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Identification of the Gulf of Mexico as an important high-use habitat for leatherback turtles from Central America

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Abstract. Endangered leatherback sea turtles (*Dermochelys coriacea*) are wide-ranging, long-distance migrants whose movements are often associated with environmental cues. We examined the spatial distribution and habitat use for 33 satellite-tracked leatherbacks from nesting beaches on the Caribbean coast of Costa Rica and Panama from 2004 to 2018, an important nesting population for the leatherback Northwest Atlantic Distinct Population Segment. Tracking revealed the use of two distinct regions, the Gulf of Mexico (GoM, n = 18) and the North Atlantic Ocean (NAO, n = 15). We developed density utilization maps to elucidate high-use habitats, migration pathways, and seasonal movements. GoM leatherbacks were found in three concentrated high-use habitats connected by a migration pathway, while NAO leatherbacks were primarily found in a single, large high-use habitat. Leatherbacks in both regions have the potential to interact with Atlantic pelagic longline fisheries based on seasonal overlap with high fishing effort. Our findings suggest that the GoM is an important destination for leatherbacks from the Caribbean coast of Central America with seasonal movements between high-use habitats within the GoM. While leatherbacks are utilizing high-use habitats in both the NAO and the GoM, the proportion of individuals migrating into the GoM increased over the study period. Additionally, NAO leatherbacks have increased the distance they travel in the first 90 d. Regional differences in movement and spatial distribution of high-use habitats are important considerations when developing conservation plans for the Northwest Atlantic leatherback population.

Key words: bycatch; high-use habitat; leatherback sea turtle; satellite telemetry; seasonal movements; spatial distribution; species conservation planning.

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Introduction

For many marine species, including turtles, food resources and suitable breeding habitat may be separated by hundreds or thousands of kilometers, necessitating long-distance seasonal migrations (Costa et al. 2012). Important habitats required for the survival of a species may be distributed across wide regions, often crossing international borders and economic exclusion zones. As a marine predator, leatherback sea turtle (*Dermochelys coriacea*) movements are associated with frontal zones (Graham et al. 2001, James et al. 2005, Bailey et al. 2012, Chambault et al. 2017, Aleksa et al. 2018*b*) where their primary prey items, jellyfish, aggregate as a result of ocean physical processes, bathymetry, and behavioral responses to environmental cues

(Powell and Ohman 2015, Aleksa et al. 2018*a*). Environmental cues, such as sea surface temperature (SST), ocean fronts, and the Gulf Stream current, can influence leatherback spatial distribution and movements across the seascape (Witt et al. 2007, Dodge et al. 2014, Chambault et al. 2017, Aleksa et al. 2018*b*).

Leatherbacks in the North Atlantic may migrate over 10,000 km from tropical nesting beaches to reach temperate foraging habitats, representing a greater migration distance for reproduction than any other marine turtle species (Ferraroli et al. 2004, Hays et al. 2004, James et al. 2005). Satellite telemetry studies of leatherbacks from nesting beaches in South America and as part of in-water projects have shown high variation in pathways, distinct migration corridors, long migration distances, and wide spatial distribution of foraging areas for leatherbacks in the North Atlantic Ocean (James et al. 2005, Eckert 2006, Witt et al. 2007, Fossette et al. 2010*a*, Dodge et al. 2014, Chambault et al. 2017). Additionally, studies have shown the occurrence of leatherbacks in the Gulf of Mexico (Evans et al. 2007; Fossette et al. 2010*a*; 2014; Aleska et al. 2018*b*; Evans 2019).

The Northwest Atlantic Distinct Population Segment (NWA DPS) of leatherbacks is listed as endangered, with nesting beaches located in Central and South America, Florida, and the Caribbean (NMFS and USFWS 2020). This population faces threats from bycatch, including artisanal nearshore and offshore gillnet, pelagic longline (PLL), and trawl fisheries, degradation of nesting beaches, and poaching of adults and eggs. Between 1992 and 2005, leatherbacks represented more than 50% of sea turtle PLL bycatch in six of the 11 North Atlantic fishing zones (Kot et al. 2010). An estimated 11.7 to 140.7 million longline hooks were set in the Atlantic PLL fishery from 2005 to 2018 (NMFS 2020), with PLL bycatch considered the greatest threat to leatherback turtles in the GoM (Garrison and Stokes 2014).

A recent report by National Marine Fisheries Service and US Fish and Wildlife Service (NMFS and USFWS 2020) indicated that in the NWA DPS, there is an overall declining leatherback nesting trend, with significant declines at some of the largest nesting beaches (Trinidad and Tobago, Suriname, and French Guiana). The Central American Caribbean leatherback nesting population (which includes Costa Rica, Panama, and Colombia) represents 17% of NWA DPS nesting female abundance. Chiriquí Beach, Panama alone has the third highest nesting female abundance in the NWA DPS (NMFS and USFWS 2020) and is considered the most important leatherback nesting beach on the Caribbean coast of Costa Rica and Panama (Ordoñez et al. 2007).

Given the importance of the Central American Caribbean leatherback nesting population to the NWA DPS, we use satellite telemetry spanning 15 yr to investigate the movements and spatial distribution of female leatherbacks migrating from nesting beaches along the Caribbean coast of Costa Rica and Panama. The goals of this study were to identify migration pathways and high-use habitats; investigate high-use habitat sea surface temperature; determine seasonal movement patterns; and evaluate the potential for turtles in high-use habitats to interact with anthropogenic activities, especially the Atlantic PLL fishery.

