



Movement behavior of satellite-tagged leatherback turtles from Panama in response to chlorophyll, primary productivity, temperature, and eddy kinetic energy

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ABSTRACT: Leatherback turtles *Dermochelys coriacea* are globally endangered. This study tracked 30 individuals from the North Atlantic population tagged on the Caribbean Panama rookery (San San Pond Sak protected area, Bocas del Toro) over a period of 3 yr. We used satellite telemetry to investigate the probability that turtles switched between migration and foraging behavioral states as a function of environmental variables. We mapped the extensive migratory routes of these turtles and analyzed these using data derived from remote sensing, including chlorophyll, productivity, and sea surface temperature (SST), to assess how these influence their migratory and foraging behaviors. We also considered oceanographic processes, i.e. mesoscale eddies coinciding with the turtles' migration paths, to understand their behavioral responses. Our observations revealed that while some turtles undertook extensive migrations to high-use areas in the Northeast and Northwest Atlantic, the majority remained within the boundaries of the Gulf of Mexico. The study effectively differentiated migration and feeding behavior, noting a clear positive relationship between feeding activities and chlorophyll concentration, while productivity played only a marginal role, and no influence was found for SST and mesoscale eddies. This study advances knowledge of North Atlantic leatherback turtle migrations, underscoring the importance of integrated, multi-disciplinary marine conservation efforts. Understanding the impact of climate warming on migration paths and food source availability necessitates a holistic approach encompassing changes in physical oceanography, nutrient dynamics, and interactions from plankton to higher trophic levels. Additionally, as leatherback turtles traverse various international territories, the research emphasizes the need for collaborative data collection for their effective protection.

KEY WORDS: San San Pond Sak · Hidden Markov model · Turtle migration · Foraging · High-use areas · Gulf of Mexico · *Dermochelys coriacea*

1. INTRODUCTION

The enduring interest in sea turtles, driven by their remarkable migrations and the growing concerns surrounding their conservation, has prompted extensive tracking efforts and analyses (e.g. Eckert et al. 2008, Shillinger et al. 2010, Bailey et al. 2012, Schick et al. 2013, Hays & Hawkes 2018, Evans et al. 2021). The

migration corridor between nesting and high-use areas can be extensive and fraught with multiple threats. Human-induced impacts, such as habitat destruction, human interference on nesting beaches, harvesting of adult turtles and eggs, fisheries by-catch mortality, pollution, and the effects of climate change collectively contribute to the overarching decline in sea turtle populations (Jackson et al. 2001, Reina et al. 2002,

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Orós et al. 2021, Prosdocimi et al. 2021). Hence, the analysis of movement patterns becomes crucial in advancing our understanding of sea turtles' biogeography, population dynamics, and the identification of critical high-use areas (e.g. Georges et al. 2007, Godley et al. 2008).

Among the 7 sea turtle species, the leatherback turtle *Dermochelys coriacea* stands out as the largest, undertaking the most extensive migration routes that can span over 10 000 km between their high-use areas and breeding areas situated on tropical and subtropical beaches across the Atlantic, Pacific, and Indian Oceans (Mazaris et al. 2017). Accordingly, leatherback turtles are divided into 7 sub-populations, or regional management units (RMUs), based on nesting sites, migratory behavior, habitat preferences, and population genetic structuring, with 3 located in the Atlantic and 2 each in the Pacific and Indian Oceans (Dutton et al. 1999, Wallace et al. 2010, 2023). Globally, the species holds a Vulnerable status on the International Union for Conservation of Nature (IUCN) Red List (Wallace et al. 2013a). However, the conservation status diverges significantly among regions, with some sub-populations classified as Critically Endangered or Data Deficient (Martínez et al. 2007, Santidrián Tomillo et al. 2007, Wallace et al. 2013b, Mazaris et al. 2017), while the Northwest Atlantic RMU remains characterized as Least Concern (Wallace et al. 2013b), although more recent assessments have noted declines of hatching females (Northwest Atlantic Leatherback Working Group 2018). The contrasting regional variations, such as those observed between the Pacific and Atlantic Oceans, are linked to unique movement patterns among individual tracked turtles, suggesting more foraging success in the Atlantic, resulting in higher reproduction, whereas the lower reproductive output of the eastern Pacific sub-population renders these turtles more vulnerable to anthropogenic threats (Saba et al. 2008, Bailey et al. 2012, Wallace et al. 2023, Rider et al. 2024).

In the Atlantic, leatherback nesting sites are widely dispersed, with rookeries found in the USA (Florida) and the Caribbean, scattered nesting sites in the southwestern Atlantic (northern Brazil), and significant rookeries in West African Gabon and South Africa, corresponding to the Northwest, Southwest and Southeast Atlantic RMUs, respectively (Dutton et al. 2013, Wallace et al. 2013b). Molecular analysis has revealed substantial population differentiation through mitochondrial and nuclear markers among Atlantic nesting sites, confirming the division into Atlantic RMUs and the connectivity of populations (Dutton et al. 2013).

The utilization of satellite tracking technology and remote sensing has begun to unveil aspects of turtle post-nesting behavior during open ocean long-distance movements, contributing to our understanding of leatherback diving and movement behaviors and the implications of these behaviors for conservation (Ferraro et al. 2004, Hays et al. 2004a,b, Eckert 2006, Luschi et al. 2006, Witt et al. 2011, Dingle 2014, Hussey et al. 2015, Sasso et al. 2021). Numerous tracking studies have been conducted on western Atlantic leatherbacks nesting in the USA, the Caribbean, and South America (e.g. Hays et al. 2004a,b, Eckert 2006, Eckert et al. 2006, Fossette et al. 2007, Rider et al. 2024). The Gulf of Mexico is an important foraging area for Caribbean and US nesting turtles (Aleksa et al. 2018, Evans et al. 2021, Sasso et al. 2021, Wallace et al. 2023). Still, many of these turtles exhibit a northward migration after nesting, likely to take advantage of seasonal prey concentrations in high-latitude waters off Canada or the United Kingdom (James et al. 2007, Dodge et al. 2014). In longer-term studies, where male and female Atlantic leatherbacks were tracked for several months, high-latitude migrations were sometimes observed annually (Eckert 1998, Eckert et al. 2006, James et al. 2005a,b, Rider et al. 2024).

This study aims to enhance the existing body of knowledge by providing new tracking data on 30 individual leatherbacks from a nesting beach along the Caribbean coast of Panama and investigate how some environmental variables drive their regional post-nesting movement behaviors. Over 3 nesting seasons, we tagged the turtles on a little studied nesting beach in a protected area of Bocas del Toro, Panama, which lacked telemetry tracking. The research focuses on analyzing the probability of switching between migration and foraging behavioral states as a function of environmental variables such as chlorophyll, productivity, sea surface temperatures, currents, and the presence of eddies.

