



Migratory corridors of adult female Kemp's ridley turtles in the Gulf of Mexico



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ABSTRACT

For many marine species, locations of migratory pathways are not well defined. We used satellite telemetry and switching state-space modeling (SSM) to define the migratory corridor used by Kemp's ridley turtles (*Lepidochelys kempii*) in the Gulf of Mexico. The turtles were tagged after nesting at Padre Island National Seashore, Texas, USA from 1997 to 2014 (PAIS; $n = 80$); Rancho Nuevo, Tamaulipas, Mexico from 2010 to 2011 (RN; $n = 14$); Tecolutla, Veracruz, Mexico from 2012 to 2013 (VC; $n = 13$); and Gulf Shores, Alabama, USA during 2012 (GS; $n = 1$). The migratory corridor lies in nearshore Gulf of Mexico waters in the USA and Mexico with mean water depth of 26 m and a mean distance of 20 km from the nearest mainland coast. Migration from the nesting beach is a short phenomenon that occurs from late-May through August, with a peak in June. There was spatial similarity of post-nesting migratory pathways for different turtles over a 16 year period. Thus, our results indicate that these nearshore Gulf waters represent a critical migratory habitat for this species. However, there is a gap in our understanding of the migratory pathways used by this and other species to return from foraging grounds to nesting beaches. Therefore, our results highlight the need for tracking reproductive individuals from foraging grounds to nesting beaches. Continued tracking of adult females from PAIS, RN, and VC nesting beaches will allow further study of environmental and bathymetric components of migratory habitat and threats occurring within our defined corridor. Furthermore, the existence of this migratory corridor in nearshore waters of both the USA and Mexico demonstrates that international cooperation is necessary to protect essential migratory habitat for this imperiled species.

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1. Introduction

Many marine vertebrates, including sea turtles, undertake energetically demanding long distance migrations between foraging grounds and breeding areas (Alerstam et al., 2003). Adult female sea turtle migrations vary in distance, duration, and speed, depending on species and geographic location. Successful migrations represent an important component of an animal's fitness, as animals transit from favorable reproductive areas to foraging grounds to obtain resources critical to survival. Only recently have migration routes been delineated for marine megafauna, including sea turtles, but relatively few studies

have statistically defined migratory corridors in terms of location, timing, depth, and distance from shore (but see Bailey et al., 2008; Shillinger et al., 2008; Hart et al., 2014a; Pendoley et al., 2014).

The endangered Kemp's ridley turtle *Lepidochelys kempii* (Garman, 1880) has been the focus of intensive population restoration efforts since the mid-1960s (NMFS, USFWS, and SEMARNAT, 2011). All individuals constitute one stock and a single regional management unit (RMU; see Wallace et al., 2010). Kemp's ridley nesting occurs almost exclusively along the Gulf of Mexico coast, with the largest concentration near Rancho Nuevo (RN 23.180° N, 97.797° W; Márquez et al., 2005) and nearby beaches in Tamaulipas, Mexico. Substantial nesting also occurs in Veracruz, Mexico (VC). About 1% of annual nesting by the species occurs in south Texas, which is the northern extent of the documented historic nesting range (Shaver, 2005; Shaver and Caillouet, 2015). Since 1978, a bi-national, multi-agency effort has been ongoing to

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increase Kemp's ridley turtle nesting at Padre Island National Seashore (PAIS), south Texas, USA to form a secondary nesting colony to safeguard against extinction (Shaver, 2005). After decades of intensive conservation and management efforts, nest numbers increased in Mexico and Texas at about 12–19% annually and it was thought that given continued protection the species could be down-listed to threatened status by 2020 (NMFS, USFWS, and SEMARNAT, 2011). However, nest numbers decreased in 2010, rebounded in 2011 and 2012 to near-2009 levels, and then decreased during 2013 and 2014 to a 7–8 year low, prompting renewed concern about the status of the species (Caillouet, 2014; Shaver and Caillouet, 2015).

Kemp's ridley turtles mature at approximately 11 years of age (Caillouet et al., 2011). They utilize habitat primarily within nearshore waters in the Gulf of Mexico (Shaver et al., 2005, 2013; Shaver and Rubio, 2008; Seney and Landry, 2008, 2011) where they forage primarily on Portunid and other crab species (Márquez, 1970; Pritchard and Márquez, 1973; Shaver, 1991). Earlier studies reported that RN females were distributed widely along the Gulf coast (Byles, 1989; Mysing and Vanselow, 1989; Márquez, 1994) and recent analysis of post-nesting movements of Texas females allowed for delineation of foraging sites used by this smaller segment of the overall Kemp's population (Shaver et al., 2013). However, little is known about migratory pathways used by the larger segment of the nesting population that nests in Mexico, so characteristics of migratory pathways remain undefined.

Multiple stressors and threats have been identified for Kemp's ridleys in the marine environment (NMFS, USFWS, and SEMARNAT, 2011). Incidental capture by shrimp trawling (Caillouet et al., 1991, 1996; Shaver, 1998, 2005; McDaniel et al., 2000; Lewison et al., 2003) and other fisheries is considered the most significant threat to the population (National Research Council, 1990). Oil spills, dredging, hypoxia (Rabalais and Turner, 2001; Rabotyagov et al., 2014), red tide, and other factors also pose potential harm. Survival of adult females is extremely important to population growth and recovery (see Wallace et al., 2008). To develop effective management strategies to protect adult females in the marine environment, it is vital to identify their marine habitat use, including migratory pathways and foraging areas, throughout their range in the USA and Mexico (Hamann et al., 2010; NMFS, USFWS, and SEMARNAT, 2011). Satellite tracking data for other sea turtle species have been used to identify important foraging and migratory habitat, assess threats to sea turtles within those habitats, and aid with marine spatial planning for conservation, in the USA (Foley et al., 2013; Maxwell et al., 2013; Hardy et al., 2014; Hart et al., 2014b) and other countries (Maxwell et al., 2011; Moncada et al., 2012; Pikesley et al., 2013; Schofield et al., 2009, 2013b; Gredzens et al., 2014; Pendoley et al., 2014; Hart et al., 2015a; Stokes et al., 2015).

