Turtles in the Gulf of Mexico: Pelagic Distributions and Commercial Shrimp Trawling

by

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May 1991

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Executive Summary

- Available data on the distribution of turtles was evaluated relative to commercial offshore shrimp trawling effort.

- The majority of data on turtle distributions was collected through pelagic aerial surveys targeting loggerhead turtles. Remaining information was provided from fishery-dependent sampling provides information on the presence of turtles within limited sampling areas.

- The distribution of loggerhead turtles overlaps and extends beyond the distribution of offshore commercial shrimp trawling.

- Aerial surveys sampled inshore and bay waters and where there were relatively few turtles as compared to nearshore and offshore waters. It is likely that within these waters, smaller turtles, including green and Kemp’s ridley turtles are more common and not detected through aerial observation.
Introduction

The loggerhead turtle is commonly found within waters of the Gulf of Mexico (Hildebrand 1982; Hildebrand 1983). Nesting of this species is limited along the Gulf of Mexico coast and is considered minor except along the Florida west coast (Marquez 1990; Hildebrand 1982). Information on the pelagic distribution of this species tends to be anecdotal and limited to hatchling and small juveniles associated with ocean fronts (Marquez 1990). The distribution of adults and sub-adults is usually referred to as "coastal" (Marquez 1990; Ehrhart 1989). Hildebrand (1982) reported that turtles have been observed in association with oil platforms, rock reefs and obstructions, and "at (a) considerable distance from the coast" while feeding on Portuguese man-of-war. The association between turtles and offshore oil platforms has recently been re-confirmed (Klima et al. 1988).

Hildebrand (1982) also discusses the relative distributions of the leatherback, Kemps’ ridley, green, and hawksbill turtles within the western Gulf of Mexico. Historically, the green turtle supported a turtle fishery along a portion of the Texas coast. Hildebrand (1982) remarks that at one time, the Kemp’s ridley turtle was referred to in the Gulf of Mexico as the Louisiana turtle. The hawksbill has never been numerous within the Gulf of Mexico (Witzell 1983). Very little information on the relative importance of leatherback turtles exists and Pritchard (1989) indicated that contrary to historical reports, this species probably does not nest in the Florida Keys and Dry Tortugas. No sampling program targetting the presumably deep water leatherback turtles has been conducted, thus, the distribution of this species in the Gulf of Mexico is not well defined. In fact, the only information on this species appears to be from capture incidental to long line fishing (Thompson 1991).

Since 1983, the Southeast Fisheries Science Center (SEFSC) of the National Marine Fisheries Service (NMFS) has collected sighting information on the sub-adult and adult life history stages of marine turtles within Gulf of Mexico waters. Because of the comparative ability to see loggerhead turtles from the most commonly utilized fishery independent sampling platform, airplanes, the vast majority of these data are specific to loggerhead turtles. Additional information on green and Kemp’s ridley turtles were collected during fishery dependent sampling conducted to evaluate mortalities of turtles incidental to commercial shrimp trawling. While the majority of the fishery independent turtle data can be statistically evaluated relative to the stratification of loggerhead distributions regionally, seasonally, and by depth, most of the fishery dependent data are only representative of where we were able to sample within the constraints of commercial trawling effort in the late 1970’s and early 1980’s. Examination of the distributions of the loggerhead from the fishery independent data provides insights into the ecology and movements of this species within and beyond the Gulf of Mexico.

Recently, the National Research Council Committee on Sea Turtle Conservation concluded that sea turtle abundance was 10 times greater in shallow than deeper water during shrimp trawling season. This conclusion prompted speculation about the seasonal and depth distribution of turtles relative to shrimp trawling effort. An
examination of loggerhead turtle distributions and shrimp trawling effort was completed to evaluate the overlap of seasonal and depth stratifications.

**Materials and Methods**

A variety of SEFC research projects have collected information relative to the distributions of turtles in the Gulf of Mexico. The only synoptic fishery independent distributional data on turtles are available from an aerial sighting program that collected sighting data on marine mammals and turtles at the water's surface from Brownsville, Texas to Key West, Florida, and from the coastline out to the 200 m isobath. Supportive site specific data on turtle distributions were provided by the SEFC Pascagoula Laboratory, Galveston Laboratory and include opportunistic turtle sightings and aerial survey sightings in the Gulf of Mexico off Louisiana. Fishery dependent data have been collected through the efforts of the Pascagoula Laboratory while obtaining information to estimate turtle mortality incidental to commercial shrimp trawling. Turtle distributional information has been collected by the Pascagoula Laboratory during site specific aerial surveys to census red drum. To evaluate the question on depth distributions of turtles relative to shrimp trawling, the defined turtle distributions were compared to the relative distribution of commercial shrimp trawling effort.

