

**SPATIAL ECOLOGY OF INTER- AND POST-NESTING GREEN
TURTLES (CHELONIA MYDAS) ON BIKO ISLAND, EQUATORIAL
GUINEA**

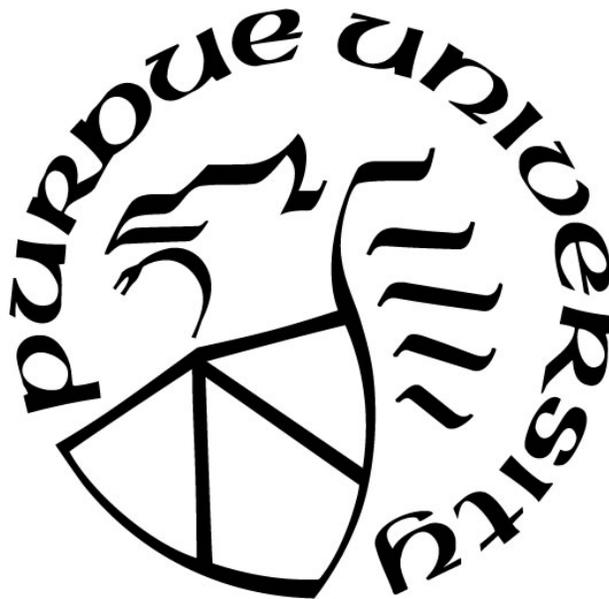
by
Emily K Mettler

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**THE PURDUE UNIVERSITY GRADUATE SCHOOL
STATEMENT OF COMMITTEE APPROVAL**

Dr. Frank Paladino, Chair

Department of Biology

Dr. Shaya Honarvar

Department of Biology

Dr. Jordan M. Marshall

Department of Biology

Approved by:

Dr. Jordan M. Marshall

Head of the Graduate Program

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ABSTRACT

Author: Mettler, Emily, K. MS

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Title: Spatial Ecology of Inter- and Post-nesting Green Turtles (*Chelonia mydas*) on Bioko Island, Equatorial Guinea.

Committee Chair: Frank Paladino

Effective conservation strategies for sea turtles require knowledge of animal movements and protection of biologically important habitats and life history stages. For breeding adult sea turtles, understanding both their inshore and pelagic spatial patterns is imperative to the successful protection of the species and the accurate identification of their vulnerabilities. This study provides insight into the inter-nesting, post-nesting, and foraging movements of green sea turtles (*Chelonia mydas*) that nest on Bioko Island, Equatorial Guinea, by using satellite telemetry to track green turtles (n=12) during two nesting seasons (2017-18, 2018-19), and as they migrated to foraging grounds after the nesting season. These tracks were fit with a switching state space model to characterize movements, and then analyzed in relation to environmental and anthropogenic factors. Dive depth data was also used to determine utilization patterns within the water column. The 12 tagged turtles migrated for an average of 1064 km to two distinct foraging grounds, with 10 migrating west for an average of 1115 km to the coastal waters of Ghana, and 2 migrating south for an average of 1563 km to the coastal waters of Angola. Migrating turtles used both direct, pelagic migration strategies, and biphasal, coastal strategies, which included intermittent foraging throughout migrations. Dive depths varied depending on behavior, with an average of 19.3 m during inter-nesting, 12.6 m during migration and 8.5 m during foraging. Knowledge of inter-nesting habitat use, migration patterns, and

foraging ground locations will be critical for the development of marine conservation management plans in the Gulf of Guinea and aide in sea turtle conservation efforts throughout the area. Additionally, spatial and dive depth data can inform zonal fishing regulators and provide information needed for modifications to fishing practices and gear that is most likely to reduce sea turtle bycatch. These data will provide a more complete understanding of marine areas critical to sea turtle conservation and aide in sustainable economic development in the Gulf of Guinea.

INTRODUCTION

Green Turtle Ecology

Sea turtles occupy tropical and subtropical oceans worldwide (Lutz et al., 2002), after entering the ocean as hatchlings they spend the majority of their lives in the water, with females emerging to lay eggs and in some cases both sexes emerging to bask (Avery, 1982). Due to their highly migratory and oceanic life history, research on sea turtles has been largely restricted to nesting females and hatchlings. This has led to conservation efforts primarily focused on nesting beaches, and on hatchlings, rather than in-water habitats utilized by breeding adults. Protecting in-water habitats of breeding adults is critical for effective species conservation as breeding individuals contribute disproportionately to sustaining populations (Maxwell et al., 2011). Adult sea turtles reproduce and forage in distinct geographic areas, which in many instances are vulnerable habitats, but once known, can feasibly be protected.

Similar to other species of sea turtles, green turtles (*Chelonia mydas*) lay multiple clutches, and will remain in the vicinity of nesting beaches for weeks at a time, making these coastal waters important sea turtle habitat. After nesting, adult green turtles have been known to migrate long distances, hundreds to thousands of kilometers, in between nesting seasons (Luschi et al., 1998; Stokes et al., 2015). Generally post-nesting migrations are direct, and turtles spend little energy on detours (Hays et al. 2002); however, a number of studies have shown individuals to take indirect routes, or a combination of open ocean and coastal routes (Cheng, 2000; Godley et al. 2002; Hays et al. 2002; Blumenthal et al. 2006; Seminoff et al. 2008). Once they have reached foraging grounds, green turtles often maintain localized, near shore home ranges (Hart and Fujisaki 2010; Christiansen et al. 2017; Levy et al., 2017).

Green turtles are the only herbivorous sea turtle, and feed primarily on sea grass and marine algae. As these food sources are limited in the open ocean, direct migration to foraging grounds is thought to be advantageous by minimizing migration time and energy expenditure (Godley et al., 2002). Just as green turtles show fidelity to nesting beaches (Bowen et al., 2002), they also typically show fidelity to foraging grounds (Broderick et al., 2007) making post-nesting migratory routes similar year after year. Consequently, protecting these regularly utilized migratory corridors could have huge benefits for populations (Stokes et al., 2015). Once at foraging grounds, there is evidence to suggest that green turtles maintain specific home ranges (Christiansen et al., 2017), which are also important to delineate and protect for conservation of green turtle populations.

In-water habitats come with a variety of unique threats including resource mining, fishing, and anthropogenic pollution (Tanner, 2014; Mahu et al., 2015; Witherington et al., 2009). Therefore, understanding the oceanic habitat use and migration patterns of sea turtles is imperative to designing effective population-level marine conservation strategies (Spotila et al., 2000). For example, endangered leatherback turtles in South Africa as well as Gabon have been unable to recover without in-water habitat protection, despite protection at nesting beaches, in part because of intensive long-line fishery operations off the coast of both countries with high rates of turtle bycatch (Witt et al., 2008; Petersen et al., 2009).

Assessing in-water movements and habitat selection in sea turtles is inherently difficult. In the 1960's, green turtles were tagged using metal flipper tags at a nesting beach on Ascension Island, these turtles were then identified by their flipper tags, at foraging grounds off the coast of Brazil, 1400 km away (Koch et al., 1969). This method was the first to reveal the long-distance migratory movements of sea turtles. Since the 1980's, satellite telemetry has expanded

our knowledge of sea turtle movements, revealing exact migratory pathways used, as well as locations of foraging grounds (Stoneburner, 1982; Timko and Kolz, 1982; Godley et al., 2008).

Satellite Telemetry

Since its inception in marine research, satellite telemetry has proven to be an effective way of tracking marine animals and has been used to track the in-water movements and distribution of all seven species of sea turtle (Godley et al., 2003; Troëng et al., 2005; Benson et al., 2007; Shaver and Rubio, 2008; Maxwell et al., 2011; Stokes et al., 2015; Whittock et al., 2014). Specifically, satellite telemetry has been used to map long-distance migration between nesting beaches and foraging grounds (Hughes et al., 1998; Nichols et al., 2000), location of migration corridors (Morreale et al., 1996), fidelity to foraging grounds (Broderick et al., 2007), overwinter hibernation locations and behavior (Hochscheid et al., 2007), movements of juveniles in foraging grounds (Limpus and Walter, 1980; Mackowski et al., 2006; Hart and Fujisaki, 2010), and more recently, clarifying how turtles move in water using state space modeling (Jonsen et al., 2007; Shimada et al., 2016). Additionally, when satellite telemetry is combined with global currents, water temperatures and other oceanographic data, it can highlight specific oceanographic factors that influence sea turtle behavior (Seminoff et al., 2008; Hart et al., 2015).

Satellite telemetry has also been used to assess the effects of human activity on sea turtle distribution. This technology has identified and highlighted the level of fishing pressures and fishing-induced mortality on sea turtles (Hays et al., 2003). Further, when overlaid with human activity maps it can provide a model of potential interaction locations that may contribute to mortality (Seminoff et al., 2008; Hart et al., 2015; Shimada et al., 2017). Synthesis of satellite

tracking studies have shown that the added protection and increased habitat quality offered by marine protected areas (MPAs) leads to increased density of green turtles in designated MPAs, highlighting the importance of spatially sensitive management strategies (Dobbs et al., 2007; Chaloupka et al., 2008; Christianen et al., 2014).

Threats to Sea Turtles

Green turtles are an endangered species, with declining global populations, as classified by the International Union for Conservation of Nature and Natural Resources (IUCN), due to their vulnerability to anthropogenic impacts, such as intentional harvesting of adults from foraging grounds, incidental bycatch in fisheries, and marine habitat degradation (Seminoff, 2004).

While sea turtles are protected under international law and by national laws in most West African nations, incidental bycatch in fisheries operations is a major threat in the Gulf of Guinea. Green turtles are common bycatch in both gillnet and pelagic longline fishing operations (Carranza et al., 2006; Wallace et al., 2010; Tanner, 2014). Oil and gas development has also rapidly intensified in the Gulf of Guinea in recent years (Brownfield et al., 2016), and poses diverse, and difficult to measure threats to sea turtle populations. Associated with oil exploration, there is an increase in channel dredging, ship traffic, oil leaks, and chemical pollution, which can affect adult turtles that forage or travel close to offshore platforms (Witherington et al., 2009). Marine and coastal pollution in the waters of the Gulf of Guinea have caused a host of environmental threats, including oxygen depletion, faunal die-offs, as well as heavy metal and hydrocarbon accumulation in marine consumers (Scheren et al., 2002; Mahu et al., 2015). These threats highlight the need to better understand the spatial ecology of green turtles during inter-nesting, migratory, and foraging periods in the Gulf of Guinea, in order to

understand their vulnerabilities and more effectively protect biologically important green turtle habitats.

Bioko Island Population

Bioko Island, Equatorial Guinea in West Africa, is home to the second largest green turtle rookery in Africa; however, this population has seen rapid decline in recent decades (Fitzgerald et al., 2011; Honarvar et al., 2016). In the 1940s, the estimated number of nesting females on Bioko Island was over 2000 individuals annually (Eisentraut, 1964). However, current annual estimates range from 454 to 649 individuals, a decline of up to 78% (Tomas et al., 1999; Seminoff, 2004; Honarvar et al., 2016). Despite the regional and global importance of this population, little is known about its in-water movements. Green sea turtles flipper tagged on Bioko in 1996-1998 have been recaptured in waters off the coast of Ghana, at least 1250 km from the nesting beaches of Bioko, in Corisco Bay, Gabon, around 280km from Bioko, and off the coast of southern Gabon, at least 760 km from Bioko (Tomas et al., 2001). Since then, there have been no studies on post-nesting migration routes from Bioko, and only one in the Gulf of Guinea, which tracked green turtles nesting in Guinea-Bissau to their foraging ground off the coast of Mauritania (Godley et al., 2010).

This study addresses the knowledge gap by using satellite telemetry to study green turtles nesting on the south coast of Bioko Island, Equatorial Guinea, 32 km off the coast of Cameroon, which has been classified as one of the most important nesting areas for green turtles within the Gulf of Guinea (Tomas et al., 2010; Honarvar et al. 2016). Green turtles nest throughout West Africa, with one of the highest densities of nesting females on the Atlantic coast of Africa occurring on Bioko's southern beaches (Fitzgerald et al., 2011; Honarvar et al.

2016). All four species of turtle that nest on these beaches are now, more than ever, threatened by anthropogenic pressures on Bioko and in the surrounding waters.

The objectives of this study are to investigate

- (1) the habitat use during inter-nesting periods;
- (2) in which direction green turtles migrate after nesting on Bioko;
- (3) if they migrate directly to their foraging grounds after nesting;
- (4) if migration routes are open-ocean, coastal, or both;
- (5) the locations of foraging grounds;
- (6) if green turtles maintain distinct home ranges once they reach foraging grounds; and
- (7) if there are multiple foraging grounds visited, and if so, how much time is spent at

each.

