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DISPERSAL SCENARIOS FOR PELAGIC POST-HATCHLING SEA TURTLES

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ABSTRACT

The major[1] reproductive effort of *Lepidochelys kempi* is restricted to a 17 km stretch of beach in the northwestern Gulf of Mexico, and most neonates begin the pelagic developmental stage of the life cycle here. The single point-source injection of all *L. kempi* hatchlings into the sea, and distributional records of where subadults assume an inshore benthic habitat, permits an hypothetical description of the relationship between oceanographic conditions and likely dispersal paths of post-hatchlings during the year or so they are "lost" at sea. The dispersal scenarios described may be of potential value in understanding the distributions and biogeographical limits of sea turtles in a general sense.

Virtually nothing is known about the distribution or biology of the oceanic developmental stages of any of the sea turtle species, and attempts to gain such knowledge have generally been unsuccessful (Collard, unpubl.[2]). We have approached the general problem of oceanic post-hatchling dispersal routes and forcing factors by relating the point source injection of *Lepidochelys kempi* hatchlings into the Gulf of Mexico, their end-point distributions as shallow water benthic-habitat preadults, and recent detailed information on circulation patterns in the Gulf of Mexico. Because of its synchronous reproductive behavior (in the form of arribadas) and limited geographical range, we feel that a simple distributional model based on *L. kempi* may provide some useful insights on the oceanic dispersal mechanisms of sea turtles in general.

Neonate sea turtles swim toward the open ocean when they leave their natal beaches (Carr, 1963; 1980; 1986; Frick, 1976; McVey and Wibbels, 1984; Meylan, 1986; Pritchard, 1969; Witham, 1976). Evidence for an oceanic developmental period in the life history of Kemp's ridley, Atlantic loggerheads (Carr, 1986) and Caribbean green turtles (Carr and Meylan, 1980) is convincing. Except for strandings usually attributable to strong onshore winds and waves (Carr, 1986; Carr and Meylan, 1980; Caldwell, 1969) or thermal shock (Henwood and Ogren, 1987; Ogren and McVey, 1982; Schwartz, 1978) individuals less than ca. 20 cm long have not been reported in nearshore waters (Ogren, in press; Schroeder, 1987[3]). As noted by Ogren (in press), ". . . the littoral zone, with its attendent predators, is clearly *not* the appropriate habitat for these young turtles." The drifting period may last 2 years or more, when larger benthic-stage individuals appear in coastal waters throughout the Gulf of Mexico and along the eastern seaboard of the United States. (Henwood and Ogren, 1987; Ogren, in press). Zug (in press[4]) has estimated the minimum age of the smallest post-pelagic individuals that we have observed

[1] Scattered nesting occurs southward to Isla Aquada, Campeche, and northward to Padre Island, Texas, but only a few (<100 females from about nine general localities) have been recorded nesting.

[2] Collard, S. B. 1987. Review of oceanographic features relating to neonate sea turtle distribution in the pelagic environment: Kemp's ridley (*Lepidochelys kempi*) in the Gulf of Mexico. Final Report Nat. Mar. Fish. Serv., Southeast Fish. Center, Panama City Lab., 71 pp.

[3] Schroeder, B. A. 1987. A summary of information on Kemp's ridley (*Lepidochelys kempi*) strandings 1980–1987 Atlantic and Gulf coasts of the U.S. Nat. Mar. Fish. Serv., Southeast Fish. Center, Miami Lab., Coastal Resources Division Contr. No. 87/88-01, 26 pp.

[4] Zug, G. In Press. Skeletochronological age estimates for juvenile *Lepidochelys kempii* from the Atlantic coast of North America. *In* Proceedings of the 9th Annual Workshop on Sea Turtle Conservation and Biology. Georgia Sea Turtle Cooperative, Jekyll Island, Georgia.

(20 cm carapace length) to be 2 years. If this is true the length of the pelagic period may be somewhat longer than 2 years, at least for North Atlantic expatriates. The results of tagging studies suggest that post-hatchlings are dispersed by surface currents until such time as they make a habitat shift to neritic waters at about 20 cm carapace length (Ogren, in press). Pelagic stage sea turtles are probably not capable of swimming speeds (Frick, 1976; Witham, 1976) sufficient for them to have reached these areas in the absence of favorable surface currents.

