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Movement patterns of immature and adult female Kemp's ridley sea turtles in the northwestern Gulf of Mexico

Erin E. Seney[1,2,3,*], André M. Landry Jr.[1,2]

[1]Sea Turtle & Fisheries Ecology Research Laboratory, Department of Marine Biology, Texas A&M University at Galveston, PO Box 1675, Galveston, Texas 77553, USA

[2]Department of Wildlife & Fisheries Sciences, Texas A&M University, 2258 TAMU, College Station, Texas 77843, USA

[3]*Present address:* Erin Seney Consulting, Woodbridge, Virginia, USA

ABSTRACT: The Kemp's ridley sea turtle *Lepidochelys kempii* is recovering from declines that reduced nesting from a single-day estimate of 10 000 to 40 000 females in 1947 to <300 during the entire 1985 nesting season. Although beach monitoring is crucial to estimating nesting population size and activity, in-water data are essential for understanding population dynamics, evaluating management strategies, and ensuring the species' continued recovery. Fifteen immature and 7 adult female ridleys were fitted with platform terminal transmitters and released off the upper Texas coast during 2004 through 2007. Immature individuals were tracked primarily during warmer months and exhibited preferences for tidal passes, bays, coastal lakes, and nearshore waters, although movement patterns varied among years. Females tracked during their inter-nesting intervals remained in the vicinity of the upper Texas coast and, upon entering the post-nesting stage, moved eastward along the 20 m isobath to foraging areas offshore of central Louisiana. Satellite telemetry indicated that inshore and continental shelf waters of the northwestern Gulf of Mexico serve as developmental, migratory, inter-nesting, and post-nesting habitat for the Kemp's ridley. Projected population growth will likely lead to increased use of the northwestern Gulf by the species and more frequent encounters with human activities. The extent of such anthropogenic interactions and need for mitigation measures should be examined and considered by natural resource managers to facilitate continued recovery of this and other sea turtle species in the Gulf of Mexico. Likewise, research efforts should be continued to better understand seasonal in-water distributions, abundances, population dynamics, and mortality risks to all life history stages.

KEY WORDS: Kemp's ridley sea turtle · Northwestern Gulf of Mexico · In-water data · Foraging · Migration · Satellite telemetry

INTRODUCTION

The Critically Endangered Kemp's ridley sea turtle *Lepidochelys kempii* (IUCN 2009) is exhibiting a recovery from declines that reduced its nesting population in Rancho Nuevo, Tamaulipas, Mexico (Fig. 1), from a single-day estimate of 10 000 to 40 000 females in 1947 (Carr 1963, Hildebrand 1963) to <300 throughout 1985 (USFWS & NMFS 1992, Márquez et al. 2005). Exponential increases in nesting of 12 to 19% yr^{-1} have since been recorded, likely due in large part to the protection of nesting females and eggs and integration of turtle excluder devices (TEDs) into the US and Mexican shrimp fisheries (Lewison et al. 2003, Heppell et al. 2007). This trend at Rancho Nuevo is complemented by the commencement and growth of Kemp's ridley nesting on the Texas (USA) coast, with a record of 197 nests documented in 2009 (Shaver 2010). Limited nesting has also been documented along Gulf

*Email: eeseney@gmail.com

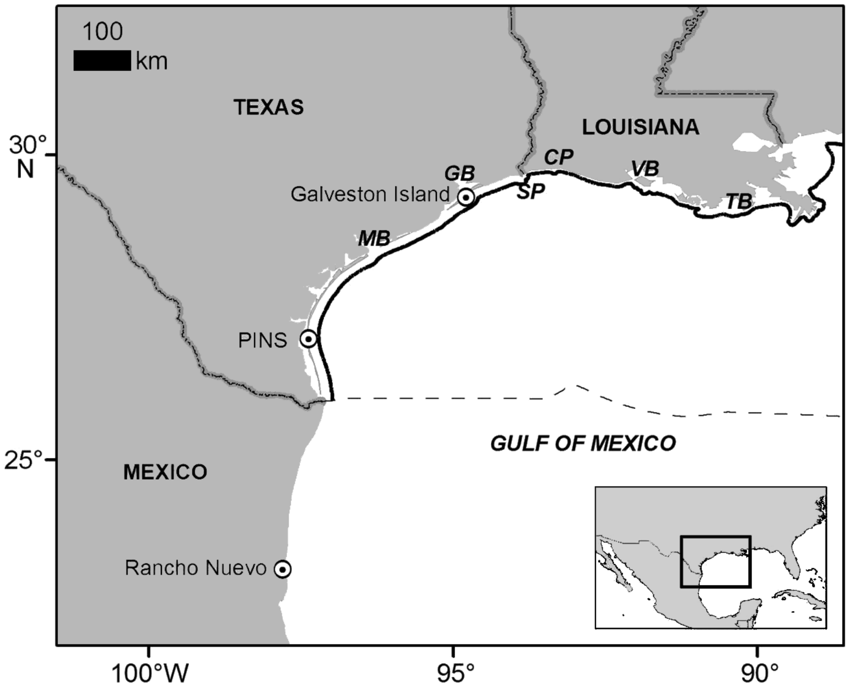

Fig. 1. Western Gulf of Mexico showing the location of Rancho Nuevo, Tamaulipas, Mexico; Padre Island National Seashore (PINS), North Padre Island, Texas; and Galveston Island, Texas, USA, as well as selected bays and passes: Matagorda Bay (MB), Galveston Bay (GB), Sabine Pass (SP), Calcasieu Pass (CP), Vermilion Bay (VB), and Timbalier Bay (TB). The solid black line marks the offshore extent of Texas and Louisiana state waters; the dashed black line marks the offshore extent of US territorial waters (Exclusive Economic Zone)

and Atlantic beaches of other southeastern US states (Shaver 2005).

Although beach monitoring is crucial to estimating nesting population size and activity, in-water data are essential for evaluating management strategies and understanding population dynamics (National Research Council 2010). The present Kemp's Ridley Recovery Plan (First Revision, USFWS & NMFS 1992) identifies the 'seasonal use of nearshore habitat by juveniles/subadults' and determining 'migratory paths and foraging areas' as necessary components of a strategy to achieve the species' recovery, but such data are currently sparse. A recent 5 yr review of the species' status (NMFS & USFWS 2007) and the draft Second Revision of the Kemp's Ridley Recovery Plan (NMFS, USFWS & Secretaría de Medio Ambiente y Recursos Naturales [Mexico], available at www.fws.gov/kempsridley/pdfs/DraftKRRP.pdf) also highlight these gaps in information.

