SPATIAL ECOLOGY OF HAWKSBILL TURTLES (*ERETMOCHELYS IMBRICATA*) NESTING AT GANDOCA-MANZANILLO NATIONAL WILDLIFE REFUGE, COSTA RICA

by

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To My Supportive Family

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ABSTRACT

Author: Bergman, Quintin, D. MS
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Title: Spatial Ecology of Hawksbill Turtles (*Eretmochelys imbricata*) Nesting at Gandoca-Manzanillo National Wildlife Refuge, Costa Rica
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The beaches in the Gandoca-Manzanillo National Wildlife Refuge (GMNWR) in southeastern Costa Rica are known to host nesting critically endangered hawksbill sea turtles (*Eretmochelys imbricata*). The spatial ecology and movement behaviors of this nesting population has never been observed. Evaluating the spatial ecology of nesting sea turtles allows for a better understanding of their local movement behavior as well as their large scale oceanic movements that inform conservation needs. Satellite tracks reveal internesting, postnesting migration, and foraging behaviors for four nesting hawksbills from the GMNWR. During the internesting behavior, satellite-tracked hawksbills remained in the coastal waters near the nesting beach for 15 to 55 days before making their postnesting migration. Home-range areas occupied by internesting hawksbills vary between 21.9 and 557.9 km^2. Hawksbill internesting high use areas overlapped with the marine boundary of the GMNWR for an average of 29% of time spent inside the refuge. The beginning of all four turtle's migrations start with a pelagic circular movement away from the coast into the Caribbean Sea before resuming a northern coastal migration pattern. Migration routes varied in length from 662 to 1,486 km and passed through three or four exclusive economic zones of various neighboring nations. Foraging areas of three hawksbills were situated east of Nicaragua and one was found along the northern coast of Honduras, near Roatan. Foraging home-range areas of satellite-tracked hawksbills varied from 205.1 to 696.1 km^2. This is the second satellite telemetry study completed on nesting hawksbills in the Costa Rican Caribbean and the first for GMNWR. These results display the use of pelagic and coastal migratory routes for the critically endangered hawksbill. Distant foraging grounds utilized by hawksbills nesting in Costa Rica reveal the importance for the preservation of the Miskito Cays and nearby ecosystems.

INTRODUCTION

Sea turtle populations around the world have been negatively impacted by the illegal harvest of meat and eggs, beach development, unsustainable fishery techniques, marine debris and climate change (Lewison et al. 2004; Hawkes et al. 2007; Tomillo et al. 2008; Fuentes et al. 2010; Gall & Thompson 2015). All seven species of sea turtles have a level of protection from the International Union for Conservation of Nature (IUCN). The olive ridley (*Lepidochelys olivacea*), loggerhead turtle (*Caretta caretta*) and leatherback (*Dermochelys coriacea*) are listed as vulnerable. The green turtle (*Chelonia mydas*) is listed as endangered. The hawksbill turtle (*Eretmochelys imbricata*) and Kemp's ridley (*Lepidochelys kempii*) are listed as critically endangered. The flatback (*Natator depressus*) is data deficient (IUCN, 2017). Hawksbill sea turtles have been historically targeted for their carapace which is used to create "tortoiseshell" commercial products such as jewelry and decorative art (Parsons, 1972; Fleming, 2001; Mortimer & Donnelly, 2008). In Central America sea turtle eggs are sought after as food items; the continued illegal harvest of eggs in these countries results in the decline of the hawksbill turtle populations in the region (Mortimer & Donnelly, 2008).

Found in the tropical waters of every ocean basin around the world, hawksbills play a unique role in the reef environment by selectively feeding on sponges which provides the competing coral space to further develop a reef (Meylan, 1988; Hill, 1998; Leon & Bjorndal, 2002). Hawksbills use their beak-like mouth to tear apart the sponge body, exposing sheltered symbionts to predators (Leon & Bjorndal, 2002). In the absence of hawksbills, sponge species would dominate reef communities and change their structure (Leon & Bjorndal, 2002). Healthy coral reefs provide a majority of tropical coast nations with substantial and economically important ecosystems (Moberg & Folke, 1999).

Like other sea turtle species, adult female hawksbills return to their natal beaches to reproduce and nest (Musick & Limpus, 1997). It is during the nesting season when adult female hawksbills typically lay 1-5 clutches of 120-200 eggs per clutch (Gaos et al. 2017). Gravid females then remain offshore during an internesting period of 12-20 days as the subsequent clutches mature (Zbinden et al. 2007; Walcott et al. 2012; Gaos et al. 2017). Habitat selection during internesting is important because some habitats facilitate resting and may minimize energy expenditures as well as can limit predation (Heithaus et al. 2007; Houghton et al. 2003).

Gravid turtles select internesting habitats close to beaches and may be exposed to anthropogenic threats such as entanglement in fishing gear, harvesting or boat strikes (Blanco et al. 2013; Hazel et al. 2009). The survival of mature breeding females plays a vital role in the conservation of sea turtle populations (Crouse et al. 1987). Understanding the movements of gravid females during the internesting period can also be used to determine important features for internesting habitat selection. Consequently this improvement of our understanding can direct conservation efforts to protect these habitats during this vulnerable life history stage. At the end of the nesting season when the last clutch has been deposited, hawksbills then migrate to distant foraging grounds where they spend 2-4 years preparing for the next season of nesting (Gaos et al. 2017; Hart et al. 2019).

Throughout the wider Caribbean, hawksbill migratory routes as well as locations of foraging grounds have been defined in the past by using flipper tag returns (Carr et al. 1966; Bjorndal et al. 1993; Meylan 1999). Recently, in Costa Rica, there have been a few spatial ecology studies that utilize satellite telemetry (Troëng et al. 2005b; Troëng et al. 2005a; Troëng et al. 2007). These tracking studies helped further our understanding of the specific routes from nesting sites to foraging areas which is vital in quantifying population-level impacts of anthropogenic threats like fishing, boat traffic, and extraction of ocean bottom resources. This more complete description of migrations and movements of these turtles are critical to designing effective conservation responses to these threats (Hamann et al. 2010). Satellite telemetry is used to elucidate the spatial ecology patterns of many species of conservation concern and determine their movements as well as habitat use (Zbinden et al. 2007; Godley et al. 2008; Seminoff et al. 2008). Satellite telemetry studies also provide insight to the spatial distribution of animals during specific behaviors such as foraging and migration of sea turtles (Polovina et al. 2004; Shillinger et al. 2010).