Methods

Satellite telemetry

From May 2004 to May 2018, 40 Argos satellite transmitters were deployed on leatherback turtles nesting in Tortuguero National Park (n = 3) and Gandoca Manzanillo Wildlife Refuge (n = 1), Costa Rica, and Chiriqui Beach (n = 25), Soropta Beach (n = 11), Bluff Beach (n = 1), and Punta Rincon (n = 1), Panama. Attachments were done in late May to coincide with the end of the leatherback nesting season at these beaches and enable tracking of females migrating from the nesting beach to foraging areas. Seven different Argos transmitter models were used: KiwiSat 101 K1G-291A (n = 12) and KiwiSat 202 Direct (n = 8) from Sirtrack (Havelock North, New Zealand); SRDL (n = 3) from Sea Mammal Research Unit (St Andrews, UK); and SPOT5-317A (n = 9) and SPOT6-352B (n = 8) from Wildlife Computers (Redmond, WA, USA). Transmitter duty cycles were set to maximize battery life, 15–24 h ON and 9–12 h OFF, and optimally provided multiple daily Argos locations. Transmitters were attached during the nesting process using either a custom-fitted harness made of nylon webbing and polyvinyl tubing (2004–2009, $n = 16$; Eckert & Eckert 1986) or by direct attachment through the dorsal ridge of the carapace using wires or cable ties (2010–2016, $n = 24$; Dodge et al. 2014). Both methods incorporated materials that were expected to eventually degrade and release the harness or transmitter. Methodology was changed to direct attachment when it was determined that the harness attachment was found to increase drag by 91% to 112%, while direct attachment increased drag by less than 2% (Jones et al. 2011). Each turtle was checked for flipper tags, and if no tags were present, a Monel tag was applied to each rear flipper. Leatherback curved carapace length (CCL) and curved carapace width (CCW) were measured to the nearest 0.1 cm with a flexible measuring tape. Tracking metrics, including total track duration, departure date (post-nesting migration start date indicated by a sustained direct movement away from the nesting beach), and total post-nesting distance, were calculated. To evaluate any changes in post-nesting distance over the study period, the cumulative post-nesting migration distance was calculated every 90 d up to 540 d. Differences in leatherback tracking metrics and post-nesting distance over time between harness and direct attachment were analyzed to determine if attachment method biased the results.

Distribution, high-use habitats, and sea surface temperature

We filtered 68,194 raw Argos locations (Kalman filtering location processing) to exclude poor quality (Z location class) and improbable locations based on a maximum rate of travel of 10 km hr^{-1} between successive locations using STAT (Coyne and Godley 2005). Gaps in daily locations were not common but did occasionally occur. Three individuals (P, T, and FF) had a transmission gap (1.5–2 months) after movement into a region, and one individual (M) had a transmission gap (7.5 months) after departing the Caribbean Sea. The best daily location from the filtered Argos data for each turtle was selected using the Douglas Argos-Filter Algorithm (Douglas et al. 2012) in Movebank (Wikelski et al. 2019). We imported the daily locations into ArcGIS (v 10.5) to map tracks and identify inter-nesting areas (locations occurring between satellite tagging date and migration start date), migration corridors, and high-use areas. Using ArcGIS, locations on land were removed ($n = 52$). For each location, we obtained sea surface temperature (SST; GHRSST daily analysis at 0.25 degree resolution, NCEI 2016) and assigned a region: North Atlantic Ocean (NAO); Gulf of Mexico (GoM); or Caribbean Sea (CAR).

To assess leatherback utilization distribution, we used Kernel Density Estimation (KDE, Spatial Analyst Tools ver 10.5.0, ArcGIS 10.5) based on all daily locations for all individuals. KDE maps were created to identify core utilization areas (50% Percentage Volume Contours) and migration pathways (an area between the nesting beach and core areas or between two or more core areas that was utilized by multiple individuals) for GoM and NAO regions. To assess seasonal habitat use, KDE maps were created by season for all locations. Seasons were defined as follows: January–March (winter), and April–June (spring), July–September (summer), and October–December (fall).

We conducted statistical analyses in R (R Development Core Team 2019) using a significance of $\alpha = 0.05$. We used a one-way ANOVA to determine differences in size, tracking distance and duration, and date of departure among regions and attachment methods. Since SST was not normally distributed, a Kruskal–Wallis test was used to determine differences in SST among core locations, regions, and seasons, with differences identified post hoc using a Pairwise Wilcoxon test with Bonferroni correction. We used linear regression analysis to evaluate trends in tracking distance over the study period for all turtles, GoM turtles, and NAO turtles, at 90, 180, 270, 360, 450, and 540 d.

Results

Satellite telemetry

We tracked leatherbacks between 8.9° N and 48.0° N and, and 9.6° W and 96.5° N, which spans the western and central Caribbean Sea, Eastern and Western NAO, and the GoM. Of the 40 tracked turtles, 33 provided sufficient tracking duration to establish a migratory route out of the Caribbean Sea (Fig. 1). Fifty-five percent ($n = 18$) of the turtles went directly into the GoM through the Yucatan Channel between Cuba and Mexico

