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Western North Atlantic Waters: Crucial Developmental Habitat for Kemp's Ridley and Loggerhead Sea Turtles

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ABSTRACT. – **Juvenile Kemp's ridley (*Lepidochelys kempii*) and loggerhead turtles (*Caretta caretta*) occur in a continuous distribution from southern Atlantic waters far into northern latitudes. Each year, during warmer months, considerable numbers of juveniles of both species migrate into shallow coastal habitats in the western North Atlantic, where they remain for many weeks, foraging on a benthic diet composed mainly of crabs. During the foraging season, individuals remain local, and exhibit high growth rates. Recapture records and satellite telemetry data reveal that during the fall, both species leave colder northern waters and migrate southward along the continental shelf. After overwintering in common coastal areas, such as near Cape Canaveral, Florida, or Onslow Bay, North Carolina, individuals move northward and again enter coastal bays and estuaries. Studies over recent years in the western North Atlantic highlight the importance to both species of bay and estuarine habitats extending from Florida to New England. Management strategies and species recovery plans must include serious consideration of these crucial developmental habitats.**

KEY WORDS. – **Reptilia; Testudines; Cheloniidae; *Lepidochelys kempii*; *Caretta caretta*; sea turtle; developmental habitat; migration; foraging; growth; juvenile; telemetry; satellite tracking; conservation; North Atlantic; USA**

Northern regions of the western North Atlantic have, in the past, not been recognized as typical habitat for sea turtles. Rather, until the past two to three decades, sea turtles were regarded as inhabitants of tropical and sub-tropical regions with a minor presence at higher latitudes. This dogmatic view of sea turtles as tropical inhabitants dated back to at least the middle 19th century (DeKay, 1842) and, until the 1980s, was pervasive throughout historical literature (citations in Morreale et al., 1992). Furthermore, because this outlook persisted for so long, it also became somewhat entrenched in current thought. This history helps explain why it took many years and numerous separate reports of leatherbacks (*Dermochelys coriacea*), loggerheads (*Caretta caretta*), Kemp's ridleys (*Lepidochelys kempii*), and green turtles (*Chelonia mydas*) in the northeastern and mid-Atlantic USA waters, before these more northern regions of the western North Atlantic were considered part of the normal range of sea turtles.

The customary tenet previously was that sea turtles lived most of their life cycles in warmer regions, and that northern temperate waters were outside their normal ranges (Hendrickson, 1980). Much of this historical inertia undoubtedly was influenced by obvious nesting activities, which are restricted mostly to tropical and subtropical beaches. Additionally, most early scientific studies were concentrated only in regions where nesting occurred. In the special case of the Kemp's ridley, which has only one major nesting beach in the Gulf of Mexico, it seemed inevitable that this species would be regarded as a warm-water sea turtle. Currently, as more and more studies have focused on details of sea turtle ecology away from the nesting beaches, it has become broadly accepted that leatherback, loggerhead, and Kemp's ridley sea turtles have distributions ranging far into temperate latitudes, and are prominent members of the sea turtle community in northern temperate waters of the western Atlantic.

Further, as studies on North Atlantic loggerheads and Kemp's ridleys have proliferated, many parallels between the two species have become obvious. The current perspective is that nesting female loggerheads and Kemp's ridleys congregate in warmer southern regions to nest while juveniles move northward, where they often become abundant in coastal waters. Although none of the sea turtles could be considered full-time residents of northern temperate waters, it is clear that large numbers of loggerhead and Kemp's ridley sea turtles move into coastal waters along the entire eastern USA seaboard each year. These turtles, which are mostly juveniles, begin appearing in nearshore habitats as water temperatures rise in spring, and remain throughout the warmer months, feeding on abundant benthic invertebrates. As temperatures decline rapidly in the fall, juveniles of both species leave their coastal habitats and join a larger contingent of other turtles migrating southward to overwinter (Musick and Limpus, 1997).

In the following discussion, in which we have incorporated data from past and recent studies, a comparison of the natural history and ecology of Kemp's ridley and loggerhead turtles in the western North Atlantic is more an accounting of their similarities, rather than of their differences. Hence, as is true for loggerheads, any accurate depiction of the ecology and distribution of Kemp's ridleys must describe them as seasonal inhabitants of northern temperate waters.

Furthermore, ecological accounts also must acknowledge the extensive migratory movements of these turtles between southern and northern habitats. Perhaps more importantly, any conservation strategies involving these endangered turtles must include serious consideration of the large numbers of turtles that occur in coastal Atlantic waters, migrate to and from habitats extending from Florida to New England, and congregate in overwintering areas such as coastal North Carolina and Florida and possibly offshore in the northern arm of the Gulf Stream.

Western North Atlantic Sea Turtle Community

Within the past few decades it has been documented that leatherback, loggerhead, green, and Kemp's ridley turtles regularly occur in North Atlantic waters of northern USA and southeastern Canada during the warmer months (Bleakney, 1965; Brongersma, 1972; Lazell, 1976, 1980; Shoop, 1980; Standora et al., 1989; Morreale and Standora, 1998). Early on, the most notable aspect of these accounts was the repeated presence of the Kemp's ridley, both because of their critically endangered status, and the great distance from their nesting beaches in the Gulf of Mexico. The unexpectedly common occurrence of Kemp's ridley turtles in extreme northern waters hinted at a much larger functional range for this species than was previously suspected. Indeed, such a range extension was strongly supported by the large numbers of Kemp's ridleys also recorded in the Chesapeake Bay region (Lutcavage and Musick, 1985; Keinath et al., 1987; Byles, 1988), squarely between the southern and northern extremes along the Atlantic seaboard.

The acceptance of far northern waters as important sea turtle habitat, however, was not immediate, as demonstrated by Hendrickson (1980), who argued that the northeastern USA was a disadvantageous environment for Kemp's ridley turtles because of the cold climate. This speculation was compelling given that many turtles, both historically and recently, have been found dead or moribund on northern shores as a result of hypothermia in early winter weeks (Murphy, 1916; Latham, 1969; Meylan and Sadove, 1986; Morreale et al., 1992; Still et al., 2003). Researchers with more moderate opinions proposed that young sea turtles could be swept occasionally into inshore waters of the northeastern USA by anomalous currents or eddies of the Gulf Stream, whereupon they might sometimes find their way back to southern waters (Carr, 1980, 1986a; Meylan, 1986; Ogren, 1989; Collard and Ogren, 1990). The implication at that time, however, remained that the occurrence of turtles in northern habitats was merely accidental, as opposed to adaptive.