Costa Rica has 166 protected areas that encompass 50% of the country's coastline, 20 of which are Marine Protected Areas (MPAs) (Alvarado et al. 2012). One of these MPAs is incorporated in the Gandoca-Manzanillo Wildlife Refuge (GMNWR) which is included in Area Conservation de la Amistad Caribe, located in southeast Costa Rica. Hawksbills are known to make nesting visits to the larger beach Playa Gandoca and the smaller beach Playita, both of which are located within GMNWR (Figgener, 2009). Designed without specific knowledge of hawksbill spatial ecology, the GMNWR may not sufficiently cover the home-range or migratory corridors of hawksbills nesting on its beaches.

The objective of this study is to use satellite telemetry to elucidate the a) internesting home-range, b) postnesting migratory routes, and c) to determine the location of foraging grounds for hawksbills nesting at GMNWR.

METHODS

Study Site

Located in southeastern Costa Rica, Gandoca-Manzanillo National Wildlife Refuge (GMNWR) (09º37’N, 082º40’W) was created in July of 1985 and consisted of 50.13 km^2 of a terrestrial area and 44.36 km^2 of a marine area for a total of 94.49 km^2 of protected habitat (MINAE, 1996). Listed as a Ramsar site by the Ramsar Convention on Wetlands of International Importance, GMNWR is a coastal lagoon consisting of seagrass beds, coral reefs, beaches and cliffs with flooded lowland areas (Ramsar, 1995). Anthropogenic uses in the area include traditional, low-scale agriculture growing cereals, cacao, plantains, yucca, and other tuberous plants; forestry; and marine and freshwater fishing (Ramsar, 1995). Large-scale banana cultivation also occurs in the area adjacent to the reserve and communities (personal observation). Created to protect species in danger of extinction and to maintain them in their natural habitat, GMNWR supports a high diversity of species including birds, reptiles, mollusks and fish (marine, estuarine and freshwater), crustaceans, including lobsters and 32 coral species (Ramsar, 1995). Four of the five sea turtles of the Caribbean nest in GMNWR including the loggerhead, green, leatherback and hawksbill turtles (Chacon et al. 1994; Ramsar, 1995; Figgner, 2009).

Transmitter Attachment

During nesting surveys in August of 2018, four adult female hawksbills were fitted with satellite transmitters (KiwiSat 202; Sirtrack) after they had nested on the beaches in the GMNWR. One hawksbill was found and satellite tagged on Playita and three on Gandoca.

We followed techniques of transmitter application from previous satellite telemetry studies (Balazs et al. 1996; Van Dam et al. 2008; Hart et al. 2017) Turtles selected for satellite transmitter application showed no apparent deformities (e.g., missing limbs, carapace malformations). This was to insure that transmitter attachment would not add an additional risk to the survivorship of injured or deformed individuals. Curved carapace lengths (taken from the nuchal notch to the posterior marginal scute tip) were collected from all tracked turtles, in addition to the application of metal Inconel and Passive Integrated Transponders (PITs) tags. To prepare the animal for transmitter attachment, an area (the first and second vertebral scutes), approximately 90 cm^2, on the turtle's carapace was cleared of all epibiota and cleaned with a new Brillo© dish pad (Armaly Brands, London, Ohio). Seawater was used to rinse the carapace of soap and debris. Sandpaper was then used to score the smooth carapace surface. Once cleaned, acetone was used as a final rinse of the carapace. Two-part epoxy (Pure50+, Powers Fasteners, Brewster, NY) was used to bind the transmitter to the carapace. First, a base layer of epoxy was spread over the prepared area, then the transmitter was placed on the first and second vertebral scutes. A period of ~15 minutes was given between each epoxy layer to allow for hardening before another layer was added; several layers were used to ensure sufficient attachment to the scutes. Special attention was given to the final layer to create a smooth surface to reduce hydrodynamic drag. During the attachment process, the turtle was safely restrained using a damp cloth over the eyes and head, while field assistants held the turtle's flippers. Once the transmitter attachment was complete, the turtle was released and crawled back into the sea unassisted. The entire process took about 60 minutes.

Telemetry Data Analysis

Location and dive data was downloaded from argos-system.clsamerica.com starting on August 24th 2018 and ended on February 1st, 2019. Signals from all four transmitters were still being received. Argos classifies each location point by a location class (LC) into six categories (LC 3:150 m, LC 2: 150–350 m, LC 1: 350–1000 m, LC 0: 1000 m, LC A and B no accuracy given). Raw location points were adjusted by removing any Z location classes (n=4) and blank coordinates (n=146). Duplicate location points were also removed (n=1,549), and the remaining location points (n=1,583) were filtered for speed in R statistical software (R Core Team, 2018) using program "argosfilter" (Freitas, 2010). The speed filter adjusts location points that are considered unrealistic based on the pre-determined speed of turtle movenments which for sea turtles was set at a maximum speed of 5km/hour (Luschi et al. 1998). When the distance between two consecutive points was more than the predetermined speed, that point was filtered (n=107).

Location points were then modeled in the program "bsam" (Jonsen et al. 2013), a Bayesian state-space model (SSM) that estimates when and where an animal changed its behavior based on their tracks. A smoothing factor is incorporated in the SSM that estimates the location of the turtle when no points are provided, this feature is based on the previous and successive movements. This SSM program was used to determine when turtle behavior changed from internesting to migrating to foraging based on the algorithm in the model. To increase model accuracy, a hierarchal correlated random walk filter was used. A tstep value of 0.5 was selected to produce two estimated locations per day. The burn-in phase was set at 5,000 and posterior samples was set at 10,000, these were selected to decrease sample autocorrelation. Samples were thinned by 10 to minimize within chain sample autocorrelation.

