



AN ASSESSMENT OF THE LOGGERHEAD TURTLE POPULATION IN THE WESTERN NORTH ATLANTIC OCEAN



A Report of the Turtle Expert Working Group

U.S. Department of Commerce
National Oceanic and Atmospheric Administration
National Marine Fisheries Service
Southeast Fisheries Science Center
75 Virginia Beach Drive
Miami, Florida 33149

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PREFACE

The loggerhead turtle occurs in the Atlantic, Pacific and Indian oceans as well as in the Mediterranean Sea, and is generally perceived as the “common” marine turtle in the eastern United States, with extensive nesting from Florida to North Carolina. In the Atlantic system, some of the largest nesting beaches are along the U.S. coastline, with the largest subpopulation from Peninsular Florida and with a separate subpopulation from Georgia to North Carolina, (whose population is about one-tenth the size of the Florida stock) and an even smaller population from the Northern Gulf of Mexico. There is some nesting in central Quintana Roo, Mexico, as well as on Cay Sal Bank, The Bahamas and Dry Tortugas, Florida. Nesting is rare throughout the Caribbean mainland and islands; Cuba and Belize have the most nests outside Quintana Roo. Low level nesting regularly occurs in Grand Cayman Island (Bell et al. 2007). Among the few tropical nesting sites are beaches on the islands off Venezuela and the Santa Marta Peninsula (northeastern Columbia), and possibly some also on the Serrano and Serranilla Banks in the Western Caribbean. However, recent quantitative data are lacking for all of these Caribbean sites. Certain beaches in south-temperate Brazil (southern Sergipe, Bahia, and southward to northern Rio de Janeiro) receive about 5,000 loggerhead nests/year (Marcovaldi and Chaloupka 2007). On the African side of the Atlantic, the best documented nesting area is in the Cape Verde Islands, with some possible nesting also occurring in Angola although recent reports cast doubt on this (Weir et al. 2007). In the Mediterranean Sea, most nesting occurs in Turkey (Dalyan, Dalaman), Greece (primarily Zakynthos), and Libya with lesser levels of nesting also occurring in Syria, Israel, and Tunisia (Margaritoulis et al. 2003). Recently, a few loggerheads nests were observed in Spain, France, and Italy (Bentivegna et al. 2005).

Peninsular Florida represents the largest loggerhead nesting aggregation in the Atlantic Ocean, representing as much as 80% of all nesting and producing 90% of all hatchlings. The number of nests has declined since peaking in 1998 (with 59,918 nests on index beaches). These beaches represent about 25% of all nesting habitat but about 70% of the total number of nests (Florida Fish and Wildlife Conservation Commission (FFWCC); <http://research.myfwc.com>). From 1989 to 1998, the number of nests increased 25% but since 1998 the number of nests has declined approximately 40% with 28,074 nests recorded on index nesting beaches in 2007 (FFWCC). On a positive note, there were 38,064 nests in 2008 on those index nesting beaches (FFWCC).

With the foregoing in mind, the global importance of the status of U.S. Atlantic loggerhead populations becomes apparent. A very significant fraction of the world loggerhead population nests in Florida. Thus, the status of this population is crucial to the species as a whole. Currently, Peninsular Florida sea turtle populations are showing changes that have resisted comprehensive interpretation. Nesting numbers of both the green turtle (*Chelonia mydas*) and the leatherback (*Dermochelys coriacea*) that share the same Florida nesting beaches with loggerheads are increasing strongly (although, at least until recently, in the typical “high year/low year” alternating fashion). For both of these species, the increases have been dramatic and significant with green turtles increasing from 5,557 in 1998 to 9,642 nests in 2005 and leatherbacks increasing from 351 to 762 over the same period (FFWCC). These species are still greatly outnumbered by loggerheads on Florida beaches, but nesting of the latter, having shown some degree of stability for over a decade, now appears to be in decline.

Along with Peninsular Florida, the productivity (measured by number of nests) of the Northern U.S. subpopulation (Georgia to North Carolina), Northern Gulf of Mexico, and Yucatán loggerhead nesting populations in the Western North Atlantic have all dropped significantly in recent years. The decrease in the Peninsular Florida subpopulation nesting is about 4 % annually (39.5% decrease since 1998), compared with 6.8 % annually in the Florida Panhandle, 1.9% annually in the Northern U.S. subpopulation, and 5% annually in the Yucatán Peninsula. However, the nesting population in Brazil has exhibited an increase over the past decade (Marcovaldi and Chaloupka 2007).

It is our purpose to update the previous Turtle Expert Working Group (TEWG) reports and a more recent assessment (NMFS SEFSC 2001) with new information, and to address the status and trends of the Western North Atlantic population of loggerhead and to evaluate possible causes of the observed trends.

The first Turtle Expert Working Group convened 1995-1998 to do an assessment of loggerhead and Kemp's ridley sea turtles. The group's work is reflected in two reports (TEWG 1998, 2000). They concluded that the Peninsular Florida loggerhead subpopulation was stable or possibly increasing and that the Northern U.S. subpopulation, after declining since the 1970's, may have stabilized. The status of the Northern Gulf and Mexico subpopulations were unknown. Subsequent to the TEWG, the original Crouse et al. (1987) population model was updated multiple times (Heppell et al. 2003; NMFS SEFSC 2001; Snover 2002; Hedges 2007) and new genetic and demographic information have become available. Importantly, the trend in nesting on the Peninsular Florida beaches has changed, recently declining.

The second loggerhead TEWG was convened December 2006 to update the previous report for loggerheads and to assess the recent decline in loggerhead nesting on South Florida beaches. Thus, this TEWG report is structured into five sections: Part I is an update of the previous TEWG reports: stock id, life stage definitions and demographics, sex ratios, and geographic distributions. Part II reviews the status and trends of the current nest numbers while Part III examines in-water population trends. Part IV explores hypotheses for the reported trends and, lastly, Part V identifies research needs.

I personally want to acknowledge all the contributions of data and hard work that were necessary to finalize this report. Considerable amounts of data were contributed that were not collected by the National Marine Fisheries Service (NMFS) or by TEWG members. Due to the need to safeguard ownership of the data and information, NMFS wants to clarify the intended use of any data shared with the TEWG. NMFS, in conjunction with collaborating parties, used these data only in producing this final TEWG report on the status of loggerhead turtles in the Western North Atlantic Ocean. All data shall remain the property of the provider and were used in this report with their permission. These data cannot be used without the explicit permission of the originator.

Dr. Nancy Thompson, chair

EXECUTIVE SUMMARY

It's been nearly a decade since the Turtle Expert Working Group (TEWG) last assessed the Western North Atlantic populations of the loggerhead sea turtle (*Caretta caretta*). An updated report at this time was deemed necessary given the apparent changes in the nesting trends of loggerhead subpopulations that were last thought to be stable or recovering and the publication of additional information on the stocks. The TEWG had assessed recovery by the increasing numbers of nests in the Peninsular Florida subpopulation while the Northern U.S. Subpopulation was at best stable. Over the past decade, the annual numbers of nests of all the loggerhead subpopulations in the Western North Atlantic were decreasing through 2007, with an upturn in 2008. Of particular concern was the recent decrease in the annual numbers of loggerhead nests in the largest subpopulation, Peninsular Florida.

We began by updating information on stock structure and definitions of life stages of Western North Atlantic loggerheads last reported by the TEWG. The TEWG previously recognized four nesting subpopulations of loggerheads in the Western North Atlantic (TEWG 2000). Continuing work on stock structure led to the discovery of a fifth nesting subpopulation in the Western North Atlantic and a better delineation of the previously identified subpopulations. In this current report, we used the designations recognized in the Loggerhead Recovery Plan (National Marine Fisheries Service and U.S. Fish and Wildlife Service 2008). These five subpopulations are:

1. Northern U.S. Subpopulation (Florida/Georgia border through southern Virginia)
2. Peninsular Florida Subpopulation (Florida/Georgia border through Pinellas County, Florida)
3. Dry Tortugas Subpopulation (islands located west of Key West, Florida and Cay Sal Bank, Bahamas)
4. Northern Gulf of Mexico Subpopulation (Franklin County, Florida through Texas)
5. Greater Caribbean Subpopulation (all other nesting assemblages within the Greater Caribbean, Mexico through French Guiana, The Bahamas, Lesser Antilles, and Greater Antilles).

It should be noted that we have added the term U.S. to the name of the first listed subpopulation to clarify its geographic location.

The 2000 TEWG last defined the life stages for the loggerhead as: pelagic immature from the time a hatchling leaves a nesting beach until it appears on coastal benthic feeding grounds at around 40-60 cm straight carapace length (SCL); benthic immature from settlement to 92 cm SCL; and adult which is ≥ 92 cm SCL. We now recognize five life stages for the loggerhead. We defined these as follows:

- I. Year One, terrestrial to oceanic, size ≤ 15 cm SCL
- II. Juvenile (1) exclusively oceanic, size range of 15-63 cm SCL
- III. Juvenile (2), oceanic or neritic, size range of 41-82 cm SCL
- IV. Juvenile (3), oceanic or neritic, size range 63-100 cm SCL
- V. Adult, neritic or oceanic, size ≥ 82 cm SCL

These new life-stage definitions recognize that recruitment to any given stage is not a knife-edged transition, but instead is associated with a distribution; the bounds of these distributions are not absolute and may overlap to some extent with adjacent stages. We made a distinction between Stages III and IV because size frequency data indicate that there are two distinct distributions/behaviors representing smaller and larger neritic juveniles.

The last TEWG assessment of the loggerhead subpopulations in the Western North Atlantic concluded that the Peninsular Florida Subpopulation (then referred to as the South Florida Nesting Subpopulation), the Northern Gulf of Mexico Subpopulation (then referred to as the Florida Panhandle Nesting Subpopulation), and the Greater Caribbean Subpopulation (then referred to as the Yucatán Nesting Subpopulation) were all either stable or increasing as indicated by rising annual numbers of nests (TEWG 2000). The Northern U.S. Subpopulation was the only one thought to be stable or decreasing (TEWG 2000). The addition of nesting data through 2007 now shows that the annual numbers of nests of all Western North Atlantic loggerhead subpopulations had been decreasing during the past decade and, by extension, indicates that the adult female component of all of these subpopulations may have been decreasing over the same time. Of greatest concern is the decrease in the annual numbers of nests of the Peninsular Florida Subpopulation. This subpopulation has the largest nesting aggregation in the Atlantic Ocean, representing as much as 80% of all nesting in the Western North Atlantic, and is one of the largest nesting aggregations in the world. The annual numbers of nests for this subpopulation decreased 49% since 1998, and now show an overall decrease of 37% from 1989 through 2007. Nest numbers were up in the Peninsular Florida subpopulation for 2008 with 38,064 nests recorded on the core nesting beaches. There were 1,159 nests in 2007 and 1,854 nests in 2008 for the Northern U.S. subpopulation which makes 2008 one of the highest counts on record. Furthermore, no long-term data suggest any of the loggerhead subpopulations throughout the entire North Atlantic are increasing in annual numbers of nests. The subpopulations in Greece and Turkey are both either stable or decreasing and there are insufficient data available to determine a nest trend for the Cape Verde subpopulation. The only loggerhead subpopulation in the entire Atlantic with recently increasing annual numbers of nests is in the Western South Atlantic (Brazil).

