Developmental Biology and Ecology of the Kemp's Ridley Sea Turtle, Lepidochelys kempii, in the Eastern Gulf of Mexico

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ABSTRACT. – Historic records, incidental captures, and tagging data were compiled to provide information on the geographic and temporal size distributions, seasonal occurrence, local movements, growth rates, physiology, and resource utilization of Kemp's ridley sea turtles (*Lepidochelys kempii*) in the eastern Gulf of Mexico. There appears to be an increasing size gradient from north to south in the eastern Gulf and a temporal shift to smaller size classes in recent years. The occurrence of Kemp's ridleys in nearshore waters is seasonal, but there are no data to indicate winter migrations. Aggregations of Kemp's ridleys in the northeastern region appear transitory, whereas the aggregations in east-central and southeast Gulf waters appear more residential. Growth data indicate a turtle would require 8–9 years to grow from 20 to 60 cm SCL and would mature in 10–11 years. Sex ratios in east Gulf aggregations of immature turtles were female-biased (2F:1M). Elevated testosterone levels and historic observations of ovarian follicles suggest gonadal maturation may begin at 40 cm SCL. Recent analyses of resource use in the northeastern Gulf suggest a possible ontogenetic shift in utilization of benthic habitats and the corresponding prey items. The eastern Gulf of Mexico is an important developmental area for Kemp's ridley sea turtles, but more information is needed in this region to adequately conserve and manage this critically endangered species.

KEY WORDS. – Reptilia; Testudines; Cheloniidae; *Lepidochelys kempii*; sea turtle; ecology; developmental habitat; growth; morphometrics; sex ratio; physiology; Florida; USA

For the past century, the coastal waters of the eastern Gulf of Mexico (Fig. 1) have been pivotal in our understanding, or lack thereof, of the Kemp's ridley turtle, Lepidochelys kempii. In the late 1800s, Garman (1880) named the species, the types being a pair of turtles sent by Richard Kemp from Key West, Florida, and applied the common name "Kemp's Gulf turtle". Efforts for the next sixty years focused on the taxonomic nomenclature for the species. Carr (1942) later reported the vernacular name "ridley" and identified Florida Bay as its center of abundance based upon his personal observations and communications with local residents. The occurrence of L. kempii was well known among fishermen from Cedar Keys to Key West (Carr, 1942), and there is a record of a large female and juvenile from Mississippi in the north-central Gulf (Smith and List, 1955). Mexican fishermen along the northern Yucatan peninsula reported a rare type of turtle that Carr (1957) believed to be a ridley, but the only known record for this region was from Isla de Mujeres, Quintana Roo (Smith and Taylor, 1950). These turtles were commonly called "bastard turtle" in all areas of the eastern Gulf and it was believed that they were a hybrid involving loggerhead, Caretta caretta, hawksbill, Eretmochelys imbricata, and/or green turtles, Chelonia mydas.

In 1955, Carr and Caldwell (1956) performed tagging experiments with "Atlantic ridley" turtles captured at the Withlacoochee-Crystal Rivers fishing grounds of west-central Florida and provided the first scientific data on size range, carapace morphometrics, and local movements for *L*. *kempii*. They also reported fishermen's observations on the seasonal occurrence of ridleys and green turtles, the habitats of each species, and the presence of ovarian follicles in larger ridley turtles. This latter observation provided evidence that *L. kempii* was reproductively active, but the natal origin and reproductive habits of the species were still not known at this time. Six years later scientists discovered a film of "Atlantic ridley" turtles nesting in the western Gulf near Rancho Nuevo, Mexico (Carr, 1963; Hildebrand, 1963).

