



Pre-nesting Movements of Leatherback Sea Turtles, *Dermochelys coriacea*, in the Western Atlantic

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Understanding high-use areas for highly migratory species and their movements within these areas may provide insight into behaviors such as foraging and mating. In the Western Atlantic, the leatherback sea turtle, *Dermochelys coriacea*, has a broad geographic range extending from nesting beaches at low latitudes to foraging areas off the coast of Eastern Canada. Biotelemetry has revealed much about the movements and habitats of leatherbacks. However, the timing and location of leatherback mating behavior remains unclear. We conducted spatial analyses of the movements of reproductive female leatherbacks prior to their first seasonal nesting events. Using kernel density estimates, high-use areas for seven female turtles originally tagged in Canadian waters were revealed from 50% volume contours depicting pre-nesting movements (120 days prior to confirmed nesting events) and inferred mating behavior (45 days prior to confirmed nesting events). All individuals initially remained offshore within a relatively small range of latitude (10–15° N) before transiting to and residing in coastal waters adjacent to nesting beaches in Colombia ($n = 2$), Trinidad ($n = 3$), Guyana ($n = 1$), and French Guiana ($n = 1$). Comparison of these movement patterns to those of mature male leatherbacks ($n = 12$) revealed similarities. Male and female residency within this offshore high-use area may be indicative of prey exploitation prior to the energetically-costly nesting season. While the offshore residency period of three males and one female extended into the interval in which mating is expected to occur, most males and females transited to coastal waters where they resided throughout this period. High-use areas determined through kernel density analysis support and corroborate previous telemetry work indicating that mature male leatherbacks exhibit seasonal residency adjacent nesting beaches for the early portion of the nesting season, presumably to exploit mating opportunities. Fine-scale analyses of fisheries interactions in both coastal and offshore waters and estimation of accompanying mortality rates is required to evaluate fishery threats to this population during the pre-nesting interval.

Keywords: *Dermochelys coriacea*, habitat, pre-nesting, mating, spatial ecology, satellite telemetry, leatherback sea turtle

INTRODUCTION

The use of satellite telemetry has provided valuable insight into the distributions and habitat use of many highly migratory species. In the marine realm, satellite telemetry has revealed the distributions and movements of threatened species such as sharks, whales, sea birds, and turtles (Weimerskirch and Robertson, 1994; Godley et al., 2002; Baumgartner and Mate, 2005; Stevens et al., 2010). The ability to remotely observe animals throughout their migrations expands not only our knowledge of their life histories, but may also help identify potential threats that populations face at each phase of their migratory cycle (Hays et al., 2003). In some cases, the use of satellite telemetry has led to the implementation of effective conservation measures such as time-area closures of recreational and industrial fisheries (Domeier, 2006; Jensen et al., 2010). For pelagic species such as most sea turtles, telemetry has provided insight into otherwise enigmatic oceanic movements and residency areas. Advancing telemetry methods have aided in the investigation of mating behavior for populations of loggerhead (Henwood, 1987; Hays et al., 2010; Schofield et al., 2010), green (Balazs and Ellis, 2000), and Kemp's ridley turtles (Shaver et al., 2005).

The leatherback sea turtle, *Dermochelys coriacea*, is the most widely distributed of all sea turtles, with mature individuals in the North Atlantic making annual migrations from their nesting beaches in the Caribbean and South America to foraging grounds in the Northeast (Witt et al., 2007; Fossette et al., 2010) and Northwest Atlantic (James et al., 2007). The species is classified as endangered in Canada (SARA (Species at Risk Act), 2002). In order to effectively protect this species, their full range of habitats and high-use areas must be understood. Advancements in telemetry have led to discoveries such as leatherback migratory routes (James et al., 2005a,b; Dodge et al., 2014) and northern foraging habitats (James et al., 2006; Jonsen et al., 2007). However, knowledge gaps in the life history of this species remain, including understanding of female pre-nesting and mating behavior. Consistent paternity documented across successive nests suggests that sperm storage occurs from mating event(s) prior to the nesting season (Crim et al., 2002; Stewart and Dutton, 2011; Figgner et al., 2016) and that mating during inter-nesting periods may be rare. Therefore, as mature male and female turtles presumably aggregate to breed in specific areas, identifying where pre-nesting season mating opportunities occur may offer conservation value to the Atlantic leatherback population.

The first published hypothesis regarding timing and location of mating activity in North Atlantic leatherbacks suggested that mating occurred in close proximity temporally and spatially to a female's first oviposition on the nesting beach (Lazell, 1980). An alternate hypothesis was published shortly thereafter, asserting that since there were no reported first-hand observations of mating near nesting beaches, such activity must occur in distant offshore waters (Pritchard, 1982). This topic was revisited again in 1988, when Eckert and Eckert inferred pre-reproductive movements of females through the study of epibionts that colonize females once they arrive in warm, tropical waters. The

results of this work suggested that females do not arrive in tropical waters early enough to allow for localized mating near nesting areas, but instead must mate prior to their arrival in tropical waters (Eckert and Eckert, 1988). The advancement of satellite telemetry allowed for these hypotheses to be re-visited in 2005, when James et al. reported that mature male leatherbacks tagged at high-latitude foraging areas migrated to waters adjacent nesting beaches, supporting the earlier hypothesis that mating likely occurs in these areas. However, these findings have yet to be corroborated with mature female movement data.