**Fishery Independent Sampling for Turtles**

*Synoptic Aerial Surveys*

From 1983 through 1986, seasonal aerial surveys were completed from the coastline of the Gulf of Mexico out to the 200 m (100 fathom) isobath. The surveys are referred to herein as GoMex for Gulf of Mexico. The purpose of these surveys was to provide data for the estimation of marine mammal and marine turtle density over continental shelf waters. Results of these surveys provide baseline information on the distributions of loggerhead turtles in the Gulf of Mexico.

To optimize seasonal and depth coverage, the study area was divided into two sampling areas (Fig. 1). The Northwestern Gulf, (NW) was defined as extending from the Rio Grande River to the mouth of the Mississippi River, a total of 144,056 km$^2$; and the Northeastern Gulf (NE), from the Mississippi River to Key West, Florida, a total of 219,514 km$^2$.

Sampling strata were established based on surface to bottom water depth, and were termed "bay", "inshore", and "offshore" sampling areas (Fig. 1). "Bays" included bays, sounds, and lagoons; inshore included waters from the coastline or oceanside from barrier islands to 18 m and "offshore" included waters from 18 m to 200 m in depth. This scheme optimized coverage over depth such that 15% of the bays, 12% of inshore, and 7% of the offshore surface waters were sampled. Overall coverage averaged 10%.

The survey platform was a twin engine Beechcraft D-18, equipped with a plexiglass observation bubble on the nose. Four observers were rotated through the observation
bubble, such that there were two observers in the bubble during surveys. All possible transects were placed at 1.4 km intervals and randomly selected.

All surveys were conducted at an altitude of 229 m (750 ft), at about 22 km/hr (120 knots) ground speed. Four surveys were completed in the northwestern Gulf and three in the northeastern Gulf. Data reported included species identification, location, time and date, various environmental conditions, and animal behavior.

**Site Specific Aerial Surveys**

From June 1988 through June 1990 the SEFC completed site specific aerial surveys with funding from the U.S. Dept. of Interior, Minerals Management Service (MMS). The purpose of these surveys was to evaluate associations between turtles and oil platforms (Lohoefer et al. 1989). Specific sampling sites off the Louisiana Coast were divided into "inshore" and "offshore" areas. (Fig. 2.).

Sampling sites were selected based on platform density and estimated sampling time. Water depth in the inshore sites varied from 6 to 65 m and were sampled from 1988 through 1990. Offshore sites were up to 200 m in depth and were sampled from 1989 through 1990.

The survey platform was a de-Havilland (DC-8) Twin Otter airplane from NOAA's Aircraft Operations Center, Miami, Florida. Downward viewing was accomplished through observation bubbles mounted on each side of the aircraft. Survey altitude was 229 m (750 ft) and speed was 167 m/hr (90 knots). Surveys were conducted weekly as possible to maximize positional information on turtles.

**Opportunistic Sightings 1985-1989**

Since 1985, the Galveston laboratory has maintained a sea turtle sighting file to compile opportunistic sightings of turtles. A sighting is defined as an event in which a sea turtle is seen, usually swimming at the surface of the water. All sightings are reported by the public or in conjunction with ongoing NMFS research programs. There is no sampling plan or research program for this and the data only represent where turtles were observed.

**Fishery Dependent Sampling**

As previously indicated, the interpretation of these data relative to turtle distributions is limited. These data were collected with the primary purpose of sampling fishing effort or a non-turtle resource. The extent of turtle distributions beyond these efforts cannot be deduced. However, these data do provide supportive information on the presence of turtles in sampling areas.