Most hatchling Kemp's ridleys are likely retained in the Gulf of Mexico, but a small percentage may be entrained in the Florida Current and transported up the Atlantic coast by the Gulf Stream (Musick & Limpus 1997, Putman et al. 2010). Post-hatchlings have been observed in floating mats of vegetation (*Sargassum* spp.), where they are assumed to spend much of their time foraging on small crustaceans and molluscs (Bjorndal 1997). The post-hatchling stage extends to approximately age 2 (<20 cm straight carapace length, SCL) and is followed by a benthic immature stage that lasts an average of 10 yr (20 to 60 cm SCL; Snover et al. 2007). Benthic-stage immature Kemp's ridleys occur in shallow, nearshore habitats of the northwestern Atlantic and Gulf of Mexico (reviewed by Ogren 1989 and Musick & Limpus 1997), where they feed primarily on crabs, other benthic invertebrates, and occasionally fishery bycatch (Shaver 1991, Burke et al. 1994, Frick & Mason 1998, Seney & Musick 2005, Witzell & Schmid 2005). Age at maturity (>60 cm SCL) is estimated at 10 to 17 yr, with a mean of 12 yr (Snover et al. 2007). Adult Kemp's ridleys occur primarily along the Gulf of Mexico's continental shelf (Morreale et al. 2007), and they feed predominantly on crabs (Shaver 1991, Frick & Mason 1998).

The northwestern Gulf of Mexico (Fig. 1) is considered developmental habitat for the Kemp's ridley (Landry & Costa 1999, Landry et al. 2005, Renaud & Williams 2005), whereas nesting females from Mexico and Texas utilize these waters seasonally (Renaud et al. 1996, Shaver & Rubio 2008, TEWG 2000). Further characterization of the Kemp's ridley's use of the northwestern Gulf is crucial to the species' management, particularly because predictive models suggest that reducing mortality of immature individuals is essential to continued recovery (TEWG 2000, Heppell et al. 2007); likewise, increased use of the Texas coast as nesting habitat warrants examination of the movements of adult females. As such, the following research objectives were identified: (1) to characterize movements of benthic-stage immature and adult female Kemp's ridleys in the northwestern Gulf of Mexico; and (2) to identify Kemp's ridley migration patterns and foraging grounds in the northwestern Gulf of Mexico.

MATERIALS AND METHODS

Satellite telemetry

Benthic-stage Kemp's ridleys (n = 22), including recreational hook-and-line captures, nesting females, dredge relocation trawl captures (see NMFS 2003), and rehabilitated strandings, were satellite-tracked in the northwestern Gulf of Mexico during 2004 through 2007. Hooked and stranded individuals received appropriate treatment at the Houston Zoo (Houston, Texas, USA) and NOAA Fisheries Sea Turtle Facility (NOAA STF, Galveston, Texas), and each was cleared by a Houston Zoo veterinarian prior to transmitter application. Data from 6 nesting females tracked in 2005 and 2006 have been examined previously within the context of nesting and inter-nesting habitat, general migration patterns, and implications for natural resource management on the upper Texas coast (Seney & Landry 2008). In the present study, we combine these data with those from an additional adult female, compare the adult females' movements to those of immature Kemp's ridleys, and include new information from spatial analyses.

All ridleys were fitted with back-pack style platform terminal transmitters (PTTs), including 1 Wildlife Computers SPOT4, 2 Telonics ST-10s, 2 Telonics ST-20s, 15 Sirtrack KiwiSat 202s, and 2 Sirtrack KiwiSat 101s. In all cases, the transmitter weighed less than 3% of the turtle's weight in air and was attached along the turtle's first and second vertebral scutes. PTTs were attached to 5 immature and 3 adult female ridleys during 2004 to 2005 using Power-Fast®+ 2-part marine epoxy (Seney & Landry 2008, Mansfield et al. 2009). A spray-on antifouling paint (Tempo® Marine) was applied to non-metal surfaces of the last 3 transmitters deployed on juveniles in 2005. This method was modified in 2006 (n = 3 immature and 4 adult females) to include a layer of Sonic-Weld® steel-reinforced epoxy putty over the Power-Fast®+ epoxy (Seney & Landry 2008, Mansfield et al. 2009). All units used in 2006 were sprayed with antifouling paint prior to attachment, and 2 coats of brush-on ablative antifouling paint (Interlux Micron® Extra) were applied to the epoxy, putty, and non-metal surfaces of the PTTs after attachment. In 2007, units were covered with Alumi-Koat® clear spray-on antifouling paint prior to attachment, and an experimental method incorporating 3.0 mm thick neoprene to accommodate growth of smaller turtles (Seney et al. 2010) was utilized for all attachments (n = 7 immature). Power-Fast®+ was used to adhere neoprene to each turtle's carapace and the PTT to the neoprene, followed by application of brush-on antifouling paint as in 2006.

A total of 14 immature ridleys (12 recreational hook-and-line captures, 1 fishing gear entanglement, and 1 relocation trawl capture) were released from the east end of McFaddin National Wildlife Refuge (NWR) near Sabine Pass, Texas, whereas each nesting female was released in close proximity to her nest site on Galveston Island (n = 5) or in Surfside, Texas (southwest of Galveston Island, n = 1). A trawl-caught adult female was released from the Bolivar Peninsula, Texas, northeast of Galveston Island, and a rehabilitated stranding from Galveston Bay was released on the Gulf side of Galveston Island (Fig. 1). Hook-and-line-caught and entangled ridleys were released according to NOAA STF protocols, which sought to minimize further hook-and-line interactions (e.g. recapture), and similar protocols were followed for the 2 relocation-trawl-caught individuals. The trawl-caught adult female was not released off McFaddin NWR due to the presence of nearshore shrimp trawlers on the day of her release. All release sites and water temperatures were within the known ranges of each life stage based upon historical stranding, hook-and-line capture, and monitoring data. The 15 immature ridleys were designated I-01 through I-15, and the 7 adult females were designated F-01 through F-07 according to release date.

PTTs were programmed with a duty cycle of 6 h on: 18 h off (n = 17) or 6 h on:6 h off (n = 5) to conserve battery life. Location messages received from satellites were processed by CLS America's Argos System and classified according to estimated accuracy and the number of messages used in processing. Location classes (LC) 3, 2, 1, and 0 were derived from at least 4 messages and had estimated accuracies of <150, <350, <1000, and >1000 m, respectively (www.clsamerica.com/argos-system/faq.html); however, actual error may be higher (Costa et al. 2010, Witt et al. 2010). LC A and B had no estimates of accuracy and were calculated from 3 and 2 messages, respectively, whereas LC Z 'indicate[d] that the location process failed' (www.clsamerica.com/argos-system/faq.html). Studies examining Argos LC accuracy using Argos-linked Global Positioning System (GPS) transmitters indicate that LC A and B can provide useful information after appropriate filtering (Hays et al. 2001, Costa et al. 2010, Witt et al. 2010).