Inter-nesting and post-nesting movements of mature female leatherbacks have been well documented (Reina et al., 2005; Eckert, 2006; Eckert et al., 2006, 2009; Hays et al., 2006); however, movements of female leatherbacks prior to their first seasonal nesting event have not yet been described. This arises from challenges associated with tracking turtles to their nesting beaches. To investigate behavior prior to the deposition of a female leatherback's first clutch of the season, satellite tags deployed on nesting females must be retained and remain operational for 2–3 years (until their next nesting season), a feat which has not yet been achieved with current technology and tag attachment methods (Hays et al., 2007). Alternatively, transmitters may be deployed on females in northern foraging areas prior to migration to nesting areas. While the required duration of tag retention and operation is considerably shorter in these cases, loss of tags and or transmissions before turtles reach nesting areas is unfortunately the norm, resulting from incidental mortality, biofouling, tag (including battery) failure, and/or tag attachment failure (Hays et al., 2007). These logistic challenges mean that documentation of pre-nesting behavior is exceedingly rare: of 57 mature females satellite tagged off the coast of Atlantic Canada (2000–2016), only six (10.5%) have retained their transmitter through to a confirmed nesting event.

Here we present the first analysis of the movements of female leatherbacks upon their arrival in tropical waters prior to their first confirmed nesting event, and compare their movement patterns to those of mature male turtles. By outlining areas of high-use habitat for both mature male and female turtles prior to the onset of nesting season, we can evaluate mating hypotheses using empirical data.

METHODS

Field Sampling

Seven female leatherback sea turtles were equipped with satellite transmitters while foraging in shelf waters off mainland Nova Scotia, Canada (~44°N, 64°W) and Cape Breton Island (~47°N, 60°W) (Table 1). Monel flipper tags (style no. 49, National Band and Tag Company, Newport, KY, USA) were applied to both rear flippers and passive integrated transponders (Avid, Calgary, AB, Canada; Biomark, Boise, ID, USA; Trovan, Douglas, UK) were implanted in the right shoulder. Individuals were equipped with satellite-linked transmitters [Wildlife Computers, Inc., Redmond, WA, USA; models SSC3 ($n = 1$), MK10-A ($n = 1$), MK10-AF ($n = 2$), SPOT5 ($n = 2$) and SPLASH10 ($n = 1$)]. All turtles were released immediately after tag attachment. Research and associated protocols were reviewed and approved

TABLE 1 | Summary data for seven mature female leatherback turtles equipped with satellite transmitters off the coast of Nova Scotia, Canada prior to confirmed nesting events.

Turtle ID	Curved carapace length (cm)	Transmitter deployment date	Date of first nest	120 Days prior to first nest	Nesting location
A	155	21-Jul-03	21-Apr-2005	22-Dec-2004	Shell Beach, Guyana
B	174.5	24-Jul-08	22-Mar-2009	22-Nov-2008	Awala Yalimapo, French Guiana
C	152.4	17-Jul-08	25-Apr-2009	26-Dec-2008	La Playona, Colombia
D	147.4	22-Jun-12	20-Apr-2013	21-Dec-2012	Bobalito, Colombia
E	151.9	25-Aug-13	22-Mar-2014	22-Nov-2013	Grande Riviere, Trinidad
F	159.2	5-Aug-14	2-May-2015	2-Jan-2015	Matura, Trinidad
G*	152	12-Jul-16	N/A	22-Jan-2017*	Trinidad-Guiana Shield

*Note that Turtle G was confirmed entangled in coastal fishing gear in Venezuela only days prior to her predicted first nesting event. Her pre-nesting interval was, therefore, estimated based on coastal residency behavior in nearshore waters off Trinidad and Venezuela.

by Dalhousie University Committee on Laboratory Animals or the Fisheries and Oceans Canada Maritimes Animal Care Committee or the Fisheries and Oceans Canada Maritimes Animal Care Committee to meet standards established by the Canadian Council on Animal Care. Research was conducted under scientific license from Fisheries and Oceans Canada and Species At Risk Act (SARA) Section 73 permits.

Spatial Analysis

Location data were acquired via the Argos satellite network¹. Locations classified as LC3, LC2, LC1, or LC0 are defined as within 150 m, 150–350 m, 350–1,000 m and >1,000 m of the true location, respectively¹. Location class A (LCA), for which Argos does not provide an estimated range of positional accuracy, has been shown to be as accurate, if not more so, than LC0 transmissions (Vincent et al., 2002). Therefore, location classes 3, 2, 1, 0, and A were analyzed in this study. Transmitters deployed in support of several research projects across multiple years had varying programming parameters, including different user-defined transmission intervals. To address this, prior to spatially analyzing these tracks, a daily median position was calculated for each individual, and tracks were linearly interpolated using packages “plyr” (Wickham, 2011) and “zoo” (Zeileis and Grothendieck, 2005) in R 3.0.2 (R Core Team, 2013) (Figure 1A). Linear interpretations assumed constant speed and direction for days in which locations were not generated. The pre-nesting interval was defined as the 120 days prior to each individual’s first seasonal nesting event; this interval allowed for discerning marked changes from migratory to residency behavior.

