources in this region could aid conservation efforts for hawksbills. Enhanced collaboration with other Caribbean nations whose hawksbill populations share these waters would improve the conservation outlook for this highly endangered species.

RESUMEN. – Para ayudar a la conservación de las poblaciones de tortugas marinas, es importante conocer sus rutas migratorias y el uso del hábitat de alimentación cuando las hembras están lejos de los sitios de anidación. En este estudio, se rastrearon por satélite cinco tortugas carey (*Eretmochelys imbricata*) entre 2000 y 2004 tras la anidación en los Cayos Perla, ubicados frente a la costa caribeña central de Nicaragua. Las cinco hembras fueron rastreadas en dirección noreste hacia tres áreas de alimentación distintas en la plataforma continental de Nicaragua, con desplazamientos desde la colonia de entre 140.8 km y 411.2 km. Los análisis de distribuciones de uso (DUs) a nivel de 50% de dos hembras, calculadas mediante las ubicaciones de Argos, reflejaron áreas núcleo entre anidaciones de 6.8 km² y 7.7 km², mientras que las DUs de alimentación al 50% ($n=5$) variaron entre 12.5 km² y 62.7 km². Nuestros resultados se suman a los de otros sugiriendo que la costa Caribe de Nicaragua, desde los Cayos Perla hacia el norte, e incluyendo la porción occidental de la *Nicaragua Rise*, es un epicentro de hábitats migratorios y de alimentación para las tortugas marinas. Interpretamos nuestros hallazgos en el contexto de otras investigaciones en la región para sugerir que el 18.9% ($n=40$) de las tortugas carey rastreadas por satélite durante sus migraciones posteriores a la anidación en 13 naciones o territorios en el Caribe, el sur del Golfo de México y el archipiélago de Lucaya se alimentaron en la parte occidental de la *Nicaragua Rise*.

Debido a esta creciente evidencia, medidas de conservación dirigidas a reducir las amenazas prioritarias que afectan a las tortugas carey y sus hábitats en la parte occidental de la Nicaragua Rise tendrían, sin duda, impactos positivos en las poblaciones de tortugas carey en el Caribe. Con este fin, el establecimiento de un acuerdo bilateral entre Nicaragua y Honduras para manejar de forma conjunta el uso de los recursos marinos en esta región contribuiría a los esfuerzos de conservación enfocados en las tortugas carey. Una mayor colaboración con otras naciones del Caribe cuyas poblaciones de tortuga carey comparten estas aguas mejoraría el futuro de conservación de esta especie en peligro crítico de extinción.

KEY WORDS. – satellite telemetry; migration routes; foraging areas; *Eretmochelys imbricata*; hawksbill turtle; Caribbean; Nicaragua

Hawksbill turtles, *Eretmochelys imbricata*, are found in circum-tropical regions of the world and rarely found outside tropical and subtropical climates. The species is listed as Critically Endangered by the IUCN because most populations have been severely depleted and continue to be under threat, primarily from human exploitation and habitat loss and degradation (Mortimer and Donnelly 2008). This was also the case in most parts of the Caribbean in previous assessments (Mortimer and Donnelly 2008; Campbell 2014). In Nicaragua, since 1999, hawksbills and their eggs have been protected from take by the establishment of a permanent closed season (MARENA 1999).

To facilitate the conservation of sea turtles, knowledge about migratory routes and foraging habitat use is needed, especially when females are away from nesting sites. Satellite telemetry has long been a foundational tool for tracking the movements and migratory routes of sea turtles (Godley et al. 2008). Tracking sea turtle movements using satellite telemetry began in the late 1970s with loggerheads *Caretta caretta* (Stoneburner 1982; Timko and Kolz 1982) and the early 1980s with Kemp's ridleys *Lepidochelys kempi* (see Byles and Keinath 1990 for a summary of early satellite tracking efforts). Satellite telemetry was first used to track movements of hawksbill turtles in the early 1990s from the Yucatán Peninsula, Mexico, and the Caribbean (Byles and Swimmer 1994; Groshens and Vaughan 1994; Hillis 1994), with the first studies in the Pacific taking place by the mid-1990s (Parker et al. 2009). By 2017, a review of scientific literature suggested that more than 7000 marine turtles worldwide were satellite tracked, of which most were loggerheads (44% of transmitters deployed) and only 4.3% were hawksbills (Hays and Hawkes 2018). However, by mid-2025, at least 232 post-nesting hawksbills from 20 nations or territories from throughout the Caribbean, southern Gulf of Mexico (sGoM), and Lucayan archipelago had been outfitted with satellite transmitters (Byles and Swimmer 1994; Groshens and Vaughan 1994; Hillis 1994; Hillis-Starr et al. 2000; Garduño Andrade et al. 2003; Tröng et al. 2005; Evans et al. 2024; Maurer and Eckert 2024; Dunbar et al. 2025; present study). Many of these studies have reported the Nicaragua Rise as an important foraging location for post-nesting hawksbills.

The Nicaragua Rise is a broad, shallow-water platform extending from Honduras and Nicaragua in the southwest to Hispaniola in the northeast, with an approximate length of 1000 km (Arden 1975) (Fig. 1A). In addition to adult female hawksbills, juvenile and male hawksbills, green turtles *Chelonia mydas*, and loggerheads have also been tracked to this area of the western Caribbean (Blumenthal et al. 2006; Moncada et al. 2012; Becking et al. 2016; Uribe-Martínez et al. 2021), highlighting the importance of the Nicaragua Rise for Caribbean sea turtle populations.

Hawksbill nesting on the mainland and nearby cays along the Caribbean and sGoM coasts of Central and North America is well documented (Eckert and Eckert 2019). In contrast, much less is known about the location and use of foraging habitats. There are 2 hawksbill rookeries in Caribbean Nicaragua, El Cocal (Lagueux and Campbell 2005a) and the Pearl Cays (Lagueux et al. 2003). Nietschmann (1981) reported high levels of female and egg exploitation from the Nicaragua coast and implied that populations were depleted. In 1999, under the auspices of the Wildlife Conservation Society (WCS), C. J. Lagueux, C. L. Campbell, and W. A. McCoy began monitoring the Pearl Cays hawksbill rookery and implemented a research and conservation program. During that first year of nest monitoring, at least 110 clutches were laid, of which 97% were poached (Lagueux et al. 2003). As a result of conservation measures that followed—e.g., employment of community members to monitor nesting beaches, engagement of local fishers, and implementation of an incentive program—the Pearl Cays nesting population showed signs of recovery from historical depletion. By 2013, there was an increase to 336 clutches laid; current nesting levels are unknown (C. J. Lagueux unpubl. data, 2013). Threats to hawksbills in the Pearl Cays include intentional take (of juveniles, adults, and eggs), fisheries bycatch, and alteration and destruction of in-water and nesting beach habitats (Lagueux et al. 2003).