Data filtering and analysis

Location data were filtered using criteria similar to those utilized previously for tracks from adult female olive ridleys *Lepidochelys olivacea* (Plotkin 1998) and adult male (Shaver et al. 2005) and female (Seney & Landry 2008, Shaver & Rubio 2008) Kemp's ridleys. Seaturtle.org's Satellite Tracking and Analysis Tool (STAT) (Coyne & Godley 2005) was employed to exclude locations that fell into any of the following categories: (1) LC Z; (2) those requiring straight-line swimming speeds >6 km h^{-1}, and (3) those at elevations >0.5 m (i.e. on land). The initial filter was modified to exclude points at elevations >1.0 m for 2 tracks that entered coastal lakes (Sabine Lake and Lake Calcasieu), but the filtering protocol otherwise remained the same. Obviously erroneous points (e.g. substantial deviations from otherwise linear or clustered movements) that remained after filtering were removed manually, and the remaining (accepted) locations were used to depict tracklines in ESRI® ArcMap™ 9.x.

Mean daily locations for each turtle were generated from accepted locations in ArcMap™ 9.x to minimize autocorrelation in spatial analyses (adapted from James et al. 2005). Immature ridley tracks and inter-nesting and post-nesting, post-migratory (foraging) portions of female tracks suitable for site fidelity and home range analysis (i.e. those of a sufficiently non-directional nature) were then selected using Rayleigh's uniformity test (Åkesson & Bäckman 1999, Mansfield et al. 2009). The Animal Movements Extension (AME) (Hooge & Eichenlaub 2000) was used to calculate Rayleigh's *Z*, and movement was considered 'directional' at an arbitrary threshold of $p < 0.05$ (cf. Åkesson & Bäckman 1999).

Site fidelity and home range analysis was conducted for non-directional immature ridley tracks >14 d in duration, as well as the inter-nesting and foraging segments of female tracks, using daily mean locations. Site fidelity was examined with AME using Monte Carlo Random Walk (MCRW) simulations of 1000 replicates per track or track segment (Hooge & Eichenlaub 2000, Mansfield et al. 2009, McGrath & Austin 2009). MCRW simulations were restricted such that they could not go onto land or leave the Gulf of Mexico. Significance was based on $\alpha = 0.05$, and tracks and segments with movements more spatially constrained than the MCRW simulations were considered to exhibit site fidelity (Hooge & Eichenlaub 2000, Mansfield et al. 2009, McGrath & Austin 2009).

The Home Range Tools for ArcGIS™ extension (Rodgers et al. 2005) was employed to conduct kernel density estimation (KDE) analyses using a fixed kernel estimator with the band width chosen via least squares cross-validation (Seaman & Powell 1996, Powell 2000, Börger et al. 2006). The 'core area of activity' for each non-directional immature ridley track and female track segment was defined by the 50% probability KDE contour (Hooge et al. 1999, Börger et al. 2006). KDE outputs were clipped in ArcMap™ 9.x to exclude land and facilitate calculation of in-water area (km^2). Relationships among in-water core areas, tracking duration, and life history stage were examined using analysis of covariance (ANCOVA). Additional KDE analyses were conducted on all mean daily locations from each life stage (immature and adult female) to generate density contours at 10% intervals from 50 to 90% (Börger et al. 2006).

Water depth and sea surface temperature (SST) at accepted locations were determined by STAT (Coyne & Godley 2005) using data produced by NOAA's National Geophysical Data Center (NGDC) and NOAA's Advanced Very High Resolution Radiometer (AVHRR) daily SST, respectively. SST values were not available for all locations; however, AVHRR was chosen in lieu of NOAA's Geostationary Operational Environmental Satellite (GOES) system to allow for maximum data coverage among all tracked ridleys. Water depth and SST were compared between life history stages with the non-parametric Mann-Whitney test during seasons with sufficient data among individuals. Average depth and SST values for spring through early summer (April to June) and late summer through autumn (July to October) from tracks >14 d were included in the analysis. Any average seasonal depth or SST calculated from 5 or fewer values was excluded from the analysis.

RESULTS

A total of 15 immature Kemp's ridleys averaging 36.3 cm SCL (SD = 4.7 cm) and 7 adult females averaging 63.8 cm SCL (SD = 2.0 cm) were fitted with PTTs and released off the upper Texas coast during 2004 to 2007 (Tables 1 & 2). These comprised 12 recreational hook-and-line captures, 1 monofilament entanglement, 1 rehabilitated stranding, 2 dredge relocation trawl captures, and 6 nesting females (3 headstarted and 3 'wild' nesting stock females; see Seney & Landry 2008). Immature ridleys were tracked 11 to 106 d ($\bar{x}$ ±1 SD = 46 ± 24 d, Table 1) as compared to 20 to 277 d ($\bar{x}$ ±1 SD = 108 ± 88 d) for adult conspecifics (Table 2). Tracks of 2 immature individuals (I-03 and I-14) were <14 d in duration and thus were excluded from spatial and statistical analyses.

A substantial increase in the number of high quality LCs and in message duration indicated I-03's PTT

Table 1. *Lepidochelys kempii*. Tracking details for 15 immature Kemp's ridley sea turtles from the northwestern Gulf of Mexico, 2004 to 2007. SCL: straight carapace length (from notch to tip); Source — E: entanglement; HL: hook-and-line capture; RT: relocation trawl; S: stranding. No. of accepted locations: locations remaining after filtering raw Argos data. KDE: kernel density estimation. Constrained movements, i.e. site fidelity, as determined using Monte Carlo Random Walk simulation. na: not applicable

Turtle ID	SCL (cm)	Source	Date of deployment	Track duration (d)	No. of accepted locations	No. of avg. daily locations	50% KDE in-water area (km^2)	Constrained movements ($\alpha = 0.05$)
I-01	34.9	HL	21 Sep 2004	58	16	12	713	No
I-02	49.6	S	25 May 2005	44	37	27	na[a]	na[a]
I-03	30.2	HL	25 Jul 2005	12	24	9	na[b]	na[b]
I-04	36.2	HL	2 Aug 2005	32	35	24	1439	No
I-05	34.4	RT	6 Sep 2005	41	26	26	2650	No
I-06	33.9	HL	17 Apr 2006	20	34	15	1151	No
I-07	33.7	HL	25 Apr 2006	57	119	47	2048	No
I-08	34.0	E	31 Jul 2006	42	48	28	240	No
I-09	34.2	HL	23 Apr 2007	51	46	27	243	Yes
I-10	41.2	HL	23 Apr 2007	106	67	47	789	Yes
I-11	37.9	HL	1 May 2007	72	48	34	351	Yes
I-12	34.6	HL	15 May 2007	50	27	15	192	Yes
I-13	31.4	HL	12 Jul 2007	56	35	24	na[a]	na[a]
I-14	38.3	HL	12 Jul 2007	11	5	5	na[b]	na[b]
I-15	39.8	HL	14 Aug 2007	35	24	18	294	Yes

[a]Analyses were not conducted for directional tracks (Rayleigh's Z, $p < 0.05$) or [b]those <14 d