Among the continuum of hypotheses, the most convincing current thought is that northeastern USA waters, as far north as New York and New England, provide critical habitat for foraging loggerhead, leatherback, and Kemp's ridley turtles (Lazell, 1976, 1980; Lutcavage and Musick, 1985; Musick, 1988; Shoop and Kenney, 1992; Morreale and Burke, 1997; Musick and Limpus, 1997). Furthermore, these assemblages of turtles are not disjunct or isolated. Rather, it is apparent that many turtles migrate into northern nearshore habitats from southern waters each summer, and return southward each fall (Lutcavage and Musick, 1985; Henwood and Ogren, 1987; Byles, 1988; Morreale and Standora, 1990; Shoop and Kenney, 1992; Keinath, 1993; Epperly et al., 1995a; Morreale and Standora, 1998). Thus, the western North Atlantic coastal sea turtles merely represent the northern portion of the same populations that mate, nest, and overwinter in southern and tropical regions, and are distributed continuously and move freely along the USA eastern seaboard. In addition, the coastal seasonal occurrence and distribution patterns appear to be nearly identical for at least two of the Atlantic species: Kemp's ridleys and loggerheads.

Ecology of Kemp's Ridleys and Loggerheads Along the Atlantic USA Coast

Seasonal Occurrence. — The yearly activity cycle for juvenile Kemp's ridley and loggerhead sea turtles along the USA east coast begins in spring. In early March, many individuals of both species reside in southern waters, but by April the numbers of juveniles in Atlantic waters of Florida decrease (Henwood, 1987; Henwood and Ogren, 1987; Schmid, 1995). At the same time, young turtles begin to show signs of activity farther north, from Georgia to North Carolina (Epperly et al., 1990, 1995a; Maley et al., 1994; Musick et al., 1994). In May, as water temperatures continue to rise even farther northward, Kemp's ridleys and loggerheads begin to appear in Virginia (Lutcavage and Musick, 1985; Keinath et al., 1987; Keinath et al., 1994), and by June, juveniles begin to arrive in New York (Morreale and Standora, 1994; Morreale and Burke, 1997) and New England (Bleakney, 1965; Shoop and Kenney, 1992). Although other species of sea turtles also occur in these nearshore habitats north of Florida, it is apparent that the most abundant are loggerheads and Kemp's ridleys.

The predictable pattern of seasonal occurrence of sea turtles, first appearing in southern waters, and then progressively northward as temperatures increase, leads to a logical assumption that sea turtles migrate northward in the springtime (Bleakney, 1965; Shoop, 1980; Lutcavage and Musick, 1985; Henwood and Ogren, 1987; Morreale and Standora, 1991; Shoop and Kenney, 1992). The similarity of turtle activity patterns from year to year, and the sequence of timing in different regions easily lends itself to the parsimonious hypothesis of annual south-to-north migration. However, the simple behavioral model that was first proposed was further refined to include the additional influxes each year of young Kemp's ridleys and loggerheads that have undergone an ontogenetic shift, from a pelagic to a benthic feeding mode (Morreale and Standora, 1994; Musick and Limpus, 1997). These young post-transition animals also appear to be an important component of the assemblages of turtles in coastal waters each year.

More recent telemetry studies have elucidated a possible third behavior in which some turtles may be migrating seasonally between Atlantic coastal habitats and warmer offshore waters. Such west-to-east movements have been documented for several loggerheads that migrated offshore during the colder months to linger in the warm Gulf Stream and North Atlantic Current waters (Byles, 1988; Keinath, 1993; Morreale and Standora, 1994; Morreale, 1999). Furthermore, loggerheads from each of these studies were later monitored as they returned back toward coastal waters, indicating a two-way journey from coastal to pelagic waters.

Offshore migration could be unique to juvenile loggerheads, but such behavior may also occur in a small portion of the coastal Kemp's ridley population. Small numbers of Kemp's ridleys have been reported captured in the Pelagic Longline Fishery in waters over the continental slope nearly 400 km offshore, and occasionally as far away as the Grand Banks, more than 2500 km from coastal USA waters (W. Witzell, *pers. comm.*). Without knowledge of their previous history, it is difficult to label these individuals definitively as members of the coastal benthic foraging community. However, juveniles in two studies have been tracked from coastal habitats to deeper waters offshore, where they may have later ended up in the Gulf Stream (Byles, 1988; Morreale and Standora, 1994). In a separate and more definitive study, a coastal juvenile Kemp's ridley was monitored as it first began to overwinter in coastal North Carolina waters, and later moved offshore into warmer Gulf Stream waters of the western Atlantic (Renaud, 1995). To date, no return trips towards the coast have been documented for Kemp's ridleys.

Size and Life Stage. — A notable characteristic of the turtles that appear in nearshore waters along the Atlantic seaboard is the small size and apparent young age of most individuals. This pattern is evident in loggerheads and is starkly obvious in Kemp's ridleys. Although many adult loggerheads breed along southeastern shores, and many appear offshore far to the north, there are few adult-sized individuals in nearshore waters north of the nesting beaches. In North Carolina and Virginia most loggerheads in bays and estuaries are medium-sized juveniles (Lutcavage and Musick, 1985; Byles, 1988; Epperly et al., 1995a). In comparable habitats farther north, virtually none are adult-sized (Morreale and Standora, 1994; Morreale and Burke, 1997).

This trend is even more conspicuous for the Kemp's ridley which, both in offshore and nearshore Atlantic waters, appears to be represented almost exclusively by juveniles. Furthermore, most individuals are from small size classes. Among the largest live Kemp's ridleys that have been reported in coastal Atlantic waters were three individuals with a straight-line carapace length (SCL) greater than 60 cm in Florida (Henwood and Ogren, 1987; Witherington and Ehrhart, 1989; Schmid, 1995), and one in Chesapeake Bay (Keinath et al., 1994). Also, there have been only a few individuals between 55 and 60 cm SCL recorded in the southern and mid-Atlantic states of Florida, Georgia, South Carolina, and Virginia (Lutcavage and Musick, 1985; Henwood and Ogren, 1987; Witherington and Ehrhart, 1989). The vast majority of Kemp's ridleys that inhabit Atlantic coastal waters are smaller than 50 cm SCL. In the far northern waters of New York and Massachusetts, Kemp's ridleys appear to be further restricted to size classes smaller than 45 cm SCL (Morreale et al., 1992; Morreale and Burke, 1997; Still et al., 2003).

It has been suggested often that there is a geographic trend in which the sizes of Kemp's ridleys increase along a continuum from north to south in coastal Atlantic waters. This has stemmed from a supposition of steadily increasing mean sizes of Kemp's ridleys along a gradient moving southward. To discern any such trend, we examined some of the larger databases containing many live captures among different habitats along the eastern seaboard (Table 1). Presented here are the comparisons of mean sizes and ranges of 883 Kemp's ridleys from eight different data sets, spanning a latitudinal gradient from New England to Florida. The overall mean size for all of the Atlantic sites was 32.9 cm SCL. Indeed, the means and ranges of sizes varied among habitats, and both the mean and maximum sizes of Kemp's ridleys from extreme northern habitats were smaller than those from southern coastal waters. However, the purported trend of steadily increasing sizes does not withstand scrutiny. More accurately, the calculated mean sizes of Kemp's ridleys are highest in the middle Atlantic states, and the maximum sizes are highest in Florida, followed by Chesapeake Bay.