Understanding hawksbill movement and habitat use, as well as direct and indirect threats to their recovery, can help identify the management actions needed to improve their conservation outlook. Herein a hawksbill tracking study is presented that was part of a coordinated Caribbean

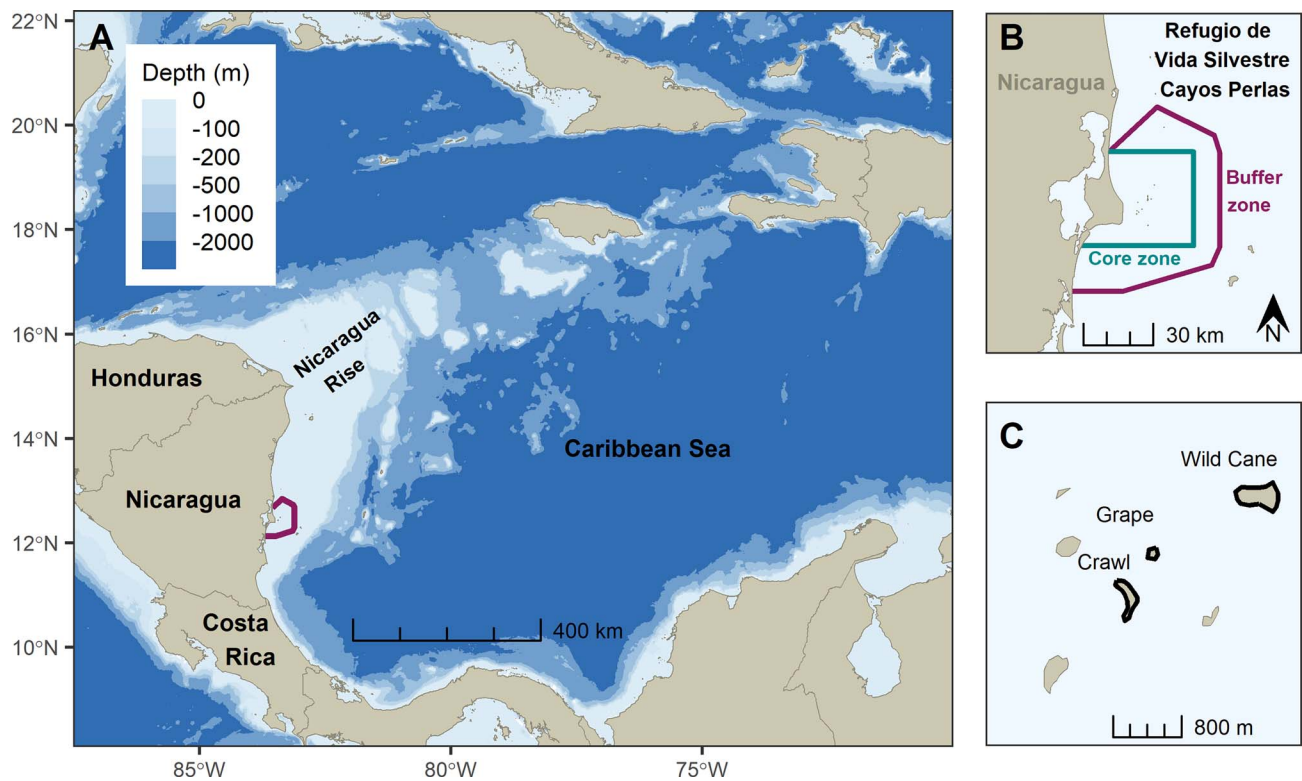


Figure 1. The Pearl Cays are located on the Caribbean coast of Nicaragua. (A) Regional map highlights the study area (magenta polygon) in the southwestern Caribbean. (B) Zoomed extent depicts the location of the Refugio de Vida Silvestre Cayos Perlas, indicating the Buffer Zone (magenta) and Core Zone (green) within central Caribbean Nicaragua (cays are barely visible at the given extent). (C) Subset of cays is mapped, with the 3 focal cays in this study highlighted in bold.

Hawksbill Tracking Consortium that included 10 nations and territories and was initiated in 1998 by the United States National Oceanic and Atmospheric Administration (NOAA) (Schroeder et al. n.d.; Hillis-Starr et al. 2000; Horrocks et al. 2001; Garduño Andrade et al. 2003; Tröng et al. 2005; Van Dam et al. 2008; Maurer et al. 2022). The primary objectives of the consortium were to determine if post-nesting hawksbills undertake long-distance migrations away from their rookeries and to identify foraging ground locations. Since the coordinated efforts of NOAA and collaborators, there has been a large increase in the use of satellite tags on hawksbills in the greater Caribbean region (see Maurer and Eckert 2024).

With this paper, we provide results from the first satellite tracking study for hawksbills nesting in Caribbean Nicaragua and contribute to the growing knowledge base of post-nesting hawksbill migrations and movement patterns in the Caribbean. We used satellite telemetry to determine 1) migratory routes between nesting and foraging grounds, 2) location of foraging grounds, and 3) movement patterns during inter-nesting and foraging phases.

METHODS

Study Area. — The Pearl Cays archipelago is located from 3 to 22 km off the central Caribbean coast of Nicaragua (Fig. 1B). The 22 cays stretch from approximately lat 12.3927°N, long 83.4630°E at their southwest limit to lat

12.5425°N, long 83.3600°E in the northeast. They are surrounded by shallow water, fringing and patch reefs, and seagrass meadows. The cays are low-lying, often with brackish water accumulated in the center of the cay during the rainy season, and comprise calcium carbonate sand, coral rubble, mangroves (e.g., *Rhizophora mangle*, *Conocarpus erectus*, and *Laguncularia racemosa*), coconut trees *Cocos nucifera*, and other tropical vegetation (e.g., seagrass *Coccoloba uvifera*, beach almond *Terminalia catappa*, and morning glory *Ipomoea sagittata*). In 2010, the cays and approximately 700 km² of marine habitat were declared a wildlife refuge, the Refugio de Vida Silvestre Cayos Perlas, by the Nicaragua government (República de Nicaragua 2010) (Fig. 1B).

In 2004 the cumulative, georeferenced coastline of the 22 cays measured 19.0 km; however, only 3.3 km were used for hawksbill nesting (Campbell et al. 2008). The remaining 15.7 km of coastline contained mangroves or coral rubble. Nesting beaches varied, ranging from longer continuous stretches to short beaches separated by non-sandy areas. The 12 cays with hawksbill nesting ranged in size from 0.2 ha to 20 ha (C. L. Campbell and W. A. McCoy unpubl. data, 2004). In more recent years, 2 cays (Maroon and Vincent) have disappeared entirely due to presumed erosion from sea level rise, exacerbated by clearing of vegetation and sand mining (Lagueux et al. 2003; C. J. Lagueux and W.A. McCoy *pers. obs.*), with only underwater remnants of the cays remaining. Furthermore, since at least

2000, nesting beaches have been altered due to increased human activities (Lagueux et al. 2003). Many small, isolated beaches have now been altered and form continuous stretches of sand. This is in part the result of the removal of thick coastal vegetation by humans. No other sea turtle species nests on the Pearl Cays; however, 3 other species occur in the surrounding waters (green turtles, loggerheads, and leatherbacks *Dermochelys coriacea*).