Table 2. *Lepidochelys kempii*. Tracking details for 7 adult female Kemp's ridley sea turtles from the northwestern Gulf of Mexico, 2005 to 2006. SCL: straight carapace length (from notch to tip); Source — N: nesting female (W: wild stock; HS: headstart); RT: relocation trawl. No. of accepted locations: locations remaining after filtering raw Argos data. KDE: kernel density estimation. Constrained movements, i.e. site fidelity, as determined using Monte Carlo Random Walk simulation. na: not applicable

Turtle ID	SCL (cm)	Source	Date of deployment	Track segment	Track/ segment duration (d)	No. of accepted locations	No. of avg. daily locations	50% KDE in-water area (km^2)[a]	Constrained movements ($\alpha = 0.05$)[a]
F-01	65.8	N(HS)	17 May 2005	Inter-nesting (whole track)	44	27	21	1340	No
F-02	62.5	N(W)	29 May 2005	Inter-nesting (whole track)	20	8	7	1929	No
F-03	63.0	N(HS)	31 May 2005	Whole track	50	93	39	na	na
				Inter-nesting	31	47	22	794	No
				Post-nesting season migration	8	17	5	na	na
				Foraging	11	29	10	2434	Yes
F-04	67.2	N(W)	28 Apr 2006	Whole track	148	170	91	na	na
				Inter-nesting	46	99	40	368	No
				Post-nesting season migration	17	19	10	na	na
				Foraging	83	52	39	1978	Yes
F-05	61.5	N(HS)	7 May 2006	Whole track	87	197	78	na	na
				Inter-nesting	39	72	35	425	Yes
				Post-nesting season migration	22	31	16	na	na
				Foraging	26	94	25	600	Yes
F-06	63.8	N(W)	27 May 2006	Whole track	132	190	112	na	na
				Post-nesting season migration	30	31	22	na	na
				Foraging	101	159	89	319	Yes
F-07	62.8	RT	16 Aug 2006	Whole track	277	202	160	na	na
				Nearshore movements	14	14	11	220	No
				Post-release migration	37	22	19	na	na
				Foraging	224	166	128	1616	Yes

[a]Analyses were not conducted for whole tracks or migration segments

was at the water surface for at least 2 d at the end of the tracking period, and mortality was the probable cause of transmission cessation (Hays et al. 2003). One post-nesting female (F-02) stranded dead 20 d after release (see Seney & Landry 2008), whereas the survival of 2 females tracked after nesting in 2006 was confirmed when they nested again on Galveston Island in 2009 (F-04) and in both 2008 and 2010 (F-05). LC and transmission data gave no indication that any of the other 18 ridleys were dead or debilitated at the time transmissions ceased, nor have any been reported as recaptures or strandings.

Movements of satellite-tracked ridleys were restricted to the continental shelf from Matagorda Bay, Texas, east to waters offshore of Timbalier Bay, Louisiana (Fig. 2). Coastal waters of the northwestern Gulf were utilized by immature ridleys as foraging areas in all years, with movements concentrated near tidal passes and fishing piers in 2004 to 2006 and near tidal passes and within bay systems in 2007. Two immature ridleys tracked during 2006 entered deeper waters and remained near the 20 m (I-08) and 30 to 40 m (I-07) isobaths for extended periods during September and May to June, respectively. Females tracked during their inter-nesting intervals remained in the Galveston region and, upon entering the post-nesting stage, moved eastward along the continental shelf (20 m isobath) to foraging areas offshore central Louisiana.

Two immature ridleys displayed 'directional' movement (Rayleigh's Z, $p < 0.05$) throughout their tracks, and 5 exhibited spatially constrained movements (site fidelity; tracks >14 d, Table 1). Directional movements were displayed by the largest immature individual (49.6 cm SCL, I-02, Fig. 2a), which stranded emaciated and lethargic in October 2004; this individual was rehabilitated, fitted with a PTT, and ultimately released in May 2005. The second directional track belonged to a hook-and-line capture from 2007 (I-13, Fig. 2d). The 5 immature ridleys that displayed track-long site fidelity were hook-and-line captures tracked for 35 to 106 d ($\bar{x} \pm 1$ SD = 63 ± 28 d) during 2007 (Table 1), with all of them entering bay systems (Matagorda Bay, Galveston Bay, Sabine Lake, or Lake Calcasieu; Fig. 2c,d).

Five nesting females remained in the Galveston area for 20 to 46 d ($\bar{x} \pm 1$ SD = 36 ± 11 d) prior to migration (n = 4) or stranding (n = 1, F-02), whereas 1 female encountered later in the nesting season (27 May 2006) left the region immediately after release (F-06). Of the 5 individuals tracked during the inter-nesting period, only 1 nesting female (F-05) exhibited true site fidelity (i.e. spatially constrained movement compared to MCRW; Table 2); others exhibited non-constrained movements, but remained offshore of the upper Texas coast during their inter-nesting periods (see Seney & Landry 2008). Five females (4 post-nesting and 1 relocation trawl-caught) were tracked during migrations of 8 to 37 d ($\bar{x} \pm 1$ SD = 23 ± 11 d; nesting females only: 8 to 30 d, $\bar{x} \pm 1$ SD = 19 ± 9 d) from Texas to waters offshore of Louisiana (Fig. 2e,f). These same 5 females were tracked for 11 to 224 d ($\bar{x} \pm 1$ SD = 89 ± 84 d) after arrival at foraging grounds offshore of Louisiana, where they exhibited site fidelity throughout the remainder of their tracks (Table 2).

Fifty percent KDE contours (core activity areas) were generated for the 11 immature ridleys with non-directional tracks over 14 d, as well as for non-migratory segments of each adult female's track. The in-water areas within each contour ranged from 192 to 2650 km^2 ($\bar{x} \pm 1$ SD = 919 ± 825 km^2, n = 11) for immature ridleys, 368 to 1929 km^2 ($\bar{x} \pm 1$ SD = 971 ± 661 km^2, n = 5) during adult females' inter-nesting periods, and 319 to 2434 km^2 ($\bar{x} \pm 1$ SD = 1389 ± 902 km^2, n = 6) for the post-migratory (foraging) portions of adult females' tracks (Tables 1 & 2). ANCOVA indicated that life history stage (fixed factor) had a significant effect on size of core activity areas (immature vs. inter-nesting female: $F_{1,13} = 3.790$, $p = 0.050$; immature vs. foraging female: $F_{1,13} = 4.978$, $p = 0.025$), whereas number of days tracked (covariate) did not (immature vs. inter-nesting female: $F_{1,13} = 0.783$, $p = 0.392$; immature vs. foraging female: $F_{1,13} = 0.107$, $p = 0.749$). Paired comparisons were not conducted for inter-nesting and post-migratory KDE areas because only 3 nesting females' tracks included both segments, but foraging core areas were, on average, ca. 50% larger than inter-nesting core areas.