2. MATERIALS AND METHODS

2.1. Satellite tagging

A group of 30 adult female leatherback turtles were satellite tagged along the nesting beach of the San San Pond Sak protected area in Bocas del Toro, Panama (9° 31' N, 82° 30' W), with 10 tagged individuals per season in 2015, 2016, and 2018 (see Table 1). Each turtle was assigned a unique identification number, and for simplicity, hereafter, they will be referred to by the last 3 digits of their platform transmitter terminal

(PTT). Turtles were tagged using SPOT-317A rectangle Ridgemount satellite tag manufactured by Wildlife Computers. Each tag weighs 180 g, measures $128 \times 72 \times 21$ cm, and is designed to transmit for 1486 d. The tags were attached to leatherbacks following a protocol prepared by Wildlife Computer (see Hamelin & James 2018, Sasso et al. 2021), where 2 horizontal holes were drilled below the apex of the medial ridge using a 4.5 mm diameter stainless steel drill bit. The tags were attached using a monofilament line covered with a thin-walled silicone tube. A base was made to fit between each side of the dorsal ridge and the tag by forming 2 parallel 'sausages' of Equinox 35 Fast One-to-One Platinum Silicone Putty (www.smo0th-on.com/). Before drilling, researchers wearing gloves rinsed the area with filtered water and cleansed it with sterile cotton gauze pads using Hibiscrub Surgical Scrub. The procedure followed The Animal Care and Use Committee of the Smithsonian Tropical Research Institute's ethical protocol. The length of the turtles was measured from the nuchal notch to the posterior tip of the pygal process along the central ridge (Robinson et al. 2017).

2.2. Track correction

The tracking devices were set to transmit 250 times during a 24 h duty cycle every day using data collected from filtered Argos satellite location classes 3, 2, 1, A, and B. To ensure high quality, we filtered out all locations with accuracy classified as 'Z' (location unknown) and dry locations. We used a state-space model (Jonsen et al. 2003, Morales et al. 2004, Patterson et al. 2008) to analyze the movements of the animals to correct the errors arising from the tracking data from the Argos satellite. In addition, this enabled us to infer the behavior of these animals at each location. We utilized move persistence, which is a measure of how consistently an animal moves. This is given as a number between 0 and 1, changing over time, and it reflects shifts in movement style based on how speed and direction correlate with each other (Jonsen et al. 2019). To estimate move persistence accurately, we employed the 'fit_ssm()' approach from the aniMotum package (Jonsen et al. 2023) with the 'model = mp' option. This approach involves fitting a continuous-time motion persistence model (MP) in state-space form, allowing us to simultaneously infer the actual locations and the degree of motion persistence. This method is effective even when handling error-prone telemetry data originating from irregularly timed Argos observations. We used the 'fit_ssm'

function in R version 4.2.3 (R Core Team 2023) with a speed filter threshold (vmax) of 3 m s^{-1} (see Eckert 2002) and 6 h time step.

2.3. Behavioral state and its relationship with environmental variables

The methodology involved associating each point along the tracks with 5 specific environmental variables: chlorophyll (Chl), productivity (Prod), sea surface temperature (SST), marine currents (U and V vectors), and the presence of eddies at the exact time and location of each transmission. Primary productivity is determined by 3 interrelated factors: chl a , incident visible surface irradiance, and SST (Behrenfeld & Falkowski 1997). These environmental variables can be utilized to identify feeding areas (Saba et al. 2008, Fossette et al. 2009). Current vectors U and V, extracted from the Copernicus Marine Environment Monitoring Service (https://data.marine.copernicus.eu/product/GLOBAL_MULTIYEAR_PHY_001_030/download?dataset=cmems_mod_glo_phy_my_0.083_P1D-m_202112) were used to calculate the eddy kinetic energy (EKE) for each location. This process entailed analyzing the square of both the eastward (U) and northward (V) velocities, reflecting the energy associated with eddies in the oceanic system. The spatial resolution of the U and V data is 0.083 degrees, and the temporal resolution is daily mean values. Eddies and marine currents significantly impact the distribution of feeding areas, leading to the movement patterns of individual turtles (Galli et al. 2012, Shillinger et al. 2012).

Monthly composite data for chl a concentration (mg m^{-3}) was obtained from the 'Chlorophyll a , North Pacific, NOAA VIIRS, 750 m resolution, 2015-present (1 Day Composite)' dataset. Daily net primary productivity of carbon (mg C m^{-2}) was extracted from the 'Primary Productivity, Aqua MODIS, NPP, Global, 2003-present, EXPERIMENTAL (1 Day Composite)' dataset, and daily SST data was sourced from the 'SST, Daily Optimum Interpolation (OI), AVHRR Only, Version 2, Final, Global, 0.25°, 1982-2020' dataset. The above datasets were obtained from CoastWatch ERD-DAP (<https://coastwatch.pfeg.noaa.gov/erddap/>) and matched with each turtle's location and date using the 'xtracto' function within the R package 'xtractomatic' (Mendelsohn 2018).

EKE represents the energy associated with oceanic eddies, but we also considered the presence of mesoscale eddies during each transmission day and location, using the Mesoscale Eddy Trajectory Atlas Product from AVISO Satellite Altimetry Data

(<https://www.aviso.altimetry.fr/en/data/products/value-added-products/global-mesoscale-eddy-trajectory-product.html>). A circular buffer zone with a diameter equivalent to each eddy's diameter on a given day (r^2) was established around each mesoscale eddy center. Subsequently, we integrated the eddy spatial layer with the turtle location data to determine turtle positions within the eddy buffer zones, keeping matches that had both spatial and temporal alignment. These analyses were carried out using the Spatial Analyst tool in ArcGIS Pro 2.4.0.

Once all turtle locations were synchronized with real-time environmental conditions, a hidden Markov model (HMM) was employed to discern various behavioral states along the adjusted tracks, including foraging and migrating (Guzman et al. 2019). Environmental factors were used as model covariates to explore potential associations between behavioral states and Chl, Prod, SST and EKE (Guzman et al. 2019). The model was fitted using the 'fitHMM' function within the R package moveHMM (Michelot et al. 2016), setting the initial values to 2 states: 5 ± 5 for the foraging state and 50 ± 20 km for the migrating state regarding the step mean, while π was configured for the turning angle. The variables were standardized in this model to ensure that they all had the same scale, facilitating fair contributions to the HMM estimation, improving numerical stability, and enhancing the interpretability of the coefficient estimates. The correlation between the variables (i.e. Chl, Prod, SST and EKE) was examined and found to be negligible, with a value close to zero. Mesoscale eddies were not incorporated into the model due to the limited sample size. A paired Wilcoxon-test was conducted to examine the relationship between the variables Chl, Prod, SST, EKE, and the foraging and migration states, with a significance level of 0.05. This test was chosen because it considers that migration and feeding data are repeated measurements on the same individuals, which makes the samples dependent. In the case where we analyzed data from a single individual turtle, the Wilcoxon rank-sum test was deemed more appropriate due to the independence of the measurements.

