ADVANCES IN UNDERSTANDING SEA TURTLE USE OF THE GULF OF MEXICO

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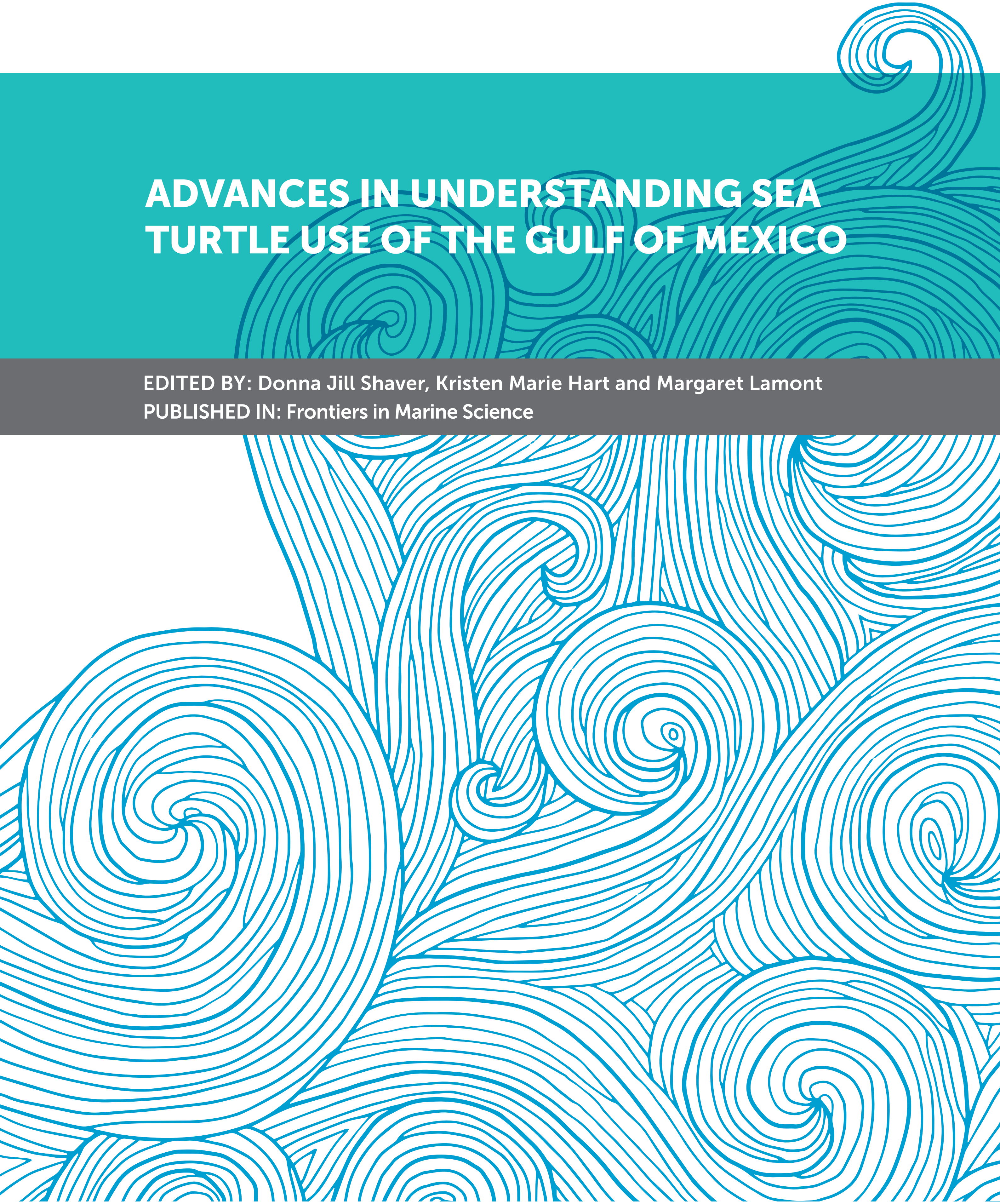

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ADVANCES IN UNDERSTANDING SEA TURTLE USE OF THE GULF OF MEXICO

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EDITORIAL
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Editorial: Advances in Understanding Sea Turtle Use of the Gulf of Mexico

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Editorial on the Research Topic

Advances in Understanding Sea Turtle Use of the Gulf of Mexico

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Six threatened and endangered sea turtle species use the Gulf of Mexico: Kemp's ridley (*Lepidochelys kempii*), green (*Chelonia mydas*), loggerhead (*Caretta caretta*), hawksbill (*Eretmochelys imbricata*), leatherback (*Dermochelys coriacea*), and olive ridley (*Lepidochelys olivacea*; Shaver, 1994; Valverde and Holzwart, 2017; USFWS, 2019; Frandsen et al., 2021). For this Research Topic, our goal was to increase knowledge of sea turtles residing in, or migrating through, the Gulf of Mexico. Though multiple threats to sea turtles exist in the Gulf of Mexico, less is known in this ocean basin in comparison to other locations. Further, most literature on sea turtles in the Gulf of Mexico has focused on the northern rather than the western and southern Gulf of Mexico (Valverde and Holzwart, 2017). In this Research Topic, contributing authors fill knowledge gaps on the behavior, ecology, habitat use, and population demographics of sea turtles in the Gulf of Mexico, and the resulting 16 papers significantly contribute to four subtopics:

1. Movements and habitat use.
2. Foraging ecology and food webs.
3. Growth, genetic stock, and population trends.
4. Conservation and management.

MOVEMENTS AND HABITAT USE

Sea turtles travel long distances using magnetic, solar, and local cues (Southwood and Avens, 2010). Satellite and GPS tags have enabled researchers to monitor migrations from nesting to foraging grounds and identify inter-nesting habitats (Block et al., 2011; Shaver et al., 2013; Shaver et al., 2016; Shaver et al., 2017a). Research has been weighted towards females from nesting beaches, and knowledge gaps exist regarding male turtle reproductive behavior, habitat use, movements, and demographic parameters due to challenges in accessing individuals in neritic and oceanic environments (Hatase et al., 2002; Plotkin, 2003; Hamann et al., 2010; Schofield et al., 2017). Contributing researchers answered lingering questions on male and female movements in the Gulf of Mexico.

Hart et al. showed that Florida's Big Bend region, a neritic northern Gulf of Mexico marine hotspot, provides year-round foraging habitat for migrating post-nesting loggerhead turtles. Thus, nearshore habitats in the northern Gulf of Mexico should be considered when discussing critical habitat designations for sea turtles in the southeastern USA. Lamont and Johnson compared multi-species aggregations in neritic northern Gulf of Mexico habitats, documenting loggerhead, and larger, turtles in coastal bay seagrass meadows, and green, and smaller, turtles in nearshore sand-bottom habitats thought to be more optimal for immature Kemp's ridley and loggerhead than green turtles. Siegfried et al. used non-invasive, stereo-video camera surveys to capture *in situ* data on species and size composition at nearshore northern Gulf of Mexico artificial habitats including reefs, jetties, and piers. From those data, they showed that species and habitat were the best predictors of size distribution.

Iverson et al. discovered high-use migration corridors for loggerhead turtles in the Gulf of Mexico: one in the eastern Gulf of Mexico and one through the Florida Straits to the Bahamas. Migration paths overlapped with anthropogenic threats including commercial line fishing (high threat), shrimp trawling (persistent threat), and shipping density (most problematic for migrating loggerhead turtles). Sloan et al. documented high-use green turtle inter-nesting and foraging areas in the Gulf of Mexico, Marquesas Keys, Florida Bay, and near the Everglades, for females tracked from nesting beaches in Florida. Sasso et al. identified the northern Gulf of Mexico as a high-use foraging area for adult leatherback turtles, and showed that the Yucatan Channel is an important migration route for Caribbean nesting leatherback turtles.

Gredzens and Shaver found most post-nesting Kemp's ridley turtles migrated to northern Gulf of Mexico foraging grounds and showed high fidelity to these areas and the migratory corridors used to travel there. This work reinforced earlier findings of Shaver et al. (2013) and showed that threats in the northern Gulf of Mexico may have a disproportionate impact on the adult population. Finally, Cuevas et al. provided a new analysis of male sea turtle satellite tracks in the southern Gulf of Mexico. Male sea turtles in that region largely resided in neritic habitats near mating areas, conducted very short migrations, and were found with post-nesting females.

FORAGING ECOLOGY

Multiple factors affect sea turtle foraging and prey availability in the Gulf of Mexico, including climate change (Sanchez-Rubio et al., 2011), hurricanes (Engle et al., 2009), fisheries (Robinson et al., 2015), hypoxic zones (Craig et al., 2001), oil spills (Wallace et al., 2017), and red tides (Dupont et al., 2010). Diet composition across species, life stages, and breeding populations differs due to geographic disparity of resources and may lead to somatic growth rate variation among these subsets (Bjorndal et al., 2003; Piovano et al., 2011). Conventional gut contents analyses are used to investigate temporal, seasonal, and ontogenetic diet trends, and improve nutrition interpretation (Parker et al., 2005; Hatase et al., 2006; Revelles et al., 2007; Casale et al., 2008; Hoarau et al., 2014; Behera et al., 2015). Contributors to this topic used novel methods and/or long-term datasets to better understand sea turtle trophic ecology in the Gulf of Mexico.

Pairing skeletal and isotopic analyses, Ramirez et al. reported strong regional variation in Kemp's ridley diet composition estimates in the Gulf of Mexico and Atlantic. Though limited by data gaps, Ramirez et al. provided a quantitative assessment of the connection between trophic ecology and somatic growth, presenting a new method for investigating drivers of somatic growth variation. Howell and Shaver presented a comprehensive assessment of green turtle trophic ecology in the western Gulf of Mexico, showing they exhibited foraging plasticity and that diet and habitat shifted between size classes.

POPULATION TRENDS

Contributing researchers provided insights on the status of several species across multiple life stages in the Gulf of Mexico. Sea turtle populations in the Gulf of Mexico have fluctuated in response to environmental and anthropogenic influences. The green turtle, once abundant in the Gulf of Mexico, was commercially exploited and overharvested in Texas in the mid-1800s, leading to population decline and sparse nesting along the western Gulf of Mexico (Hildebrand, 1981; Doughty, 1984; Shaver, 1989; Witzell, 1994a; Witzell, 1994b). Recent increases in stranding, including cold stunning, and nesting of green turtles indicate species recovery along the Gulf of Mexico (Shaver et al., 2017b). The Kemp's ridley, nearly decimated in the late 1900s, survived due to bi-national collaboration between Mexico and USA and intensive conservation strategies (Marquez et al., 2005; Bevan et al., 2016). Since 2010, exponential population growth abruptly ceased, and has since fluctuated, indicating that intensive management is still required to recover the population (NMFS, 2015; Caillouet et al., 2018).

Experimental at-sea work by Cook et al. advanced our understanding of sea turtle stranding patterns in the Gulf of Mexico. They used wooden effigy drifters and sea turtle cadavers to investigate seasonal stranding variations in the northern Gulf of Mexico. Season and distance from shore were the two greatest influences of if, and where, objects beached and the likelihood of carcass scavenging. Public reporting underestimated the actual frequency of strandings on mainland beaches based on tracked experimental carcasses.

Shaver et al. highlighted the importance of federally protected lands as green turtle nesting habitat in the western Gulf of Mexico and showed that nesting in Texas has increased since 2010, but at a lower rate than at other Gulf of Mexico beaches. Continued research, monitoring, and protection of females and nests could aid recovery efforts and help determine whether those turtles should be considered an independent management unit separate from the nesting stock in Mexico. DuBois et al. used an ocean circulation model to explore whether hurricane events could explain differences in transport distance among young-of-the-year Kemp's ridley cohorts dispersing from primary nesting areas in the western Gulf of Mexico. Shorter dispersal distances and less variance within the first months of dispersal corresponded with high hurricane activity, indicating that hurricane frequency and intensity may influence survivorship and growth rates of the Kemp's ridley.

CONSERVATION AND MANAGEMENT

Multiple threats to sea turtles exist in the Gulf of Mexico including artificial light pollution, marine debris entanglement, incidental bycatch, habitat destruction, predation, and vessel strike (Cannon et al., 1994; Rudloe and Rudloe, 2005; Witherington et al., 2014; Purvin et al., 2020; Shaver et al., 2020a; Shaver et al., 2020b; Shaver et al., 2020c; Shaver et al., 2021; Stacy et al., 2021). Contributing authors highlighted the effect of these persistent anthropogenic and environmental threats on sea turtle abundance in the Gulf of Mexico. Kemp's ridley and loggerhead foraging grounds overlap with eight spatially explicit anthropogenic threats Hart et al. Climate change, leading to increased storm frequency and severity, threatens resiliency of multiple sea turtle species (Goldenberg et al., 2001; Knutson et al., 2010).

Cook et al. developed a survey to investigate fishing practices and sea turtle interactions at northern Gulf of Mexico piers. The resulting increase in reported incidental captures indicated that outreach was an effective means to increase public awareness and reporting. Cook et al. recommended those efforts be focused on areas where anglers are likely to interact with sea turtles. Stanley et al. assessed the impact of light pollution on loggerhead nest building and hatchling orientation along the northern Gulf of Mexico. Stanley et al. found that artificial light was partially responsible for the high frequency of hatchling misorientation and that lunar fraction and altitude had strong moderating influences on hatchling misorientation rates. Further, they found nest relocation was an effective management tool to improve hatching success and reduce misorientation.

Using lidar data, generalized linear models, and random forest models, Culver et al. determined that the presence of Kemp's ridley nests in the western Gulf of Mexico were influenced primarily by average beach slope, distance from shoreline, elevation, and maximum dune slope. Those findings indicate that females avoided nesting in areas with extreme beach characteristic values. The hotspot of Kemp's ridley nesting in Texas occurs along the central section of North Padre Island, in narrow beach areas prone to sea level rise and tidal inundation.

AUTHOR CONTRIBUTIONS

All authors listed have made a substantial, direct and intellectual contribution to the work, and approved it for publication.

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Using Lidar Data to Assess the Relationship Between Beach Geomorphology and Kemp's Ridley (*Lepidochelys kempii*) Nest Site Selection Along Padre Island, TX, United States

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The Kemp's ridley sea turtle (*Lepidochelys kempii)* is the most endangered sea turtle species in the world, largely due to the limited geographic range of its nesting habitat. There has been limited research regarding the connection between beach geomorphology and Kemp's ridley nesting patterns, but studies concerning other sea turtle species suggest that certain beach geomorphology variables, such as beach slope and width, influence nest site selection. This research attempts to address the literature gap by quantifying the terrestrial habitat variability of the Kemp's ridley and investigating the connection between beach geomorphology characteristics and Kemp's ridley nesting preferences on Padre Island, TX, United States. Geomorphology characteristics, such as beach width and slope, were extracted from lidar-derived digital elevation models and associated with Kemp's nest coordinates and pseudo-absence points randomly created within the study area. Generalized linear models and random forest models were used to assess the significance of variables for nesting preferences. Kemp's ridley nest presence was successfully modeled using beach geomorphology characteristics, and elevation, distance from shoreline, maximum dune slope, and average beach slope were the most important variables in the models. Kemp's ridleys exhibit a preference for a limited range of the study area and avoid nesting on beaches with beach characteristics of extreme values. The results of this study include new information regarding Kemp's ridley terrestrial habitat and nesting preferences that have many applications for species conservation and management.

Keywords: sea turtle, lidar data, habitat model, coastal, beach geomorphology

INTRODUCTION

The range of the Kemp's ridley sea turtle encompasses the Gulf of Mexico and extends into the northwestern Atlantic Ocean (Putman et al., 2013). Most nesting occurs on beaches along the west-central Gulf of Mexico, with the greatest nesting numbers near Rancho Nuevo, Tamaulipas, Mexico (Shaver and Rubio, 2008; Caillouet et al., 2015; Shaver and Caillouet, 2015). The Mexican government began protecting the nests in 1966 because the population was rapidly declining (Caillouet et al., 2015; Shaver and Caillouet, 2015). By 1977, extinction of the species was imminent, so a bi-national, multi-agency imprinting and head-start project was implemented in order to increase Kemp's ridley nesting at Padre Island National Seashore (PAIS), known as the PAIS Restoration Program (Shaver and Rubio, 2008; Shaver and Caillouet, 2015). The overall goal of this project was to create a secondary nesting colony in a location that was both protected and within the native range of the species (Shaver and Rubio, 2008). Due to these and other efforts, both Rancho Nuevo and Padre Island National Seashore serve as main nesting sites for the Kemp's ridley sea turtle today, in Mexico and the United States, respectively (Caillouet et al., 2015). Nesting also occurs in Veracruz, Mexico and occasionally in Florida, Alabama, and the Atlantic coast in the United States (National Marine Fisheries Service and U. S. Fish and Wildlife Service, 2015).

A female sea turtle responds to various signals, both biotic and abiotic, to select the most successful site for her eggs, making nest site selection non-random (Weishampel et al., 2006; Zavaleta-Lizárraga and Morales-Mávil, 2013). According to Wood and Bjorndal (2000), sea turtle nest site selection can be divided into three stages: beach selection, emergence of the female, and nest placement. Beach selection and emergence probably depend on offshore cues and beach characteristics, such as slope and dune profile (Wood and Bjorndal, 2000). A number of selective forces drive nest placement both seaward toward the shoreline and landward away from it; nests close to the sea have a higher probability of inundation and egg loss due to erosion while nests further from the sea are more likely to result in predation and hatchling disorientation (Wood and Bjorndal, 2000; Santos et al., 2006).

The biophysical features of beaches that affect nest site selection have long been thoroughly studied, but morphological characteristics influencing nest site selection have not been researched to the same extent (Horrocks and Scott, 1991; Yamamoto et al., 2012). There has been little to no research regarding the connection between beach geomorphology and Kemp's ridley nesting site selection, but studies regarding other species of sea turtles suggest that beach characteristics may be important factors in determining sea turtle nesting site preferences (Santos et al., 2006; Yamamoto et al., 2012).

While it is well-known that females prefer to nest on beaches with fine grain sands because it is more difficult to dig egg chambers in coarse, dry sand, Mortimer (1982) predicted that slope and offshore configuration are potentially more important than sand grain properties in nesting preferences, but their relative importance was not quantified (Mortimer, 1982, 1990). One study found that segments of beaches with higher beach face slopes and narrower widths had higher nest densities of loggerhead turtles than beaches with lower slopes and wider widths (Provancha and Ehrhart, 1987). Research regarding hawksbill turtles found that nest elevation above sea level was positively related to hatching success. Furthermore, this study found that hawksbills nested further from the high tide line on beaches with less steep slopes, suggesting that they prefer to nest at a certain mean elevation above sea level (Horrocks and Scott, 1991). Similarly, Wood and Bjorndal (2000) found that out of the factors slope, temperature, moisture, and salinity, slope had the largest impact on nest site selection of loggerheads, likely because it is correlated with nest elevation. A study in Mexico discovered that green sea turtles prefer beaches with steeper slopes, specifically a steeper berm slope, while hawksbill turtles nest site selection extended to a wider range of beach morphology characteristics (Cuevas et al., 2010). A similar study regarding nest site selection by the green sea turtle in Mexico found that the most utilized nest sites were characterized by beaches at least 1,300 m long with gentle to medium slopes (Zavaleta-Lizárraga and Morales-Mávil, 2013).

Most recently, Dunkin et al. (2016) developed a model that accurately predicted loggerhead nesting habitat suitability in Florida using elevation, beach slope, beach width, and dune peak as predictors. Consistent with the findings of several of the aforementioned studies, they found that elevation was the most influential factor for nesting preferences (Dunkin et al., 2016). Similarly, Yamamoto et al. (2012) successfully modeled nest density for three different sea turtle species using a limited number of geomorphology variables. This study found that each sea turtle species exhibited a tolerance for beaches with a wide range of measured geomorphology variables but would not nest on beaches outside of this tolerance (Yamamoto et al., 2012).

The specific preference of nesting beach characteristics varies between species, possibly due to the difference in size, weight, and behavior between each species. This makes the specific preference of nesting beach characteristics for the Kemp's ridley difficult to quantify. Considering the importance that slope and elevation have in regards to nest site selection of various species of sea turtles, it is possible that they are important aspects of Kemp's ridley nesting preference. Additionally, other geomorphology features, such as dune height, rugosity, aspect, beach width, distance from shoreline, and offshore configuration, might also be important aspects of nesting preference for the Kemp's ridley. Marquez-M (1994) notes that on beaches in Rancho Nuevo, Mexico, the Kemp's ridley usually nests beyond the high tide line in front of the first dune, on the windward slope of the dune or on top of the dune. This report describes the distribution of nests at relative positions along a beach profile, but it fails to quantify the characteristics of each position, such as elevation or distance from shoreline, and to assess alongshore nesting preferences in relation to beach geomorphology characteristics, such as beach slope or width (Marquez-M, 1994).

The purpose of this study is to: (1) identify the terrestrial habitat variability of the Kemp's ridley sea turtle on the beaches of North and South Padre Islands, Texas; and (2) quantify the influence of beach geomorphology characteristics on Kemp's ridley nest site selection.

MATERIALS AND METHODS

Study Area

The study area for this research is the beaches of the Padre Island National Seashore, located on North Padre Island, and South Padre Island, TX, United States (**Figure 1**). North and South Padre Islands are barrier islands that run parallel to the coastline, separated from the mainland by the shallow estuaries of the Upper and Lower Laguna Madre, respectively (Judd et al., 1977; Weise and White, 2007). Collectively, North and South Padre Islands extend 182 km from Corpus Christi to Brazos-Santiago Pass, varying from 450 m to 4.8 km in width (Judd et al., 1977). Port Mansfield Channel is a human-made and jettied channel that separates South Padre Island from North Padre Island (Judd et al., 1977). Because Kemp's ridleys have been observed nesting from the water line to behind the foredune crest, the study area includes the area of beach extending from the wet/dry line to the landward dune boundary.

Beaches in the northern and southern sections of the study area are broad and characterized by large foredunes and grasslands (Davis, 1977; Weise and White, 2007). Washover channels and a greater extent of development also characterize the southern section (Weise and White, 2007). The shape of the Texas Gulf shoreline causes longshore currents to converge near the central section of the study area, resulting in the accumulation of sediment and shell fragments (Davis, 1977). Thereby, the beaches in this region are steeper and the mean sediment size is larger in comparison to the other regions of the study area, resembling the geomorphology of the beaches of Rancho Nuevo, Mexico (Watson, 1971; Carranza-Edwards et al., 2004; Weise and White, 2007).

Dataset

The coordinates of observed Kemp's ridley nests within the study area for the years 2009–2012 were obtained from Dr. Donna J. Shaver, the coordinator of the Sea Turtle Stranding and Salvage Network in Texas and Chief of Sea Turtle Science and Recovery at Padre Island National Seashore (**Supplementary Table 1**). The coordinates were imported into ArcGIS as XY data tables and were subsequently exported as shapefiles and projected to the coordinate system of UTM Zone 14 N. Of the total 573 nest coordinates, 8 points (1.39%) were determined to be outliers and were excluded from the study. These coordinates, comprised of three points from 2012, four points from 2011, and 1 point from 2010, were located outside of the study area, likely due to an instrumentation error when the nest coordinates were recorded.

Pseudo-absence points, or background data, establishes the characteristics of the study area while the presence data provides the attributes of the area in which a species is more likely to be present (Phillips et al., 2009). Barbet-Massin et al. (2012) found that model accuracy increased until an asymptote when the ratio of pseudo-absence to presence points reached 10:1 for generalized linear models and random forests, the statistical models used in this study. Therefore, psuedo-absence points were created randomly within the study area at a 10:1 ratio to the presence data.

In 2009, the US Army Corps of Engineers (USACE) Joint Airborne Lidar Bathymetry Technical Center of Expertise (JALBTCX) collected lidar data of the South Texas Gulf of Mexico shoreline for the West Texas Aerial Survey 2009 project. The survey was conducted between February and April, just before Kemp's ridley nesting season. Additionally, the Bureau of Economic Geology (BEG), the Center for Space Research, and Texas A&M-Corpus Christi conducted three airborne lidar surveys of the Texas Gulf of Mexico shoreline every year from 2010 through 2012. The 2010 and 2011 surveys were conducted in April at the beginning of Kemp's ridley nesting season while the 2012 survey was conducted in February, a few months prior to the start of nesting season (Paine et al., 2013). The las files for each dataset were procured from the NOAA Coastal Services Center's Digital Coast website with NAD83 horizontal and NAVD88 vertical datums. Using NOAA/NOS's VDatum, the USACE data was converted from Geoid12A to Geoid99, the same geoid as the 2010–2012 BEG lidar data. The BEG lidar data was characterized by UTM Zone 14 N projected coordinate system. Consequently, LAStools was used to project the 2009 LAS files into UTM Zone 14 N.

The last return points were used for this project in order to reduce the probability of land cover biasing topography (Starek Michael et al., 2012). The point density of each dataset was evaluated in order to determine the ideal resolution for the digital elevation models (DEMs) and outliers were located by identifying data points that exceed a height or slope difference relative to neighboring measurements within 30 m. Based on the point density of the datasets, a pixel size of 1 m was determined to be sufficient. Each LAS file was gridded using an inverse distance weighted (IDW) operation with a search radius of 2.5 m and a maximum of 3 points within each search radius. The subsequent rasters were combined to create consistent surfaces for each year.

Feature Extraction

Shoreline, potential line of vegetation, and landward dune boundaries were mapped to delineate the beach and the foredune complex within the study area for geomorphology characteristic extraction. Through the analysis of lidar data and beach profiles, Gibeaut et al. (2002) and Gibeaut and Caudle (2009) found that the wet/dry boundary typically occurs at 0.6 m above mean sea level on the Texas Gulf Coast. This elevation was mapped as the shoreline for each year. The potential vegetation line is the lowest elevation dune vegetation may thrive along the Texas Gulf shore and is 1.2 m above mean sea level. The wet/dry line is the seaward boundary of the beach and potential vegetation line is the landward boundary of the beach and seaward boundary of the foredune. The ArcGIS Contour List tool was used to map the contours, and the contours were smoothed using a 5 m tolerance with the Polynomial Approximation with Exponential Kernel (PAEK) method of the Smooth Line tool in ArcGIS. The landward dune boundaries for the 2010–2012 data were mapped by the Coastal and Marine Geospatial Lab at Harte Research Institute,

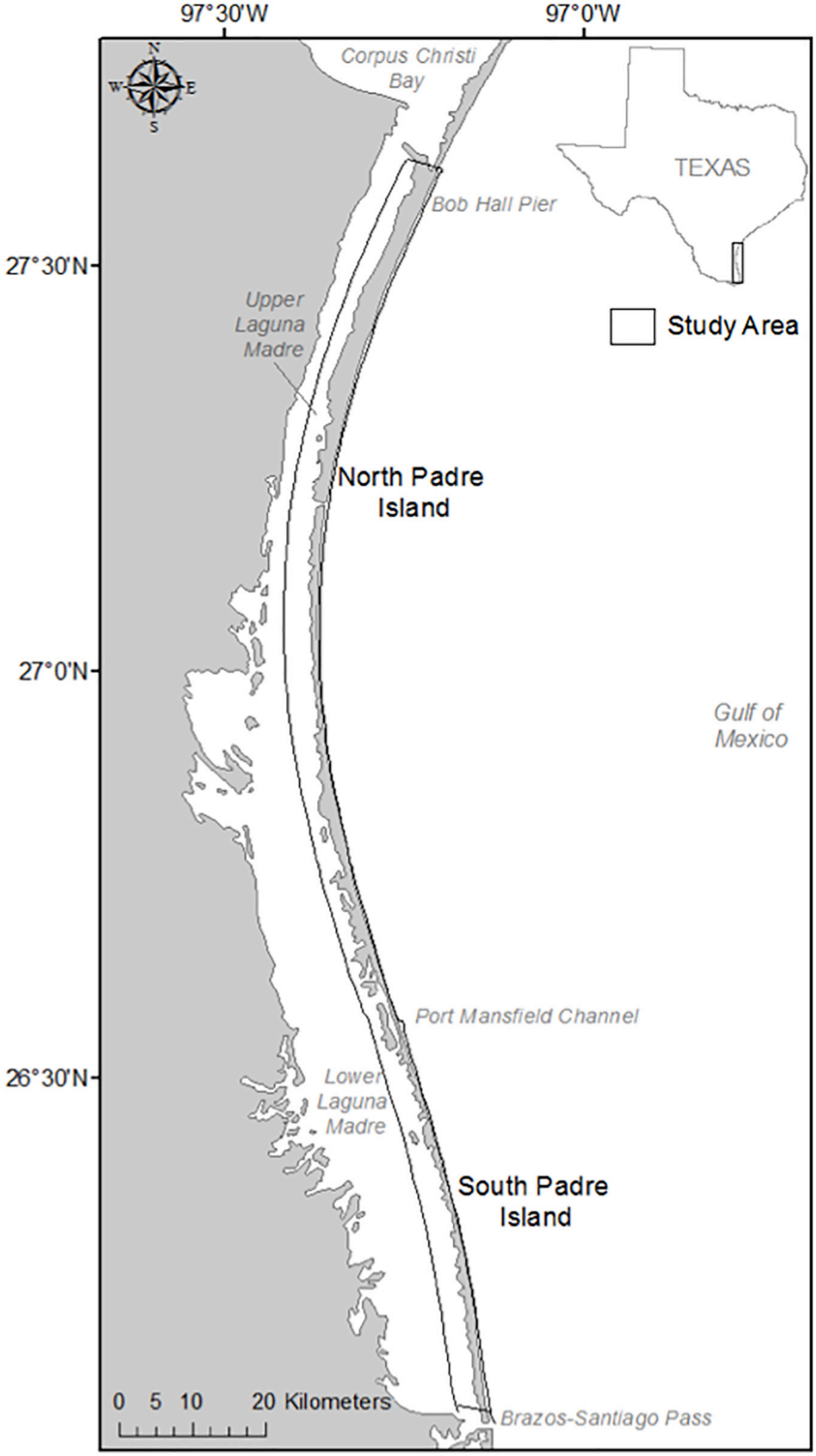

FIGURE 1 | The study area of the research, the beaches of North and South Padre Islands, TX, United States.

as outlined in Paine et al. (2013). The same systematic qualitative criteria used to generate the landward dune boundaries for 2010–2012 was used to create a landward dune boundary for 2009.

Using the ET Geowizard Extension of ArcGIS, cross-shore profiles were created at each presence and pseudo-absence point, which were then delineated by beach, or the area between the shoreline and PVL, and dune system, or the area between the PVL and landward dune boundary. Points were created every 1 m along the profiles, and elevation values from the DEMs for each year were extracted to each. The points were converted back to line segments, resulting in 3D cross-shore profiles, from which various characteristics were derived. The resulting geomorphology characteristics include beach slope, beach width, dune peak height, dune slope uphill, and dune width (**Table 1**).

Using the ET Geowizard Extension of ArcGIS, the distance of each point from the shoreline was calculated by generating and measuring a line segment that extends from each point to the shoreline. Additionally, aspect, and rugosity rasters were created for each year from the DEMs. Values from the aspect, slope, and elevation ratsters were attributed to each coordinate for each year.

Analysis

To better understand the dynamics of the system, preliminary statistical analyses were conducted. The Optimized Hot Spot Analysis tool in ArcGIS, which identifies statistically significant spatial clusters of high values and low values, was used on each year of nest coordinates, as well as all years combined. This tool aggregates incident data, identifies an appropriate scale of analysis, and corrects for multiple testing and spatial dependence. The Getis_Ord Gi* statistic is calculated for each feature in the dataset, and the resulting high and low z-scores are indicative of hot spots and cold spots, respectively. The resulting maps identified statistically significant hot spots and cold spots of nests and classified the general spatial trends in nesting.

TABLE 1 | Description of each geomorphology characteristic extracted to each presence and pseudo-absence point.

Variable	Description
Beach width	Distance (m) between the potential vegetation line and the shoreline
Beach slope	Average slope (degrees) of the profile from the shoreline to the potential line of vegetation; maximum, minimum, and average values
Dune height	Highest point (m) between the landward dune boundary and the potential line of vegetation
Dune width	Distance (m) between the potential vegetation line and the landward dune boundary
Dune slope	Average upward slope (degrees) going from the potential line of vegetation and the landward dune boundary; maximum, minimum, and average values
Distance from shoreline	Distance (m) from the coordinate to the shoreline (negative value on the seaward side of the shoreline)
Rugosity	Surface roughness or the standard deviation of elevation
Aspect	Compass direction that a slope faces
Elevation	Elevation (m) above NAVD88

Boxplots were created in R that compare the median and interquartile range of each geomorphology characteristic differentiated by nest presence and pseudo-absence. These boxplots served as tools that can be used to recognize if the Kemp's ridleys are nesting within a subset of the available habitat. Additionally, a correlation matrix composed of pairwise scatterplots and associated Pearson correlation coefficients was calculated in R to assess the collinearity between the geomorphology characteristics and to preliminarily pinpoint any geomorphology characteristics with a relationship to nest presence. Collinearity between variables can skew generalized linear models, so this information was taken into consideration during model development and selection.

In addition, the data was analyzed using statistical regression models to both quantify the relationship between beach geomorphology characteristics and Kemp's ridley nest site selection and assess the capacity of geomorphology characteristics in predicting nest presence. A generalized linear model was selected as a traditional modeling technique because it has the capacity of modeling response variables with non-normal distributions, such as discrete, binary data (Gilmour et al., 1985; Zuur et al., 2009). This modeling technique was expanded upon by the use of a machine-learning technique because recent studies have suggested that machine-learning methods may perform better than traditional algorithms, especially when the dataset includes a limited number of samples over an extensive range (Breiman, 2001; Elith et al., 2006; Mi et al., 2017).

Generalized Linear Models

Because the response variable is binary, binomial generalized linear models for all years of data combined were developed in R, with nest presence/absence as the dependent variable and the geomorphology characteristics as the explanatory variables. Models utilizing all explanatory variables were dredged in order to pinpoint the variables that comprise the relatively best model options. The best models options were then generated and evaluated using McFadden's pseudo R-squared value, K-fold cross-validation prediction error, and a boxplot of the predictions differentiated by the observation value. McFadden's pseudo R-squared value is defined as

$$R^2_{McFadden} = 1 - \frac{\log(L_c)}{\log(L_{null})}$$

where L_c denotes the likelihood value from the current fitted model and L_{null} denotes the corresponding value for the null model (McFadden, 1974). In K-fold cross-validation, the observations are split into K partitions, the model is trained on K-1 partitions, and the test error is predicted on the left out partition k (Zuur et al., 2009). This process is repeated for each partition and the result is the average test error of all partitions (Zuur et al., 2009).

Because the sampling type and ratio of the pseudo-absence data can greatly affect the model, these components were taken into consideration when developing the model (VanDerWal et al., 2009; Barbet-Massin et al., 2012). As mentioned in Section "Dataset," pseudo-absence points were generated at a ratio of 10:1 to the presence points. However, using this ratio as an input into the model would likely cause the model to be biased to predict the pseudo-absence points. Therefore, models were developed using 10:1, 5:1, 2:1, and equal ratios of pseudo-absence points to presence points in order to gauge the effect of variations in ratio pseudo-absence points on model accuracy (VanDerWal et al., 2009; Barbet-Massin et al., 2012). The models generated using a 5:1, 2:1, and equal ratios of pseudo-absence to presence points were re-constructed 100 times, resampling the pseudo-absence points each iteration, in order to fully take into consideration the distribution of the pseudo-absence points. McFadden's pseudo R-squared value, K-fold cross-validation prediction error, boxplots of the predictions differentiated by observed values, and the results of confusion matrices for each model were compared in order to evaluate model performance.

The analysis of spatial data is often complicated by spatial autocorrelation, a phenomenon that occurs when the values of variables sampled at nearby locations are not independent of each other (Dormann et al., 2007; Crase et al., 2014). In order to determine if there was spatial autocorrelation in the presence/absence data, a spline correlogram of the raw data was created in R (Zuur et al., 2009; Crase et al., 2014). A spline correlogram is a graphical representation of Moran's I for different distance classes that is smoothed using a spline function. A spline correlogram of the Pearson residuals of the model was also created in R to determine if any spatial autocorrelation was explained by the explanatory variables (Zuur et al., 2009).

Random Forest

A random forest model was determined to be a suitable machine learning methodology option due to the size of the dataset and the binary nature of the predictant (Breiman, 2001; Svetnik et al., 2003; Elith et al., 2006; Mi et al., 2017). Specifically, a random forest was preferred over other machine-learning techniques, such as a neural network, because they are less computationally expensive, do no require an extensive amount of data, are less prone to overfitting and provide information on the importance of each predictor (Breiman, 2001).

Random forests are machine learning classification and regression tools composed of a combination of trees created by using bootstrap samples of training data and random feature selection in tree induction (Breiman, 2001; Svetnik et al., 2003). A random forest model was applied to the all of the years of data combined, with the predictant as the presence or pseudo-absence of a nest site and the predictors as the geomorphology characteristics. The relative importance of each predictor in the model was quantified, providing even more insight into the relationships within the system.

As previously mentioned in regards to the development of the generalized linear models, the sampling type and ratio of the pseudo-absence data can greatly affect the model, so these components were taken into consideration during the development the random forest model as well (VanDerWal et al., 2009; Barbet-Massin et al., 2012). A subset of the pseudo-absence points of equal ratio to the presence points was constructed and then the data was further split into 75% for testing and 25% for training. The random forest model was built and then a loop was established to perform 100 iterations of each step. This effectively bootstraps the pseudo-absence data so the entire distribution is assessed. In order to assess the accuracy of each model, a confusion matrix was generated as an output for both the test subset of each model. Accuracy, sensitivity, and specificity were used to assess and compare the performance of each model iteration. Variable important plots were constructed in order to determine the role of each explanatory variable.

RESULTS

The use of the Optimized Hot Spot Analysis tool on the nest coordinates of each year and all years combined resulted in the presence of a hot spot near the central section of Padre Island, Texas each year (**Figure 2**). In particular, the analysis of all years combined exposed a notable hot spot along the central section of Padre Island and a cold spot along the northern half of South Padre Island.

Boxplots of each geomorphology characteristic differentiated by nest presence contrast the range of geomorphology values used by the Kemp's ridley sea turtle with the total range of available nesting area (**Supplementary Figures 1–7**). For most of the geomorphology characteristics, the extent used by the Kemp's ridley for nesting is limited in comparison to the breadth of the entire study area; the Kemp's ridley tends to avoid extreme values. The median value for presence points is lower than the median value for the background points for the variables elevation, distance from shoreline, maximum dune slope, dune width, and average beach slope. In particular, the interquartile range of the presence points does not overlap with the interquartile range of the background data for elevation and distance from shoreline, indicative of a distinct preference of the species.

Furthermore, **Table 2** lists statistical measures of each geomorphology characteristic for the nest coordinates for all years of data combined, which provides a detailed quantification of the terrestrial habitat range of the Kemp's ridley sea turtle.

Generalized Linear Models

A correlation matrix of the variables revealed collinearity between the following pairs of variables: maximum dune slope and average dune slope, maximum beach slope and average beach slope, and elevation and rugosity (**Supplementary Figure 8**). There was also a notable relationship between elevation and dune height, as well as between elevation and distance from shoreline. Therefore, these pairs of variables were not included in the generalized linear models in order to avoid creating a bias.

The generalized linear models created using higher ratios of pseudo-absence to presence points had a lower prediction error than models created using a lower ratio (**Table 3**). However, the results of the confusion matrices of the models created using varying ratios of pseudo-absence to presence points revealed that the ratio acts a factor for model accuracy in predicting pseudo-absence to presence points (**Table 3**). As the ratio of pseudo-absence to presence points decreases, the accuracy of the predictions for nest presence, or sensitivity, increases and the accuracy of the predictions for nest absence, or specificity, decreases. This is supported by the trends in the boxplots of the

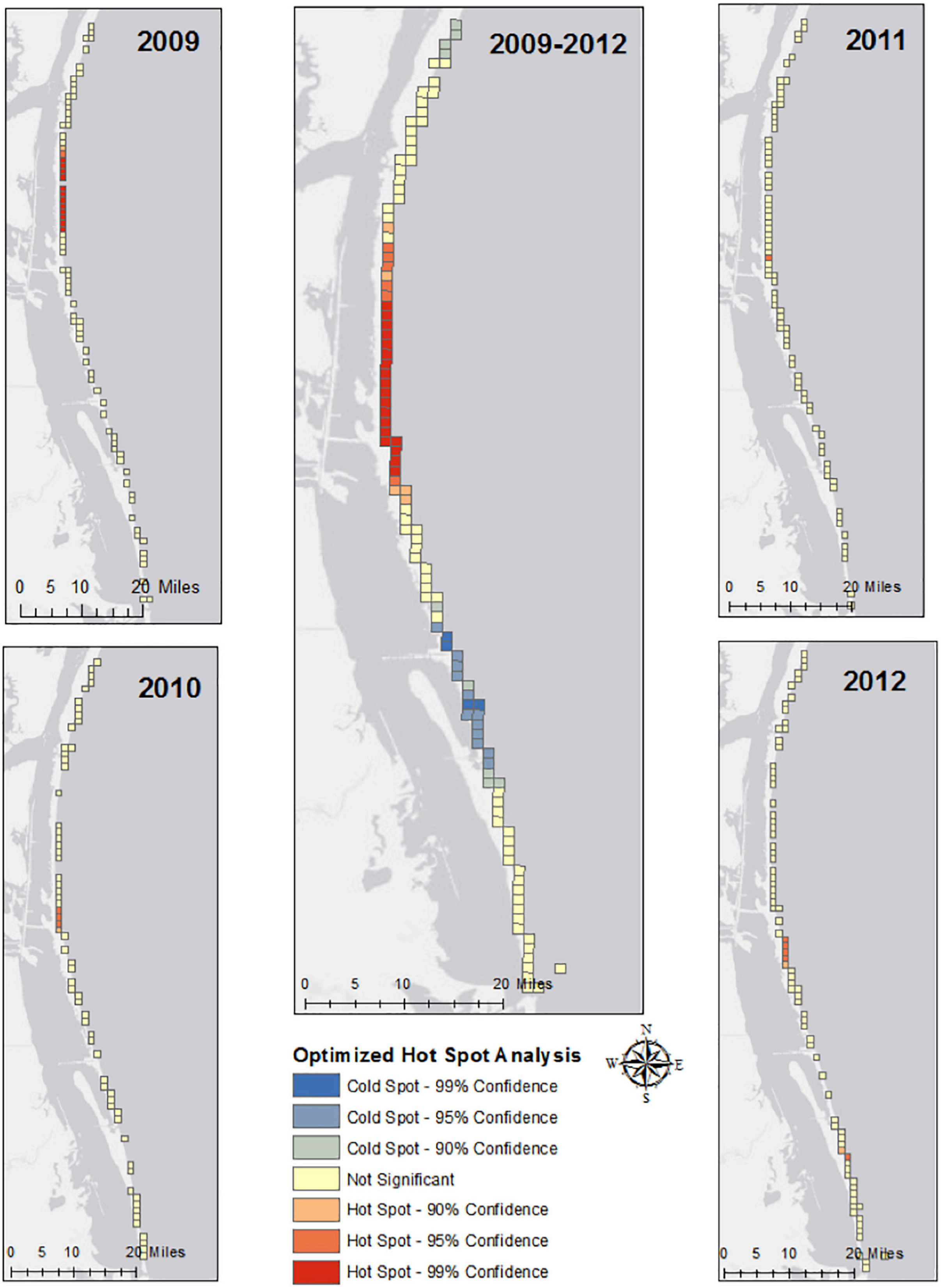

FIGURE 2 | Statistically significant hot spots and cold spots for each year of data produced using the Optimized Hot Spot Analysis tool in ArcGIS.

TABLE 2 | Statistical measures of each geomorphology characteristic for the nest coordinates of all of the years of data combined.

	Elevation (m)	Avg beach slope (degrees)	Beach width (m)	Dune height (m)	Dune width (m)	Max dune slope (degrees)	Avg dune slope (degrees)	Distance from shoreline (m)
Average	1.20	2.96	17.46	6.44	250.18	29.03	7.79	19.47
Standard deviation	0.77	0.93	9.25	1.88	75.93	7.72	2.59	61.72
1st quartile	0.75	2.27	11.02	5.38	87.93	24.01	6.07	2.71
Median	1.11	2.78	15.53	6.22	123.91	29.17	7.54	12.79
3rd quartile	1.47	3.43	21.05	7.37	189.76	33.92	9.34	23.01

TABLE 3 | Generalized linear models created using varying ratios of pseudo-absence to presence points and their respective measures of accuracy.

Generalized linear model	McFadden's pseudo R-squared	K-fold cross-validation prediction error	Ratio of pseudo-absence: presence points
5.9 – 1.64*elevation + 0.21*dune height – 0.36*avg beach slope – 0.075*max dune slope – 0.034*beach width	0.460	0.117	1:1
4.9 – 0.037*distance from shoreline + 0.13*dune height – 0.088*max dune slope – 0.43*avg beach slope	0.411	0.106	1:1
3.16 + 0.077*dune height – 0.29*avg beach slope – 0.086*max dune slope	0.097	0.220	1:1
5.8 – 1.79*elevation + 0.22*dune height – 0.44*avg beach slope – 0.074*max dune slope – 0.04*beach width	0.450	0.111	2:1
5.23 – 2.05*elevation + 0.26*dune height – 0.47*avg beach slope – 0.069*max dune slope – 0.05*beach width	0.448	0.075	5:1
4.375 – 2.16*elevation + 0.23*dune height – 0.37*avg beach slope – 0.065*max dune slope – 0.05*beach width	0.417	0.051	10:1

These models were produced using all the years of data combined.

predictions of each model differentiated by the observed values (**Supplementary Figures 9–14**). These boxplots revealed that the median prediction value for the presence points increases in accuracy at a faster rate than the median prediction value for the absence points decreases in accuracy, resulting in a somewhat balanced accuracy in the model created using an equal ratio. Consequently, an equal of pseudo-absence to presence points was determined to be optimal for the purposes of this study because the resulting model was the most accurate in predicting the presence points without exceedingly hindering accuracy in predicting the absence points.

Generalized linear models generated using an equal ratio of pseudo-absence to presence points explained 40–46% of the variability of nest presence with a relatively low prediction error (**Table 3**). In each model, each variable was significant with a *p*-value < 0.001. The top two models both contained the variables elevation and distance from shoreline, which are collinear. Additionally, these models included the variables of dune height, average beach slope, and maximum dune slope as well. A model containing the aforementioned significant variables without elevation or distance from shoreline only had a pseudo R-squared value of 0.097, indicative that the variables elevation and distance from shoreline are the most influential for the top two models (**Table 3**). Response curves of the predictions of models 1 and 2 in **Table 3** show the relationship between the probability of nest presence and elevation and distance from shoreline, respectively (**Figures 3**, **4**).

The spline correlogram of the raw data for all years of data combined revealed positive spatial autocorrelation between nests up to 250 m apart (**Supplementary Figure 15**). However, the spline correlogram of the Pearson residuals of the top generalized linear model for all the years combined (first model in **Table 4**) exhibited little spatial autocorrelation between nests, even within a short distance (**Supplementary Figure 16**). This suggests that the spatial autocorrelation in the data was explained by the explanatory variables in the model (Zuur et al., 2009; Crase et al., 2014). Therefore, the generalized linear model does not need to be adapted to account for spatial autocorrelation (Zuur et al., 2009).

Random Forest

The random forest model generated using an equal ratio of pseudo-absence to presence points improved upon the accuracy of the comparable generalized linear models (**Table 5**). A random

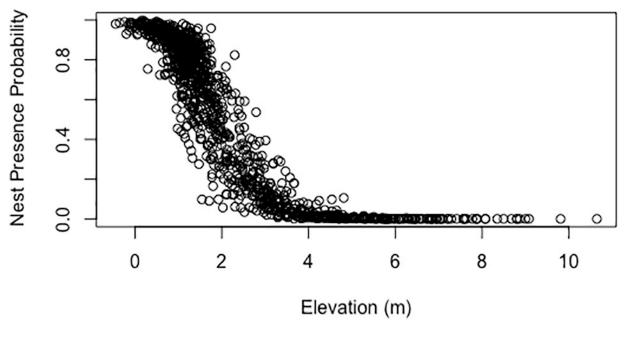

FIGURE 3 | Response curve of the predictions of model 1 in **Table 3** showing the probability of nest presence versus elevation (m).

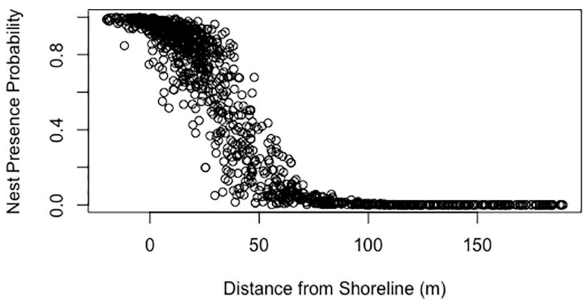

FIGURE 4 | Response curve of the predictions of model 2 in **Table 3** showing the probability of nest presence versus distance from shoreline (m).

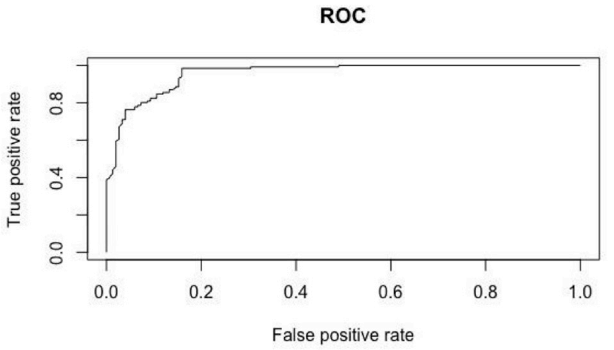

FIGURE 5 | Receiver operating characteristic (ROC) curve of the random forest model.

forest model was also generated using a 10:1 ratio of pseudo-absence points to presence points, which had a lower sensitivity in comparison to the model created using an equal ratio (**Table 5**). This is indicative that the higher ratio of pseudo-absence to presence points biases the model against the presence data, which is consistent with the trends between the generalized linear models created using varying ratios of pseudo-absence to presence points.

The receiving operating characteristic (ROC) curve, which shows the false positive rate versus the true positive rate, of the random forest model created using an equal ratio of pseudo-absence to presence points further demonstrates the accuracy of this model (**Figure 5**). The closer the false positive rate is to 0 and the closer the true positive rate is to 1, the more accurate the model. Therefore, the top random forest model for this study was the model created using an equal ratio of pseudo-absence to presence points. The variable importance plots of this model revealed elevation and distance from shoreline to be the most important variables, concurrent with the results of the generalized linear models (**Figure 6**).

DISCUSSION

Kemp's ridley nest presence was successfully modeled using a small number of geomorphology characteristics, suggestive that these characteristics may be important factors in Kemp's nest site selection. The top generalized linear models were able to explain 40–46% of the variability of nest presence with a relatively low prediction error (**Table 4**), and the final random forest model was highly accurate with a true positive rate above 85% (**Table 5**). The random forest model was superior in performance compared to the generalized linear models, which is indicative of a more complex relationship between nest site selection and beach geomorphology characteristics than can be captured in a traditional modeling technique. This indicates that ranges of the geomorphology characteristics may be more important for Kemp's ridley nesting than linear trends.

For both the random forest model and the top generalized linear models, elevation and distance from shoreline were the most important variables, but maximum dune slope, dune height, and average beach slope were relatively important variables as well. The importance of elevation and distance from shoreline strongly corresponds to the results of studies regarding both hawksbill and loggerhead sea turtles. Horrocks and Scott (1991); Wood and Bjorndal (2000), Weishampel et al. (2003), and Katselidis et al. (2013) found that the hawksbill and loggerhead prefer to nest at a certain elevation above mean sea level. Furthermore, Dunkin et al. (2016) developed a model that successfully predicted loggerhead habitat suitability using

TABLE 4 | Results of the confusion matrices for GLMs created using varying ratios of pseudo-absence to presence points.

Ratio of pseudo-absence: presence points	Balanced accuracy	Sensitivity	Specificity	Positive prediction value	Negative prediction value
1:1*	0.842	0.892	0.793	0.811	0.880
2:1	0.822	0.775	0.869	0.747	0.885
5:1	0.773	0.589	0.957	0.735	0.921
10:1	0.665	0.340	0.989	0.747	0.938

Model 1 in **Table 3.*

TABLE 5 | Results of confusion matrices for random forest models generated using varying ratios of pseudo-absence to presence points.

Ratio of pseudo-absence: presence points	Balanced accuracy	Sensitivity	Specificity	Positive prediction value	Negative prediction value
1:1	0.896	0.914	0.879	0.885	0.909
10:1	0.759	0.530	0.987	0.787	0.958

geomorphology characteristics, of which elevation proved to be the most influential factor. Multiple studies also found beach slope characteristics are an important factor for other sea turtle species in locating suitable nesting habitat (Kolbe and Janzen, 2002; Tucker, 2010; Katselidis et al., 2013).

Results showed that Kemp's ridleys nest at a median elevation of 1.04 m above mean sea level and a median distance from shoreline of 12.79 m, which corresponds to the area near the potential vegetation line or the lowest elevation dune vegetation may thrive along the Texas Gulf shore (**Table 2**). These findings are consistent with the species description by Marquez-M (1994) that the Kemp's ridley usually nests in front of the first dune, on the windward slope, or on top of the dune. A comparison of the ranges of values of geomorphology characteristics for the beaches at which Kemp's ridleys nested to the ranges for the entire study area revealed that Kemp's ridleys exhibited a preference for a limited range of the available habitat and avoided nesting on beaches with extreme values for maximum

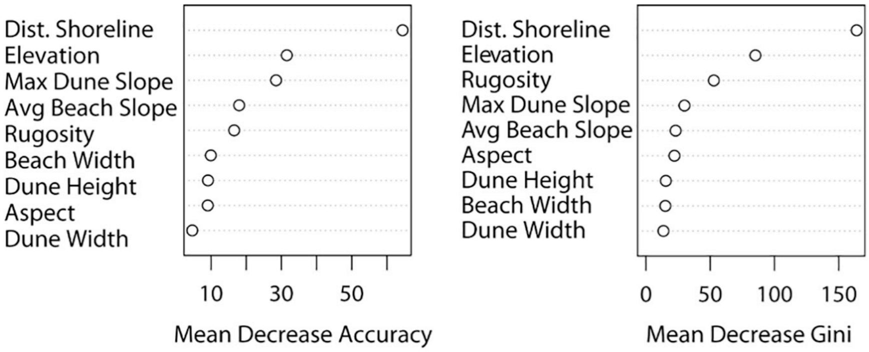

FIGURE 6 | Variable importance plots of the top random forest model. The figure on the left shows the mean decrease in accuracy of the model due to the exclusion of each variable and the figure on the right shows the relative importance of each variable.

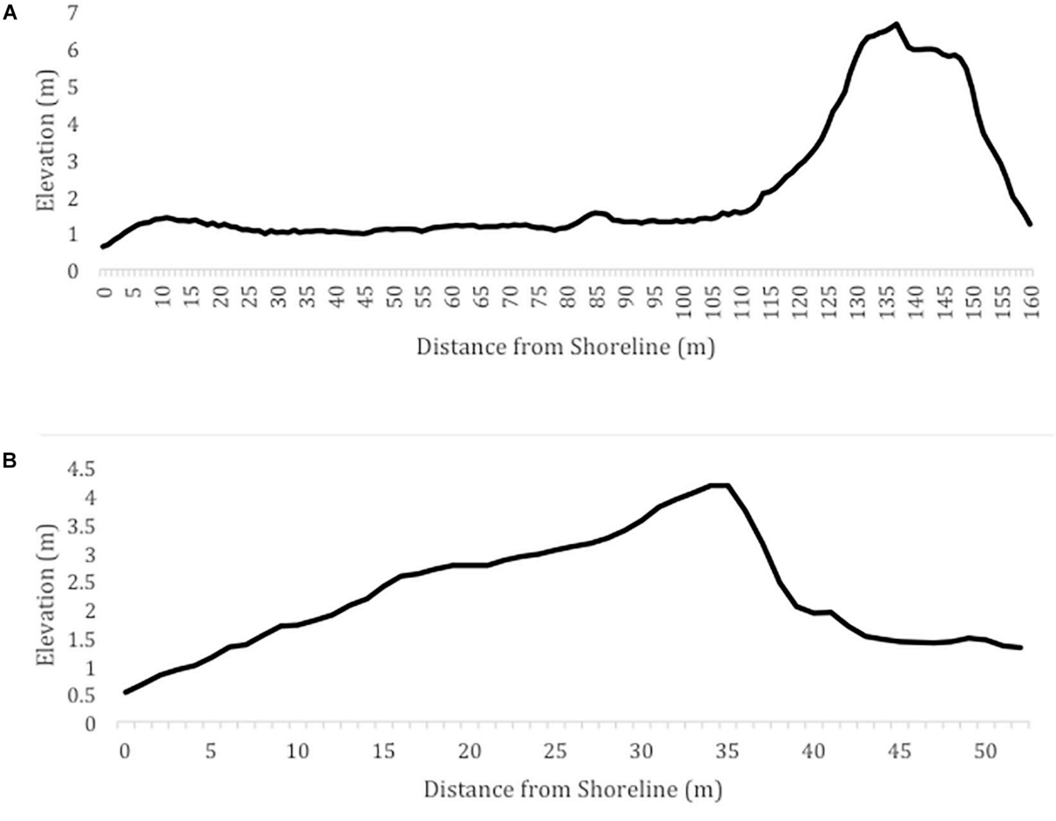

FIGURE 7 | Examples of beach profiles that would not be preferred for nesting due to **(A)** the wide, flat beach and **(B)** the narrow, steep beach and high average dune slope.

dune slope, average beach slope, and beach width. Additionally, for each geomorphology characteristic, nesting occurred at a median value that is lower than the median value for the pseudo-absence points, suggestive of an aversion to maximum values of geomorphology characteristics. This coincides with trends exhibited by other species. Yamamoto et al. (2012) documented that the loggerhead, green, and leatherback sea turtles each exhibited tolerances for a range of values of geomorphology characteristics and would not nest on beaches with values outside these tolerances.

Figure 7 shows examples of profiles that would not be preferred for nesting because they are characterized by extreme values for the beach geomorphology characteristics. On the other hand, **Figure 8** shows examples of profiles that would be preferred for nesting because they are characterized by beaches with moderate widths and slopes, as well as prominent foredune complexes.

Spatially, Kemp's ridleys nested at a higher frequency in a hot spot along the central section of the study area (**Figure 2**). The beaches in this region are on average narrower, steeper and characterized by higher dune peaks in comparison to the northern sections of the study area. The beaches in this region of the study area resemble the beaches of Rancho Nuevo, Mexico, the main nesting site of the Kemp's ridley (Carranza-Edwards et al., 2004). Both regions are also characterized by the presence of shell fragments (Carranza-Edwards et al., 2004; National Marine Fisheries Service [NMFS] et al., 2010; National Marine Fisheries Service and U. S. Fish and Wildlife Service, 2015).

The models did not explain all of the variability in Kemp's ridley nest presence, indicative that other factors, such as coastal development, alongshore currents, offshore bathymetry, sediment size, or environmental conditions, could also be influential (Weishampel et al., 2003; Pike, 2008; Garcon et al., 2010; Katselidis et al., 2013; Thums et al., 2019). Kemp's ridleys often nest in synchronous emergences called arribadas, and studies suggest that there may be cues that initiate an arribada, including strong onshore wind, lunar and tidal cycles, olfactory signals, or social facilitation (Shaver and Rubio, 2008; Shaver et al., 2017). Jimenez-Quiroz et al. (2005) found a coherence between nesting cycles and temperature and wind fluctuations, implying that these environmental variables could serve as stimuli for nesting. Shaver et al. (2017) discerned that Kemp's ridleys prefer to nest on windy days and may be prompted to nest by increases in wind speed and surf. It is possible that these conditions are preferable because the sand is cooler and the risk of predation is reduced, as any signs of nesting would be quickly erased (Shaver et al., 2017). Similarly, multiple studies regarding other species of sea turtles indicate that environmental factors, such as wind and wave exposure, oceanic currents, rainfall events, and tide levels, may be related to sea turtle nest site selection (Pike, 2008; Garcon et al., 2010; Thums et al., 2019). Future

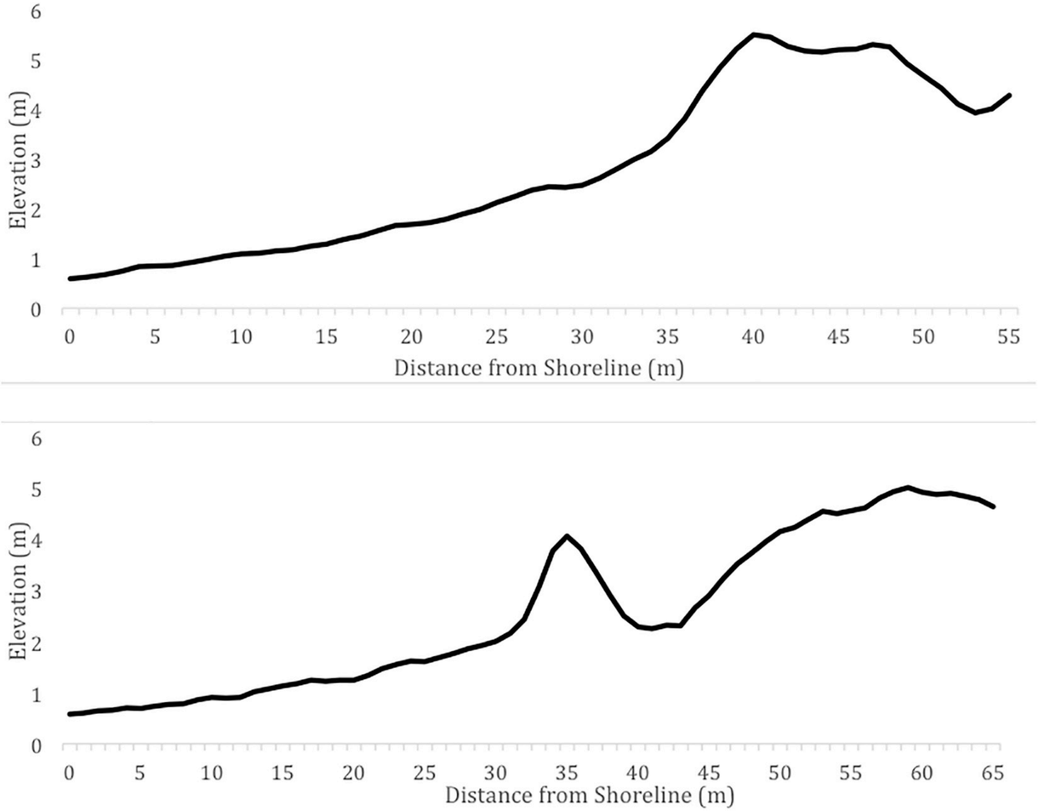

FIGURE 8 | Example of profiles that would be preferred for nesting due to the moderate beach slope and width and prominent dune complex.

modeling efforts should attempt to strengthen the predictions for Kemp's ridley nest site selection by incorporating these environmental drivers.

Kemp's Ridley Conservation and Management

There are a variety of species management and conservation applications for the results of this study that would help protect the Kemp's ridley sea turtle and its habitat. The methods developed in this study can be used to monitor and protect Kemp's ridley habitat availability along the Texas coast as both human (i.e., beach nourishment and beach maintenance) and natural processes (i.e., sea-level rise and extreme storm events) alter beach geomorphology characteristics.

Beach nourishment projects are often a necessary source protection against shoreline erosion, but beach nourishment and beach maintenance activities can result in changes to beach characteristics that may be important for sea turtle nesting, such as beach slope and width, sand compaction, gaseous environment, hydric environment, containment levels, nutrient availability, and thermal environment (Crain et al., 1995; Gallaher, 2009). This could result in a decrease in sea turtle nesting habitat suitability and may deter nesting. Resource managers and city planners can use the results of this study to limit degradation to Kemp's ridley terrestrial habitat during beach nourishment and maintenance projects by ensuring the geomorphology characteristics of all managed beaches fall within the habitat range of the species. Specifically, this data can be used to help generate a habitat suitability index for the Kemp's ridley to be considered during the permitting process.

The results of this study can also be expanded upon to calculate the extent of nesting habitat that may be at risk to sea-level rise and identify beaches where nesting may shift. Sea-level rise has the potential to cause an increase in nest inundation events and to change beach geomorphology characteristics key to sea turtle nesting, such as beach slope and elevation (Pendleton et al., 2004; Stutz and Pilkey, 2011; Williams, 2013; Santos et al., 2015). Annual and seasonal measurements of beach geomorphology characteristics could be used to calculate how the morphology of nesting beaches is changing and to predict the extent and location of optimal nesting habitat as the beaches continue to shift (Katselidis et al., 2013).

The results of this study can also be applied to Kemp's ridley nest location efforts. Because Kemp's ridleys are a relatively small and light sea turtle species, they leave only a faint track in the sand, rendering it especially difficult for nest chambers to be located on windy days. During windy conditions, searches for Kemp's ridley nests should be focused on areas where Kemp's ridleys are most likely to nest, such as near the potential line of vegetation and along the central section of North Padre Island, Texas within the Padre Island National Seashore.

CONCLUSION

This is the first study to assess the relationship between beach geomorphology characteristics and nest site selection for the Kemp's ridley, the most endangered sea turtle species in the world. This research serves as an example of how remote sensing data can be used to model wildlife habitat over an expansive study area and obtain detailed information about an endangered species that is difficult to study.

The application of high-resolution lidar data resulted in new information regarding the terrestrial habitat variability and nesting preferences of the Kemp's ridley sea turtle, which can be used to benefit the conservation and management of the species. Although other factors may influence beach selection by the Kemp's, beach geomorphology characteristics were able to be used to predict nest presence. This is suggestive of a degree of importance of geomorphology characteristics in Kemp's nest site selection, which coincides with similar studies regarding other species. Nevertheless, future work should focus on generating a more robust model that incorporates other potential factors, such as the presence of vegetation, human activity, or sand characteristics, in hopes of explaining more of the variability of Kemp's ridley nest presence.

DATA AVAILABILITY STATEMENT

The datasets for this study have been submitted to Gulf of Mexico Research Initiative Information and Data Cooperative, and publicly available at: https://data.gulfresearchinitiative.org/data/HI.x833.000:0002 (doi: 10.7266/N7445K0Z).

AUTHOR CONTRIBUTIONS

JG, DS, MS, PT, and MC conceptualized the study. DS contributed the nest coordinates. MC, JG, and PT performed the data analysis. MC wrote the manuscript with contributions from DS, JG, MS, and PT.

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SUPPLEMENTARY MATERIAL

The Supplementary Material for this article can be found online at: https://www.frontiersin.org/articles/10.3389/fmars.2020.00214/full#supplementary-material

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frontiers in Marine Science

ORIGINAL RESEARCH
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Migration Corridors and Threats in the Gulf of Mexico and Florida Straits for Loggerhead Sea Turtles

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Along migration corridors, animals can face natural and anthropogenic threats that differ from those in breeding and non-breeding residence areas. Satellite telemetry can aid in describing the timing and location of these migrations. We use this tool with switching state-space modeling and line kernel density estimates to identify migration corridors of post-nesting adult female loggerhead sea turtles (*Caretta caretta*, $n = 89$ tracks) that nested at five beaches in the Gulf of Mexico. Turtles migrated in both neritic and oceanic areas of the Gulf of Mexico with some exiting the Gulf. High-use migration corridors were found in neritic areas to the west of Florida and also in the Florida Straits. Repeat tracking of post-nesting migrations for eight turtles showed variability in track overlap, ranging from ∼13 to 82% of tracks within 10 km of each other. Migration primarily occurred in July and August. We document the longest known post-nesting migration to-date of a wild adult female loggerhead of >4,300 km, along with an apparent stopover of about 1 month. Migration corridors overlaid on three spatially explicit anthropogenic threats (shipping density, commercial line fishing, and shrimp trawling) showed hotspots in the Florida Straits, off the northwest Florida coast and off the coast of Tampa Bay. Identifying where and at what intensity multiple human activities and natural processes most likely occur is a key goal of Cumulative Effects Assessments. Our results provide the scientific information needed for designing management strategies for this threatened species. Information about this loggerhead migration corridor can also be used to inform adaptive management as threats shift over time.

Keywords: anthropogenic threats, *Caretta caretta*, Gulf of Mexico, loggerhead, migration corridors, satellite tracking, sea turtle, switching state-space modeling

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INTRODUCTION

Within migrating species there exists a large variety of migratory behavior. This can include nomadic migration where species move long distances to take advantage of irregular or ephemeral resources (e.g., banded stilt, *Cladorhynchus leucocephalus*; Pedler et al., 2014), one-way migration in which there is no return to the starting point (e.g., European corn borer moth on pre-reproductive migration, *Ostrinea nubilalis*; Dingle, 2014) and multi-generational migration where the migratory path takes multiple generations to complete (e.g., monarch butterfly, *Danaus plexippus*; Dingle, 2014). Perhaps the most well-known type of migration is seasonal migration, in which species travel seasonally between spatially separate breeding and non-breeding grounds. Seasonal migration is thought to increase fitness through the escape of deteriorating environmental conditions such as temperature extremes or predators, and/or a gain in energy or reproductive success (Alerstam et al., 2003; Dingle, 2014).

Migration corridors are the predictable routes on which seasonally migrating animals travel. Migratory corridors have been delineated for various species, both terrestrial and marine, around the world (e.g., Berger et al., 2006; Howard and Davis, 2009; Block et al., 2011). Determining migratory corridors for marine species presents unique challenges as animals may move across remote ocean basins for extended periods. However, electronic tools such as GPS and satellite tags have aided in research efforts to uncover these movements (e.g., Block et al., 2011).

While for many species seasonal migration occurs annually, for adult sea turtles migration occurs on average every 2–4 years (Southwood and Avens, 2010). Sea turtles are not the only reptile that migrates, but they are unique in the group as their migration distances are larger than other reptile species by at least an order of magnitude (Southwood and Avens, 2010). They likely navigate these long distances using magnetic and solar cues, as well as local cues, such as odor (Southwood and Avens, 2010). For the Chelonian sea turtles that make round-trip breeding migrations, these involve swimming both with and against currents (Luschi et al., 2003).

During long-distance migration, species can face increased metabolic and physiological challenges (Jenni-Eiermann and Jenni, 2000; Southwood and Avens, 2010). They can also experience a shifting predator assemblage and encounter storms or other unsuitable climate conditions. Beyond this, they may become exposed to potentially dangerous anthropogenic activities such as energy development (Henkel et al., 2014; Vander Zanden et al., 2016), direct or accidental harvesting (i.e., as bycatch, Hays et al., 2003), pollution (Henkel et al., 2012; Keller, 2013), and ship strikes (Casale et al., 2010). Similar to foraging and breeding habitats, migratory corridors represent an important habitat for migrating species. Defining the location and timing of these migratory corridors is a first step in understanding where and how migrating populations may be limited across space and time, and it offers an opportunity for targeted conservation efforts.

Loggerhead sea turtles (*Caretta caretta*) typically migrate from foraging areas to nesting beaches every 2–4 years (National Marine Fisheries Service [NMFS] and United States Fish and Wildlife Service [USFWS], 2008) sometimes moving thousands of kilometers (Hays and Scott, 2013). Loggerheads in the Gulf of Mexico (GoM) are part of the Northwest Atlantic population, which is listed as threatened (NMFS and USFWS, 2008). Knowledge of the conditions and possible threats along migration routes is important for conservation of the species, and the Loggerhead Recovery Plan lists determining the migratory pathways and management of these habitats as Recovery Objectives/Actions (NMFS and USFWS, 2008). Previous studies have identified migratory pathways for post-nesting loggerheads in the GoM for 28 turtles that nested on the southwest Florida coast (Girard et al., 2009) and 27 turtles from three Florida nesting sites (Foley et al., 2013). These studies have added important knowledge to our understanding of GoM loggerhead migration. However, it is possible that loggerheads nesting on other GoM beaches may use different migratory pathways, so expanding our understanding of loggerhead migration across spatially disparate beaches is important. Also, identifying anthropogenic threats to migratory corridors is key to conservation efforts for loggerheads and has yet to be assessed for their migration corridors in the GoM. Further, no migratory corridor has yet been designated in the GoM for loggerhead critical habitat (NMFS and NOAA, 2014).

Here, we combine 48 previously published migration tracks for post-nesting GoM loggerheads (Hart et al., 2012, 2014, 2015) with another 41 tracks, including some tagged at a new study site at a nesting beach in Everglades National Park, to discover high-use migration corridors in the GoM. We use switching state-space modeling (SSM) to identify these 89 migration routes from five nesting beaches across 8 years (2008–2015) in the GoM, including nesting beaches in both Florida and Alabama. We identify corridors, summarize the peaks in migration timing, display repeat migration patterns for individuals tracked more than once from nesting grounds, and overlay anthropogenic threats during those times onto the migration corridors to determine a migration threat index.

MATERIALS AND METHODS

Turtle Capture and SSM

Turtle tagging occurred at five study sites in the GoM including at Gulf Shores, Alabama, and four sites in Florida: Eglin Air Force Base on Santa Rosa Island in northwest Florida, St. Joseph Peninsula, Everglades National Park, and Dry Tortugas National Park which included the nesting beaches of Loggerhead Key and East Key (**Table 1** and **Figure 1**).

We tagged and outfitted 81 loggerhead females (eight of these were tagged twice for 89 tracks) with satellite transmitters after they nested. All tagging followed established protocols (National Marine Fisheries Service [NMFS]-Southeast Fisheries Science Center [SEFSC], 2008) and methods in Hart et al. (2014). These methods were approved by the United States Geological Survey-Southeast Ecological Science Center-Institutional Animal Care and Use Committee Protocol #2011-05. We fitted a platform terminal transmitter to each turtle (SPOT5 or SPLASH10, Wildlife Computers, Redmond, WA, United States). All tagged turtles were released within 2 h at their capture location.

Satellite data were available for download on the Wildlife Computers Portal.[1] We used a hierarchical SSM

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[1] www.wildlifecomputers.com

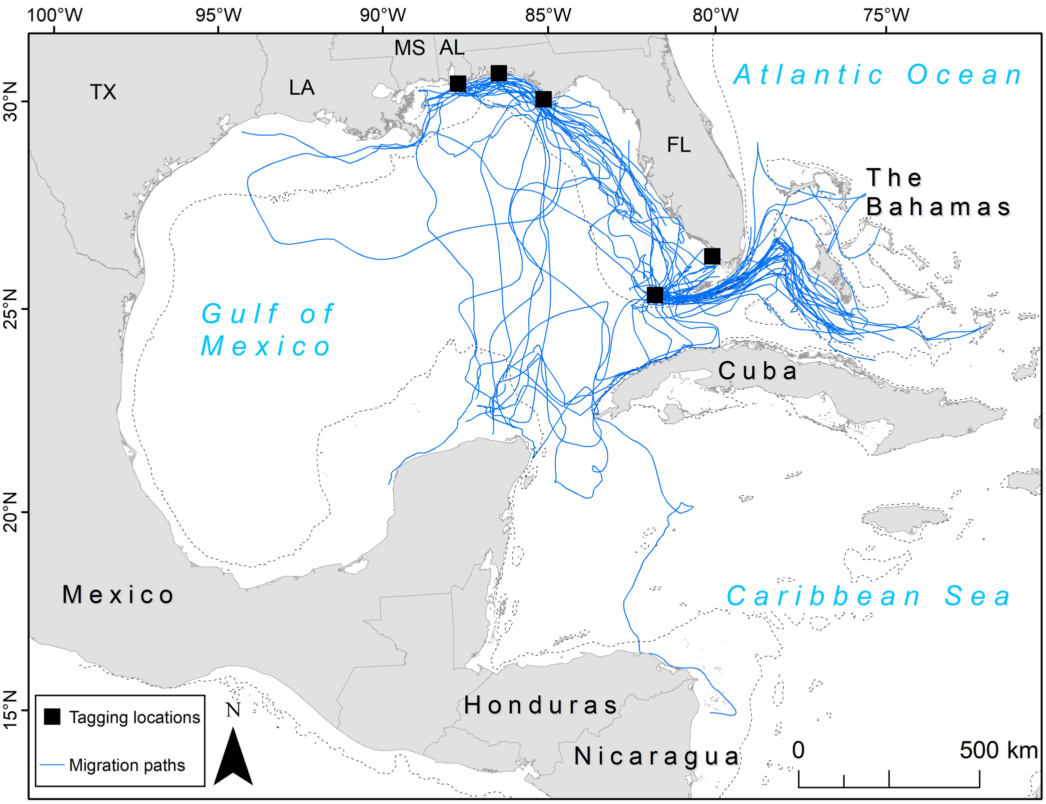

FIGURE 1 | Migration paths (blue lines) taken by 81 adult female loggerhead sea turtles (*Caretta caretta*; 89 tracks) after being tagged at nesting beaches throughout the Gulf of Mexico. Tagging locations (black squares) from top left moving clockwise: Gulf Shores, Eglin Air Force Base, St. Joseph Peninsula, Everglades National Park, Dry Tortugas National Park. U.S. states are abbreviated: TX, Texas; LA, Louisiana; MS, Mississippi; AL, Alabama; FL, Florida. The 200 m bathymetric contour is shown as a dashed line.

(Jonsen et al., 2003; Patterson et al., 2008) to characterize the movements of all turtles, following our previous studies where we determined foraging and inter-nesting periods for some of these same turtles (Hart et al., 2012, 2013, 2014, 2015, 2018a,b). Specifically, we applied a model used by Breed et al. (2009) that estimates model parameters by Markov Chain Monte Carlo (MCMC) using WinBUGS via the software program R. As input into the model, we used all tracking data except for locations defined as Location Class Z, which are considered invalid locations (CLS, 2011). We fit the model to tracks of each individual turtle to estimate location and behavioral mode every 6 or 8 h from two independent and parallel chains of MCMC. Our samples from the posterior distribution were based on 10,000 iterations after a burn-in of 7,000 and were thinned by five. We defined binary turtle behavioral modes based on SSM output as either "area-restricted searching" or "transiting" as in earlier applications (Jonsen et al., 2007).

After plotting the transiting locations, we further filtered them to remove transit locations that represented movement within inter-nesting or foraging periods. In this way, we included only the turtle's migration away from nesting beaches. The transit locations constituting the migration were determined by graphing the cumulative distance from the nesting beach, which was defined as the graph's rise after the last visit to the nesting beach to the beginning of the asymptote signifying the arrival at foraging grounds. Additionally, if a nesting event (ground-truthed) fell within the migration period, we classified the locations before the nest as "transit within the inter-nesting period."

TABLE 1 | Number of loggerhead sea turtle (*Caretta caretta*) tracks during migration in the Gulf of Mexico after being tagged at various nesting beaches.

	GS	EAFB	SJP	ENP	DTNP	Total
2008					3	3
2009					4	4
2010			4		2	6
2011	5				6	11
2012	5	2	5		9	21
2013	8		4		7	19
2014	2			2	7	11
2015	2			3	9	14
Total	22	2	13	5	47	89

GS, Gulf Shores, Alabama; EAFB, Eglin Air Force Base, Florida; SJP, St. Joseph Peninsula, Florida; ENP, Everglades National Park, Florida; DTNP, Dry Tortugas National Park, Florida.

If the input locations to SSM have large temporal data gaps or are highly imprecise, it can create SSM paths that deviate from the true path (Jonsen et al., 2013). We inspected SSM main migration output paths for 122 tracks as part of a larger project. The turtles considered here (n = 89) remain after filtering out SSM outputs that crossed large areas of land (n = 16), had no clear migration away from nesting grounds (n = 7), had three or less input locations during migration and/or had temporal gaps of a week or greater during migration (n = 10). This ensured that the SSM paths modeled the input locations as accurately as possible.

Migration Corridors

We visually identified two main migration corridors. To spatially delineate the extent of each migration corridor, we determined the line kernel density estimates (KDEs; Steiniger and Hunter, 2013) for each using the SSM migration lines in each corridor (n = 37 tracks for the GoM, n = 27 tracks for the Florida Straits). We used open source GIS software OpenJUMP (Steiniger and Hay, 2009), with the OpenJUMPHoRAE toolbox (Steiniger and Hunter, 2012) to calculate line KDEs and the 25, 50, and 75% probability contours for each migration corridor KDE. The probability contours are calculated from the KDEs, whereby a density value represents a given probability that the animal may be found in that cell, and polygons representing probability of use can then be derived from the resulting contours. The maximum percentage of 75% for the KDE distribution was applied and represents a conservative estimate of the migration corridor appropriate for assessing broad movement patterns (Pendoley et al., 2014), which aids in accounting for tracking bias (e.g., individuals tracked from the same nesting site; Almpanidou et al., 2019). We determined the line KDEs using a bandwidth of 42 km, the average distance traveled per day for the turtles in the two identified migration corridors (n = 64 tracks; Steiniger and Hunter, 2013) and implemented a raster cell size of 10 km (in agreement with other data layers). We chose 10 × 10 km grid cells to balance the spatial error of most satellite locations received ($>$1.5 km; CLS, 2011), the average daily distance the turtles moved (42 km), and a reasonably precise area for planning management actions.

Timing and Repeatability of Migration Paths

To determine the timing of migration, we obtained the dates (month and day, ignoring year) that each turtle migrated. We then separately graphed the number of turtles migrating on any given month/day for those that stayed within the GoM or went to the Bahamas or Caribbean. To describe how similar paths were for individual turtles tracked twice, we created 10 km buffers around the first path for each turtle and then determined the proportion of the second path that fell within the buffer. To compare the median threat level between migration paths for each turtle tracked twice, we extracted grid-cell threat values (see below) along each path and ran Wilcoxon rank sum tests in base R (R Core Team, 2020) for each individual.

Anthropogenic Threats

Previous work identified where foraging grounds for loggerheads and Kemp's ridleys (*Lepidochelys kempii*) in the GoM overlapped with eight spatially explicit anthropogenic threats and found that threats for turtles using the southwest coast of Florida included commercial line fishing and harmful algal blooms (HABs; Hart et al., 2018a). However, when we included only threats during the peak migration time of July and August, HABs – which occur usually between August and February[2] – were only present in a single year and in a relatively small spatial location and so we did not include HABs in our analysis. For turtles migrating through the Florida Straits, shipping lanes are a concern (Hart et al., 2018a). Additionally, while shrimp trawling effort is more concentrated in the northern GoM, trawls can present a significant threat to turtles if exclusion devices are not used and trawls are longer than 10 min (Sasso and Epperly, 2006). Therefore, we overlay these three threats on the migration corridors: commercial line fishing, shipping density, and shrimp trawling.

For commercial line fishing we used data provided by the National Oceanic and Atmospheric Administration (NOAA; Wrege, pers. comm.) that displayed the number of fisher trips that used line fishing in 2014 across the U.S. GoM. These trips were reported by fishers using a 1-degree latitude-longitude grid. For shipping density, we used Automatic Identification System data that is collected by the U.S. Coast Guard and provided for use by NOAA and the Bureau of Ocean Energy Management.[3] These data provide the locations of large vessels [≥65 ft (20 m) in length or ≥26 ft (8 m) in length for towing vessels] in monthly summaries. We downloaded the shipping density for July and August for the latest year of tracking (2015). Files were transformed into File Geodatabases using the Track Builder 3.1 tool on their website. Once points were obtained, we created lines using the ArcMap 10.4 (ESRI, 2016). Points to Line tool with separate lines for each vessel ordered by date and time. We summed the number of lines in 10 km grid cells for the 2 months to show densities across peak migration time. Shrimp trawling effort is reported by NOAA statistical zone, both of which we obtained from NOAA (Nance et al., pers. comm.). We mapped the effort as number of days fished during the summer, defined and summarized by NOAA as May to August, for years 2008 through 2015. We then averaged the effort across these years.

The threats had different units and varying degrees of intensity, so we standardized units while retaining weighted values that represented relative levels, by dividing each threat value by the maximum to get a proportion of threat level in each grid cell. Only values that intersected the final grid area in the eastern GoM were considered for obtaining the maximum value. These proportions were added together to get a total threat level value per grid cell. Any total threat level value $>$0 was added to one to ensure that multiplication of the threat to the turtle KDE value remained positive. In so doing, threats were spatially weighted in relation to themselves but not weighted

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[2] https://tidesandcurrents.noaa.gov

[3] https://marinecadastre.gov/ais

across threats based on danger level to turtles (i.e., all threat types were considered of equal danger). Once all threats were compiled, we multiplied the threat values in each grid cell by 1 – the line KDE contour value, which gave heavier weight to core areas of the line KDEs. This provided a metric to identify potential hotspots where differing levels of both migration and threats occur.

RESULTS

Turtles and SSM

We identified migration paths for 81 adult female loggerheads (89 tracks) tagged after nesting in the GoM from 2008 to 2015 (**Figure 1**). Migration tracks ranged from 1 to 115 days for a total of 1,341 days (mean ± SD: 15.1 ± 14.1 days). Most turtles were tracked for more than a week after migration ended, but five turtles stopped transmitting either during migration, or 1 day after SSM indicated that migration ended. SSM input locations during this time accounted for a total of 11,110 locations and SSM output totaled 4,008 locations. The total distance moved (successive distances between SSM locations per turtle) ranged from 23 to 4,388 km (661.8 ± 595.1 km) for a total of 58,896 km across all tracks (**Table 2**).

Migration Corridors

We identified two migration corridors for post-nesting adult female loggerheads containing 72% of satellite tracks in this study. One occurred in the eastern half of the GoM and the other was through the Florida Straits out into the Bahamas (**Figure 1**). There were a few exceptions: one turtle that nested in Dry Tortugas National Park headed south across the Caribbean Sea to waters off Nicaragua, a Gulf Shores-nesting turtle headed west to Texas, and another turtle that nested at Gulf Shores headed west toward Texas but then made a large loop back east and south, swimming through both oceanic and neritic areas eventually reaching Cuba. Oceanic areas (i.e., outside neritic areas) generally had a lower number of paths, with the middle of the GoM primarily having single, unique paths with a low degree of clustering along specific routes. However, south of mainland Florida, many tracks clustered through oceanic areas when turtles crossed the Florida Current before reaching the neritic waters of the Bahamas (**Figure 1**).

TABLE 2 | Tracking and switching state-space model (SSM) details for 81 loggerheads (*Caretta caretta*; 89 tracks).

	Days tracked in migration	SSM input	SSM output	TDM (km)	Speed (km/h)
Range	1–115	7–1,221	3–345	22.5–4388.1	0–8.0
Mean	15.1	124.8	45.0	661.8	1.9
SD	14.1	149.5	42.3	595.1	1.1
Total	1341	11110	4008	58896.4	n/a

TDM, total distance moved during migration (cumulative distance in km between successive SSM locations). Values summarized across 89 separate tracks. SSM input and output values represent number of locations. Speed calculated for turtles from SSM locations.

TABLE 3 | Migration details for loggerhead sea turtles (*Caretta caretta*) tracked from nesting grounds twice.

Turtle	Migration year	Migration dates (days)	TDM during migration (km)	Diff in TDM	% overlap
1	2013	7/13–7/28 (16)	768.9		28.0
	2015	7/16–7/25 (10)	665.2	103.7	
2	2009	7/24–7/31 (8)	490.5		82.1
	2012	7/17–7/25 (9)	569.3	78.8	
3	2011	8/5–8/22 (18)	843.7		47.5
	2013	8/6–8/18 (13)	688.6	155.2	
4	2010	8/17–8/23 (7)	438.2		24.7
	2012	8/12–8/21 (10), 8/23–8/24 (2)	835.7	397.4	
5	2010	8/19–8/31 (13), 9/2–9/8 (7)	937.4		13.5
	2013	7/29–8/13 (16)	991.2	53.8	
6	2013	8/8–9/2 (26)	1109.3		38.1
	2015	7/25–8/12 (19)	993.4	115.9	
7	2012	7/17–8/2 (17)	1090.7		19.6
	2014	7/2–7/9 (8)	809.1	281.6	
8	2011	7/21–7/26 (6)	171.8		35.0
	2012	6/7–6/13 (7), 6/17–6/27 (11)	394.5	222.6	
	Mean	13.9	737.4		36.1
	SD	6	269		21.5
	Total	223	11, 798		

All turtles were tagged in Dry Tortugas National Park, Florida except for turtle 8 which was tagged in Gulf Shores, Alabama. Turtles 4, 5, and 8 had non-transiting locations during their migration, therefore migration dates were split up. Migration dates are given as month/day. TDM, total distance moved (cumulative distance between successive SSM locations); diff, difference. The % overlap is the proportion of the second path within a 10 km buffer surrounding the first path.

The line KDE contours represent the probability that a migrating turtle would be found in that area. The line KDE created in the eastern GoM had an overlap of the 25 and 50% contours, with a probability of a given turtle being found there at 62% (**Figure 2**). The 62 and 75% contours for this corridor were relatively close in size and primarily covered neritic areas from south of Alabama to the southern tip of western Florida. The 25 and 50% contours remained separate for the corridor extending from the Florida Straits to the Bahamas, showing the core area of migration lines in a funnel shape with the tip of the funnel in the Florida Straits and the funnel opening around Andros Island, the largest Bahamian island (**Figure 2**).

Timing and the Repeatability of Migration Paths

Turtles migrated as early as 7 June and as late as 10 November (for the turtle that headed to Nicaragua). However, the majority of migration across all turtles occurred during July and August. This peak was the same regardless of whether migration began in the northern GoM or at the more southerly Dry Tortugas National Park (**Figure 3**).

We tracked eight turtles twice during migration to their foraging grounds (**Table 3**). One turtle was tagged in Gulf Shores, Alabama and the other seven were tagged in Dry Tortugas

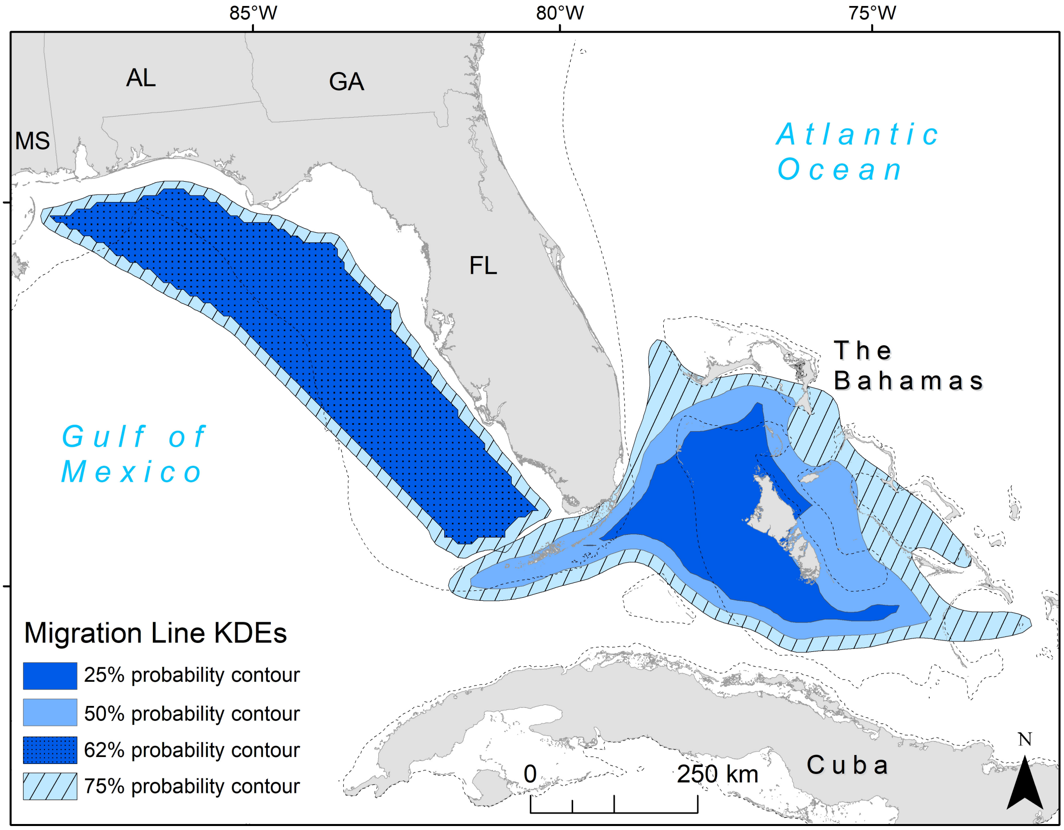

FIGURE 2 | Migration line kernel density estimates (KDEs) for adult female loggerhead sea turtles (*Caretta caretta*; 64 tracks). Two migration corridors were identified: in the eastern Gulf of Mexico and the Florida (FL) Straits into the Bahamas. The KDEs were based on multiple tracks in the Gulf of Mexico (n = 37) and FL Straits (n = 27). Values represent probability that a migrating animal will be found in each contour. U.S. states are abbreviated: MS, Mississippi; AL, Alabama; GA, Georgia; FL, Florida. The 200 m bathymetric contour is shown as a dashed line.

National Park, Florida. Paths taken by turtles were similar across years (**Figure 4**). The percent of the second path that fell within the 10 km buffer of the first path ranged from 13.5 to 82.1%, with a grand mean of 36.1% (±21.5%). Threat levels along paths were similar for turtles tracked twice; only one turtle (Turtle 8 in **Table 3**) showed a significant difference in threat levels, with the second track moving through higher threats [median threat level for track 1 = 1.23, median for track 2 = 1.36; Mann-Whitney $U = 329.00$, $n_1 = 22$, $n_2 = 43$ $P = 0.047$; we did not include Turtle 5 (**Table 3**) in these comparisons because >80% of the track was outside the threats grid]. This turtle migrated in the northern GoM, and its second track took it close to the Chandeleur Islands where threat levels were higher than off the coast of Alabama and northern Florida.

Anthropogenic Threats

When threats were multiplied by the probability of turtle presence as given by line KDE values, hotspots of high values occurred around the northwest Florida coast, off of Tampa Bay, and in the Florida Straits (**Figure 5**). Commercial line fishing was present to some degree across the entire eastern GoM, with the number of trips generally highest west and south of Florida, up to a maximum of 5,462 trips per 1-degree latitude/longitude grid cell (**Supplementary Figure 1**). Shipping density was highest in a somewhat circular path from Louisiana to the Florida Straits, where the number of vessels during the summer months reached as high as 1,500 for a 10 km grid cell (**Supplementary Figure 1**). Shrimp trawling was lower along the west coast of Florida than in the water south of Louisiana, however over 2,000 effort hours of shrimping during the summer months of 2011 (with an average of ∼1,300 h across years) was reported for waters ∼18–55 m deep in this area (**Supplementary Figure 1**).

DISCUSSION

We spatially defined areas where high-use loggerhead migration paths overlap with sea turtle-specific anthropogenic threats in the Gulf of Mexico. This is important as loggerheads are a threatened species and the GoM has a high level of disturbance and pollution. The GoM also has one of the highest levels of species per unit area in the world, yet its biodiversity is considered "most threatened" (Costello et al., 2010). Specifically, we use 89 loggerhead migration tracks to identify high-use corridors including turtles from Baldwin County, Alabama, and Okaloosa, Gulf and Monroe Counties in Florida. This includes

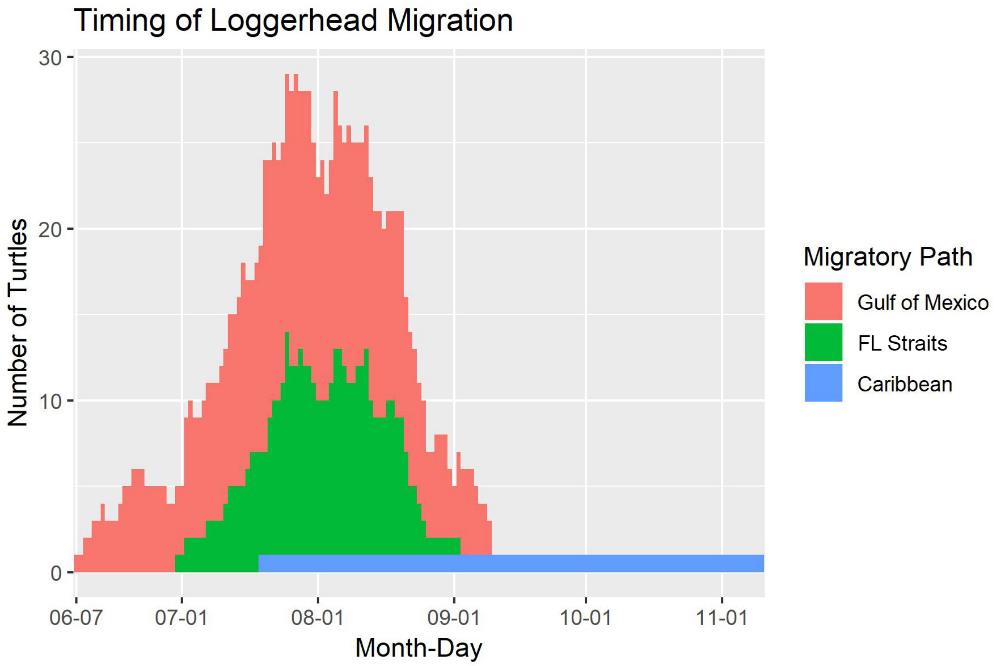

FIGURE 3 | The timing of migration paths taken by 81 adult female loggerhead sea turtles (*Caretta caretta*; 89 tracks) after being tagged at nesting beaches throughout the Gulf of Mexico. The migrations are split by which area the turtle traveled through on migration: the Gulf of Mexico, the Florida (FL) Straits, or the Caribbean. The long tail after September 6 is from the turtle that traveled to Nicaragua.

turtles tracked from a nesting beach in Everglades National Park not included in previous summaries. Based on previous work, loggerheads have been shown to use neritic waters west of Florida, as well as oceanic waters in the middle of the GoM for their migration. The corridors identified in this study align closely with many of the previously published tracks (Girard et al., 2009; Foley et al., 2013), indicating that these pathways are consistently important for loggerheads nesting through the GoM. For example, Foley et al. (2013) showed northern GoM turtles migrating in similar areas: along western Florida, loggerheads were located between 20 and 50 m bathymetry, and our core migration KDE areas overlapped these depths. In the Florida Straits, Girard et al. (2009) showed tracks in similar areas for turtles moving from western Florida to the Bahamas and Foley et al. (2013) showed many tracks along the same route but moving in the opposite direction for turtles migrating from eastern Florida into the GoM. Combined, these studies support the importance of the areas identified in this study as migratory corridors for loggerheads across years and for traveling to and from nesting beaches. Identifying corridors helps determine where management actions have potential to benefit more migrating loggerheads.

