Marine turtle populations on the west-central coast of Florida: results of tagging studies at the Cedar Keys, Florida, 1986–1995

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Abstract.–Large-mesh tangle nets were used to collect marine turtles in Waccasassa Bay, near the Cedar Keys, Florida, from June 1986 to October 1995. Tagging records were analyzed to determine the species composition, population structure, and seasonal occurrence of Kemp's ridley, *Lepidochelys kempii*, loggerhead, *Caretta caretta*, and green, *Chelonia mydas*, turtles. Additional information on local movements, morphometrics, growth, population estimation, and diet was provided for Kemp's ridley turtles. Subadult green turtles dominated the catch on the seagrass shoals of Waccasassa Reefs. Subadult Kemp's ridley turtles and, to a lesser degree, subadult and adult loggerhead turtles were primarily captured near the oyster bars of Corrigan Reef. Marine turtles were caught in these nearshore waters from April to November. Recaptures indicate that some Kemp's ridley turtles remain in the vicinity of Corrigan Reef during their seasonal occurrence and return to this foraging area annually. Seasonal and annual size distributions of Kemp's ridley turtles were investigated and regression equations were developed for carapace morphometrics. Carapace growth averaged 4–5 cm/yr for Kemp's ridley turtles, but growth analyses were confounded by the extrapolation of annual estimates from short-term recaptures. Population estimates for the Kemp's ridley mark-recapture data indicated a mean annual population size of 159 turtles at Corrigan Reef with presumably high rates of immigration and emigration by larger subadult turtles. Examination of fecal samples indicated that crabs were the primary food items of Kemp's ridley turtles captured near oyster bars.

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Historical information concerning marine turtles in the coastal waters of Florida is limited to landing statistics and observational data associated with the commercial turtle fishery (Ehrhart, 1983). During the late 1800s, large-mesh tangle nets were used to catch significant numbers of green turtles, *Chelonia mydas*, in the Indian River Lagoon and around the Cedar Keys (True, 1887; Brice, 1896). These turtles were exported to markets in the northeastern United States. Kemp's ridley, *Lepidochelys kempii*, and loggerhead turtles, *Caretta caretta*, were also captured and used as a food resource in local markets, but the landings of these species were not recorded in fisheries reports (Witzell, 1994a). The Florida fishery for marine turtles was greatly reduced by 1900 (Ingle and Smith, 1949). However, there are no quantitative data to demonstrate accurately that depletion had occurred as a result of overfishing (Caldwell and Carr, 1957). The lack of definitive data is further complicated by the fact that most of the fishery statistics reported for Florida after 1900 include green turtles imported from Costa Rica and Nicaragua by way of Key West, and no distinction was made between turtles caught in Florida and those imported from the Caribbean (Ingle and Smith, 1949; Caldwell and Carr, 1957; Witzell, 1994a, 1994b).

The first scientific investigations and conservation efforts for marine turtles were implemented fifty years after the reduction of the turtle fishery. Ingle and Smith (1949) and Carr (1952) outlined scientific data necessary for the protection and restoration of green turtles throughout their range. Carr and Caldwell (1956) conducted a one-year tagging study of green and Kemp's ridley turtles purchased from Cedar Key fish houses and provided the first details on size ranges, morphometrics, local movements, growth rates, and population estimates for these species. Florida enacted legislation in 1956 that prohibited the take of nesting female turtles and their eggs (Caldwell and Carr, 1957; Ehrhart, 1983).

Restrictions were imposed on the Florida turtle fishery in 1971, which consisted of closed seasons and size limits (Ingle, 1972). By 1978, all species of marine turtles were listed as threatened or endangered in the Endangered Species Act and protected under federal legislation.

Listing marine turtles in the Endangered Species Act outlawed their harvest and prompted surveys on nesting beaches and adjacent coastal waters in Florida (Carr et al., 1982). Entanglement nets, designed similarly to those formerly used in the turtle fishery, were employed to capture green and loggerhead turtles inhabiting the northern Indian River Lagoon System (Ehrhart and Yoder, 1978; Mendonça, 1981, 1983; Mendonça and Ehrhart, 1982; Ehrhart, 1983). These fishery-independent studies provided the first biological data on population size and structure, growth rates, and activity patterns for the previously exploited species of marine turtle in the lagoonal habitat. Trawls associated with the commercial shrimp fishery were used to collect turtles occurring in and around the Port Canaveral ship channel (Carr et al., 1980; Henwood, 1987; Henwood and Ogren, 1987). Information obtained from these fishery-dependent surveys includes size class distribution, seasonal occurrence, and migrations of loggerhead, Kemp's ridley, and green turtles.

In 1984, the National Marine Fisheries Service (NMFS) initiated long-term tagging studies of marine turtles occurring in the coastal waters of Florida, with emphasis placed on the critically endangered Kemp's ridley turtle (Ogren, 1989; Schmid and Ogren, 1990, 1992). Rudloe et al. (1991) reported on the size-class distribution, seasonal occurrence, and variations in carapace length by season and water depth for Kemp's ridley turtles incidentally captured in commercial fisheries of northwest Florida. Tagging records of turtles captured in the east-central Florida shrimp fishery provided additional data on species composition, size-class distribution, seasonal occurrence and migrations, morphometric relationships, and growth data for marine turtles along the Atlantic coast (Schmid, 1995). Fishery-independent capture techniques have also been used to collect marine turtles in the nearshore waters of west-central Florida and preliminary results of these efforts have been given by Schmid and Ogren (1990, 1992). The present paper analyzes tagging records collected near the Cedar Keys, Florida, from 1986 to 1995 in order to determine the species composition, population structure, and seasonal occurrence of Kemp's ridley, loggerhead, and green turtles. Additional information on local movements, morphometrics, growth, population estimation, and diet are provided for Kemp's ridley turtles.

Materials and methods

Study area

Marine turtles were collected east of the Cedar Keys in Waccasassa Bay, which is located on the west coast of Florida (Fig. 1). The northern and eastern boundaries of Waccasassa Bay are saltmarsh coastline inundated by numerous tidal creeks. The Waccasassa River flows into the northeast corner of the bay and is the main contributor of freshwater to the estuarine system (Wolfe, 1990). The western edge of the bay is semi-enclosed by the Cedar Keys, whereas the southern portion is open to tidal exchange with the Gulf of Mexico. Corrigan Reef, located in northwestern Waccasassa Bay, and Waccasassa Reefs, located in the eastern half of the bay, are the prominent geographic features of this shallow embayment.