3. RESULTS

All 30 leatherbacks made substantial journeys in various directions from their initial point of tagging in each of the 3 years (Table 1, Fig. 1a). The average overall distance covered was approximately 9750 km over a span of 175 d. This translates to an average speed of 55.7 km d^{-1} or 2.3 km h^{-1} .

The initial database, which encompassed all turtles, comprised 26 371 Argos locations classified into error classes as follows (in descending order): B (41.65%), A (18.35%), 0 (14.75%), 1 (12.25%), 2 (7.75%), and 3 (5.25%). Following track correction using the aniMotum model, which calculated γ_t values to indicate the likelihood of area-restricted search behavior versus directed and rapid movements, the database was reduced to 21 070 coordinate locations: 8494 for 2015 (Fig. 2), 6940 for 2016 (Fig. 3), and 5636 for 2018 (Fig. 4).

The HMM delineated 2 distinct behavioral states: migrating (47.5% of the time), characterized by a step distance (distance between time intervals) of approximately $14.35 (\pm 6.54, \text{SD})$ km and a turning angle of about $0.002 (\pm 0.005, \text{SD})$ radians, and foraging (52.5% of the time), characterized by a step distance of approximately $4.60 (\pm 3.87)$ km and a turning angle of approximately $-0.014 (\pm 0.016)$ radians. The main high-use areas were in the Gulf of Mexico and Florida (preferred by 45.1% of the turtles), Celtic Sea, the Azores archipelago, off the north coast of Canada, certain regions of the North Atlantic, and various intermediate sectors in the Atlantic Ocean (Fig. 1b).

The likelihood of transitioning between these behavioral states (from migrating to foraging or vice versa) was correlated with local environmental conditions under stationary long-term distribution (Table 2). This distribution refers to a stable pattern of behavioral states over an extended period, indicating that the frequencies of these states remain relatively constant. Specifically, turtles tended to forage more when Chl, Prod, and SST levels were higher, whereas they migrated more when these levels were lower (Fig. 5a–c). SST exhibited a critical threshold at which behaviors shifted from migration to foraging, where below-average temperatures favored migration and above-average temperatures promoted foraging behavior (Fig. 5c). Conversely, the influence of EKE manifested differently, with migrating being more probable in high EKE conditions and foraging being more likely in low EKE conditions (Fig. 5d).

Tracked turtles occupied waters with (mean \pm SD) Chl levels averaging $0.2 \pm 2.91 \text{ mg m}^{-3}$, Prod of $702.33 \pm 1040.87 \text{ mg C m}^{-2} \text{ d}^{-1}$, SST of $26.03 \pm 4.54^\circ\text{C}$, and EKE levels of $0.03 \pm 0.09 \text{ cm}^2 \text{ s}^{-2}$. When turtles were foraging, Chl levels were significantly higher (0.25 mg m^{-3}) compared to when they were in the migrating state (0.14 mg m^{-3}) (Wilcoxon signed-rank test, $V = 325$, $p = 0.0103$, Fig. 6a). In the case of Prod, turtles exhibited a preference close to the significance cut-off for areas with higher productivity, recording $202.3 \text{ mg C m}^{-2} \text{ d}^{-1}$ during foraging

Table 1. Summary of 30 tracked leatherback turtles tagged off the Pacific Coast of Panama. Final destinations are: Caribbean Sea (CS); Western Atlantic (WA); Eastern Atlantic (EA); North Atlantic (NA); Western Gulf of Mexico (WGM); and Eastern Gulf of Mexico (EGM)

Turtle PTT	Deployment (dd-mm-yy)	Last transmission (dd-mm-yy)	Turtle length (m)	Total transmission (d)	Distance travelled (km)	Final destination
149485	03-06-15	23-10-15	1.55	142	8876	EGM
149486	22-05-15	03-01-17	1.65	592	39566	EA
149487	02-06-15	16-12-15	1.57	197	6919	EGM
149488	02-06-15	03-01-16	1.46	215	10476	EGM
149489	20-05-15	29-02-16	1.60	285	8549	EGM
149490	19-05-15	28-07-15	1.42	70	4344	CS
149491	03-06-15	15-01-16	1.42	226	11428	EGM
149492	21-05-15	17-10-15	1.63	149	8210	EGM
149493	02-06-15	05-09-15	1.45	95	4913	EGM
149494	21-05-15	23-10-15	1.56	155	9157	EGM
161706	22-05-16	07-06-16	NA	16	1168	CS
161707	20-05-16	13-09-16	1.33	116	5929	WA
161708	20-05-16	07-07-16	1.65	48	4100	CS
161709	12-05-16	28-11-16	1.60	200	7956	EGM
161710	21-05-16	30-08-16	NA	101	6334	WA
161711	22-05-16	13-08-17	NA	448	13336	WA
161712	22-05-16	01-04-17	NA	314	20653	EA
161713	22-05-16	27-11-16	NA	186	6831	EGM
161714	20-05-16	03-01-17	1.60	228	13812	NA
161715	21-05-16	10-08-16	NA	81	6540	EGM
172124	12-05-18	30-04-18	1.45	49	2280	CS
175024	15-04-18	20-06-18	1.34	65	5702	WGM
175021	01-06-18	07-02-19	1.50	249	19768	EGM
175022	01-06-18	04-05-19	1.37	336	16325	EGM
175519	07-06-18	11-08-18	1.52	64	4138	CS
175521	07-06-18	14-06-18	1.58	6	234	CS
175522	08-06-18	04-11-18	1.48	149	15547	WA
172123	08-06-18	03-06-19	1.55	360	11994	WGM
175023	02-04-19	09-06-19	NA	66	4138	CS
175520	02-04-19	16-11-19	NA	227	9439	WGM

compared to $139.3 \text{ mg C m}^{-2} \text{ d}^{-1}$ during migratory behavior (Wilcoxon signed-rank test, $V = 146$, $p = 0.06236$, Fig. 6b). Remarkably, SST did not exhibit a significant difference between the 2 behavioral states, with migration state having an average temperature of 25.9°C and foraging state 26.2°C (Wilcoxon signed-rank test, $V = 236$, $p = 0.4758$, Fig. 6c). To address this uncertainty in SST, we conducted a more detailed analysis of only one turtle (ID 486) at a smaller scale, revealing a more consistently supported idea that there is a positive relationship between turtle foraging and lower SST in this specific environment (Wilcoxon rank-sum test, $W = 293631$, $p < 0.0001$), and unveiling mean SST values of 17.76°C during foraging behavior compared to 20.68°C during migration. For EKE, the values ranged between 0.035 and $0.036 \text{ cm}^2 \text{ s}^{-2}$ for foraging and migration behaviors, respectively, showing no significant differences (Wilcoxon signed-rank test, $V = 264$, $p = 0.5291$) between them (Fig. 6d).