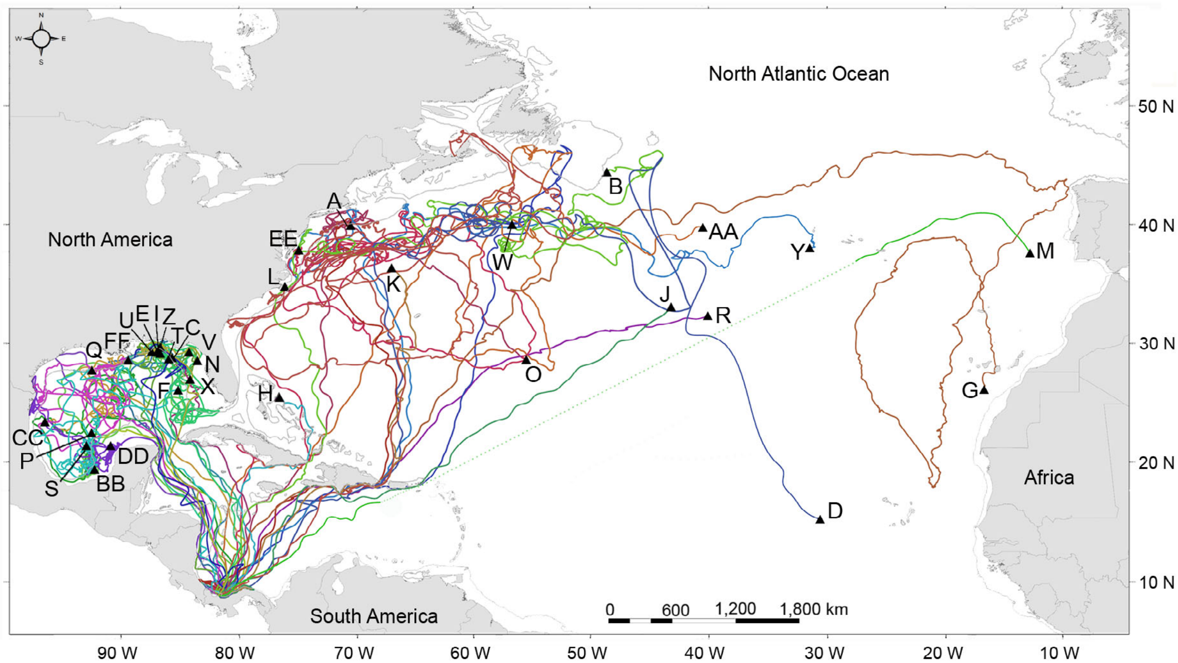

Fig. 1. Reconstructed satellite tracks (n = 33) of leatherback sea turtles from nesting beaches in Costa Rica and Panama that provided sufficient telemetry data to establish a migratory route out of the Caribbean Sea, with 200 m bathymetry (gray line). Each colored track represents an individual leatherback turtle. Letters correspond to letters of turtles listed in Table 1. Of the 33 turtles, 55% (n = 18) went into the Gulf of Mexico and 45% (n = 15) went into the North Atlantic Ocean.

(Fig. 1, GoM turtles). We tracked the remaining 45% (n = 15) entering the NAO through either the Mona Passage between Dominican Republic and Puerto Rico, the Windward Channel between Cuba and Haiti, or the Anegada Passage east of Puerto Rico (Fig. 1, NAO turtles). Of the 33 that were tracked departing the Caribbean, 32 provided sufficient tracking duration (>70 d for use in data analysis (Table 1). There was no indication of any suspicious behavior associated with final transmitter locations that would suggest any of 32 turtles had been killed. This suggests that the transmitters had either come off or the sensors had become fouled preventing additional signals.

Overall, mean CCL was 151.1 cm (133.3–164.2) and mean CCW was 109.2 cm (99.3–124.3) (Table 2). CCL between GoM and NAO turtles was not significantly different ($F_{1,31}$ = 2.5, P = 0.13), while CCW was significantly larger for NAO turtles compared to GoM turtles ($F_{1,30}$ = 6.3, P = 0.02) (Table 2). Departure date from the nesting beach was between June 3 and July 25, with tracking distances between 1303 and 24,212 km, and tracking duration between 72 and 712 d (Table 1). There was no significant difference for departure date between GoM and NAO turtles ($F_{1,30}$ = 0.228, P = 0.64) (Table 2). NAO turtles were tracked significantly further than GoM turtles ($F_{1,30}$ = 7.8, P = 0.01), but not significantly longer ($F_{1,30}$ = 0.98, P = 0.33) (Table 2).

Linear regression indicated a positive significant relationship between year and post-migration distance for NAO turtles at 90 d (n = 13; $F_{1,11}$ = 33.8, P < 0.01, R^2 = 0.755; Fig. 2). A significant positive relationship for NAO turtles was also seen from 350 to 540 d ($F_{1,3}$ = 18.3–533.4, P < 0.05, R^2 = 0.859–0.998). There was no relationship between year and post-nesting migration distance for GoM turtles (n = 14; $F_{1,12}$ = 0.00, P = 0.96, R^2 = 0.000; Fig. 2), and a positive relationship, though not significant, when regions were combined ($F_{1,25}$ = 1.68, P = 0.21, R^2 = 0.063; Fig. 2) at 90 d. There was

Table 1. Details for the 32 satellite-tracked leatherback females that were tracked for at least 70 d.

Turtle	CCL (cm)	CCW (cm)	Attachment date	Migration start date	Tracking duration (days)	Post-nesting distance (km)	Foraging region	Attachment method
A	160.0	na	05/27/04	06/23/04	156	3733	NAO	Harness
B	164.2	124.3	06/14/05	07/16/05	438	16,552	NAO	Harness
C	156.0	112.0	06/18/05	06/26/05	96	2429	GoM	Harness
D	152.0	109.0	06/17/05	07/25/05	606	15,841	NAO	Harness
E	152.0	103.7	07/07/05	07/09/05	363	7851	GoM	Harness
F	156.1	114.2	06/16/06	06/21/06	324	11,210	GoM	Harness
G	151.4	113.0	05/29/07	06/17/07	606	19,315	NAO	Harness
H	157.2	116.5	05/30/07	06/03/07	72	1644	NAO	Harness
I	151.3	106.1	06/08/08	06/28/08	112	2650	GoM	Harness
J	157.2	112.3	06/09/08	07/05/08	134	4884	NAO	Harness
K	157.0	110.0	05/31/09	06/16/09	103	3064	NAO	Harness
L	152.5	108.5	06/01/09	06/10/09	712	24,212	NAO	Harness
M	136.2	99.3	06/04/10	06/05/10	154	10,874	NAO	Direct
N	145.5	106.8	06/05/10	06/07/10	153	2772	GoM	Direct
O	159.0	113.0	05/28/11	06/08/11	244	7847	NAO	Direct
P	164.0	115.0	05/28/11	06/29/11	413	7936	GoM	Direct
Q	133.3	103.4	05/26/13	06/07/13	73	3398	GoM	Direct
R	150.9	114.3	05/27/13	07/21/13	152	4834	NAO	Direct
S	145.0	108.0	05/25/14	07/17/14	90	1303	GoM	Direct
T	144.6	108.0	05/27/14	06/28/15	459	3543	GoM	Direct
U	144.2	104.0	05/26/15	06/15/16	112	2171	GoM	Direct
V	149.7	108.1	05/30/16	06/25/16	160	2386	GoM	Direct
W	151.1	112.6	05/28/16	06/20/16	152	6539	NAO	Direct
X	152.5	102.8	05/31/16	07/01/16	244	4287	GoM	Direct
Y	151.3	111.0	05/31/17	06/21/17	351	13,397	NAO	Direct
Z	142.4	107.5	05/28/17	07/12/17	145	2058	GoM	Direct
AA	149.2	108.4	05/27/17	06/21/17	452	18,910	NAO	Direct
BB	141.2	104.8	05/31/17	06/22/17	471	13,181	GoM	Direct
CC	151.1	107.6	05/31/17	06/29/17	251	7205	GoM	Direct
DD	148.9	105.2	05/27/18	06/29/18	444	9813	GoM	Direct
EE	151.5	108.4	05/27/18	07/04/18	509	23,016	NAO	Direct
FF	156.7	106.2	05/28/18	06/28/18	508	13,144	GoM	Direct