Use of switching state-space modeling (SSM; see Patterson et al., 2008) allows for enhancement of Argos satellite tracking data for home range and long distance migration studies of marine animals (Hoenner et al., 2012). This type of modeling has been useful for quantifying foraging and migratory periods for a variety of marine taxa including whales, seals, tuna, and sea turtles (Jonsen et al., 2007; Breed et al., 2009; Bailey et al., 2009; Wilson et al., 2015). For sea turtles, SSM was recently used to define inter-nesting movements, migrations, and foraging areas for female loggerheads *Caretta caretta* in the Gulf of Mexico and Atlantic Ocean (see Hart et al., 2015b), foraging areas for Kemp's ridleys in the Gulf of Mexico (Shaver et al., 2013), migrations and foraging areas for leatherbacks *Dermochelys coriacea* and green turtles *Chelonia mydas* in the Pacific Ocean (Benson et al., 2011; Blanco et al., 2012), and inter-nesting movements of olive ridleys *Lepidochelys olivacea* in the Atlantic Ocean (Maxwell et al., 2011). Here we use SSM to characterize migratory corridors in the Gulf of Mexico for Kemp's ridleys tracked by satellite telemetry after nesting at or near PAIS, RN, VC, and Gulf Shores, Alabama, USA. Our objectives were to: (1) spatially define the migratory corridor; (2) define characteristics of the migratory corridor (i.e., bathymetry and distance from shore); and (3) examine the consistency of migratory pathways selected across years.

2. Methods

2.1. Turtles

We deployed 108 platform transmitter terminals (PTTs) on Kemp's ridleys that nested at PAIS, Texas, USA from 1997 to 2014 ($n = 80$); RN, Tamaulipas, Mexico from 2010 to 2011 ($n = 14$); Tecolutla, Veracruz, Mexico from 2012 to 2013 ($n = 13$); and Gulf Shores, Alabama, USA during 2012 ($n = 1$) (Fig. 1). Turtles were documented, measured, individually tagged with one passive integrated transponder (PIT) tag and two Inconel flipper tags, and outfitted with PTTs using established protocols (NMFS-SEFSC, 2008; Schmid and Witzell, 1997; Shaver and Rubio, 2008). PTTs included models ST-6, ST-18, and ST-20 ($n = 40$) manufactured by Telonics, Inc. (Mesa, Arizona, USA); model KS-101 and KS-202 ($n = 33$) manufactured by Sirtrack (Haverlock North, New Zealand); and models MK-10A, MK-AF, and SPOT5 ($n = 35$) manufactured by Wildlife Computers (Redmond, WA, USA). PTTs deployed from 1998 to 2007 were programmed with the transmission (duty) cycle of 6 h on/6 h off. In 2008, PTTs were duty cycled on 24 h d^{-1} for the first 106 days and then 6 h on/6 h off. From 2010 on-ward, KS-101 and KS-202 PTTs were duty cycled 6 h on/6 h off, and MK-10A, MK10AF, and SPOT5 PTTs were on 24 h d^{-1} .

We filtered satellite location data using Satellite Tracking and Analysis Tool (STAT; Coyne and Godley, 2005) available at www.seaturtle.org. We used Location Classes (LC) 3, 2, 1, 0, A, and B to reconstruct routes and calculate straight-line and total distances that turtles traveled. Argos assigns accuracy estimates of <250 m for LC 3, 250 to <500 m for LC 2, 500 to <1500 m for LC 1, and >1500 m for LC 0 (Collection, Location, Satellites, 2015); the estimated accuracy is unknown for LCs A and B. Both traditional least-squares location processing (1998–2010) as well as Kalman-filtering (initiated in 2011; Kalman, 1960) of location data were performed by Argos. This newly-implemented Kalman-filtering algorithm provides more estimated positions and significantly improves position accuracy, most significantly for locations obtained in LCs A and B (Lopez and Malardé, 2011).

2.2. SSM and migratory corridors

We attempted to use SSM to characterize the movements of all adult nesting Kemp's ridley females in the Gulf of Mexico outfitted with PTTs through 2013 ($n = 107$). The $n = 1$ turtle outfitted with a PTT during 2014 was not included in the SSM analysis (completed before the tag was deployed), but was included in the migratory corridor fidelity analysis (see below). Argos satellite locations are recorded at irregular time intervals and are often less precise than published estimates (Vincent et al., 2002), which can be misleading for developing inferences from the data, even after ad-hoc filtering of outliers (Jonsen et al., 2006). However, SSM is suggested as the best analytical technique for enhancing Argos tracking data once post processed by removing land points and adding back in good Argos locations (Hoenner et al., 2012). SSM has two components accounting for location errors (observation error) and animal behavior (Jonsen et al., 2003, 2007; Patterson et al., 2008; Breed et al., 2009); the observation error is based on the LC from Argos data. The two-state switching correlated random walk models the movement process which transits between two behavioral states (see Jonsen et al., 2005; Eckert et al., 2008; Hart et al., 2013a). Since we tagged turtles during nesting seasons, we defined the SSM behavioral modes as either 'foraging and/or nesting' which was indicated by area restricted search patterns, and 'migration' which was indicated by more directed movement (Bailey et al., 2008). The observation equation translates observed locations to true unobserved locations at equal time intervals.