METHODS

Study Site

Bioko Island, Equatorial Guinea (2027 km²) is situated 32 km off Cameroon. The southern coast has 15 km of black sand beaches suitable for sea turtle nesting, which is within the legally protected Gran Caldera and Southern Highlands Scientific Reserve (Figure 1). The remainder of Bioko's 150 km coastline is either unsuitable for nesting for structural reasons (~120 km of cliffs or narrow rocky beaches), or beaches are too close to roads and villages (approximately 15 km of sandy beaches along the northern and western coast with no known sea turtle nesting). Four species of sea turtles (leatherback, *Dermochelys coriacea*; green, *Chelonia mydas*; olive ridley, *Lepidochelys olivacea* and, hawksbill, *Eretmochelys imbricata*) nest across the five southern nesting beaches (8°66' -8°46' E and 3°22' -3°27' N), with the largest populations of nesting green turtles on beaches A, B, and C, situated west of the road to the southern beaches and the village of Ureca (Figure 1).

This study was conducted on Beach C, chosen for its accessibility and high densities of green turtles.

Turtle Selection

Nesting season for green turtles on Bioko spans October through February, therefore satellite transmitters were attached near the end of nesting season, in order to focus tracking on post-nesting migration and gather locational data from possible foraging grounds. In January and February of 2018, turtles that had laid their last nest, as determined by the absence of developing follicles when scanned with a portable ultrasound (SonoSite 180 Plus; FUJIFILM SonoSite, Bothell, WA, USA), were preferentially selected as a turtle that is about to begin

post-nesting migration (Blanco et. al., 2012). In 2019, no ultrasound was used and transmitters were attached to turtles regardless of presence or absence of follicles, to allow for the investigation of in-water inter-nesting habitat. Across both seasons, only turtles that nested and seemed to be in good health without any scarring or damage to the carapace at the location of transmitter attachment were selected. Individuals were marked using a unique injectable passive integrated transponder (PIT) tag (AVID FriendChip Identification Systems Inc., Norco, CA).

Satellite Transmitters

In January and February of 2018 and of 2019, six satellite transmitters (SirTrack, Kiwisat 202; Sirtrack, Havelock North, New Zealand) each season were attached to green turtles on beach C, Bioko Island, Equatorial Guinea, for a total of 12 transmitters deployed across both seasons. The transmitters were attached following the methods developed by Balazs et al. (1996) modified by Luschi et al. (1998), Troeng et al. (2005), and Seminoff et al. (2008). Specifically, the carapace was cleaned, first with water, then with alcohol, and then scored with sandpaper to increase the strength of attachment. Transmitters were attached using Powers Pure50+ Two-Component Epoxy Adhesive (Powers, Brewster, NY, USA) to secure each transmitter to the second central scute of the carapace (Figure 2). Each turtle was restrained by a team of 4-5 researchers, and a wet cloth placed over her eyes, to keep each turtle calm and in place while the epoxy hardened.

Movement Analysis

Location data was relayed via the Argos satellite system. All Argos location points were used except for those with location quality 0 and Z (therefore classes 3, 2, 1, A, and B in order of descending accuracy) (Witt et al., 2010). The locations were filtered using the “argosfilter”

package for R (R statistical software, R 3.4.3, Vienna, Austria), which removes any point that required a travel speed >5 km/hr (Luschi et al., 1998), and the best location per day was selected to eliminate cloud bias.

Additionally, the filtered location data was fit with a Bayesian switching state-space model (SSM) using the ‘bsam’ package (Jonsen et al., 2017) for R. Post processed locational data was used, by filtering for speed and removing land points, instead of raw data to enhance the accuracy of the state space model (Hoenner et. al., 2012). The switching SSM estimates positions based on observed satellite data, after accounting for errors through a measurement equation and for dynamics of the movement process through a transition equation. The ‘bsam’ package is based on the switching state space model developed by Jonsen et al. (2007), and was applied using a hierarchical discrete correlated random walk model (hDCRWS), with an observation model built for GPS data. The hierarchical state-space model (hSSM) was used as opposed to a single DCRWS to analyze multiple tracks at once, using data such as travel speed and turn angle to estimate behavioral states for all turtles, rather than focusing on each individual separately. This model returns a behavioral mode estimation. Behavioral mode 1 is considered migratory, and behavioral mode 2 is considered area restricted search (ARS) behavior.

This model assumes a $tstep$ parameter of one, which was kept to retain only one location per animal per day. The model was fit to the turtle tracks with two chains running in parallel for a total of 15,000 Markov Chain Monte Carlo (MCMC) samples after 5,000 were discarded as burn-in. This model assumes a burn-in of 5,000 (adapt/2) and 5,000 MCMC samples. The number of samples to generate was increased to 15,000 to achieve a better fit, due to small datasets from several turtles. The remaining samples were thinned, retaining every 20th sample,

to minimize sample autocorrelation. The results of the model were plotted with changes in latitude and longitude, and parameters were selected based on visual assessment of best fit.

The resulting locations and tracks were then mapped using ArcGIS 10.2 (Esri, Redlands, CA). Track length and daily travel distance were calculated from total track distance using ArcGIS. Distance from coastlines and other geographical features were also calculated in ArcGIS. Spatial analyses included for habitat utilization within inter-nesting habitat and foraging grounds was done by calculating Kernel Density Estimates (KDEs) with ArcGIS. This was done with the kernel density tool in the Spatial Analyst toolkit in ArcMap. A KDE grid size of 0.015° was used, and a smoothing factor of 0.15 was used to prevent over smoothing. Density estimates were calculated for 95% and 75% utilization distribution as well as core use area (50% utilization distribution).

Dive Depth Analysis

Dive data from inter-nesting behavior, migrations, and foraging behavior were separated based on the behavioral values given by the State Space Model. All recorded dive depths were used in the analysis, regardless of location quality, since depths were associated with a behavior rather than a specific location. Depths that were determined to be false due to transmission errors were discarded. Depth data included maximum dive depth for each dive, length of each dive, daily dive ratio, which represents the percentage of each day that the turtle spent diving, and tip-to-apex distance (TAD) index. The TAD index indicates the general shape of the dive, with higher numbers indicating “U” shaped dives (100 being a dive in which the total dive time is spent at maximum depth) and lower numbers indicating a “V” shaped dive, with more time spent near the surface or during descent and ascent (50 being a perfect V). TAD indices of less

than 50 indicate dives in which most time was spent near the surface, with very little time spent at maximum depth (Figure 3).

Comparative Analysis

Ocean surface current data was downloaded from the Ocean Surface Current Analysis Real-Time (OSCAR) from NASA (ESR, 2009). Current data are provided on a 1/3 degree grid with a 5 day resolution. OSCAR data used to overlay migrations was downloaded for multiple consecutive 5-day periods during migrations and averaged, giving a 10 or 15-day smoothed resolution depending on the length of migrations. OSCAR data was then scaled linearly on a scale from 0-1 and displayed in ArcMap (ESR, 2009).

Bathymetric data from ETOPO1, created by the National Geophysical Data Center (NGDC) and the National Oceanic and Atmospheric Administration (NOAA) was downloaded in NetCDF format using the grid extract tool (Amante and Eakins, 2009). Data was then displayed in ArcMap.

Seagrass distribution data was downloaded from the UN Environment World Conservation Monitoring Centre (UNEP-WCMC, Short FT (2018)). Data was displayed in ArcMap.

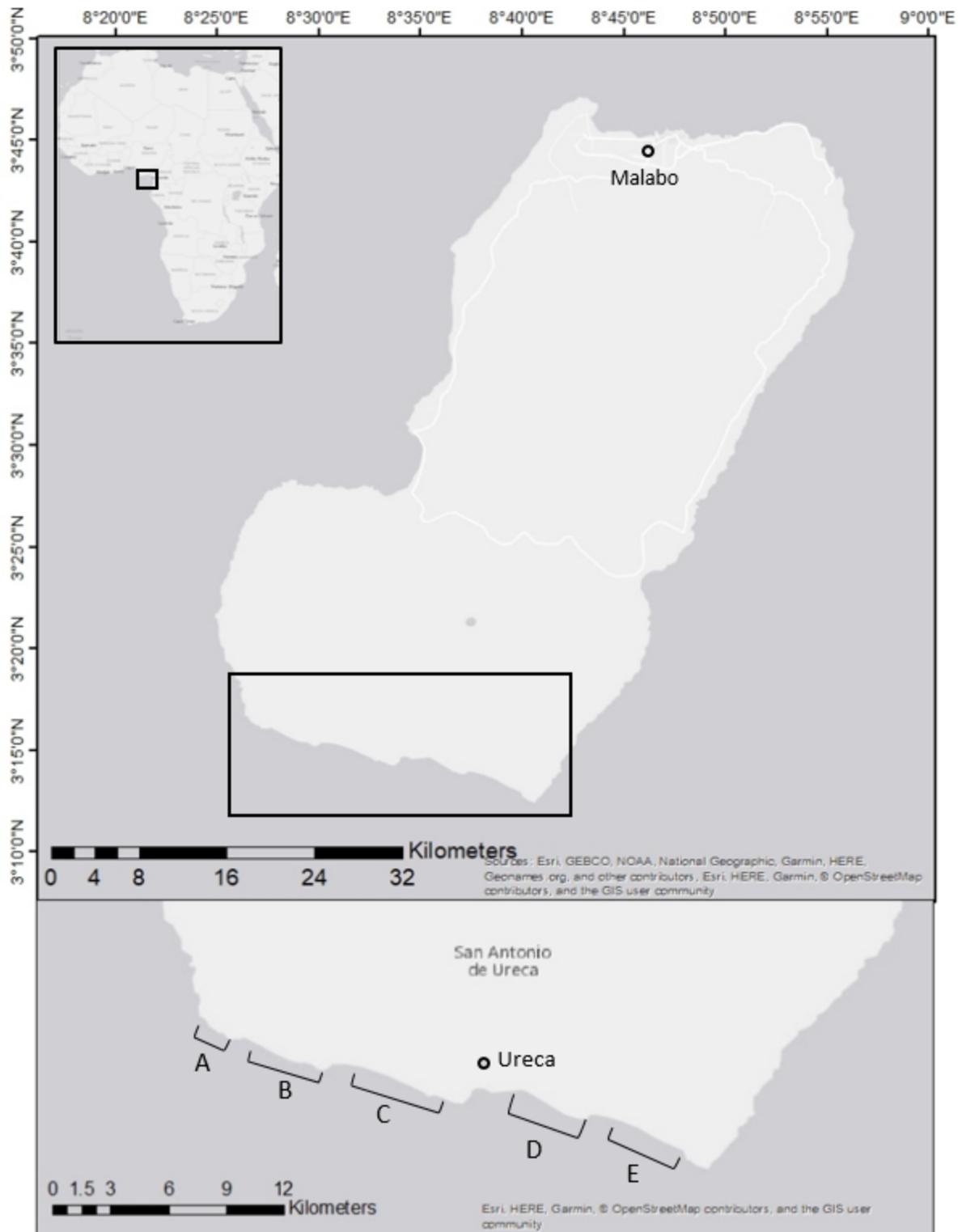


Figure 1 Map of Bioko Island. Insert shows the five sea turtle nesting beaches A-E in relation to the nearest village, Ureca.



Figure 2 Satellite transmitter attachment location. The transmitter is attached to the second medial scute of each green turtle's carapace.