Netting efforts were concentrated at three sites along Corrigan Reef (Fig. 1; site 1: 29°09'N, 82°58'W; site 2: 29°08'N, 82°58'W; and site 3: 29°07'N, 82°58'W), approximately 5 km east of the Cedar Keys. Corrigan Reef comprises a series of oyster (*Crassostera virginica*) beds in the northern region (site 1) and oyster shell bars in the southern region (sites 2 and 3). Limestone outcroppings occur among the mud and sand flats and in channels on the periphery of oyster bars. Netting was also conducted at the outer shoal of Waccasassa Reefs (29°06'N, 82°53'W), approximately 12 km east-southeast of the Cedar Keys. Waccasassa Reefs are composed of three seagrass shoals with a broad, deep-channel cutting midway through each shoal. The tides in both of these areas are mixed, with two highs and two lows of variable amplitude. Strong tidal currents flow through the channels, particularly during the new and full moon phases (spring tides).

Data collection

Seasonal netting was conducted at Corrigan Reef from 1986 to 1991 and at Waccasassa Reefs from 1986 to 1988 (see Table 1 for effort and months fished each year). A full year of sampling was performed at Corrigan Reef in 1992 and 1993. Water temperatures were recorded sporadically from 1986 to 1991 and monthly for 1992 and 1993. Netting surveys were performed for 1–3 days every other week during the neap tides. One or two nylon mesh tangle nets (61- or 51-cm stretch mesh, 20 meshes deep, and 65 m length) were set across a channel at a given site and fished over a 6- to 12-hour tidal cycle. Nets were checked hourly or immediately after an entangled turtle had been sighted. Research efforts shifted from netting surveys to telemetric monitoring during 1994

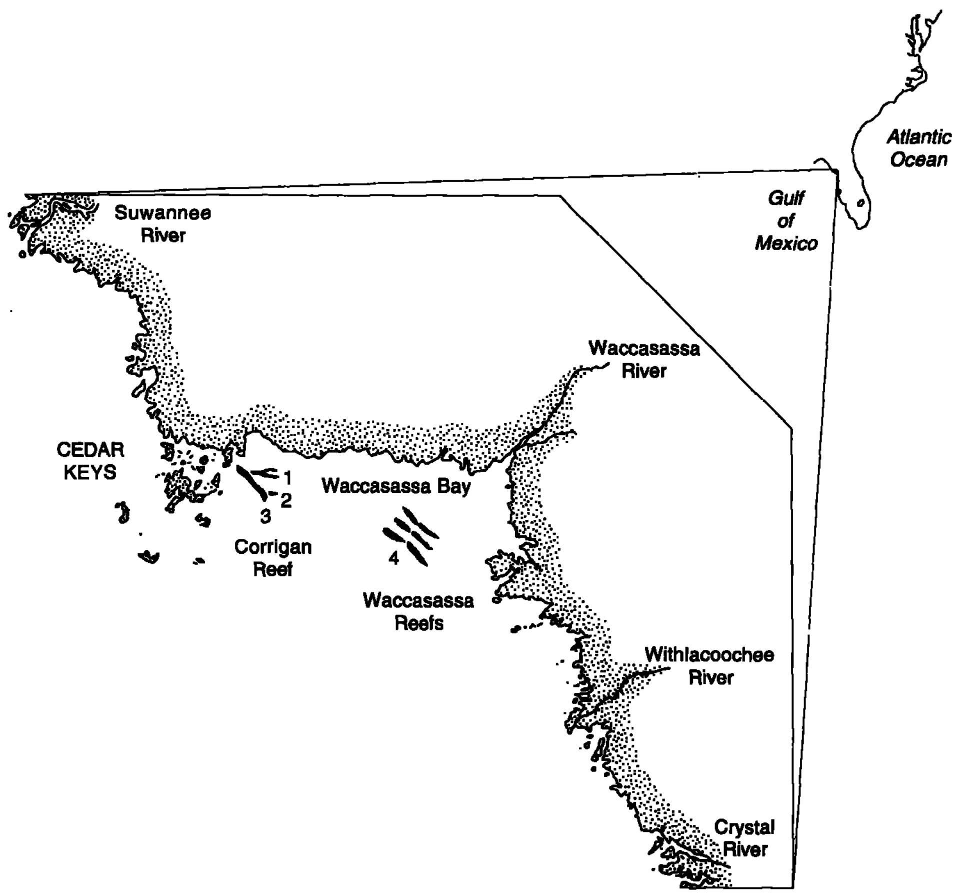

Figure 1

Map of the west-central coast of Florida showing the Cedar Keys study area. Numbers indicate the location of sampling sites described in the text.

Table 1

Annual effort (km-h) and CPUE (turtles/km-h) by species for Corrigan Reef and Waccasassa Reefs from 1986 to 1993. Lk=*Lepidochelys kempii*, Cc=*Caretta caretta*, and Cm=*Chelonia mydas*.

Year (months)	Corrigan Reef				Waccasassa Reefs			
	Effort	Lk/h	Cc/h	Cm/h	Effort	Lk/h	Cc/h	Cm/h
1986 (Jun–Nov)	153.9850	0.1104	0.0065	0.0000	9.3275	0.0000	0.0000	0.1072
1987 (May–Dec)	236.0963	0.0720	0.0000	0.0042	19.6300	0.0000	0.0509	0.2547
1988 (May–Sep)	142.3988	0.2388	0.0070	0.0000	1.2675	0.7890	0.0000	0.0000
1989 (Jun–Sep)	177.4500	0.1634	0.0394	0.0113	—	—	—	—
1990 (Jun–Sep)	233.4150	0.1499	0.0129	0.0000	—	—	—	—
1991 (Jun–Oct)	152.5225	0.1246	0.0000	0.0000	—	—	—	—
1992 (May–Dec)	461.5650	0.1148	0.0303	0.0022	—	—	—	—
1993 (Jan–Oct)	124.8000	0.1923	0.0160	0.0000	—	—	—	—

and 1995, and tag data collected on these turtles were included in the analyses.

The following morphometric measurements (Pritchard et al., 1983) were recorded for each turtle: total straight-line carapace length (TSCL, anterior most edge of carapace to posterior margin of postcentral); standard straight-line carapace length (SSCL, nuchal notch to posterior margin of postcentral); minimum straight-line carapace length (MSCL, nuchal notch to notch between postcentrals); minimum curved carapace length (MCCL, nuchal notch to notch between postcentrals); and straight-line carapace width (CW) at the widest point. Straight-line carapace lengths and width were measured to the nearest 0.1 inch with forester's calipers. Curved carapace length was measured to the nearest 0.1 cm with a flexible fiberglass measuring tape. Weight (WT) was measured to the nearest 0.25 lb with a spring scale. All measurements were performed by the author to avoid individual differences in measuring technique (Bjorndal and Bolten, 1988) and were converted to metric units for analysis. Notes on the condition of the turtle were recorded when the animal was injured or deformed (e.g. tag scars, carapace wounds, etc.).