Although turtles in this study used neritic and oceanic areas, we found corridors were primarily located in neritic areas close to the coast. In the mid-GoM oceanic areas, individual tracks showed low degrees of overlap, consistent with other studies tracking loggerheads through this area (Girard et al., 2009; Foley et al., 2013). This may be attributed to changing currents and eddies that make each path unique. Specifically, turtles migrating in oceanic GoM waters may be influenced by eddies of the Loop Current (Foley et al., 2013).

Of eight turtles tracked for two post-nesting migrations, we found a relatively high degree of spatial similarity on their paths across years. Given that sea turtles follow magnetic maps (Southwood and Avens, 2010) and generally travel between the same nesting beaches and foraging grounds across years, this is expected. The repeat SSM paths were not exact replicates for turtles, however, and this may be due in part to the limits of location accuracy with satellite tags and/or variable model inputs into the SSM (such as number of and location of input points) that caused slightly different outputs. It is also possible that shifting currents and/or shifting of local cues such as wind-borne odor (Endres et al., 2016) could influence migration paths such that we would not expect an exact overlap in space and time across years. Theoretically, changes in course across years could also be due to avoidance of the threats identified in this study, however, we did not find evidence for this.

Despite the somewhat lower location accuracy of satellite tags as compared to GPS tags, their battery longevity allows for much longer tracking periods. As the tag technology improves, researchers will be able to determine spatial consistency in migration paths for a greater sample size of turtles, and during remigration. One previously tracked loggerhead followed the same migration path post-nesting and during its remigration back to nesting grounds (Foley et al., 2013). Therefore, the corridors we identified may also be important during remigration to nesting grounds, which would occur at a different time of year when threat levels may be different. Tracking turtles from foraging grounds to their nesting beaches would help determine how consistently they use corridors for both directions of migration. The cues that drive the phenology of migration for sea turtles are not well understood, and more research on the timing of migration from foraging grounds and associated environmental conditions could help with understanding what drives this behavior for individuals in some years and not others.

One turtle migrated out of the GoM south to Nicaragua, for a total distance moved of 4,388 km. In 2017, a rehabilitated loggerhead was released from South Africa and traveled for 2 years before reaching Australia, $>10{,}000$ km from its release site.[4] For non-rehabilitated, wild turtles, the travel to Nicaragua from the GoM represents the longest reported post-nesting loggerhead migration to our knowledge. The next longest migration in this study was 2,751 km, a difference of around 1,600 km. The upper distance limit for adult Cheloniid sea turtles undertaking breeding migrations is thought to be around 3,000 km, because of limits on available fat stores (Hays and Scott, 2013). Interestingly, the turtle migrating to Nicaragua paused along the coast of Cuba from late August until early October after traveling for about 1,500 km. After this pause, the turtle resumed migrating, and then when it had traveled ~3,400 km from nesting grounds it seemingly paused migration again to make a circular loop about 50 km in diameter for 8 days in October. While the SSM identified this time as migration, it is possible that this represents a type of stopover, where the turtle may have been seeking resources for refueling. These potential stopovers occurred in the neritic waters of Cuba and then directly south of Cuba in water $>3{,}000$ m deep.

There are anthropogenic threats to sea turtles which we were not able to quantify and thus did not include in our analysis, such as plastic pollution, effects from climate change, and direct harvest. Plastic pollution presents a serious threat to sea turtles, with over half of sea turtles in the world predicted to have ingested plastic debris and a relatively high-risk of ingestion predicted specifically in the GoM for hard-shelled sea turtles (Schuyler et al., 2016), however, the spatial extent of plastic available to turtles in the GoM is not well-studied. Additionally, changes to ocean currents and sea surface temperatures due to climate change were not considered. Theoretically, sea turtles could be affected by these changes during migration, as changing temperatures and currents could alter the energetic costs of migration, however, how these changes would affect sea turtle migration is not well understood (Southwood and Avens, 2010). Direct harvest is considered the third highest threat to sea turtles based on expert opinion (Donlan et al., 2010), yet we did not include this threat because of a lack of spatial information on where direct harvest in the GoM may occur. Lastly, based on the small percentage of HABs we found occurring during the migration period, these blooms are likely of higher concern for loggerheads on foraging grounds than those migrating in the summer. However, these blooms can be variable as demonstrated by the massive bloom that started in the fall of 2017 and lasted long enough to affect over 200 km of Florida's west coast in the summer of 2018,[5] killing hundreds of sea turtles. Therefore, while this may not be a primary, consistent threat to migrating sea turtles of those we examined, it can still have important impacts in some years.

For commercial line fishing, the data represents a minimum estimate of possible impacts. This is because we included only reported line fishing trips with known gear. We also did not include trips where the gear was simply reported as combined (multiple gear types). Commercial line fishing is known to have cumulatively high sea turtle bycatch, but other forms of fishing with nets may also have impacts (Lewison and Crowder, 2007). Not all trips will have the same impact, as that depends on the effort of each trip. Here we use only the number of trips as a metric, assuming that more trips mean more impact. Even with the threat from line fishing possibly being underestimated, the potential threat to sea turtles appears relatively high across most of the GoM, as many thousands of trips were reported for just one summer.

Shipping density is most problematic for migrating loggerheads that are traveling through the Florida Straits, and a lower level of this threat occurs across all other areas considered. We mapped this layer to demonstrate areas with more potential for ship strikes, which have been shown as a common cause of sea turtle mortality in the Mediterranean (Casale et al., 2010). Lastly, shrimp trawling effort is not as high across most of the western Florida shelf as in waters surrounding Louisiana, however, this threat is persistent across neritic areas of the GoM.

Here we show that shipping density, commercial line fishing, and shrimp trawling can affect the mortality of loggerhead sea turtles in the GoM. However, we did not weigh these threats in relation to each other and were unable to consider all possible threats, therefore we consider our threats index to be a minimum estimate. Importantly, our identified corridor in the GoM overlaps with migration areas for other species of concern. Kemp's ridleys migrate slightly earlier in the year, with a peak in June, however they migrate through August (Shaver et al., 2016), so for any traveling through these same areas, they would be subject to these same threats. This corridor also overlaps with Biologically Important Areas identified for the resident population of Bryde's whale (*Baleanoptera edeni*), which are extremely rare, and represent the only year-round baleen whale population in the northern GoM (LaBrecque et al., 2015; Soldevilla et al., 2017). This whale occurs primarily between depths of 100–300 m and is listed as endangered (NMFS and NOAA, 2019).

Cumulative Effects Assessments (CEAs), sometimes referred to as Cumulative Impact Assessments, are procedures that identify and evaluate the collective impact of multiple human activities and natural processes on the environment (Jones, 2016). CEAs are considered critically important for informing effective marine policy, however, the use of CEAs in real-world management processes remains a challenge largely due to the wide variation in approaches. CEAs are complex and have

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[4] www.aquarium.co.za

[5] https://coastalscience.noaa.gov

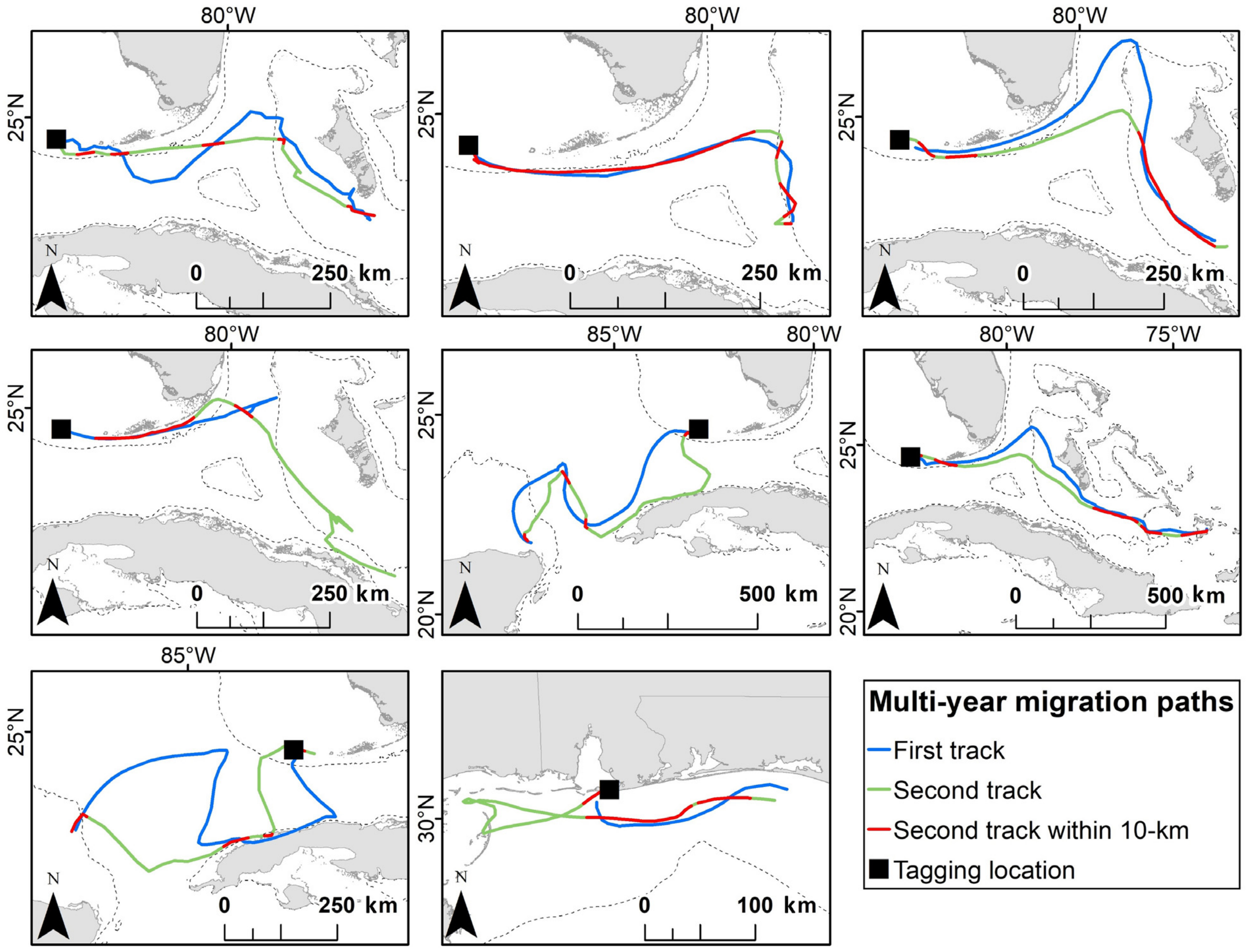

FIGURE 4 | The repeatability of migration paths taken by eight adult female loggerhead sea turtles (*Caretta caretta*) after being tagged at Dry Tortugas National Park, Florida (first seven panels) and Gulf Shores, Alabama (last panel). Parts of the track where the second post-nesting migration was within 10 km of the first post-nesting migration are indicated in red. The 200 m bathymetric contour is shown as a dashed line.

been criticized for a lack of measurable and clearly defined sustainability goals, being poorly aligned with institutional frameworks, and a lack of objective criteria (Jones, 2016). Nevertheless, attempts have been made to improve on CEAs by re-evaluating the structure and intent, reducing ambiguity, and orienting toward a common objective across regions (Willsteed et al., 2018). By incorporating CEAs within a risk-based framework that includes identification, analysis and evaluation, it may be possible to simplify and streamline CEAs while being transparent about uncertainty (Stelzenmüller et al., 2018). Ideally, CEAs show where cumulative effects most likely occur and at what intensity (Stelzenmüller et al., 2018). As we did not weight threats with additional quantitative data on mortalities and injuries caused, our analysis may be considered a Cumulative Pressure Assessment (CPA), and a step toward a fully parameterized CEA.

By overlaying anthropogenic threats onto the migration corridors, we were able to identify that hotspots of high values occurred around the northwest Florida coast, off of Tampa Bay, and in the Florida Straits. In our study, our conservation target is clear: the survival of migrating adult female loggerheads. In the Loggerhead Recovery Plan, managing migratory pathways and minimizing vessel strike mortality are listed as Recovery Objectives (NMFS and USFWS, 2008), and therefore our results directly provide scientific information needed for designing management strategies for this threatened species. In a risk-based framework, management activities are monitored and evaluated, which may lead to an understanding of thresholds for the cumulative effects (Stelzenmüller et al., 2018). In order to inform what threshold is acceptable for each threat, a future CEA would benefit from an understanding of what mortality level during migration is deemed sustainable for population recovery. As new information becomes available on the spatial intensity of threats, this estimated corridor can be used to inform adaptive management of threats during the

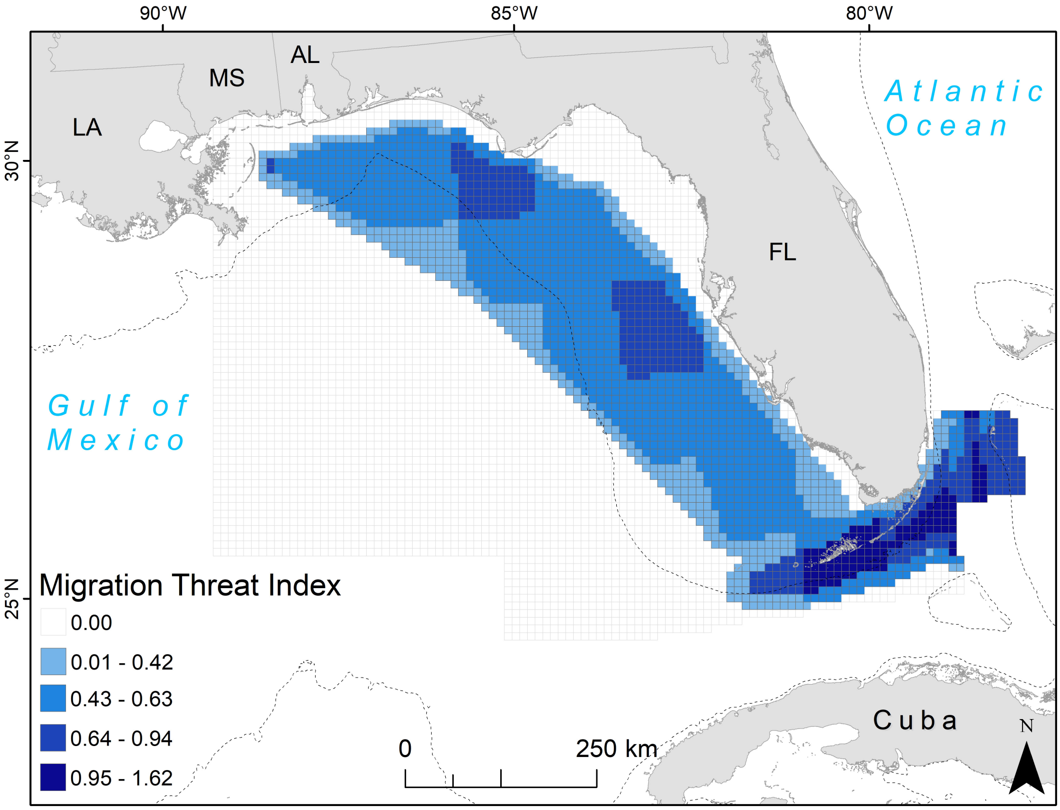

FIGURE 5 | Migration threat index for adult female loggerhead sea turtles (*Caretta caretta*; 64 tracks) after being tagged at nesting beaches throughout the Gulf of Mexico. The 10 km grid cells are color-coded by the threat index value, which accounts for the line KDE contour value in the cell and the value of three possible threats: commercial line fishing, shipping density, and shrimp trawling (see section Materials and Methods for more details). U.S. states are abbreviated: LA, Louisiana; MS, Mississippi; AL, Alabama; FL, Florida. The 200 m bathymetric contour is shown as a dashed line.

migratory period. Overall, it is imperative to understand migration patterns and threats for these highly mobile species, and our conservative estimate of threats provides valuable information for the management and recovery of loggerhead sea turtles.

DATA AVAILABILITY STATEMENT

The datasets generated for this study will not be made publicly available. Restrictions apply to the datasets. Raw data is exempt from publication due to the sensitivity of endangered species location information. Requests to access the datasets should be directed to the corresponding author. All other data used for analyses are presented in the manuscript.

ETHICS STATEMENT

The animal study was reviewed and approved by the United States Geological Survey-Southeast Ecological Science Center-Institutional Animal Care and Use Committee Protocol #2011-05.

AUTHOR CONTRIBUTIONS

AI and KH contributed to the conception and design of the study. KH acquired funding. KH and ML managed tag deployment and data collection. AI, AB, and IF organized the database and performed analyses. AI wrote the first draft of the manuscript. All authors contributed to manuscript revision, read and approved the submitted version.

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SUPPLEMENTARY MATERIAL

The Supplementary Material for this article can be found online at: https://www.frontiersin.org/articles/10.3389/fmars.2020.00208/full#supplementary-material

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ORIGINAL RESEARCH
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Brightness of the Night Sky Affects Loggerhead (*Caretta caretta*) Sea Turtle Hatchling Misorientation but Not Nest Site Selection

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Sea turtles in the Gulf of Mexico, which are listed as either threatened or endangered under the US Endangered Species Act, face numerous threats but are particularly susceptible to the negative effects of light pollution on nesting beaches. Light pollution affects the distribution, density, and placement of nests on beaches, and disrupts seafinding in hatchlings emerging from nests; often leading to their death. Rapid urban growth near Gulf Islands National Seashore (GUIS), FL, United States, over the last century has contributed to increased light pollution on its beaches. There is concern that light pollution is causing females to build nests in at-risk locations subject to erosion and flooding, and is causing the observed high rates of hatchling misorientation. From 2015 to 2016, we measured brightness of the night sky, horizon profile, and lunar variables at GUIS at loggerhead (*Caretta caretta*) nests to assess the effects of brightness on building of at-risk nests and hatchling misorientation. In addition, we quantified the effects of relocating at-risk nests on nest success. We found that contrast in brightness between the landward and seaward directions at GUIS was partially responsible for high rates of hatchling misorientation, and there was a strong moderating influence of lunar fraction and lunar altitude on hatchling misorientation: larger lunar fractions and lower lunar altitudes reduced misorientation. We did not find an effect of artificial light, horizon profile, or lunar fraction on the propensity of loggerheads to build nests in at-risk locations, and found no evidence that relocating nests at GUIS reduced loggerhead nest success. In fact, we found that nest success was improved and hatchling misorientation rates were reduced for relocated loggerhead nests.

Keywords: light pollution, loggerhead sea turtle nesting, hatchling misorientation, night sky brightness, *Caretta caretta*, nest relocation, nest success, Gulf Islands National Seashore

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INTRODUCTION

Five species of sea turtles occur in the Gulf of Mexico: Kemp's ridley (*Lepidochelys kempii*), loggerhead (*Caretta caretta*), green (*Chelonia mydas*), leatherback (*Dermochelys coriacea*), and hawksbill (*Eretmochelys imbricata*) (Valverde and Holzwart, 2017). Of these five species, two are listed under the US Endangered Species Act as threatened (*C. caretta* and *C. mydas*) and three are listed as endangered (*L. kempii*, *D. coriacea*, and *E. imbricata*) (Us Fish and Wildlife Service, 2019).

Sea turtles in the Gulf of Mexico face numerous threats including destruction of nesting and foraging habitats, incidental fisheries bycatch, entanglement in marine debris, vessel strikes, and the effects of artificial light pollution on nesting (Witherington et al., 2014). Light pollution is especially insidious due to the large number of individuals affected (Witherington, 1997). In particular, light pollution affects female placement of nests on the beach (Witherington, 1992a; Salmon et al., 1995a; Witherington et al., 2014; Price et al., 2018) and may lead to selection of sites subject to erosion or flooding, which are well-documented sources of egg mortality (Witherington, 1986; McGehee, 1990; Foley et al., 2006; Pike and Stiner, 2007; Ahles and Milton, 2016). Furthermore, it is well known that light pollution can disrupt seafinding [i.e., the tendency to move in the direction of the ocean; (Witherington et al., 2014)] of hatchlings emerging from nests, and cause misorientation [i.e., travel in any direction other than the general vicinity of the ocean; (Witherington et al., 2014)] leading to death by a variety of causes (McFarlane, 1963; Philibosian, 1976; Mann, 1978; Berry et al., 2013; Peterson et al., 2013; Witherington et al., 2014).

Gulf Islands National Seashore (GUIS), founded in 1971 and operated by the National Park Service (NPS), is located in the northeastern portion of the Gulf of Mexico and stretches across 256 km of coastline. All five species of Gulf sea turtles inhabit this region, and the beaches of GUIS are used by four of these species for nesting (hawksbill is excluded). In an effort to protect sea turtles nesting at GUIS, the NPS instituted a monitoring program in 1994. Daily beach surveys are conducted annually between May and October to identify all nesting events (i.e., non-nesting emergence, nest building, egg laying), relocate nests built in at-risk locations (e.g., below the tide line where they are susceptible to flooding or erosion), and monitor nests for predation, disturbance during incubation, and emergence of hatchlings to ensure (through redirection if necessary) they safely reach the Gulf of Mexico.

Over the course of the GUIS monitoring program, observations have suggested that selection of at-risk locations is common for loggerheads nesting at GUIS and may be increasing. Between 1996 and 2013, the percentage of at-risk nests that required relocation ranged between 20 and 78% of all nests (MN, Unpublished), and a linear regression of the data yields a positive slope of 2.66 and a 95% CI (1.47, 3.85) that does not overlap zero (TS, unpublished data); validating anecdotal observations that there has been an increase over time. Likewise, observations have suggested that misorientation in hatchlings is frequent at GUIS: from 2010 to 2018 the percentage of nests with misoriented hatchlings averaged 62% (MN, Unpublished).

Because rapid urban growth near GUIS over the last century has contributed to increased light pollution on its beaches, there is speculation by park biologists that light from anthropogenic sources is negatively influencing nest site selection by females and is causing the high rates of hatchling misorientation. However, no quantitative data exploring the association between light pollution and sea turtle nesting at GUIS have been collected. Hence, our objectives were to characterize brightness and illuminance of the night sky and assess its effects on loggerhead sea turtle nesting and hatchling misorientation on beaches at GUIS. We accomplished this by taking light measurements in a pattern covering the entire sky and horizon profile measurements at loggerhead nests the night after a nest was built and at the time hatchlings emerged from nests. This approach was novel in that, unlike other studies where only four directional measurements were taken (e.g., Salmon et al., 1995b; Price et al., 2018), the multiple nest-centered directional measurements allowed us to evaluate hypotheses regarding the range of vertical and horizontal directions from which a turtle might be perceiving light. We then used the directional light data to model the probability a nest was built in an at-risk location and the probability hatchlings were misoriented. In addition, we evaluated the effects of relocating nests on hatchling production and misorientation to quantify any possible negative effects.

MATERIALS AND METHODS

Study Site and Nest Monitoring

This study was conducted at GUIS, Florida District, near Pensacola Beach, Florida. Sea turtle nests have been monitored annually at GUIS since 1994 at three distinct areas: Fort Pickens (12.3 km of shoreline), Perdido Key (11.2 km of shoreline), and Santa Rosa Island (12.2 km of shoreline). In addition, and despite not being part of GUIS, nests at Pensacola Beach (12.9 km of publicly owned shoreline) were also monitored.

During 2015 and 2016, sea turtle nests were discovered at these four locations during daily beach surveys to locate sea turtle tracks emerging from the water and leading to a nest depression in the sand. Surveys began before 0600 h, were conducted beginning May 1, and continued through October.

When a nest was discovered an assessment was made by GUIS biologists to determine if the nest was at-risk of erosion or flooding. This at-risk determination was based on distance from the Gulf, elevation of the nest relative to the high tide line, slope of the beach, and local knowledge and experience. When a nest was considered by GUIS biologists to be at-risk it was relocated to a more suitable site, typically directly north of the nest, higher on the beach, near the primary dune line using established protocols (**Appendix**).

In general, loggerhead egg incubation time varies between 50 and 70 days (MN, Unpublished). Beginning on the 50th day after their discovery nests were monitored daily until signs of hatching appeared, whereupon nests were monitored continuously by trained volunteers until the nest hatched. Signs of hatching typically included a cone or depression in the sand, indicating the turtles were digging their way out and the cavity was slowly collapsing, or scratching noises that could be heard by placing one's ear on a towel laid over the sand near the nest, and listening. Once hatchlings emerged from the nest observers determined the direction of travel, and if they began to crawl in a direction that was clearly away from the Gulf they were placed in a bucket and counted before release into the Gulf. Since its inception in 1994 the GUIS sea turtle monitoring program has classified hatched nests as misoriented if more than 25% of the hatchlings appeared misoriented. Consequently, in the interest of continuity with standardized procedures and established reporting, we adopted this same threshold for our analysis.

Seventy-two hours after the initial hatching event, nests were assessed by GUIS biologists. Assessments were conducted after dusk to ensure that any turtles found alive in the nest cavity could be released immediately into the Gulf of Mexico. The nests were excavated and the number of live or dead hatchlings in the cavity were recorded along with any unhatched eggs. The unhatched eggs were opened to determine the stage of embryological development. Hatchlings found alive in the nest cavity were immediately released into the Gulf of Mexico, and any hatchlings that had broken partly through their egg shells, or "pipped" and were alive, were held in a cooler of sand until their carapaces uncurled. These hatchlings were held until they fully emerged from the eggshell and absorbed external yolk into their abdomen. Once ready, hatchlings were released into the Gulf of Mexico after sunset.

This study, and the field protocols affecting sea turtles, were approved by and carried out in accordance with the recommendations of the National Park Service (permits: GUIS-2014-SCI-0029, GUIS-2016-SCI-0037, GUIS-2017-SCI-001, GUIS-1017-SCI-0012, GUIS-2018-SCI-0001) and the Florida Fish and Wildlife Conservation Commission (permits: 18-830_CP_RP#811 and 17-830_CP_RP).

Light Intensity and Horizon Profile Measurements

Night sky light intensity data and horizon profile measurements for nests discovered were collected by recruiting local middle school, high school, and college students as citizen scientists under the guidance of GUIS personnel. Measurements at newly built nests were usually collected the night after discovery, began after astronomical twilight, and typically took 1 h to complete. Measurements at hatched nests were usually collected the night of hatching, but no later than 72 h after hatching. This 72 h post-hatching sampling window was necessary because the hatchling monitoring and the light measurement teams in this study were distinct. Because the exact time hatchlings emerge from a nest is inherently unpredictable, and because multiple nests might hatch on the same night, the light measurement team was sometimes unable to measure light intensity the night of hatching. Operationally, this resulted in 42% of the nests being sampled the night of hatching, and 39%, 10%, and 9% of the nests being sampled one, two, or three nights post-hatching, respectively.

We note that sampling after the night of hatching may introduce light intensity measurement error, due to differences in moonrise, lunar fraction, lunar altitude, or cloud cover. However, because lunar variables change slowly and predictably, it was our judgment that taking light intensity measurements as close to the night of hatching as possible, but within a 72 h window, would yield measurements similar enough to those at hatching that there would be little information loss. Likewise, within that 72 h window, we strived to sample on nights with cloud cover conditions that were similar enough to conditions on the night of hatching that there would likely be little information loss.

Citizen scientists collected light measurement data using two Unihedron Sky Quality Meters (with Lens, hereafter denoted as SQM; Unihedron, Grimsby, Ontario, Canada). The first SQM was left unfiltered and was sensitive to a broad spectrum of light (300–700 nm range, hereafter denoted as white light) while the second SQM was fitted with a Baader light blue bandpass filter with peak transmission at 470 nm (hereafter denoted as blue light), mounted ∼55 cm above the beach surface on a tripod with a leveler. We included blue light measurements in this study because there is evidence hatchlings are particularly sensitive to blue wavelengths, hence light pollution with greater blue spectral power may be a better predictor of misorientation than white light. The SQM-tripod unit was used to measure white and blue light intensity 360° around the horizontal plane (in 15° increments), and at vertical altitudes of 10°, 20°, 45°, 75°, and 90° (i.e., zenith), to obtain hemispheric measurements covering the night sky (the sensor detection cone has an angle of 20°). Each tripod was also equipped with a laser pointer that could be aimed at the top of dunes or buildings or other structures to obtain a horizon profile (degrees vertical altitude) over a 360°circle (in 15° increments).

Data and Statistical Methods

We modeled the binary response variables for at-risk nests at nest sites (1 if the nest was built in a location at-risk for flooding or erosion, 0 otherwise) and misorientation at hatched nests (1 if $>$ 25% of the hatchlings appeared misoriented, 0 otherwise) using logistic regression with predictor variables such as year and site, and other variables we describe below. We included only nesting data for the more common loggerhead sea turtles in our analyses because only four green sea turtle nests, four Kemp's ridley sea turtle nests, and one leatherback sea turtle nest were discovered in 2015 and 2016 combined. Furthermore, Kemp's ridley sea turtles generally nest during the day (Shaver and Rubio, 2008; Shaver et al., 2016) when the effects of night sky light intensity are irrelevant.

Two lunar variables included as predictors in our analysis were *lunar fraction* and *lunar altitude*. We considered *lunar fraction* to be important because it is an index of the moon's brightness and moonlight is a natural cue that aids hatchling seafinding (Tuxbury and Salmon, 2005); we considered *lunar altitude* to be important because the moon is brightest near moonrise and moonset (Witherington, 1992b; Witherington et al., 2014) and altitude affects reflected light from surfaces like sand or water. We let *lunar fraction* take values over the interval [0, 1] (0 = new moon, 1 = full moon), and *lunar altitude* (for the misorientation analysis only) at the time of sampling take values over the interval $[-1, 1]$ using the divisor 83.18°: the maximum possible lunar altitude at GUIS. Negative values for *lunar altitude* indicate the moon was below the horizon during sampling. Because the moon likely has no appreciable effect on risk or misorientation if it is below the horizon (Salmon and Wyneken, 1990; Witherington, 1992b), for our analysis we multiplied *lunar fraction* by an indicator variable that was set to 1 if the moon was above the horizon, and 0 otherwise. We obtained *lunar fraction* and *lunar altitude* values using the R suncalc package (R Core Team, 2017; Agafonkin and Thieurmel, 2018) and supplying the date and time (at the approximate midpoint) during which SQM measurements were made.

Witherington et al. (2014) described a useful concept for characterizing the portion of the world measured (detected) by a directional light sensor, which they call an "acceptance cone." The acceptance cone can be decomposed into both a horizontal and vertical "angle of acceptance" (AOA) which, with respect to a sea turtle, describe the range of directions from which light can be perceived (i.e., a subset of its effective field of view). We used this concept below to define subsets of data over which light intensity and horizon profile measurements were aggregated to construct predictor variables.

From the azimuth-specific horizon profile data we computed the *mean horizon* and *maximum horizon* values (in degrees altitude) from a subset of our data (described below) representing the horizontal AOA. These values were used as predictor variables for both the nest-at-risk and misorientation analyses.

For each nest site and hatched nest, we recorded 53 measurements of white light intensity and 53 measurements of blue light intensity. The SQM sensor records light intensity in magnitudes per square arcsecond and is a measure of brightness, an inverse logarithmic metric where smaller SQM readings indicate more light is hitting the sensor than larger SQM readings. We used azimuth-specific SQM data collected at a vertical altitude of 10° to compute the *mean SQM* and *minimum SQM* values (smaller values equate to brighter light) for white and blue light, and the landward minus seaward differences in these statistics (i.e., a measure of "contrast"), from a subset of our data (described below) representing the horizontal AOA. Because the SQM sensor detection cone has an angle of 20°, our measurements taken at an altitude of 10° integrate light intensity from 0° (i.e., the horizon) to 20° altitude into the SQM reading, and therefore the vertical AOA is 20°. For convenience, we will hereafter refer to these data as the 10° SQM data. There is some evidence from the literature that light closest to the horizon plays the greatest role in determining orientation direction in sea turtles (Witherington et al., 2014). For loggerheads, studies suggest that the light from 10° below the horizon to 30° above the horizon is what they are keying in on (Salmon and Wyneken, 1990; Witherington, 1992b). Consequently, we also computed the *mean SQM* and *minimum SQM* statistics from what we will hereafter refer to as the 20° SQM data, which includes both the 10° and 20° vertical altitude data so that the SQM readings integrate light from 0° to 30° altitude into the SQM reading. Thus, 30° represents the vertical AOA. We use both the 10° SQM data and 20° SQM data to construct predictor variables used in our analyses.

In addition to the SQM predictor variables, we converted the hemispheric SQM luminance measurements into 24 azimuth-specific illuminance values (in micro-lux units) using sine and cosine corrections (Duriscoe, 2016). These measures integrate light intensity measurements from 10° altitude (nearest to the horizon) to 90° altitude (zenith) into the illuminance value, and therefore the vertical AOA is 90°. We then used the azimuth-specific illuminance data to compute the *mean illuminance* and *maximum illuminance* values (log transformed; higher illuminance values indicate brighter light) for white and blue light, and the landward and seaward contrast in these statistics, from a subset of our data (described below) representing the horizontal AOA.

For the white and blue light SQM and horizon profile data for each nest a set of 24 azimuth-specific values were recorded at: 0° (true north), 15°, . . . 180° (south), . . . and 355°. Thus, we need a meaningful way of aggregating these data to characterize what a female loggerhead might perceive as she searches for a nesting site or during a hatchling's crawl to the Gulf of Mexico, but that does not impose arbitrary structure that might constrain the results. Because an adult female requires land to build a nest and a hatchling sea turtle needs to find its way to the Gulf, a natural starting point for our analysis is to distinguish between the landward and seaward data subsets.

The coast of GUIS is approximately angled such that it is oriented from 75° to 255°. Thus, we define landward as 255°–75° (inclusively, with 345° perpendicular to the shore) and seaward as 75°–255° (inclusively, with 165° perpendicular to the shore). Data were then classified so that the azimuth-specific horizon profile and light data could be meaningfully aggregated by direction.

In this study, rather than select a single subset of azimuths and analyze only those, we chose to define multiple subsets each representing the horizontal AOA over which we aggregated our azimuth-specific horizon profile, SQM, and illuminance data (**Table 1**). We accomplished this by specifying a set of azimuths, centered on the landward and seaward azimuths that are perpendicular to the shoreline (i.e., 345° and 165°, respectively), to define the horizontal AOAs considered in our analysis (**Table 1**).

Given our full set of predictor variables, we evaluated a total of 728 nest-at-risk models and a total of 288 hatchling misorientation models (with both additive and interactive effects), and we used information-theoretic model selection procedures (i.e., AICc; Akaike's Information Criterion – corrected for small sample size) to identify the set of models best supported by the data (Burnham and Anderson, 2002). We also used AICc to evaluate whether there was support in the data for a favored AOA, and whether there was evidence that blue light was a better predictor of risk or misorientation than white light.

RESULTS

Relocation Effects on Nesting

In 2015, 44.6% of all loggerhead nests (total nests = 65) were relocated and in 2016, 68.6% of all loggerhead nests (total nests = 102) were relocated. The percent nest success (a nest was successful if at least one hatchling emerged from the nest and is the opposite of complete nest failure), the percent hatching success (hatched eggs/total eggs), the percent emergence success (emerged hatchlings/total eggs), and the percentage of successful nests with >25% misoriented hatchlings, were calculated for relocated and non-relocated nests (**Table 2**). As a general pattern, hatching and emergence success rates for relocated nests were higher than for non-relocated nests, and the hatchling misorientation rate was lower for relocated nests than for non-relocated nests. We ran a *year* + *relocated* logistic regression model on these data and found the Wald Chi-Square for the *relocated* variable had $p < 0.014$ for all four of the relocation effects (**Table 2**).

Nest-at-Risk Models

For our analysis of factors influencing the probability a nest was built in an at-risk location, no strongly supported predictor variables were found. Indeed, among the set of models that do not involve an AOA we found the null model (i.e., intercept only) was most strongly supported by the data (i.e., it had the lowest AICc), with the *year* and *lunar fraction* models being somewhat competitive (i.e., their AICc values were within 2 units of the null model; **Table 3**).

Among the set of models that do involve an AOA, two models had AICc values slightly lower than the null model (**Table 4**). The best model had an interaction between *mean horizon altitude* (*mha*) and *lunar fraction* (*lf*) at a 170° AOA [β (95% CI): $\beta_{mha} = -0.196$ (−0.390, −0.028), $\beta_{lf} = -0.834$ (−2.51, 0.749), $\beta_{mha*lf} = 0.313$ (0.041, 0.641)]; and generally indicated the probability a nest was built in an at-risk location increased as *mean horizon altitude* and *lunar fraction* increased, except that when *mean horizon altitude* was near zero the probability decreased (**Figure 1**). For comparison, we also report the simpler additive model with these same variables (**Table 4**).

TABLE 1 | Horizontal angles of acceptance and the associated azimuths over which the horizon profile, SQM, and illuminance data were aggregated to construct predictor variables.

Horizontal angle of acceptance	Landward azimuths	Seaward azimuths
50°	330°–0°	150°–180°
80°	315°–15°	135°–195°
110°	300°–30°	120°–210°
140°	285°–45°	105°–225°
170°	270°–60°	90°–240°

Because the SQM sensor detection cone is 20°, the angle of acceptance is 20° larger than the angle formed by the azimuths. For example, if the sensor is pointing at 330° then it's also detecting light from the 320° azimuth, and if it's pointing at 0° it's also detecting light from the 10° azimuth, so adding 20° to the angle formed by the azimuths accounts for this.

TABLE 2 | Nest relocation effects on loggerhead (*Caretta caretta*) nesting.

	2015		2016	
	Not-relocated	**Relocated**	**Not-relocated**	**Relocated**
Nest success	97.0% (36)	100% (29)	62.5% (32)	95.7% (70)
Hatching success	76.3% (23)	85.5% (25)	65.0% (28)	77.2% (36)
Hatchling emergence success	72.3% (23)	82.3% (25)	60.7% (28)	73.3% (36)
Successful nests with misoriented hatchlings	84.4% (32)	55.2% (29)	80.0% (20)	67.2% (67)

Values are percentages (number of nests).

TABLE 3 | Model selection results for nest-at-risk models that do not involve an angle of acceptance.

Model	AICc	k
Null	**202.70**	1
Year	204.11	2
Site	207.09	4
Year*site	212.62	8
Lunar fraction	203.66	2

Lower AICc values indicate the associated model has better support from the data than models with higher AICc values, k denotes the number of estimated parameters in the model. All models included an intercept, the bolded value is the AICc for the best model.

The second-best model had a variable representing the contrast between landward (*lw*) and seaward (*sw*) blue light brightness, computed as $min(SQM_{lw}) - min(SQM_{sw})$ (170° AOA, 10° SQM data) (**Table 4**). Hereafter, we will refer to this variable as *SQMcontrast*. The 95% CI on the estimated parameter for *SQMcontrast* overlapped zero [β (95% CI): β = 0.242 (−0.073, 0.580)], suggesting the variable was not a good predictor for risk. For comparison with this model, we also report the equivalent model based on the 20° SQM data and the illuminance data (where $illumcontrast = \log(\max(illuminance_{lw})) - \log(\max(illuminance_{sw}))$), as well as the equivalent models for white light (**Table 4**). For all models we present the results for the full set of AOAs evaluated, allowing us to determine whether there was evidence for a preferred AOA. Finally, we ran a more complex model that combined the variables from the two best AOA models and got AICc = 203.75 ($k = 5$), which offered no improvement over the null model.

Hatchling Misorientation Models

Our analysis of factors influencing the probability that hatchlings were misoriented yielded multiple models with strongly supported predictor variables. Among the set of models that did not involve an AOA, we found an additive model with the variables *lunar fraction* (*lf*) and *lunar altitude* (*la*) to be the model most strongly supported by the data (**Table 5**), and in both cases the 95% confidence intervals on the parameter estimates did not overlap zero [β (95% CI): $\beta_{lf} = -3.425$ (−5.180, −1.887), $\beta_{la} = 4.124$ (0.919, 7.768)]. This suggests the variables were useful predictors for the probability hatchlings were misoriented. The *lunar fraction* * *lunar altitude* interaction model was also competitive, and both this model and the additive model were vastly better than the null model (**Table 5**).

Among the set of models that do involve an AOA, an additive model generalizing the top model was vastly superior to all other models we tried. Specifically, this model included the *lunar fraction* (*lf*) and *lunar altitude* (*la*) variables and also *SQMcontrast* (80° AOA, 10° SQM data; **Table 6**). For all three variables in this model the 95% confidence intervals on the parameter estimates did not overlap zero [β (95% CI): $\beta_{lf} = -2.327$ (−4.190, −0.594), $\beta_{la} = 6.179$ (2.493, 10.429), $\beta_{SQMcontrst} = -1.010$ (−1.655, −0.442)]; indicating the variables were useful predictors for the probability hatchlings were misoriented and generally showed that the probability of

TABLE 4 | Model selection results for nest-at-risk models that involve an angle of acceptance (AOA).

	AICc values by horizontal AOA					
Model	**50°**	**80°**	**110°**	**140°**	**170°**	***k***
Horizon profile data						
Mean horizon altitude + lunar fraction	204.35	204.53	204.35	204.27	204.40	3
Mean horizon altitude *lunar fraction	203.42	203.64	202.66	202.33	**202.15**	4
10° SQM data						
SQMcontrast (white light)	204.59	204.45	204.09	203.83	203.08	2
SQMcontrast (blue light)	204.06	204.61	204.46	203.89	**202.52**	2
20° SQM data						
SQMcontrast (white light)	204.57	204.49	204.16	204.03	203.75	2
SQMcontrast (blue light)	204.58	204.62	204.53	204.14	203.77	2
Illuminance data						
Illumcontrast (white light)	204.37	204.33	204.22	204.10	204.01	2
Illumcontrast (blue light)	204.43	204.38	204.34	204.24	203.95	2

Lower AICc values indicate the associated model has better support from the data than models with higher AICc values, k denotes the number of estimated parameters in the model. All models included an intercept, the bolded values are the AICc values for the two best models.

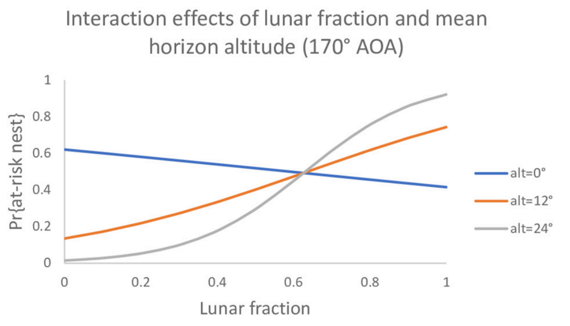

FIGURE 1 | The probability a loggerhead (*Caretta caretta*) nest was built at an at-risk location under a model with main effects and an interaction between *mean horizon altitude* and *lunar fraction* at a 170° angle of acceptance (AOA).

TABLE 5 | Model selection results for hatchling misorientation models that do not involve an angle of acceptance.

Model	**AICc**	***k***
Null	173.78	1
Year	175.73	2
Site	173.97	4
Year * site	177.66	8
Lunar fraction	159.36	2
Lunar fraction + lunar altitude	**154.92**	3
Lunar fraction * lunar altitude	155.13	4

Lower AICc values indicate the associated model has better support from the data than models with higher AICc values, k denotes the number of estimated parameters in the model. All models included an intercept, the bolded value is the AICc for the best model. The additive lunar fraction + lunar altitude model has the lowest AICc value and is the top ranked model; larger lunar fractions and lower lunar altitudes reduced misorientation.

misorientation decreased as *lunar fraction* increased, increased as *lunar altitude* increased, and decreased as *SQMcontrast* increased (i.e., it became more positive; **Figure 2**). Models with two-way and three-way interaction terms between these three variables had larger AICc values than the purely additive model.

For comparison with the top model, we included the equivalent models run on the 20° SQM data and the illuminance data (**Table 6**). We also included the single variable *SQMcontrast* white and blue light models for the 10° SQM data and 20° SQM data, and the *illumcontrast* white and blue light models. For all models we present the results for the full set of AOAs evaluated, allowing us to determine whether there was evidence for a preferred AOA. Finally, we do not present any models using the horizon profile data because the best model, which was the single variable *max*(*horizon*) model, had an AICc of 175.47 and was less supported by the data than the null model (AICc = 173.78).

For predicting the probability a hatchling was misoriented on any particular night, our data suggested the top model was the best to use (**Table 6** and **Figure 2**). However, the *lunar fraction* and *lunar altitude* variables in this model are not something over which we can exert any control. It is only the landward and seaward contrast variable, *SQMcontrast*, that we can exert influence over and we generally have more control over the landward brightness than the seaward brightness. Because the degree of control we must exert over landward brightness will likely differ on moonlit vs. moonless nights, we ran the *SQMcontrast* (white light) model using the 10° SQM data (80° AOA) separately on moonlit vs. moonless nights. We found on moonlit nights the parameter estimates (95% CI) were 0.399 (−0.110, 0.923) for the intercept and −0.897 (−1.520, −0.379) for the SQM contrast variable; whereas on moonless nights the estimates were −0.397 (−1.902, 0.977) for the intercept and −1.214 (−2.333, −0.317) for the contrast variable. Because the 95% CIs on the *SQMcontrast* parameters under both models do not overlap zero, both models are useful for predicting the hatchling misorientation we observed in this study. These models generally show the probability of misorientation decreases as *SQMcontrast* becomes more positive, and for *SQMcontrast* >-2.0 the probabilities for moonlit and moonless nights diverge (**Figure 3**).

DISCUSSION

Hatchling Results

We found three variables were strongly associated with the probability of hatchling misorientation: *lunar fraction*, *lunar altitude*, and *SQMcontrast* (the difference in white light intensity

TABLE 6 | Model selection results for hatchling misorientation models that involve an angle of acceptance (AOA).

	AICc values by horizontal AOA					
Model	**50°**	**80°**	**110°**	**140°**	**170°**	***k***
10° SQM data						
SQMcontrast (white light)	158.12	151.74	154.10	153.75	155.36	2
SQMcontrast (blue light)	158.07	156.08	154.77	154.38	155.71	2
Lunar fraction + lunar altitude + SQMcontrast (white light)	150.22	**143.70**	146.30	147.64	149.57	4
20° SQM data						
SQMcontrast (white light)	159.06	155.45	156.87	155.95	156.32	2
SQMcontrast (blue light)	159.70	158.75	156.57	155.27	155.91	2
lunar fraction + lunar altitude + SQMcontrast (white light)	148.21	145.33	146.39	146.78	147.27	4
Illuminance data						
Illumcontrast (white light)	163.11	156.76	157.39	157.33	158.14	2
Illumcontrast (blue light)	163.83	158.73	158.25	157.80	159.04	2
Lunar fraction + lunar altitude + illumcontrast (white light)	150.18	146.18	146.04	146.21	146.77	4

Lower AICc values indicate the associated model has better support from the data than models with higher AICc values, k denotes the number of estimated parameters in the model. All models included an intercept, the bolded value is the AICc for the best model. The additive lunar fraction + lunar altitude + SQMcontrast (white light) model has the lowest AICc value and is the top ranked model; larger lunar fractions, lower lunar altitudes, and larger SQMcontrast values reduced misorientation.

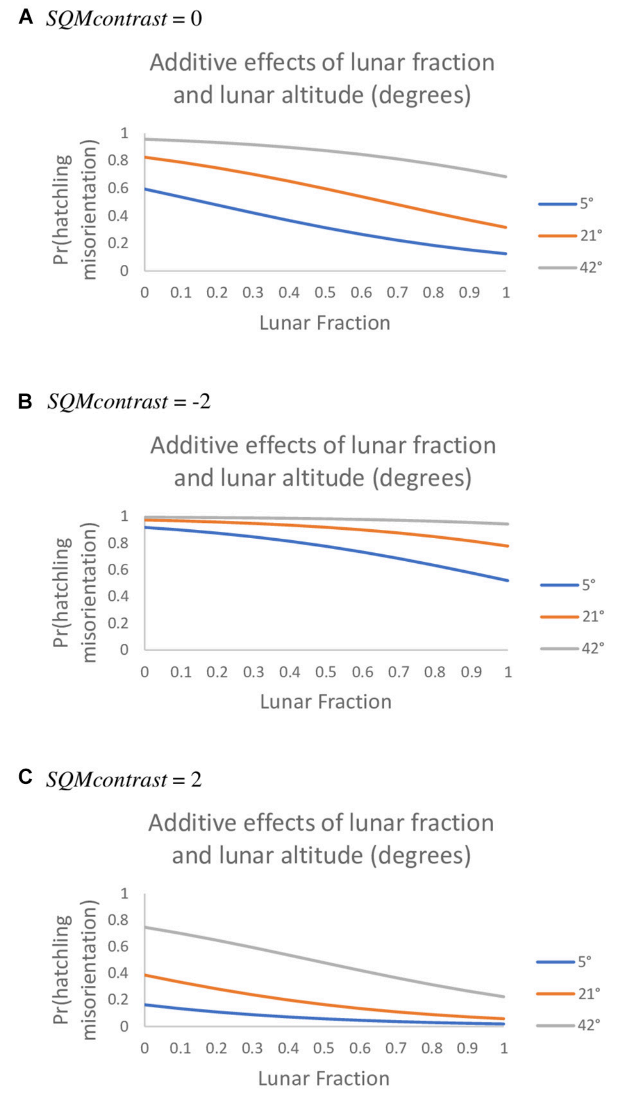

FIGURE 2 | The probability loggerhead (*Caretta caretta*) hatchlings were misoriented under an additive model with the predictor variables *lunar fraction*, *lunar altitude*, and *SQMcontrast* values of 0 **(A)**, −2 **(B)**, and 2 **(C)** (80° AOA, 10° SQM data, observed range was −5.0 to 2.7).

between the landward and seaward directions). That these variables were useful predictors was not surprising. There is ample laboratory and field evidence suggesting that brightness is an important seafinding cue (Daniel and Smith, 1947; Hendrickson, 1958; Mrosovsky and Shettleworth, 1968; Lorne and Salmon, 2007; Harewood and Horrocks, 2008; Berry et al., 2013), and it is known that, in the absence of artificial light, celestial light is reflected by the ocean and hatchlings naturally orient seaward (Mrosovsky and Shettleworth, 1968; Van Rhijn and Van Gorkom, 1983; Tuxbury and Salmon, 2005; Witherington et al., 2014). However, when artificial lighting is present hatchlings may become misoriented and have difficulty finding their way to the sea, but this will differ depending on moon phase (Salmon and Witherington, 1995; Lohmann et al., 1996; Tuxbury and Salmon, 2005; Berry et al., 2013).

When we consider only the *lunar fraction* and *SQMcontrast* variables we found the probability of misorientation was greater during a new moon than during a full moon but that, regardless of moon phase, misorientation was greater when landward brightness exceeded seaward brightness (i.e., *SQMcontrast* < 0; **Figure 2B**) than when the reverse was true (i.e., *SQMcontrast* > 0; **Figure 2C**). Salmon and Witherington (1995) obtained a similar result – most misorientation occurred on dark evenings near a new moon – and showed there was a significant inverse relationship between the frequency of misorientation and the number of days from the closest new-moon. Also like us, Rivas et al. (2015) found that the effect of artificial lighting on leatherback hatchling orientation was reduced in the presence of moonlight. Our data, along with those of Salmon and Witherington (1995) and Rivas et al. (2015), suggest there is a tension between levels of natural and artificial light that, depending on their relative brightness, influences the degree to which misorientation occurs. This tension is succinctly captured in the cue competition hypothesis of Tuxbury and Salmon (2005), which postulates a tradeoff between natural cues and the perceived magnitude of artificial light and its effect

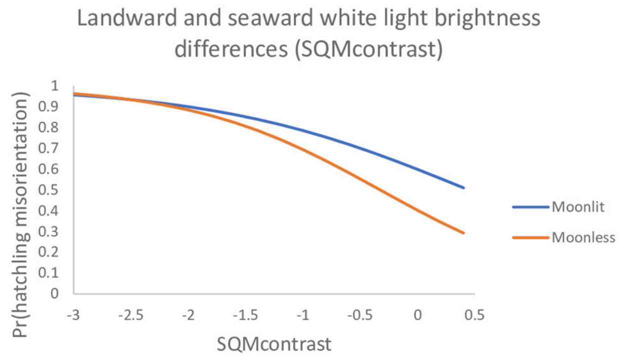

FIGURE 3 | The probability loggerhead (*Caretta caretta*) hatchlings were misoriented on moonlit vs. moonless nights under a model with *SQMcontrast* only (80° AOA, 10° SQM data). Data are plotted only over the range of *SQMcontrast* values actually observed in both subsets of the data. The full range observed for both data sets combined was −5 to 2.7.

on misorientation during a new moon vs. full moon. Our results generally support the Tuxbury and Salmon (2005) cue competition hypothesis, except our data suggest it is the contrast between landward and seaward light that is important, not just the absolute magnitude of artificial light.

The third variable we found associated with hatchling misorientation probabilities was *lunar altitude*; with misorientation probabilities increasing as *lunar altitude* increased (**Figure 2**). To our knowledge the effects of *lunar altitude* on misorientation have not previously been investigated in an explicit manner, and we found no studies that corroborate our findings or offer explanations for why this might occur. Nevertheless, we pose two hypotheses to explain the pattern we observed.

Because the coastal orientation at GUIS is ∼75°–255° the azimuth of the moon, when it is visible, typically puts it over the waters of the Gulf. Indeed, this was the case for all 80 of the hatching nests we monitored when the moon was visible, the azimuth of the moon placed it over the water. Thus, we hypothesize that, due to the amplifying effect on brightness of moonlight scattering off the surface of the water, at a lower *lunar altitude* the moon provides a stronger directional cue (*sensu* Witherington et al., 2014) toward the Gulf than it does at a higher *lunar altitude*, where scatter off the water will be more diffuse and the directional cue weaker. If true, then at GUIS we would expect the probability of misorientation to be lower at a lower *lunar altitude* and higher at a higher *lunar altitude*, as we observed.

As noted earlier there is evidence that light closest to the horizon plays the greatest role in determining orientation direction in sea turtles (Witherington et al., 2014), and that for loggerheads it is thought light from 10° below the horizon to 30° above the horizon is what they are keying in on (Salmon and Wyneken, 1990; Witherington, 1992b). Thus, our second hypothesis for the observed association between *lunar altitude* and misorientation is that at higher lunar altitudes the moon exceeds the vertical AOA for loggerheads, and therefore is effectively not perceived by them. For example, if we assume the vertical AOA is 30° above the horizon for loggerheads, then in our sample of 80 nests 49% of those nests hatched when the *lunar altitude* exceeded 30° (maximum *lunar altitude* in this study was 47°). Consequently, for our example, we would expect that for 49% of the nests in our study the moon would offer little to no directionality guiding hatchlings toward the Gulf. We note our two hypotheses regarding *lunar altitude* are not mutually exclusive and could be operating simultaneously.

As part of our analysis we fit a simple *SQMcontrast* (white light) model to hatchling misorientation data partitioned into moonlit and moonless nights. We did this to isolate the variable we can exert some control over (*SQMcontrast*) from the variables we cannot exert control over (*lunar fraction*, *lunar altitude*). Examination of the plots for these models show interesting features (**Figure 3**). First, for *SQMcontrast* < -2 the plots are somewhat flat and are essentially indistinguishable. What this tells us is that landward brightness in this region of the plot is so great it is overwhelming lunar effects, and that management actions to decrease landward brightness will be mostly ineffective until *SQMcontrast* exceeds −2.0. Second, the slope of the curve on moonless nights (−1.214) is more negative than on moonlit nights (−0.897). What this tells us is that management actions that decrease landward brightness will be more effective on moonless nights that on moonlit nights – all else being equal. Lastly, if management actions decrease landward brightness successfully, bringing it to levels equal to seaward brightness (i.e., *SQMcontrast* = 0), then misorientation probabilities will be lower but still unacceptably high (0.60 on moonlit nights and 0.40 on moonless nights). Consequently, it will be necessary to strive for *SQMcontrast* > 0 especially on moonlit nights. Our findings are unique from those of other studies in that we quantitatively identify thresholds, or transition points, identifying conditions under which controlling light pollution might be most effective. Whereas Witherington et al. (2014) suggested the higher levels of ambient light on moonlit nights may lessen the relative contribution of artificial light sources to the light fields that hatchlings perceive, they did not provide quantitative data regarding what the relative contributions might be. We believe our data are particularly informative with respect to the Tuxbury and Salmon (2005) cue competition hypothesis – which they presented abstractly without quantitative thresholds – because we report quantitative thresholds that are prospective management targets under the cue competition hypothesis. Lastly, as we noted in the methods, it is possible that the 72-h post-hatching sampling window we adopted for light intensity measurements introduced measurement error. Because we could not account for measurement error explicitly in our models it could have inflated the model deviance, thereby reducing statistical power for detecting the effects of light intensity on misorientation. Consequently, our hatchling misorientation results are likely conservative, meaning the influence of light intensity (i.e., *SQMcontrast*) had to be relatively strong for us to detect it.

For hatchling misorientation the best model was the *lunar fraction*, *lunar altitude*, *SQMcontrast* model with AICc = 143.70 (**Table 6**). Because models with AICc values within 2 units of the best model are considered to have substantial empirical support, whereas models with AICc values >4 units from the best model have considerably less empirical support (Burnham and Anderson, 2002), we can gain insights into whether loggerheads have a preferred AOA or are more sensitive to blue light than white light by comparing AICc among certain models.

We assessed the horizontal AOA by comparing among models in same row as the best model, which were identical in every way except for their horizontal AOA. Doing this we found none of the models were within two AICc units of the best model, the 110° and 140° AOA models were between two and four AICc units away, and the 50° and 170° AOA models were >4 units away. This suggests that the horizontal AOA for loggerheads was probably $>50°$ but $<170°$ and was probably closer to 80° than it was to 110° or 140°. We note that this range is much narrower than the 180° reported by Witherington et al. (2014).

We assessed the vertical AOA by comparing among the *lunar fraction*, *lunar altitude*, *SQMcontrast* models in the same column as the best model, which were identical in every way except for their vertical AOA. Doing this we found for the 20° SQM data the model was within two AICc units of the best model (AICc = 145.33), but for the illuminance data the model was >2 units from the best model (AICc = 146.18; **Table 6**). This suggests, albeit weakly, that a vertical AOA closer to 20° or 30° was better supported by the data than the vertical AOA of 90°captured by the illuminance data, and is consistent with the 10° below the horizon to 30° above the horizon values suggested by others (Salmon and Wyneken, 1990; Witherington, 1992b).

We included blue light measurements (at 470 nm) in this study because of evidence hatchlings are particularly sensitive to blue wavelengths (Witherington, 1992b, 1997; Lohmann et al., 1996; Witherington et al., 2014), with a peak behavioral sensitivity near 500 nm (Witherington, 1992b). Hence, we hypothesized light pollution with strong blue spectral power may be a better predictor of misorientation than white light pollution. However, when we compared AICc values for the *SQMcontrast* (white light) models with the AICc values for the *SQMcontrast* (blue light) models, we found no evidence that blue light was a better predictor of misorientation than white light. Of the 15 within-AOA comparisons, in only two cases were the AICc differences >2.0 units, and in both of those cases the AICc for the white light model was lower (**Table 6**). The wavelength, intensity, direction and color of light, as well as shapes of visible objects like dunes or vegetation, all provide cues to orienting sea turtle hatchlings (Witherington et al., 2014). The failure in our study to show blue light was a better predictor of misorientation than white light may have been caused by the presence of conflicting unmeasured cues. For example, in experiments loggerheads were found to be most strongly attracted to light in the near-ultraviolet to green region and showed an aversion response to light in the yellow region of the spectrum (Lohmann et al., 1996; Witherington, 1997). It is possible, therefore, that wavelengths other than the 470 nm wavelength we measured were both present and brighter and thus had a stronger influence on hatchling orientation. Alternatively, because our study was *in situ* and not a controlled laboratory experiment, there may have simply been too much environmental variation present to detect an effect with our sample sizes.

Nests-at-Risk Results

With respect to adult nest placement we investigated a very specific question: what factors were associated with female loggerheads selecting an at-risk location to build their nest rather than a not-at-risk location? Whereas several studies have assessed the effects of lighting and light intensity on the distribution, density, and placement of sea turtle nests on beaches (Witherington, 1992a; Salmon et al., 1995a; Witherington et al., 2014; Price et al., 2018), we are not aware of any studies that have addressed our specific question.

Despite the fact that we considered several predictor variables aggregated over multiple different horizontal and vertical AOAs, and evaluated 728 distinct models, we found none of the variables or models we evaluated were good predictors for the probability a female built a nest in an at-risk location. We base this conclusion primarily on the fact that the two best models (**Table 4**) had AICc values that were only marginally better than the AICc for null model (**Table 3**). Considering the top-ranked model had three more parameters than the null model and an interaction term, but the AICc value was only 0.55 units lower than that of the null model, it would be a stretch to claim that reliable prediction could be based on this more complex model. With respect to the second-best model, adding the *SQMcontrast* parameter improved the AICc value by only 0.18 units when compared to the null model, but the 95% confidence interval on the parameter overlapped zero; indicating *SQMcontrast* was not a good predictor variable. In conclusion, we found no evidence light pollution was affecting the placement of nests in at-risk locations.

As with hatchlings, we were interested in whether adult nesting in an at-risk location could be better predicted with blue light data than white light data, and whether there was any evidence of a preferred vertical or horizontal AOA. After making among model comparisons of AICc for at-risk nests (**Table 4**) equivalent to those described for the hatchlings, we found AICc differences were <2.0 units in all cases. We interpreted these results to mean there was no evidence from our study of heightened sensitivity to blue light or a preferred AOA associated with loggerheads building nests in at-risk locations.

Relocation Effects on Nest Success

In 2015 and 2016 GUIS biologists relocated multiple nests because they were judged to be at-risk, and in 2016 a beach renourishment project at Pensacola Beach required relocation of 15 additional nests that were not at-risk. Our comparison of relocated nests with non-relocated nests showed relocated nests fared better in four categories (**Table 2**). These results differ from Ahles and Milton (2016; **Table 1**), who found percent hatching success and percent hatchling emergence success were lower for relocated nests (their "12 h native" treatment) than for non-relocated nests (their "*in situ*" treatment), though only the emergence success difference was statistically significant. Interestingly, the corresponding percentages for their relocated "12 h renourished" nests were slightly higher than for their "*In situ*" nests, though the differences were not statistically significant (Ahles and Milton, 2016).

We note that the nest success, hatching success, and hatchling emergence success rates we report for non-relocated nests (**Table 2**) are likely higher than normally would be observed on beaches where none of the nests were relocated. This is because the at-risk nests in our study, which likely would have had success rates near zero if left *in situ*, were all relocated. Thus, none of the at-risk nests appeared in the non-relocated group where they would have dragged down average success rates. Consequently, rate differences between our relocated nests, and non-relocated nests in general, are likely to be even greater than is apparent from our data. What this suggests is that under the conditions prevailing at GUIS in 2015 and 2016 (with respect to storms, predation rates, etc.), relocating at-risk nests (that are almost certain to fail) is an effective management action that can actually increase average success rates. Additionally, our data show that careful selection of sites for relocated nests can reduce rates of hatchling misorientation.

CONCLUSION

Our findings support speculation that artificial light, specifically the contrast in brightness between the landward and seaward directions (i.e., *SQMcontrast*), is partially responsible for high rates of loggerhead hatchling misorientation at GUIS. Specifically, we found that:

1. Landward brightness can be so great that it overwhelms any positive effects the moon might be having, and management actions that decrease landward brightness will be mostly ineffective until $SQMcontrast > -2.0$.
2. Management actions that decrease landward brightness will be more effective on moonless nights than on moonlit nights.
3. Management actions should strive to reduce landward brightness to levels that are lower than seaward brightness (i.e., $SQMcontrast > 0$).

In addition, our results document the strong moderating influence of lunar fraction and lunar altitude on hatchling misorientation (larger lunar fractions and lower lunar altitudes reduced misorientation). With respect to factors influencing the selection of nest sites in at-risk locations, we did not document any effects of artificial light, lunar fraction, or horizon profile. Finally, we found no evidence that relocating nests at GUIS reduced loggerhead success rates, in fact relocation actually improved rates, and we found evidence that hatchling misorientation rates were lower for relocated nests. Thus, when nests are deemed to be at-risk, relocating them in accordance with the procedures outlined in the **Appendix** can be considered an effective management tool.

DATA AVAILABILITY STATEMENT

The raw data supporting the conclusions of this article will be made available by the authors, without undue reservation, to any qualified researcher.

ETHICS STATEMENT

The animal study was reviewed and approved by Florida Fish and Wildlife Conservation Commission and the National Park Service.

AUTHOR CONTRIBUTIONS

MN directed all aspects of the sea turtle monitoring program at GUIS, and was responsible for collection of the at-risk, misorientation, and nest success data. ST directed and obtained funding for the project, and coordinated personnel tasked with collecting the night sky and horizon profile data. JW designed the apparatus used to take night sky measurements, provided training on its proper use, and contributed to data analyses. TS analyzed the data and wrote the article. All authors contributed to manuscript proofing and revision.

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APPENDIX

GUIS Protocol for Marine Turtle Nest Relocation (June, 2015)

Each season several nests at Gulf Islands National Seashore (GUIS) are built in locations that are precarious. On numerous occasions since 1994, nests have been built only 1.5–3.0 m from the Gulf of Mexico (GoM). In some instances, even nests built 6.0–12.0 m from the GoM are built in areas with little elevation and can readily flood. Flooding can come from above from high surf, or from below if ground water levels are elevated by rain or high surf.

Nests deemed to be too low on the beach or in danger of flooding can be moved. Historical GUIS records witness that large numbers of nests can flood and thus fail if left *in situ*.

A new nest location can be chosen and then excavated above the high tide line. Usually a suitable area can be found directly north of the at-risk nest site.

The top of the original nest, or egg cavity, should be measured by using a wooden stake and tape measure. Care must be taken to reflect the actual surrounding grade. Measure to the top and bottom of the nest or eggs, and record.

The new nests should be excavated to the same depth as the original nest cavity. The width should have similar dimensions as well. When all the eggs are deposited into the new cavity, the depth to the top of the eggs should be recorded.

Move the eggs one by one with care, but in a timely manner. **Do not roll or rotate the eggs from their original orientation.** Use a cooler to store the eggs. Fill the bottom with a layer of sand from the nest area to prevent the eggs from rolling in the container. The sand will also cushion the eggs. Use the lid to shade the eggs while moving them. Large temperature changes need to be avoided.

After all the eggs have been deposited (not dropped) carefully in the new nest cavity one at a time, partially cover the eggs with the moist sand, using sand from the original nest site. Compress with light to moderate pressure, then use surrounding moist sand as needed. Compress the sand again with your hands with slight to moderate pressure.

Mark these nests in accordance with GUIS general guidelines for a positive nest.

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Regional Variation in Kemp's Ridley Sea Turtle Diet Composition and Its Potential Relationship With Somatic Growth

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Reptile growth is influenced by many ecological processes that can cumulatively give rise to divergent somatic growth rates within spatially structured populations. As somatic growth variation can strongly influence a species' population dynamics, identifying proximate drivers can be critical to the conservation and management of protected species. Kemp's ridley sea turtles (*Lepidochelys kempii*) exhibit spatial variation in both diet composition and growth, but whether components of this variation are linked has not been evaluated. Through an integration of skeletochronological and stable isotope analyses of stranded turtle humerus bones we characterized regional variation in Kemp's ridley diet composition and potential relationships with somatic growth rates. Turtles were divided among five regions within the United States Gulf of Mexico (GoM) and Atlantic Coast based on location of stranding, and humerus bones were sampled for stable carbon ($\delta^{13}C$) and nitrogen ($\delta^{15}N$) isotope ratios. These data were combined with region-specific prey stable isotope data sourced from the primary literature into Bayesian stable isotope mixing models (MixSIAR) to estimate the proportional contribution of five prey groups (crustaceans, bivalves, gastropods, fish, and macroalgae/seagrass) to Kemp's ridley diets. Our analysis revealed strong regional differences in mixing model-derived diet composition estimates that closely tracked published records of Kemp's ridley diet. Invertebrates generally comprised the largest proportion (43.5–97.7%) of turtle diets. However, we also observed high proportional contributions of fish (42.6–43.1%) to western GoM turtle diets and macroalgae/seagrass (42.4–47.8%), or isotopically similar prey resources (e.g., tunicates), to eastern GoM turtle diets. Growth rates were poorly correlated with $\delta^{15}N$ values—a proxy for trophic level—and diet composition estimates, suggesting that diet composition alone may not explain the regional differences in somatic growth observed in this species. This study highlights the value of complementary skeletal and isotopic analyses to understanding regional diet variation in sea turtles as well as the importance of continued collection of isotopic data for both sea turtles and their prey. These results also help fill critical knowledge gaps pertaining to the relationship between sea turtle foraging ecology and somatic growth dynamics, a topic of high importance to sea turtle conservation and management.

Keywords: stable isotope analysis, skeletochronology, mixing model, growth rates, diet analysis, foraging ecology

INTRODUCTION

Somatic growth variation manifests from the cumulative effect of multiple biological, ecological, and environmental processes (Congdon, 1989; Stearns, 1992). Environmental effects on growth rates are particularly strong in ectothermic reptiles, such as sea turtles, where resource use, quality, and availability interact with temperature to determine how much of an individuals' total energy budget is devoted to growth, maintenance, storage, and reproduction (Gibbons, 1967; Dunham et al., 1989). Spatiotemporal variation in energy allocation to growth within and among individuals can have profound effects on individual fitness and species population dynamics through influences on key life history features such as time to maturity (Frazer et al., 1993; Bjorndal et al., 2013), size-dependent mortality (Werner and Gilliam, 1984; O'Brien et al., 2005), and fecundity (Berry and Shine, 1980; Frazer and Richardson, 1986). Sea turtle somatic growth rates are highly variable within and among species and life stages, and a suite of environmental factors are thought to contribute to this variability (e.g., temperature, density-dependence, prey dynamics, diet quality, and individual behavior; Balazs, 1982; Bjorndal et al., 2003; Balazs and Chaloupka, 2004; Hatase et al., 2010; Peckham et al., 2011). Disentangling the myriad potential drivers of sea turtle somatic growth variation is challenging given the logistical limitations associated with studying highly migratory species (Omeyer et al., 2017). Nevertheless, identifying factors influential to sea turtle growth rates is of high importance to their conservation and management given that their population dynamics are sensitive to changes in demographic rates (Crouse et al., 1987; Gerber and Heppell, 2004).

Variation in resource use and availability is a primary driver of somatic growth variation within animal populations. For example, it is well-established that fish growth and population dynamics are strongly influenced by zooplankton composition, abundance, and distribution (Cushing, 1990; Brodeur and Ware, 1992; Durant et al., 2007). Similarly, variation in multiple seabird demographic rates, including growth, have been linked to differences in prey availability, composition, and energy density (Cairns, 1988; Abraham and Sydeman, 2004; Hennicke and Culik, 2005; Piatt et al., 2007). For loggerhead sea turtles (*Caretta caretta*), geographic variation in resource availability is thought to contribute to differences in somatic growth rates among life stages and breeding populations (Bjorndal et al., 2003; Piovano et al., 2011). These differences may relate to divergent prey energy densities or geographic differences in primary productivity (Bosc et al., 2004; Peckham et al., 2011). Observations of compensatory and density-dependent growth in loggerhead and green sea turtles (*Chelonia mydas*) provide further support for the importance of resource use in shaping sea turtle growth rates (Bjorndal et al., 2000, 2003). Within the Gulf of Mexico, factors that affect foraging resources for sea turtles include fisheries (Robinson et al., 2015), seasonal hypoxic zones (Craig et al., 2001), oil spills (Wallace et al., 2017), red tides (Dupont et al., 2010), hurricane activity (Engle et al., 2009), and climate change (Sanchez-Rubio et al., 2011), among others.

Kemp's ridley sea turtles (*Lepidochelys kempii*) display distinct regional differences in somatic growth rates that may be linked to differences in diet composition. During neritic life stages, this species occupies nearshore marine habitats throughout the Gulf of Mexico (GoM) and United States Atlantic (NMFS and USFWS, 2015). Comparative studies prior to the year 2000 suggest juvenile Atlantic Kemp's ridley sea turtles exhibit slower grow rates than conspecifics in the GoM (Caillouet et al., 1995; Zug et al., 1997; NMFS and USFWS, 2015; Avens et al., 2017), though causal mechanisms remain unknown. In contrast, juvenile Kemp's ridley growth rates do not appear to vary substantially within the United States GoM and Atlantic (Ramirez, 2019). Although crabs are generally thought to constitute the bulk of their diet across their range, regional differences in Kemp's ridley foraging patterns have been observed that may influence their somatic growth rates (Shaver, 1991; Burke et al., 1993, 1994; Seney and Musick, 2005; Schmid and Tucker, 2018). Diets are particularly variable among Kemp's ridleys that inhabit the GoM. For example, tunicates are a common prey item for turtles in southwest Florida (Witzell and Schmid, 2005), whereas fish—likely sourced as discards from shrimp fisheries—are often consumed by turtles in the northern and western GoM (Werner, 1994; Cannon, 1998; Stacy, 2015). Shrimp fisheries are the overwhelmingly dominant source of fish discards throughout the Kemp's ridleys' range but the availability of this potential resource is an order of magnitude higher in the western and northern GoM than in the eastern GoM and United States Atlantic (Diamond, 2004; Harrington et al., 2005; Scott-Denton et al., 2012). In contrast to their GoM counterparts, Atlantic Kemp's ridleys appear less likely to deviate from the traditional diet of crabs and molluscs (Burke et al., 1993, 1994; Frick and Mason, 1998; Seney and Musick, 2005). Ultimately, whether this spatial variability in diet composition correlates with regional differences in growth rates has yet to be evaluated.

As the isotopic composition of consumer tissues closely tracks that of their assimilated diet, stable isotope analyses provide a means of characterizing intra-population variation in diet composition over space and time (Newsome et al., 2007; Katzenberg, 2008). Importantly, the proportional contribution of different resources to a consumer's diet can be quantified using mass-balance stable isotope mixing models when isotopic data are available for both consumers and potential prey (Phillips, 2001). While many environmental and physiological processes can influence stable isotope deposition rates into consumer tissues, the latest generation of mixing models allows for incorporation of various sources of uncertainty through Bayesian inference to improve estimations of diet composition (Phillips and Koch, 2002; Semmens et al., 2009; Parnell et al., 2010; Stock and Semmens, 2016). This approach in turn yields source contribution estimates that are accompanied by probability distributions that more accurately reflect model uncertainties. Kemp's ridley humerus bones contain annual records of somatic growth that can be revealed through histological processing and analysis (Snover and Hohn, 2004; Avens et al., 2017). Combining skeletochronological and stable isotope analyses within a mixing model framework may thus provide a means of investigating the influence of diet composition on sea turtle growth rates across multiple spatiotemporal scales. The integration of these tools has already shed valuable insight into sea turtle ontogenetic growth dynamics and resource shifts (Snover et al., 2010; Avens et al., 2013; Ramirez et al., 2017, 2019; Turner Tomaszewicz et al., 2017a).

In this study we integrated skeletochronological and stable isotope analyses of Kemp's ridley humerus bones to (1) characterize regional variation in diet composition and (2) quantify the relationship between diet composition and somatic growth rates. To reduce biases associated with translating isotopic data to diet composition estimates for a highly mobile species, our analysis assesses diet composition at a broad taxonomic level (e.g., % fish, % invertebrate, and % macroalgae/seagrass). We specifically investigated if turtles inhabiting areas where fish discards are prevalent (western and northern GoM) showed evidence of consuming greater proportions of fish relative to turtles from other regions (eastern GoM and United States Atlantic). Because the energy density of fish is generally higher than that of crustaceans (Doyle et al., 2007; Peckham et al., 2011; Schaafsma et al., 2018), we also investigated whether fish subsidies to turtle diets enhance somatic growth rates, thereby contributing to regional differences in somatic growth. This investigation presents one of the first studies explicitly linking sea turtle foraging ecology to their somatic growth dynamics.

MATERIALS AND METHODS

Geographic Breakpoints

Variation in Kemp's ridley diet composition and growth was evaluated by dividing turtle and prey data among five geographic regions within the species' range (**Figure 1**): (1) western Gulf of Mexico (wGoM, n = 44 turtles; Texas/Mexico border to Vermilion Bay, LA), (2) northern Gulf of Mexico (nGoM, n = 28 turtles; Vermilion Bay, LA, to Mobile Bay, AL), (3) eastern Gulf of Mexico (eGoM, n = 24 turtles; Apalachicola Bay to Florida Bay, FL), (4) North Carolina (NC, n = 32 turtles; Long Bay to Albemarle Sound, NC), and (5) Virginia (VA, n = 25 turtles; North Carolina/Virginia border to lower Chesapeake Bay). These breakpoints were primarily determined based on known or presumed spatial variation in ocean chemistry. We explored using smaller geographic areas to more closely link turtle and prey stable isotope data in space. However, there was generally insufficient prey data for one or more prey groups to use smaller regional units for this analysis (see below).

Within the GoM, the West Florida Shelf is characterized by relatively low stable nitrogen isotope ratios (δ^{15}N) due to the presence of *Trichodesmium* (Lenes et al., 2001; Mulholland et al., 2006; Vander Zanden et al., 2015), a N_2-fixing cyanobacteria; N_2-fixation reduces δ^{15}N values (Montoya et al., 2002). Marine organisms occupying the West Florida Shelf thereby may have lower δ^{15}N values than conspecifics elsewhere due to chemical differences at the base of the food web. In contrast, the nGoM and Virginia regions may have relatively high δ^{15}N values and low stable carbon isotope (δ^{13}C) values than adjacent regions due to high nitrogen loading from agricultural runoff (i.e., high nitrogen content; Black et al., 2017; Fritts et al., 2017) and freshwater influences, respectively—freshwater systems have distinctly lower δ^{13}C values than marine systems (Fry and Sherr, 1989).

Prey Stable Isotope Ratios

Kemp's ridley sea turtles are generalist carnivores, consuming primarily invertebrates (crustaceans, gastropods, bivalves, and tunicates) but also variable amounts of fish, macroalgae, and seagrasses (Shaver, 1991; Seney and Musick, 2005; Witzell and Schmid, 2005). Although regional differences in foraging patterns have been observed for this species, such as increased consumption of fish in turtles from Louisiana and Texas (Werner, 1994; Cannon, 1998; Stacy, 2015) and tunicates in turtles from Southwest Florida (Witzell and Schmid, 2005), crabs have generally constituted >75% of their observed diet by weight (Shaver, 1991; Burke et al., 1993, 1994; Seney and Musick, 2005; Schmid and Tucker, 2018). Given the spatiotemporal extent and retrospective nature of this study, we relied on the primary literature to source stable isotope data of representative prey species for our mixing model.

We first performed a structured literature search in Web of Science and Google Scholar using the following Boolean search terms: stable isotope, crustacean, crab, shrimp, mollusc, arthropod, gastropod, sea snail, bivalve, clam, oyster, mussel, fish, tunicate, seagrass, and macroalgae. We then performed an unstructured literature search using the reference lists of relevant publications found in the structured search. Following exclusion of studies performed outside the focal geographic areas, the literature search yielded 86 studies from which stable carbon and nitrogen isotope ratios were collated. If studies reported multiple stable isotope values for a single prey species, a weighted mean and pooled standard deviation (SD) were calculated to collapse the reported data into one estimate per species per study. Tunicates, though potentially an important Kemp's ridley prey group, were excluded from our analysis given their poor representation in the literature (n = 2 studies) and overlap in isotopic values with macroalgae and seagrass. The final prey stable isotope dataset comprised 552 isotopic records (see **Table 1** for summary and **Supplementary Table S1** for full dataset). Original collection dates spanned 1975 to 2016, but primarily encompassed the years 1990 to 2016—pre-1990

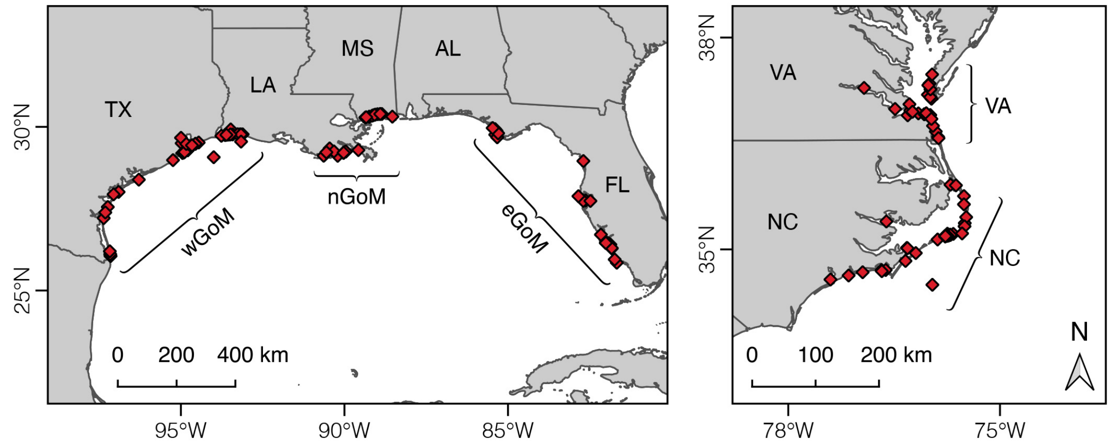

FIGURE 1 | Map of Kemp's ridley sea turtle stranding locations for the humerus bones used in this study and geographic breakpoints used to cluster turtles and prey groups. wGoM, western Gulf of Mexico; nGoM, northern Gulf of Mexico; eGoM, eastern Gulf of Mexico; NC, North Carolina; VA, Virginia.

TABLE 1 | Taxonomic and geographic summaries of Kemp's ridley sea turtle prey stable isotope data collated from the published literature.

Prey groups	Taxonomic family (Common name, *n**)	Counts* by region				
		Gulf of Mexico			Atlantic	
		W	N	E	S	N
Crustacean/Chelicerate		28	48	26	15	10
Horseshoe crab	Limulidae (horseshoe crabs, 4)	0	1	0	2	1
Crab	Portunidae (swimming crabs, 43), Panopeidae (mud crabs, 14), Epialtidae (spider crabs, 5), Menippidae (stone crabs, 4), Diogenidae (hermit crabs, 3), Aethridae (box crabs, 1), Paguridae (hermit crabs, 1), Multiple** (1)	13	26	17	9	7
Shrimp	Penaeidae (Penaeid shrimp, 48), Squillidae (Mantis shrimp, 3)	15	21	9	4	2
Bivalve	Ostreidae (Eastern oyster, 29), Mytilidae (mussels, 23), Veneridae (venus clams, 7), Mactridae (Atlantic rangia, 5), Tellinidae (tellin clams, 4), Arcidae (ark clam, 2), Pectinidae (scallops, 2)	15	27	12	13	5
Gastropod	Littorinidae (periwinkles, 18), Melongenidae (Crown conch, 3), Muricidae (murix snails, 3), Nassariidae (Nass mud snails, 3), Naticidae (Atlantic moon snail, 3), Busyconidae (whelks, 2), Calyptraeidae (slipper snail, 2), Cerithiidae (ceriths, 2), Columbellidae (dove snails, 2), Buccinidae (Tinted cantharus, 1), Neritidae (Olive nerite, 1), Potamididae (Ladder horn snail, 1), Turbinidae (West Indian starsnail, 1)	3	19	6	12	2
Fish	Sciaenidae (croaker and weakfish, 75), Sparidae (porgy and pinfish, 29), Engraulidae (anchovy, 23), Mugilidae (mullet, 20), Clupeidae (menhaden and herring, 18), Ariidae (sea catfish, 17), Paralichthyidae (flounder, 17), Haemulidae (grunt, 4), Phycidae (spotted hake, 3), Synodontidae (inshore lizardfish, 3), Achiridae (sole, 2), Pomatomidae (bluefish, 2), Triglidae (searobins, 2), Carangidae (round scad, 1)	42	52	86	20	16
Macroalgae/Seagrass		25	11	35	11	13
Seagrass	Cymodoceaceae (shoal and manatee grass, 20), Hydrocharitaceae (turtlegrass, 18), Zosteraceae (Common eelgrass, 5), Multiple** (4), Unidentified (1)	14	3	25	3	3
Macroalgae	Ulvaceae (Sea lettuce, 13), Unidentified (8), Gracilariaceae (red algae, 6), Multiple** (5), Cladophoraceae (green algae, 2), Codiaceae (Green sea fingers, 2), Dictyotaceae (brown algae, 2), Gelidiaceae (red algae, 2), Solieriaceae (red algae, 2), Ceramiaceae (red algae, 1), Ectocarpaceae (brown algae, 1), Fucaceae (bladder wrack, 1), Halymeniaceae (red algae, 1), Wrangeliaceae (red algae, 1)	11	8	10	8	10

Number of species-specific isotopic values identified in the primary literature. **Mean composite of samples from multiple families. See* ***Supplementary Table S1* *for full dataset.*

data were included in some instances to fill important data gaps for poorly represented taxa within each region, namely bivalves and gastropods.

Prey stable isotope data were grouped into five primary prey groups (crustaceans, bivalves, gastropods, fish, and macroalgae/seagrass) within each of the five geographic regions (**Supplementary Figures S1, S2**). For all animal prey groups, a simple mean and pooled SD were calculated for each region using the 552 isotopic values from the published literature. Although isotopically distinct, macroalgae and seagrass were grouped to reduce the number of sources in the mixing model. As with the other prey groups, we first calculated a simple mean and pooled SD for macroalgae and seagrass separately and then calculated a simple mean of these estimates to yield final estimates for the macroalgae/seagrass prey group, thereby weighting each prey type equally in the models. Final means and SDs for all prey groups used in the mixing model are presented in **Table 2**. We assume that isotopic data collated from the published literature accurately reflect the means and variances of these prey groups.

TABLE 2 | Mean ± SD stable carbon ($\delta^{13}C$) and nitrogen ($\delta^{15}N$) isotope ratios collated from the primary literature for Kemp's ridley sea turtle prey groups by geographic region.

Prey group	**$\delta^{13}C$ (‰)**			**$\delta^{15}N$ (‰)**		
	n_{means}	n_{total}	**Mean ± SD**	n_{means}	n_{total}	**Mean ± SD**
Western GoM						
Crustacean	28	318	−18.37 ± 1.32	27	317	9.68 ± 1.33
Bivalve	14	165	−22.74 ± 1.70	15	262	9.65 ± 1.13
Gastropod	3	11	−14.81 ± 0.78	2	6	8.95 ± 0.35
Fish	42	311	−17.40 ± 1.44	33	274	12.64 ± 1.42
Macroalgae/ seagrass	25	153	−14.56 ± 2.11	24	93	6.43 ± 1.84
Northern GoM						
Crustacean	48	1545	−18.67 ± 1.59	44	1517	10.89 ± 1.14
Bivalve	25	247	−23.63 ± 0.92	18	242	7.75 ± 0.66
Gastropod	19	478	−18.00 ± 0.74	15	461	9.36 ± 0.26
Fish	52	1334	−19.84 ± 1.13	52	1295	11.93 ± 0.79
Macroalgae/ seagrass	11	57	−15.31 ± 1.18	11	57	6.94 ± 0.94
Eastern GoM						
Crustacean	26	570	−19.58 ± 1.92	22	544	6.88 ± 0.97
Bivalve	12	301	−22.40 ± 0.75	7	258	6.51 ± 0.36
Gastropod	6	30	−19.24 ± 1.94	5	29	6.49 ± 0.83
Fish	86	1679	−17.91 ± 1.22	65	1571	10.64 ± 1.09
Macroalgae/ seagrass	29	243	−14.57 ± 2.18	30	779	4.44 ± 1.37
North Carolina						
Crustacean	15	141	−17.68 ± 0.96	15	141	10.00 ± 0.85
Bivalve	13	45	−19.98 ± 0.35	6	35	7.62 ± 0.25
Gastropod	12	40	−16.81 ± 1.25	6	23	6.32 ± 0.61
Fish	17	206	−18.33 ± 0.98	17	208	11.98 ± 0.91
Macroalgae/ seagrass	11	35	−14.70 ± 0.61	5	14	4.81 ± 1.32
Virginia						
Crustacean	10	62	−16.43 ± 0.63	8	50	11.34 ± 0.98
Bivalve	5	97	−19.59 ± 0.98	5	97	9.84 ± 0.78
Gastropod	2	6	−16.21 ± 0.64	2	6	9.83 ± 0.54
Fish	16	318	−18.42 ± 1.33	11	258	14.63 ± 0.89
Macroalgae/ seagrass	13	94	−13.59 ± 1.51	13	94	7.86 ± 1.13

*Mean ± SD is the simple mean and pooled SD of species-specific isotopic values collated from referenced studies. n_{means} is the number of mean values included in each $\delta^{13}C$ and $\delta^{15}N$ estimate. n_{total} is total number of prey items sampled in referenced studies. Values are uncorrected for trophic discrimination factors. See **Supplementary Table S1** for source list and complete prey stable isotope dataset resulting from the literature review.*

Given uncertainties in the types of fish consumed by sea turtles, potential fish prey for our analysis included species previously observed in Kemp's ridley gut and fecal contents (e.g., mullet, croaker, weakfish, menhaden, sea catfish, flatfish, and lizardfish; see Shaver, 1991; Werner, 1994; Cannon, 1998; Witzell and Schmid, 2005; Stacy, 2015; Seney, 2016) as well as ecologically similar species abundant in shrimp fishery discards (e.g., porgy, pinfish, herring, and searobin; Harrington et al., 2005; Benaka et al., 2019). When possible, fish isotopic data were restricted to specimens <30 cm in length to align with those likely to be consumed by Kemp's ridleys. However, only 45% of studies reported fish lengths, so this was not always possible. Fish stable isotope data were initially grouped based on feeding mode (e.g., piscivorous, benthophagous, and planktivorous) to evaluate trophic differences. However, isotopic data for these three fish groups tended to overlap extensively in isospace within each region and were thus collapsed to reduce the number of sources in the mixing model.

Sea Turtle Stable Isotope Ratios

Kemp's ridley humerus bones utilized in this study were originally collected as whole front flippers from 153 turtles stranded dead along the United States Gulf and Atlantic Coasts between 1993 and 2015 by participants of the Sea Turtle Stranding and Salvage Network. At time of stranding, carapace length (notch to tip), calendar date, and stranding location (state, latitude, and longitude) were recorded for each turtle. Body size was typically measured as straightline carapace length (SCL), but in cases where only curved carapace length was recorded measurements were converted to SCL following Avens et al. (2017). Sea turtle diets and growth rates vary throughout their lifetime (Bjorndal, 1997; Chaloupka and Musick, 1997). To reduce the potential for ontogenetic effects to bias our results we only sampled bone growth layers from juvenile Kemp's ridleys corresponding to their benthic life stage (i.e., age ≥ 0.75 and $\delta^{15}N$ values ≥ 10.7‰; Ramirez, 2019; Ramirez et al., 2019).

Prior to sampling, each humerus bone was cleaned of soft tissue using a knife and then boiled. To perform complementary growth and stable isotope analyses, two sequential 2–3 mm thick cross-sections were cut from each humerus bone distal to the site of the deltopectoral muscle insertion scar using a low-speed isomet saw (Buehler). One section was histologically processed using standard methods to reveal the annual growth layers contained within each bone and estimate sea turtle growth rates (see below), whereas the second was reserved for complementary stable isotope analysis. Methods for histologically processing sea turtle bones are detailed in Avens and Snover (2013) but are briefly outlined here. First, humerus bone sections were decalcified over multiple days using a fixative/decalcifier (Cal-Ex II or RDO). Then, bone sections were thin sectioned using a freezing-stage microtome or cryostat, stained using Ehrlich's hematoxylin, and finally mounted onto microscope slides and digitally imaged. Two or three independent readers (among L. Avens, L. Goshe, M. Ramirez, and M. Snover) then analyzed the bone images to determine the number and placement of lines of arrested growth (LAGs), which delimit the outer edges of each skeletal growth mark.

To characterize resource use, ∼1.5 mg of bone dust was milled from the most recently deposited growth layer of each sea turtle bone cross-section reserved for stable isotope analysis (ESI New Wave Research MicroMill). This time period represents the geochemical history within 1 year of death, dependent on individual stranding date. A 0.3 mm diameter carbide drill bit (Brasseler) was used in conjunction with transparencies of the digital skeletochronology images to guide precision drilling to a depth of ≤1.0 mm for each sample. Bulk bone dust samples were analyzed for δ^{13}C and δ^{15}N values via continuous-flow isotope-ratio mass spectrometry at the Oregon State University Stable Isotope Lab (Corvallis, OR, United States). The system consists of a Carlo Erba NA1500 elemental analyzer interfaced with a DeltaPlusXL isotope-ratio mass spectrometer (Finnigan MAT, Bremen, Germany). The standards used for δ^{13}C and δ^{15}N were Vienna Pee Dee Belemnite (VPDB) and atmospheric N_2, respectively. The internal standard IAEA-600 (Caffeine; isotopic composition of $\delta^{15}N = 1.00‰$) was calibrated at regular intervals and used to correct for instrument drift and linearity. Analytical precision was 0.08‰ for δ^{13}C values and 0.05‰ for δ^{15}N values. In addition to stable isotope ratios, %N and %C were calculated using mass 28 and mass 44 peak areas, respectively, with a precision of 0.55% for %N and 0.28% for %C. C:N ratios (%C divided by %N) for all samples were below 3.5, characteristic of unaltered protein with low lipid content (Post et al., 2007). Following stable isotope analysis, bulk bone δ^{13}C values were mathematically corrected to account for carbonate-derived carbon as recommended by Turner Tomaszewicz et al. (2015). Using their approach, we developed a δ^{13}C conversion equation ($\delta^{13}C_{\text{collagen}} = 0.975 * \delta^{13}C_{\text{bulk}} - 1.126$, $F_{1,42} = 550.1$, $P < 0.001$, adjusted $R^2 = 0.93$) that was used to mathematically correct bulk bone δ^{13}C values (see **Supplementary Mateiral** for details).

We assumed that stranding location was reflective of recent foraging location based on two lines of evidence. First, while we did not know precise locations of death in the ocean for turtles herein, it is likely that most turtles included in this study died relatively close to their stranding locations as ocean conditions were likely favorable for short carcass drift distances. The majority of turtles included in our study stranded in the spring, summer, and fall when sea surface temperatures, and thereby decomposition rates, would have been relatively high (Higgins et al., 2007). Therefore, in order for stranding to occur before carcasses dissociated due to decomposition, drift times and distances would have needed to be low (∼2–5 days, 15–30 km; Nero et al., 2013; Santos et al., 2018). Second, Kemp's ridleys display relatively high intra- and inter-annual site fidelity to nearshore, shallow (<50 m depth) foraging areas (generally <1,000 km^2) that are well constrained spatially within our defined geographic regions (Renaud and Williams, 2005; Schmid and Witzell, 2006; Shaver and Rubio, 2008; Seney and Landry, 2011; Coleman et al., 2017). Therefore, turtles that stranded within each geographic area are likely to have been foraging within their stranding location-assigned geographic area prior to death. As Kemp's ridleys have been occasionally documented migrating >1,000 km in a single year (Renaud and Williams, 2005), we acknowledge that some of our turtles may be misclassified geographically, particularly those that stranded near the edges of our pre-defined geographic areas.

Stable Isotope Mixing Model

We implemented multiple Bayesian hierarchical mixing models using the *MixSIAR* package (v 3.1.10, Stock et al., 2018) in R (v 3.5.3, R Core Team, 2019) to estimate the proportional contribution of five prey groups (crustaceans, bivalves, gastropods, fish, and macroalgae/seagrass) to Kemp's ridley diets. MixSIAR uses Markov chain Monte Carlo (MCMC) procedures to estimate posterior probability distributions of plausible proportional contributions of prey groups to consumer diets (Moore and Semmens, 2008), while accounting for uncertainty associated with trophic discrimination factors (TDFs; Parnell et al., 2010), concentration dependence (Phillips and Koch, 2002), fixed and random effects (Semmens et al., 2009), and variability in the predation process (i.e., error structure) (Parnell et al., 2010; Stock and Semmens, 2016). Initial investigations using a hierarchical structure that nested *individuals* within *regions* in a single modeling framework failed to converge after running for multiple days due to model complexity and size. Therefore, we implemented separate mixing models for each region.

