

OCEANIC MIGRATIONS OF SEA TURTLES

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Stephen J. Morreale

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Stephen J. Morreale, Ph.D.

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The present study incorporated current innovations in the field of satellite telemetry to study and compare the movement patterns and behavior of sea turtles at sea. Towable satellite transmitters were developed and attached to 14 adult female leatherback turtles (*Dermochelys coriacea*) at nesting beaches on the Pacific and Caribbean coasts of Costa Rica between 1991 and 1995, and to eight juvenile loggerhead turtles (*Caretta caretta*) from coastal New York waters between 1994 and 1996. Turtle movements were monitored by satellite and recorded along with submergence patterns and depth profiles. New algorithms also were developed to improve the filtering of satellite-derived location data for movement calculations and plotting.

Migratory movements among all pairs of study animals in Costa Rica were remarkably similar. After completion of nesting, Caribbean leatherbacks migrated along similar routes as their nesting cohorts. On Pacific nesting beaches, after nesting, all pairs of cohorts in four consecutive years traveled along a relatively narrow pathway heading southwestward. This migratory corridor appears to extend for thousands of kilometers into open Pacific waters, toward and beyond the Galapagos Islands.

The movements of the juvenile loggerheads also were strikingly similar to each other. All movements during fall were southward within a narrow corridor along coastal waters of the eastern USA. This migratory behavior conveys turtles to southern waters approximately 1000 km away, where they

become less active at the onset of winter. Individuals then spend the entire winter in southern coastal waters, or they move far offshore within the Gulf Stream. The observed migration patterns were similar to those observed for four loggerhead and three Kemp's ridley (*Lepidochelys kempii*) turtles from previous years.

From the highly similar migratory movements a generalized model was developed to predict movements of turtles at sea. The mathematical model, derived from spatial and temporal components of migrating juvenile loggerheads, was tested successfully against a separate larger data set of turtles observed in surveys. By accurately predicting migration patterns, it may be feasible to protect only minimal areas of the ocean during precise windows of time. This would minimize restrictions on human activities and maximize protection of sea turtles in the ocean.

BIOGRAPHICAL SKETCH

Stephen J. Morreale was a biology major at the State University of New York at Stony Brook from 1975-1977 and then at Buffalo State College, where he earned his Bachelor's degree in 1979. He returned to Buffalo State College to study with Jim Spotila, and earned his Master's Degree in biology in 1983. From 1982 through 1986 he was a Research Technician at the University of Georgia, Savannah River Ecology Laboratory, under the direction of Whit Gibbons. In 1986 he worked for Archie Carr as the biological director of the green turtle research station at Tortuguero, Costa Rica. The following year, he began a long-term project studying sea turtles at a marine research foundation in Long Island, New York. From 1988 through 1993, as Director of Sea Turtle Research, he worked in collaboration with Ed Standora to study and document the ecology of sea turtles in nearshore waters of the northeastern U.S. He moved to Ithaca and continued his research at Cornell University, first as a Visiting Fellow, and later with Milo Richmond as a doctoral student in the field of Zoology. Continuing his studies under the guidance of Milo, John Hermanson and Steve DeGloria, he taught undergraduate biology laboratory courses at Cornell for a year, and then became an Olin Fellow, which extended through the remainder of his doctoral studies.

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TABLE OF CONTENTS

	Page
CHAPTER ONE: Introduction	1
CHAPTER TWO: Post-nesting Migrations of the Leatherback Turtle, <i>Dermochelys coriacea</i> , From Tropical Pacific and Caribbean Waters	10
<i>Materials and methods</i>	13
<i>Results</i>	29
<i>Discussion</i>	51
CHAPTER THREE: Seasonal Migrations of Foraging Juvenile Loggerhead Turtles, <i>Caretta caretta</i> , in the Northwestern Atlantic Ocean	59
<i>Materials and methods</i>	66
<i>Results</i>	74
<i>Discussion</i>	98
CHAPTER FOUR: Predicting Spatial and Temporal Patterns of Sea Turtle Migrations	105
<i>Movement patterns of northeastern sea turtles</i>	108
<i>Model development</i>	111
<i>Model testing</i>	117
<i>Discussion</i>	121
CHAPTER FIVE: Conservation and Management Recommendations	125
<i>Recommendations</i>	128
REFERENCES	131

LIST OF TABLES

	Page
Table 2.1. Release information for 14 nesting leatherback turtles	16
Table 2.2. Program for calculating distances between locations	23
Table 2.3. Program for filtering and selecting satellite location data	24
Table 2.4. Tracking summary for 14 leatherback turtles	30
Table 2.5. Movement rates for migrating leatherbacks	44
Table 3.1. Release information for eight juvenile loggerhead turtles	67
Table 3.2. Transmitter package measurements for loggerhead turtles	70
Table 3.3. Tracking summary for eight migrating loggerhead turtles	75
Table 3.4. Percent of time spent at the surface by eight loggerheads	89
Table 3.5. Diving frequencies for eight loggerhead turtles	91
Table 3.6. Dive depths of eight loggerhead turtles	95
Table 3.7. Percent of time at different depths for eight loggerheads	97

LIST OF FIGURES

	Page
Fig. 2.1. Release sites for 14 leatherback turtles in Costa Rica	14
Fig. 2.2. Transmitter attachment design with breakaway tether	19
Fig. 2.3. Transmitter attachment position on a leatherback turtle	20
Fig. 2.4. Satellite tracks of two Caribbean leatherbacks in 1991	33
Fig. 2.5. Satellite tracks of two Caribbean leatherbacks in 1992	34
Fig. 2.6. Satellite tracks of two Pacific leatherbacks in 1992	37
Fig. 2.7. Satellite tracks of two Pacific leatherbacks in 1993	39
Fig. 2.8. Satellite tracks of two Pacific leatherbacks in 1994	40
Fig. 2.9. Satellite tracks of two Pacific leatherbacks in 1995	42
Fig. 2.10. Percent time spent at the surface by 13 leatherback turtles	46
Fig. 2.11. Diving frequency for 13 leatherback turtles	47
Fig. 2.12. Dive durations for 13 leatherback turtles	48
Fig. 2.13. Depths of dives for four leatherback turtles	50
Fig. 2.14. Migratory corridor for tropical Pacific leatherback turtles	52
Fig. 3.1. Long-distance tag recoveries of New York turtles	63
Fig. 3.2. Diagram of transmitter trailing behind a loggerhead turtle	71
Fig. 3.3. Flexible lanyard with breakaway links used for loggerheads	72
Fig. 3.4. Satellite track of loggerhead turtle 11461b	77
Fig. 3.5. Satellite track of loggerhead turtle 11459b	78
Fig. 3.6. Satellite track of loggerhead turtle 11458b	79
Fig. 3.7. Satellite track of loggerhead turtle 11460b	80
Fig. 3.8. Satellite track of loggerhead turtle 9038b	83
Fig. 3.9. Satellite track of loggerhead turtle 9039c	84

Fig. 3.10 Satellite track of loggerhead turtle 9037b	85
Fig. 3.11 Satellite track of loggerhead turtle 11462	87
Fig. 3.12 Percent time spent at the surface by 8 loggerhead turtles	90
Fig. 3.13 Diving frequency for 8 loggerhead turtles	92
Fig. 3.14 Dive durations for 8 loggerhead turtles	94
Fig. 3.15 Depths of dives for 8 loggerhead turtles	96
Fig. 4.1. Migration corridors for 15 juvenile turtles from the northeast	109
Fig. 4.2. Fall migration corridor for northeastern turtles	112
Fig. 4.3. Spatial and temporal 3-D plot of migration patterns	113
Fig. 4.4. Predicted relationship between date and latitude of turtles	115
Fig. 4.5. Predicted relationship between date and longitude of turtles	116
Fig. 4.6. Locations of turtles from CETAP survey data	118
Fig. 4.7. Locations from CETAP between October and December	120
Fig. 4.8. Illustration of a 2-D boundary line that moves through time	122

CHAPTER ONE

INTRODUCTION

Including turtles among such well-known migrants as geese, butterflies, and salmon may seem peculiar when considering these animals' impressive skills at navigation and long-distance travel. Perhaps the turtle's prominent position in lore as the symbol of plodding and steadiness contributes to the common misconception of them as sedentary animals. Nevertheless, turtles in general migrate frequently, over relatively great distances, and for many different reasons throughout their long lives. They are adept travelers that also display some remarkable abilities for homing and orientation. Therefore, any studies involving turtles must include serious consideration of their potential for long-distance migration. An extreme case can be made for sea turtles whose extensive travels have been commonly acknowledged for many years but have not been well accounted for in conservation efforts. The current endangered and threatened status of all sea turtles worldwide likely reflects the lack of protection afforded them while they are migrating.

The frequent oversight of such an important issue in turtle conservation and management may, in part, stem from an unclear definition of the concept of long-distance migration. In a discussion of migration, Baker (1982) emphasized how much this term has shifted meaning in the past few decades. From the nebulous tautology "birds migrate; therefore, migration is what birds do", that stemmed from Aristotle's observations, the term migration now broadly includes all movements of any animal through space and time. Further, the term "long-distance" is only relative to the size and capability of the organism moving (Schmidt-Koenig 1975). In this sense, the migratory movements of 50 meters per day by minuscule tropical riverine snails (Schneider and Lyons 1993),

would rank along with the trans-oceanic movements of whales (Krauss et al. 1986).

Currently the precise definition of long-distance migration is as ambiguous as ever. There are diverse forms of animal movement, many of which fall under the broad categories of long-distance migration, homing, and orientation. But the distinction between even such broad categories is unclear. It appears that long-distance migration is a relatively directed long-term movement through space that often is mediated by a mechanism such as homing or orientation (Baker 1982). Homing implies a return to an area that is already known to an animal, such as a quick return to a nest or den, or an extensive journey back to a natal rookery (Papi 1992). Orientation usually is understood to imply some sort of directional alignment in response to an external stimulus. This can take the form of a goal-oriented movement or even a stationary response (Papi 1992). However, there is much overlap inherent in the terms migration, homing and orientation, which is reflected in their often interchangeable and confusing usage (Schmidt-Koenig 1975).

Migration is also distinct from less-directed movements such as dispersal, the implied difference being one of motivational state of the organism. Migratory movements can generally be categorized as an organism's purposeful travel toward a specific goal (Papi 1992). This is unlike random dispersal, which often is the result of many stochastic processes. One of the principal implications of goal-orientation is that some direct benefit is derived as a result of migration. The traditional example is of birds moving from one site to another to benefit from improved feeding or breeding conditions, or to avoid harsh seasonal changes. A less commonly acknowledged purpose for migration is to track resources that are also migrating or shifting spatially. While these are not exclusive types of behavior, there are some important

differences that reflect in the directness of travel and the fixity and predictability of migratory routes. A caribou migrating from winter feeding to spring calving grounds tends to move directly between endpoints with minimal deviation (Craighead and Craighead 1987). The path of a nectarivorous bat, however, may be less straight as it migrates along a corridor of a specific type of cactus that fulfills its specialized dietary needs (Fleming et al. 1993). On the other extreme are migrations that have no pre-determined endpoint, such as roaming schools of tuna tracking after smaller baitfish (Arocha 1997). All of these animals are moving from a point of origin to a distant area, but their movement patterns along the way are guided by different motivations.

Notwithstanding some publicized migratory feats of sea turtles, there is a general lack of acknowledgement of the importance of long-distance movement to turtles. This is not just a minor oversight. Rather, it is the omission of a crucial element in the life cycles of most turtles. Many species of freshwater and terrestrial turtles regularly migrate for nesting (Cagle 1950, Moll and Legler 1971, Obbard and Brooks 1980, Congdon et al. 1983), overwintering (Sexton 1959, Burke and Gibbons 1995) and searching for mates or resources (Cagle 1944, Ernst and Barbour 1972, Morreale et al. 1984, Gibbons et al. 1983). Given the inherent difficulties confronted by the smaller and slower turtles, such movements can easily be defined as long-distance migrations. Similar movements by sea turtles are on the order of hundreds and even thousands of kilometers, and are obvious examples of long-distance migration, by any definition. Their travels to and from feeding areas (Carr 1967, Balazs 1976, Keinath et al. 1987, Ogren 1989, Meylan et al. 1990, Morreale and Standora 1994, Epperly et al. 1995a), overwintering sites (Mendonca and Ehrhart 1982, Henwood 1987, Henwood and Ogren 1987, Witherington and Ehrhart 1989, Morreale et al. 1992, Schmid 1995), and mating and nesting areas (Carr 1967,

Meylan et al. 1983, Cornelius and Robinson 1986, Plotkin et al. 1995, 1996, Keinath and Musick 1993, Morreale et al. 1996) are well documented. Often overlooked, however, is that all sea turtles migrate during their lives, and many individuals adopt a highly migratory general lifestyle.

Along with semantic problems, an important factor hampering our efforts to protect sea turtles is the lack of detailed information about much of their long lives. A lot of the difficulty stems from their aquatic existence and, ironically, from their propensity for oceanic travel. The generally accepted scenario for early life stages is that, as hatchlings, sea turtles swim away from their natal beaches migrating for the first time out to the open sea (Carr, 1986a; 1986b; Carr and Meylan, 1980; Collard and Ogren, 1990; Witherington and Salmon, 1992). There is convincing evidence that these young juveniles remain in a pelagic environment, feeding in surface waters until they reach a certain size (Carr, 1967; Carr and Meylan, 1980; Carr, 1986a). After this pelagic stage, which presumably culminates at lengths of 20 to 30 cm for the Kemp's ridley (*Lepidochelys kempii*) and the green turtle (*Chelonia mydas*) and at 40 to 50 cm for the loggerhead (*Caretta caretta*), juveniles of these species undergo a behavioral shift and move into shallower waters. Age estimates based on skeletochronological analyses place these size classes between the ages of two and five years old (Zug et al. 1986, Zug et al., 1997).

From that point in the lives of cheloniid turtles, the juveniles appear to establish a new behavioral pattern that will carry with them until adulthood. Although age at maturity likely differs among species and individuals, this developmental period will last from 5 to 15 years or longer (Mendonca 1981, Zug et al. 1986, Bjorndal and Bolten 1988a, Zug et al. 1997). Because young turtles cluster in specific coastal areas, more is known about their ecology during this life stage than in previous and subsequent pelagic stages. They move

into coastal waters, including inshore bays and estuaries, and become shallow water benthic foragers. In some warmer areas the juvenile turtles become year-round residents where they can be recaptured over many years (Mendonca 1981, Bjorndal and Bolten 1988a). In many coastal areas, however, the turtle populations are composed mainly of juveniles that migrate into and out of the habitat on a seasonal basis, either to overwinter (Carr and Caldwell 1956, Henwood 1987, Henwood and Ogren 1987, Ogren 1989, Witherington and Ehrhart 1989, Schmid 1995), or to feed in summer (Lutcavage and Musick 1985, Keinath et al. 1987, Morreale and Standora 1994, Epperly et al. 1995a). Mark-recapture records from these studies show that movements of turtles between distant sites are quite frequent and often extensive.

There is less consensus on early development in the leatherback turtle (*Dermochelys coriacea*), because small individuals are very rarely encountered. It has been suggested that this species attains a mature size at extremely rapid rates (Zug and Parnham 1996, Rhodin et al. 1996). Nevertheless, there is no time in their lives when they become resident in inshore waters. Once they leave the beach as hatchlings, they move quickly offshore and presumably migrate about at sea throughout their lives.

As adults, sea turtles tend to move farther offshore, and many continue to make seasonal travels to distant foraging areas. For the remainder of the adult stage they also add breeding excursions to their migratory repertoire. For adult males breeding migrations are very poorly understood. In some cases however, they do appear to migrate to and from nesting beaches to mate with females (Plotkin et al. 1996). More is known about breeding migrations of adult females from numerous studies in which turtles were tagged on nesting beaches. Piecing together the mark-recapture data, it is well established that female sea turtles can move great distances after nesting. Since some of the earliest studies, it has

also been noted that many females migrate to identifiable feeding areas, where they likely remain until they return to nest again (Carr 1967). For most turtles, however, their whereabouts once they leave the nesting beaches are obscure, and the interval between nesting episodes can span several years. Thus, most of adulthood is spent at sea, with a small window of time during which females predictably return to nesting beaches.

Because adult females are conspicuous as they crawl out on land to lay their eggs, this is the most thoroughly studied portion of the sea turtle life cycle. As a result of the high visibility and easy access to nesting turtles, there has been perhaps an inordinate emphasis placed on this single process, which comprises only a small portion of the overall ecology of sea turtles. By focusing on the female's terrestrial activity, we have biased our thinking about sea turtle ecology, which in turn has influenced our subsequent strategies geared toward their conservation. That is, much of the considerable effort to conserve sea turtles has centered upon nesting areas and surrounding waters. This has contributed to very effective protection of nesting females and eggs, but has diverted many of the available resources away from studying and protecting turtles at sea and during their frequent oceanic migrations.

The lack of emphasis on such a dominant element in sea turtle ecology is mostly due to the logistical difficulties involved in studying them in the pelagic environment. Traditionally, to monitor turtle migratory behavior, the techniques were limited to direct observation or tagging studies. Observation techniques such as aerial and shipboard surveys can effectively determine species distribution patterns at sea, and nesting and stranding surveys provide complementary distribution information about live and dead turtles on shore. These techniques do not provide much information on turtle biology, however, and even less about their migratory behavior. Capture and tagging records

provide a much better picture of an individual's basic biology because turtles captured in this mode presumably have been intercepted during their normal activities (Witzell 1984). Often these data can be used to estimate species composition, demographic data, feeding behavior, and habitat usage. In addition, recapture records of tagged sea turtles have been the traditional source of evidence of long-distance migratory movements. But, sporadic recaptures do not convey the critical details of timing and spatial patterns of oceanic movements, nor do they provide more than a rudimentary understanding of migratory behavior.

The best technique for studying ecology and behavior of individual turtles in the water is telemetry. Transmitters reduce the difficulties in identifying and following turtles and observing an individual's behavior in the water. Unlike instantaneous surveys, these techniques enable specific individuals to be monitored through time, and are not affected by attributes of the turtle. Transmitters can be effective for all sizes of turtles, in all weather conditions, and whether the individual is at or below the surface. Given enough resources, many individuals can be monitored at once to also provide a reasonable basis for quantifying behavior at the population scale (Standora et al. 1993, Morreale and Standora 1994). For decades all of these studies were conducted using traditional radio and acoustic telemetry techniques. The daunting chore of following turtles over great distances during oceanic travel, however, has been alleviated only recently through advancements in satellite telemetry.

The application of satellite telemetry to sea turtles (Timko and Kolz 1982) and subsequent refinements in recent studies (Naito et al. 1990, Standora and Morreale 1991, Keinath and Musick 1993, Keinath 1993, Morreale and Standora 1994, Byles and Plotkin 1994, Plotkin et al. 1995, Morreale et al

1996) have made it possible to remotely monitor the oceanic travels of several species. The simplified plan is that as the turtle rises to the surface to breathe, the transmitter bursts a signal to a passing satellite. The satellite identifies the unique signal and calculates the location of the transmitter by Doppler shift. Through successive improvements to hardware and software transmitters have evolved beyond simple location devices, to include environmental sensors and data loggers. These developments have provided new and exciting means to address some of the most pertinent and most elusive aspects of sea turtle biology.

The following study, which is presented here, took full advantage of the most current innovations in the field of satellite telemetry to study the movement patterns and behavior of sea turtles at sea. The over-arching objective of this study was to examine the long-distance migration patterns of sea turtles and to assess the importance of these migrations within their life cycles. Several specific objectives that were formulated for this study were:

- 1) quantify and compare the spatial and temporal patterns of migratory movements of three different species of sea turtles;
- 2) examine the migration process with respect to different life stages of the turtles;
- 3) develop and test a generalized model to describe and predict movements of turtles at sea;
- 4) evaluate the observed migration pathways of sea turtles with respect to human activities and other features that may relate to distribution and availability of marine resources.

These objectives were integrated into several different research activities which encompassed studies on nesting adult female leatherback turtles from the Caribbean coast of Costa Rica, nesting adult leatherbacks from Costa Rica's

Pacific coast, and young juvenile loggerhead turtles from New York waters. For the model development and analysis, additional data previously collected from migrating juvenile Kemp's ridley turtles (Morreale and Standora, 1994) also were incorporated. Since satellite telemetry of sea turtles is a relatively nascent field of study, this research also entailed substantial development and application of new techniques. For the juvenile loggerhead turtles, some transmitter and housing modifications were incorporated into previously developed techniques (Morreale and Standora 1994) to include some of the newest transmitter technology. For leatherback turtles, completely new designs and attachment techniques had to be devised. Also, because the available means of filtering and selecting satellite data were not well suited for tracking migrating turtles, new procedures needed to be created to analyze and interpret the transmissions.

Given the current serious concerns over the status of sea turtles, global conservation efforts that have focused upon monitoring and protecting nesting beaches appear to be inadequate. Because of continuing declines in populations worldwide, it is time to consider that appropriate management of these endangered animals may not be accomplished without allocating much more effort to safeguarding turtles of all life stages while they are in both nearshore and pelagic environments. A critical first step for the development of a sound management plan will be the accumulation of essential information on the migratory biology of individuals. Also, the delineation of migration patterns of sea turtles may have far-reaching ecological implications. If sea turtle migratory routes are linked to patterns of resource availability, then precipitous declines in sea turtle populations may be reflective of increasing pressures on concurrently diminishing resources in the marine environment.

CHAPTER TWO

POST-NESTING MIGRATIONS OF THE LEATHERBACK TURTLE, *DERMOCHELYS CORIACEA*, FROM TROPICAL PACIFIC AND CARIBBEAN WATERS.

Among the seven species of sea turtles, the most enigmatic is the leatherback turtle, *Dermochelys coriacea*. This turtle, which is endangered worldwide, has many unique physical and behavioral features that contribute to its distinction. With its pliable carapace and specialized anatomical and physiological characteristics, it is placed apart as the sole extant member of the family Dermochelyidae (Pritchard 1980). It is far larger than other turtles and, with adults weighing in excess of 400 kg, it is arguably the world's largest extant reptile.

The leatherback's distribution worldwide also adds to its distinction. This species regularly occurs at much higher latitudes than the cheloniid turtles, both in the Northern Hemisphere (Brongersma 1972, Goff and Lien 1988, Dolmen et al. 1993) and the Southern Hemisphere (Carr 1952, Hughes 1974, Limpus 1984). The leatherback's widespread distribution is partially a result of extensive travels of nesting females, which have been documented since early tagging studies (Pritchard 1973, 1976, Lambie 1983, Hirth and Ogren 1987, Boulon et al. 1988). Indeed, some of the post-nesting excursions of leatherbacks in excess of 5000 km far exceeded those reported for other turtles (Pritchard 1973).

The leatherback shares a common feature with other sea turtles, however, in that very little is known about specific migration patterns of this species, and virtually nothing of its behavior at sea. Merging the tagging data from nesting beach studies with reported observations of leatherbacks in the

ocean (Brongersma 1972, Witzell 1984, Goff and Lien 1988, Shoop and Kenney 1992), it has been possible to crudely piece together some of the migratory behavior of leatherback turtles. Along with the noted nesting migrations, many individuals appear to migrate to and from temperate waters to feed seasonally (Shoop and Kenney 1992). It is even possible that this species generally exhibits a high mobility, and that individuals travel extensively throughout their lives. Critical details in timing, spatial patterns, and frequency of migration have remained elusive, however, until the recent application of satellite telemetry.

Some of the earliest attempts to monitor leatherback movements were informative, but limited. Most were thwarted by the difficulties encountered with this species, which are unique even among the sea turtles. Impediments to tracking leatherbacks include a pliable oily carapace, to which it is difficult to attach transmitters; fast swimming speeds that can create problems with turbulence; and extreme conditions encountered during deep dives, which may exceed 1000 m (Eckert et al. 1989). The first successful track of a leatherback by radio telemetry (Standora et al. 1984) was measured in hours, and subsequent tracks by satellite telemetry ranged from 30 minutes (Dolmen et al. 1993) to 24 days (Duron-Dufrenne 1987). Among the more successful early attachment techniques was a body harness that was designed for attaching recorders to nesting leatherbacks (Eckert et al. 1986, 1989), and was later used to track a female during an interesting interval in the Caribbean for 18 days (Keinath and Musick 1993).

These novel studies demonstrated clearly that leatherback turtles could dive deeply and swim fast during the nesting season, but only one tracked a turtle upon completion of nesting (Duron-Dufrenne 1987). This early success documented the initial 800 km segment of a post-nesting excursion using a large

satellite transmitter package attached by harness. The uninterrupted movement of this turtle in the first 24 days after nesting supported the earliest reports of long-distance oceanic travel in leatherbacks, but left many questions about migratory behavior unresolved.

With steady improvements to satellite transmitters and their successful use on other species, it was inevitable that these new methodologies also would be applied toward monitoring leatherback turtles. The following study, documented here, incorporated some techniques previously designed for other sea turtles (Standora and Morreale 1991), along with new modifications, to directly investigate the details of leatherback migrations, most of which as yet remained unknown.

Objectives

The purpose of the following study was to monitor the movements and behavior of leatherback turtles after their return to the water upon completion of nesting. Because some individuals were likely to be in the midst of their nesting season, it was serendipitous to include tracking turtles both during internesting intervals and during their post-nesting migrations. The specific objectives, presented in order of priority, were:

- 1) to track leatherback turtles by satellite to reveal patterns of behavior and movement of these animals at sea.
- 2) to synthesize the observed migration patterns into a generalized framework that could be used to characterize two of the more important leatherback nesting populations in the world; and
- 3) to monitor internesting behavior, movement, and location of females and compare these to post-nesting activities.

Because of the uniqueness of this project, a fourth objective was to develop and apply new techniques that would enable the long-term tracking of leatherbacks, measuring and recording of their behavior during migration, and objectively analyzing the remotely sensed data.

This study was, of necessity, opportunistic in that it took advantage of leatherback nesting, the only known activity during which they predictably could be encountered. The intent, however, was not to learn solely about the detailed behavior of nesting adult females. Rather, this was the minimal expectation. At best, it was hoped that this satellite telemetry study would uncover new information on the oceanic existence of leatherback turtles in general.

The study was aimed at two very important populations of leatherbacks: one from Costa Rica's east coast, a large nesting colony in the Caribbean (Hirth and Ogren 1987); and the other from Costa Rica's west coast, one of the largest nesting colonies in the world (Spotila et al. 1996). The importance of both of these nesting colonies to leatherback turtles on a global scale greatly increased the value of studying the behavior of females from these populations. Furthermore, there was a heightened urgency to elucidate the ecology of leatherbacks as a result of recent estimates of huge population declines of these endangered turtles worldwide (Spotila et al. 1996, Chan and Liew 1996).

Materials and Methods

Study sites

Nesting female turtles were studied on both coasts of Costa Rica, at two separate leatherback nesting colonies (Fig. 2.1), during seven different nesting



Figure 2.1. Release sites for leatherback turtles during a five-year study of migratory behavior. Two leatherback turtles per season were selected for monitoring by satellite from nesting beaches on both coasts of Costa Rica. The first of the two study sites in the Caribbean coastal province of Limon, was within the National Park at Tortuguero ($10^{\circ}34.5'N$, $83^{\circ}30.5'W$). The following year, a study site was selected 55 km to the south at Mondonguillo ($10^{\circ}10.9'N$, $83^{\circ}14.9'W$). On the Pacific coast, studies were initiated from one of three adjacent beaches centered around Playa Grande, in the Guanacaste Province ($10^{\circ}19.0'N$, $85^{\circ}50.3'W$).

seasons. In each season, two nesting cohorts were monitored by satellite transmitter. On the Caribbean coast, turtles from two beaches in the coastal province of Limon were selected in two consecutive years between 1991 and 1992. On the Pacific coast, turtles from three adjacent beaches in the province of Guanacaste were selected over five consecutive seasons between 1991 and 1995 (Table 2.1). With the exception of the first season on the Pacific coast, nesting cohorts were selected within two days and five km of each other.

At the first Caribbean site, on 17 and 18 May 1991, two individuals were selected among the nesting leatherbacks at the National Park at Tortuguero ($10^{\circ}34.5'N$, $83^{\circ}30.5'W$). This is an active nesting area for leatherbacks each year from March through June (Leslie et al. 1996, Cambell et al. 1996). The following year, on 27 May 1992, two more cohorts were selected at a beach 55 km to the south at Mondonguillo ($10^{\circ}10.9'N$, $83^{\circ}14.9'W$). It is likely the turtles nesting at these two nearby beaches are part of the same extensive nesting population that spans from northern Costa Rica to Panama (Meylan et al. 1985, Hirth and Ogren 1987).

On the Pacific coast, studies were initiated from Las Baulas National Park, a series of three beaches centered around Playa Grande in Guanacaste Province ($10^{\circ}19.0'N$, $85^{\circ}50.3'W$). This group of beaches comprises a single nesting population (Steyermark et al. 1996), which makes it one of the largest leatherback nesting colonies in the Pacific (Spotila et al. 1996). Although other species nest along these beaches, leatherback turtles comprise the vast majority, nesting from October through March each year. Tracking at Playa Grande also began in 1991; two nesting cohorts were tracked beginning in mid-January of each of five consecutive seasons, from 1991 through 1995.

Table 2.1. Release data, locations, and measurements of 14 adult female leatherback turtles selected from Costa Rican nesting beaches and monitored by satellite transmitters. Carapace lengths (CCL) were measured over the curve.

ID	Date	Lat.	Lon.	CCL (cm)	Mass (kg)
1111A	05/17/1991	10.573	83.519	155	355
1112A	05/18/1991	10.580	83.500	151	----
1111B	05/27/1992	10.188	83.250	148	----
2107	05/27/1992	10.180	83.246	150	---
1110A	01/12/1991	10.999	83.999	999	245
1109A	01/17/1991	10.999	83.999	999	----
2105	01/15/1992	10.275	85.846	164	----
2106	01/15/1992	10.275	85.846	144	300
3560	01/11/1993	10.350	85.867	148	----
3561	01/12/1993	10.317	85.818	152	----
1109B	01/11/1994	10.317	85.838	150	----
1110B	01/13/1994	10.317	85.838	153	----
1111C	01/18/1995	10.350	85.867	153	----
1112B	01/19/1995	10.317	85.818	151	----

Satellite transmitter design

After laying their eggs, all study animals were restrained on the beach for measurements (including weights of three turtles), tagging, and attachment of satellite transmitters. The transmitters were designed to trail behind the turtles as they swam, and to float upright at the surface, with the antenna standing out of the water, as the turtle came up to breathe. As the process of attaching satellite transmitters evolved, handling time of turtles decreased from 5 h to 19 min. After the brief interruption, turtles were released to return to the water on their own.