The WCS has been conducting a long-term conservation project to monitor hawksbill nesting since 1999 (Lagueux et al. 2003). C. J. Lagueux and C. L. Campbell developed, implemented, and directed the Pearl Cays hawksbill project from its inception through 2013, and W. A. McCoy, a local fisher, served as the Field Supervisor during this period. Local community members were employed and trained to conduct diurnal beach surveys during the nesting season and periodic nocturnal patrols to encounter nesting females, during which reproductive data on individual turtles were collected.

Transmitter Deployment. — Telonics ST-14 satellite transmitters were deployed on 5 post-nesting hawksbill turtles, 3 in 2000, 1 in 2001, and 1 in 2004 (Table 1). All females were encountered and released with transmitters in August of each year to target the end of their nesting season (Balazs et al. 2000). Programming for the wet/dry sensors on the transmitters allowed the monitoring of dive duration for the final dive before a transmission (dive = any submergence lasting more than 10 secs). To conserve battery life, transmissions for 3 transmitters were duty cycled 9 hrs on followed by 3 hrs off, and 1 was programmed for 6 hrs on and 6 hrs off. Duty cycle information is not available for the fifth transmitter.

To encounter nesting females, project staff conducted night patrols on cays with higher nesting densities. The turtles captured and outfitted with satellite transmitters were encountered on 2 cays, Crawl (lat 12.4331°N, long 83.4257°E) and Wild Cane (lat 12.4435°N, long 83.4117°E) (Fig. 1C). Transmitter attachment and release of the females were conducted on the cay where the female had nested except for Turtle 1, an individual captured on Wild Cane Cay and transported 1.5 km by boat to Grape Cay (lat 12.4374°N, long 83.4232°E) where transmitter attachment and release of the turtle occurred. Prior to transmitter attachment minimum curved carapace length (CCLmin) was measured (Table 1), and flipper tags (Inconel style 681 tags, National Band and Tag Co., Newport, KY) were applied to each front flipper. Preparation of the carapace and transmitter attachment followed Balazs et al. (1996). Transmitters were placed on a silicone elastomer base at the highest point of the carapace and attached with fiberglass strips and polyester resin, with the antennae positioned posteriorly and the base of the antennae reinforced with a roll of fiberglass cloth (Troëng et al. 2005).

Transmitter deployments were used as an opportunity to educate and raise awareness among community members and local authorities about hawksbill turtles, threats to their survival, ecological importance, potential economic value to

Table 1. Transmitter deployment summaries for 5 post-nesting hawksbill turtles (*Eretmochelys imbricata*) tracked from the Pearl Cays, Nicaragua. Minimum size was measured over the curved carapace along the midline (CCLmin). Only filtered locations are included in track duration. Locations denote the number of raw Argos locations after filtering.

ID	Local name	CCLmin (cm)	Release date	Track duration (d)	No. of locations
1	Shanna	90.3	2 Aug 2000	493	828
2	Miss Pearl	86.1	3 Aug 2000	348	374
3 ^a	MIDSI	84.3	3 Aug 2000	122	142
4	Delancey	84.5	18 Aug 2001	148	353
5	Danshely	90.9	29 Aug 2004	364	604

^a Transmitter for Turtle 3 was recovered from fishers, refurbished, and redeployed on Turtle 4. We discarded transmission data for a period when the turtle presumably could have already been caught, retaining ~3.5 mos of data at the foraging area.

the local economy through ecotourism, and their conservation needs. Arrangements were made to transport local authorities, community leaders, and their families to observe transmitter attachments and turtle releases. The events were broadcast on radio stations and cable television in Pearl Lagoon and Bluefields. The local WCS High School Youth Group was involved in the activity and provided with hands-on experience with night patrols, data collection, assistance with transmitter deployments, and naming of the 5 females (Table 1).

Data Analysis. — Argos location accuracy is represented with location classes (3, 2, 1, 0, A, B, and Z), where B and Z fixes entail the most estimated error, and historically no location was determinable for some Z fixes. Obviously erroneous satellite fixes were first removed by excluding locations falling outside of a rectangle bounded by the 83.8°E and 80.2°E longitudes and 12.0°N and 15.9°N latitudes. This left 2301 locations, of which 55 were Argos Z locations, which were also excluded. Another 22 obviously erroneous locations were discarded at the beginning of Turtle 3's satellite track (18 of which were B quality), and 40 initial locations for Turtle 4 (28 B fixes). This manual filtering constrained inference of inter-nesting movements, but the high incidence of problematic B fixes made the data for these periods uninformative.

A modeling framework developed by Jonsen et al. (2023) was next used to fit a state-space model (SSM) to the remaining, filtered Argos fixes and estimated “true” turtle locations at regular timesteps (Jonsen et al. 2005, 2023; Maurer et al. 2022, 2024). Briefly, a simple correlated random walk model (i.e., no behavioral state estimation) was used to estimate locations every 24 hrs. This time step was sufficient for intended inference and set based on a minimum raw fix frequency of 1.2 locations per day (Table 1). Model-estimated locations were then used to designate individual inter-nesting, migratory, and foraging periods following manual delineation methods outlined in Maurer et al. (2024), i.e., based on patterns in displacement from the tagging location, where a migration is characterized by a rapid increase in displacement

followed by a plateau representing arrival at a foraging area.

Locations assigned to migratory periods were used to compute a total distance traveled, or path length, in addition to a straight-line displacement between the tagging location and centroid of an individual foraging area. Ocean current data were related to migratory paths by leveraging the Hybrid Coordinate Ocean Model (HYCOM; Chassignet et al. 2007), querying directional surface velocity data from the months of August and September over 2000–2005. Characterization of space use during inter-nesting and foraging periods was executed with kernel utilization distributions (UDs), employing the R package “adehabitatHR” with the default extent and bandwidth parameter settings (Calenge 2006). This treatment of inter-nesting and foraging areas is sensitive to telemetry inaccuracy, even after using the SSM to smooth error. Thus, while 95% UD are presented to depict the full observed activity space, 50% UD are a better representation of core space use. Common home-range areas, where turtles exhibited overlapping space use during breeding or foraging periods, were considered for all turtles by calculating percent overlap for 95% and 50% UD polygons.

Lastly, a linear mixed-effects model was used to assess whether dive behavior varied as a function of diel period (day versus night) or turtle behavioral phase (migrating versus foraging; inter-nesting periods were not considered given limited data). All available values for duration of the last dive preceding a transmission were used (i.e., no spatial filtering based on Argos fix quality was imposed). Thus, the response variable was dive duration (min). Binary fixed effects were included for behavioral phase (migratory/foraging, as delineated above) and day/night (determined according to sunrise and set times in the *SteamMetabolism* package in R; Sefick Jr 2016), while a random intercepts term for individual turtle ($n = 5$) modeled individual variation.