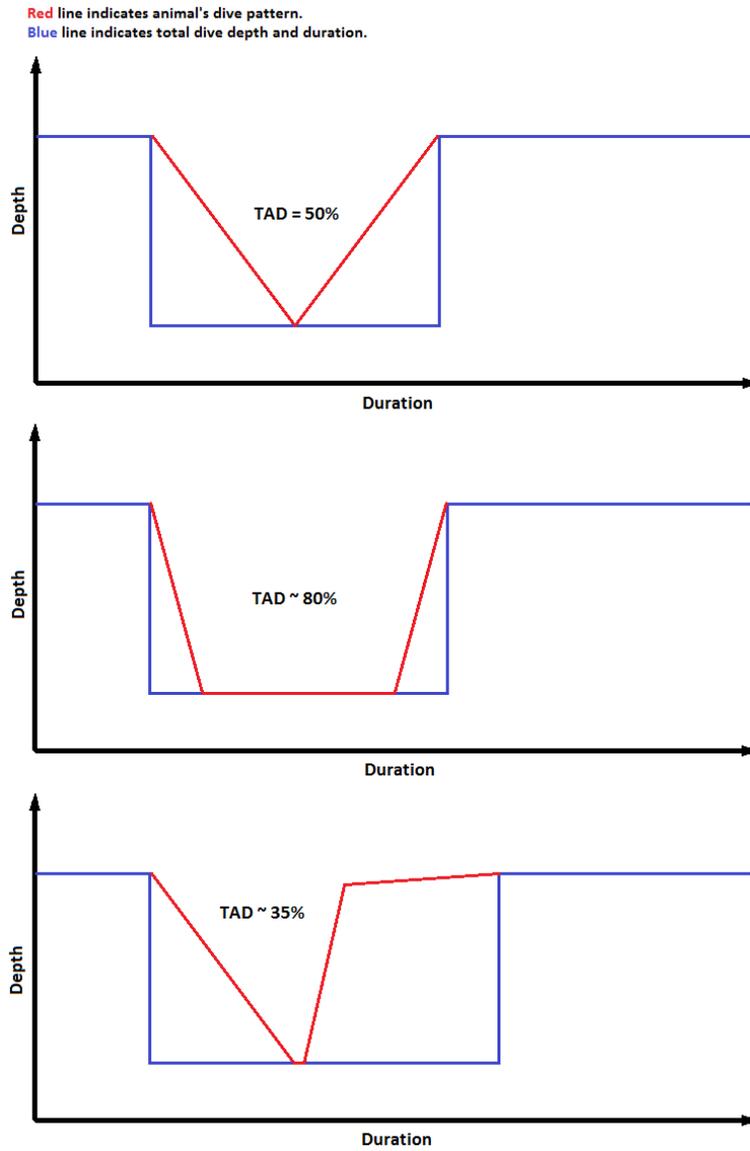


Figure 3 Illustration of TAD indices indicating general shape of each dive. A TAD index of 100 corresponds to a “U”-shaped dive, and 50 corresponds to a “V”-shaped dive.

RESULTS

Twelve satellite transmitters were deployed in 2018 (n=6) and 2019 (n=6). Tracks were analyzed for a total of 867 days. All of the turtles from the 2018 nesting season (n=6) migrated northwest from the nesting beach immediately after nesting and transmitter attachment. From the 2019 nesting season, 4 turtles began northwestward post-nesting migrations, while 2 migrated south. Four turtles returned to the nesting beach and are suspected to have nested at least once more on Bioko, before beginning migrations in either direction.

Movement Analysis

The results of the switching SSM were plotted, with the assigned behavioral state alongside the latitude and longitude of each locational point (see appendix), and the assigned behavioral states were checked against satellite data. The SSM assigned behavioral estimates of area restricted search to the movements of 4 turtles in the vicinity of the nesting beaches, before beginning a directed migration- behavioral estimates of 1. These were classified as inter-nesting movements. Area restricted search behavioral states were also assigned to movements of 9 in localized near shore habitats >1000 km away from nesting beaches, these were classified as foraging habitats. Migratory states (behavioral estimate of 1) were assigned to location points for all 12 turtles for the majority of locations in between interesting and foraging habitats.

Inter-nesting Movements

Four turtles did not immediately begin direct post-nesting movements to a foraging ground, and were suspected to have re-nested on Bioko. These four turtles maintained a core use area of 42.6 km² immediately offshore from the nesting beaches, generally remaining in the

shallow (>250 m) coastal waters (Figure 4). Two of these turtles (Cm11 and 9) remained within 5 km of the nesting beach for 12 and 9 days, respectively, before it is suspected that they renested, before beginning a directed migration (Figure 4; Table 1). Another turtle, Cm8, made a circular movement through deep oceanic waters (>1000 m), traveling ~100 km away from the nesting beach. This movement continued for 11 days before this turtle returned to the vicinity of the nesting beaches, remaining there for 4 days during which she is suspected to have renested, before beginning a directed migration. Cm10 remained within 5 km of the nesting beach for 27 days, and then made a smaller oceanic loop for 4 days, traveling ~41 km from the nesting beach, before returning for one day and then beginning a directed migration (Figure 5). These looping movements were designated as partially migratory behavior by the SSM; however, because satellite data shows that these turtles returned to the vicinity of the nesting beaches before making a directed migration and the timing of these returns corresponds to previously observed interesting intervals of about 10-15 days (Tomás et al., 2010), these movements were considered inter-nesting movements for analysis.

Post-nesting Movements

Two distinct post-nesting directions were observed. Two turtles conducted southern migrations to a neritic foraging ground off the coast of Luanda, Angola (Figure 6), and 10 turtles began a northwestern migration. Of these 10 turtles, 7 reached a neritic foraging ground east of Accra, Ghana, (Figure 7). Among these western migration routes, two migratory strategies were observed, with some turtles traveling directly to foraging grounds along mainly oceanic routes (Figure 7, blue tracks), and some conducting biphasal migrations- crossing oceanic zones and then migrating in neritic zones, and foraging intermittently at stopover foraging sites during the migration (Figure 7, green tracks).

The 7 turtles that completed northwestern migrations traveled for an average of 20.4 days and 1115 km. Cm1, Cm2, and Cm3 migrated directly to their foraging ground, with Cm2 and 3 (Figure 7, light blue tracks) traveling primarily in oceanic zones and Cm1 (Figure 7, dark blue track) traveling closer to the coast and primarily staying in shallower (<500 m) waters (Figure 7). All three direct migrations minimized travel time and traveled faster (13.7 days and 83.9 km/day on average; Table 1) when compared to biphasal migrations which included intermittent foraging (25.5 days vs 43.7 km/day on average; Table 1).

The remaining 4 turtles- Cm4, 5, 7, and 8 - migrated primarily in shallow coastal waters (<50 m) and remained within 20 km of the coast for the majority of their migration. These 4 turtles foraged for short periods (<4 days) at stopover foraging sites throughout the coastal migration (Figure 8). Turtles moving west along both oceanic and neritic migratory pathways traveled in concordance with prevailing ocean surface currents for the entirety of migration in both 2018 and 2019 (Figures 9 and 10).

All 7 of these turtles ultimately began extended periods (>15 days) of residency and foraging behavior at a neritic foraging ground off the coast of Ghana, in a 50 km stretch east of the Chemu Lagoon and west of the Volta River Delta, after migration periods of 10-29 days.

Cm9 and Cm10 traveled south, with Cm9 traveling primarily in the pelagic zone, and Cm10 remaining in the neritic zone, above shallow (<50 m) waters for almost the entirety of her migration. Both Cm9 and 10 crossed deep water to Corisco Bay, where they each foraged for two and one day, respectively then migrated to a foraging ground in the coastal waters of Luanda, Angola (Figure 11). Both turtles traveled both with and against prevailing surface currents (Figures 11 and 12). The initial portion of the southern movements of Cm9 were against clockwise, then counterclockwise rotating currents until reaching the calm waters (<0.3

m/s) of Corisco Bay. From there Cm9 traveled south, perpendicular to primarily eastern currents until $\sim 3^{\circ}20'S$, from where she traveled with prevailing southeastern currents or along the edge of rotating eddies until reaching the foraging ground (Figure 12). Cm10 traveled primarily against ocean currents, until $\sim 0^{\circ}60'S$ and then traveled perpendicular and at times in accordance with ocean currents for the remainder of her migration. Both southern migrating turtles began extended periods of foraging behavior within 15km of the shore of Luanda.

One westward moving turtle, Cm6, exhibited coastal migration and was in transit for 19 days until reaching the coastal waters of Lagos, Nigeria. Subsequently, beginning on day 20, February 20th, all location transmissions were from land, in the Amuwo Odofin suburb of Lagos. Behavioral estimates provided by the state space model indicate that this turtle was still transiting, rather than foraging, when the transmissions from land began. As this turtle had no vitellogenic follicles remaining, there is no evidence that the turtle would have naturally returned to land, and it is suspected that there was some human interaction that led to the transmitter being moved to land.

Two other turtles, Cm11 and 12, began northwestern migrations, and had traveled 240 km and 858 km, respectively when transmissions ceased, before reaching their suspected foraging areas.

Foraging Distribution and Depth Analysis

Turtles that migrated to the western foraging grounds occupied a ~ 160 km² core use area, within 20 km of the coast (Figure 14). Foraging behavior occurred in shallow waters, <50 m. During interesting behavior, the majority of dives (81.0%) were between 15 and 25m deep, with an average depth of 19.33 m, and an average maximum dive depth of 28.25 m (Figure 15) The average TAD index of interesting dives was 80.27, which corresponds to quick descents

and ascents, and most time spent at the maximum depths of each dive. On average, during interesting periods turtles spent 21.8% of each day diving, and the remainder at the surface.

Western migrations had a shallow average dive profile, with nearly half (49.6%) of dives being within 5m and most (62.3%) dives being between 0 and 10 m (Figure 16). Average dive depth was 11.1 m and average TAD index was 37.8, indicating that the majority of dives were shallow, with more time spent near the surface than at maximum depth. Southern migrations, in contrast, had a deeper average dive profile with an average dive depth of 19.5 m and nearly 70% of all dives being >10 m. The average TAD index was 70.9, indicating little time spent at the surface and at maximum depth-- between a "U" and "V" shaped dive.

The majority of dives (66.8%) during foraging behavior at the foraging ground in Ghana were <10m deep. Average depth was 8.5m, average TAD index was 63, again between "V", and "U" shaped dives with most time spent during ascent and descent (Figure 17).

Table 1 Movement summary of inter-nesting, post-nesting, and foraging periods. Turtles are grouped according to post-nesting migratory strategy and direction. Turtles that began a western migration, but for which foraging data is not available are grouped under “West unknown”.

Turtle	Inter-nesting			Migration			Foraging	
	Start Date	End Date	Duration	Duration	Distance (km)	Speed (km/day)	Duration	Distance to Coast (km)
W Direct								
Cm1	-	-	-	10	1043	104.3	258	3.86
Cm2	-	-	-	15	1126	75.1	74	0.41
Cm3	-	-	-	16	1156	72.3	63	6.92
W Biphasal								
Cm7	-	-	-	26	1125	43.3	30	3.62
Cm8	30-Jan-19	14-Feb-19	16	22	1004	45.4	16	5.84
Cm4	-	-	-	25	1118	43.6	19	0.91
Cm5	-	-	-	29	1233	42.5	73	6.76
W Unknown								
Cm11	26-Jan-19	6-Feb-19	12	5	240	48	-	-
Cm12	-	-	-	19	858	45.2	-	-
Cm6	-		-	19	742	37.1	-	-
S Biphasal								
Cm9	30-Jan-19	7-Feb-19	9	27	1559	57.7	18	2.41
Cm10	1-Feb-19	4-Mar-19	33	33	1566	47.5		

