

Movements and Home Ranges of Adult Male Kemp's Ridley Sea Turtles (*Lepidochelys kempii*) in the Gulf of Mexico Investigated by Satellite Telemetry

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ABSTRACT.—Movements of 11 adult male Kemp's ridley turtles (*Lepidochelys kempii*) captured near Rancho Nuevo, Tamaulipas, Mexico, were monitored using satellite telemetry between 1999 and 2001. Locations were obtained from 73 to 233 days and transmissions were received from 89 to 453 days following deployment. The majority of accepted locations were in near-shore waters, in 37 m (20 fm) water depth or less. One of the 11 turtles traveled northward and was last located offshore from Galveston, Texas, USA. The other 10 remained within waters off Tamaulipas, Mexico. Eight of those 10 moved multi-directionally, primarily within core home range areas, and the other two moved primarily linearly. In contrast to previous findings for adult female Kemp's ridley turtles, our results suggest that a significant proportion of the adult male Kemp's ridley population may reside in the vicinity of nesting beaches year-round. Recovery programs for Kemp's ridley turtles should incorporate considerations regarding year-round residency of adult males.

KEY WORDS.—Reptilia; Testudines; Cheloniidae; *Lepidochelys kempii*; sea turtle; telemetry; migration; site fidelity; movements; home range; conservation; management

The critically endangered Kemp's ridley turtle (*Lepidochelys kempii*) nests almost exclusively along the Gulf of Mexico coast, with the largest concentration near Rancho Nuevo, Tamaulipas, Mexico (23.180°N, 97.797°W) (Márquez et al., 1982, 1999a,b, 2001). In 1947, an estimated 40,000 females nested at Rancho Nuevo on one day (Hildebrand, 1963). Intentional human exploitation and incidental capture in various fisheries caused the population to plummet to a low of 702 nests in 1985 (U.S. Fish and Wildlife Service [USFWS] and National Marine Fisheries Service [NMFS], 1992). After decades of intensive conservation and management efforts, increasing numbers of Kemp's ridley nests have been recorded in recent years near Rancho Nuevo and at other nesting beaches in Tamaulipas and Veracruz, Mexico (Márquez et al., 1999a,b, 2001). If the Kemp's ridley population increase continues on the current trajectory, the population may be down-listed to threatened status by the year 2020 (USFWS and NMFS, 1992; Márquez et al., 1999a,b, 2001).

Kemp's ridley turtles mature at from 10–20 years of age (Chaloupka and Zug, 1997; Schmid and Witzell, 1997; Zug et al., 1997; Shaver, 2004) and roughly 60 cm carapace length (Ogren, 1989; Márquez, 1994; Chaloupka and Zug, 1997; Schmid and Witzell, 1997). Adult Kemp's ridleys are restricted primarily to the Gulf of Mexico, but are occasionally found on the Atlantic coast of the USA (USFWS and NMFS, 1992). Recaptures of nesting females tagged at Rancho Nuevo indicate northward and southward post-

nesting migrations to waters off various coastal states in the USA and Mexico (Chavez, 1969; Márquez, 1970, 1990, 1994; Pritchard and Márquez, 1973). Satellite telemetry studies have shown that adult female Kemp's ridleys are primarily near-shore, shallow-water inhabitants, capable of swimming long distances in a directed manner (Byles, 1989; Mysing and Vanselow, 1989; Renaud et al., 1996; Shaver, 2001). The waters off the western and northern Yucatan Peninsula, southern Texas coast, and northern Gulf of Mexico are important foraging areas where adult female residency has been documented (Byles, 1989; Márquez, 1990; Shaver, 1991, 1998, 2001, 2004).

In contrast, knowledge of movements and habitat use by adult male Kemp's ridleys is limited. During interviews conducted by PMB in the late 1970s and early 1980s, several fishermen and local residents reported observing Kemp's ridley turtles during the winter months in the waters off La Pesca and Barra del Tordo, Tamaulipas, Mexico. Further inquiries over the ensuing years continued to result in similar reports, including several observations of mounted pairs during the months of October through March, essentially corresponding to the non-nesting season. It was unknown whether adult males remained resident in the vicinity of nesting beaches or migrated between nesting and feeding grounds, and, if so, whether the timing and routes of their migrations differed from those of the females. Such information is important in order to develop and implement recovery actions for this critically endangered species.

This study was undertaken to gain information on adult male Kemp's ridley turtles by satellite tracking. Our objectives were to: (1) investigate the movements of adult male Kemp's ridley turtles captured in the Gulf of Mexico; (2) identify migratory paths, feeding grounds, and home ranges; and (3) investigate seasonal variations in movements and habitat use. Determining distribution and migratory pathways, and identifying marine habitat, are priority one tasks in the Kemp's ridley Recovery Plan, prepared under the U.S. Endangered Species Act (USFWS and NMFS, 1992).

METHODS

Transmitter Deployment.—Eleven adult male Kemp's ridley turtles were outfitted with model ST-14 satellite (UHF) platform transmitter terminals (PTTs) manufactured by Telonics, Inc., Mesa, Arizona. PTTs were configured in a backpack style, measured 16.5 x 9.8 x 3.0 cm, and weighed 750 g. Ten PTTs were used in the study, but one (7674) was deployed sequentially on two different turtles, without refurbishment by Telonics between deployments.

PTTs were attached to turtles that local fishermen captured by net at Barra Carrizo (7661) and Barra del Tordo (other 10), in the vicinity of Rancho Nuevo, Tamaulipas, Mexico (Fig. 1), between 11 August 1999 and 25 May 2000 (Table 1). PTTs were deployed during the fall (September–November) ($n = 3$), winter (December–February) ($n = 4$), spring (March–May) ($n = 2$), and summer (June–August) ($n = 2$). We selected males for this study based on the presence of a long tail and soft plastron. Adult male sea turtles have long prehensile tails (Rostal, 1991; Wibbels et al., 1991; Meylan et al., 1994). Soft plastron, a secondary sexual characteristic that has been documented for some adult male sea turtles during the breeding season, may be indicative of reproductive activity (Rostal, 1991; Wibbels et al., 1991; Plotkin et al., 1996).

Curved carapace length (CCL) of the males, measured from the nuchal tip to the post-central tip on the opposite side of the carapace, ranged from 60.0 to 69.5 cm (mean = 65.5 \pm 2.9 cm, $n = 11$). Straight carapace length (SCL), from the nuchal notch to the post-central tip, calculated using the length conversion equation in Schmid and Witzell (1997), ranged from 56.0 to 64.3 cm (mean = 60.8 \pm 2.5 cm, $n = 11$).

PTT weight did not exceed 10% of the weight of the turtle (Byles and Keinath, 1990). PTTs were attached to the second vertebral scute of the carapace (Byles and Keinath, 1990; Balazs et al., 1996; Plotkin, 1994, 1998; Renaud et al., 1996; Shaver, 2000), on a base of fiberglass insulation, using three thin layers of polyester resin and fiberglass cloth, with the antenna oriented anteriorly. Turtles were restrained by hand during the attachment procedure (approximately 3 hrs). After PTT attachment, each turtle was marked with a metal flipper tag and passive integrated transponder (PIT) tag, and released near its capture site.

Turtle movements were monitored via the Argos, Inc. Data Collection and Location System until transmitters were removed or transmissions ceased. Transmitters were pro-

grammed with two different transmission (duty) cycles; these two cycles were 6 hrs on/6 hrs off ($n = 4$) and 8 hrs on/52 hrs off ($n = 7$). Transmitters broadcasted data (messages) every 50 sec (repetition rate), at a frequency of 401.65 MHz, with a transmission power output of 1.0 watt. As many as five NOAA Polar Orbiting Environmental Satellites (POES) received transmissions when the PTT was "on", a satellite was within range of the PTT, and the PTT was at the surface (Eckert, 1998, 1999; Plotkin, 1998). Data received by the satellites were distributed to ground stations and processed and disseminated by Argos (Argos, 1996). From the broadcasted messages received, Argos provided data on PTT identification number, date and time, number of messages received, dive data (the duration of the turtle's submergence immediately previous to the transmission, the mean duration of all submergences in the preceding 12 h, and the number of submergences in the preceding 12 h), and internal temperature of the PTT housing reported with an accuracy of $\pm 2^\circ\text{C}$. When multiple transmissions were received from a transmitter during a satellite pass, a location and location class were provided. Locations of the turtles (latitude and longitude) were calculated by Argos from the Doppler shift in transmission frequency detected by a satellite as it approached and then moved away from the transmitter (Argos, 1996).