Immature ridleys were recorded in waters as deep as 60.1 m, but 69% of accepted locations were at depths less than 5 m or above sea level in coastal lakes or bays ($\bar{x} \pm 1$ SD = 9.0 ± 13.9 m, n = 591 locations, Fig. 3a). Adult female ridleys occurred in waters with an average depth of 14.2 m (SD = 9.6 m, n = 887 locations) and displayed peaks in occurrence nearshore at 0 to 5 m and offshore at 10 to 20 m (Fig. 3b). AVHRR SST values (Fig. 4) for immature ridleys ranged from 21.0 to 32.6°C and averaged 28.1°C (SD = 2.8°C, n = 404 locations), with similar values recorded for adult females (17.1 to 32.6°C, $\bar{x} \pm 1$ SD = 27.6 ± 3.7°C, n = 769 locations). SST values were between 24 and 32°C for 91% of immature and 82% of adult female locations, respectively. The Mann-Whitney test indicated a significant difference between immature and adult female ridleys with respect to depth values during late summer through autumn

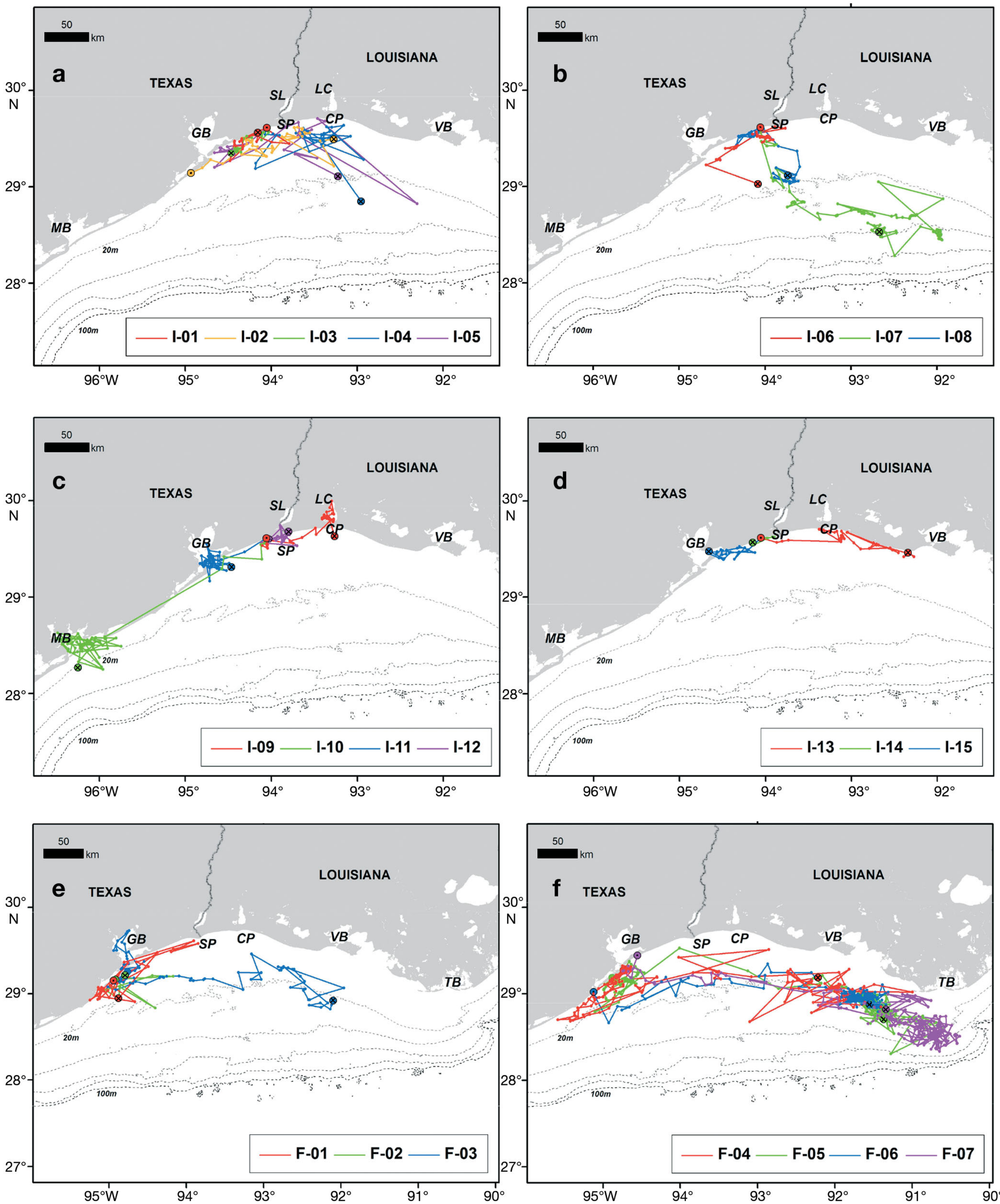

Fig. 2. *Lepidochelys kempii*. Filtered satellite tracks. ⊙: Release and ⊗: end of track. Immature individuals tracked during (a) 2004 to 2005, (b) 2006, and (c,d) 2007, and adult females tracked during (e) 2005 and (f) 2006 to 2007. MB: Matagorda Bay; GB: Galveston Bay; SL: Sabine Lake; SP: Sabine Pass; LC: Lake Calcasieu; CP: Calcasieu Pass; VB: Vermilion Bay; TB: Timbalier Bay. The gray dashed lines depict the 20 m through 100 m isobaths, in 20 m increments

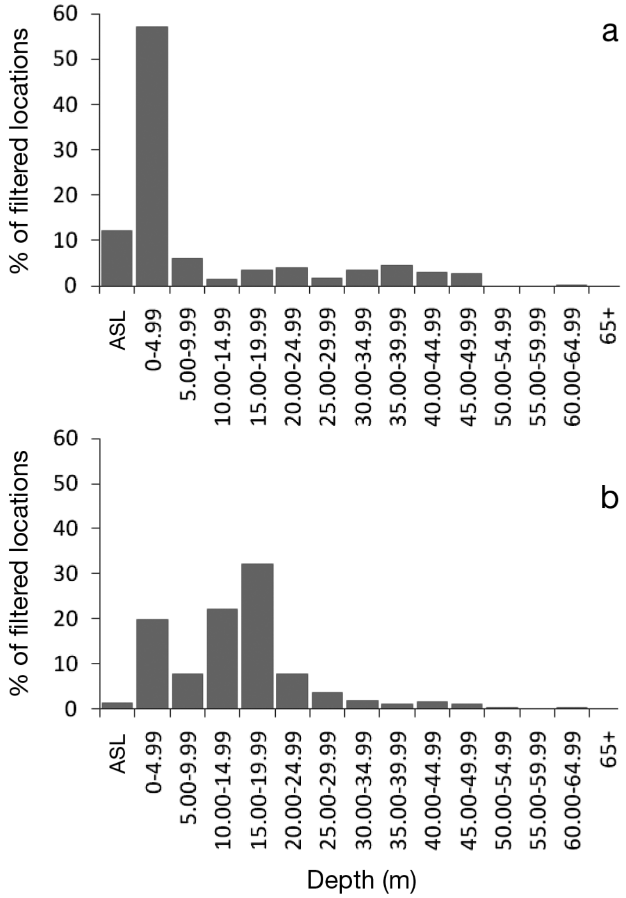

Fig. 3. *Lepidochelys kempii*. Water depth distributions of (a) 15 immature ridleys (591 locations) and (b) 7 adult female ridleys (887 locations). Depth values above sea level (ASL) represent primarily coastal lakes or bays