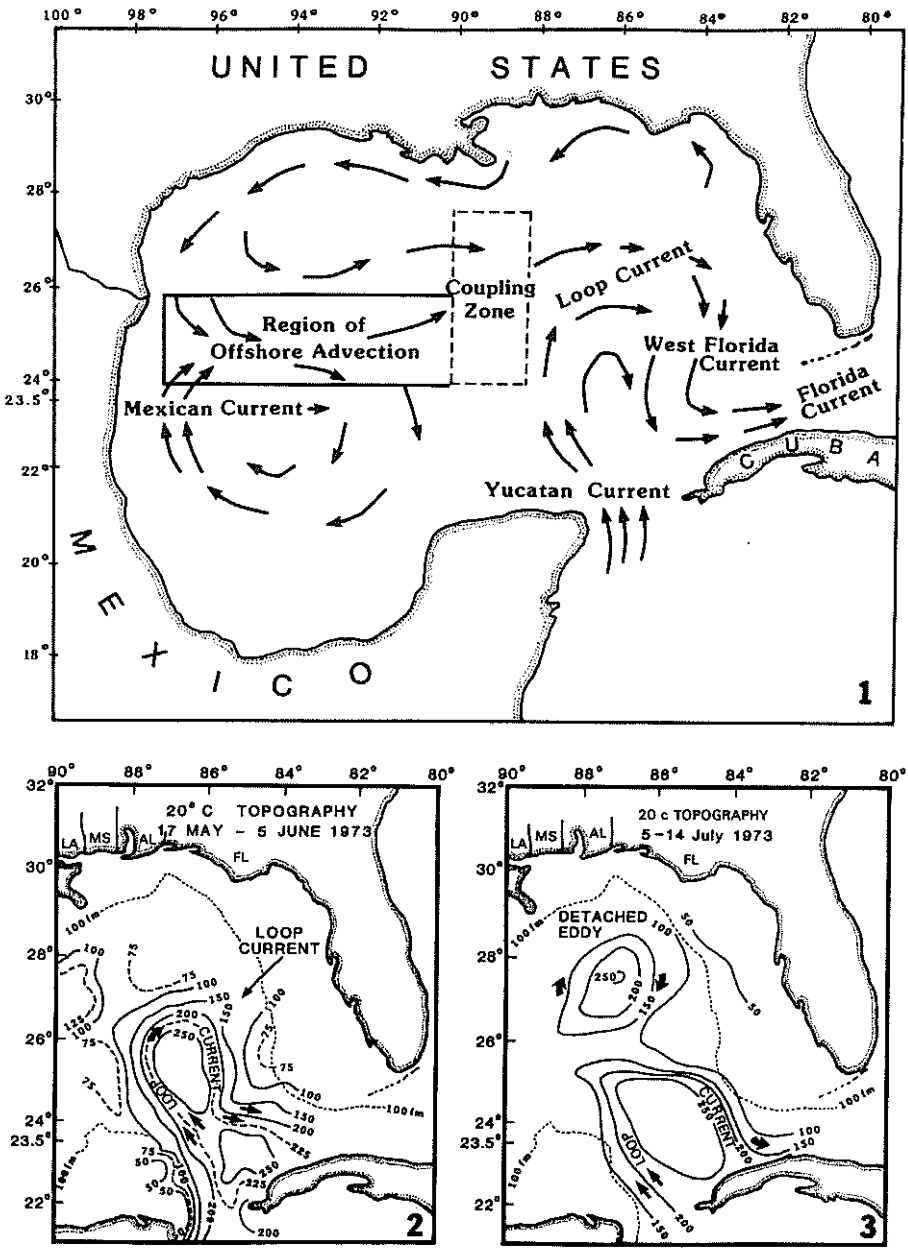
We make two assumptions: (1) That post-hatchling Kemp's ridleys probably drift farther than they swim during the first year or so of their lives, and (2) their dispersal in the Gulf of Mexico and western North Atlantic is likely to be related more to the movement of surface water masses than to wind drift. We recognize the possibility that winds may play a major role in the dispersal of pelagic post-hatchlings, but we are unable at present to evaluate the extent to which dispersal may be explained by surface drift.