**Sampling Aboard Commercial Shrimp Trawling Vessels**
Over the period 1973 through 1984, direct observations of sea turtle catches were made by observers placed on accepting shrimp trawling vessels within the Gulf of Mexico and southeastern North Atlantic (Henwood and Stuntz 1987). Three different programs included these observers and were: 1) the incidental catch and mortality program from 1979 to 1981; 2) the excluder trawl program from 1973 through 1984; and 3) the shrimp fleet discards program from 1973 through 1984. These programs are discussed in detail by Henwood and Stuntz (1987). Briefly, the incidental catch program documented the catch and mortality of sea turtles captured accidentally by commercial shrimp trawlers. The excluder trawl program included the experimental trawling using various prototypical TED designs that eventually led to the acceptance of the current NMFS TED design. The objective of the shrimp discard program was to evaluate all by-catch associated with the commercial shrimp fleet. Henwood and Stuntz (1987) summarized their results relative to water depth and turtle species.

*Aerial Surveys to Census Red Drum*

From April to December 1987, aerial surveys were conducted to census red drum within the Gulf of Mexico. Sighting information on sea turtles was also reported. Turtle sighting information was summarized from Loheofener et al. (1988) relative to water depth.

*Shrimp Trawling Effort*

Commercial shrimp trawling effort was defined as "days fished", where one day equals 24 hours that nets were in the water. Thus, for this exercise, effort represents the fishing time an individual turtle could be caught. Effort data from 1989 were used since it is the most recent data available and provide a reasonable representation of annual effort for all the survey efforts (E. Klima 1991 pers. comm.). Because shrimp trawling effort were available in 1987 and coincided with the aerial surveys to census red drum, the 1987 trawling effort data were used overlaid the turtle distributions derived from the red drum surveys. To facilitate presentation of shrimp trawling effort, grids of total shrimp trawling effort were defined in 5,000 days fished increments, with 0-5000 days fished as the lowest and 25,000 the highest increment. The distributions of loggerhead turtles from the three programs were overlaid the distributions of shrimpng effort as defined by 5,000 days fished increments. The 30 meter isobath was included in these figures as a reference. This approach was used for both the 1989 and 1987 shrimp trawling data.

*Results*

**Fishery Independent Sampling**

*Synoptic Aerial Surveys*

Seven seasonal surveys were flown; four in the northwestern Gulf and three in the northeastern Gulf. The northwestern Gulf surveys were flown in Sept. to Oct. 1983 (Fall); Jan. to Feb. 1984 (Winter); April to May 1984 (Spring); and July to Aug. 1985
(Summer). The northeastern Gulf surveys were flown June to Aug. 1985 (Summer); Sept. to Oct. 1985 (Fall); and Jan. to Feb. 1986 (Winter). The total linear kilometers flown was estimated to be 94,490.5 km in both surveys areas, with 44,071.9 km flown in the northwestern Gulf and 50,418.6 km flown in the northeastern Gulf.

The total number of loggerhead turtles sighted at the surface of the water was tabulated by survey and for each depth stratum (Table 1). The total number of turtles recorded was 1,192 with 6% of these recorded in the bays; 73% in inshore waters; and 21% in the offshore waters. It is likely that at 229 m altitude the majority of turtles sighted are in the sub-adult and adult size classes. During a previous aerial survey program targeting marine turtles, it was determined empirically that the average minimum size of turtles that are sighted at a survey altitude of 153 m is about 61 cm (2 ft.) straight line carapace length (Thompson 1984). Therefore, using a simple linear relationship at a survey altitude of 229 m, we expect that the minimum observation size was at least 92 cm carapace length. This length, 92 cm, is certainly well within the average length of nesting females throughout the southeast U.S. (Dodd 1988).

Surveys in the northwestern Gulf netted a total of 57 reported sightings of loggerhead turtles, with sightings per survey and depth stratus presented in (Table 1; Fig. 3). No sightings were recorded in the bay waters of the northwestern Gulf sampling area. This does not mean that there were no turtles in these waters, but that no adult, sub-adult or large juvenile turtle were visible at the surface under survey conditions. Water color or turbidity could not be ruled out as a factor because it is highly variable within bay waters. However, it is more likely that turtles were either too small for detection within these water (L. Ogren 1990; personal observation).

The total linear kilometers flown is presented in Table 2. Sightings per kilometer flown, or sighting rate, was estimated as an index to compare between seasons, depth strata, and areas. The sighting rate for the northwestern Gulf was estimated as .0013. Within the inshore and offshore waters, the sighting rate ranged from 0 to .0048 turtles per km (Table 3). A chi-square computation to test the independence of sighting rate from stratum and survey resulted in acceptance of the null hypothesis; that sighting rate was independent of survey or stratum ($X^2 = .23$, p. 950; Fleiss 1973). While there appears to be a greater likelihood of sighting turtles in the inshore and offshore waters during the fall, this is not supported statistically because so few turtles were recorded during any one survey. The distribution throughout this sampling area is presented in Figure 3.