We used SSM to identify foraging and migration behaviors for 68 PTTs deployed with data collected until transmitters stopped sending information or at the time of data synthesis (3 April 2014). The other $n = 39$ data sets were not robust enough for the model, which included



Fig. 1. Tagging locations for $n = 108$ Kemp's ridley turtles (*Lepidochelys kempii*) tracked by satellite telemetry in the Gulf of Mexico (from 1997 to 2014). Black stars denote tagging locations.

many of the earlier PTTs. Of the 68, $n = 2$ did not have a migratory phase because the turtles remained off PAIS after nesting and foraged there (Shaver et al., 2013). Therefore, we summarized data for $n = 66$ SSM Kemp's ridleys during migration away from nesting beaches. We applied a model used in Breed et al. (2009), which is a modified version of a model described in Jonsen et al. (2005) that estimates model parameters by Markov Chain Monte Carlo (MCMC) using WinBUGS via the software program R v2.15.2 (RCoreTeam, 2014). We used all tracking data except for LCZ, and we fit the model to tracks of each individual turtle to estimate location and behavioral mode every eight hours 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 7000 and thinned by five. The convergence was monitored by observing model parameters of two independent chains that were mixed in the trace plots (as suggested by Breed et al., 2009).

2.3. Spatial configuration and characteristics of migratory corridors

We included raw data points classified as in migration mode from the SSM output to characterize at-sea migratory pathways selected by individual turtles. We excluded locations deeper than 100 m (considered to be biologically implausible: Shaver and Rubio, 2008; Seney and Landry, 2011), locations that required swim speeds $>5 \text{ km h}^{-1}$ (considered to be unrealistically high: Luschi et al., 1998), and other obviously erroneous locations (on land, spatially very distant, etc.). We then quantified turtle tracking days in migration for these $n = 66$ turtles. Specifically, we calculated the number and proportion of migration days in grid cells ($10 \times 10 \text{ km}$) regardless of year; the grid extended across the extent of the Gulf of Mexico within the 100 m isobath. However, this can be skewed for individual tracking biases (i.e., if one turtle remained in a given grid cell for a long time). Thus, we also examined the proportion of $n = 66$ SSM turtles with a migratory phase in each grid cell. This allowed us to derive the probability of a given grid cell being used during migration by all turtles for which SSM worked. We calculated mean distance to shoreline and bathymetry for the "hotspot" grid cells (migratory corridor) where higher proportions of Kemp's ridleys migrated for the months of May through October, when most migration points occurred. For bathymetry, we used the NOAA National Geophysical Data Center (GEODAS) ETOPO1, 1 arc-minute global relief

model of Earth's surface (<http://www.ngdc.noaa.gov/m,gg/geodas/geodas.html>; accessed 26 January 2012).

2.4. Seasonality of migration

We examined seasonality of migration by calculating the proportion of migrating Kemp's ridleys in each grid cell, by month, from May through October. We also aggregated dates for all years for all SSM turtles, and calculated the proportions of Kemp's ridley turtles in migration mode by date; this summary identified timing of migration from the nesting beach to the foraging grounds. For $n = 2$ turtles that we tracked through re-migration to the nesting beach (i.e., over several years), we used SSM output to determine the date that re-migration was initiated.

2.5. Migratory corridor fidelity

To quantify long-term fidelity to the migratory corridor we compared the number of locations for $n = 39$ Kemp's ridley turtles (non-SSM and deployed during earlier study years) within and outside of the defined SSM turtle migration area. We filtered the locations by swim speeds $>5 \text{ km h}^{-1}$ and 100 m bathymetry contour, as was done for the SSM turtles. These non-SSM locations included all filtered locations after identified inter-nesting periods, and therefore may have included foraging periods after migrations.

To further visualize corridor fidelity through time, input data for figures showing entire tracks for turtles (Figs. 6, S1, S3) were filtered to exclude locations that required acute turning angles $<25^\circ$ (usually indicative of erroneous locations: Witt et al., 2010; Hawkes et al., 2011), and other locations likely implausible based on swim speed, bathymetry, etc. (see above). Repeat tracking of individuals after nesting in different years, and repeated observations of individuals along their migratory pathway through migration and re-migration, also afforded an opportunity to examine individual migratory corridor fidelity. We compared tracking maps for $n = 13$ turtles tracked after different nesting years. One of these 13 received a 4th transmitter after nesting at PAIS during 2014 and these location data (from deployment through data synthesis on 24 April 2015) were included only for visual comparison of repeated tracking periods, not in the SSM and Chi-square analyses. We also visually compared the migratory pathways for the $n = 2$ turtles

that we tracked during re-migration from the foraging grounds and back to the nesting beach.

3. Results

3.1. Turtles

Mean size of turtles ($n = 108$) was 63.3 cm straight carapace length (SCL, ± 2.4 SD; Fig. 2; see Table S1 in Supporting Information). In a total of 26,497 turtle-tracking days for the 107 PTTs included in the SSM and Chi-square analyses, mean individual tracking duration was 247.6 d (± 198.8 SD, range 8 to 1083 d; Table S1). The 108 tracks include 13 individuals that were tracked after two ($n = 10$), three ($n = 2$), or four ($n = 1$) successive nesting years (see Table S2 in Supporting Information).