RESULTS

Transmitter Deployment. — Satellite transmitters were deployed on 5 post-nesting hawksbills over a 5-yr period (2000–2004) from the Pearl Cays rookery, Nicaragua (Table 1). Individuals ranged in size from 84.3 cm to 90.9 cm CCLmin (mean = 87.2 cm $\pm$ 3.2 SD). Transmitters relayed location data until presumed failure, detachment, or removal if encountered nesting during subsequent years. Transmitters were still attached and removed by project team members from Turtles 1, 2, and 5 when they later remigrated to the Pearl Cays to nest. Turtle 3 was caught by a lobster diver working from an industrial boat; her tags and transmitter were removed, and she was released while still on her foraging ground. Her satellite transmitter was returned to the turtle program, refurbished, and redeployed on Turtle 4. Each satellite-tracked female was observed nesting at least once on the Pearl Cays in subsequent nesting seasons, and during as many as 5 different seasons at

2- and 3-yr intervals. Nevertheless, based on flipper tag returns, at least 2 of the 5 females were eventually killed by local fishers. Track durations were sufficiently long to describe a foraging area for all 5 deployments. Tracking durations after data filtering ranged 122–493 days, and individual tracks resulted in 142–828 raw Argos fixes (Table 1).

Migrations. — All 5 post-nesting hawksbills migrated in a northeasterly direction to their foraging grounds, remaining on the Nicaragua continental shelf (Fig. 2A). As they departed the Pearl Cays, they likely encountered weak and slow-moving currents, 0–0.4 m/sec, perpendicular to their heading (Fig. 2B). Speed and strength of the currents for Turtles 1, 3, 4, and 5 would have likely remained similar until they reached their foraging grounds. As Turtle 2 continued in a northeasterly direction, beyond the foraging areas of Turtles 1, 3, and 4, she likely encountered stronger and faster prevailing currents, from 0.4 to 0.6 m/sec, from the southeast that may have facilitated the later part of her journey to her foraging ground (Fig. 2B).

Three turtles (Turtles 1, 3, and 4) made similar displacements ranging 141–151 km compared to displacements of 411 km and 252 km for Turtles 2 and 5, respectively (Table 2). None of the turtles had stopovers during migration. Foraging grounds for all 5 tracked turtles were located on the Miskito Bank platform within the Nicaragua Rise (Fig. 2A). Although the track of Turtle 2 passed through the foraging area of Turtles 1, 3, and 4, she continued to the edge of the Miskito Bank platform, with her resident foraging area near a sharp drop-off, southwest of Rosalind Bank (Fig. 2A). Migratory tracks for all 5 turtles followed nearly straight-line trajectories toward their foraging grounds, with a mean difference of 7.9 km $\pm$ 8.9 SD (range = 0.2–22.9 km) between displacement and path lengths. Mean travel speeds ranged from 9.6 km/day to 21.2 km/day (Table 2).

Inter-nesting Habitat. — After data filtering, the tracks for 2 turtles contained locations depicting nonmigratory movements within an inter-nesting home range before departing the Pearl Cays (Fig. 3). Inter-nesting tracking durations for Turtles 2 and 5 were 30 and 16 days, likely indicating re-nesting an additional 2 times and 1 time before departing the rookery, respectively. The inter-nesting 50% UD for both turtles had an area < 8 km² and a 95% UD of < 27 km² (Table 3; Fig. 3). These 2 turtles showed overlap in inter-nesting space use, as expected given the proximity of the 2 cays where they nested, Crawl and Wild Cane. Their overlap was 1.3 km² for the 50% core area UD and 14.5 km² for the 95% UD.

Foraging Habitat. — Foraging periods for the 5 turtles had more robust datasets, ranging from 104–482 track days (after data filtering) and suggesting 50% UD that were between 13 km² and 63 km² and 95% UD between 87 km² and 290 km² (Table 3). Average bathymetric depth within 50% foraging UD was rather uniform for Turtles 1, 3, 4, and 5, with a mean of 19.2 m $\pm$ 4.9 SD (range = 13–24 m) (Table 3; Fig. 4A, C, D; GEBCO 2023). However,

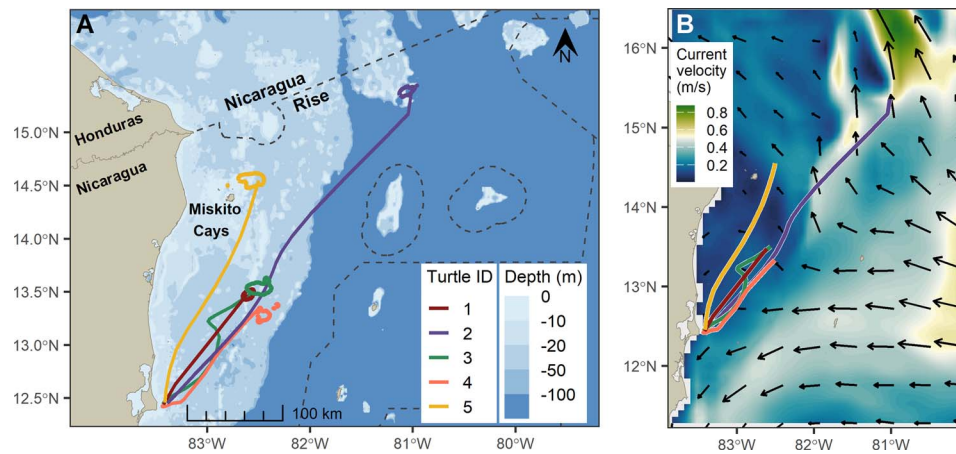


Figure 2. Post-nesting migrations to foraging areas for 5 hawksbill turtles (*Eretmochelys imbricata*) tracked from the Pearl Cays, Nicaragua. (A) Polygons indicate 95% kernel utilization distributions, dashed gray lines display national exclusive economic zones, and bathymetric depth bands (GEBCO 2023) are mapped in blue hues. (B) The same migratory routes are mapped against prevailing currents, as represented using mean HYCOM (Chassignet et al. 2007) surface velocity data over 2000–2005 for the months of August and September; background colors depict the magnitude of velocity, while arrow vectors illustrate the directional component, with bigger arrows showing stronger currents. See panel (A) for turtle IDs.

Turtle 2 foraged in an area near a cliff wall on the Nicaragua Rise with maximum depth of 349 m within its 50% UD and a mean depth of $94.7 \text{ m} \pm 105 \text{ SD}$ (Table 3; Fig. 4B). Two individuals, Turtles 1 and 3, shared space during foraging. While their 50% UDs did not overlap, their 95% UDs exhibited 16.4 km^2 of overlap, equating to 19% of Turtle 1's UD and 6% of Turtle 3's (Fig. 4A).