To characterize inter- and intra-regional differences in diet composition, we implemented four mixing models for each region in a 2 × 2 factorial design that included one of two prior distributions (uninformative vs. informative prior; **Supplementary Figure S3**) for each prey group and one of two model configurations (null model vs. individual random effect model). We first ran the models using uninformative priors that assumed a generalist diet and weighted prey groups equally ($\alpha = 1, 1, 1, 1, 1$). We then ran the model using an informative/specialist prior that weighted the prey group prior distributions using published diet composition data. Taking a weighted average of taxon-specific diet composition estimates from six Kemp's ridley diet studies (**Supplementary Table S2**), we constructed the informative priors assuming diet compositions (by dry mass) of 76.74% for crustaceans, 2.12% for bivalves, 2.12% for gastropods, 5.97% for fish, and 2.13% for macroalgae/seagrass—10.92% of diet contents were categorized as Other/Unidentified, which was excluded from this analysis. As recommended by Stock et al. (2018), the hyperparameters (α) for the informative priors were scaled to have a total weight equal to the number of sources ($\alpha = 4.31, 0.12, 0.12, 0.34, 0.12$). Between region diet variation was assessed using null models, whereas within region diet variation was assessed using models that included *individual* as a random effect. In all models, the invertebrate prey groups were aggregated *a posteriori* (Phillips et al., 2005). All models included multiplicative error (process × residual error) and were run using the "extreme" MCMC settings (chain length = 3,000,000 iterations; burn-in = 1,500,000; posterior thinning = 500; 3 chains). Convergence was assessed using Gelman–Rubin ($R_c < 1.01$) and Geweke diagnostics (Gelman and Rubin, 1992; Geweke, 1992). Most models that included an informative prior and individual random effects failed to converge with these settings. Convergence was achieved after re-running them using a chain length of 6,000,000 and burn-in of 3,000,000.

Prior to model implementation all source and consumer $\delta^{13}C$ values were corrected for the Suess Effect, the global decrease in atmospheric $\delta^{13}C$ values driven by the combustion of fossil fuels over the past 150 years (Keeling et al., 1979; Francey et al., 1999). We followed Chamberlain et al. (2005) and Fox-Dobbs et al. (2007) in applying a linear correction to standardize our data. To develop a $\delta^{13}C$ correction factor we analyzed the atmospheric $\delta^{13}C$ data for Maua Loa and La Jolla available on the Scripps CO_2 Program website[1] (Keeling et al., 2001), which indicated that atmospheric $\delta^{13}C$ values declined by ~0.025 ‰ per year since 1978. We used this rate of $\delta^{13}C$ change to correct turtle and prey $\delta^{13}C$ values to modern values (modern = 2016; i.e., $\delta^{13}C$ values were reduced by 0.025‰ in 2015, 0.050‰ in 2014, and so on). Concentrations of carbon and nitrogen for each prey group, derived from the literature (**Supplementary Table S3**), were also included in the models to account for taxon-specific differences in digestibility (Phillips and Koch, 2002).

Stable isotope mixing models require estimates of diet-tissue trophic discrimination factors (TDFs; Δ)—the difference in isotopic ratios between consumers and their diet—to estimate the proportional contribution of different prey groups to consumer diets. As diet-bone TDFs have not been quantified for Kemp's ridleys or other primarily carnivorous sea turtles, we used diet-bone TDFs estimated from dead, captive, juvenile green sea turtles (*Chelonia mydas*) ($\Delta^{13}C = 2.1 \pm 0.6$, $\Delta^{15}N = 5.1 \pm 1.1$) (Turner Tomaszewicz et al., 2017b). Although these turtles were maintained on omnivorous diets composed of ~56% animal matter (squid, shrimp, and fish) and ~43% plant matter (lettuce) by weight, percent digestible N and C from animal protein was estimated to be 96.8 and 81.9%, respectively. Even though Bayesian stable isotope mixing models account for uncertainty in TDFs, their outputs are still highly sensitive to variation in TDFs (Bond and Diamond, 2011). Given uncertainty in the diet-bone TDFs for sea turtles, we used a sensitivity analysis to characterize the influence of varying TDFs on diet composition estimates that encompass the range of diet-bone TDFs reported for sea turtles and other animal species maintained on carnivorous diets (~2–6‰; e.g., Ambrose and DeNiro, 1986; Hobson and Clark, 1992; Fox-Dobbs et al., 2007; Borrell et al., 2012; Kim et al., 2012; Cloyed et al., 2015; Webb et al., 2016; Matsubayashi et al., 2017).

Somatic Growth Rates

To examine the influence of sea turtle trophic ecology on somatic growth rates, we compared complementary diet composition data generated from the stable isotope mixed models with annual somatic growth rate data generated through skeletochronology for each stranded turtle. The somatic growth rate data presented herein are a combination of newly collected (n = 58 turtles stranded 2010–2015) and previously collected data (n = 95 turtles stranded 1993–2009) originally presented in Snover et al. (2007) and Avens et al. (2017). We followed Avens et al. (2017) to calculate growth rates for the newly processed turtles.

First, LAG diameter and humerus section diameter (HSD) were measured using image analysis software (Olympus Microsuite and cellSens) for each histologically prepared bone cross-section. The body proportional hypothesis back-calculation technique (BPH; Francis, 1990) was then used to estimate SCL for every measurable LAG, adjusted for turtle–specific SCL and HSD at death (Snover and Hohn, 2004; Avens et al., 2017). Annual somatic growth rates were calculated by taking the difference between SCL estimates of successive LAGs. However, given that LAGs are deposited in the spring and we sampled turtles that died throughout the year, only 73/153 turtles had true annual growth rate estimates.

To extend the growth dataset we calculated marginal growth rates for the 36 turtles that stranded between November and March by taking the difference between SCL at stranding and the SCL estimate of the most external LAG. While these marginal growth rates are considered minimum estimates of annual somatic growth, Kemp's ridleys likely grow little during the boreal winter when temperatures are cooler and sea turtle metabolic rates and activity patterns are reduced (Balazs and Chaloupka, 2004; Hochscheid et al., 2007; McMichael et al., 2008). Indeed, skeletal growth appears to asymptote in November (Snover and Hohn, 2004). The 44 turtles that stranded between June and October were excluded from the growth analysis, highlighting a potential disconnect in data availability for linking sea turtle growth and diet that could be overcome in future analyses through targeted sampling of only turtles that stranded in the spring.

To examine the influence of sea turtle trophic ecology on somatic growth rates, we implemented a series of Generalized Linear Models (GLMs) that included somatic growth as the response variable, age as a fixed effect, and either $\delta^{15}N$ value or estimated diet composition as a fixed effect. Separate GLMs that included $\delta^{15}N$ values as a fixed effect were implemented for each region, whereas GLMs that included estimated diet composition as a fixed effect were only implemented for regions with considerable intra-population variation in diet composition. As sea turtle growth rates change throughout their ontogeny, age was included in the model to account for ontogenetic effects on growth and diet. Age was chosen over body size to account for ontogenetic effects as models that included age had consistently lower AIC values than models that included body size. All GLMs included a Gamma distribution and were implemented in R (version 3.5.3) using the *mgcv* package (Wood, 2006; R Core Team, 2019).

RESULTS

Prey and Sea Turtle Stable Isotope Ratios

Prey $\delta^{13}C$ and $\delta^{15}N$ values were significantly different both within and among regions (Kruskal–Wallis rank sum tests, $P < 0.05$; see **Supplementary Table S4**). *Gastropod* was the only prey group that did not exhibit significant regional differences for both stable isotopes examined, although differences in $\delta^{13}C$ were sometimes evident. Despite this regional variation in isotopic composition

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[1] http://scrippsco2.ucsd.edu

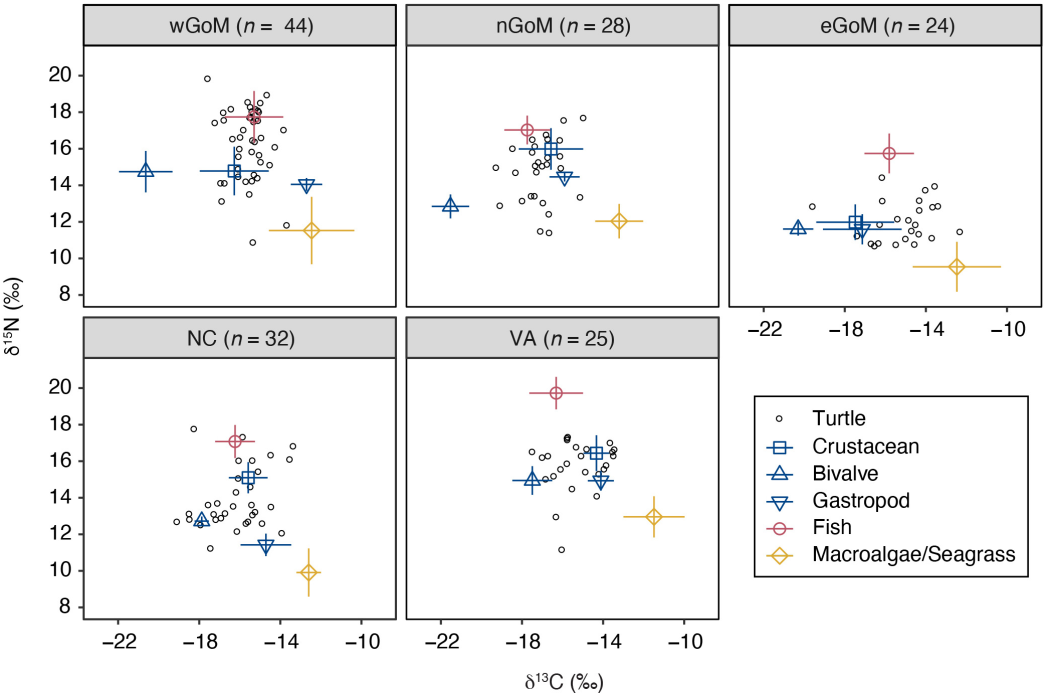

FIGURE 2 | Biplots of δ^{13}C and δ^{15}N values for Kemp's ridley sea turtles (*open circles*) and their potential prey groups (mean ± SD) by geographic region. Turtle sample sizes are presented at the top of each plot. Data are for the most recently deposited growth layer prior to death only. Prey values are corrected for trophic discrimination factors (Δ^{13}C = 2.1 ‰, Δ^{15}N = 5.1 ‰; see **Table 2** for uncorrected values). δ^{13}C values are corrected for carbonate carbon and the Suess effect.

within prey groups, the relative positioning of prey groups in bivariate isospace was similar across regions (**Figure 2**). As expected, fish δ^{15}N values were greater than the other prey groups in all cases, with mean values ranging between 10.64 and 14.63‰ (**Table 2**). Similarly, the macroalgae/seagrass group exhibited the lowest δ^{15}N values (mean range 4.44–7.86 ‰) and highest δ^{13}C values of all prey groups (mean range −15.31 to −13.59‰), reflective of their position at the base of coastal benthic food webs. Bivalves, which tended to be sampled in closest proximity to coastlines and freshwater inputs, had the lowest δ^{13}C values (mean range −23.63 to −19.59‰). Crabs and gastropods displayed the greatest variability in isospace positioning of the five prey groups but generally fell within the polygon formed by macroalgae/seagrass, bivalves, and fish (**Figure 2**). Within regions, fish, crustaceans, bivalves, and macroalgae/seagrass differed statistically for at least one stable isotope (Wilcoxon rank sum tests, $P < 0.05$; see **Supplementary Table S5**). However, gastropods tended to share isospace with at least one other prey group in each region, likely due in part to small sample sizes—gastropod stable isotope values are poorly represented in the primary literature (see **Supplementary Figure S1**).

Kemp's ridley bone stable isotope values were generally constrained by the prey stable isotope data (**Figure 2**). Summary characteristics of bone growth layers sampled for stable isotope ratios are presented in **Table 3**. An analysis of variance on these data showed there was significant variation among regions for both δ^{13}C ($F_{4,148} = 11.68$, $P < 0.001$) and δ^{15}N ($F_{4,148} = 129.19$, $P < 0.001$) values. A *post hoc* Tukey test determined that turtle bone δ^{13}C values were significantly lower in turtles stranded in the nGoM relative to all other regions ($P < 0.05$; **Supplementary Table S6**), possibly a result of influences of the Mississippi River, as freshwater systems generally have distinctly lower δ^{13}C values than marine systems (Fry and Sherr, 1989). In addition, δ^{15}N values were significantly higher in turtles from the wGoM and lower in turtles from the eGoM relative to all other regions ($P < 0.05$). Differences in δ^{15}N values between turtles in the eGoM and other regions may be driven by regional differences in nitrogen cycling or trophic ecology. The West Florida Shelf is an area of high N_2-fixation due to the presence of the cyanobacteria *Trichodesmium* (Lenes et al., 2001; Mulholland et al., 2006; Vander Zanden et al., 2015), which reduces δ^{15}N values (Montoya et al., 2002). Similarly, Kemp's ridleys in southwest Florida are known to eat tunicates, a low trophic level marine species with characteristically low δ^{15}N values (Williams et al., 2014). Along the United States Atlantic Coast, δ^{15}N values were significantly higher and less variable in turtles from Virginia relative to turtles in North Carolina, tracking differences in prey isotopic composition, which is possibly due to nutrient loading by anthropogenic activities in the Chesapeake Bay.

Regional Variation in Diet Composition

We observed distinct regional differences in diet composition (% fish vs. % invertebrate vs. % macroalgae/seagrass) for Kemp's ridleys (**Figure 3** and **Table 4**). Diet proportion estimates derived from mixing models that included both uninformative and informative priors indicated that Kemp's ridley diets were

TABLE 3 | Summary characteristics for Kemp's ridley sea turtle bone growth layers sampled for stable isotope values.

		Stranding and isotopic data							**Somatic growth data**	
Geographic region	***n***	**SCL (cm)**	**Age (year)**	**Year range**	**δ^{13}C (‰)**	**δ^{15}N (‰)**	**%C**	**%N**	***n***	**Growth rate (cm year^{-1})**
Western GoM	44	41.5 ± 8.1 (27.8, 58.9)	3.55 ± 2.62 (0.75, 12.75)	1999, 2012	−15.6 ± 0.8 (−17.6, −13.7)	16.3 ± 2.0 (10.9, 19.8)	13.8 ± 0.8	4.5 ± 0.3	38	6.5 ± 2.9 (0.8, 11.6)
Northern GoM	28	42.7 ± 8.6 (25.7, 61.8)	3.25 ± 1.84 (0.75, 7.75)	1992, 2014	−17.1 ± 1.0 (−19.3, −15.0)	14.8 ± 1.7 (11.4, 17.7)			20	6.3 ± 2.6 (3.0, 12.2)
Eastern GoM	24	43.3 ± 8.0 (26.5, 56.3)	3.38 ± 1.50 (0.75, 5.75)	1999, 2013	−15.1 ± 1.6 (−19.6, −12.3)	12.0 ± 1.1 (10.7, 14.4)			16	6.1 ± 3.0 (2.2, 13.0)
North Carolina	32	40.0 ± 7.7 (27.5, 59.6)	4.41 ± 2.50 (0.75, 12.75)	1997, 2012	−16.2 ± 1.5 (−19.1, −13.4)	13.9 ± 1.7 (11.2, 17.8)			18	5.9 ± 1.9 (1.8, 9.8)
Virginia	25	43.7 ± 5.9 (29.9, 53.1)	5.23 ± 2.10 (1.75, 10.75)	1998, 2012	−15.3 ± 1.2 (−17.5, −13.5)	15.7 ± 1.4 (11.2, 17.3)			17	5.5 ± 1.2 (2.4, 7.6)

Values reported are mean ± SD (min, max). SCL is straightline carapace length (notch to tip) at stranding. Year and age are calendar year and estimated age at start of growth layer sampled. δ^{13}C values are corrected for carbonate carbon and the Suess effect. Reported %C and %N are for all sampled growth layers. Growth rate is annual growth rate and includes both true and marginal growth rates. Only the most external, recently deposited growth layer was sampled for each turtle bone.

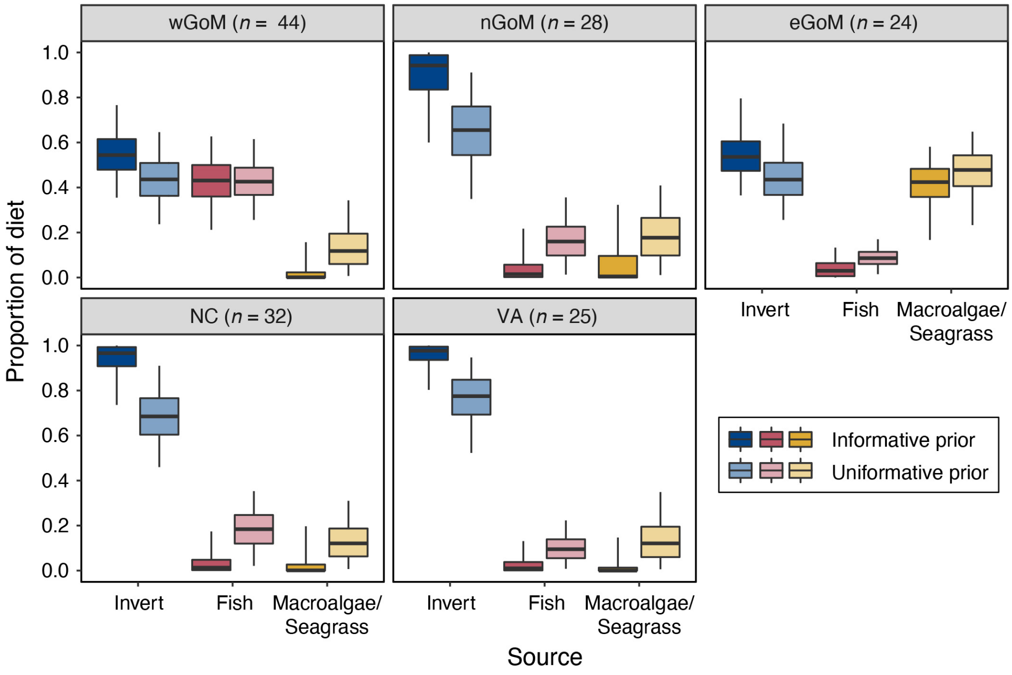

FIGURE 3 | Proportional contribution of each prey group to Kemp's ridley sea turtle diets by geographic region based on MixSIAR models that included an informative prior constructed from published diet proportion data and an uninformative prior that assigned equal probability to all prey groups. Turtle sample sizes are presented at the top of each plot. Data for invertebrate prey groups (crustacean, bivalve, and gastropod) were aggregated *a posteriori*. Lines in boxes are medians, boxes are 50% credible intervals, error bars are 95% credible intervals. See **Table 4** for samples sizes, medians, and credible interval values.

dominated by invertebrates in the nGoM, North Carolina, and Virginia (65.6–97.7%). In contrast, diets in the wGoM and eGoM were more evenly divided between invertebrates (43.6–54.5%) and fish (42.6–43.1%) or invertebrates (43.5–53.6%) and macroalgae/seagrass (42.4–47.8%), respectively. As it is unlikely that Kemp's ridleys would consume such high proportions of macroalgae/seagrass, the eGoM results likely reflect consumption of an isotopically similar benthic resource, such as tunicates (∼5.5‰; Williams et al., 2014), or incorrect parameterization of the model. Within the wGoM and eGoM regions, individual variation in turtle diets was high for wGoM turtles but low for eGoM turtles. The proportional contribution of fish and invertebrates to individual wGoM turtle diets ranged between 12 and 60% and 36 and 85%, respectively, whereas the proportional contribution of macroalgae/seagrass and invertebrates to individual eGoM turtle diets ranged between 32 and 48% and 49 and 63%.

In most cases, models that included uninformative priors estimated slightly greater contribution of fish and macroalgae/seagrass prey groups to Kemp's ridley diets

TABLE 4 | Median (95% CI) posterior Bayesian mixing model estimates of diet proportion by geographic region for Kemp's ridley sea turtles (*n* = 153).

Geographic region	Informative prior			Uninformative prior		
	Invert (%)	**Fish (%)**	**Macroalgae/ seagrass (%)**	**Invert (%)**	**Fish (%)**	**Macroalgae/ seagrass (%)**
Western GoM (*n* = 44)	54.5 (35.5, 76.6)	43.1 (21.2, 62.7)	0.1 (0.0, 15.7)	43.6 (23.7, 64.6)	42.6 (25.6, 61.5)	11.8 (0.7, 34.3)
Northern GoM (*n* = 28)	94.2 (60.0, 100.0)	1.5 (0.0, 21.7)	0.5 (0.0, 32.3)	65.6 (34.9, 91.1)	16.0 (1.3, 35.6)	17.7 (1.1, 40.9)
Eastern GoM (*n* = 24)	53.6 (36.5, 79.6)	3.0 (0.0, 13.3)	42.4 (16.7, 58.1)	43.5 (25.6, 68.4)	8.6 (1.5, 17.0)	47.8 (23.3, 64.8)
North Carolina (*n* = 32)	96.6 (73.6, 100.0)	1.3 (0.0, 17.4)	0.1 (0.0, 19.7)	68.5 (46.0, 91.0)	18.4 (2.1, 35.3)	12.1 (0.7, 31.0)
Virginia (*n* = 25)	97.7 (80.3, 100.0)	1.0 (0.0, 13.1)	0.0 (0.0, 14.7)	77.5 (52.3, 94.7)	9.5 (0.8, 22.3)	12.1 (0.6, 34.9)

The uninformative prior is constructed from the Dirichlet Bayesian prior whereas the informative prior is constructed from diet proportions published in the primary literature (see ***Supplementary Table S2****).*

relative to models with informative priors. However, posterior distributions and 95% credible intervals overlapped extensively between each set of models (**Figure 3** and **Supplementary Figure S5**). Larger differences between these model sets were evident in the pre-aggregated invertebrate data, where mixing models with uninformative priors estimated more even contribution of crustaceans, bivalves, and gastropods to Kemp's ridley diets relative to models with the informative priors (**Supplementary Figure S6**).

As expected for Bayesian stable isotope mixing models (Bond and Diamond, 2011), sensitivity analyses performed on the null mixing model with informative priors for wGoM turtles showed that changes in diet-bone TDFs affected estimated proportional contribution of prey groups to Kemp's ridley diets (**Supplementary Figure S6**). Specifically, the median estimated proportional contribution of fish and invertebrate prey to wGoM turtle diets was highly sensitive to changes in Δ^{15}N but less sensitive to changes in Δ^{13}C, unsurprising given that these prey groups primarily differ in δ^{15}N values (**Figure 2**). Diet estimates within one standard deviation of the Δ^{15}N mean ranged between 7.9 and 66.9% for fish and 30.7 and 79.2% for invertebrates, whereas estimates within one standard deviation of the Δ^{13}C mean ranged between 35.7.and 45.4% for fish and 41.7 and 62.6% for invertebrates. Mixing model estimates for proportional contribution of individual invertebrate groups to turtle diets displayed greater sensitivity to changes in Δ^{13}C values. Bivalve and gastropod diet composition estimates were more sensitive to changes in Δ^{13}C than Δ^{15}N, although their relative contribution to turtle diets remained low within one standard deviation of the mean Δ^{13}C value (0–7.4% for bivalve, 0–11.9% for gastropod). Crustacean estimates were equally sensitive to both changes in Δ^{13}C and Δ^{15}N values, with bivariate changes in both TDFs resulting in estimates ranging from 19.5 to 90.7%.

Diet Composition and Somatic Growth Rates

After controlling for the influence of age on somatic growth rates, our GLMs revealed no significant relationships between δ^{15}N values and somatic growth rates across most regions (**Table 5** and **Figure 4**). The only exception was for nGoM turtles, where there was a weakly negative relationship between δ^{15}N values and somatic growth rates ($P = 0.07$). This negative trend was still evident when marginal growth rates were excluded from the analysis, but the relationship became non-significant ($P = 0.11$). When marginal growth rates were excluded, trends across the other regions remained the same, exhibiting a shallow, non-significant decline in somatic growth rates with increasing δ^{15}N values. These patterns ran counter to our expectation of higher growth rates with increasing δ^{15}N values (i.e., foraging higher in food web), and could indicate that turtles consuming proportionally higher amounts of fish bycatch might be growing slower than conspecifics feeding primarily on invertebrates, or that physiological processes related to changes in size/age are

TABLE 5 | Summary of statistical output for Generalized Linear Models used to evaluate the influence of diet (composition and δ^{15}N values) on Kemp's ridley sea turtle annual growth rates.

Model	*n*	AIC	Var	Est	SE	*t*	Pr > |*t*|
(A) Growth ~ δ^{15}N + Age							
wGoM	38	186.11	δ^{15}N	−0.03	0.03	−0.741	0.463
			Age	−0.11	0.03	−4.234	**<0.001**
nGoM	20	83.93	δ^{15}N	−0.10	0.05	−1.902	0.074
			Age	−0.07	0.04	−1.753	0.098
eGoM	16	83.23	δ^{15}N	0.00	0.12	0.038	0.971
			Age	−0.11	0.08	−1.397	0.186
NC	18	65.90	δ^{15}N	−0.04	0.03	−1.273	0.222
			Age	−0.09	0.02	−4.410	**<0.001**
VA	17	59.31	δ^{15}N	−0.06	0.04	−1.465	0.165
			Age	−0.04	0.04	−1.196	0.252
(B) Growth ~ *p*Fish + Age							
wGoM	38	185.04	*p*Fish	−0.68	0.53	−1.295	0.204
			Age	−0.11	0.03	−4.364	**<0.001**

(A) Comparison of δ^{15}N values and growth rates across all regions. (B) Comparison of median percent of fish in diet (pFish) on growth rates for western GoM turtles only. Bold signifies statistically significant relationships.

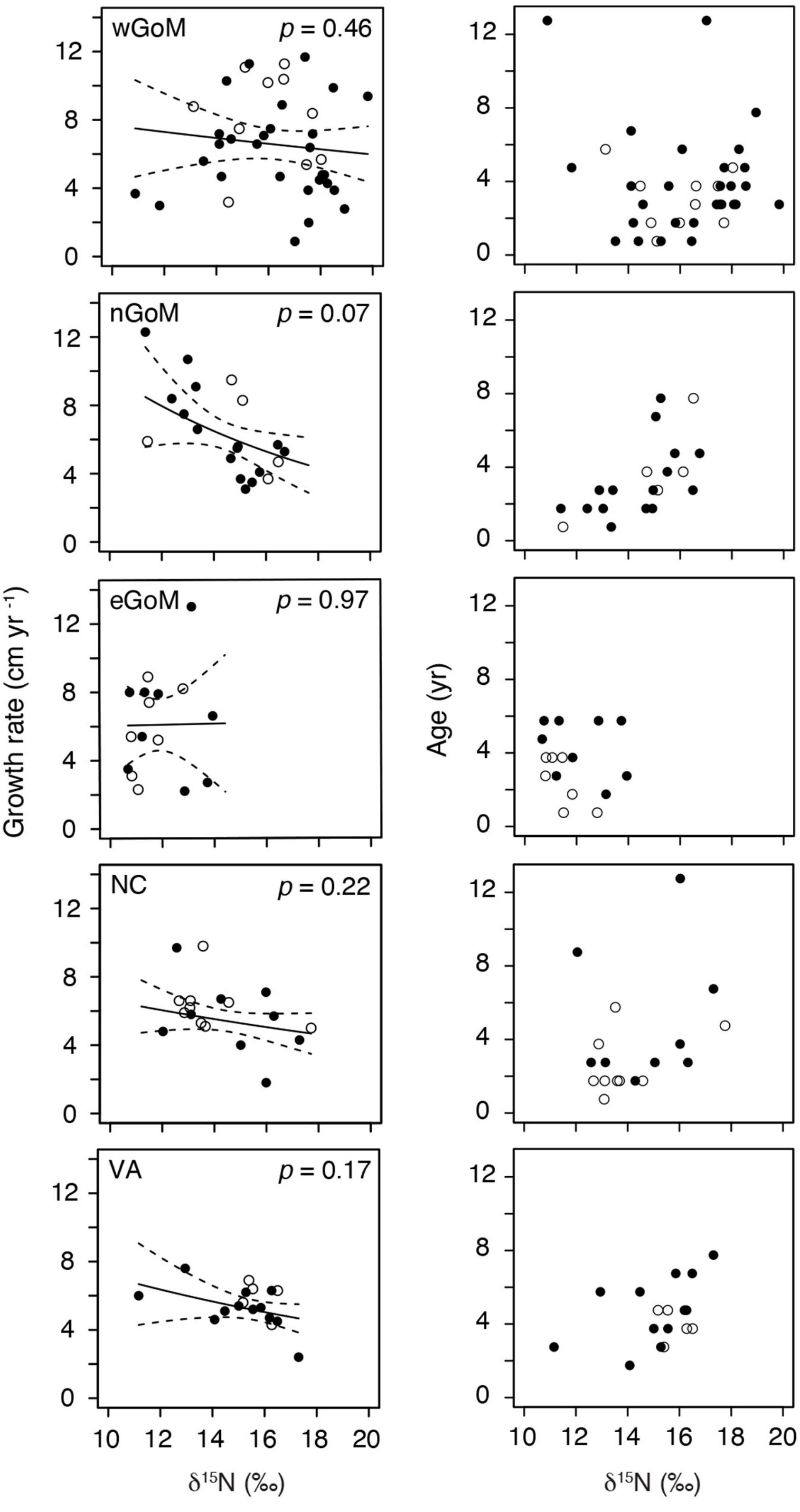

FIGURE 4 | Generalized Linear Model results examining the relationships between annual Kemp's ridley sea turtle growth rates and δ^{15}N values, and age and δ^{15}N values, for individual turtles by geographic region. Data are for the most recently deposited growth layer prior to death only. Closed circles are true annual growth rates (i.e., turtle stranded in spring, yielding a complete growth interval). Open circles are estimated annual growth rates for turtles that stranded during the winter (November–March); we assumed that annual skeletal growth asymptotes in November (see section "Somatic Growth Rates in Materials and Methods").

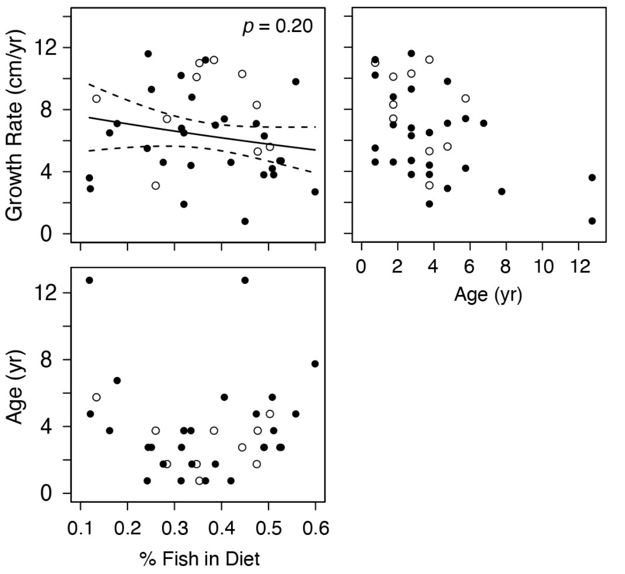

FIGURE 5 | Generalized Linear Model results examining the relationship between annual Kemp's ridley sea turtle growth rates and proportional contribution of fish to western Gulf of Mexico turtle diets. Diet estimates are derived from a stable isotope mixing model that included informative priors. Data are for the most recently deposited growth layer prior to death only. Closed circles are true annual growth rates (i.e., turtle stranded in spring, yielding a complete growth interval). Open circles are estimated annual growth rates for turtles that stranded during the winter (November–March); we assumed that annual skeletal growth asymptotes in November (see section "Somatic Growth Rates in Materials and Methods").

influencing $\delta^{15}N$ values. In nGoM and VA turtles, $\delta^{15}N$ values and age exhibited a weakly positive relationship (**Figure 4**). However, across all regions, turtles with the highest $\delta^{15}N$ values tended to span a wide range of ages, suggesting that larger/older turtles are generally not any more likely than smaller/younger turtles to feed higher in the food web.

Given the low intra-regional variation in diet composition for most regions, we only examined relationships between estimated diet composition and growth rates for turtles from the wGoM (**Figure 5**). For these turtles, growth rates were not strongly related to the proportion of fish in turtle diets ($P = 0.20$). Again, a shallow, non-significant, negative trend was evident in this relationship that did not change following exclusion of marginal growth rates from the analysis. Similar to covariate relationships with $\delta^{15}N$ values, the proportional contribution of fish was not strongly related to age (**Figure 5**).

DISCUSSION

Through an integration of multiple skeletal analyses, we provide the first population-level evaluation of Kemp's ridley diet composition and investigation into the relationship between individual foraging ecology and somatic growth. Our stable isotope mixing models revealed strong regional differences in the proportional contribution of different prey groups to turtle diets that generally followed findings of published gut and fecal content studies. We specifically observed greater contribution of fish to turtle diets in the western GoM and greater contribution of macroalgae/seagrass—or other isotopically similar benthic resources—to turtle diets in the eastern GoM, whereas invertebrates dominated turtle diets in other regions. Through comparative analyses of somatic growth rates, stable isotope values, and mixing model-derived diet composition estimates, we found that individual Kemp's ridley somatic growth rates were generally poorly correlated with stable isotope-based evidence of turtle trophic ecology within regions. Turtles that foraged higher in the food web (i.e., more fish in diet, higher $\delta^{15}N$ values) grew at the same rate as or slower than conspecifics foraging lower in the food web, even after accounting for ontogenetic effects on growth rates. Our results suggest that diet composition alone is not a primary determinant of Kemp's ridley growth rates, which may be more strongly influenced by other factors such as prey availability, foraging rate and efficiency, and nutritional condition.

Regional Diet Variation

Kemp's ridleys are opportunistic foragers, naturally feeding on a wide range of invertebrate species (Shaver, 1991). Various crab species generally constitute >75% of total dietary dry mass, whereas molluscs and vegetation generally make up <5–10% (Shaver, 1991; Burke et al., 1993, 1994; Seney and Musick, 2005; Servis et al., 2015; Schmid and Tucker, 2018). In the western and northern GoM, Kemp's ridleys also consume a significant amount of fish and shrimp. Fish can comprise up to 13.7% of total dietary dry mass and have been reported in 40.1–76.1% of stranded turtle gastrointestinal tracts in these regions (Werner, 1994; Cannon, 1998; Stacy, 2015). Fish prey are most likely obtained as discarded bycatch or bait from fisheries given that Kemp's ridleys are thought to lack the speed necessary to catch them live (Shoop and Ruckdeschel, 1982; National Research Council, 1990). This conclusion has been supported by the co-occurrence of *Nassarius* species—molluscs that scavenge dead animal tissues—in turtle stomachs that also contain fish (Shaver, 1991; Bjorndal, 1997). In contrast, fish are an uncommon prey item for Kemp's ridleys along the United States Atlantic Coast, occurring in a maximum of 16.7% of sampled turtles (Burke et al., 1993, 1994; Seney and Musick, 2005).

Results of our Bayesian isotope mixing models largely follow these patterns, with invertebrates comprising 68.5–97.7% of turtle diets along the United States Atlantic Coast but smaller and more variable proportions within the GoM. In the western GoM, where shrimp fishing effort is relatively high (Scott-Denton et al., 2012), we estimated the region-level contribution of fish to turtle diets was 42.6–43.1%. The similarity in posterior distribution estimates for models with informative and uninformative priors suggests our stable isotope data were highly informative and that these estimates are relatively robust (Moore and Semmens, 2008). Kemp's ridleys display remarkable plasticity in diet that appears largely driven by local availability rather than preferences for specific prey species (Bjorndal, 1997). Importantly, even with the implementation of bycatch reduction devices, shrimp fishery discard rates are high in the GoM, accounting for ∼50% of total

United States fishery discards (Diamond, 2004; Harrington et al., 2005; Scott et al., 2012). It is thus probable that consumption of fish bycatch discarded by shrimp trawlers is a facultative response to local availability in addition to ease of acquisition.

Diet composition estimates for turtles in the northern GoM were similar to those for turtles along the United States Atlantic Coast, with estimated contributions of invertebrates to diets ranging between 65.6 and 94.2%. These results were unexpected given our hypothesis regarding the spatial relationship between shrimp trawl activity and fish consumption, and contrast with recent necropsy results for the region which suggest higher contributions of fish to turtle diets (Stacy, 2015). Even though fishery discard rates are high in the northern GoM, natural prey availability is also high in this region and may be sufficient to support the Kemp's ridley population. Indeed, blue crab landings in Louisiana represent > 75% of all landings in the Gulf of Mexico, whereas those in Texas comprise only 7% (GSMFC, 2015). The negligible estimated contribution of fish to northern GoM turtle diets may also be due to the close proximity of fish and crustaceans in isospace (**Figure 2**). Mixing models require sources to be sufficiently separated in order for the model to be able to differentiate them (Parnell et al., 2013). It is thus possible that fish contribute more to Kemp's ridley diets in this region than our mixing models indicate. Further refinement of the prey stable isotope data to more accurately reflect fish (species and size) and invertebrate species consumed by Kemp's ridleys may improve mixing model-derived diet estimations for this and other regions.

Within the eastern GoM, we estimated Kemp's ridley diets primarily comprise invertebrates (43.5–53.6%) and macroalgae/seagrass (42.4–47.8%). These results do not align with the current understanding of Kemp's ridley diet composition and are likely due to two factors. First, the invertebrate prey groups in the eastern GoM are the most clustered in isospace relative to other regions, with δ^{13}C values for crustaceans and gastropods being particularly low (**Figure 2**). Such a δ^{13}C mismatch could arise if the eastern GoM crustaceans and gastropods included in our study derived a greater proportion of their carbon from terrestrial vs. marine sources relative to the other regions (Michener and Schell, 1994). This, combined with slightly higher turtle δ^{13}C values in this region, resulted in the largest isotopic mismatch between invertebrates and turtles of all regions after accounting for trophic enrichment. It is thus possible that the prey data included in our mixing model did not accurately reflect those prey groups or turtle diets in this region. Second, it is also possible that our mixing model is missing a key prey source. Notably, tunicates are thought to be an important prey source for Kemp's ridleys in southwest Florida, occurring in 83.3% of fecal samples and constituting 38.6% of fecal dry mass (*n* = 64 turtles; Witzell and Schmid, 2005). A dearth of tunicate stable isotope data prevented their inclusion in our mixing models. However, two tunicates sampled in Saint Joseph's Bay, Florida, had δ^{15}N values of 5.51 and 5.56‰ and δ^{13}C values of −12.72 and −12.78‰ (Williams et al., 2014), which fall within the range of seagrass and macroalgae stable isotope values included in our study. Therefore, our results may in fact reflect consumption of this or another similar benthic resource rather than macroalgae/seagrass.

While isotopic mixing models have greatly advanced our ability to discern diets from isotopic data, their utility and accuracy still rely on substantial ecological knowledge for proper parameterization—these models will always attempt to fit the data, even if the consumers fall outside the mixing space (Phillips and Koch, 2002; Parnell et al., 2010). Given the spatiotemporal scale of this study it was necessary to rely on prey isotopic data from the primary literature, which may have inserted certain biases into the analysis. We ameliorated temporal effects to the best of our abilities by using time-corrected δ^{13}C values. However, it was not possible to overcome spatial biases in sample collection and as a result this may represent the greatest source of bias in our analysis. Kemp's ridley sea turtles forage in a wide range of shallow, benthic marine habitats, including a substantial part of the continental shelf (Shaver et al., 2013; Hart et al., 2018). Unfortunately, few studies have characterized invertebrate stable isotope values for continental shelf habitats resulting in greater prevalence of estuarine and coastal organisms in our prey isotopic dataset. Given the growing application of stable isotopes to the study of sea turtle foraging and spatial ecology (Pearson et al., 2017; Figgener et al., 2019), quantifying means and variances in known prey stable isotope values across sea turtle ranges should be a high-priority research area. Future analyses using compound-specific isotope analysis of amino acids, which can more accurately estimate consumer trophic position, may also greatly aid in understanding diet variation in sea turtles (Evershed et al., 2007; McMahon and Newsome, 2018).

Trophic Ecology and Somatic Growth Dynamics

The lack of strong relationships among bone δ^{15}N values, mixing model-derived diet composition estimates, and somatic growth rates suggests that within-population variation in diet composition may not be a primary determinant of Kemp's ridley somatic growth variation, and that diet composition may not be a strong driver of the regional (Atlantic vs. GoM) somatic growth differences observed in this species. However, we measured only one component of a sea turtles' diet—composition—and foraging rate, nutrient assimilation rate, and nutritional status can also strongly influence animal growth rates. Unfortunately, these factors are difficult to study in sea turtles due to their high mobility and conservation status, which has thus far limited investigations into relationships between sea turtle trophic ecology and growth. Wallace et al. (2009) provides the only other comparison of sea turtle trophic ecology and somatic growth where they compared blood plasma δ^{15}N and δ^{13}C values with growth rates of recaptured loggerhead turtles from North Carolina, United States. They found no strong relationships between these covariates and hypothesized that intra-population growth variation may instead be driven by alternative habitat use (coastal vs. oceanic habitat; McClellan and Read, 2007). However, recent research suggests that loggerhead growth dynamics are similar between coastal and oceanic life stages and foragers (Ramirez et al., 2017), indicating that perhaps other factors underlie the observed variability in growth.

Surprisingly, our results suggest that turtles foraging at higher trophic levels may in fact exhibit lower growth rates than conspecifics foraging at lower trophic levels. Our study does not shed light on underlying mechanisms for this pattern, but these findings suggest that foraging strategies that rely on higher trophic level prey may not be energetically optimal for sea turtles. For example, that this energy rich (Williams et al., 2014; Schaafsma et al., 2018), yet presumably similarly digestible (Tibbetts et al., 2006; Peckham et al., 2011), prey does not infer a growth advantage may indicate that the energetic costs associated with searching for and consuming fish (discards) outweigh energetic gains. Similarly, Kemp's ridleys may not be well adapted to consume fish given that fish are considered an unnatural prey item. Our understanding of sea turtle nutritional ecology is poor for omnivorous species (Bjorndal, 1997), but it is plausible that sea turtles may less efficiently assimilate nutrients from fish relative to invertebrates due to evolutionary constraints.

However, it is also possible that the conditions that lead Kemp's ridleys to consume fish also contribute to reduced growth rates. If Kemp's ridleys consume fish due to low natural prey availability or poor condition, turtles may consume fewer resources overall or be nutritionally stressed which would lead to reduced growth rates. Additionally, the tissues of nutritionally stressed animals tend to have higher δ^{15}N values because they catabolize their own tissues for energy (Hobson et al., 1993; Fuller et al., 2005). Given the retrospective nature of our study, we were not able to evaluate the nutritional condition at stranding for sampled turtles. However, necropsies of Kemp's ridleys stranded in the northern GoM (Louisiana, Mississippi, and Alabama) between 2010 and 2014 suggest there was a decline in stranded turtle nutritional condition during this period (Stacy, 2015). As all but one of the northern GoM humerus bones we sampled were from turtles stranded between 2010 and 2014, the apparent decline in growth rates with increasing δ^{15}N values for this region may be attributed in part to this general decline in turtle nutritional condition in the region. Future studies combining stranded turtle nutritional assays, skeletochronology, and stable isotope analyses would greatly aid in identifying factors underpinning the observed growth patterns.

An important source of uncertainty in our growth analysis is the potential influence of growth rates on isotopic signatures and trophic discrimination factors (TDFs). For neonate loggerhead sea turtles (*Caretta caretta*), somatic growth can explain up to half of the total rate of isotopic incorporation into blood, skin, and scute tissues, and likely explains age-related differences in nitrogen TDFs (Reich et al., 2008). Indeed, multiple studies have demonstrated that faster growth can reduce Δ^{15}N values because nitrogen input greatly exceeds nitrogen loss—more ^{14}N is retained in the body which lowers δ^{15}N values and reduces isotopic differences between consumers and their prey (Fuller et al., 2004; Martinez del Rio and Wolf, 2005; Reich et al., 2008; Kurle et al., 2014). Such physiological effects, if not accounted for in stable isotope-based studies, can lead to spurious conclusions, particularly in species with distinct ontogenetic changes in size and growth (Villamarín et al., 2018). For our study, a growth-induced decline in Δ^{15}N values may have caused us to underestimate the proportional contribution of fish to turtle diets for faster growing individuals. In contrast, animals that consume large amounts of animal-derived proteins typically have higher Δ^{15}N values (Vander Zanden et al., 2012; Kurle et al., 2014; Turner Tomaszewicz et al., 2017b). A diet-induced increase in Δ^{15}N would therefore potentially have the opposite effect as growth on TDFs, causing an overestimation of the proportional contribution of fish to turtle diets for individuals that forage higher in the food web. Given the sensitivity of our results to changes in Δ^{15}N values, more studies are needed that characterize isotopic routing within sea turtle tissues and effects of diet type and physiology on TDFs, particularly for bone tissue (e.g., Turner Tomaszewicz et al., 2017b).

CONCLUSION

The integration of skeletal growth and stable isotope analysis provides a powerful tool to reconstruct sea turtle trophic ecology while simultaneously investigating relationships between diet composition and somatic growth rates. Using this approach, we elucidated substantial regional variation in Kemp's ridley diet composition that aligns with results of site-specific studies of their foraging ecology. This study also provides one of the few quantitative assessments of the relationship between sea turtle trophic ecology and somatic growth. While we present a promising new approach for studying drivers of somatic growth variation in sea turtles, our analysis was limited due to critical data and knowledge gaps. Greater characterization of sea turtle prey stable isotope values throughout the western North Atlantic Ocean, and diet-tissue isotopic discrimination factors, would substantially improve the stable isotope mixing models herein and allow for more robust isotope-based investigations into sea turtle foraging ecology (Pearson et al., 2017; Figgener et al., 2019). Additionally, applications of stable isotope mixing models to Kemp's ridleys at narrower spatiotemporal scales (e.g., specific foraging grounds, ages, and years) and using greater taxonomic specificity for prey groupings may help reduce sources of uncertainty, improve model estimates, and clarify relationships between diet composition and growth rates (e.g., Wallace et al., 2009; Lemons et al., 2011; Goodman Hall et al., 2015). Integrating additional data gleaned from dead stranded turtles (e.g., gut contents, nutritional condition, and parasite load) into these analyses may also be informative. Ultimately, our analysis further highlights the unique importance of stranded and salvaged turtles to investigating otherwise intractable questions in sea turtle ecology.

DATA AVAILABILITY STATEMENT

All prey isotope datasets, and turtle isotope and growth metadata, generated for this study are included in the article/**Supplementary Material**. Full turtle isotope and growth datasets are available upon request to the corresponding author.

ETHICS STATEMENT

Ethical review and approval was not required for the animal study because this study only utilized samples opportunistically collected from animals that died naturally and washed up on beaches.

AUTHOR CONTRIBUTIONS

MR, LA, and SH contributed to the conception and design of the study. LA and MC provided samples for analysis. MR, LA, LG, and MS performed skeletochrological analyses. MR performed stable isotope and statistical analyses and wrote the first draft of the manuscript. All authors contributed to manuscript revision and approved the submitted version.

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SUPPLEMENTARY MATERIAL

The Supplementary Material for this article can be found online at: https://www.frontiersin.org/articles/10.3389/fmars.2020.00253/full#supplementary-material

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frontiers in Marine Science

BRIEF RESEARCH REPORT
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Hurricane Frequency and Intensity May Decrease Dispersal of Kemp's Ridley Sea Turtle Hatchlings in the Gulf of Mexico

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Environmental variability can be an important factor in the population dynamics of many species. In marine systems, for instance, whether environmental conditions facilitate or impede the movements of juvenile animals to nursery habitat can have a large influence on subsequent population abundance. Both subtle differences in the position of oceanographic features (such as meandering currents) and major disturbances (such as hurricanes) can greatly alter dispersal outcomes. Here, we use an ocean circulation model to explore seasonal and annual variation in the dispersal of post-hatchling Kemp's ridley sea turtles (*Lepidochelys kempii*). We simulated the transport of 24 cohorts of young-of-the-year Kemp's ridley sea turtles dispersing from the three primary nesting areas in the western Gulf of Mexico to describe variability in transport during the main hatching season and across years. We examined whether differences in transport distance among Kemp's ridley cohorts could be explained by hurricane events. We found that years with high numbers of hurricanes corresponded to shorter dispersal distances and less variance within the first 6 months. Our findings suggest that differences in dispersal among sites and the impact of hurricane frequency and intensity could influence the survivorship and somatic growth rates of turtles from different nesting sites and hatching cohorts, either improving survival by encouraging retention in optimal pelagic habitat or decreasing survival by pushing hatchlings into dangerous shallow habitats. Considering such factors in future population assessments may aid in predicting how the potential for increasing tropical storms, a phenomenon linked to climate change, could affect Kemp's ridley and other populations of sea turtles in the Atlantic Ocean.

Keywords: dispersal, hurricane, sea turtle, ocean circulation model, movement ecology, spatial ecology

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INTRODUCTION

Many marine species move across widely separated habitats to seek conditions that are favorable for the development, growth, and survival of different life-stages (Harden Jones, 1968; Putman, 2018). These periods of habitat transition are considered "critical periods" for understanding population abundance and may be closely linked to dynamic ocean circulation processes that either facilitate or impede movement into favorable locations (Hjort, 1914; Secor, 2015). In particular, temporal fluctuations in population abundance are hypothesized to be driven by variability in the oceanic transport of juveniles to nursery grounds (Sagarese et al., 2015; Liu et al., 2016). Sea turtles are iconic examples of the life-history strategy in which juveniles disperse long-distances from their natal site to reach nursery habitat (Carr, 1987). Hatchling turtles dig out from nests deposited on sandy beaches, and upon entering the water for the first time, undertake a 1 to 2 day "swimming frenzy" to move offshore as quickly as possible, but hatchlings are small and cannot swim very quickly (Wyneken and Salmon, 1992; Lutz and Musick, 1996). The initial entrance into the water is the most dangerous, and it is estimated that an average of 30% of hatchlings do not make it through the initial gauntlet of nearshore predators (Witherington and Salmon, 1992; Gyuris, 1994). Ocean currents push hatchlings along and assist in dispersal to pelagic habitat where they remain in the open ocean traveling with the major current systems and, at a smaller scale, associating with habitats such as pelagic *Sargassum* (Carr, 1987; Collard and Ogren, 1990; Witherington et al., 2012). Upon reaching the large juvenile life stage, they depart for coastal waters and their neritic habitat (Witherington et al., 2012; Wildermann et al., 2018). Upon reaching maturity (perhaps a decade or more later), they return to the vicinity of their hatching site to reproduce (Lohmann et al., 2008). If currents move hatchlings offshore faster, they spend less time in the coastal zone, where they are presumed to be most vulnerable to predators (Witherington and Salmon, 1992; Gyuris, 1994). Owing to natal homing, locations that produce more surviving hatchings might also have higher numbers of turtles returning to nest (Putman et al., 2010a).

The role of hatchling dispersal on regional variation in population abundance is well-established: beaches positioned closer to ocean circulation features that consistently aid in the transport of hatchlings to offshore habitats host larger sea turtle populations than beaches further away (Putman et al., 2010a,b; Okuyama et al., 2011; Shillinger et al., 2012; Ascani et al., 2016; Putman, 2018). There are also indications that temporal variability in ocean circulation could influence population dynamics (Ascani et al., 2016; Scott et al., 2017). Intuitively, periods when ocean currents are more favorable for transport should result in higher survival and subsequently higher recruitment into the adult age classes, but a direct link has been challenging to demonstrate. In part, insufficient data has been collected on temporal variability in the dispersal of hatchlings to rigorously test the hypothesis (Arendt et al., 2013).

As a step toward understanding the population-level implications of temporal variability in hatchling sea turtle dispersal, we used an ocean circulation model to simulate the post-hatchling movements of Kemp's ridley sea turtles (*Lepidochelys kempii*) from their nesting beaches in the western Gulf of Mexico. Kemp's ridleys are the smallest sea turtles in both size and abundance (Lutz and Musick, 1996). Kemp's ridley sea turtles are also somewhat unique in that they often reproduce in large aggregations known as *arribadas* which occur only a few times in a season (Bevan et al., 2016). They are listed as critically endangered by the IUCN and as endangered by the United States. Endangered Species Act (NMFS, 2015; IUCN, 2019). Their three primary nesting beaches are Rancho Nuevo in Tamaulipas, Mexico, where >90% of the population nests, several beaches in Veracruz, Mexico, and a head-started population established in 1978 at Padre Island, TX, United States (Putman et al., 2013; Putman, 2018). Kemp's ridley sea turtles spend their first 2 years in oceanic habitats before recruiting to coastal waters along the Gulf of Mexico and the East Coast of the United States (Collard and Ogren, 1990; Putman et al., 2010b). Kemp's ridley sea turtles reach maturity within 10 to 15 years (Avens et al., 2017) and return to the vicinity of their natal site to reproduce, thus contributing to different demographic and genetic trajectories for distant nesting aggregations (Putman and Lohmann, 2008; Shaver et al., 2016). The Kemp's ridley sea turtle reached dangerously low numbers in the late 1900s, but responded well to intensive conservation efforts that led to a considerable population increase (Marquez et al., 2005; Bevan et al., 2016). However, since 2010, population growth appears to have abruptly stopped and has been in decline or fluctuation, and intensive management is still necessary to protect this species (NMFS, 2015; Caillouet et al., 2018). Ultimately, understanding how environmental factors influence hatchling dispersal may help increase the accuracy of population assessments that assist conservation managers in decision making for this critically endangered species.

Here, we used "hindcasts" of historical ocean conditions from the Global Hybrid Coordinate Ocean Model (HYCOM) paired with virtual particle-tracking to describe daily variability in transport during the main hatching season (June through July) and annual variability over the past quarter century (Putman et al., 2020). In these simulations, we did not attempt to simulate swimming behavior, as our aim was simply to produce indices that reflect variability in environmental conditions that influence dispersal. To better understand the processes contributing to variation in Kemp's ridley sea turtle dispersal, we examined whether tropical storm frequency and intensity contributed to yearly differences in transport predictions (Monzón-Argüello et al., 2012). Though hurricanes often have catastrophic effects on biological communities, they also may aid in the dispersal of various species both native and invasive (Eggleston et al., 2010; Johnston and Purkis, 2015; Smith et al., 2017). As hurricane season coincides with nesting and hatching seasons for many populations of sea turtles, it is plausible that hurricanes have acute impacts on nest survival, hatchling survival and hatchling dispersal (Monzón-Argüello et al., 2012). Finally, we discuss how this work to identify environmental factors that influence hatchling dispersal may help increase the accuracy of population assessments.

METHODS

To simulate the initial dispersal of hatchling Kemp's ridley sea turtles during their first year of life, we used the particle tracking software Ichthyop (v. 2.2) and velocity field outputs from the Global Hybrid Coordinate Ocean Model (HYCOM 3.1) (Chassignet et al., 2007; Lett et al., 2008). HYCOM is an eddy-resolving model that assimilates *in situ* and satellite observations to depict oceanic conditions that occurred at specific times in the past (Chassignet et al., 2007). Global HYCOM portrays ocean circulation features, such as fronts, filaments and mesoscale eddies, which are relevant to the transport of marine organisms (Chassignet et al., 2007; Putman and He, 2013). We obtained HYCOM data for the years 1993 through 2017 from Reanalysis and Hindcast Experiments 19.0, 19.1, 91.0, 91.1, and 91.2[1].

Using Ichthyop, we released particles from defined release polygons close to the shore of the three main nesting regions of Kemp's ridley sea turtles. The central points of these polygons are as follows: Padre Island, Texas (27° 14′ 9.78″N, 97° 20′ 42″W), Rancho Nuevo (23° 22′ 12″N, 97° 45′ 20.88″W), Mexico, and Veracruz, Mexico (20° 28′ 49.44″N, 97° 0′ 44.64″W, and 19° 1′ 20.28″N, 95° 58′ 30″W) and correspond to those used in Putman et al. (2019). These release locations encompass the beaches used by the majority of females in the species (Putman et al., 2013; Putman, 2018). To simulate dispersal throughout the height of the hatching season, we released 350 particles day^{-1} from June 1 to July 31, the primary hatching period for this species (Rostal et al., 1998), and repeated simulations yearly between 1993 and 2016. This 24-year period encompasses a wide range of variability in environmental conditions within the Gulf of Mexico. Particle tracking took place for 12 months after release to model the initial dispersal into the Gulf of Mexico. Ichthyop simulates movement using a Runge-Kutta 4th-order time step method with 30 min time steps and saves the particle locations daily. These simulations of sea turtle dispersal use the same methods as were applied in Putman et al. (2016) that were shown to account for variability in observed turtle distributions. Specifically, dispersal simulations from Rancho Nuevo and Veracruz predicted temporal variation in the number of small juvenile Kemp's ridley sea turtles that stranded along the west coast of Florida and dispersal simulations from Texas predicted temporal variation in Kemp's ridley strandings along the Texas coast (Putman et al., 2020). The agreement between model predictions and Kemp's ridley strandings suggests that these dispersal simulations can be used to examine the role of ocean circulation dynamics on temporal changes in sea turtle movement and distribution (Putman et al., 2020).

In this present study, we calculated the net straight-line distance from each particle's starting location to its position after 10 days, 6, and 12 months of drift. We measured the straight-line distance (km) using Python (v2.2) and geospatial data from the particle tracking simulation. Thus, for each release day, we calculated the mean and standard deviation of dispersal distance for each of the 350 particles released from a given site. With this data, our first aim was to describe temporal variation in dispersal distance for turtles hatching at different dates during the hatching season and whether differences exist across years. We then sought to explore whether annual variation in dispersal could be accounted for by major storm events (Monzón-Argüello et al., 2012).

To examine if hurricane frequency and severity affect dispersal distance and variability in dispersal distance, we compiled a list of Atlantic hurricanes, including the total number for the entire season, the number in the Gulf of Mexico each year, and the number occurring during the hatching season. We considered storms entering the ocean between the bounds of 16°N and 78°W to be near enough to the Gulf of Mexico to potentially impact Kemp's ridley dispersal. Due to the wide distribution of hatchlings throughout the Gulf of Mexico as they disperse and the wandering nature of hurricanes, we did not divide the study area further but rather sought a holistic analysis of hurricane impact. We quantified the severity of the hurricanes by two indices. First, the average maximum wind speed of storms in the entire Atlantic season (kph) (NOAA, 2019). Second, we calculated the average maximum wind speed of hurricanes that occurred in the Gulf of Mexico (kph) (NOAA, 2019). These covariates were used to determine the severity of hurricanes as a potential source of environmental variability during neonate dispersal.

We statistically analyzed if dispersal distances at 6 months varied across the three nesting sites and over time. We selected 6 months of drift to statistically evaluate for hurricane impacts, as the first 6 months of life is a critical period for hatchlings and we wanted to investigate the longer term impacts of hurricane frequency and severity on hatchling dispersal, rather than evaluate the short-term effects on early stage (<3 months) neonates. In addition, we tested whether the number of hurricanes that occurred in the Atlantic Ocean and the Gulf of Mexico annually and during the hatching season, the total average peak wind speed in the Atlantic Ocean, and the average maximum wind speed in the Gulf of Mexico resulted in a net lower dispersal distance and smaller standard deviation. All continuous explanatory variables were standardized to be centered at 0 by taking the value minus the mean divided by the standard deviation using the scale function in R, so that effects across variables could be more easily compared. The dispersal distance did not meet the assumptions of a normal distribution, based on a Shapiro-Wilkes test and visual inspection of qq plots. We tested for collinearity of the explanatory variables using variance inflation factors, and all variables were <3, our *a priori* threshold, and thus all were included in the global model (Zuur et al., 2009). Initial exploratory analyses of the simple model of hatchling dispersal over 6 months regressed with the number of Gulf of Mexico hurricanes and year suggested a degree of temporal autocorrelation, based on ACF plots, and including an autocorrelation structure substantially increased the model fit. As the sites were reasonably far apart (the two closest sites, Padre Island, Texas and Rancho Nuevo, Mexico are 561 km apart), we did not account for spatial autocorrelation (and including this as a model term did not improve fit). Thus, we used a generalized linear mixed effects model (GLMM), with year as random effect (due to the temporal autocorrelation), and a gamma distribution with a log link.

We used the information theoretic approach to evaluate if hurricane frequency and severity were predictors of hatchling dispersal, using the global model $\text{Dispersal distance}_{i,j} = \beta_0 + \beta_1 \cdot \text{Hurr\_gulf} + \beta_2 \cdot \text{Hurr\_season} + \beta_3 \cdot \text{Hurr\_hatch} + \beta_4 \cdot \text{Total\_avg\_wind} + \beta_5 \cdot \text{Peak\_wind\_gulf} + \text{Site}_i + a_i + \varepsilon_{i,j}$, where $a_i \sim N(0,\sigma^2_{\text{year}})$, and $\varepsilon_{i,j} \sim N(0, \sigma^2)$, of site *i* and year *j*. We ranked candidate models using Akaike Information

Criterion correction for small sample sizes (AICc; Burnham and Anderson, 2002; Hobbs and Hilborn, 2006). AICc, as an index of model fit to the data, balances the maximum log-likelihood and model complexity (i.e., number of model parameters; Burnham and Anderson, 2002; Johnson and Omland, 2004). As such, AICc is a superior metric to assess model fit than traditional adjusted-R^2 goodness-of-fit tests commonly used in frequentist statistical approaches (Johnson and Omland, 2004). Models with $\Delta\text{AICc} \leq 2$ from the top ranked model were considered to have comparable fit to the data while balancing parsimony in the number of explanatory variables and were included in the confidence model set. We used evidence ratios to quantify the probability of the top-ranked model compared to the null model, with an intercept only (Burnham and Anderson, 2002).

RESULTS

Temporal Variability in Dispersal Across the Nesting Beach Sites

There was considerable variation in the dispersal distance across time and sites within the first 10 days (**Figures 2B,D**), a crucial time when the turtles are small and vulnerable (Wyneken and Salmon, 1992). The first 10 days of post-hatching dispersal across all releases from all years had an absolute minimum mean dispersal distance of 22 km and an absolute maximum mean distance of 378 km (**Figure 2B**). The ocean currents at the three nesting beaches are different due to their positioning within the Gulf of Mexico (**Figure 1A**). Rancho Nuevo sits at an optimal location for hatchlings as they are transported directly into a large gyre with a western boundary current that takes them into the deep waters of the Gulf of Mexico while allowing them to avoid both inward coastal currents and the Atlantic bound Loop Current in the eastern Gulf of Mexico (Sturges and Blaha, 1976). As such, there is a consistent pattern of dispersal where Rancho Nuevo has the highest dispersal distance, followed by Veracruz, with Padre Island having the lowest yearly and seasonal dispersal (**Figures 2B,D**).

There were considerable differences in dispersal across years with a range of 45–246 km across the sites (**Figures 2A,B**). Rancho Nuevo, Veracruz, and Padre Island had average yearly distances of 165 (±54 SD) km, 89 (±47 SD) km, and 64 (±18 SD) km (**Figure 2B**). There are visible differences in the intensity and placement of currents during different years (**Figure 2A**). Rancho Nuevo and Veracruz followed a pattern of years with high and low dispersal distance. Padre Island also matched the pattern in several years. In general, and across all three sites, there was a decrease in dispersal distance between 1993 and 2016, which was most evident in Rancho Nuevo (**Figure 2A**).

In Rancho Nuevo and Veracruz, there were also distinct seasonal peaks in dispersal at 10 days based on what day the turtles hatched. A turtle hatching in early June, early July, and late July traveled much farther and much faster than hatchings in the middle of the month (**Figure 2D**). The seasonal range was from 50 to 194 km across the sites. Rancho Nuevo, Veracruz, and Padre Island had seasonal average distances of 161 (±67 SD) km, 87 (±54 SD) km, and 60 (±20 SD) km. The Veracruz beaches had smaller within-season peaks than Rancho Nuevo; dispersal started relatively higher and decreased over time with peaks in early June, early July, and late July (**Figure 2D**). Padre Island lacked within season variability, but instead dispersal distance tended to increase over the season (**Figure 2D**).

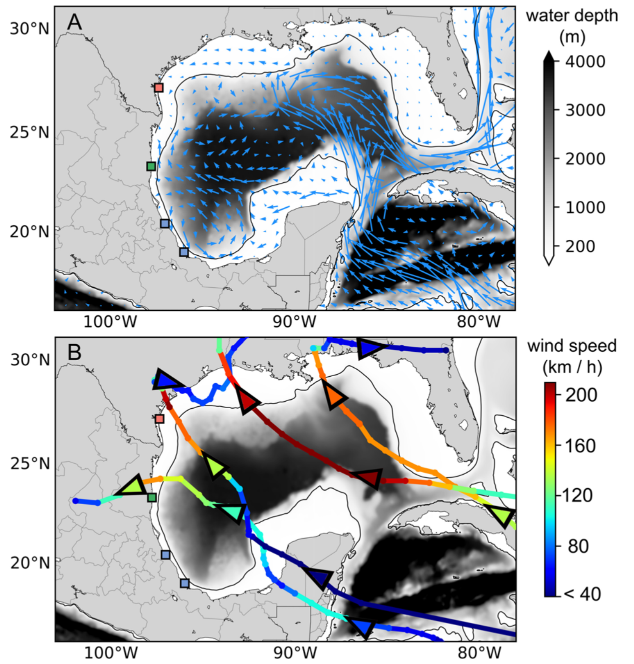

FIGURE 1 | (A) Map of the Gulf of Mexico with major circulation patterns and bathymetry. Nesting beaches of the Kemp's ridley sea turtle are indicated by colored markers. Sites from top to bottom are Padre Island, TX, United States (Red), Rancho Nuevo, Tamaulipas, Mexico (Green) and Veracruz, Tamaulipas, Mexico (Blue). **(B)** Map of Gulf of Mexico and Kemp's ridley sea turtle nesting beaches with the paths of selected hurricanes, Georges (1998), Rita (2005), Alex (2010), and Harvey (2017). Colors of tracks indicate wind speed of the storm, triangles indicate direction of travel.

Hurricane Frequency and Intensity as Predictors of Hatchling Dispersal Distance

Across 1993–2016, there were 378 Atlantic hurricanes, with 147 of them passing through or near the Gulf of Mexico, and 64 of them taking place during the hatching season for Kemp's ridley sea turtles (NOAA, 2019; **Supplementary Table S1**, see **Supplementary Material**). 2005 had the highest number of storms ($n = 31$), while 2014 and 1997 had the lowest ($n = 9$). The average yearly peak wind speed of the storms, used as a proxy for storm severity, ranged from 54 mph in 1994 to 91 mph in 2004.

We analyzed models predicting mean dispersal distance over 6 and 12 months. We included the candidate explanatory variables of (i) the number of hurricanes in the Gulf of Mexico, (ii) number of hurricanes during the hatchling season only, (iii) the number of hurricanes for the entire season in in the Atlantic and Gulf of Mexico, (iv) peak wind speed, (v) average wind speed, and (vi) nesting beach site (Texas, Rancho Nuevo, and Veracruz).

As there was significant temporal autocorrelation in the dataset, we also included year as a repeated effect in the GLMM. Model output for dispersal distance at 12 months was similar, but did not show as strong of relationships as 6 months, so we do not discuss it in the main body (but see **Table 1** and **Supplementary Material** for model output).

For the mean dispersal distance for 6 months, all models in the confidence set (ΔAICc $<$ 2) included nesting beach site as an explanatory variable, while hurricanes in the Gulf of Mexico, hurricanes in the Atlantic, peak wind speed, or average wind speed were included in some of the models as well (**Table 1**). Interestingly, the number of hurricanes during the hatching season was not included as an important variable in the confidence set. All models in the confidence set included one of the hurricane frequency variables (hurricanes in the Gulf of Mexico, or hurricanes in the Atlantic). In general, mean dispersal distance at 6 months decreased with increasing hurricanes in the Gulf of Mexico or throughout the Atlantic Ocean (**Figures 3A,B**).

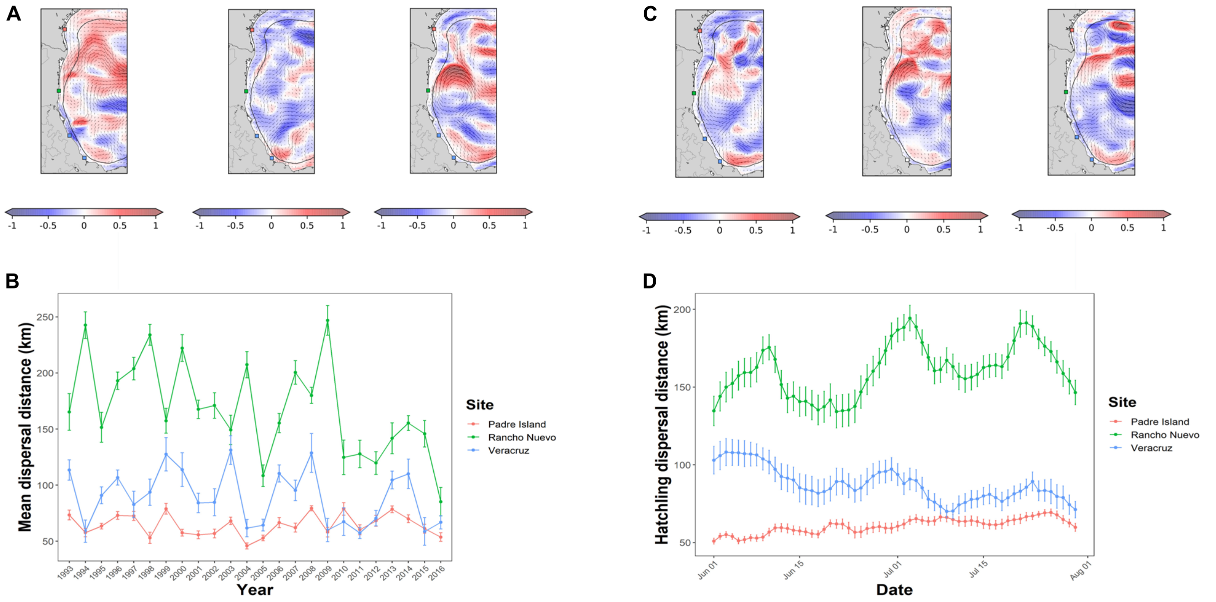

FIGURE 2 | Seasonal and annual variation in hatchling dispersal at 10 days post-hatching. **(A)** Annual variation in East/West currents (small arrows) on July 1, 2000, July 1, 2013, and July 1, 2016. Red coloration indicates stronger eastward currents, blue coloration indicates stronger westward currents (speed units are m/s). **(B)** Mean annual dispersal distance after 10 days post-hatching. Error bars indicate the 95% CI. Red corresponds to results for Padre Island, green for Rancho Nuevo, and blue for Veracruz. **(C)** Seasonal variation in surface currents in the western Gulf of Mexico on June 1, 2015, July 1, 2015, and July 30, 2015. Other conventions as in panel **(A)**. **(D)** Mean seasonal dispersal distance after 10 days based on the year of hatching. Other conventions as in panel **(B)**.

TABLE 1 | Confidence set for models describing mean dispersal distance and standard deviation of dispersal distance at 6 months.

Model	Hurricanes Gulf of Mexico	Hurricanes Hatching Season	Hurricanes Atlantic	Peak wind Gulf of Mexico	Total Avg Peak Wind	Site	Degrees of freedom	AICc	ΔAICc	AICc weight
Mean	−0.14					+	6	805.56	0.00	0.25
			−0.14			+	6	805.63	0.07	0.24
	−0.12				−0.05	+	7	807.13	1.57	0.11
	−0.12			−0.05		+	7	807.27	1.71	0.11
	−0.08		−0.07			+	7	807.34	1.78	0.10
			−0.12	−0.05		+	7	807.53	1.97	0.09
			−0.12		−0.04	+	7	807.56	2.00	0.09
St Dev	−0.20				−0.12	+	7	724.01	0.00	0.34
	−0.23					+	6	724.17	0.16	0.32
	−0.20			−0.09		+	7	725.25	1.23	0.19
	−0.29		0.12		−0.15	+	8	725.59	1.58	0.16

Model selection variables include the number of hurricanes in the Gulf of Mexico, the number of hurricanes during the hatching season, the total number of hurricanes in the Atlantic, the peak wind speed of hurricanes in the Gulf, the peak wind speed of all hurricanes in the season, and the nesting beach site. The (+) symbol indicates significance in the categorical variable of site while the values indicate the beta for the factor. All models $\Delta AIC \leq 2$ *AICc from the top-ranked model are included in the confidence set. Year was included as a random effect in the model, as there was important temporal autocorrelation in the data, and thus year was not subject to model selection process and was present in all candidate models.*

There were strong differences in dispersal distance across the three nesting beach sites, but the negative relationship between dispersal distance and hurricane frequency was conserved across the sites. As the evidence ratio of the top-ranked model, relative to the null model (Dispersal distance$_{i,j}$ = $\beta_0 + a_i + \varepsilon_{i,j}$) was 1.02 . 10^{25}, there is strong support for the effects of hurricane frequency and nesting location on dispersal outcome. The two indices of hurricane severity (total average peak wind speed for the season and the peak wind speed in the Gulf of Mexico) were also important explanatory variables and figured in the confidence model set (**Figures 3C,D**). Increasing storm severity in a season was correlated with decreased mean dispersal distance, albeit this relationship was not quite as strong as the number of hurricanes (**Figure 3**).

To assist in visualizing the effect of hurricanes on hatchling dispersal, we created maps of the years with the greatest and least numbers of storms to illustrate the positions of the released particles after 6 months (**Figure 4**). In 2005, the year with the highest number of storms, virtually no particles exited the Gulf of Mexico after 6 months - only 0.0047% of particles from Rancho Nuevo and none from Veracruz or Padre Island. In contrast, for years with the lowest numbers of hurricanes, 1997 and 2014, 3.35 and 1.16% of particles from Rancho Nuevo, 0.02 and 0.34% of particles from Veracruz entered the Atlantic within each year, respectively (but still none from Padre Island). The number of hurricanes in the Atlantic was inversely correlated with the percentage of particles entering the Atlantic from Rancho Nuevo and Veracruz within 6 months (Pearson's $r = -0.43$, $p = 0.036$, $n = 24$ for both), but less so for Padre Island (Pearson's $r = -0.28$, $p = 0.185$, $n = 24$). In contrast, there was no relationship between the percentage of particles that beached (i.e., advected into the model coastline) and hurricane frequency for Rancho Nuevo and Veracruz (Pearson's $r > -0.10$, $p > 0.641$, $n = 24$, for both), but a positive relationship was apparent for Padre Island (Pearson's $r = 0.45$, $p = 0.027$, $n = 24$). Thus, hurricanes appear to differentially impact the dispersal potential from different nesting areas, increasing retention in the Gulf of Mexico for Rancho Nuevo and Veracruz (with little impact on beaching) and increasing beaching for Padre Island (with little impact on transport to the Atlantic).

Standard Deviation in Dispersal Distance

As with mean dispersal distance, the magnitude of the standard deviation of dispersal distance typically followed the pattern of Rancho Nuevo having the highest values and Padre Island having the lowest, though the standard deviation lacked the consistency seen in the values of mean dispersal distance. Variability in dispersal distance tended to decrease with increasing hurricane frequency and storm severity (**Supplementary Figure S1** and see **Supplementary Material**). The standard deviation of dispersal distance at 6 months was most heavily influenced by both site and the number of hurricanes in the Gulf of Mexico, and all models in the confidence set included both variables (**Table 1**). Hurricane severity was also an important predictor, and all but one model included either the peak wind speed in the Gulf of Mexico or average peak wind speed. One model included two measures of hurricane frequency (seasonal total and Gulf of Mexico total) and total average wind speed. As with dispersal distance and the 6-month dispersal observations, there was a noticeable difference between the three nesting sites, where Rancho Nuevo had the highest and Padre Island had the lowest standard deviation of dispersal distance. Hurricane severity (peak wind speed or total average wind speed) also occurred in the confidence model set, and greater storm intensity was correlated with decreased standard deviation of dispersal distance across all three nesting beaches (**Supplementary Figure S3**).

DISCUSSION

Variation in Dispersal Distance Across Nesting Beaches and Time

As shown in previous modeling studies for Kemp's ridley sea turtles and other sea turtle species, ocean currents near populous nesting sites optimize hatchling movement to safe, productive nursery areas (Hays et al., 2010; Putman et al., 2010a,b, 2012a; Okuyama et al., 2011; Shillinger et al., 2012; Casale and Mariani, 2014; Putman, 2018). It is possible that better dispersal dynamics lowers hatchling mortality (Witherington and Salmon, 1992; Gyuris, 1994), causing more turtles to survive to adulthood and to lay nests at their natal beach (Putman et al., 2010a). Dispersal distance from Rancho Nuevo was consistently highest, followed by Veracruz, and then Padre Island, which coincides with the rank order of nesting population size (Putman et al., 2013). While the Padre Island nesting beach, in general, had the lowest dispersal distance nesting here was previously supplemented by translocation of eggs/hatchlings from Rancho Nuevo, and a head-starting program, making it difficult to draw conclusions about the effect of low dispersal on nesting at this location at this time (Shaver and Caillouet, 2015). Due to the *arribada* nesting strategy of Kemp's ridley sea turtles, understanding the dispersal dynamics specifically when the nests are hatching *en masse* could help us predict the impact of ocean currents during those specifically timed events (Bevan et al., 2016). For instance, dispersal distance from both Rancho Nuevo and Veracruz peaked at approximately the beginning of each month during the hatching season. Relating the seasonal variability in dispersal conditions to nesting events and subsequent hatching may provide further insight into the environmental drivers of nesting phenology (Bézy et al., 2020). Similarly, individual years also have clear distinctions in dispersal distance that could provide some insight into the overall survival of all turtles hatching by year.

Hurricanes

Our analysis revealed that there are considerable temporal differences in hatchling dispersal distance across sites and among years. Hurricane frequency and intensity appear to decrease dispersal distance and variability in that distance for Kemp's ridley hatchlings. Many hurricanes enter the Gulf of Mexico from the south and move westward (**Figures 1B**, **4**). When this occurs, hurricanes most likely push hatchlings back into the Gulf of Mexico, perhaps even back onto the continental shelf, counter to prevailing currents, and reduce the distance traveled (Monzón-Argüello et al., 2012). Hurricanes do not necessarily

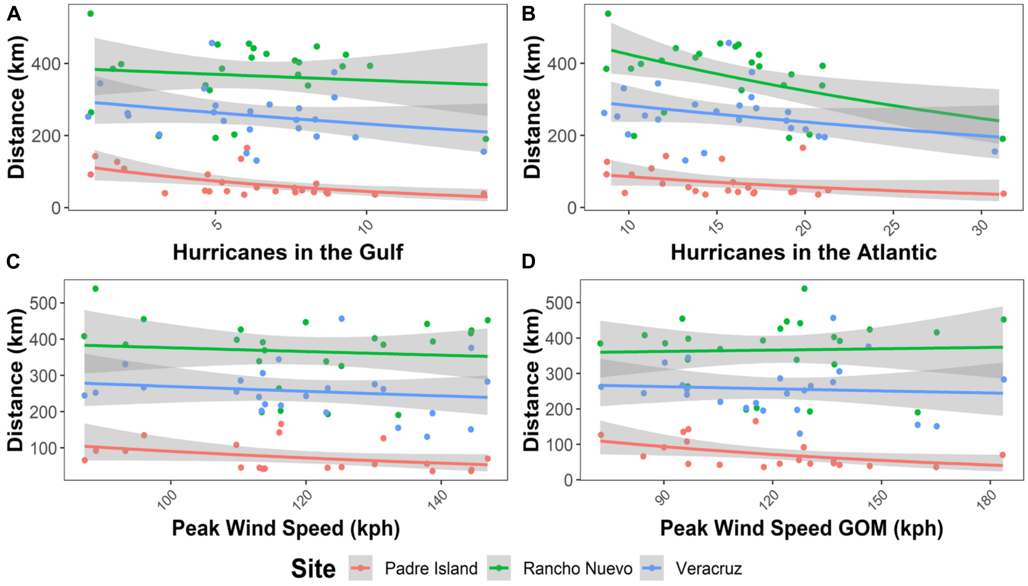

FIGURE 3 | Relationships between mean 6-month dispersal distance and **(A)** number of hurricanes in the Gulf of Mexico, **(B)** number of hurricanes in the Atlantic, **(C)** average peak wind speed for all hurricanes each year (kph), and **(D)** average peak wind speed for hurricanes in the Gulf of Mexico (kph) from 1993 to 2016. Red corresponds to results for Padre Island, green for Rancho Nuevo, and blue for Veracruz. To improve visualization of the relationships with the explanatory variables we plot unscaled variables though in the statistical analysis we standardized the variables.

have to be in the vicinity of the nesting beaches or occur during the hatching season to decrease dispersal distance. Hurricane severity, as measured by wind speed, also decreased hatchling dispersal distance. A year with many hurricanes in a season pushes the turtles back many times, and a year with strong storms likely pushes them with more intensity.

It is unlikely that there is an optimal dispersal distance to ensure the greatest survival rate for hatchlings. Generally, after the frenzy swimming period ends, Kemp's ridley sea turtles aim to associate with floating mats of pelagic *Sargassum* (Witherington et al., 2012). This habitat provides food sources and critical protection from oceanic predators. Thus, it seems likely that dispersal distances that result in reaching these offshore habitats would be ideal. However, these offshore *Sargassum* mats often become entrained in the Loop Current, which exits the Gulf of Mexico and coalesces into the Gulf Stream. There is evidence that older, oceanic-stage juvenile Kemp's ridleys orient themselves to remain in the Gulf of Mexico (Putman and Mansfield, 2015). Staying in the Gulf of Mexico keeps young turtles in comparatively warmer waters than they might encounter within the Atlantic Ocean, lessening the chance of cold stunning and keeping them out of sub-optimal habitats (Coleman et al., 2017; Avens and Dell'Amico, 2018). Thus, if hurricanes do indeed act as a retention mechanism for Kemp's ridley sea turtles in the Gulf of Mexico, there may be some benefit for juveniles. Alternatively, when hurricanes push small hatchlings back onto continental shelf habitats where predation is more likely (Witherington and Salmon, 1992; Gyuris, 1994), this could be potentially harmful. Interestingly, hurricanes seem to result in more favorable dispersal outcomes for post-hatchlings from Rancho Nuevo and Veracruz (decreasing transport into the Atlantic) than those from Texas (increasing beaching). This factor may also contribute to large population sizes at the Mexican nesting beaches (Fuentes et al., 2011).

However, survival could be impacted when hatchlings experience rough seas during hurricanes, so any purported benefit of retention in the Gulf of Mexico may be outweighed by additional losses due to physical injury (Monzón-Argüello et al., 2012). Our preliminary work using Ichthyop particles to estimate beaching, exiting the Gulf of Mexico, and approximate position at 6 months shows that there is likely a combination of both outcomes at play (**Figure 4** and **Supplementary Figures S2, S3**). The survival of turtles depends upon the circumstances of their final position in the Gulf of Mexico, as well as their natal beach and the severity of hurricanes in a given year. Though it is already known that dispersal from the Rancho Nuevo site is better at achieving transport to Gulf of Mexico foraging grounds (Putman et al., 2010b), future research addressing spatio-temporal dynamics in neonate survival and empirical estimates of hatchling migratory pathways would be beneficial for extending our understanding of population dynamics during the first year of life for this species (Scott et al., 2014).

Model Caveats/Limitations and Future Research Directions

Our simulations suggest that hatchling dispersal (and thus, potentially, survival) broadly varies over time and across nesting beaches. An important caveat is that, unlike their representatives in Ichthyop, turtles do exhibit active swimming (Wyneken and Salmon, 1992; Putman and Mansfield, 2015). Dispersal distances from our particle tracking model represent how the

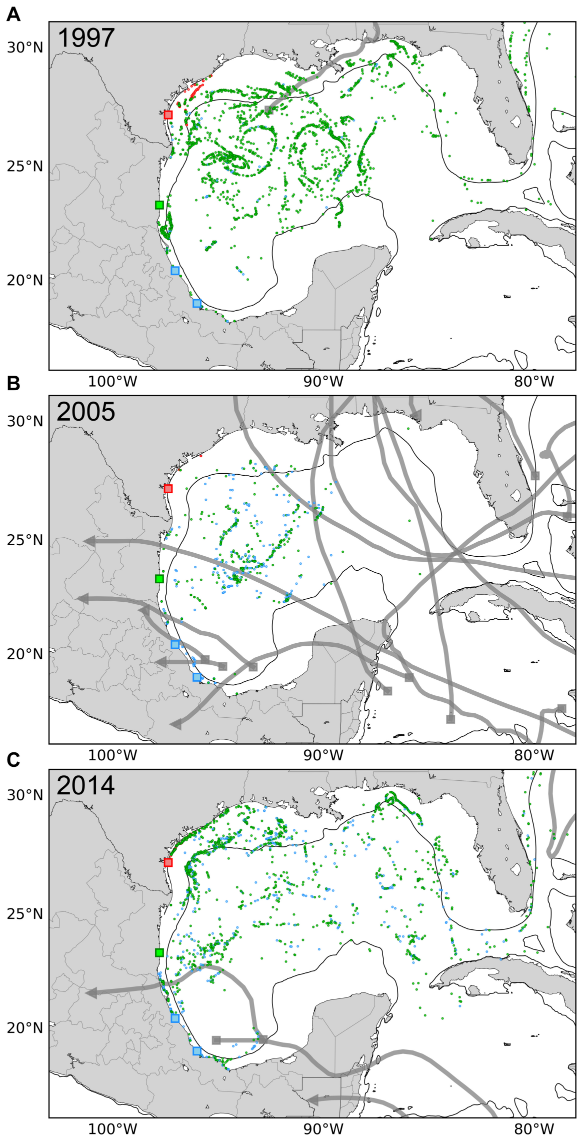

FIGURE 4 | Distribution of virtual particles released from Padre Island (red), Rancho Nuevo (green) and Veracruz (blue). Particles were released from each site (colored squares) and tracked for 6 months (*n* = 21,000 per year, per site). The thin black line delineates the continental shelf (200 m water depth) and the thicker gray lines indicate paths of hurricanes and tropical storms for a given year. Starting locations of storms are marked by a square, the end location is shown with a triangle. Results are shown for **(A)** 1997, a year with few hurricanes (9 in the Atlantic, 1 in the Gulf of Mexico); **(B)** 2005, a year with many hurricanes (31 in the Atlantic, 14 in the Gulf of Mexico); and **(C)** 2014, a year with few hurricanes (9 in the Atlantic, 2 in the Gulf of Mexico). Differences in the numbers of virtual particles shown among panels primarily result from "beaching" within the model, but also from overlap among particles and exit from the Gulf of Mexico. Annual differences in the percentage of particles that beach and exit the Atlantic from each nesting site and year (1993 through 2016) are shown in the **Supplementary Material**.

oceanic currents are acting upon the hatchlings and are not a direct prediction of location, but rather an index of whether environmental conditions are more or less favorable for dispersal.

Simulating swimming behavior in sea turtles can certainly alter modeled survivorship, dispersal routes, and the proportion of a population that encounters particular environmental conditions (Gaspar et al., 2012; Putman et al., 2012a,b, 2015; Scott et al., 2012; Lalire and Gaspar, 2019). Empirical movement data in turtles also indicates that they are not "passive drifters" during their post-hatchling and oceanic dispersal stage (Putman and Mansfield, 2015; Christiansen et al., 2016; Mansfield et al., 2017) and actively orient their movements using a suite of guidance mechanisms ranging from a large-scale geomagnetic map (Lohmann et al., 2001; Putman et al., 2011) to fine-scale movements toward pelagic *Sargassum* mats (Smith and Salmon, 2009). Swimming behavior in small-bodied marine animals appears to be relatively consistent through time and function to move animals toward regions of the ocean that are typically favorable (Putman et al., 2012a, 2020; Putman, 2015, 2018; Naisbett-Jones et al., 2017). Thus, ocean dynamics are likely to be the primary source of variability in the movements in these animals and, indeed, can account for much of the spatial and temporal variability in the distributions of many species (Putman and Naro-Maciel, 2013; Baltazar-Soares et al., 2014; Hays, 2017; Putman et al., 2020). While it is likely that the relative seasonal, annual, and site differences detected in our model are representative of actual conditions, the magnitude of these differences might differ substantially (e.g., dispersal distance from Rancho Nuevo would likely always exceed dispersal distances from Padre Island, but by how much will depend upon aspects of swimming behavior that we do not have information to parameterize) (Putman et al., 2012a,b). Thus, the dispersal metrics we present here are better suited as an index of less to more favorable dispersal conditions, rather than to determine actual survival (Putman et al., 2013).

While much work has focused on the contribution of large juvenile and sub-adult age classes for population recovery (Crouse et al., 1987; Heppell et al., 1996, 2005), our work suggests that hatchling productivity is mutable and the ability of those younger age classes to eventually recruit to the older, more demographically valuable, age classes is extremely variable. While the older age classes are more sensitive to small changes in survival and result in large increases in population growth, our research suggests that there may be *large* changes in neonate survival rate that may ultimately contribute to extreme variability in recruitment to the more sensitive age classes (Caillouet et al., 2018). Notably, empirical estimates of survival for neonate Kemp's ridley sea turtles do not exist (National Research and Council, 2010; Wildermann et al., 2018). So, it is not yet possible to parse out how variability in dispersal distance may influence hatchling survival, though it seems likely that spatio-temporal variability in dispersal would indeed influence individual survival rates. Variation in environmental conditions affect survival and reproduction across all species of sea turtles. Earlier work in sea turtles indicates that climate conditions and their influence on resource abundance are correlated with several reproductive factors, including the frequency of reproductive events, the number of offspring produced, offspring sex ratios, and offspring survival (Mrosovsky and Yntema, 1980; Lutz and Musick, 1996; Solow et al., 2002; Vincenzo et al., 2005; Pike and Stiner, 2007; Saba et al., 2007;

Piacenza et al., 2016). As such, environmental stochasticity is an important factor that influences life histories and, consequently, their representation in many population models (Lande, 1993; Legault and Melbourne, 2019). As increasingly detailed and global environmental data become available, such as we have generated with these analyses, a promising avenue for further work is to mechanistically link environmental change and population dynamics. Sources of variation such as the seasonal and yearly shifts in ocean currents and the acute disturbances caused by hurricanes impact geographically dispersed sea turtle nesting sites differently (**Figures 2**, **3**) and may be important to consider when designing management strategies and setting conservation goals.

Kemp's ridley sea turtles are endangered and in need of careful monitoring and conservation (Marquez et al., 2005; NMFS, 2015; Bevan et al., 2016; IUCN, 2019). Currently, conservation management for sea turtles implements beach protections, head-starting hatchlings, and protecting large juveniles and adults from bycatch, among other strategies (Crowder et al., 1994; Garcıía et al., 2003; Shaver and Caillouet, 2015). Given that climate change is predicted to increase hurricane frequency and severity, this species' ability to be resilient to storms is of utmost concern (Goldenberg et al., 2001; Knutson et al., 2010). A vital part of conservation management is continual monitoring and population assessment to estimate population trends and abundance. Many models integrate environmental stochasticity, but incorporation of environmental indices to improve predictive skill is rare, and variation in dispersal distance has yet to be explored and parameterized for use in these models (Crouse et al., 1987; Heppell et al., 1996; Heppell, 1998; Piacenza et al., 2017). Given the wide variability in hatchling dispersal, and potentially survival rates, it may be imprudent to parameterize hatchling survival in a population model with a static value or an internally estimated value. Our work suggests that hurricane frequency and severity could be a useful environmental index related to hatchling survival. A particular benefit of including hurricane frequency in population and stock assessment models for Kemp's ridley sea turtles is that it may also be indicative of habitat changes that are relevant to oceanic-stage turtles, such as the distribution of pelagic *Sargassum* (Witherington et al., 2012; Hardy et al., 2018). A key future step in this effort would be to relate this and other indices that are potentially associated with hatchling dispersal and survival to time-lagged indices of adult Kemp's ridley abundance, based on age-at-maturity (Caillouet et al., 2016). Detecting strong relationships would indicate the need to then empirically study the relationship between hatchling dispersal and survival rate as it could provide critical information about the early life history of Kemp's ridley sea turtles that will improve their conservation.

DATA AVAILABILITY STATEMENT

All datasets generated for this study are included in the article/**Supplementary Material**.

AUTHOR CONTRIBUTIONS

All authors contributed to writing and editing the manuscript, approved the submitted version, and contributed the figures. MD and NP conceived the study and conducted the HYCOM/Ichthyop modeling. SP and MD compiled hurricane data and conducted the statistical analyses.

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SUPPLEMENTARY MATERIAL

The Supplementary Material for this article can be found online at: https://www.frontiersin.org/articles/10.3389/fmars.2020.00301/full#supplementary-material

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frontiers in Marine Science

BRIEF RESEARCH REPORT
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The Importance of the Northeastern Gulf of Mexico to Foraging Loggerhead Sea Turtles

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Identification of high-use foraging sites where imperiled sea turtles are resident remains a globally-recognized conservation priority. In the biodiverse Gulf of Mexico (GoM), recent telemetry studies highlighted post-nesting foraging sites for federally threatened loggerhead turtles (*Caretta caretta*). Our aim here was to discern loggerhead use of additional northern GoM regions that may serve as high-use foraging sites. Thus, we used satellite tracking and switching state-space modeling to show that the Big Bend region off the northwest Florida coast is a coastal foraging area that supports imperiled adult female loggerhead turtles tracked from different nesting subpopulations. From 2011 to 2016, we satellite-tagged 15 loggerheads that nested on four distinct beaches around the GoM: Dry Tortugas National Park, FL; Everglades National Park, FL; St. Joseph Peninsula, FL; and Gulf Shores, AL. Turtles arrived at their foraging ground in the Big Bend region between June and September and remained resident in their respective foraging sites for an average of 198 tracking days, where they established mean home ranges (95% kernel density estimate) 232.7 km^2. Larger home ranges were in deeper water; 50% kernel density estimate centroid values were a mean 26.4 m deep and 52.7 km from shore. The Big Bend region provides a wide area of suitable year-round foraging habitat for loggerheads from at least 3 different nesting subpopulations. Understanding where and when threatened loggerheads forage and remain resident is key for designing both surveys of foraging resources and additional protection strategies that can impact population recovery trajectories for this imperiled species.

Keywords: Big Bend, foraging areas, home range, loggerhead, state-space modeling

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INTRODUCTION

Identification of high-use foraging sites where imperiled marine species congregate is important (Patterson et al., 2016; Augé et al., 2018). For threatened and endangered sea turtles, delineating these sites is a globally recognized conservation priority (Hamann et al., 2010; Rees et al., 2016). Such information factors into critical habitat designations in the U.S. by management agencies [i.e., National Oceanic and Atmospheric Administration (NOAA), National Marine Fisheries Service (NMFS), U.S. Fish & Wildlife Service (USFWS)] which can translate into regulations on human use in areas of human/turtle overlap (U.S. Fish and Wildlife Service and National Marine Fisheries Service, 2013). In particular, areas where multiple species or life stages overlap at foraging sties may receive enhanced priority rankings. Satellite tracking and isotopic tools have been frequently used to designate species-specific foraging areas of importance (see Bradshaw et al., 2017; Rees et al., 2017), and multi-species syntheses that take decades to collect are beginning to emerge (see Conners et al., In review).

Because nesting sea turtles are more easily observed, nesting beaches often receive more attention than in-water sites. However, sea turtles spend the majority of their time at sea and as such the locations where they remain resident provide the necessary resources for these imperiled species. Foraging resources contribute toward fat stores that allow females to attain sufficient body condition for reproductive migrations which are energetically demanding. Similarly, after a nesting season, female sea turtles recover from the energetically taxing nesting season and build energy reserves for vitellogenesis (Limpus and Nicholls, 2000; Hamann et al., 2002). Characteristics of foraging grounds can influence various aspects of reproduction (Hamann et al., 2002; Schofield et al., 2009; Weber et al., 2011; Vander Zanden et al., 2014). Thus, characterizing these areas is critical for proper management of this habitat which will help toward population recovery.

In the U.S. Gulf of Mexico (GoM), five species of sea turtle occupy various habitats, including several dense nesting assemblages along the coastline. Recent tracking work by Hart et al. (2014); Foley et al. (2014), and Tucker et al. (2014) highlighted post-nesting foraging site destinations for loggerheads (*Caretta caretta*) in the GoM, currently listed with threatened status under the U.S. Endangered Species Act (National Marine Fisheries Service and U.S. Fish and Wildlife Service, 2008, 2011). As tracking sample sizes have increased for loggerheads in the GoM, the number of questions we can address has broadened (Sequeira et al., 2019) including highlighting previously unidentified foraging areas. In the Southeastern U.S., loggerheads are considered five subpopulations (Turtle Expert Working Group, 2009) and 10 management units (Shamblin et al., 2011, 2012) based on mitochondrial DNA analyses. The subpopulations in the Dry Tortugas and northern GoM are the two smallest, with median individual nesting subpopulation estimates of 331 females and 432 females, respectively (Richards et al., 2011). Hart et al. (2012) earlier reported on the use of common coastal foraging areas for a small number of turtles tagged in these different management units. It is possible that additional tracking would highlight previously unidentified coastal areas which also serve as important foraging habitat for individuals from these same management units.

Despite several studies and relatively large sample sizes, no nesting loggerhead from the northern GoM Recovery Unit has ever been tracked outside the GoM (Hart et al., 2012; Foley et al., 2013; Lamont et al., 2015). This work highlights important foraging areas for this loggerhead subpopulation. One area that consistently emerges as important for northern GoM loggerheads are shallow waters in the northeastern GoM (Tucker, 2010; Foley et al., 2013; Hardy et al., 2014; Hart et al., 2014).

The northeastern GoM, also known as the Big Bend region of Florida, lies upon the West Florida Shelf which represents 75% of the U.S. GoM shelf area and includes "ecologically productive and biologically rich marine habitat" (Coleman et al., 2011). This region provides important nursery habitat for several ecologically and economically important species including many fish and shellfish species (Todd et al., 2014). This area has low-energy shorelines and habitat that includes seagrass beds, salt marshes, and oyster reefs (Seavey et al., 2011; Kaplan et al., 2016). The Big Bend region provides foraging habitat for juvenile sea turtles (Schmid and Barichivich, 2005), but little is known of the use of this area by other sea turtle life stages. Dramatic environmental changes in the Big Bend area have recently occurred including large decreases in oyster reef habitat (Seavey et al., 2011) and it lies adjacent to the track of Category 5 Hurricane Michael (2018, 10 October, National Weather Service)[1]. The impact of these changes to foraging turtles is currently unknown.