Upon closer examination of the size distributions of Atlantic coastal Kemp's ridleys, the greater mean sizes in

Table 1. Reported mean carapace lengths and size ranges for 883 *Lepidochelys kempii* collected from six different habitats along the USA Atlantic coast. Nearly all were juvenile-sized turtles, and most were small juveniles. No large individuals were reported in northern habitats (upper rows), but there was no discernible trend from north to south (lower rows) in other measurements.

Habitat	Mean SCL (cm)	Size Range (cm)	*n*	Reference
Massachusetts	26.9	18.4 - 37.2	216	C. Ryder, *pers. comm.*; Still et al., 2003
New York	30.7	22.5 - 42.7	261	Morreale et al., 1992; Morreale and Burke, 1997
Chesapeake Bay	37.5*	16.0 - 64.5	202	Keinath et al., 1994
North Carolina	38.8*	23.6 - 60.5	30	Anonymous, 1992
South Carolina and Georgia	34.8	20.3 - 57.2	21	Henwood and Ogren, 1987
Florida	37.4	21.5 - 66.0	153	Henwood and Ogren, 1987; Schmid, 1995
Overall	32.9	16.0 - 66.0	883	

* Converted from curved carapace lengths using same method as Schmid 1995.

southern waters are really a consequence of the presence of some big individuals there. Greater mean values do not signify that turtles in southern waters are larger, but instead that there are some larger turtles present in southern waters, while they are absent in far northern habitats. There is no discernible north-to-south trend in the minimum sizes of animals encountered. Rather, there is great similarity among all Atlantic coastal habitats in that small Kemp's ridleys comprise the majority of individuals in coastal waters. Furthermore, the smallest size classes, less than 30 cm SCL, make up a large proportion of every one of the study groups examined.

It is perhaps these small-sized turtles that reveal the nature and importance of coastal Atlantic waters for Kemp's ridleys, primarily as foraging and developmental areas for post-pelagic stage juveniles. The generally accepted scenario for early life stages is that, as hatchlings, sea turtles swim away from their natal beaches along Atlantic and Gulf shores and migrate for the first time out to the open sea (Carr and Meylan, 1980; Carr, 1986a,b; Collard and Ogren, 1990; Witherington and Salmon, 1992; Musick and Limpus, 1997). There they remain in the pelagic environment, feeding in surface waters until reaching a certain size (Carr, 1967; Carr and Meylan, 1980; Carr, 1986a). For Kemp's ridley juveniles, the pelagic stage appears to culminate at sizes of around 20 cm SCL, which translates to estimated ages between 2 and 5 years old (Zug et al., 1997; Chaloupka and Zug, 1997). At this time the young Kemp's ridleys apparently undergo a behavioral shift and make their way into shallower coastal waters (Morreale and Standora, 1994; Schmid, 1995; Musick and Limpus, 1997). An ontogenetic shift is supported not only by the obvious absence of smaller size classes along coastal waters, but by what appear to be distinct changes in growth rates around this time in the turtles' development (Chaloupka and Zug, 1997). Such a decline in growth rate may be a strong motivating force for juveniles to move out of a pelagic mode and into coastal waters. Thus, the Atlantic coastal bays and estuaries are crucial in providing habitat for small Kemp's ridleys that have undergone a transition to become shallow water benthic foragers.

Feeding and Growth. — After the juvenile loggerheads and Kemp's ridleys arrive in Atlantic coastal habitats, they remain through the rest of the summer and early fall. There they feed on a diet composed mainly of benthic invertebrates. Loggerheads seem to exhibit more breadth in dietary choice than do Kemp's ridleys, eating a variety of crabs, mollusks, horseshoe crabs, and even sea pens (Lutcavage, 1981; Plotkin et al., 1993; Burke et al., 1993a). The diet of Atlantic coastal Kemp's ridleys also can include various items such as mollusks and seahorses (Morreale and Standora, 1991; Burke et al., 1993a,b, 1994), however, nearly every Kemp's ridley stomach and fecal sample examined to date in Atlantic coastal habitats has included crabs. More importantly, crabs comprise the vast majority of the bulk of their diet (DeSola and Abrams, 1933; Hardy, 1962; Lutcavage and Musick, 1985; Bellmund et al., 1987; Morreale and Standora, 1991; Burke et al., 1993a, 1994).

It has often been reported that Kemp's ridleys specialize on blue crabs and closely related species, but there appears to be some variation in diets, even among habitats along the Atlantic coast. In studies conducted in Chesapeake Bay (Hardy, 1962; Lutcavage, 1981; Bellmund et al., 1987), blue crabs (*Callinectes sapidus*) were found to be a main food item, but rock crabs (*Cancer irroratus*) also were recorded. In Georgia the spotted lady crab (*Ovalipes stephensoni*) was identified as a main dietary component from dissected Kemp's ridley specimens (DeSola and Abrams, 1933), and in New York spider crabs (*Libinia* sp.) made up the bulk of the diet, followed by rock crabs and the lady crab (*Ovalipes ocellatus*) (Morreale and Standora, 1991; Burke et al., 1993a, 1994).

It is not clear whether dietary differences among Kemp's ridleys reflect different environmental conditions, different age-specific tendencies, or merely individual variation. In New York waters, even in habitats where spider crabs were not the most abundant crab, they were the most preyed-upon species (Morreale and Standora, 1991, 1992). The disproportionate selection of these slow-moving crabs was not attributed to habitat differences, but instead to the youth and potential inexperience of the small Kemp's ridleys arriving inshore for the first time. The premise is that, as inexperienced benthic foragers, the young Kemp's ridleys feed disproportionately on the walking crabs, and as they hone their skills, they may start feeding with greater frequency on swimming crabs, which are faster and more elusive (Morreale and Standora, 1991, 1992; Burke et al., 1994). Such a change in diet with age and experience was well supported by a comprehensive diet study in southern Texas waters, where larger Kemp's ridleys appeared to be much more selective in their diets than did smaller individuals (Shaver, 1991).

Some juveniles exhibit preferences for diets that are markedly different than other individuals. In New York, while many small Kemp's ridleys fed mainly on spider crabs, some concentrated more on rock crabs, and two other individuals appeared to eat only lady crabs (Burke et al., 1993b). Another two small Kemp's ridleys in New York ate seahorses (Burke et al., 1993a); one had at least 20 of these fish in its gut.