A total of three surveys were flown in the northeastern Gulf with a total of 1,135 loggerhead turtles recorded during these surveys. The number of turtles recorded by surveys and stratum are presented in Table 1 and illustrated in Figure 4. As before, sightings per unit of linear transect flown was estimated by season and depth stratum and included in Table 3. A statistical comparison of rates demonstrated that there were significant difference in sighting rates between season and strata ($X^2 = 11.88$, p. 005; Fleiss 1973).
The mean rate over all seasons was estimated as .0093 loggerhead turtles per kilometer. The sighting rate in all inshore surveys was greater than all offshore surveys which was greater than all bay surveys (Table 3). The smallest value was estimated for the winter bay surveys (.008) and the largest value for the fall inshore survey (.0180) (Table 3). For the bays and inshore waters, the greatest sighting rates were estimated for the fall survey, whereas the winter surveys resulted in the greatest sighting rate in the offshore strata (Table 3).

The stratified sighting rates in this area are all at least one magnitude higher than in the northwestern Gulf. However, the trend is the same suggesting that turtle behavior, environmental conditions or observer behavior was consistent throughout the Gulf during the sampling period.

When relating these turtle distributions to shrimping effort, it is obvious that the distribution of turtles overlaps and extends beyond the extent of commercial shrimp trawling. Waters in which there is no shrimp trawling and turtles are present, do not require regulation of the shrimp trawling industry. In the northwestern Gulf, the relative intensity of shrimp effort decreases when moving to offshore waters. However, the majority of sightings in offshore waters was greater than inshore waters suggesting the turtle CPUE might be higher in offshore relative to inshore waters. The results of Henwood and Stuntz (1987) are representative of the catch of turtles in inshore waters rather than offshore and bay waters, because this is where they were able to sample. Thus, their CPUE estimates are probably not applicable to offshore and bay waters of the northwestern Gulf.

In the northeastern Gulf, turtles tended to concentrate in inshore waters but were present in relatively large numbers in offshore as compared to bay waters. However, shrimp trawling effort appears to be more uniform over these waters with the exception of waters near the Dry Tortugas and in inshore waters from the Mississippi River to Mobile Bay. Over both areas, turtles were present over all depths during all seasons.

**Site Specific Surveys**

A total of 229 loggerhead turtles were sighted during this study. Turtles were sighted in all sampling areas except area 6 and 63% (145) were sighted within area 1. (Table 4). Within the sampling period, we define spring as April through June; Summer from July through September; Fall from October through December; and winter from January through March. Given this seasonal stratification, of the total 229 turtles, 40% (92) were sighted in the spring; 23% (53) in the summer; 28% (63) in the fall; and 9% (21) in the winter (Lohofener et al. 1990). Results from this seasonal sampling effort are consistent with those from the GoMex sampling.

Turtles were observed in all depth strata within a given sampling area (Fig. 5). According to Lohofener et al. (1990), the distribution of turtles by depth did not differ seasonally, although sighting rates increased with increasing depth in the fall and winter. This result is similar to that observed along the southeast Atlantic seaboard.
(Thompson 1984). Lohefner et al. (1990) speculate as did Thompson (1984) that this may be the result of turtles moving into warmer waters offshore.

**Opportunistic Sightings**

Sightings were reported by divers, oil company personnel, commercial and recreational fishermen, beach goers and NMFS employees (Fig. 6 and 7). These data are biased because the majority of the sightings were reported by NMFS observers working on oil platforms which are concentrated in shelf waters off Texas and Louisiana. Regardless of this sampling bias, sightings were reported beyond 60 m in the NW Gulf. These results are remarkably similar to those from the synoptic aerial survey program off the NW Gulf.