In 2013, the USFWS and NMFS designated critical habitat for Western Atlantic loggerheads (U.S. Fish and Wildlife Service and National Marine Fisheries Service, 2013). Since Hart et al. (2012), we continued tracking nesting loggerhead turtles from two genetically distinct subpopulations to evaluate use of foraging habitat in the northeastern GoM. Here, we report on another year-round common coastal foraging area that supports these turtles. Highlighting in-water foraging habitat should aid in future designations of critical habitat for this imperiled species.

MATERIALS AND METHODS

Field Methods

We tagged turtles at Dry Tortugas National Park, FL; Everglades National Park, FL; St. Joseph Peninsula, FL; and Gulf Shores, AL (**Figure 1**). Full details on turtle capture and satellite-tagging can be found in Hart et al. (2013, 2018). Briefly, we corralled turtles on the beach after nesting was complete and followed established protocols for sampling and tagging (National Marine Fisheries Service Southeast Fisheries Science Center, 2008). The corral was removed after tagging was completed allowing the turtle to return to the water. We used SPOT5, SPOT6, or SPLASH10 PTTs from Wildlife Computers (Redmond, WA, United States) and duty-cycled tags to transmit every 3rd day during November-April to prolong battery life. We defined the Big Bend region as the neritic zone of the GoM stretching from St. Andrew Bay at the northern end to Tampa Bay at the southern end (see **Figure 1**). We only considered tracks for this analysis that had foraging locations within this region.

Data Analysis

Processing Tracking Data

We used the raw tracking data to fit a hierarchical, behavior-switching state-space model (SSM; Jonsen, 2016), allowing us to estimate the behavioral modes of individual turtles, regularize the locations in time, and account for location error. This hierarchical SSM is similar to the model of Jonsen et al. (2005), but jointly estimates the movement parameters that define the behavioral states across all individuals, thus improving the behavioral state estimation. Using the R package "bsam" (Jonsen et al., 2017; R Core Team, 2019), we fit the SSMs then used MCMC

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[1] https://www.weather.gov/tae/HurricaneMichael2018

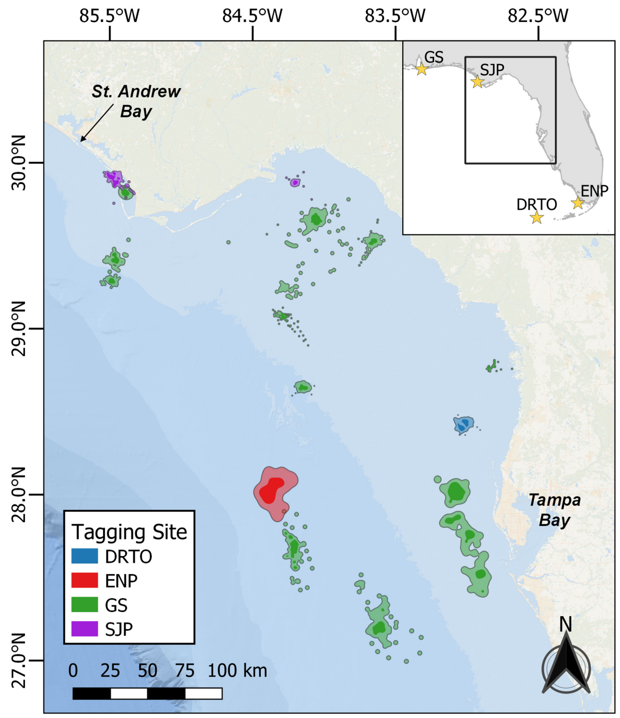

FIGURE 1 | Home range and core-use areas for loggerhead sea turtle (*Caretta caretta*) foraging periods occurring within the Big Bend region (inset box), from Tampa Bay to St. Andrew Bay. Tagging locations are shown as yellow stars on the inset map; turtles were satellite-tagged at four sites in the Gulf of Mexico and colors correspond to tagging location: Dry Tortugas National Park, Florida (DRTO, *n* = 1, blue); Everglades National Park, Florida (ENP, *n* = 1, red); Gulf Shores, Alabama (GS, *n* = 11, green); St. Joseph Peninsula, Florida (SJP, *n* = 2, purple). Kernel Density Estimates (KDEs) are shown for each turtle as lighter polygons (95% KDE; home range) with a darker color inside (50% KDE; core-use area).

parameters following our previous studies (see Hart et al., 2012), including adaptive sampling (and burn-in) for 7,000 samples, then 10,000 samples from the posterior distribution, thinned by 5 to reduce MCMC autocorrelation. As opposed to our previous studies, here we used a time step of 1 day, rather than 6 h, to reduce the autocorrelation in our home range estimation.

Large gaps in the raw data force the SSM to estimate a correlated random walk uninformed by data. These location estimates are less reliable the longer the gap becomes. To deal with this, we split individual tracks at gaps of 25 days or longer, and we passed these tracks to the model as if they were separate individuals. After fitting the SSM, we recombined the modeled daily locations for each turtle.

Delimiting Foraging Areas

The SSM separated turtle behaviors into two categories: (1) area-restricted search (ARS) which was characterized by relatively tortuous tracks and slow swim speeds; and (2) migration which was characterized by relatively straight tracks and fast swim speeds. We tagged turtles during the nesting season, so we can interpret the ARS mode to be either “inter-nesting” or “foraging.” We defined “foraging” as all the locations recorded from after the final “migration” location until the end of the tracking duration.

Home Ranges

We used all the foraging locations to fit home ranges for each turtle. We used the kernel density estimator (KDE), a common home range metric based on estimating the animal’s utilization distribution in discrete space (Worton, 1989; Kie et al., 2010). We used the R package “adehabitatHR” (Calenge, 2006) to estimate KDEs, using least squares cross-validation to select the bandwidth parameter, *h* (Worton, 1995; Seaman and Powell, 1996). We represented the overall home range with 95% KDEs and the core area of activity with 50% KDEs (Hooge et al., 2001).

For each turtle, we calculated the centroid of the 50% KDE polygon, and from that centroid, we calculated distance to shore and depth. We estimated distance to shore by using the function “gDistance()” from the R package “rgeos” (Bivand and Rundel, 2019) to calculate the distance between the centroid and the intermediate-resolution shoreline polygon from the Global Self-consistent Hierarchical High-resolution Geography database (GSHHG; Wessel and Smith, 1996). We estimated depth by extracting the value at the centroid from the ETOPO1 Global Relief model (Amante and Eakins, 2009). We estimated the relationship between home range size (area of the 95% KDE) and depth by fitting a linear model where ln(area) depended on ln(depth).

Eleven home ranges were previously published in Hart et al. (2014). In that paper, however, authors used SSM only to define time periods of migration and foraging; they then used original filtered Argos locations from within those SSM-defined time periods for analysis. Here, in contrast and as stated above, we use predicted ARS locations instead of original filtered locations, and we added additional tracking days for several turtles (after the cutoff in Hart et al., 2014). In addition, we acknowledge that aspects of one turtle’s movement is also in Hart et al. (2018), thus here we re-visited the data for these previously published home ranges, adding in additional locations for five of these turtles. We also report on three new loggerheads that were tracked to this region.

RESULTS

We documented 15 individuals using the Big Bend region from our four tagging sites: Dry Tortugas National Park, FL (*n* = 1); Everglades National Park, FL (*n* = 1); St. Joseph Peninsula, FL (*n* = 2); and Gulf Shores, AL (*n* = 11; **Table 1**). These adult female loggerhead turtles ranged in size from 87.0–106.0 cm curved carapace length (CCL; mean $\pm$ SD = 94.9 $\pm$ 4.4 cm).

We received a total of 17419 raw Argos locations for all turtles. Mean locations per turtle was 1161 (*SD* = 413, range = 390–1791). A single turtle (108965) had a gap of at least 25 days, so we split her track into two prior to fitting the SSM. After fitting the SSM, we were left with 2974 daily locations for all turtles. Mean daily locations per turtle was 198 (*SD* = 86, range = 26–317). Of those, we identified 1881 as foraging locations, and the mean daily foraging locations per turtle was 125 (*SD* = 80, range = 20–275).

TABLE 1 | Tagging and kernel density estimate (KDE) details for adult female loggerheads with resident foraging areas in the Big Bend region.

Turtle	Tagging year	Big bend foraging period (days)	Core area (km^2)	Home range (km^2)	Centroid depth (m)	Distance to shore (km)
ST. Joseph Peninsula, FL						
129498	2013	7/2/2013–11/4/2013 (125)	32.0	130.6	−6.9	4.9
129497	2013	7/20/2013–10/13/2013 (85)	6.3	35.7	−6.0	13.9
Gulf Shores, AL						
108961	2011	7/29/2011–08/17/2011 (19)	18.6	72.0	−9.6	2.1
108965	2011	8/10/2011–7/21/2012 (346)	38.0	426.9	−14.2	37.6
119923	2012	7/30/2012–1/7/2013 (161)	16.2	70.4	−37.0	115.3
119943	2012	8/2/2012–11/21/2012 (111)	11.4	59.6	−29.0	82.5
129515	2013	7/28/2013–9/22/2013 (56)	24.0	136.4	−28.6	27.5
129504	2013	8/3/2013–3/1/2014 (210)	54.6	456.9	−51.6	93.8
129510	2013	8/6/2013–10/15/2013 (70)	12.4	70.0	−45.2	42.5
129503	2013	8/10/2013–11/27/2013 (109)	210.6	1024.8	−16.1	20.6
129506	2013	9/9/2013–1/6/2014 (119)	59.1	288.9	−65.1	134.8
129505	2013	2/28/2014–4/7/2014 (38)	5.8	22.5	−2.0	10.6
53438	2016	7/30/2016–4/14/2017 (258)	15.5	128.4	−10.0	23.7
Everglades National Park, FL						
137797	2015	4/8/2016–5/18/2016 (40)	168.5	666.8	−63.2	149.0
Dry Tortugas National Park, FL						
106615	2011	6/30/2011–1/7/2012 (191)	27.7	110.0	−11.9	31.2

Turtles arrived in their foraging location in dates during June (*n* = 1), July (*n* = 6), August (*n* = 5), and September (*n* = 1); two turtles were tracked later at foraging areas in the Big Bend.

We used the SSM-derived daily ARS (i.e., foraging) locations to fit home ranges (95% KDE) and core areas (50% KDE) for each turtle. Our LSCV routine to select the bandwidth parameter converged for all turtles. The mean home range size was 246.7 km^2 (*SD* = 285.5, range = 22.5–1024.8 km^2). The mean core area size was 46.7 km^2 (*SD* = 60.7, range = 5.8–210.6 km^2). Individual home ranges were distributed throughout the Big Bend region (**Figure 1**). Depth of 50% KDE centroids ranged from 2.0 to 65.1 m (mean 26.4 m, SD 21.3) and distance to shore values for 50% KDE centroids ranged from 2.1 to 149.0 km (mean 52.7 km, SD 49.2). The relationship between ln(area) and ln(depth) was significant (p = 0.04), and this simple model explained nearly a quarter of the variation in home range size (adj-R^2 = 0.23; **Figure 2**).

DISCUSSION

Tracking studies can provide critical data for policy makers particularly when targeting specific needs and data gaps (Hays et al., 2019). This work highlights use of Florida's Big Bend region as foraging habitat by threatened adult female loggerheads from four separate nesting beaches, representing several different distinct population segments and management units. It contributes toward recognizing relative importance of foraging areas in the northern Gulf of Mexico, which has a paucity of defined foraging areas for comparison. We suspect that additional tracks in future years will complement this summary, which is derived from multiple different tracking projects across study sites and years. This summary provided here took 2011–2017 tracking data to collate, thus future effort to track additional Gulf turtles to this region would be valuable for understanding the relative use of this area by individuals from different nesting populations. We do not have foraging centroids for additional

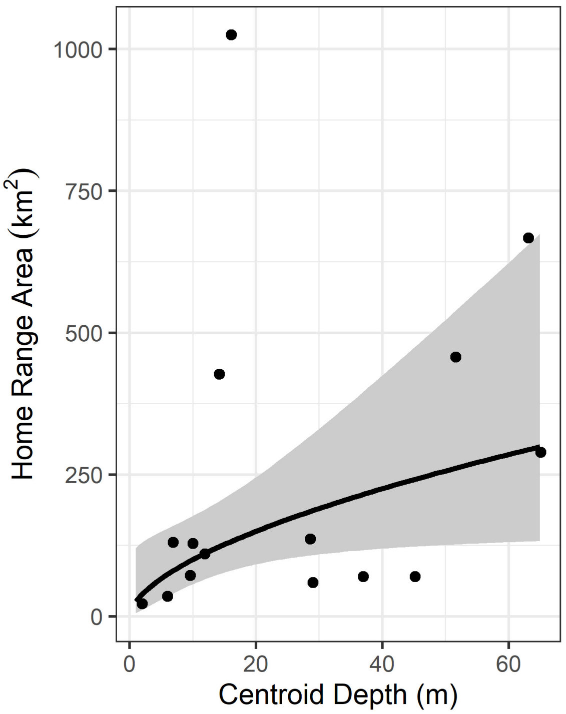

FIGURE 2 | Relationship between home range size (95% KDE) and depth. Fit line is from a linear model where ln(area) depends on ln(depth) and is significant (*p* = 0.04, adj-R^2 = 0.23). Shaded envelope represents the 95% confidence interval around the fit line.

turtles shown in Foley et al. (2014; $n = 3$) and Tucker et al. (2014, $n = \sim 13$), but it is clear that other loggerheads migrate to this region and remain resident there in at least low numbers.

We observed quite a span of individual variation in home range size (**Figure 2**), which does not appear to be a sampling artifact [i.e., it is not that large home ranges were generated due to low quality Argos locations (e.g., lots of class B and class 0 locations), as we used SSM here]. Rather, this variation reflects something real about foraging site selection, complementing previous work on loggerheads in the Mediterranean (e.g., Schofield et al., 2010), where loggerhead home ranges that were deeper and farther offshore were larger. Here, the pattern observed in Schofield et al. (2010) also holds true, as our simple linear model explained nearly a quarter of the variation we observed in home range sizes for loggerheads females in the Big Bend region. Mean values of two measurable characteristics of core use areas reported here are similar to those previously reported in Hart et al. (2014): 47.6 km mean distance to shore and 32.5 m depth, as well as a previously determined for a common coastal foraging area in the GoM, but south of the Big Bend (Hart et al., 2012; foraging centroids in that study were in waters < 50 m deep and within a mean distance of 58.5 km to nearest coastline.

The quantitative spatial ecological summary on individual home ranges presented here is key information for managers to consider as loggerhead critical habitat designations in the U.S. are refined. Recent other tracking studies highlighted areas in the GoM that serve as important foraging habitat for loggerheads (Girard et al., 2009; Foley et al., 2014; Hart et al., 2014; Tucker et al., 2014), yet it was not obvious in previous regional tracking summaries that the Big Bend was another important year-round foraging area for loggerheads from multiple distinct population segments. Our summary here also includes the first published Everglades loggerhead track (turtle 137797), representing new information for that understudied nesting sub-population.

Recently, Wildermann et al. (2019) showed the value of this area to other sea turtle species: satellite-tagged green turtles (*Chelonia mydas)*, Kemp's ridleys (*Lepidochelys kempii)*, and loggerheads partitioned habitat off of the northwest Florida Shelf. In another tracking study it was revealed that juveniles of these three species also shared habitat in coastal bays off of Northwest Florida (Lamont and Iverson, 2018). These results together highlight the potential for this area to serve as a foraging hotspot for multiple sea turtle species. Identification and delineation of foraging hotspots, particularly those used long-term and year-round like those here, are important for defining the extent of U.S. critical habitat and areas for potential protection.

Tracking studies are critical to establishment and maintenance of these protected areas (Cuevas et al., 2008; Méndez et al., 2013; Hays et al., 2019). The word "hotspot" was originated by Myers (1988) to identify areas of "exceptional concentrations" of endemic species currently experiencing exceptional loss of habitat. The goal in that paper was to highlight areas where the greatest number of species could be protected per conservation dollar (Myers, 1988, 1990, 2003; Briscoe et al., 2016). Our tracking results, coupled with previous studies that show use of this region by multiple taxa [Kemp's ridleys (Schmid and Barichivich, 2005), invertebrates (Posey et al., 1998); reef fish (Coleman et al., 2011); dolphins (Tyson et al., 2011); sharks (Bethea et al., 2015)] indicate that the Big Bend represents an important marine hotspot in the northeastern GoM. This work contributes to ongoing discussions of critical habitat designations for sea turtles in the Southeastern U.S. and highlights the importance of considering nearshore habitats on the continental shelf in these discussions, as currently, these habitats are not included in loggerhead critical habitat (U.S. Fish and Wildlife Service and National Marine Fisheries Service, 2013).

DATA AVAILABILITY STATEMENT

All datasets generated for this study are included in the article/supplementary material.

ETHICS STATEMENT

This study was carried out in accordance with the guidelines of the USGS Institutional Animal Care and Use committee who also approved the study protocol (USGS-SESC-IACUC-2011-05). In addition, all federal and state permits required were obtained for this research on turtles at Gulf Shores (USFWS permit TE206903-1 and Bon Secour Special Use Permit 12-006S); and Florida [Marine Turtle Permits #176 (issued to KH) and #118 (issued to ML)]; Dry Tortugas National Park permits DRTO-2008-SCI-0008, DRTO-2010-SCI-0009, and DRTO-2012-SCI-0008 (issued to KH).

AUTHOR CONTRIBUTIONS

KH and ML contributed to the conception and design of the study. BS performed the state-space modeling. BS and AI created the figures. All authors contributed to the writing of the manuscript, and read and approved the submitted version.

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Satellite Tracking Can Inform Population-Level Dispersal to Foraging Grounds of Post-nesting Kemp's Ridley Sea Turtles

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Understanding how populations are distributed spatially can be an effective tool for conservation and management planning. This is especially true for threatened species of mobile marine megafauna, which can use vast expanses of the ocean as foraging and reproductive habitat. Additionally, the broad distributions of these species expose them to a wide variety of threats across their range. Marine turtles are one of these mobile marine megafauna taxa, with individuals making extensive migrations between nesting beaches and foraging grounds. However, it is not well understood how many marine turtle populations distribute themselves spatially at the population or species level. In this study, 178 post-nesting female Kemp's ridley sea turtles were concurrently satellite tracked from their primary and major secondary nesting beaches between 2010 and 2017 to determine population- and species-level distribution of females to foraging grounds. Filtered tracks and switching state-space models (SSMs) were used to determine the proportion of the adult female population dispersing to, and foraging in, the northern and southern Gulf of Mexico (GoM). Fidelity to Gulf regions and foraging areas were also assessed. The majority of females dispersed to northern GoM (nGoM) foraging grounds indicating 82% of the adult female population may use the region to forage. Additionally, individuals displayed fidelity to regions, key foraging areas, and migratory corridors over time. These results suggest that the nGoM may provide the most important foraging areas for reproductively active females of the species and threats in the region may have a disproportionately higher impact on the adult female population, a population critical to the perpetuation and recovery of the species. Results highlight that continued bi-national recovery efforts are essential for recovery of Kemp's ridleys, as most females nest on Mexican beaches and forage in U.S. waters. The methodologies used could be applied to conservation and management efforts of other imperiled mobile marine megafauna.

Keywords: Gulf of Mexico, *Lepidochelys kempii*, conservation, distribution, state-space modeling

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INTRODUCTION

Determining distributions of mobile marine megafauna (e.g., marine turtles, elasmobranchs, cetaceans, and pinnipeds) is a fundamental concept for conservation and management of these imperiled species. However, determining these distributions, especially at the population level, poses significant challenges (Morales et al., 2010; Holdo and Roach, 2013; Jeffers and Godley, 2016). Specifically, mobile marine megafauna are often cryptic and their ranges can encompass entire ocean basins (Block et al., 2011; Reisinger et al., 2018) making systematic surveys impractical, both geographically and temporally. Beginning in the 1980s, telemetry studies using satellite transmitters were employed to investigate the detailed movement patterns and distributions of these species in lieu of surveys or the need to recapture an individual (Godley et al., 2008; Hart and Hyrenbach, 2009; Hays and Hawkes, 2018). However, these studies have often been plagued with low sample sizes (<10), short tracking durations, a lack of appropriate experimental design, high degrees of spatial error, and an absence of behavioral data to interpret how an animal is using the environment (Hart and Hyrenbach, 2009; Rutz and Hays, 2009).

Continued improvements in animal-borne telemetry and collaborative partnerships [e.g., Global Tagging of Pelagic Predators (GTOPP), Ocean Tracking Network (OTN), Integrated Marine Observing System Animal Tracking Facility (IMOS ATF)] have alleviated these shortcomings, allowing for increased numbers of individuals (10s to 1,000s) (Schofield et al., 2013; Fossette et al., 2014; Block et al., 2016; Queiroz et al., 2019) to be tracked over longer timeframes than in the past through data-sharing, reductions in cost, decreased transmitter size, and increased location acquisition and error processing (Rutz and Hays, 2009; Lopez and Malardé, 2011; Hays and Hawkes, 2018). These improvements, paired with advancements in quantitative techniques (e.g., state-space modeling, stable isotope analyses, genetics, remotely sensed environmental data) and computational power, allow the use of telemetry data to further our understanding of the spatial distributions of mobile marine megafauna and infer population-level dynamics (Godley et al., 2008; Hazen et al., 2012; Hays and Hawkes, 2018). Specifically, increased numbers of tracked individuals and behavioral-based modeling approaches can provide a link between individual animal movements and population metrics (Morales et al., 2010; Holdo and Roach, 2013; Schofield et al., 2013). For example, large-scale tracking studies have identified ocean basin-scale distributions (Block et al., 2011), classified migratory corridors and foraging areas (Costa et al., 2012; Shaver et al., 2013, 2016a), assessed inter-species overlap (Hart et al., 2018b), and determined exposure to anthropogenic threats (e.g., fisheries, energy production, pollution) (Maxwell et al., 2013; Hart et al., 2018a; Queiroz et al., 2019) of mobile marine megafauna. These insights can be effective tools for conservation planning and management of these species and highlight the need for continued large-scale collaborative data-sharing programs to further improve population-level knowledge.

Studies typically focus on assessing distributions and movements at the metapopulation (e.g., mixed-stock foraging aggregations, individuals from disparate breeding colonies) (Block et al., 2011; Queiroz et al., 2019) or local (e.g., specific nesting beaches or haul-out sites) (Oksanen et al., 2014; Dawson et al., 2017) level. These studies have provided significant information on how mobile marine megafauna are distributed at global and local scales and the potential broadscale and localized impacts of threats (e.g., fisheries bycatch, pollution, human development) (Maxwell et al., 2013; Hart et al., 2018a; Queiroz et al., 2019). However, implementing conservation strategies on a global scale may be hindered by differences between stakeholder priorities and cultural beliefs, while local-scale conservation may only protect a small percentage of a Regional Management Unit (RMU) or subpopulation, providing limited conservation benefit. In addition, these studies may not identify specific threats, important foraging regions, or delineate population boundaries at the subpopulation or RMU level, which can be effective targets for conservation goals. Thus, a spatial mismatch may exist between the units being studied (e.g., metapopulations, local stocks) and the units at which conservation efforts should be directed (i.e., RMUs) (Moritz, 1994; Hamann et al., 2010). Protecting RMUs can ensure genetic diversity and resiliency in metapopulations, while addressing specific regional threats and developing appropriate management plans, making them appropriate targets for short-term conservation goals (Moritz, 1994; Wallace et al., 2010).

Marine turtles are one guild of mobile marine megafauna which has received a significant amount of research focusing on delineating the movements and distributions of individuals and populations (Godley et al., 2008). To date, thousands of transmitters have been deployed on nesting and foraging marine turtles of all seven species, globally (Godley et al., 2008). Despite the level of effort that has been put into tracking individuals, there are still uncertainties in the boundaries and connections that exist within and between populations, where key foraging areas lie and the degree of site fidelity to foraging areas (Hays and Hawkes, 2018). In fact, these questions are consistently listed as priority items in marine turtle conservation and management reviews (Godley et al., 2008; Hamann et al., 2010; Rees et al., 2016; Hays and Hawkes, 2018). Generalized boundaries for marine turtle RMUs were outlined by Wallace et al. (2010) and recent progress has been made identifying key foraging regions for some RMUs (Schofield et al., 2013; Fossette et al., 2014). However, further investigations are needed to fully understand adult foraging areas and distributions. Future studies should also determine effective methods to identify the key foraging regions, specifically for RMUs (Rees et al., 2016) and identify the relative importance of each region to the conservation and/or recovery of a species.

A species of particular conservation concern is the critically endangered Kemp's ridley sea turtle (*Lepidochelys kempii*), which nests almost exclusively along the western coast of the Gulf of Mexico (GoM) (Márquez-Millán et al., 2005; NMFS and USFWS, 2015). The majority of Kemp's ridley nests are found near Rancho Nuevo, Tamaulipas, Mexico, which is considered to be the primary nesting beach for the species (Wibbels and Bevan, 2016). The majority of nests not laid at Rancho Nuevo are found at Padre Island National Seashore, Texas, United States, and Tecolutla, Veracruz, Mexico (NMFS and USFWS, 2015) which are considered here as major secondary nesting beaches. Recent pioneering work has identified foraging areas and migratory corridors within the GoM for this species through tracking post-nesting females from the primary and major secondary nesting beaches located in Mexico and the United States (Shaver and Rubio, 2008; Shaver et al., 2013, 2016a). Despite this work, the proportion of the population using identified key foraging areas is largely unknown, as is the fidelity of individuals to these foraging areas over time or the relative importance of each area. Uniquely, the Kemp's ridley is managed under one RMU and is believed to be a single genetic stock (Wallace et al., 2010) allowing for population-, RMU-, and species-level determinations of distribution and foraging area use through tracking individuals from the primary and major secondary nesting beaches. In addition, nesting beaches of this species are heavily monitored annually to obtain accurate nest counts and nesting distributions to inform the proportion of the population each nesting beach represents (Márquez-Millán et al., 2005; NMFS and USFWS, 2015; Shaver et al., 2016b). These factors allow targeted, long-term tracking studies to be used to identify the preferred foraging areas of post-nesting females to infer population- and species-level spatial dynamics of reproductively active Kemp's ridley females. This study aimed to: (1) assess the proportional distribution of the foraging adult female Kemp's ridley population within the GoM through concurrent tracking of females from the primary and major secondary nesting beaches; (2) determine key foraging areas for the adult female population; and (3) determine fidelity of females to foraging areas over time through repeated tracking of individuals to the foraging grounds. Results from objectives 1–3 were then used collectively to determine the overall importance of each GoM region to the female population. This information can then be used to inform conservation and management planning, as well as serve as a model for identifying spatial population dynamics of other mobile marine megafauna species.

MATERIALS AND METHODS

Tracking

A total of 178 adult female Kemp's ridley sea turtles were outfitted with satellite transmitters after nesting at each of the major nesting beaches in the western GoM (NMFS and USFWS, 2015) between 2010 and 2017: Padre Island National Seashore, Texas, United States (PAIS, $n = 76$, 2010–2017); Rancho Nuevo, Tamaulipas, Mexico (RNMX, $n = 44$, 2010, 2011, 2014–2016); Tecolutla, Veracruz, Mexico (VCMX, $n = 58$, 2012–2017) (**Table 1** and **Supplementary Table S1**). Each individual received a platform terminal transmitter (PTT) manufactured by Wildlife Computers (SPOT: $n = 32$, 2013–2015 or SPLASH: $n = 24$, 2010–2013) or Sirtrack (Kiwisat 101: $n = 29$, 2011–2013 or Kiwisat 202: $n = 93$, 2014–2017) (**Table 1**). Straight carapace lengths (nuchal notch to posterior tip, SCLs) were obtained at the time of PTT attachment for all turtles using straight, metal calipers or converted from curved carapace lengths (CCLs) using the equation developed by Schmid and Witzell (1997). PTTs were attached using the methods described in Shaver et al. (2013).

TABLE 1 | Tagging locations and years for satellite transmitters deployed between 2010 and 2017 of 178 post-nesting female Kemp's ridley sea turtles tracked from the primary and major secondary nesting beaches: Padre Island National Seashore, Texas, United States (PAIS); Rancho Nuevo, Tamaulipas, Mexico (RNMX); Tecolutla, Veracruz, Mexico (VCMX).

	Tagging location		
Year	**PAIS**	**RNMX**	**VCMX**
2010	6	4	·
2011	10	10	·
2012	10	·	3
2013	10	·	10
2014	10	10	10
2015	11	10	10
2016	9	10	10
2017	10	·	15
Total	76	44	58

"·": No turtles tracked for that location/year.

Platform terminal transmitters were programmed in the following ways: continuously on ($n = 44$, 2010–2014), 24-h on/24-h off ($n = 10$, 2013) and 6-h on/6-h off ($n = 75$, 2010–2017). PTTs transmitted data using the ARGOS system, which estimates each location using the following classes: 3, <250 m; 2, 250 to <500 m; 1, 500 to <1500 m; 0, >1500 m; A and B, unknown; Z, failed plausibility tests (CLS, 2011). Six PTTs deployed in 2010 were processed using least-squares analysis. The remaining PTTs were processed using the Kalman filter, which provides improved accuracy and increases the number of estimated positions (Lopez and Malardé, 2011). Kalman filtering was unavailable for the six PTTs deployed in 2010 processed using least-squares analysis. To ensure there were enough locations to identify primary foraging regions, only individuals tracked for at least 30 days after the mean last date of nesting for each specific nesting beach were used in analyses. Any tracks eliminated from analysis were confirmed to still be within or near the inter-nesting area at the last transmission. Mean last date of nesting was calculated separately for each of the three beaches using the last nesting date of each beach for each of the PTT deployment years to account for temporal differences in nesting seasons for each nesting beach. Eleven individuals were recaptured and tracked up to three times. In these instances, all tracking data were used if tracking durations were long enough. All activities were carried out according to protocols approved by the National Park Service Institutional Animal Care and Use Committee.

Modeling

A switching state-space model (SSM) was used to estimate locations and behavioral modes of each individual to determine area-restricted-search-type movements (ARS; i.e., "foraging" or "inter-nesting") and migratory-type movements (i.e., "exploratory" or "transit"). Because satellite-location data are often received at irregular time intervals and can contain large positional errors and temporal gaps, SSMs provide a means to estimate the most likely movement patterns of an animal and account for these errors while using the specific dynamics of a species' movement patterns (Jonsen et al., 2005). Location data for each individual were first fit with a continuous-time correlated random walk (CTCRW) model to predict temporally regular locations in R using the "crawl" package (Johnson, 2018; R Core Team, 2019) with an initial value centered on their release location. The CTCRW model was fit using a prior distribution and estimated the location error from ARGOS estimates. For PTTs processed using least-squares, variance parameters were fixed using ARGOS provided error estimates for the three highest quality location classes (3, 2, and 1) to estimate the error parameters. For PTTs processed using Kalman filtering, ARGOS provided error ellipse information was used (McClintock et al., 2015). Locations for each individual were simulated at 6-h time-steps over 1,000 imputations. SSMs were then modeled using a two-state continuous-time hidden Markov model using the R package 'momentuHMM' from the simulated CTCRW tracks over 1,000 imputations (McClintock and Michelot, 2018). Model parameters were set using the gamma distribution for step lengths and the wrapped Cauchy distribution for turning angles. Parameter values were set at 750 ± 200 m (ARS) and 2,000 ± 750 m (migratory) for step lengths and $\pi \pm 0.1$ rad (ARS) and 0 ± 0.7 rad (migratory) for turning angles.

Primary Foraging Regions and Dispersal

After defining movement types, migratory and inter-nesting movements, locations on land and those interpolated during tracking gaps ≥ 7 days were removed from the SSM-derived locations for foraging area analyses. Inter-nesting locations were determined from the ARS locations using the mean last date of nesting for each nesting beach. For individuals that remigrated back to the nesting beach, inter-nesting was considered to begin after a migration that coincided with the nesting season (March–July) (NMFS and USFWS, 2015). For dispersal analyses, migratory movements after the mean last date of nesting were retained in SSM-derived location data.

For PTT data that failed to converge using SSM, locations were filtered by removing locations on land, that exceeded 5 km/h, had turning angles greater than 25° or were in depths greater than 100 m. The 100 m isobath was used as greater depths have been shown to be biologically implausible for Kemp's ridleys (Shaver and Rubio, 2008; Seney and Landry, 2011). Filtered locations were used to include those individuals whose data failed to converge using SSM, but met all other criteria (e.g., tracking duration), in dispersal analyses. Mean daily locations (MDLs) were then calculated from SSM-derived and filtered locations using a custom script in R to normalize the data for all analyses. MDLs represented the centroid location of all SSM-derived or filtered locations for each day locations were available.

To determine primary foraging regions, the GoM was divided into two major areas: northern GoM (nGoM) and southern GoM (sGoM). The Exclusive Economic Zone (EEZ) boundary between the United States and Mexico demarcated the division between the nGoM and sGoM. The EEZ was chosen as the boundary as it provided a known, defined border between different environmental, anthropogenic, and political factors that may affect marine turtle turtles in the GoM. Each region included all marine waters from the coast out to the 100 m isobath in the corresponding direction from the EEZ boundary. The Atlantic coasts of Florida and Georgia were included as part of the nGoM to simplify the region.

A 25 km hex-bin grid was used to calculate the number of foraging days and identify areas of increased use throughout the Gulf using SSM-derived MDLs of ARS locations identified as foraging. This grid size was chosen as a compromise between improved data visualization and matching the spatial error of MDLs. A 10 km hex-bin grid was also investigated for comparisons to previous studies of female Kemp's ridley movements (Shaver et al., 2016a, 2017; Hart et al., 2018a,b) and is presented in the **Supplementary Material**. The ratio of SSM-derived or filtered MDLs in each GoM region was also calculated for each individual to determine regional dispersal of females from the primary and major secondary nesting beaches throughout the Gulf. Individuals with $\geq$70% of filtered or SSM-derived MDLs within a region were assigned to that region. The percentage of the total adult female Kemp's ridley population that forages in the nGoM and sGoM was then calculated using the relative proportion of the nesting population that each nesting beach represented. Relative proportions were calculated using the mean percentage of nests laid in each nesting region (Texas, Tamaulipas, and Veracruz states) between 2010 and 2017 as a proxy for adult female population size.

Regional and Foraging Area Fidelity

For individuals tracked multiple times and those tracked remigrating to the nesting beach, and then returning to foraging areas, tracks were compared between deployments and migrations to determine fidelity to Gulf regions. Utilization distributions (UDs) were then calculated using 95% kernel-density estimates (KDEs) for PTTs with SSM-derived foraging MDLs for all deployments, or during remigrations, to assess fidelity to specific foraging areas. A fixed-kernel least-squares cross-validation smoothing factor (h_{cv}) was used to calculate each 95% KDE. KDEs were compared for each turtle using the UD overlap index (UDOI) (Fieberg and Kochanny, 2005) and Bhattacharyya's affinity (BAs) (Bhattacharyya, 1943). The UDOI and BA are statistics used to determine the amount of spatial overlap in three-dimensional UDs. Values of zero describe UDs with no overlap, while values of one indicate 100% overlap. The UDOI value can be greater than one if UDs overlap significantly, but are not uniformly distributed (Fieberg and Kochanny, 2005). The UDOI has been found to be the best estimator for describing the degree of space sharing and the BA is better suited for comparing the overall similarity between UDs (Fieberg and Kochanny, 2005); thus, both are reported here. KDEs, UDOIs, and BAs were calculated in R using the package "adehabitatHR" (Calenge, 2006). All other spatial analyses were conducted in ArcGIS 10.7.

RESULTS

Tracking

Individuals measured between 58.0 and 75.2 cm SCL (mean ± SD: 63.9 ± 2.7 cm). Turtles were tracked from three to 1,554 days (mean ± SD: 368 ± 313 days) for a total of 65,466 tracking days. Overall, 150 PTTs (PAIS: *n* = 68; RNMX: *n* = 37; VCMX: *n* = 45) deployed at the primary and major secondary nesting beaches between 2010 and 2017 provided enough data to identify regional dispersal of individuals using SSM-derived MDLs or, for datasets that did not converge using SSM, filtered MDLs. Of these 150 PTTs, foraging areas were modeled for 117 PTTs (PAIS: *n* = 55; RNMX: *n* = 27; VCMX: *n* = 35) using SSM (**Figure 1**). Data from 33 PTTs did not converge using SSM and 28 PTTs had deployments too short in time for analyses. During the study period, 10 turtles were tracked twice, and one turtle was tracked three times from their respective nesting beaches. Eight of these individuals tracked multiple times had tracking durations long enough (≥30 days) for analyses. In addition, seven turtles were tracked migrating back to their nesting beaches during deployments. All remigrant turtles had tracking durations long enough for analyses. No individuals remigrated to nesting beaches other than the beach they were initially tracked from.

Primary Foraging Regions and Dispersal

Gulf of Mexico regions were assigned to all PTTs that provided enough data for analyses (*n* = 150). In total, 41,591 foraging days were modeled with 86.1% in the nGoM and 13.9% in the sGoM. Both regions of the Gulf contained areas with high numbers of foraging days with hotspots near the Yucatán Peninsula, northern and southern Gulf coasts of Florida, including the Florida Keys, the Mississippi River Delta, and the Texas-Louisiana Shelf (**Figure 2** and **Supplementary Figure S1**). Almost all PAIS turtles foraged in the nGoM with 99.8% of SSM-derived foraging days in the region and 98.5% of individuals dispersed to northern Gulf waters (**Figure 3**, **Supplementary Figure S2**, and **Table 2**). Only one individual tracked from PAIS (PTT 117512) migrated to the sGoM with its track ending offshore of the Yucatán Peninsula. Two turtles (PTTs 117515/152803 and 152804), one of which was tracked twice, foraged offshore of PAIS for the entirety of their tracking. One turtle (PTT 152808) foraged along the Atlantic coasts of Florida and Georgia (**Figure 4**). Individuals tracked from RNMX also primarily foraged in the nGoM with 90.7% of SSM-derived foraging days in the region and 83.8% of individuals dispersed to the nGoM (**Figure 3**, **Supplementary Figure S2**, and **Table 2**). Conversely, individuals tracked from VCMX were almost evenly split with 57.8% dispersing to the nGoM and 65.5% of SSM-derived foraging locations were located there (**Figure 3**, **Supplementary Figure S2**, and **Table 2**). No turtles from RNMX or VCMX foraged near the nesting beach they were tracked from.

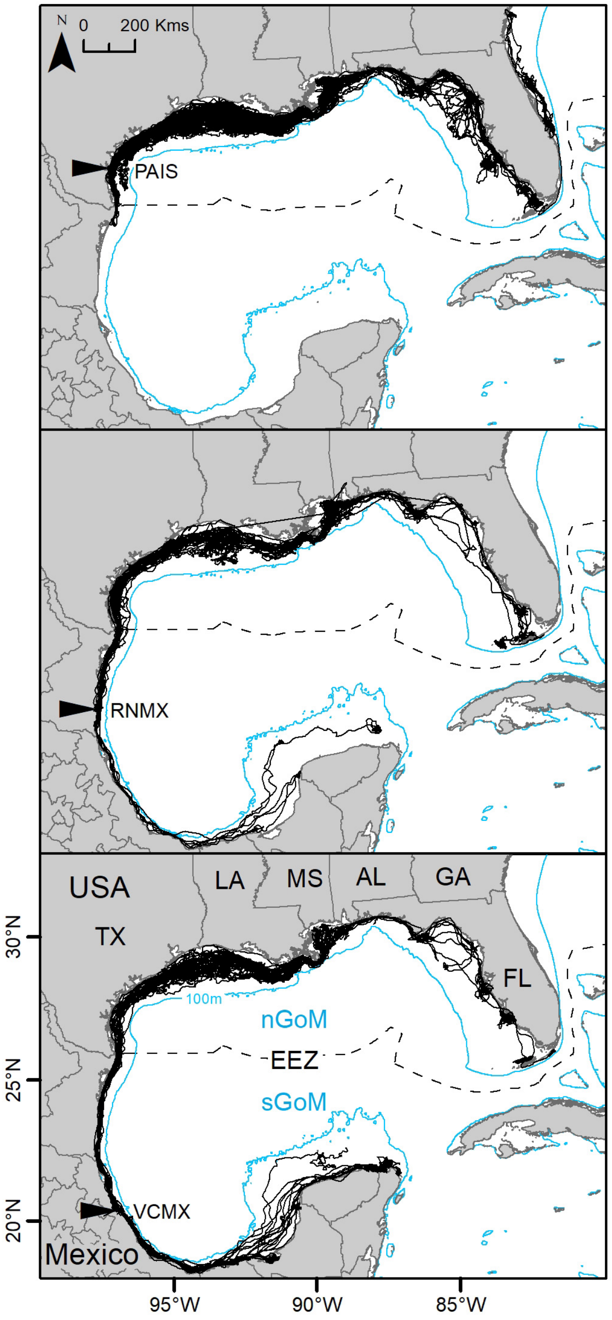

FIGURE 1 | Switching state-space model-derived tracks for 117 post-nesting female Kemp's ridley sea turtles tracked from the primary and major secondary nesting beaches: Padre Island National Seashore, Texas, United States (PAIS); Rancho Nuevo, Tamaulipas, Mexico (RNMX); Tecolutla, Veracruz, Mexico (VCMX). The Exclusive Economic Zone (EEZ) demarcates the division between the northern Gulf of Mexico (nGoM) and southern Gulf of Mexico (sGoM). Transmitters were deployed between 2010 and 2017.

All SSM-derived turtle tracks remained within the nearshore waters (≤100 m depth) of the GoM and Atlantic coast of the United States (**Figure 1**). In general, individuals foraged in either the nGoM or sGoM, but not both, and did not transition between regions over time to forage. However, there were two exceptions to this: (1) some individuals who remained within the coastal waters of southern Texas to forage and (2) individuals displaying short-duration (≤10 days) ARS-type behavior during migrations from nesting beaches in Mexico. One individual (PTT 152804) tracked from PAIS, which primarily foraged offshore of PAIS in the nGoM during its 387-day tracking period, briefly foraged in sGoM waters for 45 days before returning to its main foraging area off the south Texas coast. This individual had a maximum incursion distance into sGoM waters of 76.2 km (mean ± SD: 46.0 ± 25.7 km) from the EEZ border.

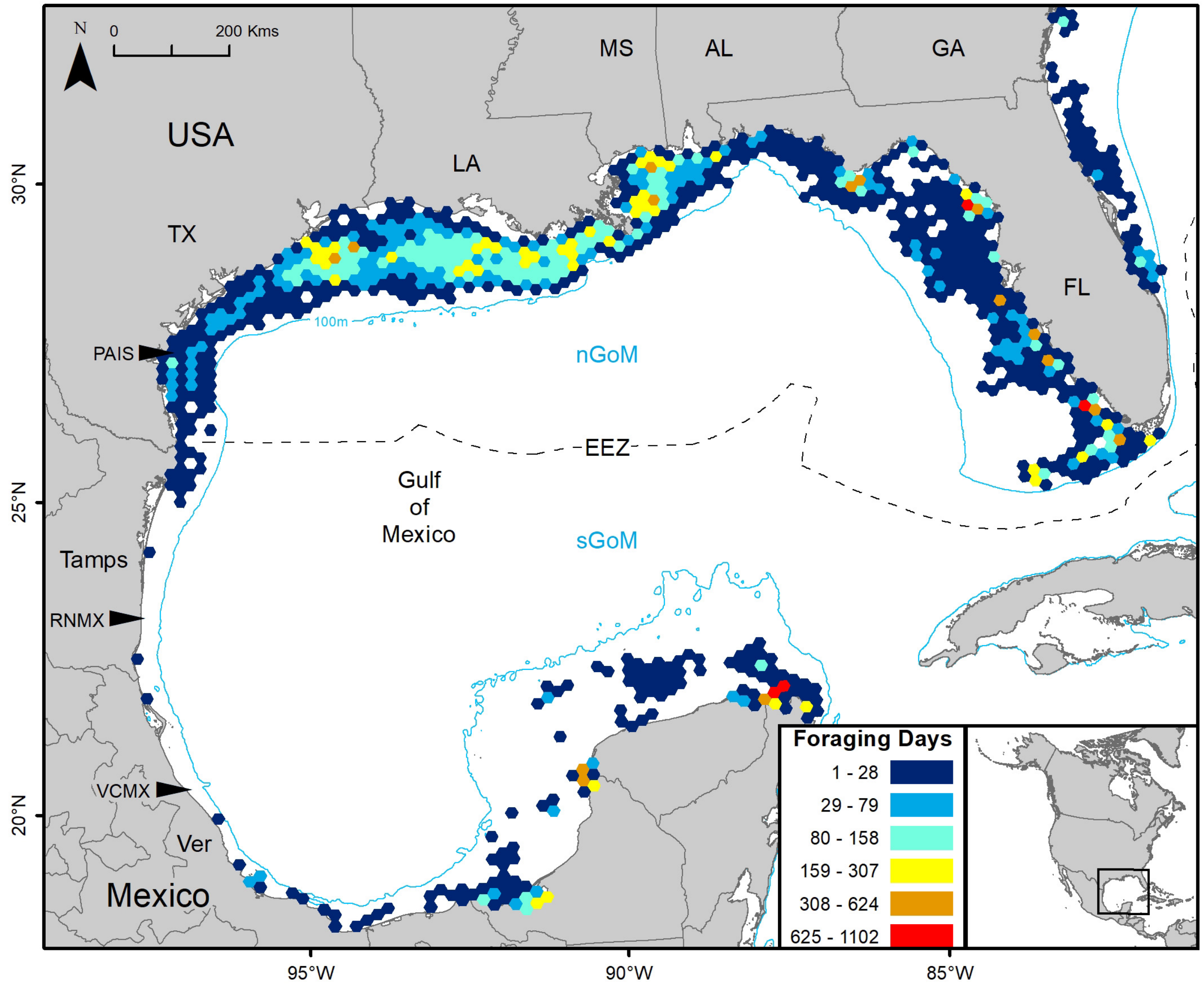

FIGURE 2 | Switching state-space model-derived foraging days for 117 post-nesting female Kemp's ridley sea turtles tracked from the primary and major secondary nesting beaches summarized in 25 km hex-bin cells: Padre Island National Seashore, Texas, United States (PAIS); Rancho Nuevo, Tamaulipas (Tamps), Mexico (RNMX); Tecolutla, Veracruz (Ver), Mexico (VCMX). The Exclusive Economic Zone (EEZ) demarcates the division between the northern Gulf of Mexico (nGoM) and southern Gulf of Mexico (sGoM). Transmitters were deployed between 2010 and 2017.

Additionally, two individuals (PTTs 126252 and 126257) tracked from RNMX displayed ARS-type behavior within the sGoM near the United States/Mexico border (mean ± SD: 47.2 ± 24.4 km south of the United States/Mexico EEZ) during their migrations to nGoM foraging areas. These individuals undertook ARS-type behaviors in the sGoM during periods just after the completion of nesting seasons in Mexico (August–September). However, these individuals displayed ARS-type behavior for $\leq$10 days before continuing their migrations north into the nGoM where they remained for the duration of their tracking periods.

The majority of Kemp's ridley nests (90.8%) were laid on the beaches of Tamaulipas, Mexico, concentrated at RNMX, between 2010 and 2017. The beaches of Veracruz, Mexico and Texas, United States accounted for relatively minor proportions of the nesting population with 8.2 and 1.0% of nests, respectively. Nesting in both of these states was concentrated at VCMX and PAIS. Using these proportions to weight the dispersal of tracked females from their nesting grounds to foraging areas indicated that 81.8% of the adult female population may use the nGoM as their primary foraging area (**Table 2**).

Regional and Foraging Area Fidelity

Eight of the 11 turtles that were tracked more than once (2X: $n = 7$, 3X: $n = 1$) had tracking durations long enough ($\geq$30 days) during each deployment to assess regional fidelity over time. All eight individuals used the nGoM, following similar migratory corridors each time they were tracked, displaying strong fidelity to the region (**Figure 5**). One individual foraged offshore from PAIS during both deployments. All other turtles migrated away from PAIS. The mean time between repeat tracking was 4.0 ± 1.3 (mean ± SD) years.

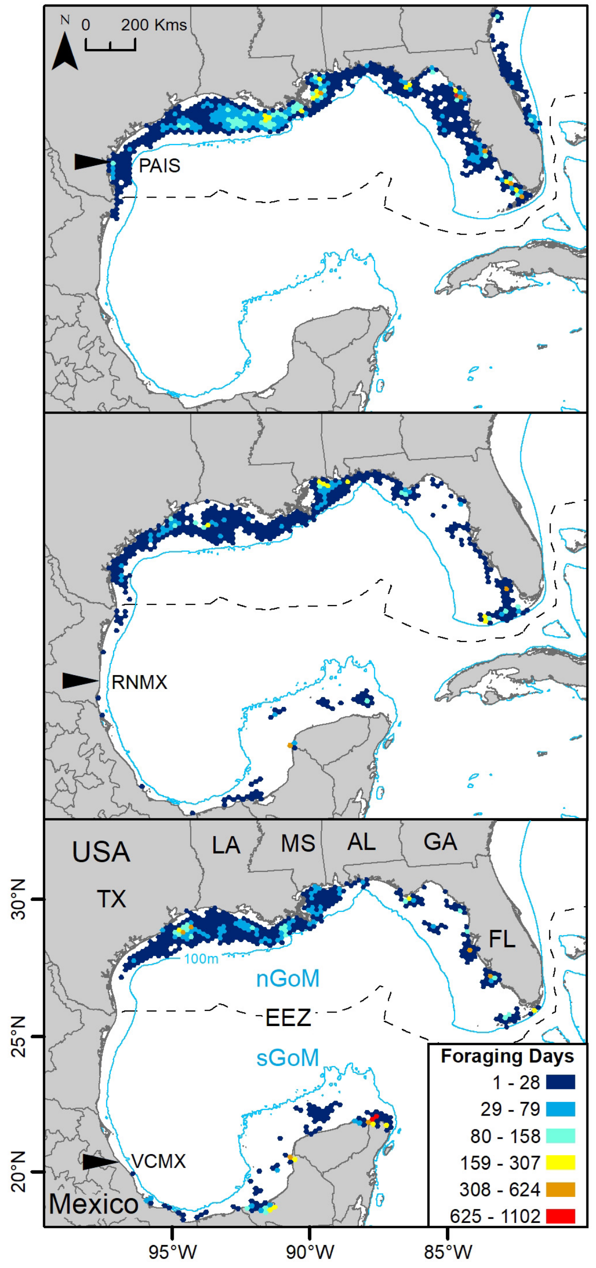

FIGURE 3 | Switching state-space model-derived foraging days for 117 post-nesting female Kemp's ridley sea turtles tracked from the primary and major secondary nesting beaches summarized in 25 km hex-bin cells and divided by deployment location: Padre Island National Seashore, Texas, United States (PAIS); Rancho Nuevo, Tamaulipas, Mexico (RNMX); Tecolutla, Veracruz, Mexico (VCMX). The Exclusive Economic Zone (EEZ) demarcates the division between the northern Gulf of Mexico (nGoM) and southern Gulf of Mexico (sGoM). Transmitters were deployed between 2010 and 2017.

Seven turtles were tracked remigrating to the nesting beach and then returning to forage during their deployments, including one of the turtles that was tracked twice. All individuals used the same region of the Gulf during successive migrations to their preferred foraging grounds, using the same migratory corridor each time (**Figure 6**). The mean time between remigrations to the nesting beach was 1.4 ± 0.5 (mean ± SD) years, but remigration intervals reported here only represent those individuals whose transmitters remained active long enough to capture a remigration during their tracking period. Seventy-six females were tracked ≥ 1 year, with seven of those tracked through a remigration, and 38 females were tracked for ≥ 1.5 years, with five of those remigrating within that period (**Supplementary Table S1**). Remigrating turtles in the nGoM initiated returns to the nesting beach during November and December while individuals returning from the sGoM began their migrations in February and March.

Individuals also showed fidelity to specific foraging areas. Twelve individuals that were tracked multiple times (*n* = 5), remigrated to the nesting beach and then back to foraging grounds during their initial deployment (*n* = 6) or both (*n* = 1) had data robust enough for SSM analysis to identify specific foraging areas and determine recurring use. For all of these individuals, overlap indices (i.e., UDOI and BA) indicated spatial overlap in their preferred foraging areas after each migration from the nesting beach (mean ± SD: 0.8 ± 0.7 UDOI; 0.6 ± 0.2 BA) (**Figure 7**). Turtles that remigrated during tracking displayed fidelity over successive nesting years (mean ± SD: 0.9 ± 0.8 UDOI; 0.6 ± 0.2 BA) and turtles that were tracked more than once displayed fidelity to foraging grounds over time (mean ± SD: 0.7 ± 0.6 UDOI; 0.6 ± 0.2 BA).

DISCUSSION

Long-term, concurrent tracking of adult female Kemp's ridley sea turtles from the primary and major secondary nesting beaches identified dispersal patterns to key foraging areas within the GoM. This study adds an additional five years of tracking data and 115 adult female Kemp's ridleys not previously described in the literature, with a significantly increased sample size from VCMX. Female Kemp's ridleys showed preferential selection for nearshore nGoM foraging areas, with the majority of the female population likely using these areas to forage. The proportion of the female population from each of the primary and major secondary nesting beaches using the nGoM to forage decreased with latitude, with more individuals dispersing to the sGoM from more southerly nesting beaches. Individuals showed fidelity to foraging regions over time, with animals migrating back to the same foraging regions (nGoM or sGoM) they used previously after each nesting season and when tracked more than once. Turtles also displayed strong fidelity to previously used foraging grounds, with large overlaps between individual foraging areas after repeat migrations or additional PTT deployments. Furthermore, migratory routes remained consistent for individuals between migrations and deployments. No individuals were observed nesting in areas other than the one they were initially tracked from, indicating fidelity to nesting beaches. These results are consistent with patterns seen in Kemp's ridleys and other marine megafauna species, showing strong fidelity to foraging sites, migratory corridors,

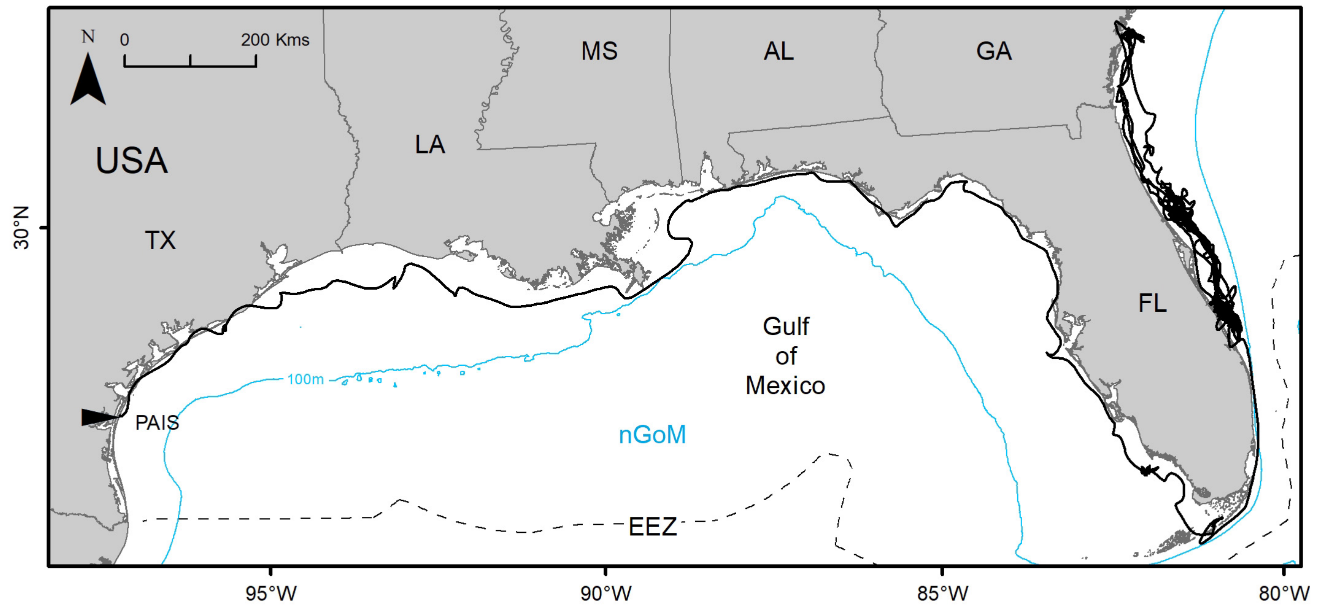

FIGURE 4 | Switching state-space model-derived track of PTT 152808 tracked between 02 July 2016 and 24 March 2019 (995 days) from Padre Island National Seashore, Texas, United States (PAIS) to the Atlantic coasts of Florida and Georgia, United States. The Exclusive Economic Zone (EEZ) demarcates the division between the northern Gulf of Mexico (nGoM) and southern Gulf of Mexico.

and nesting/breeding areas (Shaver and Rubio, 2008; Kelly et al., 2010; Horton et al., 2017; Shimada et al., 2019). Because large numbers of individuals were tracked from regions representing nearly 100% of the nesting population (NMFS et al., 2011), these results have the potential to be applied to the entire adult female Kemp's ridley population to infer population-level and species-level spatial dynamics.

Results complement and add to findings from previous work identifying key foraging areas and migratory corridors of female Kemp's ridleys, showing consistency over 22 years of satellite tracking (Seney and Landry, 2008, 2011; Shaver and Rubio, 2008; Shaver et al., 2013, 2016a; Hart et al., 2018a,b). SSM identified additional foraging areas along the panhandle and central coast of Florida and the Yucatán Peninsula, adding to previously identified foraging areas in these regions (Shaver et al., 2013; Hart et al., 2018a,b). Furthermore, foraging areas were identified along the Atlantic coasts of Florida and Georgia that had previously not been described. The importance of the U.S. Atlantic coast to adult Kemp's ridleys is still largely unknown, with only one confirmed migration from the nesting beaches to the region (PTT 152808), as are the mechanisms leading to these migrations or if these individuals return to the GoM to nest in later years. These additional foraging areas may be the result of increased tracking of individuals, which were not identified in previous studies, indicate a shifting range of female Kemp's ridleys over time or are controlled by other environmental factors (e.g., seasonal currents, resource availability). Further analysis is warranted to describe these differences. However, foraging areas on the Texas-Louisiana Shelf and off of the Mississippi River Delta in the nGoM remain the most heavily used areas (Shaver and Rubio, 2008; Shaver et al., 2013; Hart et al., 2018a,b).

TABLE 2 | Proportions of individual dispersal (Dispersal) and switching state-space model-derived foraging days (Foraging Days) of post-nesting female Kemp's ridley sea turtles in the northern Gulf of Mexico (nGoM) and southern Gulf of Mexico (sGoM) tracked from the primary and major secondary nesting beaches: Padre Island National Seashore, Texas, United States (PAIS); Rancho Nuevo, Tamaulipas, Mexico (RNMX); Tecolutla, Veracruz, Mexico (VCMX).

	Dispersal		**Foraging Days**	
	Region			
Location	**nGoM**	**sGoM**	**nGoM**	**sGoM**
PAIS	98.5%	1.5%	99.8%	0.2%
RNMX	83.8%	16.2%	90.7%	9.3%
VCMX	57.8%	42.2%	65.5%	34.5%
Total	81.8%	18.2%	86.1%	13.9%

Total percentages for individual dispersal are weighted by the proportion each nesting beach represented of the nesting population.

It is still unknown how Kemp's ridleys, and marine turtles in general, select their key foraging areas and distribute themselves spatially. However, it has been suggested that dispersal of hatchlings by oceanic circulation patterns may play a role in determining where individuals recruit to forage as adults. Specifically, individuals recruiting to neritic foraging areas from the pelagic zone may retain fidelity to productive or known areas as they mature, either through imprinting to geomagnetic fields, memory or other factors (Hays et al., 2010; Putman et al., 2015a,b; Shimada et al., 2019). Consequently, oceanic circulation patterns may explain preferential use of the nGoM. In fact, dispersal modeling of hatchlings from the primary and major secondary Kemp's ridley nesting beaches indicates

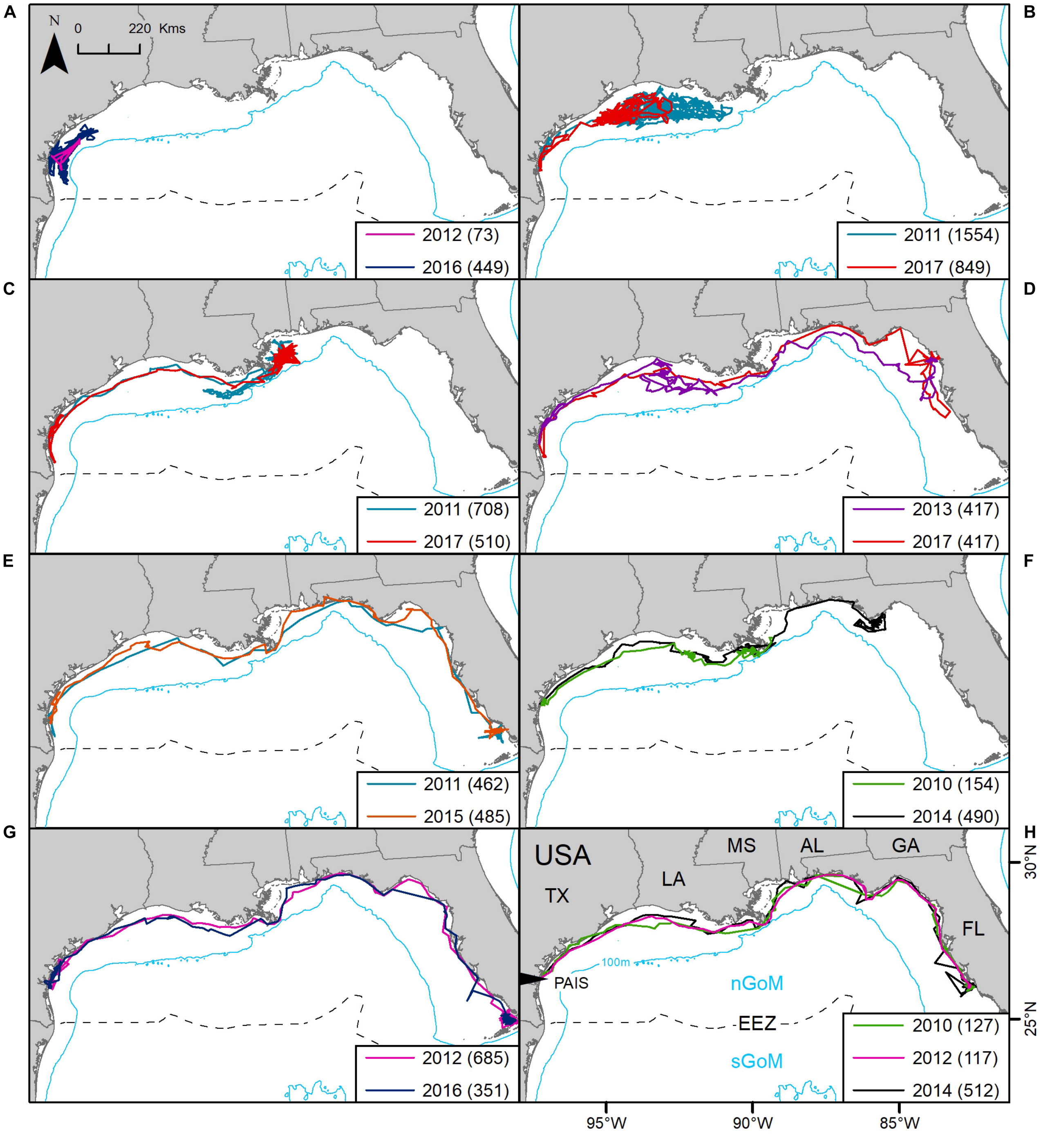

FIGURE 5 | Repeat tracking of eight post-nesting female Kemp's ridley sea turtles in the northern Gulf of Mexico tracked from Padre Island National Seashore, Texas, United States (PAIS): **(A)** platform terminal transmitters (PTTs) 117515 and 152803; **(B)** PTTs 101137 and 152828; **(C)** PTTs 101138 and 152827; **(D)** PTTs 112763 and 152829; **(E)** PTTs 106343 and 141781; **(F)** PTTs 47562 and 133286; **(G)** PTTs 112758 and 152802; **(H)** PTTs 47524, 112762 and 133285. The Exclusive Economic Zone (EEZ) demarcates the division between the northern Gulf of Mexico (nGoM) and southern Gulf of Mexico (sGoM). Numbers in parentheses equal the number of tracking days for each deployment. Tracks were reconstructed from mean daily locations of filtered location data. Transmitters were deployed between 2010 and 2017.

a strong relationship between where hatchlings are predicted to disperse and where identified key adult foraging areas are located, with most hatchlings predicted to disperse to U.S. nGoM waters (Putman et al., 2010, 2020). Other modeling work has suggested that the location of the major nesting beaches correlates to areas with circulation patterns which are more

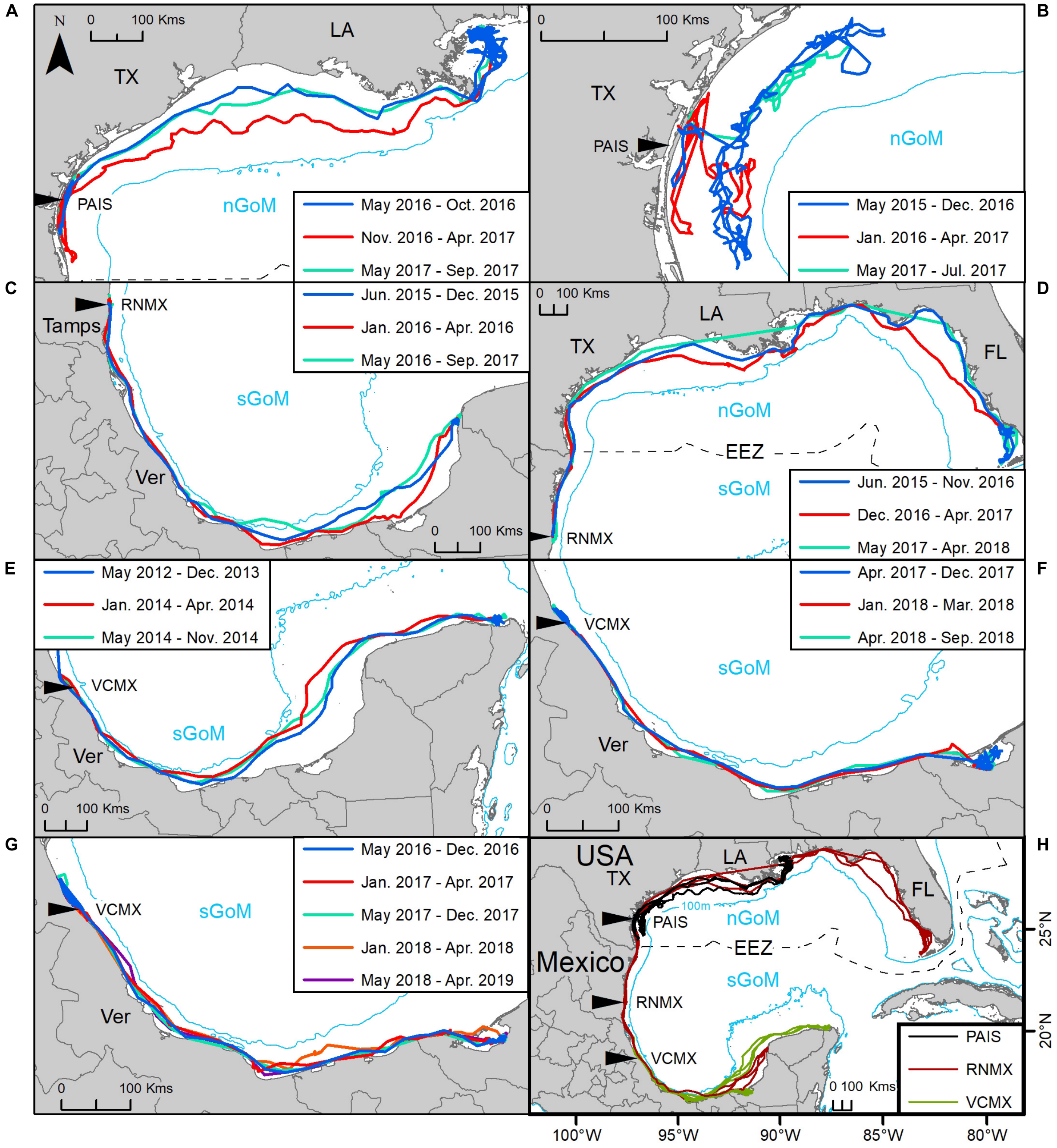

FIGURE 6 | Tracking of seven post-nesting female Kemp's ridley sea turtles from the primary and major secondary nesting beaches that remigrated from foraging areas to their nesting beach: **(A,B)** Padre Island National Seashore, Texas, United States (PAIS); **(C,D)** Rancho Nuevo, Tamaulipas (Tamps), Mexico (RNMX); **(E–G)** Tecolutla, Veracruz (Ver), Mexico (VCMX). **(H)** Tracks of all individuals. The Exclusive Economic Zone (EEZ) demarcates the division between the northern Gulf of Mexico (nGoM) and southern Gulf of Mexico (sGoM). Tracks were reconstructed from mean daily locations of switching state-space model-derived location data. Transmitters were deployed between 2010 and 2017. Line colors correspond to each migration; blue: first migration from the nesting beach to foraging grounds; red: first return migration to the nesting beach; turquoise: second return migration from the nesting beach to foraging grounds; orange: second return migration to the nesting beach; purple: third migration from the nesting beach to foraging grounds.

likely to transport hatchlings to productive foraging grounds (Putman et al., 2010). Thus, the distribution of key foraging areas may be interlinked between hatchling dispersal patterns, major nesting beach locations, and resource availability. In light of this, key foraging areas may have the potential to shift due to predicted changes in ocean circulation patterns and resource distributions caused by climate change (Pikesley et al., 2015; Willis-Norton et al., 2015). For example, sGoM sites appear to

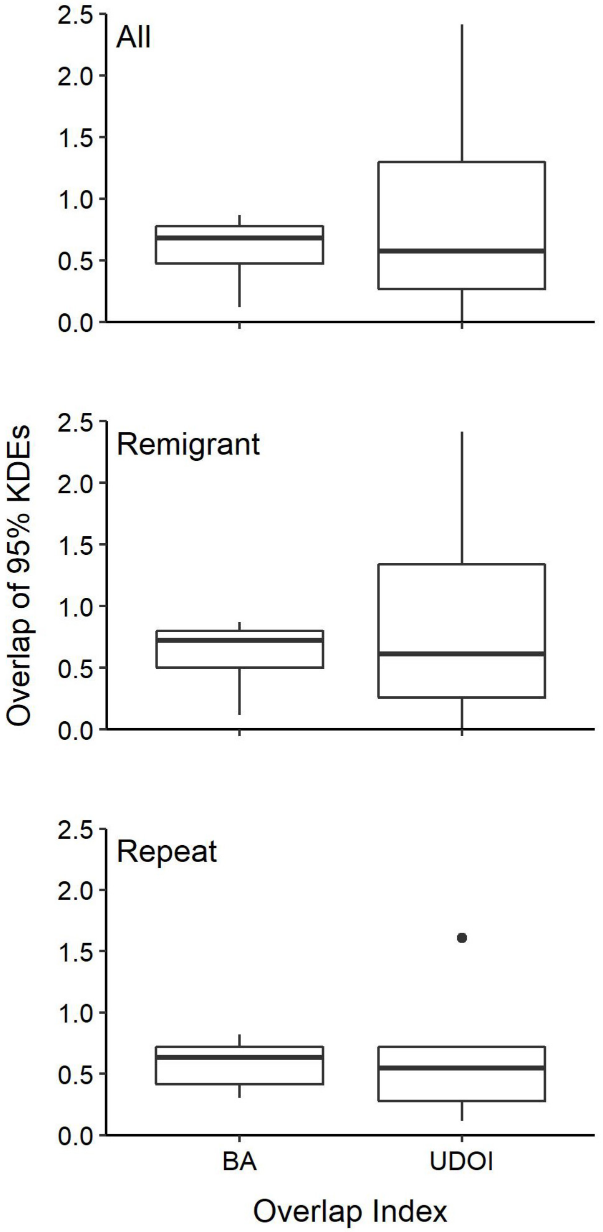

FIGURE 7 | Kernel-density estimates (KDEs) of foraging area overlap for individual post-nesting female Kemp's ridley sea turtles with transmitters deployed between 2010 and 2017. Individuals were tracked multiple times (Repeat) or tracked remigrating back to the nesting beach and then returning to the foraging grounds during their deployment (Remigrant). Remigrant and Repeat tracks were also combined (All) to show overall intra-individual overlap of foraging areas. BA, Bhattacharyya's affinity; UDOI, utilization distribution overlap index. Boxes bound the 25th and 75th percentiles, the solid line indicates the median, dots represent outliers, and the whiskers extend 1.5 times the interquartile range.

provide suitable habitat for juvenile and adult Kemp's ridleys (Carr, 1980; Márquez-Millán, 1994). However, these areas are seemingly underused by the species, with approximately 18% of the female population foraging in the region.

This study focused only on the movements and distributions of reproductively active female Kemp's ridleys from the primary and major secondary nesting beaches who had successfully nested at least once during their lifetime. While Kemp's ridleys have been reported to nest in other areas along the GoM and U.S. Atlantic coast, these events are rare, accounting for only a few individuals annually, and are not considered significant portions of the population (NMFS et al., 2011; Shaver and Caillouet, 2015). However, it is unknown if additional foraging areas are used by females on the verge of reaching maturity, newly mature individuals who have not yet nested in their lifetime or those that are no longer in the breeding population (e.g., post-reproductive, chronically ill, or disabled individuals). Thus, these portions of the female population and the foraging areas they use, if different, were not captured in this study. Further investigations are needed to identify potential differences in foraging distributions of other life-stages.

In addition, only a few studies have investigated the movement patterns of adult males, with comparatively low numbers of individuals tracked (Shaver et al., 2005; Hughes and Landry, 2016). Nevertheless, tracking has shown that some males appear to overlap with female distributions in the nGoM, specifically on the Texas-Louisiana Shelf, and use the same migratory corridor as females (Shaver et al., 2005; Hughes and Landry, 2016). The spatial overlap of some males and females in this area of the northwestern GoM reinforces the importance of the region as key foraging habitat for the species and spatial protections and policies may encompass both genders. However, many of the males tracked remained in the vicinity of the primary and major secondary nesting beaches throughout the year (Shaver et al., 2005). This is in sharp contrast to female migration patterns, where very few individuals remain near the nesting beaches outside of the nesting season. The results of the current and previous studies suggest that additional research and conservation actions may be needed to protect male Kemp's ridleys in their foraging grounds. Specifically, key areas are still undescribed, and males may not follow the same patterns as females for site selection, making spatial protections for females potentially inadequate for males. In fact, increased protections of males are becoming progressively more important due to the predicted feminization of marine turtle populations as a result of climate change (Jensen et al., 2018; Patrício et al., 2019). Thus, additional studies should be undertaken to determine key foraging areas and distributions of males to inform a complete picture of adult Kemp's ridley spatial population dynamics. In addition, spatial segregation of genders has also been shown in other mobile marine megafauna species such as blue sharks (*Prionace glauca*) (Maxwell et al., 2019), Indo-Pacific bottlenose dolphins (*Tursiops aduncus*) (Fury et al., 2013), and Australian fur seals (*Arctocephalus pusillus doriferus*) (Kernaléguen et al., 2015) highlighting the need for research across genders to determine the spatial dynamics of a species.

Conservation Implications

Preferential selection of nGoM waters as foraging grounds, fidelity to foraging regions, and narrow migratory corridors across the Gulf indicate that the adult female Kemp's ridley nesting population may be more susceptible to regional threats and that the nGoM may be the most significant foraging region for females of the species. Importantly, point source events have the potential to significantly affect a high proportion of the nesting population in the foraging grounds or along migratory routes. For example, the Deepwater Horizon oil spill in 2010 may have had a population-wide effect on nesting females due to its centralized location within the nGoM, overlap with key foraging areas and lying directly within the migratory corridor (Beyer et al., 2016; Shaver et al., 2016a; Hart et al., 2018a). Due to its location, any individuals migrating to central or eastern nGoM foraging grounds, or returning to the nesting beaches, would have had to pass directly through the oiled area. In fact, it has been estimated that >50% of Kemp's ridleys that forage in the region may have been exposed to oil (Reich et al., 2017) and it has been hypothesized that the spill may have affected, in part, the recovery of the species (Caillouet, 2014; Gallaway et al., 2016a,b).

The nGoM region is also used heavily by a variety of anthropogenic activities, including commercial fisheries, commercial shipping traffic, and oil and gas production (Hart et al., 2018a). Shrimp trawling has been linked with high incidents of marine turtle bycatch, with large numbers of mortalities of Kemp's ridleys in the nGoM (Lewison et al., 2003; Finkbeiner et al., 2011) and the fishery has been plagued with compliance issues in the past (Lewison et al., 2003; Cox et al., 2007). Vessel traffic has been connected with marine turtle mortalities (Hazel and Gyuris, 2006; Casale et al., 2010) and mortalities in a host of other threatened mobile marine megafauna [e.g., North Atlantic right whales (*Eubalaena glacialis*) (van der Hoop et al., 2012) dugongs (*Dugong dugon*) (Marsh et al., 2011) manatees (*Trichechus manatus*) (Lightsey et al., 2006)]. Vessels have also been identified as a significant threat to marine turtles in the nGoM (Hart et al., 2018a). Hypoxic events and harmful algal blooms are becoming more common in the GoM and are predicted to increase (Brand and Compton, 2007; Justić et al., 2007) which can affect individuals, including marine turtles, and their prey resources (Landsberg et al., 2009; Capper et al., 2013; Walker et al., 2018; Foley et al., 2019).

Not only is a high proportion of the nesting population exposed to varying threats within their foraging regions, there are increasing threats along their migratory corridor, both in United States and Mexican waters. Illegal, unreported and unregulated (IUU) fishing using long-line and gill net gear, primarily targeting red snapper (*Lutjanus campechanus*) and sharks, may be the most significant inadequately addressed threat and marine turtles are frequently incidentally caught and killed by these operations. Large numbers of stranded marine turtles have been reported in south Texas, including adult female Kemp's ridleys, during recent years, presumably a result of incidental capture from IUU fishing vessels, called lanchas, operating out of Mexico (Oliver and Jacobs, 2019; Donna Shaver, unpublished data). The U.S. Coast Guard reported seizing 74 of the 175 detected lanchas from south Texas waters in 2019, a new record, and have noted a significant increase of vessels since 2017 (USCG, 2019). Additionally, only an estimated 5–15% of total lancha incursions are detected annually, suggesting the total volume of illegal fishing activity in the GoM may be much higher than what has been reported (Frazer, 2020). These interactions have the potential to impact a high proportion of mature females as these operations occur directly in the primary migratory corridor leading from the nGoM to the major nesting beaches (Shaver and Rubio, 2008; Shaver et al., 2016a).

CONCLUSION

The nGoM appears to be the most important foraging area for adult female Kemp's ridleys and management of threats in the region may play a significant role in the conservation and recovery of the species. Preferential use of foraging regions, consistency in foraging region selection, and fidelity to migratory corridors highlights the need for a continued bi-national cooperation between the United States and Mexico. These cooperative actions are needed for effective management and conservation of Kemp's ridleys, with most females foraging in U.S. waters, migrating across the Mexico–United States border and nesting on Mexican beaches. This calls for maintaining and building upon existing nest and marine protection efforts in Mexico and marine protections and policies in the United States.

DATA AVAILABILITY STATEMENT

All datasets presented in this study are included in the article/**Supplementary Material**.

ETHICS STATEMENT

The animal study was reviewed and approved by the National Park Service Institutional Animal Care and Use Committee.

AUTHOR CONTRIBUTIONS

CG and DS contributed to the conception and design of the study and revised and wrote the final manuscript. CG conducted the modeling, performed the statistical analyses, wrote the first draft of the manuscript, and produced the figures and tables. All authors contributed to the article and approved the submitted version.

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SUPPLEMENTARY MATERIAL

The Supplementary Material for this article can be found online at: https://www.frontiersin.org/articles/10.3389/fmars.2020.00559/full#supplementary-material

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Green Turtle (*Chelonia mydas*) Nesting Underscores the Importance of Protected Areas in the Northwestern Gulf of Mexico

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Knowledge of the spatial and temporal distribution of green sea turtle (*Chelonia mydas*) nesting is crucial for management of this species. Limited data exist on the nesting patterns of green turtles along the northwestern Gulf of Mexico (GoM) coast. From 1987 to 2019, 211 green turtle nesting activities were documented on the Texas coast, including 111 confirmed nests and 100 non-nesting emergences. Of the 111 nests, 99 were located on North Padre Island (97 at Padre Island National Seashore (PAIS), two north of PAIS) and 12 on South Padre Island (six within the Laguna Atascosa or Lower Rio Grande Valley National Wildlife Refuges (NWR), six outside of a NWR). Of the 100 non-nesting emergences, 75 were on North Padre Island (70 at PAIS, 5 north of PAIS), 21 on South Padre Island (nine within a NWR, 12 outside of a NWR), one on Boca Chica Beach, two on San Jose Island, and one on Mustang Island. Nearly all of the nests (92.8%) and most of the non-nesting emergences (79.0%) were on property protected by the United States Department of the Interior as PAIS or a NWR, and confirmed nest density was largest at PAIS, highlighting the importance of these federally protected lands as nesting habitat for this threatened species. Of the 111 located nests, eight were predated. Mean hatching success of the 103 non-predated nests was 77.4%, and 9,475 hatchlings were released from the predated and non-predated nests. The largest annual number of green turtle nests documented was 29 in 2017. Nesting appeared to increase since 2010, but at a much lower rate than at other GoM nesting beaches. To aid with recovery, efforts should be undertaken to monitor long-term nesting trends, protect nesting turtles and nests, and investigate potential causes for the slower recovery in Texas. Additionally, the genetic structure of the population that nests in Texas should be determined to reveal if the population warrants recognition as a unique management unit, or if it is part of a broader unit that is a shared nesting resource with Mexico which is already being considered as a unique management unit.

Keywords: conservation, endangered species, texas, hatching success, spatial trends

INTRODUCTION

Green turtles (*Chelonia mydas*) are distributed world-wide in tropical and warm temperate oceans. Green turtles in the Gulf of Mexico (GoM), Caribbean, and North Atlantic Ocean are part of the North Atlantic Distinct Population Segment and are classified as threatened under the United States Endangered Species Act (Seminoff et al., 2015; NMFS and USFWS, 2016). Systematic harvest decimated the tens of millions of green turtles that once existed in the Caribbean and GoM, but after decades of conservation, green turtle nesting numbers have increased in many areas (Shamblin et al., 2015, 2018; Cuevas et al., 2018).

In Mexico, the annual number of nests documented in Quintana Roo increased from 500 to more than 23,000 from 1996 to 2017 (Tzeek Tuz et al., 2019), and the most recent total nester abundance for the five Mexican states of Tamaulipas, Veracruz, Campeche, Yucatan, and Quintana Roo was estimated to be 24,330 turtles (Seminoff et al., 2015). Despite this progress, green turtles continue to be vulnerable at inter-nesting sites in Veracruz and the Yucatan Peninsula (Cuevas et al., 2019).

Historic nesting levels of green turtles in Florida are not known. The first green turtle nest scientifically confirmed in peninsular Florida was in 1957 near Vero Beach in Indian River County (Carr and Ingle, 1959). Green turtle nesting was sparse in Florida through the early 1980s and then began to surge on both Atlantic and GoM coast beaches (Chaloupka et al., 2008; Witherington et al., 2009; Weishampel et al., 2016). The epicenter of nesting in Florida is on the Atlantic coast at the Archie Carr National Wildlife Refuge, on Melbourne Beach, which recorded 11,000 nests in 2013 (Shamblin et al., 2015).

In Texas, the green turtle was once abundant and commercially exploited during the mid-1800s (Witzell, 1994a,b). Turtle harvesting peaked during April–November (Hildebrand, 1981), aligning with the breeding season for green turtles in North America (Hirth, 1997). This timing, combined with the average weight of the harvested turtles recorded at 113 kg/turtle (Doughty, 1984), indicates that adult green turtles were likely among the individuals slaughtered. By 1963, when sea turtle fisheries were prohibited in Texas, green turtle catch had already precipitously declined and was almost non-existent (Hildebrand, 1981; Doughty, 1984). Presently, most green turtles inhabiting Texas waters are juveniles, and Texas inshore waters (i.e., bays, lagoons, and passes) serve as important developmental and foraging habitat for them (Metz and Landry, 2013; Shaver et al., 2017b). Some hypothesize that green turtles historically nested in Texas in abundance (Neck, 1978), but the first confirmed record of green turtle nesting in Texas was not until 1987 (Shaver, 1989). Neck (1978) relayed observations by Robert A. F. Penrose of 91–122 cm long turtles nesting near the mouth of the Rio Grande river in south Texas in 1889 (Fairbanks and Berkey, 1952) and concluded that these were likely green turtles. Hildebrand (1981) hypothesized that they were Kemp's ridley turtles (*Lepidochelys kempii*), but the size described is more indicative of green turtles, which nest at about 90–120 cm straight carapace length (SCL) (NMFS and USFWS, 2007; Seminoff et al., 2015), than of Kemp's ridley turtles, which nest at about 58.5–72.5 cm SCL (Márquez-Millán, 1994).

Green turtle nesting is low in Texas, with lower increases in nesting, compared to other GoM nesting beaches. Without historical data, it is unknown whether this nesting population is rebuilding from an exploited, once abundant nesting population or represents a spread of nesting from Mexico. The closest nesting beaches to Texas are in Tamaulipas, Mexico and along the Florida GoM coast. Little has been published in peer-reviewed literature regarding green turtle nesting on the Gulf coast of Mexico and tracking data from adult green turtles in the GoM is very limited. Adults tracked from Veracruz and Quintana Roo, Mexico, have migrated to foraging grounds in southwest Florida or remained in Mexico (Bresette et al., 2010; Méndez et al., 2013; Seminoff et al., 2015). We undertook this study to investigate the spatial and temporal trends of green turtle nesting in Texas, which have not been described in the peer-reviewed literature, and to establish a baseline to compare future green turtle nesting patterns in the northwestern GoM. This analysis is vital for evaluating population status and developing future monitoring strategies and management actions to aid with recovery efforts for this threatened species.

MATERIALS AND METHODS

Patrol Effort and Study Area

Efforts to find, document, and protect nesting sea turtles and their eggs in Texas were initiated on North Padre Island in 1986 and later expanded to include more Texas GoM beaches, days of the sea turtle nesting season, and hours of the day. The temporal and spatial variations of these patrols are described in NMFS et al. (2011) and Shaver et al. (2016b). Since 1986, daytime patrols have been conducted on the entire 128 km GoM shoreline of North Padre Island, including the southernmost 105 km protected by the United States Department of the Interior (DOI), National Park Service (NPS), as Padre Island National Seashore (PAIS). Established in 1962, PAIS preserves the longest stretch of undeveloped barrier island beach in the United States. Daytime patrols on North Padre Island were conducted a few days each week until 1995–1997, when patrol frequency increased to seven days per week (Shaver, 2005). Beginning in 1998, North Padre Island was repeatedly patrolled each day, from approximately 0630 to 1830 h, from April through mid-July, to target when Kemp's ridleys typically nest. Kemp's ridley is the most frequent nesting sea turtle in Texas and is the focus of a long-term, bi-national, multi-agency effort to form a secondary nesting colony at PAIS (Shaver and Caillouet, 2015). In 1999, repeated daytime patrols began on Boca Chica Beach, and on South Padre Island repeated daytime patrols began in 2000 (Shaver et al., 2016b). Of the 55 km long Gulf beachfront of South Padre Island, 15.3 km is currently protected by the DOI, United States Fish and Wildlife Service, as Laguna Atascosa and Lower Rio Grande Valley National Wildlife Refuges (NWRs) in a mosaic of fragmented parcels of land added to the refuges since 2000, and concentrated on the northern end of South Padre Island. Patrols began on other Texas beaches starting in 2003 and have been conducted on most Texas beaches since 2005, however, patrols from the upper Texas coast to San Jose

Island were conducted only a few days per week. Patrollers also watched for signs of green turtle nesting activity, especially during their first patrols of the morning, since green turtles nest predominantly at night.

From 2002 to 2004, exploratory patrols were conducted on North Padre Island to determine the nesting season for the five sea turtle species that have been recorded nesting in Texas (Hildebrand, 1981; Shaver, 1989; Shaver and Frandsen, 2019; Shaver et al., 2019a) and protect the nests that were found. In addition to the annual April through mid-July patrols, surveys were conducted once a day from 1 February–24 March and 12 July–30 September 2002, 1 February–29 March and 11 July–30 September 2003, and 1 February–3 April and 18 July–30 September 2004. In the years following the exploratory study, from mid-July through as late as early-October, patrols were sometimes conducted during morning hours to document green turtle and loggerhead (*Caretta caretta*) nesting activity on North and South Padre Islands. Late-season dawn patrols were conducted with more regularity beginning in 2010, with patrols terminating 2 weeks after the last documented nest each season. Nesting green turtles and green turtle tracks were also located and documented by biologists while they conducted other research and conservation activities, by other personnel working on the beach that were trained to identify signs of nesting, and by the public.

Documentation and Protection of Adult Females and Nests

Locations of all green turtle nesting activity found on the Texas coast from 1987 to 2019 were recorded using a hand-held GPS. Adult females encountered on the beach were measured for SCL using calipers or curved carapace length (CCL) using a flexible tape measure. An attempt was made to find eggs at all nesting activity locations. Due to significant threats from anthropogenic activities, predation, and high tides, eggs from all green turtle nests located were retrieved for protected incubation. Eggs from nests found on North Padre Island were placed into polystyrene foam boxes lined with sand from the nest site and relocated to the PAIS incubation facility (Shaver and Caillouet, 2015). Starting in 2008, eggs from nests found on South Padre Island were incubated in an outdoor screened enclosure called a corral, unless found after 15 July, in which case they were placed into polystyrene foam boxes containing sand from the nest site and transported to the PAIS incubation facility to protect them from the increased threat of hurricane activity from July through October. Eggs were monitored through the incubation period. After hatching, the number of hatchlings produced, number of unhatched eggs, and hatching success were recorded for each clutch. From 1987 to 2006, prior to release, hatchlings from all green turtle nests found in Texas were weighed to the nearest hundredth of a gram using an electronic balance and measured to the nearest hundredth of a millimeter using calipers. Hatchlings from all years were released at the surf line on the islands where they were hatched. All activities were carried out according to protocols approved by the NPS Institutional Animal Care and Use Committee.

Analysis

Locations where eggs were found were categorized as nests and locations where no eggs were found were categorized as non-nesting emergences. The numbers of nests and non-nesting emergences were determined for each year. The numbers of nests and non-nesting emergences found on North and South Padre Islands were categorized as within and outside of PAIS and NWRs, respectively. Density and optimized hot spot analyses were performed in ArcGIS 10.4 to determine preferred nesting areas. Nesting success was defined as:

$$\text{Nesting Success} = \frac{\text{Nests}}{\text{Nests} + \text{Non} - \text{nesting Emergences}} \times 100$$

A chi-squared test was conducted to examine whether the proportion of emergences that were nests differed inside and outside of the DOI protected lands. The numbers of confirmed nests per year were calculated for the entire study period (1987–2019) and linear regression was used to examine the nesting trend between 2010 and 2019, when patrol efforts were more consistent in time and area. Nesting female abundance was determined using the formula developed by Seminoff et al. (2015):

$$\begin{array}{c}\text{Nesting Female}\\\text{Abundance}\end{array} = \frac{\text{Nests}}{\text{Clutch Frequency}} \times \text{Remigration Interval}$$

Nesting female abundance is the total number of reproductive females using Texas beaches over time and is not an annual nester count (Seminoff et al., 2015).

Mean SCL was quantified for the females; if only CCL was obtained for a turtle, CCL was converted to SCL using the regression equation published by Teas (1993). Mean weights and lengths were calculated for hatchlings weighed and measured from 1987 to 2006. All statistical analyses were conducted in R version 3.4.4 (R Core Team, 2018).

RESULTS

Two hundred and eleven green turtle nesting activities were documented on the Texas coast from 1987 through 2019, including 111 confirmed nests and 100 non-nesting emergences (**Figures 1**, **2**). Nearly all nests (92.8%) and most non-nesting emergences (79.0%) were on federally protected lands. Of the 111 nests, 99 were found on North Padre Island (97 at PAIS, 2 north of PAIS) and 12 on South Padre Island (6 within the Laguna Atascosa or Lower Rio Grande Valley NWR, 6 outside of a NWR). The 100 non-nesting emergences included 75 on North Padre Island (70 at PAIS, 5 north of PAIS), 21 on South Padre Island (9 within a NWR, 12 outside of a NWR), 1 on Boca Chica Beach, 2 on San Jose Island, and 1 on Mustang Island (**Figure 1**). Confirmed nest density was greatest at PAIS, particularly between the PAIS 31.1 km (19.3 mile) and 74.8 km (46.5 mile) markers (**Figure 1**). Optimized hot spot results confirmed density findings with $\geq$95% confidence for nests to be found within this area.

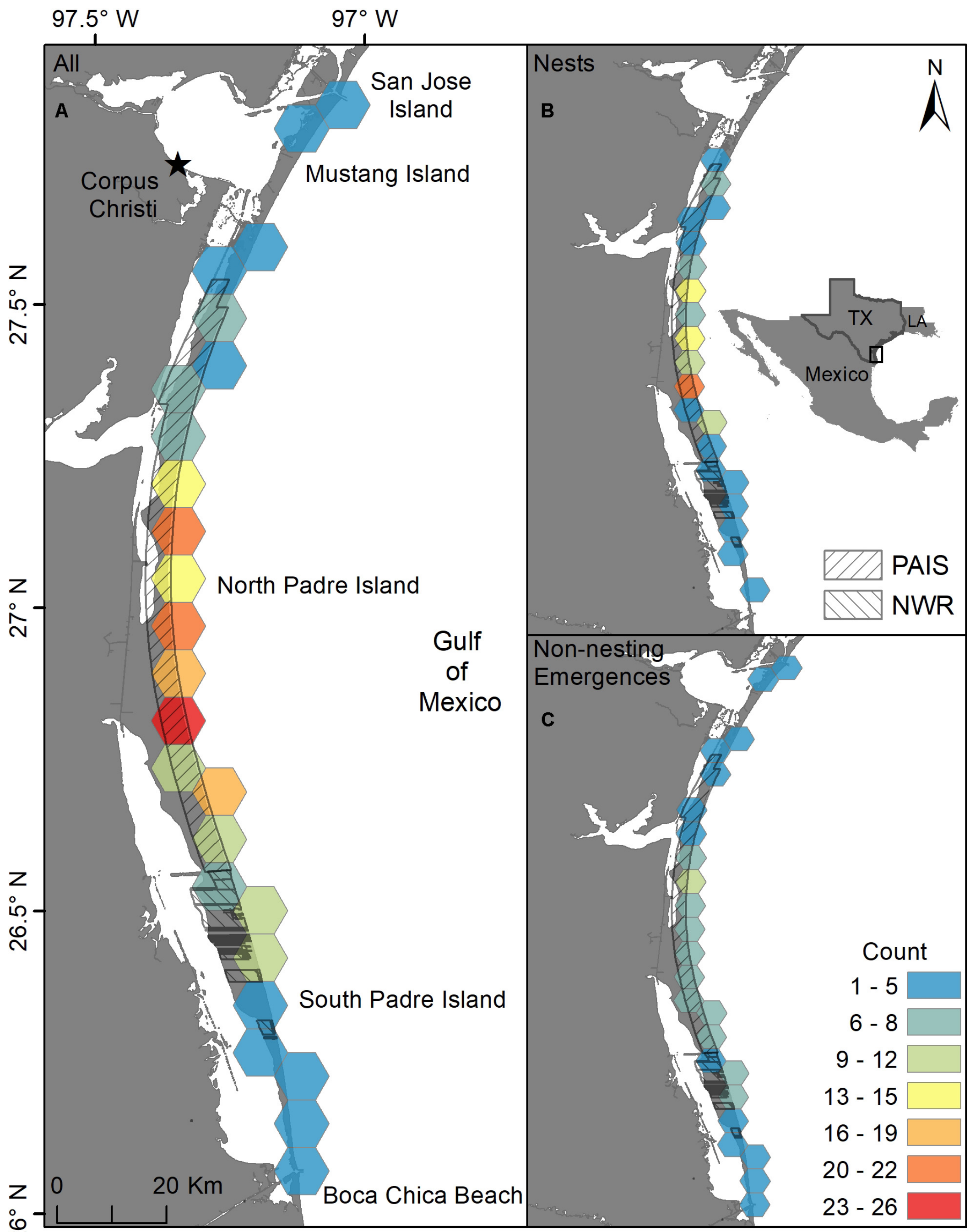

FIGURE 1 | Ten km hex-bin density of all green turtle (*Chelonia mydas*) nesting activity (nests and non-nesting emergences) in Texas from 1987 to 2019. **(A)** Density of all nests and non-nesting emergences, **(B)** density of all nests, **(C)** density of all non-nesting emergences. PAIS = Padre Island National Seashore, NWR = Laguna Atascosa and Lower Rio Grande Valley National Wildlife Refuges.