Turtles were double tagged on the trailing edge of the fore flippers with no. 681 Inconel tags (June 1986 to May 1988; May 1994 to October 1995), with Jumbo Roto plastic tags (June 1988 to October 1991), or with both (May 1992 to September 1993). Beginning in 1988, two holes were drilled in specific marginal scutes of Kemp's ridley turtles in order to identify the year of capture (1988—left postcentral, 1989—right postcentral, 1990—left 12th marginal, 1991—right 12th marginal, 1992—left 11th marginal, 1993—right 11th marginal, 1994—left 10th marginal, and 1995—right 10th marginal). Passive integrated transponder (PIT) tags were applied to the left front flipper of Kemp's ridley turtles from June 1992 to October 1995. Turtles were immediately released after data collection approximately 100 m down-current from the netting site.

Data analysis

Marine turtle life history stages were defined according developmental habitats and carapace lengths (Schmid, 1995). The term "juvenile" was reserved for immature turtles in the epipelagic stage of development. A turtle was considered "subadult" after recruiting to its respective coastal-benthic habitat and "adult" when sexually mature. Loggerhead turtles greater than 80 cm (Carr, 1986), green turtles greater than 83 cm (Witherington and Ehrhart, 1989), and Kemp's ridley turtles greater than 60 cm (Pritchard and Márquez M., 1973) were considered adult based on sizes of nesting females.

Capture records were analyzed to evaluate species composition within the Cedar Keys study area, length-frequency distribution of each species, and patterns of seasonal occurrence. Additional analyses of morphometrics, growth rates, population estimates, and dietary composition were performed for Kemp's ridley turtles. Standard straight-line carapace length was used in the analyses of size distribution and growth. Means are followed by ± one standard deviation unless noted otherwise. Turtle catch per unit of effort (CPUE) was standardized according to Shaver (1994) with the formula

$$E = \left(\frac{Nets \times Length}{1000} \right) Hrs,$$

where E = the netting effort in hours fished by a 1-km tangle net;
$Nets$ = the number of tangle nets fished;
$Length$ = the length (m) of a net; and
Hrs = the number of hours fished.

Kemp's ridley turtle morphometric relationships were investigated by regressing carapace width on length and log-transformed weight on length. Conversion formulae for Kemp's ridley turtle carapace lengths were calculated by regressing paired straight-line and curved carapace lengths. Turtles with carapace wounds or deformities were not included in regression equations.

Yearly growth rates for Kemp's ridley turtles were calculated with the formula

$$G = \left(\frac{\Delta Length}{Days} \right) 365,$$

where G = the growth rate in cm/yr;
$\Delta Length$ = difference between the recapture length and the initial length; and
$Days$ = the number of days at large.

Growth rates were grouped and analyzed in terms of the recapture interval duration, recaptures between versus recaptures within netting seasons, and size classes of recaptured turtles. Growth rates were assigned to 10-cm size classes on the basis of mean of the initial and recapture carapace measurements (Bjorndal and Bolten, 1988). The von Bertalanffy growth interval equation was fitted to the recapture data with a nonlinear least-squares regression procedure (SAS Institute Inc., 1989). The von Bertalanffy growth interval equation (Fabens, 1965) for recapture data is:

$$CL_2 = a - (a - CL_1)e^{-kt},$$

where CL_2 = the carapace length at recapture;
a = the asymptotic length;
CL_1 = the length at first capture;

k	=	the intrinsic growth rate; and
t	=	the time in years between captures.

Kemp's ridley turtle mark-recapture data for 1986–93 were tallied in a method B table (Krebs, 1989) and analyzed with the computer program JOLLY (Hines, 1988; Pollock et al., 1990). Summary statistics for the Jolly-Seber computer analysis include the total number of turtles captured and released each year (n), the number of marked (m) and unmarked (u) turtles captured each year, the number of turtles released each year that are captured again later (r), and the number of turtles captured before a given year and captured again later (z). The data were applied to a Jolly-Seber model that assumes that the population parameters survival rate (Φ) and capture probability (p) are constant per unit time. Annual estimates of the number of marked turtles in the population (M), population size (N), and the number of individuals recruited to the population (B) were computed with the reduced parameter model.

Dietary analyses were conducted on Kemp's ridley fecal specimens fortuitously encountered during the tagging process. Fecal specimens were initially examined in the field and the contents were noted in tagging records. Additional examinations were performed from photographs and samples of feces. Components of the feces were identified to the lowest taxon possible and were analyzed to determine the percentage of specimens containing each component (Burke et al., 1994). Nomenclature of molluscs was identified by using the field guide of Abbott and Morris (1995).

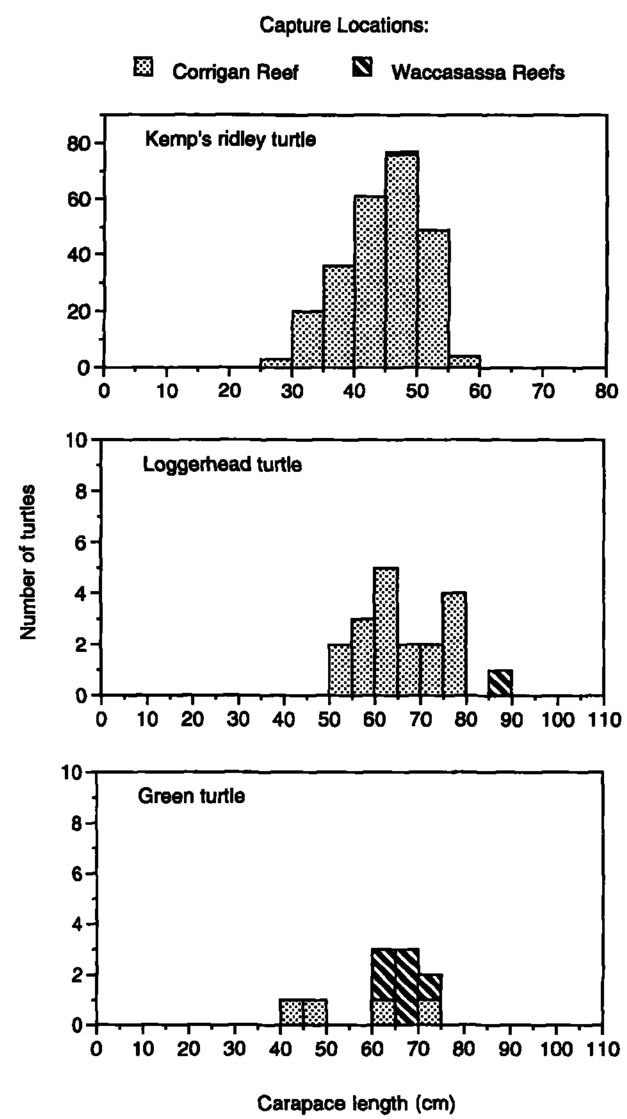

Figure 2
Length-frequency distributions for Kemp's ridley turtles, *Lepidochelys kempii*, loggerhead turtles, *Caretta caretta*, and green turtles, *Chelonia mydas*, collected in Waccasassa Bay, Florida, from 1986 to 1995. Note the different scale in y axis of upper graph.