We assessed data from long-term studies of loggerheads in the water to identify any changes in (i) the overall numbers of loggerheads found along the eastern U.S. and (ii) loggerhead size distributions. Such changes may signal changes in recruitment and/or survival rates. The data for neritic loggerheads were primarily from immature, Stage III animals. Four studies spanning the southeastern U.S. (from central North Carolina through central Florida) indicated a possible increase in the abundance of neritic loggerheads in this area over the past one to two decades. However, aerial surveys and one other in water study in the northeastern U.S. (north of Cape Hatteras, N.C.) suggest a decrease in abundance over similar time periods for some areas.

The apparent overall increase in the abundance of neritic loggerheads in the southeastern U.S. may be due to increased abundance of the largest Stage III loggerheads and may indicate there is a relatively large cohort that will be reaching maturity in the near future. Other complications suggest that any increase in adults may be temporary because in-water studies throughout the entire eastern U.S. also documented a substantial decrease in the abundance of the smallest Stage

III loggerheads. This pattern was also corroborated by data on dead or debilitated (*i.e.*, stranded) loggerheads found in the northeastern U.S. and we are concerned that subsequent recruitment could be low.

We investigated various hypotheses to explain the decreases in the annual numbers of loggerhead nests throughout the Western North Atlantic. The decline in loggerhead nests appears to be species-specific. We first noted that the cause(s) of the decrease in loggerhead nests was not apparently affecting either green turtles (*Chelonia mydas*) or leatherbacks (*Dermochelys coriacea*) on some of the same nesting beaches. During the period of time when the annual numbers of loggerhead nests were decreasing in both Florida and Mexico, the annual numbers of green turtle nests at both sites and the annual numbers of leatherback nests in Florida were rising. We also noted an interesting parallel at Kurashima Island, Japan, where annual numbers of loggerhead nests are declining but annual numbers of green turtle and hawksbill (*Eretmochelys imbricata*) nests are increasing. Because other species on the same beaches are increasing in numbers, we could not attribute loggerhead decline to loss or degradation of nesting habitat (at least in Florida and Mexico)

It is possible that random variation in demographic parameters within the range reported (such as fecundity) could result in the observed decline in nest number in both an increasing population or in a decreasing population. This phenomena coupled with other well known processes, such as transient dynamics (see Caswell 2001), that can result after one or more population perturbations may also explain the current decline in nest counts that could result with either an increasing or decreasing population. Unfortunately we have no time series of any demographic parameters that are appropriate to examine this hypothesis quantitatively.

We recognize that a decrease in the annual numbers of nests could reflect a decrease in individual reproductive output, in numbers of nesting females or some combination of both. It is conceivable that the quality or quantity of forage for adult loggerheads in the Western North Atlantic may have recently decreased resulting in increased remigration intervals of the adult females. Because adult female loggerheads forage over large areas of the Western North Atlantic, we would expect such decrease in nutrient availability or quality would be noticeable. Yet, we know of no direct evidence to indicate changes in prey abundance but hypothesize that competition for food resources with commercial harvest could potentially impact productivity via decreased reproductive output.

One known mechanism by which the average reproductive output per adult female loggerheads might be lowered is if the proportions of putative first-time nesters in the nesting assemblages have risen. First-time nesters typically produce fewer clutches per season and smaller clutches. We analyzed tagging data from the Quintana Roo rookery and determined that over the short period for which data are available, there was an increasing trend in the proportion of putative first-time nesters in the population. We lack similar data for any of the beaches in other subpopulations.

We explored the hypothesis that losses of adult female loggerheads have remained unchanged and that a recent lack of new recruited females accounts for the change. That does not appear to be the case for the Mexico Subpopulation where the proportion of putative first-time nesters has

been increasing. Evidence from in-water studies of measured loggerheads suggests crests and troughs in abundances of individuals in sequence among the studies. The in-water studies indicated that we may soon see a crest in newly recruited females perhaps followed by another trough. Similarly, we found no shift in sex ratio that would explain the decline.

To better characterize the recent rate of loss of adult female loggerheads, we estimated the current adult female survival rates. We estimated annual survival rates from tagging data collected on one beach for each of the subpopulations: Peninsular Florida (Melbourne Beach), Greater Caribbean (Quintana Roo), and Northern U.S. (Wassaw Island). The survival estimate for resident females nesting on Melbourne Beach was the lowest (0.73, 95% CI 0.71 – 0.76). The survival estimate for resident females nesting in Quintana Roo was the highest (0.85, 95% CI 0.81 – 0.88). The survival estimate for resident females nesting on Wassaw Island was 0.81 (95% CI 0.77 – 0.84) and was slightly higher than a previous estimate (0.79). All models suggested that annual survival did not vary over time. In addition, the results from Melbourne need further study to ensure they are correct as this study is not a dedicated mark-recapture study and these results may be biased low.

Recalling that while the annual numbers of loggerhead nests in the Western North Atlantic have been decreasing, the annual numbers of green turtle and leatherback nests have been increasing, we concluded that any mortality factors that may account in large part for decreasing numbers of adult female loggerheads must be restricted to this species. We reviewed the recent history of the directed harvest of loggerheads in the Western North Atlantic and found that the commercial fishery in Cuba would have been the only one to harvest substantial numbers of loggerheads during the past several decades. However, the take from this fishery was reduced to a relatively low level in the early 1990's and has been reported as being close to zero since 1996. Interestingly, as fewer loggerheads were harvested in Cuban waters in the late 1980s through the late 1990's, there was a concurrent increase in the annual numbers of loggerhead nests of several of the loggerhead subpopulations in the Western North Atlantic. If the past directed harvest of loggerheads in Cuba has a role in the current decline in the numbers of nests in the Peninsular Florida and Northern U.S. Subpopulations, that role is likely the loss of immature turtles a decade or more ago that would have eventually transitioned to the adult population.

The greatest source of added mortality for sea turtles during the last half century has been from incidental takes in commercial fisheries. For loggerheads in the Western North Atlantic, loss of relatively large-sized individuals (Stages III, IV, and V) in shrimp trawls has been chronic and was a major source of mortality at least until 2003 when larger Turtle Excluder Devices were mandated. There has been mortality of small-sized loggerheads (Stage II) in pelagic longline fisheries. There has also been loggerhead mortality of larger animals (Stages III-V) in finfish trawl, gill net, drift net, and pound net fisheries. The incidental capture of loggerheads in commercial fisheries may certainly be playing a role in the recent apparent decrease in the numbers of adult female loggerheads in the Western North Atlantic either through recent mortality of adult females or through past mortality of immature loggerheads that would have recently matured.

The overall mortality of loggerheads in Florida as indicated by stranding numbers has been increasing at an increasing rate since the mid 1990's. There have also been several, recent

epizootics of loggerheads in Florida. Some were likely caused by harmful algal blooms and others were likely caused either by previously undetected diseases or by emergent diseases. Most of the epizootics have been centered in southwest Florida where large numbers of adult loggerheads are resident along the wide continental shelf there.

In summary, we could not determine whether or not the decreasing annual numbers of nests among the Western North Atlantic loggerhead subpopulations were due to stochastic processes resulting in fewer nests, a decreasing average reproductive output of the adult females, decreasing number of adult females, or both factors. Many factors are responsible for past or present loggerhead mortality that could impact current nest numbers, however no single mortality factor stands out as a likely primary factor. It is likely that several factors compound to create the current decline. Regardless, it is clear that the current hatchling output will result in depressed recruitment to subsequent life stages over the coming decades.

Our ability to assess the current status of all segments of the Western North Atlantic loggerhead subpopulations is limited. We have bits and pieces of the information, but lack the specific census and mortality data necessary to characterize and monitor trends for these populations. To improve future assessments, fundamental life history and census data must be collected, compiled, made available, and evaluated for these subpopulations.

PART I. UPDATES ON STOCK STRUCTURE, LIFE-STAGE DEFINITIONS, BIOLOGY, AND BEHAVIOR OF LOGGERHEADS

Stock Structure –Alan Bolten and Sheryan Epperly

Loggerheads from the Western North Atlantic have a complex population structure. Based on mtDNA, oceanic juveniles show no structure, neritic juveniles show moderate structure, and nesting colonies show strong structure (Bowen et al. 2005). In contrast, a survey using microsatellite (nuclear) markers showed no significant population structure among nesting populations of the Western North Atlantic (Bowen et al. 2005), indicating that while females exhibit strong philopatry, males apparently provide an avenue of gene flow between nesting colonies in this region. Earlier reports by the TEWG (1998, 2000) identified four subpopulations in the Western North Atlantic, based solely on mtDNA. We now identify five nesting subpopulations of loggerhead sea turtles in the Western North Atlantic: four subpopulations in the U.S. were identified in the Loggerhead Recovery Plan (National Marine Fisheries Service and U.S. Fish and Wildlife Service 2008) (Northern U.S. Subpopulation, Peninsular Florida Subpopulation, Northern Gulf of Mexico Subpopulation, and Dry Tortugas Subpopulation), and one in Mexico (Quintana Roo). Within the North Atlantic basin, there is a sixth subpopulation: Cape Verde in the Northeast Atlantic. These six subpopulations are genetically independent based on mtDNA haplotype frequencies (AMOVA, $F_{ST} = 0.256$, $p < 0.001$; Bolten and Bjorndal, unpublished). The loggerhead nesting population on Cay Sal Bank, Bahamas, is not genetically distinguishable from the Dry Tortugas Subpopulation (AMOVA, $F_{ST} = 0.018$, $p = 0.708$; Bolten and Bjorndal, unpublished); therefore, these two rookeries were combined for analyses. To assess genetic independence for all of the known subpopulations in the Atlantic, we evaluated these six subpopulations along with the rookeries in Brazil, Greece, and Turkey and determined that the nine subpopulations were genetically distinct (AMOVA, $F_{ST} = 0.409$, $p = 0.000$; Bolten and Bjorndal, unpublished) with all F_{ST} pair wise comparisons significantly different ($\alpha = 0.05$). At this time we do not have data for Cuba, the only major North Atlantic rookery not included in our analyses.

Five subpopulations of nesting loggerheads in the Western North Atlantic previously have been identified (Encalada *et al.* 1998, Francisco Pearce 2001). Until recently, the definition of the nesting range of the Northern U.S. Subpopulation included northern Florida. However, recent increases in genetic sample sizes and more complete sampling of rookeries along the Atlantic coast of the southeast U.S. suggests that there is a cline for each of the two primary haplotypes (CC-A1 and CC-A2; Archie Carr Center for Sea Turtle Research unpubl. data; National Marine Fisheries Service and U.S. Fish and Wildlife Service 2008). Analyses using these new data indicate that there is no genetic difference between loggerheads nesting on adjacent beaches along the Florida Peninsula. This lack of genetic structure makes it difficult to designate specific boundaries for the subpopulations based on genetic differences alone. Therefore, the Loggerhead Recovery Team (National Marine Fisheries Service and U.S. Fish and Wildlife Service 2008) used a combination of geographic distribution of nesting densities, geographic separation, and geopolitical boundaries in addition to genetic differences to identify the four U.S. subpopulations as recovery units, in addition to identifying the Greater Caribbean as a fifth subpopulation in the Western North Atlantic.