The satellite transmitters used for all 14 turtles in this study were 1/2 watt ST-6 transmitters made by Telonics (Mesa, AZ). All were capable of relaying location information, but the earlier models had limited sensing capacity. Equipped with a saltwater switch and a timer, these first 10 devices recorded mean dive durations and dive frequencies. The supplemented transmitter packages used in 1994 and 1995 included specially designed satellite-linked time-depth recorders (SLTDR) engineered by Wildlife Computers (Redmond, WA). The SLTDR extended the basic ST-6 transmitter by incorporating a microprocessor, a pressure transducer, and a conductivity sensor. It also had the ability to record and archive information for later transmission. All of the transmitters were expected to transmit for one year based on calculated transmission rate and nominal battery life.

The satellite transmitter housings were custom-designed to be pressure-resistant, buoyant, and hydrodynamic. These were modified and improved as the study progressed. The initial housings made of delrin were machined into tubes with walls thick enough to withstand very high pressures that might be experienced at great depths. The dimensions were further expanded to enable the entire package, including transmitter and batteries, to float. Transmitters

were potted into the tubes with only the antenna and salt-water sensors protruding. After using this larger housing on the first four turtles, the package size was reduced to less than 1/2 the original diameter and mass. Although the design for the next six turtles was basically the same, smaller batteries and a floatation collar enabled its reduction in size to a cylinder of 40 cm x 5 cm, weighing less than 1100 g. For the last four turtles, transmitters were upgraded and new housings were fabricated from a high-performance syntactic foam (Emerson and Cumming Inc., Canton, MA) which was poured into a mold around the electronic components. This buoyant foam has a density of .38 g/cm³ and withstands pressures at depths greater than 3600 m. With the lighter material, the final overall package was further reduced to a cylinder weighing less than 900 g, and with a buoyancy of approximately 100 g.

The floating transmitters were attached to the turtle's carapace using modifications of techniques previously developed for smaller Kemp's ridley (Morreale and Standora 1991, 1992) and loggerhead turtles (Standora et al. 1993, Morreale and Standora 1994). Each transmitter was fastened to a flexible lanyard, which was connected to the turtle through a series of corrosible links to prevent long-term encumbrance (Fig. 2.2). To reduce abrasion, rubber surgical tubing was stretch-fitted into a 4 mm hole in the overhanging pygal region of the turtle's carapace. The monofilament lanyard was passed through the tubing, around a lower button, and back up through a smaller upper button to distribute the forces more widely over the carapace. The position of attachment far back on the turtle's shell was well-suited for the satellite transmitters and the sonic transmitters that were used in simultaneous studies (Fig. 2.3). Due to the streamlined shape of the turtle, this site at the posterior-most portion of the carapace is a region of very reduced drag behind the swimming turtle.

Pygal Region of Carapace

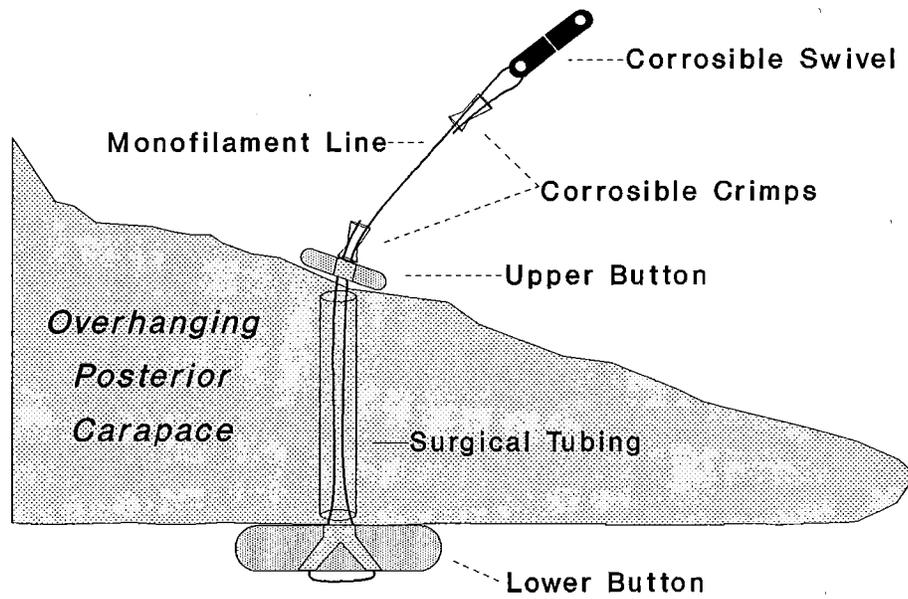


Figure 2.2. Lateral diagrammatic view of the low-strain breakaway tether used to attach the hydrodynamic satellite transmitter to the overhanging rear portion of the carapace of the leatherback turtle.

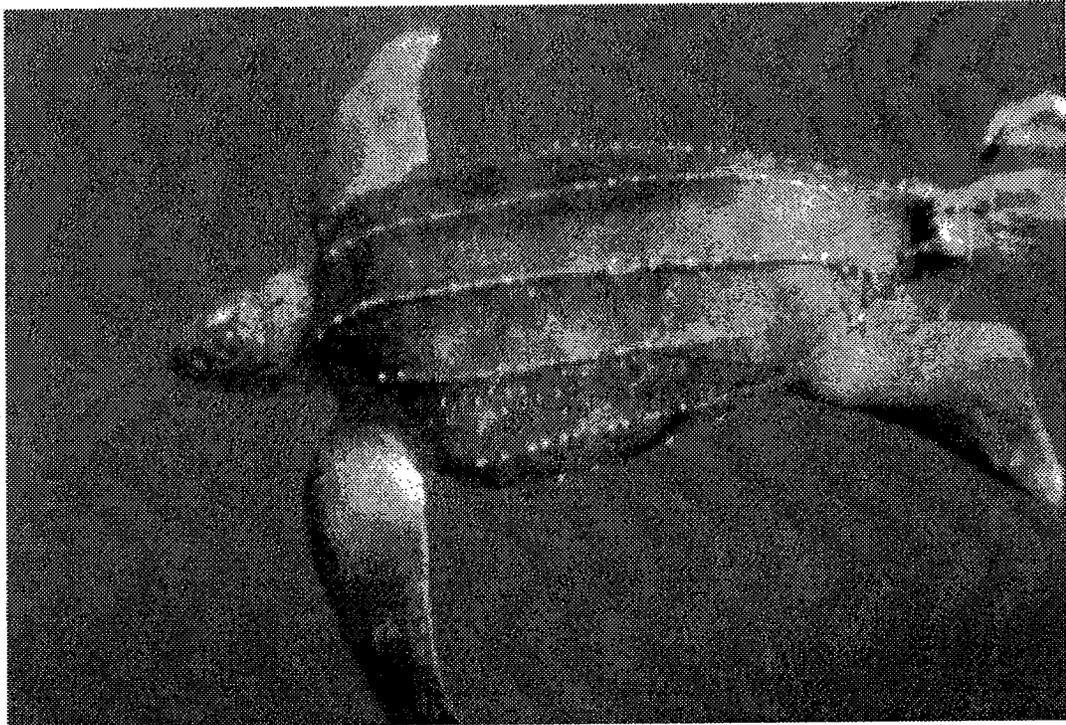


Figure 2.3. Underwater photo of a free-swimming leatherback turtle approximately 10 km off the Pacific coast of Costa Rica. The position of attachment of the sonic transmitter far back on the turtle's shell was well suited for these and satellite transmitters because of the reduced drag in that region. The sonic transmitter is in the process of being removed as the turtle begins to dive.

Location data

Turtle migratory movements were recorded at remote terminals where data were downloaded from the satellites daily for as long as the transmitters continued to send signals. Transmissions were monitored and relayed using the French-American ARGOS telemetry system (ARGOS, Landover, Maryland). ARGOS uses the TIROS-N series satellites, which are a series of polar orbiting satellites operated by NOAA and used mostly for environmental data. Much of the instrumentation is for spectral recording of radiation, but there are additional features, such as microwave and infrared sounding units, and radio reception and transmission. The transmitters attached to the turtles take advantage of the satellite's radio capabilities by emitting a UHF signal at a controlled frequency (approximately 401.650 Mhz). Because the satellite is always in a precisely known position in space and time, it can calculate the transmitter's location through Doppler shift. For this technique to be most effective, it is better to have a series of at least three transmissions as the satellite passes overhead.

Because the ability to pinpoint the signal varies greatly, the ARGOS system classifies the location data into four levels of certainty. Some factors that are important in accurately locating sea turtles are satellite position, transmitter orientation, and amount of time the turtle spends at the surface (Standora and Morreale 1991). As a result of the interactions of these and many other factors, a large proportion of the locations are relegated to the lowest level of certainty; Level 0. For example, more than three-fourths of the locations of the Pacific leatherbacks in this study were designated by ARGOS as Level 0 (Morreale et al. 1996). To enhance these sorting routines, which were designed for stationary platforms, a new set of algorithms had to be developed to more appropriately assign acceptance criteria for locating sea turtles.

In the first process, only ARGOS high-certainty locations were used to calculate rates of movement of individual turtles (Table 2.2). The resultant output file from this dBase program yields travel distances and movement rates between successive locations, along with mean and maximum values of daily movement rates. The use of only these high-certainty locations to measure turtle movements provides an objective way to determine which low-certainty data points are more likely to be accurate. Any location that is within the calculated maximum allowable distance from its neighboring points can be included along the plotted turtle track. This program also can be applied to calculate movements of turtles in different locations, for different behaviors, and even for different species.

In the second process, all original turtle location data of all levels of certainty were resubmitted to a second program for calculating, sorting, and selection (Table 2.3). Using the newly established threshold for maximum allowable movement rates, the series of algorithms then culled out any excessive movements. Individual points were ultimately selected or rejected based on a hierarchy of criteria: 1) certainty level; 2) maximum movement threshold; and 3) distance from previous and subsequent locations along the turtle's path. A low-certainty location was accepted only if the turtle's calculated rate of movement to and from that point were below the movement threshold. The accepted locations were then used along with the original high-quality data to reproduce the turtles' specific paths of movement in much greater detail.

Plots of the turtle locations were designed to reflect the various levels of certainty assigned by the different sources: 1) Solid symbols for locations that were high certainty using ARGOS criteria; 2) lines connecting to open symbols that were deemed acceptable locations based on the new algorithms, and 3) detached open symbols for locations that were unlikely by both measures. Lines

Table 2.2. The dBase program DISTDAY is designed to calculate distances in km and decimal days between successive high-certainty location data: categories LC1, LC2, and LC3, as reported by ARGOS. Distances are calculated using spherical coordinates and the following formula for calculating distances on the surface of a sphere:

$$\text{Cos } A = (\text{Sin Lat}_1)(\text{Sin Lat}_2) + (\text{Cos Lat}_1)(\text{Cos Lat}_2)(\text{Cos}(\text{Lon}_1 - \text{Lon}_2))$$

In the output file DISTDAY1, mean movement rates of turtles and the maximum acceptable threshold of movement per day are calculated.

&& Program DISTDAY

CLEAR MEMORY

SET DECI TO 8

USE DISTDAY && Satellite location data file with high-certainty
 && ARGOS categories: LC1, LC2, and LC3

DO WHILE .NOT.EOF()

 STORE DTOR(LAT) TO LAT10 && converts lat lons to radians to
 && match Sin() and Cos() functions

 STORE DTOR(LON) TO LON10

 STORE DATE TO DATE1

 STORE HOUR TO HOUR1

 SKIP

 STORE DTOR(LAT) TO LAT20

 STORE DTOR(LON) TO LON20 && these are just to follow the
 && convention established in my related programs.

 REPL DAY WITH DATE-DATE1+(HOUR-HOUR1)/24

 REPL DIST WITH 1.852*60 * RTOD(ACOS(SIN(LAT10)*SIN(LAT20) +
 COS(LAT10)*COS(LAT20)*COS(LON10-LON20)))

 REPL RATE WITH DIST/DAY

ENDDO

SET SAFE OFF

COPY FIELDS TRAN,DATE,LC,HOUR,LAT,LON,DIST,DAY,RATE TO
 DISTDAY1

USE DISTDAY1 && output file

LIST

SET SAFE ON

AVER RATE TO MEAN

CALC MAX(RATE) TO KMPERDAY && newly established maximum
 && allowable movement in the form of a memory variable.

Table 2.3. The dBase program NEWDIST uses all of the original location data relayed by satellite to calculate distance in km and time in decimal days between successive points. After assigning distance and rate values on the first pass, it examines each data point and selects or culls them in a stepwise fashion. Decisions to include or omit locations are hierarchical, based on original certainty level; maximum allowable threshold of movement; and previous, penultimate, and subsequent locations.

&& Program NEWDIST

```

CLEAR MEMORY
KMPERDAY=110 && calculated maximum allowable rate of movement
SET DECI TO 8
USE NEWDIST && file containing all unsorted satellite location data
STOR DTOR(LAT) TO ALAT
STOR DTOR(LON) TO ALON
STOR DATE TO ADATE
STOR HOUR TO AHOUR
STOR LC TO ALC

DO WHILE .NOT.EOF() && 1st record on 1st pass, then current acceptable record
  STORE DTOR(LAT) TO LAT10 && converts lat lons to radians to match format
  STORE DTOR(LON) TO LON10 && of the Sin() and Cos() functions
  STORE DATE TO DATE10
  STORE HOUR TO HOUR10
  STORE LC TO LC10
  SKIP && 2nd record on 1st pass, then subsequent record
  STORE DTOR(LAT) TO LAT20
  STORE DTOR(LON) TO LON20 && these are just to follow the convention
  STORE DATE TO DATE20 && in DISTDAY.prg
  STORE HOUR TO HOUR20
  STORE LC TO LC20
  REPL DAY WITH DATE20-DATE10+(HOUR20-HOUR10)/24
  REPL DIST WITH 1.852*60 * RTOD(ACOS(SIN(LAT10)*SIN(LAT20) + ;
  COS(LAT10)*COS(LAT20)*COS(LON10-LON20)))
  REPL RATE WITH DIST/DAY
  IF RATE > KMPERDAY
    IF ALC#1'.AND.ALC#2'.AND.ALC#3'.AND.ALC#9' && if previous lc = 0
      REPL DAY WITH DATE20-BDATE+(HOUR20-BHOUR)/24
      REPL DIST WITH 1.852*60 *
RTOD(ACOS(SIN(BLAT)*SIN(LAT20) + ;
      COS(BLAT)*COS(LAT20)*COS(BLON-LON20)))
      REPL RATE WITH DIST/DAY
      && tries to correct by recalculating to penultimate record

```

Table 2.3 (Continued).

```

IF RATE<KMPERDAY.OR.LC='1'.OR.LC='2'.OR.LC='3'.OR.LC='9'
    && If corrected value is good or if this
        SKIP-1
        DELE && reco is an LC>0, then prev reco is
            && deleted as long as prev reco is an LC 0
            && this will occur regardless of its value
        PACK
        LOCA FOR DATE=DATE20.AND.DTOR(LAT)=LAT20;
            .AND.DTOR(LON)=LON20
            && moves on, whether or not problem is solved
        STOR BLAT TO ALAT
        STOR BLON TO ALON
        STOR BDATE TO ADATE
        STOR BHOUR TO AHOUR
        STOR BLC TO ALC
ELSE && if corrected value is unacceptable
    DELE
    PACK
    LOCA FOR DATE=ADATE.AND.DTOR(LAT)=ALAT;
        .AND.DTOR(LON)=ALON
    STOR BLAT TO ALAT
    STOR BLON TO ALON
    STOR BDATE TO ADATE
    STOR BHOUR TO AHOUR
    STOR BLC TO ALC
    STOR LAT10 TO LAT20
    STOR LON10 TO LON20
    STOR DATE10 TO DATE20
    STOR HOUR10 TO HOUR20
    STOR LC10 TO LC20
ENDIF
ELSE && If previous lc= 1 or 2 or 3 or 9
    DELE
    PACK
    LOCA FOR DATE=ADATE.AND.DTOR(LAT)=ALAT;
        .AND.DTOR(LON)=ALON
    STOR BLAT TO ALAT
    STOR BLON TO ALON
    STOR BDATE TO ADATE
    STOR BHOUR TO AHOUR
    STOR BLC TO ALC

```

Table 2.3 (Continued).

```
        STOR LAT10 TO LAT20
        STOR LON10 TO LON20
        STOR DATE10 TO DATE20
        STOR HOUR10 TO HOUR20
        STOR LC10 TO LC20
    ENDIF
    ENDIF          && if initial rate is below allowable threshold, move on.
    STOR ALAT TO BLAT
    STOR ALON TO BLON
    STOR ADATE TO BDATE
    STOR AHOUR TO B HOUR
    STOR ALC TO BLC
    STOR LAT20 TO ALAT
    STOR LON20 TO ALON
    STOR DATE20 TO ADATE
    STOR HOUR20 TO AHOUR
    STOR LC20 TO ALC
ENDDO

SET SAFE OFF
COPY TO NEWDIST1
USE NEWDIST1
LIST
SET SAFE ON
```

plotted between consecutive acceptable points, therefore, represent the calculated migratory pathways of the individual turtles.

Base maps for the plots were derived from the Micro World Data Bank digitized world map. Maps and plotted tracks were displayed as Mercator projections for viewing only. Distances between points were calculated using spherical geometry and a spherical Earth model, which was more simply applied than ellipsoid models; distances calculated by this method were less than 0.5% different than the values calculated for the turtle movements using the reference ellipsoid NAD83.

Sensor data

The satellite transmitters used for the first 10 turtles were equipped with a saltwater switch and a timer that recorded average dive durations and total number of dives over the 4 h period prior to transmission. To account for wave splash, only submergence times longer than one minute were counted as dives. Because the transmitters were activated for only eight hours each day, these dive measurements were available for the pre-dawn period, between 0300 and 0700, and the morning period, between 0700 and 1100, Costa Rican local time. The functions and the daily duty cycle of these earlier models were preset and hard-wired into the sealed units.

The SLTDR devices used on the four turtles in 1994 and 1995 offered greater flexibility. By connecting a computer through a communication port, the SLTDR could be programmed to collect and store data while remaining quiescent. For extended life of the transmitters, active duty cycles were programmed for 12 h of transmission each day, between the hours of 0500 and 1700 Costa Rica time. During active transmissions, the data, stored as summaries of 6 h periods, were relayed in chronological order starting with the

most recent time period. Thus, if a turtle were at the surface long enough, it was possible to receive a record of its activity for up to 18 h previous to the current time period. Although there were some differences from the earlier transmitters, the sampling scheme was designed to maximize data collection during pre-dawn and morning hours for comparative purposes.

The extra sensors on the SLTDR provided the capability to record and store information to be transmitted to the satellite later along with the location signal. The most exciting new feature was the ability to remotely monitor diving behavior of the turtles as they migrated through open waters. A pressure transducer, which was preset to measure depths ranging from 0 to 1500 m with a resolution of 2 m, recorded the maximum depth of each individual dive made by the turtle. Also, a programmed timer recorded total duration of each dive, in addition to the percent of total time spent by the turtle at different depths within the water column. Thus, the data relayed by satellite for each turtle were: global position, dive depth profiles, dive duration profiles, and surface and submergence activity profiles.

To conserve storage space, individual dive sequences of turtles were not recorded. Rather than recording depth at specific times, as do many depth recorders (Eckert et al. 1986, 1989, Naito et al. 1990, Sato et al. 1994), dives were condensed into frequency histograms that accumulated diving activity into 14 depth and 14 duration categories summarized over six-hour periods. Percentage of the six-hour period that was spent at the surface, and at different depths within the water column, was also calculated. Only movements below a depth of 6 m were considered dives; all time spent within the upper 6 m was categorized as surface activity.

Results

During the seven seasons of study, beginning in January 1991, 14 adult female leatherback turtles were monitored by satellite transmitter for periods ranging from 1 to 87 d (Table 2.4). Using the first and last positions of the turtles, net movements were calculated to range from 20 to 2780 km within those intervals. These measurements, which are the calculated shortest distances between endpoints, are conservative underestimates of actual travel distances. Similarly the broad range of rates of average movement from 1.2 to 40.4 km/d represents a dampening effect from including minimal interesting movements for some turtles.

In all but three cases, the tracks were truncated by the inexplicable termination of signals long before the expected end of the battery life. The transmitters from the earliest two turtles bobbed at the surface after 1 and 17 days, and continued to send signals for more than a year afterward. The transmitter from the first turtle to be tracked on the Caribbean coast was retrieved from a fisherman after the turtle was caught in his fishing net in the Antilles.

Notwithstanding the somewhat abbreviated tracks, the attachment of transmitters to trail behind the turtles proved to be a feasible and successful technique in terms of ease and speed of attachment, and minimal impact on the turtles. The final attachment process, without glues, bone screws or a body harness, entailed only restraining the turtle for a maximum of 20 minutes before it returned to the water. The low-profile package, and its design to trail behind the turtle, appeared to be an appropriate solution for decreasing drag, which is perhaps the single-most important factor for these aquatic animals (Logan and Morreale 1994). Also, all transmitters were less than 1% of the animal's overall

Table 2.4. Tracking summary of 14 adult female leatherback turtles from nesting beaches in Limon and Guanacaste provinces of Costa Rica from 1991 through 1995. Two nesting cohorts in each of seven consecutive seasons were selected. All movements were monitored via satellite for as long as transmissions continued. Distances were calculated using a spherical earth model. Net movements are calculated using beginning and end locations and, as such, represent underestimates of actual values.

ID number	Release date	Tracking duration	Net movement	Net rate (km/d)
<i>Caribbean</i>				
1111A	05/17/91	86 days	2368 km	27.5
1112A	05/18/91	17 days	686 km	40.4
1111B	05/27/92	58 days	969 km	16.7
2107	05/27/92	54 days	1813 km	33.6
<i>Pacific</i>				
1110A	01/12/91	1 day	60 km	60.0
1109A	01/17/91	17 days	20 km	1.2
2105	01/15/92	63 days	1639 km	26.0
2106	01/15/92	39 days	820 km	21.0
3560	01/11/93	29 days	417 km	14.4
3561	01/12/93	3 days	67 km	22.3
1109B	01/11/94	87 days	2780 km	32.0
1110B	01/13/94	54 days*	888 km	21.1
1111C	01/18/95	46 days**	1451 km	38.2
1112B	01/19/95	75 days	1886 km	25.1

* 54 days of data; last position on day 42.

** 46 days of data; last position on day 38.

body mass, and were minimally buoyant. This streamlined package minimized hindrance to the turtles in the water and on land. This was illustrated many times throughout the study when six different individuals with transmitters returned on schedule to nest again. On the Caribbean coast where there were no observers, one turtle apparently nested three additional times, before embarking on its post-nesting migration. At the Pacific sites, five different individuals were observed directly upon their return, four of these by researchers; all were reported to be seemingly unaware of the attached transmitters. Once in open water, all individuals swam immediately and directly away from the nesting beaches, for the most part, maintaining unwavering courses during migration.

Location data and migratory paths

Location data were available for all 14 turtles in the study. In all, there were 407 positional fixes that were relayed by satellite. In the original classification scheme, ARGOS designated 75 % of these as LC0, leaving only 100 acceptable data points. By submitting these same data through the new filtering algorithms, the number of plausible locations was boosted considerably. First, using only the 100 data points of high reliability, movement rates were calculated. The maximum rates for nine turtles ranged from 15.2 to 104.1 km/d (mean = 60.9; SD = 27.9). This measured value gives support to previous and subsequent estimates of swimming rates for leatherbacks between 1.2 and 9 km/h (Duron 1978, Standora et al. 1984, Keinath and Musick 1993, Papi et al. 1997). Thus, the upper limit of travel was established at 104 km/d. Using this threshold value as the highest allowable rate of movement between consecutive turtle locations, the sorting program increased the usable data points to 344, an increase of over 60 % of the total. Taking advantage of the higher resolution, plots of turtle tracks with greater detail were created using

both the ARGOS-selected data and those from the custom-made program.

Movements of Caribbean turtles. The first two nesting cohorts on the Caribbean coast were released at Tortuguero National Park on 17 and 18 May 1991. Soon after nesting both turtles embarked upon migration, heading eastward through Caribbean waters (Fig 2.4). Over the first two weeks, their movements for several hundred kilometers were along roughly parallel paths, one through open waters, the other more close to the shoreline. In the shorter track, turtle # 1112A moved more than 650 km in 17 days, continuing along the same general heading at an average rate of 40 km/d, until last contact with the satellite transmitter.

The nesting cohort of this turtle (# 1111A) similarly migrated eastward along the shelf waters of Central and South America for more than 500 km, slowed its movements for two weeks, then crossed the open waters of the Caribbean and continued eastward along the Antillean Island chain. During the two different segments of steady movement, the turtle traveled at average rates of 49 and 24 km per day respectively. On day 86, after migrating more than 2300 km, all movement halted. The functioning transmitter was tracked down and retrieved from a fisherman on the Island of St. Kitts, who reported that the turtle had drowned in his net.

The following year at Mondonguillo, two turtles were tagged and released for monitoring in the early morning hours of 27 May. Upon completion of nesting, both turtles headed directly northward (Fig. 2.5). But after the first few days, it became apparent that one had finished, while the other was in the midst of its nesting season. The first of these turtles to leave the nesting area, # 2107, headed northward passing the Nicaraguan border by day four, and through open Caribbean waters to the southern coast of Cuba by day 22.

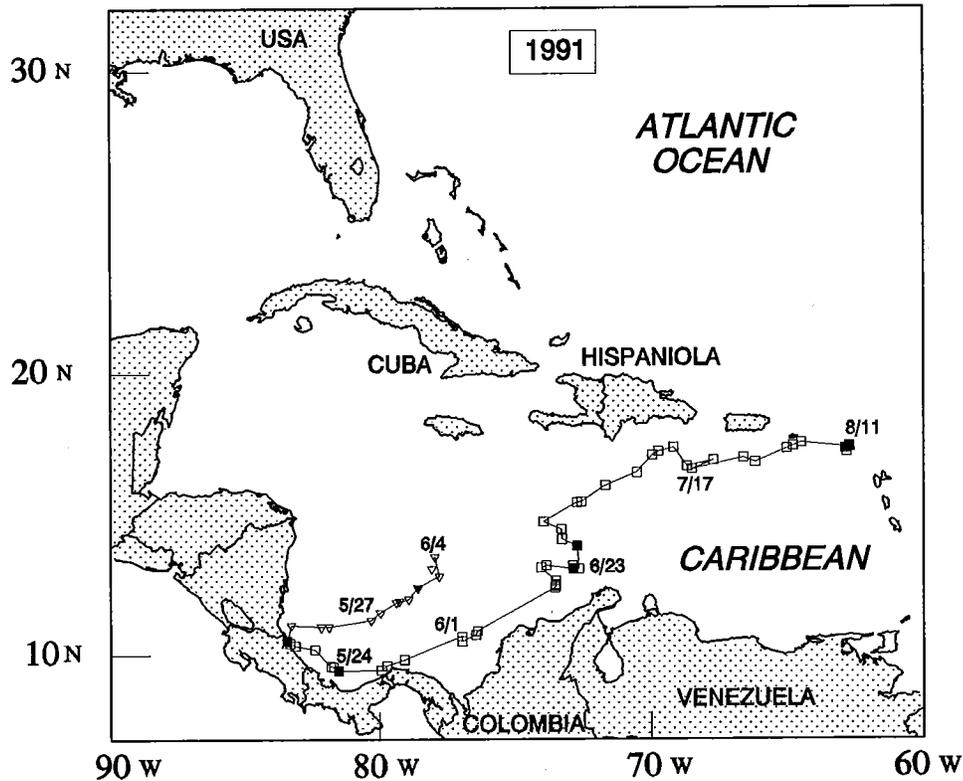


Figure 2.4. Satellite tracks of two nesting leatherback turtles from the Caribbean nesting beach at Tortuguero National Park in 1991. After nesting, both turtles migrated eastward along roughly parallel paths. Transmissions stopped for turtle # 1112A (triangles) after migrating 650 km in 17 days. The nesting cohort, # 1111A (squares), migrated along Central and South America for more than 500 km, crossed the Caribbean Sea to the Antilles, and became entangled in a fishing net after 86 days and more than 2300 km. Solid symbols represent high-certainty locations assigned by ARGOS; lines connect all the points that were included by the filtering algorithms; detached open symbols were unlikely locations by both measures.

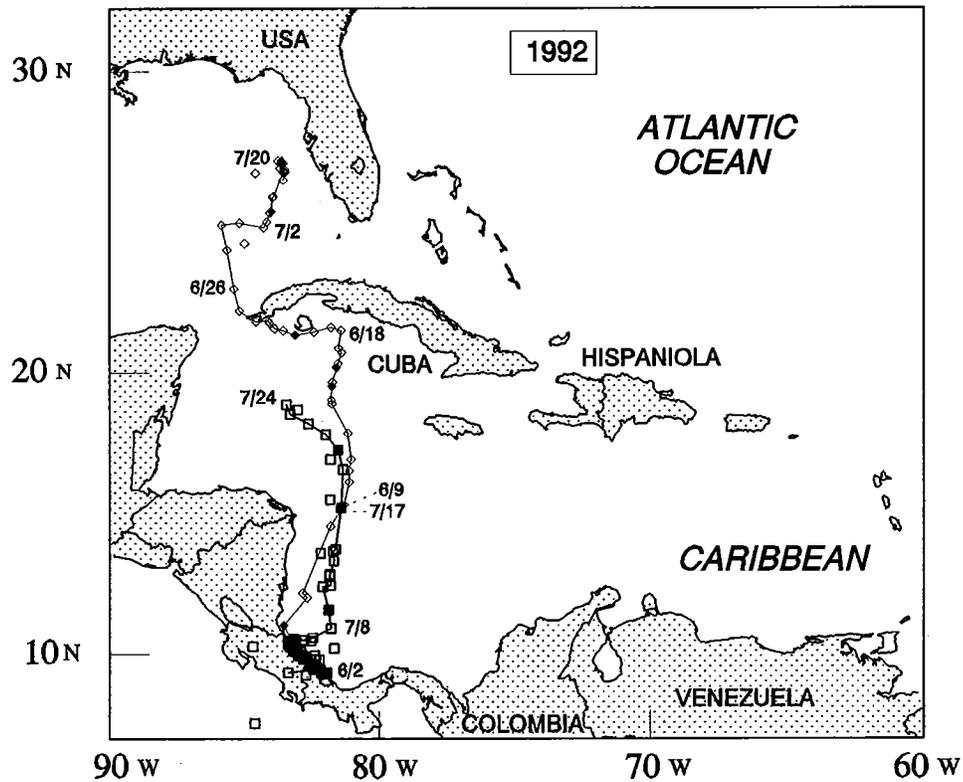


Figure 2.5. Satellite tracks of two nesting leatherbacks from the Caribbean nesting beach at Mondonguillo in May 1992. Turtle # 2107 (diamonds) headed northward, ultimately skirting the southern coast of Cuba and settling offshore of Sarasota, Florida in July. The nesting cohort # 1111B (squares) remained behind to nest apparently three more times before striking out along a migratory path of over 900 km that was almost an exact replica of its cohort five weeks earlier. Symbols are the same as in Fig. 2.4.