Nesting success for all years and areas combined was 52.6% and was higher at the federally protected lands (56.6%) than outside of them (27.6%) [$\chi^2(1, 211) = 8.44$, $p = 0.00367$]. Of the nests with reported beach positions ($n = 102$), 81.4% were situated between the embryonic dunes and the top of the first foredune. Nesting appeared to increase from 1987 to 2019, but predictive modeling of this data was deemed inappropriate due to high variability, both in time and space, of patrol effort. Linear modeling of nests laid between 2010 and 2019, when patrol effort was increased and more consistent between years, indicated a 0.7× annual increase of nests, but was not statistically significant with low explanatory power [$y = -1359.02 + 0.68x$,

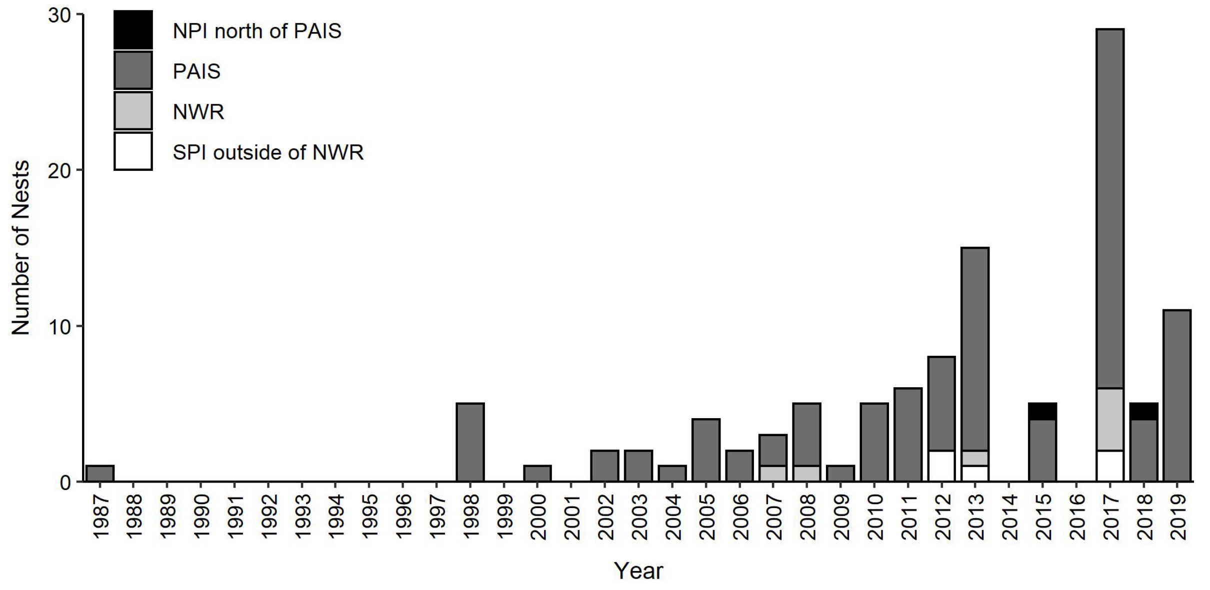

FIGURE 2 | Annual numbers of green turtle (*Chelonia mydas*) nests documented in Texas from 1987 to 2019 (non-nesting emergences not included). NPI = North Padre Island outside of PAIS, PAIS = Padre Island National Seashore, NWR = Laguna Atascosa and Lower Rio Grande National Wildlife Refuges, SPI = South Padre Island outside of a NWR.

$F(1, 8) = 8.79$, $R^2 = 0.06$, $p = 0.503$]. The largest numbers of nests ($n = 29$) and non-nesting emergences ($n = 47$) were documented in 2017 (**Figure 2**). Nesting occurred from May through September, but was most frequent in July ($n = 53$), with 47.7% of all confirmed nests documented that month (**Figure 3**). Non-nesting emergences were documented from June through October and were most frequent in August ($n = 46$), with 46.0% of non-nesting emergences documented that month (**Figure 3**). Collectively, from 1987 to 2019, 74.4% of all green turtle nesting activity (nests and non-nesting emergences) occurred between July and August.

Females were observed at 18 of the 211 nesting activity sites, but at all other sites the females had already returned to the GoM by the time that biologists arrived. Nine females were tagged, including four at nest sites and five at non-nesting emergence sites. Mean SCL of the nine females measured was 105.7 cm (SD = 5.3 cm, range = 98.6–113.2 cm). One female tagged in 2019 at a non-nesting emergence site was observed expelling a prolapsed oviduct (Frandsen et al., 2020). Through tag returns, two nesting females (1 in 2017 and 1 in 2018) were confirmed to have nested twice in a season. One female that was tagged and documented nesting in 2006 was observed during a non-nesting emergence in Hampton Bays, New York in 2011 (Shaver et al., 2019b). Based on total nests, a clutch frequency of three (Seminoff et al., 2015), and a re-migration interval of 2.27 years (del Méndez Matos et al., 2019), it is estimated that 84 adult female green turtles have nested in Texas since 1987.

During the 32-year study, 12,598 eggs were located at 111 nests, of which 9,486 hatched. Ten hatchlings died prior to release (0.1%), 1 weak hatchling was recaptured after unsuccessful release and retained for rehabilitation, but later died, and 9,475

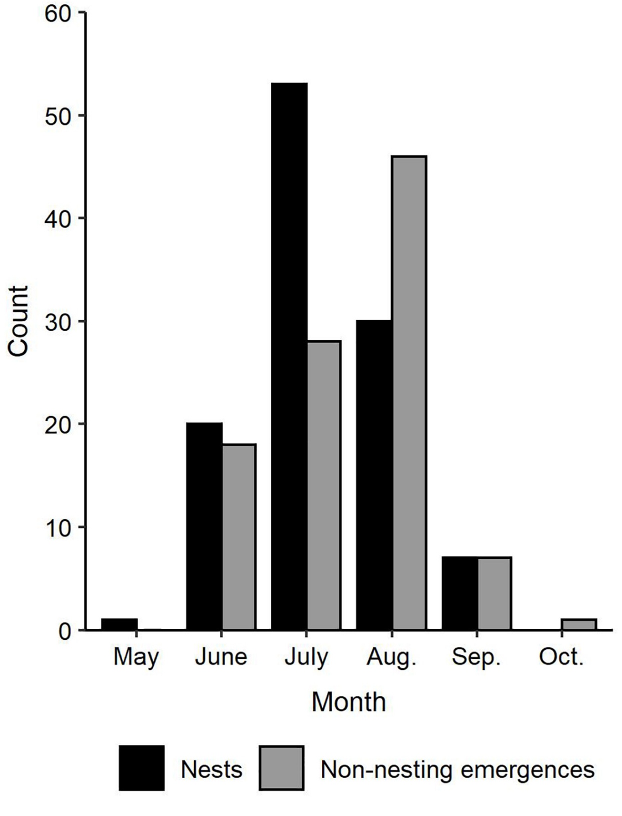

FIGURE 3 | Monthly trends in total number of green turtle (*Chelonia mydas*) nesting activity (nests and non-nesting emergences) documented in Texas from 1987 to 2019.

TABLE 1 | Summary of incubation, hatching, and release information for green turtle (*Chelonia mydas*) nests documented on the Texas coast from 1987 through 2019, including the annual number of nests found, number of nests by incubation method, number of nests predated, hatching success, and number of hatchlings released.

Year	No. nests	No. nests PAIS[1] incubation facility	No. nests SPI[3] corral	No. nests predated (no. intact eggs)	Percent hatched[5]	Total no. hatchlings released[6]
1987	1	1	0	0	50.0%	0
1998	5	5	0	0	84.0%	436
2000	1	1	0	0	97.1%	169
2002	2	2	0	0	81.0%	189
2003	2	2	0	0	48.6%	68
2004	1	1	0	0	92.9%	105
2005	4	3	0	1(5)	88.1%	380
2006	2	2	0	0	68.6%	189
2007	3	3	0	0	87.0%	298
2008	5	4	1	0	90.8%	495
2009	1	1	0	0	94.9%	130
2010	5	5	0	0	82.3%	529
2011	6	5	0	1(111)	78.4%	499
2012	8	7	0	1(109)	51.4%	450
2013	15	14	0	1(107)	66.7%	1,135
2015	5	5	0	0	91.1%	636
2017	29	24	3	2(22)	71.7%	2,358
2018	5	5	0	0	94.6%	574
2019	11	9	0	2(80)	75.8%	835
Total	111	99[2]	4[4]	8(434)	77.4%[7]	9,475

[1] PAIS = Padre Island National Seashore, [2] Total does not include 6 nests that were incubated after predation. [3] SPI = South Padre Island. [4] Total includes one nest relocated from the SPI corral to Laguna Atascosa National Wildlife Refuge for protected incubation in polystyrene boxes. [5] Percent hatched of non-predated nests. [6] Totals include hatchlings released from both non-predated and predated nests. [7] Mean hatch percentage of non-predated nests.

hatchlings were successfully released and entered the surf at PAIS ($n = 9{,}078$) or South Padre Island ($n = 397$) (**Table 1**). The 103 non-predated nests contained 12,038 eggs, with a mean clutch size of 117 eggs (SD = 29.4, range = 2 to 177 eggs). Mean hatching success for the 103 non-predated clutches was 77.4% (SD = 31.4, range = 0.0–99.3%) (**Table 1**). The 8 nests predated by badgers (*Taxidea taxus*), coyotes (*Canis latrans*), and/or ghost crabs (*Ocypode quadrata*) before nest detection contained 560 identifiable eggs (total does not include shredded egg shells found at nest sites), of which 434 eggs were still intact when found. The 434 eggs were salvaged, incubated, and produced 169 hatchlings. Using our mean clutch size of 117 eggs as a proxy for clutch size in the eight predated nests, estimated mean hatching success for the predated nests was 18.1%. Combining estimates for the eight predated nests with results for the 103 non-predated nests, the estimated mean hatching success of the 111 green turtle nests found in Texas from 1987 to 2019 was 73.1%. For the 1,537 hatchlings weighed and measured from 1987 to 2006, mean SCL was 52.97 mm (SD = 1.90 mm, range = 43.62–58.06 mm) and mean weight was 28.61 g (SD = 2.51 g, range = 19.95–34.07 g) (**Figure 4**).

DISCUSSION

Spatial Trends

All green turtle nests confirmed on the Texas coast through 2019 were on North and South Padre Islands, with 92.8% of nests documented on lands protected by the DOI as PAIS ($n = 97$ nests) or NWR ($n = 6$ nests) (**Figures 1**, **2**). During the study period, nesting success was 52.6%, which is slightly higher than the 50% recorded for green turtles in the southeast United States (Weishampel et al., 2003). Green turtles demonstrated a preference for nesting on DOI property and had higher nesting success at the federally protected lands (56.6%) than outside of them (27.6%). Not only is PAIS the most important green turtle nesting beach in Texas, it is also the most important nesting beach in Texas for loggerhead turtles and the most important nesting beach in the United States for Kemp's ridley turtles, with more Kemp's ridley nests recorded there annually than at any other United States beach (Shaver et al., 2016b, 2017a; **Figure 5**). Although green turtle nests have only been confirmed in Texas on North and South Padre Islands, Kemp's ridley and loggerhead nests have been recorded state-wide (Shaver et al., 2016b; Shaver pers. obs.), indicating that green turtles strongly prefer to nest on North and South Padre Islands over other Texas beaches that have been used for nesting by other sea turtle species. Additionally, the only hawksbill (*Eretmochelys imbricata*) and leatherback (*Dermochelys coriacea*) nests confirmed in Texas were documented on North Padre Island at PAIS (Shaver and Frandsen, 2019; Shaver et al., 2019a), indicating that PAIS is the most important sea turtle nesting beach for all five GoM species on the Texas coast.

Green turtle nest density was highest at PAIS, particularly between the 31.1 km (19.3 mile) and 74.8 km (46.5 mile) markers (**Figure 1**). This nesting epicenter encompasses the

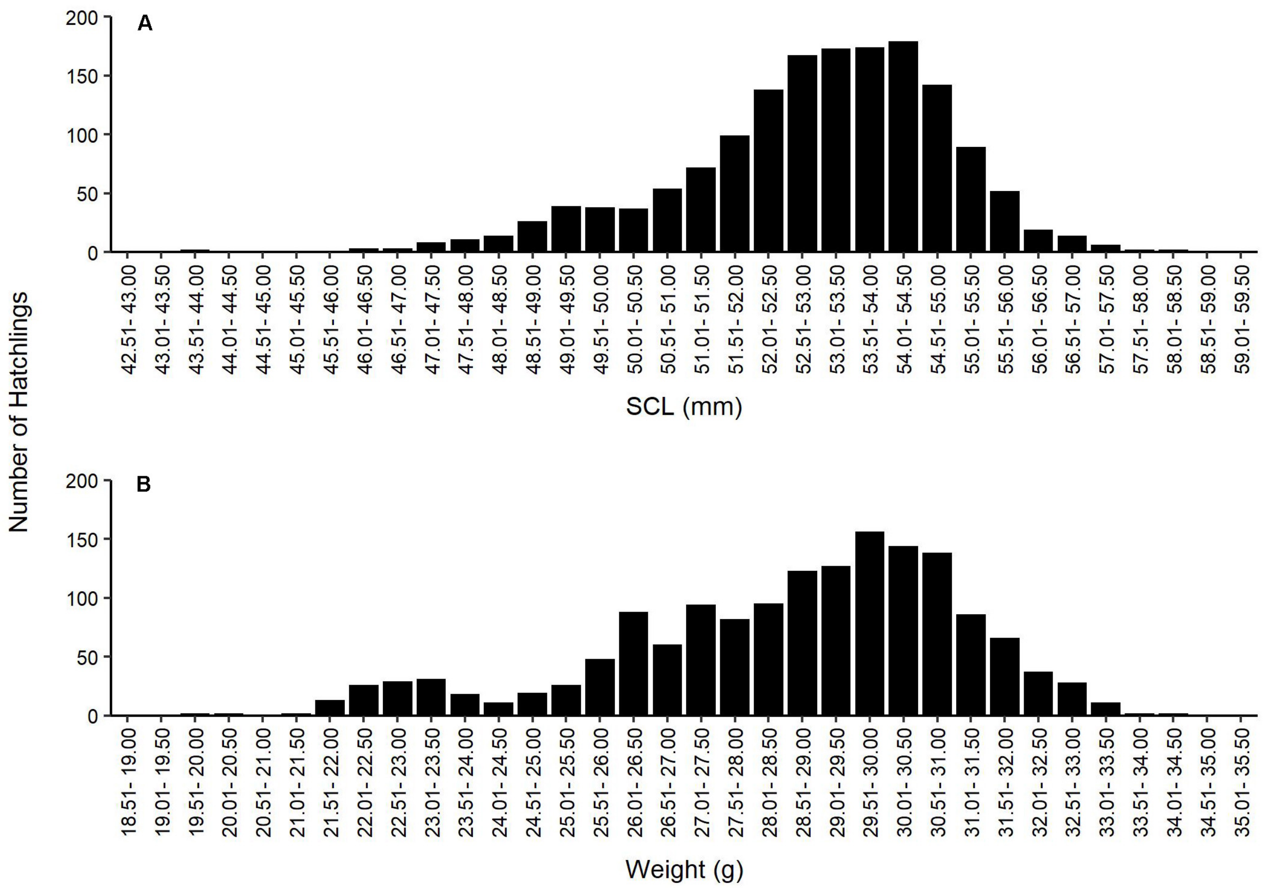

FIGURE 4 | (A) Straight carapace lengths (SCL) (mm) and **(B)** weights (g) measured for green turtle (*Chelonia mydas*) hatchlings that emerged from eggs hatched at the Padre Island National Seashore (PAIS) incubation facility, and released on the beach at PAIS, from 1987 to 2006.

southernmost 25.2 km of "Big Shell Beach", which extends from the PAIS 27.4 km (17 mile) to 56.3 km (35 mile) markers (Weise and White, 1980; USDA NRCS and NPS, 2005), and 18.5 km immediately south of Big Shell Beach. Culver (2018) found that Kemp's ridley nest density on North and South Padre Islands was highest between approximately the PAIS 27.4 km (17 mile) and 67.6 km (42 mile) markers, which encompassed all of Big Shell Beach and the 11.3 km stretch of beach immediately south of it. The nesting epicenters for green and Kemp's ridley sea turtles at PAIS are nearly identical and include beaches with geomorphological characteristics that are unique on the Texas coast, but resemble the geomorphology of beaches at Rancho Nuevo, Tamaulipas, Mexico (Carranza-Edwards et al., 2004; Culver et al., 2020), where Kemp's ridley and green turtle nesting are prolific. Longshore currents converge near the center of PAIS and cause sediment and shell fragments to accumulate in this area (Davis, 1978).

Multiple factors may influence where sea turtles choose to nest (Mortimer, 1990, 1995; Weishampel et al., 2003, 2006; Cuevas et al., 2010), including magnetic fields (Brothers and Lohmann, 2018), offshore habitat structure (Hughes and Richard, 1974), offshore and near-shore oceanographic conditions (Carr and Carr, 1972; Marcovaldi and Laurent, 1996; Weishampel et al., 2003), beach morphology and covering (Whitmore and Dutton, 1985; Kikukawa et al., 1996; Fujisaki and Lamont, 2016; Maurer and Johnson, 2017), sand characteristics, and anthropogenic factors (Crain et al., 1995; Steinitz et al., 1998; Davis et al., 1999; Kikukawa et al., 1999). However, multiple factors, including human or predator disturbance, lighting, unfavorable topography or sand characteristics, marine debris, and others, can also cause green turtles to abandon nesting attempts.

At other beaches, green turtles tended to nest on beaches with 1–2 mm sand particles (Salleh et al., 2018), moderate to steep slope (Cuevas et al., 2010; Zavaleta-Lizárraga and Morales-Mávil, 2013), vegetated dunes (Whitmore and Dutton, 1985), and little to no development or recreational activity (Weishampel et al., 2003; Zavaleta-Lizárraga and Morales-Mávil, 2013). Though nesting has been observed on highly developed beaches (Shamblin et al., 2015), lighting from development can deter nesting and cause disorientation of hatchlings (Witherington, 1992; Salmon and Witherington, 1995; Salmon et al., 1995; Fuentes et al., 2016; Price et al., 2018).

Beaches on the three DOI properties are more remote and primitive and are less heavily visited by the public. The remoteness of the properties may attract green turtles to nest

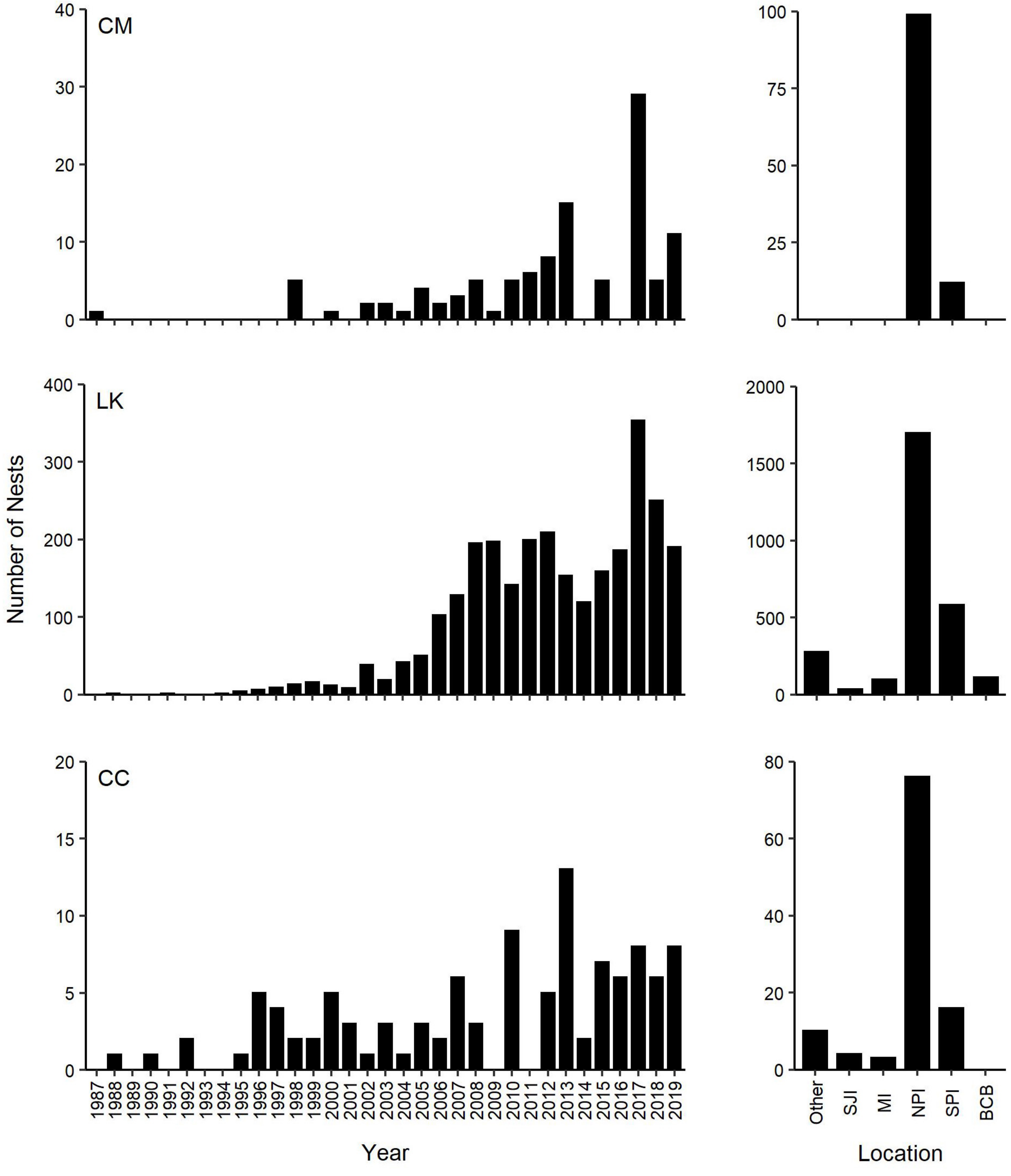

FIGURE 5 | Nesting trends of green (CM, *Chelonia mydas*), Kemp's ridley (LK, *Lepidochelys kempii*), and loggerhead (CC, *Caretta caretta*) turtles in Texas, United States between 1987 and 2019, with total documented nests each year and total numbers of nests documented on specific Texas beaches. Other: All other Texas beaches where green turtle nesting activity has not been observed that are monitored annually for nesting activity; SJI, San Jose Island; MI, Mustang Island; NPI, North Padre Island; SPI, South Padre Island; BCB, Boca Chica Beach.

there due to nearly non-existent levels of development, light pollution, and anthropogenic disturbance (Fuentes et al., 2016). There is no road behind the dunes on most of the DOI property, so visitor activities there are limited to beach driving by 4-wheel drive vehicles, fishing, wildlife watching, and primitive camping; therefore, boating and visitation is often sparse there. Of the combined total length of 120.3 km, only approximately 1.6 km (1.0 miles) on North Padre Island in front of the PAIS Visitor

Center and Campground is mechanically raked and graded to remove marine debris and *Sargassum* spp. when large influxes periodically occur. Large items that wash ashore (i.e., logs, poles) are not removed unless they pose a safety hazard to the public, and marine debris clean-up is restricted to hand work by volunteers. But since these beaches are remote, clean-ups are not as frequent as in the developed areas.

In contrast, developed beaches on the north end of North Padre Island, south end of South Padre Island, and multiple other locations in Texas, are more accessible, manipulated, and visited by the public. Some of these beaches are reinforced with seawalls and these beaches are sometimes re-nourished. Mechanical grading and raking are routinely used to remove marine debris, trash left on the beach by visitors, and *Sargassum* spp. from the beachfront. Heavy equipment is used to remove loose sand accumulated there to facilitate beach driving, which is permitted on most Texas beaches under the Texas Open Beaches Act.

Temporal Trends and Genetic Structure

Numbers of green turtle nests recorded on the Texas coast appear to have increased from the late-1980s through 2019. However, nesting detection efforts have been incomplete through the years and the 111 nests recorded is a minimum estimate of the total number of nests laid on the Texas coast by this species. Nesting green turtles and their tracks could have been missed as a result of minimal visitation to PAIS prior to 1962 when it was designated as a unit of the National Park System. Sea turtle nest detection patrols did not begin on North Padre Island until 1986, and patrols were limited by the number and proficiency of patrollers until 1995. The documentation of five nests in 1998, and virtually none before then, is likely a result of increased patrol effort and skill. Additionally, for many years, patrols were only conducted from April through mid-July, to target Kemp's ridley nesting, and thus missed most of the green turtle nesting season, which can extend through early-October. During a three-year exploratory study beginning in 2002, patrollers found green turtle nests (n = 2) during late season surveys, indicating that patrols for this species should be extended through at least July 31. Late season, early-morning patrols were conducted on parts of North and South Padre Islands starting in 2010, but they rarely extended through the entire green turtle nesting season due to funding limitations. Biologists were watchful for nesting activity when they drove on North and South Padre Islands at night to release hatchlings, but this typically was not a full sweep of both islands and did not occur nightly throughout the green turtle nesting season. Nighttime patrols designed to detect nesting green turtles were only conducted on North Padre Island in 2018 and 2019. However, due to grant funding limitations, patrols were only conducted on a portion of North Padre Island during a portion of the nesting season.

To understand nesting trends and inform conservation efforts, the genetic population structure of green turtles nesting in Texas must be identified. It is unknown whether green turtles nesting in Texas are remnants of a formerly much larger nesting population, represent a spread of nesting from Tamaulipas and Veracruz, Mexico, or originate from elsewhere. Furthermore, it is unknown how many of the exponentially increasing numbers of juvenile green turtles now occurring in Texas waters will someday nest on Texas Gulf beaches. Recent increases in documented nests may indicate that this population is recovering from past exploitation and that western GoM beaches served as important nesting habitat for green turtles. Increases in green turtle nesting have been documented in Florida and on the Gulf coast of Mexico (Weishampel et al., 2003; Cuevas et al., 2010). However, the rate of increase in nesting in Texas is less than at these other GoM nesting beaches, which may reflect higher mortality of turtles from this population during one or more of their life stages. It is unknown why green turtle nesting is so sparse in Texas compared to nesting on GoM beaches in Mexico and Florida. It is impossible to reference historical nesting levels since overharvesting of green turtles in GoM waters prior to 1900 likely eliminated nesting activity in Texas before baseline levels could be reported. Additionally, a thriving fishing and shrimping industry in Brownsville and Port Isabel, Texas, may have killed adult green turtles in southern Texas GoM waters where shrimping intensity and sea turtle abundance were high (McDaniel et al., 2000). The industry flourished in the 1940s–1990s and in 1989, Brownsville/Port Isabel was ranked the sixth most valuable commercial fishing port in the United States and the most valuable port in the GoM (Haby et al., 1993). The port potentially sustained the largest offshore shrimping fleet in the world (Haby et al., 1993) and subsequent trawling activities likely exacerbated the precipitous decline of adult green turtles along the Texas coast. When turtle excluder devices (TEDs) were initially implemented in the United States, the opening size required in the GoM was smaller than the opening size required in Atlantic waters (Epperly and Teas, 2002). Thus, larger turtles were more at risk in the GoM until 2003, when regulations were changed requiring larger TED openings to enable escape of leatherback and all other sea turtle species in both Atlantic and GoM waters (Finkbeiner et al., 2011). However, it is unknown whether adult green turtles captured in Texas fisheries were at their foraging grounds or near their nesting beaches. Currently, there are no known adult green turtle foraging grounds along the Texas coastline.

Alternatively, nesting increases in Texas may reflect a spread of nesting northward from Tamaulipas. Although sea turtles are thought to return to their natal beaches for reproduction through geomagnetic imprinting and magnetic navigation (Brothers and Lohmann, 2018), some sea turtles have been recorded nesting on multiple beaches and colonization of nesting beaches occurs over geologic time. Rabon et al. (2003) suggested that the nesting colony of leatherbacks in Florida could have been the source population of the females that nested sporadically between 1981 and 2011 on the Atlantic coast of the United States north of Florida, which was outside the historical nesting range of this species. Carreras et al. (2018) found that sporadic loggerhead nesting events in developmental feeding grounds in the western Mediterranean may be an adaptation to changing environmental conditions and can be considered new populations in this context.

The spread of green turtle nesting northward from Tamaulipas may be a compensatory mechanism that may allow this population to adapt to changing environmental conditions (Shamblin et al., 2018). As ocean surface temperatures increase (Cheng et al., 2017), earlier nesting dates (Hawkes et al., 2007; Weishampel et al., 2010) and smaller clutch sizes (Mazaris et al., 2008) at other sea turtle nesting beaches have been observed. With rising sand temperatures, many nesting beaches are predicted to produce 100% female clutches by 2070 (Fuentes et al., 2011). Sand temperatures recorded on western GoM beaches during the Kemp's ridley nesting season (April–August) indicate that northern nesting beaches (PAIS and South Padre Island, United States and La Pesca, Mexico) are consistently cooler than southern nesting beaches in Mexico (Bevan et al., 2019). Though modeling by Pike (2013) predicts that habitat suitability in Texas is marginal for green turtle nesting, the preferential use of DOI property by nesting green turtles indicates that these areas along the Texas GoM coast are important for this species. A spread of nesting northward may be evidence that green turtles in the western GoM are able to utilize new nesting habitat as those areas become more suitable due to climatic change (Araújo et al., 2005).

The juvenile green turtle population has increased substantially in Texas since 2010. Although it originates predominantly from nearby rookeries on the western Gulf coast of Mexico (Anderson et al., 2013; Shamblin et al., 2017; Shaver et al., 2017b), more work needs to be done to determine if the nesting adults and juveniles in Texas are of the same genetic stock, and whether some individuals that use Texas waters as juveniles for foraging also use Texas beaches for nesting. Kemp's ridley is considered one genetic stock and one Regional Management Unit (RMU) (Wallace et al., 2010). Annual counts of Kemp's ridley nests in Texas and Mexico trended similarly from the 1990's through 2019, although numbers in Texas were greatly reduced compared to the numbers in Mexico (Shaver et al., 2016b; Shaver pers. obs.).

There is a slight possibility that the green turtles that have nested in Texas were from Operation Green Turtle, where over 130,000 hatchlings and eggs were shipped from Tortuguero, Costa Rica, to 17 Greater Caribbean countries from 1959 to 1968, with the goal of re-establishing decimated green turtle nesting populations (Carr, 1967; Owens et al., 1982; Bjorndal et al., 1999). Numbers released at each site were not well documented, but some hatchlings were released into the GoM in south Texas. Based on estimated age to maturity of about 23–45 years (NMFS and USFWS, 2007; Seminoff et al., 2015), green turtle hatchlings released could have reached maturity by 1987, when the first green turtle nest was confirmed in Texas.

Distinct green turtle rookeries and foraging aggregations must be conserved to effectively protect the genetic diversity of the species (Ng et al., 2017). Green turtles nesting in Texas may represent an emerging subpopulation and warrant recognition as a unique management unit separate from those nesting in Mexico, which are already being considered a unique management unit (Shamblin et al., 2017). Haplotypes CM-A1.1 and CM-A3.1 accounted for 87% of the green turtles sampled within 10 Florida rookeries (Shamblin et al., 2015). Haplotype frequencies were strongly partitioned by latitude and supported recognition of at least two management units based on a genetic break between rookeries separated by a 1 km wide inlet (Shamblin et al., 2015). This population structure was reassessed using the mitochondrial microsatellite short tandem repeat (mtSTR), which further identified four management units in Florida instead of two and demonstrated discrete fine-scale natal homing to island groups (Shamblin et al., 2020). Further study is needed to identify the degree of demographic partitioning among green turtle rookeries along the western GoM coast. Depending on the results, preservation of green turtle nesting in Texas may be vital to conserving rare haplotypes only found in a new management unit there, or in the broader GoM unit shared with Mexico.

Conservation Implications

North and South Padre Islands are the epicenter of sea turtle nesting in the northwestern GoM. All green turtle, hawksbill, and leatherback nests confirmed in Texas, 84.5% of loggerhead, and 81.5% of Kemp's ridley nests confirmed in Texas through 2019 were located there (Shaver et al., 2016b, 2019a; Shaver and Frandsen, 2019; Shaver pers. obs.). The concentration of green turtle nesting on DOI property on these islands will aid with conservation of this nesting population in the northwestern GoM into the future. DOI properties have prohibitions against future development and restrictions on the activities allowed within their boundaries, whereas development continues on the northern end of North Padre Island and the southern end of South Padre Island. Interestingly, PAIS was initially planned to include all but 22.5 km on the northern end of North Padre Island and 22.5 km on the southern end of South Padre Island, which would be reserved for development (Jones, 1999). Although only a small portion of South Padre Island was preserved within PAIS when it was established (Jones, 1999), over the last 60 years several land parcels on South Padre Island have been added to the Laguna Atascosa and Lower Rio Grande Valley NWRs, now achieving much of the initial intended protection through a mosaic of DOI lands.

The Archie Carr National Wildlife Refuge was established to protect important nesting habitat for the largest nesting rookeries of loggerhead and green turtles on the United States Atlantic coast (Weishampel et al., 2003). About 70.6% of North and South Padre Island is currently preserved as PAIS and NWR, and though these properties were not established to help conserve sea turtles, as green turtle and Kemp's ridley nesting has increased on the northwestern GoM coast, these properties have become an important sanctuary for sea turtle nesting. The continued purchase of additional parcels of undeveloped land on South Padre Island, and transfer of those parcels to a NWR, could benefit green, Kemp's ridley, and other sea turtles nesting on South Padre Island by establishing a unified nesting habitat with North Padre Island, similar to the Archie Carr NWR, but for the western GoM.

Establishment of a Marine Protected Area (MPA) surrounding this unified nesting habitat would also help protect green turtles and other marine species from various anthropogenic threats occurring there. Nearshore GoM waters off south Texas are critical for multiple life stages of multiple sea turtle species (Shaver, 1992; Plotkin et al., 1993; Shaver et al., 2005, 2013a,b, 2016a, 2017a, 2020b). On 10 July 2019, a green turtle mating pair was observed off the coast of South Padre Island (Mariana Devlin, pers. comm., Sea Turtle, Inc., South Padre Island, Texas, United States). Turtles foraging off the Texas coast are threatened by shipping, commercial fisheries, oil and gas platforms, surface oiling, hypoxia (Hart et al., 2018), entanglement in marine debris and ghost fishing gear (Purvin et al., 2020), and continued illegal red snapper (*Lutjanus campechanus*) fishing practices in south Texas (Shaver pers. obs.). In addition, Texas hosts the longest-term land-based recreational shark fishery in the United States (Ajemian et al., 2016). MPA's, if managed and enforced appropriately, can benefit mobile, wide-ranging species and prevent further decline of their populations (Doherty et al., 2017).

The large stretch of undeveloped coastline protected by DOI on North and South Padre Islands could help absorb future changes in shorelines and sea turtle nesting distributions along the western GoM coast due to climate change. Sea level is projected to rise in the GoM over time and at PAIS, sea level is projected to rise 0.46–0.69 m by 2100 (Caffrey et al., 2018). Some important green turtle nesting beaches in the Caribbean are already eroding and being destroyed (Zavaleta-Lizárraga and Morales-Mávil, 2013). In contrast, parts of PAIS accrete sand, with the greatest accretion measured at the center of the park (Pendleton et al., 2004; KellerLynn, 2010). With no development on the beach, the coastline of the DOI properties on North and South Padre Islands can be allowed to move as the beach is eroded or accretes over time. In contrast, at other areas where seawalls, hotels, residences, and other structures line the beach, great lengths are undertaken to maintain the beachfront through sand re-nourishment and other practices. Developed beaches (particularly those with hotels) have been shown to be the most vulnerable to sea-level rise (Fish et al., 2005), indicating that the substantially developed northern end of North Padre Island and southern end of South Padre Island may no longer contain viable nesting habitat in the future.

If the population of green turtles that nests in Texas continues to grow, there could be a surge in nesting in Texas within the next few years as has been documented on the closest other green turtle nesting beaches in the GoM, in Mexico and the east coast of Florida. Though the magnitude of historic nesting in Texas is unknown as late-season patrol effort (July–October) was not conducted with regularity until 2010, and predominantly from North Padre Island (including PAIS) to South Padre Island, data collected from 2010–2019 establishes a baseline for comparison of future nesting levels. However, these estimates only provide minimum estimates of green turtle nesting activity on the south Texas coast and nighttime patrols targeting green turtle nesting were only conducted in 2018 and 2019 on a portion of North Padre Island during a portion of the green turtle nesting season due to grant funding limitations.

This study defined the temporal and spatial trends of green turtle nests confirmed in Texas, which is the first step needed for developing a monitoring and protection program. We recommend that systematic nighttime patrols be instituted on North and South Padre Islands through the green turtle nesting season (June though early-October), to locate, document, and protect nesting green turtles and their nests. Additionally, these nighttime patrols will protect the females and nests of the other GoM species that nest later in the year than Kemp's ridley turtles. Leaving nests unprotected allows mammalian predators to develop habits of nest predation (Pritchard and Marquez, 1973; Worth and Smith, 1976) and associate females and their tracks with a reliable food source, which has led to predation upon the smaller Kemp's ridley nesters at PAIS (Shaver et al., 2020a). Non-nesting emergences should also be documented and tracked through the potential incubation and hatching seasons, to confirm whether they are actually non-nesting emergences or nest sites. On-going daytime patrols conducted from April through mid-July that target Kemp's ridley nesting would not enable detection and protection of nesting green turtles, and would only enable location of green turtle nests during first patrols of the morning in June and early July, and opportunistically during release of hatchlings and through reports from the public. Continued data collection through a systematic program will be essential for developing an accurate assessment of trends and demographics for the population of green turtles that nest in Texas. Continued detection, documentation, and protection efforts will aid with recovery efforts for this threatened species as well as for the other four GoM species that utilize Texas for nesting. Preservation of this genetic stock is vital to population viability. If this green turtle population is a shared stock with Mexico, this highlights the critical need for international collaboration across political boundaries. However, this stock is still poorly defined and could be a rare remnant, essential for preservation of the species.

DATA AVAILABILITY STATEMENT

The datasets presented in this article are not readily available as National Park Service (NPS) policy prohibits disclosure of endangered species location data, and we are unable to provide the GPS locations of the nesting activities presented in the article. Requests to access the datasets should be directed to DS, donna_shaver@nps.gov.

ETHICS STATEMENT

The animal study was reviewed and approved by National Park Service Institutional Animal Care and Use Committee.

AUTHOR CONTRIBUTIONS

DS conceived the study and methodology and acquired funding. DS, HF, JG, and CG provided resources and wrote and reviewed the original draft. DS, HF, and CG performed the data analysis. CG created the figures. All authors contributed to the article and approved the submitted version.

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An Interview-Based Approach to Assess Angler Practices and Sea Turtle Captures on Mississippi Fishing Piers

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During 2010–2015, the Mississippi Sea Turtle Stranding and Salvage Network (STSSN) documented 1,073 sea turtles, primarily juvenile Kemp's ridleys (*Lepidochelys kempii*), incidentally caught by recreational anglers. Due to increases in interactions, an angler interview survey was conducted during 2013 at six Mississippi fishing piers. Anglers were interviewed about fishing practices and sea turtle interactions. Interviewers conducted outreach and distributed Rehabilitation Hotline business cards. Angler participation was 86%, and over 60% used J-hooks and were not targeting specific species, which was similar to data collected from incidental captures reported to the STSSN. Over 58% of anglers used dead shrimp followed by cut up fish for bait. This greatly differs from STSSN reported captured sea turtles where 60% were caught on cut up fish and only 6% on dead shrimp. Over 18% of participants captured at least one sea turtle in the last 12 months. Anglers stated that nearly half of the sea turtles were taken for rehabilitation, 41% were released by the angler and 10% broke the line and swam away. Only 60% of anglers reported the capture because many were unaware they should report it. During and after the survey period, there was an increase in reported incidental captures, possibly indicating outreach is an effective means of increasing awareness and reporting. Recently, NOAA Fisheries developed a survey that can be used nationally to conduct similar research. We recommend conducting angler surveys every few years unless there is a noticeable change in incidental capture trends or angler practices.

Keywords: sea turtle, incidental capture, fishing pier, angler survey, outreach, recreational angler, bycatch, Kemp's ridley

INTRODUCTION

Although the Mississippi (MS) coast is small with only 71 km of general coastline, the highly productive waters of MS Sound draws anglers from all over the state and the rest of the country (National Marine Fisheries Service, 2016). To provide access to fishing and other coastal marine resources, MS has over 200 public access points such as fishing piers, boat launches, and marinas[1] in its three coastal counties. Access points increased following destruction of most

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[1] https://gis.dmr.ms.gov/PublicAccess/

fishing infrastructure by Hurricane Katrina in 2005 (Abbott-Jamieson and Ingles, 2015), and are relevant because recreational anglers in MS more than doubled from 2005 to 2015 (National Marine Fisheries Service, 2016, 2017). Piers and marinas are frequented by anglers whose fishing gear hooks many species of fish, sharks, and also sea turtles (Lyn et al., 2012; Coleman et al., 2016b). From 1998 to 2009 there were a total of ten reported sea turtle incidental captures in MS (Sea Turtle Stranding and Salvage Network [STSSN][2]). However, beginning in 2010, the number of incidental sea turtle captures reported by recreational anglers began to rise considerably (Lyn et al., 2012; Coleman et al., 2016b). Whether the increased numbers were due to actual increases in numbers of captures, or rather increased awareness to report the captures is unknown. The increase occurred the same year as the *Deepwater Horizon* oil spill which resulted in hundreds of sea turtle strandings along the MS coast and considerable media attention. These data were collected through the National Oceanic and Atmospheric Administration (NOAA) STSSN, which works to document sea turtle strandings from Maine to Texas (TX). During 2010–2015, the STSSN documented 1,073 incidentally caught sea turtles along the MS coast (**Figure 1**), primarily caught from 29 different access points.

The majority of incidental captures in MS from 2010 to 2015 were juvenile Kemp's ridleys (89%) (*Lepidochelys kempii*) (STSSN[2]), which are the smallest and most endangered of all sea turtle species (Marquez, 1994; Caillouet et al., 2018; Wibbels and Bevan, 2019). Neritic zones in the Gulf of Mexico and western North Atlantic Ocean represent important foraging habitats for Kemp's ridleys (National Marine Fisheries Service, U. S. Fish and Wildlife Service, and SEMARNAT, 2011). Satellite telemetry has shown the northern Gulf of Mexico as a primary foraging ground for Kemp's ridleys (Shaver et al., 2013, 2016), and, specifically, the MS Sound represents an important recruitment and developmental habitat (Coleman et al., 2016a). This species was on the brink of extinction in the 1970s and 1980s, but it experienced a population recovery due to intense management and conservation efforts (National Marine Fisheries Service, U. S. Fish and Wildlife Service, and SEMARNAT, 2011). The higher number of turtles, combined with an increased number of anglers using recently constructed piers in coastal MS, may have resulted in the increases in incidental captures. Due to the high number of interactions, a pilot survey was developed in 2013 by NOAA's National Marine Fisheries Service (NOAA Fisheries), NOAA's MS Laboratories (MS Labs), and the Institute for Marine Mammal Studies (IMMS) to collect data on angler fishing practices and sea turtle interactions. Each survey concluded with outreach efforts aimed to educate anglers and curtail incidental captures. The ultimate goal was to determine if mitigation measures could be developed to minimize the number of recreational hook and line captures on MS fishing piers.

MATERIALS AND METHODS

To address the sudden rise of incidental sea turtle captures in MS, NOAA, and IMMS created a pilot survey with several objectives. The first was to gather data on angler practices and experiences on MS coastal access points, and the second was to determine frequency of both sea turtle incidental captures and reporting of captures to local agencies. The survey also served as

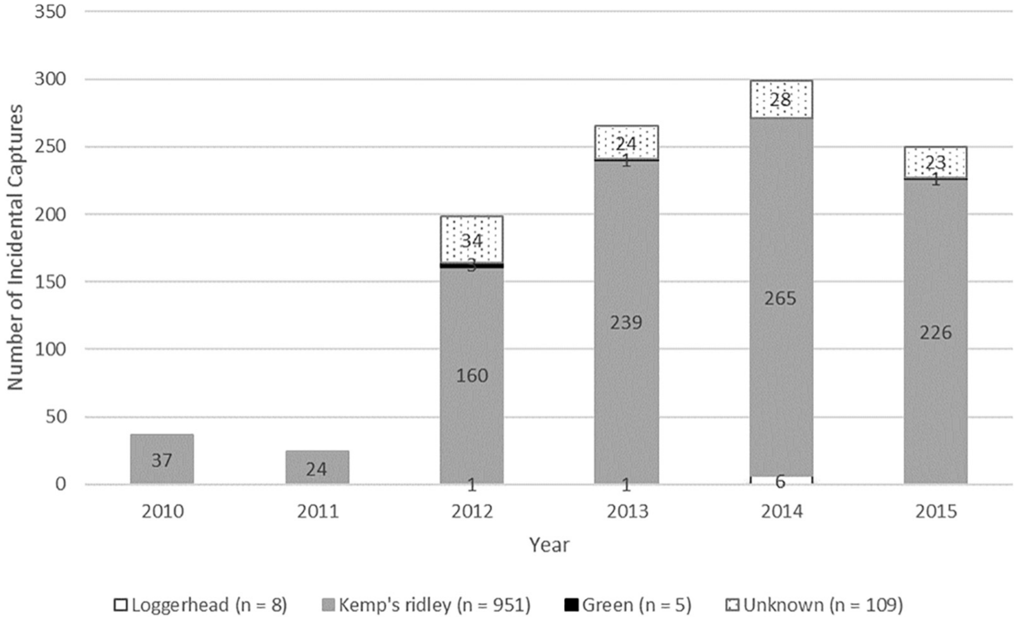

FIGURE 1 | Reported sea turtle species (*n* = 1,073) caught on hook and line by recreational anglers fishing on Mississippi piers from 2010 to 2015. Source: (NOAA Sea Turtle Stranding and Salvage Network [STSSN], https://grunt.sefsc.noaa.gov/stssnrep/).

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[2] https://grunt.sefsc.noaa.gov/stssnrep/

an educational outreach tool to inform anglers about procedures they should take if they hooked a sea turtle.

Study Sites

Six fishing sites (**Figure 2**) were selected along MS's three coastal counties. Sites were selected based on several factors including availability (many fishing piers and marinas in western MS were destroyed in 2012 storms), location, type of fishing access point, and number of previously reported incidental captures. If possible, the site with the highest number of incidental captures in each county was selected and also sites with zero or low reports to allow for comparison. Reported incidental captures at the sites ranged from zero to 56 reports (prior to the start of the survey). Sites included four fishing piers, a fishing bridge and a former marina. Jackson County piers included Pascagoula Beach Park Pier (PB; 30° 20.595 N, −88° 32.019 W; 305 m long), Chester M. McPhearson, Jr. Pier (CM; 30° 24.31 N, −88° 49.768 W, 165 m long) and the Ocean Springs Fishing Pier (OS; 30° 24.681 N, −88° 50.484 W; 402 m long) which opened in February 2012. Harrison County contained the two largest sites in the study. The newly constructed Old Biloxi Fishing Bridge (OBB) (30° 23.792 N, −88° 51.552 W) opened on April 30, 2013 and had reported incidental captures within 2 weeks. The OBB is 1,433 m long, has two lanes of traffic, sidewalks and lighting. The second site in Harrison County was the old Broadwater Marina (BW; 30° 23.503 N, −88° 57.760 W) site. The Broadwater Marina was destroyed in 2005 during Hurricane Katrina but the land is still accessible to anglers by vehicle and offers over 2,100 m of water access. Hancock County had the highest number of reported incidental captures at the survey start time. However, the Washington Street Fishing Pier (WS; 30° 18.137 N, −89° 19.642 W) was the only site selected because the other piers in Hancock County were still closed due to damage from Hurricane Isaac in 2012. The WS was also damaged in Hurricane Isaac and was closed from August 2012 through early June 2013. The WS has a 110 m fishing pier but also has an expansive parking area with fishing access and two jetties which add an additional 450 m of fishing access. In February 2012, informational signs about sea turtle incidental capture, handling, and reporting were placed on any MS fishing piers not already equipped with signs.

Angler Survey

The MS Fishing Pier Angler Survey Cover Sheet (**Supplementary Table 1**) and Angler Survey (**Supplementary Table 2**) were designed based on similar surveys conducted by the Chicago Zoological Society/Sarasota Dolphin Research Program and the NOAA Fisheries Southeast Regional Office. The survey was designed using established methods (Robson and Jones, 1989) and incorporated a variety of questions to assess MS angler fishing practices and sea turtle interactions. All documents

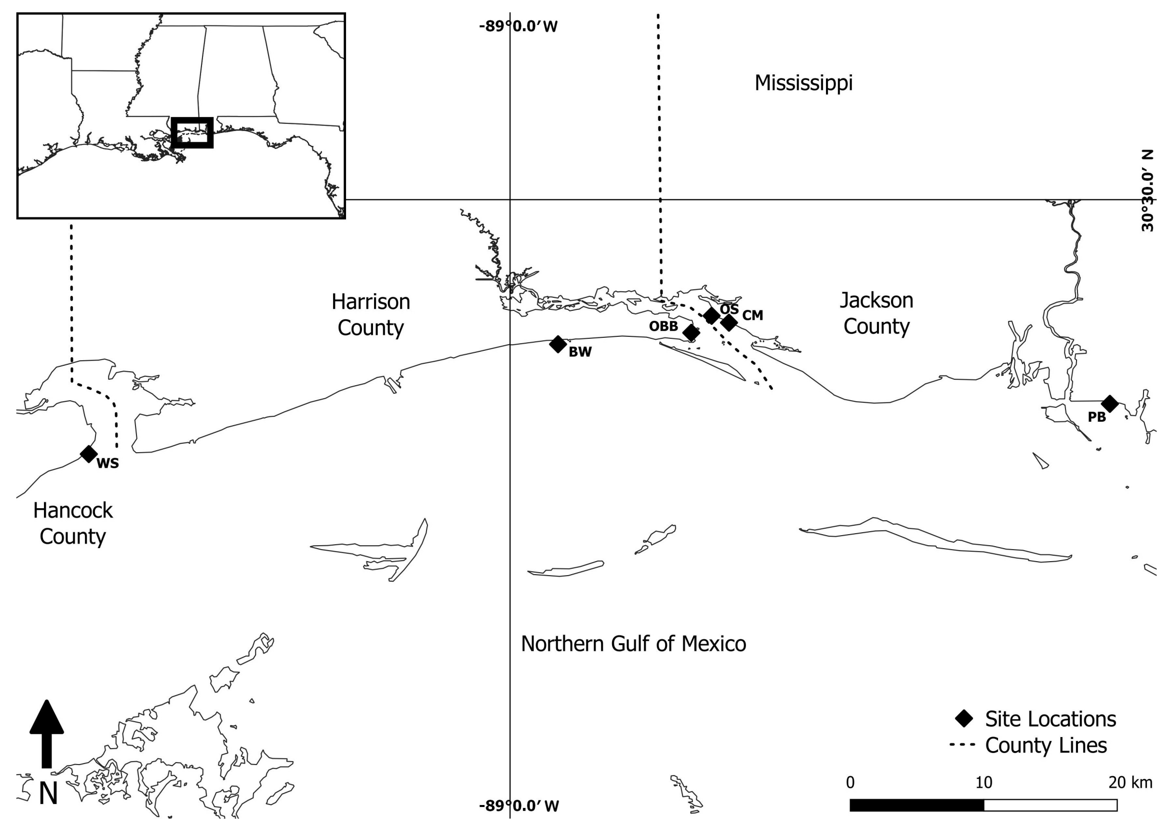

FIGURE 2 | Fishing sites selected for Mississippi angler surveys. Washington Street Pier (WS), Broadwater Marina (BW), Old Biloxi Fishing Bridge (OBB), Ocean Springs Fishing Pier (OS), Chester M. McPhearson, Jr. Pier (CM), and Pascagoula Beach Park Pier (PB).

have undergone independent review pursuant to the Paperwork Reduction Act (PRA) of 1995 (44 U.S.C. 3501 et. seq.), OMB Control Number 0648-0774, and are compliant with The Privacy Act of 1974 (5 U.S.C. 552a). Collection of these data on sea turtle interactions in the pier-based recreational fishing sector is necessary to fulfill statutory requirements of the Endangered Species Act (16 U.S.C. 1531 et. seq.). All recorded data were entered and archived in a Microsoft^{TM} Access database.

Angler Interviews

Preceding the start of the survey, interviewers read a statement identifying that they were working with NOAA Fisheries and the IMMS to conduct a research study on angler fishing practices, the information collected would be combined with responses provided by other recreational anglers and used only for scientific research, statistical and publication purposes. Anglers were advised the survey would take about 5 min, participation was completely voluntary and all answers were confidential. No minors were interviewed for this study and no personally identifiable information was recorded. Lead researcher contact information was available upon request if participants had questions about the research or respondent rights.

Prior to conducting the interviews, eight staff and interns were trained to deliver the survey in a consistent manner to ensure standardized measurement (Fowler, 2014). Interviewers received training on survey objectives, and sea turtle outreach information, and were supervised during initial surveys to ensure consistency. All interviewers were also trained on how to safely handle an incidentally caught sea turtle, in the event that one was hooked while interviewers were present at fishing locations. Interviewers were equipped with survey materials, Rehabilitation Hotline business cards, and large plastic bins to safely transport a sea turtle, if necessary.

Interviews were conducted one-on-one by staff and interns from MS Labs and IMMS. These were done opportunistically (due to staff availability) from late June through September 2013, and occurred on weekends and week days. Starting time (morning, midday, and evening) and survey site varied to achieve a representative sample (Fowler, 2014). Interviewers documented wave height and tidal conditions, number of anglers and lines in the water and number of anglers declining to participate. The goal was to interview all anglers present at the site, if possible. If time or weather prevented completion of angler interviews, counts of anglers and lines fished were conducted for missed anglers. Anglers were asked questions such as state residency, where and when they preferred to fish, target catch, bait and hook type, fish cleaning and bait disposal practices. The final set of questions was specific to sea turtles observed or incidentally captured within the last 12 months in MS. If the angler had incidentally captured a sea turtle they were asked where and when the most recent capture occurred, interaction type (hooked or entangled), outcome of the capture (line broke, turtle released, turtle taken to rehabilitation facility) and if the angler reported the capture to the stranding network or state agency.

Interviews concluded with angler outreach where anglers were told about sea turtles found in MS waters, fishing practices that can reduce interactions (i.e., do not cast in the direction of a sea turtle or discard unused bait in the water), and what to do if they accidentally caught a sea turtle. This included advice to immediately call the rehabilitation center hotline, do not pull a sea turtle up by the line but instead use a net or walk it down to the beginning of the pier, and do not cut the fishing line and release the animal. Business cards with the rehabilitation center hotline number were distributed and advised to be placed in anglers tackle boxes, wallets, or glove boxes since vehicles were often in close proximity to anglers. Typical interviews and outreach lasted 5 to 10 min but frequently took longer as anglers were interested in learning about sea turtles and sharing stories of incidental captures.

Sea Turtle Incidental Capture Data Collection

Beginning in 2012, the MS STSSN introduced the Sea Turtle Incidental Capture Intake Form (STICIF) to collect information on fishing gear and interaction type. This was collected in addition to the standard STSSN data (e.g., date, location, species, size, etc.). When an angler reported an incidental capture they were asked about fishing practices such as target species, hook type, and bait type used at time of capture. Details on interaction type (i.e., hooked, entangled), gear location (i.e., tongue, esophagus, beak) and outcome (i.e., released by angler, rehabilitated and released, died) were recorded by the veterinarians and staff at IMMS upon admission into rehabilitation. STICIF data from 2012 to 2015 were then compared to angler survey results.

RESULTS

Study Sites

The six selected piers comprised 45% of reported incidental captures prior to the start of the survey, and 53% of reported captures post survey. From 2010 to 2015, the WS pier followed by BW site had the highest numbers of reported captures, 254 and 160, respectively (STSSN[2]). Anglers interviewed also reported catching the majority of sea turtles at these two sites but reported more captures at the BW site than the WS pier. The PB site, which had zero reported incidental captures prior to the survey, had 19 reported captures post survey through 2015. The other sites (CM, OS) with low reports pre survey (9 total) continued to have low numbers post survey, 12 additional reports. Site size did not have any apparent influence on the numbers of incidental captures.

Angler Demographics

Surveys were conducted on 28 days at 81 site visits over the 3-month period. Angler and line counts were completed at 91% of site visits. Interviewers observed 1,042 anglers fishing using 1,283 fishing poles. The majority of anglers were observed at the two largest fishing sites, OBB (44%, *n* = 459) and BW (24%, *n* = 246). Over half (63%) of the site visits were conducted Monday through Thursday. Although only 37% (*n* = 30) of site visits were Friday through Sunday, 42% of surveys (*n* = 160) were completed during weekends. Over 54% of anglers (*n* = 565) were fishing during a falling tide followed by nearly equal numbers fishing during high (20%, n = 211) and rising (18%, n = 186) tides, and only 8% of anglers (n = 82) were fishing during low tide.

Anglers had a high willingness to participate, resulting in 382 completed surveys from 534 anglers approached. During the survey period, 15% (n = 79) of anglers approached had already participated in the survey and were not interviewed a second time. Only 12% of approached anglers (n = 63) declined to answer survey questions and 2% (n = 10) of anglers did not participate due to language barriers. Therefore, only 14% of approached anglers were unwilling to participate resulting in 86% of anglers participating. The majority of anglers surveyed (89%, 336 out of 377 responses) were from MS, 83% were from the three coastal counties. Anglers from Louisiana (LA), Alabama (AL), and Florida (FL) comprised 5% of anglers surveyed. Almost half of the anglers interviewed reported they fished year round. Although seasonal fishing also occurred, 36% fished primarily in summer, 13% in spring, 5% in fall, and only 1% in winter. Few respondents were "new to fishing" (15%) or "occasional" (1–15 times per year) anglers (8%). The majority were experienced anglers who fished 16–50 days (25%) or more than 50 days per year (52%). Time of day anglers reported fishing varied for most (43%) although ∼38% of anglers preferred to fish in the morning. A preference for all day fishing was reported 19% of the time and ∼11% of respondents reported fishing in evening or night hours.

Unused bait was discarded into the water by 44% (n = 163 of 374 responses) of anglers surveyed and sometimes discarded 12% (n = 44) of the time. The remaining 45% (n = 167) of anglers either said they fished until all of the bait was gone or kept it for another day. While bait was discarded into the water nearly half of the time, that was not the same for fish discards. Most anglers surveyed (86%, n = 318 of 371 responses) did not clean fish at the fishing piers or discard carcasses into the water. Although, the few anglers who cleaned carcasses on the pier discarded those remains 85% of the time.

Angler Survey and STSSN/STICIF Comparisons

Most anglers surveyed (65%, n = 247) were not targeting a specific fish species. Those that were targeted were drum (14%, n = 53), primarily red drum (*Sciaenops ocellatus*) or black drum (*Pogonias cromis*), and trout (Sciaenidae) (11%, n = 41), speckled trout (*Cynoscion nebulosus*) or sand seatrout (*C. arenarius*). Even fewer anglers targeted sharks (Carcharhinidae), flounder (*Paralichthys* sp.) or other species (≤4% each). Over 63% of anglers (n = 239) reported using J-hooks and 22% (n = 84) reported using circle hooks. Considerably fewer anglers used kahle hooks, jigs and other hook types (**Table 1**). Those results were very similar to STICIF data collected at the time of incidental capture during 2012–2015. Those data found J-hooks comprised over half of documented captures, followed by circle hooks, kahle hooks and other types of gear (**Table 1**). Overall, an average of 58% of anglers interviewed were using dead shrimp (*Penaeus* sp., range: 28–73%) followed by cut up fish (21%, range: 3–69%) for bait and 10% (range: 0–13%) of anglers used live shrimp (**Table 2**). Results for individual piers varied considerably, 69% of anglers on the WS pier and 48% of anglers on PB pier used cut up fish as their primary bait. Mullet (*Mugil cephalus*) and Atlantic croaker (*Micropogonias undulatus*) were the most common fish used as cut bait. Dead shrimp was the primary bait used at the remaining sites. According to the STICIFs, over 60% of sea turtles were caught by anglers using cut up fish and only 8% on dead shrimp (**Table 2**). Mullet and Atlantic croaker were still the top species consumed by sea turtles at fishing piers, according to STICIF data. Bait data were not available for 23% of sea turtle captures.

TABLE 1 | Hook type used by recreational anglers during the 2013 Angler Survey and 2012–2015 sea turtle incidental captures.

Hook type	2013 Angler survey (n = 378)	2013 STICIF (n = 262)	2012–2015 STICIF (n = 1,008)
Circle	22%	17%	16%
J-hook	63%	52%	54%
Jig	3%	0%	0%
Kahle	6%	7%	4%
Other	4%	1%	1%
Treble	1%	0%	1%
Unknown	0%	23%	24%

Incidental capture data from Sea Turtle Incidental Capture Intake Form (STICIF) used by the MS Sea Turtle Stranding and Salvage Network.

TABLE 2 | Bait type used by recreational anglers during the 2013 Angler Survey and 2012–2015 sea turtle incidental captures.

Bait type	2013 Angler survey (n = 378)	2013 STICIF (n = 262)	2012–2015 STICIF (n = 1,008)
Crab	1%	2%	2%
Cut fish	21%	69%	63%
Dead shrimp	58%	8%	8%
Live fish	2%	2%	1%
Live shrimp	10%	1%	0%
Other	8%	5%	4%
Unknown	0%	13%	21%

Incidental capture data from Sea Turtle Incidental Capture Intake Form (STICIF) used by the MS Sea Turtle Stranding and Salvage Network.

Sea turtles were observed swimming near fishing piers by 37% of anglers surveyed (n = 139), and 28% of anglers (n = 104) we spoke to reported they saw someone catch a sea turtle within the last 12 months. During the last year, 18% of anglers (n = 66) had personally caught one sea turtle and some reported capturing multiple sea turtles. Anglers reported the majority of sea turtle captures (75%) occurred between June and August. Results are similar to STSSN data (n = 1,073) where 80% of captures occurred in May through August with an additional 10% of captures reported in September. According to the MS STSSN[2], all sea turtles captured and measured (n = 876) were juveniles or sub-adults [range 19.5–72.5 cm straight carapace length (SCL)]. The mean SCL for Kemp's ridleys, loggerheads (*Caretta caretta*) and greens (*Chelonia mydas*) was 31, 36, and 33 cm, respectively.

The anglers interviewed reported that most sea turtles were hooked (94%) by the fishing gear and 3% were entangled in the line. Some sea turtles (3%) were both hooked and entangled in the line. Data regarding specific hook location were not collected. STICIFs documented similar trends. Not all anglers were available for interview when responders arrived to pick up the incidentally caught sea turtle. As a result, approximately 12% of interaction types were unknown. Of those captures where STICIF data are available (*n* = 1,012), the majority (84%) of sea turtles were hooked, 2% were entangled and only 1% were both hooked and entangled. Most sea turtles (92%, *n* = 737) were hooked while actively targeting the bait and only 8% (*n* = 63) were externally foul hooked. The esophagus was the most common (57%) internal hook location followed by unspecified mouth areas (17%). Most sea turtles were foul hooked in the flipper (*n* = 52, 83%). Interviewed anglers in our study stated that hooked sea turtles broke the line and swam away in 11% of the incidents. Many anglers (41%) released the sea turtles at the fishing pier while others (48%) called the stranding hotline so the sea turtle could be taken to IMMS for rehabilitation. Surveyed anglers said they reported the incidental capture 60% of the time, therefore, nearly half of incidental captures beginning summer 2012 to summer 2013 were undocumented. During angler outreach, interviewers learned that many anglers were unaware that sea turtles were in MS waters or that they should report incidental captures.

DISCUSSION

The interactions between sea turtles and commercial fishing has been studied extensively (Henwood and Stuntz, 1987; Poiner and Harris, 1996; Sasso and Epperly, 2006) but limited information is publicly available for sea turtle interactions with recreational hook and line fisheries. The TX STSSN has documented recreational captures since the early 1980s (Cannon et al., 1994), and Rudloe and Rudloe (2005) reported on Kemp's ridleys incidentally captured by Florida (FL) anglers from 1991 to 2003. Incidental captures have occurred along both the Gulf of Mexico and western North Atlantic coasts (STSSN[2]). Observations in MS were similar to those in Virginia (VA) where incidental captures increased from 2013 to 2017 and Kemp's ridleys were the dominant species captured (Rose et al., 2018). It is likely that incidental captures are also unreported because anglers are either unaware, unable or unwilling to report the incident. The Federal Kemp's Ridley Recovery Plan identifies the reduction of hook and line interactions as a high priority action (National Marine Fisheries Service, U. S. Fish and Wildlife Service, and SEMARNAT, 2011). A nearly eightfold increase in reported incidental captures in Mississippi in 2012 (**Figure 1**) prompted the development of the STICIF to gather data on hook and line captures. However, data on angler practices must also be obtained in order to determine if mitigation measures could be developed to minimize the number of recreational hook and line captures.

Data from the MS STSSN and STICIF indicated incidental captures in MS were similar to those in VA, TX, and FL. Juvenile Kemp's ridleys (20–40 cm SCL size range) were the dominant species captured in all locations (Cannon et al., 1994; Rudloe and Rudloe, 2005; Seney and Musick, 2005; Rose et al., 2018). Although crustaceans, mainly crabs, are known as the primary diet for Kemp's ridleys, fish bait was heavily consumed in all locations (Cannon et al., 1994; Rudloe and Rudloe, 2005; Rose et al., 2018). Diet studies and necropsies of stranded Kemp's ridleys also indicate that fish, likely bycatch discards, are a common prey item (Stacy, 2015; Ramirez et al., 2020). However, regional differences did exist because angler practices often vary by location and target species. In VA, squid was the primary bait type for anglers and the majority of hooked turtles (Rose et al., 2018). In MS, squid was rarely used as bait on fishing piers. In both MS and VA, J-hooks were the most commonly observed hook type followed by circle hooks (Rose et al., 2018). Based on our survey results, the most promising mitigation measure to reduce sea turtle incidental captures is to limit or eliminate the use of fish as bait. There was a notable difference between the bait type used by anglers interviewed (dead shrimp) and the bait type used by anglers that incidentally caught sea turtles (dead fish). This idea is supported when individual fishing sites were examined. Anglers interviewed at WS, were primarily using fish as bait, which may explain the high number of incidental captures at this location. Anglers at BW, second highest reported captures, reported using dead shrimp (44%) and fish (31%). During 2012–2015, 635 sea turtles were captured by anglers using dead fish as bait versus only 81 sea turtles caught on dead shrimp. However, this would likely not be favored by the fishing community and prove very difficult to enforce. It would also not reduce foul hooking interactions. Anglers could be encouraged to use non-stainless steel or barbless hooks, especially during spring and summer when turtles are present (Coleman et al., 2016a), and according to our findings, anglers are most likely to be fishing. Areas with fishing piers should promote the safe handling of captured sea turtles and reporting of captures so animals can receive proper medical attention. The IMMS has successfully rehabilitated and released 96% of incidentally captured sea turtles (Coleman et al., 2016b). Many of these sea turtles had multiple ingested hooks indicating that they were previously captured (Heaton et al., 2016). Depending on the hook location, medical intervention, if available, is necessary to decrease the likelihood of a mortality.

The STSSN has no way of knowing how many incidental sea turtle captures go unreported annually, however, since 2013 the number of sea turtles released by anglers on site has decreased over time. According to the STSSN, in 2012, 18% of incidentally caught sea turtles were released by anglers or broke the line and swam away. Our 2013 Angler Survey included outreach and education at the end of every interview to ensure that anglers were aware of what to do if they caught a sea turtle and who to call to report the incident. During discussions with anglers, interviewers learned that many of the anglers did not know they should report all sea turtle incidental captures. The number of reported sea turtle incidental captures increased throughout the survey period and continued into the fall; according to the STSSN, 2013 had the highest number of reported captures to date (*n* = 265). Post survey, reports occurred from every site, including PB, which had zero reports prior to our survey. Three times more incidental captures were reported to the STSSN in August through October 2013 than in the three previous years. The following 2 years also had high reported incidental captures of 250 or more. Anglers began reporting sea turtle incidental captures when the line broke and the sea turtle swam away. Outreach efforts likely helped contribute to this increase in reported captures and sea turtles receiving treatment and rehabilitation for any injuries.

The 2013 pilot survey was one of the first attempts nationally to obtain information from anglers regarding fishing practices and sea turtle interactions on fishing piers. Since sea turtles are a protected species we were not sure if anglers would be willing to discuss past interactions. This created the potential for social desirability bias among respondents, especially in regards to sensitive questions such as asking respondents if they reported incidental sea turtle captures (Connelly et al., 2012). Techniques such as randomized response or having participants self-administer sections of the questionnaire (Nederhof, 1985) could address biases in future studies. We had an 86% response rate; on average only one angler (range 0–9) refused to participate at each site. Therefore, anglers were willing to participate and the majority of anglers answered all questions. Only questions regarding discarding unused bait and location of fish cleaning were not answered by all anglers. Many federally funded surveys strive for response rates of 75–80% (Draugalis et al., 2008; Hendra and Hill, 2019) and those targets were exceeded in this survey. Staff and intern availability limited the survey to summer months and opportunistic rather than standardized sampling design. Although the timing was ideal to match up with when anglers are most likely fishing (according to our findings), and sea turtles are present in MS waters (Coleman et al., 2016a). Interviewers even encountered 15% of anglers that had already participated in this study. In the future it would be useful to conduct Angler Surveys in the spring, fall, and winter months to both compare against and confirm these preliminary findings.

The incidental capture of juvenile sea turtles by hook and line, and the impacts of those captures are not documented as consistently as sea turtle strandings. It is recommended that stranding networks conduct outreach and education in areas where sea turtles are likely to interact with recreational anglers. Implementation of the STICIF by all STSSN partners would greatly increase our knowledge of factors associated with sea turtles feeding on fishing piers. Since 2013, the original survey has been amended and improved. The success of this pilot survey resulted in NOAA Fisheries developing a survey and instruction manual[3] that can be used by other states and organizations to conduct similar research in their respective areas. Since recreational interactions have increased, funding is becoming available to study this issue. The Region-wide Trustee Implementation Group (TIG) noted projects that "Reduce sea turtle bycatch in pier- and shore-based recreational fisheries by evaluating, developing, and implementing conservation measures (Approach 4: Technique 1)" were considered a priority area for Region-wide TIG restoration consideration[4]. By expanding the survey regionally or nationally, data can be compared to determine if trends exist throughout the Gulf of Mexico and Atlantic states. Other stranding networks are now using the STICIF and results could be compared to angler surveys. The combination of these two data sets could allow managers to determine types of mitigation measures that could be implemented to reduce the number of sea turtle incidental captures on fishing piers.

Angler surveys likely only need to be conducted every few years unless there is a noticeable change in incidental capture trends. The number of reported incidental captures in MS in 2014 (n = 299) and 2015 (n = 250) were consistent to the previous years (2012–2015 mean = 255) before drastically falling from 2016 to 2019 (averaging 24 captures annually). It is unknown whether this decrease was due to lower populations of immature Kemp's ridleys in the MS Sound, decreased numbers of sea turtles feeding at fishing piers, a need for regular angler outreach or a recent hesitance of recreational anglers to report captures. During 2012–2019, documented sea turtle strandings in MS also varied greatly from as low as 68 in 2015 or as high as 213 in 2013 with an annual mean of 142. Interestingly enough, a large-scale mortality event occurred in Kemp's ridleys in 2010, and the population trajectory has not recovered from pre-2010 estimates (Gallaway et al., 2016; Caillouet et al., 2018). Instead, annual nesting numbers have shown fluctuations since 2010, and these fluctuations may indicate that this species has reached carrying capacity within the Gulf of Mexico, potentially because of decreased prey population levels (Gallaway et al., 2016; Caillouet et al., 2018). These decreased prey population levels (particularly blue crabs) could have partially provided impetus for immature Kemp's ridleys to forage around recreational fishing piers. Nevertheless, the recent decline in reported incidental captures could be a reflection of decreased nesting numbers, given the 2–4 years of lag time for immature individuals to recruit to neritic habitats. This may be the case in 2017, which had both low stranding and incidental capture numbers. During 2016–2019, the annual stranding average was 132 animals, suggesting that sea turtles are still present in the MS Sound. If incidental capture numbers continue to be low throughout MS, researchers should determine if recreational anglers are still willing to report incidental captures by initiating another Angler Survey and outreach.

DATA AVAILABILITY STATEMENT

The datasets generated for this study are available on request to the corresponding author.

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[3] https://www.fisheries.noaa.gov/national/marine-life-distress/sea-turtles-and-recreational-fishing

[4] https://www.gulfspillrestoration.noaa.gov/2019/09/submit-your-ideas-region-wide-trustee-implementation-group-restoration-planning

ETHICS STATEMENT

The studies involving human participants were reviewed and approved by the United States Office of Management and Budget via the Paperwork Reduction Act (PRA) of 1995 (44 U.S.C. 3501 et. seq.), OMB Control Number 0648-0774. Written informed consent for participation was not required for this study in accordance with the national legislation and the institutional requirements.

AUTHOR CONTRIBUTIONS

MC and AC contributed conception and design of the study. VD conducted the fieldwork. MC wrote the first draft of the manuscript. VD and AC wrote sections of the manuscript. All authors contributed to manuscript revision, read and approved the submitted version.

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SUPPLEMENTARY MATERIAL

The Supplementary Material for this article can be found online at: https://www.frontiersin.org/articles/10.3389/fmars.2020.00655/full#supplementary-material

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BRIEF RESEARCH REPORT
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First Spatial Distribution Analysis of Male Sea Turtles in the Southern Gulf of Mexico

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In the Gulf of Mexico, the bulk of published studies for sea turtles have focused on northern (United States) waters where economic resources are centered, with fewer studies in the southern portion of the basin, resulting in significant knowledge gaps in these underrepresented areas. Similarly, publications on adult sea turtles are dominated by research on females that come ashore to nest and can be readily studied (e.g., through the collection of biological samples and the application of satellite-telemetry devices), whereas information on adult male sea turtles is scarce. The goal of this paper is to begin filling these knowledge gaps by synthesizing available data on adult male sea turtles in the southern Gulf of Mexico. We used satellite-telemetry, boat- and drone-based surveys, and stranding records combined with ocean circulation modeling to better understand the spatial distribution of male loggerhead (*Caretta caretta*), green (*Chelonia mydas*), hawksbill (*Eretmochelys imbricata*), and Kemp's ridley (*Lepidochelys kempii*) sea turtles in the southern Gulf of Mexico. These spatially explicit analyses will provide context for opportunistically collected data on male sea turtles and better contribute to the management and restoration of sea turtle populations that use the Gulf of Mexico. Moreover, this synthesis can serve as a launching point for directed studies on male sea turtles in this region.

Keywords: numerical simulations, satellite tracking, reproductive individuals, stranding, spatial ecology

INTRODUCTION

Though sea turtles have been intensively studied for decades, major knowledge gaps persist that limit the ability to prioritize conservation plans (Bjorndal et al., 2011). These gaps primarily arise from differences in the ease in which scientists can study certain parts of the sea turtle life-cycle (Hamann et al., 2010; Hays et al., 2016). Sea turtles nest on sandy beaches at tropical, subtropical, and temperate latitudes. After nesting, adult females return to the sea and their offspring incubate in egg chambers before hatching and then immediately migrate offshore (Bolten, 2003). A large portion of the juveniles returns to coastal habitats as they grow and, upon reaching maturity, return to the vicinity of their natal site to reproduce (Bowen et al., 1996). Research has focused mostly on nesting beaches (where scientists can easily access turtles on land) and is weighted toward regions where economic resources are centered (locations of relative wealth where scientific endeavors are prioritized and infrastructure exists to support research). Thus, knowledge gaps tend to exist for the demographic segments of sea turtle populations that are exclusive to marine habitats (Godley et al., 2008) and in areas where there is less economic development.

Within the Gulf of Mexico (GoM), information on sea turtles is predominantly on adult females, eggs, and hatchlings, and centered in the northern portion of the basin (Valverde and Holzwart, 2017). Thus, information on in-water life-stages of sea turtles in the southern GoM is particularly scarce. Focusing on areas associated with the reproduction of a species is important and continued work on nesting beaches is needed. However, potentially problematic knowledge gaps associated with reproduction in sea turtles involve adult males (Hamann et al., 2010). In contrast to the relative ease to access reproductive females, adult males occupy mostly offshore neritic and oceanic habitats, which are more complicated to access (Hatase et al., 2002; Plotkin, 2003; Schofield et al., 2017). Due to the complexity and cost of in-water research, and the low-profile behavior of adult males, less is known about their reproductive cycles and dynamics. Published studies have reported some behavioral features such as that males and females frequently occur at the same foraging areas, males display mating site fidelity, they likely spend less time away from their residency areas, undertake shorter migrations than females, and likely breed annually (Fitzsimmons et al., 1995; van Dam et al., 2008; Hays et al., 2010; Varo-Cruz et al., 2013). However, much more research on male demographic parameters, habitat use, and movements are needed to complete the integrative population analyses necessary for restoring sea turtle populations, particularly in underrepresented regions such as the southern GoM.

In this context, a better understanding of the spatial ecology of males would provide a foundation for designing conservation plans that explicitly account for males within a region harboring some of the largest nesting populations in the West Atlantic for at least three species (Spotila, 2004; Mortimer and Donnelly, 2008; Ceriani et al., 2019). Therefore, the objective of this study was to construct a regional panorama of this demographic segment of sea turtle populations by integrating multiple data sources including satellite telemetry, stranding records coupled with ocean/wind models, as well as boat censuses and unmanned aerial vehicle (UAV) records obtained in the southern GoM and north Mexican Caribbean.

This study represents the state of the art on male sea turtle spatial ecology in the southern GoM, provides new information for the management and restoration of sea turtle populations and serves as a launching point for other studies on male sea turtles in this region.

MATERIALS AND METHODS

Study Area

The geographic scope of this study was the southern GoM and the northern Mexican Caribbean (extreme points at 29.19°N/−96.84°W – 15.09°N/−82.82°W) (**Figure 1A**). These areas have unique biological and oceanographic conditions that influence the spatial ecology of marine megafauna (Woolley et al., 2020). Our area of study is within the Northwest Atlantic Regional Management Unit for sea turtles (Wallace et al., 2010); and in oceanic regions delimited by the Yucatan shelf and the Yucatan Current (Wilkinson et al., 2009; Uribe-Martínez et al., 2019).

Satellite Telemetry

By 2008 (Godley et al., 2008), there was only one paper on satellite tracking of male hawksbill turtles (*Eretmochelys imbricata,* $N = 8$), another on male leatherback turtles (*Dermochelys coriacea,* $N = 11$) in the Wider Caribbean (James et al., 2005; van Dam et al., 2008); and one of Kemp's ridley turtles (*Lepidochelys kempii,* $N = 11$) in the GoM (Shaver et al., 2005). In more recent years, in northwest Atlantic and Caribbean region Arendt et al. (2012) tracked male loggerheads ($N = 16$, b $N = 29$), Becking et al. (2016) tracked male hawksbills in the Lesser Antilles ($N = 2$), and Hughes and Landry (2016) tracked one male Kemp's ridley in northwest GoM. Notably, most of these tracking studies have a small sample size, a reflection of the challenge to obtain information on this demographic segment of marine turtles and that research on this topic is at the "innovation and discovery" initial phase of tracking studies (Sequeira et al., 2019).

Over 8 years (2010–2017), six adult male sea turtles [five hawksbills -*Eretmochelys imbricata (Ei)*-, and one green turtle -*Chelonia mydas (Cm)*-] were tracked from different locations in the southern GoM (**Supplementary Table S1**). All hawksbills were tagged after stranding on the beach, three of them were kept in captivity for rehabilitation in specialized hospitals for more than 1 year, and the other two received a medical evaluation and were released the same day or 1 day later. The sixth male, a green turtle, was captured by hand in a sea turtle aggregation at the northwest corner of the Yucatan Peninsula, Mexico (**Figure 1**).

Though there is uncertainty regarding whether the movements of turtles that have been exposed to human interventions are representative of counterparts that remain in the wild, there are indications that even prolonged periods of captivity may not greatly alter sea turtle behavior (Cardona et al., 2012; Lyn et al., 2012; Mestre et al., 2014; Baker et al., 2015; Kuo et al., 2017; Robinson et al., 2017; Innis et al., 2019). Obtaining

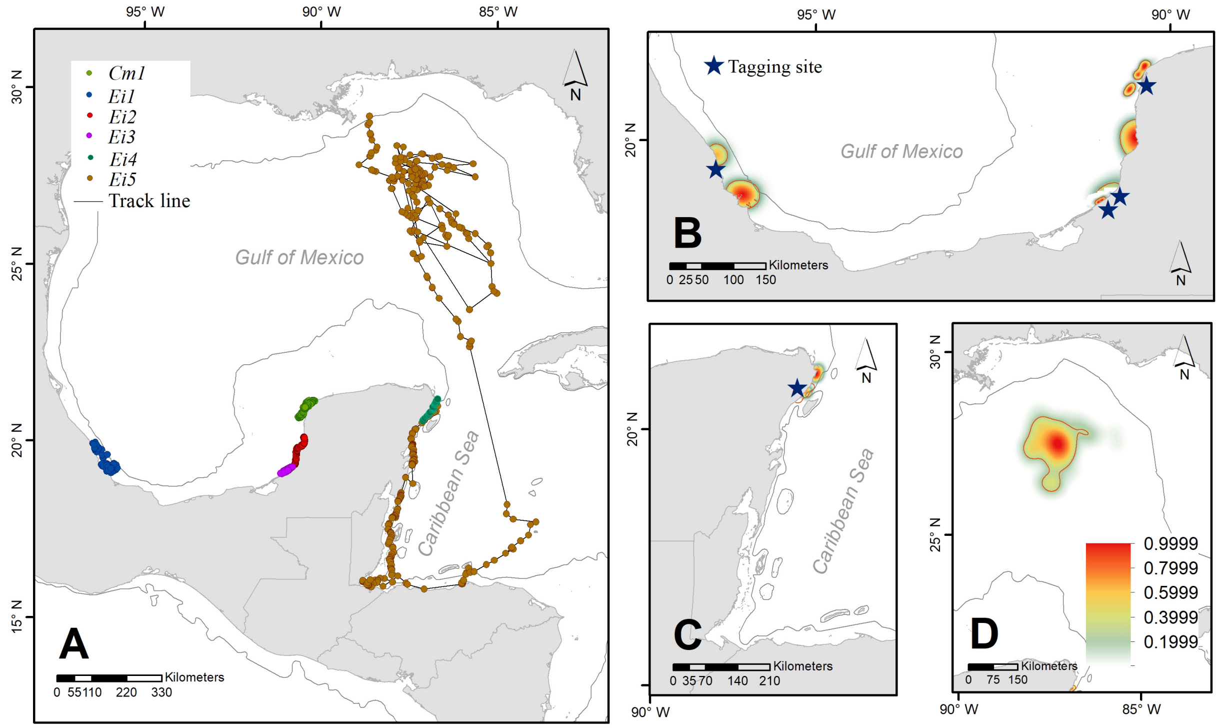

FIGURE 1 | Pathways of six satellite-tracked male sea turtles (five hawksbills and one green) after stranding, subsequent rehabilitation, and release from capture locations on shore (blue stars) **(A)**. Their home ranges (75%, red polygons) are presented together with space use distribution kernels for all individuals (*Ei*1, *Ei*2, *Ei*3, and *Cm*1) **(B)**, *Ei*4 and *Ei* 5 **(C)**, and the open ocean home range *Ei* 5 **(D)**.

individuals for this study required opportunistic sampling, using incidentally caught, recovered, and rehabilitated individuals.

Satellite transmitters were deployed on turtles following the protocol recommended by Gallegos-Fernández et al. (2018). Given the tag availability, five of these individuals were tagged with TAM4510 Telonics ARGOS transmitters and one was tagged with a Wildlife Computers Mk10-AF ARGOS transmitter. The telemetry data were filtered for quality control (*adehabitat* filters by Freitas et al., 2008), and in cases where the male displayed a discernable migratory phase (based on speed, turning angle and increasing rate of distance to release site), the data were split into separate stages (Cuevas et al., 2008, 2019). The home range isoline polygon (75%) of the aggregation data for each individual was obtained from functions of space use distribution kernels (Worton, 1989; Schofield et al., 2013). The latter analysis was done in a lattice of 1 km^2 (an area in which most of the maximum location error by ARGOS system are embedded) (Bradshaw et al., 2007; Lowther et al., 2015), and a smoothing factor (h) calculated by *ad hoc* methods (Calenge, 2006).

Beach Stranding Data and Probable Death Sites

Although data on sea turtle strandings may potentially present a biased view of distribution (e.g., they are more likely to occur when and where ocean/wind conditions are favorable to washing ashore), when they are derived from systematic long-term monitoring projects, their relevance for spatial inferences are robust (Koch et al., 2013; Nero et al., 2013; Putman et al., 2020). Given that recordings of sea turtle adult males are otherwise scarce, stranding data are particularly useful for building a regional panorama of the spatial ecology of this population segment.

We compiled stranding records of male individuals from the Mexican coasts along the western and southern GoM from 1994 through 2018. These data were obtained as part of 13 long-term sea turtle nesting beach monitoring programs, in which 525 km of the coastline are systematically monitored during nesting season, and from response units for stranding events throughout the year. The individuals were identified to species level, standard carapace morphometrics, date, time and geographic coordinates of each event were recorded. Stranding data were mapped, and their geographic locations and dates served as input for a numerical model that estimated probable death sites.

To determine where stranded turtles might have been before washing ashore, we simulated their transport using an ocean circulation model paired with satellite-based wind-fields, and a virtual particle tracking tool. This approach followed established methods where ocean current and wind models were applied to estimate the death sites of individual marine turtles (Nero et al., 2013; Santos et al., 2018a,b). We used surface currents from the GoM Hybrid Coordinate Ocean Model (GOM-HYCOM) experiment 50.1 (1994–2012), experiment 31.0 (2013–2014), and experiment 32.5 (2014–2018). These products provided surface current velocities at 0.04° × 0.04° grid resolution (~4 km) at three (1994–2012) and one (2013–2018) hour time steps. GOM-HYCOM uses data assimilation of satellite and *in situ* measurements to produce hindcast estimates of the oceanic conditions that existed in the past (Chassignet et al., 2009).

While GOM-HYCOM represents the main features of ocean circulation relevant for the movement of marine organisms (Putman and Mansfield, 2015), objects at the ocean surface will experience additional forces that are not depicted in the model (Putman et al., 2016), such as windage (direct momentum transferred from the wind to an object at the ocean surface) and Stokes drift (residual transport due to waves) (Putman et al., 2018; Olascoaga et al., 2020). The influence of these processes can be accounted for, in part, using a "leeway model," whereby a fraction of the wind velocity is added to the surface current velocity (Nero et al., 2013). To account for these effects, we used NOAA Blended Sea Winds to provide estimates of wind velocity at 0.25° × 0.25° resolution (~25 km) at 6 hourly time steps (1994 – 2018) (Zhang et al., 2006). We spatially and temporally interpolated wind velocity data to the GOM-HYCOM grid and time steps and added 3% of the 10 m wind velocities to those surface velocities of GOM-HYCOM (Putman et al., 2018). The 3% windage value that we applied falls within the range of values obtained by studies that examined the drift of sea turtle carcasses [e.g., 3.5% (Nero et al., 2013), 1–4% (Santos et al., 2018a)]. The decomposition state of carcasses can be useful to infer time spent adrift (Santos et al., 2018a,b), however, this information was not available for all stranding records and was not considered in the analysis. Rather, we assessed in which oceanic locations the turtle most likely occurred during the 5 days prior to the stranding date (Nero et al., 2013).

The combined GOM-HYCOM and NOAA Blended Sea Winds velocity fields served as inputs for virtual particle tracking simulations that were run using ICHTHYOP v.3.3 (Lett et al., 2008). We created a ~200 km buffer from the Mexican coastline across the southern GoM (18°/−98° – 24°/−86°), within which we selected 20,600 random locations to release virtual particles. We released virtual particles from these sites 5 days prior to the recorded stranding date and tracked their movement using a Runge–Kutta 4th-order time-stepping method to compute trajectories at 15-min intervals. Daily latitude and longitude were recorded for subsequent analysis. For each day of the 5-day tracking period, the distance between each virtual particle and the stranding site was measured using a custom Python script based on the pyproj module geod[1]. We determined the 100 virtual particles that were closest to the stranding site and each particle was weighted proportionally to the inverse of its distance to the stranding site (i.e., particles closer to the stranding site were weighted more heavily than those farther from the site). The weighting factor was applied to the initial release sites of those 100 particles to map the most likely locations of the stranded turtle each day of the previous 5-day period and to integrate with the other distribution data available for male sea turtles.

For analysis and spatial representation purposes, the probable at-sea locations for each of the 99 stranded males were averaged into a lattice of 10 km diameter hexagons, and the values were scaled 0 to 1 to have a standard variation range, so that both individual species distributions and cumulative values for all species together could be evaluated.

Point Location Data

In the northeastern corner of the Yucatan Peninsula, systematic surveys were conducted to record the number of in-water sea turtle individuals using small boats (27–30 ft.) in focal areas (hundreds of square kilometers). Between June and November 2016, and May through July 2017, an array of systematic line-transects adding 100 km in length was conducted (Buckland et al., 2012) in one of three different areas of interest (two at 51 and one at 31 km off the coast). This area was close to one of the largest sea turtle aggregations in the region and near the nesting beach of Isla Holbox (1,200 km were surveyed). Also, in 2019 in this same region, individual males and mating aggregations were recorded using drones at southeast Isla Mujeres. Given *a priori* knowledge of the presence of mating couples in this region, an area <10 km^2 was surveyed twice in April, when mating season started, as prospective surveys using a Phantom (Dji) drone flying at 30 m and covering a 300 m transect. Sea turtle species were identified using aerial photographs based on size, carapace color and general silhouette shape.

Because of the spatial scope of these efforts, and the variability in survey consistency of the drone surveillance, the data were not included to estimate the cumulative probability of occurrence. However, in the context of multi-source data for building the regional distribution of male turtles, they were displayed as points and polygons over the probability of occurrence map, complementing the regional panorama of the distribution of males in the southern GoM.

Cumulative Probability of Occurrence of Male Sea Turtles

As an integrative and wrapping procedure of our outputs, we used the same hexagonal lattice (10 km diameter) to transfer all calculated probabilities of space use distribution kernels and scaled the values at the hexagons in the range 0–1. This allowed us to put the drift modeling and satellite telemetry kernels in the same numerical and spatial context, and conduct an arithmetic sum of both datasets (Tougaard et al., 2008; Downs et al., 2014; Domingues et al., 2016) to obtain a final cumulative probability of occurrence of males in the southern GoM.

RESULTS

The compilation of data sets from different sources allowed us to integrate the first synthesis of the regional probability panorama of the presence of adult male sea turtles in the southern GoM. The outputs include spatially explicit information at different scales.

Satellite Telemetry

Track durations ranged from 5 to 185 days (Median = 55 days) (**Supplementary Table S1**). Five of the six tracked turtles moved close to the shoreline and stayed at nearshore residency areas

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[1] https://pyproj4.github.io/pyproj/stable/_modules/pyproj/geod.html

traveling <120 km from the site of release. The shortest distance traveled by individuals of both species was displayed by *Ei*3, moving a net distance of 10.8 km from the coast of Campeche in 55 days. Even when some tracks were very short, that minimum time was enough to show individuals moving far from their release point, like *Ei4*. *Cm1* traveled no more than 62 km from its capture/release site and remained in the region for 78 days, which we therefore assumed was its residency area (**Figure 1**).

Individual *Ei*5 traveled the longest distance, moving 775 km from Quintana Roo to an oceanic residency area in 185 days (**Figure 1**), with a home range of nearly 20,000 km^2 (**Figure 1C**). Unlike the other individuals that stayed in neritic waters, *Ei5* moved in neritic waters from June to July, and then moved to oceanic habitats. During 4 months (August–December), *Ei*5 moved inside an anti-cyclonic eddy linked to the Loop Current. Instead of leaving the Gulf of Mexico with the main flow of the Loop Current, the turtle remained within the eddy. The eddy detached from the Loop Current in November and the turtle traveled with it. By December *Ei5* appeared to have departed from the eddy and moved northwards toward the United States continental shelf when transmissions were lost (**Figure 2**).

Probable Death Sites for Stranded Individuals

The stranding dataset included 99 adult male turtles (14 loggerheads 34 greens, 33 hawksbills, and 18 Kemp's ridley), of all the stranding records, an average of 8.8% (± 2.9) were males (Tamaulipas 9.38%, Veracruz 4.9%; Campeche 9.1%; north Yucatan 11.8%) and there were no significant differences between states ($X^2{}_{(d.f\ =\ 3,\ n\ =\ 99)} = 3.1$, $p = 0.3765$). Most of them came from Campeche (53.33%), followed by the northern Yucatan Peninsula (17.14%), Veracruz (17.14%), and Tamaulipas (12.38%). Green turtles comprised 38.09% of stranding records, followed by hawksbills (18.86%), Kemp's ridleys (17.14%), and loggerheads (13.21%). The average curved carapace length of the stranded individuals was 92.51 cm ± 11.27 (loggerheads), 91.43 cm ± 17.35 (green turtles), 79.07 cm ± 10.50 (hawksbills), and 65.67 cm ± 3.50 (Kemp's ridleys). Though size is not entirely indicative of maturity, these sizes fall into the range of what are likely reproductive adults (Goshe et al., 2010; Bell and Pike, 2012; Bjorndal et al., 2014; Avens et al., 2015).

Drift modeling indicated that the most probable locations of turtles in the 5 days prior to stranding tended to be close to shore, over the continental shelf, and relatively near the points of stranding (**Figure 3**). Along the north and west coasts of the Yucatan Peninsula, there are high probabilities of the presence of male sea turtles of these four species. A similar scenario occurs in central and north Veracruz (**Figure 3E**). The standard deviation of these probabilities is mainly dictated by the combination of both high and low values near shore (**Figure 3F**).

Cumulative Probability of Occurrence of Male Sea Turtles

We found high probabilities of space use at the northeast and west coast of the Yucatan Peninsula, together with south Veracruz and Tamaulipas (**Figure 4**). Locations of observed sea turtle mating occurred close to the areas identified as high cumulative probability of male sea turtle occurrence.

This integration of data supports and strengthens local empirical knowledge on the location of mating aggregations close to shore, and together with a few directed surveys supports the hypothesis of sea turtles mating near their nesting beaches, as in other parts of the world (Miller, 1997). An apparent exception, however, is for hawksbills as no reported evidence exists on locations of consistent mating aggregations in the southern GoM.

DISCUSSION

Satellite Telemetry

As reported in other studies, tracking rehabilitated sea turtles is a reliable alternative to the complex and often expensive enterprise of capturing in-water males (Mestre et al., 2014; Hughes and Landry, 2016; Robinson et al., 2017, 2020). To what extent subsequent behavior is influenced by exposure to humans remains an important question as it has implications for how conservation efforts for sea turtles are prioritized (Caillouet et al., 2016). The data we present can be used in future meta-analyses that address that issue. Nevertheless, our findings suggest: (1) favorable outcomes can occur for individual sea turtles rehabilitated in local specialized hospitals (i.e., Xcaret Park and Acuario de Veracruz), and (2) the tracks of rehabilitated individuals can contribute to the knowledge of the spatial ecology of male sea turtles.

Our results show that male sea turtles are prone to stay in neritic habitats nearshore of mating areas, and conduct very short migrations when these neritic habitats are located in wide, productive areas (such as those in the Yucatan Peninsula) (van Dam et al., 2008; Hughes and Landry, 2016). Another relevant result is that males occupy some of the same habitats as post-nesting females in the Yucatan Peninsula (Cuevas et al., 2008, 2019; Méndez et al., 2013), and present broadly similar movement behaviors as those observed in loggerhead males (Varo-Cruz et al., 2013; Hughes and Landry, 2016).

Male turtles in the Yucatan Peninsula may also move to oceanic habitats to feed as reported in other regions (van Dam et al., 2008; Varo-Cruz et al., 2013; Saito et al., 2015). The movement of individual *Ei5* correspond to an area dominated by the Loop Current, where intensive biological activity occurs as a result of upwelling and the accumulation of drifting material along ocean current fronts, or by eddy-induced Ekman pumping (McGillicuddy, 2016). Similar broad-scale pelagic feeding areas are reported for loggerhead females in the Atlantic (Varo-Cruz et al., 2013).