Mesoscale eddies that spatially and temporally coincided with the presence of turtles were observed in only 15 distinct locations. The eddies exhibited an average radius of $63.1 \pm 18.6 \text{ km}$, with a distribution of 40% being anticyclonic and 60% cyclonic in nature. Within both these types of eddies the turtles exhibited a combination of migratory and foraging behaviors. Notably, among the eddies coinciding with the presence of turtles, 69% featured turtles engaging in foraging behavior, while the remaining 31% were involved in migration.

4. DISCUSSION

4.1. Leatherback foraging behavior

Using Argos satellite tracking data, our study provided insights into adult female leatherback turtles' movement behavior in Caribbean Panama, revealing

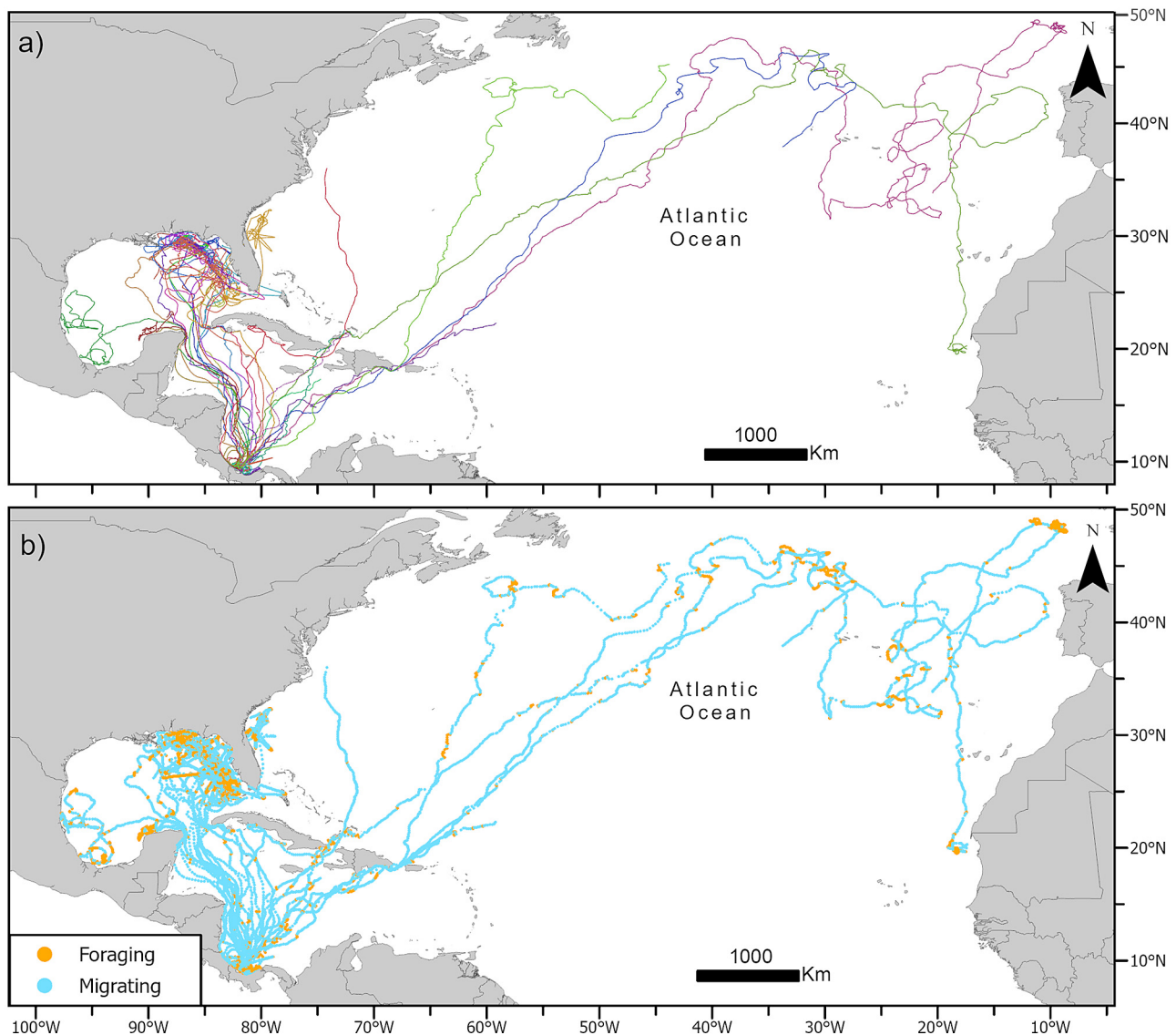


Fig. 1. (a) Tracks and (b) migration and foraging states inferred by hidden Markov modeling of 30 leatherback turtles tagged off the Pacific coast of Panama during 2015, 2016, and 2018 ($n = 10$ per year)

their extensive migrations from nesting beaches into the Greater Caribbean and North Atlantic. Twelve out of the 30 tagged turtles transmitted data for over 200 d, and only 3 transmitted data for over a year, with one turtle transmitting data for 592 d. Overall, the HMM analysis revealed that for all turtles combined 52.5% of the time was spent foraging and 47.5% of the time was spent migrating. We observed that half the leatherback turtles (45.1%) tended to prefer the confines of the Gulf of Mexico, particularly near the southern shores of the USA (Louisiana, Alabama, and Florida) as their primary high-use areas. In contrast, there were fewer occurrences in the Northeast Atlantic and the Northwest Atlantic, with only 1 individual tracked off the coast of Newfoundland (Fig. 1 but see Rider et al. 2024).

Similarly, data obtained from other Caribbean rookeries indicated the Gulf of Mexico as a major high-use area (Aleksa et al. 2018, Evans et al. 2021). Our findings are consistent with those of Fossette et al. (2010), who found that of 3 individuals tagged in Panama, 2 traveled to the Gulf Stream to identified Temporary Residence Areas (TRAs), and one traveled to the North Atlantic, covering the greatest distance. Similarly, animals tagged in the Gulf of Mexico predominantly remained in west Florida for feeding, while 1 group traveled south from the Caribbean to Costa Rica, Panama, and Colombia (Sasso et al. 2021). Additionally, an individual tagged in Massachusetts traveled to Panama in 133 d for foraging (Rider et al. 2024). These studies highlight the Gulf of Mexico and Florida as crucial