Months-old Kemp's ridleys swim directly out to sea after being released on the beach, changing course to compensate for longshore drift (Wibbels, 1984) and objects in their paths, such as swimmers (Frick, 1976). In at least some species, hatchlings apparently do not circumvent sargassum, and have been observed to enter patches of the weed, possibly for rest or refuge (Fletemeyer, 1978; Frick, 1976) and it has been suggested that they may actively search for sargassum for these purposes (Collard, submitted[5]; Frick, 1976; Stoneburner et al., 1982). In our opinion, hatchlings do not stay with sargassum when they encounter it close to shore, but may "rest" in the weed for some time before continuing to swim offshore. Whether swimming by neonates subsequent to interruptions of the frenzy period is active or passive, is unknown (Collard, submitted). Based on stranding records of post-hatchlings associated with beached sargassum, we suggest that hatchlings whose energy supply (residual yolk) has been depleted (Frick, 1976; Kraemer and Bennett, 1981) may have entered and been stranded in nearshore sargassum.

Upon termination of the swim frenzy, hatchlings presumably slow or stop directional swimming and become relatively passive drifters whose subsequent pelagic distribution is determined by surface currents (Carr, 1980; 1986; Witham, 1980) such as the Mexican (Sturges and Blaha, 1976) and Loop Currents in the Gulf of Mexico and the Florida Current/Gulf Stream system in the North Atlantic (Pritchard and Marquez, 1973). General schemes to explain the probable current-mediated transport of young pelagic turtles have been proposed (Carr, 1958; 1980; 1986; Collard, unpubl.; summarized in Marquez, 1986). Individuals swept out of the Gulf of Mexico may become waifs or may return to the Gulf of Mexico at some later period in their development (Byles, 1985; Carr, 1980; Hendrickson, 1980; Henwood and Ogren, 1987; Lazell, 1980; Meylan, 1986; Pritchard, 1969; Pritchard and Marquez, 1973). The pelagic phase of Kemp's ridley may be spent entirely in the Gulf of Mexico (Hildebrand, 1980) or some or all of a given year-class may be swept out of the Gulf with the Loop Current, to complete the remainder of the pelagic phase in the North Atlantic (Pritchard and Marquez, 1973).

Mean Circulation of the Gulf of Mexico.—The Gulf of Mexico receives its major source of water through the Yucatan Straits from the Caribbean Sea (Fig. 1). This stream of water becomes the Gulf of Mexico Loop Current, whose meanders and eddies form the ocean basin circulation of the eastern Gulf. Anticyclonic eddies

[5] Collard, S. B. Aspects of the pelagic developmental habitat of Kemp's ridley (*Lepidochelys kempi*) in the Gulf of Mexico. Submitted.



Figures 1–3. (1) Brucks' suggested generalized circulation regime in the Gulf of Mexico showing the region of coupling between the eastern and western basins. (From Brucks, pers. comm.). (2) Depth of the 20°C isotherm during May and June 1973, showing the position of the Loop Curent intrusion. (Adapted from Molinari et al., 1977, fig. 1A.) (3) Depth of the 20°C isotherm during July 1973, after a Loop Current eddy has been pinched off. (Adapted from Molinari et al., 1977, fig. 1B.)

("rings") shed periodically from the Loop Current migrate into and across the western Gulf of Mexico, which results in an overall clockwise circulation pattern in the western Gulf. Sturges and Blaha (1976) suggested that a western boundary current similar to the Gulf Stream system is characteristic of the western Gulf of

Mexico. The frequency of ring shedding by the Loop Current is variable from year to year (Waddell, 1986) but there is general agreement that circulation in the eastern and western Gulf basins are coupled. Mean circulation in the western basin is largely determined by Loop Current events.

Primary shelf circulation patterns in the Gulf of Mexico are primarily wind driven (Cochrane and Kelly, 1985; Sturges, unpubl.[6]). In shelf waters along the north-south trending coasts of northeastern Mexico and southern Texas, southeasterly winds tend to induce a northerly surface drift. Along east–west coasts outer shelf currents flow to the east during most of the year (Shaw et al., 1985).