Research efforts during the 1960s and 1970s focused on the rapidly declining number of Kemp's ridley females at the Rancho Nuevo nesting beach (Pritchard and Márquez-M., 1973). The primary source of information for Kemp's ridley turtles in the eastern Gulf during this period was records of captures in commercial fishing operations (Fig. 1). A female tagged at the nesting beach in Rancho Nuevo was recaptured by a shrimp trawler between the Dry Tortugas and Marquesas Keys (Sweat, 1969). Gillnet fishermen reported captures of Kemp's ridley turtles in the nearshore waters around Sanibel Island and shrimp trawlers reported occasional captures offshore of southwest Florida (LeBuff, 1990). A few turtles captured by trawlers in the vicinity of Mississippi Sound and Mobile Bay were tagged and later recaptured in this region or to the west (Carr, 1980). A locality known as Big Gulley, located east of the entrance to Mobile Bay, was identified as an area where trawlers captured significant numbers of Kemp's ridley turtles (Carr, 1980; Ogren, 1989). Caldwell (1962) reported the capture of 3 small turtles off Ft. Walton



Figure 1. Locations (stars) of historic records, incidental captures, and tagging studies for Kemp's ridley turtles in the eastern Gulf of Mexico: (1) Mississippi Sound, (2) Big Gulley, (3) Ft. Walton Beach, (4) St. Joseph Bay, (5) Apalachicola Bay, (6) Apalachee Bay, (7) Deadman Bay, (8) Cedar Keys, (9) Withlacoochee-Crystal Rivers, (10) Tampa Bay, (11) Charlotte Harbor, (12) Sanibel Island, (13) Ten Thousand Islands, (14) Florida Bay, (15) Key West, (16) Marquesas Keys, (17) Dry Tortugas, (18) Islas de Mujeres. Nesting beach (19) at Rancho Nuevo.

Beach, but the capture method was not identified. By the late 1970s, it was apparent that commercial fishing operations, particularly shrimp trawling, were a major source of mortality for marine turtles and research efforts were concentrated on reducing the incidental capture of turtles in fishing gear (Magnuson et al., 1990).

In 1984, the National Marine Fisheries Service initiated long-term tagging studies to characterize the aggregations of Kemp's ridley turtles occurring in the coastal waters of western Florida (Fig. 1). There were also limited tagging efforts with trawl-caught turtles in the northern Gulf, which again demonstrated a westward movement from Mississippi Sound (Ogren, 1989). Rudloe et al. (1991) documented the length frequency distribution, variation in size classes by season and depth, bottom type preferences, and local movements of animals captured incidentally in the fisheries of western Apalachee Bay. Entanglement nets from the former turtle fishery were used to collect marine turtles east of Cedar Keys in order to determine their species composition, population structure, and seasonal occurrence in these nearshore waters (Schmid and Ogren, 1990, 1992). These latter fishery-independent methods provided additional data on the length frequency distribution, seasonal and annual size distributions, morphometrics, growth, population estimates, and diet of Kemp's ridley turtles (Schmid, 1998).

During recent years, research efforts have filled the gaps in the documented distribution of Kemp's ridley turtles in the eastern Gulf and sought to characterize the coastal habitats utilized by this species. A fishery-independent gill net survey for sharks demonstrated that Kemp's ridley turtles occurred in Tampa Bay and Charlotte Harbor on the west-central coast of Florida (Manire and Foote, 1996). Tagging studies have documented the presence of Kemp's ridley turtles within Deadman Bay and the Big Bend region in northwestern Florida (Barichivich, 1998) and the Ten Thousand Islands (Witzell and Schmid, 2004) and Florida Bay (B. Schroeder, *pers. comm.*) in southwestern Florida. Other research efforts have included documenting the feeding ecology of this species in the Deadman Bay-Big Bend region (Barichivich, 1998) and characterizing its habitat associations near the Cedar Keys (Schmid, 2000; Schmid et al., 2003). The following account is a synopsis of the biological and ecological data available for wild Kemp's ridley turtles inhabiting the coastal waters of the eastern Gulf of Mexico. Information is provided on their geographic and temporal size distributions, seasonal occurrence, local movements, growth rates, physiology, and resource utilization.