Observed differences in diet could contribute to differences in growth rates among individuals. It is likely also that differences in food availability, environmental quality, and temperature among the Atlantic coastal habitats and among years could similarly affect growth. Possibly for these reasons, the rates of growth of Kemp's ridleys in Atlantic coastal habitats are somewhat variable. In studies in Florida (Schmid, 1995) and New York (Morreale and Standora, 1994), growth estimates based on recapture measurements of wild-caught turtles ranged from negligible changes in SCL to as high as 12.2 cm/yr in New York waters, and from 0 to 29.2 cm/yr in east-central Florida. In both cases, the highest values were extrapolations of measured growth increases over periods of less than 180 days. For longer-term recaptures over 180 days the highest rate of growth was 7.8 cm/yr in the Florida study (Schmid, 1995). This may be a more reasonable yearly estimate, since northern Atlantic

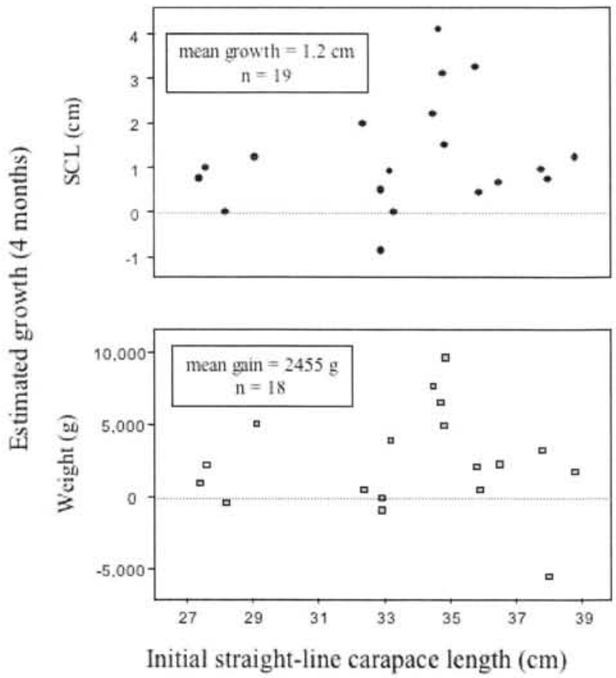

Figure 1. Growth measurements for carapace length (top) and weight (bottom) of juvenile *Lepidochelys kempii* individuals captured and later recaptured in New York waters. Because growth probably is limited to a 4-month season in New York, estimates are presented for that interval. Initial sizes of the turtles ranged from 27–39 cm. There was no detectable linear relationship between initial size and growth rates; $p > 0.3$ for both length ($n = 19$) and weight ($n = 18$). Actual measurements (before estimates) were all taken within 90 days of initial capture. The highest measured growth in this time frame was 2.4 cm in length, with a weight gain of 1497 g.

coastal turtles probably do not exhibit year-round growth. In New York, the activity season is more likely condensed to approximately four months of the year. This would yield a conservative maximum growth estimate of 4.1 cm/yr for northern Kemp's ridleys (Fig. 1), if their sole food source were from northern habitats.

Increases in mass also can be a good indicator of feeding and growth, but must be interpreted cautiously. Weights of animals can vary greatly over relatively short periods of time with fluid gain or loss through ingestion, evaporation, and defecation. In the case of small Kemp's ridleys, changes of a few hundred grams could cause significant differences in total weight. Presumably, because of these fluctuations and logistical reasons, there are few available written reports of weight changes in coastal Atlantic Kemp's ridleys. To examine growth more completely, we compiled all of the weight data from recaptures of Kemp's ridleys in New York waters (Standora et al., 1989a,b; Morreale and Standora, 1990, 1991, 1992; Burke et al., 1993b) for summarization (Fig. 1). In general, weight measurements followed the observed patterns in carapace measurements. Weight increases varied among individuals, ranging from a loss of 228 g to increases of as much as 1497 g within recapture intervals of less than 90 days. The measured weight gains represented increases of as great as 27% of the turtles' initial body weights, with a mean increase of 8%. The combination of increases in length and weight in these studies is strongly indicative of good potential for feeding and growth in Atlantic coastal habitats.

There are growth estimates also for Atlantic coastal Kemp's ridleys based on skeletochronological data (Chaloupka and Zug, 1997; Zug et al., 1997). These calculated growth rates from age and length relationships provide an excellent alternative technique to compare the measurements of the wild-caught turtles. In addition, the use of independent measures on large samples composed mainly of Kemp's ridleys from Atlantic coastal habitats, allowed for the development of a better model to describe growth in juveniles. Many previous studies used von Bertalanffy, Gompertz, or logistic functions to portray turtle growth (Chaloupka and Musick, 1997). However, a more realistic way to look at growth in early life stages is to imagine it occurring in spurts, with rates of increase changing depending on ontogenetic stage, size class, or habitat. With this premise, Chaloupka and Zug (1997) proposed a polyphasic growth model which better reflects the variable rates observed among individual Kemp's ridleys, both in bone growth and in measured growth rates. The predicted rates by this method compare nicely with the estimated rates from mark-recapture studies in New York and Florida waters (Table 2).

Long-Distance Movements. — In some warmer Atlantic habitats such as coastal Florida, juvenile Kemp's ridleys and loggerheads may be found year-round. However, these coastal southern populations appear to swell during winter months due to an influx of juvenile turtles immigrating from more northern waters (Carr and Caldwell, 1956; Henwood, 1987; Henwood and Ogren, 1987; Ogren, 1989; Witherington and Ehrhart, 1989; Schmid, 1995). Coupled with these observed wintertime increases are numerous observations of emigration out of every coastal habitat north of North

Table 2. Growth estimates for juvenile *Lepidochelys kempii* from northern and southern Atlantic coastal habitats compared with growth rates predicted by skeletochronological analysis. Florida data from Schmid (1995). Measurements were taken from recaptured wild turtles. All recapture intervals for New York turtles were less than 90 days; in Florida 3 turtles were captured more than 180 days later. Growth rates for recaptured turtles are presented as yearly estimates for comparison. In New York the actual yearly rate may be closer to the four-month estimate. Similarly, in Florida, the long-term recapture rates may be more representative of actual annual growth. Initial turtle sizes were within the ranges reported; SCL = straight-line carapace length; n = number of turtles.

Habitat	Range SCL (cm)	n	Estimated Growth from Recaptures	Predicted Growth (Chaloupka and Zug, 1997)
New York	27 – 39	19	cm/yr: negative – 12.2	cm/4 mo: negative – 4.1; cm/yr: 2.3 – 4.5
Florida	21 – 60*	10	cm/yr (all): 0 – 29.2	cm/yr (>180 d): 4.3 – 7.8; cm/yr: 1.3 – 10.3

* Reported size range of all captures; sizes of recaptured turtles were not specified.

Carolina. The timing of these movements into and out of geographically separated habitats indirectly supports an assumption of seasonal movements up and down the Atlantic coast. However, the direct link between northern and southern habitats only comes from observations of travel between these sites.

Synthesis of many observation and distribution studies, which include shipboard surveys and fishermen and observer records, suggests that there is seasonal movement of turtles into and out of coastal Florida and Georgia (Henwood, 1987; Henwood and Ogren, 1987; Schmid, 1995), Pamlico Sound (Epperly et al., 1995a), Chesapeake Bay (Lutcavage and Musick, 1985; Keinath et al., 1987; Byles, 1988; Keinath, 1993), New York (Morreale and Standora, 1989, 1990, 1991, 1992, 1994; Morreale and Burke, 1997), and New England (Lazell, 1980; Shoop, 1980). Moreover, timing of movements out of southern waters in spring corresponds to the influx of turtles in more northern habitats, and the pattern is reversed each fall. Further observational studies that included aerial surveys (Shoop et al., 1981; Keinath et al., 1987; Byles, 1988; Shoop and Kenney, 1992; Hopkins-Murphy and Murphy, 1994; Musick et al., 1994; Epperly et al., 1995b,c) have provided complementary data that strongly support the assumption of directed seasonal movements of turtles between southern and northern Atlantic coastal habitats.