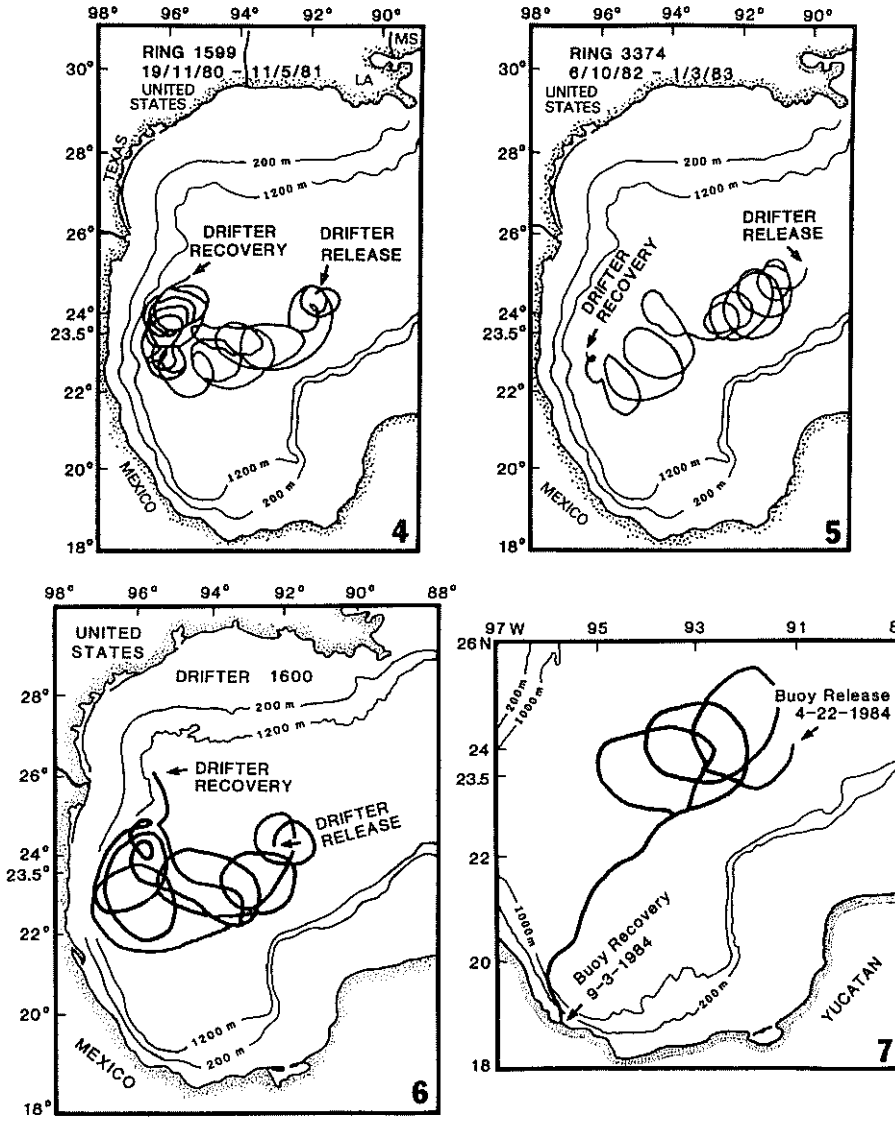
When coupling of boundary currents between the western and eastern basins occurs (i.e., across the Mississippi Delta region) net slope boundary water transport is generally clockwise throughout the Gulf of Mexico (Waddell, 1986; Wallcraft, 1986). In the absence of coupling, eastern and western basins may have, for variable periods of time from several months to a year essentially independent clockwise circulation patterns (Elliott, 1982).

Eastern Gulf of Mexico Loop Current.—The east–west boundaries of the Loop Current lie between 90°W Longitude, and the west Florida shelf (Sturges, unpubl.[6]). Variation in the position of the northern boundary of the Loop Current have been attributed to both up and downstream conditions (Hurlburt and Thompson, 1980; Sturges and Evans, 1983; Vukovich et al., 1979; Waddell, 1986). Leipper (1970) suggested that northern intrusions of the Loop Current had an annual cycle, beginning in the spring and reaching highest latitudes in the summer and fall. During its northernmost penetration the current was either continuous from Yucatan to the northeast Gulf (Fig. 2) or a northern eddy detached from the current leaving a remnant of the Loop Current in the southeast Gulf (Fig. 3 from Molinari et al., 1977). Molinari et al. (1977) noted that from the period 1974–1977 the Loop Current extended farthest north during winter months. Prior to 1974, winter intrusions north of 26°N (a parallel connecting Cape Romano and the U.S.–Mexican border) had not been reported.