Results

Marine turtle captures and effort

One (12.5%) Kemp's ridley, 1 (12.5%) loggerhead, and 6 (75%) green turtles were collected during 64.75 h of netting at Waccasassa Reefs. The Kemp's ridley turtle measured 47.6 cm SSCL, the loggerhead turtle measured 86.4 cm SSCL, and green turtles ranged from 63.0 to 73.9 cm SSCL (mean=68.0 ±3.9 cm; Fig. 2). Three of the green turtles captured at Waccasassa Reefs exhibited fibropapillomas (1–4 cm diameter), primarily in the axillary region of the flippers. Maximum CPUE for green turtles at Waccasassa Reefs was 0.255 turtles/km-h in 1987, and values of CPUE for loggerhead and Kemp's ridley turtles were 0.051 turtles/km-h in 1987 and 0.789 turtles/km-h in 1988, respectively (Table 1). Netting effort was conducted at this location from June through November and turtles were captured in July and August.

Two hundred and fifty-three (91.7%) Kemp's ridley, 19 (6.9%) loggerhead, and 4 (1.4%) green turtles were collected during 980.00 h of netting at Corrigan Reef. Kemp's ridley turtles ranged from 26.8 to 58.6 cm SSCL (mean=44.5 ±6.3 cm), loggerhead turtles ranged from 50.0 to 77.4 cm SSCL (mean=65.0 ±8.7 cm), and green turtles ranged from 42.9 to 70.9 cm SSCL (mean=56.8 ±12.9 cm; Fig. 2). Loggerhead turtles greater than 80 cm SSCL were caught at

Corrigan Reef but could not be landed for data collection. One such turtle was identified as a male because its tail extended considerably beyond the posterior marginal scutes. Fibropapillomas were not observed on green turtles captured at Corrigan Reef. Annual CPUE for Kemp's ridley turtles at Corrigan Reef ranged from 0.072 turtles/km-h in 1987 to 0.239 turtles/km-h in 1988 (Table 1). Maximum CPUE for loggerhead and green turtles at Corrigan Reef was 0.039 turtles/km-h and 0.011 turtles/km-h in 1989, respectively. Kemp's ridley and loggerhead turtles were captured in this area from April to November, whereas green turtles were captured from June to September.

Recaptures and local movements

Thirty-four Kemp's ridley turtles (23 with tags and 11 with tag scars), five loggerhead turtles (3 with tags and 2 with tag scars), and one green turtle (with a tag scar) were identified as recaptures. All recaptured turtles with tags, with the exception of two NMFS Galveston laboratory headstart Kemp's ridleys, were initially captured and tagged at Corrigan Reef. Thirty-five percent of the recaptured turtles exhibited tag scars, which is indicative of moderate tag loss and may account for the lack of recaptures or recoveries in other areas. Schmid and Ogren (1992) identified barnacle fouling as a potential problem with the otherwise corrosion-resistant Inconel flipper tag. The increased drag and weight produced by the barnacle clusters and the necrosis of flipper tissue by the encrusted tag (Fig. 3A) resulted in the eventual shedding of the tags and the formation of a conspicuous notch in the trailing edge of the flippers (Fig. 3B). Barnacle growth was observed on both Inconel and plastic tags in as little as 14 days and tag loss was observed within 10 months after application. Similar retention times were noted for both types of tags, but a quantitative analysis of retention rates was not performed because of small sample sizes. The use of marginal markings allowed for the identification of tag-scarred turtles originally tagged at the Cedar Keys and the tabulation of recapture data by year classes. PIT tags were successfully used to identify tag-scarred Kemp's ridley turtles in the later part of the study.