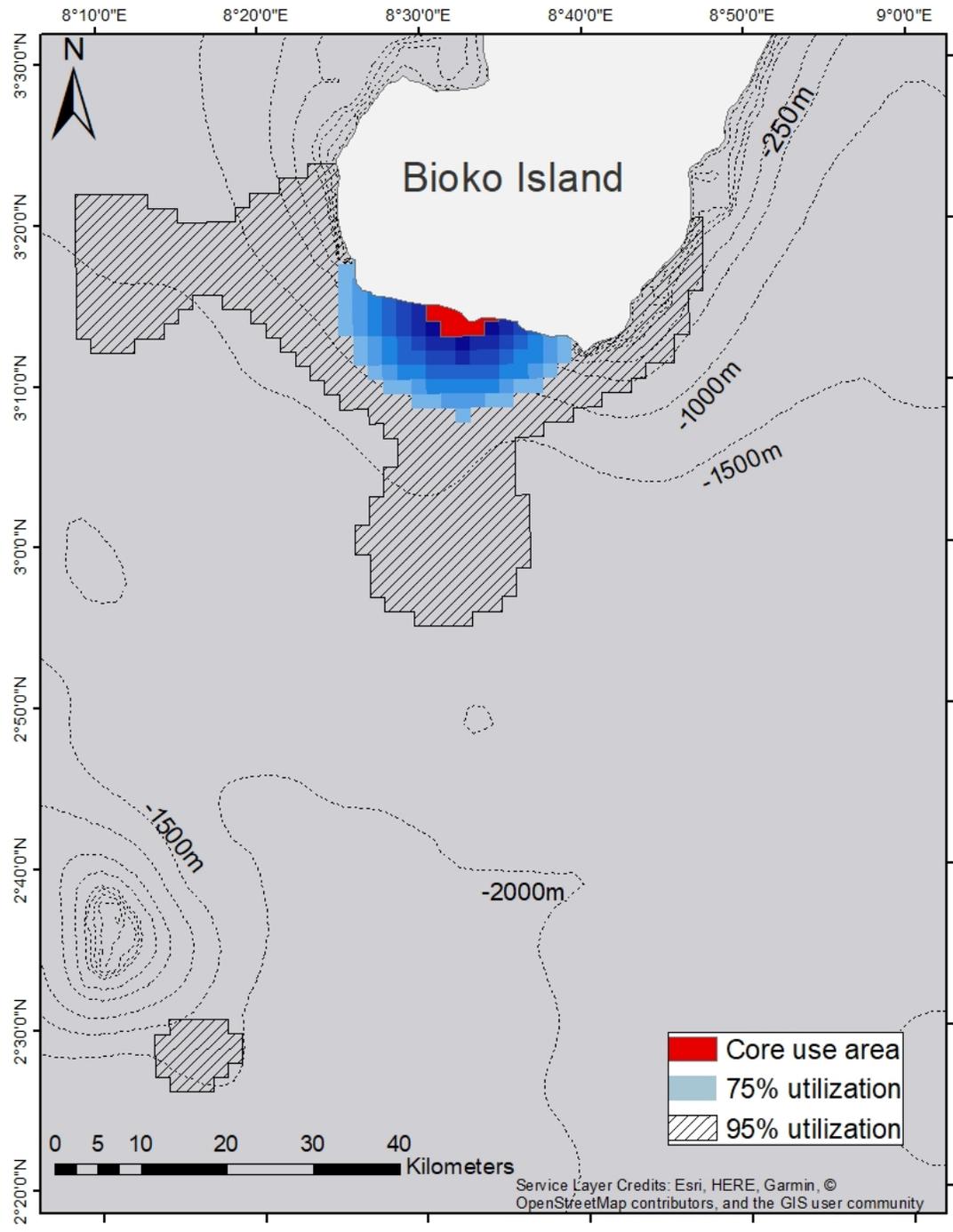
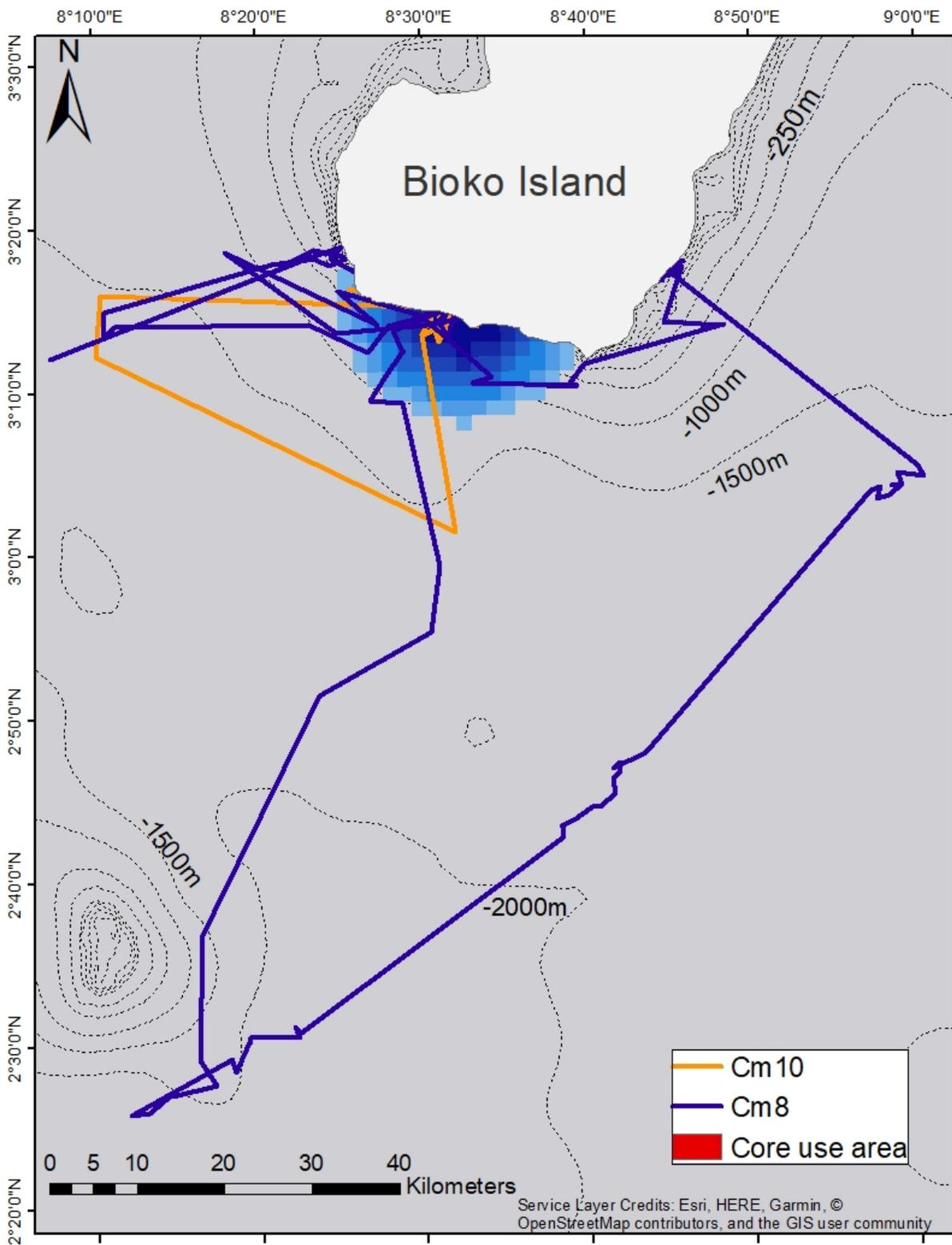


Figure 4 Map of inter-nesting behavior. Cm8, 9, 10, and 11 remained in the vicinity of the nesting beach for 12-33 days, maintaining a core use area (50% utilization) of 42.6m². 95% and 75% utilization distributions are also shown.



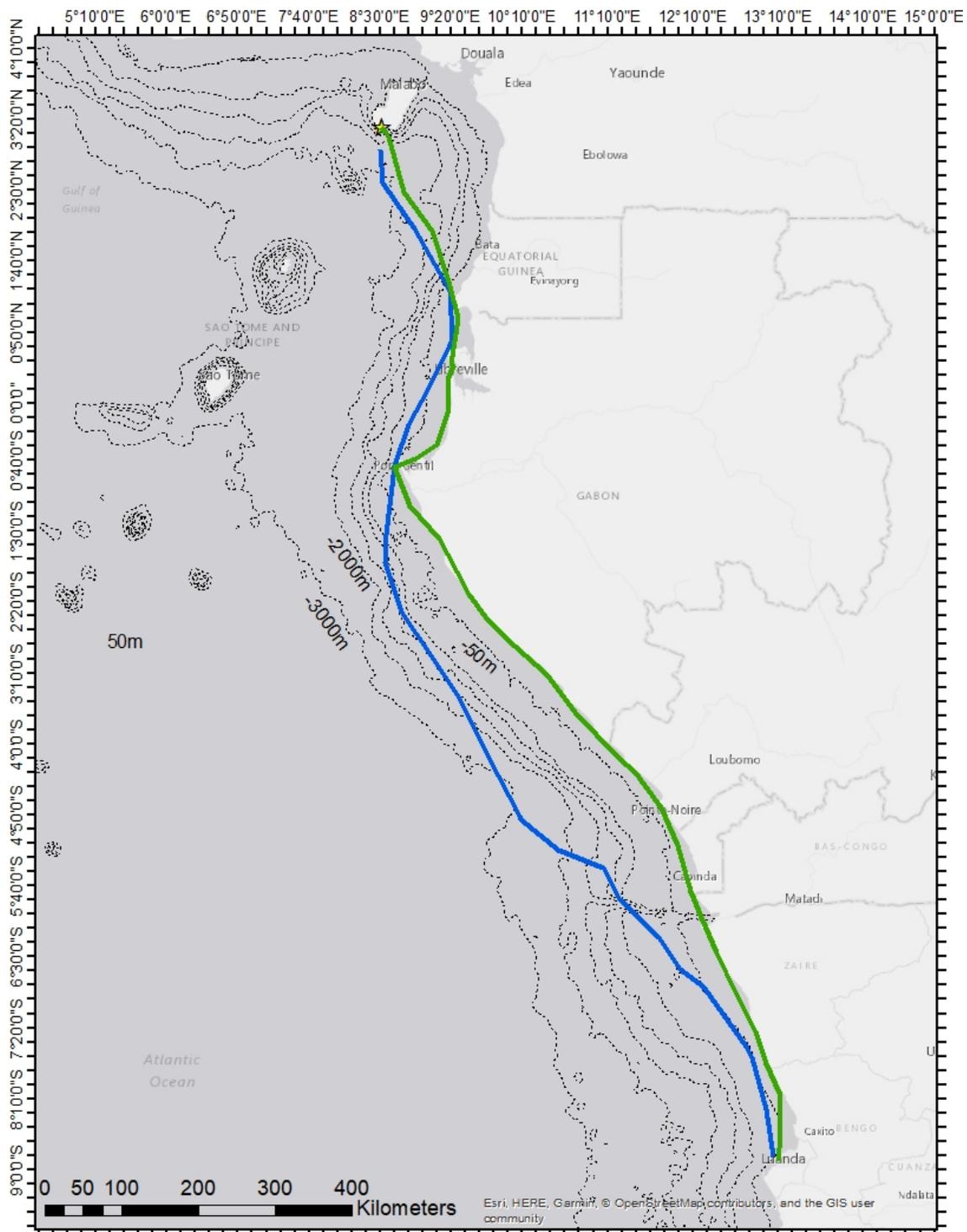


Figure 6 Post-nesting movements of two green turtles tracked from Bioko Island after the 2019 nesting season. Individuals traveled an average of 1563km, one using a coastal migratory route (green track) and one using a primarily oceanic migratory route (blue track).

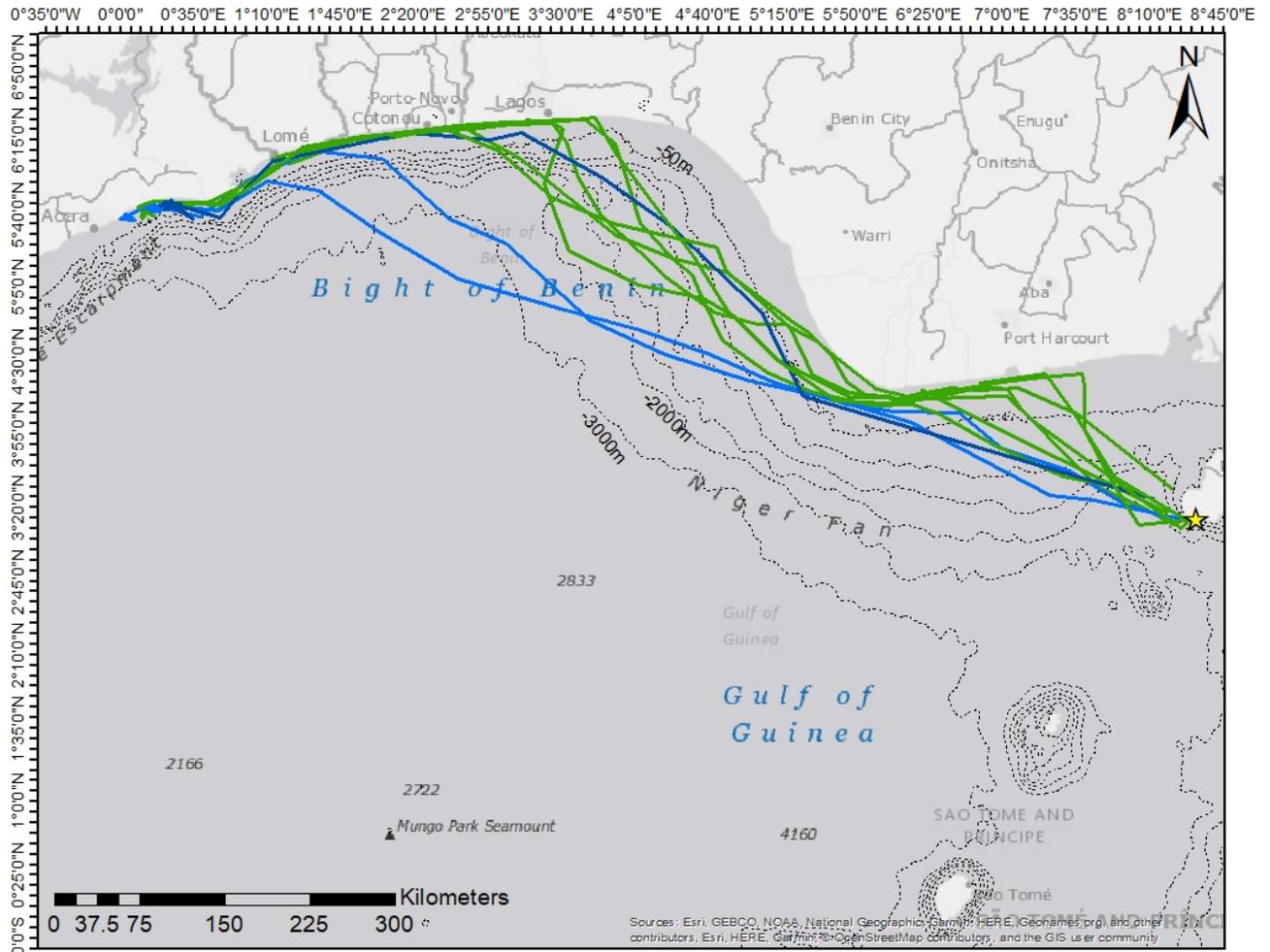


Figure 7. Post-nesting movements of ten green turtles tracked from Bioko Island (yellow star), after the 2017-18 and 2018-19 nesting season. Individuals traveled an average of >1,000 km using a combination of oceanic (light blue tracks) and coastal migratory routes. Most coastal migrations were interspersed with brief periods of foraging at stopover foraging sites (green tracks), while one was a direct migration with no stops (dark blue track).