Geographic Size Distribution

Ogren (1989) described the life history of the Kemp's ridley turtle as composed of a juvenile epipelagic stage (<20 cm SCL; standard straight-line carapace length [nuchal notch to tip of postcentral scutes]), a coastal-benthic subadult stage (20–60 cm SCL), and a coastal-benthic adult stage (>60 cm SCL). A clinal size pattern was suggested for Kemp's ridley turtles along the Atlantic seaboard, with smaller turtles occurring in northern waters (Carr, 1980; Ogren, 1989), but a similar pattern had not been observed in the eastern Gulf. However, a comparison of the mean sizes and size class compositions from recent tagging studies in northwestern and west-central Florida does suggest an increasing size gradient from north to south in the eastern Gulf (Fig. 2). Sixty-six percent of the turtles captured in the



Figure 2. Length data for Kemp's ridley turtles in the eastern Gulf of Mexico: (a) Mississippi Sound (Smith and List, 1955; Carr, 1980), (b) Ft. Walton Beach (Caldwell, 1962), (c) Apalachicola-Apalachee Bays (Rudloe et al., 1991), (d) Big Bend-Deadman Bay (Sulak and Barichivich, unpubl. data), (e) Cedar Keys (Schmid, 1998), (f) Withlacoochee-Crystal Rivers (Carr and Caldwell, 1956), (g) Sanibel Island (LeBuff, 1990), (h) Ten Thousand Islands (Witzell and Schmid, 2004), and (i) Key West (Garman, 1880; Sweat, 1969).

northern Apalachicola-Apalachee Bays (Rudloe et al., 1991) and 75% of those captured in the northern Big Bend region (Barichivich, unpubl. data) were early to mid-subadults (20– 40 cm), compared to only 24% in the mid-coastal Cedar Keys (Schmid, 1998). The northeastern Gulf has been identified as an ejection point for Kemp's ridley turtles that have completed their epipelagic development (Collard and Ogren, 1990) and these length-frequency distributions appear to support this supposition.

Alternatively, the observed size distributions in the northeastern Gulf may be the result of gear bias associated with each of the studies. Commercial shrimp trawls were the primary collection gear in the Apalachicola and Apalachee Bays, but any capture selectivity by this fishery-dependent method has not been addressed. Fishery-independent strike netting was the most commonly employed method in the Big Bend region. Mesh sizes of these nets were decreased from a 25 cm bar to a 10 cm bar as smaller turtles were observed to escape through the larger webbing (Barichivich, 1998). The Cedar Keys study was also based on fishery-independent captures, but with anchored entanglement nets of 25-30 cm bar mesh. Smaller mesh nets were not used in this study owing to an increase in bycatch (e.g., stingrays) with decreasing mesh size. Large-mesh entanglement nets are known to favor the capture of larger turtles (Carr and Caldwell, 1956; Schmid and Ogren, 1992), while small-mesh nets may favor the capture of smaller turtles as larger turtles do not become entangled (W. Barichivich, pers. obs.). Therefore,

the observed size distributions may have resulted from the different mesh sizes used in the fishery-independent studies.

Temporal Size Distribution

A temporal size distribution was noted for Kemp's ridley turtles collected in west-central Florida (Schmid, 1998). All but one of the turtles examined by Carr and Caldwell (1956) in the mid-1950s were greater than 40 cm and 8% of these specimens were greater than 60 cm (Fig. 2). By comparison, 24% of the turtles captured from 1986 to 1995 were 20-40 cm and 76% were 40-60 cm. Both studies reported similar measurement techniques and gear bias between the studies was ruled out as both utilized largemesh entanglement nets. However, Carr and Caldwell (1956) relied on captures from the commercial fishery, and larger turtles may have been preferentially landed given their higher market value. Interestingly, some Cedar Key turtle fishermen referred to smaller turtles as "housekeepers" which were customarily released to "tend the house" of larger turtles on the fishing grounds (Schmid, pers. obs.). This anecdote may explain the lack of smaller size classes in the turtle fishery and suggests the fishermen may have been practicing the first conservation efforts for this species.

Conversely, the temporal difference in size distributions could be indicative of the demographic shift in the Kemp's ridley population which has resulted from the initial exploitation and subsequent protection of the nesting beach.

 Table 1. Records of multiple recaptures for Kemp's ridley turtles in the eastern Gulf of Mexico.