To infer potential areas of high use during the pre-nesting interval, interpolated tracks were spatially analyzed in ArcGIS 10.2.2 software (ESRI) using the kernel density tool within the Home Range Tools toolbox (MacLeod, 2013) (Figure 1B). Smoothing parameters for this analysis were calculated using the *ad hoc* approach in order to minimize fragmentation of potential high-use areas (Kie, 2013; Schuler et al., 2014). From kernel density results, percent volume contours were generated, outlining areas in which 50 and 95% of each individual’s locations have the probability of being detected within the 120-day pre-nesting interval (Figure 1C). The 50% volume contours were

used to infer high-use areas, while 95% contours showed the range of each individual throughout the pre-nesting interval.

To corroborate leatherback high-use areas derived from female pre-nesting telemetry data, we also considered tracking data from 12 mature male leatherbacks, including data from seven turtles previously analyzed by James et al. (2005a) (Table S1). Male tracking data were analyzed for all dates spanning 120 days prior to the earliest recorded nest (March 22; Female B) through to the onset of each male’s northward migration (Figure S2). Male and female high-use areas defined by their 50% volume contours were overlaid to determine areas of overlap using the Clip tool within the Spatial Analysis toolbox (ESRI).

Inference of Mating

Unlike other sea turtles, the timespan between mating and nesting events has not been directly observed in leatherbacks. Therefore, we inferred this period from known follicular development intervals of other sea turtles. Studies of captive green turtles indicate the first oviposition typically occurs ~34–45 days after observed copulation (Simon et al., 1975; Wood and Wood, 1980); however, this interval may reach up to 60 days (Wood and Wood, 1980). The mating period for loggerhead sea turtles has been documented to last up to 42 days (Miller et al., 2003). Leatherbacks are predicted to have a similar timespan between mating and nesting to that recorded for loggerhead and green turtles, as egg incubation and inter-nesting intervals are similar across these species (Hirth, 1980). This interval is also supported by the findings of Eckert and Eckert (1988), who estimated an interval of ~30 days between mating and egg production based on the colonization of tropical epibionts on nesting leatherback females. To remain conservative in our estimation of follicular development time, we assumed the period between mating and first nesting spans 45 days.

To identify potential areas of mating activity, individual female movement datasets were truncated to the inferred mating period (45 days prior to first seasonal nesting events), and spatial analyses applied to the pre-nesting interval (see above) were repeated (Figure S3). Male movement data were analyzed for all dates spanning 45 days prior to the earliest recorded nest (March 22; Female B) through to the onset of each male’s northward migration. From kernel density estimates, 50% volume contours were generated for both females (Figure 4) and males (Figure 5). Movement data for turtle F were not analyzed within the mating