Western Gulf of Mexico.—Hurlburt and Thompson (1980) determined that anticyclonic eddies can be shed in a regular manner from the Loop Current, and described a three gyre circulation pattern observed in the Gulf during October–November 1976: The Loop Current in the east; a detached eddy in the central Gulf, and a gyre in the western Gulf which filled the deep basin. A similar pattern occurred in 1967, 1969, and 1972, and it was suggested that a large exchange of water between the eastern and western Gulf occurred at 90.5°W, especially in the spring, due primarily to transport created by wind stress curl (Smehil et al., 1978). Recent studies have shown that, on an annual basis, there are often from one to three closed, westward-drifting rings in or entering the western Gulf as a result of eddy-shedding or breakdown of the northern portion of the Loop Current (Brooks, 1984; Kirwan et al., 1984; Lewis, 1984; Waddell, 1984; Wallcraft, 1986).

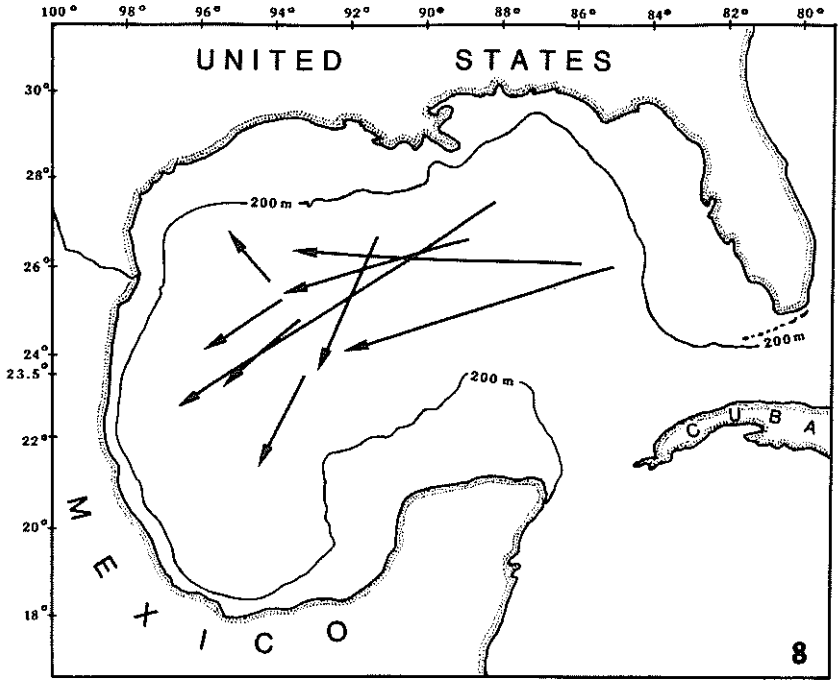
Waddell (1986) described the paths of three rings seeded with Lagrangian drifters as being identical, with a total travel time across the Gulf of Mexico, from shedding by the Loop Current to contact with the Mexican shelf, of 6 to 8 months (Figs. 4–7). Figure 8 (from Waddell, 1986) shows the mean paths of nine separate rings that were followed. Net movement of most of the rings was toward the southwest. Characteristic paths of warm rings based upon GOES and NOAA

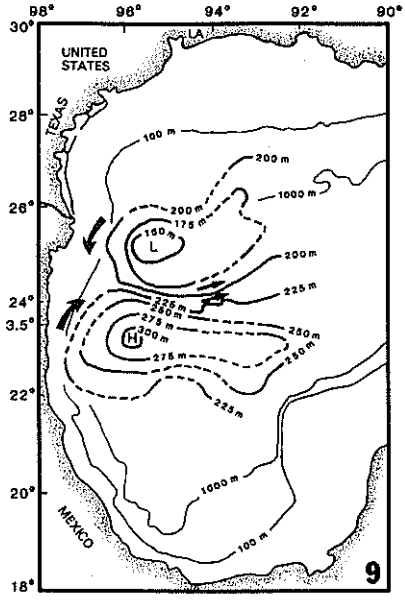
[6] Sturges, W. 1978. Coherence between winds and currents at a nearshore mooring on the west Florida shelf north of Key West. Informal Tech. Note, Florida State University, unpublished.