ArcGIS (10.5, ESRI, Redlands, CA) was used to map turtle behaviors: internesting locations, migration routes, and foraging grounds. The oceanic areas used during the internesting behavior delineated by the SSM was then assessed by applying a Kernel Density Estimate (KDE), as well as the creation of Minimum Convex Polygons (MCP). These analyses are used to display the home-range areas of the near beach and oceanic habitat the turtles utilize during this behavior state. The KDE tool was used to show the 50%, 75%, and 95% usage of each turtle's internesting area. Subsequently, a MCP tool was applied to each of the turtles internesting and foraging behavior locations to show the 95% home-range of each behavior state.

Turtles performed dives when as the transmitter becomes submerged in water. Data from these dives were decoded and processed into proportion histograms. Daily maximum dive depth is reported for each turtle, to make comparisons data was first separated by behavior state for each turtle. Once divided dives were binned at 10 meter intervals (0-10 m, 10-20 m, 20-30 m, 30-40 m, and >40 m) which then are displayed proportionately in histograms.

RESULTS

All four turtles were tracked from their nesting beach to their foraging areas (Table 1). The SSM-estimated internesting, migration, and foraging behavior for each turtle. The postnesting migrations exhibited a counter-clockwise circular path before returning close to the coast and then moving northward towards foraging grounds (Figure 1). The mean duration of internesting behavior was 29 ($\pm$ 20) days with the mean duration of postnesting migration behavior being 28 ($\pm$ 11) days (Table 1). All tracks ended February 1st of 2019 for analysis, which resulted in a mean duration of 100 ($\pm$ 11) days for foraging behavior recorded at time of writing (Table 1). At time of analysis all four transmitters continue to send signals, this endpoint allows for analysis of sufficient foraging behavior.

Internesting

All four tagged hawksbills (Ei01, Ei02, Ei03, and Ei04) exhibited internesting behavior directly in front of the nesting beach or in nearby waters (Figure 2). During the internesting behavior hawksbills remained mostly over the continental shelf (<200m). MCP analysis indicated that internesting home-range areas occupied by the hawksbills varied between 21.9 and 1104.8 km^2 (Table 1). KDE analysis indicated that 50% utilization area of the internesting area ranged between 1.91 and 100.05 km^2. Turtle Ei01 spent 55 days near the nesting beach. This turtle remained within 28 km of the nesting beach, with the majority of its locations 10 km away from the original nest location (Figure 3). Turtle Ei02 spent 15 days within 8 km of the nesting beach, with the majority of its locations <1 km away from the orginal nesting location (Figure 3).

Imminently following release turtle Ei03 went directly east into the Caribbean Sea for 263 km, turned northward, and then returned to the coast. This loop was 808 km long and lasted for 13 days. Once back along the Costa Rican coast turtle Ei03 spent 4 days remaining within 15 km of the shore near Puerto Limon, which was 62 km north of the primary nesting beach (Figure 3). Immediately post release, turtle Ei04 moved south along the coast for 64 km, remained in the Bocas del Toro Archipelago for 14 days before returning to the nesting beach (Figure 4). Subsequently, the turtle repeated the movement south, after 1 day in GMNWR, to the Bocas del Toro Archipelago for another 14 days before returning to the original nest location. From this point, the turtle Ei04 moved 15 km to the north of the primary nesting beach and remained in these waters for 15 days before making what SSM determined to be their postnesting migration.

Postnesting Migration and Foraging

The postnesting migrations for all four turtles started in a counter-clockwise circular pattern in the Caribbean Sea before making a northern migration (Figure 1). Each turtle's postnesting migration ended at what the SSM designated as foraging areas, traveling an average of 1,156.3 km^2 (SD $\pm$ 349.3 km^2; range: 662-1,486 km^2). On average the postnesting migration took 28 (SD $\pm$ 11; range: 12-40) days (Table 1). The counter-clockwise circular movement pattern in the open Caribbean Sea ended for all turtles near Nicaragua's Bluefields. Turtle migrations then turned northward along the coast and continued northerly for an average of 526 (SD $\pm$ 276) km and remained on average 18 (SD $\pm$ 16) km near the coast. Turtles Ei01 and Ei02 passed through four Economic Exclusive Zones (EEZ), while turtles Ei03 and Ei04 only passed through three EEZs (Table 2).

Foraging areas of hawksbills (Figure 1) were identified along the eastern coast of Nicaragua (n=3) and also one area along the northern coast of Honduras (n=1). The mean distance of the foraging areas from shore was 90 (SD $\pm$ 52.7) km. The mean home-range of the foraging areas for all four hawksbills were 371.7 (SD $\pm$ 192.5) km^2 (Table 1). Size of foraging home-range areas varied, the largest foraging home-range is utilized by turtle Ei01, with a total 696.1 km^2 and it is located in Honduran waters, 87 km from the coast partially located inside the boundary of the Miskito Cays Marine National Park. The foraging area for turtle Ei03 is second largest at 329.9 km^2 and is located on the border of the EEZ of Honduras and Nicaragua, 165 km from the coast (Figure 5). Turtle Ei02 has a foraging area of 255.7 km^2 and is located in Honduran waters 16 km from the coast. The foraging area of turtle Ei02 is partly located inside the boundary of Honduras' Bay Islands Marine National Park. Lastly, the foraging area for turtle Ei04 is 205.1 km^2 and is located in Nicaraguan waters 92 km from the coast.

Dive Behavior

Comparison of the daily maximum dive depth of all turtles show difference between behavior states. Turtles use shallow waters or the surface during the internesting behavior (Figure 4a), average dive depth for all turtles during this behavior was 16.59 (SD $\pm$ 9.0) m.

Turtle Ei02, which remained close to the coast (~5 km) resulted in the highest proportion of dives in the 0-10 m bin. Depths frequented during the postnesting migrations (Figure 4b), varied between all the bins, the average dive depth for all turtles during migration was 26.42 (SD $\pm$ 14.82) m. Upon reaching the foraging ground, we observe each turtle assigning to separate dive bins (Figure 4c). Mean dive depth for all turtles during foraging behavior was 28.24 (SD $\pm$ 9.67) m.