The five subpopulations (= recovery units) are:

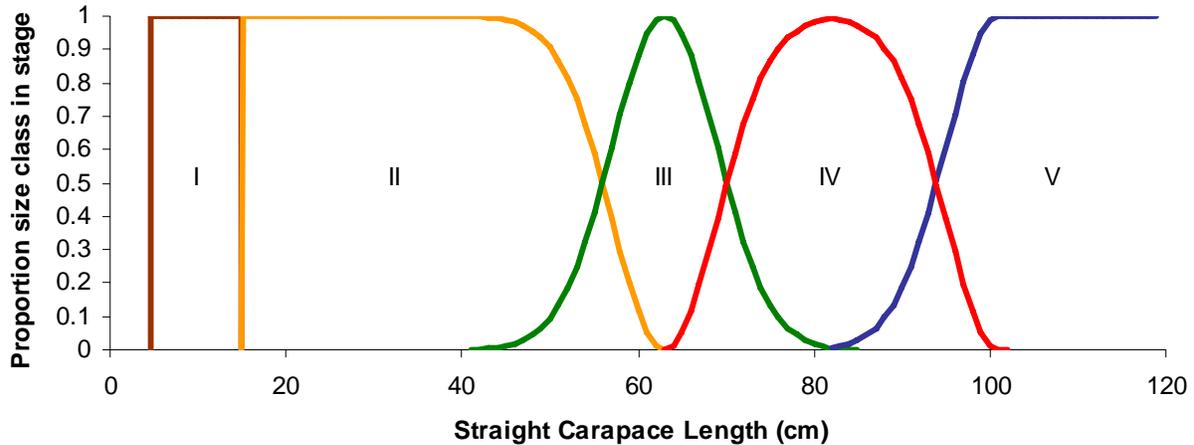
1. Northern U.S. Subpopulation (Florida/Georgia border through southern Virginia)
2. Peninsular Florida Subpopulation (Florida/Georgia border through Pinellas County, Florida)
3. Dry Tortugas Subpopulation (islands located west of Key West, Florida and Cay Sal Bank, Bahamas)
4. Northern Gulf of Mexico Subpopulation (Franklin County, Florida through Texas)
5. Greater Caribbean Subpopulation (all other nesting assemblages within the Greater Caribbean, Mexico through French Guiana, The Bahamas, Lesser Antilles, and Greater Antilles).

Further sampling throughout the greater Caribbean may yield compelling information to identify additional subpopulations in the future. Although the largest rookeries appear on the mainland U.S., the Mexico Subpopulation has the greatest genetic diversity (Encalada et al. 1999). During glaciation periods, the temperate beaches were too cool to incubate eggs and nesting could have continued only on the tropical beaches. Thus, the contemporary distribution of nesting is the product of colonization events from the tropical refugia during the last 12,000 years (Encalada et al. 1998; Bowen and Karl 2007). This underscores the historic importance of the tropical rookeries, although small in size, to the genetic diversity and persistence of the North Atlantic population through time.

Life Stages and Demographics –Sheryan Epperly, Melissa Snover, and Alan Bolten

The first TEWG identified four life stages, but recognized that large immature turtles in the coastal environment represented a larger proportion of the strandings and in-water captures along the south and western coasts of Florida as compared with the rest of the coast (TEWG 2000). To date, virtually all population models for loggerheads have distinguished between small and large neritic juveniles (Table 1). Herein we define five life stages of the loggerhead sea turtle, denoting the large immature neritic animals as a separate stage (Figure 1): I. Year One, terrestrial to oceanic; II. Juvenile (1) exclusively oceanic; III. Juvenile (2), oceanic or neritic; IV. Juvenile (3), oceanic or neritic; V. Adult, neritic or oceanic. These correspond roughly to stages used in past matrix models: egg to post hatchling, pelagic juveniles, small benthic juveniles, large benthic juveniles, and adults (Table 1). We retained the distinction between Stages III and IV because size frequency data indicate two modes and differing geographic distributions of the neritic juveniles, but there was not consensus on this; some members believed these stages should be combined as was done in the loggerhead recovery plan (National Marine Fisheries Service and U.S. Fish and Wildlife Service 2008). The new stage definitions recognize that except for Stage II juveniles, which are exclusively oceanic, all other stages may occur in both the oceanic and neritic environments (Witzell 2002; Bolten 2003; McClellan and Read 2007; Spatial Distribution section in this report). The new stage definitions also recognize that recruitment to any given stage is not a knife-edge, but instead is associated with a distribution; the bounds of these distributions are not absolute either. The stages are explained below. Table 1 summarizes their use in matrix models to date. Since the first TEWG reports (see Appendix 4 in their 1998 report) there have been many updates to the demographic parameters for each stage. Table 2 provides updated information on the demographic parameters.

Figure 1. Conceptual model of size distributions for each life stage of the loggerhead turtle.



Stage I. Year One, terrestrial to oceanic - 1 year post-hatchlings. Ranges from size at hatching (4.5 cm straight carapace length {SCL} average: van Buskirk and Crowder 1994) to 15 cm SCL (Bjorndal et al. 2000).

Stage II. Juvenile (1) exclusively oceanic - Ranges from 1 year (15 cm SCL; end of stage 1) to 63 cm SCL. According to Bjorndal et al. (2000), recruitment out of the oceanic stage begins at 42 cm SCL (46 cm curved carapace length {CCL} converted using their equation). From the neritic size distribution data (see section ‘In-Water Trends and Size Distributions’), 41 cm SCL is commonly the smallest length, and thus animals begin to shift from Stage II to Stage III at 41 cm SCL. According to the length frequency analysis of Bjorndal et al. (2000), Atlantic loggerheads are nearly fully recruited out of the oceanic stage (Stage II) by 59.5 cm SCL (64 cm CCL converted using their equation). The inshore length frequency data from North Carolina (Epperly et al. 2007; NMFS unpublished data; Figure 2) do not show the bimodal distribution that most of the other southeast U.S. inshore/nearshore datasets show, but the one mode described by the N.C. data also is present in the other datasets of the southeast (see below). Hence, the N.C. data describe juvenile lengths for Stage III. The mean for the N.C. dataset is 63 cm SCL, similar to the size at which nearly all Stage II loggerheads have departed oceanic environments (Bjorndal et al. 2000). Thus, we used 63 cm SCL as the end of Stage II. We assigned a normal probability distribution to describe the drop from the proportion of individuals in Stage II at 41 cm to the proportion of individuals in Stage II at 63 cm.

Stage III. Juvenile (2), oceanic or neritic - Ranges from 41 cm SCL to 82 cm SCL with a peak at 63 cm SCL. The justifications for selecting 41 and 63 cm SCL is described above. The distribution of Stage III in the figure is essentially that of the N.C. dataset (Figure 2); 82 cm SCL is approximately the 98th percentile of that distribution and 82 cm SCL is also the 2.5 percentile of the putative neophyte data analyzed and described in this TEWG report (using data from all beaches, 87.2 cm CCL_{std} converted to SCL_{std}) and what we determined should be the beginning of Stage V (Adults).

Stage IV. Juvenile (3), oceanic or neritic - The start (63 cm), middle (82 cm) and endpoint (100 cm) of this distribution were determined by the other distributions as the curves need to link and sum to one at every length. The presence of a bimodal size distribution of juvenile loggerhead turtles can be found in other datasets from the southeast U.S. with greater prominence in the southernmost study sites (see In-Water section in this TEWG report; Hillestad et al. 1978); it is most pronounced near Cape Canaveral (Bolten et al. 1994; Henwood 1987) and in Florida Bay, indicating that the habitat and threats likely differ among the two juvenile stages in the neritic environment. This second mode often is confounded by the presence of adults, with an overlapping size distribution.

Stage V. Adult, neritic or oceanic - Begins at 82 cm SCL (2.5 percentile of neophytes) with full recruitment to the adult stage at 100 cm SCL (see Size of Putative Neophyte Nesters below). Females move briefly from the neritic to the terrestrial environment to nest.

Table 1. Life table for loggerhead models used to date. Lengths are standard (notch-to-tip) measurements of the carapace unless noted otherwise. Note that Frazer's (1983a) age-structured life tables are not included, but the early model all were based on his original table.

TEWG's definition of stages	I. Year One, terrestrial to oceanic			II. Juvenile (1), exclusively oceanic	III. Juvenile (2), oceanic or neritic	IV. Juvenile (3), oceanic or neritic	V. Adult, oceanic or neritic	Comments
Historical definition of stages	Egg	Hatchling	Post-Hatchling	Oceanic, pelagic juvenile	Neritic, benthic juvenile, small	Neritic, benthic juvenile, large/subadult	Adult female	
Crouse et al. (1987)	<10 cm SCL age < 1yr S=0.6747		10.1-58.0 cm SCL age=1-7 yr S=0.7857	58.1-80.0 cm SCL age=8-15 yr S=0.6758	80.1-87.0 cm SCL age=16-21 yr S=0.7425	>87.0 cm SCL age=22-54 yr S=0.8091	6-stage-classified model; one sex (female); different fecundity for novice breeder, 1 st yr remigrant, and mature breeders	
Crowder et al. (1994)	Duration=1 yr S=0.6747		Duration=7 yr S=0.75	Duration=8 yr S=0.6758	Duration=6 yr S=0.7425	Duration > 32 yr S=0.8091	5-stage model (Crouse's 3 adult stages collapsed); annual fecundity=76.5	
Heppell et al. (2003)	F=nests x eggs x sex ratio x survival from egg to age one 4.1 nests/female; 115 eggs/nest; 1:1 sex ratio S=fitted (pre-1990 $\lambda=0.95$) ¹			5-45 cm SCL 8 or 10 yr S=fitted (pre-1990 $\lambda=0.95$) ¹ S ₁ =0.745 S ₂ =0.875	45-72 cm SCL 6 or 11 yr S ₁ =0.6758 S ₂ =0.7	72-92 cm SCL 8 or 13 yr S ₁ =0.7425 S ₂ =0.8	92+ cm SCL 23 or 35 yr to maturity S ₁ =0.8091 S ₂ =0.85	Age-classified model; incorporated variable remigration intervals (3%, 56%, 31%, 7%, and 3% for 1-5 yr, respectively); 2 growth models; 4 TED scenarios
NMFS SEFSC (2001)	F=nests x (eggs x egg survival) x sex ratio x survival from hatchling in water to age one; 4.1 nests/female; 115 eggs/nest; 0.675 egg survival, % female=35%, 50%, 80% S=fitted ¹ (pre-1990 $\lambda=0.95, 0.97, 1.0$) Duration=1 yr			Minimum <42cm SCL Average<49cm Duration ₁ =6yr Duration ₂ =7yr Duration ₃ =6yr Duration ₄ =7yr S=fitted ¹ (pre-1990 $\lambda=0.95, 0.97, 1.0$)=0.585-0.894	Minimum=42-72 SCL Average=49-72 Duration ₁ =7yr Duration ₂ =6yr Duration ₃ =13yr Duration ₄ =11yr S _{1,2} =0.6758 S _{3,4} =0.893	Minimum=73-82 SCL Average= 73-90 Duration ₁ =7yr Duration ₂ =14yr Duration ₃ =11yr Duration ₄ =21yr S _{1,2} =0.7425 S _{3,4} =0.893	Minimum=83cm SCL Average=90cm Duration=indefinite S _{1,2} =0.809 S _{3,4} =0.812	Same as Heppell et al., plus two growth models and based on minimum and average size-to-stage; 2-sex model @ three sex ratios

¹ With empirical inputs for all other parameters in the projection matrix and a knowledge of the dominant eigenvalue (λ ; or population growth rate), the only unknown value, the oceanic, pelagic stage survival rate, can be solved for; this value also is used in the fecundity term.