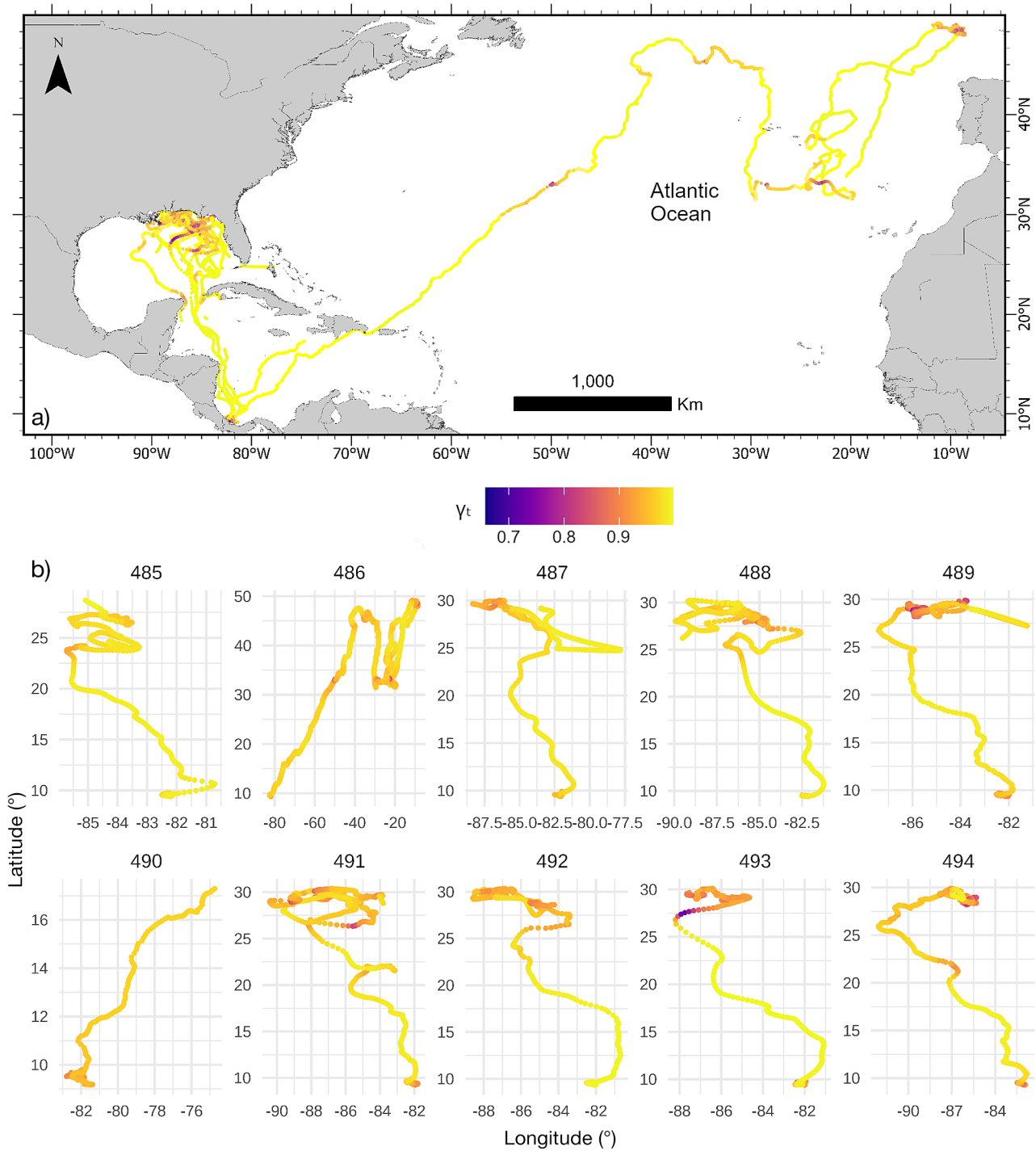


Fig. 2. Leatherback turtle migration using the aniMotum model for turtles tagged in 2015. (a) Overall migration map; (b) individual tracks modeled for each turtle by PTT. Lower γ_t values (from orange to purple) highlight regions where the turtles are likely engaged in area-restricted search behavior, while higher γ_t values (from light orange to yellow) indicate areas where turtles exhibit directed, rapid movements. These γ_t values represent the likelihood of these behaviors. The numbers on the graphics refer to turtle IDs (last 3 digits of turtle PTT; see Table 1)

high-use areas for leatherbacks, emphasizing the significant round-trip migratory routes between Panama and the Gulf of Mexico. Routes from nesting areas in South America (French Guiana and Suriname) also in-

tersect with key feeding areas mentioned above in the Gulf of Mexico, Gulf Stream, Florida, and the North Atlantic (see Ferraroli et al. 2004, Hays et al. 2004a, Fossette et al. 2009, Bailey et al. 2012).