Location	Initial SCL (cm)	Date Tagged	Dates of Recaptures	Days at Large
Deadman Bay	32.0	11 Jun 1998	30 Jul 1998	49
			18 Aug 1998	19
			8 Sep 1998	21
	21.8	26 Jun 1998	18 Aug 1998	53
			1 Dec 1998	105
	22.4	13 Aug 1998	18 Aug 1998	5
		2	3 Dec 1998	107
Cedar Keys	37.1	4 Sep 1991	3 Oct 1991	30
			27 May 1992	237
	35.6	12 Jul 1990	19 Jun 1991	332
			11 Jun 1992	357
	34.3	3 Oct 1991	20 Sep 1992	353
			29 May 1994	617
	30.5	3 Oct 1991	19 Sep 1993	717
			5 Aug 1995	685

Prior to the mid-1970s, there are a few reports of adult-size (60+ cm) Kemp's ridley turtles, primarily females, captured in the eastern Gulf (Garman, 1880; Smith and List, 1955; Carr and Caldwell, 1956; Carr, 1980; LeBuff, 1990). Reports during and after the 1950s correspond to a period of rapid decline for the once abundant west Gulf nesting aggregation (U.S. Fish and Wildlife Service and National Marine Fisheries Service, 1992). Recent tagging studies in the eastern Gulf have not reported the capture of wild Kemp's ridley turtles greater than 60 cm (Rudloe et al., 1991; Schmid, 1998; Barichivich, 1998; Witzell and Schmid, 2004), although strandings of adult-size turtles have been reported (Teas, 1993) and nesting females have been observed on the Florida gulf coast (Johnson et al., 1999). Protection of the Rancho Nuevo nesting beach over the last 30 years has increased hatchling production, which has presumably led to greater recruitment of post-pelagic turtles to coastal waters (Ogren, 1989). This may account for the higher frequency of subadult Kemp's ridley turtles in the eastern Gulf during recent years, though there are no quantitative data to confirm an increase in abundance.

Seasonal Occurrence

Kemp's ridley turtles were typically captured in the nearshore waters of the northeastern Gulf from April to November (Carr and Caldwell, 1956; Schmid and Ogren, 1990, 1992). Recent investigations indicate that turtles occur in these coastal waters when water temperatures are above 20 JC (Schmid, 1998) and sightings and captures have been reported in December and March during unseasonably warm periods (Barichivich, 1998, *pers. obs.*). Conversely, cold-stunned turtles have been collected from St. Joseph Bay after the passage of strong cold fronts in December (L. Ogren, *pers. comm.*; Foley, 2001). Ogren (1989) proposed

an offshore emigration in winter based upon the capture of turtles in deeper waters during December, January, and February (Rudloe et al., 1991). Kemp's ridley turtles may be moving to warmer waters offshore and/or may travel southward along the west coast of Florida. Tag recoveries (Henwood and Ogren, 1987; Schmid, 1995) and satellite telemetry (Renaud, 1995; Gitschlag, 1996) have demonstrated a seasonal migration for Kemp's ridleys in the Atlantic. However, there are no tag recoveries that indicate seasonal movements in the eastern Gulf (Schmid, 1998). Surveys in the Ten Thousand Islands region were inconclusive as to whether Kemp's ridley turtles overwinter along the southwestern Florida coast. Although captures or sightings were reported during all months of the year, turtle abundance decreased during the winter months (December-February) and turtles were not observed in nearshore waters during some of the colder winters (Witzell and Schmid, 2004).

Local Movements

All tagging studies in the eastern Gulf have reported recaptures at the sites of initial capture, which indicate site fidelity by Kemp's ridley turtles. Carr and Caldwell (1956) first noted that a turtle released in the Cedar Keys traveled approximately 35 km to the original capture site at the Withlacoochee-Crystal Rivers fishing grounds within 43 days. Short-term fidelity has also been observed in Apalachicola-Apalachee Bays (Rudloe et al., 1991) and the Big Bend region (Barichivich, 1998). Multiple recaptures within a netting season have been recorded at the latter locality (Table 1). Short-term recaptures suggest that Kemp's ridley turtles may establish restricted foraging ranges while in coastal waters of the eastern Gulf. Telemetric monitoring in the Cedar Keys demonstrated that turtles occupied 5-30 km2 foraging ranges for at least 2-3 months (Schmid et al., 2003). Telemetered turtles also oriented their movements with the prevailing tidal currents, presumably as an energyefficient means of transport (Schmid et al., 2002). Recaptures between netting seasons and multiannual recaptures in the Cedar Keys (Table 1) demonstrate that some turtles remigrate to capture sites in this area and may return to previously utilized sites over a period of years (Schmid, 1998). A similar pattern of recaptures was observed in the Ten Thousand Islands (Witzell and Schmid, 2004). Based on these data, aggregations of Kemp's ridley turtles in the Florida panhandle region appear transitory, as all recaptures have been recorded in the same season and year, whereas the aggregations in west-central and southwest Florida appear more residential.