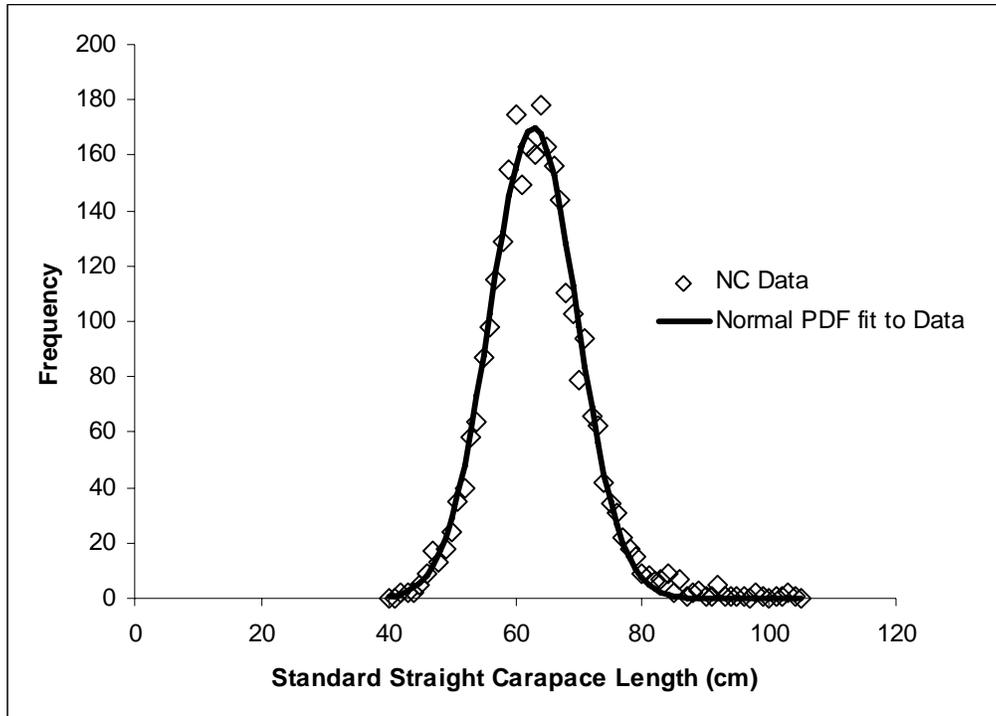
Snover (2002)	Duration=1 yr S=0.3700 (from Heppell et al. 2003)	<49 cm SCL Duration=14 yr S=0.8100	49-80 cm SCL Duration=10 yr S=0.6758	80-90 cm SCL Duration=7 yr S=0.7425	>90 cm SCL S=0.8091	Similar to NMFS SEFSC (2001), but updating stage durations based on skeletochronology, and without all the runs using different growth models and sex ratios
Hedges (2007)	Duration=1 yr 2.1, 3, and 4 nests/female, 118 eggs/nest, 58% female (from Hawkes et al. 2007), $S_{\text{egg-hatchling}}=0.386$ $S_{\text{hatchling-1yr}}=0.875$	S=0.875	S=0.81 (SD 0.06) from Sasso et al. (2006)	S=0.8	S=0.853 (SD 0.0365)	Simulations using six models to evaluate effect of uncertainty in clutch frequency, survival rates, and remigration intervals (breeder state + 3 non- breeder states); based on Bald Head Island data. Unless noted, structure same as Heppell et al. (2003)

Table 2. Recent information on loggerhead life stages. Lengths are standard (notch-to-tip) measurements of the carapace unless noted otherwise.

I. Year One, terrestrial to oceanic	II. Juvenile (1), exclusively oceanic	III. Juvenile (2), oceanic or neritic	IV. Juvenile (3), oceanic or neritic	V. Adult, oceanic or neritic
<p>Stewart and Wyneken (2004) Hatchling survival for first 15 min in water=94.9%</p> <p>Whelan and Wyneken (2007) hatchling survival for first 15 min in water = 95.4%</p>	<p>Bjorndal et al. (2003a) Total sample: $S_{2-6}=0.910 (0.872-0.951)^2$</p> <p>Tuna sample: $S_{4-6}=0.894 (0.880-0.909)^2$</p> <p>Sasso and Epperly (2007) $S_{-6-12}=0.814 (0.557-0.939)$</p> <p>Bjorndal et al. (2000) Duration$_{\leq 46\text{cm CCL}}=6.5$ yr and Duration$_{<64\text{cmCCL}}=11.5$ yr</p> <p>Bjorndal et al. (2003b) Duration$_{<46\text{cmCCL}}=7$ yr</p> <p>Snover (2002) Duration$_{\text{average}(48.5-51.1 \text{ cm SCL})}=14.8$ yr (SD 3.3) (range 9-24 yr)</p>	<p>Sasso et al. (2006) $S_{\text{apparent}}=0.81$ (SE 0.06)</p> <p>Braun-McNeill et al. (2007a) $S_{\text{realized}}=0.83 (0.74-0.89)$</p> <p>Bjorndal et al. (2001) Duration$_{46-87\text{cmCCL}}=20$ yr</p> <p>Snover (2002) Duration$_{49-90\text{cmSCL}}=17$ yr</p> <p>Braun-McNeill et al. (2008) Duration$_{50-80 \text{ cmSCL}}=17.4$ yr (15.6-19.4)</p> <p>Braun-McNeill et al. (2007b) Sex Ratio 2.1:1 females:males</p>	<p>Bjorndal et al. (2001) Duration$_{46-87\text{cmCCL}}=20$ yr</p> <p>Snover (2002) Duration$_{49-90\text{cmSCL}}=17$ yr</p>	<p>Bald Head Island, NC Hedges (2007) $S=0.853 (0.781-0.925)$</p> <p>Wassaw Island, GA (this TEWG report) $S=0.81 (0.77-0.84)$</p> <p>Melbourne Beach, FL (this TEWG report) $S=0.73 (0.71-0.76)$</p> <p>Quintana Roo, Mexico (this TEWG report) $S=0.85 (0.81-0.88)$</p> <p>Sex ratio = 34-47% (this TEWG report)</p> <p>Average size of neophyte nester among Northern, Peninsular Florida, and Mexico subpopulations is 98.2 cm CCL$_{\text{std}}$ (91.2 cm SCL$_{\text{std}}$) and 95% of the neophytes' measurements fell in the range of 87.2–109.3 cm CCL$_{\text{std}}$ (82.0-100.5 cm SCL$_{\text{std}}$) (this TEWG report).</p> <p>Snover (2002) age at maturity (90 cm SCL)=30.8yr</p> <p>Byrd et al. (2005) Min size of S.C. nester = 80.7 cm SCL and 86.4 cm CCL</p> <p>Dahlen et al. (2000) Min mean number nests per female=3.6 for neophytes and 4.1 for remigrants</p> <p>Scott (2006) number of nests per female = 4.5 for Wassaw Island nesting females</p>

² Note that these 95% confidence intervals were not presented in the original publication but were calculated from the raw data presented therein.

Figure 2. Size frequency data of loggerheads captured in North Carolina (Epperly et al. 2007; NMFS unpublished data).



Nesting Females, Adult Stage, and Sizes –Sheryan Epperly

Few long-term nesting beach datasets exist within the five subpopulations and even fewer have long-term mark-recapture data that identify individual nesters and track individual females' fecundity over time. The first TEWG (1998) analyzed Wassaw Island, Georgia tagging data to determine size at sexual maturity for female loggerheads. They determined that the average size of first-time nesters was 92.9 cm SCL_{std} ; this information was provided in a summary of demographic parameters for a deterministic model (their Appendix 4). NMFS SEFSC (2001) examined Cooperative Marine Turtle Tagging Program (CMTTP) data “for original tagging events” from nesting beach survey products and calculated a different average size of 90.4 cm SCL_{std} .

To provide a more current and broader perspective on adult size, fecundity, and survival, this TEWG examined nesting beach data for three purposes. First, we explored the size distribution of putative first-time nesters to define the beginning of the Adult Stage (V) which is used at several points in our report. Second, we examined the data to determine if the size of putative first-time nesters had shifted to smaller or larger size. The direction of any size-at-maturity change could account for the reduction in nesting activity and reproductive output through longer remigration intervals, decreased number of clutches laid, and/or smaller clutch size (see Part II).

Lastly, the full nesting beach mark-recapture datasets were examined to estimate survival rates and to evaluate whether there had been changes in survival over time (see Part III).

We acquired data from five beaches, representing three subpopulations, with adequate long-term mark-recapture data: (1) Bald Head Island, (2) Wassaw Island, (2) Casey Key and Manasota Key, (4) Keewaydin Island, and (5) Aventuras, Chemuyil, Xcacel, and Xel-ha beaches. Three of these beaches represent the few locations where there has been almost-complete saturation tagging of nesting females for several years. Unmarked females were inferred to be putative first-time nesters, but it is important to note that previously they may have nested elsewhere or had not been detected on the sampled beach. While the probability of not being detected within their first nesting season on a monitored beach, given multiple emergences, is low, we have no way of knowing whether a female had previously nested on unmonitored beaches. We acknowledge that our estimates of the size of putative first-time nesters likely are biased high. Generally, marked animals were considered remigrants, even if they had not been detected on that particular beach earlier. It is possible that these animals received their marks during in-water captures and may not have nested previously. Animals with tagging scars were re-marked, but considered remigrants; this may overestimate the remigrant population as the lost marks could have been applied before the animal reached maturity (or while nesting on a different beach). In nearly all cases, the investigators identified putative first-time nesters and remigrants in the databases provided to us.

Northern U.S. Subpopulation

Bald Head Island, North Carolina U.S. – Since 1980, turtles have been intercepted and marked nightly on 15.3 km of beach between late May and mid August (Hawkes et al. 2005; Hedges 2007). Double flipper tagging with inconel tags began in 1991. PIT tagging began in 2002 to augment flipper tags. Animals with existing marks or tag scars were identified as remigrants. Unmarked and unscarred turtles were identified as putative first-time nesters. Standard measurements of carapace length (SCL and CCL) were taken through 2003; beginning in 2004, minimum SCL and CCL lengths were taken instead (straight and curved). We were provided with the entire dataset from 1980-2007.

Wassaw Island, Georgia U.S. – Nightly monitoring of the ~14 km island started in 1973 (Williams and Frick 2001). Monitoring begins in early May and ends in the middle of August. Project personnel intercept and identify an average of 82% of the nesting females using the beach (K. Williams pers. comm.). Double flipper tagging with inconel tags began in 1988. PIT tagging began in 1992, but it was not until 1999 that tags and readers were standardized and the investigators were certain that they were capable of detecting all PIT tags (Prior to 1999 personnel used 128 kHz tags and Trovan readers to scan the turtles). Thus, based on PIT tags alone, they could detect animals that they tagged but not animals tagged by other researchers with a different frequency of PIT tag – e.g., immigrants). Animals with existing marks previously applied at Wassaw Island were identified as remigrants; for the purpose of our analyses, we also included immigrants (previously marked in another location), and tag-scarred turtles. Since 1995, 45 animals were identified as remigrants/immigrants based on the presence of PIT tags alone. Unmarked and unscarred turtles were identified as putative first-time nesters. Standard straight carapace lengths were taken through 1989. In 1990, standard measurements of

straight or curved carapace length were taken (but not both on the same animal) and after 1991 the standard CCL was taken. We were provided the entire dataset spanning 1973- 2008.