Dive Behavior. — There were 2135 observations of dive duration, ranging 131–798 observations per turtle, that provided inference into variation in dive behavior. Overall, mean dive durations for individual tracks ranged from 45.2 to 71.6 min (Fig. 5). The linear mixed model provided evidence that dive durations were significantly longer at night as compared to the day ($\beta = 24.7 \pm 0.7 \text{ SE}$; $p < 0.001$) and longer during foraging periods compared to migrations ($\beta = 18.2 \pm 1.3 \text{ SE}$; $p < 0.001$). The estimated variance of the random intercepts term for individual turtle was $106.1 \pm 10 \text{ SD}$ and for the residuals was $218.2 \pm 15 \text{ SD}$. Turtle 2, whose foraging residence was along the edge of a cliff wall, had the longest dive durations compared to the other 4 turtles for all data groupings—overall track, nighttime, daytime, while migrating, and while foraging (Fig. 5).

Table 2. Summary of post-nesting migratory movements for 5 hawksbill turtles (*Eretmochelys imbricata*) satellite tracked from the Pearl Cays, Nicaragua. Durations are presented as whole days (1 location was estimated per day). Displacement is the straight-line distance between nesting site and centroid of an individual foraging area, and path is the inferred migration route taken.

ID	Start	Duration (d)	Displacement (km)	Path (km)	Speed (km/d)
1	2 Aug 2000	11	144.3	144.5	13.1
2	2 Sep 2000	23	411.2	416.8	18.1
3	30 Aug 2000	18	150.5	173.4	9.6
4	4 Sep 2001	13	140.8	149.0	11.5
5	14 Sep 2004	12	251.5	254.2	21.2

DISCUSSION

This study presents the first 5 post-nesting hawksbill turtles satellite tracked from Caribbean Nicaragua. These satellite tracking results contribute to the knowledge base for post-nesting hawksbill migrations and nonmigratory habitat use (inter-nesting and resident foraging) for the region. Previously published satellite tracking results for post-nesting hawksbills from the southwestern Caribbean were from rookeries in Costa Rica, Honduras, and Panama (Troëng et al. 2005; Dunbar et al. 2025).

Inter-nesting Habitat. — Inter-nesting habitat use by 2 hawksbills for both core 50% utilization distributions (UDs) and 95% UDs in the Pearl Cays ($< 8 \text{ km}^2$ and

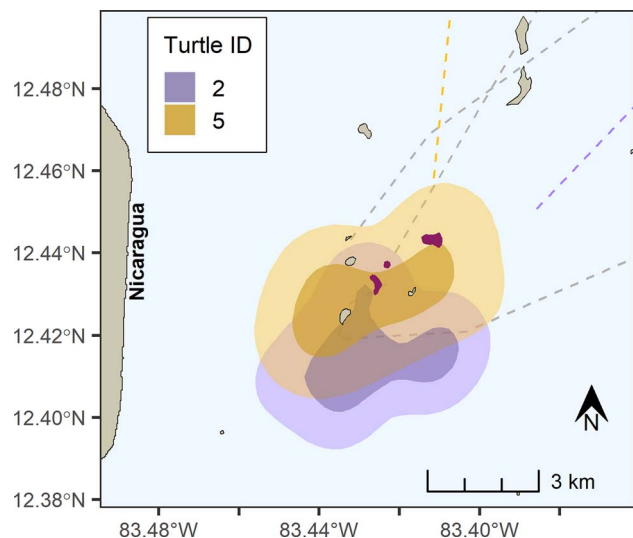


Figure 3. Inter-nesting home ranges for 2 hawksbill turtles (*Eretmochelys imbricata*) satellite tracked from the Pearl Cays, Nicaragua. Turtles are shown in unique color palettes, with the 50% and 95% UDs shown in darker versus lighter hues, respectively. Dashed lines depict migratory departure paths for the 5 turtles; the 2 with inter-nesting data are shown in their respective color.

Table 3. Summaries of space use by 5 post-nesting hawksbill turtles (*Eretmochelys imbricata*) during nonmigratory inter-nesting and foraging periods. A dash denotes no inter-nesting data were available. Mean $\pm$ SD depth within 50% foraging utilization distributions (UDs) is presented, along with minimum and maximum values in parentheses, as calculated from GEBCO (2023) bathymetry data.

ID	Inter-nesting			Foraging			
	Duration (d)	50% UD (km ²)	95% UD (km ²)	Duration (d)	50% UD (km ²)	95% UD (km ²)	Depth (m)(range)
1	—	—	—	482	12.5	87.2	13 $\pm$ 4 (6–20)
2	30	6.8	22.7	295	13.0	104.4	94.7 $\pm$ 105 (1–349)
3	—	—	—	104	62.7	267.4	21.7 $\pm$ 8 (4–36)
4	—	—	—	135	14.4	130.9	24.3 $\pm$ 2 (20–28)
5	16	7.7	26.8	336	19.8	289.9	17.6 $\pm$ 7 (4–29)

< 27 km², respectively) were consistent with results from some turtles tracked in other Argos telemetry studies in the Caribbean, including Martinique (Nivière et al. 2018), Buck Island, US Virgin Islands (Hart et al. 2019), Anguilla (Soanes et al. 2022), Antigua (Maurer et al. 2024), Nevis (Evans et al. 2024), and Panama (Dunbar et al. 2025). Nevertheless, at some sites there was a wide range of inter-nesting habitat sizes for females within the same rookery, ranging from tens of square kilometers (Hart et al. 2019; Fossette et al. 2021; Maurer et al. 2022, 2024; Evans et al. 2024; Dunbar et al. 2025), to hundreds (Nivière et al. 2018; Uribe-Martínez et al. 2021; Dunbar et al. 2025), and even thousands of square kilometers (Dunbar et al. 2025). This range in size of habitat use could be due to differences in habitat structure and resource availability. There may be a greater range in the size of inter-nesting habitat use for Pearl Cays hawksbills; however, our sample size was too small to determine habitat size variability for this population.

The marine habitat within the Pearl Cays archipelago is comprised of fringing and patch reefs interspersed with seagrass meadows, apparently providing ample food resources for juvenile hawksbills as indicated by the resident juvenile aggregation (C. J. Lagueux, C. L. Campbell, and W. A. McCoy unpubl. data, 2000). Although we are

not aware that females were foraging during the inter-nesting periods, females may take advantage of these resources during the nesting season, as may be occurring in Nevis (Evans et al. 2024).