¹www.argos-system.org

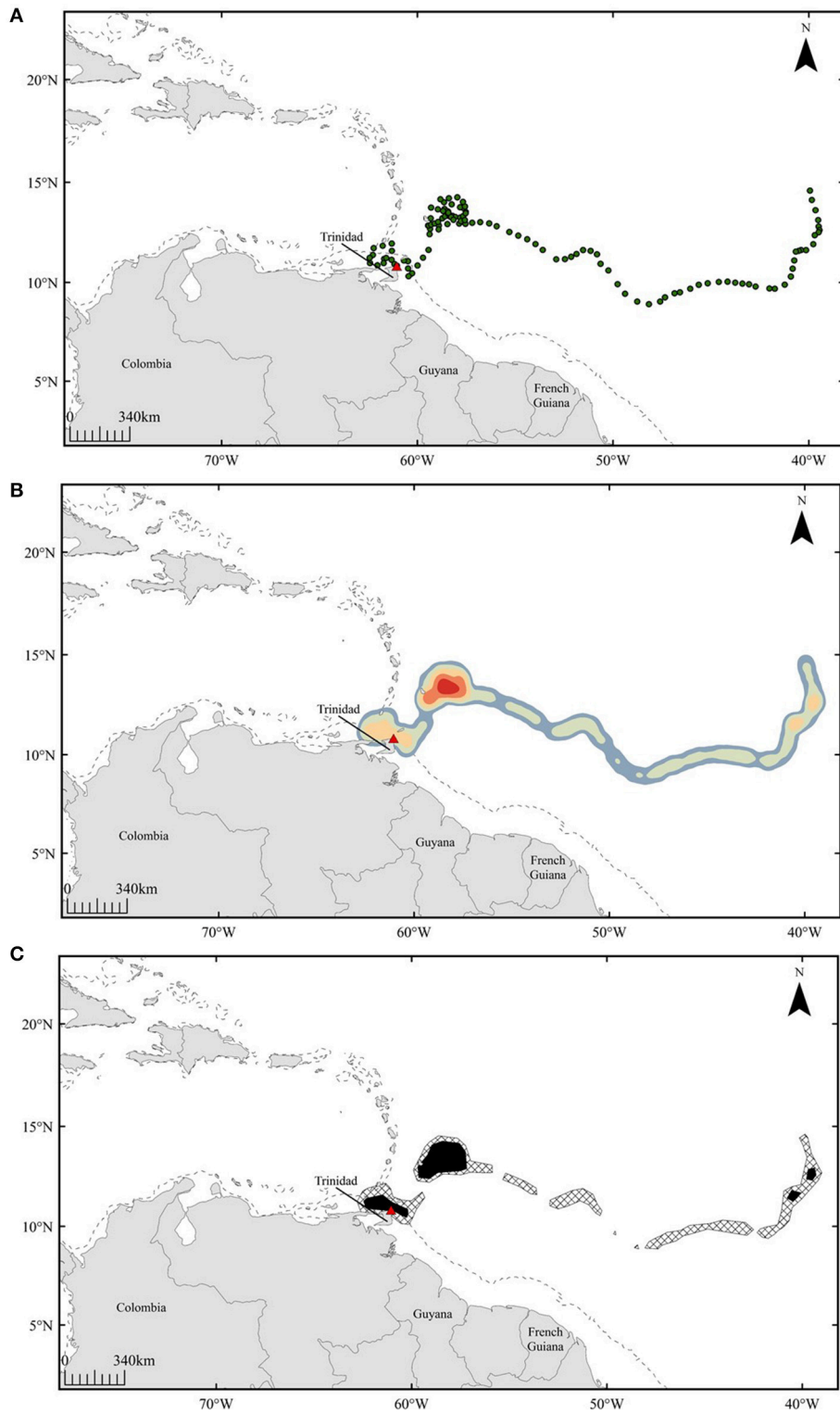


FIGURE 1 | Representative example of spatial analyses conducted for pre-nesting leatherbacks: turtle E. Panels show interpolated positions for 120 days prior to nesting **(A)**, heatmap displaying areas of high density (red) **(B)**, and 50% (black) and 95% (hatched) volume contours generated from kernel density results **(C)**. Dashed line represents 200 m isobath.

period (45 days prior to nesting), as transmissions temporarily ceased during this time interval. Nesting events were confirmed through observations of high-quality coastal Argos locations derived from continuous tag transmissions during satellite passes and/or extended surface/dry time logged by tag depth sensors, consistent with turtles coming ashore at known nesting areas ($n = 1$), or through encounters of tagged animals by collaborating beach monitoring organizations ($n = 4$). For one female (turtle G), the pre-nesting and mating intervals were estimated based on coastal residency behavior in nearshore waters off Trinidad and Venezuela prior to her fatal entanglement just days before her first predicted nesting event.

RESULTS

Female Movements within the Pre-nesting Interval

All mature female leatherbacks equipped with satellite transmitters off Nova Scotia exhibited seasonal residency in Atlantic Canadian waters from the time of tagging through to late September ($n = 2$), October ($n = 4$), or November ($n = 1$) of their respective deployment years before assuming southward migration. Females traveled southward within a narrow longitudinal range ($\sim 35^{\circ}$ – 50° W). Upon reaching southern waters corresponding roughly to the North Equatorial current (~ 10 – 15° N), seven females (turtles A–G) traveled westward toward beaches in Colombia ($n = 2$), Trinidad ($n = 3$), Guyana ($n = 1$), and French Guiana ($n = 1$) (Figure S1).

Combining the 50% volume contours produced from kernel density estimates for all seven female leatherbacks revealed patterns in female behavior during the 120-day pre-nesting interval (Figure 2). While offshore high-use areas spanned a wide longitudinal range ($\sim 40^{\circ}$ – 60° W), $\sim 75\%$ of activity in these areas (across all corresponding pre-nesting seasons) occurred within a narrow range of latitude ($\sim 5^{\circ}$; 10 – 15° N). After initially departing