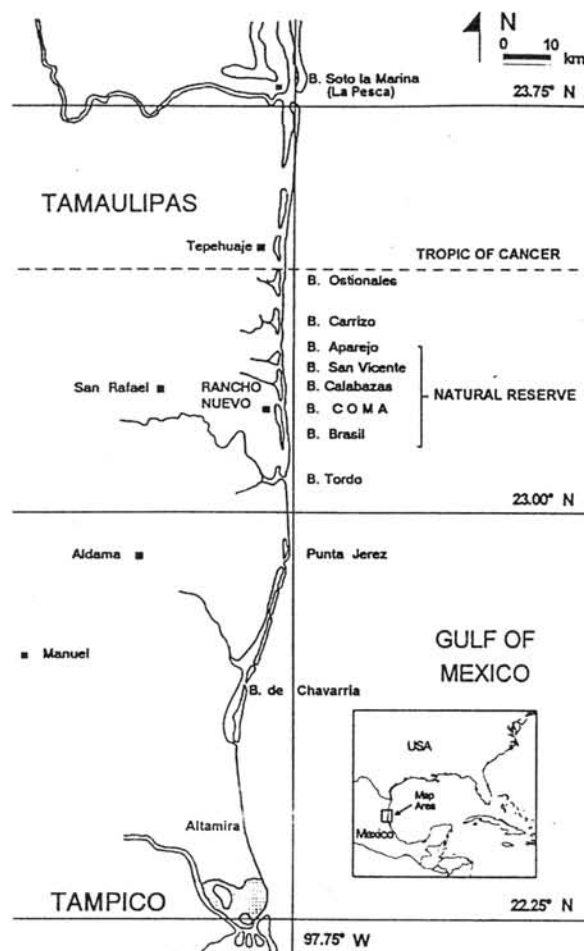


Figure 1. Map of the western Gulf of Mexico showing locations where turtles were captured and released near Rancho Nuevo, Tamaulipas, Mexico (adapted from Márquez et al., 1999b).

The calculation and accuracy of latitude and longitude was dependent on the number of messages received from a PTT during a satellite pass and the angle of the satellite relative to the PTT. Argos supplied location classes (LC) for each calculated latitude and longitude; these included LC 3, 2, 1, 0, A, B, or Z (Argos, 1996). However, locations of LC 0, A, B, and Z are only supplied by request to users subscribing to Argos multi-satellite service and Auxiliary Location Processing (ALP). Argos has estimated that accuracy in latitude and longitude for LC 3 is less than 150 m, for LC 2 is from 150-350 m, for LC 1 is from 350-1000 m, and for LC 0 is more than 1000 m (Argos, 1996). Argos provides no estimation of location accuracy for LC A and LC B, but this does not mean that locations are necessarily less accurate than LC 3, 2, 1, or 0. LC Z are rejected, invalid locations (Argos, 1996).

Location data were reviewed and either accepted or rejected based on criteria established by Plotkin (1994, 1998). Locations were rejected if they met one or more of the following criteria: (1) only two transmissions were received for a transmitter during a satellite pass and both were identical; (2) the location calculated for a transmitter was on land; (3) the rate of movement of a turtle between two consecutive locations exceeded 6 km/hr; and (4) the movements among consecutive locations were deemed unlikely (Plotkin, 1994, 1998). For each turtle, accepted locations were plotted sequentially to depict sequence of movement.

Analysis of Data. — The number of locations mapped (L), number of days from the date deployed to the date of the last location mapped (M), and number of days from the date deployed to the date of the last transmission (D) were calculated for each turtle. Data were tested for normality and homogeneity of variance prior to using parametric procedures. When parametric assumptions were not met, equivalent non-parametric procedures were used. T-tests were used to compare the mean L, mean M, and mean D from turtles with the two different duty cycles. All means are followed by \pm one standard deviation.

Using the Geographic Information Systems program ArcView® with Tracking Analyst Extension® and Animal Movement Analyst Extension (AMAE) (Hooge et al., 2001), home range was calculated for those turtles for which the assumptions of the individual home range models used were met. All PTT data were analyzed for site fidelity (i.e., the animal's locations did not exhibit significant dispersion or significant linearity) and those that failed to meet this assumption were eliminated from all home range analyses (Hooge et al., 2001). For those with adequate sample size, minimum convex polygon (MCP) home range was calculated; for those without serial autocorrelation, kernel home ranges with 95% and 50% probabilities were calculated, with the 95% contour considered as the area that the animal actually used and the 50% contour as the core of activity (Hooge et al., 2001). When the calculated home range encompassed land area, that land area was omitted from the home range reported.

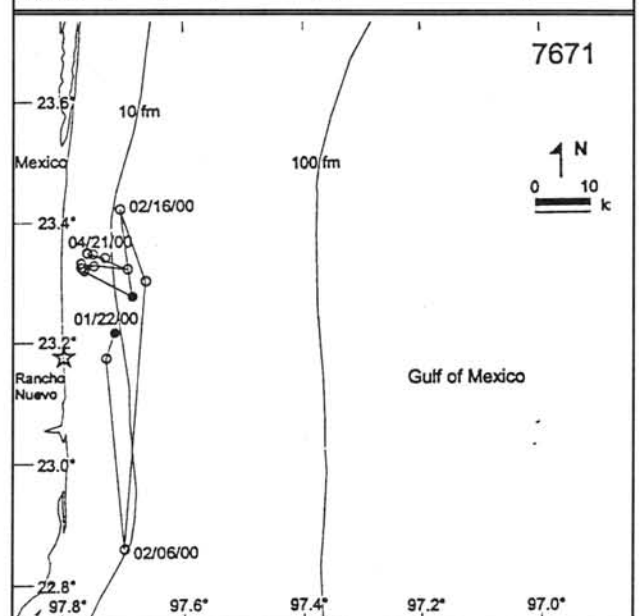
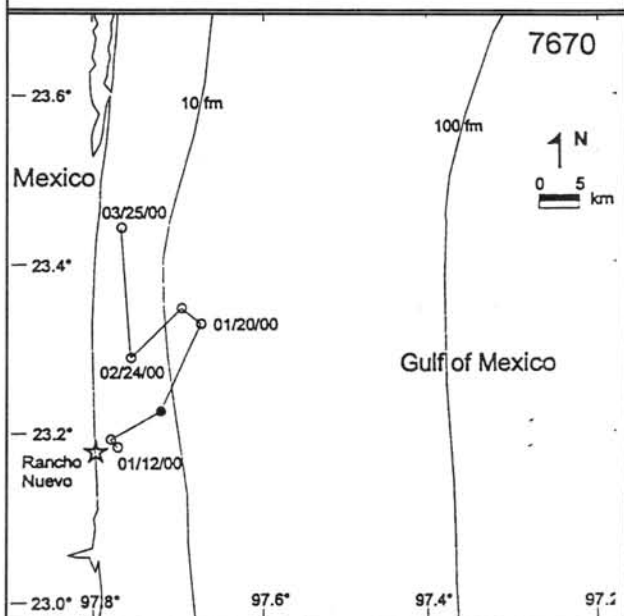
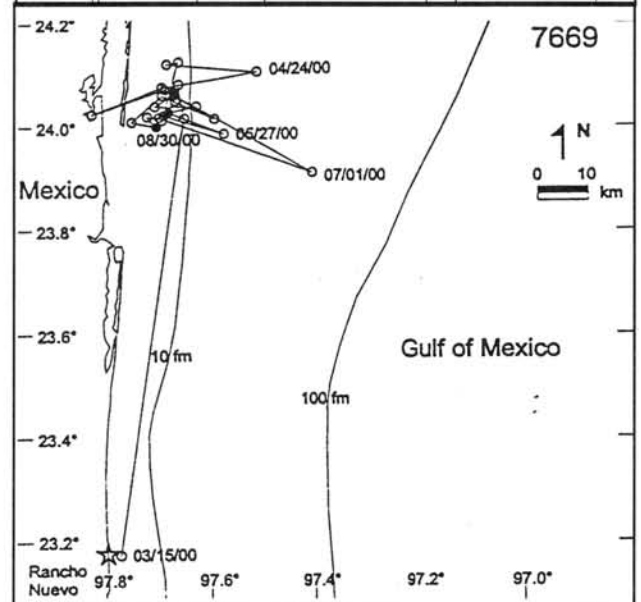
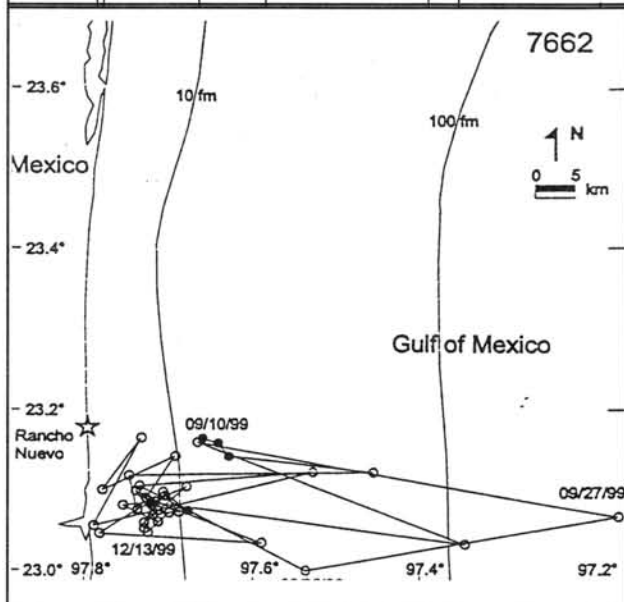
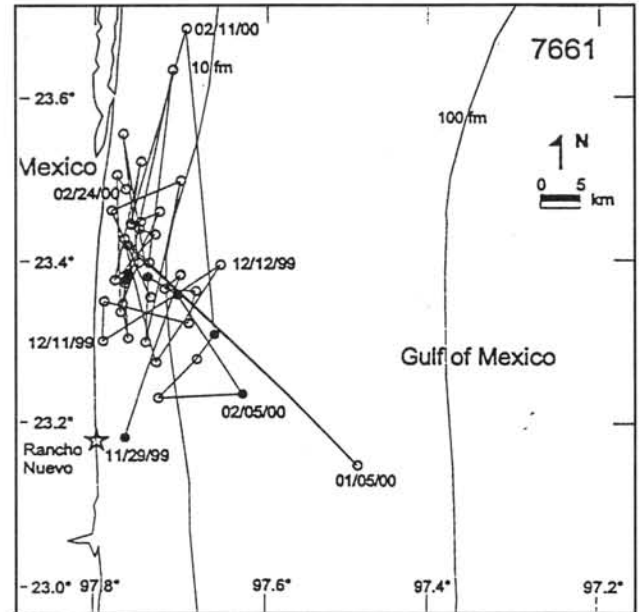
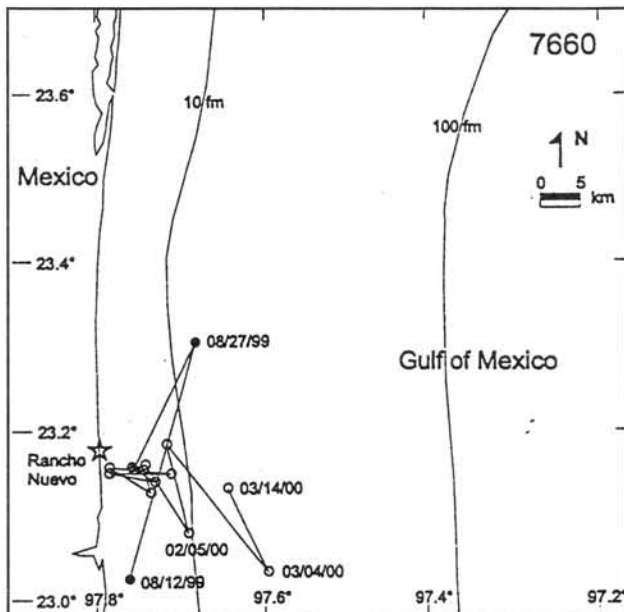
RESULTS