Notes: Assigned foraging areas are abbreviated as in text: CCL, curved carapace length (cm); CCW, curved carapace width (cm); GoM, Gulf of Mexico; NAO, North Atlantic Ocean.

no significant relationship for GoM turtles, or when regions were combined, for 180 to 540 d.

Attachment method comparison

Total tracking duration for harness attachment ranged from 72 to 712 d, with a mean duration of 310 d, while direct attachment duration ranged from 73 to 509 d, with a mean duration of 280 d (Tables 1, 2). There was no significant difference between attachment methods for date of departure ($F_{1,30}$ = 0.107, P = 0.75), number of tracking days ($F_{1,30}$ = 0.192, P = 0.67), or post-nesting tracking distance ($F_{1,30}$ = 0.386, P = 0.54) (Table 2). Overall mean remigration for tracked leatherbacks was 2.2 yr (n = 24), with no significant difference between harness (2.3 yr) and direct attachment (2.2 yr; $F_{1,10}$ = 0.054, P = 0.82) turtles. There was no significant difference in distance traveled at 90, 120, 180, 270, 360, or 450 d (χ^2 = 0.002–0.04, P = 0.83–0.96) between attachment methods. When turtles were separated by attachment method, there was a positive, but not significant, relationship between year and post-nesting migration distance for both harness ($F_{1,7}$ = 0.73, P = 0.42, R^2 = 0.094) and direct ($F_{1,16}$ = 3.54, P = 0.08, R^2 = 0.181) attachment.

Distribution, high-use habitats, and sea surface temperature

Leatherback location SST ranged from 10.1° to 31.7°C (mean = 24.0°C; ± 4.7), with ten turtles tracked between two and 13 consecutive days in

Table 2. Summary for the 32 satellite-tracked leatherback females that were tracked for at least 70 d.

Variable	Overall	GoM	NAO	Harness	Direct
CCL					
Mean	151.1	149.1	153.4	155.6	148.4
Range	133.3–164.2	133.3–164.0	136.2–164.2	151.3–164.2	133.3–164.0
SD	7.0	7.3	6.4	3.8	7.1
CCW					
Mean	109.2	107.3*	111.5*	111.8	107.7
Range	99.3–124.3	102.8–115.0	99.3–124.3	103.7–124.3	99.3–115.0
SD	4.8	3.6	6.1	5.3	3.9
DD					
Mean	24-Jun	25-Jun	24-Jun	28-Jun	26-Jun
Range	3-Jun to 25-Jul	7-Jun to 17-Jul	3-Jun to 25-Jul	3-Jun to 25-Jul	5-Jun to 21-Jul
SD	13	10	16	15	12
Dur					
Mean	289	260	323	310	280
Range	72 - 712	73-508	72-712	72-712	73 - 509
SD	185	155	214	233	159
Dis					
Mean	8500	5726*	11,644*	9449	7931
Range	1303–24,212	1303-13,181	1644-24,212	1644-24,212	1303-23,016
SD	6621	4085	7620	7763	5978

Notes: Values listed as mean, range, and standard deviation (SD). CCL, curved carapace length (cm); CCW, curved carapace width (cm); DD, Date of departure from nesting beach; Direct, Direct attachment method; Dist, tracking distance (km).; Dur, tracking duration (days); GoM, Gulf of Mexico; Harness, Harness attachment method; NAO, North Atlantic Ocean.

* Difference between regions significant at $P < 0.05$.

waters with SST between 10.1° and 14.6°C. Mean SST was calculated for both core (KDE 50% PVC) and non-core locations by region for all locations and by season (Table 3). SST was significantly different between GoM and NAO core areas ($\chi^2 = 1640.2$, $P < 0.01$), and between core and non-core locations in both GoM ($\chi^2 = 54.7$, $P < 0.01$) and NAO ($\chi^2 = 54.9$, $P < 0.01$) (Table 3). There were significant differences among seasons in core SST for GoM ($\chi^2 = 812.2$, $P < 0.01$) and for NAO ($\chi^2 = 494.2$, $P < 0.01$), and significant differences between core and non-core locations for each season in GoM ($\chi^2 = 313.0$ to 602.8, $P < 0.01$) and in NAO ($\chi^2 = 6.6$ to 78.3, $P < 0.05$) (Table 3).

The KDE map based on all post-nesting locations identified multiple leatherback high-density areas in the GoM and moderate-density areas along the Mid-Atlantic coast of the USA, Caribbean coasts of Costa Rica, and Panama (post-nesting migration), and south of Newfoundland, Canada (Fig. 3a). The density of locations in the GoM biased the KDE map toward the GoM, possibly because of tagging site bias that may underestimate the use of areas farther away from the tagging site (Hays et al. 2020). To address this, a separate KDE map was created for each region and then combined to create a single composite map. The composite KDE map indicates high-use habitats in the northern GoM (south of Louisiana and along the Panhandle of Florida, USA) and in the southern GoM (Campeche Bay, Mexico) (Fig. 3b). In the NAO, high-use habitat is located along the Northeast coast of the USA and south of Newfoundland, Canada, with several moderate use habitats in the western NAO and one northeast of the Cape Verde Islands (Fig. 3b). There is a shared east-west movement corridor connecting the Mid-Atlantic and south of Newfoundland high-use habitats, a north-south migration pathway between the Caribbean Sea and the NAO high-use habitat, and a north-south migration pathway between high-use habitats in the GoM (Fig. 3b). Within the CAR, there are three migration pathways between nesting beaches and both the GoM and NAO (Fig. 3b).