DISCUSSION

The telemetry data collected from these four hawksbills provided a substantial outline of their behaviors starting at the original nesting beach and ending at their individual foraging areas. The aim of this study is to delineate the home-range areas of internesting hawksbills, the postnesting migration routes, and the location of their foraging grounds. Satellite telemetry data from Argos resulted in a high quantity of lower quality “Location Class,” which was to be expected based on other satellite telemetry studies on sea turtles (Hoenner et al. 2012, Thomson et al. 2017). Using the “argosfilter” (Freitas 2010) and “bsam” (Jonsen et al. 2013) analysis packages in R Statistical Software, behavioral states were then modeled for each of the tagged turtles. For the internesting period, the turtles displayed varying numbers of days for this behavior, which was used to estimate the number of nests laid, without actually observing the turtle on the beach after transmitter application. Postnesting migration behavior resulted in delineating the routes taken, which also identified a strong counter-clockwise oceanic circular pattern in the Caribbean Sea. This movement pattern demonstrated that hawksbills nesting at GMNWR briefly utilize pelagic habitat off the coasts of Costa Rica and Panama which was previously unknown. Home-range analyses for foraging areas and internesting areas results in delineating these habitats for tracked hawksbills, revealing the sizes and locations of where hawksbills spend a majority of their time.

State-Space Model Analysis

State-space models (SSM) derived from satellite telemetry data have been a useful tool in understanding the spatial ecology for marine species which utilize large areas of the ocean (Jonsen et al. 2007; Patterson et al. 2008; Hoenner et al. 2016). This analysis was able to delineate the different behaviors of each tracked turtle, categorized as internesting, migrating, and foraging behaviors. Due to the technological limits of satellite telemetry, poor or duplicate location points were not incorporated in these analyses, however, the SSM was still able to produce viable estimations of the timing when turtles changed their behavior.

This study is the first satellite telemetry study conducted on nesting hawksbills from the GMNWR and the second satellite telemetry study of nesting hawksbills along the Caribbean coast of Costa Rica. Troëng (2005b) reported on satellite tracks of two nesting hawksbills that migrated northward to Nicaraguan waters from their nesting beaches in northern Tortuguero National Park, Costa Rica. The tracks from this study show that Costa Rican hawksbills are capable of traveling further along the Central American coastline than previously thought and utilize waters north of Honduras near the island of Roatan. A dramatic circular pelagic movement out into the Caribbean Sea was identified for all four hawksbills. This circular pelagic postnesting movement was previously documented in green turtles nesting in Tortuguero National Park near the same area of the Caribbean Sea (Troëng et al. 2005a).

Internesting Behavior

Locations of turtles during the internesting behavior illustrates which part of the regional habitat the turtles are utilizing during subsequent clutch development. Turtles Ei01 and Ei02 were tracked to habitats near the nesting beach and inside the GMNWR marine boundary (Figure 2). Location points near the nesting beaches of the GMNWR reveal that nesting hawksbills utilized habitat within the MPA protected waters. A total of 29% of the internesting locations of the four tracked hawksbills occurred inside the GMNWR marine MPA boundary. Satellite transmissions from tracked hawksbills indicate that not all of the internesting locations fall within the protection of the GMNWR marine boundary. For example, while 80% of internesting activity for turtle Ei02 occurred within the MPA, 0% of the internesting activity for turtle Ei03 fell within the same boundary, along with 23% and 13% of activity for turtles Ei03 and Ei04 fell within the MPA (Table 1). This indicates that the MPA boundary may not offer sufficient protection for all internesting females. Turtle Ei04 spent 64% of its time (27 days) south of the nesting beach in the waters of Bocas Del Toro Archipelago of Panama. Turtle Ei03 exhibited all of its nesting behavior 65 km north of the nesting beach (Figure 4), which is 53 km outside of the protected waters of GMNWR. Turtle Ei02 is the only turtle with a majority of its transmissions within the GMNWR marine boundary (Figure 3). This data provides crucial information on the habitat use of internesting females with regards to the boundary of the MPA. Providing such data from satellite telemetry studies is useful and informative when delineating MPA management areas (Dawson et al 2017; Maxwell et al. 2011).

Based on a study by Bjorndal et al. (1985) it is estimated that the internesting period of hawksbills is 16.8 days. In light of these data for this study, we estimate that turtles Ei01 and

Ei04 remained close to the beach habitats in order to oviposit two to three more nests after attachment of the transmitters. We also estimate that turtle Ei02 oviposited only one more consecutive nest with an internesting behavior that lasted 15 days.

In contrast, turtle Ei03 departed the nesting beach and made the counter-clockwise oceanic circular movement pattern, before returning to the coast of Costa Rica near Puerto Limon 46 km north of the orginal nesting beach. Ei03 then remained within close proximity of the shore for four days (Figure 3) before initiating a northern migration. This time the turtle migrated to a northern foraging ground, similar to the other three females. The SSM identified a behavior change for this turtle during the four days off the coast of Puerto Limon that was similar to internesting behavior. We conclude that turtle Ei03 probably laid one more nest in the Puerto Limon area before migrating to the northern foraging grounds. In particular interest to the conservation of the species, Puerto Limon is a highly populated coastal town with a high volume of ship traffic and therefore an increase exposure to fisheris, pollution and other anthropogenic impacts on the survival of this reproductive female and the nest deposited.

A notably different internesting behavior compared to the other females was observed for turtle Ei04. After release, this turtle was tracked to Panamanian waters within the Bocas Del Toro Archipelago. After spending 13 days turtle Ei04 returned to waters directly in front of the nesting beach inside the GMNWR marine boundary for one day. Subsequently this turtle then returned to the Bocas Del Toro Archipelago for another 15 days. In a similar movement, turtle Ei04 then returned once more to waters in front of the original nesting beach inside the GMNWR marine boundary for one day, then moved north to the northern part of the GMNWR MPA, and remained within the marine boundary for an additional 12 days before displaying migration behavior (Figure 4). This behavior of selecting an internesting habitat 64 km away from the nesting beach has been previously seen in hawksbill turtles in Barbados (Walcott et al. 2012). Based on the high proportion of dives at 20 m depth (Figure 4), it is possible that this turtle could have been seeking specific thermal regimes of foraging during its internesting period (Hochscheid & Wilson 1999).