Tracking Duration and Location Class. — Overall, 936 transmissions were received (Table 1) including LC 3 ($n = 10$), LC 2 ($n = 17$), LC 1 ($n = 17$), LC 0 ($n = 22$), LC A ($n = 93$), LC B ($n = 202$), and LC Z ($n = 575$) (Table 1). From these, 297 locations were accepted and mapped including LC 3 ($n = 10$), LC 2 ($n = 17$), LC 1 ($n = 15$), LC 0 ($n = 18$), LC A ($n = 82$), and LC B ($n = 155$). The majority of the 639 transmissions that were not mapped were transmissions that failed to yield a location. However, 64 locations were rejected because they were on land ($n = 44$), the calculated rate of movement of a turtle > 6 km/hr ($n = 14$), or the locations were deemed unlikely ($n = 6$). These rejected locations were of LC 1 ($n = 2$), LC 0 ($n = 4$), LC A ($n = 11$), and LC B ($n = 47$).

For the 11 turtles monitored, L ranged from 7 to 65 (mean = 27 ± 17), M from 73 to 233 days (mean = 131 ± 52 days), and D from 89 to 453 days (mean = 183 ± 104 days) (Table 1). The last mapped locations for the vari-

Table 1. Adult male Kemp's ridley turtles captured and released in Tamaulipas, Mexico, and tracked in the Gulf of Mexico using satellite telemetry. CCL = curved carapace length; SCL = straight carapace length calculated using Schmidt and Witzell (1997); DC = PTT duty cycle designated as number of hours on/number of hours off; M = the number of days from the date deployed to the date of the last location mapped; D = the number of days from the date deployed to the date of the last transmission; LC = location class for all transmissions (prior to screening using location rejection criteria); L = number of locations mapped; MCP = minimum convex polygon home range; K95 = kernel home range, 95% probability; K50 = kernel home range, 50% probability.

PTT ID No.	Carapace Length (cm)			Date Released	Date Last Location (M)	Date Last Transmission (D)	LC								Home Range (km ²)		
	CCL	SCL	DC				3	2	1	0	A	B	Z	L	MCP	K95	K50
7660	67.0	62.1	8/52	11 Aug 1999	14 Mar 2000 (216)	21 Mar 2000 (223)	0	0	2	2	12	4	35	15	356	363	44
7661	65.3	60.6	6/6	28 Nov 1999	24 Feb 2000 (88)	25 Feb 2000 (89)	2	2	4	1	7	37	98	44	1018	770	116
7662	62.0	57.8	6/6	9 Sep 1999	13 Dec 1999 (95)	18 Dec 1999 (100)	0	2	3	3	8	28	38	38	654	367	63
7669	68.4	63.3	8/52	15 Mar 2000	30 Aug 2000 (168)	30 Aug 2000 (168)	0	0	4	4	10	15	60	25	2398	845	184
7670	66.5	61.7	8/52	12 Jan 2000	25 Mar 2000 (73)	5 Oct 2000 (238)	0	1	0	0	4	3	33	7	-	-	-
7671	66.0	61.2	8/52	12 Jan 2000	21 Apr 2000 (100)	24 May 2000 (133)	1	1	0	1	3	12	21	16	-	-	-
7672	67.1	62.2	8/52	18 Aug 1999	7 Apr 2000 (233)	7 Apr 2000 (233)	2	4	1	1	9	27	104	32	3626	856	140
7674	69.5	64.3	8/52	1 Sep 1999	28 Dec 1999 (118)	31 Dec 1999 (121)	4	3	1	0	1	7	18	12	-	-	-
7674B	60.0	56.0	8/52	25 May 2000	11 Sep 2000 (109)	14 Sep 2000 (112)	1	2	1	0	4	11	20	17	-	-	-
7682	65.8	61.1	6/6	18 Dec 1999	9 Apr 2000 (113)	15 Mar 2001 (453)	0	1	0	3	25	46	79	65	490	124	19
7683	62.4	58.1	6/6	19 Dec 1999	24 Apr 2000 (127)	15 May 2000 (148)	0	1	1	7	10	14	69	26	1320	1077	100