3.2. SSM and migratory corridors

We obtained SSM results for 68 turtles, of which 66 had a migratory phase away from the nesting beach (see Table S1). We quantified turtle tracking days in migration for these $n = 66$ turtles (Fig. 3) and the proportion of them with a migratory phase in each grid cell (see Fig. S2 in Supporting Information). Filtered locations for these 66 turtles included locations from LC 0 ($n = 692$), 1 ($n = 486$), 2 ($n = 314$), 3 ($n = 155$), A ($n = 1978$), and B ($n = 6747$). We found consistently high numbers of turtle migration days in specific grid cells, particularly off the coasts of Texas and Louisiana (see ‘warmer’ colored cells in Figs. 3, S2). With both analyses, high-use grid cells depict the corridor used by many different individuals for post-nesting migration in both the northern and southern Gulf of Mexico. These high-use migration areas were located adjacent to nesting beaches in RN and Texas, and also in Louisiana.

Migration sites were relatively close to land, and in relatively shallow water. During migration, turtles used waters that were on average 26 m deep and 20 km from shore (Table 1). However, turtles that migrated in May through August did so closer to shore than those that migrated in September through October. Additionally, water depths used by turtles were deeper, but more variable, during May and June compared to depths used during July through October. We were unable to quantify these parameters for November through April since there were too few migration points during these months. In some of the lesser used areas of the migratory corridor, turtles used shallower waters, some very close to the shore.

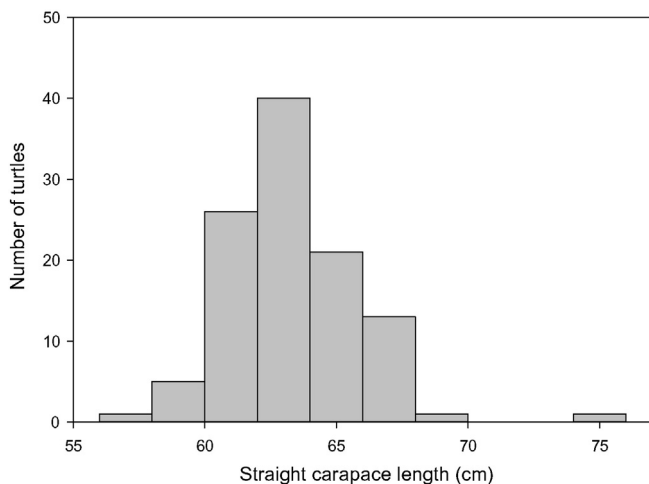


Fig. 2. Straight carapace lengths of $n = 108$ Kemp's ridley turtles (*Lepidochelys kempii*) tracked by satellite telemetry in the Gulf of Mexico.

3.3. Seasonality of migration

Migration for post-nesting Kemp's ridleys occurred from late-May through August, and the migratory area shifted clockwise around the northern Gulf, and counterclockwise around the southern Gulf, during this time (Fig. 4). Migration from the nesting beach is a relatively short phenomenon, and by fall, fewer turtles were in migration mode (by September and October, there were fewer grid cells with migration points). Migration peaked in June (Fig. 5); for all years combined, by 1 June approximately half of all SSM turtles ($n = 68$) were in migration mode, transitioning from the nesting grounds to foraging sites. By 1 August, that proportion dropped to about 30%. Post-nesting Kemp's ridleys forage at multiple sites (Shaver et al., 2013) and there was more limited movement between foraging sites during fall periods. Migration dates in late winter and early spring are migrations between foraging sites, and did not reflect re-migration back to nesting beaches. The mean re-migration interval for Kemp's ridley is 2 years (NMFS, USFWS, and SEMARNAT, 2011), but battery life in relatively few PTTs lasted that long.

3.4. Migratory corridor fidelity

Turtles often showed remarkable fidelity to migratory pathways over the 16 year tracking period. Filtered locations for the $n = 39$ non-SSM Kemp's ridley turtles included LC 0 ($n = 1013$), 1 ($n = 542$), 2 ($n = 245$), 3 ($n = 99$), A ($n = 2011$), and B ($n = 4679$). We found that significantly more locations from the $n = 39$ Kemp's ridley turtles (non-SSM) were inside the SSM-defined migration area ($\chi^2 = 2456.7$, $p < 0.0001$), which indicates consistent use of this migratory area over time, despite any environmental fluctuations.

We observed that the migration pathway was consistently used year to year, supporting the migratory corridor concept. For all turtles (see Supporting Information Fig. S3, Table S2; Shaver and Rubio, 2008), tracks were in nearshore northern Gulf of Mexico waters. Individuals tracked after different nesting years generally used the same migratory corridor, and some returned to the same foraging grounds after two, three, or four nesting years. Overall, we were able to track $n = 13$ turtles more than once, and thus visually compare their successive post-nesting migration pathways. Most of the 13 turtles traveled to the same foraging grounds during successive tracking periods, but five did not, including one (Turtle ID #P8) that may have died and two others (Turtle IDs #P9 and #P68) that stopped transmitting before reaching and establishing residency in foraging grounds during their second tracking periods. Turtle #P12, one of the $n = 2$ turtles that we tracked during re-migration from foraging grounds to nesting beaches, followed a similar migratory pathway during her migration and re-migration in her second tracking event, but traveled approximately twice as far during her first tracking period compared to her second tracking period. However, during the second tracking period Turtle #P12 re-migrated to near the nesting beach at a one-year re-migration interval, whereas during the first tracking period the turtle did not re-migrate during the 14 month tracking duration.