Growth Rates

Little information is available on the growth of wild, subadult Kemp's ridley turtles. A mean growth rate of 5.1 ± 3.1 cm/yr was calculated for turtles collected in the northeastern Gulf by Schmid (1998) and Barichivich (1998). However, 61% of the individual growth rates were derived

Table 2. Mean annual growth rates (SCL in cm/yr) for Kemp's ridley turtles in the eastern Gulf of Mexico by (a) recapture interval, (b) netting season, and (c) size class. Turtles were assigned to size classes by mean of initial and recapture SCL (standard straight-line carapace length).

Data treatments	n	Growth (cm/yr)	S.D.	Range
(a) Recapture Interval				
All recaptures	33	5.1	3.1	1.2 - 13.0
Recaptures > 90 days	19	4.2	2.6	1.2 - 12.3
Recaptures > 180 days	13	3.6	1.2	1.2-5.4
(b) Netting Season				
Within season	20	6.1	3.6	1.7 - 13.0
Between seasons	10	3.3	1.1	1.2-4.7
(c) Size Class				
20.0–29.9 cm	5	3.7	2.3	1.2 - 6.5
30.0–39.9 cm	11	4.7	2.8	1.2 - 9.4
40.0-49.9 cm	13	6.2	3.7	2.9 - 13.0
50.0–59.9 cm	4	4.6	2.5	2.2-7.9

from recapture intervals of less than 180 days duration and extrapolating annual growth rates from short-term recaptures will amplify any errors associated with the measurements. Error was minimized in both studies as all measurements were performed by a single person using the same techniques and similar types of equipment. Nonetheless, increasing the amount of time elapsed between initial capture and recapture increased the precision of the growth rate estimate (Table 2). Mean growth rate within netting seasons was significantly greater ($\chi^2 = 5.23$, d.f. = 1, p = 0.022) than between seasons (Table 2), but all within-season growth rates were calculated from recapture intervals of less than 180 days and may have been overestimated due to extrapolation. Growth rates by 10 cm size classes appear polyphasic (Table 2), as has been suggested with skeletochronological age estimates for Kemp's ridley turtles (Zug et al., 1997; Chaloupka and Zug, 1997). There was not a significant difference in mean growth rates among the size classes (F = 0.96, p = 0.42), although there was also a high degree of variability associated with the estimates. Using the mean growth rates by size class, a turtle would require 8-9 years to grow from 20 to 60 cm. A similar duration has been

derived using mark-recapture growth equations (Schmid and Witzell, 1997). Therefore, a Kemp's ridley turtle would mature in 10–11 years assuming a 2-year epipelagic stage (Zug et al., 1997) and sexual maturity at 60 cm.

Physiology

Plasma corticosterone, glucose, and testosterone concentrations have been used to investigate the stress response and sex ratio of Kemp's ridley turtles captured in westcentral Florida (Gregory and Schmid, 2001). Mean corticosterone and glucose concentrations increased significantly after 60 min of captivity, but no significant difference was observed for mean testosterone concentrations. The results of this study demonstrated that immature Kemp's ridley turtles respond to handling stress with elevated levels of glucocorticoids and hyperglycemia. Furthermore, initial corticosterone concentrations of Kemp's ridley turtles were almost 6 fold higher than those recorded for loggerhead turtles collected at the same time and location (Gregory et al., 1996), which may have implications concerning the behavior and stress-induced mortality of both species.