Peninsular Florida Subpopulation

Casey Key and Manasota Key, Florida U.S. – These two beaches are in very close proximity to each other and animals detected nesting on one sometimes also nesting on the other (T. Tucker pers. comm.). Hence, they are reported together. The consistent data and standardized tagging and measurement dataset for the 11.8 km of Casey Key and 13.8 km of Manasota Key extends from 2002-2006. During this period, all turtles intercepted were double tagged with flipper tags and PIT tags on Casey Key. Tagging effort occurs only on the southern 6 km of the Casey Key beach and on the northern 7.4 km of Manasota Key (during 2007 they could survey only 5.7 km due to extremely soft sand). While monitoring effort has been nightly, all night, at Casey Key (T. Tucker pers. comm.), effort at Manasota Key has been more variable (often efforts end by 1-3 am). It is estimated that 20-40% of the nesting females are intercepted on Casey Key (T. Tucker pers. comm.) and about 5% are intercepted on Manasota Key (J. Grimes pers. comm.) Animals with existing marks or tag scars were identified as remigrants. Unmarked and unscarred turtles were identified as putative first-time nesters. We acknowledge that with such low tagging effort, assuredly some remigrants are included as putative first-time nesters. Standard and minimum SCL and CCL were recorded. We were provided the size data for putative first-time nesters 1997-2006 for both beaches and 2007 data were later provided for Casey Key (T. Tucker pers. comm.) for the survival rate analysis. The putative first-time nester analysis was based on the 2002-2006 data.

Keewaydin Island, Florida U.S. – Nightly monitoring began in 1985 and occurs from May 15 through August 15 (Addison et al. 2004). The island is approximately 12 km in length, but only 7.2 km is surveyed regularly at night; beginning in 1993 the remaining 4.8 km to the north was surveyed for nesting activity each morning. It is estimated that they intercept 75-95% of females nesting annually (D. Addison pers. comm.). Double tagging with inconel tags began in 1990 and PIT tagging began in 2007 (D. Addison pers. comm.). Animals with tag scars or existing marks were identified as remigrants. Unmarked and unscarred turtles were identified as putative first-time nesters. They also identify as putative first-time nesters animals tagged elsewhere but seen on Keewaydin Island only once. Standard and minimum measurements were taken for both straight and curved carapace lengths. We were provided the size data for putative first-time nesters 2002-2005 (D. Addison pers. comm.).

Mexican Subpopulation

Quintana Roo: Aventuras, Chemuyil, Xcacel, and Xel-ha beaches, México - Nightly monitoring on these beaches from early May to the end of October began on a regular basis in 1987, but it was not until 1996 that tag supplies were sufficient to mark all animals intercepted; animals were single tagged with inconel tags (Zurita et al. 1997). The tagging efficiency³ since 1996 has been estimated at 79-87% (Zurita et al. 2003) and at >90% since 2000 (J. Zurita pers. comm.). Animals with tag scars or existing marks were identified as remigrants. Unmarked and unscarred turtles were identified as putative first-time nesters. No immigrants from other areas have been detected on these beaches (J. Zurita pers. comm.). Standard measurements of curved

³ Tagging efficiency is defined by Hopkins and Richardson (1984): The efficiency of a tagging program at a nesting beach is directly related to the proportion of nests that can be identified with a female in the nesting area.

carapace length were taken. We were provided the size data for putative first-time nesters 1987-2005 and were provided annual estimates of percent putative first-time nesters for 1996-2006 (J. Zurita pers. comm.).

Size of Putative First-Time Nesters –Sheryan Epperly

We used standard curved carapace length (CCL_{std}) for our analysis because it was the measurement most often recorded for nesting females. For 2002-2006 all beaches reported CCL_{std} , except for Bald Head Island which reported CCL_{min} for 2004-2006. Data from Keewaydin Island and Casey Key were used to derive a relationship between CCL_{std} and CCL_{min} , and the CCL_{min} data of Bald Head Island were converted to CCL_{std} with the following equation:

$$CCL_{std} = 7.529 + (0.938 * CCL_{min}), \text{ r-square} = 0.920, N = 65$$

The relationships between CCL_{std} and SCL_{std} for nesting turtles are expressed in following equations. The measurement relationships were based on data available from Bald Head Island, Casey Key, and Keewaydin Island.

$$SCL_{std} = 8.879 + (0.838 * CCL_{std}), \text{ r-square} = 0.798, N=556$$
$$CCL_{std} = 11.381 + (0.953 * SCL_{std}), \text{ r-square} = 0.798, N=556$$

The distribution of putative first-time nester sizes (CCL_{std}) during 2002-2006 was compared among beaches (Table 3, Figure 3). The average size of putative first-time nesters was significantly larger on Bald Head Island (100.4 cm) than the average size on either of the two Florida beaches (96.9 cm and 97.0 cm), but not significantly larger than the average size of putative first-time nesters on Wassaw Island (98.4 cm) or in Quintana Roo (98.7 cm). The average size of putative first-time nesters on the two Florida beaches were not significantly different from each other nor from any other beach except Bald Head Island.

Despite the difference in sizes between Bald Head Island and two other beaches, data were pooled among beaches to assess the size distribution of all putative first-time nesters. Univariate statistics for the pooled CCL_{std} data also are provided in Table 3. The mean size of a putative first-time nester was 98.2 cm CCL_{std} (91.2 cm SCL_{std}) and 95% of the putative first time nesters' measurements fell in the range of 87.2–109.3 cm CCL_{std} (82.0-100.5 cm SCL_{std}). We were not able to examine the size data over time for trends. We note that the average size of remigrants on Bald Head Island (104.5 cm) was significantly larger than the average size of putative first-time nesters on that North Carolina beach, and that remigrants of Wassaw Island (100.2 cm) also were larger than putative first-time nesters on the Georgia beach; we did not have access to data on remigrants elsewhere.

Summary

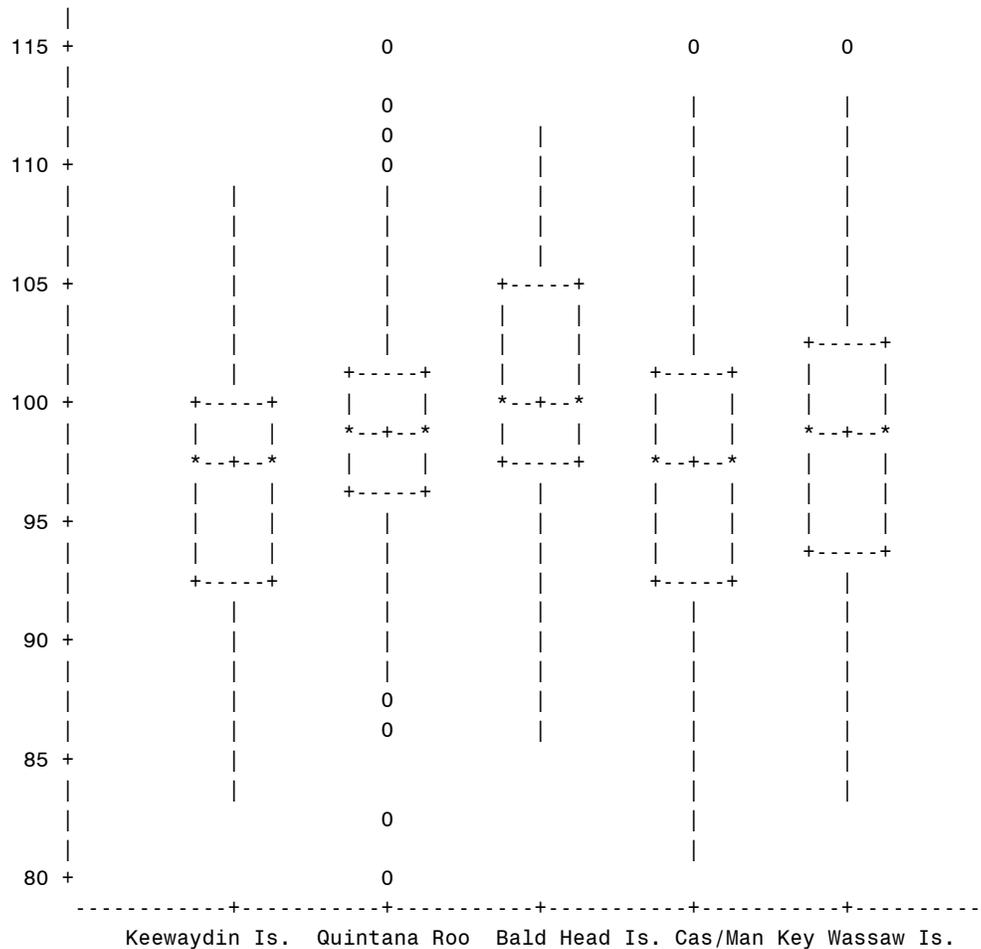
Based on tagging data from nesting beaches in North Carolina, Georgia, Florida, and Quintana Roo, the minimum size of the adult stage (V) is 87.2 cm CCL_{std} (82.0 SCL_{std}). These sizes, are smaller than the sizes used the first TEWG, but are derived from broader geographic coverage. The minimum size is based on the 2.5 percentile of the size distribution of all putative first-time

nesters. These results provide a conservative estimate, yet one that undoubtedly includes bias, as unmarked females, while inferred to be putative first-time nesters, possibly could have nested elsewhere and were not detected and marked. Putative first-time nesters were found to be significantly smaller than remigrant turtles on the North Carolina and Georgia beaches representing the Northern U.S. Subpopulation.

Table 3. Putative first-time nester sizes (CCL_{std}) for Bald Head Island, N.C. (2000-2006), Wassaw Island, Ga. (2000-2006), Casey Key and Manasota Key, Fla. (2002-2006), Keewaydin Island, Fla. (2002-2005), and Quintana Roo, México (2000-2005).

	Mean	Median	Mode	Std. Dev.	Std. Error of Mean	95% CI	Range	2.5-97.5 Percentiles	N
Northern U.S. Subpopulation	99.4	99.0	99.0	5.9	0.47	98.5-100.3	84.0-115.0	86.8-110.2	158
Bald Head Island	100.4	100.4	105.1	5.7	0.65	99.1-101.7	85.8-111.5	85.9-110.4	77
Wassaw Island	98.4	99.0	99.0	6.0	0.67	97.1-99.7	84.0-115.0	86.0-109.0	81
Peninsular Florida Subpopulation	97.0	97.0	100.0	6.7	0.33	96.3-97.6	81.0-115.0	86.0-109.0	300
Casey Key Manasota Key	97.0	97.0	100.0	5.6	0.38	96.2-97.8	81.0-115.0	86.0-109.9	219
Keewaydin Island	96.9	97.0	97.0	5.7	0.64	95.7-98.2	84.0-109.1	84.0-107.5	81
Mexico Subpopulation	98.7	99.0	99.0	4.9	0.25	98.2-99.2	80.5-115.0	80.4-109.3	368
Quintana Roo	98.7	99.0	99.0	4.9	0.25	98.2-99.2	80.5-115.0	80.4-109.3	368
All Beaches	98.2	98.4	100.0	5.5	0.19	97.8-98.6	80.4-115.0	87.2-109.3	826

Figure 3. Schematic plot of distributions of putative first-time nester sizes, 2002-2006 (2005 for Keewaydin Island). The y-axis is CCL_{std} (cm). The 75, 50, and 25 percentiles are depicted, along with the ranges and the means (+).



Sex Ratios –Jeanette Wyneken

Data on sex ratios are important in a number of contexts including the identification of shifts in vital rates and population vigor, recognition of impacts from climate change or other environmental alteration, and in understanding mating systems. Both prior TEWG reports summarized the available information on sex ratios from the literature. The 2001 assessment (NMFS SEFSC) estimated juvenile sex ratios of the Peninsular Florida (80% female), Northern U.S. (35%), and Mexico (69%) Subpopulations based on necropsied stranded animals, testosterone titers, and laparoscopies of in-water captures, and related information on the natal origins of animals on foraging grounds. Here we provide updated information on sex ratio data for loggerheads in the Atlantic, with a focus on the Northwestern Atlantic region.