During her second tracking period, Turtle ID #P12 entered SSM migration mode and began to leave the northern Gulf foraging grounds on 1 January 2007 (Fig. 6a). However, she only remained in migration mode through 6 January 2007, and then resumed foraging mode until she reached the nesting beach in late-March 2007. Based on visual examination of her tracking map, it appeared that she initiated re-migration during November, the same month that the adult female tracked by Renaud et al. (1996) appeared to begin departure from northern Gulf foraging grounds. Her transmitter stopped functioning a few days after she arrived near the nesting beach, before nesting began in Texas; she was not observed nesting in 2007. The second turtle tracked during re-migration, Turtle ID #VC03, entered migration mode and left her foraging grounds on 27 February 2014 (Fig. 6b). She arrived near the nesting beach around 11 April 2014, and was observed nesting

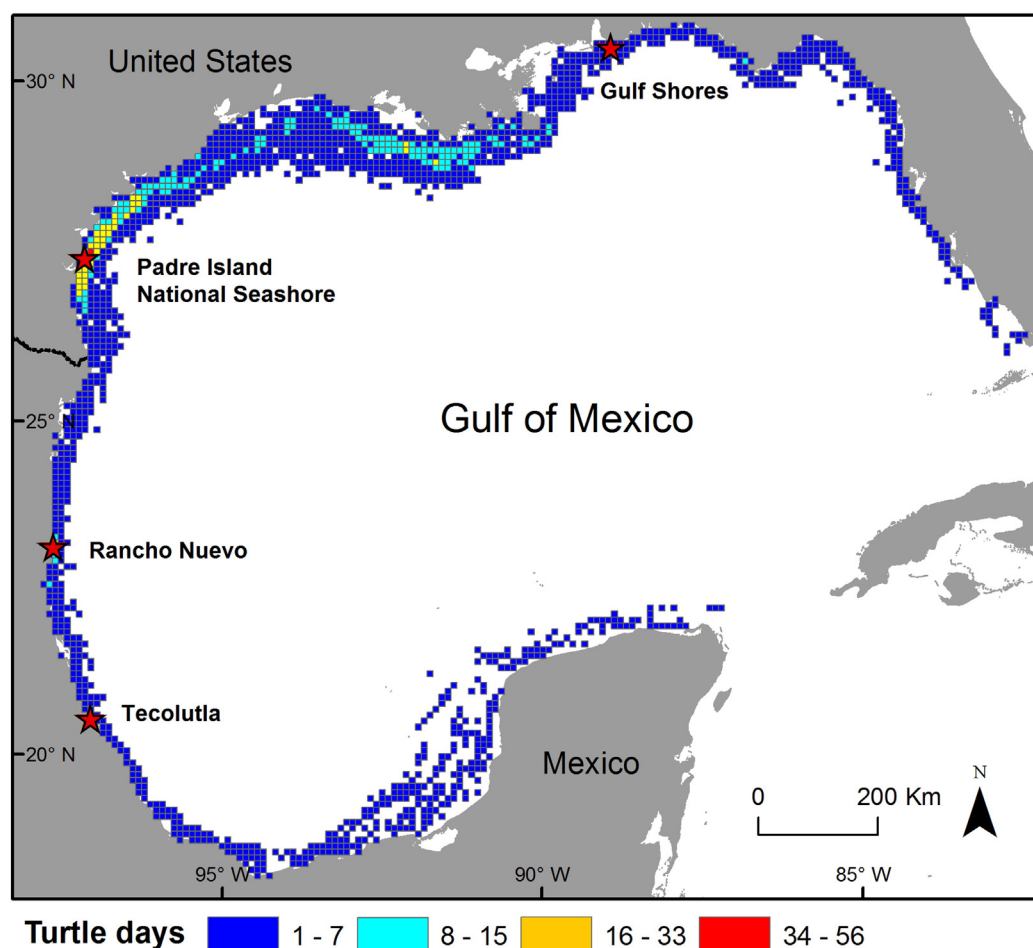


Fig. 3. Number of days used by $n = 66$ Kemp's ridley turtles (*Lepidochelys kempii*) (turtle days) in each 10×10 km grid cell during identified migration periods (from 12 May 1998 to 2 April 2014) by switching state-space model in the Gulf of Mexico. Red stars denote tagging locations.

there on 30 April and 19 May 2014. The two re-migration pathways were relatively similar to their corresponding migration pathways, except that sections of the re-migration pathways were in deeper waters than were the post-nesting migratory pathways, possibly reflecting use of slightly deeper waters during winter versus summer months.

4. Discussion

Through analysis of the largest ($n = 108$ PTTs) and longest-term ($n = 16$ yr) satellite tracking data set for the species, we demonstrate and quantify the importance of nearshore waters in both the northern and southern Gulf of Mexico as migratory habitat for endangered post-nesting Kemp's ridleys. We tracked individuals from the nesting

epicenter for the species and from the northern and southern extents of the documented historic nesting range. Nearly all nesting by this species occurs within the range of these study sites and no separate genetic populations or sub-populations have been identified (Wallace et al., 2010; NMFS, USFWS, and SEMARNAT, 2011). Because we deployed PTTs over many years and found consistent use of this corridor through time, we believe that our results are representative of post-nesting migratory habitat for the adult female component of the population. We suggest that a critical migratory corridor exists for this imperiled species in the Gulf of Mexico, particularly off Rancho Nuevo, PAIS, and Louisiana. No other sea turtle study conducted to date has identified and quantified a migratory corridor that is consistently used by most adult females of the species.