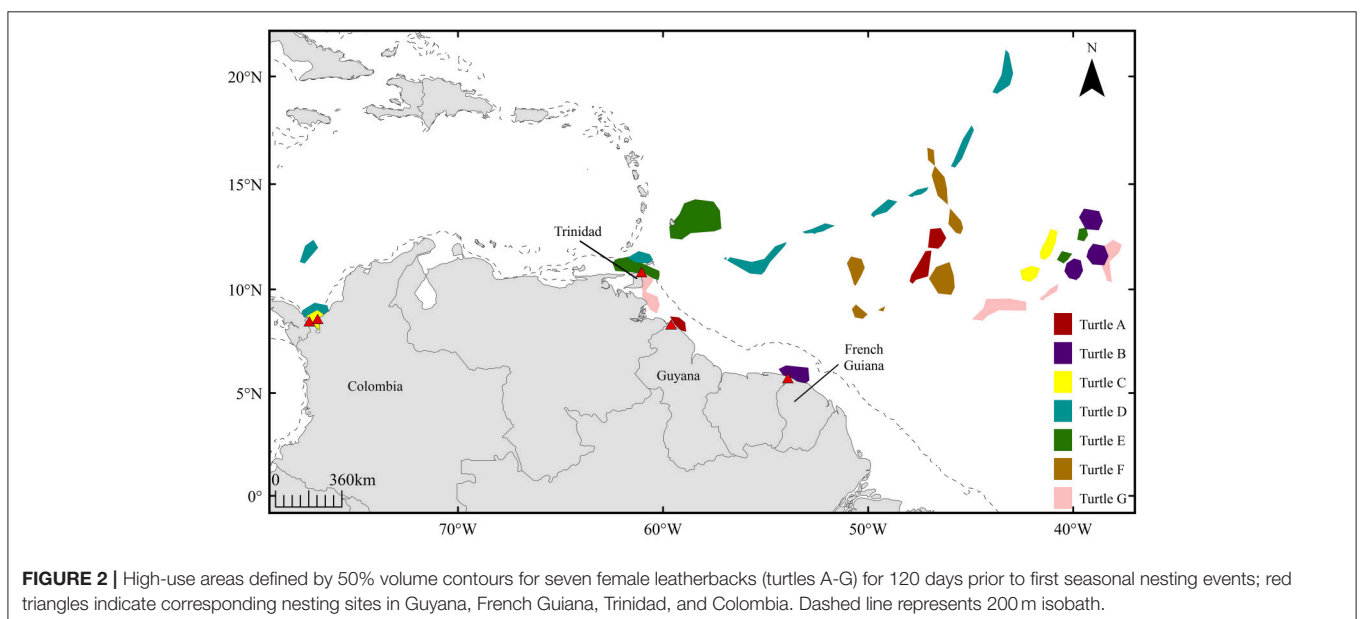
offshore high-use areas, tracking data from six females (turtles A–E, G) revealed secondary residency areas in coastal waters proximate to their respective nesting beaches, used immediately prior to their respective first nesting events.

Male Movements within the Pre-nesting Interval

Male satellite tracking data ($n = 12$) also revealed offshore high-use areas within the pre-nesting interval (Figure 3). Similar to patterns observed in female tracking data, 76.4% of total male residency fell within the 10 – 15° N latitudinal range. Overlap between mature male and female leatherback high-use areas (revealed from 50% volume contours) occurred in offshore areas spanning latitudes of 40 – 60° W, as well as in coastal waters off Trinidad and French Guiana (Figure 3). Within the 10 – 15° N latitudinal range, each female exhibited at least one high-use 50% volume contour that corresponded to male residency areas, representing a strong affinity for both males and females for this area over the course of multiple breeding seasons ($n = 13$).

Female and Male Movements within the Mating Period

Throughout the inferred mating period, six females (turtles A–E, G; turtle F not included due to transmission gaps) resided in coastal waters proximate to nesting beaches in Trinidad ($n = 2$), French Guiana ($n = 1$), Guyana ($n = 1$), and Colombia ($n = 2$) (Figure 4). Offshore residency throughout the mating period was observed in one female, turtle E, which occupied waters beyond the 200 m isobath prior to transiting and residing in coastal waters proximate to Trinidad. Each female was present in continental shelf waters (inshore of the 200 m isobath) in the days immediately preceding confirmed nesting events. Mature male tracking data were analyzed to corroborate probable mating areas. Three males exhibited offshore residency throughout the mating period (Figure 5, Figure S4); however, the majority of