Migratory Routes. — From the Pearl Cays rookery, all 5 post-nesting females took a nearly direct path to 3 separate foraging areas within the Nicaragua Exclusive Economic Zone on the Nicaragua Rise. The small difference between the length of the migratory path and straight-line distance (ranged from 0.2 km to 22.9 km) was likely due, in part, to weak and slow-moving currents they encountered during their migrations. Only Turtle 2 encountered stronger and faster moving currents during the later part of her journey. Thus, the velocity and direction of currents at the time of this study apparently did not cause turtles to deviate appreciably from a straight-line path during their migration. Currents may have a range of influences on sea turtle migrations (Luschi et al. 2003). In some cases, turtles appear influenced by velocity and direction of currents causing them to use a less-direct route to their foraging grounds (e.g., Horrocks et al. 2001; Esteban et al. 2015; Nivière et al. 2018). In other cases, current velocity and direction appear to have little impact on migratory paths, as sea turtles were able to take direct routes to their foraging ground (e.g., Cuevas et al. 2008;

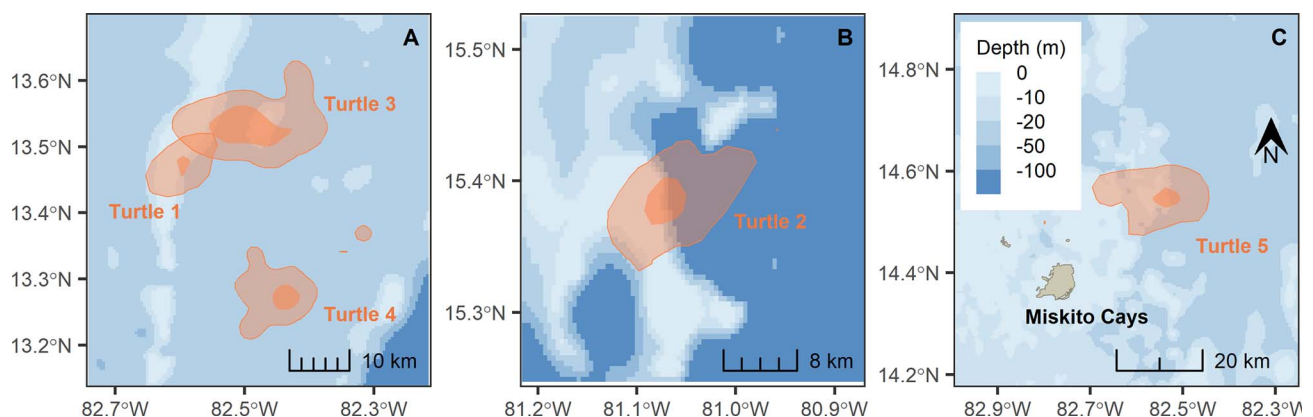


Figure 4. Overlapping polygons show 50% and 95% utilization distributions (shown in darker versus lighter hues, respectively) representing foraging home ranges for 5 hawksbill turtles (*Eretmochelys imbricata*) satellite tracked from the Pearl Cays, Nicaragua. Per the numbering of individual turtles in Table 1, (A) depicts overlapping home ranges for Turtles 1 and 3, and the proximity of Turtle 4, (B) depicts the home range for Turtle 2, and (C) depicts the home range for Turtle 5. Refer to Fig. 2 for broader geographic context. The blue backgrounds show GEBCO bathymetry data (GEBCO 2023).

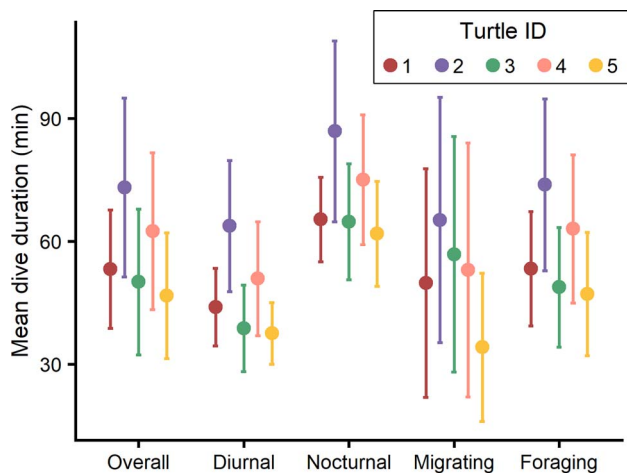


Figure 5. Summary of dive durations for 5 post-nesting hawksbill turtles (*Eretmochelys imbricata*) from the Pearl Cays, Nicaragua. Mean $\pm$ SD is presented in minutes for all measurements for an individual track (overall), in addition to 4 subsets. Inferences are based on measurements of the last dive preceding a satellite transmission.

present study). Gaspar et al. (2006) state that the impact of currents on the tracks of marine animals can be highly variable, although they suggest that such impacts are rarely negligible.

Four of the hawksbills (Turtles 1–4) took a similar path away from the rookery, possibly indicating the location of an important migratory corridor for post-nesting Pearl Cays hawksbills. Three females (Turtles 1, 3, and 4) migrated to a foraging area between 98 km and 120 km offshore from Prinzapolka, Nicaragua. Four females from other rookeries in the Dominican Republic (Hawkes et al. 2012), Antigua (Maurer et al. 2024), and Costa Rica (Dunbar et al. 2025) were also satellite tracked to this area off the Nicaragua central Caribbean coast. Combined, these 7 foraging sites indicate that the continental shelf off the central Caribbean coast of Nicaragua is an important foraging area for post-nesting hawksbills. A fourth Pearl Cays female (Turtle 5) migrated to the Miskito Cays area, and a fifth (Turtle 2) migrated to an area approximately 225 km from the Nicaragua-Honduras mainland border. Both areas were previously identified as foraging areas for hawksbills from other rookeries (see “Importance of Nicaragua Rise” subsection).

Post-nesting hawksbills tracked to date from the southwest Caribbean (i.e., from Panama to Nicaragua) appear to migrate in a northerly direction to the western Nicaragua Rise, although some paths have not been as direct as those from the Pearl Cays (Troëng et al. 2005; Dunbar et al. 2025). Post-nesting hawksbills tracked from the sGoM and Yucatán peninsula have either migrated to foraging grounds within Mexico’s waters or to the Nicaragua Rise (Cuevas et al. 2008; Uribe-Martínez et al. 2021). Interestingly, the direction of travel for 5 females tracked from Utila, Honduras, the country to the immediate north of Nicaragua, was westward within Honduras or northward

to Belize and Mexico and not southward to the Nicaragua Rise (Dunbar et al. 2025).

Migrations from other hawksbill rookeries in the Caribbean indicate that migration distance varies among females from the same rookery, from shorter to longer migrations near their rookery (e.g., Horrocks et al. 2001; Hawkes et al. 2012; Moncada et al. 2012; Maurer et al. 2022, 2024; Evans et al. 2024). All 5 hawksbills from Nicaragua traveled short distances (< 420 km), with 3 of the 5 tracks < 175 km. Although our results could be an artifact of a small sample size, females were tracked during 3 nesting seasons thereby sampling across at least 2 cohorts. The short distance traveled to foraging habitats by Pearl Cays hawksbills within the Nicaragua Rise helps confirm the suitability of this habitat for hawksbills, indicating adequate food availability.