**Fishery Dependent Sampling**

*Sampling Aboard Commercial Shrimp Trawling Vessels*

Henwood and Stuntz (1987) presented results of catch and mortality of turtles incidental to commercial shrimp trawling. They estimated catch and mortality of turtles relative to commercial shrimp trawling effort. Notably, all fishing effort was in offshore waters or those beyond the barrier islands out beyond the 30 meter (15 fathom) isobath. Their results did not show any significant deviation in turtle CPUE between depths sampled within the Gulf of Mexico. Loggerhead turtles were most abundant with Kemp's ridleys next in abundance and green turtles the least in abundance.

*Aerial Surveys for Red Drum*

Lohefner et al. (1988) divided the study area 6 geographical study areas identified as South Texas from the Texas/Mexico border to the northern end of Matagorda Bay; North Texas to the Louisiana border; Louisiana to the mouth of the Mississippi River; the North Central Gulf of Mexico to Perdido Bay, Al.; North Florida from Cape San Blas, Fl. to Waccasassa Bay, Fl.; Central Florida to Charlotte Harbor; and South Florida to Key West (Fig. 8). Note that the coast between Perdido Bay, Al. to Cape San Blas, Fl. was not sampled due to military air space restrictions. Sampling was conducted in two seasons, spring and fall, except in the Central Florida area which was only sampled in the fall. According to Lohefner et al.(1988), all transects were terminated within 20 minutes of flight time perpendicular to the mainland coast. Given a ground speed of about 100 knots, survey effort was concentrated within the 60 meter isobath or are equivalent to the inshore survey area described under the synoptic aerial surveys. Lohefner et al.(1988) estimated densities within study areas for each seasonal survey. They only distinguished between hard-shelled turtles and leatherbacks. However, based on the relative ease at observing loggerhead turtles of the adult and sub-adult size relative to green and Kemp's ridleys we expect that the vast majority of these sightings were loggerhead turtles. Turtles were observed in all surveys at all depths for all seasons. Estimated turtle density in the spring ranged from a minimum of .04 turtles/km$^2$ in the Louisiana area to a maximum of 1.13 turtles/km$^2$ in South
Florida. In the fall, turtle density ranged from .05 turtles/km² in Louisiana to .64 turtles/km² in South Florida. Overall leatherback turtles were rarely reported.

Discussion

Results from these surveys efforts serve as a baseline for the seasonal and spatial distribution of loggerhead turtles in the Gulf of Mexico. Large loggerhead turtles are clearly a successful target for pelagic aerial surveys. Results of these surveys show that the distribution of sub-adult and adult turtles is skewed toward the eastern Gulf, from the Mississippi River Delta to Key West, Florida. The relative lack of sightings in the western Gulf is not to be interpreted to mean that there are no marine turtles in this area. Historically, the green turtle was known as the Texas turtle and was the focus of an active fishery in the Corpus Christi area at the turn of the century (Hildebrand 1982). The Kemp’s ridley turtle was known historically as the Louisiana turtle and while not fished with the same intensity as the green, was taken opportunistically (Hildebrand 1982). Results of our own research have produced data on both Kemp’s ridley and green turtles in Gulf waters (Henwood and Stuntz 1987). Thus, both species are present throughout the Gulf by were not detected by pelagic aerial surveys. The carapace coloration of the green turtle does no provide the same contrast as that of the loggerhead and is probably easily overlooked. The Kemp’s ridley coloration also does not provide a visual contrast against the water and being the smallest species is probably not large enough for detection at 229 m altitude and at 222 km/hr speed.

This east-west dichotomy in the distribution of loggerhead turtles is supported by results of previous aerial surveys in the Gulf conducted by the US Fish and Wildlife Service (USFWS) in 1980-1981 (Fritts et al. 1983). In these surveys loggerhead turtles were sighted 50 times more frequently off the southwest coast of Florida compared to off the Louisiana and Texas coasts (Fritts et al. 1983). Results of these bimonthly surveys indicated that this distribution showed seasonal shifts as well, with the highest frequency of sightings occurring in the spring and the lowest in the winter (Fritts et al. 1983). Our results suggest that there may be seasonal movements also from the central Florida inshore and offshore waters in the fall to the southwest Florida inshore and primarily offshore waters in the winter. Fritts et al. (1983) estimated turtle density off the southwest coast of Florida and the highest was estimated for February 1981 (.22 turtles per km²) and lowest in October 1980 (.061 turtles per km²). Our results also demonstrated an aggregation of turtles in southwest Florida waters during the winter.