Continuing along at an average rate of 50 km per day, the turtle skirted the eastern tip of Cuba and continued again northward into Florida coastal waters. For the last two weeks of radio contact, the turtle exhibited minimal movements, confined within a radius of 40 km in the shelf waters of the Gulf of Mexico. Over the 54 days of both migration and reduced activity, the turtle traveled more than 1813 km, conservatively averaging 34 km per day.

The nesting cohort of this turtle, # 1111B, remained in the nesting region for quite some time after its release. First it moved slowly southward to Bocas del Toro, Panama, where it stayed for several days, before apparently nesting again in northern Panama. Heading back northward, it appeared to nest for a third time again near Mondonguillo, and after a 10-day excursion to and from northern Panama, a fourth nest at the original beach. On 4 and 5 July the turtle remained off Tortuguero beach, before moving farther offshore, to begin a steady migration northward along Nicaraguan shelf waters. The highly directed movements carried it northward through the open Caribbean at an average rate of 52 km/d, along a path which was almost an exact replica of its cohort five weeks earlier. Upon last transmission, the turtle was still moving steadily at a net distance of over 969 km from the release site.

Movements of Pacific turtles. On the Pacific nesting beaches in the vicinity of Playa Grande, migratory movements were observed for the turtles in the four consecutive years between 1992 and 1995. There were no migratory movements recorded in 1991 because of the early detachment of one transmitter after one day, and the other before the turtle completed the nesting season. Transmitter detachment was assumed based on several characteristics of the transmissions, the change in movement rate, and the sensor data, which indicated no diving activities. In the subsequent years all but the last transmitter stayed attached at

least as long as the transmissions continued; the last transmitter detached after 75 days.

The two nesting females monitored in 1992 were released on 15 January from their nest sites less than 900 m apart on Playa Langosta. The first turtle, # 2105, probably had nested numerous times since its first of two observed nests nearly two months earlier. In addition, using ultrasound imagery, it was evident that the turtle was mostly depleted of eggs. This was supported when, on the fourth day of monitoring, the turtle began a steady migration southwestward through open Pacific waters (Fig. 2.6). Traveling at rates between 20 and 40 km/d, the turtle swam more than 1300 km before slowing down at the Galapagos Islands. After meandering through the island group for 12 days, the turtle increased its pace to a rate of 64 km/d and resumed its original course for the last three days of transmissions.

In the first two weeks of monitoring, the behavior of the second turtle, # 2106, was much different. Instead of leaving within a few days, it lingered in the vicinity of the nesting beach. In addition to its seven previously recorded nests, the turtle returned to nest again on the eleventh night. By day 17, however, the turtle was moving southwestward at a rate of 28 km/d, along a path that was virtually the same as the route taken by its nesting cohort. Their similar migratory behavior became more obvious over the next 21 days as the gap between the two migrating turtles steadily closed. On 21 February, after more than 700 km of open ocean travel, both turtles were located within 20 km of each other on the same satellite pass. The last transmission was received two days later from a final position approximately 350 km northeast of the Galapagos Islands.

The following year, for undetermined reasons, neither transmitter lasted very long. These were of the same model used six months earlier on the

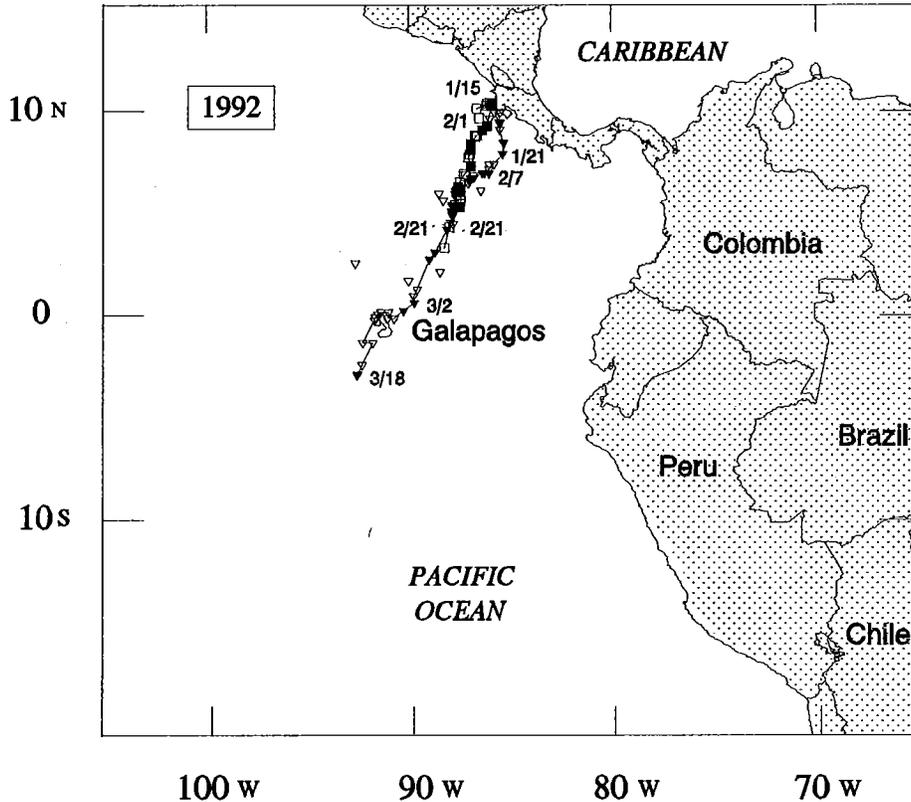


Figure 2.6. Satellite tracks of two nesting leatherback turtles from the Pacific nesting beaches near Playa Grande in January 1992. Turtle # 2105 (triangles) soon began a steady migration southwestward, passing through the Galapagos Islands, to a position of last contact more than 1600 km away in 63 days. The nesting cohort # 2106 (squares) remained to nest again before also migrating southwestward. On 21 February, after five weeks and more than 700 km of open ocean travel, both turtles were located within 20 km of each other. Symbols are the same as in Fig. 2.4.

Caribbean coast. Nevertheless, these brief tracks appeared to encompass at least the initial movements of both turtles as they started their post-nesting migrations (Fig. 2.7). Turtle # 3560 was monitored as it stayed within 50 km of the nesting beach, apparently nesting again after approximately 14 days. By day 21 it was heading offshore and then began migrating southwestward for more than 400 km along a path similar to the previous year's turtles. The turtle was traveling at a rate of 66 km/d upon last contact. The initial movements of its nesting cohort, # 3561, appeared to be along the same migration route. Over the first three days after release, it travelled southwestward at a rate of 20 km/d until last transmission.

Tracks of the two nesting cohorts in 1994 were exceptional in terms of duration and distance. However, the paths taken away from the nesting beach were very similar to those taken by the migrating turtles in the previous two seasons (Fig 2.8). During the first week turtle # 1109B stayed close by the nesting beach, and returned to nest on the ninth night (nesting was observed by researchers from Drexel University). Over the next several days it moved slowly offshore, and then began moving at a pace between 30 and 40 km/d along a southwestward course. This 87 day migration of over 2700 km became the longest track of the entire study. As the turtle moved far beyond the points of last contact of the other turtles, its path turned southward. At last contact the turtle was still swimming steadily in open Pacific waters at a position more than 2000 km offshore of Lima, Peru.

Although the track of the nesting cohort # 1110B was not as impressive, it was similar in many aspects. After 10 days of little movement, the turtle was observed nesting again for at least its sixth time of the season. Soon after departing from the beach, it then headed along a southwestward course just a few days behind its cohort. During the 31 days of post-nesting migration, the

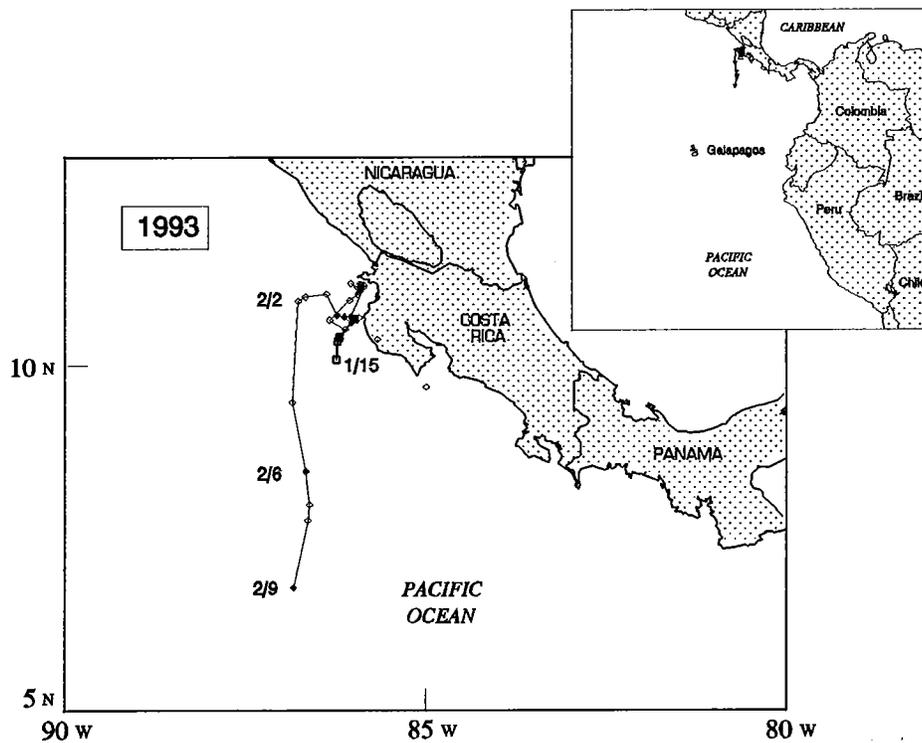


Figure 2.7. Full-scale and expanded views of the satellite tracks of two nesting leatherback turtles from the Pacific nesting beaches near Playa Grande in January 1993. Turtle # 3560 (diamonds) apparently nested again on day 14, after which it migrated southwestward over more than 400 km by last contact on day 29. During its post-nesting migration, the turtle traveled at rates between 40 and 60 km/d. Initial migratory movements of turtle # 3561 (squares) also were southwestward over the three days of tracking. Symbols are the same as in Fig. 2.4.

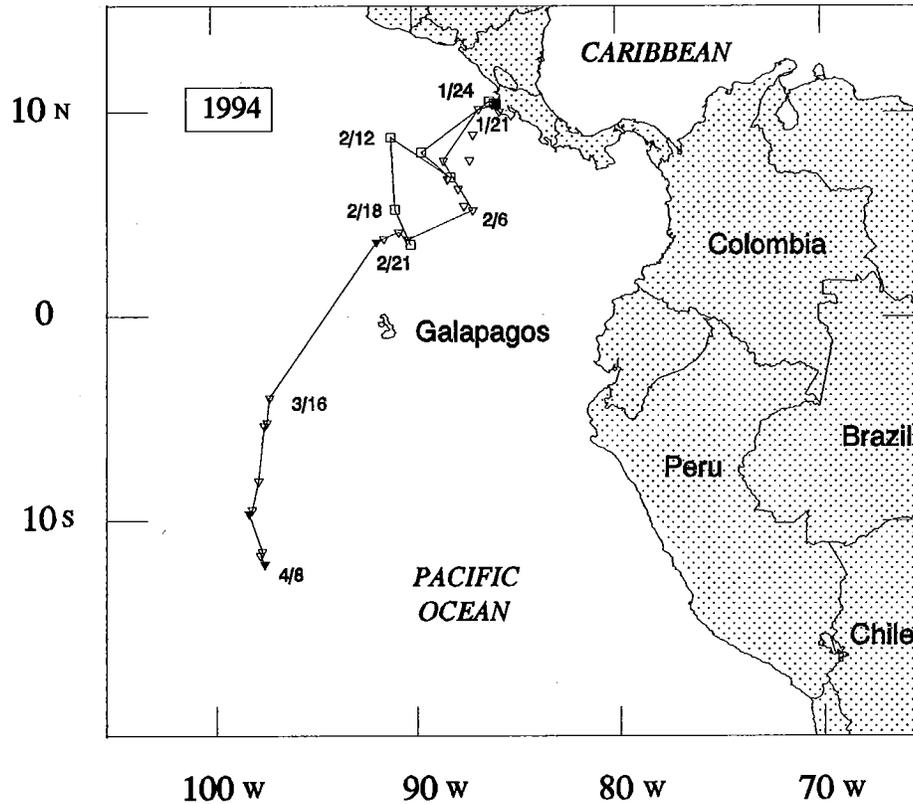


Figure 2.8. Satellite tracks of two nesting leatherback turtles from the Pacific beaches near Playa Grande in January 1994. The longest track of the study was recorded for turtle # 1109B (triangles) after it returned to nest for its sixth time of the season on day nine. Its subsequent 78 days of migration conveyed the turtle along the southwestward path of its predecessors, and then beyond, for a total of more than 2700 km. The nesting cohort # 1110B (squares) also returned to nest for the sixth recorded time 10 days after transmitter attachment. Over the next 31 days it too moved southwestward more than 880 km before last contact. Symbols are the same as in Fig. 2.4.

turtle had moved more than 850 km. It transmitted sensor data until three weeks later, but this location, approximately 330 km north of the Galapagos Islands, was the last satellite fix received.

In 1995, the final season of the study, both turtles selected for tracking were observed renesting after intervals of limited movements near the nesting beach. The first turtle, # 1111C, was reported by a beach volunteer to have nested on day 10. Soon afterward, it began a steady post-nesting migration along the same southwesterly course as its predecessors of the three previous years (Fig 2.9). The 38 day track traced the turtle's movements beyond the Galapagos Islands before the last location was reported. The transmitter continued to relay sensor data for eight more days. The second transmitter continued sending signals long after it broke free of the turtle. Turtle # 1112B was observed by researchers (Buffalo State College) on day 10, nesting for the first of apparently two subsequent times during the first three weeks of monitoring. After day 26, the turtle began its post-nesting migratory movements, which also carried it steadily southwestward, past the Galapagos Islands. On day 75, after six weeks traveling at a rate of 42 km/d, the transmitter detached and floated to the surface. The last satellite locations for both turtles were more than 1450 km away from the nesting beach.

Rates of migratory movement. Although the primary emphasis of the study was to monitor post-nesting migrations of the leatherbacks, the tracks also included the interesting movements of seven females as they returned to nest at intervals between 9 and 14 days after transmitter attachment. Since the calculations of overall net movements (Table 2.4) included these periods of relative inactivity, they generally represent underestimates of travel rates. While turtles remained in the area to nest, net displacements were minimal, and measurements of these

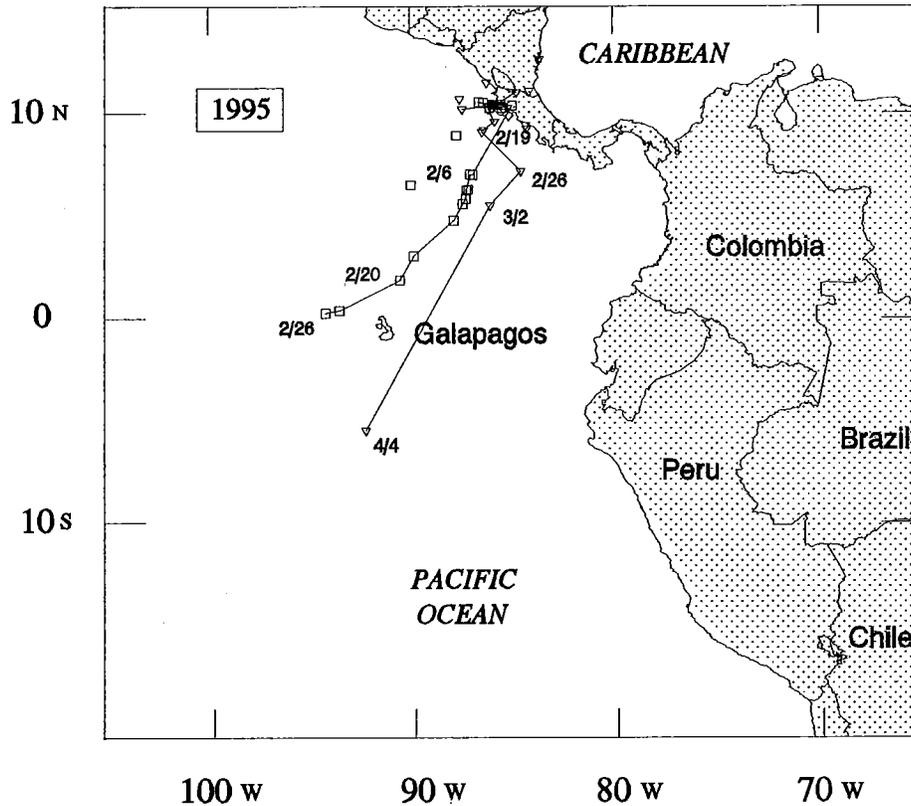


Figure 2.9. Satellite tracks of two nesting leatherback turtles from the Pacific nesting beaches near Playa Grande in January 1995. Both turtles nested again after transmitter attachment, and both subsequently migrated southwestward past the Galapagos Islands. Turtle # 1111C (squares) remained for 10 days to nest again, before migrating along a southwestward course, traveling over 1450 km over the next 28 days. On 20 February the turtle dove to a depth of 744 m; this is the deepest dive ever reported for a turtle. Turtle # 1112B (triangles) apparently nested twice more before heading along a similar course, traveling more than 1880 km in the final six weeks before the transmitter broke free. Symbols are the same as in Fig. 2.4.

interesting movements were considerably below the limits of resolution of the satellite transmitters. To yield better estimates of movement during migration, mean and maximum rates were calculated only from the ARGOS high-quality location data that were available after each turtle obviously had begun its post-nesting migration (Table 2.5). Interesting turtles and migrating turtles without data of this category were excluded from these analyses.

The mean rates of travel of nine migrating leatherbacks ranged from 15 to 52 km/d. The grand mean of 37.9 km/d probably represents a good estimate of a turtles daily travel during its active hours. To estimate actual swimming speeds, these values should more appropriately be doubled to account for the half day of light in the Tropics. The maximum rates up to 104 km/d, with a grand mean of 60.9 km/d, reflect some of the higher values that were calculated over short intervals. As such, these probably are closer to the actual swimming speeds of leatherbacks during migration.

Sensor data, activity, and diving behavior

Surface behavior patterns were calculated as mean percentage of time spent at or near the surface. For the earlier nine transmitters, the values were calculated from the cumulative time in a four-hour period the turtles were not submerged for more than one minute. The comparable measure of surface behavior for the four depth transmitters was the percentage of time spent in the upper 6 m of the water column over a six-hour period. The overall mean time at surface calculated from 346 recorded time periods was 19.4% (SD = 14.1). The grand mean for the 13 individuals was a similar 20.6% (SD = 9.3). Leatherbacks were at the surface more during daylight hours (Standora and Morreale, *in press*) but the difference was only a slight 3%. Turtles also spent slightly more time at the surface during interesting periods (20.8%) than

Table 2.5. Rates of daily movement calculated from high-certainty satellite fixes for nine leatherback turtles during their post-nesting migrations. All interesting movements have been excluded. Overall and grand mean and maximum rates were calculated in km/d.

ID	n	Mean	S.D.	Min.	Max.
1109B	3	35.8	6.1	31.2	42.8
1111A	5	41.0	30.2	17.3	93.5
1111B	3	50.4	20.8	29.1	70.6
1112A	1	42.5	---	42.5	42.5
2105	34	33.8	23.0	3.8	104.1
2106	8	30.7	6.4	23.5	43.2
2107	7	39.0	22.0	17.2	71.7
3560	2	52.4	17.5	40.0	64.8
3561	1	15.2	---	15.2	15.2
Overall	64	35.8	21.0		104.1
Grand	9	37.9	11.1		60.9

during post-nesting migration (18.3%). The largest differences in surface activity showed up between daylight periods (20.0%) and dark periods (14.0%) while turtles were migrating (Fig. 2.10). This is most likely reflective of high activity by day and sleeping below the surface at night.

A further indicator of diurnal differences in physical activity by the turtles was the diving frequency. The overall mean diving rate was 29.1 dives/4 h (SD = 24.7) for 373 recorded intervals. This was the intermediate value that resulted from merging the lower nighttime values, which averaged 23.9 dives/4 h, with the higher daylight value of 32.0 dives/4 h. During interesting intervals the diving frequency of 23.3 dives/4 h was also lower than the value of 32.6 dives/4 h observed during active migration. The highest mean diving frequency of 36.5 dives/4 h was observed for migrating turtles during the daylight hours, a time of most likely highest physical exertion (Fig. 2.11).

The two measures of behavior and activity were complemented by a third measure of diving activity in which the durations of 373 individual dives were recorded for the 13 turtles (Fig. 2.12). The overall mean of 11.9 minutes per dive included values for interesting turtles, where there were no apparent diurnal differences, and migrating turtles, where the average dive was shorter during the day (11.7 min.) than at night (16.3 min.). The larger diurnal differences among the migrating turtles reinforced the inferred pattern of higher energy expenditure by day, which would prompt more frequent shuttling to and from the surface to breathe.

With the added depth features on the SLTDR-type transmitters, the sub-surface behavior of four turtles also was monitored in two different ways. In one set of summary data, the maximum depth over the 24 hours prior to transmission was reported. The maximum depths over 33 of these complete-day records ranged from 24 m for turtle # 1112B, during an interesting interval, to

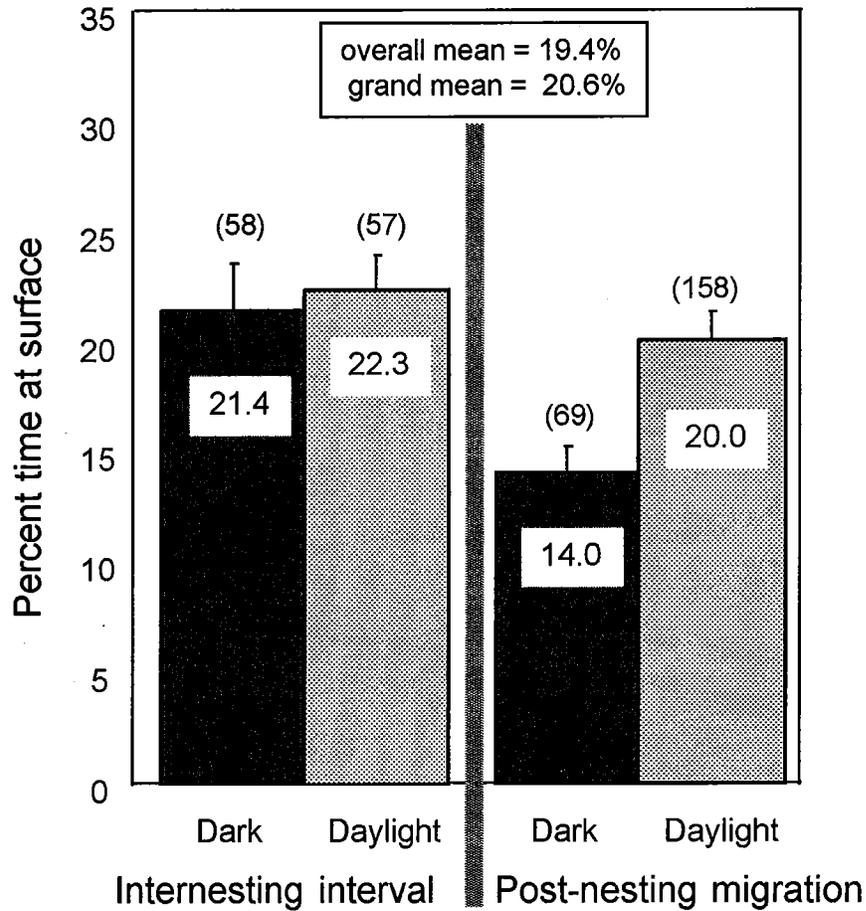


Figure 2.10. Diurnal and behavioral differences in mean duration at the surfaces for 13 leatherback turtles during internesting intervals and post-nesting migrations. The large diurnal difference in surface time during migration probably reflects large differences in daytime and nighttime activity levels. Values of histograms represent overall mean durations for each group; sample sizes are in parentheses.

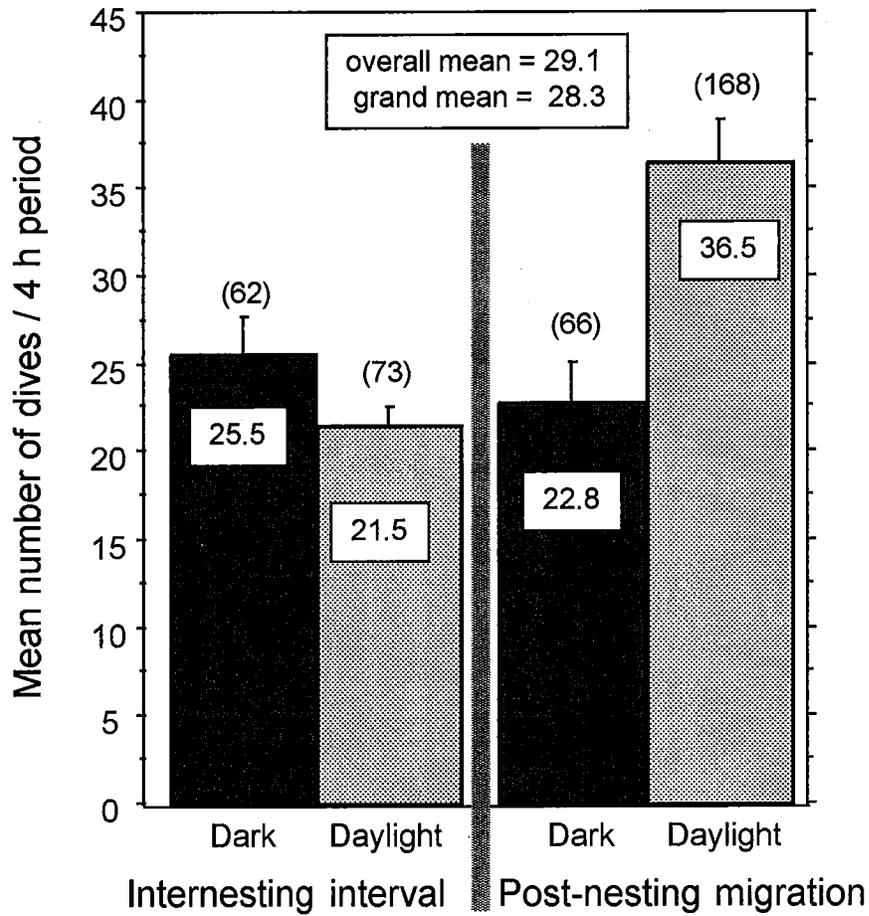


Figure 2.11. Diurnal and behavioral differences in mean diving frequency for 13 leatherback turtles during internesting intervals and post-nesting migrations. Higher frequency of dives by day during migration indicates higher physical activity than at night. Values of histograms represent overall mean durations for each group; sample sizes are in parentheses.

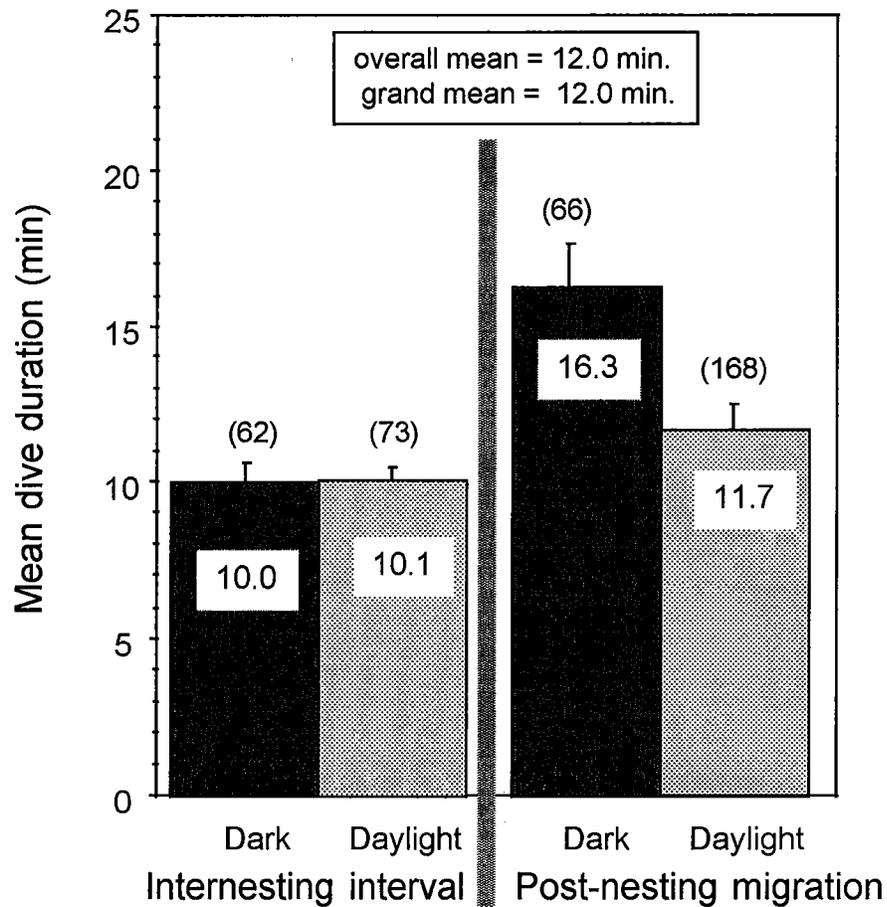


Figure 2.12. Diurnal and behavioral differences in mean durations of dives for 13 leatherback turtles during internesting intervals and post-nesting migrations. Shorter dives by day during migration indicate higher activity levels and increased respiration than at night. Values of histograms represent overall mean durations for each group; sample sizes are in parentheses.