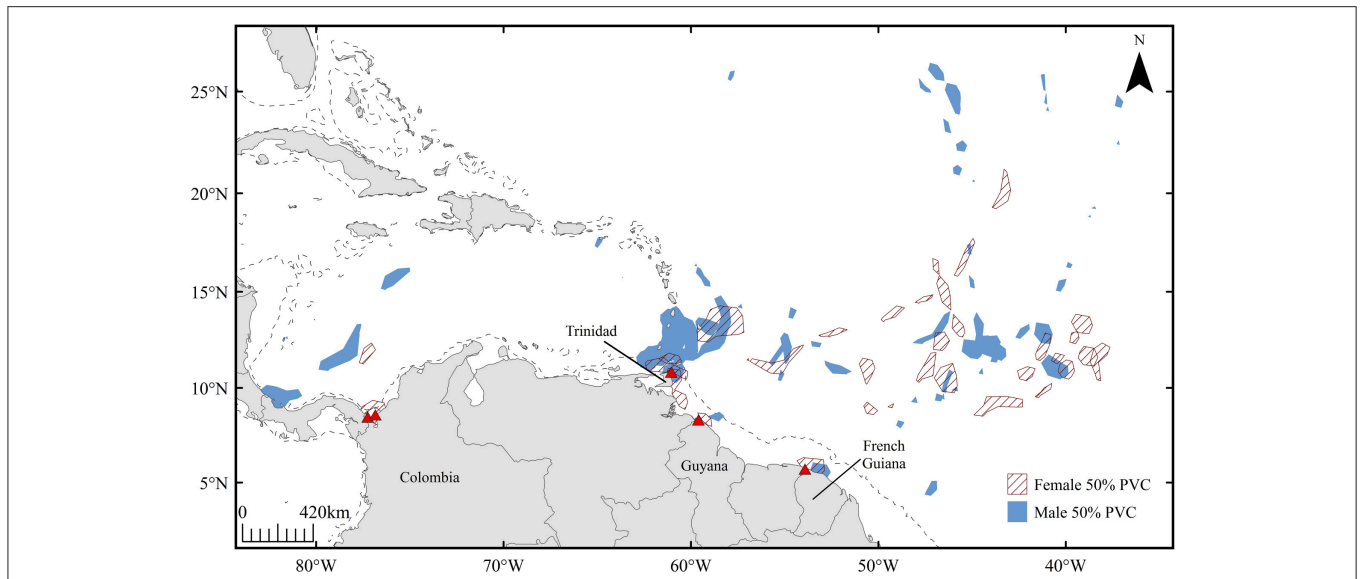


FIGURE 3 | High-use areas defined by 50% volume contours for mature male ($n = 12$, blue) and female ($n = 7$, red hatched) leatherbacks throughout the 120-day pre-nesting interval. Dashed line represents 200 m isobath.

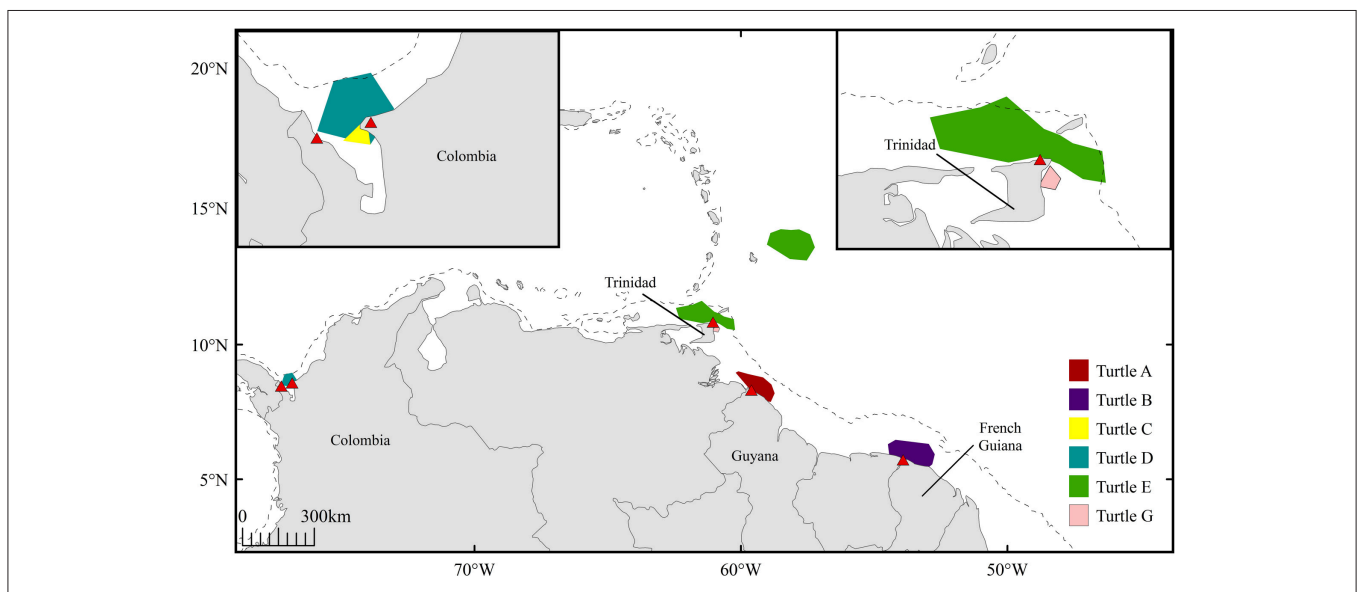


FIGURE 4 | High-use areas defined by 50% volume contours for 6 female leatherbacks (turtles A-E, G) during inferred mating period 45 days prior to confirmed nesting events; red triangles indicate corresponding nesting sites in Guyana ($n = 1$), French Guiana ($n = 1$), Trinidad ($n = 1$), and Colombia ($n = 2$). Dashed line represents 200 m isobath.