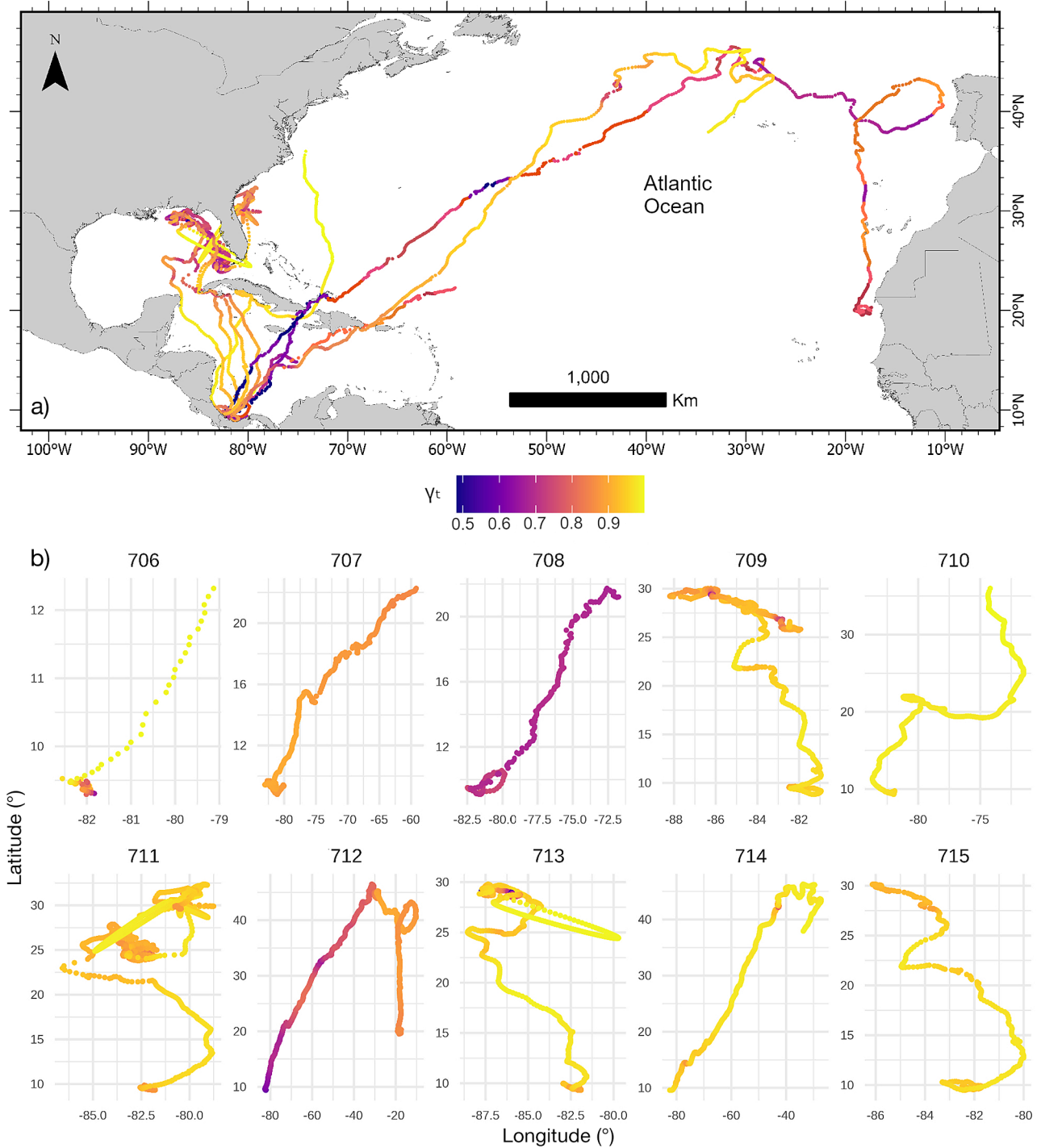


Fig. 3. As in Fig. 2 but for turtles tagged in 2016

4.2. Environmental influences on movement patterns

Investigating how environmental conditions influence turtles' behaviors during migration and foraging, our study employed HMM to distinguish between these 2 distinct states in leatherback turtles. We identified high-use areas in various regions,

including the Gulf of Mexico, Florida, the Celtic Sea, the Azores archipelago, and several locations in the North Atlantic. The correlation between these behavioral states and examined environmental factors shed light on how leatherback turtles respond to their surroundings. Currently, there is limited knowledge about this relationship, particularly in terms of rela-

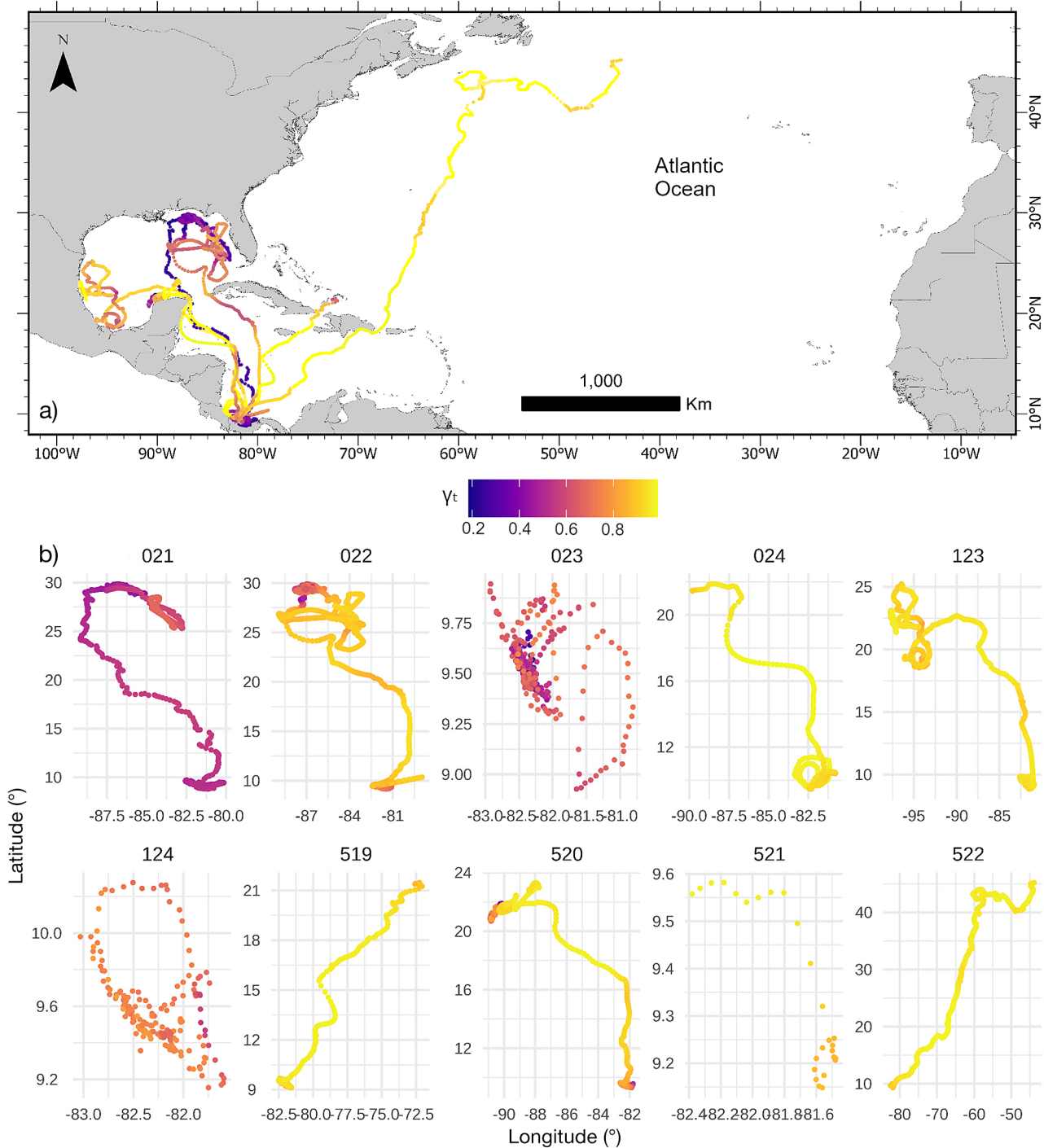


Fig. 4. As in Fig. 2 but for turtles tagged in 2018

tionships of foraging activity and environmental variables, SST in particular (Okuyama et al. 2021). Notably, our findings show that higher levels of chlorophyll, primary productivity, and sea surface temperature are linked to an increased likelihood of turtles being in the foraging state, decreasing migration long-term probability (see Table 2).