744 m for turtle # 1111C, during post-nesting migration. This was the deepest dive ever recorded for a turtle in reported literature. The single deep dive came when the leatherback was migrating over water approximately 2000 m deep, north of the Galapagos Islands (Fig. 2.9).

Since roughly 80% of the leatherbacks' time is spent submerged, the characterization of their diving profiles proved to be relatively important. As a turtle dived, its maximum depth was measured. At the end of the dive the record was added to one of 14 different pre-selected depth intervals ranging from 6 m to 1500 m. After each six-hour period, the bin totals were then compiled and reported in the subsequent satellite message. In this fashion, 3301 individual dive depths were reported. To reconstruct a general picture of the diving behavior of leatherbacks, the averages of the 104 recorded six-hour periods were calculated (Fig. 2.13). On average, 84% of the dives were to depths within the upper 54 m of the water column, and more than 97% were within the upper 102 m. Undoubtedly, the average dive depth was diminished by interesting behavior in shallower coastal waters, where 96% of all dives were shallower than 54 m. However, even while turtles were migrating in water mostly deeper than 2000 m, more than 70% of their dives did not exceed 54 m, and 25% more were to depths between 54 and 102 m. The deepest dives recorded in these binned messages were to depths between 300 and 402 m, but these were more than 300 m shallower than the maximum recorded in the daily summaries. As would be expected from such a diving summary, the overall average time turtles spent either at the surface or at depths shallower than 54 m was 94%; average time spent between 54 and 102 m was 5%; and time at depths between 150 and 402 m was less than 1%.

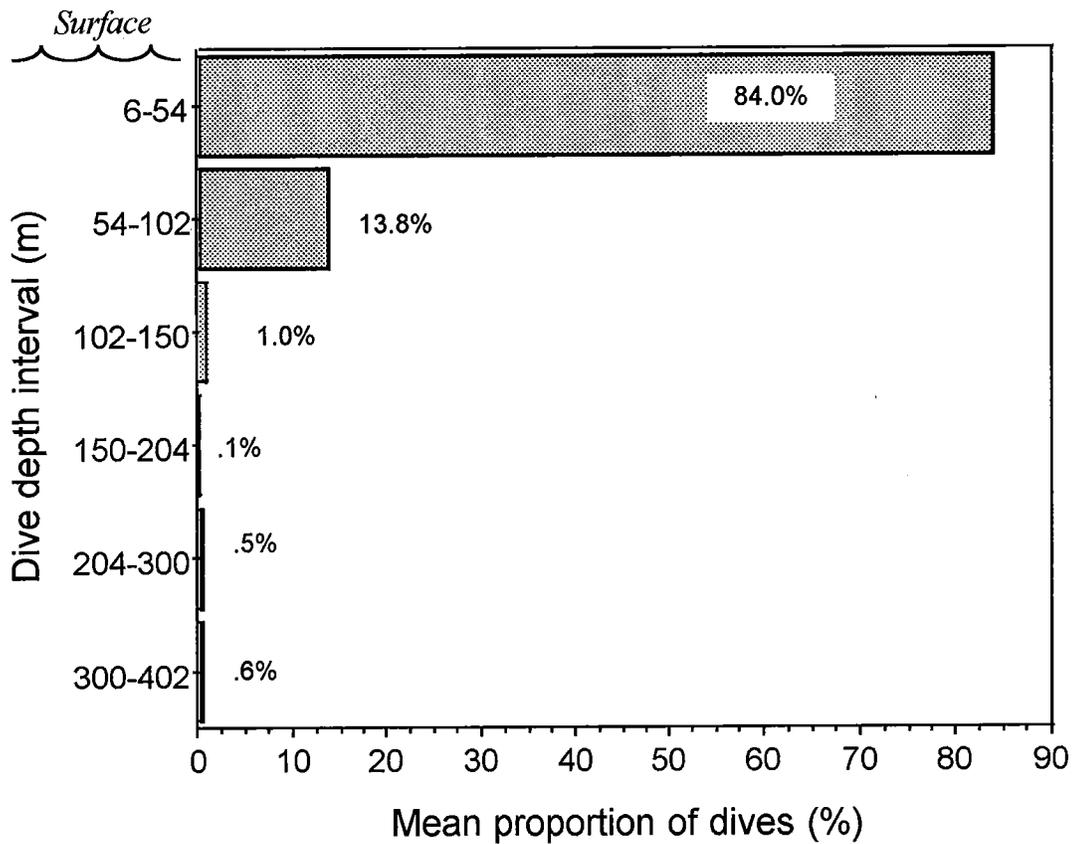


Figure 2.13. Overall mean percentages of dives culminating at selected intervals from the surface to depths of 402 m. Averages were calculated for 104 six-hour periods in which 3301 dives were recorded and relayed by satellite. In an average six-hour period, some dives were deeper than 300 m, but nearly all were within the upper 100 m of the water column.

Discussion

Definite and obvious patterns of oceanic movement were observed as a result of monitoring the migratory behavior of several leatherback turtles in the same study. First, a similar migratory behavior was evident between all six pairs of nesting cohorts. Upon completion of nesting, turtles within the same season invariably traveled along similar, and in some cases virtually identical, pathways. Even after long intervals between departure, nesting cohorts followed the same migratory routes. There were some very striking examples of this observed pattern. The first of two migrating turtles tracked from the Caribbean beach at Mondonguillo swam along a northward course to Cuba and ultimately to Florida. Its cohort, tagged on the same night, remained in the region shuttling between Panama and Costa Rica, apparently nesting three more times, before beginning migration. Even though the cohorts' movements were separated by five weeks, the second turtle migrated 900 km northward over a route that was virtually identical to the first turtle. On the Pacific coast in 1992, one turtle departed immediately after nesting, while its cohort remained in the region to nest one more time. After 17 days of separation, it became obvious that the turtles were traveling along a very similar course. Within 24 more days, the second turtle had traveled more than 700 km to a position less than 20 km away from its nesting companion.

A further remarkable migration pattern developed among the Pacific leatherbacks. All four separate pairs of nesting cohorts monitored in each of four consecutive years leaving from Playa Grande beaches migrated along a southwesterly course across open ocean waters (Fig. 2.14). Despite the vastness of the Pacific, and the separation of as much as four years, the tracks of all eight turtles when superimposed, were all within a relatively narrow corridor

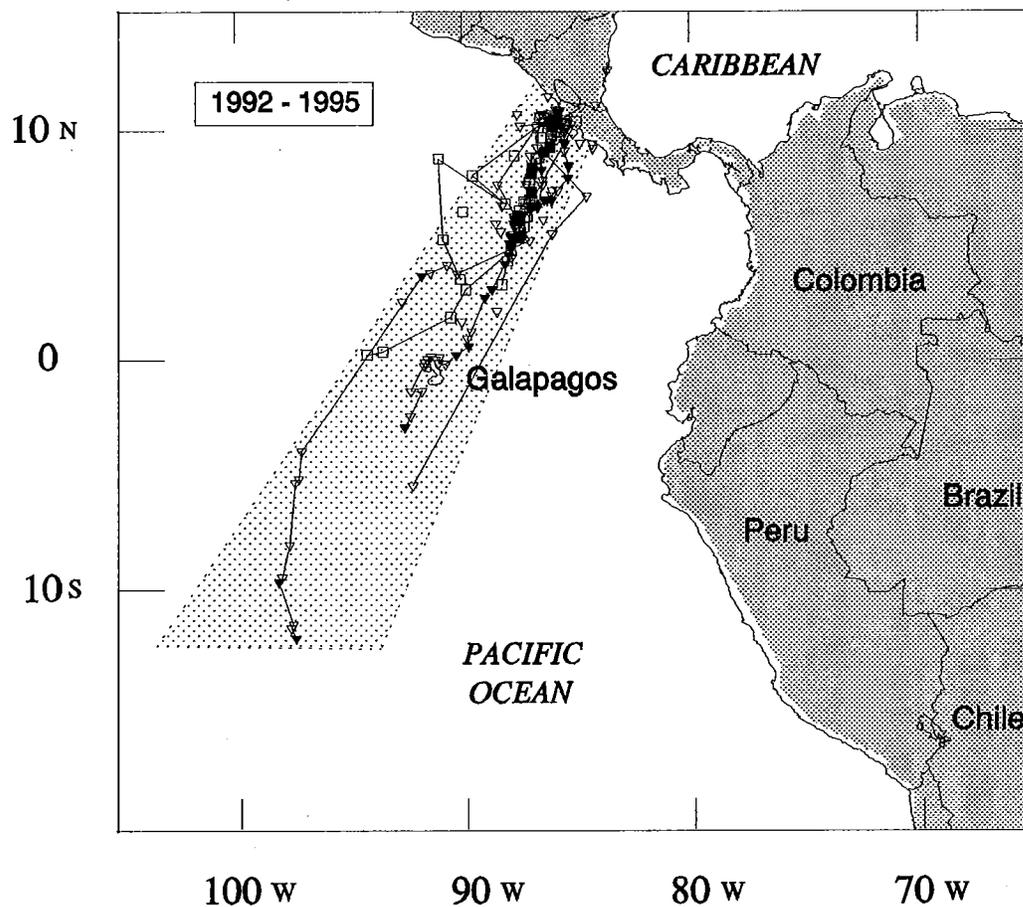


Figure 2.14. Satellite tracks of the post-nesting migrations of all eight leatherback turtles from the Pacific nesting beaches near Playa Grande, between 1992 and 1995. All but the two most extreme locations were within a narrow corridor through open Pacific waters. This corridor was conservatively estimated to be less than 500 km wide, from Central America to at least as far as the Galapagos Islands, and perhaps as far as 2700 km away. Symbols are the same as in Fig. 2.4.

extending out thousands of kilometers into the Pacific Ocean. Once the turtles completed nesting, their movements were direct and steady along this same heading, which pointed roughly toward and beyond the Galapagos Islands. Five of the turtles were tracked as they passed by the Galapagos; one turtle slowed down, dwelling among the islands for nearly two weeks before continuing into deeper ocean waters.

This persistent oceanic route, which was conservatively estimated to be narrower than 500 km, was the first such migratory corridor ever documented for migrating sea turtles (Morreale et al. 1996). The probability of all eight turtles migrating within such a restricted corridor was considered to be extremely low. It was calculated that a turtle leaving the Pacific coast has the option of heading out along an arc of roughly 160°. Even if this were simplistically divided into four sectors of 500 km each, and the turtle tracks were evenly distributed, the chance of two turtles traveling within that same sector would be 0.06; for four turtles it would be 0.004; and for all eight turtles it would be 1.5×10^{-5} . This was in great contrast to the post-nesting movements of olive ridley turtles, *Lepidochelys olivacea*, from a nearby beach, which were diverse and widespread from year to year, and even among nesting cohorts (Plotkin et al. 1995).

The fixed behavior of the leatherbacks over several years can best be explained by the presence of a fixed migratory corridor heading southwestward through open waters of the Pacific. This observed migratory pattern may be representative of the migratory route used by all of the Pacific coast leatherbacks in Costa Rica, or possibly by all leatherbacks in the region. The farthest location a turtle was monitored along this path was a position roughly 2000 km west of Lima, Peru. However, all turtles were still moving at last contact, and these deep ocean waters may only be part of the way toward their

destination. It is not yet known how such a corridor is maintained through time, or how it would be detected by the migrating leatherbacks. Their migratory patterns may be influenced by any number of environmental factors including currents, magnetic cues (Lohman and Lohman 1993, Papi et al. 1997), persistent ocean fronts (Yoder et al. 1994), or bathymetric features (Morreale et al. 1994).

In analyzing the physical properties of the observed migration routes, there seemed to be at least some connection with underlying bathymetric features. Using National Geophysical Data Center's ETOPO5 topographic data set, the tracks of the Caribbean turtles were observed to parallel bathymetric contours ranging from depths of 200 to 3000 m. Moreover, most of the turtles' movements were along the steep slopes of the continental shelf, but appeared to avoid the featureless abyssal plains. The two turtles that migrated eastward both skirted the edge of the Columbian Basin which exceeds 3500 m in depth. One turtle appeared to be crossing the Caribbean along the basin's northern rim, while its cohort followed along the southern rim and continued across to the Antilles along the Beata Ridge, a high point which separates the Caribbean basin from the 4000 to 5000 m depths of the Venezuelan Basin. The following year, both Caribbean turtles followed along the contours of the Nicaraguan rise northward toward the Gulf of Mexico. In the longer of the two tracks the turtle's path conveyed it precisely around the eastern boundary of the abyssal depths of the Yucatan Basin.

The bathymetry along the initial segment of the Pacific corridor supports this connection between topography and migration. The pathway used by the Pacific turtles for much of the first 1500 km traces over the northwestern boundary of the Cocos Ridge. This is a substantial geologic feature that rises from depths of greater than 3500 m to less than 1000 m, with some sea mounts,

including Cocos Island and the Galapagos Islands. While following along the ridge, turtles spent most of their time in waters ranging from 1200 to 3000 m in depth.

These movements could be viewed simply as the avoidance of shallow areas, and of the very deep areas greater than 3000 m in depth. However, this did not account for the observed behavior in the latter parts of some of the longest Pacific tracks. Beyond the Galapagos Islands, the ridge drops off to the ocean floor with depths in excess of 3000 m. When four turtles were tracked beyond this point, they continued off the ridge and through the deeper Pacific waters without a noticeable change of heading or behavior.

If the underlying bathymetry does influence leatherback migration for some of the journey, it seems unreasonable to assume that individuals are following along such deep-water contours by shuttling to and from the bottom. More likely, they would be responding to some environmental signal that is expressed in shallower depths closer to the surface. The deepest dive ever recorded was 744 m, and even if they do dive deeper, as has been suggested (Eckert et al. 1989), the deep dives are rare.

Indeed, regardless of water depth, turtles remained almost exclusively in the upper 100 m of the water column. There was an observed tendency to dive deeper during migration, but even during the deeper dives of 300 to 400 m, the turtles did not penetrate beyond the upper fifth of the entire water column. These patterns in diving depth were in close agreement to two other studies that measured diving depths of leatherback turtles (Eckert et al. 1986, 1989, 1996). Interesting females from St Croix spent more than 95% of their time in the upper 200 m, with overall mean depths of less than 100 m. The deepest dives recorded in these studies also were to similar depths of 475 m and 315 m respectively. In the latter study, two of the turtles exceeded the 315 m scale

several times, and it was estimated that one turtle may even have dived deeper than 1000 m. This conjecture was supported in the present study when one of the Costa Rican leatherbacks was recorded diving to a depth of 744 m. Even this deepest single dive ever recorded for a turtle, however, was also within the upper half of the water column.

For interesting turtles, there was little indication that there were any major behavioral differences by day or night. The activity levels, as indicated by diving frequency, length of dives and amount of time spent at the surface, showed minimal diurnal variation. The general impression is that these turtles remain relatively inactive during the days between nesting bouts. This contrasted with the diving behavior reported for interesting turtles from a nesting beach at St. Croix (Eckert et al. 1986, 1989), but was similar to the lack of diurnal difference in diving behavior reported for another interesting leatherback from St. Croix (Keinath and Musick 1993).

The general pattern for migrating turtles was one of higher activity by day (characterized by more frequent breathing), and reduced activity at night (with fewer and more protracted dives, and minimal surface time). It was presumed from these data that the turtles were not traveling at night, but were sleeping. In a more recent study on a single leatherback migrating away from a nesting beach in Natal, the turtle was reported to travel equally by day and night (Hughes et al. 1998). The movements of this turtle, however, were probably mediated by the Alguhas Current, which would have transported the turtle even while it was resting.

A common feature in all post-nesting leatherback turtles studied to date, is their similar motivation to migrate fast and far after nesting. The first few migratory excursions recorded in this study were the longest detailed tracks of leatherback turtles recorded at the time. However, in the past few years there

have been other successful tracks of leatherback turtles, and some have even exceeded these tracks by thousands of kilometers (Papi et al. 1997, Eckert 1997). Thus, it appears that in Costa Rica and at other nesting beaches, extensive migratory movements are expected behavior for leatherbacks after nesting is completed. The additional large sample of turtles from the Costa Rican study further revealed that in some regions oceanic travel of many individuals can occur along migratory corridors.

The existence of specific migratory corridors for leatherbacks is important for understanding their ecology and evolution, especially with respect to environmental patterns. The ability to predict specific routes for migrating turtles also may have as much relevance to their conservation and international management. The clustering of individuals in both space and time during migratory events could facilitate monitoring, censusing and, protecting entire populations. To date, global conservation efforts have focused primarily upon monitoring and protecting nesting beaches. However, the observed patterns of migration of turtles along specific routes may offer an excellent means to shift the emphasis of future management out to sea, where the turtles spend most of their time. Thus, sea turtles could be protected, not only in nesting and foraging areas, but also as they move along the interconnecting migratory corridors at sea.

With mounting concerns over the status of leatherback turtles, global conservation efforts need to acknowledge that they are a shared resource, with individuals readily traveling through the waters of many different nations. Because of continuing declines in leatherback populations worldwide, an understanding of migration patterns could have immediate impact on their protection. The delineation of migration routes of sea turtles also could have more far-reaching conservation implications. It is possible that the routes of

leatherback turtles described in this study may be linked to oceanographic features, which may be highly related to broader scale patterns of resource availability. The observed convergence of turtles along narrow routes then, may be linked to tightly clustered resources along these limited corridors. If such a relationship exists between migration patterns and environmental conditions, then current declines in leatherback turtle populations may reflect concurrently diminishing resources in the marine environment.

CHAPTER THREE

SEASONAL MIGRATIONS OF FORAGING JUVENILE LOGGERHEAD TURTLES, *CARETTA CARETTA*, IN THE NORTHWESTERN ATLANTIC OCEAN.

Northwestern Atlantic waters are not generally noted as typical habitat for sea turtles. Rather, sea turtles traditionally have been regarded as inhabitants of tropical regions of the world. This conventional outlook dates at least to the middle of the 19th century (Dekay, 1842) and is pervasive throughout the historical and contemporary literature (Morreale et al., 1992). The customary tenet was that sea turtles live their entire life cycles in warmer regions, and that northern waters are outside their normal ranges. Although leatherback (*Dermochelys coriacea*), loggerhead *Caretta caretta*, Kemp's ridley (*Lepidochelys kempii*), and green turtles (*Chelonia mydas*) were reported in northeastern U.S. waters repeatedly over the past century (Morreale et al. 1989), the dogmatic view of them as inhabitants of the south persisted. Much of the historical inertia undoubtedly was influenced by obvious nesting activities, which are mostly restricted to tropical and subtropical beaches. It is more accurate, however, to describe sea turtles as tropical nesters, with distributions ranging from the Tropics to the higher temperate latitudes.

More recently there has been a willingness to concede that sea turtles inhabit northern temperate waters seasonally. Within the past three decades it has been documented that leatherback, loggerhead, green, and Kemp's ridley turtles regularly occur in northeastern U.S. waters during the warmer months (Bleakney 1965, Brongersma 1972, Lazell 1980, Shoop 1980, Morreale and Standora 1994). The acceptance, however, was not complete. It was argued that the northeast U.S. was clearly a disadvantageous environment for Kemp's ridley

turtles (Hendrickson 1980) and, by implication, for other species. This speculation was perhaps more compelling given that many of the turtles in both recent and historical accounts had been found dead or moribund, from hypothermia in early winter weeks. (Murphy 1916, Latham 1969, Meylan and Sadove 1986, Morreale et al. 1992). Researchers with more moderate opinions surmised that young sea turtles are swept occasionally into inshore waters of the northeast by anomalous currents or eddies of the Gulf Stream, whereupon they may sometimes find their way back to southern waters (Carr 1980, 1986a, Meylan 1986, Ogren 1989, Collard and Ogren 1990).

Among the continuum of hypotheses, the most convincing current thought is that New England and New York waters are a critical habitat for foraging loggerhead, Kemp's ridley, and leatherback turtles during warmer months each year (Lazell 1980, Shoop and Kenney 1992, Morreale and Burke 1997). Extensive long-term studies in New York have substantiated this contention through detailed examination of demographics, feeding ecology, and behavior of the sea turtles that occur in northern coastal waters (Morreale and Standora 1994). With the exception of a few leatherbacks, the turtles in nearshore waters are small juveniles. The loggerhead is the most abundant, followed by the Kemp's ridley. Each year the young turtles appear in early summer and remain for up to several months, feeding heavily on a diet composed mainly of crabs. The abundant resources in the nearshore environment result in extremely high measured growth of the juveniles, before they slow down in the fall (Morreale and Standora 1994). As temperatures decline rapidly, turtles change their behavior and begin to move toward open ocean waters.

The patterns of behavior observed in these long-term studies indicated for the first time that large numbers of juvenile turtles migrate into northern

temperate waters each year to forage, and then migrate out in the fall.

Furthermore, once they return to ocean waters, they become part of a large contingent of northeastern turtles that appear to be migrating southward (Shoop and Kenney 1992, Morreale and Standora 1994, Morreale and Burke 1997).

Hence, the resulting image is no longer one of a group of waifs, disjunct and lost from the main body of the sea turtle populations that inhabit distant southern waters. Rather, the sea turtles of the northeast represent a substantial constituent that probably moves freely among the widespread habitats in the western Atlantic.

In western North Atlantic waters there are thousands of sea turtles, many of which probably migrate similarly along continental shelf waters. In the southeastern U.S. there are numerous nesting beaches for sea turtles, with an estimated 14,000 loggerhead turtles nesting in the region annually (National Marine Fisheries Service and U.S. Fish and Wildlife Service 1991).

Loggerheads are joined in southern waters by three other species that, although they mostly nest farther south, also occur in great numbers: the Kemp's ridley, the leatherback, and the green turtle. The overall distribution of these species is scarcely limited to the south, however. Instead, these turtles are much more widespread, extending along the entire length of the Atlantic seaboard. With nesting and overwintering sites in the south, and developmental habitats and feeding grounds extending far into the northeast, by all expectations, there should be numerous accounts of frequent long-distance travel of turtles among these distant habitats. Indeed, it has been shown that individuals of all three species are at least capable of migration between these widely separated regions. Yet, it is surprising that there is so little known about specific movements of turtles; namely, timing, extent of movement, and the routes of travel used during their long-distance migrations.

There are three main sources of evidence of long-distance migratory movements of sea turtles along the Atlantic coast: observation studies; mark-recapture records; and telemetry studies. The nature of information from these diverse study techniques is both fundamentally and qualitatively distinct, each providing important information toward a general understanding of oceanic movements of turtles in this region of the Atlantic.

Synthesis of many observation studies that included shipboard surveys and incidental captures by fishermen suggests that there is seasonal travel along the Atlantic coast to and from Pamlico Sound (Epperly et al. 1995*a, b*), Chesapeake Bay (Lutcavage and Musick 1985, Keinath et al. 1987, Byles 1988), New York (Morreale and Standora 1989, 1990, 1991, 1992, 1994, Morreale and Burke 1997), and New England (Lazell 1980, Shoop 1980). Further observations by aerial surveys have provided complementary data that were strongly supportive of the capture studies (Shoop et al. 1981, Keinath et al. 1987, Byles 1988, Shoop and Kenny 1992, Hopkins-Murphy and Murphy 1994, Musick et al. 1994, Epperly et al. 1995*b, c*). The overall pattern that emerges from the observed distributions appears to be one of extensive seasonal migration of sea turtles along the eastern seaboard.

Recapture data, providing start and end points of travel of individual turtles, also collectively indicate considerable movement of sea turtles along the Atlantic coast. 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, Schmid 1995, Epperly et al. 1995*a*), a loggerhead from Rhode Island to Georgia (Shoop and Ruckdeschel 1989) and over a dozen individuals of three species that have migrated from New York to southern waters (Fig. 3.1; Morreale and Standora 1989, 1994, Morreale and Burke, 1997).

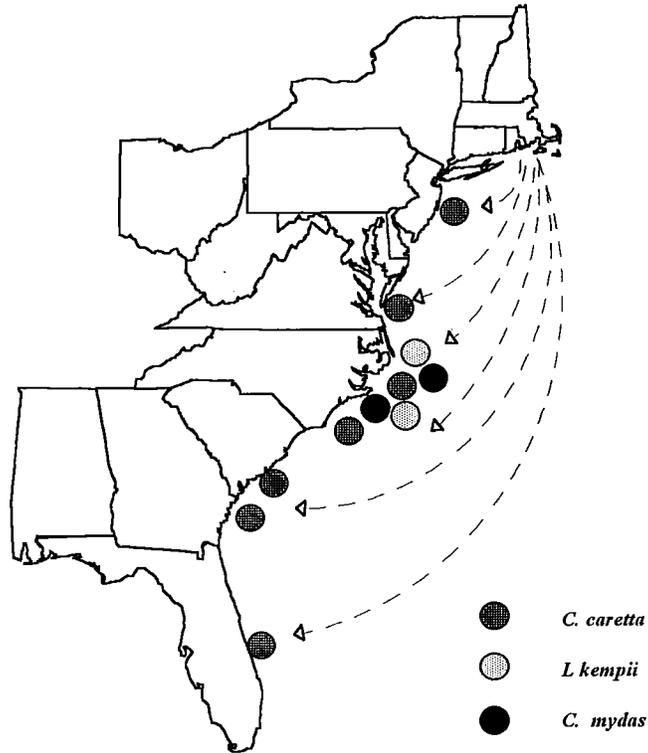


Figure 3.1. Long-distance recoveries of 11 juvenile sea turtles of three different species originally tagged in New York waters. Dashed lines indicate unknown migration routes from New York to the other regions along the Atlantic coast (modified from Morreale and Standora 1994).

Evaluating sea turtle movements by observation studies and long-distance recaptures is not without shortcomings. Both methods present one-dimensional information on location and neither provides much information about migratory pathways and timing of movements. Additionally, the success of both techniques depends on turtle behavior. Turtles must be accessible in the case of captures, or at the surface and visible in the case of aerial or shipboard surveys. Moreover, difficulties arise in assuming that the behavior of the relatively few turtles observed is truly representative of the majority. Nevertheless, observation and mark-recapture data were the only tools available for most of the history of sea turtle research.

In later years, the advent of telemetry offered a new source of information on sea turtle ecology. With transmitters, individual behavior and movements could be monitored for the first time, and these techniques were first applied in nearshore developmental habitats. More recently, with technological advances in satellite telemetry, some excellent information also has been accumulated on turtles at sea. Again, these studies supported a pattern of seasonal migration along the Atlantic habitats with reported movements of Kemp's ridley and loggerhead turtles between Florida and North Carolina (Renaud 1995, Gitschlag 1996), from Chesapeake Bay to North Carolina and into Gulf Stream waters (Byles 1988, Keinath et al. 1989, Keinath 1993), and even from New York to southern waters (Morreale and Standora 1991, 1992, 1994). The information on migratory behavior that satellite transmitters are able to provide is far and above the incomplete information from all other sources combined. Turtle movements can be monitored as they happen, which is extremely useful in interpreting patterns in the northwestern Atlantic where seasonal climate changes probably influence migration. In addition, the vastly increased resolution obviates the need to infer the pathways and timing between

distant endpoints.

By incorporating some of the newest satellite technology and expanding on some of the methods discussed in previous chapters, the study presented here was designed to carefully examine the fall migration patterns of sea turtles from northeastern U.S. waters. The study plan also benefitted greatly from the extensive knowledge of the ecology of sea turtles in the New York bight (Morreale and Standora 1994). The predictable capture of turtles during early October, and their presumable readiness to migrate at this time, enabled higher precision in planning and much more uniformity in the sampling scheme. In addition, the similar ecology, documented among the loggerheads and Kemp's ridleys in New York, increased the chance that the patterns observed in this study would be more broadly applicable to other species.

Objectives

This study was designed primarily to document patterns of movement of loggerhead turtles as they migrated through the open ocean from inshore waters of the northeast. The specific objectives of this study, in order of importance were:

- 1) to monitor the oceanic movements of individual turtles as they migrated out of nearshore waters in the fall;
- 2) to detect emergent patterns of migratory behavior through a synthesis of detailed observations on the timing and pathways of movement; and
- 3) to quantify behavioral attributes during migration, such as diving activity, surfacing behavior, and the turtles' positions within the water column.

As an interesting adjunct to the stated objectives, the design of the study enabled a means to assess the proportion of resident turtles that migrate out of northeastern waters to other regions. Young loggerhead turtles were selected

from eastern New York waters based on the time of year only. The turtles selected were not very distinct in terms of species, size, state of health, or location of capture. As such, their behavior was considered to be representative of a much larger group of turtles. A high proportion of turtles migrating between the northeast and distant regions would underscore the connection among these seemingly separate populations along Atlantic seaboard, including the northeast, which until recent years was considered a remote and disjunct region.

Materials and Methods

Turtles were collected from commercial fishermen on Long Island, New York as water temperatures began to decline in early October of each of the two years of the project: 1994 and 1995. The eight turtles chosen for this study were loggerhead turtles that had been captured in pound nets by fishermen and transported to an aquarium. Three turtles were housed in a 2100 l tank for periods ranging from 5 to 14 d prior to release, two individuals for less than 48 h, and three others for less than 24 h (Table 3.1). All turtles were weighed, measured, and tagged with metal flipper tags. In preparation for satellite transmitters, a 3 mm hole was drilled through the carapace where it overhangs the rear of the turtle at one of the posterior-most marginal scutes. The attachment process, which lasted from four to eight minutes per turtle, was done on the beach before release.

Four loggerhead turtles were selected for monitoring beginning in fall 1994, and four more beginning in fall 1995 (Table 3.1). All were juveniles ranging in straight-line carapace length (SCL) from 46.4 cm to 59.1 cm ($n = 8$;

Table 3.1. Capture and release locations of eight juvenile loggerhead turtles selected for monitoring by satellite transmitter as they began their fall migrations from New York waters during 1994 and 1995. Locations are presented as degrees north latitude (Lat.) and degrees west longitude (Lon.).

ID	Capture			Release			SCL (cm)	Mass (Kg)
	Date	Lat.	Lon.	Date	Lat.	Lon.		
11458b	10/11/94	41.13	72.33	10/12/94	41.98	72.10	47.7	16.9
11459b	10/11/94	41.17	72.24	10/12/94	41.98	72.10	46.4	12.9
11460b	10/06/94	41.08	72.10	10/11/94	41.98	72.10	59.1	30.5
11461b*	10/10/94	41.06	72.10	10/11/94	41.98	72.10	55.5	26.5
9037b	10/01/95	41.11	72.38	10/09/95	41.98	72.10	58.9	31.6
9038b	09/26/95	41.02	72.38	10/10/95	41.98	72.10	54.4	24.6
9039c**	10/07/95	41.06	72.10	10/09/95	41.98	72.10	54.1	24.8
11462	10/07/95	41.06	72.10	10/09/95	41.98	72.10	52.2	26.3
						mean	53.5	24.3
						S.D.	4.65	6.39

* Captured twice before during summer in New York and captured once before during spring in Florida.