The similarity in migration pathways for western Caribbean rookeries contrasts with the migratory paths of post-nesting hawksbills from the insular Caribbean, where migrations occur in multiple directions and often end thousands of kilometers from their origins (e.g., Horrocks et al. 2001; Hart et al. 2019; Soanes et al. 2022; Evans et al. 2024; Maurer et al. 2024). This dichotomy of migrating across ocean basins versus along landmasses is seen in other ocean basins where hawksbills nesting on or near large land masses migrate over continental shelves along coastlines (e.g., Marcovaldi et al. 2012; Fossette et al. 2021), whereas hawksbills from insular rookeries migrate in a variety of directions (e.g., Mortimer and Balazs 2000; Madden Hof et al. 2023; Nivière et al. 2024). Additionally, none of the satellite tracked hawksbills from the sGoM or Caribbean have migrated eastward into deeper waters of the Atlantic Ocean, reinforcing our knowledge that hawksbills are tied to neritic, coastal waters for foraging and developmental habitat. Nevertheless, they may make migrations over deeper Caribbean waters to reach their foraging grounds (Becking et al. 2016; Nivière et al. 2018; Hart et al. 2019; Evans et al. 2024).

Importance of the Nicaragua Rise. — As early as the late 1950s, the Miskito Cays (within the Nicaragua Rise) was identified as a potentially important foraging area for post-nesting hawksbills based on flipper tag returns (Carr et al. 1966). Other flipper tag recovery studies since then have also reported this area as important for hawksbills (Carr and Stancyk 1975; Bjørndal et al. 1985; Hillis 1994; Meylan 1999; Hillis-Starr et al. 2000; Troëng et al. 2005; Horrocks et al. 2011). Tag returns do not, however, necessarily indicate a foraging ground, as turtles may have been migrating through the area when captured.

A literature review identified 232 post-nesting hawksbills satellite tracked in the Caribbean prior to mid-2025, 212 were tracked to their foraging grounds, of which 18.9% ($n = 40$) had home ranges within the western portion of the Nicaragua Rise. Hawksbills tracked to the Nicaragua Rise originated from 13 nations or territories: Antigua, Bonaire, Costa Rica, Cuba, Dominican

Republic, Jamaica, Martinique, Mexico, Nevis (Nevis and St. Kitts), Nicaragua, Panama, Puerto Rico, and the US Virgin Islands (Troëng et al. 2005; van Dam et al. 2008; Hawkes et al. 2012; Moncada et al. 2012; Becking et al. 2016; Nivière et al. 2018; Hart et al. 2019; Uribe-Martínez et al. 2021; Maurer et al. 2022, 2024; Evans et al. 2024; Dunbar et al. 2025; present study). This growing body of work reinforces the importance of the western Nicaragua Rise for foraging and migratory habitat for adult female hawksbills in the Caribbean. Furthermore, tag recoveries of juvenile hawksbills indicate this area is also an important developmental habitat (C. J. Lagueux and C. L. Campbell unpubl. data, 1998). As a subregion of the Caribbean, the western Nicaragua Rise is a clear candidate for concerted multinational efforts to reduce threats to hawksbills and promote recovery of regional populations.

Identifying Critical Habitat Through Tagging. — Concerted efforts to flipper tag and satellite track more juvenile and adult hawksbills are needed to provide a more complete understanding of foraging habitats for rookeries throughout the region. Not until flipper tagging almost 1800 nesting hawksbills in Barbados and subsequent recovery of flipper tags was the western Caribbean confirmed as a possible foraging area for this most eastern Lesser Antilles hawksbill rookery, a straight-line distance of approximately 2600 km (Horrocks et al. 2001, 2011). In 1998, 4 post-nesting hawksbills were satellite tracked from Antigua, and none migrated more than 130 km to foraging grounds (Maurer et al. 2022). However, when 22 additional post-nesting hawksbills were tracked from Antigua between 2016 and 2019, the Nicaragua Rise was identified for 2 of these females as a foraging ground, a straight-line distance of approximately 2250 km (Maurer et al. 2024). Results from these studies illustrate that sample size is a critical factor for both flipper and satellite tagging to understand the full scope of migratory routes and foraging grounds for specific rookeries. Tagging efforts at unstudied rookeries would add to the growing body of knowledge of hawksbill migratory and foraging habitats.

Foraging Habitat. — In general, there was consistency in the small size ($< 20 \text{ km}^2$) of core-use foraging areas among the 5 tracked turtles, except for Turtle 3. Turtle 3 was the outlier with a core foraging area roughly 3 times (62.7 km^2) the size of the other 4 hawksbills, despite being near Turtle 1 and likely with access to similar resources. Core foraging areas reported in some Argos studies were also small, even with larger sample sizes (e.g., Hart et al. 2019; Evans et al. 2024; Maurer et al. 2024). However, other studies demonstrated higher variability in core foraging area size, ranging from < 10 to hundreds of square kilometers (Dunbar et al. 2025). Variation in core foraging area size for hawksbills is likely linked to habitat type (e.g., reef versus cliff wall), quality, and resource availability.

Studies indicate sea turtles demonstrate fidelity to resident foraging areas over several breeding migrations (Broderick et al. 2007; Hart et al. 2015; Shimada et al.

2019; Hamilton et al. 2021; Maurer et al. 2025), with changes to resident foraging locations occurring only rarely (Cheng 2000; Shimada et al. 2019). Interestingly, Turtle 3, based on the recovery of her flipper tags, was reportedly recaptured on a green turtle fishing bank south of the Miskito Cays and subsequently killed. The recapture location was approximately 100 km northwest of her foraging ground previously identified from satellite tracking. It is unknown if Turtle 3 was in the process of changing her putative resident foraging ground (first identified in 2000) or if she was still migrating when captured in-water the second time. It is also possible that she was displaced by Hurricane Felix (Category 5) during remigration to her area of residence, although we have no direct evidence. Nevertheless, she was last observed nesting in the Pearl Cays on 22 August 2007, after which Hurricane Felix made landfall on the northern Nicaragua coast on 4 September 2007, which heavily impacted the area. It seems possible that this weather event impacted her return to her previously identified foraging site.

Population Threats. — In Nicaragua, juvenile and adult hawksbills and eggs are illegally taken from foraging and nesting habitats. Meat and eggs are consumed locally by fishers and their families or shared with community members, and the shell is illegally sold to local artisans who fashion the scutes into jewelry (e.g., bracelets, earrings, rings) (Lagueux 1998; Lagueux et al. 2003; Lagueux and Campbell 2005a, 2005b; Bräutigam and Eckert 2006). There is directed take of hawksbills in the green turtle fishery and opportunistic take in lobster and sea cucumber artisanal and industrial fisheries. Bycatch of hawksbills occurs in gill and lobster net fisheries (Lagueux and Campbell 2005a, 2005b). Other threats include unregulated and uncontrolled alteration of nesting habitat in the Pearl Cays, destruction of foraging habitat due to sedimentation from mainland runoff and erosion of the cays, anthropogenic debris and waste discarded at sea from fishers and those providing services while living at sea, and alteration and destruction of habitats from fishing methods (Lagueux 1998; Lagueux et al. 2003; Lagueux and Campbell 2005b).