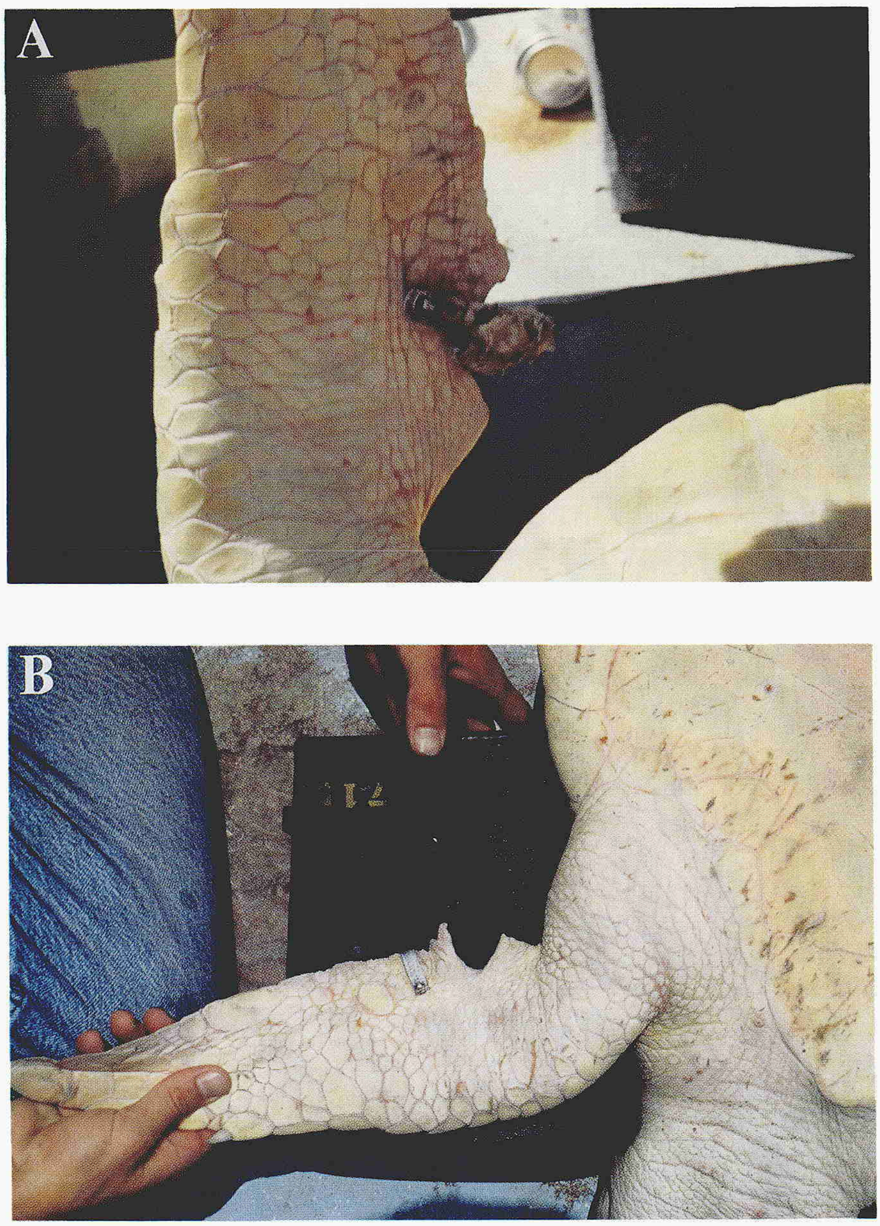

Figure 3

Photographs of recaptured Kemp's ridley turtles, *Lepidochelys kempii*, demonstrating (**A**) a barnacle-encrusted tag and (**B**) a flipper scar from tag loss.

Kemp's ridley recaptures ranged from 14 to 839 days and loggerhead recaptures ranged from 142 to 189 days. The two headstart Kemp's ridley turtles were recaptured approximately 3–4 years after their release in Texas waters as was determined from the location of the living tag in the carapace (Fontaine et al., 1993; Caillouet et al., 1995). Seven Kemp's ridley turtles with tag scars had marginal scute markings indicating the year of initial capture at Corrigan Reef. Four of these were at large for 1 year, one was at large for 2 years, and two were at large for 3 years. Four Kemp's ridley turtles had multiple recaptures in the vicinity of Corrigan Reef. One turtle was tagged at site 2 in September 1991 and recaptured at this site in October 1991 and May 1992 (0.7 year duration). Another turtle tagged at site 1 in July 1990 was recaptured at this site in June 1991 and June 1992 (1.9-year duration). A turtle tagged at site 2 in October 1991 was recaptured at this site in September 1992 and at site 3 in May 1994 (2.6-year duration). The fourth turtle had a 1991 marginal marking and was recaptured at site 2 in September 1993 and August 1995 (≈4-year duration).

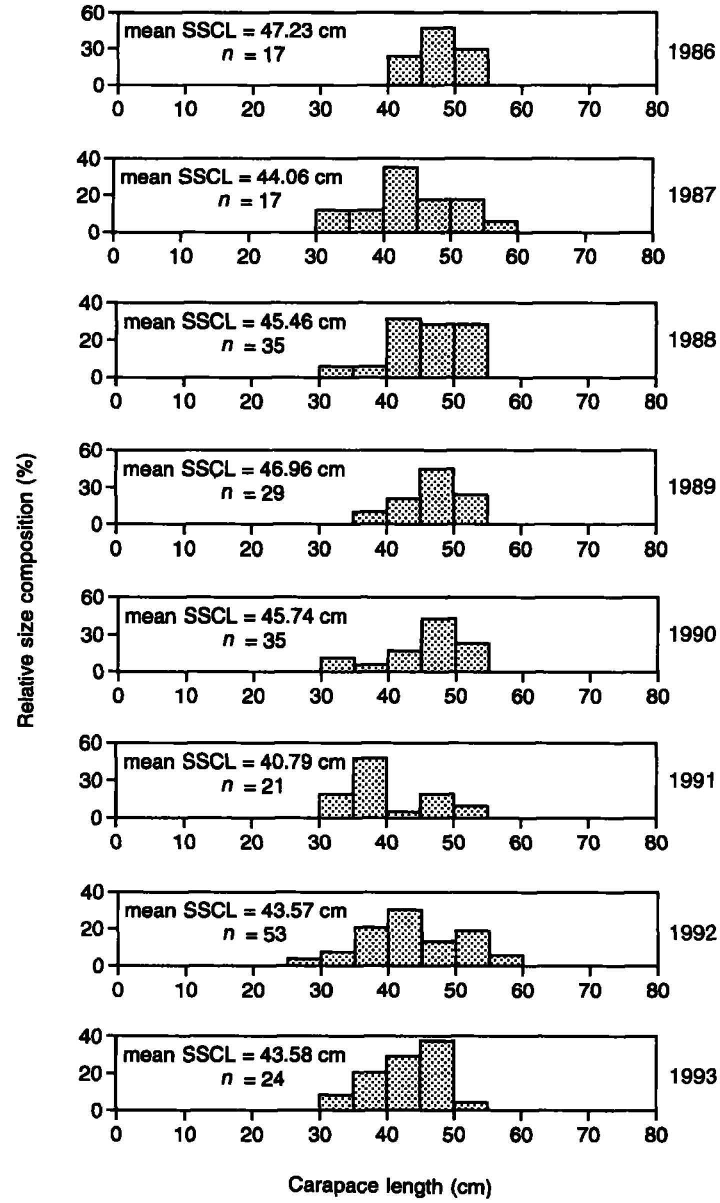

Figure 4

Annual relative size composition of Kemp's ridley turtles, *Lepidochelys kempii*, captured at Corrigan Reef from 1986 to 1993.

Seasonal and annual size distributions

Mean water temperatures at Corrigan Reef were calculated by season (Table 2): winter (Dec–Feb), spring (Mar–May), summer (Jun–Aug), and fall (Sep–Nov). Turtles were captured in water temperatures greater than 20°C. Carapace lengths for Kemp's ridley turtles captured from 1986 to 1995 were pooled by season (spring, summer, or fall) according to the month of capture (Table 2). A significant difference (F=3.76, P=0.025) was detected between the mean SSCL of at least two seasons. Multiple comparisons with the Bonferroni procedure demonstrated no significant difference in mean SSCL between spring and summer, or spring and fall. However, mean SSCL in summer was significantly larger than that of fall.

Analysis of the annual relative composition of Kemp's ridley turtle carapace lengths from 1986 to 1993 indicated that the 40–50 cm size class dominated the catch during all years except 1991 (Fig. 4). The majority of turtles captured during 1991 were in the 30–40 cm size class. The carapace length distributions for 1986 through 1990 were not significantly different when compared with the Kolmogrov-Smirnov two-sample test. The distribution of carapace lengths for 1991 was significantly different from all years except 1987, and the distribution for 1992 was significantly different from all years except 1987 and 1988. The carapace length distribution for 1993

Table 2

Seasonal water temperatures and Kemp's ridley turtle, *Lepidochelys kempii*, carapace lengths at Corrigan Reef from 1986 to 1995 (standard deviations given in parentheses).