Probable Death Sites for Stranded Individuals

Strandings represent a complex interaction among anthropogenic and environmental conditions that influence mortality, the probability of washing ashore and the probability of being reported (Putman et al., 2020). Further examination of the movement of turtle carcasses in response to wind and current conditions, decomposition rate, variability in survey

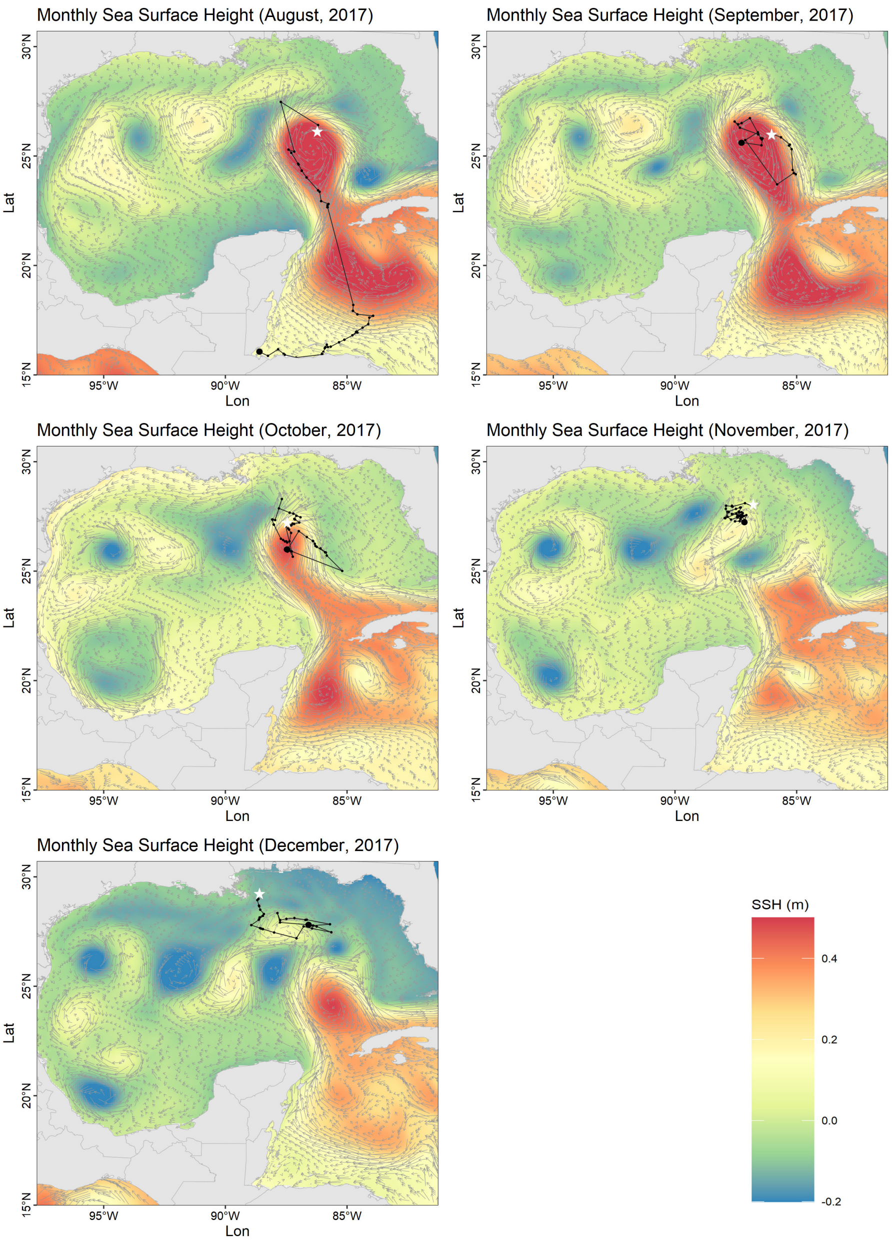

FIGURE 2 | Monthly means of sea surface height (SSH) and ocean current velocity vectors produced by Copernicus Marine Environment Monitoring System (CMEMS) (Copernicus Marine Environment Monitoring Service [CMEMS], 2020) during the oceanic movement of a male hawksbill (*Ei5*) from September to December 2017. Current direction and speed are represented by gray arrows and the sea turtle tracks are plotted as black dots and lines. Largest black dots are the start of the mapped tracking period and white stars the end.

effort, among other considerations are important for gathering more information from stranding records and numerical analyses (Nero et al., 2013; Santos et al., 2018a,b). However, even considering the present limitations of the stranding data available for synthesis here, valuable information was obtained. We showed that the peaks of stranding occurrence differed among species (April for Kemp's ridleys, May for loggerheads and hawksbills, and June for greens), possibly because of an association with the reproductive season of each species (Xavier et al., 2006; Castro, 2016; Cuevas, 2016; Delgado, 2016; Koch et al., 2016).

Based on the latter context and their sizes, we might assume that at least the larger males were in a reproductive state when they died, suggesting that the areas with the highest probabilities of occurrence (**Figure 3**) may also be mating spots. Directed *in situ* research surveys will be needed to verify those areas are occupied by adult male turtles. We already demonstrated the feasibility of implementing these strategies using water and aerial

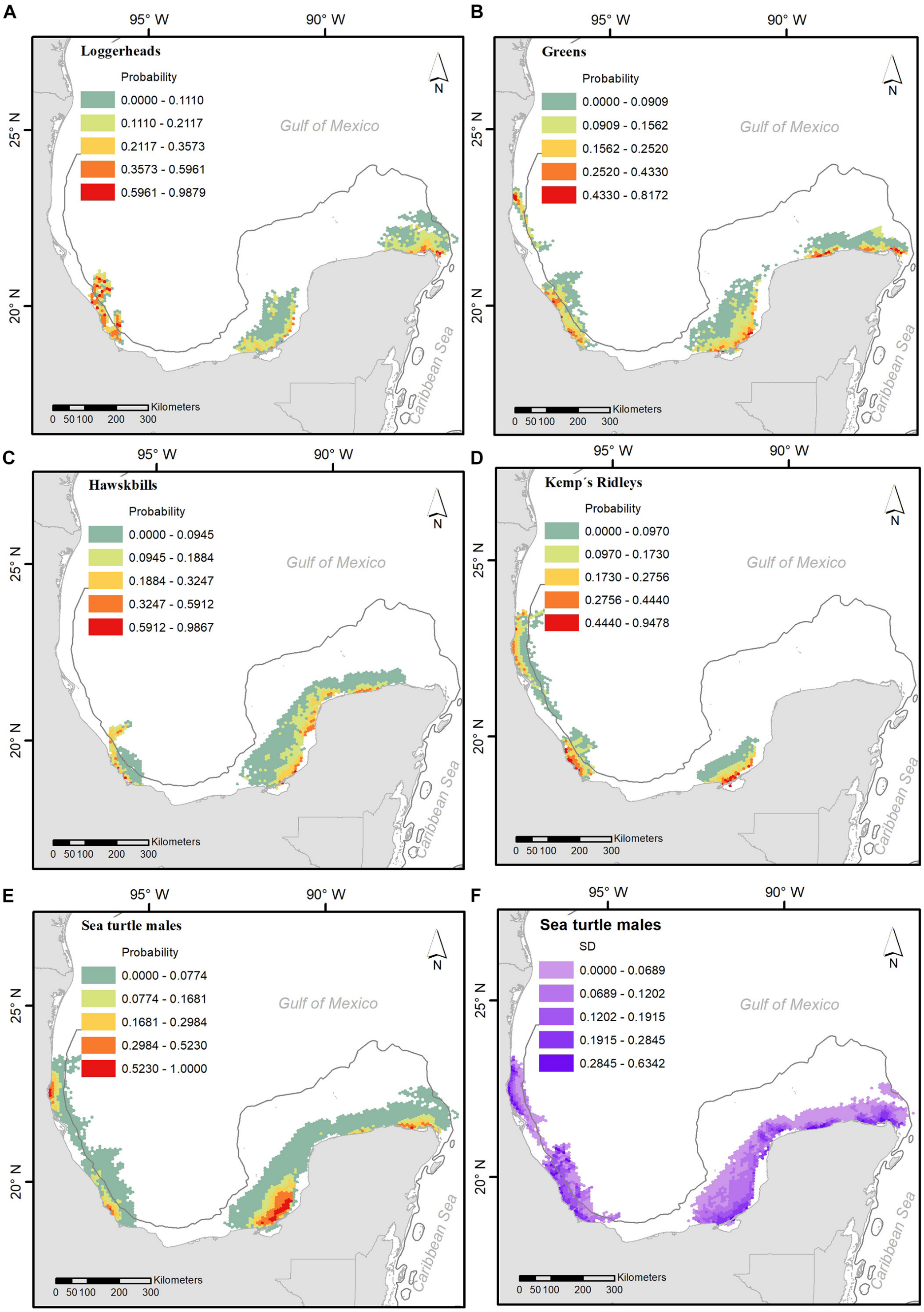

FIGURE 3 | Average probability of death site occurrence for stranding sea turtle males along the coast, for *Caretta caretta* **(A)**, *Chelonia mydas* **(B)**, *Eretmochelys imbricata* **(C)** and *Lepidochelys kempii* **(D)**; and an average of occurrence probability for all species **(E)** and its standard deviation values **(F)**.

vehicles (manned and unmanned). The areas adjacent to Isla Mujeres and Isla Holbox (17 individual sea turtles, and 16 mating aggregations of up to three turtles were recorded) are example sites for more precise, local scale, systematic in-water monitoring (**Supplementary Figures S3, S4**). Additionally, projects designed to encourage the participation of local communities to report

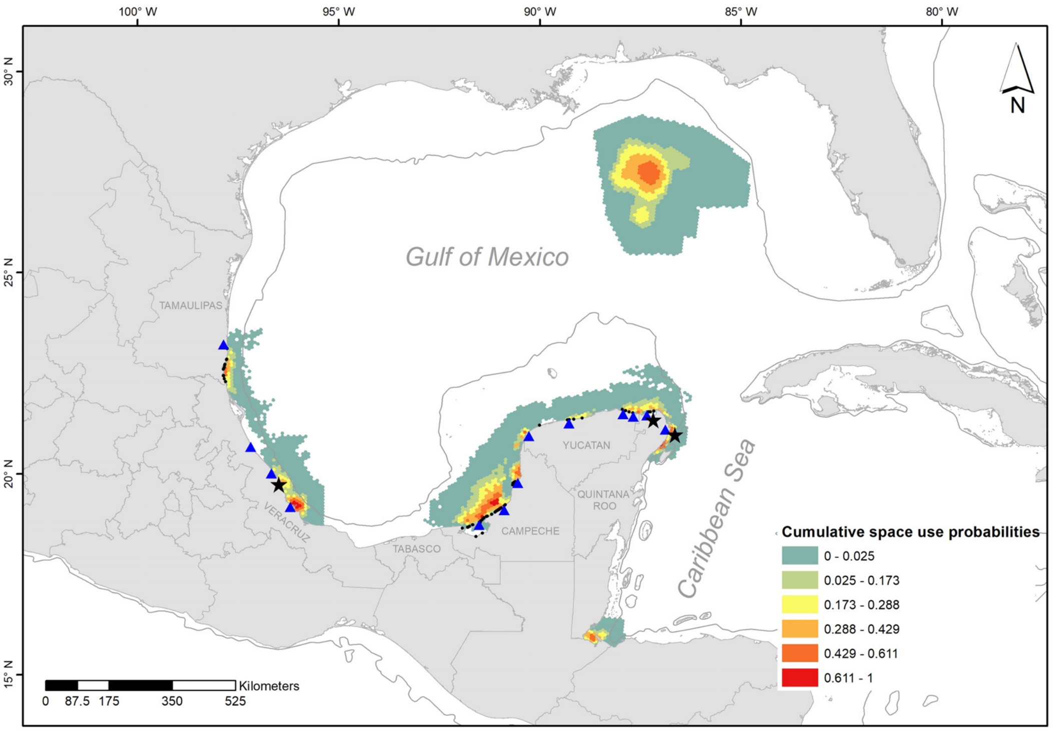

FIGURE 4 | Cumulative space use probabilities for adult male individuals of *C. caretta*, *C. mydas, E. imbricata,* and *L. kempii*. The black points on the shoreline represent the sites of stranding records, the black stars are point locations where mating couples of green and loggerhead individuals have been recorded, and the blue triangles are some of the main sea turtle nesting beaches in the region.

bycatch of male turtles such as the one in southern Veracruz, Mexico should be prioritized.

Cumulative Probability of Occurrence of Male Sea Turtles

This study contributes to filling information gaps of basic biology and ecology of these species and expands the knowledge frontier in this region. We show a spatial overlap in important areas along the coasts of Quintana Roo, Campeche, and Veracruz, where more detailed targeted research and monitoring should be implemented. In this context, the waters adjacent to Isla Holbox and Isla Mujeres in Mexico are of significant biological relevance in this region (Cárdenas-Palomo et al., 2015; Reyes-Mendoza et al., 2016), including aggregations of under studied male individuals of endangered sea turtles.

We also identified an important in-water information gap in front of Tabasco State (**Figure 4**) where there is not sea turtle nesting; therefore, no systematic surveillance exists. However, there is evidence of important in-water areas that are sensitive for sea turtles in this area (Cuevas et al., 2019). Further research is needed to understand how this region functions in the ecology of sea turtles in the southern GoM.

Finally, the spatial integration of stranding datasets from long term survey projects (more than two decades), as well as the efforts of satellite-tracking individuals in this study area, are an essential contribution to the ecological knowledge of four sea turtle species in the GoM. The synthesis of this formerly dispersed data expands our knowledge on sea turtle ecology, sets new research goals, and highlights the need for long-term monitoring efforts. It also demonstrates a critical need to formally systematize the recent in-water research efforts on male sea turtles to increase the information about this underrepresented population segment in a way that can contribute to the recovery of sea turtle populations.

DATA AVAILABILITY STATEMENT

Some of the datasets presented in this article are not readily available because of restrictions by funding sources. Requests to access the datasets should be directed to EC, amir.cuevas@gmail.com.

ETHICS STATEMENT

This work was carried out in the respect of Mexican regulations regarding the reporting of stranded dead sea turtles during beach patrolling (SGPA/DGVS/008368/18 and SGPA/DGVS/04900/19; No. SGPA/DGVS/05895/19); and those that were alive and went to rehabilitation processes were treated under the direct supervision of the Federal Attorney for Environmental Protection in Mexico, and the tracking study was performed with the permit SGPADGVS/SEMARNAT, Mexico, No. 09583/15.

In water data at Isla Holbox were collected under permit SGPA/DGVS/06712/16. No samples were used for this study.

AUTHOR CONTRIBUTIONS

EC, AU-M, SG-F, VG-H, MCLC, MALC, JT-C, RG-D-M, HA-S, RM-P, ML-H, PH-R, and JS collected the data. EC, NP, AU-M, SG-F, and JT-C performed the analyses. EC, NP, AU-M, SG-F, MCLC, and JT-C drafted the manuscript. NP, VG-H, MCLC, RG-D-M, AN-P, HA-S, RM-P, ML-H, PH-R, MALC, and JS reviewed and edited the manuscript. All authors contributed to the article and approved the submitted version.

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SUPPLEMENTARY MATERIAL

The Supplementary Material for this article can be found online at: https://www.frontiersin.org/articles/10.3389/fmars.2020.561846/full#supplementary-material

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Variation in Species Composition, Size and Fitness of Two Multi-Species Sea Turtle Assemblages Using Different Neritic Habitats

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The neritic environment is rich in resources and as such plays a crucial role as foraging habitat for multi-species marine assemblages, including sea turtles. However, this habitat also experiences a wide array of anthropogenic threats. To prioritize conservation funds, targeting areas that support multi-species assemblages is ideal. This is particularly important in the Gulf of Mexico where restoration actions are currently ongoing following the Deepwater Horizon oil spill. To better understand these areas in the Gulf of Mexico, we characterized two multi-species aggregations of sea turtles captured in different neritic habitats. We described species composition and size classes of turtles, and calculated body condition index for 642 individuals of three species captured from 2011 to 2019: 13.6% loggerheads (*Caretta caretta*), 44.9% Kemp's ridleys (*Lepidochelys kempii*) and 41.4% green turtles (*Chelonia mydas*). Species composition differed between the two sites with more loggerheads captured in seagrass and a greater proportion of green turtles captured in sand bottom. Turtles in sand bottom were smaller and weighed less than those captured in seagrass. Although small and large turtles were captured at both sites, the proportions differed between sites. Body condition index of green turtles was lower in sand habitat than seagrass habitat; there was no difference for Kemp's ridleys or loggerheads. In general, smaller green turtles had a higher body condition index than larger green turtles. We have identified another habitat type used by juvenile sea turtle species in the northern Gulf of Mexico. In addition, we highlight the importance of habitat selection by immature turtles recruiting from the oceanic to the neritic environment, particularly for green turtles.

Keywords: multi-species, neritic, Gulf of Mexico, Kemp's ridley, body condition index, sea turtle, fitness

INTRODUCTION

Habitat loss in marine environments is occurring at an alarming rate and many of these habitats are found in neritic waters (Millennium Ecosystem Assessment, 2013; Babcock et al., 2019). Mangroves have declined 35%, coral reefs have been reduced 20% with an additional 20% identified as degraded, and seagrasses have been disappearing at a rate of 110 km^2 $year^{-1}$ since 1980

(Waycott et al., 2009; Millennium Ecosystem Assessment, 2013). These losses have necessitated conservation actions for many marine species that rely on neritic habitats such as sea turtles (Sellas et al., 2005; Wakefield et al., 2011; Hart et al., 2018a). Neritic habitat plays a consistent and important role for foraging hard-shelled sea turtles (Hays et al., 2004) throughout their entire lives (Bolten, 2003; Lamont et al., 2015). Juvenile sea turtles forage in neritic habitat for a decade or longer, after undertaking an ontogenetic habitat shift from the oceanic environment (Bolten, 2003). However, different turtle species shift into different habitats. For example, hawksbill turtles typically use coral reefs whereas green turtles migrate into seagrass beds. Identifying habitats used by juvenile turtles is crucial because this life-stage is the most important to protect when trying to recover populations (Crouse et al., 1987). Managers cannot ensure that a necessary habitat is available for turtles if managers are unaware that turtles rely on that habitat. In addition, as adults, sea turtles maintain foraging home ranges that are often located in neritic waters (Hart et al., 2014; Braun McNeill et al., 2020; Gredzens and Shaver, 2020), although variation in habitat use occurs among individuals (Hawkes et al., 2007; Hatase et al., 2013; Cameron et al., 2019).

Neritic habitat is also where most anthropogenic threats occur in the oceans. The majority of oil and gas platforms are in water depths < 300 m (Muehlenbachs et al., 2013), commercial shrimping activity occurs primarily in neritic waters (McDaniel et al., 2000), vessel strikes appear to have higher mortality rates in nearshore than offshore waters (Foley et al., 2019), and because of its proximity to land, neritic waters suffer from increased levels of pollution (Fang et al., 2017). Although these activities result in broadscale impacts to habitats that most likely affect organisms on the community-level, many studies focus only on single-species (Hart et al., 2014; Eguchi et al., 2020; Ramirez et al., 2020). However, individual species respond to environmental stressors in different ways; for example, species at a higher trophic level appear to be disproportionally impacted by habitat fragmentation (Didham, 1998; Hovel and Lipcius, 2001; Layman et al., 2007; Roslin et al., 2014; Rielly-Carroll and Freestone, 2017). To identify areas that support multi-species assemblages and, as such. represent high conservation priority (Brodie et al., 2015; Rich et al., 2016), more information on habitats used by these assemblages is needed, particularly those that rely on neritic waters for survival (Easter et al., 2019).

Multi-species assemblages of marine animals have been studied, however, most research has focused on invertebrates or fish (Barnes, 2019; Moyes and Magurran, 2019; Palumbi et al., 2019). Large marine vertebrates also maintain multi-species groups (Augé et al., 2018; Drymon et al., 2020; Sutton et al., 2020) and because these species typically inhabit a higher trophic level, changes in habitat may have serious consequences. Sea turtle foraging assemblages provide the ideal opportunity to examine multi-species groups of marine vertebrates in neritic habitats (Hart et al., 2018a; Lamont and Iverson, 2018; Wildermann et al., 2019). In the Gulf of Mexico (GoM), sea turtles forage in groups that include herbivores such as green turtles (*Chelonia mydas*) and carnivores such as loggerheads (*Caretta caretta*) and Kemp's ridleys (*Lepidochelys kempii*; Lamont and Iverson, 2018; Wildermann et al., 2019). This provides us with a unique opportunity to collect information across species that may differ in their vulnerability to human disturbances, environmental change, and habitat fragmentation (Easter et al., 2019). Characterizing multi-species assemblages of sea turtles in neritic habitats can help maximize conservation dollars and prioritize restoration efforts, particularly in the GoM where restoration actions following the Deepwater Horizon oil spill are currently being conducted.

Juvenile turtles throughout the world have been shown to exhibit multi-year fidelity to foraging areas (González Carman et al., 2016; Metz et al., 2020; Siegwalt et al., 2020), which further highlights their importance in the conservation and recovery of these species. In Australia, green turtles and loggerheads remained in foraging habitats for 17 and 23 years, respectively. The size of these home ranges varies greatly among species and studies, most likely a factor of study methods used, duration of tracking periods, and environmental conditions (Metz et al., 2020). For example, mean size of core use areas for green turtles in Northeast Florida was 4.4 ± 1.3 km^2 (Wildermann et al., 2019) while along the Texas coast, the mean size for green turtles in summer was much larger (125.4 ± 47.5 km^2) and when examining only winter core use areas, the mean size in Texas was even greater (543.7 ± 230.6 km^2). This variability illustrates the importance of understanding habitat use by turtles under wide array of conditions and habitat types.

In this study, our goal was to characterize immature sea turtles of three species that were captured at two sites in the GoM: a sand bottom habitat in nearshore GoM waters and seagrass-dominated habitat in a coastal bay. We compared species composition and size classes of individuals captured at both locations. In addition, we calculated a body condition index (BCI) for captured turtles as a proxy for fitness to assess whether resource quality between sites affected turtle fitness (Bjorndal and Bolten, 2010; Peig and Green, 2010).

MATERIALS AND METHODS

St. Joseph Bay (SJB), located in northwest Florida (**Figure 1**) in the northern GoM, covers approximately 26,000 ha. It has a mean depth of 7 m, the greatest depth being 13.3 m in the northern end and the shallowest being <1 m in the southern end (Florida Department of Environmental Protection, 2008). Seagrass beds cover approximately 16% of the bay (4,000 ha) and are most abundant in the shallow southern end (Florida Department of Environmental Protection, 2008). The most abundant seagrass species is *Thalassia testudinum.* The sediments in St. Joseph Bay are predominantly sand, sand-silt-clay, sandy clay, and silty clay (Florida Department of Environmental Protection, 2008). The bay is considered one of the most pristine coastal bays in all of Florida. The high salinity and clear water found immediately nearshore in a shallow, low-energy environment in the northern Gulf of Mexico is unique and provides for a diverse ecosystem (Florida Department of Environmental Protection, 2008). St. Joseph Bay offers some of the world's best fishing grounds for a variety of

FIGURE 1 | Location of Santa Rosa Island (SRI) and St. Joseph Bay (SJB) in Northwest Florida where immature sea turtles were captured from 2011 to 2019 (SJB) and 2014–2019 (SRI). Also included are individual images of each study site. These maps (with self-created symbols/shapes/text) were created using ESRI (Environmental Systems Resource Institute; http://www.esri.com/software/arcgis) ArcMap software, version 10.7.1. Basemap sources for all Figures, except c (terrapin), include: Esri, Maxar, GeoEye, Earthstar Geographics, CNES/Airbus DS, USDA, USGS, AeroGRID, IGN, and the GIS User Community.

species including bay scallops *(Argopecten irradians)* and these activities serve as the foundation for the economy of this area (Florida Department of Environmental Protection, 2008).

The Santa Rosa Island (SRI) site encompasses approximately 21 km of GoM coastline that is owned by Eglin Air Force Base. The nearshore sediments in this area are predominately fine silica sand (Williams et al., 2012). The study site is bordered by Okaloosa Island to the east, with the Okaloosa pier located approximately 4 km east of the study site boundary and the Destin pass approximately 8 km beyond the pier. The Destin pass serves as the entrance to Choctawhatchee Bay, which supports approximately 2,300 ha (7%) of seagrass habitat. The western end of the study site is bounded by Navarre Beach. The Navarre Beach pier is located approximately 1.4 km from the study site boundary. In addition, about 0.5 km west of the study site is the Navarre Beach Marine Sanctuary, an artificial reef that consists of 78 structures constructed of piling-mounted concrete disks located 340 feet south of the mean high tide line.

All turtles were captured between March and November 2011–2019 (SJB) and 2014–2019 (SRI). In SJB, turtles were surveyed for and captured from a boat using a set net, dip net, cast net or by hand. At SRI, turtles were surveyed for from all-terrain vehicles (ATVs) ridden on the beach. Once observed, turtles were captured using a modified set net technique. In this method, turtles were observed in nearshore waters typically less than 2 m deep and within 100 m of shore. When a turtle was observed, biologists deployed a short (approximately 20 m) set net about 100 m in front of the turtle while additional personnel entered the water behind the turtle. As the turtle swam forward to avoid the personnel approaching from its rear, it became tangled in the net. All captured turtles at both locations were individually marked with a metal Inconel tag placed along the trailing edge of each front flipper and a passive integrated transponder (PIT) tag placed subcutaneously in the left shoulder. Turtles were measured using two methodologies: (1) straight carapace length (SCL) and width (SCW) using calipers and (2) curved carapace length (CCL) and width (CCW) using a cloth tape measure. Weight (Wgt; in kilograms) was determined by placing the turtle in a harness and hanging the harness from a hand-held Pesola spring scale.

Straight carapace lengths were used in all analyses. If SCL was not gathered for an individual, CCL was converted to SCL using the following regression equations from Teas (1993):

$SCL = -1.442 + (0.948 \times CCL)$ for loggerheads

$SCL = 0.013 + (0.945 \times CCL)$ for Kemp's ridleys

$SCL = 0.294 + (0.937 \times CCL)$ for green turtles.

Body condition was calculated as Fulton's K ($BCI = \text{body mass}/SCL^3 \times 10^4$; Bjorndal et al., 2000).

A generalized linear model (GLM) was used to evaluate relationships among years, species, sites, size classes and seasons. To account for differences in life-stages within species, we placed individuals into two groups: small juveniles and large juvenile/adults. For Kemp's, small juveniles were <45 cm SCL and for greens they were <60 cm SCL. Because loggerheads were all large juveniles/adults, we did not divide them into groups. The response variables were SCL, BCI, and Wgt. We ran three univariate models on SCL, BCI, and Wgt and calculated the residuals. Using Pearson's correlation test on the residuals, we found that BCI and Wgt were not correlated ($p > 0.5$), yet SCL and Wgt were correlated for both sites ($p < 0.0001$). Hence, a 2-way MANOVA was run on the correlated responses of SCL and Wgt and an ANOVA was run on BCI. Loggerheads were dropped from the analyses because of a lack of samples at SRI ($n = 1$). We used the Wilks' Lambda statistic for the MANOVA tests. PROC GLM in SAS 9.4 was used to run the analyses and an alpha = 0.05 was established for all analyses. Models were checked for homogeneity and normality of residuals. Mean differences for main effects were compared using Tukey's test and significant interactions were compared using a Bonferroni correction test. Finally, a Log Likelihood model comparison test was used to identify the best final model for BCI.

RESULTS

From 2011 to 2019 (SJB) and 2014–2019 (SRI), 642 turtles were captured at both sites (**Table 1**). Mean water depth at capture in SJB was 1.32 ± 0.45 m (range 0.18–3.26 m) and at SRI was 1.13 ± 0.61 (range 0.60–3.66). The majority (78.0%) of turtles were captured in SJB. Captured turtles included 88 (13.7%) loggerheads, 288 (44.9%) Kemp's ridleys, and 266 (41.4%) green turtles. Of all turtles captured, we had SCL and weight for 535 (83.3%) individuals, which allowed for calculation of BCI (**Table 1**). The majority of turtles captured at both sites were juveniles. Using 87.0 cm SCL as size at sexual maturity for loggerheads (NMFS and USFWS, 2008) only 5.7% of loggerheads captured in SJB were adults. Using the minimum size of nesting Kemp's of 57.2 cm (Shaver et al., 2016) and size at reproduction for greens of 83.2 cm SCL (Goshe et al., 2010), none of the Kemp's ridleys we captured at either site were adults. We captured two adult male green turtles at SRI but all other green turtles captured at both sites were juveniles.

St. Joseph Bay

From 2011 to 2019, 501 turtles of all three species were caught in SJB (**Table 1**). Most (54.7%) of turtles were captured by hand, while 27.8% were captured in a set net, 17.0% in a dip net, and 0.4% in a cast net. Turtles were captured in every month of the year with most captured in July (17.4%) and October (18%). Mean SCL and weight for all turtles captured in SJB are presented in **Table 1** and proportion per size class in **Figure 2**. Mean recapture rate for all turtles in SJB was 10.2% and was lowest for loggerheads (5.8%) and highest for Kemp's ridleys (11.7%). Recapture rate for green turtles was 9.1%. Mean recapture interval for all turtles in SJB was 399 days ($n = 29$; SD 411.3; range 6–1,649).

Mean BCI for loggerheads in SJB was 1.46 (SD 0.20, range 0.90–1.87). Mean BCI for Kemp's ridleys in SJB was 1.46 (SD 0.22, range 0.47–3.17). Mean BCI for green turtles was 1.38 (SD 0.29, range 0.87–4.13). Mean BCI per size class for each species is presented in **Table 2**.

Santa Rosa Island

From 2014 to 2019, 141 turtles were captured off SRI (**Table 1**). All turtles (except one which was captured by hand) were captured using the modified set net technique. Turtles were captured May through October with most captures occurring in September (26.2%) and October (44.7%). Mean SCL and weight for all turtles captured in SJB are presented in **Table 1** and proportion per size class in **Figure 2**. Two of the green turtles captured at SRI were adult males; with those two individuals excluded the mean size of remaining green turtles was 29.9 cm (SD 4.86, range 22.0–55.0 cm) and weight was 3.79 Kg (SD 2.50, range 1.5–17.0 kg). Mean recapture rate for all turtles was 28.4% and was highest for green turtles (30.8%) and Kemp's ridleys (25.0%) and lowest for loggerheads (0%). Mean recapture interval was 133 days ($n = 27$; SD 176.2; range 1–724).

TABLE 1 | Characteristics of loggerhead (Cc), Kemp's ridley (Lk) and green (Cm) turtles captured in St. Joseph Bay (SJB) and off Santa Rosa Island (SRI), Florida from 2011 to 2019 (SJB) and 2014–2019 (SRI).

	SJB			SRI		
	Cc	**Lk**	**Cm**	**Cc**	**Lk**	**Cm**
Sample size	86	240	175	2	48	91
SCL (cm)	70.7 ± 12.01	36.5 ± 7.6	37.4 ± 8.87	68.3 ± 2.3	30.8 ± 7.02	30.7 ± 8.80
Weight (kg)	43.34 ± 17.01	7.46 ± 4.69	7.78 ± 5.33	39.8 ($n = 1$)	4.96 ± 3.73	4.64 ± 7.90
BCI	1.46 ± 0.20 ($n = 36$)	1.46 ± 0.22 ($n = 222$)	1.38 ± 0.29 ($n = 152$)	1.13 ($n = 1$)	1.52 ± 0.14 ($n = 46$)	1.31 ± 0.18 ($n = 77$)

This includes mean straight carapace length (SCL; ±SD) measurements, mean weight (±SD) and mean body condition index (BCI ± SD). Sample sizes for each species and each location are also included.

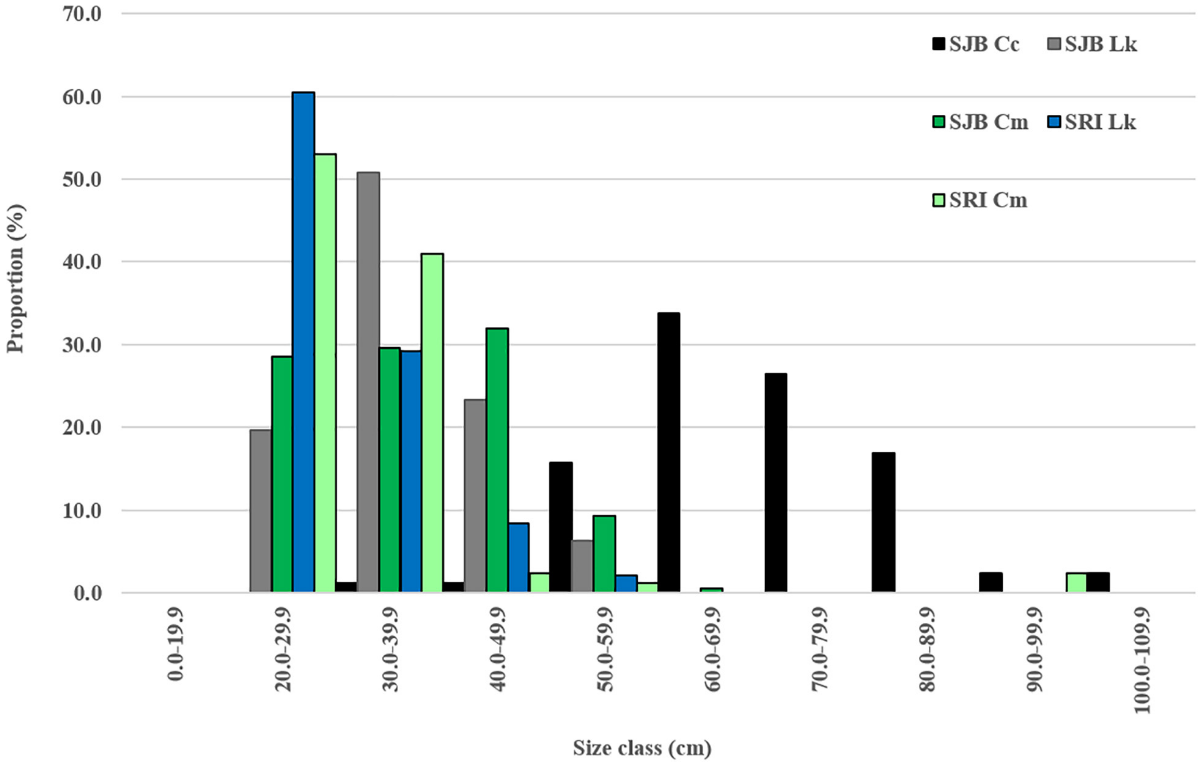

FIGURE 2 | Proportion of all captures that were loggerheads (Cc), Kemp's ridleys (Lk) and green turtles (Cm) per size class (straight carapace length in cm) at two sites in Northwest Florida: off Santa Rosa Island (SRI) from 2014 to 2019 and in St. Joseph Bay (SJB) from 2011 to 2019. Dashed vertical lines illustrate minimum size at maturity for all three species.

Of the 141 turtles captured at SRI, we had SCL and weight on 123 turtles allowing for calculation of BCI (**Table 1**). We were unable to record weight for one of the loggerheads captured at SRI therefore we were unable to include this individual in BCI calculations. As such, we also dropped the one remaining loggerhead from statistical comparisons. The 123 turtles used in statistical analyses included 46 Kemp's ridleys and 77 green turtles. Mean size of all turtles was 30.23 cm (SD 5.78, range 22.0–52.7 cm). Mean BCI per size class for Kemp's ridleys and green turtles is presented in **Table 2**.

Data Analyses

In the MANOVA, the only significant parameters were site ($p = 0.0001$), year ($p = 0.0003$), and group ($p \leq 0.0001$; **Supplementary Table 1A**). The overall model for BCI was significant ($p < 0.0001$). Of the independent variables (species, site, size class and season), the highest order significant interactions (**Supplementary Table 1B**) were species * site ($p = 0.0084$) and species * size ($p = 0.0164$). All additional comparisons were not significant. Means comparisons using Tukey's test revealed that SCL and weight were smaller at SRI than SJB. All other comparisons were not significant. Because the model suggested year had no influence on BCI, we did not adjust for year in the analyses. However, because year and size (i.e., group) was shown to influence SCL, we adjusted for those two variables in the model and found differences in SCL between sites was still significantly different.

Green turtles off SRI had lower BCI than green turtles in SJB ($p = 0.0115$). At SRI, BCI of greens turtles was lower than BCI of Kemp's ($p < 0.0001$). Among all size classes of green turtles at both sites, BCI of 20.0–29.9 and 30.0–39.9 cm SCL turtles was lower than BCI of similarly sized Kemp's ridleys (there was no difference among larger turtles). Within all green turtles (combined between sites), BCI of individuals 30.0–39.9 cm SCL was lower than BCI of individuals 20.0–29.9 cm SCL. All other comparisons were not significant.

DISCUSSION

The role neritic habitat plays in the development of immature sea turtles has been broadly acknowledged (Musick and Limpus, 1997; Bolten, 2003; Broadbent et al., 2020). However, our results highlight variability in composition and habitat use of multi-species assemblages within this zone and suggest sea turtles in the northern GoM recruit into at least two different neritic habitats: seagrass meadows in coastal bays and nearshore sand bottom habitat. This variation in habitat selection may have consequences to turtles in the form of lower fitness (Diez and Van Dam, 2002). In addition, results of this study may contribute to restoration activities currently underway in the

TABLE 2 | Body condition index (BCI), calculated as body mass/SCL^3 × 10^4, per size class (straight carapace length, SCL, in cm) for Kemp's ridleys (Lk) and green turtles (Cm) captured off Santa Rosa Island (SRI) from 2014 to 2019 and in St. Joseph Bay (SJB), Florida from 2011 to 2019, and for loggerheads (Cc) captured in SJB from 2011 to 2019. Only two loggerheads were captured off SRI.

Size classes (cm)	BCI	*n*	
30–39	1.60	1	SJB Cc
40–49	1.62	1	
50–59	1.51	8	
60–69	1.50	15	
70–79	1.33	9	
80–89	1.42	2	
20–29	1.49	47	SJB Lk
30–39	1.47	122	
40–49	1.43	44	
50–59	1.39	13	
20–29	1.41	47	SJB Cm
30–39	1.34	46	
40–49	1.37	90	
50–59	1.36	12	
30–39	–	–	SRI Cc
40–49	–	–	
50–59	–	–	
60–69	–	1	
70–79	1.13	1	
80–89	–	–	
20–29	1.54	29	SRI Lk
30–39	1.52	12	
40–49	1.41	4	
50–59	1.18	1	
20–29	1.35	41	SRI Cm
30–39	1.25	33	
40–49	1.30	2	
50–59	1.32	1	

GoM in response to the Deepwater Horizon oil spill. Many of those activities are occurring in nearshore waters; a better understanding of what habitats are important to juvenile Kemp's ridleys and green turtles can help optimize these restoration projects for juvenile sea turtles. This is particularly important considering the juvenile life-stage is the most responsive to recovery actions (Crouse et al., 1987). Although new recruits to the neritic environment must move through nearshore waters on their way to coastal bays, the long-term and consistent presence of individuals off SRI supports the idea that this area may also serve as developmental habitat for immature turtles until they reach reproductive maturity.

Immature sea turtles exhibit variability in foraging habitat selection (McClellan and Read, 2010; Seney and Landry, 2011; Lamont and Iverson, 2018; Schmid and Tucker, 2018). For example, green turtles forage in habitats ranging from tidal creeks in the Florida Everglades (Hart and Fujisaki, 2010) to pristine seagrass beds (Lamont and Iverson, 2018) to human-made and/or altered environments (Kubis et al., 2009; Eguchi et al., 2020). As such, it was not unusual for us to document immature turtles of all three species in two different habitat types in the northern GoM. Green turtles and Kemp's ridleys represented the majority of captures at both sites (82.8% in SJB; 98.6% off SRI) but loggerheads represented a larger proportion of captures in SJB (17.2%) than off SRI (1.4%). The difference in proportion of loggerheads captured may reflect dispersal patterns by hatchling loggerheads (Putman et al., 2020) or differences in recruitment by immature loggerheads (Bolten, 2003), however, it may also simply reflect variation in capture methods between the two sites. In SJB, we used a boat to survey for and then hand capture loggerheads, whereas at SRI, we conducted surveys from land. These land-based surveys limit the distance from shore at which we are able to capture individuals. Loggerheads may not travel as close to the coast as green turtles and Kemp's ridleys (Hart et al., 2018b) thereby making them less available for capture at SRI than in SJB.

The proximity of SRI to fishing piers may contribute to differential habitat use by species between the two sites, particularly for Kemp's ridleys and green turtles. Both of those species are captured frequently in recreational fishing activities from piers (Coleman et al., 2016; Cook et al., 2020) even though the prey available at fishing piers (i.e. bait) are not typical foraging items for these species (Williams et al., 2013; Ramirez et al., 2020). If juvenile Kemp's ridleys and green turtles are attracted to fishing piers as foraging locations, the presence of those structures in nearshore sandy-bottom habitats across the GoM may provide foraging sites for multi-species assemblages. The quality of that habitat may not be ideal, however, and the lower BCI we documented for juvenile green turtles at SRI versus in SJB support that theory. Further studies examining turtle use of fishing piers are needed to better understand the impacts of these structures on turtle populations.

In addition to species composition, we documented variation in size classes of turtles captured at the two sites. Green turtles and Kemp's ridleys at SRI were smaller than those in SJB. Although small individuals (<25 cm SCL) of both species were captured at SJB and SRI, a larger proportion of small individuals were captured at SRI (**Figure 2**). As with loggerheads, differences in size classes captured at both sites could reflect capture methods. Larger green turtles and Kemp's ridleys might remain in deeper waters more often than smaller individuals making them less available for capture, however, this would seemingly affect turtles in SJB also since we are typically unable to hand capture turtles in deep (>4 m) waters in SJB due to turbidity. Therefore, we suspect this difference reflects ontogenetic habitat shifts by immature turtles in the neritic environment. The smallest turtles captured at both sites are most likely new recruits to neritic habitat. Analysis of cloacal microbiome in green turtles captured at SJB and SRI showed bacterial communities of turtles at SRI were more similar to turtles captured in the oceanic environment than to those captured in seagrass habitat in SJB (Price et al., 2017), which suggests these small individuals may have recently recruited from the oceanic zone.

However, long-term recaptures (>365 days) of green turtles and Kemp's ridleys at SRI demonstrates multi-year fidelity by some individuals to that site. The longest recapture at SRI for green turtles was 388 days and for Kemp's was 724 days. Without movement data (i.e., satellite or acoustic tracking), it is not possible to say for certain that turtles did not move from SRI into seagrass habitat and back again during these time periods. Tracking studies in SJB are limited but show that distance moved from core use areas differed among species (Lamont and Iverson, 2018). Loggerheads moved a mean distance of 59.6 km from the core use areas whereas greens moved a mean distance of 14.6 km and Kemp's ridleys traveled 28.8 km. If turtles at SRI moved similar distances, they would have access to seagrass habitat in Choctawhatchee Bay (located approximately 13 km from the eastern boundary of our study site). Additional diet studies, including gut bacteria and stable isotopes (Burgett et al., 2018; Campos et al., 2019), could help clarify whether SRI serves only as a stop-over area for new recruits moving into the neritic zone or also as a long-term developmental habitat for immature turtles.

If SRI is a developmental habitat for immature turtles, it appears to provide sub-optimal foraging resources for green turtles. The BCI for green turtles was lower off SRI than in SJB, even though SRI green turtles were on average smaller than SJB green turtles, and mean BCI of smaller (20.0–29.9 cm) green turtles was greater than mean BCI of larger (30.0–39.9 cm) green turtles (see **Table 2**). Body condition index is a rough proxy for nutritional status and health (Diez and Van Dam, 2002) and our two sites differ in availability of one major source of nutrition for green turtles: seagrass. SJB supports more than 4,000 ha of seagrass while SRI has none. Diet of green turtles at SRI is unknown, however, we have observed turtles foraging on algal-covered structures and analyses of cloacal bacteria of green turtles at SRI suggested an algal diet (Price et al., 2017). Although it is not uncommon for immature green turtles to forage on algae (Bjorndal, 1980; Williams et al., 2013), growth rates of individuals in seagrass beds along Florida's east coast was higher than that of turtles using algal habitat (Kubis et al., 2009). The lack of difference in BCI for Kemp's ridleys between the two sites support this idea, as Kemp's ridleys forage on benthic invertebrates, particularly crabs (Shaver, 1991; Witzell and Schmid, 2004) that are common at both sites.

Foraging in atypical habitat does not always result in negative consequences for sea turtles. For example, hawksbills in the Bahamas foraged in seagrass beds rather than on coral reefs, however, growth rates and BCI of individuals did not differ between the two habitats (Bjorndal and Bolten, 2010). Although there is seagrass habitat in coastal bays near SRI (e.g., Choctawhatchee Bay and Santa Rosa Sound), it appears from recaptures that at least some green turtles remain off SRI rather than moving into the nearby bays. Why they choose to remain in seemingly suboptimal habitat is unknown. Off the Cape Verde Islands, Africa most adult loggerheads forage in oceanic waters even though neritic foragers were larger and laid bigger clutches (Eder et al., 2012). Eder et al. (2012) suggest these loggerheads forage in oceanic waters as juveniles and as such select that habitat as adults (Hays et al., 2010). As they mature, however, some individuals may become aware of the productive neritic habitat and move into those waters. This may be the case with immature green turtles; as they recruit from oceanic to neritic habitat, some may encounter algae resources and remain to forage whereas others do not and continue into seagrass meadows. Examination of movement patterns and diet of green turtles in these two habitats is needed to address that question.

Mean BCI for all species was within the range reported at other sites and we found no differences in BCI among species

TABLE 3 | Body condition index (BCI) values for green, Kemp's ridley or loggerhead sea turtles reported from sites throughout the world.

BCI values	Species	Size (SCL cm)	Sample size	Location	Source
1.48 ± 0.15 (1.14–2.09)	Loggerhead	45.7–77.3	45	North Carolina, United States (Atlantic)	Keller et al., 2004
1.54 (1.35–1.75)	Loggerhead	52.3–72.7	57	North Carolina, United States, (Atlantic)	Stamper et al., 2005
1.46 ± 0.9	Loggerhead	68.9 ± 3.8	5	Hawaii, United States, (Pacific)	Clukey et al., 2017
1.60 ± 0.20 (1.30–2.00)	Kemp's ridley	47.0–61.0	14	Galveston, TX, United States (Gulf of Mexico)	Bjorndal et al., 2014
1.56 ± 0.08 (1.37–1.70)	Kemp's ridley	33.6–55.8	26	Big Bend, FL, United States (Gulf of Mexico)	Perrault et al., 2017
1.14 ± 0.3	Kemp's ridley	34.6 ± 5.3	21	Texas/Louisiana, United States (Gulf of Mexico)	Swarthout et al., 2010
1.42 ± 0.02 (1.03–2.19)	Green	46.0–100.0	102	Baja California, Mexico (Pacific)	Seminoff et al., 2003
1.21 ± 0.02 (0.98–1.38)	Green	Juvenile	323	Baja California, Mexico (Pacific)	Caldwell, 1962
1.22–1.36	Green	25.3–82.3	701	Union Creek, Bahamas (Atlantic)	Bjorndal et al., 2000
1.39 ± 0.1	Green	43.9 ± 5.2	10	Hawaii, United States (Pacific)	Clukey et al., 2017
1.37 ± 0.08	Green	43.9–92.4	24	Punta Abreojos, Mexico (Pacific)	Labrada-Martagón et al., 2010
1.47 ± 0.07	Green	39.7–62.2	5	Laguna San Ignacio, Mexico (Pacific)	Labrada-Martagón et al., 2010
1.67 ± 0.06	Green	40.4–80.3	25	Bahía Magdalena, Mexico (Pacific)	Labrada-Martagón et al., 2010
1.20 ± 0.10 (1.0–1.3)	Green	29.5–77.5	93	Brazil (Atlantic)	De Deus Santos et al., 2015
1.46 ± 0.20	Loggerhead (SJB)	35.2–101.1	86	Northwest Florida United States (Gulf of Mexico)	This current study
1.46 ± 0.22	Kemp's ridley (SJB)	20.8–55.6	240	Northwest Florida United States (Gulf of Mexico)	This current study
1.52 ± 0.14	Kemp's ridley (SRI)	23.4–52.7	48	Northwest Florida United States (Gulf of Mexico)	This current study
1.38 ± 0.29	Green (SJB)	23.2–62.6	175	Northwest Florida United States (Gulf of Mexico)	This current study
1.31 ± 0.18	Green (SRI)	22.0–96.5	91	Northwest Florida United States (Gulf of Mexico)	This current study

Mean BCI values (± SD; range when available), species (green, loggerhead, Kemp's ridley), size (except for Caldwell, 1962 for which exact size data were unavailable), sample size (number of individual turtles), location (including ocean basin in parenthesis), and the source of the data.

(**Table 3**; Labrada-Martagón et al., 2010; Bjorndal et al., 2014). However, differences in morphology among sea turtle species limit among-species comparisons of Fulton's BCI (i.e., a lower BCI for green turtles as compared to Kemp's ridleys does not suggest green turtles have lower fitness than Kemp's ridleys). Fulton's BCI is based on the relationship between mass and body length. Sea turtle species differ in size and shape; for example, of the hard-shelled sea turtles, green turtles are the largest whereas Kemp's ridleys are the smallest (Wyneken, 2001). Peig and Green (2010) found Fulton's BCI produced CI's that decreased with size therefore we would expect variation in BCI among larger and smaller turtle species. Although Fulton's index has received some criticism (see Stevenson and Woods, 2017), it performed well in a comparison of different CI methods (Peig and Green, 2010). In general, body condition has been shown to be closely related to an animal's health (Peig and Green, 2009) and has been widely considered an important indication of fitness (Peig and Green, 2010). This is exemplified in the loggerhead we captured off SRI. This individual was lethargic and sent to a rehabilitation center after capture. The BCI for this individual was 1.13 compared to the mean BCI of 1.46 for loggerheads captured in SJB. The low BCI for the SRI loggerhead highlights the functionality of Fulton's BCI for this species. However, among species comparisons must consider morphological differences among those the species being examined (Peig and Green, 2010).

Body condition index for green turtles has also been linked to population density and growth rates (Bjorndal et al., 2000). As population densities increase, growth rates and BCI decrease (Bjorndal et al., 2000; Seminoff et al., 2003; Labrada-Martagón et al., 2010). It has been suggested that green turtles in SJB are reaching carrying capacity and may be a threat to the bay's seagrass beds through overgrazing (Rodriguez and Heck, 2020). However, high population densities should result in lower growth rates and BCIs (Bjorndal et al., 2000), and in our study, the BCIs we calculated for green turtles from 2011 to 2019 were similar to or higher than those reported for green turtles captured in SJB from 2001 to 2004 by McMichael et al. (2008), and for green turtles that stranded in SJB in 2010 by Avens et al. (2012; **Supplementary Table 2**). Growth rates of green turtles captured during a mass stranding event in SJB in 2010 fell within the range of growth rates reported from elsewhere in the world (Avens et al., 2012) and did not appear to decrease over time when compared to rates reported by McMichael et al. (2008). An updated analysis of growth rates for green turtles in SJB is warranted to address this question, however, the data that are currently available on BCI (this study) and growth rates (McMichael et al., 2008; Avens et al., 2012) do not support the theory that the green turtle population in SJB has reached carrying capacity.

Our characterization of these multi-species sea turtle assemblages that utilize two different neritic habitats identifies high value areas that may be targeted for conservation actions and raises questions about habitat selection by new recruits to the neritic environment, particularly for green turtles. Additional studies across the Gulf of Mexico, and other ocean basins, would increase sample sizes and clarify habitat needs for neritic turtles. Gulf-wide studies are particularly needed in light of the intense habitat restoration occurring in neritic waters. Nearshore sand bottom habitat appears optimal for immature Kemp's ridleys but less ideal for green turtles. This habitat selection may therefore have serious consequences to the fitness of immature turtle populations. This study also highlights the need for more research on diet and fine-scale habitat use to further explore these questions.

DATA AVAILABILITY STATEMENT

The datasets generated for this study will not be made publicly available. Restrictions apply to the datasets. Raw data is exempt from publication due to the sensitivity of endangered species information. Requests to access the datasets should be directed to the corresponding author. All other data used for analyses are presented in the manuscript.

ETHICS STATEMENT

The animal study was reviewed and approved by the USGS IACUC committee.

AUTHOR CONTRIBUTIONS

ML conceived of and designed the study. DJ performed statistical analyses. ML and DJ created figures. Both authors contributed to writing the manuscript, read, and approved the submitted version.

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SUPPLEMENTARY MATERIAL

The Supplementary Material for this article can be found online at: https://www.frontiersin.org/articles/10.3389/fmars.2020.608740/full#supplementary-material

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Foraging Habits of Green Sea Turtles (*Chelonia mydas*) in the Northwestern Gulf of Mexico

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Knowledge of green turtle (*Chelonia mydas*) foraging ecology in the northwestern Gulf of Mexico (GOM) is critical as populations begin to recover from heavy harvesting in prior centuries. We present a comprehensive long-term assessment of green turtle diets from carcasses salvaged from 1987 to 2014 along the Texas coast. Digestive tract contents were examined from 420 green turtles, ranging in size from 7.3 to 86.0 cm in straight carapace length (SCL_{max}). Green turtles as small as 16.2 cm SCL_{max} recruit from the oceanic environment to nearshore foraging habitat in the northwestern GOM and consume macroalgae principally. A successive shift in diet and habitat to inshore seagrasses was evident by the seagrass-dominated diet of turtles larger than 30 cm SCL_{max}. Animal matter remained a frequently ingested diet item suggesting these immature green turtles are better classified as omnivores. The overall evidence indicates that Texas' recovering green turtle assemblage is exhibiting foraging plasticity within seagrass meadows changing species composition and density.

Keywords: sea turtle, *Chelonia mydas*, gut content analysis, foraging ecology, Texas

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INTRODUCTION

Green turtles (*Chelonia mydas*) were once so abundant in Texas waters that they supported a commercial fishery, with a peak annual landing of approximately 265,350 kg of turtles in 1890 (Hildebrand, 1982). Pressures on this marine turtle assemblage were inexorable. By 1903 the green turtle fishery had virtually collapsed due to the commercial harvest and severe hypothermic stunning events in the winters of 1894–1895 and 1899, which decimated the turtle population (Hildebrand, 1982; Doughty, 1984). Since green turtles were listed under the protection of the U.S. Endangered Species Act in 1978 and Mexico banned the commercial harvest of all sea turtles in 1990, Texas waters once again support a rapidly growing immature green turtle aggregation (Shaver et al., 2013). In-water research indicates increased green turtle population growth, with a catch per unit of effort on the lower Texas coast at 10 times greater in 2002–2010 than in 1991–1994 (Metz and Landry, 2013). Furthermore, the Sea Turtle Stranding and Salvage Network (STSSN) provides evidence of an increased Texas green turtle population. The STSSN reports increasingly high stranding numbers of immature green turtles (Stacy et al., 2020) and record-breaking stranding events from cold weather. From 1980 through 2015, the largest totals (>450 turtles) of turtles cold-stunned were during the winters of 2009–2010, 2010–2011, 2013–2014, and 2014–2015 (Shaver et al., 2017).

Immature green turtles in Texas primarily originate from Mexican rookeries in the western Gulf of Mexico (GOM) (Shamblin et al., 2016). They disperse from their nesting beaches as hatchlings and occupy an oceanic stage in the offshore waters of the GOM (Bolten, 2003). During this life-history stage, young green turtles reside and feed within the large *Sargassum* mats floating in the GOM (Witherington et al., 2012). The aforementioned algae mats break away in massive segments and wash ashore in the spring and summer seasons in massive wracks along the Texas gulf coast (Gherskiere et al., 2006; Gower et al., 2006; Webster and Linton, 2013). Large recruitment pulses of immature oceanic green turtles frequently accompany these *Sargassum* mats (Shaver et al., 2017; Stacy et al., 2020). Post-oceanic recruits often reside at neritic granite rock jetties designed to stabilize channels that connect to inshore bays and lagoons (Manzella et al., 1990; Renaud et al., 1992; Williams and Manzella, 1992; Coyne, 1994; Renaud et al., 1994; Shaver, 1994; Renaud and Williams, 1997; Williams and Renaud, 1998). These structures provide protection and abundant invertebrate and macroalgae food sources, with over 80 macroalgae species reported at the Port Mansfield jetty in south Texas (Edwards and Kapraun, 1973; Kaldy et al., 1995). Green turtles have been documented to inhabit jetty channels for up to 1,100 days (Shaver, 2000), where they consume macroalgae (Coyne, 1994). Some of the smallest daily movements recorded for juvenile green turtles were at a jettied pass in South Texas (Renaud et al., 1995), further evidence of the green turtles' dependency on this habitat.

Texas green turtles exhibit a size-based transition, typically at 25–45 cm SCL, from jetty inhabitation to residency in inshore seagrass beds (Gorga, 2010; Howell, 2012). Among these beds, there are macroalgal communities (Breuer, 1962; Hildebrand and King, 1978). Data on the green turtle foraging habits in the northern GOM are historically limited. While Atlantic green turtles are known to maintain and selectively feed within seagrass plots (Bjorndal, 1985), only recently was this identified for the first time in the northern GOM (Rodriguez and Heck, 2020). Research suggests seagrasses are the dominant diet item for turtles captured in Texas' lagoon and bay systems (Landry et al., 1992; Coyne, 1994). The three most common species of seagrass in Texas waters are shoal (*Halodule beaudettei*), Gulf manatee (*Cymodocea filiformis*), and turtle (*Thalassia testudinum*) grass (Quammen and Onuf, 1993; Withers, 2002). The 209-km long Laguna Madre accounts for 81% of the Texas coast's entire seagrass coverage (Mendelssohn et al., 2017). Consequentially, the Laguna Madre supports the greatest abundance of inshore green turtles in the state (Doughty, 1984; Metz and Landry, 2013).

Ecological succession in seagrass beds typically starts with the colonization of shoal grass in disturbed or barren areas and climaxes with turtle grass (Patriquin, 1975). Historically, shoal grass dominated Texas' estuaries. However, from the mid-1960s to 1998, bare regions increased, and shoal grass acreage declined by 36%, with partial replacement by turtle and manatee grass (Quammen and Onuf, 1993; Onuf, 1996; Pulich and Onuf, 2007; Gutierrez et al., 2010; Hobson and Whisenant, 2018). The changes in seagrass coverage and composition are attributed to maintenance dredging, propeller scarring, brown tide algae blooms, and natural processes (Onuf, 1994; Pulich and Calnan, 1999; Dunton et al., 2002). With the drafting of a Seagrass Conservation Plan for Texas in 1999, efforts to protect and enhance Texas seagrass beds' health and quality were implemented. They were expected to be effective at seagrass restoration within 2 years once high-priority actions were accomplished (Pulich and Calnan, 1999). Although seagrass distribution and density are essential to Texas's green turtle occurrence (Shaver et al., 2017), the impact of changes in seagrass composition and coverage on turtles' foraging habits is unknown.

The Texas coast is temperate to a subtropical system, with long hot summers and short, mild winters. Temperature frequently drives the macroalgal seasonality in warm-water regions like Texas (Mathieson and Penniman, 1986). Seagrass beds in Texas have displayed similar growth and biomass changes from the seasons' light and temperature-dependent fluctuations (Kowalski et al., 2009). Variability in resource availability can bring about variation in turtle foraging habits (López-Mendilaharsu et al., 2008; Guebert-Bartholo et al., 2011). For these reasons, it is critical to understand Texas green turtle foraging habits within their year-round range and how the diet might change with seasonal environmental fluctuations.

Describing the diet of green turtles found stranded in Texas for nearly three decades may discern any food-related changes due to seagrass composition and abundance variations. Further, examining the diet of multiple life-history stages in this rapidly increasing assemblage will provide a baseline for future diet studies. The significance of conventional gut contents analyses (GCA) to improve nutrition interpretation is highlighted in the sea turtle literature (Parker et al., 2005; Hatase et al., 2006; Revelles et al., 2007; Casale et al., 2008; Hoarau et al., 2014; Behera et al., 2015). We used GCA to examine the dietary composition of all size ranges of green turtles stranding on the Texas coast and to explore ontogenetic, temporal, and seasonal diet trends.

MATERIALS AND METHODS

Study Area

Seven major estuaries are covering 2.6 million acres along the Texas coast (**Figure 1**). Across the 350 miles long Texas coast, nine federally maintained jettied ship channels (Army Corps of Engineers, 2021) provide access to the bays and the Laguna Madre. Red algae species are most numerous in the jetty habitat, followed by brown and green algae (Fikes and Lehman, 2010). There are five species of seagrass in Texas, including widgeon (*Ruppia maritima*), star (*Halophila engelmannii*), shoal (*Halodule beaudettei*), Gulf manatee (*Cymodocea filiformis*), and turtle (*Thalassia testudinum*) grass. Amongst the seagrass beds, there are macroalgal communities dominated by *Cladophora* sp., *Digenea simplex, Gracilaria* spp., *Hypnea musciformis*, *Ulva lactuca*, and *Yuzurua poiteaui* (Breuer, 1962; Hildebrand and King, 1978).

Sample collection. We collected diet samples from 306 green turtles stranded from 1987 to 2014 from the Texas coast's inshore and offshore waters, and we incorporated the unpublished weight data from 114 Texas green turtles (Howell et al., 2016); for

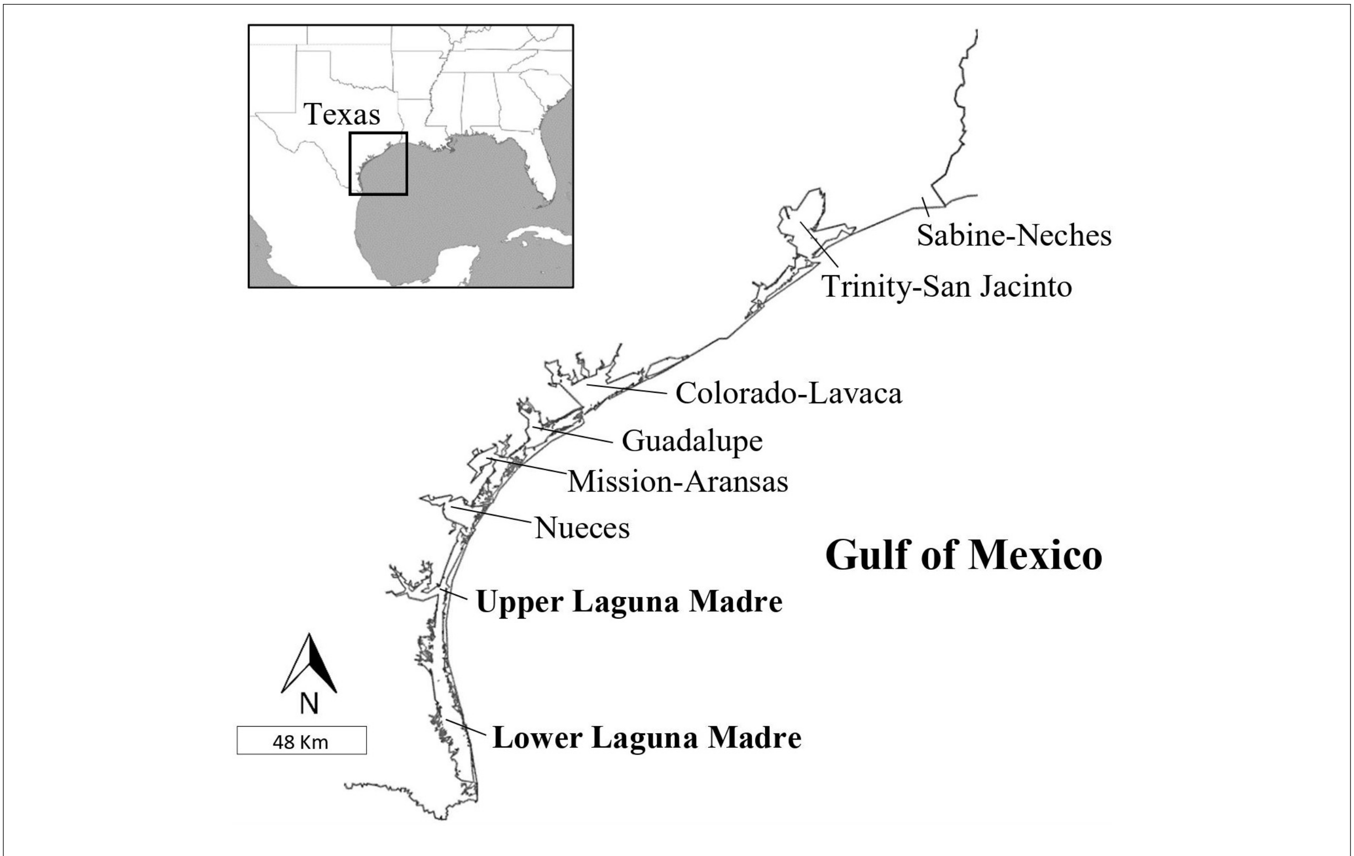

FIGURE 1 | Map of the Texas, United States, and coast, showing the major estuaries and the geographic area where green turtles (*Chelonia mydas*) were stranded from 1987 to 2014. The Laguna Madre is one estuary but is labeled upper and lower for illustrative purposes and is given in bold. Inset shows the location of Texas in the western Gulf of Mexico.

TABLE 1 | The number of stranded green sea turtles (*Chelonia mydas*) analyzed temporally and seasonally in this study ($n = 306$) and from previously unreported data from Howell et al. (2016) ($n = 114$), within each size class.

	Samples		**Temporal**		**Seasonal**			
Size class, straight carapace length (cm)	**Present study (dry gravimetric)**	**Howell et al., 2016 (wet gravimetric)**	**1987–2000**	**2001–2014**	**Spring**	**Summer**	**Fall**	**Winter**
Oceanic (≤20.0 cm)	10	5	6	9	8	6	1	0
Recruit (20.1–30.0 cm)	88	42	67	63	50	29	28	23
Transitional (30.1–40.0 cm)	139	43	93	89	31	28	34	89
Inshore (≥40.1 cm)	69	24	46	47	16	15	10	52
Total	306	114	212	208	105	78	73	164

a total of 420 samples from individual turtles (**Table 1**.) All measurements presented are maximum straight carapace length (SCL_{max}); ±0.1 cm, measured from carapace notch to the posterior-most tip. Turtles sampled for this study ranged in size from 7.3 to 86.0 cm SCL_{max}, and their body condition suggested normal behaviors (i.e., actively foraging) prior to death. Data were grouped into four size classes, based on previous size-based distribution studies in Texas, to improve our assessments of size-based diet and habitat differences (Coyne, 1994; Shaver, 2000; Shaver et al., 2013; Howell et al., 2016). These size classes are referred to herein as oceanic (≤20.0 cm), recruit (20.1–30.0 cm), transitional (30.1–40.0 cm), and inshore (≥40.1 cm).

Necropsies were performed on carcasses following standard sampling procedures (Wyneken, 2001), and the entire digestive tracts were extracted and frozen for subsequent analysis. Diet items were removed from the whole gastrointestinal tract and identified to the lowest taxon possible with a dissecting microscope. Diet items were quantified by dry ($n = 306$) and wet ($n = 114$) gravimetric analyses (Hyslop, 1980; Bigg and Perez, 1985; Forbes, 1999). Dry weights were obtained by drying identified taxa samples for 24–48 h at 60°C and measuring the cooled samples to the nearest hundredth of a gram. The wet mass of each identified taxa was weighed to the nearest hundredth of a gram.

Sample Analysis

Cumulative prey curves were employed to determine if an adequate number of samples had been collected to describe Texas's green turtle diet (Ferry and Cailliet, 1996). The order in which the samples were analyzed was randomized 10 times to reduce bias to construct the prey curve. The cumulative number of prey types was plotted against the cumulative number of guts analyzed. The number of samples analyzed is considered sufficient for describing dietary habits when the resulting curve reaches an asymptote.

The percent weight (*Wi*) by individual diet taxon was used as a more effective measure to reduce variance, minimize bias from the difference in individual sample weights, and standardize amongst quantification methods. The *Wi* calculated by dividing each diet taxon's weight in a given sample by the total weight of that turtle's foregut contents (×100). The gravimetric method may overestimate the relative importance of slowly digested hard-bodied items (George and Hadley, 1979); accordingly, additional metrics are useful to interpretations (Amundsen and Sánchez-Hernández, 2019). The frequency of occurrence (*Fi*) for each diet item was determined by dividing the number of samples containing each food item by the total number of samples examined (×100). The relative importance of each item in the diet was determined using an index of relative importance (IRI; Bjorndal et al., 1997):

$$IRI\ (\%) = \frac{100\ (FiWi)}{\sum_{n=1}^{i}\ (FiWi)}$$

where F is the frequency of occurrence of the target taxon i, and W is the mean percent taxon weight in all individual turtles (Wi) for the collective gravimetric methods.

The IRI is a compound index incorporating frequency of occurrence and weight into a single numerical measure to estimate dietary importance. While single metrics aid diet interpretations, compound indices can additionally provide a general picture of prey items' importance in predators' diets (Liao et al., 2001). Higher IRI values indicate a less diverse diet. Depending on the gravimetric method employed, hard-bodied prey can bias prey importance outcomes by contributing more to the *Wi* (Hyslop, 1980). The IRI values for each gravimetric method were calculated independently and collectively to explore differences between them. There were no differences detected amongst the principal diet groups' estimated dietary importance. Therefore, all gravimetric data were collectively combined and analyzed.

Food habits were analyzed in relation to the size class, the season of stranding (northern meteorological seasons of winter, spring, summer, fall), and two time periods (1987–2000, 2001–2014). The year divisions of 1987–2000 and 2001–2014 were used to compare general diet information after the 2-year implementation of the 1999 Texas Seagrass Conservation Plan. The frequency of occurrence approach provides a comprehensive and reliable account of diet composition, is unaffected by the diet item's condition, and can be used to make comparisons across studies (Baker et al., 2014). With a large sample size for this study, the frequency of occurrence allows for population-wide assessments with minimal bias. The frequency of occurrence was the consistent metric used for statistical analyses. Chi-square tests were conducted using the software package IBM SPSS 25.0 to examine the relationship between size class and whether a particular diet taxon was consumed. The Cochran-Armitage test of trend was used to determine whether there was a linear trend in the primary diet group chosen within each life-history stage over the study period. The Cochran-Armitage test was additionally conducted to examine any linear trends in seagrass species selected by all combined size classes. The binomial logistic regression procedure in SPSS Statistics was used to generate the result of the Cochran-Armitage test of trend. The Goodman and Kruskal's lambda test was used to measure the strength of the association between the diet items selected by each size class within the stranding season. For all analyses, $\alpha = 0.05$.

RESULTS

The cumulative prey curve reached asymptote indicating most major prey items had been collected to describe green turtles' diet in Texas waters (**Figure 2**). Green turtles consumed 73 unique species, comprised of five seagrasses, 33 red algae, 12 green algae, eight brown algae, and 15 animals (**Supplementary Table 1**). Food items were classified as six major diet groups based on an overall F ≥ 25%: seagrasses, animal matter, anthropogenic debris, red, green, and brown macroalgae. All F values presented refer to the frequency of occurrence from all 420 turtles. Results were collectively presented on *Sargassum* species and *Gelidium* species, which intermix in their respective habitat.

Ontogenetic Shifts

Multiple size-based diet shifts were evident in the IRI values (**Figure 3**). There was a significant association between the ingestion of brown macroalgae and size class [$\chi^2(3) = 70.149$, $p < 0.0001$]. Brown macroalgae, specifically *Sargassum* spp., were the principal diet item of oceanic stage turtles ($F = 93.3\%$, IRI = 73.9%). Red macroalgae and the size class feeding on them were significantly associated [$\chi^2(3) = 21.538$, $p < 0.0001$]. The highest IRI values for recruits demonstrated red and brown macroalgae were the most important diet groups (IRI = 24.2%, IRI = 27.4%, respectively). The relationship between the frequency of green algae consumption and size class was significant [$\chi^2(3) = 9.563$, $p = 0.022$]. The food items with the highest frequency of occurrence in the recruits were *Sargassum* spp. (63.0%), turtle grass (38.5%), mollusks (36.9%), shoal grass (33.1%), red algae *Gelidium* spp. (29.2%), and green algae *Ulva* spp. (23.1%). A secondary size-based diet shift was apparent with significant differences in seagrass consumption among the size classes [$\chi^2(3) = 46.0047$, $p < 0.0001$]. Seagrass was the principal diet item for the transitional class (IRI = 51.2%) and inshore class (IRI = 83.6%). The highest frequency of occurrence among food items in the transitional turtles was shoal grass (44.5%), turtle grass (43.9%), *Gelidium* spp. (41.7%), mollusks (38.4%), manatee seagrass (24.2%), and *Ulva* spp. (21.3%). Turtles of the

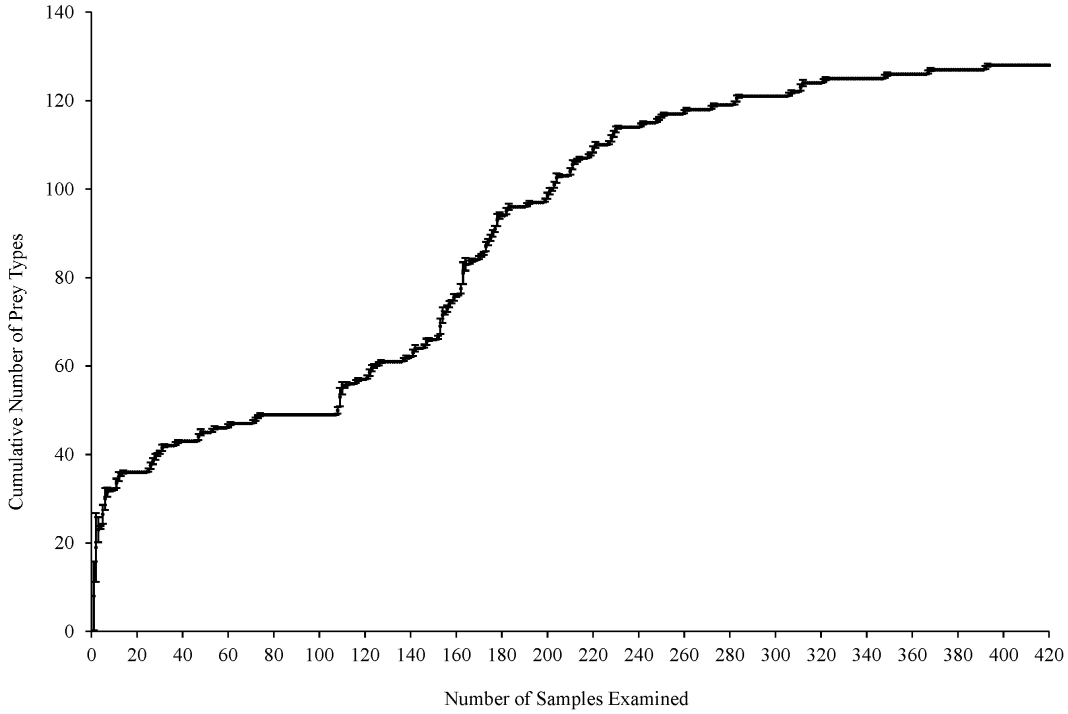

FIGURE 2 | Cumulative prey curve (prey taxa per gastrointestinal tract) for green turtles (*Chelonia mydas*) (n = 420) collected along the Texas coast. Error bars represent one standard deviation.

inshore class most frequently consumed turtle grass (62.4%), shoal grass (51.6%), mollusks (36.56%), manatee grass (33.3%), and star grass (*Halophila englemannii*) (33.3%). Foraging on anthropogenic debris occurred most frequently ($F = 60.0\%$) in oceanic class turtles with significant variation amongst all size classes [$\chi^2(3) = 19.521, p = 0.0002$]. In all collective size classes, ≥53.3% of individuals ingested animal matter. There was not a significant association between animal matter consumption and the size class feeding on it [$\chi^2(3) = 2.965, p = 0.397$].

Temporal Trends

There was a significant decrease in the frequency of seagrass consumption in recruits ($p < 0.0001$) and transitional turtles ($p = 0.031$) between the two study periods (**Figures 4B,C**). Ingestion of red macroalgae by recruits increased significantly ($p = 0.028$) over time while there was no significant change in transitional turtles ($p = 0.131$). The presence of anthropogenic debris in gastrointestinal tracts decreased significantly between the two time periods for oceanic and recruits ($p < 0.05$) (**Figures 4A,B**). Inshore class turtles consumed red algae ($p = 0.045$) and brown algae ($p < 0.0001$) less frequently over time (**Figure 4D**). Among all size classes combined, turtle grass consumption decreased significantly over time, from $F = 50.0\%$ to 40.0% ($p = 0.023$). The ingestion of shoal grass decreased across the collective size classes, from $F = 50.9\%$ to 31.8% between the two periods ($p < 0.0001$). Manatee grass consumption did not change over time ($F = 21.6$–22.2%, $p = 0.989$).

Seasonal Differences

The interseasonal differences in oceanic turtles' diet were not statistically analyzed as samples were unavailable for all seasons (**Figure 5A**). The proportion of recruits consuming red algae was significantly associated with the time of year of stranding ($\lambda = 0.022, p = 0.037$), with red algae consumption documented the least in the spring months (**Figure 5B**). The proportion of brown algae recorded in recruits was predicted by the season ($\lambda = 0.150, p = 0.006$), present in 92% of the spring turtles. In the winter and spring months, recruits ingested animal matter proportionally more than the other seasons ($\lambda = 0.020, p = 0.050$). There was a significant association between seagrass consumption and season of stranding in transitional turtles ($\lambda = 0.060, p = 0.0005$), wherein seagrass was documented more frequently in the winter months (**Figure 5C**). The presence of red algae in the diet was significantly associated with the season in which transitional turtles were stranded ($\lambda = 0.026, p = 0.003$). It was documented less frequently in the winter months than any other season. The consumption of green algae by the inshore class was significantly associated with the time of year ($\lambda = 0.039, p = 0.014$). Inshore size class turtles ingested green macroalgae most frequently in the spring (**Figure 5D**).

DISCUSSION

The green turtle population in Texas is increasing rapidly, and, as such, understanding the diet of this growing assemblage is critical

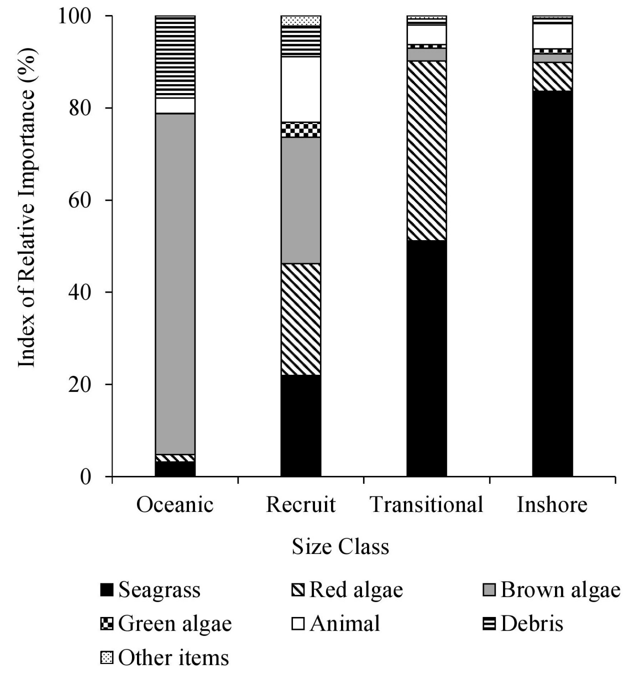

FIGURE 3 | Percent index of relative importance (IRI) (%) of major diet items from size classes of stranded green sea turtles (*Chelonia mydas*) in Texas.

to endangered species management. Conservation managers can then prioritize preservation areas and policies designed to protect these essential green sea turtle foraging grounds. We characterized the diet of green turtles stranding along the Texas coast for 28 years to evaluate changes over time. This first long-term diet study of Texas green turtles demonstrated turtles ingest a diversity of food items across size classes with foraging differences observed seasonally and temporally.

Diet of the smallest size class suggested this group was mostly representative of the oceanic life-history stage. The frequency of brown macroalgae ($F = 93.3\%$), specifically the *Sargassum* spp., in oceanic turtles diet, was similar to the esophageal and fecal samples ($F = 86, 87\%$, respectively) from oceanic size green turtles captured in pelagic *Sargassum* habitat off Florida, United States (Witherington et al., 2012). The authors suggested the ingestion of *Sargassum* was incidental to foraging on sessile, epiphytic animals on the brown algae. Furthermore, the high occurrence of *Sargassum* in the oceanic size class is similar to studies that have reported turtles foraging at the surface (Carr, 1987b; Morais et al., 2014). Stable isotope results ($\delta^{15}N$ values) from the scutes of some of our oceanic-sized green turtles indicate they are not assimilating the *Sargassum*-dominated diet. Instead, they had tissue isotope values reflective of the animals that frequent the floating algae mats (Howell et al., 2016). Primarily the animals ingested by this size class are organisms known to be closely associated with the *Sargassum* community (e.g., Cnidarians, Schypozoans, Teleosts) (Witherington, 2006; Boyle and Limpus, 2008; Jones and Seminoff, 2013).

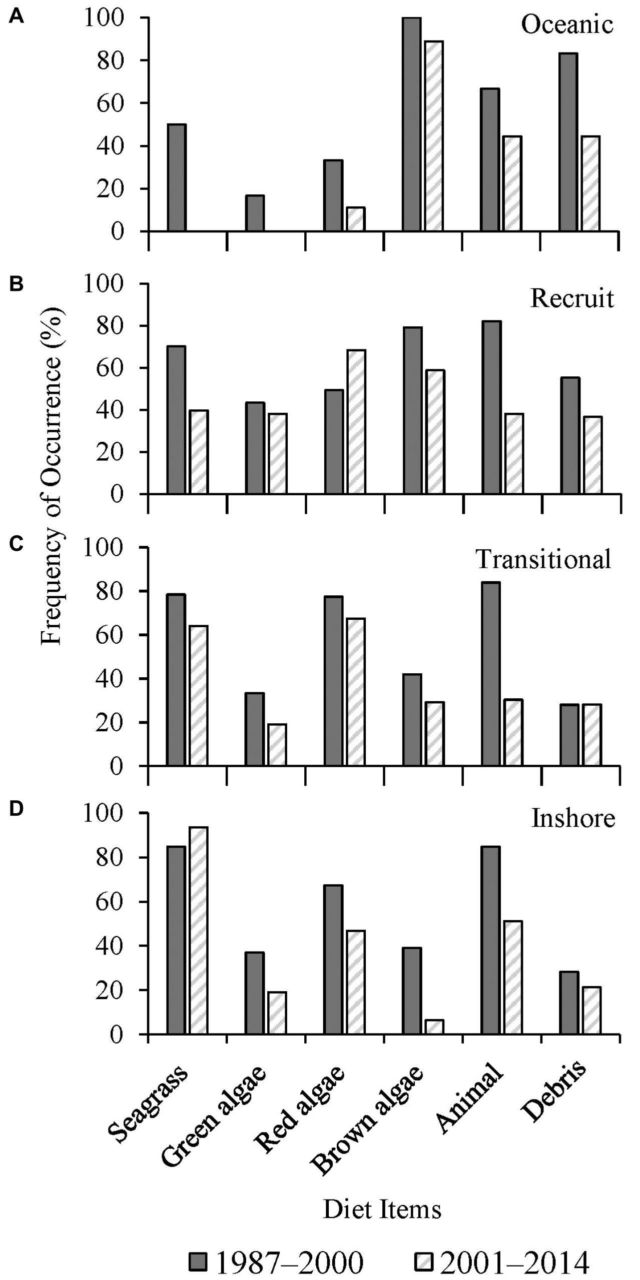

FIGURE 4 | Frequency of occurrence (F) (%) of major diet items from **(A)** oceanic (1987–2000, $n = 6$; 2001–2014, $n = 9$), **(B)** recruit (1987–2000, $n = 67$; 2001–2014, $n = 63$), **(C)** transitional (1987–2000, $n = 93$; 2001–2014, $n = 89$), and **(D)** inshore (1987–2000, $n = 46$; 2001–2014, $n = 47$) size classes of stranded green sea turtles (*Chelonia mydas*) in Texas, grouped by years (1987–2000, $n = 212$; 2001–2014, $n = 208$).

Convergence zones are oceanographic features that collect *Sargassum* and marine debris (Carr, 1987a), and as such, anthropogenic debris consumption was highest in oceanic turtles ($F = 60\%$). Anthropogenic rubbish ingestion by marine turtles has been linked to numerous health issues, including blockage and compaction of the digestive tract, ultimately with lethal

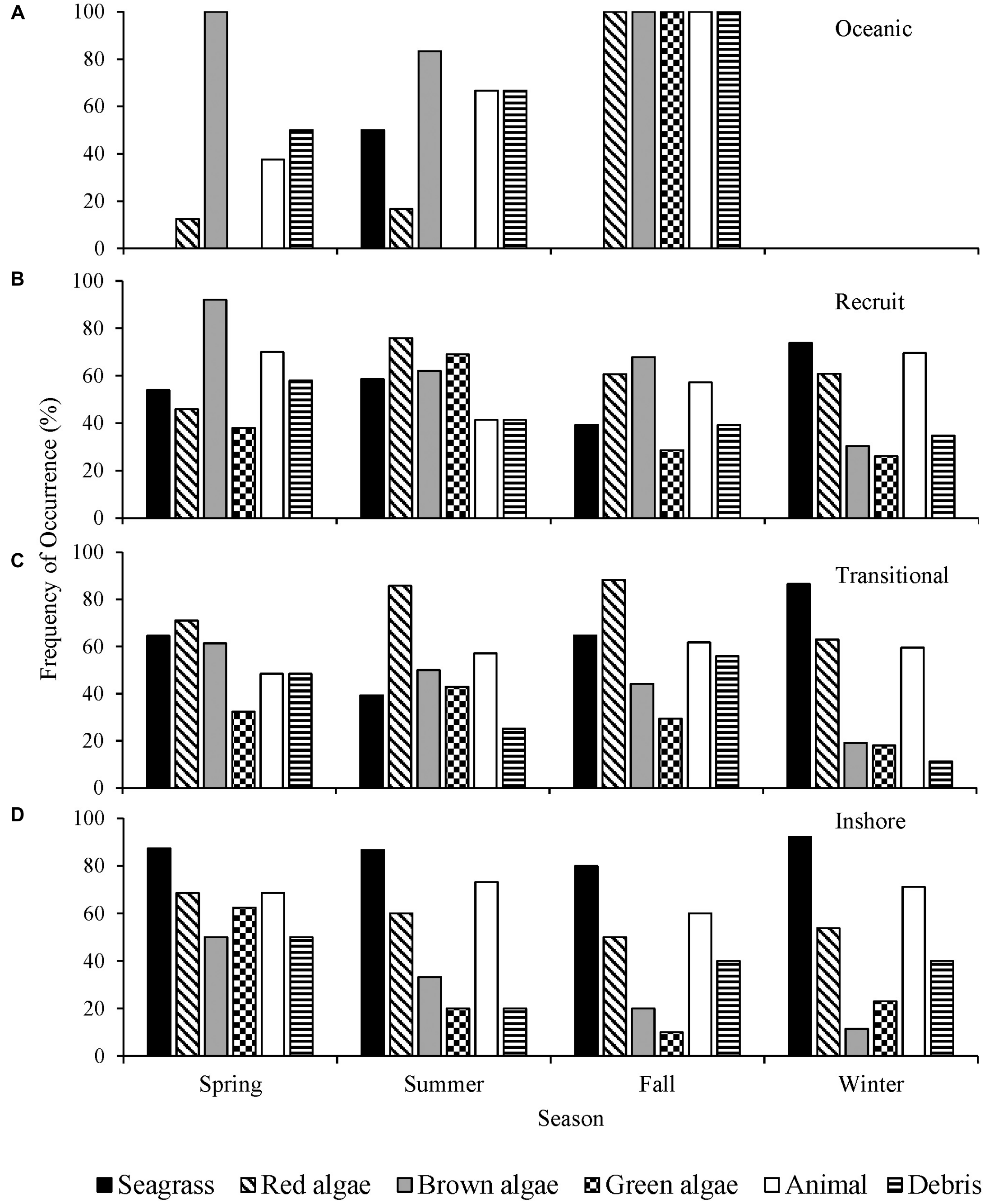

FIGURE 5 | Frequency of occurrence (F) (%) of major diet items from **(A)** oceanic, **(B)** recruit, **(C)** transitional, and **(D)** inshore size classes of stranded green sea turtles (*Chelonia mydas*) in Texas, grouped by northern meteorological seasons.

effects (Bjorndal et al., 1994; Tourinho et al., 2010; Gonzalez Carman et al., 2014; Wilcox et al., 2016). Our findings were similar to a study on oceanic green turtles captured in the *Sargassum* habitat, where synthetic material was the third most frequently ingested diet item (Witherington et al., 2012). Reduction of marine debris is identified as a recovery action in the Atlantic green turtle's ESA Recovery Plan (NMFS, 1991), and prioritization should continue.

Previous diet studies in Texas showed seagrass was not present in turtles $\leq$20 cm SCL$_{max}$ in Texas (Howell, 2012); therefore, our finding of seagrass in the diet of $\geq$16.2 cm–20 cm SCL$_{max}$ turtles ($F = 20.0\%$) was unexpected. These oceanic size class turtles also consumed macroalgae frequently found along the Texas coast (Kaldy et al., 1995; Agan and Lehman, 2002; Fikes and Lehman, 2008, 2010), suggesting nearshore occupancy for them. Young green turtles inhabiting jetty channels feed on flotsam, including seagrass blades detached from nearby inshore grass beds (L. N. Howell, D. J. Shaver, per. obs.). Our diet data suggest these individuals were likely foraging on benthic algae and floating seagrass blades in the nearshore environment before death. There are inherent variabilities in obtaining these smallest turtles, and our interpretations are based on a limited sample size. Nonetheless, the presence of multiple benthic species of neritic diet items in the oceanic class demonstrates recruitment at ≤20 cm SCL_{max} to Texas' nearshore waters. Marine turtles are vulnerable to being taken as bycatch in coastal fishery operations and other anthropogenic threats (Magnuson et al., 1990). An explicit understanding of size ranges occupying Texas nearshore waters is critical to protected species management, as threats vary depending on the size class.

While green turtles in neritic foraging grounds typically consume benthic items (Redfoot, 1997; Holloway-Adkins, 2001; Gilbert, 2005; Makowski et al., 2006; Foley et al., 2007), floating *Sargassum* spp. were the most frequently ingested item in recruits and dominated the diet of turtles found in spring months. The mean digestive passage time for a food item consumed by immature green turtles was determined to be 23.3 ± 6.6 days (Amorocho and Reina, 2008). The size at recruitment to the neritic zone varies for oceanic stage green turtles (summarized in Avens and Snover, 2013). Consequently, the *Sargassum*-dominated diet of oceanic stage turtles could still be present in newly recruited turtles' gastrointestinal tracts. Alternatively, it is equally plausible that Texas recruits are resourcefully foraging inside the massive wracks of *Sargassum* that enter the channel passes in the spring months (Breuer, 1962) while continuing to feed benthically within the jetty environment. Immature neritic Atlantic green turtles foraging amongst artificial structures in Florida, United States, were noted to opportunistically consume flotsam in addition to their benthic macroalgae-dominated diet (Holloway-Adkins and Hanisak, 2017). The stomach contents of multiple recruits contained jetty algae (e.g., *Gelidium* spp. and *Ulva* spp.) and *Sargassum* spp., indicating this size class inhabits the jetty habitat. Dedicated surveys of turtle feeding behavior within the channel environment when *Sargassum* mats are present would help elucidate the foraging activity of turtles resident in these channels. Collectively, benthic macroalgae found on the Texas coast (Wynne, 2008) dominated the recruits' diet indicating this size group is in the jetty habitat.

Several recruits ($F = 23.3\%$) ingested all three primary species of seagrasses, suggestive of foraging in seagrass beds and not on the floating matter in the jetty channels. Tracking data revealed that turtles occupying the jetty environment made brief expeditions into the nearby inshore habitat but returned to jettied-channels (Shaver, 2000). Recruitment may not represent a distinct unidirectional shift from one habitat to the next. As an alternative, younger turtles may display an intermediate stage sampling on macroalgae and seagrasses in diverse environments (Arthur et al., 2008). Considerably, the fluctuation in density and concentration of macroalgae on jetty structures (Kaldy et al., 1995; Renaud et al., 1995; Fikes and Lehman, 2008) could force turtles to feed at alternative sites. Studies incorporating fecal analysis and esophageal lavage may provide a more precise understanding of recruitment size and principal diet.

Green turtles in the western Atlantic are frequently considered obligate seagrass consumers (Mendonca and Ehrhart, 1982; Bjorndal, 1997), with omnivory reported in the Atlantic southwest (Bugoni et al., 2003) and the Pacific (Bjorndal, 1997; Seminoff et al., 2006; Fukuoka et al., 2019). More than half the individuals in all collective size classes ingested animal matter, indicating that Texas's immature green turtles are omnivores in these developmental foraging grounds. This finding is similar to other studies that have demonstrated animal consumption persisting through ontogeny (Amorocho and Reina, 2008; Cardona et al., 2010; Carrión-Cortez et al., 2010; Morais et al., 2014). The relative importance of animal matter varied across the size classes, with the highest collective IRI value noted in recruits, primarily due to mollusk consumption. Mollusc ingestion may occur incidentally to foraging on macroalgae in the jetty habitat or represent a selective effort. The more frequent ingestion of animals in the winter and spring months by the recruit size class could be proportional to the seasonal variation in the macroalgal abundance documented in the Texas jetty habitat (Fikes et al., 2010). In a previous study in the northern GOM, immature green turtles consumed animal matter more in the winter months due to the seasonal fluctuations in seagrass and algae biomass (Williams et al., 2014). Furthermore, green turtle digestive efficiency decreases when water temperatures drop (Bjorndal, 1980); and animal matter is easier to digest than plant material for green turtles (Bjorndal, 1985). Conceivably, the recruit class selects easier to digest animal matter more frequently during the cooler months when jetty algae composition changes. Regardless of seasonal environmental variations, we recommend that juvenile green turtles foraging in Texas be described as omnivores. Multisource stable isotope mixing models have highlighted invertebrate consumption and assimilation among omnivorous green turtles (Lemons et al., 2011). Therefore, future diet studies in Texas should incorporate isotope mixing models to gain supplemental information on the nutritional contribution and importance of animal matter to all size classes' diets.

The recent seagrass conservation efforts in Texas have achieved some success. Seagrass acreage was reported to have increased to cover a mean area of 87.7 ± 25.5% in the upper and 50.0 ± 38.4% in the Lower Laguna Madre (Dunton et al., 2013). However, transitional turtles consumed seagrass less frequently over time, indicating that this size class utilizes different habitat niches. Any beneficial effects of recovering seagrass meadows may be negated by an exponentially growing turtle population (Shaver et al., 2017). Plausibly driven by resource competition from turtles in the seagrass beds, transitional turtles incorporate a varied diet of seagrasses and algae. Satellite tracking data revealed green turtles (mean SCL 37.9 ± 5.2 cm) migrate in and out of the Laguna Madre seagrass beds via the jetty habitats (Shaver et al., 2013). The high frequency of ingestion of the typical jetty red algae, *Gelidium* spp. by transitional turtles indicates turtles supplement their seagrass diet with benthic macroalgae as they transit from inshore waters to the GOM. The concept above is further supported by analyzing digesta boluses throughout the gastrointestinal tract, which indicate separate feeding sessions. Some transitional turtles alternated their diets between seagrass (e.g., *Cymodocea* sp.) and jetty algae (e.g., *Gelidium* spp.).

In contrast to transitional turtles, the more frequent consumption of seagrasses by the inshore size class indicates these larger turtles have become highly reliant on the seagrasses with time. Immature green turtles are more susceptible to cold stunning in Texas as they overwinter and show strong site fidelity for inshore habitats (Arms, 1996). Cold stunning is the most significant cause of stranding events in Texas (Shaver et al., 2017) and cold-stunned turtles comprised most winter samples for transitional and inshore size classes. The high frequency of seagrasses in the diet of the two largest classes of turtles stranded in the winter months most certainly reflects this strong seagrass bed dependency.

Shoal grass in the lower Laguna Madre has declined in abundance and increased in bed fragmentation, while the upper Laguna Madre has indicated some expansion in coverage (Onuf, 2007; Wilson and Dunton, 2017). Previous research revealed green turtles in the Laguna Madre selected shoal grass over the other seagrasses (Coyne, 1994). Interestingly, we documented a significant decrease of shoal grass in all size classes' diet over time with no parallel increase in the frequency of other seagrass species consumed. Turtle grass was still frequently consumed and dominated the diet of our inshore size classes. Conceivably, immature turtles are exhibiting foraging plasticity within their changing seagrass meadows by consuming a variety of macroalgae and animal matter species. Overall, seagrass collectively dominated the diet of turtles larger than 30 cm SCL_{max}, illustrating the necessity of conserving and monitoring seagrass habitats along the northwestern GOM coast. Potential impacts of changes in seagrass composition and distribution on this green turtle assemblage's diet should be rigorously monitored through future diet studies.

Management and Conservation Implications

Marine turtles inhabiting the Texas coast face a variety of threats, both human-related and natural. As this green turtle population continues to increase rapidly, it is critical to incorporate foraging ecology studies into conservation management decisions that strengthen the species and habitat protection. Size-related variation in sea turtle foraging habits necessitates integrated management strategies that reduce impacts to immature turtles in Texas jetty and seagrass habitats. Gear modifications in commercial fisheries could be implemented to reduce the incidental take in our nearshore waters, hence providing increased protection of this threatened species. Additionally, it is essential to manage the seagrass beds fundamental to the survival of this exponentially growing green turtle assemblage that will eventually recruit to the breeding population.

DATA AVAILABILITY STATEMENT

The original contributions presented in the study are included in the article/**Supplementary Material**, further inquiries can be directed to the corresponding author/s.

ETHICS STATEMENT

Ethical review and approval was not required for the animal study because the animals used in this study were deceased upon discovery.

AUTHOR CONTRIBUTIONS

DS and LH conceived and designed the study. LH performed the statistical analysis, created the figures, and wrote the manuscript's first draft. Both authors contributed to manuscript revision, read and approved the submitted version.