Postnesting Migration Behavior

Using the SSM-estimated postnesting migration locations, each turtle's route was mapped through the Caribbean Sea. Figure 1 depicts the coastal corridor these nesting hawksbills utilize between their nesting beach and foraging areas in the north. All four tracked turtles made a similar counter-clockwise circular pattern into the pelagic portion of the Caribbean Sea. It appears that all these hawksbills utilized strong surface currents in this area, which are associated with the local bathymetry in order to navigate towards northern foraging grounds. During October and November the surface currents in this part of the southeastern Caribbean Sea move in the same counter-clockwise direction, producing a strong coastal current moving southwards and then out into the central Caribbean Sea. It is possible that postnesting hawksbills move with this strong current into the pelagic zone compared to moving against these strong currents thus saving energy. Once turtles have reached a point in the gyre that returns close to the Central American coastline, the northward portion of their migration routes commences past Costa Rica, up near the Bluefields of Nicaragua.

The United Nations Convention on the Law of the Sea states that a country has individual rights regarding the exploration and use of marine resources of their Exclusive Economic Zone (EEZ). Postnesting migration routes taken by satellite-tracked hawksbills resulted in various distance and time spent in different EEZs. As an organism that migrates vast distances throughout the ocean, hawksbills have a high likelihood to pass through different EEZs. We tracked turtles Ei01 and Ei02 through 4 nations EEZs while turtles Ei03 and Ei04 were tracked through 3 nations EEZs (Table 2). When compared, Nicaragua's EEZs hosted 52% and Panama hosted 25% of all satellite-tracked hawksbill migration routes. Tracked turtles migrated the least amount of distance through Costa Rica's and Honduras' EEZ at 12% and 11%, respectively. This data illustrates that hawksbills nesting at the GMNWR begin their postnesting migration in Panamanian waters and spend very little time in Costa Rican waters (Figure 5).

Foraging Behavior

Using the SSM-estimated foraging locations we can map the home-range minimum convex polygons of each turtle's foraging area. Studies conducted across the wider Caribbean have tracked hawksbills to similar foraging grounds in coastal waters along known reefs. A total of 15 hawksbills from previous studies (Troëng et al. 2005, Revuelta et al. 2015, Moncada et al. 2012, van Damn et al. 2008, and Hart et al. 2019) have been tracked to foraging grounds off the coast of Honduras and Nicaragua. Our study increases this number to 18 hawksbills that utilize this specific region as a home foraging ground. Turtle Ei02 was tracked to a foraging ground near the Honduran island of Utila, which has previously not been delineated as a hawksbill foraging area.

Conclusions and Conservation Implications

Most conservation efforts are limited by fiscal resources, therefore there is a high demand to find the most responsible and effective methods when implementing conservation management strategies. Based on the large oceanic spatial movements of sea turtles, conservation of these marine reptiles can be challenging. Spatial ecology studies, like this, provide a better understanding of the large scale turtle movements and behavior, and in turn can potentially inform management policies. From the internesting behavior, we observed that while some of the tracked hawksbills utilize habitat within the GMNWR marine boundary, and three out of the four tracked hawksbills primarily utilize habitats outside of the refuge boundary. This will most likely play a role in the survival of the species since during this internesting phase adult female turtles are exposed to higher threats of anthropogenic interactions. Based on the dive depth analysis during their internesting phase turtles are exploiting shallow waters and could therefore be more readily targeted for capture for their valuable carapace.

It is inevitable that sea turtles will migrate in and out of various nations' jurisdictions. The cross-country migration routes highlight that more attention needs to be diverted to the issue of how to approach differing international policies to ensure adequate protection for this critically endangered species. The results from this study provide evidence that the current MPA at GMNWR offers protection to 29% of the nesting hawksbills during their crucial internesting period. In the end the nesting beach is protected which accounts for a portion of a turtle's life history and important for the recruitment of new individuals. Postnesting migrations ended at the hawksbill foraging grounds where they will spend the following 2-3 years preparing for the next nesting season. Outlining the need to protect this high-use habitat, this study recommends that foraging grounds for this critically endangered species receive more monitoring and protection.

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Table 1: Summary of behavior states for satellite-tracked hawksbills nesting at the Gandoca-Manzanillo National Wildlife Refuge. CCL = curved carapace length, MCP = minimum convex polygon, MPA = marine protected area.

				Internesting Behavior			Postnesting Migration			Foraging Behavior		
Turtle ID	**CCL**	**Transmitter Attachment**	**Total Tracking Days**	**Duration (days)**	**MCP (km^2)**	**% of points within GMNWR MPA**	**Duration (days)**	**Track Distance (km)**	**Speed (km/day)**	**Duration (days)**	**MCP (km^2)**	**Distance to coast (km)**
Ei01	85	24-Aug-18	160	55	557.9	23%	24	992	41.3	81	696.1	87
Ei02	88	26-Aug-18	157	15	21.9	80%	36	1,486	41.3	106	255.7	16
Ei03	94.5	29-Aug-18	155	4	45.9	0%	40	1,485	37.1	111	329.9	165
Ei04	86	29-Aug-18	156	42	1,104.8	13%	12	662	55.2	102	205.1	92
AVERAGE	88.38		157	29	432.6	29%	28	1156	44	100	371.7	90
SD	3.70		2	20	443.2	31%	11	349	7	11	192.5	53

Table 2: Breakdown of the Exclusive Economic Zones (EEZ) each hawksbill postnesting migration route.

Turtle ID	Duration of Migration (days)	Total Distance of Migration Track (km)	Distance of Track in EEZ (km)		Proportion
Ei01	24	992	Panama	247	25%
			Costa Rica	40	4%
			Nicaragua	650	66%
			Honduras	55	6%
Ei02	36	1,486	Panama	335	23%
			Costa Rica	71	5%
			Nicaragua	604	41%
			Honduras	476	32%
Ei03	40	1,485	Panama	394	27%
			Costa Rica	350	24%
			Nicaragua	757	51%
Ei04	12	662	Panama	203	31%
			Costa Rica	72	11%
			Nicaragua	387	58%