** Captured once before during summer in New York.

mean = 53.5 cm; SD = 4.65) and in mass from 12.9 to 31.6 kg (n = 8; mean = 24.3 Kg; SD = 6.39). All eight turtles were intercepted in nets in eastern Long Island waters, presumably beginning their migratory movements eastward at the time of capture. Six of the turtles had not been captured previously, while two others had been captured earlier in the summer in Long Island waters. One of these had a somewhat extraordinary previous capture record. This 59 cm loggerhead was initially tagged in St. Lucie Inlet, Florida after being captured in a power plant intake canal in April 1994 (Eric Martin, pers. comm.). By 21 July it had migrated more than 1700 km to the inshore waters of Long Island, where it was again captured. Remaining within Long Island's eastern bays through the summer, the turtle was recaptured less than 5 km away after a two-month interval, and again in early October as it headed eastward through the bays; upon final capture it was outfitted with a satellite transmitter, as were the others. All eight turtles were released from a point on shore near Napeague State Park, a location within 13 nautical miles of all of the capture sites. In 1994, turtles were released on 10 and 11 October; in 1995 they were released on 9 and 10 October.

The transmitter packages used in this study were specially designed satellite-linked time-depth recorders (SLTDR) engineered by Wildlife Computers (Redmond, WA). These combined a basic 1/2 watt Telonics ST-6 transmitter (Telonics Corp; Mesa, AZ) with a microprocessor, a pressure transducer, and a conductivity sensor. Each unit was powered by four 2/3-A lithium batteries and included a fifth smaller battery for memory backup. The components, which were stacked to minimize width, had the final dimensions of 3.9 x 1.7 x 18.3 cm with a total mass of 158.6 g.

After numerous modifications and design tests (Standora and Morreale 1991; Morreale and Standora 1994; Morreale et al. 1996), a towable, buoyant,

pressure-resistant housing was developed to encase the transmitter packages. Protective housings were hydrodynamically shaped to minimize drag, and were slightly buoyant to enable transmission to the satellites. They were fabricated of a high-performance syntactic foam (Emerson and Cumming Inc., Canton, MA) that was poured into a mold around the electronic components. This buoyant foam has a density of 0.38 g/cm^3 and withstands pressures at depths greater than 3600 m. The final cylindrical package measured approximately $6.0 \times 23.6 \text{ cm}$, contributing to an overall average mass of 612 g with an average buoyancy of 44 g (Table 3.2). This design enabled the towed transmitter to float at the surface, with the antenna standing upright and out of the water, as the turtle emerged to breathe (Fig. 3.2).

The floating transmitters were attached to the turtle's carapace using techniques previously developed for Kemp's ridley (Morreale and Standora 1991, 1992), loggerhead (Standora et al. 1993, Morreale and Standora 1994), and leatherback turtles (Morreale et al. 1996). Transmitters trailed behind, connected by a flexible lanyard with breakaway and corrosible links to prevent entanglement of turtles or long-term encumbrance (Fig. 3.3). The overall design was intended to maximize transmissions, while reducing mass and buoyancy and minimizing drag, which is a very important factor in transmitter attachment (Logan and Morreale 1994).

Data processing

During pre-deployment tests in September of 1994 and 1995, transmitters were programmed and prepared for attachment to migrating turtles. Programming was by computer through a communications port connected to the microprocessor. To extend the life of the transmitters, active duty cycles were programmed for 8 h on and 16 h off each day. Two of the transmitters in 1994

Table 3.2. Satellite transmitter package dimensions and proportions relative to the body mass of the juvenile loggerhead turtles to which they were attached during 1994 and 1995.

Transmitter ID	Width (cm)	Length (cm)	Mass (g)	Proportion body mass	Buoyancy (g)
11458b	6	23.6	610	0.036	33
11459b	6	23.6	648	0.050	60
11460b	6	23.6	619	0.020	60
11461b	6	23.6	650	0.025	34
9037b	6	23.6	573	0.018	41
9038b	6	23.6	607	0.025	37
9039c	6	23.6	581	0.023	42
11462	6	23.6	611	0.023	47

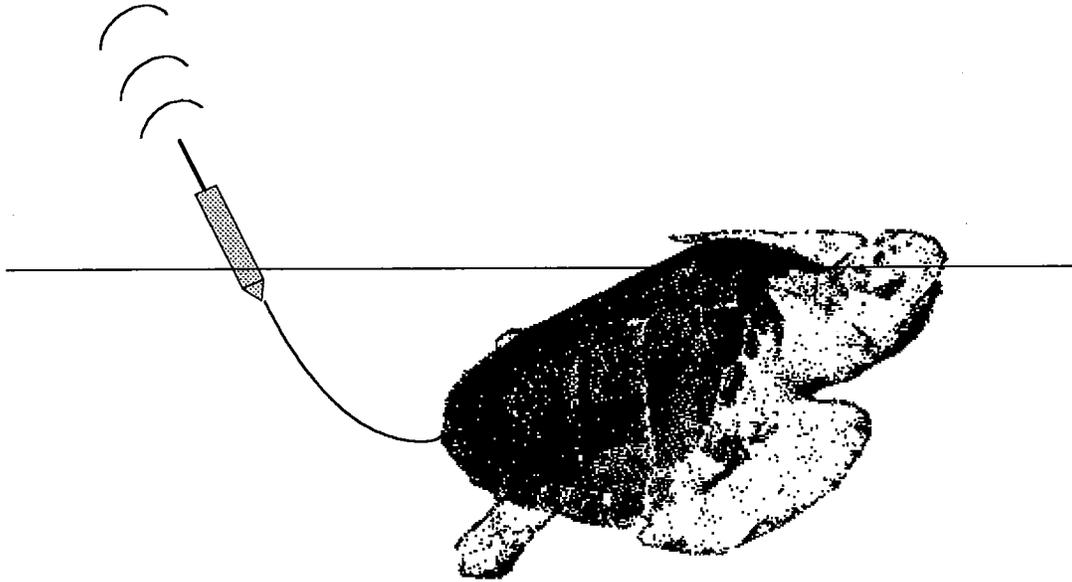


Figure 3.2. The buoyant, pressure-resistant housing allowed the depth-sensing satellite transmitter to trail behind the turtle. The hydrodynamic package stood upright, primed for data transmission, as the turtle came to the surface to breathe.

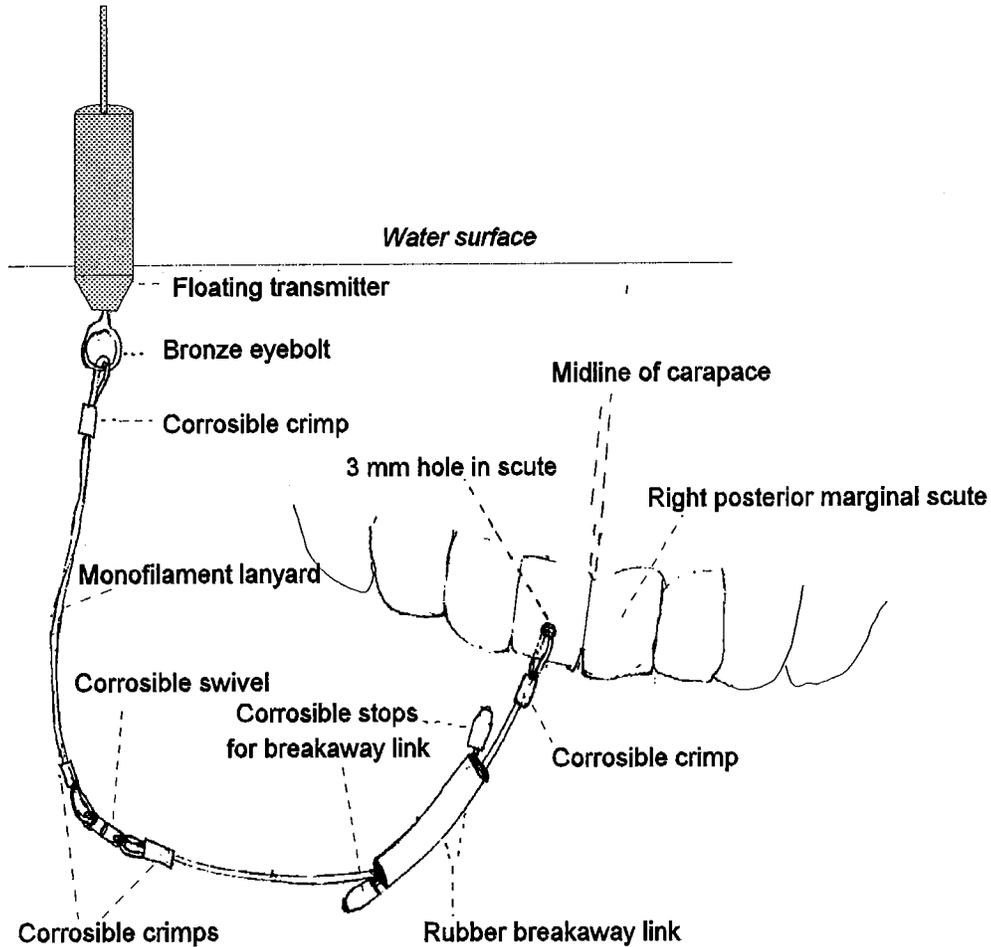


Figure 3.3. Satellite transmitters were attached to a posterior marginal scute of the turtles' carapaces. The attachment process took from four to eight minutes, and was done on the beach. The flexible lanyard with rubber and corrosible breakaway links prevented entanglement or long-term encumbrance by the transmitter.

were programmed to transmit every second day; the other six sent signals daily. Data were transmitted to satellites between 1300 and 2100 GMT. These are the daylight hours (between 0800 and 1600 EST) that correspond to the period of highest surface activity by the turtles in northeastern U.S. waters (Morreale and Standora, 1991). The expected life of the transmitters was between 50 and 100 days, depending on the surfacing activity of the individual turtle. Generally, the more time a turtle spent submerged, the longer the battery lasted.

The data that were collected and stored by the SLTDR's for later transmission to the satellite were in the same format as those described for the leatherback model in Chapter 2. However, the pressure transducer for the loggerhead model was preset to measure shallower depths, ranging from 0 to 233 m with a resolution of 1 m. Thus the data relayed by satellite for each turtle were global position, dive depth profiles down to 233 m, diving frequencies, and percent of total time spent at different depths within the water column. Diving records for the loggerheads were also condensed into frequency histograms that accumulated diving activity into 14 depth and 14 duration categories, summarized over six-hour periods. Percentage of the six-hour period that was spent at the surface and at different depths within the water column was also calculated. Since these turtles were smaller than the leatherbacks, movements below a depth of 3 m were considered dives, and all time spent within the upper 3 m was categorized as surface activity.

Turtle activity during migration was relayed by TIROS-N series, polar orbiting satellites. Positional fixes and data were calculated and reported using the same ARGOS system described in the previous chapter. Also, the same custom-made algorithms were used to enhance the filtering process for turtle locations (Tables 2.2 and 2.3). These first determined the maximum allowable travel rate for migrating loggerheads, and then applied the selection criteria to

the entire set of location records. All locations were then plotted using the same digitized base map, and displayed as calculated migratory pathways using Mercator projections. Estimated tracks of the turtles reflected the various levels of certainty assigned by the different sources: 1) acceptable by ARGOS; 2) acceptable by the new algorithms; and 3) unlikely by both sources. Distances between points were calculated using spherical geometry and a spherical Earth model.

Results

During the two years of study, beginning in October 1994, eight loggerhead turtles were monitored by satellite transmitter for periods ranging from 8 to 283 d (Table 3.3). Mean rate of travel for the eight turtles was 15.6 km per day as they moved net distances from 317 to 2360 km. The actual movement rates were, at times, much greater than this conservative average, sometimes exceeding 100 km per day as turtles traveled along in the Gulf Stream.

Movements

1994-1995. Almost immediately after release in eastern Long Island, all four turtles swam southwestward across the New York bight toward the southern New Jersey coast. Two individuals headed in a direct path, unswervingly through mid-shelf waters ranging from 30 to 60 m in depth. The other two followed more closely along the shores of Long Island and New Jersey, remaining in waters shallower than 40 m. All four turtles continued to migrate southward at approximately the same rate (roughly 20 km per day)

Table 3.3. Net tracking durations, distances traveled, and mean rates of travel of eight loggerhead turtles tracked by satellite transmitter during their migrations from New York waters in 1994 and 1995.

ID	Release			Last contact			Duration (days)	Distance (km)*	Rate (km/d)
	Date	Lat.	Lon.	Date	Lat.	Lon.			
11461b	10/11/94	40.98	72.10	10/19/94	38.96	74.74	8	317	41.4
11459b	10/12/94	40.98	72.10	11/04/94	37.45	75.53	23	492	21.5
11458b	10/12/94	40.98	72.10	03/29/95	38.54	50.85	168	1831	10.9
11460b	10/11/94	40.98	72.10	07/21/95	39.15	74.71	283	**300	2.6
9038b	10/10/95	40.98	72.10	11/07/95	37.48	75.29	28	476	17.0
9039c	10/09/95	40.98	72.10	12/29/95	34.70	75.90	81	772	9.6
9037b	10/09/95	40.98	72.10	01/28/96	32.49	78.44	111	1098	9.9
11462	10/09/95	40.98	72.10	04/20/96	36.20	45.52	194	2360	12.2
						mean	105	991	15.6

* These are net distances based on beginning and end points only. All are underestimates of distances traveled.

** Turtle 11460b migrated 855 km southward to overwinter, then returned 575 km back northward the following spring.

during the first week. On the eighth day, upon reaching waters offshore of Delaware Bay, one transmitter stopped abruptly (Fig. 3.4).

The other three turtles were tracked farther southward through Delaware, Maryland, and Virginia waters. During this portion of the journey they remained always within the 40 m contour, which runs at a distance of less than 50 km offshore. Within three weeks, all three individuals swam as far as Chesapeake Bay, which was the last point of contact for the second turtle (Fig. 3.5).

The remaining two turtles continued along into North Carolina waters by the second week of November, where both began to linger within 60 km from shore. One stationed itself in water inside the 40 m contour due east of Cape Hatteras (Fig. 3.6), and the other settled at equivalent water depth a bit farther south beyond Cape Lookout (Fig. 3.7). Once in these warmer southern waters, both turtles remained in their respective locales, seemingly sedentary, until late January when the northernmost of these turtles became more active.

After remaining in place east of Cape Hatteras for 81 days, the third turtle began to move again, but instead of moving southward, its movements carried it slowly offshore (Fig. 3.6). After many days of undirected travel during the last week of January the turtle encountered the warmer waters of the Gulf Stream, where the current transported it first northward, and then into deep ocean waters. Over the next two months of pelagic travel, the turtle swam mainly in the upper water column as it traveled steadily eastward, tracing the path of the Gulf Stream. By 29 March, this turtle was in pelagic waters more than 1800 km offshore of its origin in New York. With greater surface time, the remaining battery reserves were dissipated more quickly. Thus, the last location data for this turtle were transmitted on 29 March, although there were additional bursts of data from this transmitter relaying surfacing and diving activity of the

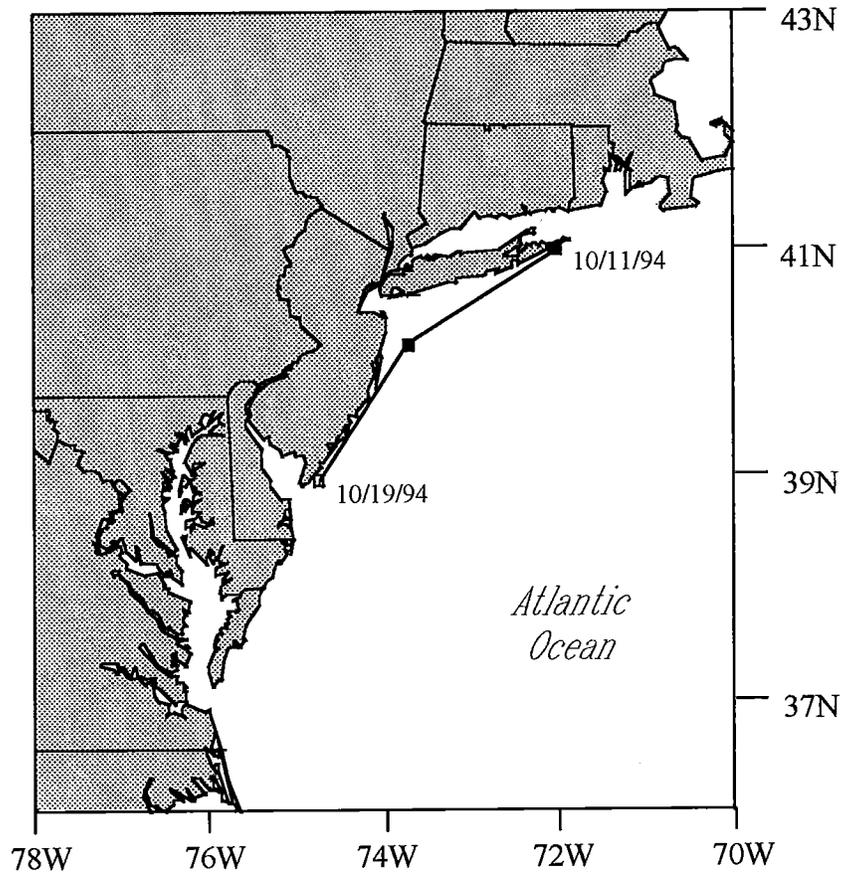


Figure 3.4. Loggerhead turtle 11461b migrated southward following the shores of New York and New Jersey soon after its release on 11 October 1994. The turtle moved a net distance of 317 km during the eight days of satellite tracking. Solid symbols represent high-certainty locations assigned by ARGOS; lines connect all the points that were included by the filtering algorithms; detached open symbols were unlikely locations by both measures.

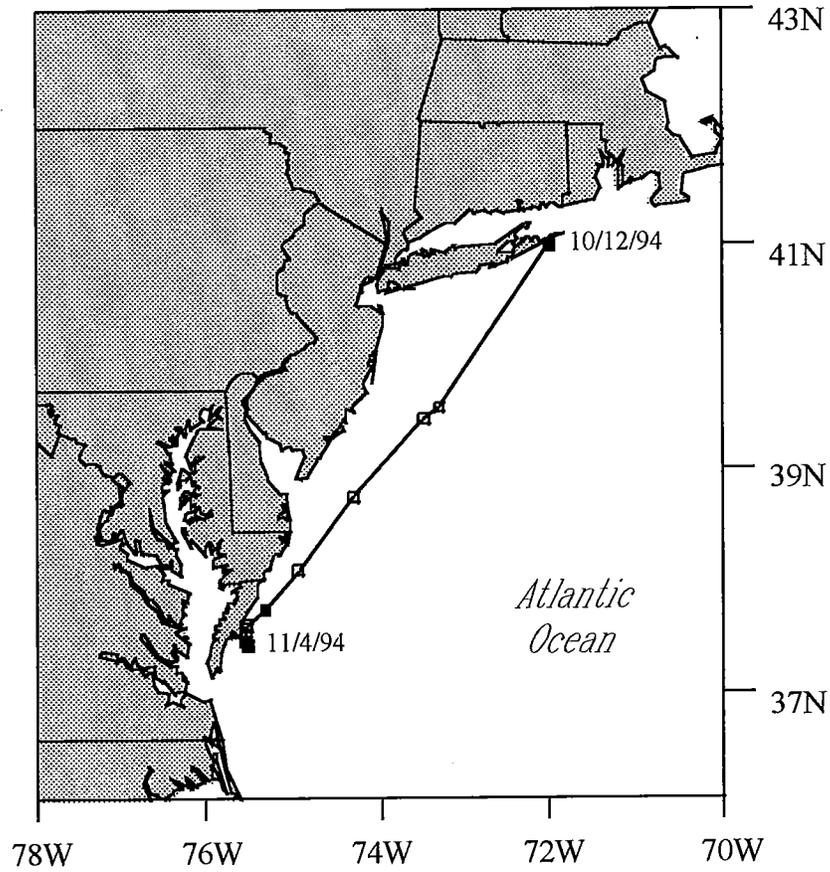


Figure 3.5. Loggerhead turtle 11459b was tracked by satellite transmitter for 23 days as it migrated southward soon after release on 12 October 1994. The turtle had migrated to Virginia waters, over 492 km away, and was still moving steadily southward upon last contact. Symbols are the same as in Fig. 3.4.

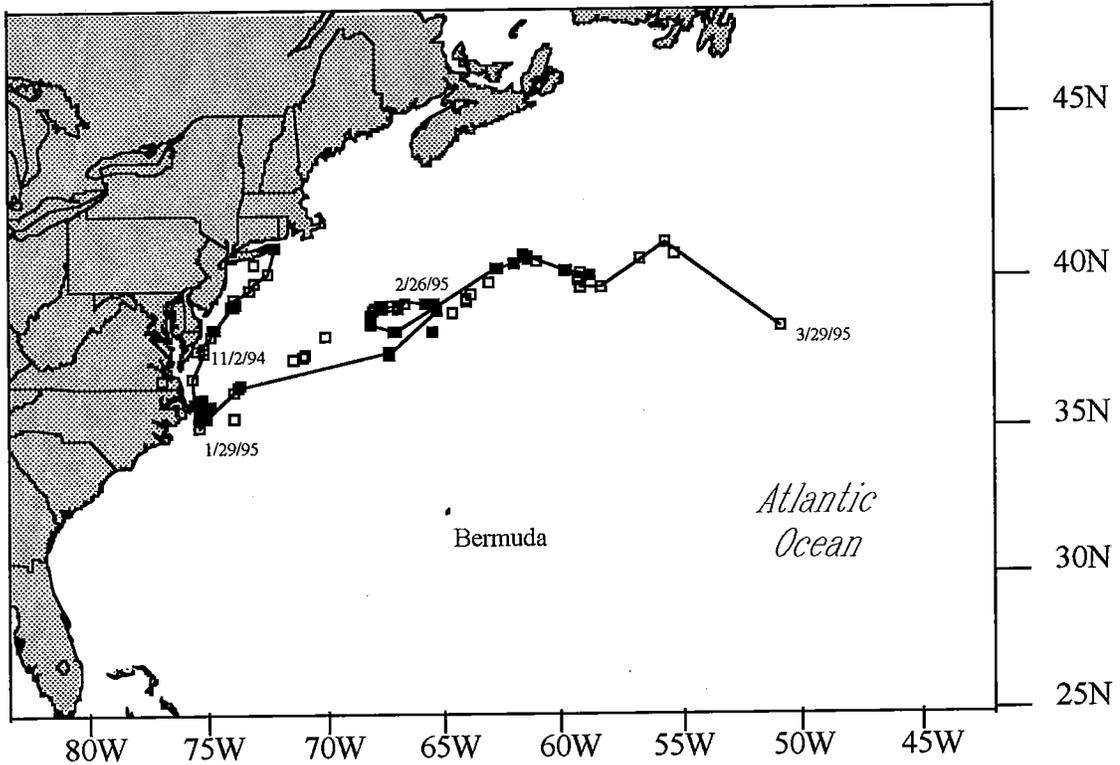


Figure 3.6. Loggerhead turtle 11458b was tracked by satellite transmitter as it migrated southward to North Carolina during the first month after release on 12 October 1994. After spending 81 days in a relatively sedentary state offshore of Cape Hatteras, the turtle began to move slowly eastward. Upon joining the Gulf Stream in early February, it moved rapidly into pelagic waters. By the end of winter, it was at a position more than 1800 km offshore. Symbols are the same as in Fig. 3.4.

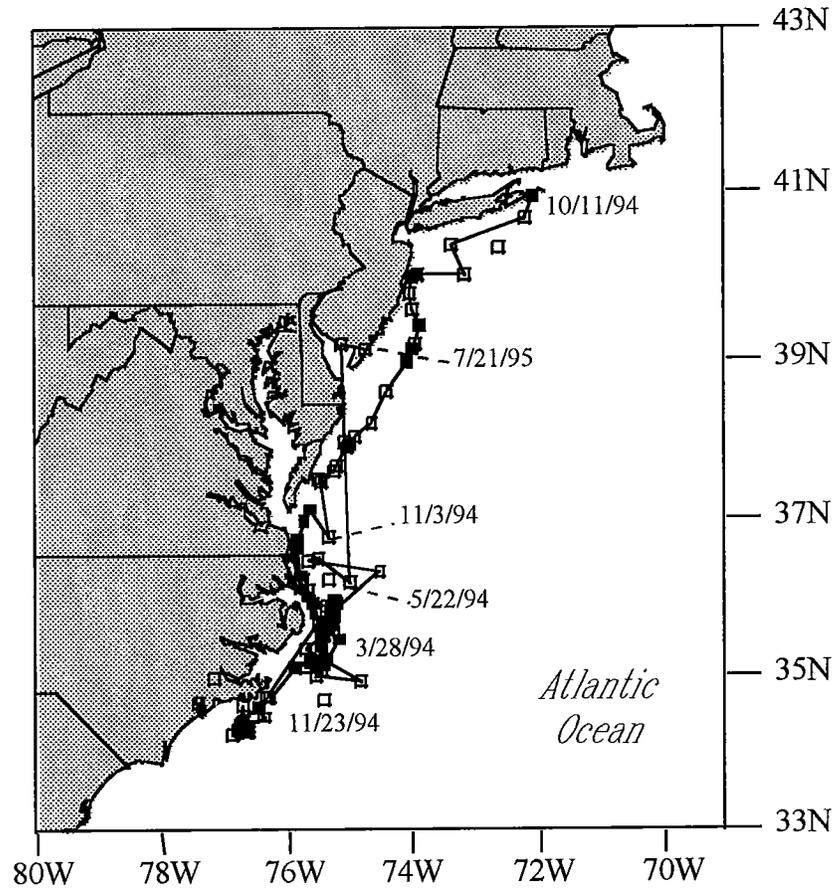


Figure 3.7. Loggerhead turtle 11460b was tracked by satellite transmitter as it migrated southward to North Carolina in the first month after its release on 11 October 1994. After traveling more than 800 km by late November, it settled near Cape Lookout Shoals. By late March, the turtle began its return migration northward. The last contact was in New Jersey waters the following July, culminating 283 days of tracking. Symbols are the same as in Fig. 3.4.

turtle from April through June.

The track of the fourth turtle was at least as impressive and informative. Its movement of an additional 100 km southward, before settling down beyond Cape Lookout, North Carolina, apparently had far-reaching effects on its overwintering behavior (Fig. 3.7). After late November this turtle's net movement was minimal, as it remained relatively inactive in shallower waters near Cape Lookout Shoals. This area, bounded also to the south by Frying Pan Shoals, presumably provided a suitable overwintering site. The turtle remained in the vicinity until temperatures increased the following spring. By 28 March, this turtle became active again and began to retrace its path of the previous fall, heading northward through coastal waters.

By early April the turtle moved north of Cape Hatteras, where it remained between there and the Virginia border for several weeks. As the batteries dwindled, signals became more sporadic and no locations were available through May and June. During the first three weeks of July, however, some very clear final signals from the transmitter pinpointed the turtle as far north as New Jersey. The transmitter appeared to have broken free and washed ashore by 21 July at Cape May.

This was not only the longest tracking duration of the study, but was the first turtle to ever be monitored through a complete migration cycle from the northeast, to a southern overwintering site, and northward back into northeastern waters the following spring. Although the turtle had traveled more than 1430 km, its final net movement over the 283 day cycle was less than 300 km from its release site.

Collectively there were some emergent patterns of movements of all four turtles during the first year. When superimposed, all four migration tracks could be encompassed in an imaginary corridor running southward over 800 km along

the northeast coastline, with a maximum width of less than 60 km. This tight grouping of turtles was observed not only spatially, as individuals migrated along the same paths, but also temporally, as they traveled within the same time frame. On the 2nd and 3rd of November, all three remaining turtles were located off of Cape Charles, Virginia. After nearly three weeks of ocean travel, covering more than 450 km, all three turtles were within a radius of 30 km.

1995-1996. Again in year two, movements of all four of the turtles were highly similar to each other. Soon after release all four individuals headed southwestward toward the New Jersey shoreline, remaining nearly always in waters shallower than 40 m in depth. After two weeks of travel all four turtles were offshore of Atlantic City, swimming steadily southward parallel to the coastline. They continued along this same heading, southward into Virginia waters where, after 28 days of tracking, one of the transmitters came free (Fig. 3.8).

The continued southward movements of the other three turtles carried them into North Carolina waters, where they remained shoreward of the 40 m contour. All three turtles stayed within 60 km of the coast of North Carolina throughout November and December. One of the three, after traveling more than 770 km, became sedentary just north of Cape Lookout Shoals (Fig. 3.9). After 81 days of tracking, on 29 December, it shed its transmitter, which then was carried off by the nearby Gulf Stream.

The other two turtles continued a little farther south of Cape Lookout before slowing down. One turtle spent the month of December moving slowly southward between Cape Lookout Shoals and Frying Pan Shoals (Fig. 3.10). It then continued into South Carolina waters. Throughout the 111 day migration, which covered 1100 km from New York to Charleston, South Carolina, the turtle remained always within the 40 m contour. At this location, which is the

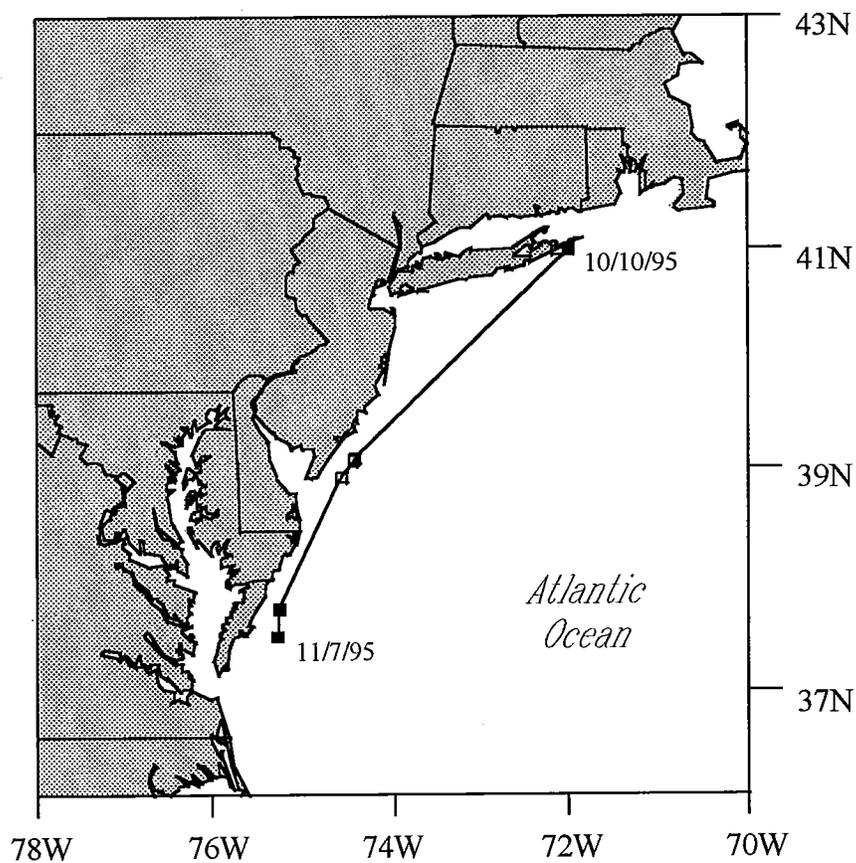


Figure 3.8. Loggerhead turtle 9038b was tracked by satellite as it began its migration on 10 October 1995. By early November it reached Virginia waters. As the turtle continued moving southward, it shed its transmitter. In the 28 days of tracking, it covered more than 476 km. Symbols are the same as in Fig. 3.4.