Season	Mean water temperature	Mean carapace length	n	Size range
Spring	22.5°C (3.0)	44.1 cm (7.4)	24	26.8–58.6 cm
Summer	30.4°C (0.6)	45.5 cm (5.9)	142	28.2–54.4 cm
Fall	22.9°C (4.2)	43.1 cm (6.6)	85	27.3–56.6 cm
Winter	15.7°C (2.0)	—	0	—

Table 3

Formulae for converting between straight-line and curved carapace measurements of Kemp's ridley turtles, *Lepidochelys kempii*. TSCL = total straight-line carapace length, SSCL = standard straight-line carapace length, MSCL = minimum straight-line carapace length, and MCCL = minimum curved carapace length.

Converted length	Conversion formula	n	r^2
TSCL	1.0118 SSCL + 0.0650	227	0.9990
TSCL	1.0214 MSCL + 0.3800	227	0.9982
TSCL	0.9720 MCCL + 0.2203	107	0.9920
SSCL	0.9874 TSCL – 0.0199	227	0.9990
SSCL	1.0094 MSCL + 0.3155	227	0.9990
SSCL	0.9598 MCCL + 0.1941	107	0.9929
MSCL	0.9773 TSCL – 0.2896	227	0.9982
MSCL	0.9897 SSCL – 0.2658	227	0.9990
MSCL	0.9495 MCCL – 0.0864	107	0.9933
MCCL	1.0205 TSCL + 0.1368	107	0.9920
MCCL	1.0345 SSCL + 0.1162	107	0.9929
MCCL	1.0462 MSCL + 0.3913	107	0.9933

was not significantly different from the distributions of 1986 through 1990. The observed shift in size-class distribution for 1991 may have been caused by changes in fishing conditions that year. Beginning in July 1991, a smaller mesh (25.4-cm bar) net was deployed either singly or in combination with the larger mesh (30.5-cm bar) net that was used the previous years. The smaller mesh net may have resulted in the increased capture of 30–40 cm turtles in 1991, although the frequency of 40–50 cm turtles increased in the following years. Also, during August 1991, a massive influx of pelagic Sargassum occurred along the west coast of Florida and the majority of netting effort was conducted in the months following this unusual event. It is not known how this latter condition may have affected the relative frequency of carapace lengths, either by increasing the frequency of 30–40 cm turtles or decreasing the frequency of 40–50 cm turtles.

Carapace regression equations

There was a strong correlation between carapace width and carapace length (r=0.9883, n=227) for Kemp's ridley turtles. Regression of width on length resulted in the equation

$$CW = -3.7415 + 1.0530\,(SSCL).$$

A strong correlation (r=0.9886, n=225) was calculated for the weight-to-length data transformed with the natural logarithm. Regression of these variables resulted in the equation

$$\ln WT = -8.1570 + 2.8128\,(\ln SSCL).$$

Conversion equations were computed between the straight-line and curved carapace length measurements (Table 3). These equations will allow for comparisons between studies with different measuring techniques.

Growth analyses

Twenty-one Kemp's ridley turtles were recaptured a total of 24 times, yielding 24 annual growth rates. However, 83% of the recaptures occurred within a year of initial tagging and extrapolating annual growth rates from short-term recapture intervals will amplify any error associated with the measurements. The removal of short-term recaptures decreased the range of annual growth rates and increased the precision of the mean growth rate estimate (Table 4A). Subsequent analyses of growth by netting seasons and size classes were confounded by short-term recaptures. The mean growth rate of Kemp's ridley turtles recaptured within netting seasons (see Table 1 for months fished each year) was significantly larger (χ^2=7.93, df=1, P=0.005) than that of turtles recaptured between netting seasons (Table 4B). However, the duration of all recaptures within netting seasons was less than 180 days (mean=49.6 ± 44.5 days) and the annual growth rates may have been overestimated owing to extrapolation error. Although mean growth rates did not vary significantly when compared by size class (F=0.753, P=0.484), Kemp's ridley turtles in the 40–50 cm size class appeared to have a higher mean growth rate than those in the 30–40 cm and the 50–60 cm size classes (Table 4C).

Deletion of data with recapture intervals less than 90 days reduced the mean growth rate of the 40–50 cm size class (4.7±3.0 cm/yr; n=9, range: 2.9–12.3 cm/yr).

The von Bertalanffy growth interval equation was fitted to each of the recapture interval data treatments. Estimates of asymptotic length ranged from 77.3 to 91.4 cm and estimates of intrinsic growth rate ranged from 0.0852 to 0.1167 (Table 5). The growth interval equation for all Kemp's ridley turtles recaptured at Cedar Key had the lowest residual mean square, a standard that has been used to select the best fit growth model (Dunham, 1978). However, the estimated asymptotic length for this model (a=91.4 cm) is considerably larger than the average carapace length reported for nesting females (65 cm; Márquez M., 1994) and should therefore be considered biologically unrealistic (Frazer et al., 1990). The estimated asymptotic length for recapture intervals greater than 180 days (a=77.3 cm) would be more appropriate if this latter criterion is used. This model has the least amount of error from short-term recaptures, but suffers from a reduced sample size and a truncated range of carapace lengths.

Population estimations

The computer program JOLLY computed a survival rate of 0.41 (± 0.07 SE) and a capture probability of 0.18 (±0.05 SE) for Kemp's ridley turtles at Corrigan Reef. Population estimates ranged from 98.05 turtles in 1987 to 262.79 turtles in 1992 (Table 6). For 1987 through 1993, the mean annual population size was 158.50 (±112.40 SE) turtles and there was a mean of 15.35 (±11.58 SE) marked turtles in the population (10% of the estimated mean population size). For 1987 through 1992, there was a mean annual recruitment of 102.71 (±48.23 SE) turtles (65% of the estimated mean population size).

Food

Fecal specimens from 12 Kemp's ridley turtles were examined during the course of this study. Crab components were identified in all specimens. In addition, two (17%) of the fecal specimens contained mollusc shells and two (17%) specimens contained a portion of undigested seagrass (*Halodule wrightii* in one and *Halophila engelmannii* in the other). Seven (58%) of the fecal specimens contained unidentified crab fragments. Five (42%) of the turtles had consumed chelipeds of stone crab, *Menippe* spp., and three (25%) had consumed chelipeds of blue crab, *Callinectes sapidus*. Two (17%) Kemp's ridley turtles had consumed shark eye shells (*Polinices duplicata*), one of which also consumed a common eastern nassa shell (*Nassarius vibex*), that contained hermit crabs (Paguridae). The two turtles that consumed hermit crabs also ingested mollusc components. Cancellate cantharus shells (*Cantharus cancellarius*) and oys-

Table 4

Mean annual growth rates of Kemp's ridley turtles, *Lepidochelys kempii*, by recapture interval, netting season, and size class (standard deviations given in parentheses). Turtles were assigned to size classes by mean of initial and recapture SSCL.