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SUPPLEMENTARY MATERIAL

The Supplementary Material for this article can be found online at: https://www.frontiersin.org/articles/10.3389/fmars.2021.658368/full#supplementary-material

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Leatherback Turtles in the Eastern Gulf of Mexico: Foraging and Migration Behavior During the Autumn and Winter

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We deployed 19 satellite tags on foraging adult leatherback turtles, including 17 females and 2 males, captured in the northeastern Gulf of Mexico in 2015, 2018, and 2019 in order to study regional distribution and movements. Prior to our study, limited data were available from leatherbacks foraging in the Gulf of Mexico. Tag deployment durations ranged from 63 to 247 days and turtles exhibited three distinct behavior types: foraging, transiting, or rapidly switching between foraging and transiting. Some females were tracked to nesting beaches in the Caribbean. Most of the leatherbacks remained on and foraged along the west Florida continental shelf whereas a few individuals foraged in waters of the central Gulf of Mexico during the autumn and winter. In addition, migration of adult females through the Yucatan Channel indicate that this is a seasonally important area for Caribbean nesting assemblages.

Keywords: movement ecology, migration, foraging, leatherback turtle, Gulf of Mexico

INTRODUCTION

Movement characterizes the life cycles of marine animals (Putman, 2018) and understanding the role of individual movements on species distributions and habitat use is an important component of scientifically sound management efforts (Blumenthal et al., 2006; Oppel et al., 2018). Satellite-telemetry methods have been widely used in large-bodied marine animals to determine their movements and habitat associations, and have yielded considerable insights into sea turtle biology and behavior (Hays et al., 2019). Sea turtles are particularly well-suited for satellite telemetry because tags can be affixed to their carapaces, and their obligate air-breathing and other surface behaviors allow data to be reliably transmitted to satellites. The majority of satellite tags are deployed on nesting female sea turtles because of easy access by researchers (James et al., 2005). While this approach provides useful information, the data are biased toward females and inter-nesting and post-nesting periods.

Leatherback turtles (*Dermochelys coriacea*) inhabiting the Northwest Atlantic are one of seven populations that comprise the global distribution of this endangered species (National Marine Fisheries Service, and U.S. Fish and Wildlife Service, 2020). Multiple researchers have deployed satellite tags on female leatherbacks in nesting locations in the United States (Florida), Central America, the Caribbean, and South America (e.g., Hays et al., 2004; Eckert, 2006; Eckert et al., 2006; Fossette et al., 2007). Fewer in-water studies of this population have been conducted and mostly tagged turtles off the Atlantic coast of North America, documenting foraging areas that extend into high-latitudes (e.g., in waters near Canada and the United Kingdom; James et al., 2007; Dodge et al., 2014). Thus, the movement behavior of leatherbacks in the Atlantic, and movements to tropical nesting sites are relatively well known (James et al., 2005; Mills Flemming et al., 2010).

However, Northwest Atlantic leatherbacks also forage in the western Equatorial Atlantic and Gulf of Mexico, but there has been little directed research in these areas. The Gulf of Mexico may be a particularly important area for leatherbacks based on a recent study by Aleksa et al. (2018b) that identified foraging hotspots using telemetry data from Caribbean nesting turtles ($n = 10$) and turtles sampled off the Florida Panhandle ($n = 6$). The northeastern Gulf of Mexico off the Florida Panhandle and the southeastern Gulf of Mexico in the Bay of Campeche off the state of Tabasco, Mexico were identified as primary foraging areas. These two areas exhibit high primary productivity partly due to nearby high discharge-rate rivers (the Mississippi River and Rio Grijalva; David and Kjerfve, 1998).

Leatherbacks are present in the Gulf of Mexico year-round as demonstrated by Aleksa et al. (2018b), and recorded bycatch in pelagic longline fisheries (Garrison and Stokes, 2017). Leatherback abundance in the Gulf of Mexico is greater during summer and early autumn months as post-nesting turtles enter the Gulf from Caribbean nesting beaches during the summer, and depart to the Caribbean in the late autumn (Aleksa et al., 2018b and here). This seasonality coincides with the increased abundance of preferred gelatinous zooplankton prey (e.g., jellyfish, Aleksa et al., 2018a).

Salinity, temperature, nutrients, distance from shore, and water movements are factors that affect the abundance of jellyfish in the Gulf of Mexico (Aleksa et al., 2018a). These factors, along with physical oceanic features, such as convergence zones and eddies, provide conditions that concentrate leatherback prey. Leatherbacks are noted to forage along physical oceanic features where jellyfish are aggregated in the open ocean (Benson et al., 2011), and selectively feed on preferred jellyfish prey at foraging areas (Benson et al., 2007; Heaslip et al., 2012; Dodge et al., 2014). In the northern Gulf of Mexico, leatherbacks have been observed selectively feeding on pink meanie jellyfish (*Drymonema larsoni*, Aleksa et al., 2016). The pink meanie is a large scyphomedusa that is a predator on other jellyfish such as *Aurelia* spp.

Leatherbacks that forage in the northeast Gulf of Mexico appear to follow similar paths when leaving the Gulf in the autumn. Previously tagged turtles that departed the foraging area to return to the Caribbean mostly migrated southward on the west Florida shelf and used a secondary foraging area off southwestern Florida (Aleksa et al., 2018b).

A greater understanding of foraging and migration behavior by leatherbacks in the eastern Gulf of Mexico first described in Aleksa et al. (2018b) requires a larger sample size of satellite tagged leatherbacks that use the northern Gulf of Mexico foraging area. To elucidate the behavioral state of individuals during their movements, we used oceanographic features in combination with satellite telemetry data from nineteen leatherbacks tagged in the northern Gulf of Mexico. Data were assessed in a hierarchical Bayesian state space model with joint estimation over all individuals to infer behavioral states of leatherbacks, identifying whether portions of the track were associated with migration, foraging, or nesting behavior (Jonsen, 2016).

MATERIALS AND METHODS

Leatherback turtles were located by a spotter aircraft that directed the capture vessel to the turtles. Turtles were captured with a 2-m breakaway hoop net attached to the vessel and, upon successful capture, the turtle was lifted out of the water in a basket (2015) or brought aboard a small inflatable craft for examination and attachment of a telemetry tag (2018 and 2019). The general health of each captured turtle was evaluated based on visual examination and metal flipper tags and passive integrated transponder tags were documented or applied, if not already present. Curved carapace length and width measurements were obtained, and sex identification was determined based on tail length. A satellite-linked transmitter with FASTLOC GPS capacity (Wildlife Computers MK-10AF) was attached via a tether attached to the caudal peduncle prior to release (NMFS SEFSC –National Marine Fisheries Service Southeast Fisheries Science Center, 2008). Only robust, active turtles without any evident major injuries were tagged. The entire process from capture to release required approximately 30 min. GPS locations were determined using Wildlife Computers DAP processor for all FASTLOC locations with a maximum number of four GPS locations per day for each tag.

Behavior state and track positions were estimated with a hierarchical state space model (Jonsen et al., 2007; Jonsen, 2016) for all individuals that had transmitter durations lasting longer than 10 days. Behavior state was determined by estimating the parameters of a 2-state correlated random walk model. The behavior states were "transit," relatively fast and directional movement ($b = 1.0$), or "foraging," an area-restricted search ($b = 2.0$) characterized by frequent changes in speed or direction of movements. The terms "transit" and "foraging" are used here as a convenient shorthand to describe differences in turtle movements, but do not necessarily imply that turtles are engaged in goal-oriented swimming ("transit") or consuming food ("foraging"). Determining the relative contributions of ocean currents to the net movement of a sea turtle is critical to inferring volition from track data (Gaspar et al., 2006). Location uncertainty was estimated based on Argos location codes (6 categorical codes) that have estimated error, we also had GPS data that were assigned to Argos location code = 3 (the most accurate) for all analysis. We excluded all Argos "Z" location codes because they have no estimated error.

All estimated tracks and behavior states were calculated in R (3.6.0, R Development Core Team, 2019) using the r-package bsam (Jonsen, 2016). Although the hierarchical model corrects points based on location quality, proximity to previous positions,

TABLE 1 | Turtle summary data.

PTT	Curved carapace length	Release date	End date	Days of deployment	Nesting beach flipper tag	Nesting beach from satellite track
140161	147.0 cm	20-Sep-2015	30-Nov-2015	71		
140164	153.0 cm	19-Sep-2015	11-Dec-2015	82		
140165	142.0 cm	20-Sep-2015	18-Apr-2016	210		Trinidad
140166	158.0 cm	20-Sep-2015	6-Jan-2016	108		
140168	148.5 cm	20-Sep-2015	5-Apr-2016	198	Panama	Panama
151391	150.0 cm	22-Sep-2015	4-Dec-2015	72		
174484	130.2 cm	14-Sep-2018	30-Dec-2018	107	Costa Rica	
174485	170.5 cm	13-Sep-2018	22-Nov-2018	70		
174486	147.5 cm	14-Sep-2018	12-Apr-2019	210		Honduras
174494	155.4 cm	16-Sep-2018	24-Feb-2019	161		
174495	148.0 cm	13-Sep-2018	17-Nov-2018	64		
174496	157.8 cm	14-Sep-2018	17-Sep-2018	3	Costa Rica	
174497	151.2 cm	17-Sep-2018	19-Nov-2018	63		
174500	152.7 cm	13-Sep-2018	18-May-2019	247		Costa Rica
174503	150.4 cm	17-Sep-2018	24-Mar-2019	187	Columbia	Columbia
181707	148.0 cm	8-Sep-2019	11-Jan-2020	125	Columbia	
181709	153.3 cm	7-Sep-2019	5-Jan-2020	120		
181711	152.9 cm	8-Sep-2019	15-Dec-2019	98	Panama	
181714	157.7 cm	8-Sep-2019	10-Jan-2020	123		(Trinidad?)
184107	155.4 cm	7-Sep-2019	15-Dec-2019	99	Panama	

Tag 181714 stopped transmitting before nesting but she was off the north coast of Trinidad.

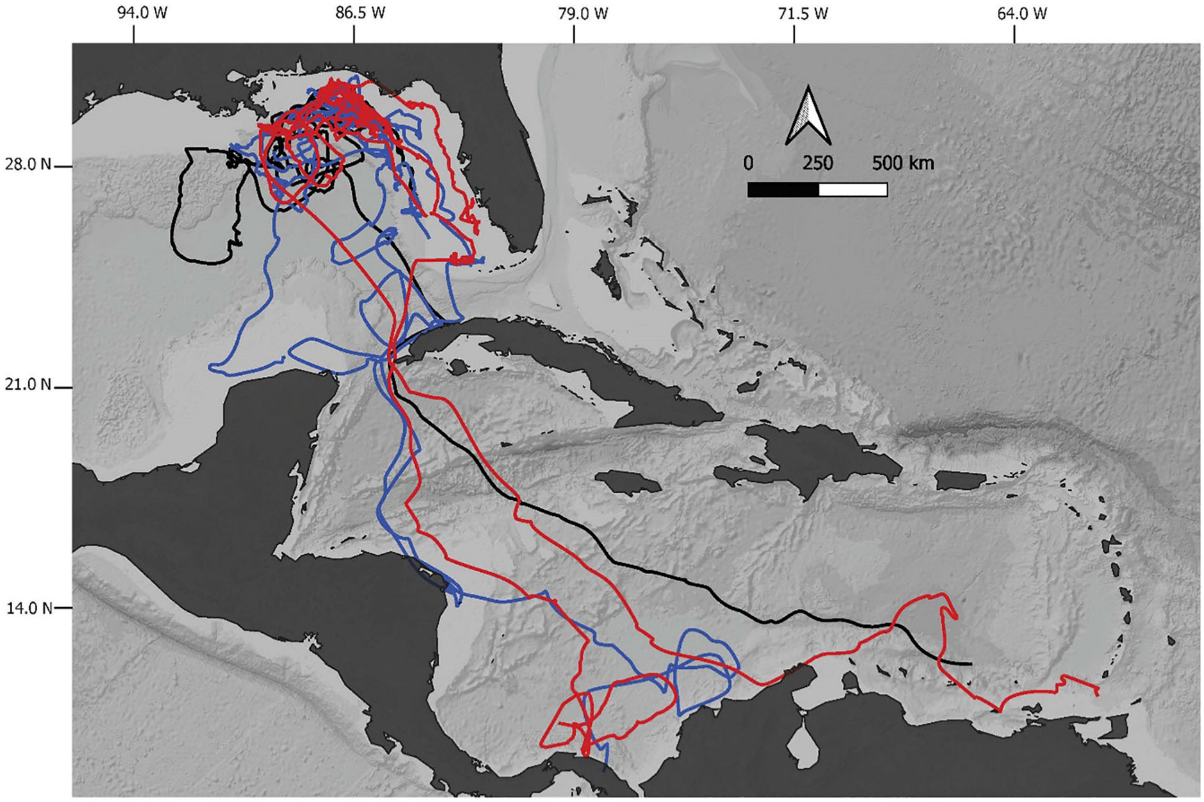

FIGURE 1 | Leatherback tracks by Year 2015 are in red, 2018 in blue, and 2019 in black.

and the parameters of other individuals, some data were removed before analysis by inspection. ARGOS satellite location data were first filtered removing all points north of latitude 30.30, west of longitude -94.4, south of latitude 7.55, east of longitude 66.00, and all positions on land (<1 km from shoreline). Track lines may appear over land if two consecutive points were on opposite sides of a landmass but no positions on land were included in analysis. We also removed all locations after a transmitter prematurely detached.

Due to the nature of ARGOS data, large gaps in transmission are common. Under optimal conditions, we achieved the programmed transmission of 6 positions per 24-h period. Many days had missing data, thus we chose to model time steps of 1 (1 interval per day), 0.5 (2 intervals per day or one every 12 h), and 0.25 (4 intervals per day or regular intervals of 6 h). For three individuals (140165, 174494, and 174500) large gaps in transmissions (1 to 3 months) between a portion of the southern movement in the GOM until transmissions resumed at or near presumptive nesting beaches near the coast of Honduras resulted in unrealistic estimated pathways (e.g., cross land, long straight lines). In each case, too few data points remained after the large temporal gap in data to facilitate analysis. The inclusion or exclusion of these data points near nesting beaches had no noticeable impact on behavior state analysis for all other individuals.

We used a kernel density estimator (KDE) to visualize the distribution of high use areas from the SSSM predicted leatherback locations each year. To be comparable to Aleksa et al. (2018b) the KDE was approximated in QGIS3 using the heatmap tool with radius set to 56.419 km (or 10,000 km^2) and color densities in increments of 12.5% of the maximum density. Warm colors (reds) to cooler colors (blues) represent the gradient from maximum density to minimum density. We masked densities less than 12.5% of the maximum.

RESULTS

In 2015, 2018, and 2019, a total of twenty leatherback turtles were satellite tagged (**Table 1**). All turtles were sexually mature based on carapace length (>113 cm, Avens et al., 2020). 18 of the turtles were female and two were males based on tail length (turtle IDs, 140161, and 140166). Seven of the females had been previously flipper tagged on nesting beaches (**Table 1**) in Colombia (*n* = 2), Costa Rica (*n* = 2), and Panama (*n* = 3).

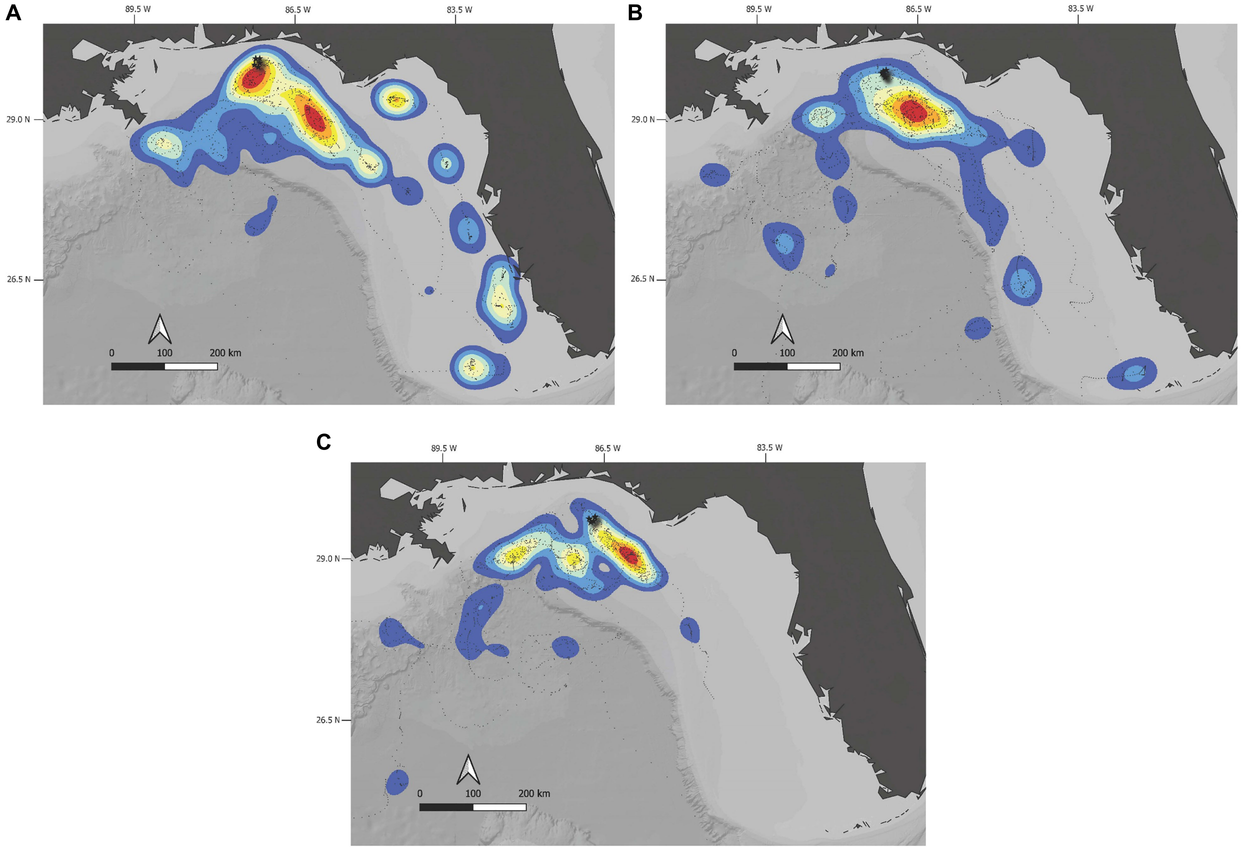

FIGURE 2 | Kernel density maps by year. Colors represent 12.5% increments of the proportion of total density; warmer colors (reds) are greater density and cooler colors (blues) are lower density. The lowest 12.5% of densities are not shown. Initial capture locations are shown with a star, all other estimated locations are shown by black dots. Kernel density radius was 56.419 km. **(A)** 2015 Kernel Density Map. **(B)** 2018 Kernel Density Map. **(C)** 2019 Kernel Density Map.

We successfully tracked 19 of these turtles between 63 and 247 days (**Table 1** and **Figure 1**). One tag deployed in 2018 prematurely failed and was excluded from analysis. Between mid-October and the first week of December, ten of these turtles left the foraging area in the northern Gulf and began southward migrations, presumably to breed or nest in Central and South America. One of the males (140166) migrated and foraged along the Florida Coast until January 6, and did not appear to be returning to the Caribbean to breed at the end of its transmission (**Table 1** and **Figure 2**). Five of the females were tracked to nesting beaches, and nested in Colombia, Honduras, Panama, and Trinidad (**Figure 1**). Female turtle 181714 returned to the Caribbean but stopped transmitting in February 2020 north of Trinidad (**Figure 1**).

We delineated transit from foraging behavior with a state space model (Jonsen, 2016) and inspection of the statistically corrected positions. We observed three large scale patterns, a general foraging behavior delineated by behavior parameter $b > 1.7$, transit shown by movement parameter $b < 1.4$, and a series of estimates that switch rapidly between foraging and searching behavior $1.4 < b < 1.7$ (**Figure 3**).

Kernel Density maps are presented by year (**Figures 2A–C**) to demonstrate intensity of area use by leatherbacks in the eastern Gulf of Mexico for turtles tagged in this research. Use was generally similar among years with use of the west Florida shelf along with a few turtles foraging in the central Gulf of Mexico.

DISCUSSION

Our results build upon previous studies and fisheries bycatch records to demonstrate consistent use of the northeastern Gulf of Mexico as a foraging area for leatherback turtles (Garrison and Stokes, 2017; Aleksa et al., 2018b). Moreover, capture of turtles previously tagged on nesting beaches, as well as tracking turtles returning to nesting beaches, demonstrate the importance of the region for leatherbacks from numerous nesting areas. The northeastern Gulf of Mexico is likely advantageous due to its proximity to nesting assemblages in the Caribbean and availability of abundant prey. The leatherbacks we tracked leatherbacks spent nearly all their time foraging while on the continental shelf of the Florida Panhandle (**Figure 3**). Migration off the presumed foraging area began in late October and continued through early December, but it is not clear whether changes in water temperature, photoperiod, or prey abundance triggered movements from the presumed foraging area. Most of the leatherbacks moved south into waters of the west Florida continental shelf with the prevailing current direction. A smaller number moved across the deeper water of the central Gulf of Mexico during their southern migration, swimming against the Loop Current. The turtles migrating along the shelf likely foraged as they moved and engaged in intermediate behavior, perhaps due to the patchy availability of prey. In contrast, the turtles that migrated across the central Gulf tended to

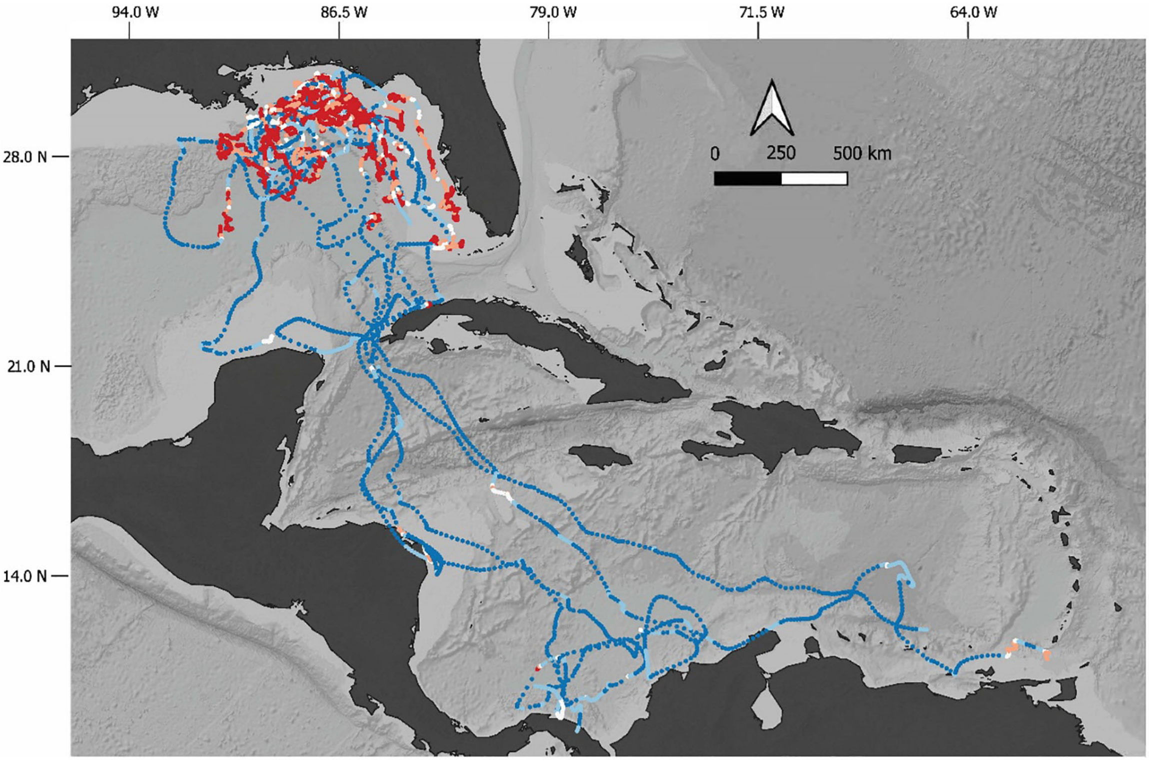

FIGURE 3 | Tracks and behavior states of leatherbacks along satellite tracks. Red represents foraging, blue represents migration, and orange/white/light blue represents searching/foraging.

engage in direct movements south until reaching the continental shelf in the southern Gulf of Mexico. The female turtles that entered the Caribbean migrated for a period, switched to the intermediate searching/foraging behavior, and then returned to transit behavior in a repeating cycle on their way to nesting beaches.

Neither of the male leatherbacks left the Gulf of Mexico, and male turtle 140161 was not tracked long enough to leave the northeastern Gulf foraging area. This turtle grouped genetically with the Florida nesting assemblage (Peter Dutton pers. comm.) which is of note as no females have been tracked from Florida into the Gulf, nor was this assemblage represented in leatherbacks captured in the pelagic longline fishery in the Gulf (Stewart et al., 2016). Male turtle 140166 (**Figure 4**) left the foraging area in the northeast Gulf, and remained on the west Florida shelf until the tag stopped transmitting in early January 2016, 108 days after deployment. The turtle was genetically linked to the Caribbean (Peter Dutton pers. comm.) but did not appear to be migrating back to the Caribbean for mating, suggesting that males do not necessarily return from the Gulf every year for mating near nesting beaches.

The possible secondary foraging area off southwest Florida identified in Aleksa et al. (2018b) was based on data from a limited number of turtles from our 2015 deployments. One of those turtles was the male 140166, which used the area extensively after migrating south from the foraging area off the Florida Panhandle. With the larger sample size presented here, the entire west Florida shelf is a heavily used foraging area as turtles migrate south in the autumn and winter. Fine scale distribution and abundance of foraging turtles in high use areas along the shelf is likely variable based on prey availability in a given year; however, it is clear that this foraging area provides a source of jellyfish as turtles make their migration back to the Caribbean and/or the northern Gulf of Mexico foraging area.

For those turtles that migrated south in the Gulf and returned to the Caribbean, all followed a similar pattern and entered the Caribbean using the eastern half of the Yucatan Channel (**Figure 1**). In contrast, when migrating from the Caribbean into the Gulf, turtles used the western half of the Yucatan Channel (see Aleksa et al., 2018b, **Figure 1a**). This pattern is likely due to prevailing currents in the channel which flow northward in the west and southward in the east. The passage between Cuba and the Yucatan is a corridor between nesting beaches in Central and South America and the Gulf of Mexico, and should be considered for protected area status due to its importance to leatherback migration.

Our results indicate the high use of the eastern Gulf of Mexico compared to the prediction of relative abundance of leatherbacks in Gulf of Mexico presented in Grüss et al. (2018, see **Figure 7**). Their results are based on reported bycatch of leatherbacks in the pelagic longline fishery rather than telemetry data as presented here. We found extensive use of the west Florida shelf that was not

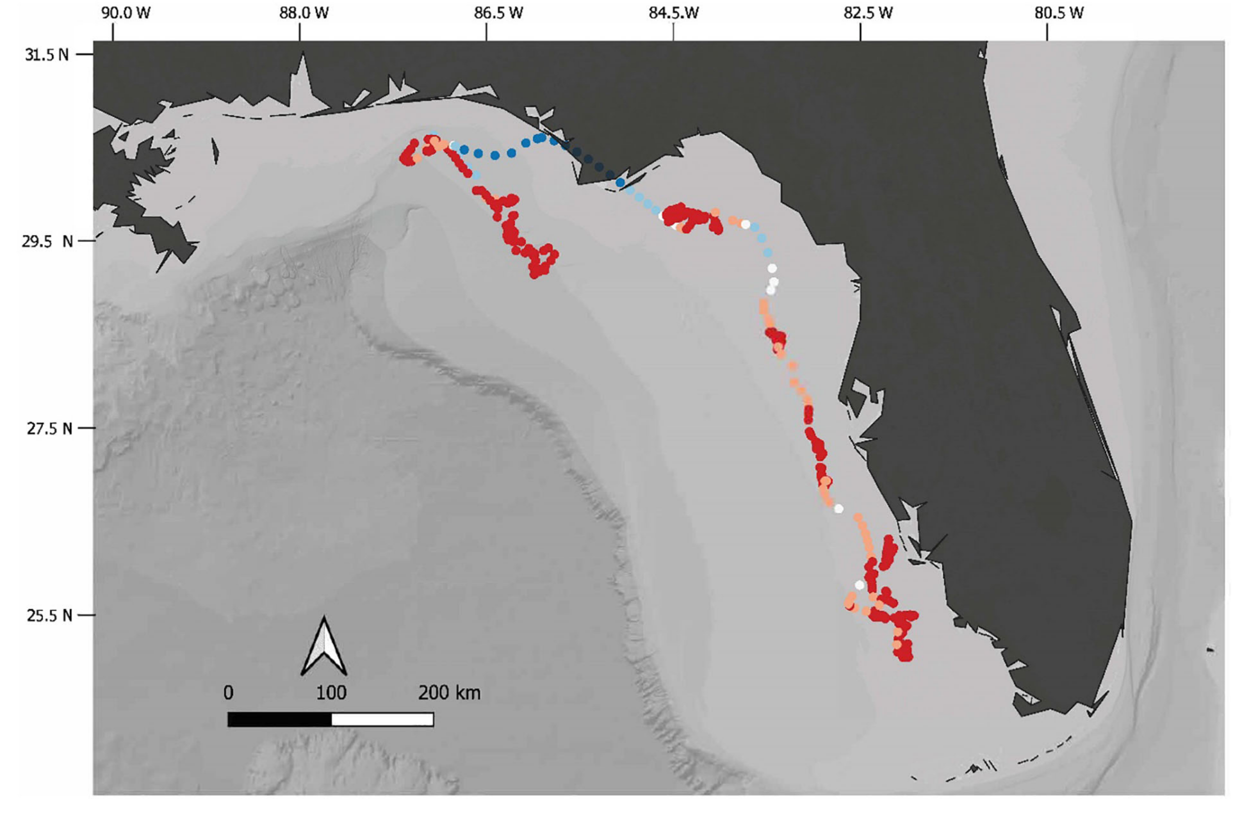

FIGURE 4 | Track and behavior of turtle 140166. Red represents foraging, blue represents migration, and orange/white/light blue represents searching/foraging.

predicted by Grüss et al. (2018), but this is likely because pelagic longline effort data were used to generate their predictions, and effort is extremely low in this region. Bycatch of leatherbacks in the pelagic longline fishery in the Gulf of Mexico is highest in the spring and summer (Quarters 2 and 3) with 11 of 14 observed captures of presumed adult turtles in 2015 occurring in these seasons (Garrison and Stokes, 2017, **Table 4**). Most of our telemetry data are from autumn. The majority of turtles tracked here did not use the high abundance central Gulf of Mexico area identified in Grüss et al. (2018), but the higher bycatch in spring and summer in the Gulf of Mexico suggests that the central Gulf of Mexico area is an important migratory route for leatherbacks returning to the Gulf from the Caribbean. Aleksa et al. (2018b) showed tracks of returning females that used the central Gulf as such a route on their way to the foraging areas off the Florida Panhandle or the Bay of Campeche. Furthermore, our research demonstrates use of the central Gulf in the autumn for foraging as well as when migrating back to the Caribbean (**Figures 1**, **3**). The central Gulf areas used by some of the leatherbacks in our research overlaps with areas of high pelagic longline fishery effort and observed bycatch (see **Figure 3** in Garrison and Stokes, 2017). These areas are also consistent with those predicted to have high abundance by Grüss et al., 2018. Bycatch of leatherbacks in the pelagic longline fishery and post-release mortality are a concern and needs further research to provide quantitative estimates of impacts on annual survival. Future research should also track turtles in other seasons as bycatch records clearly indicate that leatherbacks are present in the Gulf year-round as well as assess the importance of the central Gulf as a migratory pathway to and from the Caribbean.

These results build on the previous research on leatherbacks in the Gulf of Mexico. We have identified several areas that are used by leatherbacks in the Gulf, especially in the late summer through the early winter. Leatherbacks occur in the Gulf year-round so continued research is needed to understand their distribution and behavior throughout the entire year as well as the effects of fisheries bycatch and other anthropogenic threats. The northeastern Gulf is a highly used foraging area in the summer and autumn as is the west Florida shelf and central Gulf as leatherbacks move south in the autumn and winter. In addition, the distinct pattern of entry and exit from the Gulf into the Caribbean makes the Yucatan Channel a seasonally important area for all Caribbean nesting leatherback assemblages.

DATA AVAILABILITY STATEMENT

The datasets presented in this article are not readily available because these data are part of an ongoing study. All data will be uploaded to a public repository once the study is complete. Requests to access the datasets should be directed to CS, chris.sasso@noaa.gov.

ETHICS STATEMENT

National Marine Fisheries Service's Atlantic Institutional Animal Care and Use Committee (IACUC) reviewed and approved all procedures and methods. The animal study was reviewed and approved by NOAA Fisheries.

AUTHOR CONTRIBUTIONS

CS contributed to conception, field operations, analysis, and writing. SB contributed to conception, field operations, and writing. PR and NP contributed to analysis and writing. MJ, BS, and DS contributed to field operations and writing. All authors contributed to the article and approved the submitted version.

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Use of Drift Studies to Understand Seasonal Variability in Sea Turtle Stranding Patterns in Mississippi

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Stranded sea turtles provide valuable information about causes of mortality that threatens these imperiled species. Many potential factors determine whether drifting sea turtles are deposited on shore, discovered by people, and reported to stranding networks resulting in successful documentation. We deployed 182 sea turtle cadavers and 115 wooden effigy drifters with affixed GPS-satellite tags to study stranding probability in the northern Gulf of Mexico (nGOM) in an effort to better understand seasonal stranding variations in this region. Public reports of beached carcasses were recorded to determine reporting rates. Season and distance from shore greatly influenced beaching results. During winter months when strandings are infrequent and sea turtle abundance is likely low in cold nearshore waters, carcasses had an 80–90% probability of beaching. Beaching probability was reduced to 37–50% during the spring, which is the period of greatest strandings in this region. During summer months when relatively few strandings are documented, the probability of a carcass beaching dropped to only 4–8%. Low summer stranding rates were coincident with higher rates of decomposition (7%) attributed to warmer water temperatures, more frequent scavenging (69% of carcasses), and shifting wind and current patterns which drive carcasses offshore or to remote locations. As waters cooled in the fall, probability of carcasses beaching increased to 40–48%, coincident with a small pulse in strandings that often occurs during this period. Only 28% of carcasses and effigies came ashore on mainland beaches and were easily available for discovery by the public, 49% were on barrier islands that are publicly accessible and 23% beached in dense salt marshes where discovery would be unlikely. The 47% of objects that did not beach included those lost at sea and carcasses that were likely scavenged or decomposed. Only 22% of beached carcasses were reported due to infrequent (11%) reporting on barrier islands.

Notably, only 50% of carcasses deposited on mainland beaches were reported, which was lower than anticipated. We recommend additional efforts to increase reporting rates of carcasses by the public and use of dedicated surveys to detect stranded sea turtles, especially on barrier islands in this region.

Keywords: carcass drift, carcass decomposition, sea turtle strandings, endangered species, stranding seasonality, stranding reporting rates, sea turtle effigies

INTRODUCTION

Sea turtle strandings are one of the few direct indicators of at-sea mortality. Stranding data provide critical information about mortality sources, locations where such threats occur, and other informative characteristics, such as temporospatial trends (e.g., Mancini et al., 2011; Koch et al., 2013; Foley et al., 2019). However, the number of documented sea turtle strandings only represents a minimum measure of mortality, as the probability that a dead or impaired sea turtle will drift ashore and become documented is influenced by oceanographic and atmospheric conditions, decomposition and scavenging rates, shoreline characteristics, as well as the extent of human presence and the effectiveness of detection, and reporting mechanisms. These factors, particularly those related to environmental conditions, can be highly variable by locality and time of year.

Previous studies conducted in the United States south Atlantic derived mortality estimates using stranding data (Epperly et al., 1996; Hart et al., 2006). By comparing observer data and stranding reports, Epperly et al. (1996) determined the number of strandings on North Carolina beaches represented only 7–13% of the estimated fishery-induced mortality. They also noted that strandings during the winter months were a poor indicator of at-sea mortalities because carcasses were often transported offshore by bottom currents. Hart et al. (2006) evaluated the influence of nearshore physical oceanographic and wind regimes on sea turtle strandings to decipher seasonal trends and stranding patterns on North Carolina oceanfront beaches. To accomplish this, results from 1967 and 1973 oceanographic drift bottle experiments were reevaluated and used in conjunction with stranding data. Return rates of drift bottle experiments provided an upper limit estimate that only 20% of sea turtle carcasses will strand on local beaches. Findings suggest that carcasses are only likely to strand if mortality occurs within 20 km or less from shore. Mortalities occurring farther from shore have an even lower, perhaps negligible, probability of stranding on beaches. Additionally, the probability of a carcass stranding varies by season due to variable oceanographic conditions (Hart et al., 2006). Koch et al. (2013) also used drifters combined with stranding data and found similar results off Baja California Sur; stranding rates varied widely and usually do not exceed 10–20% of total mortality, even in nearshore waters.

Despite the importance of stranding (and reporting) probability in the use of stranding-derived data, there have been very few studies of this topic and none in the Gulf of Mexico (GOM). Because strandings are influenced by oceanographic and seasonal conditions, the probability of carcasses stranding in the GOM could be considerably different than reported elsewhere. The United States South Atlantic Bight (SAB), which is the closest area previously studied, is generally a more energetic region in comparison to the northern Gulf of Mexico (nGOM). The SAB is strongly influenced by the Gulf Stream on its outer shelf and has greater overall wind generated wave and current fields than occur in the nGOM. Seasonal shifts in atmospheric conditions favoring onshore drift in spring and early summer, transitioning to conditions favoring offshore flows in fall and winter, occur in both systems. However, the more northerly latitude of the SAB results in a stronger pre-frontal setup, frontal passage, and return current flow than the nGOM. The nGOM attains higher spring and summer inshore temperatures, resulting in more benign winds, current flows, and likely faster decomposition of carcasses.

Beginning in 2010, the Sea Turtle Stranding and Salvage Network (STSSN) documented high numbers of strandings, primarily of Kemp's ridley (*Lepidochelys kempii*) sea turtles, along the Mississippi (MS), Alabama (AL), and Louisiana (LA) coasts (STSSN[1]). Surveillance and documentation of sea turtle strandings in this region was highly variable prior to this period and was enhanced considerably following the *Deepwater Horizon* oil spill in April 2010. Over the last decade, sea turtle strandings have exhibited a relatively consistent seasonal occurrence characterized by peak activity during March to June followed by a marked reduction during summer months and slight resurgence in the fall (October–November). Necropsy findings also have been consistent and indicate a sudden cause of mortality in the majority of these strandings based on normal body mass, evidence of recent feeding prior to death (often on fin fish), frequent presence of sediment within the respiratory tract, and absence of significant disease or other apparent cause (Stacy, 2014). These findings are similar to previous reports of mortality attributed to incidental capture (bycatch) by fisheries (Shoop and Ruckdeschel, 1982; Shaver, 1991; Caillouet et al., 1996; Casale et al., 2010); however, a specific cause(s) of the spring peaks in strandings on the nGOM coast remains unidentified. Better understanding of the drivers of seasonal variation and distribution of strandings could significantly improve ongoing mortality monitoring and investigation, and enable comparisons of stranding data with anthropogenic activities of concern.

The objectives of this study were to (1) use floating sea turtle cadavers and effigy drifters to determine how environmental conditions influence seasonal variability in sea turtle stranding patterns in MS, where many nGOM strandings are found and (2) determine the proportion of stranded sea turtles originating from nGOM waters reported to the STSSN. By using actual sea

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[1] https://grunt.sefsc.noaa.gov/stssnrep/

turtle carcasses, we were able to determine the percent of dead turtles that strand on nGOM beaches as well as the effectiveness of stranding detection and reporting. Our methodology has wide applications for use to determine stranding probabilities and detection in other regions. Improved information on stranding rates will help scientists and managers further understand how reported strandings relate to total mortality and potential causes in the nGOM.

MATERIALS AND METHODS

Carcasses and Effigies

All carcasses used in this study were sea turtles that died during cold-stunning events, which occur when nearshore water temperatures persistently fall below 10°C in susceptible localities in the Atlantic and GOM. These events provide the most readily available source of non-decomposed carcasses for research purposes. All sea turtles were determined dead by qualified, permitted individuals based on absence of detectable cardiac contraction and were frozen at 0°C until use. We previously studied decomposition rates of unfrozen or frozen sea turtle carcasses and found no differences that are pertinent to our study objectives (Cook et al., 2020). Kemp's ridley (*Lepidochelys kempii*, $n = 57$) and green (*Chelonia mydas*, $n = 125$) sea turtles were used based on availability. Carcasses ranged in size from 18.4 to 38.9 cm straight carapace length (SCL) (mean = 27.2 cm SCL).

Prior to deployment, frozen sea turtle carcasses were flipper tagged for identification, thawed in a water bath, and allowed to decompose until they achieved positive buoyancy due to accumulation of postmortem gases. This treatment ensured postmortem condition was similar among study animals and was developed to resemble the state at which dead turtles first reach the surface and begin to drift (Reneker et al., 2018). The target carcass condition was <50% of the carapace exposed above the waterline and all appendages underwater at the time of deployment. The use of actual bloated sea turtle carcasses allowed for us to incorporate natural decomposition and scavenging into our study design.

In addition to sea turtle carcasses, wooden effigies were deployed for comparison. The use of an effigy removed the influence of decomposition and scavenging and allowed us to monitor object drift and temporal trends in strandings with greater sample sizes. Effigy use also offered the potential for comparison to future studies where use of actual turtles is infeasible. Wood-block effigies were constructed of three square pieces of commercial southern yellow pine (middle block, 11.25″ × 11.25″ × 1.5″; upper and lower blocks, 5.5″ × 5.5″ × 1.5″) centered and attached with glue and screws. Small, 2″ × 3″ × 1″ SPOT Trace (SPOT) GPS satellite transmitters were vacuum sealed in plastic, placed in small 0.5 L plastic jars and attached to all carcasses and effigies using 4 mm braided polyethylene twine. The twine was tied through a hole drilled through the effigy or marginal bone of the carcasses. The jars were positioned so they would float approximately 30 cm behind the objects (**Figure 1**). The SPOT transmitted locations every 10 min and battery life lasted an average of 27 days before the signal was lost. GPS location was accurate to within a meter and objects were monitored in real-time over the course of their deployment.

Drift Study Methodology

Sea turtle carcass and effigy deployments began in January of 2017, in coastal and offshore waters in the nGOM. Deployments occurred at five sites (**Figure 2**) selected in areas with documented sea turtle occurrence (Coleman et al., 2016), known shrimping effort, or in areas of other potential mortality sources (i.e., ship traffic). Sites were also selected in various depths because the time required for a dead sea turtle to decompose and float, in the case of sinking carcasses, varies depending on temperature and depth (influenced by water pressure) (Cook et al., 2020). More gases are needed to float at greater depths. For example, if the bottom temperature was 24°C at the three sites, the time required for a carcass to float would increase from ∼1.5 days (at 5 m), ∼2.5 days (at 10 m), and ∼5.3 days (at 25 m) as depth increased. Drift studies consisted of both biweekly (sites A, B, and C) and monthly (sites D, E) deployments (**Figure 2** and **Table 1**).

Approximately every 2 weeks, from January through December 2017, a deployment date was chosen based on favorable weather conditions. For each deployment, 2–3 bloated

FIGURE 1 | Sea turtle carcasses, wood effigies and satellite tags at deployment location.

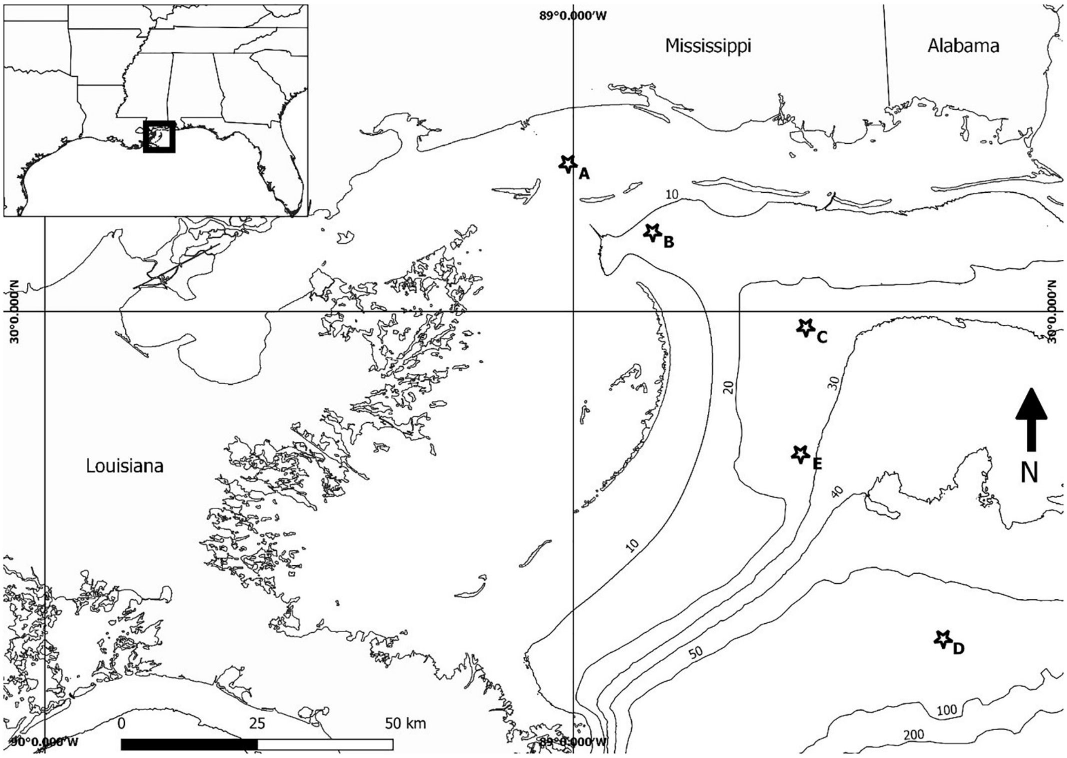

FIGURE 2 | Sea turtle carcass and wood effigy deployment locations. Deployments occurred twice a month from January to December at sites A, B, C and monthly from February–May and July at sites D and E. Depth contours are in meters.

sea turtle carcasses (Reneker et al., 2018) and 1–3 wooden effigies, hereafter referred to collectively as floating “objects,” were released at three pre-selected deployment locations (A, B, and C), which were ∼11, 27, and 41 km, respectively, from mainland MS. In addition, five monthly deployments were conducted in February–May and July at sites ≥68 km from mainland MS (D, E). The objective of these two more distant sites was to determine the maximum distance a carcass could drift and still strand in MS. Due to logistics, only wooden effigies were used for the monthly, distant deployments. The first two deployments occurred at Site D (110 km from mainland MS). Drift tracks from the first two deployments indicated objects that far south of MS would likely never beach on the MS mainland or barrier islands. Therefore, the site location was moved to Site E (68 km from mainland MS) for the remaining three deployments.

TABLE 1 | Location of carcass and effigy deployments.

Site ID	Name	Latitude	Longitude	Distance from mainland MS (km)	Distance to closest point of land (km)
A	Inshore	30.28	−89.01	11.39	6.40
B	Nearshore	30.15	−88.85	27.32	9.93
C	Offshore	29.97	−88.56	40.70	27.00
D	Louisiana	29.38	−88.30	108.62	70.89
E	Chandeleur	29.73	−88.57	68.02	28.60

At each deployment site, sea turtle carcasses and effigies were released off the side of the boat simultaneously. GPS location, deployment time, weather, and sea conditions were recorded. A YSI-85 was used to measure dissolved oxygen, temperature, and salinity of the surface water at each deployment location. Air temperature, wind speed, and wind direction were collected with an anemometer. Photographs and video were taken for reference. Once objects were deployed, they were allowed to float naturally with the winds and currents. We observed them for ∼10 min to ensure nothing was tangled and all were floating well before departing. Real-time monitoring occurred throughout the entire deployment to determine where objects travelled, if a transmitter stopped working, or if the object came ashore. At the conclusion of each deployment, carcasses and effigies were assigned outcomes of beached or did not beach. Objects were classified as beached if the object came ashore with the SPOT still attached. Outcomes classified as not beached included instances where the tag ceased transmitting or when the carcass/effigy was never recovered. Secondary determinations were made when only SPOT tags beached. If we recovered a SPOT without the turtle attached, we attributed the loss to probable scavenging if the twine was missing or parted, or shark bite marks were observed on the plastic jar, which was not observed in any of the effigies (**Figure 3A**). If the twine was intact and the carcass was missing or tethered to disarticulated bone, we attributed likely loss of the carcass to decomposition (**Figure 3B**).

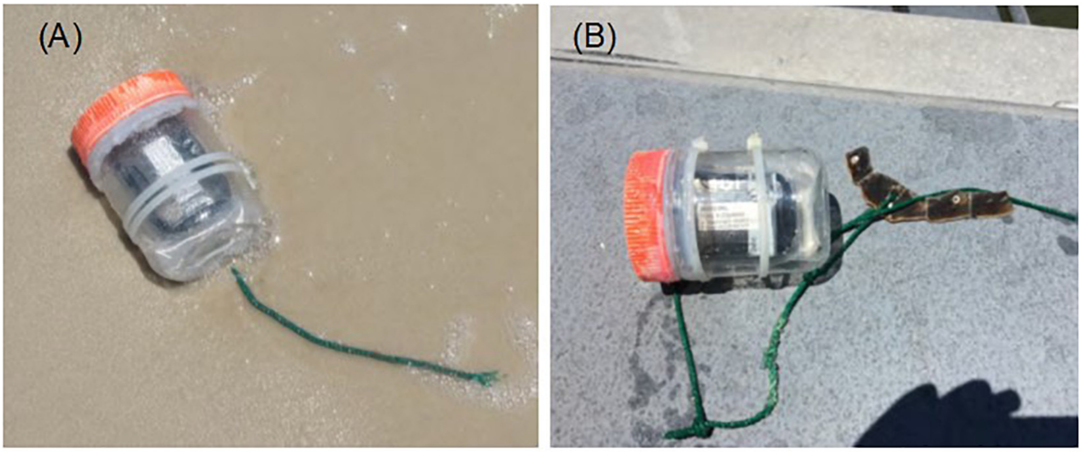

FIGURE 3 | (A) Example of beached jar with the twine still attached but broken prior to where a carcass was attached. These carcasses are presumed to have been scavenged prior to the jar beaching. There are no instances where a jar broke free from an effigy. **(B)** Example of beached jar with a portion of the rear carapace remaining attached to the twine. These carcasses are presumed to have decomposed prior to the jar beaching.

Once objects reached the beach, they were located as quickly as possible to evaluate whether the carcass or effigy were still attached to the SPOT tag. If the carcass was still attached, it was photographed and the decomposition code was evaluated using the same scale as the pre-deployment classifications (Reneker et al., 2018). The second portion of the study was to determine the proportion of strandings that were reported by the public to the STSSN. Therefore, all study carcasses that beached were left in place after initial documentation. In addition, we removed the SPOT tag and twine at the time of discovery, whenever possible, to minimize any influence on later discovery or reporting. Local STSSN participants were notified of the location of the carcass as well as its unique identification number. If the carcass was subsequently reported to the STSSN by the public, the date and time of the call were recorded. If reported multiple times, authorized individuals removed the carcasses from the beach.

Environmental Data

Water temperature at the surface and seafloor as well as surface current and wind speed at sites A–E were obtained from the Northern Gulf of Mexico Operational Forecast System (NGOFS) to investigate the seasonal variations of environmental conditions of the study region. NGOFS is a three-dimensional model that provides hourly wind, currents, water temperature and salinity over the northern Gulf of Mexico continental shelf (Wei et al., 2014). NGOFS grid resolution ranges from 10 km on the open ocean boundary to ~600 m near the coast. The NGOFS sea surface temperature and wind at the five sites were compared with *in situ* observations collected during the 2017 deployments to evaluate modeling data. Both model temperature and wind were concurrent with observations. The modeled and observed wind magnitudes were generally on the same order and direction, the difference was mostly less than ± 45°. A 40 h low-pass Lanczos filter was applied to wind and current data to remove any high frequency oscillations with periods shorter than 40 h (e.g., diurnal and semi-diurnal tides, near-inertial oscillations). The 40 h low-pass filtered data showed the long-term wind and current variations. Turtle carcasses and effigies were tracked as Lagrangian surface particles forced by the drifting velocity, which is a combination of wind $W_{\mathrm{u,v}}$ and surface current $C_{\mathrm{u,v}}$ in the east (u) and north (v) direction in the north central Gulf of Mexico (Nero et al., 2013). The drifting velocity $U_{u,v}$ was estimated using a similar formula as in Nero et al. (2013):

$$U_{u,v} = C_{u,v} + \left(W_{u,v} - C_{u,v}\right) K$$

The second term on the right-hand side of the equation is the apparent wind forcing $W_{\mathrm{u,v}} - C_{\mathrm{u,v}}$ adjusted by a leeway drift coefficient K. The leeway coefficient K ranged from 0.02 to 0.05, and the average value of 0.035 was used for K in this study as suggested by Nero et al. (2013).

Statistical Analysis

Generalized linear mixed models (GLMM) were used to estimate the binomial probability (of drifting carcasses and effigies) to beach by season and deployment site. Two separate models were run. The first utilized a combination (n = 263) of carcasses and effigies. To maximize comparability of effigies and carcasses, only effigies with drift durations that did not exceed observed carcass decomposition rates were selected. Maximum drift durations were calculated monthly for all beached carcasses and effigies. Any effigy drift duration that exceeded the maximum carcass drift duration for that month was excluded from the analysis. The second GLMM only included carcasses (n = 163). In both instances, all deployments from sites D and E were excluded because deployments did not occur monthly. Additionally, all transmissions lost within ≤5 h were removed. Season was divided into four periods of interest that characterize the typical seasonal variation in strandings for the study area: winter pre-season (January–February), spring peak (March–June), summer lull (July–September), and fall pulse (October–December). Season, deployment site (A, B, or C) and object type (carcass or effigy) were examined as fixed effects in the model utilizing both carcasses and effigies, but only season and deployment site effects were examined for the carcass only model. Individual carcasses and effigies within a deployment event were treated as replicates. A Type III Test of Fixed Effects (alpha = 0.05) was used to test for significant effects of season, deployment site and object type. Binomial probabilities by season and site location were based on predicted marginal means (Searle et al., 1980). Multiple comparisons in the differences of estimated marginal means among seasons and deployment sites were tested at an alpha = 0.05 with a Tukey–Kramer correction. The GLMM models, estimated marginal means and multiple comparison tests were implemented using the GLIMMIX procedure in the SAS/STAT component of SAS, version 9.4 (SAS Institute Inc., Cary, NC, United States).

RESULTS

Carcass and Effigy Drift Results

Deployments were conducted from January–December 2017. Over the course of 26 trips, 297 objects, 182 carcasses (61%; **Figure 4A**) and 115 effigies (39%; **Figure 4B**) were released. Over half (53%) of the objects deployed beached (*n* = 156). Beached objects were comprised of 41% (*n* = 64) sea turtle carcasses and 59% (*n* = 92) effigies. The remaining 47% (*n* = 141) of objects that did not beach were primarily sea turtle carcasses (84%, *n* = 118); only 16% (*n* = 23) of effigies did not beach. The fate of these objects included 23% of carcasses (*n* = 46) and effigies (*n* = 23) classified as unknown because either the SPOT stopped transmitting, the SPOT battery life expired while still drifting, or we were unable to recover the object. Forty percent (*n* = 72) of SPOT tags attached to carcasses beached without the sea turtle attached or with only part of the shell remaining; this did not

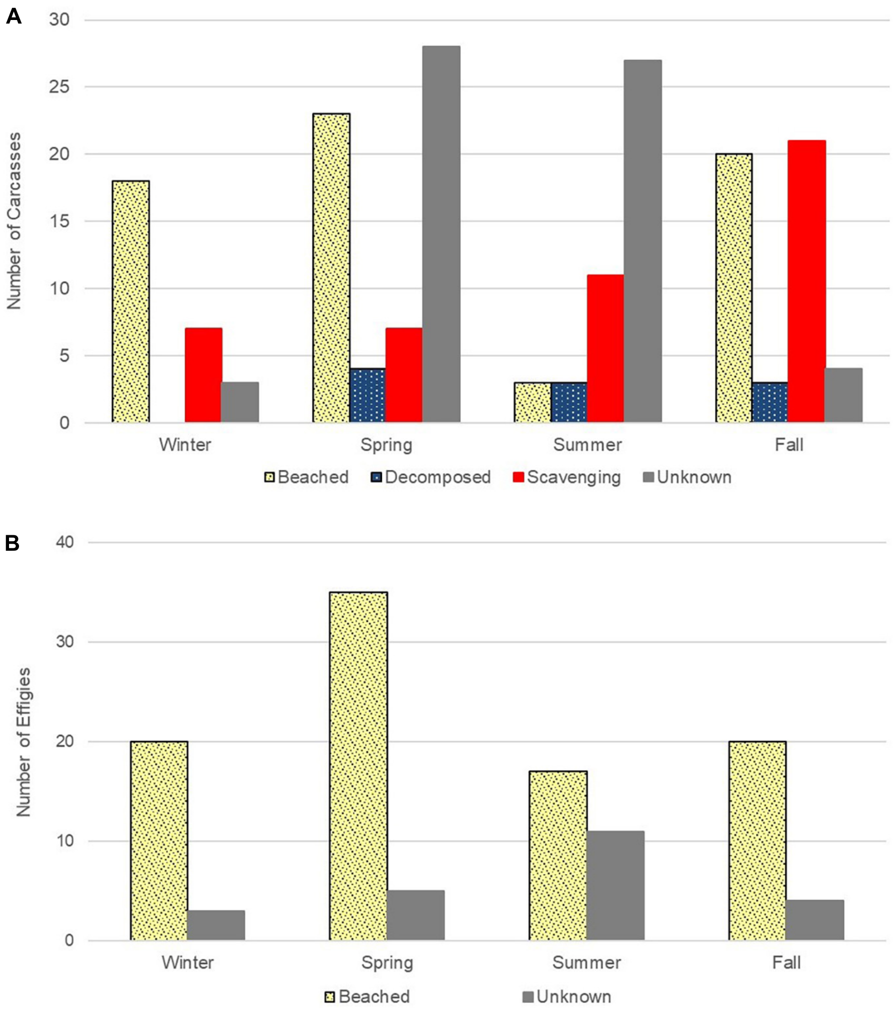

FIGURE 4 | (A) Sea turtle carcass (*n* = 182) and **(B)** wood effigy (*n* = 115) outcome results by season. Both carcasses and effigies beached (*n* = 64 and *n* = 92, respectivly). Carcass (*n* = 46) and effigy (*n* = 23) outcomes were classified as unknown if the SPOT stopped working (*n* = 21), the SPOT battery life expired (*n* = 24) while still drifting, or we were unable to recover the object (*n* = 10). Only carcasses were decomposed (*n* = 10) or scavenged (*n* = 62).

occur with effigies. Based on the condition of twine, we suspect 62 were scavenged and 10 detached due to decomposition. **Figure 5** shows the outcome summary of all objects deployed over the 12-month period, and the Supplemental depicts monthly deployment results. The carcasses and effigies that beached drifted for an average of 3.7 days (range: 0.4–14.6 days) and travelled an average of 86.1 km (range: 9.4–411.8 km). The longest drift track, 411.8 km, of a beaching object was from an effigy deployed at site B in August. Over the course of 13.1 days, it drifted east toward Orange Beach, AL then drifted west and beached on Horn Island, MS. Although over half of deployed objects beached, where they beached was greatly impacted by the geography of the nGOM. Nearly half (49%, n = 76) of beached objects were located on barrier islands off MS (n = 62), LA (n = 12), or AL (n = 2). Only 28% (n = 43) of beached effigies and carcasses were found on mainland beaches, primarily in MS (n = 38). Four effigies beached in AL and one effigy beached in Pensacola, Florida. The remaining 23% of objects came ashore within remote marsh areas of MS (n = 10), LA (n = 26), and AL (n = 1) and would likely never be discovered if they were an actual stranded sea turtle.

Deployment site greatly influenced if and where objects eventually beached; as distance from shore increased, the likelihood of objects beaching greatly decreased. Also, as distance from mainland MS beaches increased the likelihood of carcass scavenging also increased (**Figure 5** and **Table 2**). Out of a total of 156 beached objects, 46% (n = 71) were from site A, 31% (n = 48) from site B, 20% (n = 31) from C, and 4% (n = 6) from E. Site A is closer to both Cat and Ship Islands (6 and 8 km, respectively) than Gulfport, MS (11 km). Although the barrier islands were closer, 42% (n = 30) of objects deployed from site A beached on the MS mainland and 31% (n = 22) beached on the MS barrier islands, followed by 17% (n = 12) beaching in northeastern LA marshes. Objects released from site A beached in all three MS coastal counties, but the majority beached in central Harrison County. Just over half (54%, n = 26) of objects deployed at site B beached on Cat, Ship, and Horn Islands. Objects from site B also beached in all three MS counties (10%, n = 5), the MS marsh (4%, n = 2), and on AL beaches (4%, n = 2). Although the Chandeleur Islands are only 11 km south of site B, only 8% (n = 4) of objects beached there. However, 19% (n = 9) beached farther west in the marshes of northeastern LA and the MS River Delta. Objects deployed at site C had the largest geographical drift distribution. Only a third

TABLE 2 | Final outcomes of sea turtle carcasses and effigies deployed at sites A, B, C, D, and E in the northern Gulf of Mexico during 2017.

Site	Beached	Decomposed	Scavenged	Unknown outcome	Total objects
A	76% (71)	7% (7)	11% (10)	7% (6)	94
B	51% (48)	3% (3)	26% (24)	20% (19)	94
C	33% (31)		30% (28)	37% (35)	94
D				100% (6)	6
E	67% (6)			33% (3)	9
Total	53% (156)	3% (10)	21% (62)	23% (69)	100% (297)

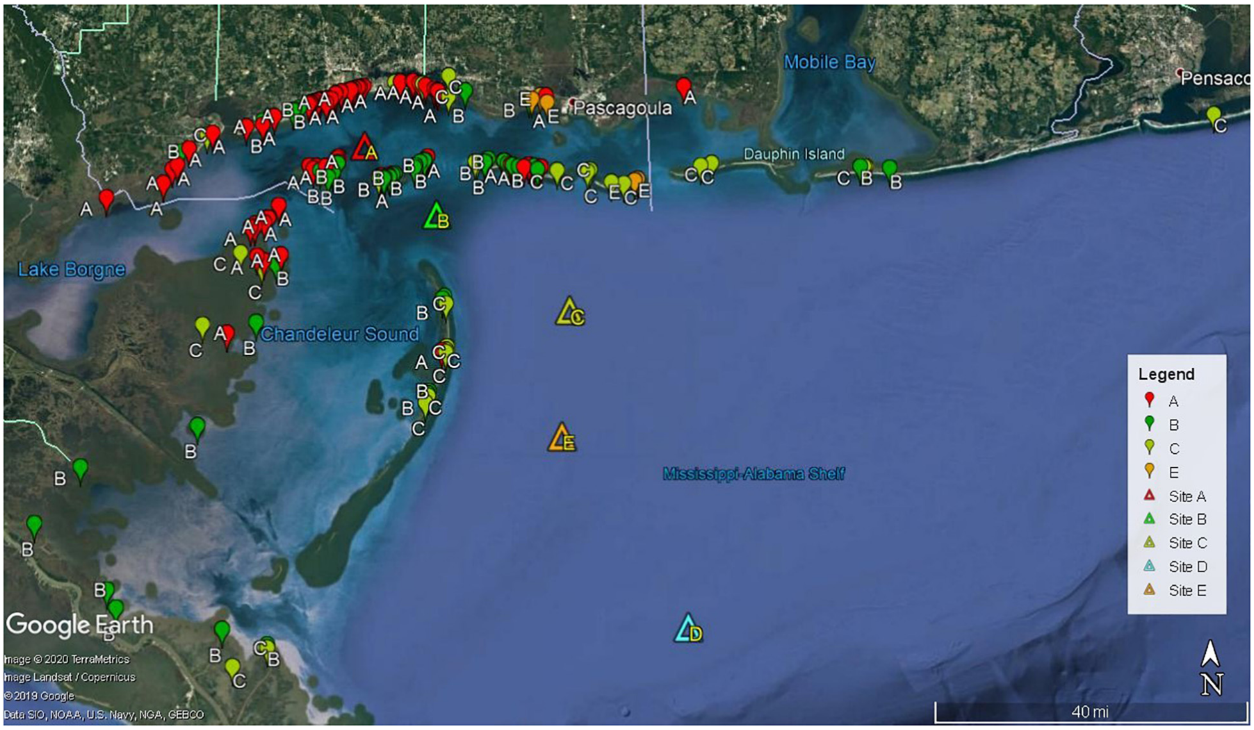

FIGURE 5 | Locations of beached sea turtle carcasses (n = 64) and effigies (n = 92) color coded by release site (triangles). The effigy that beached on Timbalier Island, LA is not shown.

of objects (*n* = 31) deployed from site C beached, 65% (*n* = 20) of them beached on nGOM barrier islands. In MS, objects were found on Ship Island, Horn Island, and Petit Bois Islands. Site C deployment objects also beached on Dauphin Island, AL, the Chandeleur Islands and one effigy drifted around the MS River Delta and beached on Timbalier Island, LA. This effigy, deployed in June, beached on Timbalier Island, LA after 6.2 days and a 359 km drift track. The only object to beach in Florida was an effigy released from site C in February; it drifted for 10 days and washed up on Pensacola Beach. Results from offshore sites D and E indicated that objects beyond approximately 100 km south of MS are very unlikely to drift northward to MS beaches or barrier islands. No effigies from site D (71 km from the closest point of land) beached; all six drifted over the continental shelf for 27 days before the SPOT batteries died. However, 67% of the effigies deployed at site E (68 km from mainland MS) beached on MS barrier islands and MS marshes. Although site E is only ∼29 km from the Chandeleur Islands, no effigies beached there.

Deployment site ($P \leq 0.0001$) had a significant effect on GLMM estimates of beaching probability for the model examining both sea turtle carcasses and effigies. Beaching probabilities while accounting for the significant covariates of season ($P \leq 0.0001$) and object type ($P = 0.0011$) varied among deployment sites with probability decreasing the further offshore an object was released (**Figures 2**, **6**). Beaching probability at deployment site A ($M = 0.80$, SE = 0.07) was significantly higher than at site B ($M = 0.48$, SE = 0.10) and site C ($M = 0.17$, SE = 0.06), and beaching probability was also significantly higher at site B than site C. Deployment site ($P \leq 0.0001$) was also found to have a significant effect on GLMM estimates of beaching probability for the model examining only sea turtle carcasses. Beaching probability when accounting for the significant covariate of season ($P = 0.0008$) indicated a similar decrease in probability with distance from shore as did the model utilizing carcasses and effigies (**Figure 6**). Beaching probability at deployment site A ($M = 0.71$, SE = 0.09) was significantly higher than at site B ($M = 0.26$, SE = 0.09) and site C ($M = 0.12$, SE = 0.06). However, unlike the model utilizing turtles and effigies the probability of beaching was not significantly different between at sites B and C.

Object type ($P = 0.0011$) was found to have a significant effect on beaching probability. Effigies ($M = 0.62$, SE = 0.08) had a higher probability of beaching than carcasses ($M = 0.33$, SE = 0.07). Since effigies cannot be scavenged or decompose, effigies sometimes had considerably longer drift tracks than carcasses deployed at the same time and location, especially during summer months. Overall, effigies that eventually beached traveled an average of 96 km and 94 h (site E excluded). Beached carcasses averaged 61 km drift tracks over an average of 73 h per deployment. Although six of nine effigies deployed from site E beached, they likely did not all represent actual carcass behavior. During April deployments, the three effigies beached within 72–94 h, which overlapped the drift times (72–97 h) of the five sea turtle carcasses that also beached. In May, all three site E effigies beached within 266–272 h, while only one sea turtle carcass beached after only 94 h adrift.

Testing the effectiveness of effigies as a proxy for sea turtle carcasses was one goal of this study. Notably, carcasses and

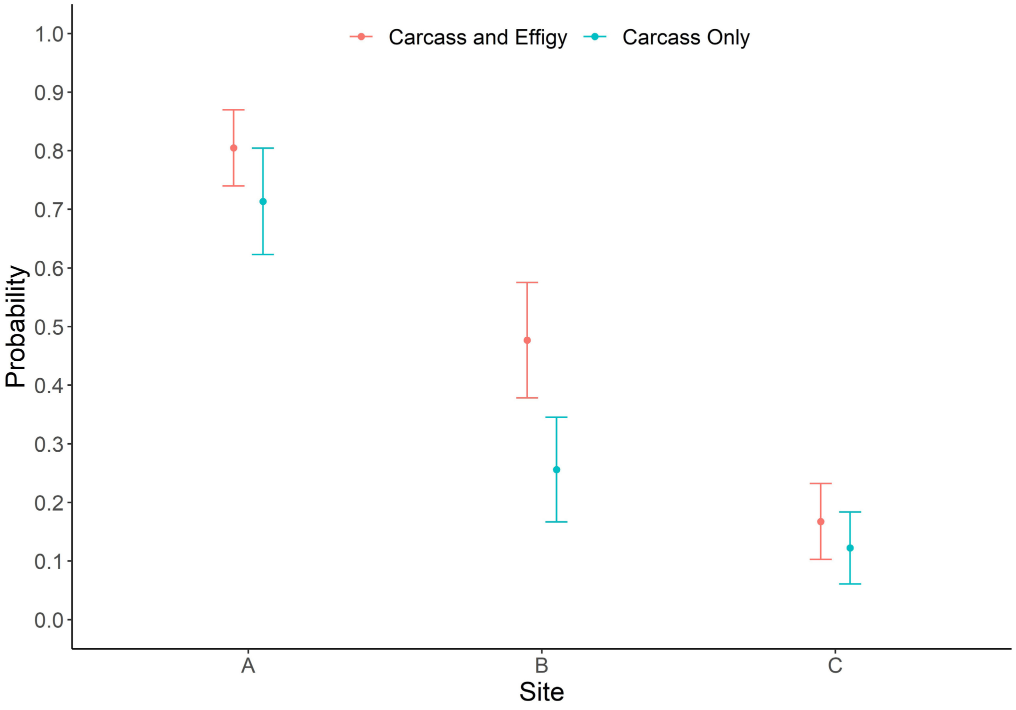

FIGURE 6 | Probability of beaching by deployment site (A, B, and C) ± 1 standard error for carcass and effigy and carcass only models.

effigies had very similar drifting patterns in the nGOM. During numerous deployments, their drift tracks mirrored each other (**Figure 7**) and they often beached in close proximity and within hours or minutes of each other. For example, objects released at site A on April 25, 2017 drifted an average 18.7 km and all beached within 2.7 h of one another (**Supplementary Figure 4**). During the same trip, two of the effigies released at site E beached within a minute of each other and drifted 93.8 and 94.2 km. Similar patterns were observed offshore at site C where an effigy and two carcasses had nearly identical tracks, beaching ~140 m apart within 38 min of each other (**Supplementary Figure 2**) on one of the Chandeleur Islands, LA. The separation of objects deployed at the same site and time was influenced by the intensity of the horizontal eddy diffusivity. In the examples above, the horizontal eddy diffusivity must be small to keep the objects following similar trajectories. In general, the longer the objects drifted, the further apart from each other they usually beached (**Supplementary Figures**). Both effigies and carcasses also tended to follow similar inertia circles due to the Coriolis Effect, which were reflected in the motions of the objects (e.g., **Supplementary Figure 7**).

Environmental Conditions

Environmental conditions mainly have two impacts on carcasses during their drifting on the sea surface. The combination effect of wind and current drive the movement of the carcasses and determines the drifting trajectories and final stranding destinations. The sea surface temperature impacts the decomposition rate with faster decay rate under higher temperature conditions. In **Figures 8**, **9**, we show the water temperature (A), wind (B), current (C), and wind and current combined drifting velocity (D) from NGOFS model at site A and C in 2017, respectively. Site A is an inshore station, while Site C represents the ocean conditions offshore.

The modeled temperature agreed reasonably well with the observed temperature in **Figure 8A**, suggesting model temperature could be used to investigate the seasonality in the study region. Due to the shallow depth, the inshore water at Site A was well mixed throughout 2017 indicated by the small difference between surface and bottom temperature (**Figure 8A**). The coolest temperature (~13.5°C) was obtained in mid-January and the highest temperature (~31°C) appeared in July and August at Site A. The offshore water temperature at Site B, C and E all showed similar trends and patterns. The water was well mixed and steady at approximately 20°C between January and early March. GOM waters started to warm and became weakly stratified starting in mid-March when the weather began to warm (**Figure 9A**). The water continued warming between April and July and enhanced stratification until the water became well mixed again in mid-September. The offshore water at Site C in general was warmer in the winter than the inshore water.

The wind vectors at all five sites followed similar patterns, though the offshore wind magnitude was slightly larger than the inshore wind (**Figures 8B**, **9B**). The wind was stronger in fall (October–December) and winter (January–February) than in late spring (March–May) and summer (June–September). During winter, there was no obvious dominant wind direction. Wind direction could switch between onshore and offshore in

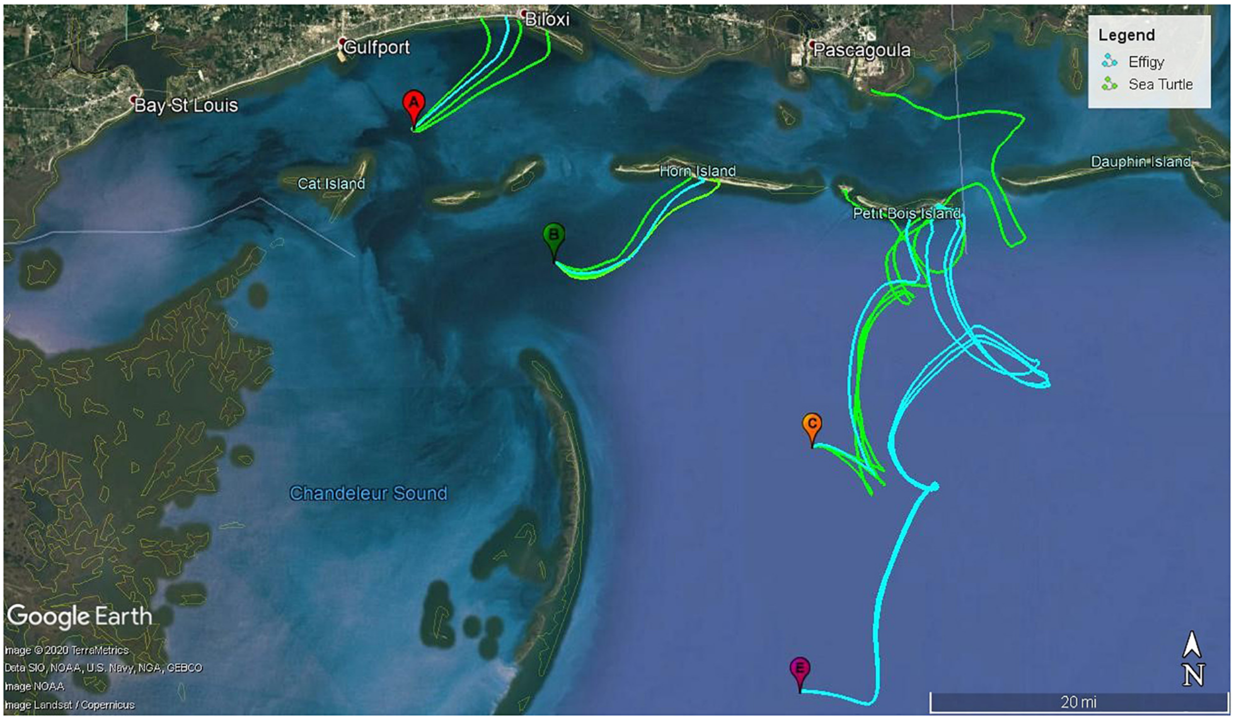

FIGURE 7 | Carcass (green) and effigy (blue) drift tacks from sites A, B, C and E deployed on 25 April 2017. All objects beached on or before 29 April 2017.

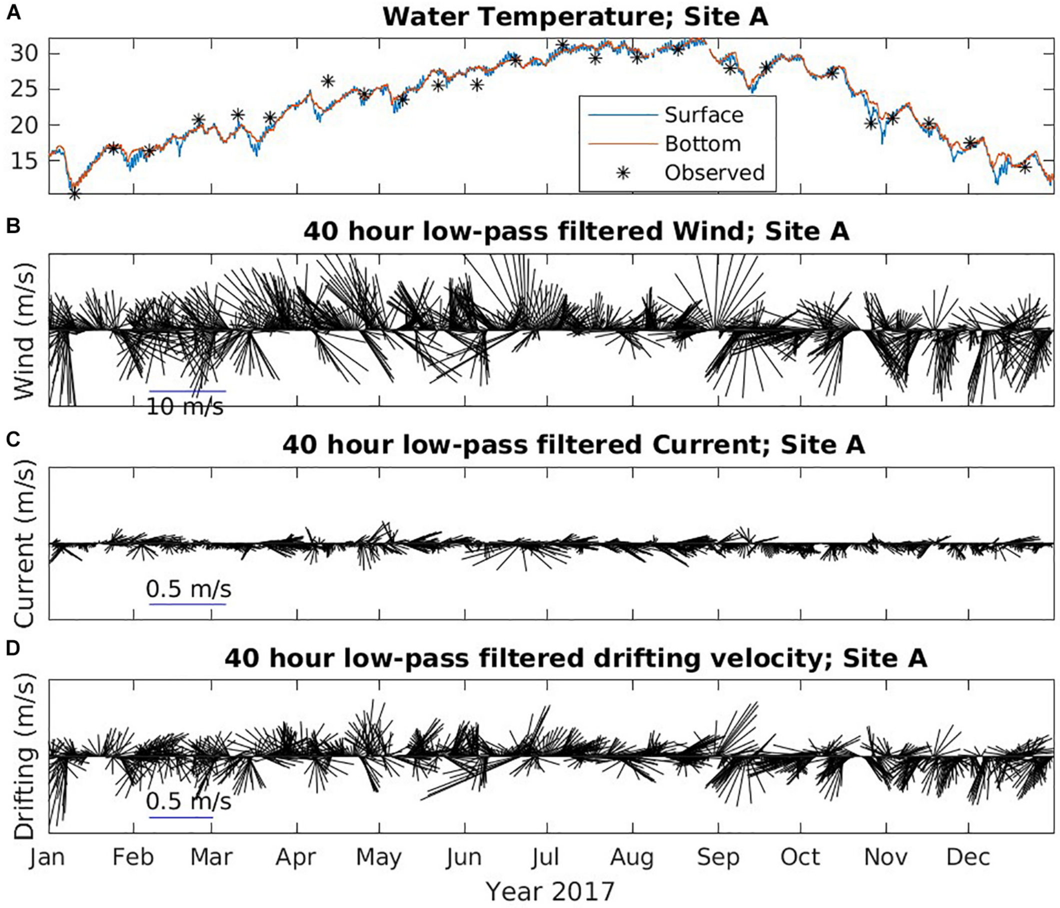

FIGURE 8 | Time series of environmental data at Site A from NGOFS. **(A)** Water temperature (°C); **(B)** Wind vector (m/s); **(C)** Surface current vector (m/s); and **(D)** drifting velocity vector (m/s). A 40-h low-pass filter was applied to wind, current, and drifting velocity to remove the fluctuations with periods less than 40 h. Vectors pointing "up" indicate northward flow.

hours to days. From March through the end of August, the dominant wind direction was onshore, though it changed to offshore occasionally. The wind mostly blew offshore between September and December. The water surface current at site A was small (~0.1 m/s) and mostly along shore direction (**Figure 8C**). In contrast, the current at site C was much stronger and mainly toward offshore direction throughout the year (**Figure 8C**). The magnitude of current at site C during spring and summer is larger than fall and winter. The current at site B was also small. Site D and E had similar strong offshore current as Site C.

Due to the weak current, the direction of the drifting velocity at site A (**Figure 9D**) and B followed similar patterns as the wind. The drifting of surface objects was dominated by wind nearshore. Therefore, from mid-March to the end of August, the drifting was mainly northward, toward the mainland. This might explain why, although the barrier islands were closer to Site A, more objects (42%) stranded on the mainland than on the barrier islands (31%). At Site C, in fall and winter, the drift velocity had similar direction as wind suggesting that wind predominantly influenced drift. Moreover, current became weaker in fall and winter at Site C (**Figures 9B,C**). During spring and summer, the current and wind were generally in opposite directions. The current was strongest in the spring, while the wind was also strong. Combined drifting velocity could be onshore or offshore. In the summer, wind became weaker, but offshore current was still relatively strong. In most cases, the direction of drifting velocity followed current direction (**Figure 9**), suggesting current was the dominant influence in the summer at site C. Because wind and current were opposite during summer, the drift velocity tended to be the smallest among all seasons. The wind at Site D and E was similar to Site C, but the current was stronger and directed offshore, which resulted in an offshore drift. Besides the long distance to land, the strong offshore directional current might also contribute to the low stranding rate at Site D and E. We assume that fine-scale drift was more complicated than we infer because both wind and current might have changed once an object moved away from the deployment location.

Stranding Seasonality

Actual sea turtle strandings during 2017 (*n* = 66) were below the annual average based on the previous 5 years (*n* = 153) but

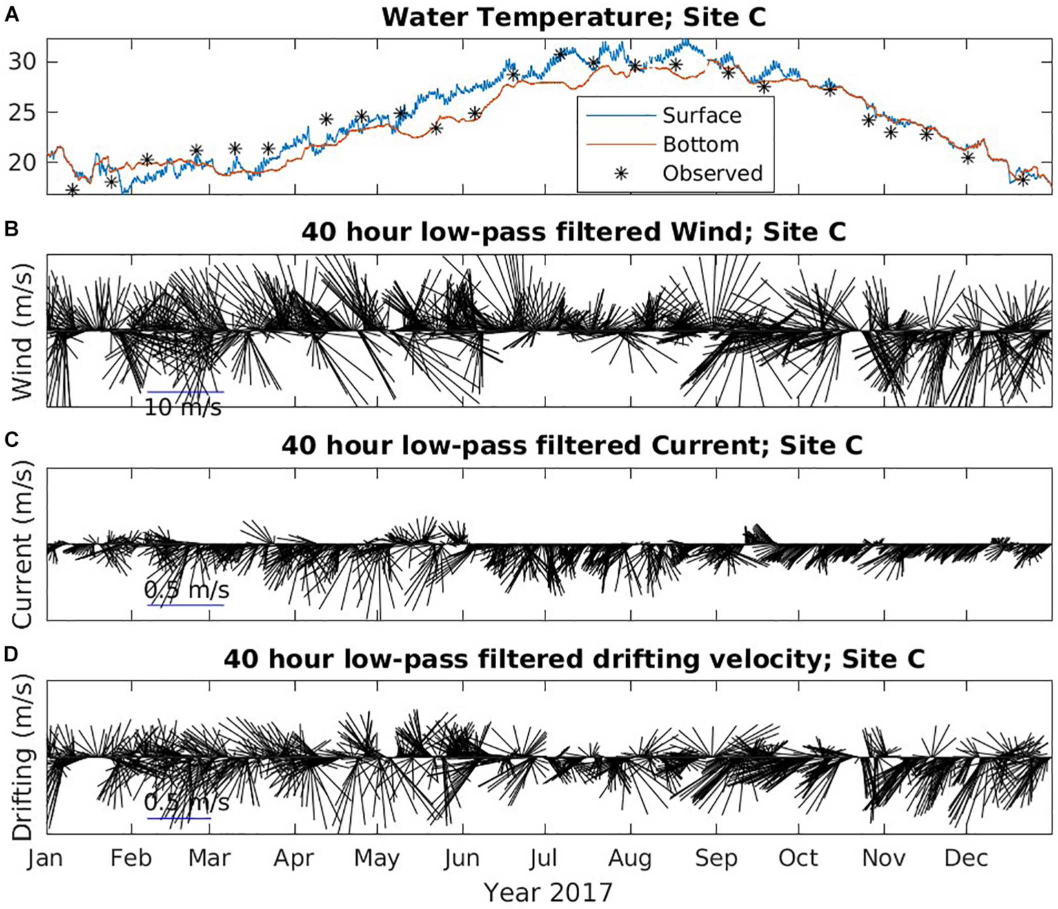

FIGURE 9 | Time series of environmental data at Site C from NGOFS. **(A)** Water temperature (°C); **(B)** Wind vector (m/s); **(C)** Surface current vector (m/s); and **(D)** drifting velocity vector (m/s). A 40-h low-pass filter was applied to wind, current and drifting velocity to remove the fluctuations with periods less than 40 h. Vectors pointing "up" indicate northward flow.

followed the expected aforementioned seasonal trend [STSSN (see text footnote 1)]. Our study carcasses exhibited a similar pattern (**Figure 10**). Season ($P \leq 0.0001$) was found to have a significant effect on GLMM estimates of beaching probability for the model examining both sea turtle carcasses and effigies (**Table 3**). Beaching probability, while accounting for the significant covariates of deployment site ($P \leq 0.0001$) and object type ($P = 0.0011$), was highest during the spring and lowest during the summer (**Figure 11**). Beaching probability during the summer ($M = 0.08$, SE = 0.04) was significantly lower than winter ($M = 0.90$, SE = 0.06), spring ($M = 0.50$, SE = 0.09) and fall ($M = 0.48$, SE = 0.11). The probability of beaching was also significantly lower during the spring and fall than during the winter, but not significantly different between spring and fall. Season ($P \leq 0.0008$) was also found to have a significant effect on GLMM estimates of beaching probability for the model examining only sea turtle carcasses (**Table 3**). Beaching probability, when accounting for the significant covariate of deployment site ($P = 0.0003$), showed a similar pattern to the model utilizing both turtles and effigies (**Figure 11**). Beaching probability during the summer ($M = 0.04$, SE = 0.03) was significantly less than winter ($M = 0.80$, SE = 0.11), spring ($M = 0.37$, SE = 0.10) and fall ($M = 0.40$, SE = 0.12). However, differences in beaching probability among winter, spring and fall were not significant.

Deployment site, season and environmental conditions are all factors that contribute to the stranding seasonality observed in this study (**Table 4**). Overall beaching probability ranges include results from both carcasses ($n = 163$) and effigies ($n = 100$) combined and carcasses only released at sites A, B and C. We attribute the significant differences between objects to lower persistence of carcasses since drift tracks and travel times were similar. Results of scavenging and decomposition apply to carcasses only. During winter, 88% of objects beached (**Supplementary Figures 1, 2**). No carcasses were lost due to decomposition and probable scavenging was observed in 13% of carcasses deployed in winter. Recorded surface water temperatures at deployment averaged 15.9–19.2°C, in January and February, respectively. Additionally, during winter months, greater differences in temperature were noted among sites, with colder temperatures documented inshore, e.g., 13.5°C at site A compared to 17.7°C at site C in January. Beached objects

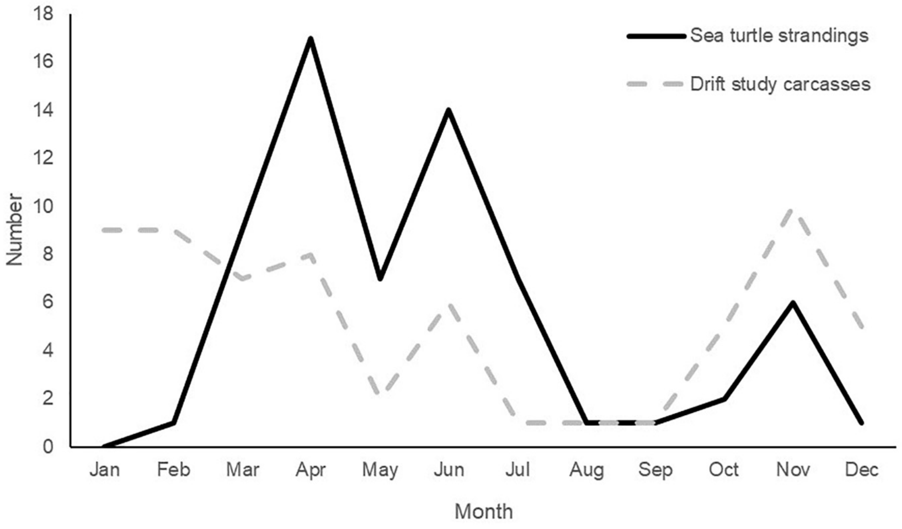

FIGURE 10 | Number of documented sea turtle strandings (*n* = 66) and drift study carcasses (*n* = 51) that beached in Mississippi in 2017. Stranding data from the Mississippi Sea Turtle Stranding and Salvage Network database (https://grunt.sefsc.noaa.gov/stssnrep/).

TABLE 3 | Estimated least square means of beaching probability by season [winter pre-season (January–February), spring peak (March–June), summer lull (July–September), and fall pulse (October–December)], deployment site (A, B, or C) and object type (effigy, *n* = 100 or carcass, *n* = 163).

	Carcasses and effigies		Carcasses only	
Effect	**Mean**	**Standard error mean**	**Mean**	**Standard error mean**
Winter	0.8956	0.0601	0.7971	0.1121
Spring	0.4977	0.0942	0.3703	0.0951
Summer	0.0818	0.0420	0.0365	0.0280
Fall	0.4765	0.1069	0.4021	0.1156
A	0.8049	0.0651	0.7137	0.0909
B	0.4768	0.0983	0.2559	0.0893
C	0.1675	0.0647	0.1223	0.0614
Effigy	0.6245	0.0775		
Carcass	0.3329	0.0656		

drifted for an average of 58.6 km (range: 12.5–214.0 km) and travelled an average of 3.0 days (range: 0.5–10.6 days). Overall, stranding probability was highest in winter (80–90%) than any other time of year.

In March, when strandings typically begin to occur, (**Supplementary Figure 3**), water temperatures began to warm and became nearly uniform between sites (21.0–21.4°C). In the following months, surface water temperatures at all sites increased to ∼27°C by June. Of the 90 objects deployed during spring, 58% beached (**Supplementary Figures 4–6**). The objects drifted for an average of 53.5 km (range: 15.2–148.7 km) and travelled an average of 2.3 days (range: 0.6–5.6 days). Probable scavenging of carcasses increased considerably to 47% and 7% of carcasses decomposed before beaching. Stranding probability during the peak stranding season dropped substantially following winter and was only 37–50%.

Summer surface water temperature averaged 29.4°C at all sites. Only 31% of the 64 objects deployed in summer beached (**Supplementary Figures 7–9**), including only three of 39 carcasses. Drift distance decreased slightly, averaging 48.4 km (range: 17.9–75.7 km), and drift duration was an average of 2.6 days (range: 1.0–4.3 days). Probable scavenging peaked at 69% during summer months, and decomposition was documented in 8% of deployed carcasses. Stranding probability dropped to 4–8% during summer months.

Surface water temperatures decreased in the fall from ∼24°C in October to ∼17°C in December. The cooler water temperatures likely contributed to the observed increase in object beaching (up to 61%) and predicted stranding probability of 40–48%. Beached carcasses were less decomposed than those observed during the summer months. Although more carcasses beached, they had similar drift durations to those that beached in late spring. During the fall, objects had the shortest drift distance and time. Objects beached in an average of 2.8 days (range: 0.4–9.6 days) (**Supplementary Figures 10–12**). Carcasses drifted an average of 55.1 km (range: 9.4–188.1 km). Loss of carcasses attributed to decomposition and scavenging were 7% and 10% of the documented outcomes, respectively. Unknown object outcomes were highest in fall (29%), because many of the objects drifted southwest and either never beached or came ashore along the marshlands of the eastern MS River Delta and were not recoverable.

Stranding Reports

The final portion of the study was to determine what percent of the 64 beached carcasses were reported to the STSSN in MS and adjacent states. Only 34.4% of carcasses beached on MS mainland beaches, while 40.6% of carcasses washed up on the MS barrier islands. Carcasses also beached on the LA barrier islands (4.7%), primarily the Chandeleur Islands, and the LA

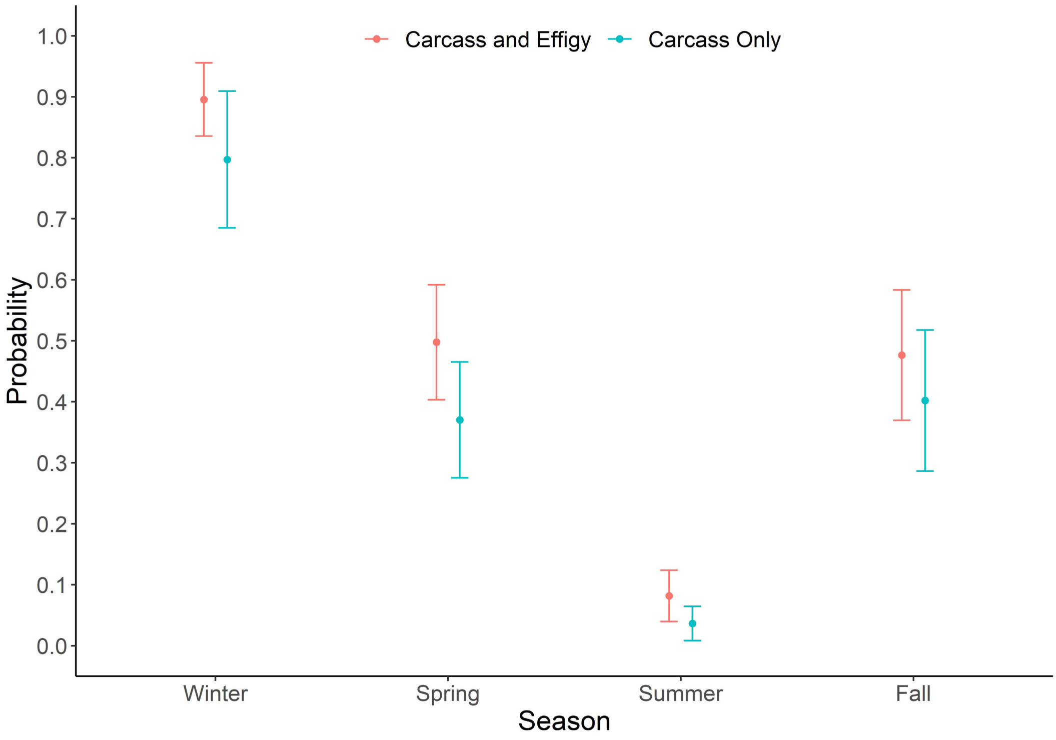

FIGURE 11 | Probability of beaching by season ± 1 standard error for carcass and effigy and carcass only models.

TABLE 4 | Summary of seasonal mean water temperature, distance travelled and time traveled for beached objects [carcasses (*n* = 64) and effigies (*n* = 56)] by season [(January–February), spring (March–June), summer (July–September), and fall (October–December)]. Beaching probability ranges include results from both carcasses (*n* = 163) and effigies (*n* = 100) combined (higher values) and carcasses only released at deployment sites (A, B, and C).

Season	Mean water temperature (°C)	Mean distance travelled (km)	Range distance travelled (km)	Mean travel time (days)	Range travel time (days)	Beaching probability
Winter	17.71	58.57	12.49–214.04	3.04	0.45–10.58	79.7–89.6%
Spring	24.11	53.47	15.18–148.70	2.25	0.58–5.63	37.0–49.8%
Summer	29.44	48.41	17.93–75.67	2.59	0.99–4.33	3.6–8.2%
Fall	21.20	55.04	9.43–188.04	2.83	0.43–9.61	40.2–47.7%

marshes (14.1%). Only 4.7% and 1.6% of carcasses beached in the MS and AL marshes, respectively. The MS STSSN (see text footnote 1) received 37 stranding reports for 23 carcasses from this study; several of the reports were for the same carcass. While every effort was made to remove the SPOT tags as soon as the carcasses beached or just after sunrise, it was not always possible, especially for the barrier islands and remote locations, where it took us an average of 138 h to reach them after they came ashore. However, we were successful in arriving at carcasses on the MS mainland within an average of 7 h after beaching (range: 0–27 h). As a result, SPOT tags and twine had been removed from carcasses for 25 of the public reports and 12 carcasses still had the tags attached when they were reported. There was only a 21.5% reporting rate for all beached carcasses, which can be attributed to the low reporting rate of carcasses that beached on the barrier islands and in marshes (**Table 5**). None of the carcasses that beached on the LA barrier islands or any of the MS, AL, and LA marshes were reported. Only 50.0% of carcasses from MS mainland beaches and 11.1% of sea turtle carcasses from the MS barrier islands were reported.

DISCUSSION

Numerous factors must come together for a sea turtle carcass to beach and be reported to a stranding network. First, the mortality must occur close enough to shore to allow environmental and oceanic conditions to move the carcass toward the beach. Second, the carcass must persist in the environment long enough to make it to shore and not decompose or be scavenged. Next, the carcass must beach in an area that is publicly accessible and frequently accessed. Finally, the public must be aware that sea turtle strandings should be reported and know the mechanism for doing so. This study was the first to examine how all these factors contribute to sea turtle mortality documented by a stranding network. Our results provide evidence and a plausible

TABLE 5 | Location and public reporting of drift study carcasses that beached in Mississipi (MS), Alabama (AL), and Louisiana (LA) during 2017. Several carcasses were reported more than once.