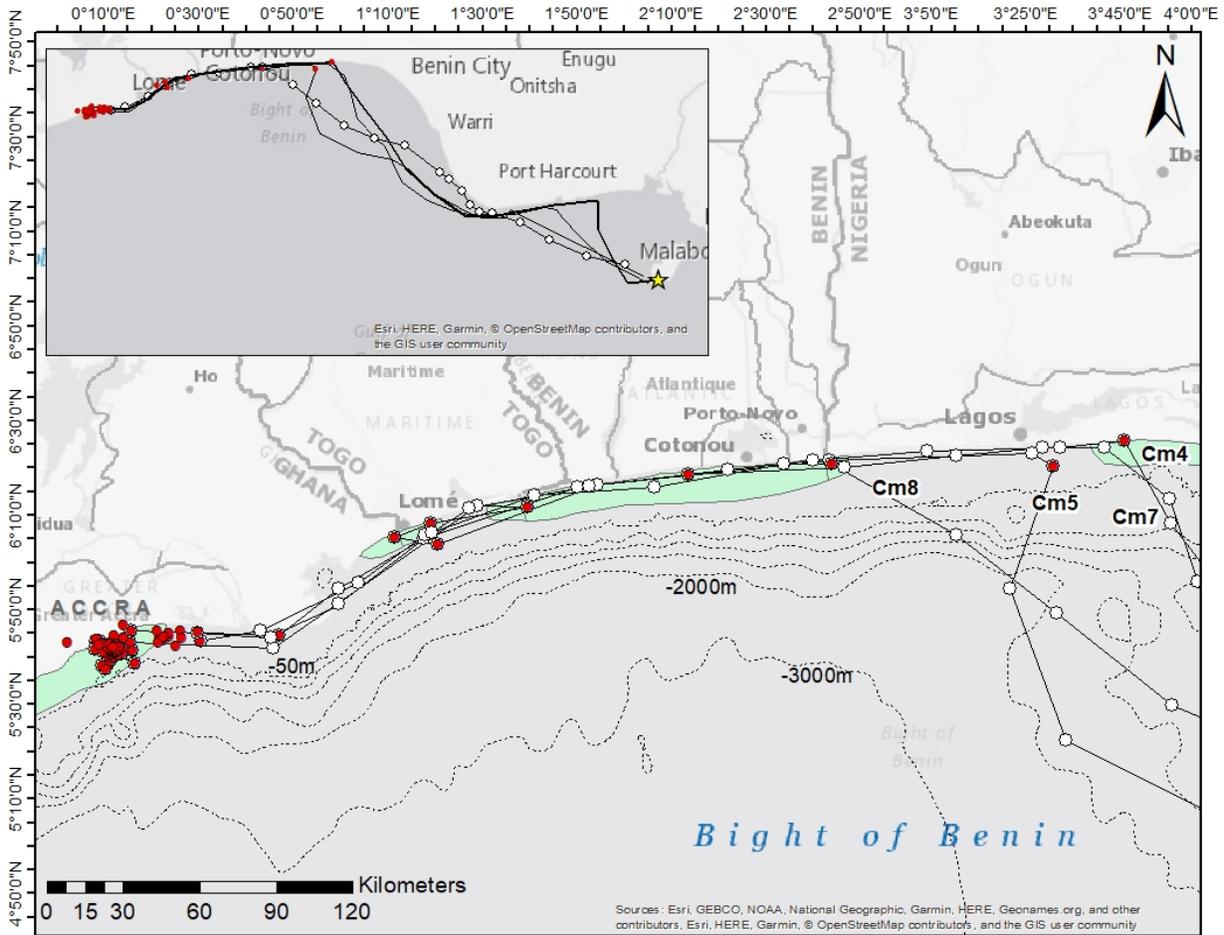


Figure 8 Daily locations (circles) of 4 turtles tracked from Bioko Island. White circles indicate transiting behavior and red circles indicate foraging behavior. Green areas indicate known seagrass beds. Four turtles exhibit migrations interspersed with short (<4 days) periods of foraging.

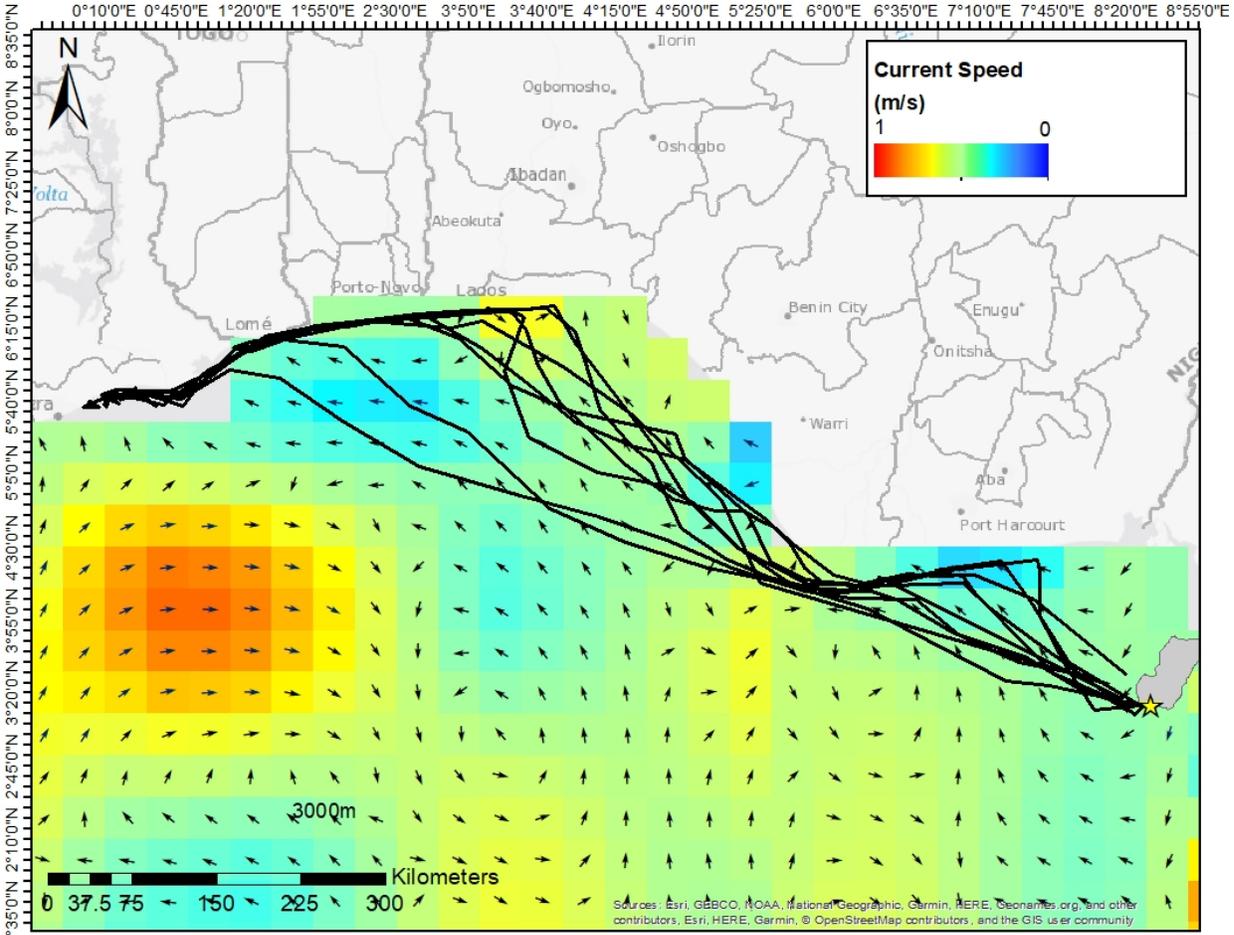


Figure 9 Western migrations of 6 turtles traveling from Bioko Island after the 2017-18 nesting season overlaid with surface current data. Migration routes are overlaid onto averaged ocean current data for the 10 day period from 2/10/18 to 2/20/18.

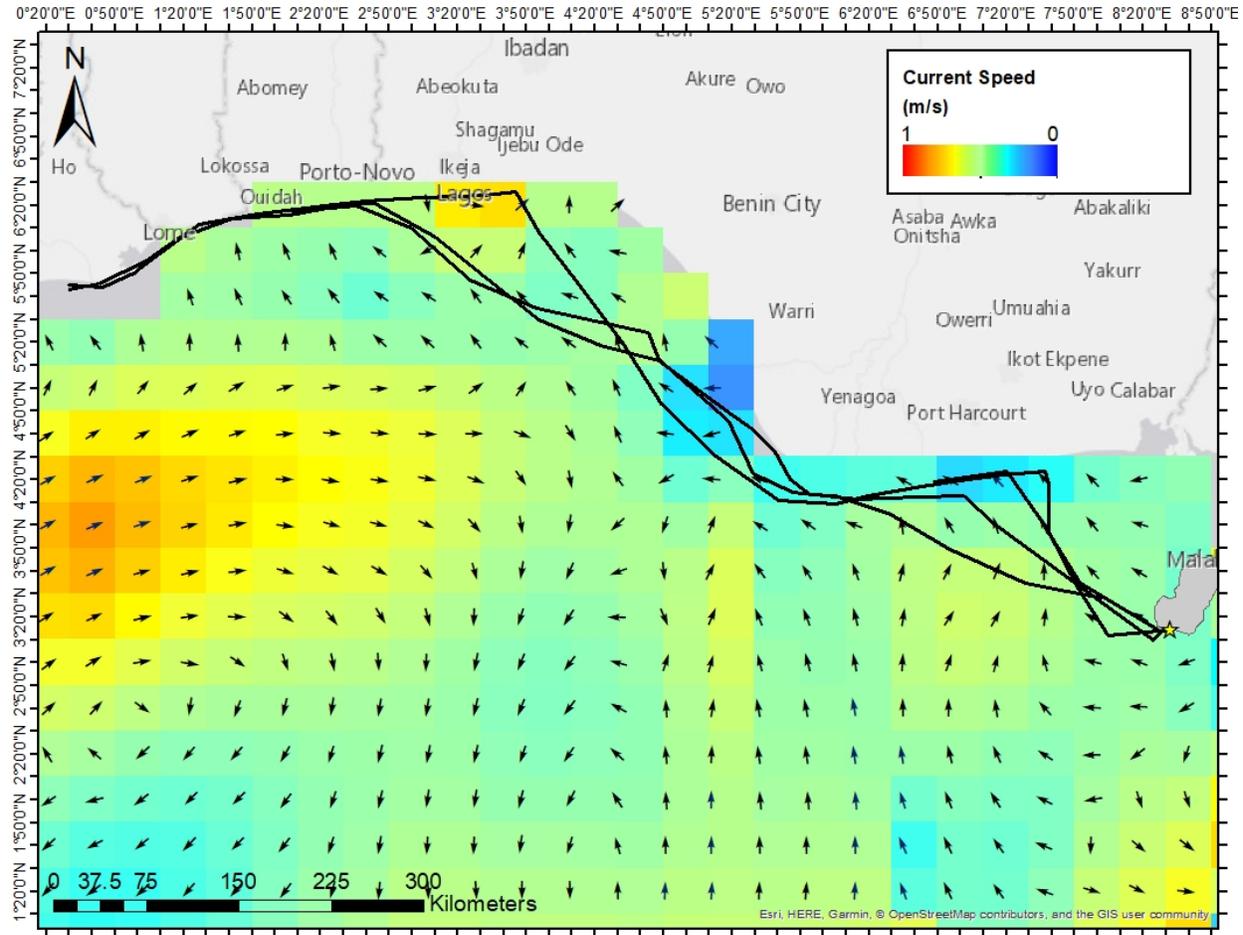


Figure 10 Western migrations of 6 turtles traveling from Bioko Island after the 2018-19 nesting season overlaid with surface current data. Migration routes are overlaid onto averaged ocean current data for the 15 day period from 2/15/18 to 3/2/18.