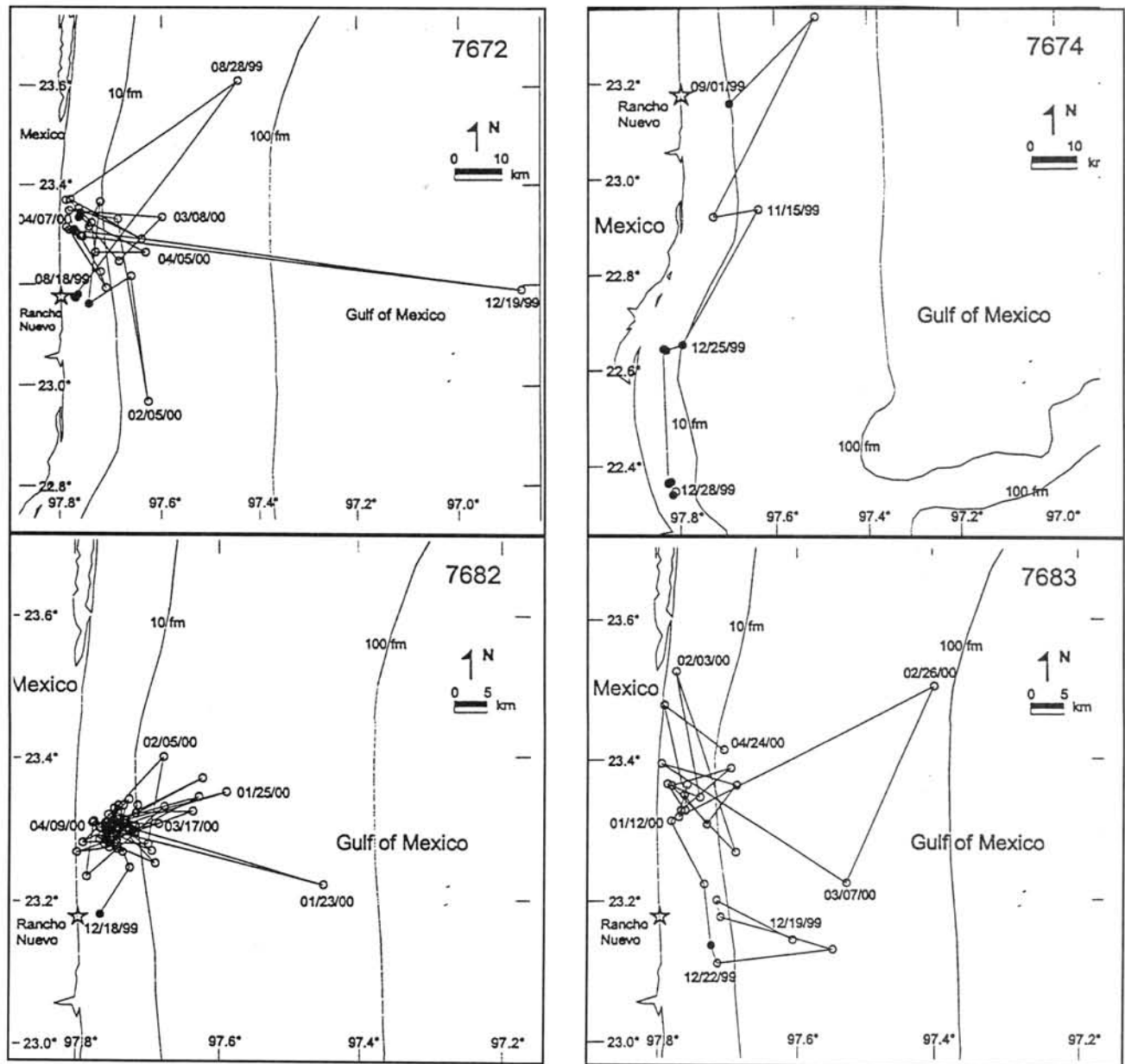


Figure 2. (previous page and this page) Locations of 10 satellite-tracked adult male Kemp's ridley turtles in the Gulf of Mexico, off Tamaulipas, Mexico. (●) = locations of LC 3, 2, and 1; (○) = locations of LC 0, A, and B; (☆) = Rancho Nuevo.

ous PTTs were between 13 December 1999 and 11 September 2000 and the last transmissions between 18 December 1999 and 15 March 2001 (Table 1). Some PTTs ceased transmitting location data, but continued to transmit dive data for days to months. One turtle (7674) was found washed ashore dead in Tampico, Tamaulipas, Mexico on 31 December 1999, 121 days following PTT deployment. From 25–28 December 1999, the number of messages per satellite pass ranged from 5–13 and all locations were LC 3, 2, or 1 for this PTT. In contrast, before 25 December, far fewer messages were received per pass and most locations were LC B. The marked increase in transmissions after 25 December indicates that the turtle was primarily at the surface because it had died and was floating, had suffered an acute injury that

altered its diving ability prior to death, or had died on the deck of a boat and then discarded. No other turtles exhibited a similar pattern. The PTT was removed from the dead turtle and later deployed on a different turtle (as 7674B).

The mean L from PTTs with a duty cycle of 8/52 (mean = 18 ± 8 , $n = 7$) was significantly smaller than from PTTs with a duty cycle of 6/6 (mean = 43 ± 16 , $n = 4$) ($t = -3.508$, $df = 9$, $p = 0.007$), the mean M from PTTs with a duty cycle of 8/52 (mean = 145 ± 61 days, $n = 7$) was not significantly different from PTTs with a duty cycle of 6/6 (mean = 106 ± 18 days, $n = 4$) ($t = 1.235$, $df = 9$, $p = 0.248$), and the mean D from PTTs with a duty cycle of 8/52 (mean = 175 ± 55 days, $n = 7$) was not significantly different from PTTs with a duty cycle of 6/6 (mean = 198 ± 172 days, $n = 4$) ($t = -0.322$, $df = 9$, $p = 0.754$). Performing these statistical comparisons

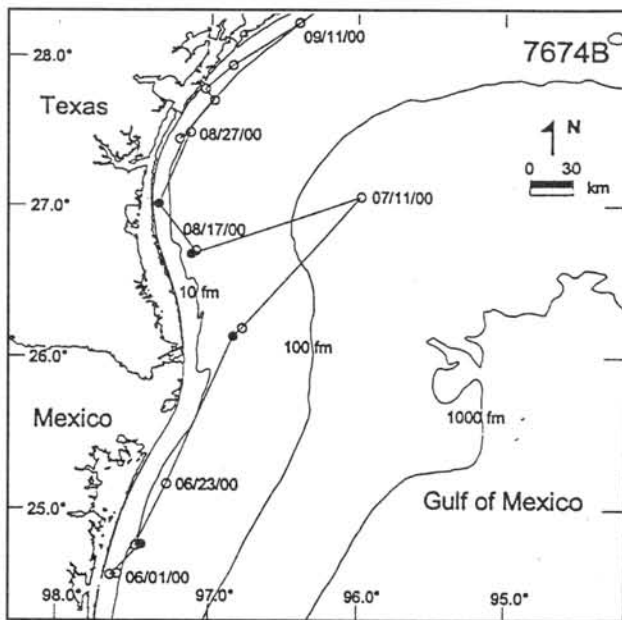


Figure 3. Locations of a satellite-tracked adult male Kemp's ridley turtle (7674B) in the western Gulf of Mexico off Tamaulipas, Mexico and Texas, USA. (●) = locations of LC 3, 2, and 1; (○) = locations of LC 0, A, and B.

again, after excluding the PTT that was deployed twice (7674, 7674B), did not alter the overall results, although the *p* values differed slightly.

Movements. — All turtles remained in the western Gulf of Mexico and adjacent bays for the duration of the tracking period (Figs. 2, 3). Collectively, locations ranged from approximately 22.341°N (7674) to 28.227°N (7674B) latitude and 95.982°W (7674B) to 97.833°W (7674) longitude. However, the vast majority of locations were within a much smaller area centered in Gulf of Mexico waters off the coast of Tamaulipas, Mexico. Most of the tracked turtles were located near Rancho Nuevo on at least one occasion after PTT deployment and many were located there several times.

Eight turtles (7660, 7661, 7662, 7669, 7671, 7672, 7682, 7683) exhibited multi-directional movements within localized core areas, which differed slightly for each turtle (Fig. 2). The core areas for seven of the eight (all but 7669) were in a region between 23 km south and 42 km north of Rancho Nuevo. The core area for 7669 was about 100 km north of Rancho Nuevo. Movements for seven of the eight (all but 7671) met the assumptions of the home range models used; for these seven, the mean MCP home range was 1409 km² (range = 356–3626 km²), mean kernel home range with 95% probability was 629 km² (range = 124–1077 km²), and mean kernel home range with 50% probability was 95 km² (range = 19–184 km²) (Table 1).

Three turtles (7670, 7674, 7674B) moved primarily in one direction and their last identified location was their most distant from Rancho Nuevo (Figs. 2, 3). One turtle (7674) moved southward after release and was last located about 92 km south of Rancho Nuevo, while another (7670) moved northward after release and was last located about 29 km north of Rancho Nuevo. Only one turtle (7674B) left Mexi-

can waters during the tracking period. This turtle moved northward after release, generally traveled parallel to the Gulf of Mexico coastline, and was last located just south of Galveston, Texas, USA, about 565 km north of Rancho Nuevo.

Temperatures recorded by the PTTs ranged from 13–33°C. Collectively, turtles were located near Rancho Nuevo at all times of the year and site fidelity to localized core areas did not vary seasonally. Additionally, the locations with the highest accuracy (LC 3, 2, 1) were not concentrated during any particular season. Movements to the north and south and further offshore did not appear related to temperature or season, with two possible exceptions. One turtle (7674B) moved northward and left the Tamaulipas coast in late June, towards the end of the nesting season. Another turtle (7674) moved slightly southward during the fall after the PTT-recorded temperature dropped by 7°C, but very few locations were available for this turtle and it was later located dead.

Most of the locations identified for the 11 turtles and most of the locations with the highest accuracy were in near-shore waters that were 0–37 m (0–20 fm) deep. Decreasing numbers of locations were found in 37–183 m (20–100 fm) and 183–1829 m (100–1000 fm) water depths. All four locations outside the 183 m (100 fm) contour were LC B.