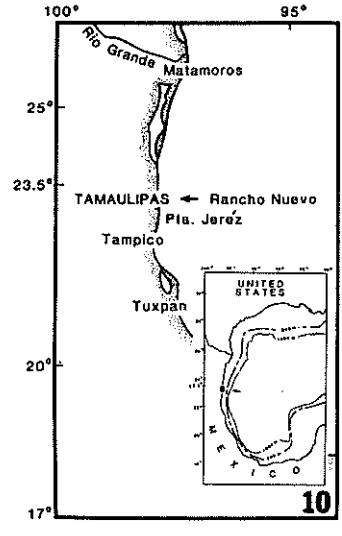


Figures 4–7. (4) Trajectory of Lagrangian drifter number 1599 tracked from 19 November 1980 to 11 May 1981. (Adapted from Lewis, 1986, fig. 3C–6.) (5) Trajectory of Lagrangian drifter number 3374 tracked from 6 October 1982 to 1 March 1983. (Adapted from Lewis, 1984, fig. 4.2-50B.) (6) Trajectory of Lagrangian drifter number 1600 tracked from 20 November 1980 to 11 May 1981. (Adapted from Kirwan et al., 1984, fig. 1C.) (7) Trajectory of Lagrangian drifter number 3350 tracked from 22 April 1984 to 3 September 1984. (Adapted from Waddell, 1984, fig. 41.)

satellite data during the period 1973 to 1984, ". . . suggest that all paths converge to a region in the northwestern Gulf of Mexico best defined by 25°N to 28°N and 93°W to 96°W. Average ring diameters are estimated to be on the order of 185 km, and their westward translation speeds range from 1 to 5 km per day" (Elliott, 1982). The typical life span of a ring or eddy shed by the Loop Current is about 1 year.







Figures 8–10. (8) Linear paths based on the connection of endpoints on nine different Loop Current rings as evidenced by the movements of Lagrangian drifter buoys. (After Waddell, 1986, fig. 4.3–35.) (9) Counter-rotating vortices in the western Gulf of Mexico near Rancho Nuevo. Water flows to the east between the northern cyclone and the southern anticyclone. (Adapted from Merrell and Morrison, 1981.) (10) Location of Rancho Nuevo (adapted from Marquez, 1978) and (inset) proximity of the shelf break off Rancho Nuevo.

Shelf Currents.—Wind is a primary cause of currents along much of the Texas–Louisiana coasts (Cochrane and Kelly, 1985). The known effects of wind stress along other Gulf of Mexico coasts indicates that winds are probably of primary importance in directing surface water movements over and along the north-south trending coast of northeastern Mexico, as well (Brooks, 1984; Csanady, 1982; Sturges and Blaha, 1976). Cochrane and Kelly (1985) concluded that a cyclonic gyre prevails over much of the shelf except during July and August (Fig. 9). Downcoast currents (east or south, with respect to shoreline orientation) dominate much of the coast except during July and August, and form the inner (i.e., shoreward) limb of the cyclone. A countercurrent (north, east, or northeastward flowing) is present near the shelf break, and includes the outer limb of the gyre. Part of the countercurrent extends south and east beyond the gyre. Water flows offshore in the gyre's southwestern limb, and toward the Louisiana coast in its eastern limb. In late August or September after an abrupt change in prevailing wind direction, which becomes again downcoast, the cyclonic gyre is reestablished and reaches its maximum southward extent beyond the Rio Grande. While the eastern limb of the gyre remains in place until July, the southwestern limb (in which surface water flows offshore) contracts to the east beginning in March or April due to increasingly southerly and southwesterly winds; by July, the gyre has disappeared. The overall picture of Texas–Louisiana shelf circulation dominated by a counterclockwise gyre is in good agreement with the findings of Lewis (1984). The persistent anticyclonic boundary current discussed above would presumably reinforce an eastward flowing surface current near the shelf break. Weisenburg (1984) described an east and south flowing jet along a front separating coastal water in the Mississippi River plume and the northern limb of a large (200 km in diameter) anticyclonic Loop Current eddy near 28°53′N, 88°31′W, in December, 1982. The presence of this jet, located somewhat south and east of the Mississippi delta, suggests a mechanism for the transport of floating organisms and debris from the western to the eastern basin of the Gulf. Shaw et al. (1985) noted that juvenile organisms emigrating from estuaries along the Texas–Louisiana coasts during summer, would be carried eastward during the period of longshore current reversal.