Sex ratios are described for hatchling, juvenile and adult. Hatchling sex ratios are most often established at the level of the clutch and are measured in various ways. They are often calculated from the sexes of the hatchlings produced. Loggerhead hatchling sex ratio is influenced by the incubation environment, and the embryo initially develops a gonadal ridge that is neither male or female. During the middle third of incubation the period of incubation gonadal sex is directed to become either testis or ovary (Yntema and Mrosovsky 1980; Maxell et al. 1988). The primary factor implicated in sex determination is incubation temperature (critically reviewed by Limpus et al 1983; Mrosovsky 1994; Miller and Limpus 2003; Miller et al. 2003; Wibbels 2003). The sex ratio response of eggs and nests to temperature appears to vary (Limpus et al. 1985; Godfrey and Mrosovsky 2001) and may not be well represented by average nest temperatures (Georges et al. 1994; Wibbels 2003; Blair 2005). Other environmental factors (e.g. rainfall, soil moisture, or shade) directly or indirectly influence sex ratios (Godfrey 1997; Mrosovsky et al. 1995).

Juvenile and adult sex ratios are derived from animals that have already hatched (e.g. juveniles captured at sea, adults captured at sea, or stranded animals). Juvenile and adult sex ratios of sea turtles typically differ from hatchling sex ratios because they integrate a number of life history events including the effects of mortality in younger stages, spatial and temporal variations in distribution, and a single stage class being studied may include individuals produced from rookeries over a number of different seasons. Additionally, sex ratios of juveniles and adults may reflect the integration of mixed stocks. Operational sex ratios are based on the reproductively active males and females in an assemblage at any given time. There are no data available that quantify operational sex ratios in Northwestern Atlantic loggerhead turtles.

Hatchling sex ratios serve as the starting point for both juvenile and adult sex ratios. Although more datasets have been published on hatchling sex ratios than other life stages, overall relatively little is known about population-wide sex ratios at any level (hatchling, juvenile or adult) and so we restrict our discussion to sex ratios by size or stage classes, except where supporting documentation allows more specific categorization of the sex ratios.

Hatchling sex ratios are important in part because they represent the pools from which future sex ratios arise. Shifts in hatchling sex ratios may have cascading effects on future generations if changes are extreme enough to impact productivity. Often, hatchling sex ratio estimates vary greatly across locations and years. Loggerhead sex ratios have been calculated variously and are summarized below by their sources (Table 4). Generally, in the Atlantic, there is a tendency for larger loggerhead rookeries located closer to the equator producing more female hatchlings on average, with smaller rookeries located further away from the equator producing more variable sex ratios (Table 4). A major caveat associated with this statement is that few rookeries have been rigorously studied for multiple years. Also, many studies reporting beach-based sex ratios are based on nest or beach temperature but lack adequate validation for temperature ranges found at the study sites. Most studies with validation are based on relatively small sample sizes, and are frequently under-sampled to accommodate local conservation goals. Also, some sex ratios are also estimated from dead hatchlings remaining in the nest after emergence. It is unlikely that sex ratios calculated for individual nests from dead-in-nest hatchlings are accurate measures because of insufficient samples (based on binomial probabilities) and/or because of the potential for sex-biased mortality of embryos or hatchlings.

For juvenile sex ratios, more recent data have been made available for foraging populations (Table 5). However, foraging areas are often visited by turtles that originated from different rookeries, which in turn may have different hatchling sex ratios. Therefore, it is often difficult to link juvenile sex ratios directly to hatchling sex ratios, because of the lack of direct genetic sourcing of individual juveniles to rookeries.

In the case of adult sex ratios, there remain profound gaps in our knowledge and we lack sex ratio data for all regions in the Atlantic. Yet, such information is important because shifts in productivity are difficult to interpret without an understanding how many animals of each sex breed in a season and how this varies temporally and spatially. Sex ratios may be important in the context of loggerhead mating systems and in clutch quality. Promiscuous mating systems are characteristic of sea turtles (Miller 1997; Pearse and Avise 2001). In promiscuous mating systems, several factors potentially may impact egg production and hatching success. These may include numbers of bouts of mating by individuals, duration of mating (important in *Chelonia mydas*; Wood and Wood 1980), mate selection, and multiple paternity within a single clutch of eggs (Zbindin et al. 2007; Bollmer et al. 1999). Factors that are important in many lower vertebrates such as possible sperm competition or social induction of follicle maturation or ovulation are unstudied in sea turtles. If adult sex ratios are too skewed, potential negative impacts from the Allee effect (Berec et al. 200; Marcovaldi and Chaloupka 2007) have been postulated, but remain unstudied or understudied in marine turtles (Wyneken and Heppell 2007).

Table 4. Sex ratios as percent of female *Caretta caretta* hatchlings, dead and alive, summarized and modified from Godfrey (1997). Here we do not classify sex ratios as primary of secondary because there is currently no uniform definition. We note that in sea turtles, primary sex ratio may be the sex ratio all of eggs or all hatchlings and that ratio does not account for post-deposition or post-hatching mortality. Secondary sex ratios in sea turtle hatchlings may be either the ratio at hatching or emergence.

Location	Year	Sex ratio (% female)	Comments Code	Reference
South Carolina and Georgia, U.S.	1979, 80, 82	56.3%	A, H	Mrosovsky et al. 1984
North Carolina, South Carolina and Georgia, U.S.	2002 2003	80% 60%	A, F, G	Blair et al. 2005
North Carolina, South Carolina Georgia, U.S.	2002 2003	79% 37%	A, F, H	Wyneken et al. unpub. data
North Carolina, U.S.	1980-2005	58%	D, J, H	Hawkes et al. 2007
Florida, U.S.	1987-89	~90%	A, H	Mrosovsky and Provanca 1989, 1992
SE Florida, U.S.	1998	~92.5%	D, J	Hanson et al. 1998
SE & SW Florida, U.S.	2002 2003 2004	84% 90% 100%	A, F, G	Blair et al. 2005
SE & SW Florida, U.S.	2002 2003 2004	67% 88% 97%	A, F, H	Wyneken et al. unpub. data
Peninsular Florida, U.S. (= Southern Subpopulation)	1995-1999	80%	I, L	NMFS SEFSC 2001
Sergipe and Bahia, Brazil	1988-1994	92.6-96.9%	J, H	Marcovaldi et al. 1997
Espirito Santo, Brazil	1988-1994	57.3%	J, H	Marcovaldi et al. 1997
Boa Vista Island, Cape Verde archipelago	2003-2004	67%	B, E	Delgado 2008

Table 4 and 5 Comment Codes:

- A. Estimate based on small sample size or sample results extrapolated
- B. Only part of season was studied
- C. Changes in nesting frequency not taken into account
- D. No *in situ* nests actually sampled
- E. Only dead hatchlings investigated
- F. Verified through laparoscopy and/or biopsy
- G. Sample sex ratio, not scaled for production
- H. Sex ratio scaled for production or estimated assemblage size

- I. Necropsied strandings
 - J. Calculated using temperature or other indirect estimate
 - K. Hormonal assay
 - L. Calculated from Texas, North Carolina, and South Carolina strandings sex ratio & natal origin probabilities 1995-97, assuming stable mortality
- 1 % female calculated from published ratio.
 2. Sampling of mixed stock on foraging grounds

Table 5. Sex ratios as percent of *Caretta caretta* juveniles, modified from Godfrey (1997).

Comment codes are provided in key of Table 4.

Location	Year	Sex ratio (% female)	Comments Code	Reference
North Carolina U.S.	1995-2002	68%	F, 1	Braun-McNeill et al. 2007b
Florida	1980s	65%	K, 1	Wibbels et al. 1987
Peninsular Florida U.S. (= Southern Subpopulation)	1995-1999	80%	I, L	NMFS SEFSC 2001
Northern U.S. Subpopulation	1995-1999	35%	I, L	NMFS SEFSC 2001
Yucatán Subpopulation Mexico	1995-1999	69%	I, L	NMFS SEFSC 2001
Gulf of Mexico (Texas, Florida Gulf coast) U.S.	1995-1999	74.5%	I	NMFS SEFSC 2001
Southeast Florida, U.S.	1995-1999	70.5%	I	NMFS SEFSC 2001
NE Florida through Maine, U.S.	1995-1999	67.5%	I	NMFS SEFSC 2001
Eastern Atlantic	2000s	66%	F, 1, 2	Delgado 2008
Eastern Atlantic	2000s	66.7%	F, K, 2	Dellinger 2007

Sex Ratios Estimated from Stranded Turtles

Strandings data represent an alternative sampling source for sex ratios based on dead or moribund turtles that are found ashore (beach-cast). However, because juvenile and adult sea turtles, while foraging or migrating, are of mixed stock (*i.e.*, they come from different source nesting beaches, which may have different hatchling sex ratio production values), sex ratios calculated from stranded sea turtles (strandings) only reflect those of the standing stock if death rate and stranding rate by stage are the same for both sexes. Death rates by life stage appear not to be the same for both sexes. In various marine fish populations, there is often a sex ratio bias of captured individuals, despite a presumed 1:1 offspring sex ratio (*e.g.* Bessa et al. 2007). Thus, sex ratio data of stranded turtles remain challenging to interpret because of the many unknown factors that bias these samples. Sources of bias may include temporal variation in spatial

occurrence of immature turtles, differences in sex-specific death rates, influences of sex-specific behavior differences, sex-specific risks, and resolution differences due to integration of multiple year-classes of immature turtles (and even mature turtles). The probability of a carcass washing ashore is greater for turtles that die closer to shore (Hart et al. 2006). If the sexes differ in their proximity to shore, such a spatial difference could bias results as well. However, with the recognition that strandings, like many biological samples, have some biases, they nonetheless are a sample source of disabled or dead turtles that we can quantify. These turtles became stranded if they were killed or debilitated near shore and, while they clearly are an incomplete sample, they represent multiple year classes. As such, if one selects data that meet the most rigorous criteria for sex identification, they may indicate juvenile or adult sex ratios (or trends in sex ratios) of turtle assemblages. Where sampling or observer effort is uniform, changes in sex ratios of these multiyear classes of strandings deserve attention as they may reflect long scale shifts in production of one sex, changes in spatial occurrence, mortality variation, major mortality events (that removed reproductive turtles or pre-reproductive immature turtles that should have recruited to reproductive stages), or some combination of these factors. Thus, sex ratios of stranded turtles warrant investigation.

We examined the sex ratios in stranded turtles using several subsets of the Sea Turtle Stranding and Salvage Network (STSSN) database (Appendix A). Here we summarize those results:

- Sex ratios of immature and mature turtles are not the same. About 70% of the immature turtles were females and the percent females decreased between the immature and the mature stages. These changes suggest that mortality rates and/or the probabilities of stranding are not uniform for both sexes by life stage (length classes).
- We did not detect large changes in sex ratios over time in two sets of years surveyed. If long-term shifts in sex ratio occurred, we cannot detect them from strandings at this time. Because multiple year classes contribute to each stage class, and loggerhead turtles are late maturing animals, several more decades of data are needed to detect sex ratio shifts over time and only if such a shift persists for a biologically sufficient period to allow detection.
- While the sex ratios of immature turtles were female-biased in all regions, the sex ratios of mature turtles tended to be nearly 1:1 or slightly male-biased across most regions. We failed to reject the null hypotheses that observed sex ratios were similar across regions for most size classes.
- The sex ratios of stranded turtles were not similar among regions when we examined the largest acceptable dataset (1987-2004), but when we examined only data from animals with verified sex assignments, we could not reach the same conclusion. The significant differences were attributed to the adult-sized animals. We found female bias common when data were grouped by state.
- In states and regions that host nesting, the sex ratios were usually female-biased, and tended to be slightly more female-biased during the nesting season of May-September. The numbers of female strandings were much higher in the Northeast and in North Carolina-Georgia during May-September. This combination may reflect the return of nesting turtles to nearshore waters and the return of non-nesting or post-nesting turtles to temperate feeding grounds during warmer months. The increase in nesting season

mortalities probably also heralds increases in spring-summer fisheries and recreational activities.