Migratory corridors are most well-defined for seabirds and whales. Attempts have been made for various sea turtle species, but few have quantified and identified the physical features of these corridors (Morreale et al., 1996; Griffin et al., 2013; Pendoley et al., 2014; Stokes et al., 2015). Morreale et al. (1996) concluded that leatherback migration was influenced by ocean currents. Other researchers also found that ocean currents, for some species and life states, may play a major role in shaping location and extent of migratory corridors (Hays et al., 2001; Luschi et al., 2003; Fossette et al., 2010). However, ocean currents may be less influential for adult female Kemp's ridleys in the Gulf of Mexico, where temperatures are relatively warm and currents not as strong. Instead, depth and distance from shore are likely more important predictors of optimal migratory pathways than currents.

Our findings document that nearshore Gulf of Mexico waters, in the USA and Mexico, must be considered important migratory habitat for

Table 1

Mean distance to shoreline and bathymetry in "hotspot" grid cells (10×10 km) which were used by at least one satellite-tracked Kemp's ridley (*Lepidochelys kempii*) during identified migration periods.

Month	Number of grid cells	Distance to shore line (km)		Bathymetry (topography) (m)	
		Mean	SD	Mean	SD
May	460	21.2	20.0	18.8	16.5
June	883	24.0	21.9	20.2	17.2
July	720	26.4	22.0	17.7	16.9
August	382	23.3	22.4	16.0	14.8
September	290	39.1	33.7	22.2	19.1
October	67	42.7	28.3	22.8	14.8
All	1556	26.3	25.2	20.0	18.3

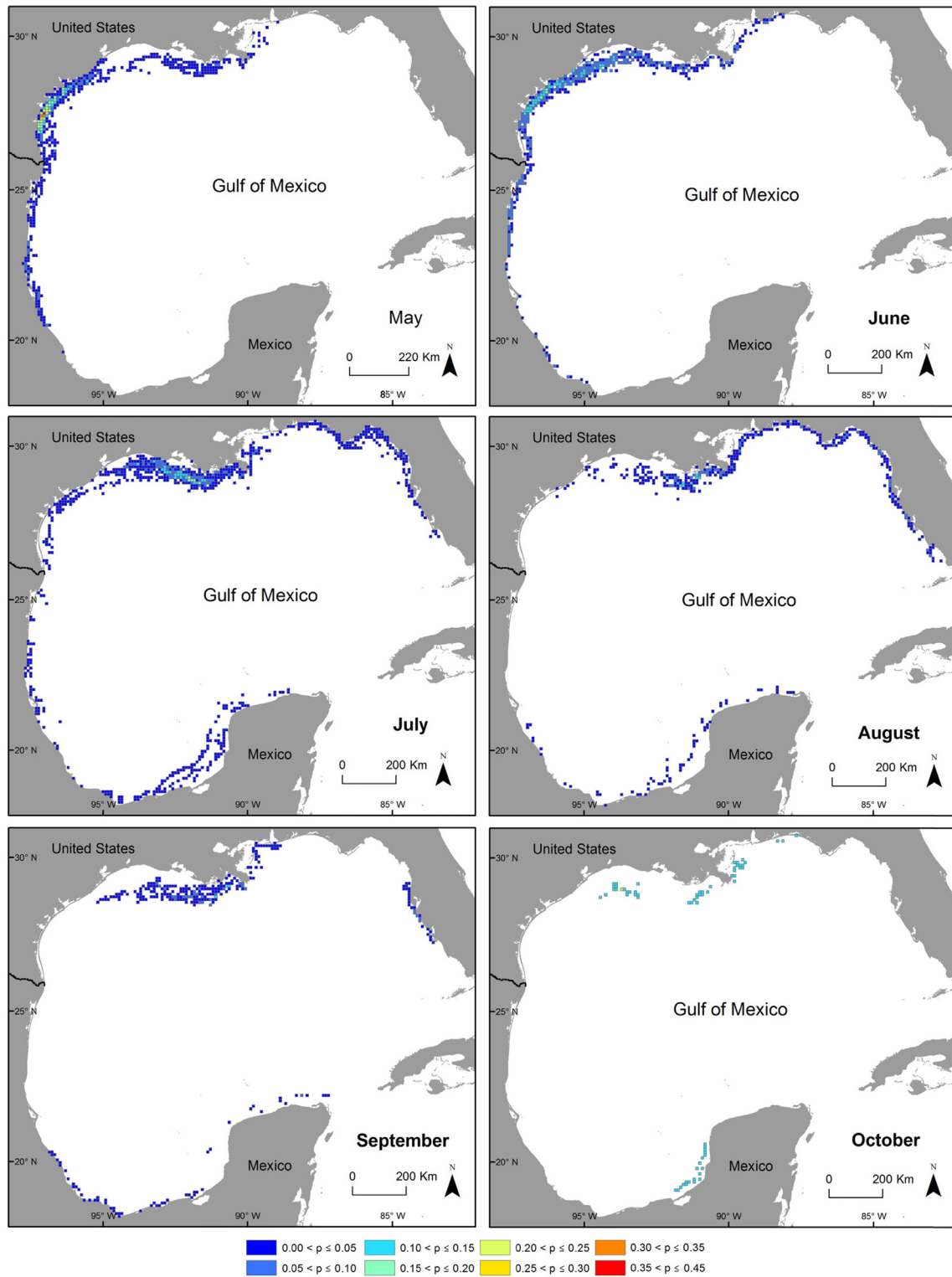


Fig. 4. Migration area for $n = 66$ satellite-tracked Kemp's ridley turtles (*Lepidochelys kempii*) as indicated by proportion of turtles that used each 10×10 km grid cell for each month, during migration periods (from 12 May 1998 to 2 April 2014) identified by switching state-space model.

this species. Although mean monthly distance from shore and depth of high use migration grid cells varied slightly, the overall mean distance to shore (20 km) and depth (26 m) of the high use migration grid cells were relatively similar to those means for the high use foraging grid cells used by adult female Kemp's ridleys in the Gulf of Mexico; the mean distance to the nearest land from centroids at foraging sites was 25.2 km (± 27.0 SD, $n = 18$) and mean bathymetry values at foraging centroid locations ranged from 20.4 m to 18.5 m (Shaver et al., 2013).