In addition, mark-recapture data from several independent studies collectively have indicated considerable movement of sea turtles along the Atlantic coast (Fig. 2). All told, there have been several published reports of tagged turtles traveling between Florida and the mid-Atlantic states (Meylan et al., 1983; Lutcavage and Musick, 1985; Henwood, 1987; Henwood and Ogren, 1987; Byles, 1988; Epperly et al., 1995a; Schmid, 1995), a loggerhead from Rhode Island to Georgia (Shoop and Ruckdeschel, 1989), and over a dozen individuals that have migrated from New York to southern waters (Morreale and Standora, 1989, 1994; Morreale and Burke, 1997). In general, the more intensively a habitat has been studied, the more data there are on long-distance coastal movements. Most of these recapture records were of juvenile loggerheads, followed by juvenile Kemp's ridleys, with only a few green turtles. The longest recorded movements, which span the 1700 km from the northeastern USA to Florida, really underscore the connectedness of all of the Atlantic coastal habitats. Not only do juveniles appear to move up the coast in spring, but their emigration in fall appears to ultimately lead them back southward.

Fall Emigration. — More recently, with technological advances in satellite telemetry, some excellent information has been compiled for individual turtles after they move out of inshore coastal habitats. The observed satellite tracks of turtles traveling between Atlantic habitats include records of juvenile Kemp's ridleys and loggerheads migrating between Florida and North Carolina (Renaud, 1995; Gitschlag, 1996), from Chesapeake Bay to North Carolina and southward to Florida, or into Gulf Stream waters (Byles, 1988; Keinath et al., 1989; Keinath, 1993), and from New York to southern coastal and Gulf Stream waters (Standora and Morreale,

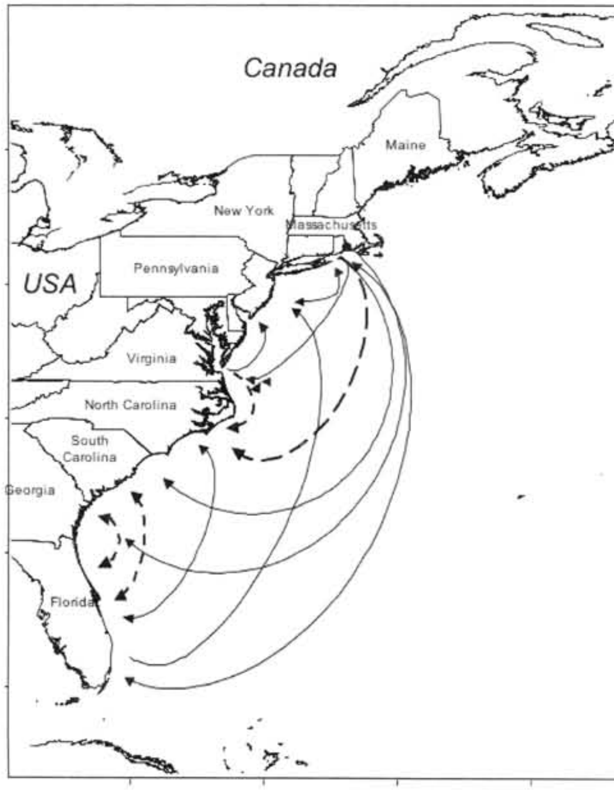

Figure 2. Extensive movements of turtles northward and southward along most of the Atlantic USA coast as determined by recaptures. Lines represent connections between recapture points of 11 *Lepidochelys kempii* (dashed lines) and 51 *Caretta caretta* individuals (solid lines) that traveled among 12 different coastal sites. Arrows indicate the direction of travel into and out of the coastal sites, but lines do not indicate actual paths of travel. Turtles migrated into and out of nearly every site, and some movements spanned the entire distance between New York and Florida.

1991, Morreale and Standora 1991, 1992, 1994; Morreale, 1999). These studies definitively support the premise of seasonal travel that was initially based on distribution and mark-recapture data. Furthermore, these first detailed accounts of migration have revealed extremely similar patterns of movement of coastal juveniles, from year to year, and among individuals of loggerheads and Kemp's ridleys.

Just as in the observation and mark-recapture studies, each telemetry study individually reinforces the pattern of emigration out of inshore habitats and southward in fall. Also, when taken together, the telemetry data are extremely complementary in providing a cohesive overview of the patterns of migration of coastal Kemp's ridleys (Fig. 3). In October and November, Kemp's ridleys were observed migrating southward from northern Florida, Georgia, North Carolina, Virginia, and New York habitats (Byles, 1988; Morreale and Standora, 1992; Keinath, 1993, Renaud, 1995; Gitschlag, 1996). Along the entire length of the Atlantic coast, the timing and pattern of fall movements was similar. All of the observed fall movements were oriented southward, most movements were within continental shelf waters, and migrating turtles in all the studies exhibited relatively directed, steady travel which carried them away from colder waters.

Carolina. The timing of these movements into and out of geographically separated habitats indirectly supports an assumption of seasonal movements up and down the Atlantic coast. However, the direct link between northern and southern habitats only comes from observations of travel between these sites.

Synthesis of many observation and distribution studies, which include shipboard surveys and fishermen and observer records, suggests that there is seasonal movement of turtles into and out of coastal Florida and Georgia (Henwood, 1987; Henwood and Ogren, 1987; Schmid, 1995), Pamlico Sound (Epperly et al., 1995a), Chesapeake Bay (Lutcavage and Musick, 1985; Keinath et al., 1987; Byles, 1988; Keinath, 1993), New York (Morreale and Standora, 1989, 1990, 1991, 1992, 1994; Morreale and Burke, 1997), and New England (Lazell, 1980; Shoop, 1980). Moreover, timing of movements out of southern waters in spring corresponds to the influx of turtles in more northern habitats, and the pattern is reversed each fall. Further observational studies that included aerial surveys (Shoop et al., 1981; Keinath et al., 1987; Byles, 1988; Shoop and Kenney, 1992; Hopkins-Murphy and Murphy, 1994; Musick et al., 1994; Epperly et al., 1995b,c) have provided complementary data that strongly support the assumption of directed seasonal movements of turtles between southern and northern Atlantic coastal habitats.

In addition, mark-recapture data from several independent studies collectively have indicated considerable movement of sea turtles along the Atlantic coast (Fig. 2). All told, there have been several published reports of tagged turtles traveling between Florida and the mid-Atlantic states (Meylan et al., 1983; Lutcavage and Musick, 1985; Henwood, 1987; Henwood and Ogren, 1987; Byles, 1988; Epperly et al., 1995a; Schmid, 1995), a loggerhead from Rhode Island to Georgia (Shoop and Ruckdeschel, 1989), and over a dozen individuals that have migrated from New York to southern waters (Morreale and Standora, 1989, 1994; Morreale and Burke, 1997). In general, the more intensively a habitat has been studied, the more data there are on long-distance coastal movements. Most of these recapture records were of juvenile loggerheads, followed by juvenile Kemp's ridleys, with only a few green turtles. The longest recorded movements, which span the 1700 km from the northeastern USA to Florida, really underscore the connectedness of all of the Atlantic coastal habitats. Not only do juveniles appear to move up the coast in spring, but their emigration in fall appears to ultimately lead them back southward.