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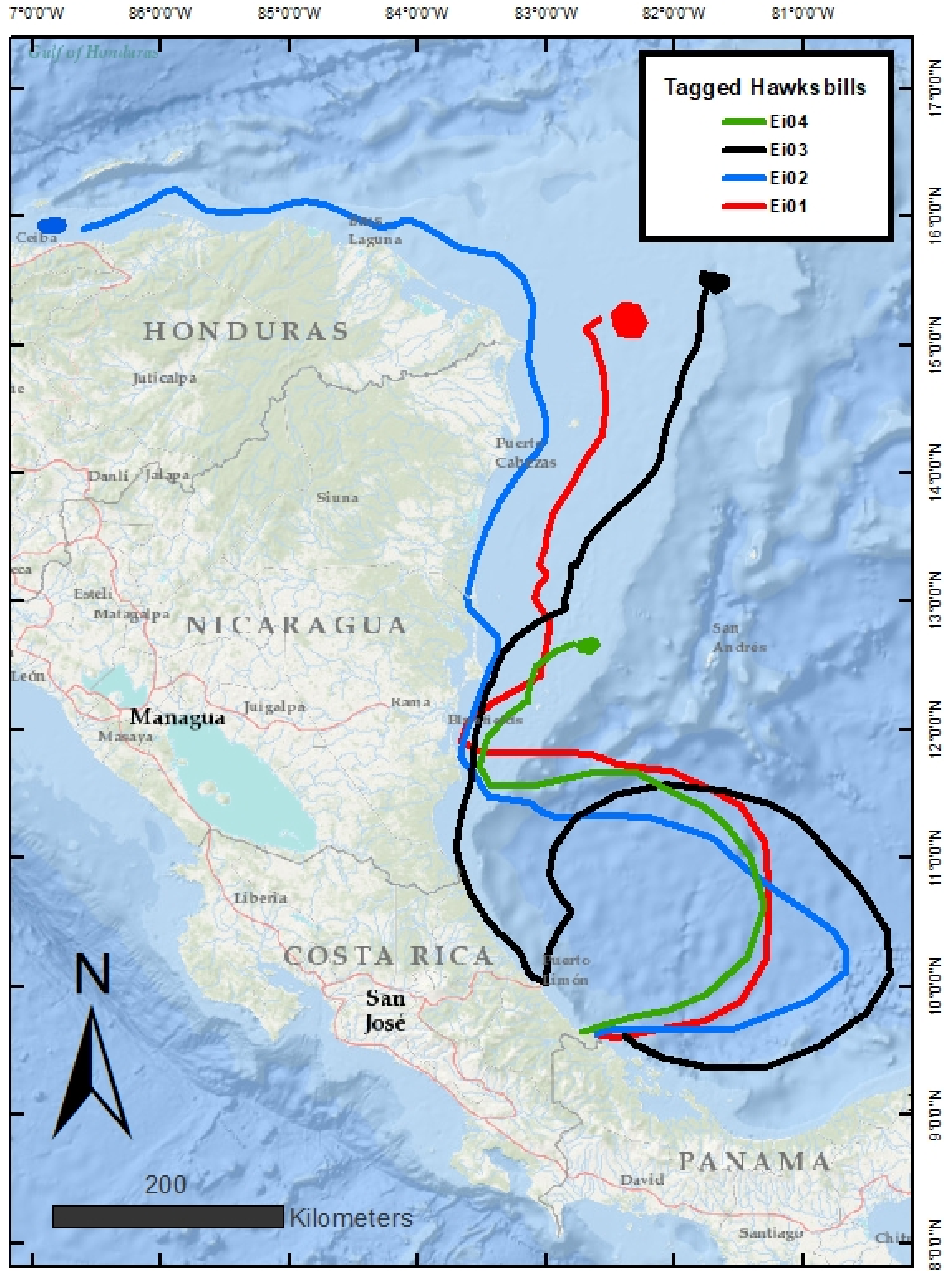

Figure 1: Postnesting migrations and foraging grounds of based satellite-tracked hawksbills nesting at the Gandoca-Manzanillo National Wildlife Refuge.