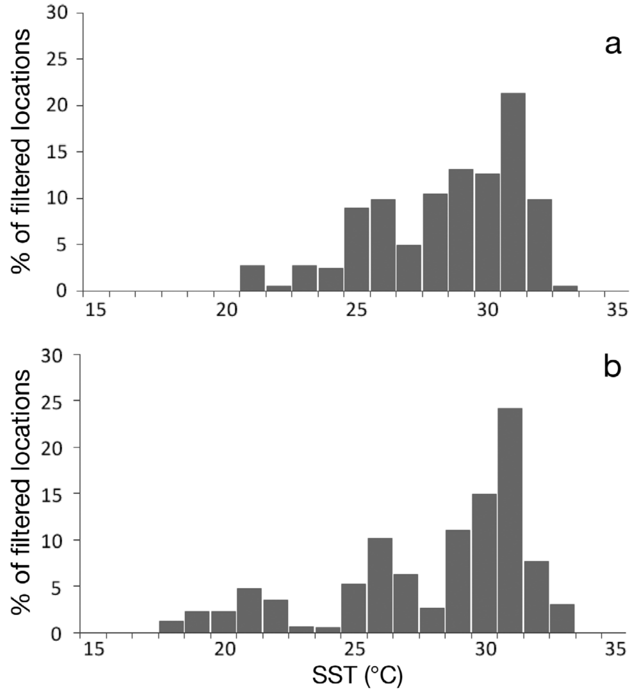

Fig. 4. *Lepidochelys kempii*. Advanced Very High Resolution Radiometer (AVHRR) sea surface temperature (SST) distributions for (a) 15 immature ridleys (404 locations) and (b) 7 adult female ridleys (769 locations). Sea surface temperature (SST) data were not available for all accepted locations

(9 immature tracks vs. 5 adult tracks, p = 0.003), but not for spring through early summer (7 immature vs. 7 adult, p = 0.064) or for SST (spring through early summer: 7 immature vs. 7 adult, p = 0.277; late summer through autumn: 7 immature vs. 5 adult, p = 0.570).

KDE analyses combining daily average locations for all immature ridleys (Fig. 5a) and adult females (Fig. 5b) reinforced the aforementioned trend in water depth between life history stages. Most high-use areas for tracked immature ridleys occurred within shallow Texas state waters (up to 9 nautical miles [n miles; ~16.7 km] from shore) between Galveston Island and Sabine Pass. Tracked females exhibited 2 high-use areas: (1) Texas state waters along Galveston Island during the nesting season; and (2) deeper federal waters (US territorial waters outside of the states' jurisdictions) offshore of central and eastern Louisiana (>3 n miles [~5.6 km] from shore) after migrating along the 20 m isobath.

DISCUSSION

Immature ridleys

Tidal passes, bays, and coastal lakes within Texas and Louisiana state waters served as foraging areas for immature Kemp's ridleys in the northwestern Gulf of Mexico during 2004 to 2007 (Figs. 2a–d & 5a). Four out of 7 individuals tracked in 2007 entered and exhibited fidelity to 4 different bay systems, whereas 2 out of 3 ridleys tracked in 2006 moved offshore (20 to 40 m depth) for extended periods. These results contrast with those for immature ridleys tracked during 2004 to 2006 and in prior studies (Renaud & Williams 2005) that favored tidal passes of the northwestern Gulf of Mexico. This disparity suggests that the preferred habitat (e.g. passes, bays, or offshore) of immature ridleys may differ among years. Variation in habitat use among similar-sized individuals has also been observed for immature loggerhead sea turtles *Caretta caretta* tracked from North Carolina (McClellan & Read 2007) and Virginia, USA (Mansfield et al. 2009). These loggerheads were observed to have 2 distinct migratory patterns: (1) nearshore,

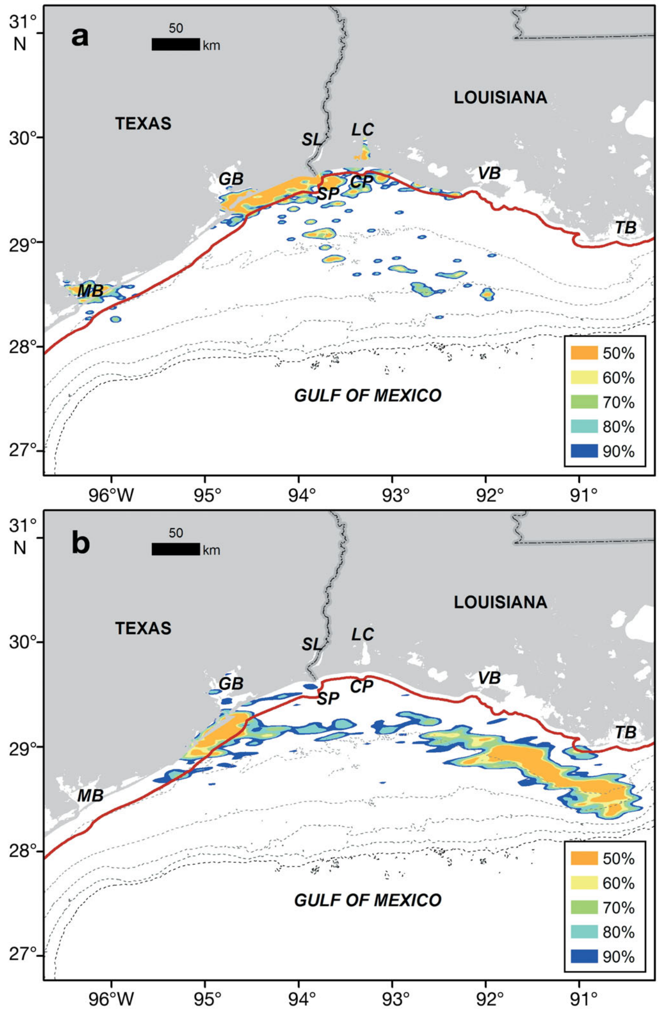

Fig. 5. *Lepidochelys kempii.* Use of the northwestern Gulf of Mexico, as estimated with kernel density estimation (KDE) by (a) 15 immature ridleys (358 average daily locations) and (b) 7 adult female ridleys (508 average daily locations). MB: Matagorda Bay; GB: Galveston Bay; SL: Sabine Lake; SP: Sabine Pass; LC: Lake Calcasieu; CP: Calcasieu Pass; VB: Vermilion Bay; TB: Timbalier Bay. The solid red lines mark the offshore extent of Texas and Louisiana state waters. The gray dashed lines depict the 20 m through 100 m isobaths, in 20 m increments

with individuals overwintering between North Carolina and Florida, USA; and (2) prolonged oceanic movements, with no apparent seasonality or relationship to SCL.