The USFWS surveys extended from the coastline out to the approximate 1000 m bathymetric curve with some sightings beyond the 100 m curve (Fritts et al. 1983). Both inshore and offshore waters of central and southwest Florida support numerous turtles out to the western boundary of the offshore sampling areas (Fig. 4). Thus, it appears from these most recent surveys, that loggerhead turtles are abundant and conspicuous in the eastern Gulf off the coast of Florida and significantly less abundant or less conspicuous in the northern and western Gulf waters where they are probably replaced by green and/or Kemp’s ridley turtles. Loggerhead turtles probably move from north central Florida to the southwest offshore waters in response to reduce temperatures in the winter or as they follow an available resource.
Based on the examination of turtle and shrimp trawling effort distributions, it appears that the distribution of turtles extends beyond the extent of trawling and throughout the shrimp trawling season. Thus, wherever shrimping occurs, loggerhead turtles are observed in significant numbers. The absence of sightings in bay waters from these aerial surveys does not mean juvenile turtles or green Kemp's ridley turtles were not present. These aerial surveys only target adult and sub-adult loggerhead and leatherback turtles. Notably, Hildebrand (1982) suggested that the Kemp's ridley historically was the "Louisiana" turtle, and the green turtle, the "Texas" turtle. Both species are rarely sighted using current survey methods but, both species utilize inshore and nearshore waters (Hildebrand, 1982). Thus, within bays of the Gulf of Mexico green and Kemp's ridley turtles are present and cannot be been detected via our aerial survey efforts (Ogren 1989).
Literature Cited


List of Figures

Figure 1. Survey area for synoptic aerial sampling of the Gulf of Mexico. Line at the mouth of Mississippi River separates northwestern Gulf and northeastern Gulf. Bays includes bays and sounds; inshore waters includes waters from the coast or coeanside of barrier islands to 18 m in surface to bottom depth; and offshore waters are 18 m to 200 m in depth.

Figure 2. Aerial survey sampling area from site specific surveys to evaluate turtle-oil platform distances. Shrimp trawling effort is overlaid in 5,000 days fished grids.

Figure 3. Turtle sightings for the northwestern Gulf of the synoptic surveys. Each dot represents a single sighting of a loggerhead turtle. Shrimp trawling effort is overlaid in 5,000 days fished grids.

Figure 4. Turtle sightings from the northeastern Gulf of the synoptic survey. Each dot represents a single loggerhead turtle sighting. Sightings in offshore blocks line up along sampled transects. Shrimp trawling effort is overlaid in 5,000 days fished grids.

Figure 5. Aerial surveys sightings from site specific sampling. Each dot represents a single sighting. Shrimp trawling effort is overlaid in 5,000 days fished grids.

Figure 6. Opportunistic sightings of turtles in the northwestern Gulf. Shrimp trawling effort in 5,000 days fished grids are overlaid.

Figure 7. Opportunistic sightings of turtles in the northeastern Gulf. Shrimp trawling effort in 5,000 days fished grids are overlaid.

Figure 8. Turtle sightings from red drum aerial overflights over the western Gulf of Mexico. Shrimp effort grids in 5,000 days fished increments from 1987 effort data are overlaid.

Figure 9. Turtle sightings from red drum aerial overflights over the eastern Gulf of Mexico. Shrimp effort grids in 5,000 days fished increments from 1987 effort data are overlaid.
1989 TOTAL EFFORT
(DAYS FISHED)

- 0 to 5000
- 5000 to 10000
- 10000 to 15000
- 15000 to 20000
- 20000 to 25000

15 Fathoms
30 Fathoms
Table 1. Numbers of loggerhead turtles sighted in the Northwestern and Northeastern Gulf of Mexico during seasonal surveys from 1984-1987. Sightings are reported by season and for each depth stratum.

<table>
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<td>371</td>
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Table 2. Total transect kilometers flown for each season in the Northwestern and Northeastern Gulf of Mexico. Linear distance is reported for each depth stratum within each season.

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Table 3. Mean number of turtles sighted per linear kilometer of selected transects flown. These sighting rates are presented for the Northwestern and Northeastern Gulf study areas by depth stratum and season. The mean sighting rate over all states for each season is included.

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Table 4. Number of loggerhead turtles sighted by month and sampling area from site specific survey. Data were pooled over years 1988 and 1989 (Lohofner et al.). NS = not sampled.

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