Seasonal KDE maps suggest that tracked leatherbacks moved in response to seasonal changes. Winter locations show a large high-use

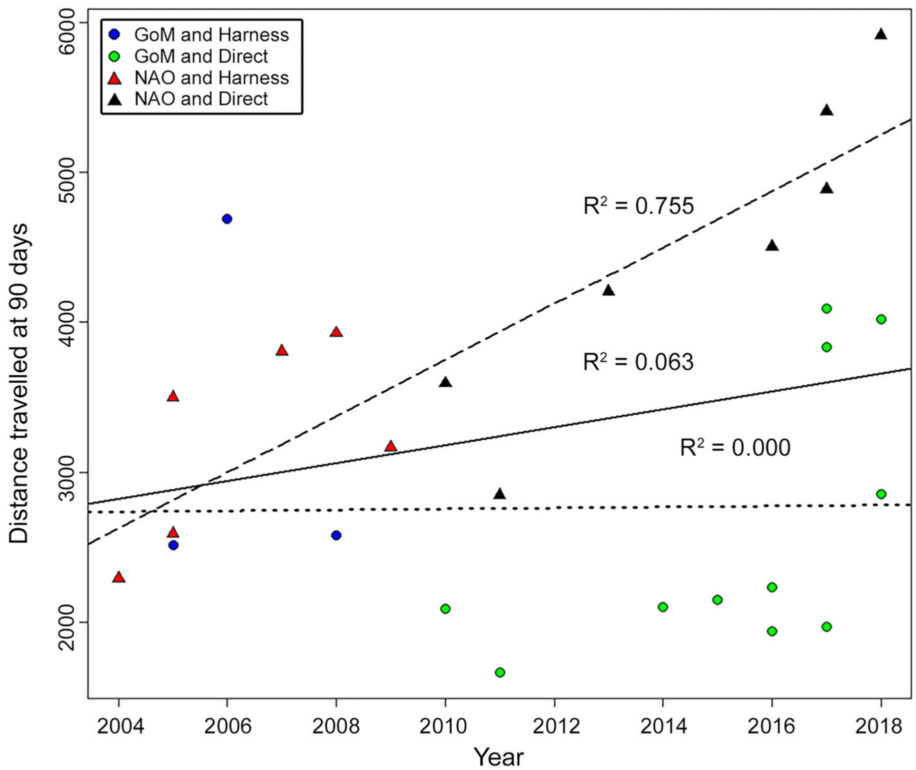

Fig. 2. Scatter plot of distance traveled by individual turtles at 90 d after post-migration started away from the nesting beach over the study period (2004–2018). Triangles represent turtles that migrated into the North Atlantic Ocean (NAO) and circles represent turtles that migrated into the Gulf of Mexico (GoM). Blue and red colored icons represent turtles with the harness attachment (2004–2009), green and black colored icons represent turtles with the direct attachment (2010–2018). The three regression lines represent GoM turtles (dotted line), NAO turtles (dashed line), and all turtles (solid line).

area in the southwestern GoM and south of Novia Scotia, Canada (Fig. 4a). Spring locations were associated with nesting beaches, a high-use area in the southern GoM, and low use areas southeast of Novia Scotia, Canada (Fig. 4b). Summer locations were associated with high-use areas in the northern GoM and off the Northeast coast of the US (Fig. 4c). Fall locations were associated with three high-use areas: two in the northern GoM and the third off the Northeast coast of the US (Fig. 4d). When the seasonal KDE maps from this study were compared to the bycatch maps from Swimmer et al. (2017), we noticed a slight overlap in GoM during winter, little overlap in NAO during Spring, high overlap in both GoM and NAO during summer, and very high overlap in both GoM and NAO during fall (Fig. 4).

Discussion

Leatherbacks nesting along the Caribbean coast of Costa Rica and Panama migrated to high-use habitats in both tropical (GoM) and temperate (NAO) regions using four distinct passages to leave the Caribbean Sea. Once leatherbacks departed the Caribbean, those traveling into the NAO displayed a large spatial dispersal, possibly only limited by environmental factors, such as SST zone of between 10° and 15°C being a barrier to leatherback movement (McMahon and Hays 2006, Witt et al. 2007). Ten of the turtles tracked in the NAO did venture into waters with SST in this range, though the time they spent in these areas was short, suggesting that this SST zone constrains northern leatherback movement. Leatherback movements in the NAO

Table 3. Summary of sea surface temperature for core locations (50% Percentage Volume Contours) and non-core locations by region and by season.

	GoM turtles		NAO turtles	
Season	Core locations	Non-core locations	Core locations	Non-core locations
All (*n*)	1280	1275	1570	1572
Mean	27.9†	26.9‡	20.7†,§	21.9§
Range	20.9–31.7	16.9–31.6	12.2–30.4	10.1–30.1
SD	2.1	2.9	3.8	4.8
Winter (*n*)	164	289	295	439
Mean	24.7‡	23.3‡	18.33§	19.4§
Range	22.4–26.9	16.9–26.1	12.2–24.1	10.4–24.8
SD	0.7	1.7	2.5	3.0
Spring (*n*)	135	90	263	162
Mean	27.7‡	25.9‡	20.6§	19.7§
Range	21.7–30.0	12.5–29.6	12.9–28.0	16.4–23.7
SD	1.3	2.3	3.1	1.9
Summer (*n*)	652	481	412	591
Mean	29.3‡	29.7‡	24.2§	25.6§
Range	27.1–31.7	27.2–31.3	15.8–30.4	12.2–30.1
SD	0.9	0.7	3.3	4.6
Fall (*n*)	329	415	597	380
Mean	26.7‡	26.2‡	19.5§	19.9§
Range	20.9–29.2	18.5–29.5	13.0–27.7	10.1–28.1
SD	1.8	1.6	3.1	4.1

Notes: Values listed as n, mean, range, and standard deviation (SD). GoM, Gulf of Mexico; NAO, North Atlantic Ocean.