Transport of Pelagic Stage Kemp's Ridley.—Kemp's ridley hatchlings emerge from the nest during summer and early fall. As they enter the water and swim toward the open sea the direction of local nearshore currents is probably of less significance to the turtles' initial heading than other orientation cues such as horizon brightness. In conditions of heavy waves, hatchlings might be thrown back upon the beach, where they would likely perish.

Assuming that Kemp's ridley neonates swim vigorously for 24 h or so upon entering the water for the first time; that they swim in a net direction normal to the beach; and can maintain, in the absence of onshore wind drift or longshore currents an average speed of about 1 kn, the turtles would have to swim for about a day before they encountered a western boundary current at the shelf/slope boundary. This amount of effort in terms of energy reserves (yolk) seems to be within the capabilities of Kemp's ridley neonates. The swim frenzy may last for longer than 24 h in which case further swimming would more deeply embed them in the current. In the presence of adverse currents (i.e., inhibiting seaward movement) hatchlings may continue to swim until they encounter a boundary current or swim more slowly until a favorable current is encountered. In the cases mentioned, the likely end result would be eventual entrainment of the turtles in a northward or eastward flowing limb of an anticyclonic eddy.

All anticyclonic eddies derived from the Loop Current translate to the west or southwest across the western basin of the Gulf of Mexico, and contact the shelf/slope boundary of southwestern Texas or Mexico. After contact with the slope most eddies move to the north, either independently or after coalescing with another eddy. These eddies result in a western boundary current which seems to be present much of the time in a given year. This flow will continue to the north until it reaches an area dominated by a cyclonic eddy. As it approaches the northwestern corner of the Gulf, the flow will be in an easterly direction. As noted, the area between the southern limb of a cyclonic eddy, and the northern limb of an anticyclone often results in an eastward jet of some magnitude flowing between them.

A number of distributional scenarios may be postulated for Kemp's ridley hatchlings once they have crossed the continental shelf off Mexico (Fig. 10). They may be captured within an anticyclonic eddy that remains in the southwestern Gulf and spend the entire pelagic phase there (Fig. 7). Second, hatchlings may be swept to the east off the Texas–Louisiana shelf and be entrained in the Loop Current (Fig. 1). Depending upon transit time from the western to the eastern Gulf, and whether the hatchlings fetch up in a northeastern Gulf eddy, and are carried back into the western basin, some them are carried out of the Gulf of Mexico through the Straits of Florida, and drift with the western edge of the Florida Current/Gulf Stream until they are either strong enough to leave the current and disperse shoreward, or are passively transported toward the coast by current meanders or warm-core rings. Some individuals are swept into the open North Atlantic and are presumably lost to the population. We think it unlikely that Kemp's ridley could survive a complete circuit around the North Atlantic Gyre. However, we do not entirely discount the possibility that, as Carr (1986) suggested for loggerheads, some individuals embedded in the warmer central part of the gyre might cross the Atlantic, travel south in the Canary Current, and approach the North American coast via the North Equatorial–Antilles Currents.

While large scale movements of pelagic stage Kemp's ridleys are attributable to wind drift and surface watermass movement, they may be capable of substantive position changes within currents. It is possible that some of the hatchlings "escape" from a given current to be swept into another one; perhaps into one with an entirely different future path or lifespan.