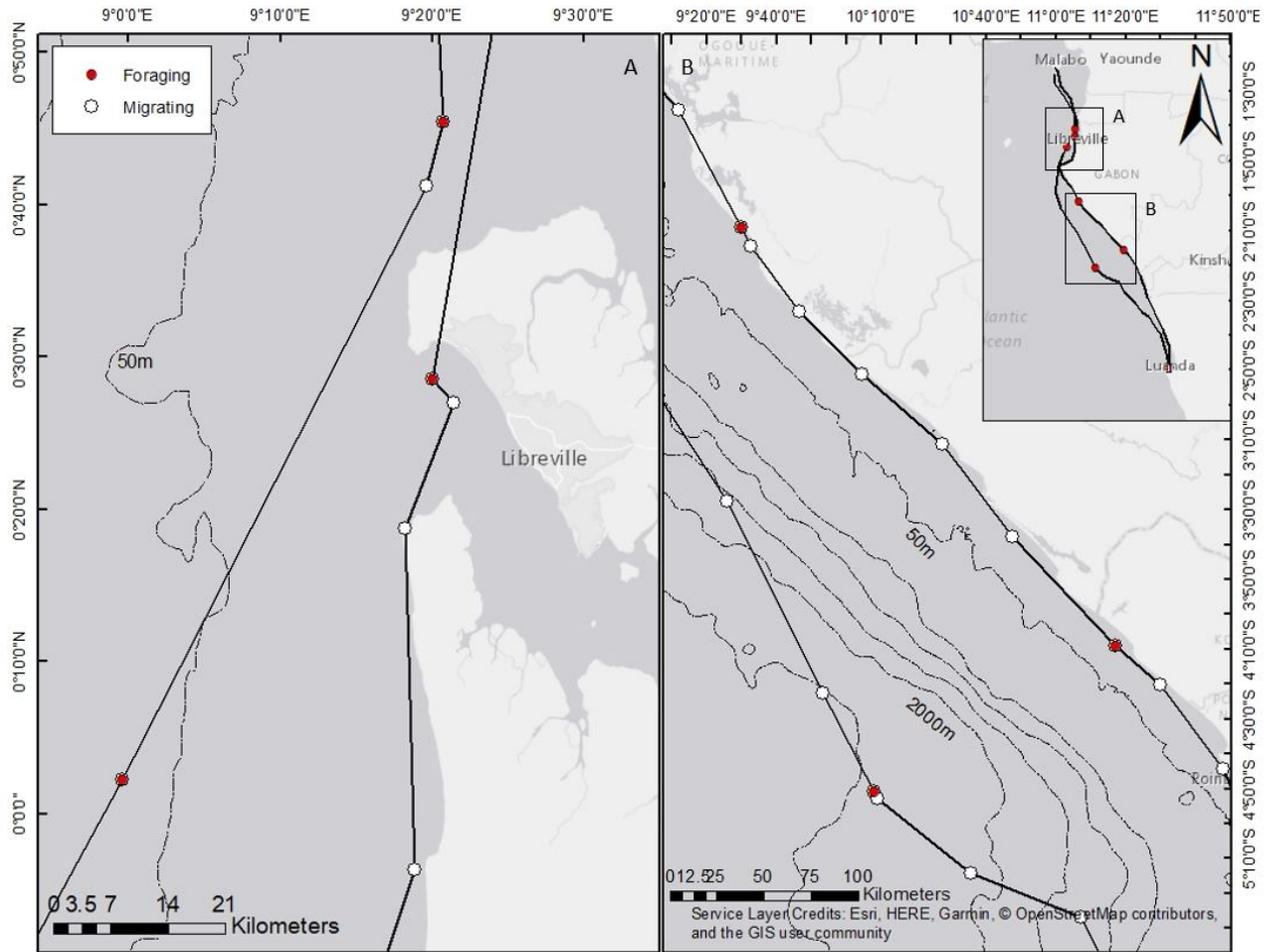


Figure 11 Daily locations (circles) of 2 turtles migrating south from Bioko Island after the 2018-19 nesting season. White circles indicate transiting behavior and red circles indicate foraging behavior. Both Cm9 and Cm10 foraged in Corisco Bay (9A) and in another location ~100 km north of Pointe Noire, Congo (9B) during their migrations.

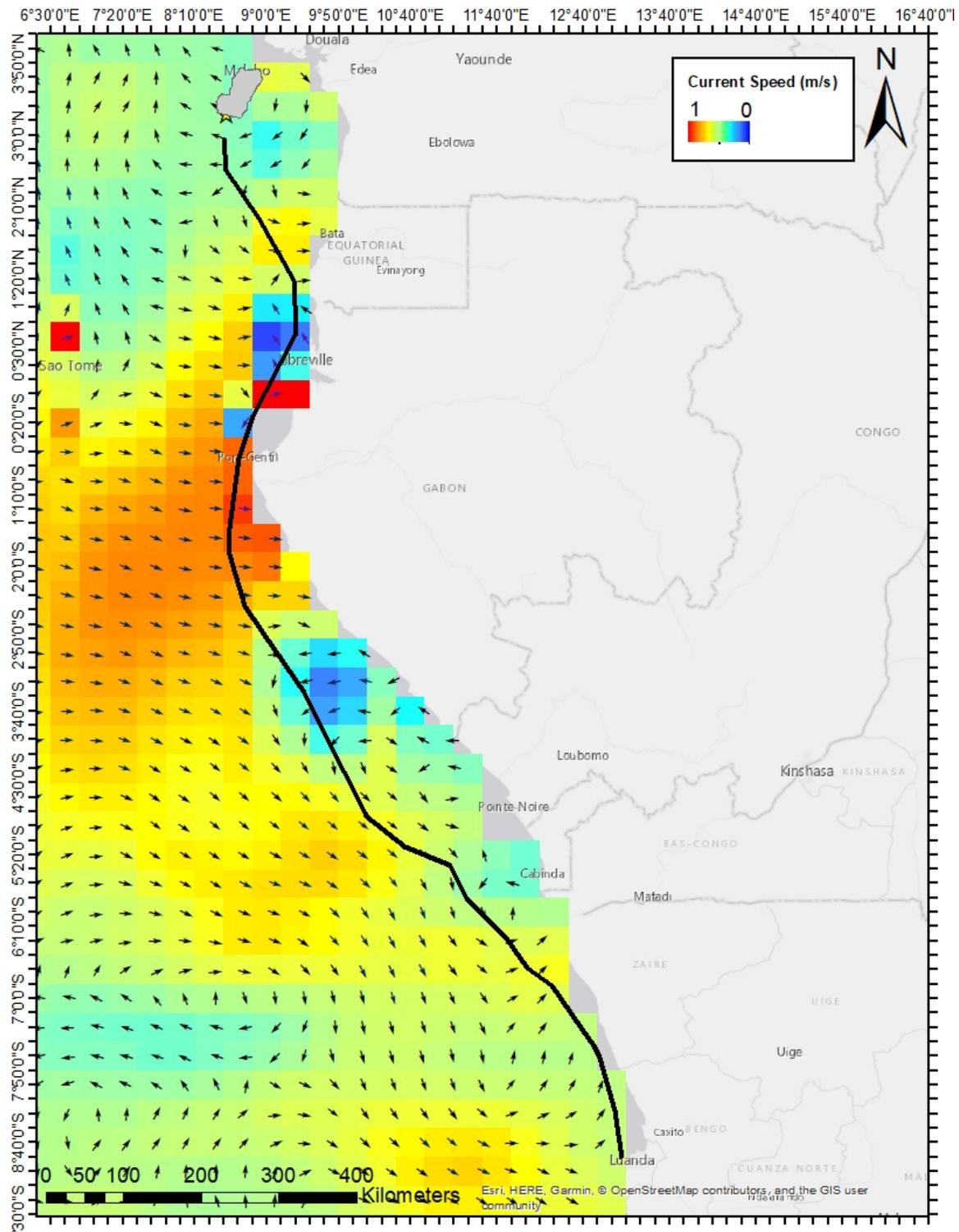


Figure 12 Southern migration of 1 turtle traveling from Bioko Island after the 2018-19 nesting season overlaid with surface current data. Migration route is overlaid onto averaged ocean current data for the 15 day period from 2/15/18 to 3/2/18.

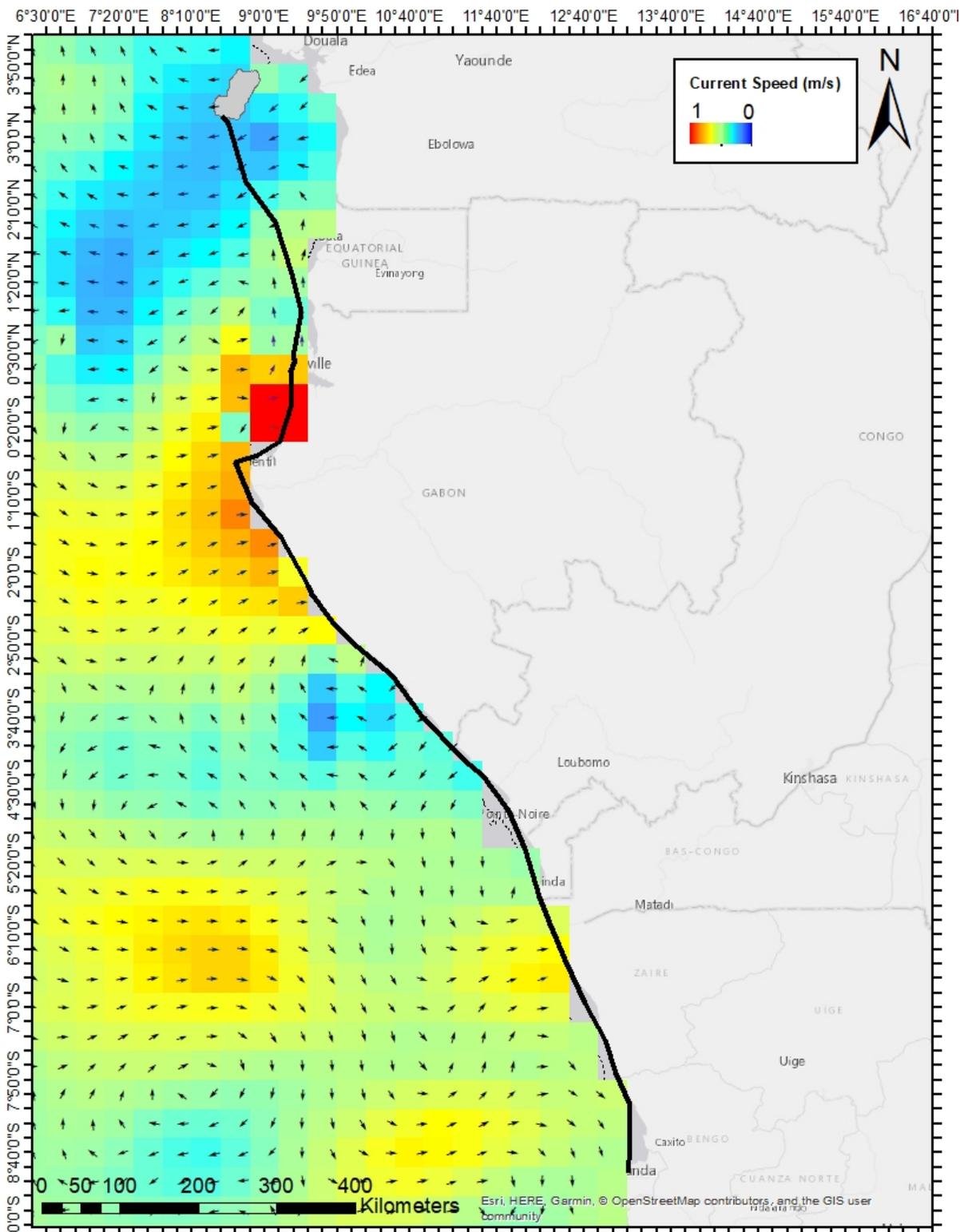


Figure 13 Southern migration of Cm10 traveling from Bioko Island after the 2018-19 nesting season overlaid with ocean current data. Migration route is overlaid onto averaged ocean current data for the 15 day period between 3/7/19 and 3/22/19.