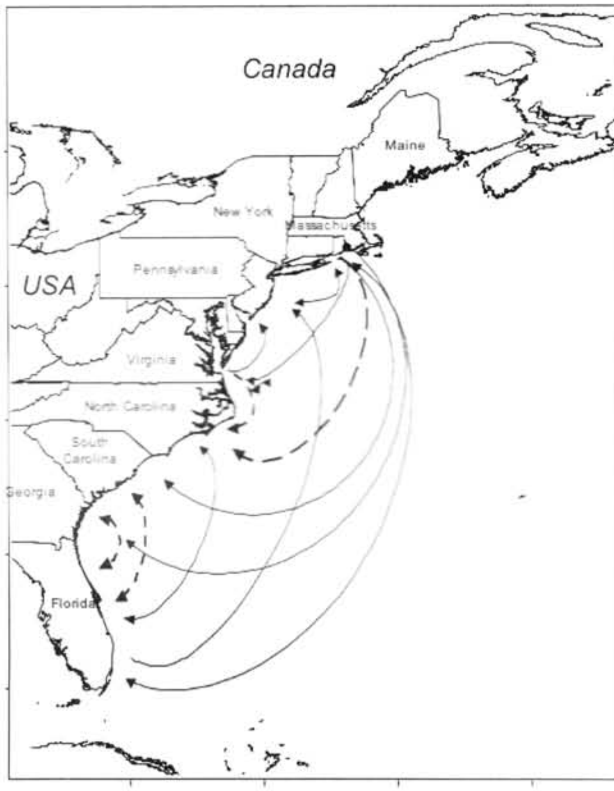

Figure 2. Extensive movements of turtles northward and southward along most of the Atlantic USA coast as determined by recaptures. Lines represent connections between recapture points of 11 *Lepidochelys kempii* (dashed lines) and 51 *Caretta caretta* individuals (solid lines) that traveled among 12 different coastal sites. Arrows indicate the direction of travel into and out of the coastal sites, but lines do not indicate actual paths of travel. Turtles migrated into and out of nearly every site, and some movements spanned the entire distance between New York and Florida.

Fall Emigration. — More recently, with technological advances in satellite telemetry, some excellent information has been compiled for individual turtles after they move out of inshore coastal habitats. The observed satellite tracks of turtles traveling between Atlantic habitats include records of juvenile Kemp's ridleys and loggerheads migrating between Florida and North Carolina (Renaud, 1995; Gitschlag, 1996), from Chesapeake Bay to North Carolina and southward to Florida, or into Gulf Stream waters (Byles, 1988; Keinath et al., 1989; Keinath, 1993), and from New York to southern coastal and Gulf Stream waters (Standora and Morreale, 1991, Morreale and Standora 1991, 1992, 1994; Morreale, 1999). These studies definitively support the premise of seasonal travel that was initially based on distribution and mark-recapture data. Furthermore, these first detailed accounts of migration have revealed extremely similar patterns of movement of coastal juveniles, from year to year, and among individuals of loggerheads and Kemp's ridleys.

Just as in the observation and mark-recapture studies, each telemetry study individually reinforces the pattern of emigration out of inshore habitats and southward in fall. Also, when taken together, the telemetry data are extremely complementary in providing a cohesive overview of the patterns of migration of coastal Kemp's ridleys (Fig. 3). In October and November, Kemp's ridleys were observed migrating southward from northern Florida, Georgia, North Carolina, Virginia, and New York habitats (Byles, 1988; Morreale and Standora, 1992; Keinath, 1993, Renaud, 1995; Gitschlag, 1996). Along the entire length of the Atlantic coast, the timing and pattern of fall movements was similar. All of the observed fall movements were oriented southward, most movements were within continental shelf waters, and migrating turtles in all the studies exhibited relatively directed, steady travel which carried them away from colder waters.

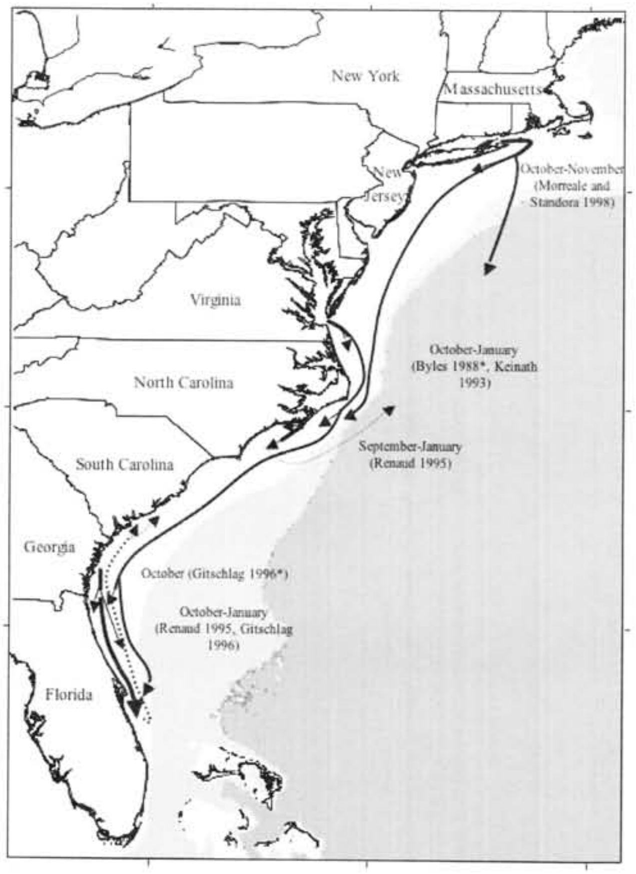

Figure 3. General characterizations of the observed migration paths of 13 *Lepidochelys kempii* from five separate studies along the USA east coast, strongly supporting the premise of seasonal migration of juvenile Kemp's ridleys among coastal habitats. All of the 10 turtles that were tracked by satellite, along with the three that were monitored by radio transmitters(*), swam southward in the fall (solid lines). After remaining sedentary for many weeks, one turtle made a late-winter move offshore from North Carolina, and two returned northward from Florida in the following spring (dotted lines). Thickened lines represent the common pathways of more than one individual.

The similar fall migration patterns are not exclusive to Kemp's ridleys. Rather, the patterns observed for juvenile Kemp's ridleys and loggerheads traveling from many of the same habitats are virtually identical (Byles, 1988; Keinath, 1993; Morreale and Standora, 1998; Morreale, 1999). When long-distance migration patterns of turtles from New York waters were analyzed, it was shown that their paths each fall were statistically similar (Morreale, 1999). Moreover, the predictable spatial pattern persisted, despite using different techniques on two turtle species, in separate studies, and over five separate years. When all of the migratory paths of these northern turtles are superimposed (Fig. 4), it is apparent that both species move southward each fall, mostly within a relatively well-defined corridor that extends for more than 1000 km along continental shelf waters.