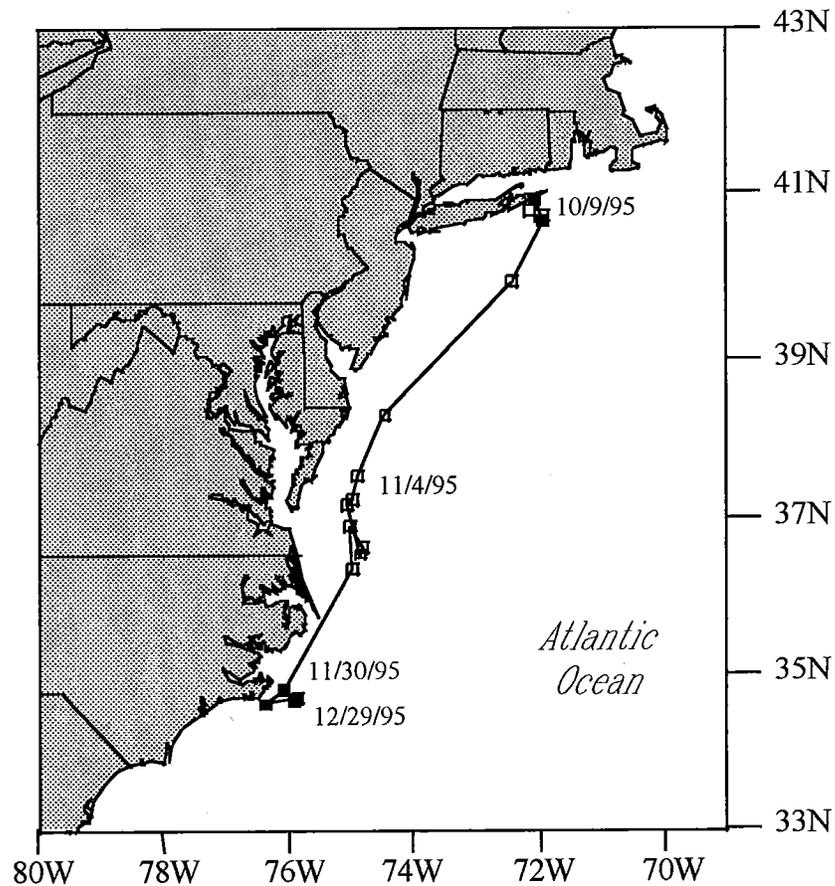


Figure 3.9. Satellite tracking of loggerhead turtle 9039c began on 9 October 1995. As the turtle headed along a southward path it reached Virginia waters by the first week of November. After migrating steadily for nearly 800 km, the turtle became sedentary on the north side of Cape Lookout Shoals for the month of December. After 81 days of tracking it shed its transmitter, which then was transported eastward by the Gulf Stream. Symbols are the same as in Fig. 3.4.

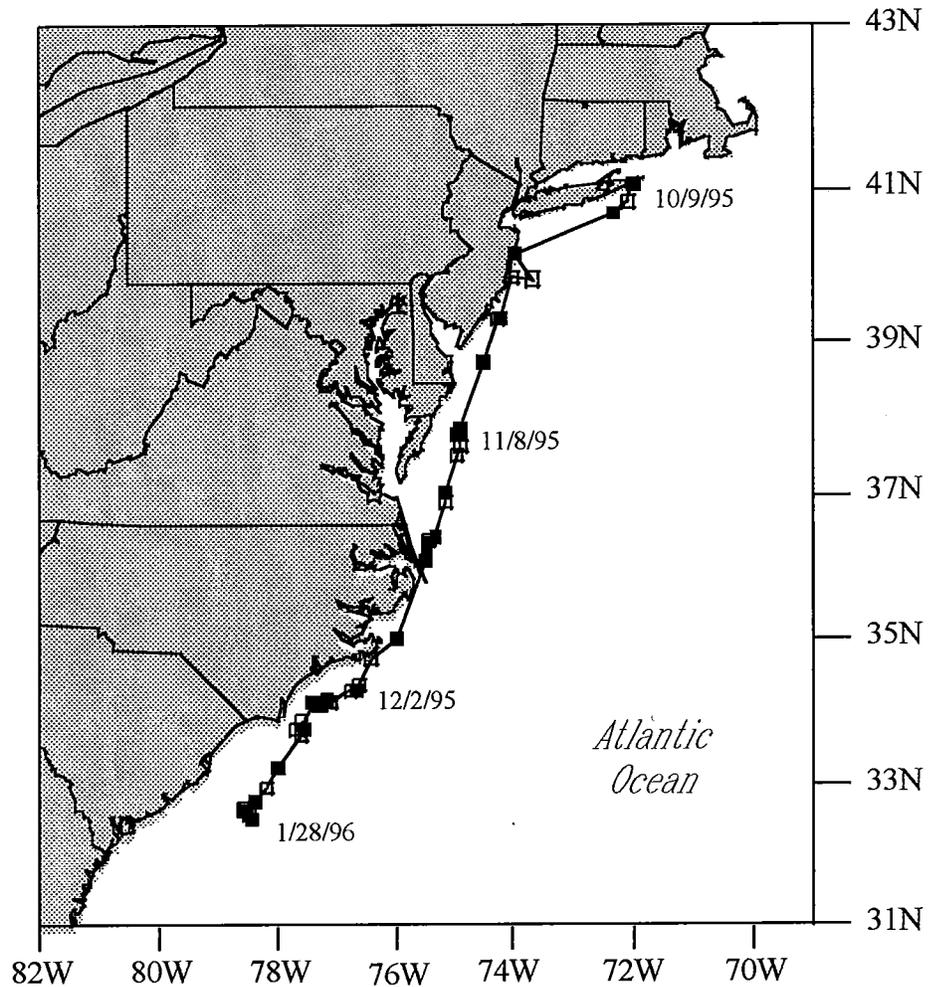


Figure 3.10. Loggerhead turtle 9037b headed southward upon its release on 9 October 1995. The turtle reached Virginia waters by the first week of November, and moved to the area between Cape Lookout Shoals and Frying Pan Shoals for the month of December. Continuing slowly southward into South Carolina, it reached the farthest point south that a turtle was ever tracked from northeastern waters. At a distance of nearly 1100 km away, the turtle shed its transmitter, which soon afterward was transported off into the Gulf Stream. Symbols are the same as in Fig. 3.4.

farthest point south a turtle has ever been tracked from northern waters, the turtle shed its transmitter. Over the next week this transmitter also was carried off by the Gulf Stream.

The last turtle also spent several weeks between Cape Lookout Shoals and Frying Pan Shoals, before heading slowly into South Carolina waters in late January (Fig. 3.11). Between Cape Fear and Cape Romaine its movements were minimal until the second week of February. On 9 February, the turtle apparently entered the western fringe of the Gulf Stream, where it was carried quickly into pelagic waters. During the first leg of the migration, a movement of over 1000 km southward, the average rate of travel was approximately 12 km/d. After moving into open Atlantic waters, however, the average pace increased to 54 km/d, as the turtle traveled a distance of more than 3100 km. By the last transmitted location on 20 April, the turtle had slowed its pace again and remained in a region nearly 2500 km due south of Greenland and 1300 km southeast of Newfoundland.

The strong resemblance that was evident among the chosen migration pathways of the four turtles was also obvious in the timing of the movements. After nearly six weeks and after having migrated southward more than 500 km, three of three turtles being monitored were within 80 km of each other. Furthermore, these late fall migratory patterns were nearly identical to those recorded for the loggerheads during 1994 both spatially and temporally.

Overall patterns. When the migration data from turtles in both years are combined, the similarities are striking. The conspicuous orientation southward highly contrasted with any expectations of random dispersal away from New York. For turtles emigrating from coastal northeastern waters, the range of alternative potential pathways extends roughly between bearings of 30° and 230°. The eight actual turtle bearings, however, ranged narrowly between 210°

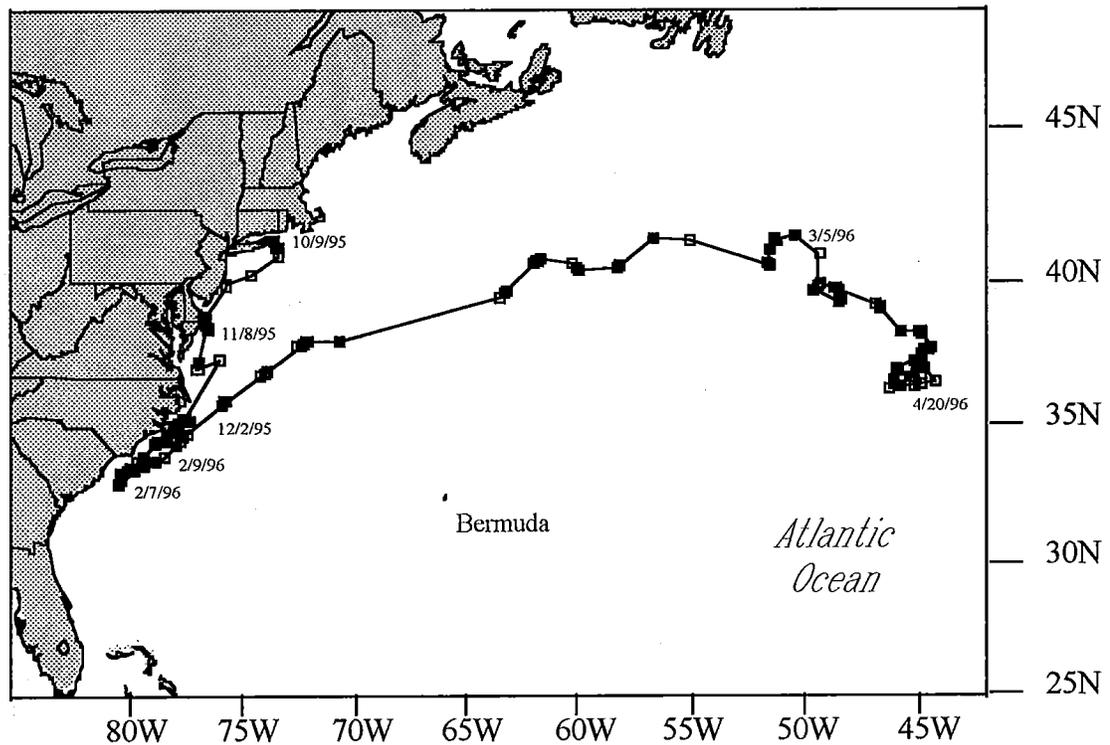


Figure 3.11. Loggerhead turtle 11462 was tracked by satellite as it migrated southward soon after its release on 9 October 1995. Its continued movements carried it into Virginia waters by the first week of November, and southward to Cape Lookout by one month later. In early February, after two months of minimal movements southward, the turtle began moving northeastward. Within a week it was moving rapidly in the Gulf Stream. In early March it passed south of the Grand Banks, and by late April it had moved more than 3100 km offshore. When it slowed its pace over the mid-Atlantic Ridge, the turtle had traveled more than 3/4 of the distance to the Azores. Symbols are the same as in Fig. 3.4.

and 230°. There was a highly significant difference between these observed values and a uniform distribution (Wilcoxon signed-rank test; $P < 0.01$). Furthermore, the range of variation among turtle pathways was minuscule (variance = 56.7) compared with that expected from a uniform distribution (variance = 3332).

Surface Activity and Diving Behavior

Surface behavior patterns were calculated as mean percentage of time spent in the upper 3 m of the water column. The overall mean time at surface for 498 recorded six-hour periods was 32% and the grand mean for the eight individuals was 29% (Table 3.4). These undifferentiated averages, however, obscure the obvious diurnal variability in surfacing behavior, which ranged from values of 20% to 70% among different periods of the day (Fig. 3.12). An ANOVA on the arcsin-transformed percentage values, revealed highly significant differences among diurnal periods ($F_{3,24} = 24.68$, $P < 0.001$). In both years the pattern was consistent. Turtles spent significantly more time at the surface (Tukey HSD test) during the early daylight period ($p < 0.05$) than the night periods, and the nearly threefold increase during the mid-day period was significantly greater than all other periods ($p < 0.01$).

Diurnal variability was also evident in diving frequency, as calculated from the number of recorded excursions deeper than 3 m below the surface. The overall mean number of dives for 560 six-hour periods was 7.3 per period, and the grand mean for the eight individuals was 6.2 dives per 6 h period (Table 3.5). There were notable diurnal differences in diving frequency (Fig. 3.13) with a pattern that was similar to the previously observed surfacing pattern. A correlation between individual dive frequency and time at surface among time periods yielded a relationship that, although not strongly linear ($R^2 = 0.2$), was

Table 3.4. Average percent of time spent at the surface by eight individual loggerhead turtles during 498 six-hour periods. Durations are presented as average percent of time the turtle was in the upper 3 m of the water column per six-hour period. Averages were calculated for individual turtles, overall, and by period of day in Eastern Standard Time. Both the overall means and the grand means are presented for comparison. Sample sizes for individual calculations are in parentheses.

ID	All periods	Period of Day (Eastern Standard Time)			
		2100-0300	0300-0900	0900-1500	1500-2100
11458	48.7% (71)	40.9% (30)	59.5% (25)	76.7% (6)	27.9% (10)
11459	46.0% (8)	41.9% (2)	59.2% (2)	64.4% (2)	18.5% (2)
11460	21.9% (61)	17.3% (28)	24.9% (24)	65.6% (2)	17.8% (7)
11461	7.9% (2)	7.9% (1)	----- (0)	----- (0)	7.9% (1)
9037	24.8% (76)	20.4% (35)	29.3% (32)	59.2% (1)	21.2% (8)
9038	23.1% (17)	20.3% (8)	27.9% (7)	----- (0)	17.3% (2)
9039	25.5% (45)	22.2% (22)	31.4% (18)	----- (0)	18.6% (5)
11462	34.0% (218)	18.8% (96)	47.8% (88)	78.5% (10)	26.0% (24)
Overall	32.2% (498)	22.4% (222)	41.4% (196)	74.5% (21)	23.2% (59)
Grand	29.0% (8)	23.7% (8)	40.0% (7)	68.9% (5)	19.4% (8)
SD	13.4%	11.8%	15.1%	8.3%	6.1%

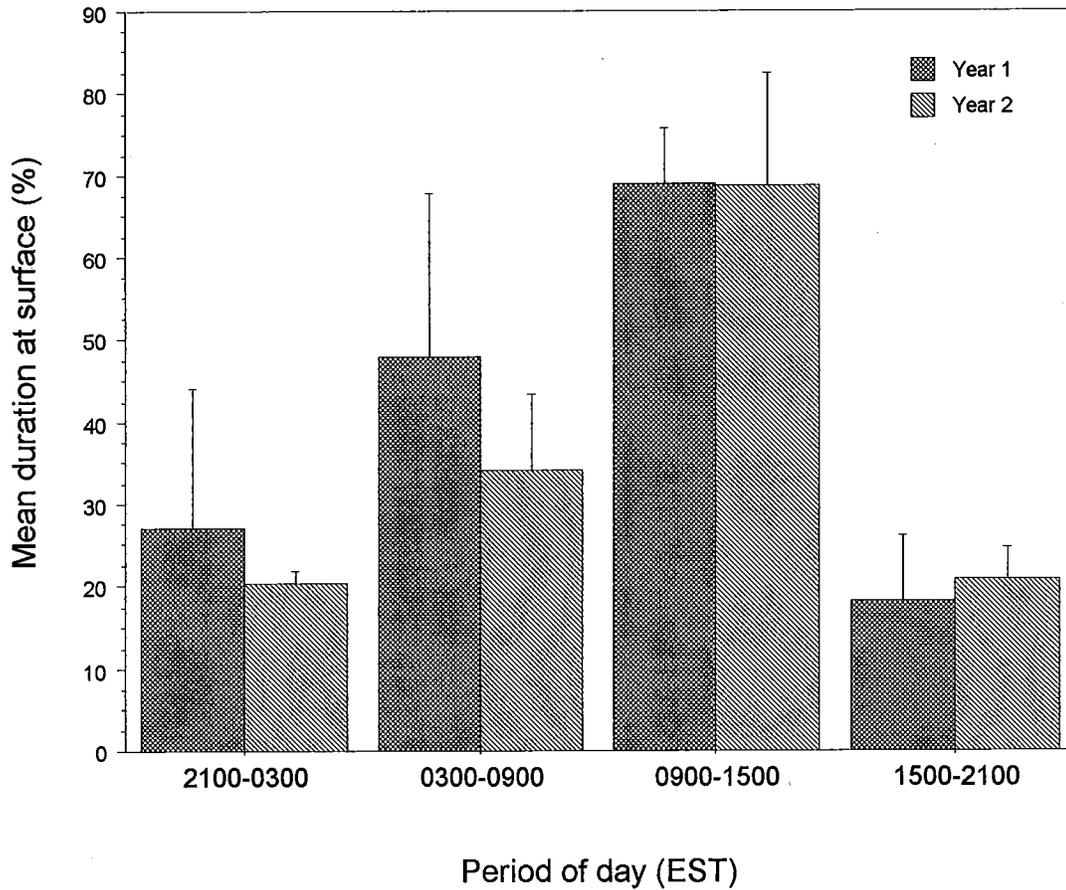


Figure 3.12. Average percentage of time spent in the upper 3 m of the water column by eight loggerhead turtles. Grand means and standard deviations are presented for 498 six-hour intervals monitored by satellite telemetry. Diurnal patterns were highly similar in both years. Turtles generally spent twice as much time at the surface during daylight periods.

Table 3.5. Summary of numbers of dives deeper than 3 m made by eight individual loggerhead turtles. A total of 4068 dives were recorded by satellite transmitter during 560 individual six-hour periods. Mean values were calculated from numbers of dives per six-hour period. For individual and overall calculations, n = number of six-hour periods; for grand means, n = number of turtles.

ID	Total # dives	# 6 h periods	Mean # per 6 h period	S.D.	Period of Day			
					2100 to 0300	0300 to 0900	0900 to 1500	1500 to 2100
11458	948	102	9.3	12.2	4.1	12.1	12.2	9.3
11459	40	10	4.0	2.6	4.0	3.0	6.0	4.0
11460	1116	113	9.9	18.1	6.3	11.8	13.4	7.3
11461	0	1	0.0	0.0	0.0	----	----	----
9037	334	66	5.1	4.9	2.5	5.6	9.3	5.2
9038	154	18	8.6	4.5	9.0	9.5	7.0	8.7
9039	255	37	6.9	4.4	5.1	6.9	8.7	5.7
11462	1221	213	5.7	7.6	5.3	4.6	8.4	5.2
Overall	4068	560	7.3	11.1	4.8	7.7	10.3	6.6
Grand	4068	8	6.2	3.3	4.5	7.6	9.3	6.5

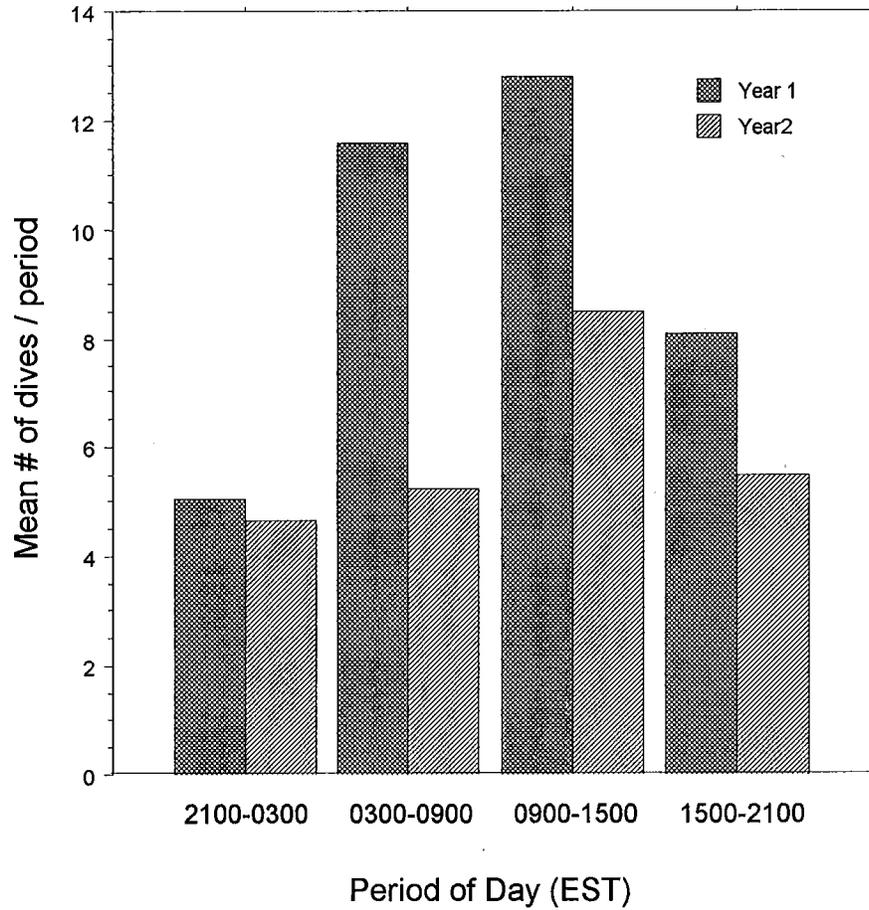


Figure 3.13. Diurnal pattern of the average number of dives deeper than 3 m made by eight loggerhead turtles. Mean numbers of dives per 6 h period were calculated for each year. In both years there generally were more dives made during daylight hours. Dive frequency was positively correlated with the time spent at the surface ($P = 0.02$).

significantly positive ($P = 0.02$). The combined results of these two measures reliably represents the turtles' level of activity. More cumulative time at the surface, along with more frequent diving, strongly indicates more vigorous activity that demands more frequent breathing during daylight hours.

These inferred activity patterns were supported by an independent measure of diving activity in which the recorded durations of 3559 individual dives also were grouped by period of day (Fig. 3.14). During daylight periods more than 50% of dives were shorter than 20 min. in duration, while at night more than 70% of all dives were longer than 40 min.

Although there were some seasonal differences in activity, the general pattern was one of higher activity by day, characterized by many shorter dives, and reduced activity at night, with fewer protracted dives and reduced surface time.

Dive depth profiles were summarized by calculating the percentages of 4068 dives that culminated at 14 different pre-selected depth intervals ranging from 3 m to >200 m (Table 3.6). The overall means for 517 recorded 6 h periods were similar to the grand means, which indicated that roughly equal numbers of dives occurred between the depths of 3 to 15 m as occurred between 15 and 30 m. Although the deepest dives were in the 150 to 200 m interval, 97% of all dives were within the upper 50 m of the water column (Fig. 3.15). As would be expected from such a diving summary, the turtles spent more than 99% of their time at depths shallower than 50 m, including the surface (Table 3.7). The similar patterns observed among the dive depth and depth duration profiles can be most simply explained by assuming that when turtles were diving, they mostly stayed near the bottom.

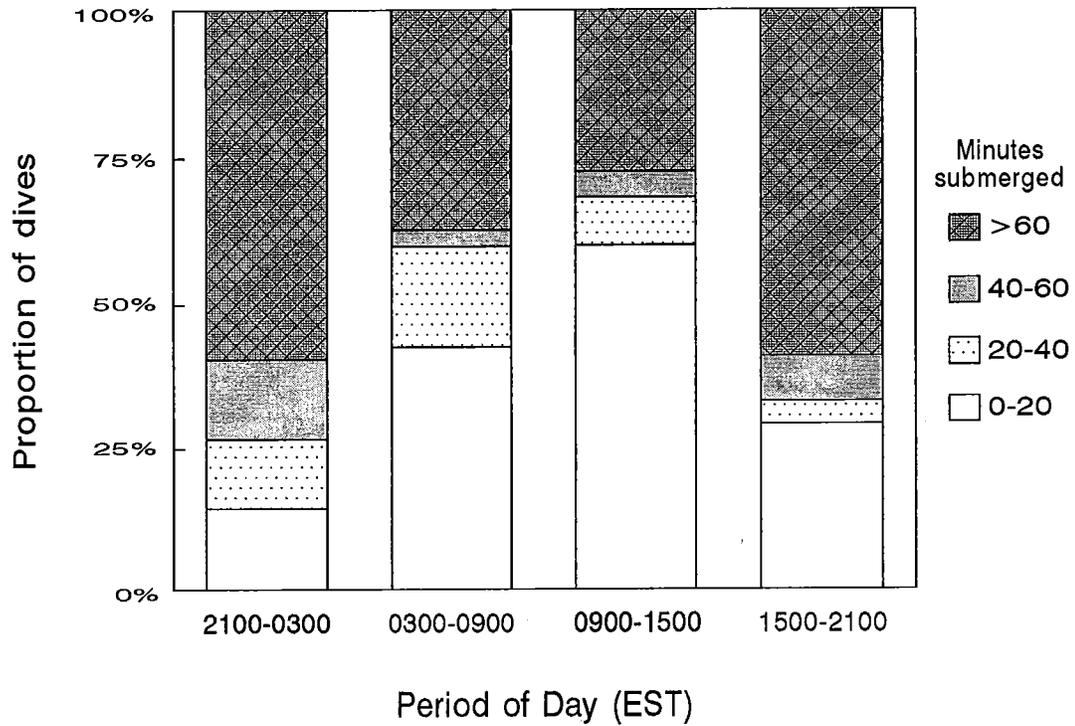


Figure 3.14. The diurnal pattern of the dive durations were a further indicator of activity levels of the eight loggerhead turtles monitored by satellite. Records from 3559 individual dives were averaged over four periods of the day. At night more than 70% of all dives were longer than 40 min., while more than 50% of daytime dives were shorter than 20 min.

Table 3.6. Mean percentages of dives culminating at 14 selected depth intervals down to depths greater than 200 m. Individual, overall, and grand means were calculated from 517 six-hour periods recorded by satellite transmitters.

ID	n	Depth Intervals (m)													
		3-6	6-9	9-12	12-15	15-30	30-40	40-50	50-60	60-70	70-80	80-100	100-150	150-200	>200
9037	63	16.4	2.4	1.9	4.0	41.7	21.0	8.1	4.2	0.1	0.1	0.1	0.0	0.0	0.0
9038	17	2.7	1.7	6.7	13.1	54.9	17.9	1.0	2.0	0.0	0.0	0.0	0.0	0.0	0.0
9039	36	10.4	0.8	0.5	0.0	31.8	31.4	13.8	0.0	3.2	6.8	1.4	0.0	0.0	0.0
11458	96	45.8	5.7	4.6	9.7	19.2	9.3	3.8	1.7	0.0	0.0	0.1	0.0	0.1	0.0
11459	9	11.1	0.0	4.4	25.6	56.1	2.8	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
11460	92	32.5	2.1	0.6	2.8	43.0	18.2	0.8	0.0	0.0	0.0	0.0	0.0	0.0	0.0
11462	204	27.7	3.6	2.6	6.7	47.8	11.3	0.0	0.2	0.0	0.1	0.0	0.0	0.0	0.0
Overall	517	28.2	3.2	2.5	6.3	40.2	14.8	2.9	1.0	0.2	0.5	0.1	0.0	0.0	0.0
Grand	7	20.9	2.3	3.0	8.8	42.1	16.0	3.9	1.2	0.5	1.0	0.2	0.0	0.0	0.0
SD		15.1	1.9	2.3	8.6	13.1	9.3	5.2	1.6	1.2	2.5	0.5	0.0	0.0	0.0

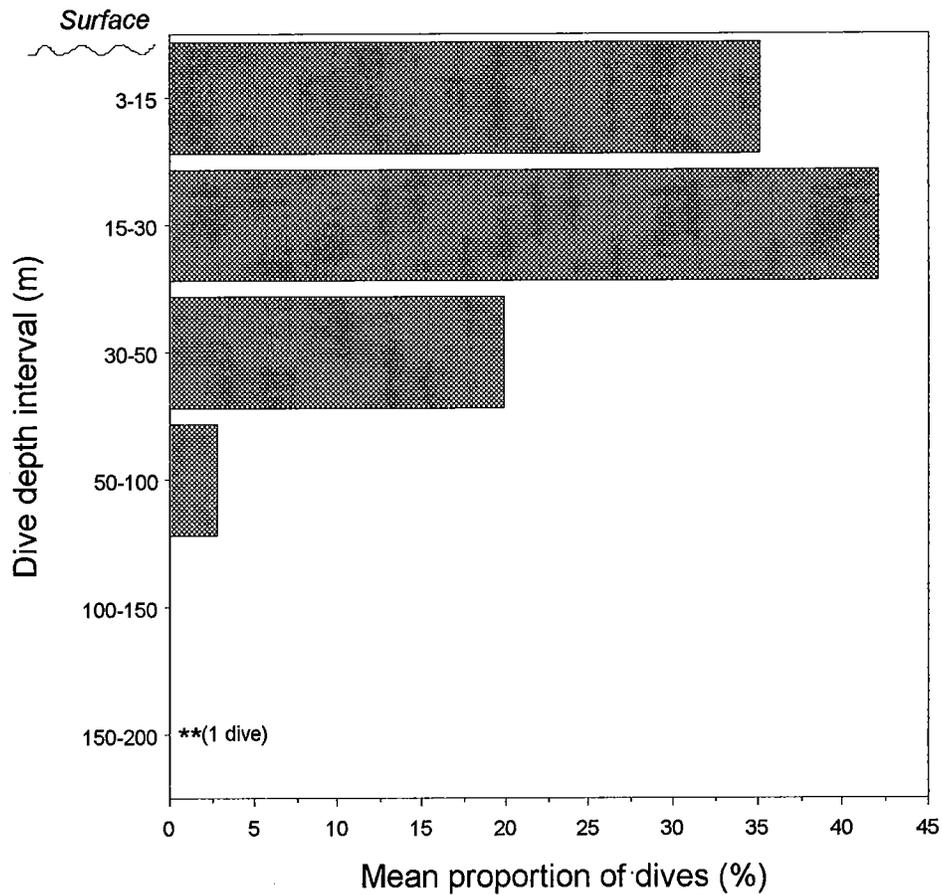


Figure 3.15. Migrating turtles spent much of their time in shallower waters along the continental shelf. The relatively high proportions of dives culminating at the first three depth intervals probably reflect numerous dives to the bottom. However, even when the turtles moved into deep pelagic waters, they remained mostly in the upper reaches of the water column. All told, 97% of all dives were shallower than 50 m in depth. Out of 4068 recorded dives of the loggerhead turtles, one was between 150 and 200 m.