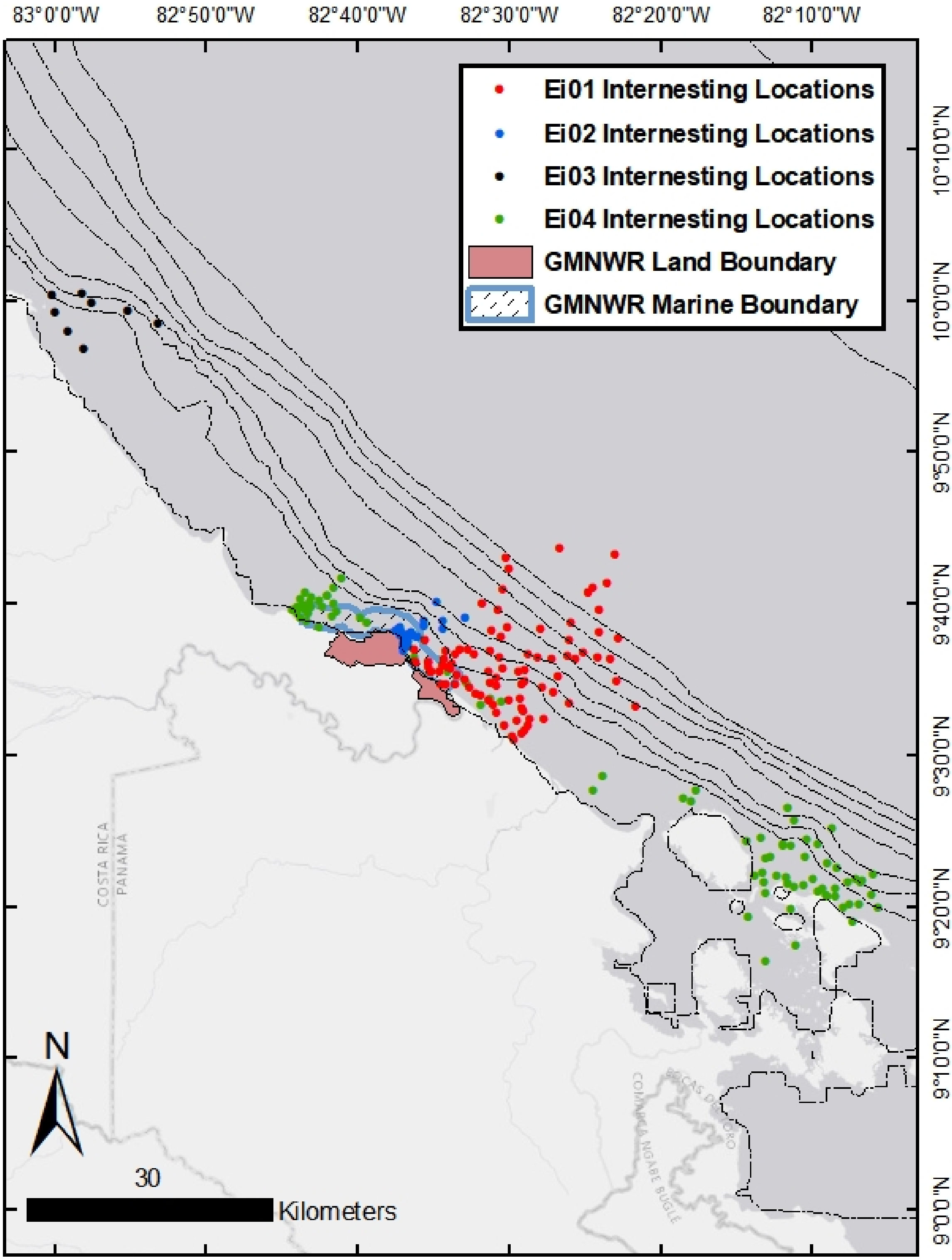

Figure 2: Internesting location of all tracked hawksbills nesting at the GMNWR over bathymetric contour lines.

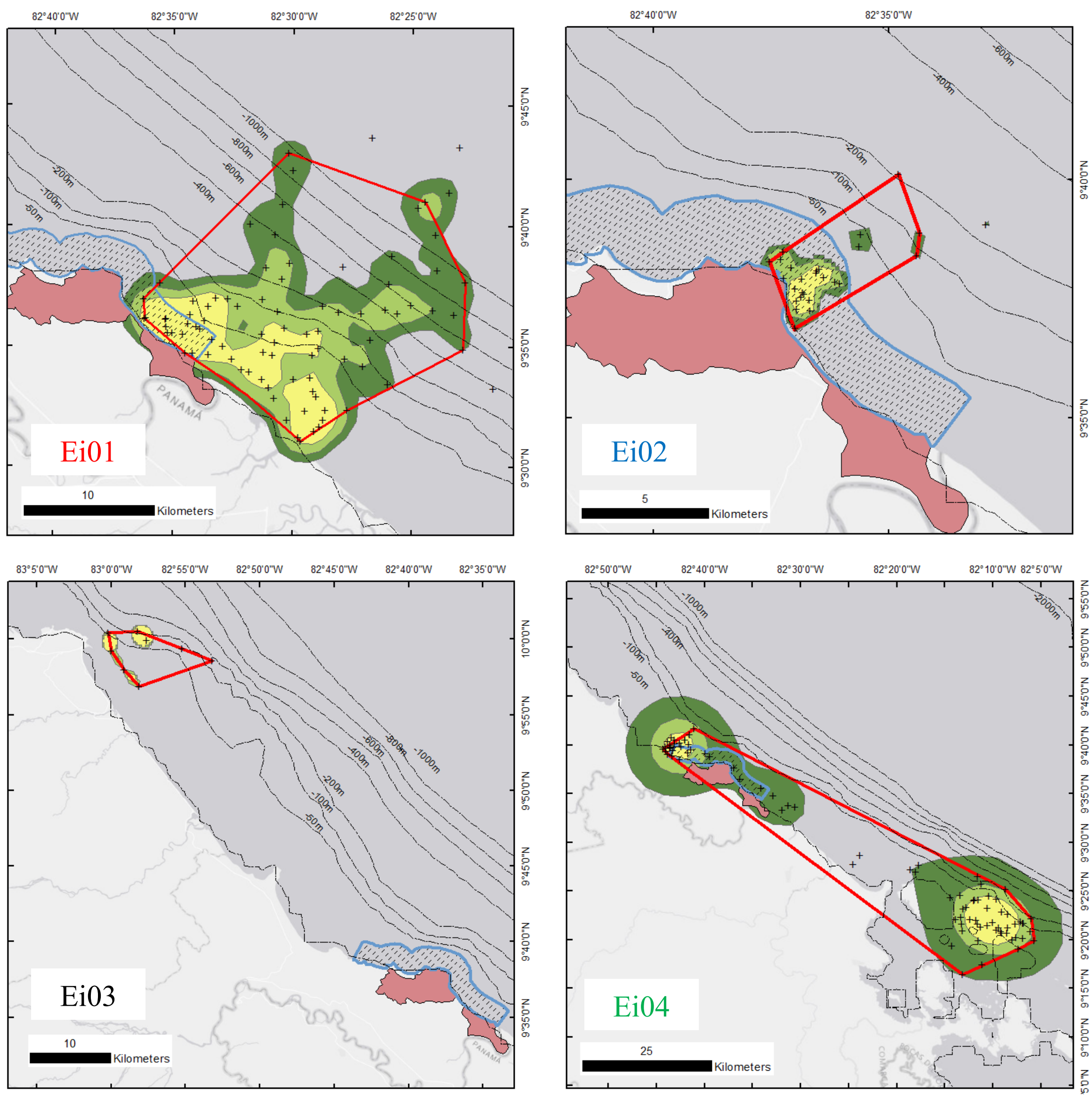

Figure 3: Home-range analysis of internesting hawksbill habitats. Red polygon is the 95% MCP, dark green, light green, yellow isopleths are 95%, 75%, and 50% KDE, respectively. GMNWR boundaries are depicted by the coral polygons (terrestrial) and blue with dashes polygons (marine).