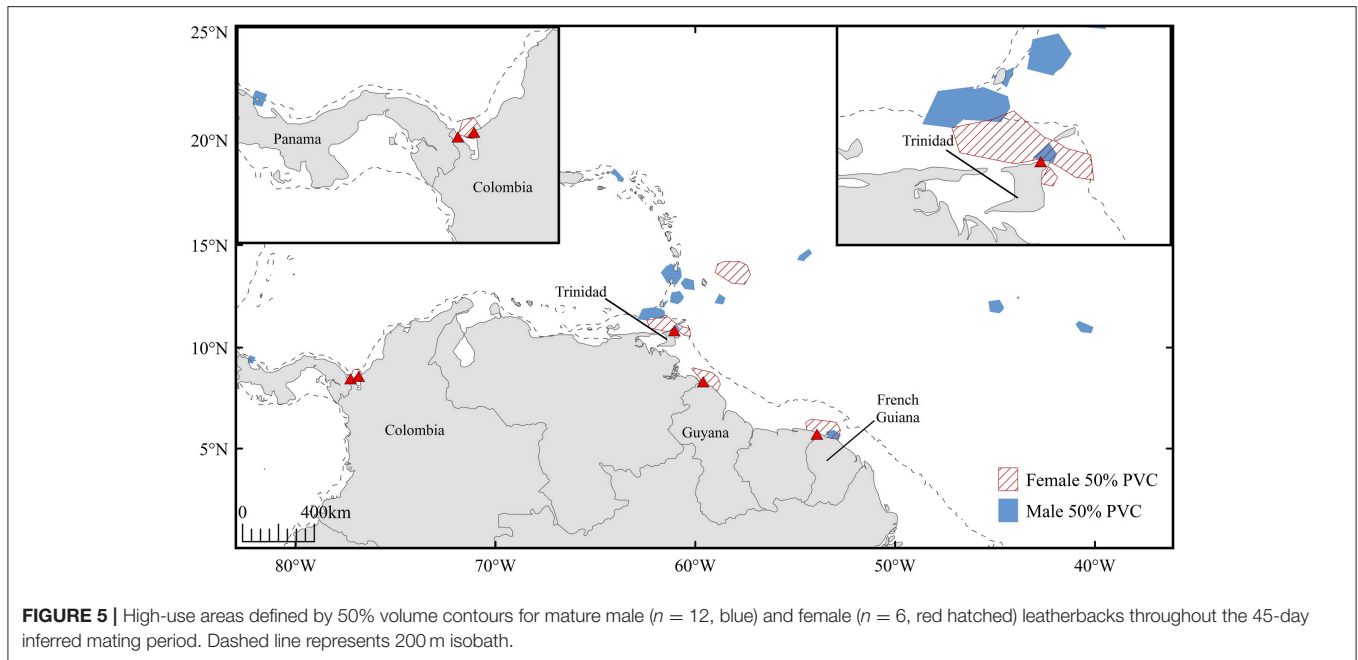
male high-use areas corresponded to coastal waters directly adjacent nesting beaches in Trinidad, French Guiana, St. Lucia, St. Vincent, Grenada, and Panama prior to the onset of their northward migration.

DISCUSSION

Offshore High-Use Areas

Satellite telemetry data from mature leatherbacks tagged in Canadian foraging habitat can be used to identify probable

mating areas and provide the first insights into the pre-nesting behavior of this species. Consistent with James et al. (2005a), results of the present spatial analyses showed that mature males spend extended time proximate to nesting beaches within the inferred mating interval. However, this study highlights an additional high-use area for both mature males and females prior to their arrival in coastal waters proximate to nesting beaches (Figure 3). All seven female leatherbacks and seven of 12 males we tracked frequented this offshore area prior to assuming directed movement toward nesting beaches. Residency



of reproductively-active females and males in this offshore area over multiple breeding seasons ($n = 13$) underscores the importance of these waters to the Northwest Atlantic leatherback turtle population.

The fundamental goals of long-distance migrations are often resource driven linked to exploitation of spatially limited food, mates, or shelter, all of which may result in temporary aggregation (Dingle and Drake, 2007). The foraging grounds of Atlantic Canada have been identified as critical habitat for mature leatherbacks (James et al., 2006), and both morphometric and physiological indicators have been used to determine that leatherbacks are capital breeders (James et al., 2005b; Davenport et al., 2011; Plot et al., 2013). Throughout the nesting season, leatherbacks rely on energy stores and become anorexic (Plot et al., 2013). The sub-Equatorial region spanning 5–15°N has previously been posited as an area of foraging success for post-nesting leatherbacks, corroborated by low leatherback travel rates and modeled annual zooplankton biomass (Fossette et al., 2010). It is possible that this offshore high-use area provides foraging opportunities for pre-nesting leatherbacks as well, enabling acquisition of valuable energy reserves prior to the start of the energetically-costly nesting season.

Inferred Mating Behavior

After exhibiting seasonal residency in offshore waters, presumably to exploit available prey, reproductively active male and female leatherbacks transited to coastal waters where they resided throughout the inferred mating period preceding first seasonal nesting events (Figure 5). While three males remained in offshore waters throughout this time interval, six females and nine males exhibited coastal residency during the inferred mating period. Our results corroborate the findings of James et al. (2005a), suggesting that mature leatherbacks

frequent coastal waters adjacent to nesting beaches in order to exploit mating opportunities prior to the nesting season.

Coastal mating areas have also been identified for various populations of other sea turtle species. Mature male and female green sea turtles have been documented in coastal waters of Hawaii (Dizon and Balazs, 1982), Costa Rica (Carr et al., 1978), and Australia (Booth and Peters, 1972) prior to the onset of seasonal nesting. Satellite tracking data of male green sea turtles near Ascension Island have revealed temporary residency in the coastal waters of high-density nesting beaches (Hays et al., 2001). Male green turtles have also been observed transiting through coastal waters of multiple high-density nesting sites prior to and during the nesting season, potentially mating in coastal waters of multiple rookeries in Cyprus and Turkey (Wright et al., 2012). Mating pairs of olive ridley sea turtles have been documented offshore from nesting beaches just prior to high-density arribada nesting events (Kalb et al., 1995; Jensen et al., 2006). Similarly, coastal mating has been confirmed in the Laganas Bay population of loggerhead sea turtles, where mating pairs have been directly observed in close proximity to rookeries over the course of multiple breeding seasons (Schofield et al., 2006). Our results suggest that leatherbacks behave similarly to other sea turtle species, with mature males and females residing in coastal waters prior to the onset of seasonal nesting.