DISCUSSION

Movements and Habitat Use. — Adult male Kemp's ridley turtles in this study appeared to be mostly year-round residents in the vicinity of the Rancho Nuevo nesting beach. Only one of the 11 migrated from the nesting beach area and the other 10 remained within waters off the coast of Tamaulipas, Mexico, for the duration of their tracking period (range = 73–233 days). Most of the 10 had restricted home ranges and exhibited site fidelity during the study period. Movements for two of the 10 were primarily in one direction. However, fewer locations were recorded for these two turtles than for any others and if more locations had been available, multi-directional movement within localized core areas might also have been recorded for them. The lack of migratory behavior in most of these adult male Kemp's ridleys was in sharp contrast to most adult female Kemp's ridleys and most adult males of other sea turtle species that have been monitored using satellite telemetry. The attraction of year-round prey availability and mating opportunities offshore the principal nesting beaches may obviate the need for adult male Kemp's ridley turtles to migrate from waters off the Tamaulipas coast.

Satellite telemetry studies of adult female olive ridley (*Lepidochelys olivacea*), green (*Chelonia mydas*), loggerhead (*Caretta caretta*), leatherback (*Dermochelys coriacea*), and hawksbill (*Eretmochelys imbricata*) turtles have demonstrated reproductive migrations between foraging and nesting areas (Balazs, 1994; Balazs et al., 1994; Byles and Swimmer, 1994; Plotkin et al., 1995; Schroeder et al., 1996; Sakamoto et al., 1997; Hughes et al., 1998; Luschi et al., 1998).

Similar migratory behavior has been displayed by satellite-tracked adult female Kemp's ridley turtles (Byles, 1989; Mysing and Vanselous, 1989; Renaud et al., 1996; Shaver, 2001), which nest primarily between April and July (Márquez, 1990, 1994). An adult female Kemp's ridley captured at a foraging area off the coast of Louisiana, USA, and outfitted with a satellite transmitter on 13 August 1994, moved to waters offshore from the upper Texas coast in late November 1994, arrived offshore from Rancho Nuevo in early March 1995, nested there on 23 April and 19 May 1995, and ceased transmitting there on 16 May 1995 (Renaud et al., 1996). Sporadic Kemp's ridley nesting also occurs on the south Texas coast (Shaver and Caillouet, 1998; Shaver 1999a,b, 2001, 2004). Most adult female Kemp's ridleys outfitted with satellite transmitters after nesting left waters offshore from their nesting beaches in Tamaulipas and Texas between May and July, traveled within near-shore Gulf of Mexico waters, and swam directly to distant feeding areas, where they established relatively circumscribed ranges (Byles, 1989; Mysing and Vanselous, 1989; Shaver, 2001).

A primary factor that may contribute to non-migratory behavior in adult male Kemp's ridley turtles would be the opportunity for mating. Some male sea turtles migrate to breeding grounds located near nesting beaches and most mating is thought to take place before or during the beginning of the nesting season, about 30 days before oviposition of the first clutch (see Plotkin et al., 1996; FitzSimmons, 1997; Hays et al., 2001b). Kemp's ridley turtles held in captivity at the Cayman Islands displayed a seasonal reproductive cycle with a distinct mating period (March) followed by a 3-month nesting period (mid-April to mid-July) (Rostal et al., 1998). Males did not display reproductive behavior (courtship or mounts) or increased activity (swimming, moving, and/or feeding versus remaining stationary on the bottom of the pond) in the summer and fall (Rostal, 1991; Rostal et al., 1998). The timing and location of mating in the wild is poorly known for Kemp's ridley. Fishermen supplied anecdotal information that mating presumably occurs from March through May, before and during the beginning of the nesting season, in the vicinity of the Rancho Nuevo nesting beach (Pritchard, 1969; Márquez, 1990; USFWS and NMFS, 1992). More recently they have reported observing mounted pairs in that area between the months of October and March and capturing both adult males and females during the fall and winter. Additionally, a mounted pair was documented in waters within the Mansfield Channel, Texas, on 3 June 1991 (Shaver, 1992). However, in none of these field observations were copulations actually confirmed and hence additional data are needed to elucidate the Kemp's ridley mating season under natural conditions.

The presence of adult males off the Tamaulipas coast during the few months prior to the nesting season and during the beginning of the nesting season, when sea turtle mating is thought to occur, was not unexpected. However, the preponderance of year-round residency by adult males was in contrast to results from most similar satellite-tracking investigations of males of other sea turtle species. Most adult

male olive ridley, green, and loggerhead turtles monitored by satellite telemetry traveled large distances from breeding grounds or other capture sites (Beavers and Cassano, 1996; Plotkin et al., 1996; Sakamoto et al., 1997; Balazs and Ellis, 2000; Garduño et al., 2000; Hays et al., 2001b; Meylan, *pers. comm.*). Adult male olive ridley and green turtles left the breeding grounds at the peak of the nesting season, possibly because most of the females had already mated by then (Plotkin et al., 1996; Balazs and Ellis, 2000). However, as with the anecdotal reports from fishermen for Kemp's ridley, some adult males and mounted pairs of olive ridley and green turtles have been visually observed offshore from nesting beaches after the mid-season peak in nesting (Plotkin, *pers. comm.*; Alvarado and Figueroa, 1989). Copulation was not confirmed in most of these instances and these observations may represent opportunistic mounting by stragglers remaining in the area after the departure of most other males or by various males that arrive and depart at irregular times. However, these observations could indicate mating after the mid-season nesting peak or year-round (Alvarado and Figueroa, 1989).

Male sea turtles would be expected to maximize their reproductive fitness by mating with as many females as possible. If mating takes place off the Tamaulipas coast, those males that remain there year-round would have the potential to mate with more females than those that migrate to distant foraging grounds, especially if the times that adult females arrive at the breeding grounds vary (Márquez, 1990) and if some mating occurs in the fall and winter. This strategy of year-round residency would save the energetic costs of migration, but could only occur if adequate foraging opportunities were available. Crabs, the preferred food item of adult Kemp's ridleys (Shaver, 1991), are abundant off the Tamaulipas coast and a large proportion of the male population should be able to locate food there without exceeding the local carrying capacity. The gastrointestinal tracts of two dead adult male Kemp's ridley turtles captured incidentally in shrimp trawls operating off Tampico were full of crabs, clams, shrimp, vegetation, and fish (Márquez, 1970). One of these males was captured on 7 February 1968 and measured 66 cm CCL; the date of capture and length of the other male were not reported. The gastrointestinal tract of an adult male (68 cm CCL, soft plastron, long tail), found dead at Rancho Nuevo during the breeding season (12 April 1988), was full of crabs (Shaver, unpubl. data). Although it cannot be proven with certainty, it is reasonable to assume that these turtles were foraging in waters off the Tamaulipas coast immediately prior to their death, since prey items were present in the upper portion of their gastrointestinal tract. In contrast, olive ridley turtles tracked by Plotkin et al. (1996) and green turtles tracked by Hays et al. (2001b), left breeding areas where there was little suitable food and migrated to foraging areas. They hypothesized that these adult males shortened their length of residence on the mating grounds due to a lack of local food availability.

One male tracked during this study traveled northward and left waters off the Tamaulipas coast and all of the others

tracked remained locally resident for up to 233 days. In contrast, most of the post-nesting females tracked were migratory (Byles, 1989; Mysing and Vanselous, 1989; Shaver, 2001). Differences in movement patterns for these turtles may be indicative of flexible strategies, where some individuals migrate and some remain resident. Such flexibility would be important with the mobile prey exploited by Kemp's ridley turtles, which can vary in abundance temporally and spatially. Females may migrate more frequently in search of optimum foraging sites, thought to be located off the mouth of the Mississippi River, USA, and Campeche Banks, Mexico, since the energetic costs of producing eggs are greater than for producing sperm.

However, we may have underestimated migratory behavior among adult male Kemp's ridleys. Some tracking periods may not have been long enough to see a post-breeding season migration. Seven of the PTTs ceased transmitting location data between February and April. Only two transmitted location data during May, June, and July, when migratory males would be expected to leave waters off the nesting beaches. Additionally, it is possible that we underrepresented sampling a component of the male population that migrates to a distant non-breeding season foraging area due to sampling bias, by deploying most of the PTTs during the non-breeding season on turtles that were already resident off the nesting beaches. The two PTTs that yielded location data during May, June, and July were the only two deployed during the spring and the only two tracked north of 24.0°N latitude. One of these two was the only turtle that left waters off the Tamaulipas coast during the tracking period and it might represent some significant percent of the population. Kemp's ridley male migration patterns could be different from other species, but only true mating-season capture and study may confirm this hypothesis.