- We found no significant shift in the median sizes of either sex of stranded adult loggerheads. We note that it is possible that the time range covered may not be sufficient to detect a trend towards onset of breeding at a smaller size.
- We note that the strandings data reflect large numbers of dead females in both the immature and adults size classes. The nearly uniform tendency for female bias in the data set of verified sex turtles suggests significant female mortality occurs which removes potential nesting turtles from population at all locations.

Summary

Overall, the available data on sex ratios in Atlantic loggerhead sea turtles are intriguing but limited. At the current time, there is no indication that changes in hatchling, juvenile or adult sex ratios have contributed directly to the decline in nest numbers observed in the Southeast U.S. However we note that there is a clear data need from a wider spatio-temporal stretch to firmly characterize the sex ratios of different life stages of loggerheads.

Spatial Distribution –Kate Mansfield, Heather Haas, and Sheryan Epperly

Sea turtles are highly migratory, long lived animals. The previous TEWG reports provided brief summaries of the geographic range of loggerheads while the 2001 NMFS SEFSC assessment provided more information, particularly on the distribution on each of the subpopulations. Identifying core areas of habitat use, seasonal dispersal patterns and size- or sex-specific patterns of movement will allow for a better understanding of the potential hazards these animals may encounter and will provide the basis for spatially targeted management strategies. Understanding the spatial distributions of loggerheads captured within the Western North Atlantic will provide insight to:

- 1) The degree of spatial overlap among turtles originating from different subpopulations;
- 2) Whether high use areas seasonally exist for turtles from different subpopulations, size classes or sex; and
- 3) Whether these high use areas overlap with known sources of sea turtle mortality, or with regions subjected to ecological change and habitat degradation;

We used three approaches to identify spatial overlap, high use areas and seasonal movements and habitat occupancy among loggerheads captured along the eastern U.S. seaboard and the Gulf of Mexico. The first approach includes an examination of available conventional tag data. The next approach included analyzing available satellite telemetry data to determine areas of high use based on seasonal sex-, size-, or subpopulation-specific data. The final method utilized historic aerial survey data to provide verification for the observed distributions derived from satellite telemetry.

Conventional tag data

While tag returns from conventional tagging methods using inconel, monel, or Passive Integrated Transponder (PIT) tags are valuable for inferring growth rates or general dispersal and movement information for loggerhead sea turtles, recapture data must be interpreted with caution. Not only are recapture records highly dependent on tags being reported by the public, but recapture data only provide information at the time of original capture ('Point A'), and at the time of recapture ('Point B'). With the exception of localized in-water mark and recapture programs in North Carolina, Virginia and Florida, and a few long-term nesting beach tagging programs (North Carolina, Georgia, and Florida), the majority of recaptures usually reflect mortality events occurring along a journey or at a specific time in their life histories, rather than a destination for these turtles ('Point C'). As such, the reliability of returns, if trying to evaluate the proportion of a stock of turtles that travel to specific areas, is problematic.

Methods

We examined the flipper and PIT tag records from 1980 through 2007 in the Cooperative Marine Turtle Tagging Program (CMTTP) database (<http://accstr.ufl.edu/cmttp.html>) From 1980-through 2007, the CMTTP distributed nearly 250,000 inconel, monel, and plastic tags.

Turtles were initially tagged and/or found by a variety of sources including: nesting beach surveys; headstart programs; general TED testing; rehabilitation and display turtles (for education purposes in an aquarium); stranding networks; cold stunning events; incidental capture (shrimp trawls, including try nets and bib nets, fish trawls, gill nets, longline, hook and line, pound net, dredges, etc.); pound net mark and recapture research; gill net mark and recapture research (including stationary entanglement, turtle, stop, block, trammel, and tangle nets; encircle netting, purse seine and long haul seines); hand capture for research purposes (including cast and dip nets, scuba, and any methods which require human effort alone); shrimp and fish trawl research; power plant impingement; captures in water intake canals; and other miscellaneous or unknown sources. Because the tagging purposes were so varied, we focus only on inferred turtle movements on a broad scale.

Inconel and monel tags are applied externally, typically to the front and/or rear flippers; PIT tags are inserted into the muscle tissue of a turtles' shoulder, front flipper or in between the digits of a turtle's front or rear flipper.

Over 10,000 first-time loggerhead tagging events and more than 9,100 subsequent recaptures have been reported since 1980; approximately 700 loggerhead recaptures are reported annually. These returns originate from the same sources reported above with the largest proportion of recovered tags reported by nesting beach surveys (71%). Geographic regions were assigned based on the reported state or country of capture, but if these data were missing, regional assignments were made by assessing the zone of capture or the reported capture latitude and longitude (Table 6). We included data from only those turtles that were reported to be captured in the United States on their first tagging event, because not all releases outside the U.S. are

reported to the CMTTP. Note that the CMTTP database does not represent all turtles tagged within the United States. Additional tag databases exist, most notably one managed by the University of Florida (UFL). The UFL database has been existence since 1950 and contains information for over 220,000 tags. While portions of this database were merged with the CMTTP database in April 1999, some older and/or proprietary data were not merged with the CMTTP.

We tallied the number of loggerheads that were originally tagged in each region within the U.S. and subsequently recaptured (Table 7). For each original tagging region (Table 6), only the number of turtles recaptured is reported by recapture region (rather than the total number of recapture events). This approach decreases the bias associated with differential reporting rates between the regions and protects the proprietary nature of these data.

A total of 3,797 individual animals had recapture histories recorded in the CMTTP database. Although some movement between regions was reported, the majority of recaptures occurred in the same region where the original tagging occurred (Table 7).

Turtles tagged within the GOM region likely remain within the southern geographic regions (GOM, SEU, and CCA) and are less likely to range into the northern regions (NAO, NEC). Genetics data from developmental habitats in the NEC and North Carolina indicate that immature turtles foraging in these areas originate from several subpopulations (Norrgard 1996; Rankin-Baransky et al. 2001; Bass et al. 2004; Bowen et al. 2004). It is not surprising, therefore, that there is overlap in both the SEU and NEC region-based recaptures.

Table 6. Description of regional strata. Cap_ST refers to the reported state or country of capture. CAP_ZONE refers to NMFS statistical zones (<http://www.sefsc.noaa.gov/seaturtleSTSSN.jsp>). CAP_LAT and CAP_LONG refer to the reported latitude and longitude of capture (respectively) coded as five digits: degrees, minutes, tenths of minutes. Unknown locations are coded as ‘99999’; we assumed ‘--999’ (last three digits) also refers to unknown information.

	Region	Included data
NAO	North Atlantic Oceanic	Cap_ST=Azores, Bermuda CAP_LAT=45270 and CAP_LONG=41510
CCA	Caribbean and Central America	Cap_ST=Antigua, Belize, Bahamas, British West Indies, British Virgin Islands, Cuba, Costa Rica, Dominica, Dominican Republic, Grenada, Cayman Islands, Honduras, Haiti, Jamaica, Guiana, Panama, Puerto Rico, U.S. Virgin Islands, St. Kitts, British West Indies, Trinidad, Turks and Caicos, Nicaragua
GOM	Gulf of Mexico	Cap_ST=Alabama, Gulf of Mexico, Mississippi, Louisiana, Texas, Gulf Coast of Florida, Gulf Coast of Mexico (which represented all Mexico tags used in this analysis)
		CAP_ZONE>=1 and CAP_ZONE<=21
		CAP_LAT=27999 and CAP_LONG=82999
		CAP_LAT=28999 and CAP_LONG=82999
		CAP_LAT=30999 and CAP_LONG=84999
NEC	Northeast U.S. and Canada	Cap_ST=Canada, Connecticut, Massachusetts, Maine, New Hampshire, New Jersey, New York, Rhode Island, Delaware, Maryland, Virginia
		CAP_ZONE>=37 and CAP_ZONE<=44
SEU	Southeast U.S.	Cap_ST=Georgia, Atlantic Coast of Florida, North Carolina, South Carolina
		CAP_ZONE>=24 and CAP_ZONE<=35
		CAP_LAT=27999 and CAP_LONG=80999
		CAP_LAT=28999 and CAP_LONG=80999
		CAP_LAT=30999 and CAP_LONG=81999
		CAP_LAT=33999 and CAP_LONG=79999

Table 7. Tagged and recaptured turtles by region. The number of turtles tagged in the United States and later reported recaptured in our regions of interest (Table 6) are shown in the “Recaptured Tags” column. The values in the regional columns represent the number of turtles that were recaptured in that region (rather than the number of recapture events). In addition to the turtles reported in the recapture locations, there were 21 loggerhead recaptures with missing information for the recapture location (state, country, zone, latitude, and longitude). Approximately 250,000 tags have been distributed to turtle projects by the CMTTP.

Tagging Region	Recaptured Turtles	Recapture Locations of Tagged Individuals				
		CCA	GOM	NEC	NAO	SEU
GOM	1,268	4	1,245	0	0	19
NEC	63	0	0	38	0	25
SEU	2,466	11	18	60	2	2,355

Satellite Telemetry

In contrast to the “snapshot” perspective provided by conventional tag return data, satellite telemetry can identify sea turtle distribution patterns and habitat utilization (*e.g.* foraging areas, inter- and post-nesting movements, seasonal migratory behavior), and movement rates or survival. Spatial ranges of nesting stocks may be identified, as may seasonal distributions based on size classes and sex.

Due to the high cost associated with satellite telemetry, as well as the time to meet set criteria to successfully navigate the permitting process in the U.S., and because that satellite telemetry is a relatively new method, few research programs have large or long-term datasets. As more datasets are established or built upon, there is potential for monitoring spatial trends over time (changes in distribution, seasonal distribution, changes due to the potential effects of global warming, etc.).

Replicating the analyses used by the Leatherback Turtle Expert Working Group (TEWG 2007), we established a baseline analysis of sea turtle distributions within the Western North Atlantic using existing satellite data. We standardized our approach with the Leatherback TEWG by analyzing spatial composites that incorporate multiple tracking datasets. Several proprietary satellite data repositories currently exist including seaturtle.org’s tracking site and the OBIS-SEAMAP program. However, a neutral, management-based repository does not exist. Thus, the composites generated in this report required that TEWG members approach individual researchers, requesting tracking data for these analyses. There was a very high level of voluntary participation in these analyses resulting in approximately 85% of the existing track data for loggerheads tagged within the Western North Atlantic along the east coast of the U.S. and within the Gulf of Mexico (as of fall 2007). A complete list of contributors is provided in Table 8.