Table 3.7. Mean percentages of time spent by eight loggerhead turtles at 14 selected depth intervals throughout the water column. Individual, overall, and grand means were calculated from 533 six-hour periods recorded by the satellite transmitters. Time spent at each depth includes stationary behavior and passage through that portion of the water column. Depth intervals vary in breadth. The first interval also includes all time spent at the surface.

ID	n	Depth Intervals (m)													
		0-6	6-9	9-12	12-15	15-30	30-40	40-50	50-60	60-70	70-80	80-100	100-150	150-200	>200
11458	88	59.4	2.0	3.4	8.6	11.0	11.7	3.8	0.1	0.0	0.0	0.0	0.0	0.0	0.0
11459	10	38.7	7.0	12.6	29.7	11.9	0.1	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
11460	105	34.4	5.1	5.8	5.2	26.6	21.6	1.2	0.0	0.0	0.0	0.0	0.0	0.0	0.0
11461	1	100.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
9037	62	34.2	2.6	2.3	4.3	36.8	14.5	1.9	2.9	0.1	0.2	0.2	0.1	0.0	0.0
9038	17	36.4	2.8	3.9	5.1	50.3	1.5	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
9039	33	27.4	2.3	2.8	3.8	26.3	20.7	13.8	0.0	1.9	0.7	0.2	0.0	0.0	0.0
11462	217	41.6	2.6	7.5	12.2	29.6	6.4	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Overall	533	41.3	3.1	5.6	8.9	26.8	11.8	2.0	0.4	0.1	0.1	0.1	0.0	0.0	0.0
Grand	8	46.5	3.1	4.8	8.6	24.1	9.6	2.6	0.4	0.2	0.1	0.1	0.0	0.0	0.0

Discussion

All of the turtles that were tracked embarked upon a long-distance journey soon after they were released in the fall of both study years. With the satellite transmitters, oceanic movements were monitored with relative ease and apparently with little bother to the turtles. The tracking durations of four of the turtles exceeded the anticipated length of the study; one turtle was tracked for 283 days, which carried it through both a fall migration and a spring migration. Erring toward the side of caution, the breakaway links allowed three of the transmitters to detach while the transmitters were still active. Nevertheless, even in the shortest movement, the turtle was tracked as it traveled steadily more than 300 km southward.

In earlier studies it was documented that the young turtles exhibit very similar behavior while residing in northeastern nearshore waters (Morreale and Standora, 1994). In fact, the predictability of turtles moving out to sea in the fall was a major consideration in the present study design. Therefore, it was not too surprising that all of the turtles captured in October were on their way out of the estuarine habitats. As turtles left nearshore waters, however, the similarity of behavior became remarkable. All turtles left soon after release, and all migrated steadily out of northeastern waters at similar rates. Furthermore the pathways of all eight turtles intertwined along the same relatively narrow band of ocean extending along shallower portions of the continental shelf toward southern waters.

From the synthesis of the observed movements it is obvious, both intuitively and statistically, that each fall, sea turtles migrate along a well-defined oceanic corridor that extends southward for more than 1000 km, from the northeast to the south. This pattern was not only observed for the eight

loggerhead turtles in this study, but was also exhibited by four other young loggerhead and three young Kemp's ridley turtles in preliminary satellite tracking studies from New York (Morreale and Standora 1994). This is also a phenomenon similar to the migration corridor that was observed for adult leatherback turtles in the tropical Pacific (Morreale et al. 1996, Chapter 2), but differs in some details. An obvious distinction between the two routes was the depth of water along the paths. The leatherbacks traveled in more open waters of depths mostly greater than 1200 m, while the loggerheads traveled along shelf waters shallower than 60 m during their migration southward. For the loggerhead turtles that later migrated offshore, however, this distinction disappeared as they swam beyond the continental slope into deep pelagic waters. Another difference was that the Atlantic coastal corridor appears to be quite constricted, estimated to be within a band narrower than 60 km wide. The wider Pacific corridor, however, may reflect the liberal inclusion of a few widely separated points that may not have been true locations.

An important feature that is unique to the narrow corridor for turtles migrating from northeastern U.S. waters is the equally narrow time frame in which migration occurs. Thus, the Atlantic corridor appears to be condensed temporally, existing within time only from October through December. The general trend for the northeastern turtles is to migrate southward beginning in early October and to pass the Virginia border by the first week of November. Continuing along to the terminus of the corridor, off the coast of North Carolina, turtles then slow their southward movement and apparently become sedentary south of Cape Hatteras.

The pulse of fall migratory movements means that, in December, there is likely a confluence of sea turtles from more northern waters joining with many others from Virginia and North Carolina waters that evidently follow the same

pattern (Byles 1988, Keinath 1993, Renaud 1995). Indeed, such congregations of turtles south of the Cape Hatteras faunal barrier during winter months have been corroborated in separate observation studies (Musick et al. 1994, Epperly et al. 1995*a, b*). With this clustering of turtles in time, it is immediately obvious that any disturbance during migration along the corridor, within the 50 m contour, could drastically affect east coast populations. The potential threat is probably exacerbated as turtles pass along Cape Hatteras. There, the corridor becomes even more constricted, possibly to less than a few kilometers wide. With the acknowledgement that turtles migrate along similar routes, must come the acceptance that such clustering can greatly increase their vulnerability.

Another gathering area for migrating turtles, worthy of specific mention, is in Onslow Bay near Latitude 34W and Longitude 77N, approximately 100 km offshore of Wilmington, North Carolina. This recessed section of coastline between Cape Lookout Shoals and Frying Pan Shoals appears to be a suitable overwintering site in most years. The shallow reefs, which jut out more than 40 km offshore, and the nearby Gulf Stream waters combine to make this a unique site where turtles may become highly concentrated during winter months. It also appears very similar in physical character to the major overwintering site at Cape Canaveral. Although Onslow Bay's northern location may make it too cold in more severe winters, nearly all of the turtles that were tracked through December settled in this relatively small area. Some remained there for months, and at least one was monitored as it spent the winter there before migrating north again in spring. The potential occurrence of a winter gathering site in the Onslow Bay area has been suggested previously (Epperly et al. 1995*b*, Keinath 1993) and this was confirmed by the behavior of the turtles in the present study. Also, upon review of the literature, there have been some other isolated examples of telemetered loggerheads and Kemp's ridleys that have spent some

or all of the winter near that same spot (Keinath 1993, Renaud 1995). This winter gathering site for turtles also may warrant special attention.

It is not until after turtles remain in North Carolina for one to two months that the first divergent behavior becomes noticeable. The renewed activity, usually in January or February, is most likely due to a decrease in temperature that usually affects waters south of Cape Hatteras at that time (Epperly et al. 1995*b*). Because of the complexity and mixing of waters in that region, in some years a subtle difference in overwintering location may affect whether a turtle experiences suitable conditions or is prompted to change position. From North Carolina, the result of a mid-winter move for warmer water may have great consequences. The nearness of the Gulf Stream ensures that there is a close source of warm water so there appears to be little threat of cold-stunning. However, once the turtles enter the flow, they are transported quickly and very far offshore. In some cases this resulted in movements of thousands of kilometers. Although seemingly extreme, such a strategy may also represent a viable overwintering behavior. Turtles apparently were able to slow their movement along the way. One loggerhead even began what appeared to be a return trip, traveling back toward the coast more than 400 km before last contact. The same type of open ocean travel has been reported previously for loggerheads (Byles 1988, Keinath 1993, Morreale and Standora 1994) and a Kemp's ridley (Renaud 1995).

Whether the loggerheads occupied coastal areas or deeper pelagic waters, most of their biological activity was confined to the upper 50 m of the water column. From the diving profiles, the turtles were observed to spend about one third of their time at the surface, and the rest of their time submerged mainly at shallower depths. In coastal waters, this usually translated to dwelling along the bottom, whereas in pelagic waters turtles remained in the upper 5% of

the water column. It is not clear whether this depth limitation represents a general preference of the species, or merely of the juvenile turtles observed in this study. In a diving record of an adult loggerhead tracked in Japan, however, the turtle also remained mostly within the upper 50 m of the water column, with only a few brief excursions down as deep as 200 m (Sato et al. 1994).

The careful synthesis of the observed behaviors from this study, along with selected data from previous studies, has revealed some clear patterns in sea turtle migratory behavior. As a consequence, it appears that the temporal and spatial positions of sea turtles can be well predicted during their extensive fall migrations from the northeast, and perhaps upon their return in the spring. This includes the early travels southward along the coastal migratory corridor, and possibly the subsequent overwintering activities in southern waters. In addition, it may even be possible to reasonably predict the pelagic migration patterns based on a few observations. The path of the turtle that was tracked into the Gulf Stream beginning the second week of February 1996 was nearly identical to the path followed by a turtle the second week of February 1995. When plotted together, these tracks intertwine for a distance of more than 1000 km with the path of a third loggerhead turtle that was tracked through pelagic waters in the winter of 1993 (Morreale and Standora 1994). With the added information on the diving activities, it may be possible to extend our predictive potential also to anticipate the turtles' positions in the water column.

Predicting where and when sea turtles occur will have immediate and practical application by allowing us to sharpen the focus of management activities. With an understanding of migration patterns it may be feasible to protect only minimal areas, such as narrow migratory corridors, rather than face the daunting task of protecting the entire ocean. It may also be possible to define windows of time during which stringent restrictions could be imposed,

and then free up migratory pathways of turtles for alternative uses during the rest of the year. Although effective management might be easier in shelf waters, the confinement of turtles to the upper water column may simplify the task of managing turtles in pelagic waters also.

Contrary to the historical perception of northeastern sea turtles as waifs, it has become apparent that northeastern waters provide important foraging habitat for loggerhead, Kemp's ridley, leatherback and some green turtles during warmer months. Furthermore, through direct observation of numerous turtles, it is apparent that they swim into and out of northeastern waters readily and frequently. Two of the turtles in this study were followed through complete north-south migration cycles; one was tracked completely by transmitter, the other through combined tagging and transmitter data. The patterns of these two loggerheads seem to characterize the behavior of northeastern sea turtles in general. Turtles migrate into the northeast during spring, they remain to feed for up to several months, and then migrate back southward before winter. Moreover, this pattern of long-distance migration along the eastern seaboard likely is prevalent and persistent throughout much of the lives of many turtles. It is important to note that these present-day patterns of activity of northeastern sea turtles also apparently are very similar to historical patterns (Morreale et al. 1989). Therefore, the annual fluxes of turtles into and out of the region probably have been occurring for a long time, whether or not it was acknowledged by scientists.

The skewed outlook we have had that for a long time depicted sea turtles as southern animals has surely influenced, not only our perception, but also our conservation strategies. As a result of inappropriately labeling sea turtles, we have not properly acknowledged the importance of annual seasonal migrations to and from northern temperate waters. By not considering that potentially

tremendous numbers of threatened and endangered turtles participate in these long-distance excursions, our management plans have been, at the least, inadequate. More likely, our neglect of such an important part of their life cycles makes sea turtles highly vulnerable to undesired interactions at sea. The extensive migration routes documented here may represent avenues by which sea turtles shuttle to and from northern temperate waters for many years. This greatly augments the significance of such fixed migratory routes, and this importance should be reflected in future conservation efforts.

CHAPTER 4

PREDICTING SPATIAL AND TEMPORAL PATTERNS OF SEA TURTLE MIGRATIONS.

Numerous anthropogenic threats, both traditional and current, have contributed greatly to the endangered and threatened status of sea turtles worldwide. The harvesting of nesting females and their eggs on beaches has long been identified as a major influence in the global decline of sea turtles (Carr 1967). Since these early studies, management strategies on many beaches worldwide have responded by protecting adults and eggs through stringent regulations. However, the continued decline of many populations of sea turtles, despite these protective measures, is evidence that other major sources of mortality need to be examined and properly addressed.

With our long-standing myopic concern over the terrestrial phases of the sea turtle life cycle, we have well accounted for the sources and magnitude of mortality of turtles on nesting beaches. Because a sea turtle's existence is mainly aquatic, however, a tremendous amount of mortality also occurs in the ocean. Although this is widely recognized, it has been difficult to quantify mortality in many marine environments and, therefore, much more difficult to devise adequate management practices for sea turtles. In addition, protecting aquatic habitats is more problematic than protecting nesting beaches. These beaches are generally discrete with turtle activity predictably confined to certain times of the year. In contrast, the distribution of sea turtles in the oceans is extremely widespread, and movements of individuals vary both seasonally and throughout their lifetime. The inaccessibility and high mobility of turtles contributes greatly to our lack of knowledge of their biology.

There is a certain amount of irony in not knowing much about the

ecology of sea turtles while they are in the sea. Even more ironic is that a large portion of our information on sea turtle biology in their natural habitat comes from their entanglement and death. Although sea turtles are directly hunted in many parts of the world, huge numbers are caught incidentally in fishing gear that is targeted for other species. While capture and restraint in gear can be damaging to many marine animals, turtles are especially susceptible because they need to reach the surface to breathe.

The possibility of being drowned in fishing gear may be one of the largest threats to sea turtles, rivaling those on nesting beaches. Much of the mortality in international waters throughout the world has been from incidental capture by gillnets (Margaritoulis 1986, Chan et al. 1988), longlines (Chan et al. 1988, Nishemura 1990, Laurent et al. 1993, Bolten et al. 1993, Thoulag 1993, Miller 1993, Aquilar 1995), and trawling (Chan 1988, Poiner et al. 1990, Robins 1995, Poiner and Harris 1996). There is much variability and unpredictability in capture rates among gear types, season of activity, and location of fishing, but the cumulative impact of commercial fishing on turtles appears to be generally high. Although it is seldom the intent of these fisheries to catch turtles, many types of gear are not designed precisely enough to catch only the targeted species. Some types of fishing practices are even unwittingly prone to capturing highly protected species, such as marine mammals and sea turtles (Scott and Brown 1997).

The very large problem of incidental capture and drowning of sea turtles is not restricted to commercial fishing. Rather, it frequently occurs wherever there is much overlap in activities and habitat usage between humans and turtles. Deaths of sea turtles numbering in the thousands have been documented in protected swimming areas in Australia (Paterson 1979, 1986, 1990) and in South Africa (Dudley and Cliff 1993) as a result of drowning in Anti-shark nets.

Regardless of the source, the bycatch of many other animals, is often unforeseen and, in most instances, undesirable.

Clearly, there is not always an easy remedy for human activities that impact sea turtles, even after a problem has been detected. The commercial longline fishery has been regarded as a source of mortality to turtles for more than two decades (Witzell 1984). In this fishing technique, hooks baited with squid or fish are dangled from mainlines that can extend for distances of more than 100 km each. All told, the millions of hooks and lines each year contribute to some alarmingly high numbers of entangled and hooked turtles. In northeastern U.S. waters observers randomly assigned to 54 different longline fishing trips targeted for tuna, swordfish and sharks, observed the incidental capture of 85 sea turtles (Gerrior 1996). Comparably high numbers were recorded in the western North Atlantic waters, where 501 turtles were captured on 395 randomly observed fishing trips (Hoey 1997), and 2601 captured turtles were recorded in fishing logbooks between 1992 and 1995 (Witzell, in press). Despite much deliberation on the problem (Balazs and Pooley 1993, Williams et al. 1996), no comprehensive solution, short of complete closure of the longline fishery, has yet been proffered.

Even with the high rates of interactions with sea turtles reported in pelagic longline, pelagic drifnets, and deep-water trawl fisheries (Scott and Brown 1997), there is a burgeoning concern over the nearshore gillnet, driftnet, and lobster fisheries that saturate coastal waters. The current concern over these fishing activities does not stem from high rates of entanglement of turtles, but rather the sheer numbers of lines and nets in the water that result in many reported turtle drownings, and probably many more that are unreported.

A chief deterrent to managing such a diffuse problem in coastal waters has been the lack of details on the activities of sea turtles and, hence, a lack of

ability to predict and avoid interactions. However, with the information that is now being accumulated on sea turtle biology using satellite telemetry, it may be possible to reduce the incidental capture of turtles by pinpointing times and locations where overlap is most likely. In addition, an effective plan developed for coastal waters may provide a good template for tackling the pervasive problems faced by turtles at sea.

Movement Patterns of Northeastern Sea Turtles

The finding that turtles from the northeastern U.S. migrate along a common pathway (Chapter 3), similar to the adult turtles studied in Costa Rica (Chapter 2; Morreale et al. 1996), may offer a solution toward their conservation within coastal waters. Moreover, a predictive model based on observed movements of turtles along the coast could be readily adapted to predict movements of turtles in nearby pelagic waters, and even in other regions of the world.

The synthesis of the observed migratory behaviors of turtles in this study, along with data from preceding studies in northeastern U.S. waters (Morreale and Standora 1994) has revealed some distinct patterns of movement along the eastern seaboard. All told, the migratory movements of 15 juvenile turtles monitored by satellite transmitter were along highly similar routes (Fig 4.1). This pattern persisted, despite using different techniques on two turtle species (Kemp's ridley and loggerhead), in two separate studies, and over five separate years (between 1990 and 1995). Turtles appear in northeastern coastal waters in the early summer each year. There they remain and flourish for up to several months, foraging on the abundant benthic fauna. By fall, the rapidly

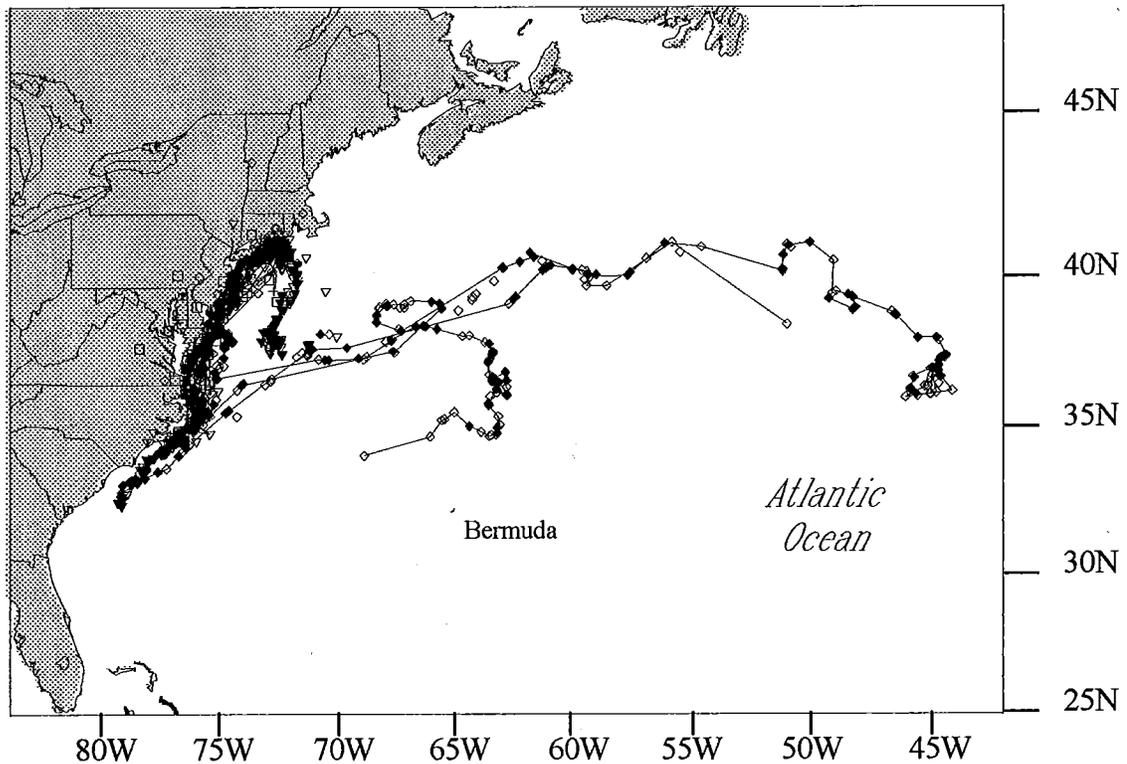


Figure 4.1. The similar migration paths of 15 juvenile sea turtles tracked by satellite transmitter from New York waters beginning in the summer or fall of five different years. Three Kemp's ridleys in 1990 and 1991, along with 4 loggerheads in 1992 were tracked in previous studies (Morreale and Standora 1994); eight more loggerheads were tracked in the present study in 1995 and 1996. Turtles remained in near shore waters, until fall, when they migrated out to sea and southward along coastal shelf waters by early winter. Some overwintered in the Carolinas and others moved into pelagic waters in late winter, traveling with the Gulf Stream to positions thousands of kilometers offshore.

declining water temperatures stimulate the turtles' departure and they migrate out of northeastern waters. After observing 15 of the 15 turtles migrate southward from New York waters, it became apparent that their plotted movements were defining a narrow migratory corridor along which turtles predictably travel between northern and southern waters.

The high degree of similarity in movements was also evident with respect to timing. Furthermore, these nearly identical patterns transcended different species and different years. On the same date of October 30 in three separate years, there were five turtles that were released in New York (a Kemp's ridley and four loggerheads) all within a radius of 40 km from a central location near the Maryland-Virginia border. The comparable timing among years is not very mysterious. The impetus to migrate is probably mediated by abrupt temperature declines each year around early October. The very predictable timing of these temperature changes (Morreale and Standora 1994) is the likely cause of such a predictable migration schedule. The outcome is a pulse of turtles that depart from inshore waters each year and swim southward along a coastal corridor that appears to be predictable both spatially and temporally.

Objectives

The objective of this portion of the study was to develop a generalized model of migratory movements of sea turtles. Such a model, constructed from a synthesis of observed movement patterns, could provide a powerful tool for predicting temporal and spatial positions of sea turtles during the course of their extensive migrations southward, and possibly by extension, while overwintering and throughout the rest of the year. Predicting where and when sea turtles occur should have immediate and practical application by sharpening the focus of management activities. Areas in which turtles are migrating could be more

specifically delineated, and windows of time in which to regulate these areas could be defined with greater precision.

Model Development

The predictive model was generated from the satellite-monitored tracks of the eight loggerhead turtles along the eastern seaboard of the U.S. in 1994 and 1995 that were presented in the previous chapter. The standardized study protocol among these eight individuals contributed in making them ideal subjects for developing a general model of sea turtle migration patterns. Furthermore, their highly similar movements along a narrow corridor for the first several weeks of migration (Fig. 4.2) offered the prospect that these could be synthesized into a mathematical model that could be useful in predicting turtles' positions simply by knowing the date.

The movements of the turtles between 1 October and 1 December of both years first were broken down into three simple dimensional components: latitude, longitude, and day of the year (Fig. 4.3). These movements were then analyzed using two different statistical models to produce predicted pathways through time and space. Both models partitioned the three-dimensional data into two segments: day of year versus latitude of turtles, and day of the year versus longitude of the turtles.

In the first analysis a mixed model, which accounts for both random and fixed effects, was used to compare migration patterns among individuals, and to generate a predicted pathway for all turtles. The mixed model (Proc Mixed; SAS Institute, Inc. 1997) allowed locations along each turtle's track to be correlated through time by incorporating a first-order auto-regressive function.

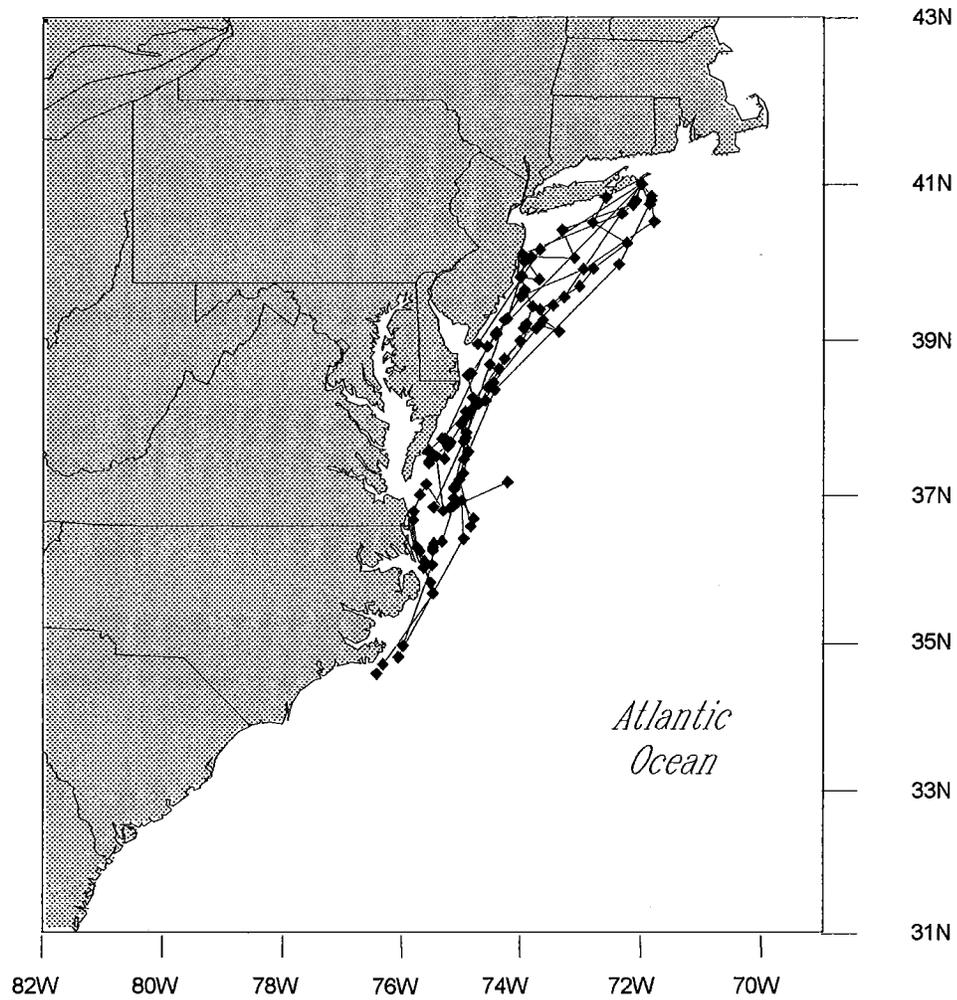


Figure 4.2. The migratory tracks of eight loggerhead turtles between the dates of 1 October and 1 December in 1994 and 1995 as they traveled southward from northeastern U.S. waters along a coastal migratory corridor. Each point represents a satellite-determined position of a turtle along its migration path. The general movement for all turtles was from north to south.

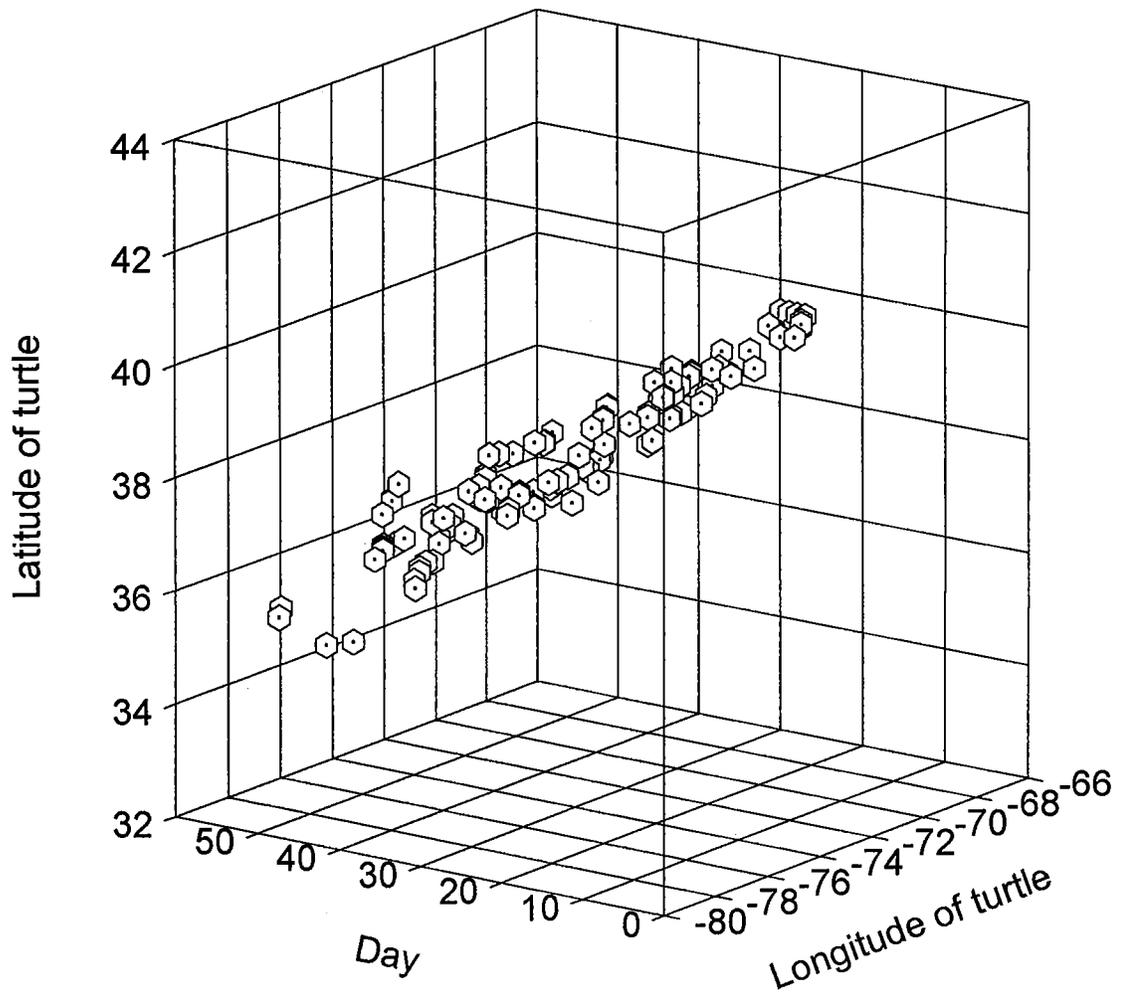


Figure 4.3. The satellite tracks of eight turtles during fall migration, depicted as three-dimensional coordinates through time and space. The migratory movements of all eight turtles were tightly grouped both spatially and temporally. Turtle positions are presented in degrees north latitude and west longitude. Dates between 1 October and 1 December of both study years are represented as the number of days since 1 October.