Data treatments	n	Mean SSCL growth rate (cm/yr)	Range of growth rates (cm/yr)
Recapture interval			
All recaptures	24	5.4 (3.3)	1.2–13.0
Recaptures > 90 days	16	4.5 (2.6)	1.2–12.3
Recaptures > 180 days	13	3.6 (1.2)	1.2–5.4
Netting season			
Within season	10	7.7 (3.6)	1.7–13.0
Between seasons	11	3.3 (1.1)	1.2–4.7
Size class			
30–40 cm	7	4.6 (2.8)	1.2–9.4
40–50 cm	13	6.2 (3.7)	2.9–13.0
50–60 cm	4	4.6 (2.5)	2.2–7.9

Table 5

Estimated values of asymptotic length (a) and intrinsic growth rate (k) from nonlinear regression of von Bertalanffy growth interval equation for Kemp's ridley turtles, *Lepidochelys kempii* (one asymptotic standard error in parentheses).

Data treatment	n	a	k
All recaptures	24	91.4 cm (41.9)	0.0852 (0.0720)
		Residual mean square error = 1.3872	
All recaptures > 90 days	16	90.9 cm (51.1)	0.0858 (0.0892)
		Residual mean square error = 2.1179	
All recaptures > 180 days	13	77.3 cm (29.2)	0.1167 (0.0957)
		Residual mean square error = 2.0085	

Table 6

Summary statistics and estimated parameters for the Jolly-Seber analysis of Kemp's ridley turtle, *Lepidochelys kempii*, mark-recapture data (standard errors given in parentheses). Descriptions of the notation are as follows: n = total number of turtles captured and released each year; m = number of marked turtles captured each year; u = number of unmarked turtles captured each year; r = number of turtles released each year that were captured again later; z = number of turtles captured before a given year and captured again later; M = annual estimate of the number of marked turtles in the population; N = annual estimate of population size; and B = annual estimate of the number of individuals recruited to the population.

	Summary statistics					Estimated parameters		
Year	n	u	m	r	z	M	N	B
1986	17	17	0	3	—	—	—	—
1987	17	16	1	3	2	10.91 (5.49)	98.05 (32.11)	139.87 (42.90)
1988	35	31	4	1	1	18.20 (7.41)	187.03 (55.83)	96.38 (32.86)
1989	29	28	1	3	1	7.30 (4.70)	159.79 (50.22)	107.25 (34.87)
1990	32	29	3	2	1	14.17 (6.72)	172.66 (52.53)	45.54 (24.72)
1991	20	18	2	6	1	11.32 (6.05)	109.35 (35.92)	201.60 (58.21)
1992	49	43	6	2	1	28.61 (10.55)	262.79 (75.59)	25.64 (28.35)
1993	22	19	3	—	—	16.34 (9.53)	119.81 (39.34)	—

ter shell fragments were identified in both of the fecal specimens. Furthermore, one of these specimens contained hooked mussels (*Ischadium recurvus*) attached to an oyster shell fragment.

Discussion

The results of this study indicate the importance of seagrass beds and oyster reefs as developmental habitats for Kemp's ridley, loggerhead, and green turtles. Furthermore, these species may be preferentially utilizing the two habitat types on the basis of their respective feeding strategies. The extensive seagrass flats along the west coast of Florida have been identified as foraging habitat for the herbivorous green turtle (True, 1887; Carr and Caldwell, 1956; Caldwell and Carr, 1957). Netting effort at the seagrass shoals of Waccasassa Reefs resulted in captures of mid- to late subadult green turtles, comparable to the size class of green turtles reported by Carr and Caldwell (1956). The Kemp's ridley turtle is primarily cancivorous (Shaver, 1991; Burke et al., 1994), and the distribution of this species can be correlated to areas with abundant crab populations (Ogren, 1989). Intertidal oyster bars provide refuge for stone crabs (McRae, 1950; Bender, 1971; Wilber and Herrnkind, 1986), whereas the mud bottom adjacent to these bars is the preferred substrate of blue crabs (Evink, 1976; Wolfe, 1990). Subadult Kemp's ridley turtles dominated the aggregation of marine turtles captured in the vicinity of Corrigan Reef and the food items for these turtles were typical of the macroinvertebrate fauna inhabiting nearshore oyster bars. Subadult and adult loggerhead turtles were also captured at Corrigan Reef; this species also feeds on benthic invertebrates, particularly molluscs (Dodd, 1988). The possibility of competition for food resources between loggerhead and Kemp's ridley turtles is unknown and could be investigated by comparing fecal specimens of both turtles captured in the same location.

Tagging studies of Kemp's ridley turtles have revealed reproductive migrations of females in the Gulf of Mexico (Pritchard and Márquez M., 1973), seasonal migrations of subadults along the Atlantic coast (Henwood and Ogren, 1987; Schmid, 1995), and an east–west movement of subadults in the northern Gulf (Ogren, 1989). However, there are no mark-recapture data to indicate a seasonal migration of subadult turtles in the eastern Gulf of Mexico. As stated by Carr (1980) and observed in the present study, turtles apparently immigrate to the nearshore waters of the Cedar Keys in April and emigrate to some unknown locality in November, presumably in response to changes in water temperature. Ogren (1989) suggested a seasonal offshore movement of Kemp's ridley turtles in the northern Gulf on the basis of capture of subadult turtles in deeper waters off Apalachicola Bay during the winter (Rudloe et al., 1991). Satellite telemetry has demonstrated that Kemp's ridley turtles on the Atlantic coast respond to a decrease in water temperature by moving to warmer waters southward or offshore (Renaud, 1995). Marine turtles in the Cedar Keys area could be moving westward to deeper waters offshore or southward within the shallow coastal waters. Alternatively, some Cedar Key fishermen believe that turtles overwinter in the remote coastal waters by "burying up" in mud bottom holes (Carr and Caldwell, 1956; Schmid and Ogren, 1990). Loggerhead turtles have exhibited this behavior in the Port Canaveral ship channel at water temperatures below 15°C (Carr et al., 1980; Ogren and McVea, 1982). Water temperatures as low as 12–14°C were recorded at the Cedar Keys study area from December to February. The possibility of winter dormancy or migration (or both) by west coast turtles requires additional information (Ogren and McVea, 1982) and could be investigated by attaching satellite transmitters to turtles during the fall.