The known mortality of 2 of the tracked females (Turtles 1 and 3) occurred in local artisanal fisheries. These turtles were killed 2 and 7 yrs post-transmitter deployment. Turtle 1 was captured in 2002 by an artisanal fisher in coastal waters southwest of her resident foraging area. She nested in the Pearl Cays during the same season and was likely captured during her migration to her foraging area. See details on the mortality of Turtle 3 described in the “Foraging Habitat” section. The known mortality for 2 of 5 females tracked in this study highlights the significant threat posed by local fisheries to this population. This threat has been demonstrated in green turtles exposed to fishing activities in Nicaragua, where large juvenile and adult sea turtles are known to have lower than expected survival rates (Campbell and Lagueux 2005). The impact of these lower green turtle survival

rates is perhaps reflected in the decline of the nearby green turtle rookery at Tortuguero, Costa Rica (Restrepo et al. 2023), and green turtles share foraging habitats with hawksbills in this region.

Based on a region-wide analysis, Nicaragua is ranked as having medium to high levels of artisanal fishing pressure (Dunn et al. 2010). Sea cucumbers (Class Holothuroidea) and the Caribbean spiny lobster (*Panulirus argus*) were ranked second and third in annual fishery production on Nicaragua's Caribbean coast, respectively (INPESCA 2023). Hawksbills inhabit the same coral reef environments as sea cucumbers and spiny lobsters, making them highly vulnerable to being captured by divers in these fisheries. The magnitude of hawksbills caught is unknown, but their capture in these fisheries is well established from flipper tag recoveries (C. J. Lagueux and C. L. Campbell unpubl. data, 1998; present study). Hawksbills and loggerheads are also caught in large mesh entanglement nets set in the legal artisanal green turtle fishery and in gill-net fisheries (Lagueux 1998; Lagueux and Campbell 2005a). From 1991 through 1996, > 170 hawksbills of all size classes were reported caught in the green turtle fishery (Lagueux 1998).

Oil and gas exploration on the Nicaragua continental shelf is also a potential threat to foraging sea turtles and the Pearl Cays hawksbill rookery. However, the extent and magnitude of this threat to sea turtles is not well known (Nelms et al. 2016). To conduct seismic surveys offshore, air guns are used to create sound waves. The potential harm to sea turtles includes exclusion from critical habitats, damage to hearing, and entanglement in seismic survey equipment (Nelms et al. 2016). Drilling of wells can also degrade seagrass meadows and coral reefs. Petroleum exploration in Caribbean Nicaragua waters began as early as 1930 with an active exploration and exploratory well drilling period between 1960 and 1978 (MEM 2010). In the early 2010s, the Nicaragua government awarded 4 exploratory concessions in their Caribbean waters (MEM 2023). In late 2013, the first well in 30 yrs was drilled in offshore Caribbean Nicaragua (Bunge et al. 2017). Exploration and production of oil and gas on the Nicaraguan continental shelf is of concern for hawksbill populations throughout the region, as evidenced by the catastrophic impact on marine life by the Deepwater Horizon explosion and subsequent oil spill in the GoM in 2010 (Deepwater Horizon Natural Resource Damage Assessment Trustees 2016).

Conservation Considerations. — Satellite tracking of marine turtle movements provides a range of information (e.g., location of inter-nesting, breeding, and foraging areas; and potential migratory corridors) that may be used by community and government authorities to improve protection measures for endangered species (Hamilton et al. 2021; Jim et al. 2022). The inter-nesting habitat of at least 2 hawksbills in this study are within the boundaries of the core zone of the Refugio de Vida Silvestre Cayos Perlas (RVSCP). However, enforcement of regulations within the RVSCP is insufficient to protect

hawksbills. An additional measure that would benefit hawksbills is to establish a seasonal closed area within the core zone of the RVSCP to reduce human disturbance to nesting hawksbills, as well as reduce opportunistic take and bycatch in fisheries (e.g., lobster, entanglement net, and sea cucumber). Although our small sample size is insufficient to draw strong conclusions about habitat use during their inter-nesting period, it is a good starting point to implement actions to reduce threats within the RVSCP. Additional satellite tracking of this population would help to confirm inter-nesting habitat use, breeding areas, migratory corridors, and potential additional foraging areas to solidify appropriate management actions needed to protect the Pearl Cays rookery. Male hawksbills should be included in future tracking studies to ensure that important habitats for them are also identified and included in protection efforts.

The importance of the Nicaragua Rise for Caribbean hawksbills cannot be overstated. Nearly 19% of 212 post-nesting hawksbills satellite tracked from throughout the region were tracked to foraging grounds on the Nicaragua Rise. These results suggest that these waters are an epicenter for hawksbills of multiple life stages from numerous rookeries. Furthermore, they also provide important habitat for green turtles and loggerheads (Carr et al. 1978; Campbell and Lagueux 2005; Troëng et al. 2005; Blumenthal et al. 2006; Becking et al. 2016; Uribe-Martínez et al. 2021).

Nicaragua's multitude of governmental authorities (i.e., communal, territorial, municipal, regional autonomous, and national) on the Caribbean coast not only have an opportunity to protect the Pearl Cays hawksbill rookery but also the migratory routes and foraging habitats on which they depend (Hernández Munguía and González 2005; Luna et al. 2005; Jim et al. 2022). Implementation of strong conservation measures within Nicaragua may be sufficient to reduce mortality of Pearl Cays nesting hawksbills because at least a portion of the population forages within Nicaragua. Furthermore, the presence of turtles from disparate rookeries in Nicaraguan waters means that local authorities can also contribute to the protection and recovery of sea turtle populations throughout the Caribbean. Internally, Nicaraguan authorities could, for example, conduct a wide-reaching awareness campaign, but especially in coastal Caribbean communities and towns, by framing targeted messaging in appropriate languages. Existing laws that fully protect hawksbill eggs, juveniles, and adult turtles would benefit from stricter enforcement, e.g., at-sea inspections of artisanal and industrial fishing vessels and at *acopios* (offshore lobster purchasing stations), which would likely reduce mortality and improve the conservation outlook for hawksbills in this region. Full implementation of existing laws would include addressing the open sale of hawksbill jewelry in coastal towns, markets, and tourism centers throughout the country (C. J. Lagueux and C. L. Campbell, *pers.*

obs.). However, enforcement of regulations would require funding for staff and resources, and political willingness.

Internationally, the Nicaragua and Honduras governments could benefit sea turtles and other marine biodiversity by establishing a legally binding bilateral agreement to provide protection for their shared continental shelf and develop actionable items to guarantee compliance with regulations. Nation states whose sea turtle populations share these waters could provide support to the Nicaragua government in a variety of ways, e.g., logistical, scientific, strategic, and most importantly financial assistance to manage human use of marine resources on the western Nicaragua Rise. Local conservation actions alone are not sufficient to guarantee the protection of sea turtle populations and their habitats throughout the Caribbean due to their highly migratory behavior. Thus, implementation of management actions at the local, national, regional, and international levels is imperative for hawksbill conservation and recovery.

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