Coastal migration by adult female Kemp's ridleys may be influenced by locations of their foraging resources. Adults forage primarily on crabs and shrimp trawling by-catch that occur in nearshore areas (Shaver, 1991). Shaver et al. (2013) previously found evidence of Kemp's foraging behavior during migration and suggested that a foraging "hotspot" exists for the species in nearshore Gulf of Mexico waters in both USA and Mexico. The foraging hotspot and our migratory corridor defined here spatially overlap. Combining our findings with known

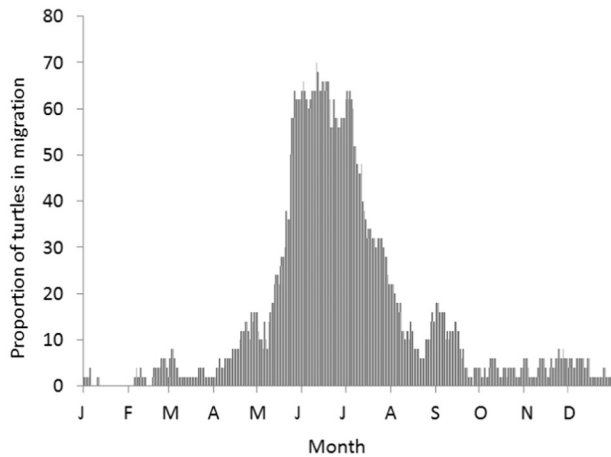


Fig. 5. Proportions of $n = 66$ Kemp's ridley turtles (*Lepidochelys kempii*) in migration mode by date. Migration days occurred from 12 May 1998 to 2 April 2014.

locations of foraging areas identified for adult females tracked after nesting in Texas and Mexico (see Fig. S1; Seney and Landry, 2008, 2011; Shaver and Rubio, 2008; Shaver et al., 2013) underscores the vital importance of nearshore Gulf of Mexico waters to adult female Kemp's ridley turtles, and thus to the conservation of the entire species.

All migrating adult female and male Kemp's ridleys tracked to date have migrated through coastal waters; none have crossed the Gulf of Mexico through oceanic waters (Byles, 1989; Mysing and Vanselow, 1989; Renaud et al., 1996; Seney and Landry, 2008, 2011; Shaver et al., 2005, 2013; Shaver and Rubio, 2008). This is in contrast to adult olive ridley (Plotkin, 2010; Maxwell et al., 2011; Plot et al., 2015) and leatherback turtles (Morreale et al., 1996; James et al., 2005b; Eckert et al., 2006; Shillinger et al., 2008; Benson et al., 2011; Schick et al., 2013; Fossette et al., 2014; Roe et al., 2014) that migrate primarily through

oceanic waters. Both oceanic and coastal migrations have been documented for adult loggerhead, green, hawksbill (*Eretmochelys coriacea*), and flatback (*Natator depressus*) turtles (Godley et al., 2002; Blumenthal et al., 2006; Cuevas et al., 2008; Seminoff et al., 2008; Van Dam et al., 2008; Marcovaldi et al., 2010, 2012; Hart et al., 2012b, 2013b, 2014a, 2014b, 2015b; Hawkes et al., 2012; Foley et al., 2013; Griffin et al., 2013; Schofield et al., 2010, 2013a; Hays et al., 2014b; Pendoley et al., 2014; Baudouin et al., 2015; Stokes et al., 2015). The consistent use of a coastal migration route where potentially harmful human activities are concentrated renders the Kemp's ridley population disproportionately vulnerable compared to other species with more oceanic and varied migration routes. Thus, anthropogenic impacts in the coastal zone may warrant further consideration when Kemp's ridley protection strategies are evaluated.

Our delineation of a coastal migratory corridor is paramount for understanding at-sea migratory habitat site selection and therefore, areas of potential conservation concern. Satellite tracking data are particularly useful for identifying threat overlaps and developing boundaries for Marine Protected Areas and other conservation strategies for sea turtles (Maxwell et al., 2011, 2013; Hart et al., 2013b, 2014a, 2014b; Schofield et al., 2013b; Gredzens et al., 2014; Pendoley et al., 2014). The concentration of Kemp's ridley high-use migratory grid cells off the coasts of Texas and Louisiana across study years and individuals is noteworthy as these areas are known for heavy fishing effort and oil production. Incidental capture by fisheries is a threat to marine megafauna worldwide (Komoroske and Lewison, 2015), including Kemp's ridleys (Caillouet et al., 1991, 1996; NMFS, USFWS, and SEMARNAT, 2011). The Deepwater Horizon (DWH) Oil Spill released over 4.4 million barrels of oil into the northern Gulf of Mexico during 2010 (Crone and Tolstoy, 2011). Deaths and impairments of sea turtles, bottlenose dolphins (*Tursiops truncatus*), and other marine organisms have been linked to the DWH Horizon Oil Spill (Carmichael et al., 2012; Antonio et al., 2011; Powers et al., 2013; Incardona et al., 2014; Landers et al., 2014; Etnoyer et al., 2015; Venn-Watson et al., 2015a, 2015b). Although habitat characteristics