Recaptures of Kemp's ridley turtles tagged and released in the northeastern Gulf of Mexico have provided information on their use of coastal foraging grounds. Carr and Caldwell (1956) observed that Kemp's ridley and green turtles released from Cedar Key returned to the Withlacoochee-Crystal River fishing grounds within a short period of time. The authors implied that the turtles may be exhibiting a homing behavior and maintaining home ranges at the site of initial capture. Schmid and Ogren (1990) suggested that Kemp's ridley turtles in the Florida panhandle region were transitory because of the lack of long-term recaptures (Rudloe et al., 1991). By comparison, recaptures in the Cedar Keys area were indicative of a more residential aggregation. Although the majority of Kemp's ridley turtles tagged near the Cedar Keys were recaptured within a year of initial capture, almost equal numbers of turtles were recaptured within netting seasons and between netting seasons. Recaptures within a netting season suggest that some turtles remain in the vicinity of Corrigan Reef during their seasonal occurrence in this region. Recaptures between netting seasons indicate that some turtles return to the previously utilized oyster bar habitat annually and may do so for up to four years. Efforts are currently underway to determine the activity patterns and habitat associations of Kemp's ridley turtles in the Cedar Keys area (Schmid, 1994).

Kemp's ridley turtles were numerous in the coastal waters of Florida prior to the 1950s (Carr, 1980). Data provided by Carr and Caldwell (1956; p. 21, Fig. 3) indicated that approximately 1% of the Kemp's ridley turtles captured at the Withlacoochee-Crystal River fishing grounds were early to mid-subadults (20–40 cm), 88% were mid- to late subadults (40–60 cm), and 11% were adult (60+ cm). There was also an unconfirmed report of a vitellogenic female weighing 42 kg with an estimated length of 75 cm. The presence of adult turtles in this 1955 survey corresponds to a period when there were relatively large, though declining, nesting aggregations of Kemp's ridley turtles (U.S. Fish and Wildlife Service and National Marine Fisheries Service, 1992). The lack of 20–40 cm turtles may be indicative of lower subadult recruitment resulting from the intensive egg harvesting that was occurring at this time (Hildebrand, 1982). In contrast, the catch at the Cedar Keys from 1986 to 1995 comprised 24% early to mid-subadults and 76% mid- to late subadults. Observations and captures of adult Kemp's ridley turtles at sea have become extremely rare owing to the greatly reduced nesting population, whereas the higher frequency of 20–40 cm turtles may suggest higher subadult recruitment as a result of nesting beach protection (Ogren, 1989).

Carr and Caldwell (1956) also described an apparent, though not statistically significant, seasonal shift in the mean carapace length of Kemp's ridley turtles taken in the commercial turtle fishery. Larger turtles (mean=54.9 cm) were captured early in the April to November fishing season, whereas smaller turtles predominated the mid- and late season catch (mean=50.3 cm and 52.1 cm, respectively). The seasonal mean carapace lengths reported in this earlier study were 5–10 cm greater than those recently recorded at the Cedar Keys. The authors' description of their measurement technique (". . . from the center of the anterior end of the carapace and the greatest posterior projection of the carapace.") corresponds to the standard straight-line carapace length. Furthermore, the entanglement nets used in the present study were the same mesh size as those used in the commercial turtle fishery. The perceived difference could be due to preference by the former turtle fishermen for larger, higher-priced turtles. Alternatively, the smaller mean carapace lengths of the present study may be indicative of an increased aggregate of smaller Kemp's ridley turtles along the west coast of Florida.

Despite numerous tagging studies, there is very little information available on the growth rates of wild Kemp's ridley turtles (Márquez M., 1994). The data treatments used to analyze Kemp's ridley turtle growth at the Cedar Keys indicated an average increase of 4–5 cm/yr in carapace length. Growth rates of 6–9 cm/yr were obtained for Kemp's ridley turtles at Cape Canaveral with the same data treatments (Schmid, 1995). The higher growth rates observed for east coast turtles are possibly due to measurement errors identified in the Cape Canaveral study. Error was minimized in the Cedar Key study because all measurements were determined by the author using the same equipment and techniques. Assuming a constant growth rate of 4–5 cm/yr, a Kemp's ridley turtle would require 8–10 years to grow from a 20-cm postpelagic subadult (Ogren, 1989) to a 60-cm adult. An estimate of 10–12 years to maturity is calculated by combining the duration of the subadult stage with the estimated 2-year pelagic juvenile stage (Schmid and Ogren, 1990). This calculated age to sexual maturity is in agreement with Kemp's ridley growth models computed from skeletochronological age estimates (Zug and Kalb, 1989; Zug, 1990) and the combination of recapture data for Cape Canaveral and Cedar Keys (Schmid and Witzell, 1997).

The Kemp's ridley turtle aggregation at the Cedar Keys was considered an open "population" with recruitment in terms of postpelagic turtles and subadult immigrants from other locations and with losses in terms of death and permanent emigration to other subadult or adult aggregations. Annual estimates from the Jolly-Seber analysis were indicative of the catchable turtle population at Corrigan Reef within the months fished, which may or may not be representative of the entire aggregation in this area (Krebs, 1989). The relatively low number of recaptures, and corresponding low estimated capture probability, reduced the precision of the population estimates as evidenced by their high standard errors (Pollock et al., 1990). Nonetheless, general comments can be made concerning the estimates of recruitment and survival of Kemp's ridley turtles in the Cedar Keys area. The majority of turtles captured in this locality were mid- to late subadults; there were very few captures of postpelagic turtles. Therefore, provided that sampling bias due to the large-mesh nets was minimal, the high level of recruitment estimated from the Jolly-Seber analysis was presumably a result of immigration by larger subadult turtles. The low estimated survival rate was probably a function of emigration rather than high turtle mortality. However, there were no recaptures of turtles tagged at Cedar Key to indicate emigration to other localities and there was no systematic sampling of turtle strandings to demonstrate the extent of mortality in this region.

In conclusion, tagging studies conducted at the Cedar Keys are models for characterizing foraging populations of marine turtles and these efforts must be expanded to include regions not yet sampled in order to accurately manage these threatened and endangered species (Magnuson et al., 1990; Thompson et al., 1990; U.S. Fish and Wildlife Service and National Marine Fisheries Service, 1992). Areas where marine turtle congregate need to be identified through anecdotal information, historical records, incidental captures, and stranding data. In-water sampling programs should be conducted over an extended period of time to establish the distribution and abundance of turtles in areas of aggregation. After implementing a mark-recapture study, supplementary research activities may include the following: holding turtles for fecal sample collection; sampling blood for stress response, sex determination, and genetic analyses; monitoring local movements via radio and sonic telemetry; discerning migrations via satellite telemetry; and developing GIS models for marine turtle habitat associations.

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