An alternative hypothesis about why one male left waters off the Tamaulipas coast and the other 10 remained resident is that some of the turtles may have been immature or not reproductively active during their tracking period. The migratory individual was the smallest of the turtles studied. Although all the turtles were within the size range documented for nesting females (Márquez, 1994; Schmid and Witzell, 1997), size is a poor predictor of maturity since female sea turtles mature at various sizes (Miller, 1997; Musick and Limpus, 1997) and little is known about the size at maturity for male Kemp's ridleys. The 11 turtles tracked all possessed long tails and soft plastra, characteristics thought to indicate maturity in males (Wibbels et al., 1991; Meylan et al., 1994). However, immature male sea turtles can possess a long tail and show initial signs of plastron dekeratinization, indicating a prolonged period of puberty (Hickerson, 2000). Additionally, males may not be reproductively active on an annual basis (Wibbels et al., 1991). It would have been useful to examine the epididymis of each male for further validation of maturity and reproductive activity (Meylan et al., 1994; Plotkin et al., 1996), but this would have required laparoscopic examination beyond the scope of this study.

Location Class, Depth, and Seasonality.—After screening location data using the rejection criteria, 297 locations remained, of which only 42 were of LC 3, 2, and 1. The scarcity of high quality locations during this study likely relates to the study site, study animal, and one of the PTT duty cycles used. First, since this study was conducted at relatively low latitudes, there were fewer satellite passes per day and hence fewer opportunities for location data to be collected than had it been conducted at higher latitudes. Additionally, these turtles were adults inhabiting relatively warm-water coastal feeding areas and hence they likely spent more time below the surface than would turtles that were smaller or migrating within colder ocean waters. Another factor that diminished the number of locations was the use of a duty cycle of 8 hrs on/52 hrs off for seven of the 11 turtles tracked. It was hoped that the 8 hrs on/52 hrs off duty cycle would extend the tracking period, but the four PTTs with the 6 hrs on/6 hrs off duty cycle had similar tracking periods and yielded more locations. In retrospect, to maximize the likelihood of receiving transmissions, all PTTs should have been programmed with a 6 hrs on/6 hrs off or 12 hrs on/12 hrs off duty cycle. PTTs with these duty cycles can be synchronized with a 24 hr clock and satellite overpasses, whereas those with the 8 hrs on/52 hrs off duty cycle cannot be in continuous synchronization with a 24 hr clock and thus would probably be "on" more when no satellite was in range. Additionally, Plotkin (1998) recommended that transmitters should be "on" as often as possible for turtles that occupy coastal waters, turtles with short migrations, and turtles with a restricted home range.

The 297 locations that were mapped included data of LC 3, 2, 1, 0, A, and B. If the tracking maps had been prepared using only LC 3, 2, and 1 data, only 42 locations would have remained. Although the general conclusions regarding site fidelity to the Tamaulipas coast would have been the same, many of the details about movements would have been lacking, home ranges could not have been calculated due to insufficient sample size, and the tracking periods would have been shortened. Facing similar shortages of LC 3, 2, and 1 locations, some other researchers studying sea turtle movements have also included locations of LC 0, A, and B after extensive data screening (Hughes et al., 1998; Morreale, 1999; Hays et al., 1999, 2001b).

Hays et al. (2001a) found that the accuracy of LC A was comparable to that of LC1, and LCB had poorer accuracy than LC A, but the worst level of accuracy was found in LC 0. It is important to note that some of the locations mapped, especially of LC 0 and B, may have been inaccurate. Most of the locations identified for the 11 adult males monitored during this study were in near-shore waters 0–37 m depth and most of the locations of LC 3, 2, and 1 were within this region. Those locations furthest offshore into the Gulf of Mexico (particularly between the 183 m and 1829 m depth contours) were questionable, but could not be ruled out using the rejection criteria we selected. Other immature and adult Kemp's ridleys monitored using satellite telemetry generally inhabited waters less than 50 m deep (Byles, 1989;

Mysing and Vanselous, 1989; Keinath, 1993; Byles and Plotkin, 1994; Renaud, 1995; Keinath et al., 1996; Renaud et al., 1996), but sometimes ventured into waters with depths comparable to those found during our study (Keinath, 1993; Renaud, 1995; Keinath et al., 1996; Renaud et al., 1996).

Movements and habitat usage by most of the adult males tracked during this study did not appear related to season or temperature, although many of the tracking periods only spanned two seasons. In contrast, most adult female Kemp's ridleys tracked moved in relation to the nesting season (Byles, 1989; Renaud et al., 1996; Shaver, 2001). Most juvenile Kemp's ridleys tracked in USA waters moved southward or further offshore into warmer waters during the fall and winter (Byles, 1988; Standora et al., 1992; Keinath, 1993; Renaud, 1995; Keinath et al., 1996; Gitschlag, 1996), but waters that these juveniles moved from were generally cooler than Gulf of Mexico waters off Tamaulipas, Mexico.

Conservation Implications. — Evidence of a resident population of adult male Kemp's ridleys underscores the need for protection of the marine habitat adjacent to the Rancho Nuevo nesting beach year-round. Currently, under Mexican law, the Natural Reserve of Rancho Nuevo incorporates 15 km of coastline and a 4 km offshore zone that is closed to commercial fisheries during the sea turtle breeding season (Márquez et al., 1982, 1999a,b). When this zone was established in 1977, it encompassed the area where most Kemp's ridley nests were being recorded. These data support an expansion of the offshore zone to the north and south, especially to encompass the region where the core areas were located. Additional satellite transmitters should be deployed on adult males, especially ones captured during the nesting season, to gather more information on seasonality, residency, movements, and habitat use. It would be useful to monitor adult males captured far away from the nesting beach and adult males captured in March or April, during actual mating activity, near the nesting beaches in Tamaulipas and Veracruz, Mexico, and Texas, USA. At least 10 individuals should be tracked from each location and each should be examined via laparoscopy to verify that they are reproductively active. This information, coupled with additional data needed on the reproductive condition, mating, and foraging ecology of adult male Kemp's ridley turtles, would be very useful for enhancing and developing effective recovery strategies, including protected marine areas, for this critically endangered species.

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LITERATURE CITED

- ALVARADO, J. AND FIGUEROA, A. 1989. Breeding dynamics of the black turtle (*Chelonia agassizi*) in Michoacan, Mexico. In: Eckert, S.A., Eckert, K.L., and Richardson, T.H. (Compilers). Proceedings of the Ninth Annual Workshop on Sea Turtle Conservation and Biology. NOAA Technical Memorandum NMFS-SEFC-232, pp. 5-7.
- ARGOS. 1996. User's manual. Toulouse, France: Service Argos, 176 pp.
- BALAZS, G.H. 1994. Homeward bound: satellite tracking of Hawaiian green turtles from nesting beaches to foraging pastures. In: Schroeder, B.A. and Witherington, B.E. (Compilers). Proceedings of the Thirteenth Annual Symposium on Sea Turtle Biology and Conservation. NOAA Technical Memorandum NMFS-SEFSC-341, pp. 205-208.
- BALAZS, G.H. AND ELLIS, D.M. 2000. Satellite telemetry of migrant male and female green turtles breeding in the Hawaiian Islands. In: Abreu-Grobois, F.A., Briseno-Duenas, R., Márquez-Millan, R., and Sarti-Martinez, L. (Compilers). Proceedings of the Eighteenth International Sea Turtle Symposium. NOAA Technical Memorandum NMFS-SEFSC-436, pp. 281-283.
- BALAZS, G., CRAIG, P., WINTON, B.R., AND MIYA, R.K. 1994. Satellite telemetry of green turtles nesting at French Frigate Shoals, Hawaii, and Rose Atoll, American Samoa. In: Bjorndal, K.A., Bolten, A.B., Johnson, D.A., and Eliazar, P.J. (Compilers). Proceedings of the Fourteenth Annual Symposium on Sea Turtle Biology and Conservation. NOAA Technical Memorandum NMFS-SEFSC-351, pp. 184-187.
- BALAZS, G., MIYA, R.K., AND BEAVER, S.C. 1996. Procedures to attach a satellite transmitter to the carapace of an adult green turtle, *Chelonia mydas*. In: Keinath, J.A., Barnard, D.E., Musick, J.A., and Bell, B.A. (Compilers). Proceedings of the Fifteenth Annual Symposium on Sea Turtle Biology and Conservation. NOAA Technical Memorandum NMFS-SEFSC-387, pp. 21-25.
- BEAVERS, S.C. AND CASSANO, E.R. 1996. Movements and dive behavior of a male sea turtle (*Lepidochelys olivacea*) in the eastern tropical Pacific. *Journal of Herpetology* 30(1):97-104.
- BYLES, R.A. 1988. Behavior and ecology of sea turtles from Chesapeake Bay, Virginia. Ph.D. Thesis, College of William and Mary, Williamsburg, Virginia.
- BYLES, R.A. 1989. Satellite telemetry of Kemp's ridley sea turtle, *Lepidochelys kempi*, in the Gulf of Mexico. In: Eckert, S.A., Eckert, K.L., and Richardson, T.H. (Compilers). Proceedings of the Ninth Annual Workshop on Sea Turtle Conservation and Biology. NOAA Technical Memorandum NMFS-SEFC-232, pp. 25-26.
- BYLES, R.A. AND KEINATH, J.A. 1990. Satellite monitoring sea turtles. In: Richardson, T.H., Richardson, J.I., and Donnelly, M. (Compilers). Proceedings of the Tenth Annual Workshop on Sea Turtle Biology and Conservation. NOAA Technical Memorandum NMFS-SEFC-278, pp. 73-75.
- BYLES, R.A. AND PLOTKIN, P.T. 1994. Comparison of the migratory behavior of the congeneric sea turtles *Lepidochelys olivacea* and *L. kempi*. In: Schroeder, B.A. and Witherington, B.E. (Compilers). Proceedings of the Thirteenth Annual Symposium on Sea