Elevated Chl levels observed in our data align with our expectations regarding enhanced foraging activity, as these levels are indicative of a greater availability of the leatherback turtles' preferred food source (Bailey et al. 2012). Chl appears to be the most influential variable driving foraging behavior, showing a strong statistical relationship, while Prod showed only mar-

Table 2. Model coefficient of correlation between each environmental variable (model covariate) to the probabilities of switching between behavioral states (foraging and migration), with 95% confidence intervals in parentheses

	From migrating to foraging	From foraging to migrating
Intercept	−2.638 (−2.730, −2.547)	−2.765 (−2.861, −2.669)
Chlorophyll	0.052 (0.007, 0.096)	−0.539 (−1.112, 0.034)
Productivity	0.069 (−0.025, 0.163)	−0.265 (−0.646, 0.116)
Sea surface temperature	0.082 (−0.009, 0.173)	−0.020 (−0.113, 0.074)
Eddie kinetic energy	0.011 (−0.073, 0.095)	0.040 (−0.048, 0.127)

ginal significance. However, our study yielded an intriguing finding regarding leatherback turtles' SST preferences during foraging. Contrary to some expectations and prior research (Jonsen et al. 2007, Shillinger et al. 2011), our HMM results indicated that turtles, on average, favored warmer waters for feeding compared to their migration state, where they preferred cooler waters; however, this difference was not statistically significant. This unexpected pattern, especially when considering that colder waters are often associated with higher marine Prod (Sarhan et al. 2000), prompted a closer examination of our findings. The mean SST during migration and foraging states showed a surprising similarity, initially suggesting a possible deviation in our data, as shown by the behavior of turtle 486 where a positive relationship between turtle foraging and lower SST was observed.

Oceanographic processes have been shown to significantly influence the migratory paths of leatherback turtles, impacting both hatchlings and actively swimming adult sea turtles (Luschi et al. 2003, Lambardi et al. 2008, Galli et al. 2012), affecting turtles either by physically influencing their movements or by altering the distribution of their planktonic prey (Hays et al. 2004a, Eckert 2006, Lambardi et al. 2008). Specifically, mesoscale eddies are known for their ability to concentrate nutrients, creating abundant food patches (Lambardi et al. 2008). Hence, it was reasonable to anticipate prolonged stays in areas characterized by these oceanographic conditions. In line with this expectation, our study revealed that when eddies coincided with the presence of leatherback turtles, a notable proportion, approximately 69%, exhibited foraging behavior. This finding implies that leatherback turtles likely exploit eddies as advantageous environments for procuring food resources. Nevertheless, it is worth noting that the remaining 31% of observed turtles continued their migration activities within these eddies, suggesting that eddies may not invariably function as primary

high-use areas and may serve additional roles in influencing various facets of turtles' migratory behavior.

4.3. Implications of movement patterns for conservation

Satellite tracking data plays a crucial role in developing effective conservation and management strategies (e.g. Hays & Hawkes 2018). With mounting pressures from human impacts such as

global fisheries bycatch and climate change on marine turtle populations, robust estimation of population sizes and the identification of key habitats have gained even greater significance (e.g. James et al. 2005c, Shillinger et al. 2008, Weber et al. 2013, Hetherington et al. 2018). Understanding foraging success is particularly important, as it is closely linked to reproductive success and, consequently, the viability of populations (e.g. Lescreol et al. 2010).

We used proxies (i.e. HMM) for foraging success, expecting animals to spend more time in areas of high prey abundance, resulting in reduced travel rates during foraging compared to transiting between feeding areas. This method, drawn from concepts used in studies of other marine megafauna (e.g. Robinson et al. 2007, Kuhn et al. 2009), allowed us to distinguish between foraging and transit periods by observing changes in transit rates.

Our findings highlight the leatherback turtle as a transboundary species crossing exclusive economic zones (EEZs) of 25 countries, including Panama, Costa Rica, Colombia, Nicaragua, Honduras, Jamaica, Cuba, Haiti, Dominican Republic, Puerto Rico, Turks and Caicos, British Virgin Islands, Anguilla, Cayman Islands, Mexico, USA, Bermuda, Canada, Portugal (Azores/Madeira), Spain (Canaries), France, UK, Ireland, Western Sahara, and Mauritania, as well as international waters. This extensive geographical spread underlines the necessity for collaborative conservation efforts across multiple nations (Fossette et al. 2014), also considering the recent Biodiversity Beyond National Jurisdiction (BBNJ) Agreement adopted by the United Nations in June 2023 (Deasy 2023). The latter provides a framework for establishing Marine Protected Areas (MPAs) in international waters. MPAs are considered instrumental in mitigating various threats faced by leatherback turtles, such as fisheries bycatch, boat strikes, and other human impacts (Snape et al. 2018 and citations therein). However, the BBNJ Agreement stops short of imposing a complete ban on com-

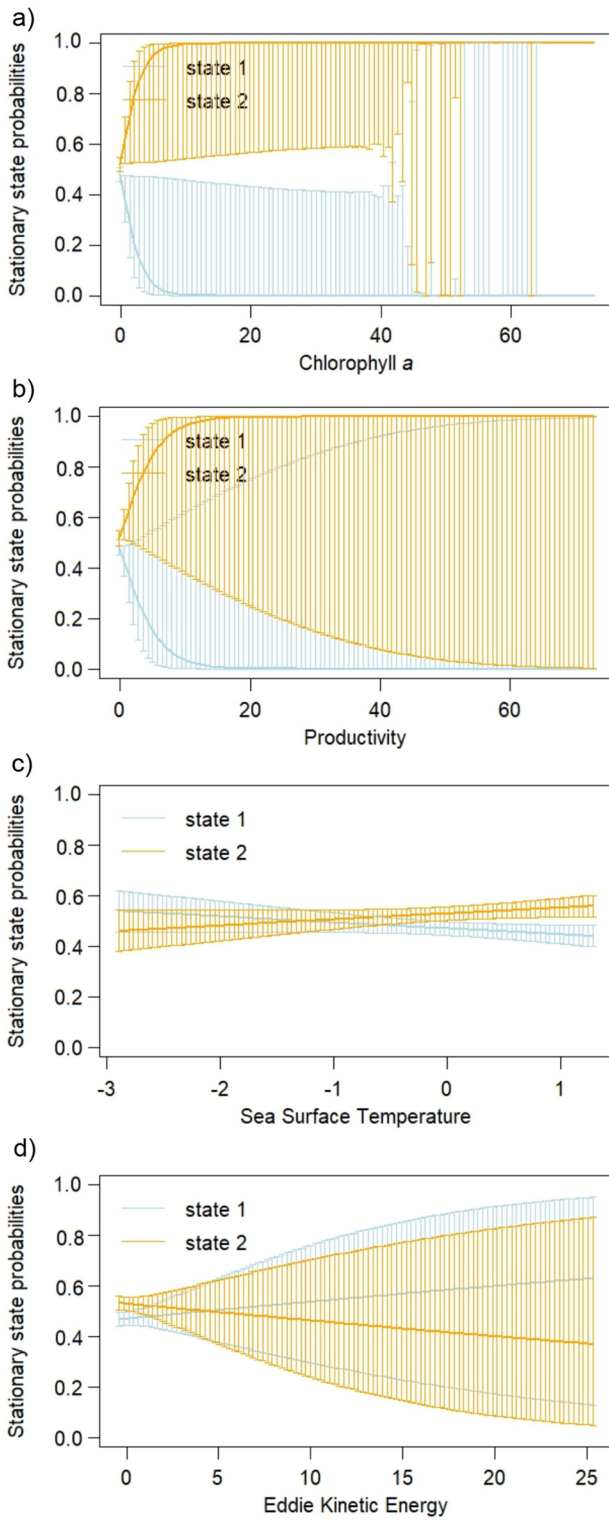


Fig. 5. Long-term probabilities of turtles at different values of the covariates (95% confidence intervals) from the hidden Markov model. (a) Chlorophyll a , (b) productivity, (c) sea surface temperature, and (d) eddy kinetic energy; in each behavioral state: foraging (state 2) and migrating (state 1). All variates have been standardized