Genetic analyses have previously identified reproductively isolated leatherback nesting assemblages within the Northwest Atlantic. Stewart et al. (2013) combined the use of passive identification tagging, satellite telemetry, and mitochondrial DNA analyses to identify the natal origins of 288 leatherbacks sampled off the coast of Atlantic Canada. Results indicated that individuals from the Guiana Shield population (encompassing nesting populations from Trinidad, Guyana and French Guiana)

were genetically distinguishable from individuals originating from Costa Rica, Panama, and Colombia. The present telemetry results, also representing turtles sampled in Canadian waters, support the findings of Stewart et al. (2013), as both Colombian-nesting females (turtles C and D) spent their presumed mating period in coastal waters of Colombia. In contrast, females nesting in Trinidad, French Guiana and Guyana (turtles A, B, and E) exhibited longer residency in the North Equatorial Current offshore area throughout their pre-nesting interval, followed by secondary residency periods in waters proximate to their respective nesting beaches throughout the mating period (Figure 4).

A metric of reproductive success among oviparous organisms is the quantity of eggs successfully fertilized (Parker, 1984). As such, reproductively successful males will have morphological or behavioral adaptations that increase their likelihood of fertilizing as many eggs as possible. For male leatherbacks, these adaptations may include the areas they select to intercept females prior to the nesting season. While all species of sea turtle exhibit polyandry (Kichler et al., 1999; Ireland et al., 2003; Jensen et al., 2006; Zbinden et al., 2007; Theissinger et al., 2009; Joseph and Shaw, 2011), multiple paternity in Atlantic leatherback clutches has been observed in low proportions (10–41.7%; Crim et al., 2002; Stewart and Dutton, 2011, 2014; Figgenger et al., 2016). Few instances of inter-nesting mating have been identified in leatherbacks (Figgenger et al., 2016), and successive nests laid by most females reveal consistent paternities throughout the nesting season, indicative of sperm storage from mating event(s) occurring prior to the nesting season (Crim et al., 2002; Stewart and Dutton, 2011; Figgenger et al., 2016). Therefore, male leatherbacks must intercept reproductive females upon arrival in low latitude waters prior to the onset of nesting, highlighting the importance of leatherback high-use areas prior to the nesting season.

Confirmation of leatherback mating interactions during the inter-nesting interval in nearshore waters off Pacific Costa Rica has been achieved through deployments of animal-borne video recorders on nesting turtles (Reina et al., 2005). However, logistical challenges have so far precluded application of this technology on turtles during the pre-nesting period; thus direct confirmation of the times, areas, and behaviors associated with mating remains elusive. With the rapid evolution of animal-borne imaging systems, visual confirmation of pre-nesting mating behavior may eventually be possible.

Fishing Interactions and Significance for Conservation

Identification of high-use areas for leatherbacks is critical to evaluating where this species may be vulnerable to fisheries interactions (James et al., 2005c; Fossette et al., 2014). Artisanal gill net fisheries have been identified as a serious threat to nesting leatherbacks in Trinidad and Tobago (Lee Lum, 2006) and Grenada (Georges et al., 2007), as well as in French Guiana and Suriname (Chevalier et al., 1999; Georges et al., 2007). One female leatherback in this study (turtle G) exhibited pre-nesting behavior

consistent with other females (turtles A-F), however, she was confirmed dead, entangled in coastal fishing gear, just prior to the date of her first predicted nesting event. This case highlights the threat coastal fishing gear presents to mature leatherbacks in waters proximate to nesting beaches prior to and during the nesting season.

While artisanal fisheries adjacent to many nesting beaches are an important source of mortality for the Northwest Atlantic leatherback population, this species may also be vulnerable in the additional high-use offshore area identified here, where mature turtles aggregate prior to their arrival in nearshore coastal waters.

Atlantic basin-wide analyses have identified areas where leatherbacks may be vulnerable to interactions with high seas fisheries (Hays et al., 2004; Lewison et al., 2004; Wallace et al., 2010; Fossette et al., 2014). However, where satellite telemetry data has been incorporated into such analyses, mainly post-nesting movements have been considered, potentially missing key areas of reproductive leatherback aggregation including the pre-nesting movements described here. A detailed bycatch analysis quantifying leatherback-fishery interactions and subsequent mortality rates in offshore high-use areas is required to better evaluate the potential impact on the Northwest Atlantic population at this stage of their migratory cycle.

AUTHOR CONTRIBUTIONS

EPB led the analysis and writing of the manuscript. MCJ conceived the study, conducted fieldwork, collected data, and contributed to the analysis and writing of the manuscript.

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SUPPLEMENTARY MATERIAL

The Supplementary Material for this article can be found online at: <http://journal.frontiersin.org/article/10.3389/fmars.2017.00223/full#supplementary-material>

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