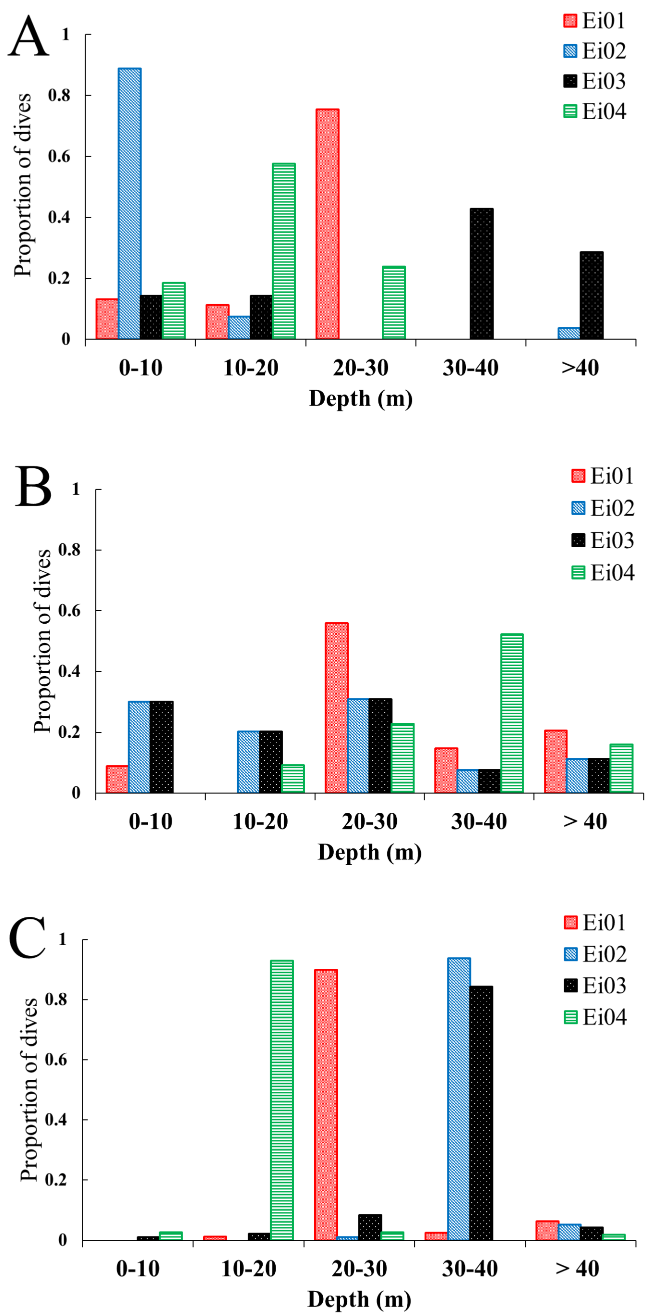

Figure 4: Maximum dive depths of hawksbills nesting at Gandoca-Manzanillo National Wildlife Refuge. Comparison of dives in the internesting (A), postnesting migration (B), and foraging (C) behavior states.

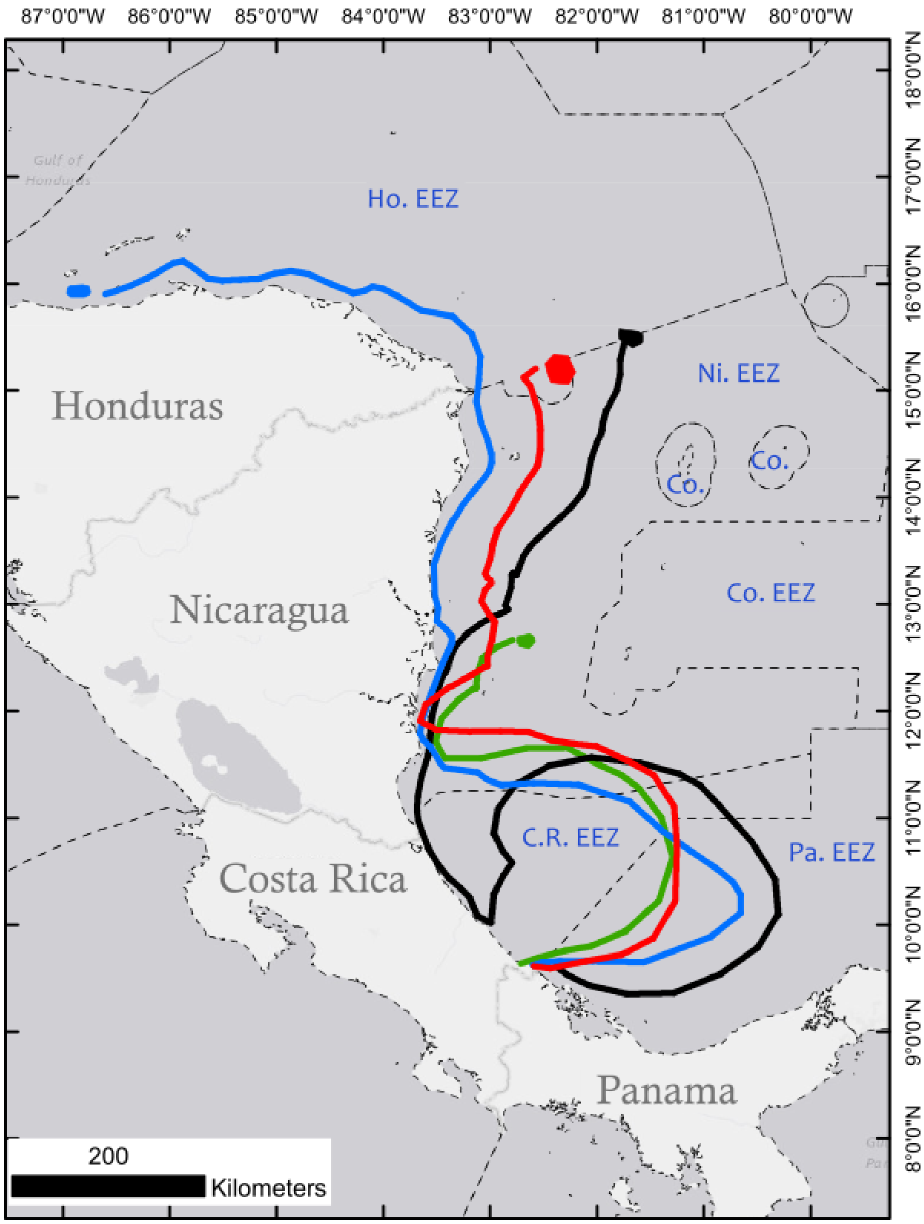

Figure 5: Migration routes of the four satellite-tracked hawksbills and Exclusive Economic Zones of each nation in the region.