- Turtle Biology and Conservation. NOAA Technical Memorandum NMFS-SEFSC-341, p. 39.
- BYLES, R.A. AND SWIMMER, Y.B. 1994. Post-nesting migration of *Eretmochelys imbricata* in the Yucatan Peninsula. In: Bjorndal, K.A., Bolten, A.B., Johnson, D.A., and Eliazar, P.J. (Compilers). Proceedings of the Fourteenth Annual Symposium on Sea Turtle Biology and Conservation. NOAA Technical Memorandum NMFS-SEFSC-351, p. 202.
- CHALOUPKA, M. AND ZUG, G.R. 1997. A polyphasic growth function for endangered Kemp's ridley sea turtle, *Lepidochelys kempi*. Fishery Bulletin 95:849-856.
- CHAVEZ, H. 1969. Tagging and recapture of the lora turtle (*Lepidochelys kempi*). International Turtle and Tortoise Society Journal 3(4):14-19, 32-36. Reprinted from Instituto Nacional de Investigaciones Biologicas Pesqueras, Mexico, No. 19.
- ECKERT, S.A. 1998. Perspectives on the use of satellite telemetry and other electronic technologies for the study of marine turtles, with reference to the first year-tag tracks of leatherback sea turtles. In: Epperly, S. and Braun, J. (Compilers). Proceedings of the Seventeenth Annual Sea Turtle Symposium. NOAA Technical Memorandum NMFS-SEFSC-415, pp. 44-46.
- ECKERT, S.A. 1999. Data acquisition systems for monitoring sea turtle behavior and physiology. In: Eckert, K., Bjorndal, K.A., Abreu-Grobois, F.A., and Donnelly, M. (Eds.). Research and management techniques for the conservation of sea turtles. Publication No. 4. Washington, DC: IUCN/SSC Marine Turtle Specialist Group, pp. 88-93.
- FITZSIMMONS, N.N., LIMPUS, C.J., NORMAN, J.A., GOLDIZEN, A.R., MILLER, J.D., AND MORITZ, C. 1997. Philopatry of marine turtles inferred from mitochondrial DNA markers. Proceedings of the National Academy of Sciences, USA 94:8912-8917.
- GARDUÑO, M., MALDONADO, A., MÁRQUEZ-M., R., SCHROEDER, B., AND BALAZS, G. 2000. Satellite tracking of an adult male and female green turtle from Yucatan in the Gulf of Mexico. In: Kalb, H. and Wibbels, T. (Compilers). Proceedings of the Nineteenth Annual Symposium on Sea Turtle Conservation and Biology. NOAA Technical Memorandum NMFS-SEFSC-443, pp. 158-159.
- GITSCHLAG, G.R. 1996. Migration and diving behavior of Kemp's ridley (Garman) sea turtles along the U.S. southeastern Atlantic coast. Journal of Experimental Marine Biology and Ecology 205:115-135.
- HAYS, G.C., LUSCHI, P., PAPI, F., DEL SEPPIA, C., AND MARSH, R. 1999. Changes in behaviour during the inter-nesting period and post-nesting migration for Ascension Island green turtles. Marine Ecology Progress Series 189:263-273.
- HAYS, G.C., ÅKESSON, S., GODLEY, B.J., LUSCHI, P., AND SANTIDRIAN, P. 2001a. The implications of location accuracy for the interpretation of satellite tracking data. Animal Behaviour 61:1035-1040.
- HAYS, G.C., BRODERICK, A.C., GLEN, F., GODLEY, B.J., AND NICHOLS, W.J. 2001b. The movements and submergence behavior of male green turtles at Ascension Island. Marine Biology 139:395-399.
- HICKERSON, E.L. 2000. Assessing and tracking resident, immature loggerheads (*Caretta caretta*) in and around the Flower Garden Banks, northwest Gulf of Mexico. M.S. Thesis, Texas A&M University, College Station.
- HILDEBRAND, H.H. 1963. Hallazgo del área anidación de la tortuga marina "lora", *Lepidochelys kempi* (Garman), en la costa occidental del Golfo de México (Rept., Chel.). Ciencia (Mexico) 22:105-112.
- HOOGE, P.N., EICHENLAUB, W.M., AND SOLOMON, E.K. 2001. Using GIS to analyze animal movements in the marine environment. <http://www.absc.usgs.gov/giba/gistools/>, 20 pp.
- HUGHES, G.R., LUSCHI, P., MENCACCI, R., AND PAPI, F. 1998. The 7000-km oceanic journey of a leatherback turtle tracked by satellite. J. of Exp. Mar. Biol. and Ecol. 229:209-217.
- KEINATH, J.A. 1993. Movements and behavior of wild and head-started sea turtles. Ph.D. Thesis, College of William and Mary, Williamsburg, Virginia.
- KEINATH, J.A., MUSICK, J.A., AND BARNARD, D.E. 1996. Abundance and distribution of sea turtles off North Carolina. U.S. Dept. of the Interior, Minerals Management Service, Gulf of Mexico OCS Region, MMS 95-0024.
- LUSCHI, P., HAYS, G.C., DEL SEPPIA, C., MARSH, R., AND PAPI, F. 1998. The navigational feats of green sea turtles migrating from Ascension Island investigated by satellite telemetry. Proc. R. Soc. Lond. B 265:2279-2284.
- MÁRQUEZ M., R. 1970. Las tortugas marinas de Mexico. Thesis, I.P.N., Escuela Nacional de Ciencias Biologicas.
- MÁRQUEZ M., R. 1990. FAO species catalogue. Vol. 11: Sea turtles of the world. An annotated and illustrated catalogue of sea turtle species known to date. FAO Fisheries Synopsis. No. 125, Vol. 11. Rome: FAO, 81 pp.
- MÁRQUEZ M., R. 1994. Synopsis of biological data on the Kemp's ridley turtle, *Lepidochelys kempi* (Garman, 1880). NOAA Technical Memorandum NMFS-SEFSC-343, 91 pp.
- MÁRQUEZ M., R., VILLANUEVA O., A., AND SÁNCHEZ P., M. 1982. The population of the Kemp's ridley sea turtle in the Gulf of Mexico – *Lepidochelys kempi*. In: Bjorndal, K.A. (Ed.). Biology and Conservation of Sea Turtles. Washington, DC: Smithsonian Institution Press, pp. 159-164.
- MÁRQUEZ M., R., BURCHFIELD, P., SÁNCHEZ-P., M., DÍAZ-F., J., PEÑA-V., J., CARRASCO-A., M.A., AND LEO-P., A.S. 1999a. Shared resources: Marine turtle programs' Rancho Nuevo Kemp's Ridley Sea Turtle Project. In: Proceedings: Seventeenth Annual Gulf of Mexico Information Transfer Meeting. Minerals Management Service, Gulf of Mexico OCS Study MMS 99-0042, pp. 327-338.
- MÁRQUEZ M., R., DÍAZ, J., SÁNCHEZ, M., BURCHFIELD, P., LEO, A., CARRASCO, M., PEÑA, J., JIMÉNEZ, C., AND BRAVO, R. 1999b. Results of Kemp's ridley nesting beach conservation efforts in Mexico. Marine Turtle Newsletter 85:2-4.
- MÁRQUEZ M., R., BURCHFIELD, P., CARRASCO, M.A., JIMENEZ, C., DÍAZ, J., GARDUÑO, M., LEO, A., PEÑA, J., BRAVO, R., AND GONZALEZ, E. 2001. Update on Kemp's ridley turtle nesting in Mexico. Marine Turtle Newsletter 92:2-4.
- MEYLAN, P.A., DAVIS, K., AND MEYLAN, A.B. 1994. Predicting sexual maturity of male green turtles from morphological data. In: Schroeder, B.A. and Witherington, B.E. (Compilers). Proceedings of the Thirteenth Annual Symposium on Sea Turtle Biology and Conservation. NOAA Technical Memorandum NMFS-SEFSC-341, pp. 108.
- MILLER, J.D. 1997. Reproduction in sea turtles. In: Lutz, P.L. and Musick, J.A. (Eds.). The Biology of Sea Turtles. Boca Raton, FL: CRC Press, pp. 51-81.
- MORREALE, S.J. 1999. Oceanic migrations of sea turtles (*Dermochelys coriacea*, *Caretta caretta*). Ph.D. Thesis, Cornell Univ., Ithaca, New York.
- MUSICK, J.A. AND LIMPUS, C.J. 1997. Habitat utilization and migration in juvenile sea turtles. In: Lutz, P.L. and Musick, J.A. (Eds.). The Biology of Sea Turtles. Boca Raton, FL: CRC Press, pp. 137-163.
- MYSING, J.O. AND VANSELOUS, T.M. 1989. Status of satellite tracking of Kemp's ridley sea turtles. In: Caillouet, C.W., Jr. and Landry, A.M., Jr. (Eds.). Proceedings of the First International Symposium on Kemp's Ridley Sea Turtle Biology, Conservation and Management. Texas A&M University Sea Grant College Publication TAMU-SG-89-105, pp. 112-115.
- OGREN, L.H. 1989. Distribution of juvenile and subadult Kemp's ridley sea turtles: preliminary results from the 1984-1987 surveys. In: Caillouet, C.W., Jr., and Landry, A.M., Jr. (Eds.). Proceedings of the