The high degree of similarity in movements is evident also with respect to timing of travel. On the same date of 30 October in three separate years, five turtles (a Kemp's ridley and four loggerheads) that had been tracked from New York were all located within a radius of 40 km from a central point near the Maryland–Virginia border. The comparable timing of travel among years is easily explained. The impetus to migrate probably is mediated by abrupt temperature declines each year around early October. The very predictable timing of these temperature changes (Morreale and Standora, 1998) is the likely cause of such a predictable migration schedule. The outcome is a pulse of turtles of mixed species departing simultaneously from northern inshore habitats each year. After moving into open ocean waters they swim southward along a corridor that conveys them to warmer southern coastal waters.

The general trend for the New York and New England coastal Kemp's ridleys and loggerheads is to migrate southward beginning in early October. Along the way the northernmost turtles likely are joined by others migrating southward from coastal New Jersey and Delaware waters. By the first week of November, turtles head southward past the Virginia border, where they presumably become part of an ongoing procession of migrants out of Chesapeake Bay (Lutcavage and Musick,1985; Byles, 1988; Keinath, 1993; Renaud, 1995) and North Carolina inshore waters (Epperly et al., 1995b,c). This group of northern migrants joining the stream of migrating mid-Atlantic coast turtles means that each December there probably is a rather large confluence of sea turtles in that region continuing their migration southward. Indeed, such large clusters of turtles have been reported in separate observation studies during winter months in North Carolina waters (Musick et al., 1994; Epperly et al., 1995a,b).

Thus, the fall migration pattern for northern Atlantic coastal Kemp's ridleys and loggerheads can be readily summarized. They respond similarly by emigrating from their coastal foraging habitats as water temperatures decline beginning in October. Once in ocean waters they swim southward along a corridor that appears to be quite constricted in a narrow band running within continental shelf waters. This is similar to the migration corridor that was observed for adult leatherback turtles in the tropical Pacific (Morreale et al., 1996). However, migration of Atlantic coastal juveniles is much more condensed, existing within time only for several weeks, as turtles move southward at least as far as North Carolina. Because Kemp's ridleys and loggerheads probably are joined by migrating green and leatherback turtles (Shoop and Kenney, 1992; Morreale, 1999), some rather high densities of turtles can be expected along this fall migration route.

Overwintering and Re-Migration. — For migrating turtles south of Cape Hatteras, North Carolina, there appear to be some different patterns of behavior that emerge. Some individual Kemp's ridleys continue swimming southward to as far as Cape Canaveral, Florida (Keinath, 1993; Renaud, 1995; Gitschlag, 1996), which appears to be a common destination for overwintering juveniles. Nevertheless, the numbers of tracked Kemp's ridleys are small, and tracking durations have not always extended for the entire winter. It is possible that the turtles moving to Cape Hatteras from the more northern habitats (Morreale and Standora, 1998) also continue on to central Florida, paralleling the Kemp's ridleys observed migrating from Virginia (Keinath, 1993), Georgia (Gitschlag, 1996), and northern Florida (Renaud, 1995). However, there have been other observations that may reflect additional strategies by overwintering turtles.

A Kemp's ridley tracked from Beaufort, North Carolina, moved south into neighboring Onslow Bay during fall 1989 (Renaud, 1995). Rather than continuing southward, it remained in the vicinity until early January, when colder temperatures likely prompted a second movement offshore and into the nearby Gulf Stream (Fig. 3). By itself this behavior may appear anomalous, except it nearly exactly mirrored the early winter stopover locations of two large loggerhead turtles tracked from Virginia in 1991 (Keinath, 1993), and four juvenile loggerhead turtles migrating from New York in 1994 and 1995 (Morreale, 1999). Two of these juveniles from New York also made late-winter movements offshore and into the Gulf Stream (Fig. 4), as did wild and head-started loggerheads migrating from Virginia and North Carolina (Keinath, 1993). In both of the studies, it was concluded that the overwintering behavior displayed by these loggerheads was a viable strategy for northern foraging turtles. Such an alternate overwintering strategy could easily be available to juvenile Kemp's ridleys as well.

In this more encompassing scenario, all turtles migrate southward to overwinter in warmer waters, but achieve their objective in different ways. Some continue moving to a position far enough south to ensure reasonable temperatures throughout the winter, such as Cape Canaveral. Others move to a position that provides reasonable conditions for an extended stay, such as southern North Carolina. In some years, this strategy may greatly shorten the turtles' fall migration southward, and their subsequent return northward the following spring. In other years, when cold winter temperatures penetrate the shelf waters south of Cape Hatteras, turtles may have to make a late winter move toward more suitable temperatures. Some do this by continuing on southward to South Carolina (Morreale, 1999). Others react by moving in an offshore direction (Keinath, 1993; Renaud, 1995; Morreale, 1999). Such a move from the shelf waters of North Carolina can result in an immediate encounter with the Gulf Stream, which runs northeastward only tens of kilometers away, and sometimes closer. This places the turtles in warm water for the remainder of the winter, but can also transport them fast and far from shore.

Apparently the oceanic movements, whether intentional or accidental, are not a one-way trip. After spending the winter up to thousands of kilometers offshore, several loggerheads began to return directly shoreward during the following spring (Keinath, 1993; Morreale and Standora, 1998; Morreale, 1999). In fact, turtles overwintering in Florida, South Carolina, and North Carolina, as well as in pelagic waters, have been directly monitored making a return trip back to more northern coastal waters. This included the springtime movements not only of many juvenile loggerheads, but also of two Kemp's ridleys that were tracked moving northward after overwintering near Cape Canaveral, Florida (Renaud, 1995; Gitschlag, 1996).