The narrow shelf off Rancho Nuevo, may enhance the probability of neonates reaching a western boundary current. Once entrained in a current, hatchling turtles are probably committed to completing the pelagic dispersal phase in the same direction, and at the same speed as the host current path dictates. Five possible distributional patterns seem more likely to us than others that could be suggested. (1.) Post-hatchlings remain in the central-southwestern Gulf of Mexico. (2.) They are swept out of the western Gulf, are entrained by the Loop Current, and finish the pelagic phase in the Florida Current/Gulf Stream. (3.) As in (2.), but they are captured by a northern Loop Current eddy, and return to the western Gulf. (4.) They do not make it to a major dispersing current, or are ejected from a current, find themselves in coastal waters, and perish there because of presumably higher predation pressure or cold winter temperatures not found in the Loop or Florida Currents. (5.) As an alternative to (4.), older individuals of post-pelagic size (ca. >20 cm) might find themselves in coastal waters, their subsequent developmental habitat, and survive there as benthic carnivores.

Distribution of Post-Pelagic Lepidochelys kempi.—The distribution of coastal benthic habitat (i.e., post-pelagic) *L. kempi* shows an increasing size gradient from

New England waters south to Florida (mean carapace length 30–37.6 cm) (Ogren, in press). This suggests that some post-hatchlings drift to the north in the Florida Current-Gulf Stream. Such individuals may continue to drift in the Gulf Stream and be carried further out to sea, or leave the current at some point as a result of easterly winds or shoreward transport in meanders or eddies that advect them across shelf waters to the coastal zones of the eastern seaboard. In response to seasonal temperature increases small juveniles may actively migrate along the coast to Florida and account for the larger juveniles found there. Tag recapture data indicate that some individuals undergo seasonal migrations along the eastern seaboard of the United States for more than a year. Very few adults, however, have been recorded from the Atlantic coast (Henwood and Ogren, 1987; Schroeder, 1987[3]).

The smallest (20 cm carapace length) coastal-benthic *L. kempi* are commonly found in the coastal zones of western Louisiana and the Florida Panhandle east of Cape San Blas (Ogren, in press). The coastal water distributions of post-pelagic Kemp's ridleys is discussed in Henwood and Ogren (1987) and Ogren (in press). We suggest that these turtles have undergone their entire pelagic developmental stage in the Gulf of Mexico, and have either been ejected from eddies, or have been transported shoreward as a result of surface wind drift.

Summary and Conclusions

Within rather broad limits the likely dispersal patterns of oceanic post-hatchling sea turtles are related to specific ocean surface currents and wind drift. Even small scale variation in these currents should result in dispersal variation between Kemp's ridley cohorts, which we view as a type of imposed bet-hedging of potential benefit to the species.

As circulation models become more refined it may be possible to predict to some degree where a given cohort of *L. kempi* post-hatchlings will leave the pelagic zone and become benthic carnivores. Although environmental and biological variability admittedly limit predictive confidence levels, such knowledge may be useful in conservation efforts.

Circulation in the western Gulf is dominated by a western boundary current formed by anticyclonic eddies derived from the Loop Current. Hatchling Kemp's ridleys cross the narrow continental shelf off Rancho Nuevo and are entrained in this current, which then transports them to the Loop Current or a Loop Current eddy via an eastward flowing jet in the northwestern Gulf. Individuals embedded in the Loop Current will be swept out of the Gulf of Mexico through the Straits of Florida and transported to the north in the Florida Current and Gulf Stream. Post-hatchlings entrained by a Loop Current eddy may remain in the northeastern Gulf, or be carried back to the central-southwestern Gulf, depending on the movement and lifespan of the eddy.

The size distribution of post-pelagic juveniles suggests that the smallest post-pelagic individuals found in coastal waters of western Louisiana and the eastern Florida Panhandle, have spent their entire pelagic developmental period in the Gulf of Mexico which has been estimated to last about 2 years (Zug, in press[4]). Intermediate size post-pelagic individuals are found in coastal New England waters, and the largest animals are found off the east coast of Florida (Ogren, in press). This distribution may indicate that, of those pelagic-stage Kemp's ridleys swept out of the Gulf of Mexico, many or most are transported a considerable distance to the north, then actively migrate south (toward the Gulf of Mexico) as coastal water temperatures rise (Henwood and Ogren, 1987).

Acknowledgments

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