Not surprisingly, the eight separate turtle tracks were deemed not to be significantly different than each other in relationships between day of year and latitude ($P > .05$), and between day of year and longitude ($P > .05$). For all calculations, latitude and longitude were measured in decimal degrees, and day of year was calculated as number of days since 1 October. The predicted line for the relationship between day and latitude of turtle was linear, described by the formula: $\text{Latitude} = 41.9817 - 0.1221 * \text{Day}$. Since this line was intended to represent the predicted generalized turtle track, it was useful also to designate some confidence limits (Fig. 4.4). The confidence boundaries were established at a distance of 3 S.D. from the central line, which, for both latitude and longitude, encompassed more than 94% of all plotted locations. The resultant confidence interval for predicting latitude of turtles was designated as 1.05 degrees. For the relationship between day of year and longitude of turtle, the formula used for the predictive line was quadratic, in the form of: $\text{Longitude} = -70.4658 - 0.1997 * \text{Day} + 0.0019 * \text{Day}^2$; the confidence interval was 1.12 degrees (Fig. 4.5).

The second analysis, which used a more traditional parametric linear model (Proc GLM), was performed as a check of the first model which was more appropriate in theory. The general linear model does not account for autocorrelation, and therefore assumes that all locations in time and space were independent points drawn from a random population. This was not the case for turtle tracks in which each point along a migration path is highly influenced by the location of the previous point. The shortcoming of the traditional parametric model also precluded the comparison of tracks of turtles. The resulting analysis, nevertheless, was in close agreement with that of the mixed model. The predicted line for latitude and day was described by the formula: $\text{Latitude} = 41.7321 - 0.1166 * \text{Day}$. The relationship between day and longitude was

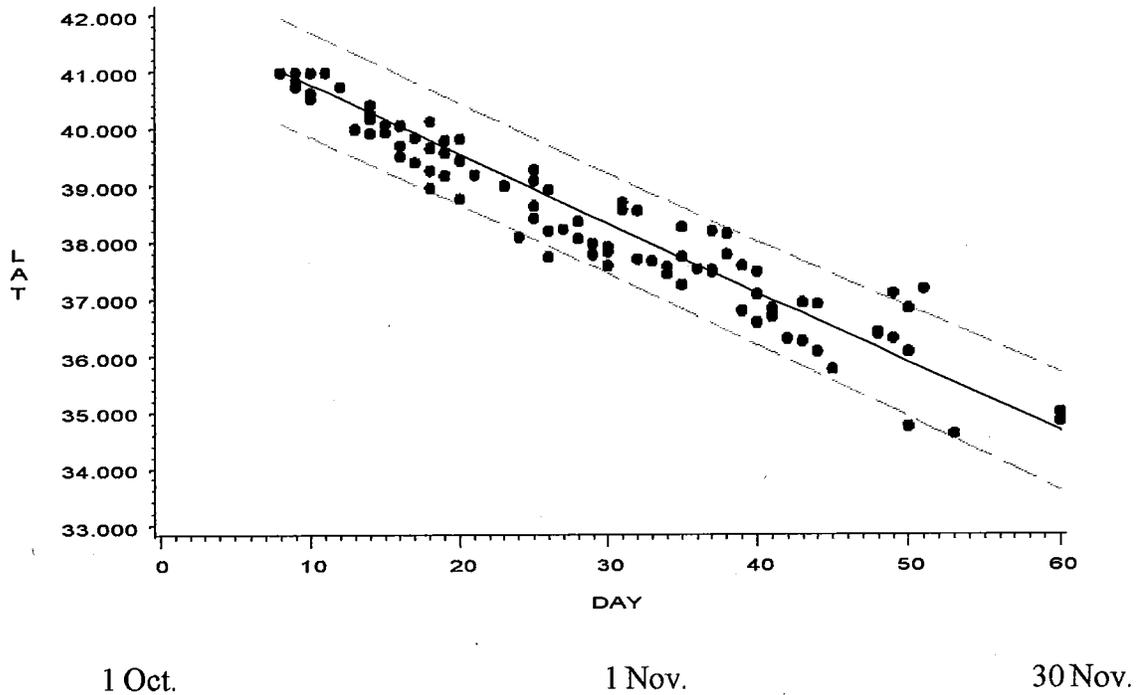


Figure 4.4. The relationship between day of the year and latitude of eight turtles during migrations from northeastern U.S. waters in October and December. A mixed model was used to compare migration patterns of eight turtles and to generate a predicted migratory pathway. There was no significant difference ($P > .05$) among the eight turtles; the predicted line (solid line) for the relationship between day of year and latitude of turtle is linear: $\text{Latitude} = 41.9817 - 0.1221 * \text{Day}$. A confidence interval of 1.05 degrees (depicted by dotted lines) encompassed >94% of the plotted locations.

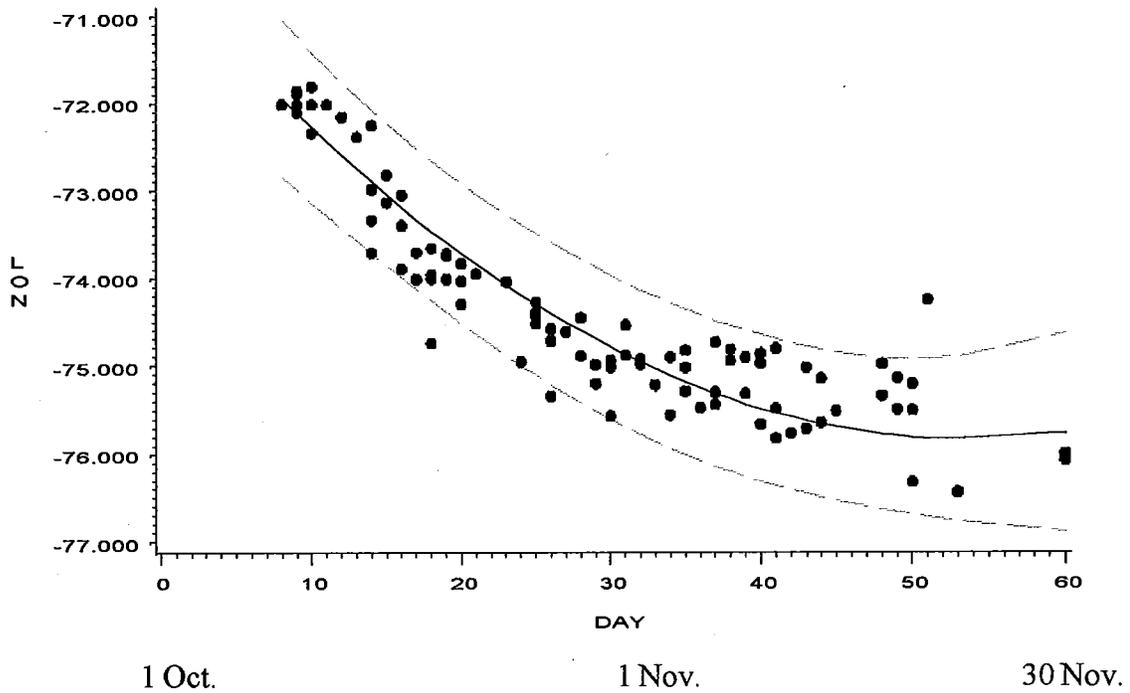


Figure 4.5. The relationship between day of the year and longitude of eight turtles during migrations from northeastern U.S. waters in October and December. A mixed model was used to compare migration patterns of eight turtles and to generate a predicted migratory pathway. There was no significant difference ($P > .05$) among the eight turtles; the predicted line (solid line) for the relationship between day of year and longitude of turtle is quadratic: $\text{Longitude} = -70.4658 - 0.1997 * \text{Day} + 0.0019 * \text{Day}^2$. A confidence interval of 1.12 degrees (depicted by dotted lines) encompassed >94% of the plotted locations.

described by the predicted quadratic line: $\text{Longitude} = -70.3795 - 0.2178 * \text{Day} + 0.0023 * \text{Day}^2$. The 95% confidence intervals, calculated at 0.93 degrees for both predicted lines also were similar to the intervals used in the mixed model. The similar depiction of the data by the parametric analysis gave further support to the predictive ability of the much preferred mixed model.

Model Testing

The predictive model of turtle positions by date was mathematically derived solely from the observed movements of eight loggerhead turtles during migration in 1994 and 1995. The objective, however, was to develop a model that would adequately predict timing and location of turtles on a broader scale. To test its effectiveness at predicting more generalized movements, the newly developed model was applied to an independent data set, composed of locations of four species of sea turtles, sighted in aerial and shipboard surveys between 1978 and 1982, along the continental shelf of the northeastern U.S. (Fig 4.6). These data were collected during the Cetacean and Turtle Assessment Program surveys (Shoop and Kenney 1992) and derived from a much more extensive data set compiled and maintained by the University of Rhode Island (R. Kenney, personal communication).

At first inspection, the pattern of spatial distribution of the turtles observed from the aerial surveys is strikingly similar to the spatial patterns of migrating turtles observed by satellite transmitters. Most of the turtle sightings occur within the same narrow band along coastal shelf waters that was described in the telemetry studies as the turtle migration corridor. Furthermore, in analyzing the patterns of loggerhead and leatherback distributions, Shoop and

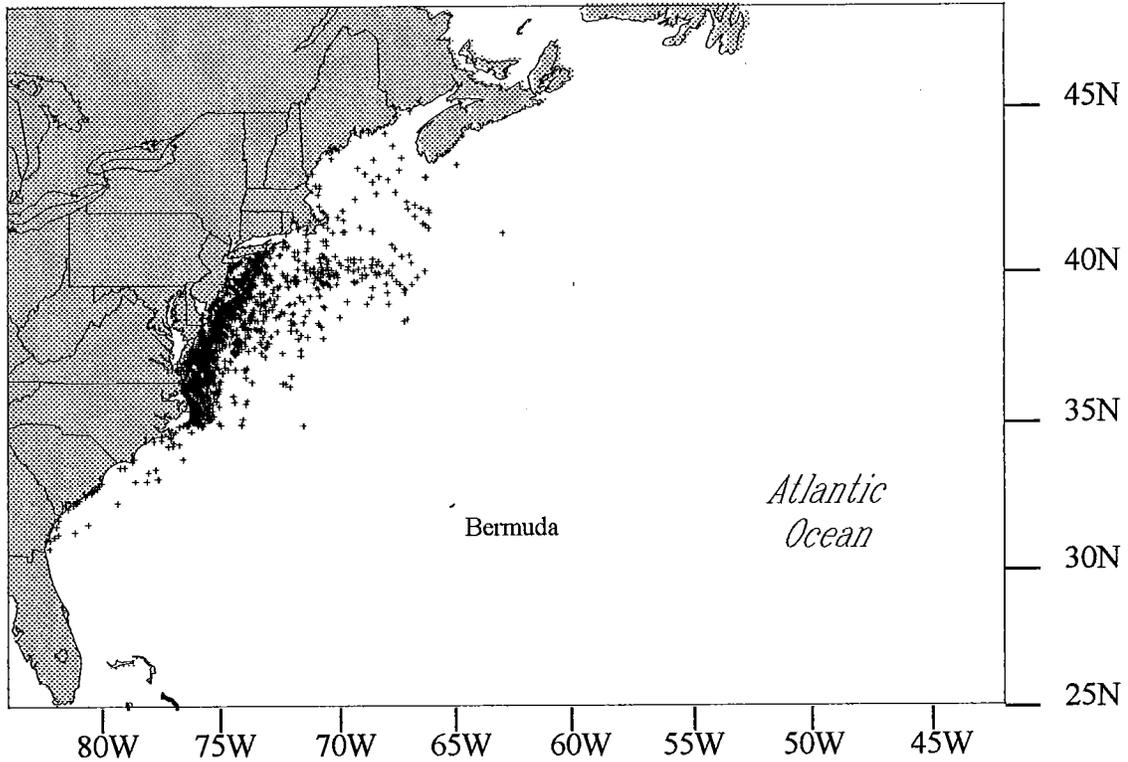


Figure 4.6. The locations of four species of sea turtles that were observed along the continental shelf of the USA between the dates of 30 September 1978 and 30 July 1982. The 2816 points represent observations of sea turtles from shipboard or aerial surveys. Data were compiled by the University of Rhode Island during a larger study (Shoop and Kenney 1992). (Data were used with permission of R. Kenney).

Kenny (1992) also noted a strong seasonal component. In that study the trend in the fall was interpreted as indicative of wholesale movements of turtles from northeastern waters to the south.

Upon a much more detailed examination of the survey data, the predictive model also performed extremely well. The survey data were pared down to include 305 observations of turtles between the dates of 1 October and 1 December (Fig. 4.7). Thus, the survey data were limited to within the realm of the first 60 days of migration that was observed by satellite telemetry more than a decade later. The turtle migration model was then applied to these data to measure its predictive abilities. The strength of the model was not in making pinpoint predictions of where turtles occurred, but instead in its accuracy of defining outer boundary lines of turtle occurrence.

Using the tight confidence intervals for both latitude and longitude, less than 5% of the turtle positions were predicted accurately on their specific dates. Thus, an appropriate use of the model would not be to predict sea turtle distribution within such a small window. However, the model values were very good at depicting the tail end of an advancing wave of turtles moving southward. This was accomplished by using only the upper confidence limits for latitude and longitude to define a northern and eastern boundary line around the turtles. Applying the formula and these upper confidence limits for any given day yielded a precisely defined perimeter, inside of which (eastward and toward shore) turtles occurred, and outside of which (northward and away from shore) turtles did not occur. Using this application on the 305 observations of turtles, the locations of more than 94% of all individuals were accurately predicted.

This solution is not merely of academic value. Rather, it provides a means to objectively predict with great confidence the areas where sea turtles

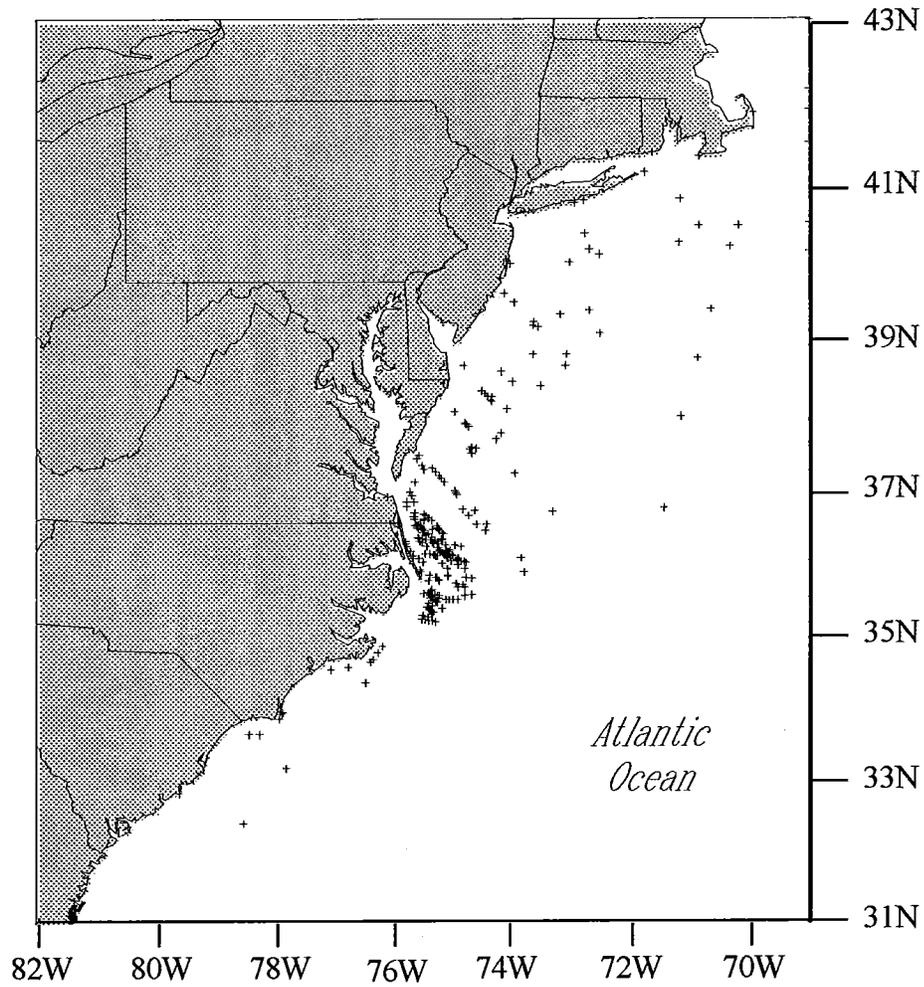


Figure 4.7. The locations of 305 sea turtles between the dates of 1 October and 1 December that were observed in the shipboard and aerial surveys between 1978 and 1982. These include all of the turtle sightings on the continental shelf from the Gulf of Maine to South Carolina. Data were compiled by the University of Rhode Island during a larger study (Shoop and Kenney 1992). (Data used with permission of R. Kenney).

will not occur. This is better visualized as a two-dimensional boundary that moves in time from northeastern to southern waters each fall (Fig. 4.8). Since nearly all observed turtles in the study area are southward and westward of the boundary, activities outside of the demarcated area at any time are unlikely to overlap with turtles. The immediate outcome of this model is a readily comprehensible and easily used guideline to avoid undesirable interactions between humans and turtles. At the same time, the fine temporal resolution and well-defined perimeter minimize the disruption of human activities by reducing the likelihood of unnecessary restrictions.

Discussion

Through the synthesis of the observed migratory behavior presented here, a convincingly robust model has been made to predict sea turtle locations during their fall movements. This model was developed for the primary purpose of designating buffers to protect turtles. It was designed to be simple and practical to apply by using two formulas to assign boundaries between high- and low-risk areas that move through time along with the turtles.

This specific model was constructed to predict movements of turtles in coastal waters and was not intended to be the paradigm for all turtle movements. It is expected, however, that this model be used as a template. The same methodology can be employed for protecting turtles in other oceanic regions. In that regard, it was encouraging that the turtles monitored by transmitter exhibited patterns similar to their study cohorts, and to turtles from the surveys many years earlier.

Even when migrating in distant ocean waters, there were surprisingly

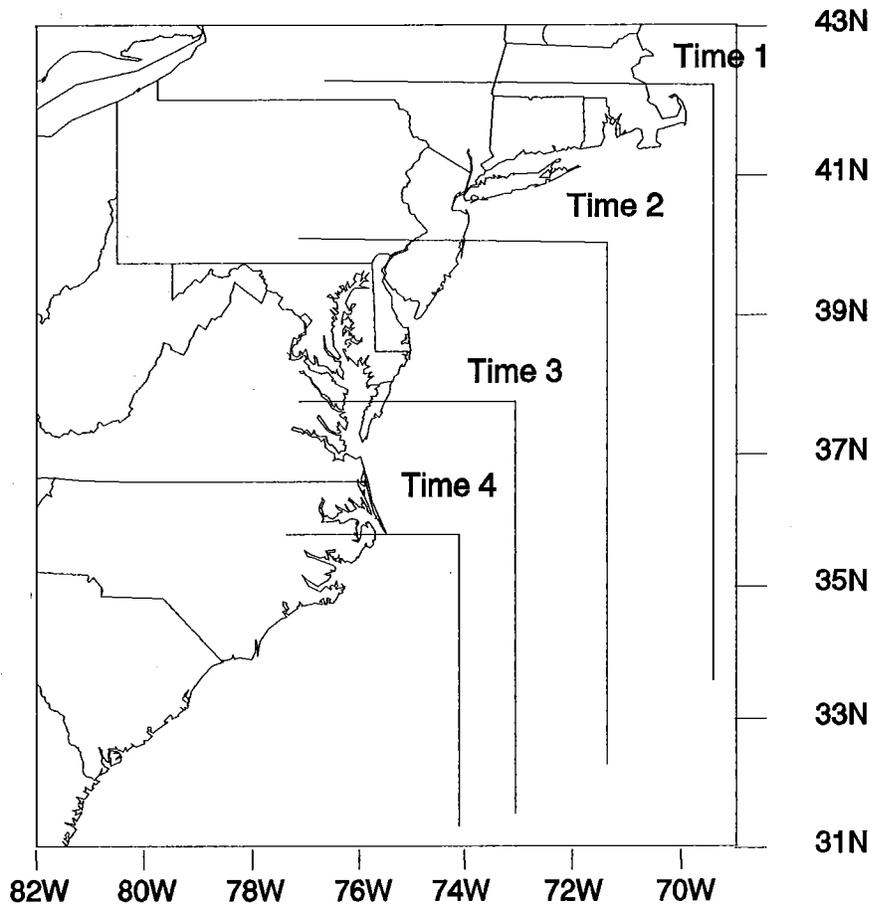


Figure 4.8. An illustration of a two-dimensional boundary line that moves southward and westward during the fall. The model is constructed so that, at each chosen time interval, the region to the north and to the east of the boundary line will contain almost no turtles.

similar movements among individuals and among years. The path of the turtle that was tracked into the Gulf Stream beginning the second week of February 1996 was nearly identical to the path followed by a turtle the second week of February 1995, and another in 1992. When plotted together, these tracks intertwine for a distance of more than 1000 km through the open ocean. The uniformity of migratory behavior undoubtedly will alleviate some of the difficulty in the chore of modeling and predicting oceanic movements.

The apparently fixed migratory behavior of sea turtles along narrow corridors probably has made them more vulnerable to human pressures historically. For example, the turtle migration route from the northeastern U.S. is within coastal shelf waters where resources are plentiful and accessible. Because of these attributes, these same coastal waters have been heavily fished by humans for centuries. Thus the frequent interactions between humans and sea turtles have not been merely serendipitous. Even the pelagic movements of these turtles do not relieve them of human interactions. Rather, the observed offshore movements of the turtles alarmingly coincide with the fishing locations of the U.S. distant water longline fishery, which accounts for a large proportion of this country's turtle entanglements at sea (Witzell 1996; in press). In retrospect, the chronic overlap between humans and migrating turtles along these and other migration routes has probably been one of the primary sources of sea turtle decline.

The recognition of predictable migratory behavior of sea turtles also has armed us with much greater ability to protect them in the water. If we can adequately predict where sea turtles will occur, we can restrict potentially harmful activities in these areas. In addition, the development of more accurate models to predict sea turtle movements may alleviate some less desirable impacts of conservation activities. There may not be a need for complete

shutdowns, but instead, only slight adjustments to the operations of the major fisheries. With a good model of oceanic movements of turtles, human activities may need only be restricted within narrow windows in time and space.

Moreover, the judicious use of the knowledge of turtle behavior may afford protection to sea turtles of all ages that otherwise may be forced to run a gauntlet of traps, nets, and longlines during their frequent long-distance migrations at sea.

CHAPTER 5

CONSERVATION AND MANAGEMENT RECOMMENDATIONS

To be most effective, management schemes designed to protect sea turtles must account for the biological and behavioral traits of these marine organisms. During the small portion of the life of sea turtles that is spent on nesting beaches, they are well protected in the U.S. and elsewhere. The most successful conservation programs in these areas are those that afford blanket protection to beaches and turtles during the nesting season. Similar protection should be considered for migration corridors and for turtles while they are migrating at sea.

The similarity in migration patterns among the sea turtles was a common theme throughout all of the telemetry studies presented here. Similar, and sometimes identical, patterns of movement were observed among adult female leatherback turtles in tropical Caribbean and Pacific waters, and among juvenile loggerhead and Kemp's ridley turtles along the northeast coast of the USA. The observed patterns of oceanic movements also persisted through time, sometimes over many years. In the tropical Pacific, the migration paths of nesting leatherbacks in four consecutive years defined a corridor extending out thousands of kilometers away from the nesting beach (Morreale et al. 1996). Likewise, the paths of juvenile loggerheads and Kemp's ridleys over several years were all within a narrow migratory corridor extending more than 1000 km along the U.S. Atlantic coast.

The persistent use of the same corridors probably means that patterns of migratory behavior are ingrained in sea turtles. In the Eastern Pacific, leatherback turtles leaving from a nesting beach in Mexico in 1997 also were

tracked southward as they migrated past the Galapagos Islands (Eckert 1997), just as did the Costa Rica turtles several years earlier (Morreale et al. 1996). In the earlier study (Morreale et al. 1996), concern was raised over the vulnerability of turtles traveling within narrow oceanic corridors. On that basis, it was recommended that potentially harmful activities to turtles be restricted within migratory corridors. Eckert (1997) reiterated these concerns and discussed some potentially devastating interactions between turtles and commercial fisheries along these oceanic routes. As it becomes increasingly apparent that turtles are exhibiting fixed behavior during migration, it is crucial that commercial fishing be curtailed along migratory corridors.

In coastal waters of the northeastern U.S., the migratory patterns of turtles that were tracked by satellite in the present study represented the distribution patterns of turtles observed in the region more than a decade earlier (Shoop and Kenney 1992). Each year in early fall, turtles migrated southward within a narrow corridor, and over a predictably limited time frame. Furthermore, there is much ancillary evidence throughout recorded history to suggest that similar seasonal migration patterns have prevailed for hundreds of years in northeastern waters (Morreale et al. 1989).

As sea turtles continue to migrate unchangingly along the east coast corridor there has been considerable overlap between turtle and human activity. Unfortunately, turtles were rarely considered in conservation schemes until recently. When the impact to turtles by commercial fishing was assessed, it was startling how much a single industry had contributed to long-term declines in sea turtles (National Research Council 1990).

The overlap in activities is often a result of a convergence on the same resources. Shallower shelf waters provide abundant resources for turtles, and these resources comprise part of the rich ecosystem that also attracts

commercial fishing. For many years, a major source of incidental capture and mortality of turtles was the shrimp trawling industry, where many thousands of turtles were being drowned in nets each year (Henwood and Stuntz 1987). Most of the captures of turtles were in water shallower than 18 m, where shrimp, turtles, and the shrimp trawlers were all converging.

Much overlap also occurs while turtles are in the midst of migrating through ocean waters. As sea turtles from northeastern waters migrate southward in the fall, they converge with many more turtles along the coastal corridor. The concentration of turtles in North Carolina coastal waters precisely coincides with peak concentrations of summer flounder and flounder trawlers migrating into the area (Epperly et al. 1995*b*). The simultaneous convergence of sea turtles and trawlers along this narrow coastal area, was directly linked to high levels of turtle mortalities in early winter.

There is similar convergence of turtles and humans even in deeper waters offshore. In pelagic Atlantic waters, turtles appear to be clustered near the Gulf Stream, which provides needed warmth in colder months. The nutrient rich waters also support plankton communities and the associated fauna of higher trophic levels, which also makes them desirable areas for fishing. Many of the interactions between turtles and the U.S. pelagic longline fleet are along the Gulf Stream and where it passes by the edge of the Grand Banks (Witzell, in press). The viewpoint is that turtle occurrence in these waters is unpredictable and irregular, and encounters tend to be in short pulses (Sutton 1996, Witzell 1996).

The frequent migration of sea turtles and their changing positions through time makes the problem of management even more difficult. In U.S. waters, much has been done to decrease the incidental capture of sea turtles. This has been achieved through the required use of Turtle Excluder Devices in

U.S. shrimp trawls and with restrictions on flounder trawling, dredging, and other human activities that have been well-documented sources of sea turtle mortality. Using the current management techniques, however, the progress is slow. To protect sea turtles, the fisheries management approach is to assess the impact of each specific activity on each species, and then develop appropriate solutions, usually in the form of area closures. Using only this conservation method, which is more reactive than pre-emptive, the outlook for sea turtles is not good. Relatively few resources are available to monitor and document captures of sea turtles, and there are not large standing stocks of turtles to absorb losses. It is my recommendation that the current management strategy be modified to increase its effectiveness.

Recommendations

- 1) Maximum protection to sea turtle migration corridors while turtles are migrating. Management activities should take into account the predictable timing of migration of sea turtles along corridors, as was demonstrated by satellite telemetry, survey data, and mathematical models presented here. All activities that are potentially harmful to sea turtles should be curtailed or eliminated within the migratory corridor while sea turtles are migrating.

- 2) Maintenance of corridor habitat. Migratory corridors should be treated as sensitive habitats that are critical to sea turtles, even during times of year when turtles are not present. Activities within these narrow spatial corridors should be carefully evaluated for their impact on resources and habitat quality. Activities that are judged to have potentially high negative impact on habitat quality within the corridor should be prohibited.

3) Model application. The model that was developed here to describe and predict migratory patterns should be used as a more encompassing and effective tool to regulate corridors. Using the model to predict geographical limits of turtle occurrence on different days of the year, time-area closures can be implemented efficiently and with pre-determined confidence limits.

4) Future refinements. The turtle migration model was developed to describe and predict the movements of turtles along the east coast of the U.S. during fall. This methodology can be more generally applied, however, to include predictive models of similar migrations during spring, nesting migrations, or movements in other regions. An important feature of this model was that it was derived using one data set (telemetry data) and tested using another (region-wide survey data). Similar telemetry studies should be conducted on sea turtles in pelagic waters. Using the techniques developed for this study, it would be simple to place transmitters on turtles caught in pelagic fisheries. For other regions of the world the development of alternative schemes to monitor turtles would be useful. For immediate purposes, however, general models of turtle behavior can be made using the available survey information.

Because of the highly migratory nature of sea turtles, even impacts on a regional level can affect their populations on a much broader scale. Many threats to sea turtles are posed by humans activities, and many interactions occur when humans and turtles interact at sea. To date, extensive efforts have been made to modify and restrict activities that have been demonstrated to be harmful. These efforts need to be augmented through improvements to management practices in ocean waters. By incorporating a detailed

understanding of the ecology of sea turtles in their marine environment, it should be possible to develop better conservation schemes with greater precision to ensure minimal impact both to humans and to sea turtles.

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