Initial testosterone concentrations were used to determine the sex of individual Kemp's ridley turtles in the Cedar Keys using the criteria of Coyne and Landry (2000). Fiftynine percent of the turtles were classified as female, 33% as male, and 8% as indeterminate (Fig. 3). The resulting sex ratio was female biased (1.8F:1.0M) but was not significantly different from 1:1 ($\chi^2 = 2.78$, d.f. = 1, p = 0.096). A similar sex ratio (2F:1M, n = 12) was reported for turtles collected in the Big Bend region (Campbell and Sulak, 1997). In the Cedar Keys, predicted males with carapace lengths 38-45 cm SCL exhibited elevated levels of testosterone (Fig. 3), which may indicate that turtles at this size are entering puberty. Carr and Caldwell (1956) observed follicles the size of "BB shot" in butchered Kemp's ridley turtles as small as 18-23 kg (51-55 cm converted SCL; Schmid, 1998). This observation indicates the ovaries of females begin developing at 50 cm SCL, though it may still take several years to reach sexual maturity. Owens (1997) identified the period of gonadal maturation as the subadult



Figure 3. Plasma testosterone concentrations for Kemp's ridley turtles in the Cedar Keys (from Gregory and Schmid, 2001). Numbers in parentheses indicate sample sizes.

stage of marine turtle development and Coyne and Landry (2000) suggested redefining the size classes of Kemp's ridley turtles using physiological data. Gregory and Schmid (2001) concurred with these authors and suggested the following modifications to Ogren's (1989) life history stages: pelagic juvenile (< 20 cm SCL), coastal-benthic juvenile (20–39 cm), coastal-benthic subadult (40–59 cm), and coastal-benthic adult (> 60 cm). Using the aforementioned growth rates (Table 2), the duration of the prepubescent juvenile stage would be 4–5 years and the duration of the adolescent subadult stage would be 3–4 years.

Habitat Analyses

The mangrove-bordered coastline of southern Florida, particularly Florida Bay, was first identified as a preferred habitat of the Kemp's ridley turtle (Carr, 1942). Carr and Caldwell (1956) later noted that this species was also captured on the seagrass flats of western Florida. They speculated that Kemp's ridley turtles were feeding on crabs and other invertebrates in the channels cutting through the grassbeds. During recent years, research efforts have focused on characterizing the benthic habitats and prey items utilized by Kemp's ridley turtles. Ogren (1989) broadly described the habitat of immature turtles as the shallow seagrass beds and mud bottom bays of coastal marshes, particularly in association with portunid crab distribution. Schmid (1998) identified an oyster bar complex east of the Cedar Keys as important developmental habitat and noted the occurrence of both stone crab (Menippe sp.) and blue crab (Callinectes sapidus) fragments in fecal specimens collected during tagging operations. Recent analyses of Kemp's ridley habitat associations in the Cedar Keys indicated that turtles were preferentially utilizing hard bottom communities surrounding the oyster reef (Schmid et al., 2003). Barichivich (1998) collected fecal specimens from smaller turtles inhabiting the seagrass beds of Deadman Bay and noted that spider crabs (Libinia sp.) were present in all samples but blue and stone crabs occurred in only a few. A cursory comparison of the Kemp's ridley aggregations in these two areas suggests a possible ontogenetic shift in utilization of benthic habitats and the corresponding prey items.

Conclusions

The eastern Gulf of Mexico has been recognized as an important developmental area for Kemp's ridley turtles, but more information is required to adequately conserve and manage this critically endangered species (Magnuson et al., 1990; U.S. Fish and Wildlife Service and National Marine Fisheries Service, 1992; Turtle Expert Working Group, 1998). Long-term and concurrent tagging studies are needed throughout the species' range to provide more data on site fidelity and growth rates, and to demonstrate possible movements among aggregations in different areas. Capture methodology for these studies should be standardized, or at least kept constant within a study, in order to monitor trends in abundance (Bjorndal and Bolten, 2000). Satellite telemetry is needed to identify migration routes and overwintering areas in the eastern Gulf. Characterization of Kemp's ridley turtle habitat has been identified as a priority (Thompson et al., 1990; U.S. Fish and Wildlife Service and National Marine Fisheries Service, 1992), but research to date has been limited in scope and geographic coverage. These efforts must be expanded in order to identify and protect the developmental habitats that are critical to the survival of this species.

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