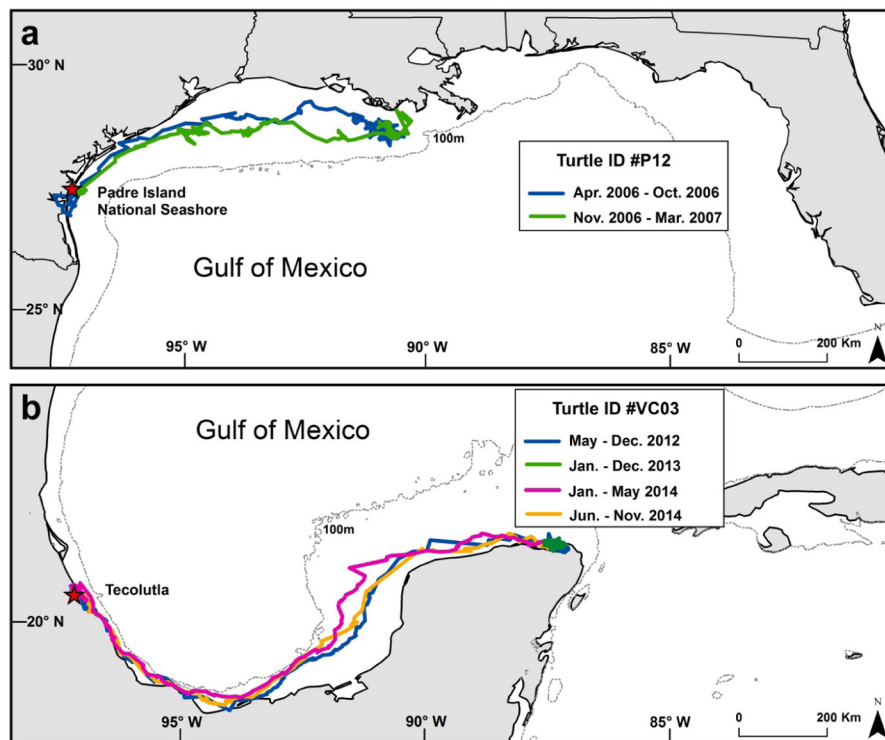


Fig. 6. Tracks for the two Kemp's ridley turtles (*Lepidochelys kempii*) that included re-migration to the nesting beach (a) #P12 tracked during post-nesting migration to foraging grounds and re-migration to the nesting beach during 2006–2007 and (b) #VC03 tracked during post-nesting migration to foraging grounds in 2012, foraging ground residency in 2013, re-migration to the nesting beach in 2014, and post-nesting migration to foraging grounds in 2014. Stars indicate nesting beaches of deployment at Padre Island National Seashore, Texas, USA (a) and Tecolutia, Veracruz, Mexico (b).

and suitability for sea turtles in this region are poorly understood, locations of the migratory corridor identified here and core-use foraging areas previously identified (Shaver and Rubio, 2008; Shaver et al., 2013) indicate that important habitat exists for Kemp's ridley (Shaver and Rubio, 2008; Shaver et al., 2013) and loggerhead turtles (Hart et al., 2012a, 2013a, 2014a; Foley et al., 2013) at these sites in the northern Gulf of Mexico. Future monitoring efforts are suggested to fully understand impacts of this massive oil spill on sea turtles in this area.

In our study, only two turtles were tracked during re-migration back to the nesting beach from foraging areas and only one other adult female Kemp's ridley has ever been tracked from her foraging grounds to the nesting beach (Renaud et al., 1996). Based on our two observations and findings presented in Renaud et al. (1996), re-migration from northern Gulf foraging grounds may be relatively slow and interrupted by periods of foraging, whereas re-migration from southern Gulf foraging grounds may be faster. However, there is a paucity of data on the migration pathways of turtles from foraging grounds to nesting beaches. Van Dam et al. (2008) tracked two adult male hawksbills from breeding areas to foraging grounds, and back to breeding areas one year later. A few adult male leatherbacks and adult male and female loggerheads have also been tracked from foraging grounds to nesting beaches (James et al., 2005a; Hays et al., 2010, 2014a). PTTs deployed on Kemp's ridley females at the nesting beach rarely transmit data long enough to capture re-migration. Efforts to deploy PTTs on sea turtles at foraging sites are suggested to allow for determination of the timing of re-migration to the nesting beach and quantification of behaviors (e.g., dives, stopover foraging locations) during this phase of migration. This information could identify threats to the turtles along both post-nesting and pre-nesting migration routes.

Nearshore waters of the Gulf of Mexico serve as essential migratory habitat for post-nesting Kemp's ridley turtles. Our results define this migratory corridor for this species in the northern and southern Gulf of Mexico, and demonstrate consistent selection of these nearshore waters by turtles tracked from nesting beaches in both the USA and Mexico over a 16 year period. These findings underscore the importance of this habitat across time for adult females of this species, and highlight the need for international cooperation on conservation efforts. Additional and continued tracking of adult females from PAIS, RN, and VC nesting beaches is suggested to further delineate this corridor and threats to turtles within it. Furthermore, efforts to deploy transmitters on adult females in the foraging grounds to investigate timing and corridors of re-migration to nesting beaches would be valuable.

Author contributions

D.S. and K.H. conceived the ideas; D.S., K.H., C.R., J.P., D.G.G., R.G.D.M., P.B., H.M., and J.O. collected the data; D.S., K.H., I.F., C.R., and A.S. analyzed the data; D.S. and K.H. led the writing, and I.F., C.R., and A.S. contributed to writing the manuscript.

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Appendix A. Supplementary data

Supplementary data to this article can be found online at <http://dx.doi.org/10.1016/j.biocon.2015.12.014>.

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