Although movements of immature ridleys varied in direction and destination, all traversed shallow nearshore areas, remaining primarily in waters less than 5 m deep during most or all of the tracking period. Water depth and SST ranges inhabited by immature ridleys in the present study were also similar to those recorded for 5 slightly larger individuals (38.6 to 51.1 cm SCL) tracked in the Cedar Keys on the Gulf coast of Florida (Schmid & Witzell 2006). Both groups preferred shallow nearshore areas, and SST values recorded for the Florida conspecifics during May (21 to 28°C) and June to August (26 to 31°C) mirrored values in this study. In contrast, the Florida ridleys occupied foraging areas (100 % minimum convex polygon: 3.8 to 48.0 km^2) an order of magnitude smaller than the 50 % KDE estimates for immature ridleys from Texas (Table 1).

A preference for nearshore habitats was also reported by Renaud & Williams (2005), who found that 57 out of 78 juvenile ridleys (<50 cm SCL) satellite- and/or radio-tracked during 1988 to 1996 remained in shallow northwestern Gulf waters during June through September. Daily locations of 60 'habitat faithful' juvenile ridleys (Renaud & Williams 2005) were often concentrated outside of Sabine and Calcasieu Passes on the lee side of jetties, but these turtles were both captured and released in these areas. The remaining 18 juveniles tracked by Renaud & Williams (2005) departed from their release sites, typically moving from Sabine Pass to Calcasieu Pass and vice versa or between Calcasieu Pass and Mermentau Pass, Louisiana. Three loggerhead sea turtles (56 to 93 cm SCL) tracked in the northwestern Gulf of Mexico during 1988 to 1991 (Renaud & Carpenter 1994) exhibited similar 'habitat faithfulness', maintaining relatively small core areas; however, these loggerheads remained further offshore and in deeper waters (average depth of 13 to 16 m) than did immature ridleys.

Movements of immature relocated Kemp's ridleys contrasted not only with site fidelity previously observed in the northwestern Gulf (Renaud & Williams 2005), but also with fidelity of immature conspecifics to Florida Panhandle fishing piers (Rudloe & Rudloe 2005), loggerheads to northwestern Gulf petroleum structures (Renaud & Carpenter 1994), and seasonal and inter-annual fidelity exhibited by immature ridleys to Florida's Cedar Keys (Schmid & Witzell 2006). Only one of the 15 immature ridleys in the present study, a 2004 hook-and-line capture (I-01), returned to the vicinity of its capture location (Gilchrist, Texas) during the tracking period, whereas the 2005 relocation trawl capture (I-05) approached its capture location (Calcasieu Pass, approximately 110 km straight-line distance from release) near the end of its 41 d track (Fig. 2a). This apparently low rate of return to piers contrasted with recapture rates documented for ridleys caught by anglers at piers, commercial shrimp trawls, or other fishing gear along the Florida Panhandle: 9 out of 38 ridleys released at the point of capture were recaptured at or near this site, and 3 out of 19 relocated 1 to 32 km were recaptured near their initial capture site (Rudloe & Rudloe 2005). These results suggest that relocation of hook-and-line-caught Kemp's ridleys to McFaddin NWR may be a viable option for reducing recapture rates at Galveston County, Texas, fishing piers.

Despite differences between movement patterns of immature ridleys tracked in the present study and those tracked previously in the northwestern Gulf of Mexico (Renaud & Williams 2005) and Florida (Schmid & Witzell 2006), the habitat characteristics of some seasonal foraging sites are likely similar, although specific prey items and abundances may vary. For example, Texas and Louisiana bays, in providing protection from adverse sea conditions, better visibility for foraging, and access to abundant populations of blue crabs *Callinectes sapidus* and other benthic prey (More 1969, Britton & Morton 1989, Metz 2004, Minello et al. 2008), may offer immature ridleys the same foraging advantages as does the lee side of tidal passes. Nearshore Gulf waters, through which all immature ridleys tracked in 2004 to 2007 moved and some established short-term residency, also provide foraging opportunities. Such areas are often characterized by abundant blue crab assemblages (Metz 2004) as well as bycatch discarded by shrimping vessels (Caillouet et al. 1996). Baited recreational fishing hooks and associated discard of bait and/or fish from piers, beaches, jetties, and groins also serve as a food source for ridleys (Seney 2008). Additionally, state-mandated removal of abandoned crab traps (Texas Parks and Wildlife Code, Section 78.115) and recent reductions in the Texas shrimping effort (Caillouet et al. 2008) have likely reduced mortality of blue crabs and other benthic organisms, and, in turn, rendered Texas coastal waters and bays more attractive to foraging ridleys.

Adult females

Adult females inhabited nearshore waters along Galveston Island during the nesting season and then utilized the 20 m isobath as a migratory path to foraging grounds offshore of Louisiana (Figs. 2e,f & 5b), a pattern similar to that of many post-nesting ridleys tracked along the continental shelf from Padre Island National Seashore (PINS) (Fig. 1) to foraging areas ranging from Sabine Pass to the Florida Keys during 1997 to 2006 (Shaver & Rubio 2008). The single migration pattern observed for 5 upper Texas coast females contrasts with migratory patterns documented for olive ridleys and loggerheads, which, like Kemp's ridleys, feed primarily on invertebrates. Movements of 20 post-reproductive female and 7 male olive ridleys tracked in the eastern tropical Pacific Ocean were widely distributed and nomadic, with all but one individual displaying no fidelity to specific feeding habitats (Plotkin 2010); in contrast, North Atlantic and Pacific loggerheads exhibit intra-population variation in migratory patterns. Smaller female loggerheads nesting on Cape Verde, West Africa (Hawkes et al. 2006), and in Japan (Hatase et al. 2002) forage oceanically, with larger conspecifics from the same nesting populations foraging in coastal waters (neritically). Female loggerheads tracked from North Carolina exhibit 2 distinct post-nesting migration patterns: (1) northward movement to summer foraging grounds followed by a southward autumn migration: or (2) southward coastal migration immediately following the nesting season (Hawkes et al. 2007). Loggerheads from Sarasota, Florida, displayed 5 distinct patterns during 2005 to 2007: movement locally or migration to the southwestern Florida shelf, northeast Gulf of Mexico, southern Gulf of Mexico, or Bahamas (Girard et al. 2009). The neritically foraging Cape Verde loggerheads and the Sarasota conspecifics reached their post-nesting foraging grounds in 35 to 50 d ($n = 2$) and 3 to 68 d ($n = 28$), respectively, as compared to 8 to 30 d for 4 post-nesting ridleys in the present study. Additionally, inter-nesting and foraging core areas (50% KDE) utilized by female Kemp's ridleys (Table 2) were larger than total foraging areas calculated for loggerheads in the North Atlantic. Neritically foraging West African female loggerheads established total foraging areas of 112 to 421 km^2 (Hawkes et al. 2006), while post-nesting conspecifics from North Carolina established summer and winter foraging areas of 34 to 207 km^2 and 18 to 95 km^2, respectively (Hawkes et al. 2007). Female Kemp's ridleys also established larger core areas than those calculated for neritic (3 to 11 km^2) and oceanic (20 to 210 km^2) track segments of adult male loggerheads from Greece (Schofield et al. 2010), although some differences may be attributable to differences in analysis methods.