† Difference between regions significant at $P < 0.05$.

‡ Difference between locations within GoM region significant at $P < 0.05$.

§ Difference between locations within NAO region significant at $P < 0.05$.

indicate several shared pathways between nesting beaches and high-use habitats, though there was some individual variation. Chambault et al. (2017) and Fossette et al. (2010*b*) reported similar movements, but our findings are in contrast to in-water tracking by James et al. (2005) and Dodge et al. (2014). This difference may be a result of our study only tracking post-nest females, while the in-water studies included female, male, and juvenile turtles. Similar NAO high-use habitats were identified for leatherbacks satellite tagged in-water (James et al. 2005, Jonsen et al. 2007, Dodge et al. 2014), as well as leatherbacks satellite tagged while nesting in the eastern Caribbean and northern South America (Eckert 2006, Hays et al. 2006, Fossette et al. 2010*a*, *b*, Chambault et al. 2017). In contrast, GoM leatherback movements were confined to a specific region, but not constrained within the GoM by SST. Movements suggested preference for three high-use habitats connected by a migration corridor. The CAR region appears to be primarily used as a migration corridor for both NAO and GoM leatherbacks. Additionally, seasonal movements documented in this paper are consistent with those reported by Dodge et al. (2014) for NAO turtles and Aleska et al. (2018*b*) for GoM turtles.

Our tracking supports the hypothesis that leatherbacks are found in the GoM year-round (Stewart et al. 2016, Aleksa et al. 2018*b*) and supports the idea proposed by Evans et al. (2007) that leatherbacks use the GoM as a destination rather than just a pass-through region. Genetic analysis by Stewart et al. (2016) suggests the majority of leatherback turtles caught in the GoM were from Costa Rica and Trinidad nesting beaches, with a higher number of individuals having >80% probability of being from the Costa Rican nesting population. There is evidence of individuals moving between Costa Rican and Panamanian nesting beaches (Ordoñez et al. 2007), suggesting that the genetic markers identifying the Costa Rican nesting population may actually represent the larger Costa Rica/Panama nesting population.

Within the GoM, turtles are utilizing three primary areas: the northeastern GoM along the Panhandle of Florida (FLPH), south of Louisiana (SLA), and the southern GoM in the Bay of Campeche, Mexico (BOC). All three of these areas are connected by a shared corridor. The FLPH was also identified as important to leatherbacks satellite tagged in-water (Aleska et al 2018*b*), while the SLA is consistent with reported PLL fishery bycatch (Fossette et al. 2014, Stewart et al. 2016).

The use of the GoM by the tracked leatherbacks may represent an energetic advantage with lower energy requirements (shorter migration) and lower energy expense (core body temperature is easier to maintain in warmer water) (Aleska et al. 2018*b*). With approximately 80% of reproductive energy costs associated with round-trip migrations (Wallace et al. 2006), the shorter migration distance to the GoM compared to the NAO could put GoM turtles at a reproductive advantage with a decreased breeding migration interval. Surprisingly, when we examined the remigration intervals of the tracked turtles, we found no significant difference between GoM