- First International Symposium on Kemp's Ridley Sea Turtle Biology, Conservation and Management. Texas A&M University Sea Grant College Program Publication, TAMU-SG-89-105, pp. 116-123.
- PLOTKIN, P.T. 1994. The migratory and reproductive behavior of the olive ridley, *Lepidochelys olivacea* (Eschscholtz, 1829), in the eastern Pacific Ocean. Ph.D. Thesis, Texas A&M Univ., College Station.
- PLOTKIN, P.T. 1998. Interaction between behavior of marine organisms and the performance of satellite transmitters: A marine turtle case study. *Marine Technical Society Journal* 32:5-10.
- PLOTKIN, P.T., BYLES, R.A., ROSTAL, D.C., AND OWENS, D.W. 1995. Independent versus socially facilitated oceanic migrations of the olive ridley, *Lepidochelys olivacea*. *Marine Biology* 122:137-143.
- PLOTKIN, P.T., OWENS, D.W., BYLES, R.A., AND PATTERSON, R. 1996. Departure of male olive ridley turtles (*Lepidochelys olivacea*) from a nearshore breeding ground. *Herpetologica* 52:1-7.
- PRITCHARD, P.C.H. 1969. Studies of the systematics and reproductive cycles of the genus *Lepidochelys*. Ph.D. Thesis, Univ. Florida, Gainesville.
- PRITCHARD, P.C.H. AND MÁRQUEZ M., R. 1973. Kemp's ridley or Atlantic ridley, *Lepidochelys kempii*. IUCN Monograph No. 2., (Marine Turtle Series), 30 pp.
- RENAUD, M.L. 1995. Movements and submergence patterns of Kemp's ridley turtles (*Lepidochelys kempii*). *Journal of Herpetology* 29:370-374.
- RENAUD, M.L., CARPENTER, J.A., WILLIAMS, J.A., AND LANDRY, A.M., JR. 1996. Kemp's ridley sea turtle (*Lepidochelys kempii*) tracked by satellite telemetry from Louisiana to nesting beach at Rancho Nuevo, Tamaulipas, Mexico. *Chelonian Conservation and Biology* 2:108-109.
- ROSTAL, D.C. 1991. The reproductive behavior and physiology of the Kemp's ridley sea turtle, *Lepidochelys kempi* (Garman, 1880). Ph.D. Thesis, Texas A&M Univ., College Station.
- ROSTAL, D.C., OWENS, D.W., GRUMBLES, J.S., MACKENZIE, D.S., AND AMOSS, M.S., JR. 1998. Seasonal reproductive cycle of the Kemp's ridley sea turtle (*Lepidochelys kempi*). *General and Comparative Endocrinology* 109:232-243.
- SAKAMOTO, W., BANDO, T., ARAI, N., AND BABA, N. 1997. Migration paths of adult female and male loggerhead turtles *Caretta caretta* determined through satellite telemetry. *Fisheries Science* 63:547-552.
- SCHMID, J.R. AND WITZELL, W.N. 1997. Age and growth of wild Kemp's ridley turtles (*Lepidochelys kempi*): cumulative results of tagging studies in Florida. *Chelonian Conservation and Biology* 2:532-537.
- SCHROEDER, B.A., EHRHART, L.M., AND BALAZS, G.H. 1996. Post-nesting movements of Florida green turtles: preliminary results from satellite telemetry. In: Keinath, J.A., Barnard, D.E., Musick, J.A., and Bell, B.A. (Compilers). *Proceedings of the Fifteenth Annual Symposium on Sea Turtle Biology and Conservation*. NOAA Technical Memorandum NMFS-SEFSC-387, p. 289.
- SHAVER, D.J. 1991. Feeding ecology of Kemp's ridley in south Texas waters. *Journal of Herpetology* 25:327-334.
- SHAVER, D.J. 1992. Life history notes: *Lepidochelys kempii* (Kemp's ridley sea turtle). *Reproduction*. *Herpetological Review* 23:59.
- SHAVER, D.J. 1998. Sea turtle strandings along the Texas coast, 1980-94. In: Zimmerman, R. (Ed.). *Characteristics and causes of Texas marine strandings*. NOAA Technical Report NMFS 143, pp. 57-72.
- SHAVER, D.J. 1999a. Kemp's ridley sea turtle project at Padre Island National Seashore, Texas. In: McKay, M. and Nides, J. (Eds.). *Proceedings from the 17th Annual Gulf of Mexico Information Transfer Meeting*. U.S. Dept. of the Interior, Minerals Management Service, Gulf of Mexico OCS Region, MMS 99-0042, pp. 342-347.
- SHAVER, D.J. 1999b. Sea turtle strandings in the Gulf of Mexico. In: Owens, D.W. and Evans, M. (Eds.). *Sharing Our Gulf: A Challenge For Us All*. Conference Proceedings. Texas Sea Grant Program, TAMU-SG-99-104, pp. 31-33.
- SHAVER, D.J. 2000. Distribution, residency, and seasonal movements of the green sea turtle, *Chelonia mydas* (Linnaeus, 1758), in Texas. Ph.D. Thesis, Texas A&M University, College Station.
- SHAVER, D.J. 2001. U.S. Geological Survey/National Park Service Kemp's ridley sea turtle research and monitoring programs in Texas. In: McKay, M., Nides, J., Lang, W., and Vigil, D. (Eds.). *Proceedings of the Gulf of Mexico Marine Protected Species Workshop*. U.S. Dept. of the Interior, Minerals Management Service, Gulf of Mexico OCS Region, MMS-2001-039, pp. 121-124.
- SHAVER, D.J. 2004. Analysis of the Kemp's Ridley imprinting and headstart project at Padre Island National Seashore, Texas, 1978-88, with subsequent nesting and stranding records on the Texas coast. *Chelonian Conservation and Biology* 4(4):844-857.
- SHAVER, D.J. AND CAILLOUET, JR., C.W. 1998. More Kemp's ridley turtles return to south Texas to nest. *Marine Turtle Newsletter* 82:1-5.
- STANDORA, E.A., MORREALE, S.J., AND BURKE, V.J. 1992. Application of recent advances in satellite microtechnology: Integration with sonic and radio tracking of juvenile Kemp's ridleys from Long Island, New York. In: Salmon, M., and Wyneken, J. (Compilers). *Proceedings of the Eleventh Annual Workshop on Sea Turtle Biology and Conservation*. NOAA Tech. Memo. NMFS-SEFSC-302, pp. 111-113.
- WIBBELS, T., OWENS, D.W., AND ROSTAL, D. 1991. Soft plastra of adult male sea turtles: an apparent secondary sexual characteristic. *Herpetological Review* 22:47-49.
- U.S. FISH AND WILDLIFE SERVICE AND NATIONAL MARINE FISHERIES SERVICE. 1992. *Recovery plan for the Kemp's ridley sea turtle *Lepidochelys kempii**. St. Petersburg, FL: National Marine Fisheries Service, 40 pp.
- ZUG, G.R., KALB, H.J., AND LUZAR, S.J. 1997. Age and growth in wild Kemp's ridley sea turtles *Lepidochelys kempii* from skeletochronological data. *Biological Conservation* 80:261-268.

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