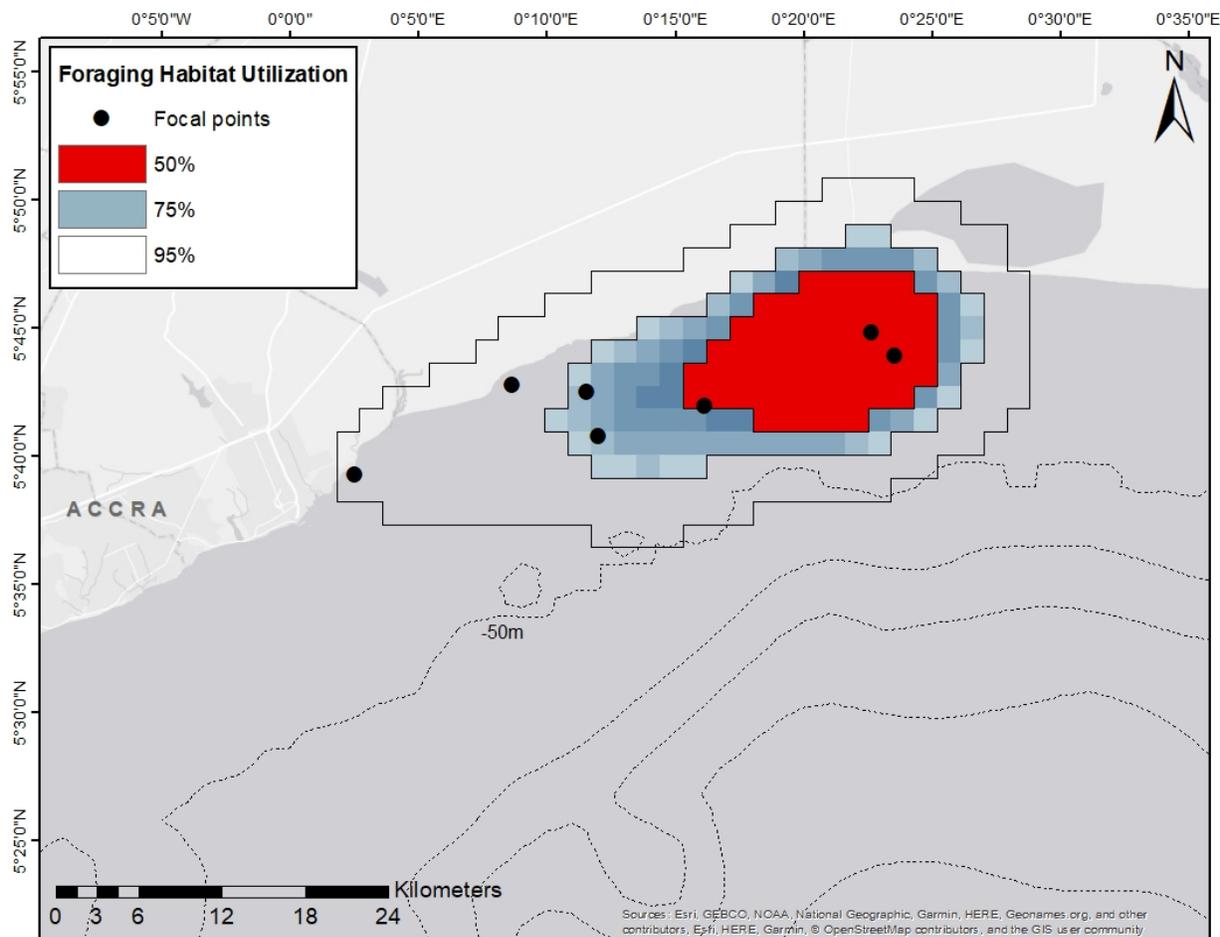


Figure 14 Foraging behavior of 7 turtles near the coastal waters of Accra, Ghana. Turtles occupied a core use area of 160 km², in waters <50 m deep. 95% and 75% utilization distributions are also shown.

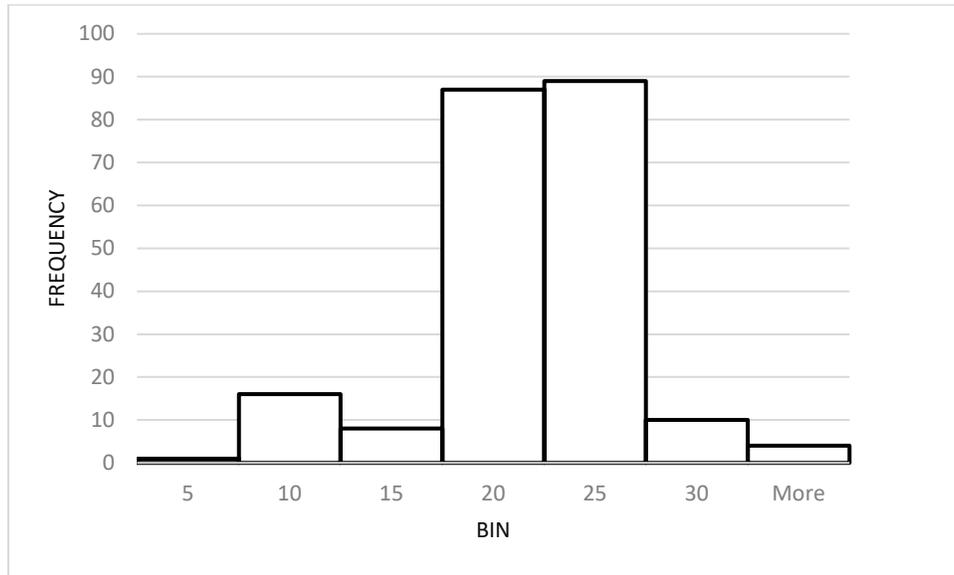


Figure 15 Frequency distribution showing maximum depths of all dives during interesting behavior.

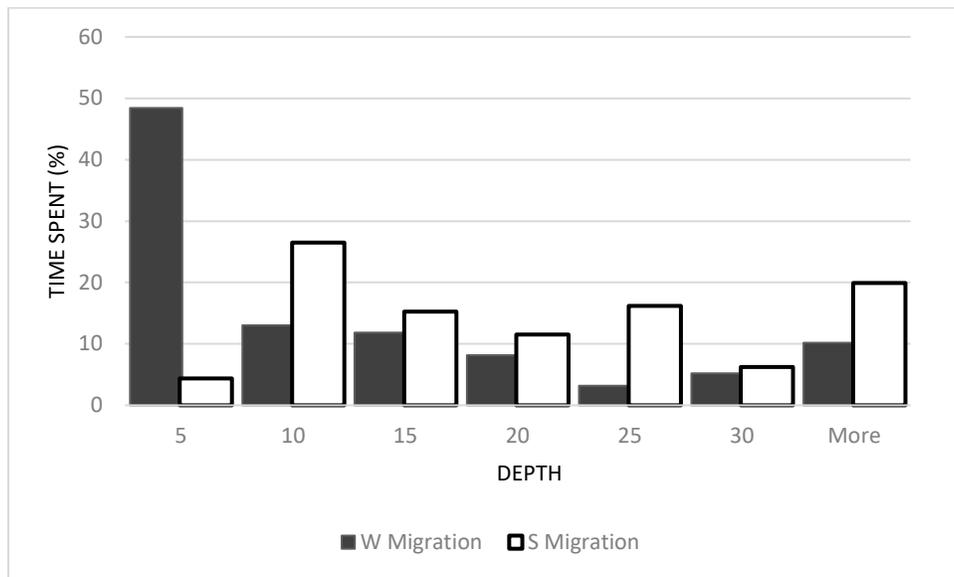


Figure 16 Frequency distribution showing maximum depths of all dives during western and southern migrations.

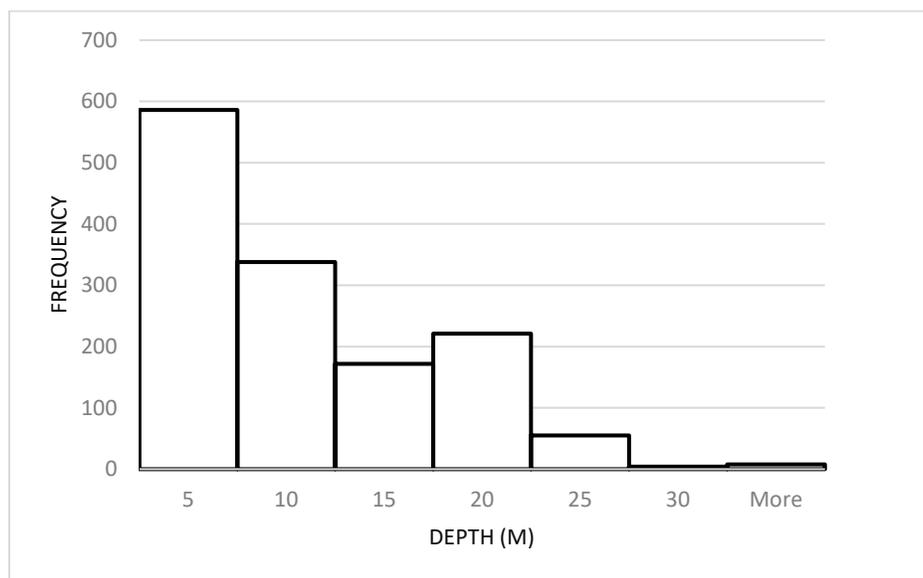


Figure 17 Frequency distribution showing maximum depths of all dives during foraging behavior.

DISCUSSION

Inter-nesting Movements

Tomás et al. (2010) observed inter-nesting intervals for green turtles nesting on Bioko with the most frequent inter-nesting intervals being 10-15 days. Due to limitations in accuracy of satellite locations it is impossible to confirm that turtles nested again on Bioko beaches with the satellite data, but three of the four turtles (Cm8, 9 and 11) that exhibited suspected inter-nesting behavior began directed migration from the coastal waters of the nesting beach 12-16 days after a confirmed nesting event and transmitter attachment, indicating one possible re-nesting event before migration.

Of these four turtles, Cm11 and Cm9 remained within a few kilometers of the nesting beach before beginning directed migrations, which is consistent with previous records of green turtle inter-nesting and migration behavior (Papi and Luschi, 1996; Godley et al., 2002; Hart et al., 2013). It has been suggested that turtles spend inter-nesting intervals resting, and therefore remain nearby nesting beaches to minimize energy expenditure (Cheng, 2009). Green turtles exhibit plasticity in inter-nesting behavior, and may also feed opportunistically when there are foraging grounds or other available food items close to the nesting beach (Hays, 2002; Richardson et al., 2013); however, there is evidence to suggest that green turtle inter-nesting habitat preference is driven primarily by bathymetry, rather than presence or absence of foraging habitat (Hart et al., 2013). The average dive depth during inter-nesting behavior for these four turtles was 19.33 m, and 81.9% of dives were within 15-25 m, which may correspond to the depth of seagrass beds in the area or to optimal resting depth in these coastal waters (Figure 15). Average TAD indices (80.27%) indicate that dives during inter-nesting periods

were typically U-shaped, with steep descents and ascents, and the majority of time spent at maximum depth. These typically correspond to resting dives (Cheng, 2009). The rocky coastline, steep drop-off, and existing data on seagrass distribution also make it unlikely that these coastal waters provide suitable foraging habitat, and suggest that inter-nesting habitat may primarily be used for resting (Cheng, 2009; Hart et al., 2013; UNEP-WCMC, 2018).

Based on the observed inter-nesting interval for this population, the 11 day oceanic loop made by Cm8, followed by 4 days in the vicinity of the nesting beach, is likely a circular inter-nesting movement followed by a nesting event. The much smaller, 4-day loop made by Cm10 may have been followed by another nesting event, or may have taken place after the last nest was laid, but before a directed migration. While green turtles more commonly remain nearby nesting beaches during interesting intervals, a number of studies have documented oceanic loops prior to directed migration (Cheng, 2000; Troeng et al., 2005; Blumenthal et al., 2006). It has been suggested that looping behavior may be an attempt to locate a new foraging ground (Luschi et al., 1998).

Looping behavior, whether as inter-nesting or post-nesting movements, may also be associated with oceanic foraging (Troeng et al., 2005). Green turtles are typically benthic herbivores, and ocean depths throughout both loops were too deep for benthic foraging (>1,000 m). Additionally, data from depth sensors shows that the turtle's maximum dive depths during these oceanic loops were 35.75 m and 31.25 m, making it highly unlikely that these movements were driven by benthic foraging activity. Oceanic foraging on surface level planktonic food sources by green turtles has also been demonstrated by stable isotope and stomach content analyses (Hatase et al., 2006; Parker et al., 2011). It is possible that these oceanic loops were associated with oceanic foraging on planktonic food sources being carried by surface currents.