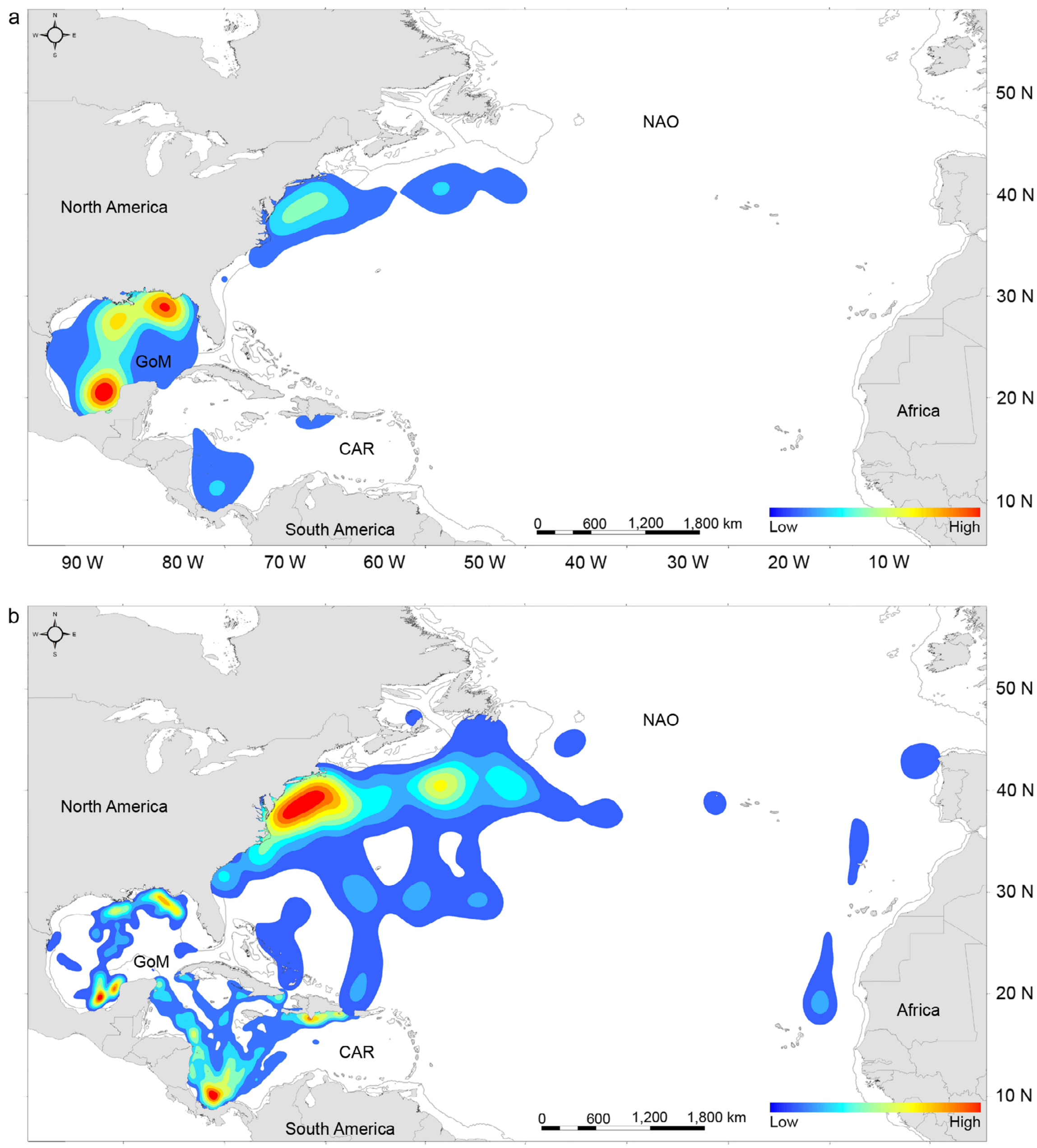

Fig. 3. Kernel Density Estimation (KDE) maps with 200 m bathymetry (gray line). (a) For all post-nesting movement locations. Multiple leatherback high-density areas were located in the Gulf of Mexico (GoM), with moderate-density areas along the Eastern coast of the USA and Southeast of Novia Scotia, Canada. The low-density area along the Caribbean coast of Costa Rica and Panama represents post-nesting migration. (b) Composite KDE map based on analysis within each region. High-use habitats were located in both northern and southern GoM, the Northeast coast of the USA, and south of Newfoundland, Canada. There is an east-west corridor connecting the Northeast US and south of Newfoundland high-use habitats, a north-south migration pathway between the Caribbean Sea (CAR) and the North Atlantic Ocean (NAO) high-use habitats, and a north-south migration pathway between high-use habitats in the GoM. Within the CAR, there are migration pathways from nesting beaches to both the GoM and NAO.

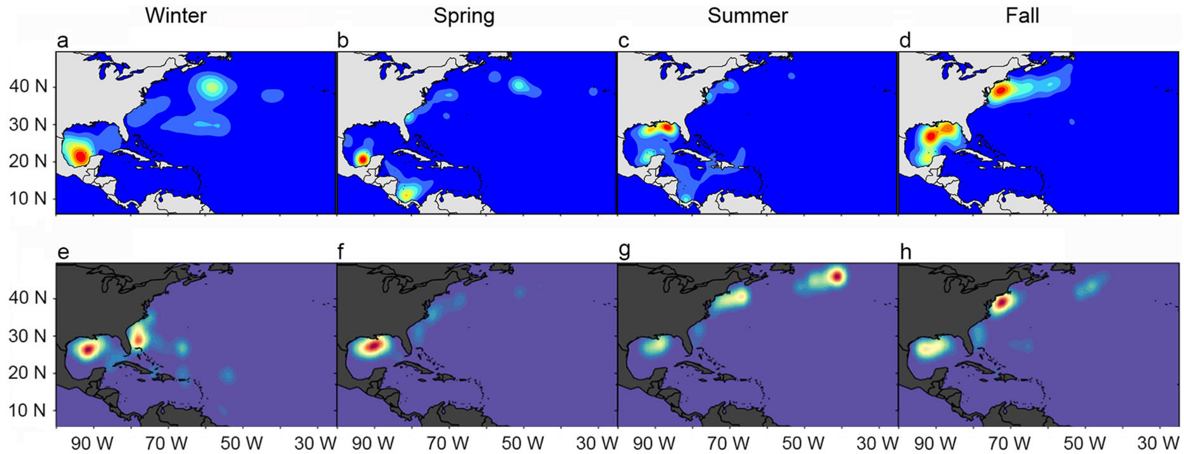

Fig. 4. Seasonal kernel density estimation (KDE) maps of leatherback locations (a–d) and leatherback bycatch in US longline fisheries (e–h; from Swimmer et al. 2017). KDE location maps suggest that tracked leatherbacks are moving in response to seasonal changes. Winter locations show a high-use area in the southwestern Gulf of Mexico (GoM) and a moderate use area south of Novia Scotia, Canada (a). Spring locations show high use of the southern GoM and multiple moderate use areas along the Atlantic coast of the US and southeast of Novia Scotia, Canada (b). Summer locations are dominated by migration away from the nesting beaches with high-use areas in the northern GoM and off the Northeast coast of the US (c). Fall locations show two high-use areas in the north GoM and a high-use area off the Northeastern coast of the US (d). When the location KDE maps are compared to bycatch KDE maps, there is slight overlap in GoM during Winter (a, e), little overlap in North Atlantic Ocean (NAO) during Spring (b, f), high overlap in both GoM and NAO during Summer (c, g), and very high overlap in both GoM and NAO during Fall (d, h).

(2.2 yr) and NAO (2.1 yr) turtles, suggesting that use of the GoM may not provide an energetic advantage. An alternative possibility driving the use of the GoM is that adult sea turtle distribution is related to locations encountered by drifting hatchlings in ocean currents (Hays et al. 2010, Scott et al. 2014, Lalire and Gasper 2019). The Caribbean Current would be the first strong current encountered by leatherback hatchlings from nesting beaches along the Caribbean coast of Central America, pushing them into the GoM via the Loop Current, before traveling into the NAO via the Gulf Stream. This is supported by the genetic results of Stewart et al. (2016) with a high number of leatherbacks identified as being from Costa Rica (n = 43) and Trinidad (n = 43), a low number from French Guiana (n = 11), St. Croix (n = 2), and none from Florida.