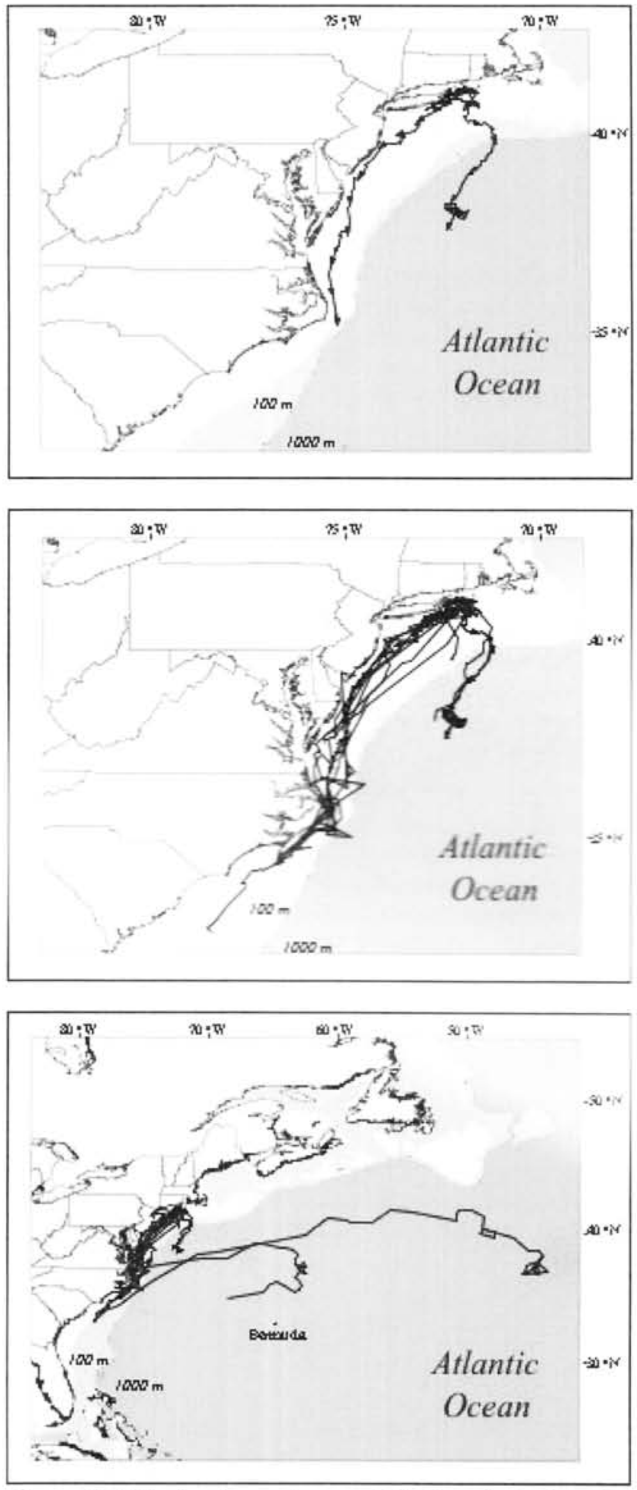

Figure 4. Fall migratory pathways of 15 juvenile turtles after leaving New York waters, monitored by satellite in studies over five different seasons. The upper panel shows the migratory paths of three *Lepidochelys kempii* (arrow lines); the middle panel shows how these paths are hard to distinguish from those of 12 *Caretta caretta* (solid lines) migrating from the same habitats. All of the turtles monitored swam directly southward in response to temperature declines in the fall. Most of the turtles traveled along a relatively narrow coastal corridor that conveyed them to North Carolina by early winter. After remaining sedentary for many weeks, three loggerheads made a late-winter move offshore from North Carolina (lower panel). Once in the Gulf Stream, they were transported from1100 to 3100 km offshore, before slowing their movements again.

All in all, any of the observed overwintering strategies that begin with an initial migration to North Carolina seem to be successful. All lead the turtles to warmer waters, and none of them prevent the turtles from returning the following spring. One strategy that apparently does not work north of North Carolina, however, is hibernation. From early on, in virtually all of the studies in more northern coastal waters, it has been noted that turtles lingering into winter will most likely become cold-stunned and die. This phenomenon affects loggerhead and green turtles, but seemingly disproportionately affects juvenile Kemp's ridleys. Cold-stunning occurs frequently in some northern areas (Morreale et al., 1992; Still et al., 2003), but even occurs occasionally in southern coastal waters (Witherington and Ehrhart, 1989). Thus, the cold-stunning phenomenon is a factor that coastal Atlantic turtles may need to contend with during their juvenile years.

Conservation Considerations

The importance of the western North Atlantic region to relatively large portions of the world's populations of Kemp's ridley and loggerhead turtles underscores the value of preserving these crucial coastal areas. During a juvenile life stage that extends for many years, these turtles are highly dependent on coastal resources. Thus, each year thousands of young Kemp's ridleys and loggerheads move into inshore foraging habitats along the USA Atlantic coast. These include the major estuaries and bays of Massachusetts and New York, Delaware Bay, Chesapeake Bay, Pamlico Sound, Charleston Harbor, and coastal waters of Georgia and Florida.

The major attraction of sea turtles to the key coastal habitats is likely the high productivity, especially among the benthic biota. The success of the seasonal foraging strategy for young turtles in northern waters may depend on the use of those specific coastal habitats. The abundance of resources in the bays and estuaries undoubtedly contributes to juvenile health and growth, and turtles are able to move freely among widespread coastal habitats. However, because this region also hosts some of the highest human densities in the western North Atlantic, foraging young turtles can be exposed to high levels of human disturbance.

Increasing the potential for negative impacts on turtles is the timing of their foraging activity, which is at its highest level during warmer months. This coincides with human activity cycles, which also peak in coastal waters in warmer weather.

Coastal foraging habitats, however, are not the only sites in which western North Atlantic Kemp's ridley and loggerhead populations are highly vulnerable to disturbance. It is very important to consider the coastal corridor along which turtles cluster during fall, and probably spring, migration. This relatively narrow band, which possibly extends along the entire length of the USA Atlantic coastline, appears to be heavily used by Kemp's ridleys and other species moving between northern and southern waters. It is obvious that activities that negatively impact migrating turtles within that corridor could drastically affect their populations. The potential threat is probably exacerbated as turtles pass Cape Hatteras, North Carolina, where the corridor becomes more constricted and turtle densities can be very high.

As juvenile turtles migrate to southern waters, once again they cluster in certain areas such as Cape Canaveral, Florida. The combination of warmer temperatures, shallow water, and relative protection all contribute to making Cape Canaveral a common overwintering area for turtles. Another area where turtles may become highly concentrated during winter months is in Onslow Bay, North Carolina, up to approximately 100 km offshore. This section of coastline between Cape Lookout Shoals and Frying Pan Shoals is protected and warmer because of the nearby Gulf Stream. In early winter, it appears that Kemp's ridleys and loggerheads migrating from the north often settle here. In some years, they may even spend the entire winter. Such winter gathering sites for turtles warrant special attention. At the least, certain activities such as bottom trawling should be limited near overwintering habitats.

The diverse behaviors, widespread habitats, and the highly mobile lifestyle adopted by these seasonal migrants can make management difficult. Yet, while increasing their vulnerability, the tendency of young turtles to converge to feed, migrate, and overwinter makes appropriate management easier. With the accumulated research that has focused on early developmental stages, we can now identify principal sites and key times of turtle activity, and we can construct better predictive models of turtle behavior. Using such detailed understanding of the ecology of sea turtles in their marine environment, it should be possible to develop improved conservation strategies with increased precision to ensure minimal impact both to humans and to sea turtles.

There have been considerable amounts of time, energy, and resources committed toward the recovery of Kemp's ridleys from critically low population levels. It now appears that many years of beach protection and modification of trawling techniques have successfully resulted in increased numbers of juveniles and even adults. The continuing goal is to bring Kemp's ridleys back from their critically endangered status by increasing their numbers up to more sustainable levels. We could go a long way toward achieving that goal by wisely managing and preserving the Atlantic coastal habitats that are so crucial to juveniles.

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