Typically, during interesting intervals, reproductive females are concentrated in a distinct area nearby nesting beaches, making them more vulnerable to predation, and more recently to anthropogenic threats (Meylan, 1995). Therefore, it may be advantageous for turtles to undertake long oceanic movements during this interval to avoid predation, despite the higher energy cost.

Circular movements were also observed in disoriented turtles after displacement (Luschi et al., 2001). The track made by Cm8 was indirect, meandering through deep open-ocean until reaching a seamount, at which point the turtle nearly reversed directions, and traveled in two near-straight lines back to the nesting beach (Figure 5). This behavioral switch may suggest the use of this sea mount as a navigational aid.

Post-nesting Movements

A prior tag recapture study demonstrated movement of green turtles from Bioko northwest towards Ghana, as well as south, where a turtle was recovered in southern Gabon (Tomas et al., 2001); however, this study reveals the specific migration routes and locations of foraging grounds that are used. The multiple migration routes discovered in this study, including both northwestern and southern migrations, as well as oceanic and coastal routes, demonstrates the behavioral plasticity in migratory strategies and foraging ground locations for this nesting population.

Turtles migrated to two distinct foraging grounds, and exhibited both open-ocean and coastal migration routes. Of the turtles that completed northwestern migrations to the Ghanaian foraging ground (n=7), two different migration strategies were observed. Several turtles took a more direct route over deeper oceanic water, minimizing total migration distance, while the remainder made a short oceanic crossing to shallow coastal waters, then continued migrating

above the coastal shelf or along the coast until reaching the foraging ground. The SSM indicates that 4 turtles exhibited periods of coastal foraging during their migrations. Similarly, the SSM indicates that both Cm9 and Cm10 spent 2 days and 1 day, respectively, foraging at the known green turtle foraging ground in Corisco Bay, before continuing the migration to the coastal waters of Luanda.

Variation in migration strategies and foraging ground locations within green turtle populations is becoming more commonly demonstrated by satellite telemetry studies, and has been observed in Japan, the Galapagos, the Cayman Islands, and Guinea-Bissau (Godley et al., 2003; Blumenthal et al., 2006; Hatase et al., 2006; Seminoff et al., 2008). Biphasal migrations, consisting of direct pelagic routes followed by slower coastal migrations, have been previously documented and, in some cases, have been associated with opportunistic benthic foraging along coastlines (Cheng, 2000; Godley et al., 2002; Hays et al., 2002). Turtles that exhibited this migration strategy may decrease the overall energy cost of migration, despite a longer total migration distance (Godley et al., 2002; Hays et al., 2002).

This flexibility in migration patterns has been observed on the individual level as well. A green turtle tracked for two consecutive seasons in the Caribbean exhibited a direct migration one season followed by a biphasal migration the following season (Blumenthal et al., 2006). Variations in migration strategies may be driven by nutrient levels in post-nesting turtles, with more nutrient-depleted turtles taking the most direct route possible (Seminoff et al., 2008). It has also been suggested that minimizing open ocean travel and migrating along the coast may serve to facilitate navigation (Hays et al., 2002).

Both open ocean and biphasal northwestward migration routes in 2018 and 2019 occurred in the same direction as prevailing ocean currents (Figures 9 and 10). Southern

migrations occurred against ocean currents at times, and with currents or in areas with little to no current at times (Figures 11 and 12). While green turtles typically show foraging ground fidelity, migrating to a specific foraging ground whether with or against ocean currents, surface currents have been shown to affect swim speed and orientation, ultimately affecting overall energy cost of migration (Cheng and Wang, 2009). Currents in shallow coastal waters have been shown to have little effect on green turtle migrations when compared to stronger oceanic currents (Cheng and Wang, 2009). Therefore, turtles that exhibited an open-ocean migration strategy in the same direction as surface currents may utilize these stronger currents to decrease the energetic cost of migration compared to a coastal migration.

Foraging Behavior

Exactly why or how turtles select foraging grounds is unknown, however, in many cases green turtles show fidelity to foraging grounds, returning to the same location year after year (Godley et al., 2002; Broderick et al., 2007). Current hypotheses suggest that after hatching green turtles emerge from their nests and enter the ocean, they enter a pelagic phase, lasting between 5 and 10 years (Zug et al.; 2002; Reich et al.; 2007). It is assumed that dispersal mechanisms during this phase are primarily caused by ocean surface currents, and hatchlings are transported along these currents until they become juveniles, at which point they recruit to neritic foraging habitats (Carr and Meylan, 1980, Bass et al., 2006). Whether juveniles from Bioko recruit to the same foraging ground that adults return to after nesting is unknown, but is a possible explanation for foraging ground selection.

Opportunistic foraging along the northwestern migration pathways may indicate that suitable foraging habitat for green turtles exists closer to the nesting beaches, however turtles continued past these habitats to a more distant foraging ground. Similarly, Cm9 migrated south,

foraging for two days near a known green turtle foraging ground at Corisco Bay, on the border of Gabon and mainland Equatorial Guinea, and foraging again in the pelagic zone, before continuing south for 1277 km until taking up residence at a foraging ground off the coast of Luanda, Angola (Figure 11). Cm10 migrated south as well, and foraged for one day in Corisco Bay, and again for two days along the coast further south, before continuing migration to Luanda (Figure 11).

This foraging activity, as well as environmental data indicate that there are seagrass beds along both migratory routes (UNEP-WCMC, Short FT, 2018). While it is possible that a portion of this population forages at these closer foraging habitats, this study found no turtles across two seasons foraging for extended periods at these foraging grounds. It is likely that these are stopover habitats, and may not be large enough to support sustained foraging of a larger population. Furthermore, studies on bycatch in artisanal and commercial fisheries in these areas suggest that fishing-induced mortality of green turtles may be a significant threat (Formia et al., 2003; Riskas and Tiwari, 2013). Some suitable foraging habitats along the northwestern migration route have been recently compromised or diminished due to coastal erosion caused by dredging and development (Formia et al., 2003). These pressures may have either reduced the numbers of turtles from this population that migrate to these foraging grounds, or caused them to travel further to more suitable habitats.

All 7 turtles that foraged at the Ghanaian foraging ground remained within 20 km of the coast and in relatively shallow waters, <50 m deep, with an average maximum dive depth of 8.5 m. This likely corresponds to the depth of sea grass beds in the area.

Anthropogenic Threats and Conservation Implications

While green turtles are internationally protected, these turtles inhabit waters with little to no protection, and are threatened by fishing operations in the coastal waters of Bioko during their interesting periods, as well as at their neritic foraging grounds (Riskas and Tiwari, 2013; Belhabib et al., 2016; FAO, 2016). Tracked turtles spent time in the Exclusive Economic Zones (EEZs) of 9 different countries, all of which have been shown to have green turtle bycatch in artisanal fisheries (Fretey, 1998, 2001; Tomas et al., 2001; Formia et al., 2003, 2008; Weir et al., 2007; Moore et al., 2010; Riskas and Tiwari, 2013).

During their inter-nesting period, green turtles remained within the vicinity of the southern beaches on Bioko, going no more than 100 km away, and spending the majority of their time within 5 km of the coast. These waters support small-scale fishing boats, with coastal communities relying heavily on fisheries for both subsistence and income (Belhabib et al., 2016). While intentional take of green turtles by coastal communities is estimated to be much higher on the beach than for in-water turtles on Bioko, the use of these coastal waters for small-scale fisheries increases the risk of fishing-induced mortality during interesting periods (Fitzgerald et al., 2011; Riskas and Tiwari, 2013; Belhabib et al., 2016).

In waters along both the western and southern migratory routes, intentional take with nets and harpoons, as well as incidental bycatch with a variety of gear has been documented (Fretey, 2001; Carranza et al., 2006; Dossa et al., 2007; Formia et al., 2008; Riskas and Tiwari, 2013). Small-scale longline and gillnet operations have been shown to have high rates of incidental sea turtle bycatch for all five species of sea turtles found in the waters of the Gulf of Guinea (Carranza et al., 2006; Moore et al., 2010; Riskas and Tiwari, 2013). Nearly 50% of fishermen in Nigeria reported incidental sea turtle bycatch, with limited data from Togo and

Benin showing bycatch occurrence, although at much lower rates (Fretey, 2001; Dossa et al., 2007).

The two turtles that migrated south foraged for one day in the heavily fished waters of Corisco Bay, a known foraging ground for adult and juvenile green turtles. Intentional take of sea turtles by fishermen in Corisco Bay is common, with estimates of 300-500 individuals caught per year (Formia et al., 2008). Stranding data from Gabon and the Congo provide evidence of fishing-induced mortality of sea turtles from small-scale fisheries (Parnell et al., 2007); however, bycatch in industrial fisheries has a larger impact on all sea turtle species in this area, with recent annual estimates ranging from 1026-2581 individuals to over 1,000 tons caught in trawls and pelagic longlines (FAO, 2011; Casale et al., 2017).

Foraging grounds are especially vulnerable habitats for green turtles as that is where they spend that majority of their adult lives, and in-water threats at these neritic foraging habitats can have long-lasting population-level impacts (Blumenthal et al., 2006; Maxwell et al., 2011). Interviews and returns of tagged turtles from fishermen in Ghana provide evidence for green turtle bycatch (Tomas et al., 2001; Amiteye, 2002). Furthermore, studies suggest that both incidental and intentional sea turtle take is common, and fishermen interviews indicate that as much as 60% of coastal fishermen have tasted and/or still eat turtle meat (Amiteye, 2002). The ~50 km of Ghanaian coastline where these turtles forage supports extensive small-scale fisheries, with over 70% of marine catch coming from artisanal fisheries (FAO, 2016). Most fisheries in this area use purse seines and handlines, with gillnets, driftnets, and beach seines occasionally used (FAO, 2016). Dive behavior at this foraging ground was relatively shallow, with 67% of dives being <10 m, making them most vulnerable to beach seines, gillnets, handlines, and longlines, with driftnets posing a lesser threat.

In Angola, artisanal fishing is common within 4 nautical miles of the coast, and there is evidence that industrial fisheries also use this near-shore zone, putting foraging turtles at risk from both small-scale and industrial fishing gear (Agostinho et al., 2005).

The western end of this foraging ground lies off the coast of Tema, the most industrialized city and the largest harbor in Ghana (FAO, 2016). Tema contains the Chemu Lagoon and the Sakumo Lagoon, both of which are heavily polluted with industrial, agricultural, and domestic waste, leading to an increase in nutrient levels, as well as high levels of heavy metal pollution in water flowing from the lagoon into the ocean (Entsua-Mensah, 2002; Cynthia et al., 2011).

The southern foraging ground in Angola lies in the Luanda Bay, which has been shown to contain pollutants from oil drill mud disposal and sewage (Vale et al., 2009; Garcia-Rodriguez et al., 2013). A variety of pollutants have been shown to have direct negative impacts on sea turtles, including heavy metals, oil, marine debris, and nutrient pollution (through habitat degradation) (Komoroske et al., 2011; Lutcgavage et al., 2017).

While prior conservation efforts have been focused primarily on nesting beaches, the growing knowledge of both the importance and the locations of migratory corridors and neritic foraging grounds have made protecting these habitats a growing priority. The two foraging grounds identified in this study are not only important locations for green turtles in the Gulf of Guinea, but are especially vulnerable due to their close proximity to largely populated urban areas. The level of fishing activity in these areas, and the depth analysis of foraging turtle can inform the implementation of known adjustments to decrease bycatch in currently used fishing gear and adopting lower-impact fishing gear. Green turtles in these areas occupy relatively

shallow waters, therefore fishing gear used at >30 m would likely decrease the possibility of sea turtle bycatch.

Establishments of no-take zones or an MPA in the area of the foraging grounds would target reduction of sea turtle bycatch and intentional take, as well as decrease general overexploitation of the foraging habitat. The occurrence of nesting sea turtles on the beaches at the Ghanaian foraging ground also creates the opportunity for a protected area to encompass both marine and terrestrial habitats, protecting multiple species during both in-water and nesting activities. With major ports occurring near both foraging grounds, heavy ship traffic occurs increases the potential for ship strikes, and highlights the need for management strategies such as speed restrictions and designated shipping lanes.

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APPENDIX

The behavioral estimates given by the switching state space model were plotted alongside the latitude and longitude of each locational point and visually assessed to determine best fit. The results of the model for Cm1, 2, 3, 4, 5, 7, 8, 9, 10, show changes in longitude and latitude above changes in behavioral estimates.