Beaching location	Reported	Not reported	Total
Barrier Islands-MS*	3	24	27
Barrier Islands-LA	0	3	3
Mainland MS	11	11	22
Marsh-AL	0	1	1
Marsh-LA*	0	9	9
Marsh-MS	0	3	3
Grand Total	14	50	65

**Turtle-Green A1 orginally beached in the LA marsh and then restranded on the MS barrier islands and was reported.*

explanation for the annual pattern of strandings observed in MS and, likely, other nGOM states. We demonstrate that the likelihood of a sea turtle carcass beaching is significantly impacted by the time of year, environmental conditions, and proximity to shore. Moreover, similar to previous studies in other regions, our findings also show that a relatively low proportion of sea turtles that die at sea are subsequently documented as beached strandings.

On average, approximately 80% of sea turtle strandings in MS occur during March through June, with a peak in April. The proportion of carcasses we deployed during this study that came ashore mirrored the actual seasonal trend in stranding numbers during 2017, which was similar to previous years [STSSN (see text footnote 1)]. We observed that as the waters began to warm, fewer carcasses beached and losses attributed to scavenging and decomposition began to increase. During the spring peak in strandings, only 37–50% of objects are predicted to beach. Strandings begin to decline throughout June due to changing environmental conditions, such as increased water temperatures and calm winds. However, we observed a spike in beached study carcasses in June that deviated from this expected trend. Notably, this spike corresponded with an unusual number of actual sea turtle strandings (see text footnote 1). These anomalies are attributable to Tropical Storm (TS) Cindy that impacted the nGOM in June 2017. Our second June deployment occurred on 19 June, just days before TS Cindy brought strong onshore winds (**Figure 8B**) and increased sea states to the waters off MS. All objects from this deployment beached within 3 days of release; four were dislodged from their original beached location in the LA marsh and washed ∼120 m inland. Two effigies originally beached on Cat Island within 24 h of deployment but refloated due to TS Cindy and both beached a second time, within an hour of each other, on the mainland in Long Beach, MS (**Figure 12**). A second striking observation from this event was, that despite high winds and tumultuous sea state from a TS, both of the effigy tracks were nearly identical and they beached within 1.1 km of each other. This opportunistic observation highlights the impacts tropical storms may have on sea turtle strandings and the likelihood of public reporting. None of the carcasses deployed during TS Cindy were reported to the STSSN, likely a result of carcasses being pushed farther inland and absence of people on MS public beaches.

Summer stranding probability was only 4–8%, which explains the low number of strandings documented by the MS STSSN during summer months. The two largest biological factors impeding a drifting sea turtle carcass from eventually beaching are decomposition and scavenging (or predation if the turtle is still alive), both of which follow similar temporal trends in the nGOM. Sharks are known to prey on sea turtles and scavenge sea turtle carcasses (Heithaus et al., 2008; Delorenzo et al., 2015). Both live and dead stranded sea turtles are often observed with shark bites. Stacy et al. (2021) found that 79% of shark wounds observed on a sub-set of dead stranded sea turtles from the GOM and eastern FL occurred postmortem. Although none of our carcasses beached with apparent shark bite wounds, we are considering that tags recovered with damaged tether or shark bites likely reflect scavenging of the carcass by sharks. The nGOM is a shark nursery area and habitat to adult and juvenile sharks (Parsons and Hoffmayer, 2007; Bethea et al., 2014). The area contains a diverse number of shark species including Atlantic sharpnose, *Rhizoprionodon terraenovae*, blacktip shark *Carcharhinus limbatus*, finetooth shark, *C. isodon* and bull shark, *C. leucas* (Parsons and Hoffmayer, 2007; Bethea et al., 2014). We observed predation highest in spring and fall which coincides with the movement of shark species migrating in and out of coastal MS waters (Parsons and Hoffmayer, 2005).

Another peak in beached carcasses from this study was recorded in November (n = 10) and was concurrent with a small peak in actual sea turtle strandings (see text footnote 1) (n = 6), which is typical for winter based on stranding data from prior years. This trend may reflect decreased water temperatures, which slow decomposition (Santos et al., 2018). Fall stranding probabilities, 40–48%%, are similar to those of spring. One reason the stranding numbers are likely not as high as in the spring is because sea turtles begin to migrate to warmer offshore waters as the temperature drops in the fall (Lyn et al., 2012). Also, study results and environmental conditions suggest that if sea turtles die while they are migrating out of MS waters, they will drift southwest and end up offshore or in LA marshes and never be discovered. Only sea turtles that die nearshore in the fall are likely to strand on MS mainland beaches.

Stranding location greatly affects whether sea turtles are discovered and reported. The nGOM is a diverse habitat comprised of mainland beaches, bays, bayous, marshes and barrier islands. According to NOAA,[2] of the 30 United States' states with shorelines, LA (12,426 km) is the third largest, AL (977 km) ranks 21st and MS (578 km) is 24th. MS only has 100 km of mainland shoreline, which includes only 42 km of sandy beaches[3]. Much of the northern GOM shoreline comprises remote habitat that is not frequented by the public. Therefore, carcasses that strand there will likely never be reported. Our study found that up to a third of carcasses beach in these remote areas. When carcasses strand, they usually remain in the same location as they initially beach. However, high tide and storm events can

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[2] https://coast.noaa.gov/data/docs/states/shorelines.pdf. Accessed October 8, 2020.

[3] https://www.gulfcoast.org/plan/secret-facts/secret-facts-page-four/#:~{}:text=Coastal%20Mississippi%20has%2062%20miles,with%2026%20miles%20of%20beaches. Accessed October 9, 2020.

FIGURE 12 | Effigy tracks from 25 June 2017 site B deployment. Two effigies originally beached on Cat Island within 24 h of deployment but refloated due to Tropical Storm Cindy and both beached a second time, within an hour of each other, on the mainland in Long Beach, MS.

cause carcasses to drift and float to other locations. We observed such translocation in early March when a carcass beached in the LA marsh, where the SPOT was removed, but was reported as a stranding on West Ship Island, MS 10 days later. Translocation of stranded turtles from their original stranding site appears to be relatively rare in this region and if it does happen, carcasses are likely to be highly decomposed once they beach again.

Strandings are one of few direct methods by which we identify and monitor threats to sea turtle populations. It is possible to use location data from stranded carcasses to backtrack the carcass's drift path to the likely area of the initial mortality (Nero et al., 2013). Backtracking can occur for individual carcasses or a combination of strandings to determine if there are specific areas of concern. Results from our drift study deployments were used to test improvements made to the model created by Nero et al. (2013). The new model now also incorporates water depth and decomposition state in addition to the previously included environmental conditions. A manuscript detailing decomposition study results, backtracking equations and drift study comparisons is currently in review.

Data derived from stranded sea turtles are frequently used for various types of research. Such valuable applications are only possible if carcasses are detected soon after discovery, i.e., with sufficient time to be located and examined. The stranding network in MS, as in many other areas, largely relies on members of the public to report stranded sea turtles. The 22% stranding reporting rate for carcasses deployed in this study was much lower than anticipated. Since the 2010 *Deepwater Horizon* oil spill, the MS STSSN has undertaken efforts to enhance stranding reporting within MS through public outreach, television and social media broadcasts, coordination and training of stranding response organizations and volunteers, and regimented reporting. While the MS STSSN receives reports from both the mainland beaches and offshore barrier islands, ~80% come from the highly trafficked inland beaches. This study clearly shows that sea turtles strand along the offshore barrier islands at a comparable rate to the mainland. However, due to their relative remoteness, only a small fraction of these strandings are documented. Based on these findings, additional effort is needed to increase stranding detection and reporting on barrier islands, such as through dedicated stranding surveys or greater encouragement of opportunistic reporting by those travelling to these areas. Furthermore, the stranding reporting rate on mainland beaches was only 50%, which was also much lower than anticipated. Local organizations should enhance efforts to educate the public on what to do if they find a stranded sea turtle and seek out ways to increase public awareness, such as posting signs with stranding reporting information and through the media.

Our methods are applicable to studies of stranding probability and detection in other regions. We acknowledge that using sea turtle cadavers can be challenging and infeasible for various reasons, thus we incorporated easily fabricated effigies into our study design and demonstrate their value as a valid surrogate. By using actual carcasses, we were able to study persistence in the environment, a key variable in stranding probability; however, factors such as decomposition rates also can be inferred based on experimental studies and temperature (Cook et al., 2020).

We also demonstrated a surprisingly low rate of reporting of carcasses that landed on beaches that we know are visited regularly by beachgoers. In general, structured stranding networks with established reporting mechanisms within developed areas tend to assume a relatively high rate of reporting by the public. Our findings caution against making such assumptions without having some empirical measure. We anticipate that comparable studies in other regions would have similar benefits with regard to understanding stranding patterns and trends, monitoring sources of sea turtle mortality, and evaluating the efficacy of stranding detection and reporting.

DATA AVAILABILITY STATEMENT

The raw data supporting the conclusions of this article will be made available by the authors, without undue reservation.

ETHICS STATEMENT

Ethical review and approval was not required for the animal study because we only used carcasses so it was not necessary. This study was authorized under United States Fish and Wildlife Service permit number TE 676395-5. No live animals were killed or harmed for this study.

AUTHOR CONTRIBUTIONS

MC, RN, and BS contributed to conception and design of the study. MC, JR, and RN conducted fieldwork. MC wrote the first draft of the manuscript. DH and ZW conducted environmental and statistical analysis. JR, DH, and ZW wrote sections of the manuscript. All authors contributed to manuscript revision, read, and approved the submitted version.

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SUPPLEMENTARY MATERIAL

The Supplementary Material for this article can be found online at: https://www.frontiersin.org/articles/10.3389/fmars.2021.659536/full#supplementary-material

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Insights Into Sea Turtle Population Composition Obtained With Stereo-Video Cameras *in situ* Across Nearshore Habitats in the Northeastern Gulf of Mexico

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Population size estimates are key parameters used in assessments to evaluate and determine a species' conservation status. Typically, sea turtle population estimates are made from nesting beach surveys which capture only hatchling and adult female life stages and can display trends opposite of the full population. As such, in-water studies are critical to improve our understanding of sea turtle population dynamics as they can target a broader range of life stages – though they are more logistically and financially challenging to execute compared to beach-based surveys. Stereo-video camera systems (SVCS) hold promise for improving in-water assessments by removing the need to physically capture individuals and instead extract 3D measurements from video footage, thereby simplifying monitoring logistics and improving safety for the animals and surveyors. To demonstrate this potential, snorkel surveys were conducted at artificial habitats in the northeastern Gulf of Mexico (neGOM) to collect size and photo-identification data on sea turtles *in situ* using a SVCS. Over 29.86 survey hours, 35 sea turtles were observed across three species (*Caretta caretta, Chelonia mydas,* and *Lepidochelys kempii*) and all neritic life stages (juvenile, sub-adult, and adult) utilizing different habitats, including artificial reefs, jetties, and fishing piers. Greens straight carapace length ranged from 28.55 to 66.96 cm ($n = 23$, mean 43.07 cm ± 11.26 cm standard deviation; SD) and loggerheads ranged from 59.71 to 91.77 cm ($n = 10$, mean 74.50 cm ± 11.35 cm SD), and Kemp's ridleys ranged from 42.23 cm to 44.98 cm (mean 43.61 cm ± 1.94 cm SD). Using a linear mixed model, we found that species and habitat type were the most important predictors of sea turtle body length distribution. Overall, this case study demonstrates the potential of SVCS surveys to enhance our understanding of the population structure of sea turtle species within the neGOM and elsewhere.

Keywords: green sea turtle, loggerhead sea turtle, Kemp's ridley sea turtle, abundance, size distribution, photogrammetry, stereo-video camera system

INTRODUCTION

Population assessments are crucial to determine population trends and status (i.e., trends in size class distribution; Crouse et al., 1987; Summers et al., 2017). For a population assessment to be considered robust it requires demographic data on all life stages, survival rates, habitat distribution, species-specific size data, and movement patterns (Heppell et al., 2003). Typically, only abundance data are used to assess population size and to estimate extinction risk for sea turtles and other endangered species (Schroeder and Murphy, 1999; Caswell, 2002; Morris and Doak, 2002; National Research Council (U.S.) et al., 2010). While abundance-centered assessments are essential, these data alone are insufficient to predict sea turtle population trends (Heppell et al., 2003). Abundance-based data alone can be misleading and lead to potentially erroneous conclusions about the direction and severity of population decline or recovery, especially if the population index is based on only one life stage, e.g., reproductive females (Esteban et al., 2017; Piacenza et al., 2019; Casale and Ceriani, 2020; Ceriani et al., 2021). Incorporating demographic data, specifically morphometric data, would lead to more effective modeling of populations and allow for researchers to estimate age at maturity, growth rates, and survival rates (Heppell et al., 2003; Casale et al., 2011). These vital rates allow researchers and conservation management agencies to determine if a population is declining or recovering and which, if any, conservation management actions are needed to aid in recovery (Bjorndal et al., 2011; Redfoot and Ehrhart, 2013). Collecting morphometric data in addition to abundance data can also be used to predict recruitment to reproductive life stages, particularly when populations are unstable, and the population structure is transient (O'Farrell and Botsford, 2006; White et al., 2013; Froese et al., 2018; Rudd and Thorson, 2018). Moreover, size-frequency distributions which encompass juvenile sizes can be powerful tools to understand population recovery that may not yet be reflected in adults, who are more commonly monitored (Hilborn and Walters, 2001; Ault et al., 2008; Heppell et al., 2012).

Sea turtle populations in general are commonly monitored by observing the number of females nesting or numbers of nests laid [National Research Council (U.S.) et al., 2010]. While nesting surveys provide readily accessible data for population assessments, sea turtles only spend 1% of their life on nesting beaches (as embryos to hatchlings and as nesters), yet 90% of sea turtle literature is derived from these surveys (Bjorndal, 1999; Wildermann et al., 2018). Studying a single life stage, such as nesting females, has been equated to studying human maternity wards with the assumption that the results represent the entire species (Bjorndal et al., 2011). In addition, a stage-based matrix model of loggerhead sea turtles (*Caretta caretta*) suggests juvenile life stages of sea turtles can have the largest impact on population growth and recovery (Crouse et al., 1987). However, due to their highly migratory behavior and difficulty to capture, studying in-water life stages presents a unique set of challenges (Wildermann et al., 2018).

Traditional methods for studying turtles in-water are to capture them via rodeo or tangle netting (Limpus and Walter, 1980; Ehrhart and Ogren, 1999; Fuentes et al., 2006). Both methods are time- and labor-intensive, which could result in additional stress on the animal, the turtle evading capture, and can leave researchers with small sample sizes, especially on short-term projects. However, observing turtles *in situ* using a stereo-video camera system (SVCS) can allow researchers to expand efforts to study different demographic classes while eliminating difficulty related to capturing turtles, thus improve the accuracy of population status estimates (Goetze et al., 2015; Araujo et al., 2016, 2019; Logan et al., 2017; Boldt et al., 2018). The SVCS is a non-invasive, remote method that allows for 3D measurements to be extracted from video footage (Harvey et al., 2002). The SVCS requires no handling of sea turtles and is highly accurate when compared to traditional hand measurements. Mean percent bias of the SVCS across three species of sea turtles ranged from −0.61% (±0.11 SE) to −4.46 % (±0.31 SE; Siegfried et al., 2021). Body size data is incorporated into length-based population assessment models, such as length-frequency analysis, which can be used to estimate growth rates, size at maturity, survival rates, and abundance of sea turtle populations (Casale et al., 2011). Length-frequency analysis requires relatively high sample numbers of turtles (Casale et al., 2011). Fortunately, since SVCSs do not require time-intensive capture methods, it is possible to achieve a larger sample size than methods that require capture.

The nearshore estuarine habitats and artificial reefs of the northeastern Gulf of Mexico (neGoM) have been recognized as geographic gaps in in-water sea turtle research in Florida (Eaton et al., 2008). For sea turtle species in these coastal waters, fewer studies have been conducted *in situ* to assess population structure and size-class distributions for loggerhead (*C. caretta*), green (*C. mydas*), and Kemp's ridley (*L. kempii*) sea turtles known to use this region (but see: Avens et al., 2012; Hart et al., 2012, 2013, 2014, 2020; Metz and Landry, 2013; Lamont et al., 2015; Lamont and Iverson, 2018; Wildermann et al., 2019; Broadbent et al., 2020; Chabot et al., 2021; Lamont and Johnson, 2021). These existing studies have either focused on satellite telemetry studies, or have used in-water capture methods for other regions in the northern GOM, i.e., the lower Texas Coast, St. Joseph's Bay, Florida, or off Crystal River, Florida, and only one included a study site in northwestern Florida. To demonstrate how SVCS surveys could be used to fill these data gaps and improve the accuracy and completeness of sea turtle population assessments, this study sought to (1) record sea turtle population size distributions, and (2) relate this distribution to artificial habitat preferences in the western Florida Panhandle as a case study for the application of SVCS.

MATERIALS AND METHODS

Study Sites

The neGOM is a dynamic coastal environment composed mostly of soft, sandy bottom interspersed with inlets of estuarine seagrass beds and sparse natural hard-bottom or reefs (Locker et al., 2000) used by loggerhead, green, and Kemp's ridley sea turtles (Lamont and Iverson, 2018; Wildermann et al., 2019). However, since the Deepwater Horizon oil spill in 2010, local and state authorities began adding additional artificial reef habitats to aid

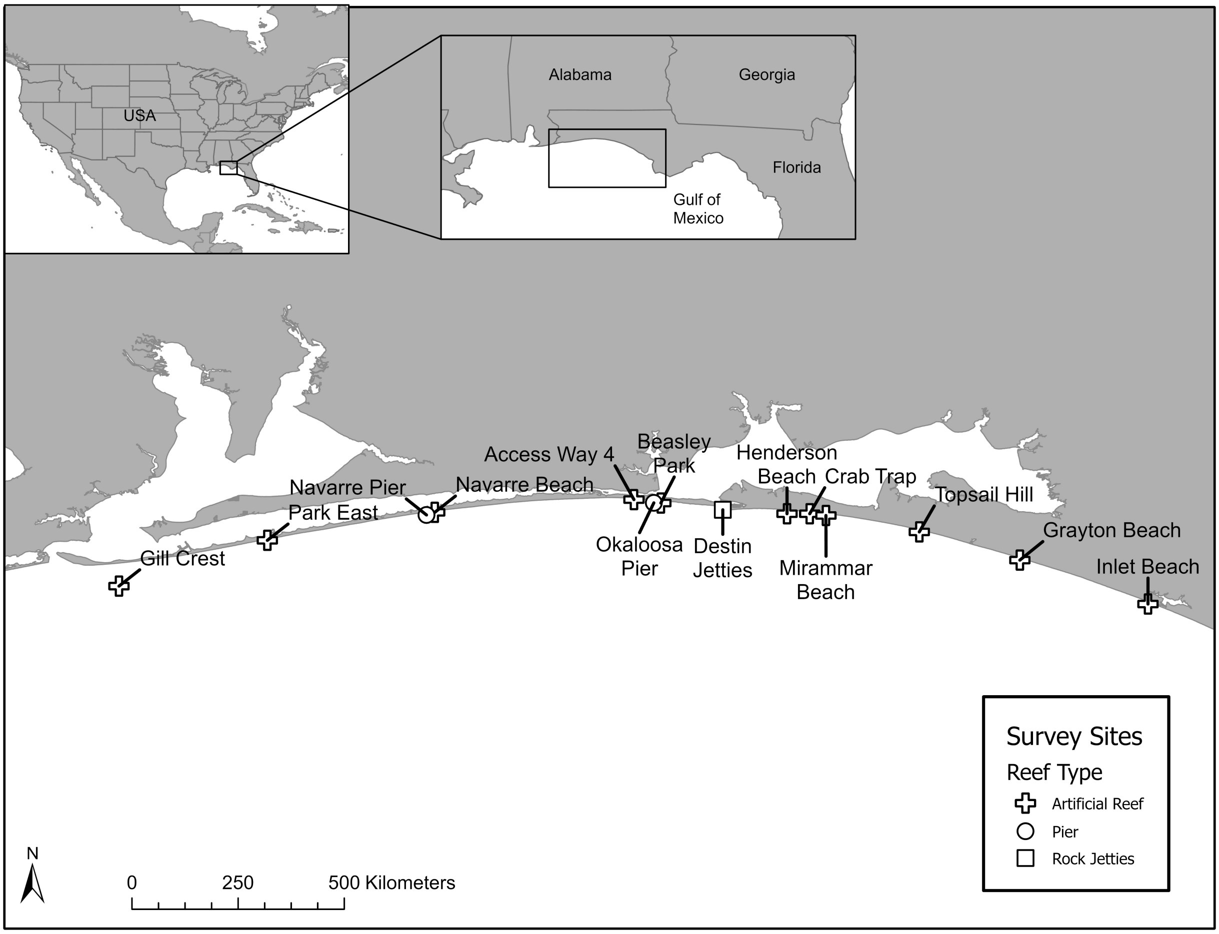

FIGURE 1 | Northeastern Gulf of Mexico survey sites from Escambia County to South Walton County, Florida.

in fish recovery (Nelson, 2017). As of 2019, there have been 1,065 artificial reefs installed in the region from the Alabama border to Mexico Beach, Florida to attract marine wildlife and sustain ecotourism (Barnette, 2017; FWC Database, 2019).

Shore-based dive surveys on local artificial reefs, piers, and jetties from Santa Rosa to South Walton Counties of Florida with a SVCS were conducted weekly, weather permitting, from May 2019 to August 2020 with locations selected on an opportunistic rotating basis (**Figure 1**). We conducted a total of 58 dive surveys (29.86 total observation hours, surveys typically took ∼ 30 min to complete) at 14 sites from the Florida-Alabama border to just west of Panama City, FL, United States (**Table 1** and **Figure 1**). Artificial habitats included artificial reefs, fishing piers, and rocky jetties. We attempted to survey each site an equal number of times; however, certain conditions, such as sea state, water visibility, or reef accessibility influenced the number of dive surveys at each site.

Stereo-Video Camera System Surveys

The SVCS was used to conduct video surveys throughout the neGOM. The SVCS was comprised of two GoPro® cameras attached at a fixed distance apart (0.8 m) that were inwardly converged at an angle of ∼4°. The SVCS was calibrated following the procedure described by Harvey and Shortis (1998) at the University of West Florida Aquatic center in <1 m depth of water using the SeaGIS CAL software v.3.23 (SeaGIS, 2008a Pty., Ltd., Bacchus Marsh, VIC, Australia). In previous work, the SVCS measurements were validated by comparing hand-captured measurements to stereo measurements and percent error was between −0.61% (±0.11 SE) and −4.46% (±0.31 SE) across three sea turtle species (Siegfried et al., 2021).

Opportunistic searches for sea turtles were conducted via snorkel, covering the entire artificial reef site while visually inspecting around and under each reef module at least once per survey. Surveys at all reefs were conducted at equivalent times of the day, typically between 10 am and 3 pm. The survey methodology was modified slightly for the fishing piers and jetties, where we swam linearly along the center of the pier pilings or along the edge of the jetty, rather than systematically swimming around the reef pilings. One researcher swam with the SVCS while the other researcher carried a secondary GoPro® camera to assist in obtaining facial identification photos. At each field site, water temperature, maximum depth, visibility, and weather conditions

TABLE 1 | Relative filming catch per unit effort (CPUE) of all species of sea turtles (n) per survey hour among locations during snorkel surveys. CPUE calculation includes Kemp's ridleys.

Site location	Number of dives	Survey hours	Total turtles	CPUE
Miramar Beach	4	1.91	0	0.00
Access Way 4	4	1.6	0	0.00
Topsail Hill	3	1.63	0	0.00
Beasley Park	7	2.97	2	0.67
Navarre Beach	12	5.85	6	1.03
Park East	8	4.98	6	1.20
Inlet Beach	4	1.56	2	1.28
Henderson Beach	2	0.75	1	1.33
Gill Crest	1	0.72	1	1.39
Okaloosa Pier	3	2.02	3	1.49
Crab Trap	2	1.15	2	1.74
Grayton Beach	3	2.08	4	1.92
Navarre Pier	2	0.88	2	2.27
Destin Jetties	3	1.76	6	3.41
TOTAL		29.86	35	1.17

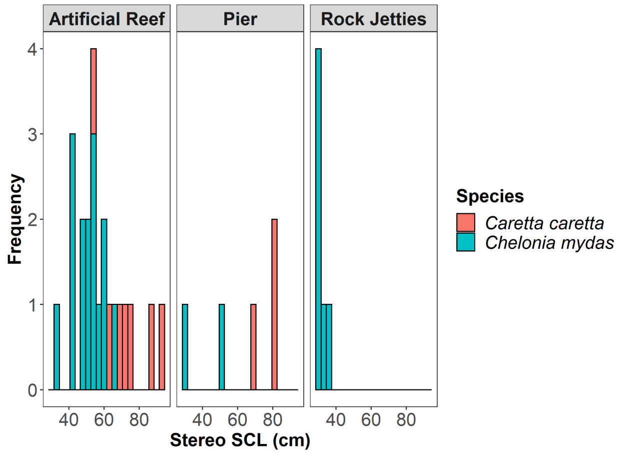

FIGURE 2 | Size-frequency distribution of sea turtle species across our study sites in the northeastern Gulf of Mexico.

were recorded. We also noted if flipper tags were apparent, however, we usually could not read the tag identification codes, due to distance of turtle or bioaccumulation on tags. To be included in the data set, a survey was considered successful when the entire artificial reef assemblage was inspected and visibility was ≥ 2 m to allow for adequate detection of sea turtles. Visibility was visually estimated based on the divers' experience. If these conditions were not met, the survey was not considered part of the sample set and was not included in the analysis.

Video footage was analyzed using SeaGIS EventMeasure software, v.5.22 (SeaGIS, 2008b Pty., Ltd., Bacchus Marsh, VIC, Australia) to record straight carapace length (SCL; cm). The measurement points for SCL were selected at the nuchal scute and the tip of one of the supracaudal scutes (Bolten, 1999) when both were clearly visible in the same frame. To reduce measurement error, the average of ten SCL measurements from separate video frames was calculated for each turtle (Harvey et al., 2001).

Catch per unit effort (CPUE) was calculated as the number of turtles filmed (i.e., "caught") per dive time:

$$CPUE = \frac{N_t}{t}$$

Where *Nt* is the number of turtles filmed and t is the time (in hours) at a given location (**Table 1**). When applicable, photo-identification using the I^{3}S software with the random pattern search was used to check for re-sighting events (Calmanovici et al., 2018). I^{3}S has a high success rate for positively identifying resighted individuals; for free-swimming turtles I^{3}S has an 85% success rate (Calmanovici et al., 2018). Additionally, all matches identified by I3S were visually inspected to confirm potential match. To avoid pseudoreplication, all resighted turtles were treated as an individual average measurement as resightings happened <1 year apart and no substantial growth was observed.

Statistical Analysis

To examine factors that may be influencing size distribution, we evaluated individual body size (i.e., SCL) as a function of water temperature, species, and habitat type in a linear mixed effects model (LMM). Survey site was used as a repeated effect to account for spatial autocorrelation as we made multiple visits to each site. We ran model diagnostic tests to evaluate which model type was appropriate for the data and model residuals were assessed for homoscedasticity and normality. Visual inspection of the quantile-quantile plot and fitted values vs. residuals plot conformed to the model assumptions. Therefore, we evaluated factors influencing body size using LMM using R package *lme4* (Bates et al., 2015).

We used the information-theoretic approach for model selection based on Akaike Information Criterion correction (AICc) for small sample sizes (Burnham and Anderson, 2002; Johnson and Omland, 2004) to identify explanatory variables that influence the size distribution using the dredge function in the R package *MuMin* (Barton, 2020). In the dredge function, we limited the number of allowed explanatory variables to 2 due to our small sample size. Models with ΔAICc < 2 from the top-ranked model were retained in the confidence model set. Lastly, we examined the 95% confidence intervals of all explanatory parameters to identify uninformative parameters, i.e., parameters that had confidence intervals crossing zero (Burnham and Anderson, 2002; Arnold, 2010; Leroux, 2019). All candidate models were tested against our global model:

$$SCL = \beta_0 + \beta_1 \times Species + \beta_2 \times Habitat\ Type + \beta_3 \times$$

$$Water\ Temperature\ (^{\circ}C) + \varepsilon_{i,j},$$

Where SCL is the predicted mean body length at site *i*, β_0 is the intercept, and $\varepsilon_i \sim \mathrm{N}(0, \sigma^2)$ of site *i*. All analyses were

TABLE 2 | Straight carapace length ranges, with mean ± SD, of each species at each habitat type.

Habitat type	*N*	Range	Mean ± SD
Artificial Reef			
Green	15	33.49–66.96 cm	50.68 ± 8.38 cm
Loggerhead	7	54.86–91.77 cm	73.44 ± 13.06 cm
Kemp's ridley	2	42.23–44.98 cm	43.61 ± 1.94 cm
Jetties			
Green	6	30.76–34.57 cm	31.81 ± 1.51 cm
Piers			
Green	2	28.53–52.02 cm	40.27 ± 16.61 cm
Loggerhead	3	69.20–81.70 cm	77.04 ± 6.83 cm

Kemp's ridley turtle sightings are included here for reference but were not included in the statistical analyses due to their small sample size.

performed in R v.3.5.2 (R Development Core Team, 2021) and R Studio v.1.0.153 (RStudio Team, 2021 Inc.).

RESULTS

Throughout our study, 35 sea turtles were recorded, but only 33 sea turtles were measured using the SVCS. CPUE among the different site locations varied considerably (**Table 1**). Destin Jetties had the highest CPUE with 3.41 turtles/h, while three sites (Dolphin Reef, Access Way 4, and Topsail Hill) had zero observed turtles despite over 5 h of surveying, combined. Overall, the average filming frequency across all dive surveys were 1.17 turtles/h. Three turtles were resighted at the same artificial reefs. Two individuals were resighted once, while the third individual was resighted three times.

We observed body lengths of green turtles ($n = 23$) ranging from 28.55 to 66.96 cm (mean 43.07 cm ± 11.26 cm standard deviation; SD) and loggerhead turtles ($n = 10$) ranging from 59.71 to 91.77 cm (mean 74.50 cm ± 11.35 cm SD) across all sites and locations (**Figure 2**). Green turtles were primarily juveniles, with only one subadult (defined as 65 < SCL < 90 cm; Bresette et al., 2010) observed (**Table 2**). Of the loggerhead turtles observed, 26% were classified as adults (SCL > 82 cm) and 74% were subadults (SCL < 82 cm; Márquez, 1990), and no juveniles were filmed. It should be noted that recent research indicates that the size at maturity cut-off for adult loggerhead and green turtles may be lower than previously thought (Phillips et al., 2021). However, we decided to use a more broadly accepted cutoffs for these species as this study was just recently published and was based on data from one nesting beach, albeit with very high numbers of nesters. In the future, it may be worthwhile to use these lower cut-offs for size-at-maturity, as well as to consider regionally specific cut-offs. One adult male loggerhead turtle was confirmed based on tail length. Kemp's ridley turtles were observed as well (**Figures 3A-D**), but because their sample size was small ($n = 2$), they were excluded from the statistical analysis, and their size ranged from 42.23 cm to 44.98 cm (mean 43.61 cm ± 1.94 cm SD).

When evaluating the effect of water temperature, habitat, and species on the size distribution, the model confidence set included one top ranked model (**Table 3**). In the top ranked model, habitat type and species best predicted SCL of sea turtles in the neGOM. Upon evaluating the explanatory variables in the confidence set, only one variable's confidence intervals crossed zero: the fishing pier habitat type. Overall, the rock jetties supported the smallest green turtles, with the fishing pier and artificial habitat supporting a wider range size of this species (**Figure 4**). The artificial reefs supported a wider range of loggerhead turtles, subadult to adult, while we observed only sub-adult loggerhead turtles at the fishing piers (**Figure 4**).

DISCUSSION

The SVCS successfully collected length-based data on sea turtle populations at nearshore artificial habitats. Research on artificial reefs in Florida's nearshore coastal waters is generally lacking due to the difficulty in capturing and accessing the turtles on these reefs with traditional research methods. However, the use of SVCS provided a snapshot of the local sea turtle populations in the neGOM, with minimal cost and without the need for direct capture methods. The SVCS allowed us to remotely measure SCL from each turtle encounter, separate each animal into the appropriate size class, and then examine the size class distribution among different habitat types.

Our LMM analysis indicated that habitat type and species greatly influenced size distribution of sea turtles throughout the neGOM. In our study, all green turtles except one were considered juveniles (SCL < 65 cm), and were observed at almost all sites, except Beasley Park and Okaloosa fishing pier. A reasonably high density of juvenile green turtles may suggest that the area is serving as an important foraging and recruitment area for this species (León and Diez, 1999). Once green turtles reach SCL ≥ 35 cm, they undergo an ontogenetic habitat shift from the open ocean to the nearshore reefs (Summers et al., 2017). Often, these smaller juvenile green turtles can be found at rock jetties as they transition from open ocean to nearshore foraging habitats (**Figure 3D**; Coyne, 1994; Metz and Landry, 2013). Rock jetties serve as resting grounds, providing juvenile green turtles shelter and adequate food, primarily algae, during this transition (Coyne, 1994; Metz and Landry, 2013). In our study, the Destin Jetties supported the smallest size range of green turtles (range 30.76 cm–34.57 cm;

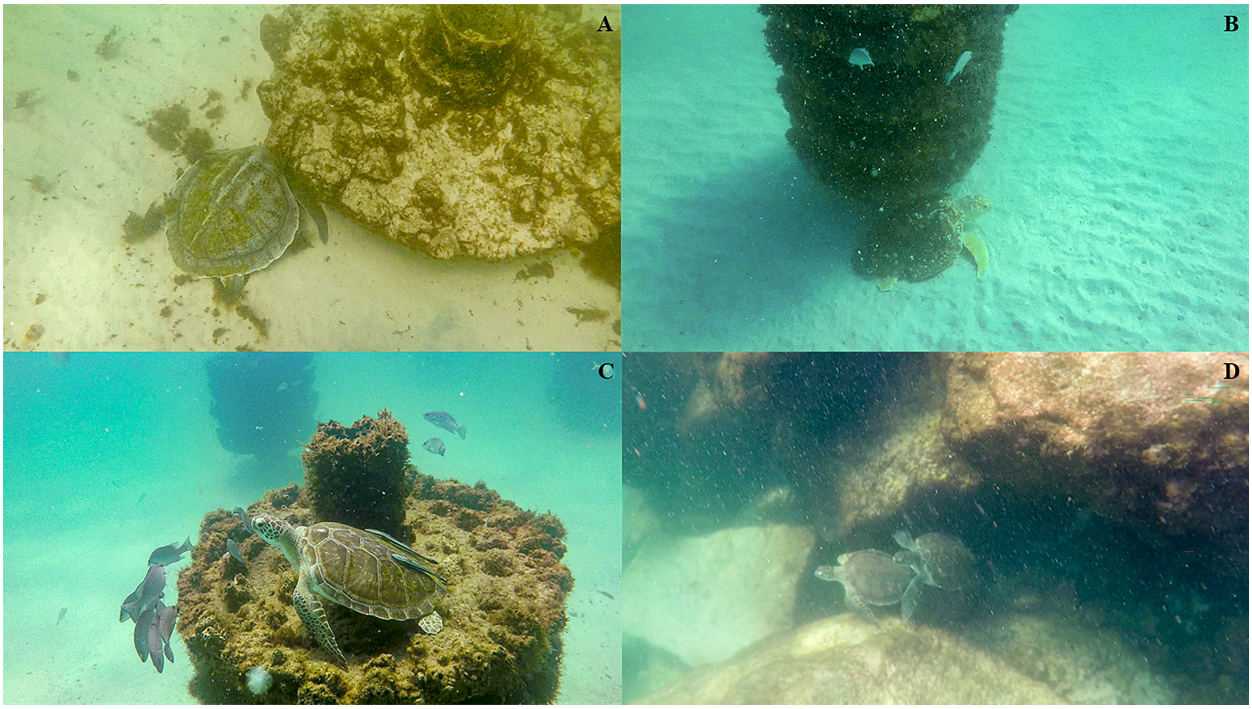

FIGURE 3 | All species of sea turtles using artificial habitats for resting and protection in the northeastern Gulf of Mexico. **(A)** Kemp's ridley (*Lepidochelys kempii*), **(B)** Loggerhead (*Caretta caretta*), **(C)** green (*Chelonia mydas*), observed sitting on top of reef module, and **(D)** two juvenile green turtles observed resting and swimming together at the Destin East Pass Jetties.

TABLE 3 | Model confidence set (ΔAICc < 2) for LMM analysis of body length and environmental correlates.

Model terms				**Model support**			
	Habitat	Species	Temperature	df	AICc	ΔAICc	Weight
Model 1	+	+	–	6	234.68	0	1

+, variable included in the model; –, explanatory variables not included in the model; df, degrees of freedom; AICc, Akaike's Information Criterion corrected for small sample size; ΔAICc, difference in AICc from the top ranked model and model in consideration.

mean 31.81 ± 1.51 cm). The observed size distribution may be a result of size-specific habitat requirements and predation risk (Bresette et al., 2010).

Loggerhead turtles observed in the study area were sub-adults and adults, with no observations of juveniles. Loggerhead turtles are highly migratory and travel between foraging grounds and breeding grounds (Hart et al., 2014) and may be attracted to fish and encrusting invertebrates, such as sponges and cnidarians, present at the artificial reefs (Mendonça et al., 1982). Loggerhead turtles may use the artificial reefs as resting grounds while migrating into the neGOM for breeding and nesting. Notably, most of the loggerhead turtles observed coincided with the nesting season (May–October), which may be because several beaches in the neGOM are known nesting beaches for loggerhead turtles (Fuentes et al., 2016 and Silver-Gorges et al., 2021). However, only 26% of the loggerhead turtles observed during our surveys were classified as adults, so this also suggests that the Florida panhandle is important habitat for sub-adult loggerheads.

Flipper-tagged green turtles were present at Navarre Beach, Park East, and the Navarre Beach fishing pier; however, untagged green and loggerhead turtles were present at all site locations. Most local tagging efforts in the region occur at nearby sea turtle rehabilitation centers, rather than in-water research tagging efforts, although sustained in-water capture and tagging programs exist in St. Joseph's Bay and in the Big Bend area (Lamont and Johnson, 2020; Wildermann et al., 2020; Chabot et al., 2021). Regardless, the SVCS allows researchers to collect data on turtles that have not yet been tagged and of various size classes. Green turtles were observed year-round, with three individuals being re-sighted at the same artificial reef, which may suggest site fidelity and residency. Juvenile hawksbills have fidelity to specific sites (Limpus, 1992; van Dam and Diez, 1998), thus, it is not unlikely that juvenile green turtles may experience this same sort of site fidelity. Past studies have confirmed that green turtles tend to overwinter in the neGOM (Lamont et al., 2018), so, perhaps, it should not be unexpected that green turtles inhabit artificial reefs year-round even at such northerly sites. This could be discerned with longer-term monitoring programs at artificial reefs in the neGOM. If conditions in an area are favorable (i.e., feeding, protection, adequate temperatures, and

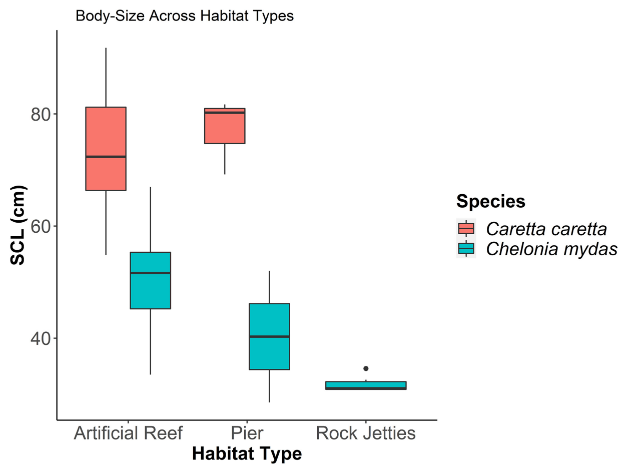

FIGURE 4 | Sea turtlestraight carapace length (SCL) in relation to habitat type and species.

nesting for adults), despite the higher latitude location, then there would be no need for migration elsewhere (Carr, 1980).

In considering the efficacy of using SVCS to obtain morphometric data, we calculated catch per unit effort. Notably, our survey sites differed significantly in survey effort and was heavily influenced by weather and sea state, and therefore sample sizes were higher at some artificial reefs and between habitat types (**Table 1**). Anecdotally, there is probably also an observer effect, which we did not calculate as our survey team was consistent throughout the study period. It seems likely that observers that conduct surveys at different swim speeds, or other variables, may have different CPUE. In practice, swimming with the SVCS slows the diver down, and thus this individual would set the pace for the survey. In the future, it may be useful to physically measure distance traveled during the survey (e.g., using GPS) or include survey team as a random effect, when evaluating patterns in carapace length and SVCS CPUE. In addition, it is likely that sites with higher turtle abundance would also have higher CPUE. Future surveys that compared different types of surveys, e.g., in-water SVC and aerial surveys with unmanned aerial vehicles, in locations with high water visibility and calm conditions may help to better ascertain sighting efficiency and CPUE for the SVCS.

Our CPUE (range: 0.0–3.41 turtles/h) was comparable to capture frequencies seen in the Dominican Republic (range: 0.0–3.43 turtles/h; León and Diez, 1999) and Mona Island, Puerto Rico (range: 0.48–2.38 turtles/h) during snorkel surveys. For example, our maximum CPUE was slightly less than the maximum sighting frequency observed in the Dominican Republic (sighting frequency (3.41 vs. 3.43 turtle/h) and slightly less than maximum capture frequency (3.41 vs. 3.43 turtles/h; León and Diez, 1999). Our average CPUE was 1.17 turtles/h, which is comparable to the sighting frequency in the Dominican Republic (1.67 turtles/h) and slightly less than their capture frequency (1.42 turtles/h; León and Diez, 1999). During our dive surveys, only four sea turtles were sighted in the water, but not successfully filmed. This is substantially less than snorkel capture surveys in the Dominican Republic, where they sighted 324 turtles and successfully captured 275 of those turtles (León and Diez, 1999). Ultimately, incorporating the use of SVCS to conduct dive surveys at artificial habitats would greatly increase the amount of data collected on a given sea turtle population.

Conclusion

Many mark-recapture studies are commonly conducted in seagrass beds, which are important habitats for sea turtles. However, few mark-recapture studies have been conducted in the coastal waters of the neGOM, and even fewer at artificial habitats (i.e., fishing piers, jetties, and reefs), due to logistical and financial challenges associated with direct capture methods (but see Coleman et al., 2016). SVCS allows researchers to study sea turtle population structure in areas where it is otherwise difficult to capture a range of size classes. Importantly, SVCS may be used in various locations, such as deep offshore artificial reefs, nearshore habitats, seagrass beds, and mangrove creeks (Santana-Garcon et al., 2014; Cundy et al., 2017; Logan et al., 2017; Siegfried et al., 2021); however, decent water visibility is required for turtle detection (Siegfried et al., 2021). With the implementation of the SVCS over time, residency and site fidelity traits may be monitored at selected sites. The use of SVCS gives researchers a greater chance to study sea turtles in-water, where they spend most of their lives, without the need to capture or to physically tag. Therefore, this methodology may give scientists a more comprehensive understanding of the sea turtle populations in each area. Through our remote in-water study, we have observed three species and all neritic life stages using artificial habitats. Thus, by implementing and collecting demographic data in-water using novel approaches, such as the SVCS, we demonstrate the use of an in-water non-invasive monitoring study while also collecting baseline population data and size structure for loggerhead and green sea turtles.

DATA AVAILABILITY STATEMENT

The raw data supporting the conclusions of this article will be made available by the authors, without undue reservation.

ETHICS STATEMENT

Ethical review and approval was not required for this animal study because no handling of animals occurred. Therefore, no ethical committee evaluation was required.

AUTHOR CONTRIBUTIONS

TS contributed to the conception and design of study, data collection, data analysis, grant writing, and writing of the manuscript. CN and JR contributed to data collection, post-processing video footage, and extensively reviewing the manuscript. MW contributed R code analysis support, GIS mapping consultation, and extensively reviewing the manuscript. MF contributed to an extensive review of the manuscript. SP was the advisor of TS and contributed data analysis, aiding in grant writing, aiding in research development, and manuscript writing. All authors contributed to manuscript revision, read, and approved the submitted version.

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Inter-Nesting Movements, Migratory Pathways, and Resident Foraging Areas of Green Sea Turtles (*Chelonia mydas*) Satellite-Tagged in Southwest Florida

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Globally, sea turtle research and conservation efforts are underway to identify important high-use areas where these imperiled individuals may be resident for weeks to months to years. In the southeastern Gulf of Mexico, recent telemetry studies highlighted post-nesting foraging sites for federally endangered green turtles (*Chelonia mydas*) around the Florida Keys. In order to delineate additional areas that may serve as inter-nesting, migratory, and foraging hotspots for reproductively active females nesting in peninsular southwest Florida, we satellite-tagged 14 green turtles that nested at two sites along the southeast Gulf of Mexico coastline between 2017 and 2019: Sanibel and Keewaydin Islands. Prior to this study, green turtles nesting in southwest Florida had not previously been tracked and their movements were unknown. We used switching state space modeling to show that an area off Cape Sable (Everglades), Florida Bay, and the Marquesas Keys are important foraging areas that support individuals that nest on southwest Florida mainland beaches. Turtles were tracked for 39–383 days, migrated for a mean of 4 days, and arrived at their respective foraging grounds in the months of July through September. Turtles remained resident in their respective foraging sites until tags failed, typically after several months, where they established mean home ranges (50% kernel density estimate) of 296 km^2. Centroid locations for turtles at common foraging sites were 1.2–36.5 km apart. The area off southwest Florida Everglades appears to be a hotspot for these turtles during both inter-nesting and foraging; this location was also used by turtles that were previously satellite tagged in the Dry Tortugas after nesting. Further evaluation of this important habitat is warranted. Understanding where and when imperiled yet recovering green turtles forage and remain resident is key information for designing surveys of foraging resources and developing additional protection strategies intended to enhance population recovery trajectories.

Keywords: green turtle, home range, movement paths, satellite tracking, state space modeling

INTRODUCTION

Green turtles (*Chelonia mydas*) are widely distributed, nesting circumglobally in temperate and tropical waters. A 2004 study estimated that green turtle populations had declined by 37–61% worldwide over the previous 141 years (Seminoff, 2004) and consequently the species is classified as globally endangered (Baillie et al., 2004). However, a more recent assessment of global trends in green turtle nesting patterns indicated that four out of five regional management units (RMUs; Wallace et al., 2010) for the species are significantly increasing in abundance (Mazaris et al., 2017).

Although the green turtle is listed as federally endangered under the United States Endangered Species Act (Endangered Species Act [ESA], 1973, as amended), green turtles nesting in the Gulf of Mexico appear to be increasing in abundance. Modest increases in green turtle nest counts have been reported on northwestern Gulf of Mexico beaches in Texas (Shaver et al., 2020) and nest counts for Florida green turtles have risen at an exponential rate [Chaloupka et al., 2008; Valdivia et al., 2019; Florida Fish and Wildlife Conservation Commission (FWC) unpublished data]. Green turtle nesting activity is concentrated along the east-central and southeast coasts of Florida, but a marked increase was documented on the Gulf coast in recent years, including in Dry Tortugas National Park at the western end of the Florida Keys reef tract in the National Marine Sanctuary boundary (see text footnote 1). Green turtle nesting in southwest Florida was first documented in 1994 (Foley, 1997) and from 1994 to 2012, no more than 60 green nests were ever reported annually on the west coast of peninsular Florida during statewide nesting beach surveys. An exponential increase has been observed since 2013 and 841 green turtle nests were documented on the west coast of Florida in 2019 (FWC, unpublished data).

While decades of targeted conservation efforts have resulted in population recovery (Valdivia et al., 2019), optimizing strategies to protect sea turtles requires an in-depth understanding of their temporal and spatial distributions, migratory patterns, habitat utilization, trends and identification of source populations. International sharing of tracking data is becoming more common (Hays and Hawkes, 2018) and these large-scale datasets have proven to benefit conservation by creating management actions that successfully reduce fisheries by catch and vessel strikes, and establish marine protected areas (Hays et al., 2019). Documenting inter-nesting behavior, migratory routes, foraging grounds, and high-use areas is vital in assessing threats that coincide with turtles in the marine environment (e.g., incidental capture, oil spills, dredging, and red tide).

Because nighttime tagging operations are rare in southwest Florida, and extensive remote wilderness exists in this area, it is likely that many green turtles nesting in the region have never been encountered. This data gap creates complications in understanding the population structure as it is unknown if green turtles nesting on Gulf coast beaches represent a subset of the population that nests on Florida's east coast or if the population source is instead elsewhere. Genetic analyses of mitochondrial DNA indicate that colonization of northwest and west-central Florida *via* the Atlantic Coast rookeries cannot be ruled out (Shamblin et al., 2020).

Satellite telemetry is a widely used tool to study movements and habitat use patterns of marine megafauna, and thousands of turtles have been tracked around the world (Hays and Hawkes, 2018). Data from satellite transmitters and dive sensors suggest that there is remarkable variability in the at-sea behavior of breeding green turtles. During the nesting season, turtles typically migrate from feeding grounds to nesting beaches where they lay several clutches of eggs. However, there can be a great deal of plasticity in each phase of this process, including migration strategy (Godley et al., 2002; Blumenthal et al., 2006; Seminoff et al., 2008; Baudouin et al., 2015; Hays et al., 2020), the extent of movement during the inter-nesting period (Hays et al., 1999); the number of days between nesting events, and foraging behavior (Hatase et al., 2006), with variability documented even within a single nesting beach. Currents (Chambault et al., 2015), learned behavior (Scott et al., 2014), water temperature (Godley et al., 2002; Hays et al., 2002; Santos et al., 2015), predator avoidance (Mettler et al., 2020), resource availability (Dalleau et al., 2019), and diel cycles (Hays et al., 1999) have been proposed to influence such behaviors.

Research using telemetry to track juvenile green turtles in the Gulf of Mexico has revealed that they generally use small core use areas in nearshore foraging habitats at this life stage (Hart and Fujisaki, 2010; Lamont et al., 2015; Wildermann et al., 2019), although seasonal differences in foraging ranges have been reported (Metz et al., 2020). Satellite tracking data for adult green turtles nesting on United States Gulf of Mexico beaches are currently limited to studies at Dry Tortugas, where post-nesting movements have been documented both within the park and the surrounding areas of the Florida Keys (Hart et al., 2013). In-water captures at Dry Tortugas (Fujisaki et al., 2016) and the Eastern Quicksands (Herren et al., 2018) have identified these sites as high-density foraging grounds for adult green turtles.

Movements and residence areas for green sea turtles nesting in peninsular southwest Florida have not been previously identified. Thus, our objectives were to document adult female green turtle inter-nesting behavior, delineate migratory corridors used, identify foraging sites selected, and spatially define home ranges and core use areas.

MATERIALS AND METHODS

Study Sites

Keewaydin Island and Sanibel Island are coastal barrier islands located on the lower southwest coast of Florida (**Figure 1**; Sanibel – N 26.46481°, W 81.16714°, Keewaydin – N 26.04844°, and W 81.78139°). Sanibel Island is 21 km in length with a land area of 4,429 ha while the more linear Keewaydin Island is 12.5 km long and encompasses 526 ha. Eighty-five percent of Keewaydin is state-owned and is within Rookery Bay National Estuarine Research Reserve. Keewaydin is a relatively pristine island that can only be visited by boat, while the coastline of Sanibel is much more developed and readily accessible. The

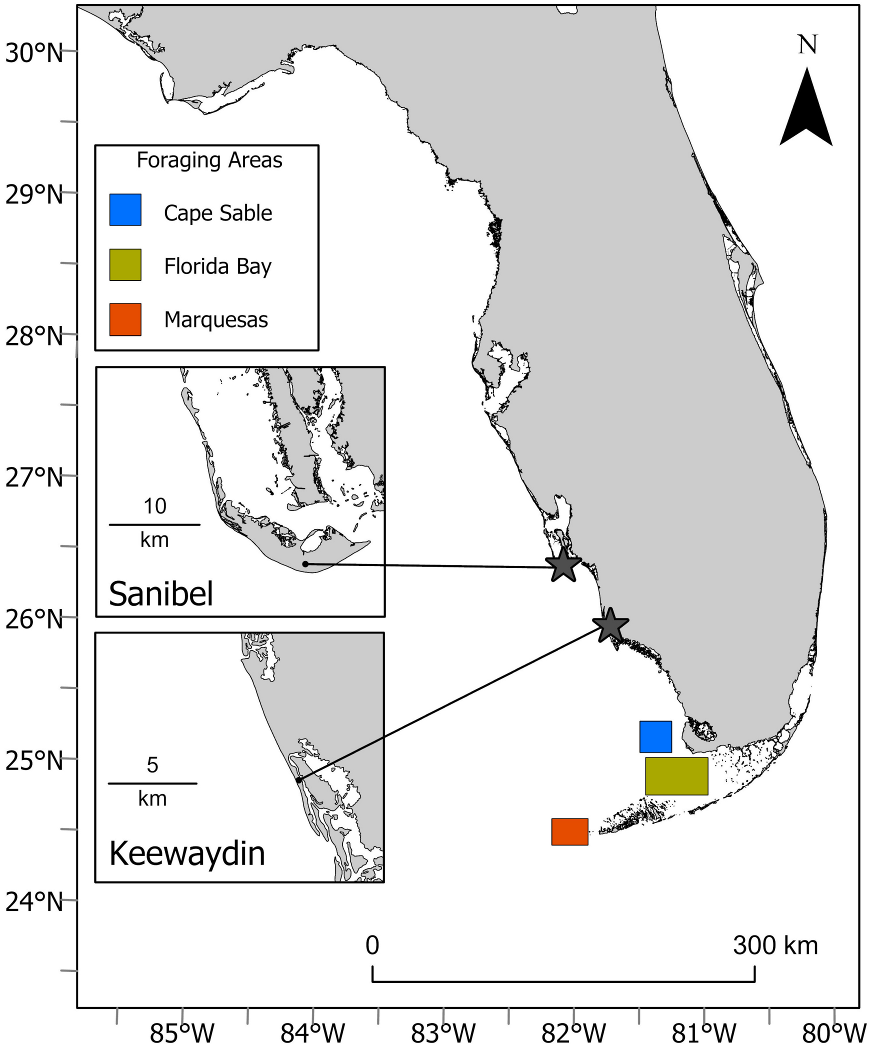

FIGURE 1 | Study sites: stars indicate tagging beaches and squares indicate foraging grounds.

straight-line distance between the two sites is approximately 30 km.

Satellite Tagging

Nighttime tagging surveys run from May 1 to July 31 on Sanibel Island and May 15 to July 31 on Keewaydin Island. Staff patrol these two beaches on ATVs from sundown to sunrise seven nights per week. We captured turtles during night patrols by temporarily corralling them after nesting in an adjustable plywood box. We tagged the trailing edge of front flippers with 681/C Inconel self-piercing sea turtle tags (National Band and Tag Company, Newport, KY, United States) and inserted subcutaneous passive integrated transponder (PIT) tags (Biomark FDX-B HPT12 PIT) in the right front flipper (NMFS-SEFSC, 2008). We recorded morphometric data and took biopsies for genetics and stable isotope analysis for each individual. We used Sirtrack K2G 575E KiwiSat 202B Argos platform terminal transmitters (PTTs) that were adhered according to Mansfield et al. (2009). We cleaned the carapace, prepped it with a drying agent and attached the transmitter using a two-component adhesive (DeWalt Pure50+^{TM}) followed by a two-part steel reinforced epoxy putty (Sonic Weld®). Additionally, we coated the transmitter and surrounding epoxy with antifouling paint. We released the turtles on site immediately after all attachment methods had dried or set. Sirtrack Argos PTTs were programmed by the manufacturer with a 24-h on/24-h off duty cycle to conserve battery life in 2017 and were continuously on in 2018 and 2019.

Analysis

We used switching state space modeling (SSM) to characterize the movements of tagged turtles. The model was previously described in Jonsen et al. (2005) and has been applied to model movement of many marine animals (Bailey et al., 2009; Shillinger et al., 2010; Maxwell et al., 2011; Shaver et al., 2016; Iverson et al., 2020). Specifically, we applied a Bayesian hierarchical movement model with behavioral-state switching in the R package "bsam" (Jonsen et al., 2005, 2017; Jonsen, 2016; R Core Team, 2020) by calling JAGS (package rjags; Plummer, 2019) to run the Markov Chain Monte Carlo (MCMC) algorithm. The model was fit with the function "fit_ssm()," using the "hDCRWS" specification (hierarchical first difference correlated random walk switching model); we applied a time step of 1 day. The MCMC parameters were set following Hart et al. (2020), using adaptive sampling for 7,000 draws, taking 10,000 samples from the posterior distribution, and thinning by 5 to reduce MCMC autocorrelation, resulting in 2,000 posterior samples for inference. The SSM estimates location and behavioral mode at regular time intervals, improving accuracy of tag data by accounting for positional errors and dynamics of animal movements. The SSM assigned either area restricted movement (ARS) or directed movement to a location based on the swimming speed and turning angle of the animal. The ARS movements corresponded to either inter-nesting or foraging behavior, and directed movement (transiting) corresponded to migration. Switching SSMs utilize raw track data to determine behavioral state in a bimodal context by providing a behavioral index between 1 and 2, referred to as a "*b*" value. Mode 1 (e.g., "migrating") is represented by *b* values <1.5 and mode 2 (e.g., "resident/foraging") is represented by *b* values >1.5 (Jonsen et al., 2005; Breed et al., 2009). We used the model to classify ARS and migratory behavior, determine the dates of migration, and identify the date of arrival at foraging grounds (i.e., when ARS behavior resumed post-migration).

To assess inter-nesting movements, we determined the mean distance traveled per day during inter-nesting for each turtle by calculating the distance traveled per day from the SSM points using the geosphere package (successive distance between points from 1 day to the next; Hijmans, 2019) in R (R Core Team, 2020), and then calculated the mean distance traveled per day for each turtle over their inter-nesting period. We calculated the inter-nesting interval (the number of days between nesting events) using recapture data when available, as telemetry locations that appeared on the beaches had high estimated error associated with points (i.e., spatial data were unreliable). Means were accompanied by ±SD.

We used the Optimized Hot Spot Analysis in ArcGIS Pro 2.4.3 to identify areas of high use during inter-nesting and migration (Environmental Systems Research Institute [ESRI], 2019). The program uses inter-nesting and migratory data from the SSM and the Getis-Ord Gi* statistic to generate a fishnet grid of 18 km squares, assigning them a color based on statistical significance (Getis and Ord, 1992). We calculated bathymetry from the "hotspot" grid cells comprising the migratory corridor where higher proportions migrated. We layered the NOAA National Geophysical Data Center (2001) United States Coastal Relief Model Vol.3 – Florida and East Gulf of Mexico in ArcGIS Pro to estimate depth associated with each migration grid cell (CRM, NOAA National Geophysical Data Center, 2001; Environmental Systems Research Institute [ESRI], 2019).

Post-migration ARS points were considered "foraging" and we used the first date of these ARS points to delineate the turtle's date of arrival to the foraging area. We corroborated these dates using cumulative distance plots (not shown Hart et al., 2021). To determine core use areas upon arrival at foraging grounds, SSM locations for each turtle were used for kernel density estimation (KDE) analysis for all individuals. Kernel density is a tool used in spatial ecology to identify areas of heavy use (i.e., core areas) within a home range boundary. We used the (the adehabitatHR package via Home Range App created by Cyril Bernard, SIE, CEFE-CNRS) for each KDE. We used 95% KDEs to represent the home foraging range and the 50% KDEs to represent core areas of activity at foraging sites.

RESULTS

The 14 turtles tracked include 4 individuals that were instrumented twice to assess consistency of foraging site selection; one of these turtles nested in two consecutive years and three had a 2-year inter-nesting interval (**Table 1**). Turtles ranged in size from 93.1 to 109.3 cm SCL (straight carapace length, notch to tip), with a mean size of 102.9 ± 4.01 cm. Over the 3-year study period we tracked turtles for a total of 1,707 days, with individual tracking durations ranging from 39 to 383 days (mean = 122 ± 83 days).

Argos assigns location classes (LCs) 3, 2, 1, A, and B in order of descending accuracy to each location point. Argos (2016) states that the estimated accuracy in latitude and longitude is <250 m for LC 3, 250–500 m for LC 2, 500–1,500 m for LC 1, $>1,500$ m for LC 0, and unbounded accuracy for LC A and B. LC B represented the highest proportion of data (mean = 6.4 locations per day) followed by LC A (mean = 0.97 locations per day). Location data in classes 3, 2, and 1 were less common, with means of 0.17, 0.22, and 0.20 locations per day, respectively (see **Supplementary Table 1**).

Inter-Nesting Behavior

Eight turtles had clear migrations identified by SSM (**Figure 2**), providing a well-defined end date for their nesting season and allowing us to characterize inter-nesting movements prior to initiation of migration. Turtle J was instrumented at her last nesting event of the season, which precluded any inter-nesting observations. Turtle A did not have a migration identified by SSM and therefore an end date for her nesting season was not defined, prohibiting the calculation of distance traveled per day. However, she clearly remained close to the Sanibel nesting beach throughout the tracking period. With the exception of this individual, all turtles were highly mobile between nesting events, exhibiting mean track lengths between 11 and 30 km/day during the nesting season (**Table 2**). For the eight turtles that had migrations identified by SSM, the mean distance traveled per day between the tagging date and the start of migration (i.e., the nesting season) was 21 km/day. Turtle C traveled the longest distance during the nesting season, logging 1,489 km between the tagging date and initiation of migration (June 16, 2017–August 22, 2017; **Figure 2A**). The mean water depth associated with inter-nesting movements was 6.3 m.

Six of the 14 turtles traveled between the nesting beach and a distinct in-water location ∼30 km west of Cape Sable, southwestern tip of Florida, between consecutive nesting events

TABLE 1 | Tracking summary for satellite-tagged green turtles.

Turtle	Tagging site	Size: SCL n–t (cm)	Date tagged	Last transmission	Tracking period (days)
Turtle A	Sanibel	105.3	June 4, 2017	September 21, 2017	109
Turtle B	Sanibel	93.1	June 14, 2017	November 5, 2017	144
Turtle C	Sanibel	101.2	June 16, 2017	November 20, 2017	157
Turtle D	Sanibel	103.3	June 27, 2017	September 29, 2017	94
Turtle E	Sanibel	102.9	July 10, 2017	October 13, 2017	95
Turtle F	Keewaydin	107.5	July 7, 2017	July 25, 2018	383
Turtle G	Keewaydin	101.4	June 1, 2017	November 7, 2017	159
Turtle G	Sanibel	101.4	June 21, 2018	July 30, 2018	39
Turtle A	Sanibel	105.3	May 30, 2019	September 2, 2019	95
Turtle F	Keewaydin	107.5	June 5, 2019	May 21, 2020	175
Turtle E	Sanibel	102.9	June 10, 2019	August 27, 2019	78
Turtle H	Sanibel	109.3	June 17, 2019	August 3, 2019	47
Turtle I	Keewaydin	102.0	June 19, 2019	September 11, 2019	84
Turtle J	Sanibel	97.7	July 21, 2019	September 7, 2019	48
					Total tracking days = 1,707

SCL is straight carapace length, notch–tip.

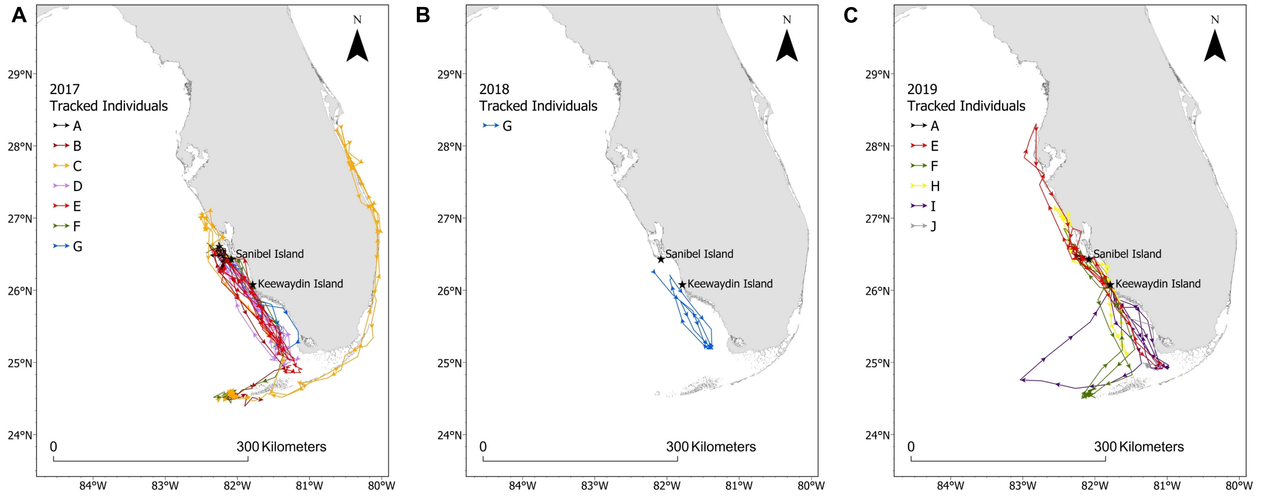

FIGURE 2 | Daily switching state space modeling tracks throughout the tracking period for all individual adult female green turtles (*Chelonia mydas*) satellite-tagged in southwest Florida for **(A)** 2017, **(B)** 2018, and **(C)** 2019.

(**Figure 3**). These individuals traveled as far as 300 km roundtrip and spent 2–6 days at the site before returning to the nesting beach. Three of these tracks were documented in 2017, one in 2018, and two in 2019. Turtle E and Turtle G were satellite-tagged twice but only exhibited this behavior during one of the 2 years.

Logistical limitations prevent a true saturation tagging project (in which every turtle is observed and tagged) at each of the study sites. As such, the satellite-tracked turtles in this study were not observed during every nesting event on Sanibel and Keewaydin Islands. However, on the 10 occasions when a satellite tagged turtle was seen during two consecutive nesting events, the internesting interval ranged from 9 to 14 days (mean = 11 days; $n = 5$ turtles).

Migration

Eight turtles had migration periods (**Table 2**). Two turtles (Turtle G in 2017 and Turtle F in 2019) had well defined foraging grounds but SSM did not delineate a clear migratory phase. Each turtle traveled south after their presumed final nesting event. A nearshore migratory hotspot was identified along the coast of southwest Florida (**Figure 4**). Initiation of migration to foraging areas ranged from July 6 to August 28. Turtle G and Turtle J were the only individuals that departed for their foraging grounds in July. For the other turtles, migration start dates ranged from August 5 to August 28. The average time spent migrating to the foraging grounds was short, at 4 ± 5.7 days (range 1–18). Migratory movements identified through SSM took place in shallow waters (mean depth was 14.6, 8.3, and 8.0 m in 2017, 2018, and 2019, respectively) off the southwest coast of Florida, with the exception of two turtles: one who had a migratory phase to and from the Dry Tortugas prior to settling in Florida Bay, and another who traveled beside the continental shelf while migrating to Florida's east coast as far north as the Patrick Space Force Base in Brevard County.

TABLE 2 | Distance traveled during the nesting season and migration dates.

Turtle	Year	Total distance traveled in nesting season (km)	Distance traveled per day in nesting season (km)	Migration start date	Migration end date
Turtle A	2017	NA	NA	NA	NA
Turtle B	2017	394.9	10.7	8/5	8/10
Turtle C	2017	1489.6	22.6	8/22	9/9
Turtle D	2017	991.8	22.5	8/11	8/12
Turtle E	2017	1247.4	25.9	8/28	8/29
Turtle F	2017	472.1	15.2	8/11	8/13
Turtle G	2017	NA	NA	NA	NA
Turtle G	2018	277.4	19.8	7/6	7/7
Turtle A	2019	NA	NA	NA	NA
Turtle F	2019	NA	NA	NA	NA
Turtle E	2019	NA	NA	NA	NA
Turtle H	2019	NA	NA	NA	NA
Turtle I	2019	1094.4	29.6	8/7	8/8
Turtle J	2019	NA	NA	7/22	7/25

NA indicates that the data were not available to complete the calculation. When no migration phase was identified the end date for the nesting season was not clearly defined, so the exact dates for the nesting season could not be delineated.

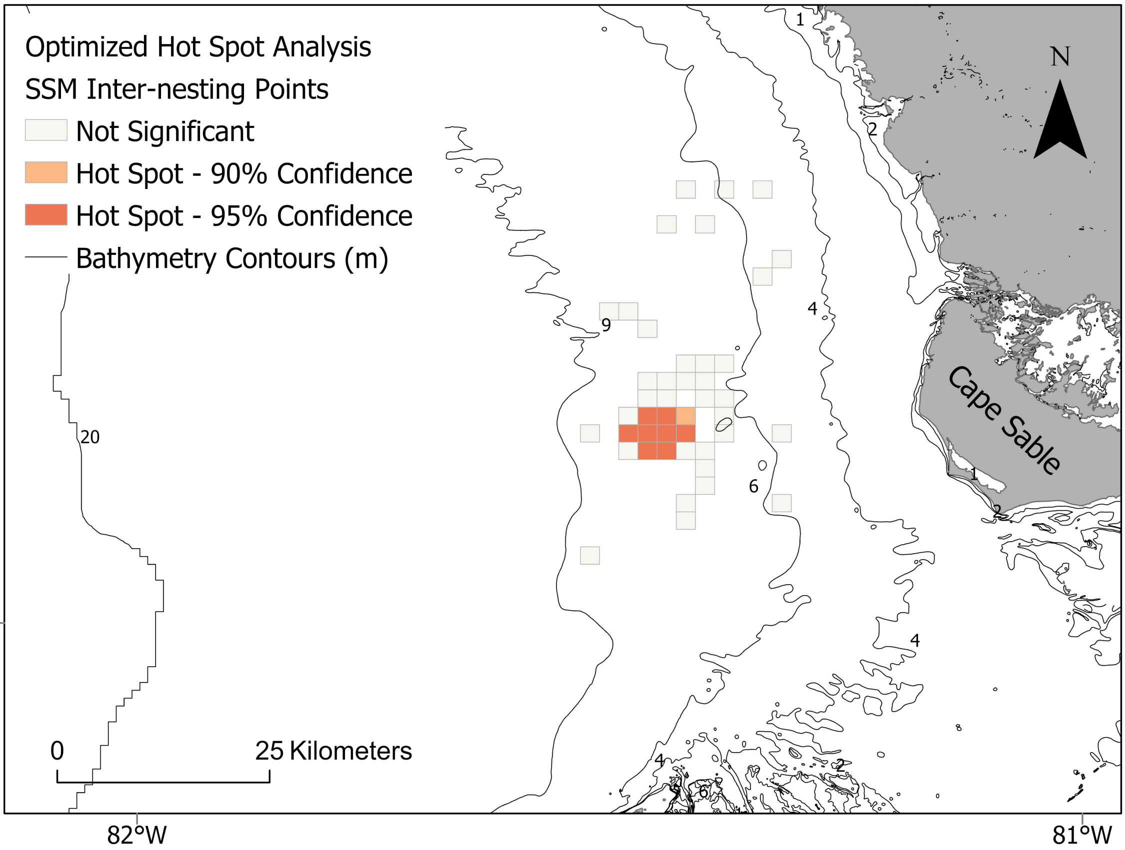

FIGURE 3 | Inter-nesting hotspot for adult female green turtles satellite-tagged in southwest Florida, ~25 km west of Cape Sable, Everglades, FL, United States.

Of the four turtles that were tagged twice, there were no instances when migration data were identified in both seasons. Turtle F and Turtle E were not sending transmissions at the likely time of migration in 2019 and did not transmit long enough to determine foraging areas. Turtle G did not have migratory points defined by SSM in 2017. Turtle A did not migrate away from the coast of Sanibel either year (2017 or 2019) during the migratory period defined in this study and could be a resident

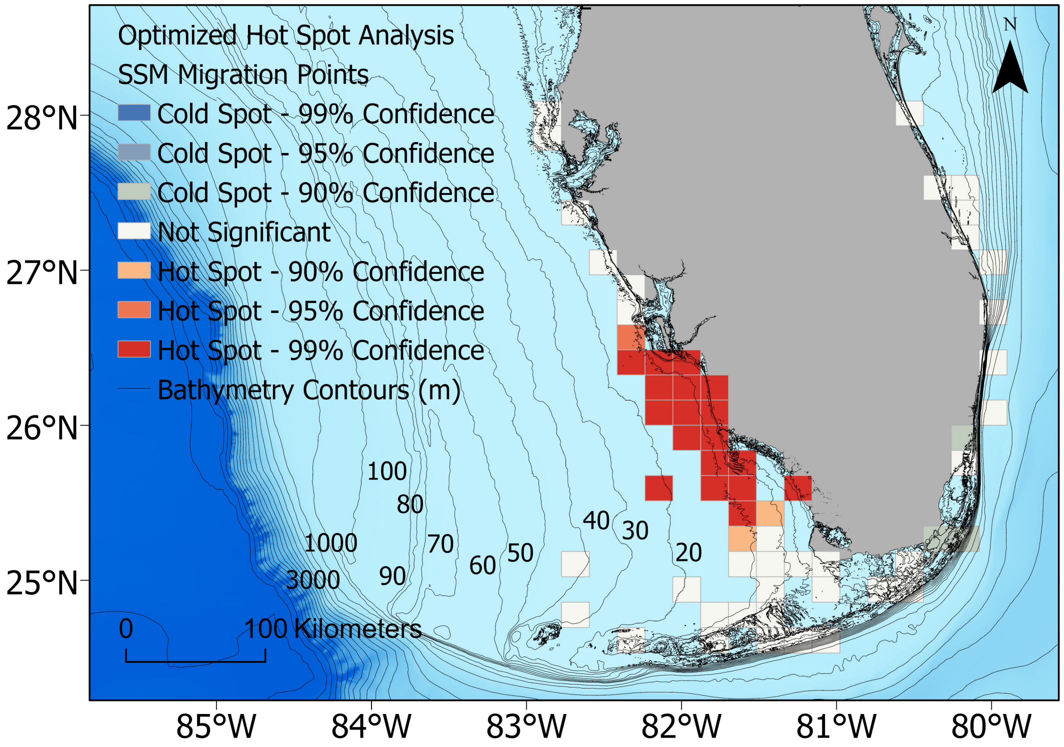

FIGURE 4 | Migratory corridors of adult female green turtles (*Chelonia mydas*) nesting in southwest Florida with hotspots of high-use.

turtle that forages and nests in the same area, but the dataset acquired during the presumed foraging period was too limited to make this assumption.

Foraging Grounds

We tracked turtles to foraging grounds in the Marquesas Keys ($n = 4$), western Florida Bay ($n = 4$), and an area offshore Cape Sable ($n = 2$; **Table 3** and **Figures 5**, **6**). Turtles were tracked at resident foraging sites for 333–345 days (mean = 94 ± 90.5 days). The size of the 50% core use resident areas for each individual ranged from 8 to 904 km^2 (mean = 296 ± 309.3 km^2; **Figures 5**, **7**). In every case the foraging period ended when the PTT stopped transmitting rather than the turtle leaving the location, and thus is not a true reflection of time spent at the foraging grounds. Nonetheless, the transmitter for Turtle F was sending high quality data until August 12 of the following nesting season.

Four individuals (Turtle D, Turtle E, Turtle I, and Turtle J) used a previously unidentified foraging hotspot in the western Florida Bay region (see **Figure 6**). The centroid locations for core use areas were very close to the shoreline for turtles foraging in the Marquesas Keys (mean = 2.3, range 1.4–3.0 km) compared to turtles foraging in western Florida Bay (mean = 21.4 km, range 11.3–23.7 km). The mean water depth at centroids in these two sites was comparable (4.2 and 4.1, respectively). The distance to shore for Turtle G that used the Cape Sable residence area in two separate years was 25 km, considerably farther than the other two sites, and the water depth at the foraging centroid was slightly deeper at 5.5 m.

For the foraging centroids, the mean distance to the closest foraging centroid was 3.1 km (range 1.1–5.5 km) for turtles foraging in the Marquesas Keys and was 19.6 km (range 4.2–36.5 km) for turtles foraging in western Florida Bay. Turtle G and Turtle F were tracked to their foraging grounds twice, and both turtles exhibited fidelity to the same foraging areas, one off Cape Sable and the other at Marquesas Keys. Turtle G's centroid locations were 4.7 km apart and Turtle F's centroid locations were 1.6 km apart (**Figure 6**). The other two turtles that were tracked twice (Turtle A and Turtle E) did not have defined foraging grounds for both tracking years and thus we could not assess the extent of their interannual site fidelity.

DISCUSSION

The 10 animals in the current study provided the first movement data for green turtles nesting on the west coast of the Florida peninsula. The inter-nesting behavior of the turtles in this study was highly variable, both among and within individuals. This behavioral plasticity may allow green turtles to adapt and survive in a dynamic environment that is exposed to frequent hurricanes, harmful algal blooms, seagrass die offs, and other shifts in food availability. Despite individualized behavior during the nesting season, there was strong site fidelity to core use areas.

Loggerhead (*Caretta caretta*) data suggest that the rookery on Sanibel may reflect dispersal of Sarasota County females, consistent with tag returns. Recapture data from loggerheads on Sanibel indicate nesting exchange between Casey Key (∼85 km),

TABLE 3 | Location, size, and depth of core use areas.

Turtle	Year	Foraging grounds start date	Foraging grounds location	Residence period (days)	Cape Sable inter-nesting (Y/N)	50% KDE area (km^2)	95% KDE area (km^2)	Centroid distance to shore (km)	Depth at centroid (m)
Turtle B	2017	August 11, 2017	Marquesas	86	Y	152.8	1225.6	3	3.7
Turtle C	2017	September 10, 2017	Marquesas	71	N	178	1337.6	2.6	5.5
Turtle D	2017	August 13, 2017	Florida Bay	47	Y	704.7	2796.3	23.7	5.5
Turtle E	2017	August 30, 2017	Florida Bay	44	Y	904	4170.5	23.5	5.5
Turtle F	2017	August 14, 2017	Marquesas	345	N	23.6	175.2	2.3	3.7
Turtle G	2017	July 1, 2017	Cape Sable	129	N	7.6	41.2	27.3	5.5
Turtle G	2018	July 8, 2018	Cape Sable	22	Y	442.9	3378.3	22.9	5.5
Turtle F	2019	January 18, 2020*	Marquesas	124	N	18.2	143.8	1.4	3.7
Turtle I	2019	August 9, 2019	Florida Bay	33	Y	16.9	90.4	11.3	1.8
Turtle J	2019	July 26, 2019	Florida Bay	43	N	20.9	127.6	19.1	3.7

**Turtle G did not send data between July 26, 2019 and January 8, 2020 and transmitted at foraging ground thereafter.*

Manasota Key (∼60 km), and Keewaydin (∼50 km), with 23, 8, and 16 tag returns from each beach since 2016, respectively (Sanibel-Captiva Conservation Foundation [SCCF], unpublished data). Green turtle recapture data are very limited due to the relatively small number of individuals nesting on the west coast of Florida, telemetry locations during known nesting events had high associated error, preventing reliable identification of nesting events from satellite-derived data alone. In this study, the only exchange documented among green turtle nesting beaches on Florida's west coast is Turtle H, who has been observed on Keewaydin, Sanibel, Englewood, and Manasota Key, and Turtle G, who has confirmed nests on both Sanibel and Keewaydin (SCCF, unpublished data). Natal homing to islands separated by more than 70 km can occur within a distinct subpopulation (Shamblin et al., 2020), and data showing exchange among these west coast beaches may provide insight into stock structure and population connectivity that complements genetic analysis.

The location data collected by Fastloc-GPS are more accurate than Argos, and thus home range estimates presented in this study are not directly comparable to those collected using other techniques (Thomson et al., 2017). When the transmitters were set to a 24-h on/24-h off duty cycle in 2017, 90% of the data collected were categorized as LC A or B (see **Supplementary Table 1**). The cycle was changed to collect data continuously in 2018 and the proportion of the less accurate A and B locations decreased to 70%. However, only one turtle was tracked this year for a total of 39 days, which may not provide a dataset robust enough for comparison. In 2019 the duty cycle remained continuously on, and the A and B location data totaled 87% of the total dataset. The similarity in location accuracy in 2017 and 2019 suggests the duty cycle may play a less important role than other variables, such as tracking equipment, in collecting highly accurate data. It is unclear why tags stopped transmitting, as sensor data for tags was not available at the time of analysis.

Inter-Nesting

State space modeling model output did not produce discrete inter-nesting, migration, and foraging phases; instead, there were numerous ARS and migration points intermingled throughout the entire tracking period. It is likely that these turtles were foraging to some extent during the nesting and migration periods. While it was previously believed that turtles do not forage while nesting (Limpus, 1973; Carr, 1975), there is mounting evidence that foraging occurs in the inter-nesting period when forage is available. Dive data from nesting green turtles near Cyprus suggests that foraging behavior may occur between nesting events (Hochscheid et al., 1999) and studies analyzing gut contents have confirmed that opportunistic foraging occurs at nesting sites (Tucker and Read, 2001; Hays et al., 2002). These inter-nesting foraging sites are typically located in close proximity to the nesting beach, as nesting turtles generally limit their movement in order to minimize energy expenditure (Cheng, 2009). However, it appears that the six turtles in our study which made the 300 km trip to Cape Sable area may be exhibiting intentional food-seeking behavior rather than opportunistic feeding. Future studies are needed to determine why turtles are using this site in between nesting events.

We found considerable inter-annual variability in the relative importance of the Cape Sable area. The Cape Sable area was used all 3 years, but by different individuals each year, and never by the same animal twice. Seagrass beds are prevalent in this area and it is likely that these turtles used this site for feeding. Environmental conditions, including ocean currents, can influence turtle movements, but the use of this site each season suggests local conditions are favorable for these adult green turtles. The distribution and abundance of seagrasses in south Florida vary annually (Fourqurean et al., 2001), and the quality of the forage resources at this location may influence energy reserves available for turtles in the next non-breeding seasons.

Inter-nesting intervals lie within the general range reported for green turtles at other sites, with 9–18 day intervals between nests (Carr et al., 1974; Mortimer and Portier, 1989; Broderick et al., 2002; Van de Merwe et al., 2009; Hart et al., 2013). Cooler water temperatures can lengthen the number of days between nesting events for green turtles (Hays et al., 2002), but this phenomenon does not apply to the turtles in this study due to the consistently warm water temperatures in the Gulf of Mexico during the nesting season (Turner et al., 2017). Transiting

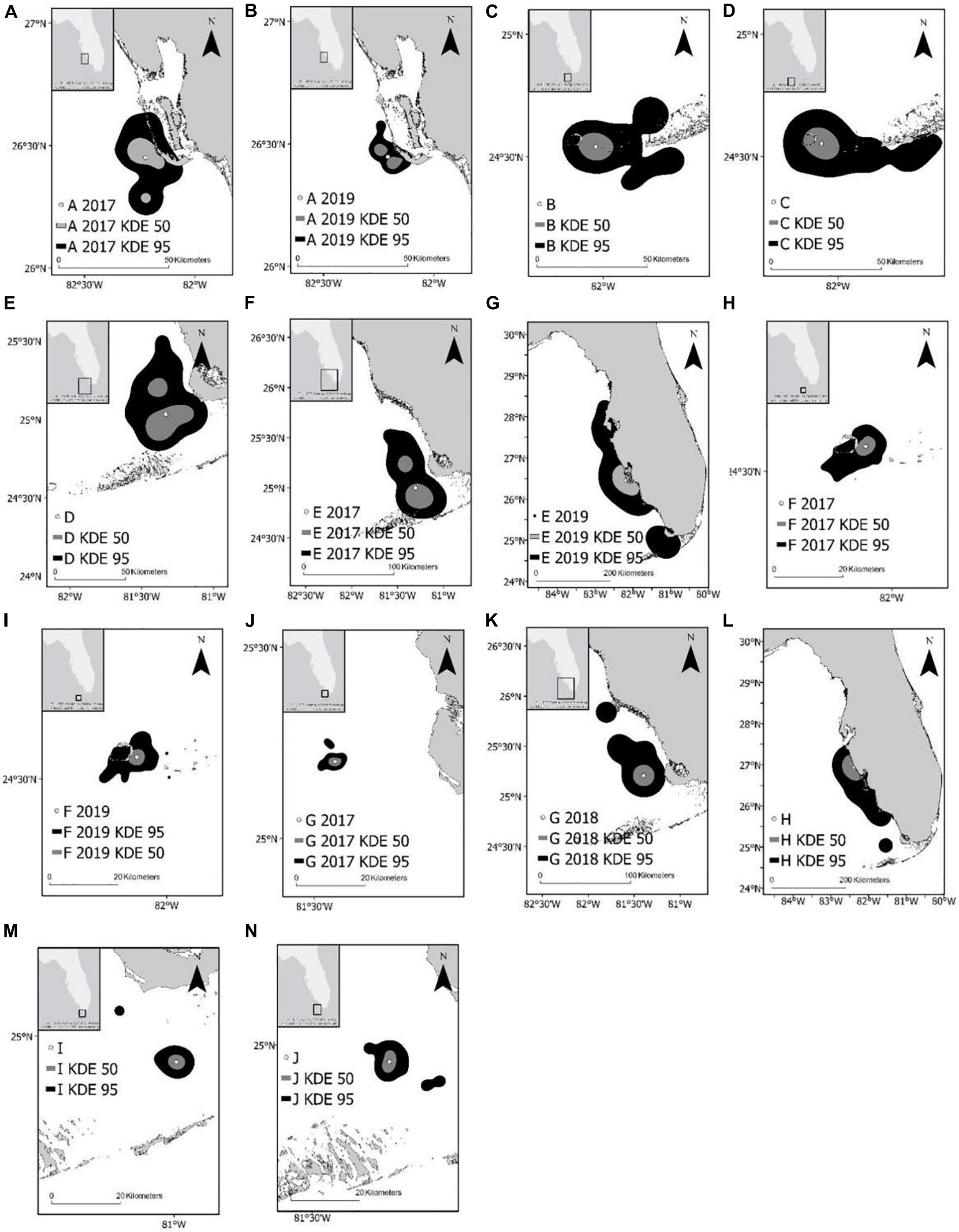

FIGURE 5 | Kernel density estimates (KDE) for 50% core use areas and 95% home ranges, and centroid locations of core use areas during foraging for green turtles (*Chelonia mydas*; turtles **A–J**) that nested in southwest Florida. **(A)** Turtle A in 2017, **(B)** Turtle A in 2019, **(C)** Turtle B in 2017, **(D)** Turtle C in 2017, **(E)** Turtle D in 2017, **(F)** Turtle E in 2017, **(G)** Turtle E in 2019, **(H)** Turtle F in 2017, **(I)** Turtle F in 2019, **(J)** Turtle G in 2017, **(K)** Turtle G in 2018, **(L)** Turtle H in 2019, **(M)** Turtle I in 2019, and **(N)** Turtle J in 2019.

behavior between nesting events was highly variable within and among individuals, but collectively the turtles exhibited more nomadic behavior than previously reported for nesting green turtles. Studies on inter-nesting behavior in green turtles suggest that turtles generally remain close to their nesting beach (Mortimer and Portier, 1989; Hays et al., 1999; Troeng et al., 2005; Blanco et al., 2013; Hart et al., 2013, 2017; Esteban et al., 2015; Chambault et al., 2016), although individual exceptions have been

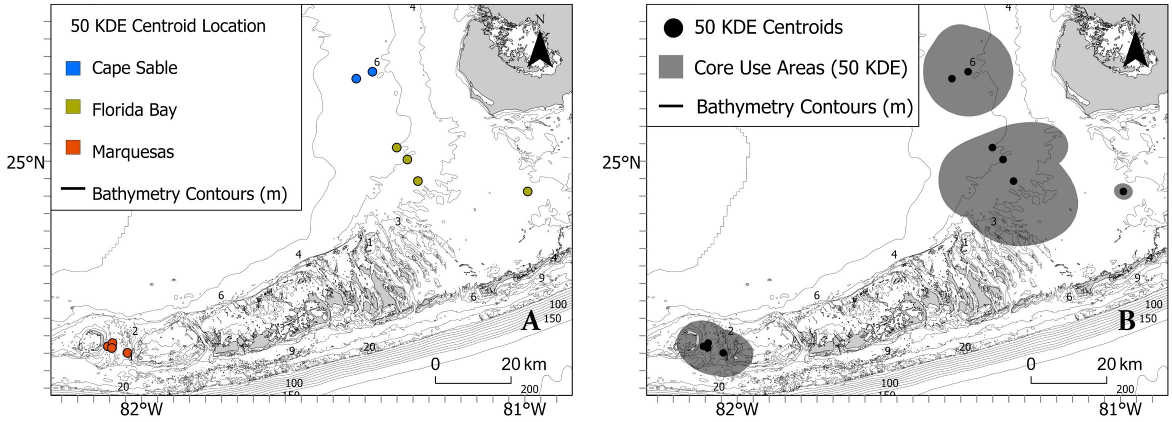

FIGURE 6 | (A) Centroid locations and **(B)** Core use areas [50% kernel density estimation (KDE)] for all green (*Chelonia mydas*) turtles tracked from southwest Florida nesting beaches to their respective foraging grounds.

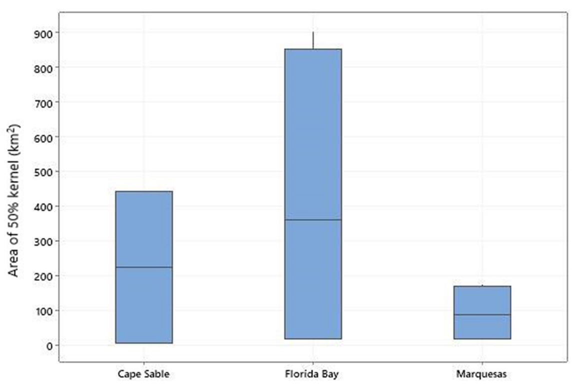

FIGURE 7 | Box plots of the 50% kernel density areas (in km^2) for turtles in each foraging ground.

noted (i.e., Esteban et al., 2015; Chambault et al., 2016; Mettler et al., 2020). Overall, the individuals in our study had greater displacement in between nests than has been previously reported for green turtles, but they all used relatively shallow Gulf waters (mean 6.3 m) in between nesting events.

Migration

The mean migration distance using a compilation of tracks from adult green turtles worldwide was estimated at 806 ± 602 km (Hays and Scott, 2013). However, highly variable migration distances have been recorded for green turtles both among study sites and also within individuals from the same study site. The variation in migration distances for individual turtles nesting on a single beach can be over 1,000 km (Luschi et al., 1998; Godley et al., 2002; Hays et al., 2020). On a global scale, the range of distances reported for migration from nesting beach to foraging grounds can be less than 100 km (Whiting et al., 2007; Hart et al., 2017), while distances up to 4,619 km have been recorded in the Indian Ocean (Hays et al., 2020) and 5,278 km along the coast of French Guiana, Suriname, and Brazil (Baudouin et al., 2015).

Our findings are consistent with migration data for turtles nesting within the Gulf of Mexico at Dry Tortugas (5–282 km; Hart et al., 2013) and Buck Island (0.2–694 km; Hart et al., 2017), and also in the Indian Ocean (33–37 km; Whiting et al., 2007). Turtles in these studies traveled less than 200 km to shallow foraging areas after the breeding seasons. It has been hypothesized that these variable migration patterns may reflect the oceanic drift that individuals experienced in their early years as hatchlings or young turtles (Scott et al., 2014). The hatchling drift scenarios for Keewaydin, Sanibel, and Dry Tortugas are similar due to the relatively close proximity of the three sites within the Gulf of Mexico, and post-hatchling turtles from these beaches would likely encounter the same locations along their routes, possibly accounting for the similarity in consistent migration behavior among individuals at the three sites.

The mean migration depth in 2017 was deeper (14.6 m) compared to 2018 and 2019 (8.3 and 8.0 m, respectively). Turtle E migrated southbound along the east coast of Florida in 2017, using much deeper waters in the Atlantic Ocean. Migrations within the Gulf of Mexico were shallow and generally close to the shoreline. Some turtles in this study briefly visited the Cape Sable site along their migration route, and others remained in the area for longer periods of time before initiating migration. Foraging during migration has been reported in sea turtles (Baudouin et al., 2015; Shimada et al., 2020) and these animals may be maintaining foraging site fidelity to the Cape Sable area while *en route* to their final destinations.

Resident Foraging Areas

The geographic locations of the three hotspots (Cape Sable, Florida Bay, and Marquesas Keys) determined by the model provided novel information on the foraging grounds for green turtles that nest on the west coast of Florida. Four turtles used the Marquesas Keys as foraging grounds. Turtle F returned to the same location in both 2017 and 2019 and remained there for 345 days in 2017, implying strong site fidelity to this area. High levels of fidelity to foraging grounds is common for both adult and juvenile green turtles (Broderick et al., 2007; Siegwalt et al., 2020).

Unpublished satellite telemetry data indicate that turtles nesting on the east coast also use the Marquesas Key as a foraging site (Bagley et al., 2021, Department of Biology, University of Central Florida, written communication, August 19, 2021). The Eastern Quicksands area is adjacent to the Marquesas Keys and provides important foraging grounds for green turtles that nest along the central Atlantic coast of Florida. Tag returns revealed that these turtles also nest in Quintana Roo, Mexico and Tortuguero, Costa Rica (Bresette et al., 2010), demonstrating that females from multiple nesting populations are using the area as their foraging grounds. Aggregations of foraging adults from multiple nesting beaches have also been reported in other areas such as Dry Tortugas National Park (Naro-Maciel et al., 2017), the Great Barrier Reef (Limpus et al., 2009; Jones et al., 2018), and Nicaragua (Bass et al., 1998). The source rookeries for the green turtles nesting on the west coast of Florida are unknown; genetic analyses of samples collected from nesting females will be required to assess relatedness to Florida east coast turtles.

Four turtles in this study used areas in western Florida Bay area as foraging grounds. The two turtles that foraged closer to shore (Turtle I and Turtle J) maintained much smaller core use areas compared to the turtles that used slightly deeper water into the Gulf of Mexico (Turtle D and Turtle E). This behavior may be a function of food availability, with higher density forage potentially located in shallower waters. One turtle tracked from Dry Tortugas used the Florida Bay area (Hart et al., 2013), and several turtles from an Atlantic coast nesting beach also foraged at this location during the non-nesting season (Bagley et al., 2021, Department of Biology, University of Central Florida, written communication, August 19, 2021), suggesting there could be individuals from multiple rookeries mixing at this foraging ground.

Foraging areas for the turtles in this study were located in relatively shallow habitats (2–6 m) that are likely to support seagrass beds. This is consistent with previous studies on green turtles nesting in Florida. The Eastern Quicksands was identified as a high-density adult green turtle foraging area by the Inwater Research Group (Herren et al., 2018). The depth of the waters at this location (3.1–6.0 m) are similar to those reported in this study and contain a bottom of shifting sand areas interspersed with seagrass beds of *Thalassia testudinum* and *Syringodium filiforme*, supporting a density of 58.5 green turtles/km^2. Seagrasses are widespread and conspicuous in the marine waters surrounding the southern tip of the Florida peninsula (Schomer and Drew, 1982; Fourqurean et al., 2001; Carlson and Fourqurean, 2016). Future work to determine if the Florida Bay and Cape Sable sites identified in this study contain similar foraging habitat would be worthwhile.

In addition to its importance in the nesting season, the Cape Sable site is a previously unidentified foraging hotspot and core use area. One turtle tracked from Dry Tortugas also used the same areas after nesting (Hart et al., 2013), putting this location on the map, but it was not characterized as a true hotspot prior to this study. A comprehensive study that mapped seagrasses in South Florida revealed exceptionally high biomass of *T. testudinum* at this exact location (Fourqurean et al., 2001), but more research is needed to confirm current benthic cover. Juvenile green turtles have been reported near this area (Hart and Fujisaki, 2010), and adult turtles may remain faithful to this site as a known high-quality foraging habitat. Future work at this site that includes a combination of underwater video (e.g., Hart et al., 2010), direct observations, and benthic sampling would be valuable.

The results of this study are particularly relevant from a conservation standpoint because of the noteworthy contribution of these foraging grounds to Florida's green turtle population. The high concentration of green turtles foraging in the neritic habitat in the Florida Keys and Florida Bay region indicates that conservation efforts focused in this region could be beneficial for these imperiled turtle populations. The additional knowledge provided by this study about the convergence of sea turtles found at these important at-sea sites can inform resource management strategies intended to protect turtles nesting in many different areas. Concerted management and restoration plans focused on protecting the turtles in these areas from threats posed by fisheries and watercraft interactions could augment plans in place that protect them from nesting habitat degradation.

DATA AVAILABILITY STATEMENT

The raw data supporting the conclusions of this article will be made available by the authors, without undue reservation.

ETHICS STATEMENT

The animal study was reviewed and approved by the Sanibel Captiva Conservation Foundation. All research was conducted in accordance with federal and state protected species guidelines as stipulated under permitted activities in Florida Marine Turtle Permit #116.

AUTHOR CONTRIBUTIONS

DA conceived the study. DA, KS, and AG contributed to the design of the study and completed the field components of the study. KS and AG organized the database. AB and AG performed the statistical analysis. KS wrote the first draft of the manuscript. KH, AG, DA, and AB wrote sections of the manuscript. All authors contributed to manuscript revision, read, and approved the submitted version.

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SUPPLEMENTARY MATERIAL

The Supplementary Material for this article can be found online at: https://www.frontiersin.org/articles/10.3389/fmars.2021.775367/full#supplementary-material

Supplementary Figure 1 | Area restricted movement and migration data assigned by SSM for all turtles (2017–2019).

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