Life history stage comparisons

Statistical analysis indicated that the large core areas of activity displayed by inter-nesting and foraging adult female Kemp's ridleys (Table 2), as compared to those of immature individuals tracked during 2004 to 2007 (Table 1), were not a function of the adults' longer track durations. Similarly, the inter-nesting and foraging core areas of adult females in the present study were an order of magnitude larger than those of 7 male Kemp's ridleys tracked from Rancho Nuevo, Mexico, during 1999 to 2000 (50% KDE: 19 to 184 km^2, $\bar{x} \pm 1$ SD = 95 ± 57 km^2; Shaver et al. 2005). These differences suggest that adult female Kemp's ridleys may need to move more frequently, and into deeper waters, to find sufficient prey and/or appropriate environmental conditions offshore of Louisiana; however, longer track durations for immature individuals and increased efforts to track adult males are required to better compare movement patterns between life stages. The slightly larger range of SST values encountered by adult female ridleys (17.1 to 32.6°C), as compared to that for immature individuals tracked in this study (21.0 to 32.6°C), was due in large part to temporal distribution of tracking, and SST values did not differ significantly between the 2 life history classes during periods of overlapping data (spring to autumn).

Track durations

The track durations recorded in this study, particularly those of immature ridleys, were shorter than those typically recorded by other projects deploying Argos-linked satellite transmitters on sea turtles. The shortest nesting female track (20 d) was associated with a known mortality event, and a 12 d track recorded for an immature individual was likely due to the turtle's death. Other potential causes of premature transmission cessation relative to expected battery life include antenna damage, biofouling of saltwater switches, poor adhesion of transmitter, and shedding of transmitter due to high growth rate (discussed further in Seney et al. 2010). High levels of epibiont and algal growth and/or high immature turtle growth rates promoted by the northwestern Gulf of Mexico's elevated spring and summer water temperatures (often >30°C) were suspected factors in the reduced track durations in 2004 and 2005, prompting use of antifouling paint, more thorough attachment site preparation (sanding), and a less rigid attachment technique in later deployments.

Management considerations

Texas and Louisiana state waters and nearby US federal waters of the northwestern Gulf clearly serve as developmental, migratory, inter-nesting, and post-nesting habitat for the Critically Endangered Kemp's ridley; however, shrimping regulations currently afford sea turtles more protection along the lower half of the Texas coast (US–Mexico border to Corpus Christi) than that on the upper coast (Corpus Christi to Texas-Louisiana state line) or along the Louisiana coast (TPWD 2010, LDWF 2011). Gulf of Mexico waters offshore of the entire Texas coast (state waters and US exclusive economic zone [EEZ], Fig. 1) are annually closed to shrimping during the 'Texas closure' that typically extends from 15 May through 15 July. Additionally, Gulf waters within 5 n miles (~9.3 km) of the lower half of the Texas coast have been closed to shrimping during 1 December to 15 May annually since December 2000 (Shaver 2005). This regulation, along with mandated use of TEDs in shrimp trawls, has helped reduce the mortality of adult ridleys between Corpus Christi and Mexico and likely contributed to increased nesting along the lower half of the Texas coast (Lewison et al. 2003, Shaver & Rubio 2008). Many Texas bays, including portions of Galveston and Matagorda Bays, are typically open to shrimping during the May to July Texas closure (TPWD 2010), as are inshore and Gulf waters off Louisiana (LDWF 2011). Louisiana shrimp seasons are set by the Louisiana Wildlife and Fisheries Commission based upon shrimp population data. Gulf waters offshore of Louisiana are typically open to shrimping year-round except for closed seasons in some areas, which usually begin in mid- to late December and extend into April or May (LDWF 2011). Shrimp trawlers without a power trawl retrieval system, vessels retaining shrimp as live bait, and those hauling several specific net types are exempted from US TED requirements, but these vessels are subject to tow-time restrictions (US Code of Federal Regulations, Title 50, Part 223.206).

CONCLUSIONS

Immature Kemp's ridleys that recruit to coastal waters of the northwestern Gulf of Mexico during early spring also occupy these habitats during the summer and autumn, whereas adult females utilize these waters for nesting, foraging, and migrating during spring and summer. Favorable water temperatures and abundant food, presumably in the form of blue crabs, other invertebrates, bycatch, and bait, render shallow nearshore waters ideal habitats for foraging ridleys. During 2004 to 2007, ridley movements were documented primarily along the upper Texas–southwestern Louisiana coast, with individuals' activity scattered among nearshore Gulf waters, tidal passes, bays, and coastal lakes. Migratory behavior of immature and inter-nesting individuals was largely confined to a narrow, nearshore area in Texas and western Louisiana state waters, whereas post-nesting females migrated across deeper, US federal waters on the Texas–Louisiana continental shelf.

Projected population growth (Lewison et al. 2003, Heppell et al. 2007) will likely lead to increased use of the northwestern Gulf by Kemp's ridleys and, in turn, more frequent encounters with human activities such as commercial and recreational fishing, channel dredging, and oil and natural gas operations. The extent of these interactions and need for mitigation measures such as regulations affording increased protection for Kemp's ridleys in coastal waters should be examined by natural resource managers to facilitate the continued recovery of this and other sea turtle species in the Gulf of Mexico. Likewise, the Kemp's ridley's dependence on the northwestern Gulf of Mexico for seasonal foraging and migratory habitat should be considered when revising the Kemp's Ridley Recovery Plan, and research efforts should continue in the region to better determine in-water seasonal distributions, abundances, population dynamics, and mortality risks. Future research efforts can aid managers by reducing data gaps for the species, particularly with respect to in-water temporal and spatial distributions of the less-studied pelagic and benthic-stage immature life history stages, as well as adult males.

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