The distance traveled by NAO leatherbacks appears to have significantly increased over the study period, with turtles tagged later in the study (2016–2018) traveling further over the first 3 months of post-nesting migration compared to turtles tagged early in the study (2004–2006). The increase in distance during the study was also significant at longer time intervals. While it has been suggested that the shorter distances traveled during the first 90 d could be an artifact of the harness attachment method (Fossette et al. 2008, Benson et al. 2011), a positive increase in distance traveled was seen in both harness and direct attachment turtles. Additionally, the distance traveled at 90 d up to 450 d was not significantly different between attachment methods. While the attachment method may be considered as a potentially confounding factor in the analysis, none of the metrics compared between the two attachment methods were significantly different. It is also interesting to note that two-thirds of the turtles between 2004 and 2009 migrated a further distance into the NAO compared to only one-third of turtles between 2010 and 2018, potentially signaling a shift in destination from NAO to GoM.

Sea turtle bycatch probability has been associated with SST and time of year, with the highest probability of bycatch for leatherbacks occurring during fall months and SST between 18 and 24°C (Kot et al. 2010, Swimmer et al. 2017). Swimmer et al. (2017) reported the highest levels of leatherback bycatch in the GoM during winter and spring (Fig. 4e, f), while the highest bycatch levels in the NAO occurred in summer and fall (Fig. 4g, h). Between 1992 and 2005, the GoM fishing zone had the highest number of PLL hook sets, followed by the Florida East Coast, Mid-Atlantic Bight (MAB), Northeast Coastal (NEC), and Northeastern Distant (NED) (Kot et al. 2010). Fossette et al. (2014) showed that between 1995 and 2010, leatherbacks had a medium susceptibility to PLL in GoM and high susceptibility in the NED, MAB, and South Atlantic Blight fishing zones, all areas utilized by the turtles tracked in this study. Leatherbacks accounted for over 50% of the sea turtle bycatch in six of the 11 PLL fishing zones, with the highest rates in the GoM swordfish PLL fishery and the NAO tuna PLL fishery (Kot et al. 2010, Garrison and Stokes 2014). The NAO-tracked turtles utilized core habitats with a mean SST of 20.7°C in the NEC zone during fall months, exposing them to a high probability of bycatch, while GoM turtles had the highest probability of interacting with the PLL fishery during the summer and fall months.

The number of hooks in the US Atlantic PLL fishery has changed over time with an overall decrease in the number of hook sets from 7899 in 2005 to 5635 in 2018 (NMFS 2020). In late 2004, PLL fishery zone closures and regulations related to hook type (switching from J to circle) and bait (switching from squid to fish) were implemented to reduce sea turtle bycatch. While these measures have resulted in an overall 40% decline in leatherback bycatch, and a 64% decline in the NED though limiting squid bait and requiring larger circle hooks, the post-release mortality of caught individuals has increased (NMFS 2020). In the NAO high-use habitats, leatherbacks also face bycatch in fixed gear fisheries, potentially with a higher mortality rate due to entanglement occurring at depth (James et al. 2005, Hamelin et al. 2017), while the GoM is being utilized by more than half of the turtles tracked, making nesting females from the Caribbean coast of Central America highly susceptible to fisheries bycatch. In addition to overlapping with PLL fisheries, GoM leatherback high-use habitats overlap some of the highest density areas for oil and natural gas platforms off the coasts of Alabama, Mississippi, and Louisiana, USA (Sinclair 2011). Currently, oil and natural gas exploration is banned (BOEM 2020), and there is limited PLL fishing since 2004 (Walter et al. 2008, Carruthers et al. 2010, Swimmer et al. 2017), on the continental shelf along Florida's gulf coast, which provides an area of relative safety for leatherbacks in the northern GoM.

Changes to the marine environment as a function of climate change have likely impacted both the biotic and abiotic variables that influence leatherback turtle behavior. While there was no support that turtles were traveling further north in search of cooler SST, an increased post-migration distance may be a result of leatherbacks finding it harder to locate suitable prey. An increase in travel distance may be due to leatherbacks being able to access additional areas as thermal restraints in the NAO shift northward (McMahon and Hays 2006). Changes in SST and currents could result in changes to jellyfish abundance and distribution in the NAO, similar to the predicted decline in core leatherback pelagic habitat in the Pacific (Willis-Norton et al. 2015), while causing shifts in the spatial and temporal distribution of jellyfish in the GoM, affecting the movement of leatherback sea turtles. Climate changes may also be leading to a shift in the number of leatherbacks migrating into the GoM instead of NAO, even though individuals may not see an energetic advantage of a shorter migration. Continued research into leatherback high-use habitats can include identifying possible foraging areas and strategies through switching space-state models, assessing changes in environmental conditions that may influence prey availability, and the shifting of pelagic habitat, and analyzing genetic samples from individuals nesting along the Caribbean coast of Panama.

To protect the Central American Caribbean leatherback nesting population, conservation efforts could be enhanced by addressing climate change and other anthropogenic impacts in both regions and may benefit from continued work to reduce bycatch mortality in Atlantic PLL fisheries. GoM leatherbacks are found in specific, highly productive areas all year long that overlap with known fishery efforts and stand to benefit from designation of critical habitat, establishment, or strengthening of Marine Protected Areas, fisheries closures off the southern coast of Louisiana during summer and fall months, and cooperative agreements with Mexico to encourage the protection of the southern GoM high-use habitat. NAO leatherbacks are wider-ranging and dispersed and may benefit from additional management of human activities, such as decreasing leatherback bycatch even more, through exclusive use of fish bait and larger circle hooks in the NEC and MAB fishing zones. Ultimately, developing conservation and management strategies to reduce potential interactions with anthropogenic activities can be informed by consideration of the different regional movements of the NWA DPS Central American Caribbean leatherback nesting population.

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Data Availability

Data are not publicly available due to the sensitivity of location data for an endangered species. Data may be obtained from Dr. Daniel R. Evans, Sea Turtle Conservancy, and is available to researchers with appropriate credentials.