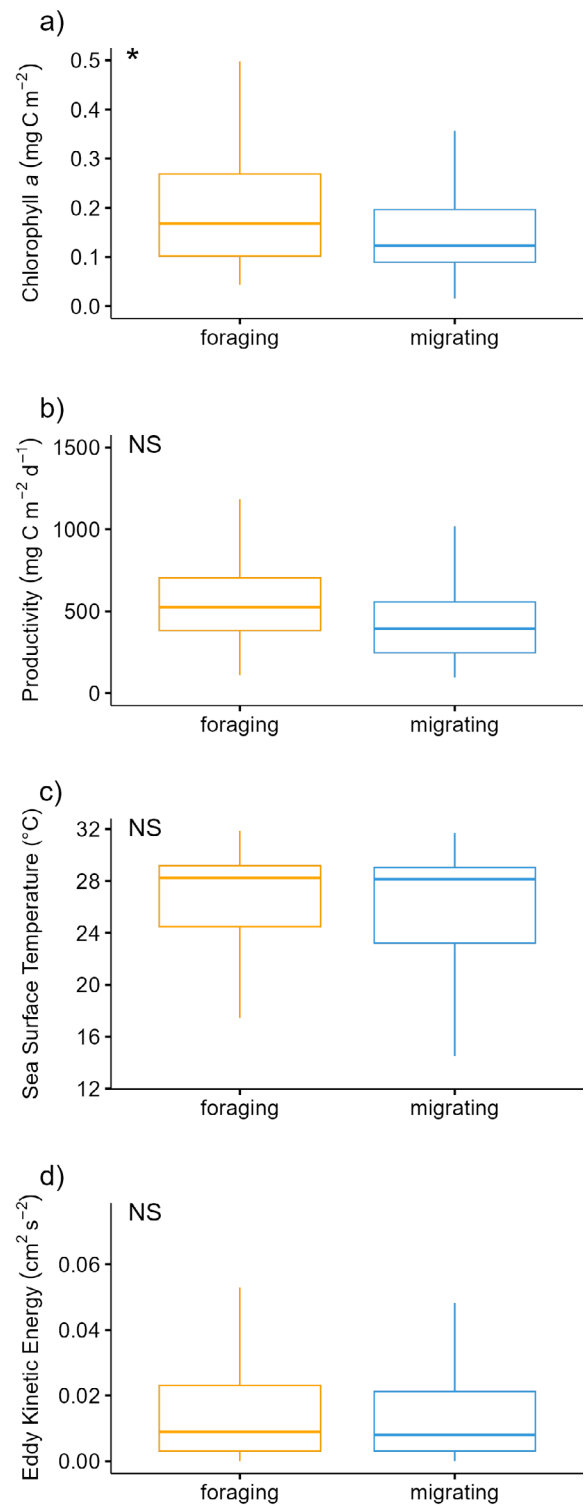


Fig. 6. Environmental conditions during migration and foraging states modeled by a hidden Markov model; turtles preferred to forage when chlorophyll and primary productivity levels were higher. The boxplots show the median (horizontal line) and the interquartile range (boxes). *Significant ($p < 0.05$); NS: not significant difference determined by the paired Wilcoxon-test

mercial fishing within these MPAs, but it necessitates compelling reasons for regional fisheries management organizations to advocate for a complete prohibition of fishing in these areas to safeguard marine life. Furthermore, the conservation of leatherbacks cannot be implemented in a few specific fishing grounds or MPAs and should include all leatherback high-use areas (*sensu* Hays et al. 2004a).

Considering that our study has revealed a strong correlation between foraging activity and Chl levels, while the correlation with Prod and SST, and hydrodynamic features such as eddies was less pronounced, it becomes imperative to explore how ongoing climate change might affect the migratory routes of these turtles. Global ocean warming is poised to significantly alter marine ecosystems with complex and uncertain effects on marine food webs (e.g. Murphy et al. 2020). Rising sea temperatures could enhance strobilation, growth rates, and abundance of gelatinous organisms (Purcell 2005, Lucas et al. 2012), and alter plankton community structures (Barton et al. 2016, Murphy et al. 2020). The North Atlantic has experienced particularly severe warming over the last decades (Barnett et al. 2001, Lee et al. 2011), which may lead to the northward expansion of leatherback turtles' high-use areas following their prey trajectories (McMahon & Hays 2006, Nordstrom et al. 2020). However, there is a counteracting trend: the potential weakening of the global thermohaline circulation might reduce heat transfer to northern latitudes, leading to cooler sea temperatures and possibly causing leatherback turtles to retreat from their current northern foraging limits (IPCC 2001). Thus, forecasting the impact of climate change on leatherback turtle distribution is complex requiring consideration of various interrelated environmental factors across different trophic levels.

5. CONCLUSION

In our study, satellite tracking has been instrumental in uncovering the migratory routes and foraging habits of the leatherback turtles originating from a Caribbean Panama rookery. The extensive migratory paths of these turtles, traversing international and various national waters, highlight the complexities of cross-border conservation and the necessity of sharing data and research methodologies (Shillinger et al. 2008, Witt et al. 2011, Dutton et al. 2013, Fossette et al. 2014, Wallace et al. 2023, Rider et al. 2024). Coordinated efforts by these countries are critical to developing and implementing effective conserva-

tion strategies. Mitigating risks arising from fishing necessitates a collaborative effort in monitoring and managing fishing activities, both nationally and internationally, with the potential establishment of protective areas to reduce conflicts between leatherback turtle migration paths and human activities (Schuter et al. 2011, Snape et al. 2018). Additionally, our findings indicate that Chl levels significantly affect turtles' migratory and foraging behaviors. Given potential climate-induced alterations of these oceanographic parameters, a comprehensive research approach is essential to devise conservation strategies for the evolving marine environment influenced by climate change. This necessitates integrating data on environmental factors affecting leatherbacks' prey and their primary high-use areas with insights from climate science (e.g. Nordstrom et al. 2020, Rider et al. 2024). Addressing the rapid environmental changes demands collective action and enhanced data on leatherback turtles' oceanic habitats and migration to ensure their effective protection and long-term survival.

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