Methods

Track data from adult female nesters and foragers, adult and immature males, and immature foragers (Stage III Juveniles) were compiled through the fall of 2007 in order to identify areas of high use and to determine any stock-, size class- or sex-specific patterns of habitat use. We obtained ARGOS location data for 248 individual turtles intercepted on nesting beaches or from captures in in-water studies ranging from New York, south along the east coast of the U.S., and in the Gulf of Mexico from Florida and Texas. These included in-water captured juveniles, nesting and foraging adult females from the Northern U.S. and Peninsular Florida nesting beaches and foraging grounds, and in-water captured male loggerheads (Table 8). The majority of telemetry tracks provided for this analysis were derived from the spatial region associated with the Northern U.S. Subpopulation. Among the adult nesting females represented, all originated from three nesting assemblages: the Northern U.S., Peninsular Florida, and Northern Gulf of Mexico. Juveniles from all of these sources commingle on the neritic foraging grounds (Bowen et al. 2004). The only track data available for Florida and the eastern Gulf of Mexico were derived from adult female nesters, resulting in some spatial bias related to tracking effort. All tracks were of varying duration and duty cycles resulting from different research priorities.

Location data provided by ARGOS have a range of associated accuracies classified as Z, B, A, 0, 1, 2, 3, with 3 as the highest accuracy and B as lowest. Locations are not determined for Location Class Z. Locations of lower quality tend to be less predictable. We filtered all data to exclude aberrant locations with a filtering algorithm for PC-SAS-Version 9.0 created by David C. Douglas (U.S.G.S.): <http://alaska.usgs.gov/science/biology/spatial/douglas.html>. We used the hybrid filter which combines the minimum redundant distance and distance angle criteria. A list of the input parameters used (and associated rationale) for this analysis are included in Table 9.

We selected median daily locations for each turtle based on the filtered positions to reduce the effects of autocorrelation. Positions for missing days, within periods of less than eight days and greater than one day from known positions, were estimated using a simple linear interpolation with the distance between the known positions divided evenly between the missing days. Thus, each daily position represents one track day per individual turtle. Locations were tallied into hexagonal area bins standardized for horizontal distance from 45° W over the curvature of the earth using $\cos(\text{lat}) * (\text{lon} + 45)$ (James et al. 2005; TEWG 2007). Data were combined and plotted by size class (neritic juvenile or adult females), males, and nesting females by subpopulation to elucidate habitat use. For seasonal analyses, we defined Winter as January through March; Spring as April through June; Summer as July through September; and Fall as October through December.

We did not analyze 38 proprietary tracks from nesting females in Florida during 1998-2000, but provide a summary taken from Foley et al. (2008). The tracks include 15 turtles from the Archie Carr National Wildlife Refuge (Atlantic coast, Brevard County), 13 turtles from Manasota Key (Gulf coast, Sarasota County), and 10 turtles from Cape San Blas (Gulf coast, Gulf County).

Results

All animals

A total of 248 individual turtle tracks were analyzed including 24,535 track days. Track data were collected between 1986 and 2007. Figure 4 represents the movements and habitat use for all sea turtles in this analysis. The majority of both turtles and track days were found to occur along the continental shelf out to the 200 m bathymetric contour line. Another high use area occurred along the southern Gulf coast of Florida between the Dry Tortugas and Cape San Blas (Figure 4). There were some turtles that tracked beyond the continental shelf to the northern Atlantic. Those turtles ranged as far east as approximately 35° W and between 30° N to 46° N.

Juveniles

Track data from 108 neritic juveniles (Stage III) were analyzed, spanning from 1986 through 2007 (9,833 track days). With the exception of seven juvenile turtles tracked from Texas and Louisiana, all immature loggerheads were captured and tracked from waters ranging from Georgia north to Long Island, N.Y. (Figure 5). No juvenile loggerheads were captured and tracked from the eastern Gulf of Mexico or from Florida. The majority of tracked juveniles were found to occur along the continental shelf out to the 200 m bathymetric contour line. However, almost a fifth of the turtle tracks ranged beyond the continental shelf into the northern Atlantic (Keinath 1993; Mansfield 2006; McClellan and Read 2007). Those turtles ranged as far east as approximately 35° W and between approximately 30° N and 46° N (Figure 5). Another high use area occurred along shelf waters off of eastern Texas and western Louisiana. Some juveniles tagged and released north of Florida, including as far north as Virginia, migrated south along the eastern Florida shoreline (Keinath 1993). Turtles tagged and released in Texas, remained on the shelf offshore of the Texas and Louisiana coastlines (Renaud and Carpenter 1994; Renaud et al. 1994; J. Williams unpub. data).

Seasonal composites (Figures 6A-D) indicate few to no juvenile turtles occurring close to shore north of Cape Hatteras, N.C. during the Winter. From Spring through Fall, turtles were found to occur in nearshore coastal waters with high use areas occurring from the North Carolina-South Carolina border north into Virginia's Chesapeake Bay and coastal waters of the mid-Atlantic Bight. During the colder Fall and Winter months, turtles had a high frequency of days spent south of Cape Hatteras off of the Carolinas' shorelines.

Males

We analyzed tracks from 36 male loggerheads (mostly adults) collected between 1991 and 2007, representing 2,612 track days (Figure 7). Four originated from the west coast of Florida, 29 from the east coast off Cape Canaveral. The remaining three originated from Virginia. The majority of males remained along the continental shelf out to the 200 m bathymetric contour line. A small number of males moved beyond the continental shelf into waters as far east as 60° W from the Delmarva Peninsula (Mansfield 2006; M. Arendt SCDNR unpub. data). High use areas occurred in shelf waters off of Cape Canaveral, Florida, along the west coast of Florida, and in the vicinity of Cape Hatteras, N.C. Turtles released from Florida's west coast ranged from the southern tip of the state up to the Panhandle. Seasonal composites (Figures 8A-D) indicate no male turtles occurred coastally north of Cape Hatteras, N.C. during the winter months.

Adult Females

We processed data for 100 adult female turtles tagged on nesting beaches between 1992-2007 representing 11,863 days of tracking (Figure 9). The majority of adult female tracks originated from Northern U.S. Subpopulation nesting beaches ranging from Georgia to Virginia. Thirty-three of the 100 adult nesting females originated from the west coast and Panhandle region of Florida. With few individual exceptions, the majority of adult females remained on the continental shelf. High use areas occurred near shore from the North Carolina-South Carolina border north to Delaware Bay, and from Tampa Bay south to the Dry Tortugas (Figure 9). Turtles ranged as far south as the Gulf side of the Yucatán Peninsula and north and west coasts of Cuba.

Seasonal composites (Figures 10A-D) indicate few to no turtles occurring coastally north of Cape Hatteras, North Carolina during January through March. Turtles also occurred more frequently offshore, remaining in deeper waters closer to the edge of the continental shelf. Fewer track data were available for the winter months resulting in the fewest track days occurring during this season. By the Spring and Summer, turtles occurred in near shore coastal waters with high use areas occurring from the North Carolina-South Carolina border north into Virginia's Chesapeake Bay and coastal waters. Additional discrete areas of higher use occurred adjacent to the nesting beaches from which the turtle tracks originated. Some nesting females originating from Northern U.S. nesting beaches have been documented migrating north of Cape Hatteras post-nesting (Plotkin and Spotila 2002; Hawkes et al. 2007; D. Griffin SCDNR unpub. data).

Nesting Females by Subpopulation

For Northern U.S. Subpopulation nesting females (n=64; 11,863 track days), high use areas occurred coastally from the North Carolina-South Carolina border north into the Chesapeake Bay and Delaware Bay and directly offshore of the Georgia nesting beaches where several turtles were captured and tagged (Figure 11A). There was some movement by northern nesters south into Florida (Mansfield 2006), as well as some movement off the shelf, particularly east of the mid-Atlantic Bight. There were two turtles that migrated from Virginia post-nesting south along the coast to the southern tip of Florida and into the Gulf of Mexico (Mansfield 2006). Turtles tracked from the west coast of Florida mostly remained on shelf waters within the eastern Gulf of Mexico (Figure 11B). These turtles ranged as far south as the Gulf side of the Yucatán Peninsula, along the north and west coasts of Cuba, and coastally along the northern Gulf of Mexico offshore of Louisiana and the Florida Panhandle. The few turtles tracked from the Northern Gulf of Mexico Subpopulation of nesting females ranged from their nesting beaches (Gulf Islands NWR) south to the Florida Keys and Dry Tortugas; none left the Gulf of Mexico (Figure 11C).

Other Florida Nesting Females (from Foley et al. 2008)

Most post-nesting movements were directed and only a few of the turtles appeared to wander (Figure 12). Some of the turtles traveled along coastal routes but some crossed deep-water even when a coastal route was available. Females departing from the same nesting beach and sharing a similar post-nesting destination did not necessarily follow the same route. However, half of the females from the east coast (8 of 15) moved close along southeast Florida and the Florida Keys as they moved into the Gulf of Mexico. Within a few weeks of departing their nesting beach, the females took up residence in well-defined, relatively small areas (median of 2,000 km²) on the continental shelf off Florida, Texas, Mexico, the Bahamas, and Cuba (Figure 12). The majority

of the females (22 of 38; 60%) from both subpopulations took up residence off the west coast of Florida between the Dry Tortugas and Cape San Blas. With few exceptions, turtles remained in their resident areas for the duration of the transmitter life (mean of 364 days, range 11–712 days). Some turtles had resident areas that were near their nesting beach (<50 km) and some had resident areas distant from their nesting beach (>700 km). Most turtles migrated to a more distant nesting beach even though there were nesting beaches that were closer to their resident area. The resident areas of females from both subpopulations overlapped (Foley et al. 2008).

Conclusions

Nesting beaches and in-water foraging grounds were not sampled in proportion to their population sizes. The majority of tracks were obtained from research programs occurring from Georgia north to New York. Nevertheless, these data provide a foundation for the identification of temporal trends and distributions over time and provide insight into regional and seasonal movement patterns. However, effort should be made to include a greater spatial representation of Western North Atlantic loggerheads in the future.

Despite ongoing research, data are still few or lacking for juvenile loggerheads in Florida; for oceanic loggerheads, particularly loggerheads from the eastern Atlantic; for loggerheads of all age classes in the Gulf of Mexico; male loggerheads throughout the Atlantic; from underrepresented subpopulations in Mexico, the Dry Tortugas, etc.; and for post-hatching and neonate turtles originating throughout the range for this species. The ideal approach would be to identify and track a proportional spatial representation of turtle populations within the Western North Atlantic.

There are some spatial biases associated with tracking effort among the datasets used for these analyses, including:

- 1) Lack of sampling consistency over time (including standardization of methods and/or temporal consistency);
- 2) Lack of funding (particularly to sustain projects over time or to ensure strong spatial representation of data throughout the Atlantic and among size class or sexes);
- 3) Availability of existing proprietary data for management purposes.

Funding should be encouraged to support telemetry studies throughout the Atlantic, particularly for underrepresented size classes, sexes and stocks. Despite recognized data needs for the youngest size classes (TEWG 2000; Heppell et al. 2005), significant data gaps remain. Post-hatching and neonate *in-situ* tracking studies have historically been limited by funding, logistics and the availability of small-scale technologies that allow for the remote tracking and characterization of where these animals are within the water column over extended periods of time. Few *in-situ* empirical data of neonate behavior, dispersal and survivorship exist. These data tend to have small sample sizes, are limited in spatial scope, and are constrained by labor-intensive visual observations.

Table 8. List of satellite telemetry data contributors.

Researcher	Program	Release Location(s)	Turtle Source(s)	Number of tracks contributed
Steve Morreale	Cornell University	Long Island, New York	Immature foragers	12
Jennifer Dittmar	National Aquarium, Baltimore	Outer Banks, North Carolina	Immature forager	1
Kate Mansfield	Virginia Institute of Marine Science	Virginia coast, Chesapeake Bay	Immature foragers; post-nesting adult females; adult male	33
Catherine McClellan	Duke University (Marine Lab)	North Carolina coast and Sounds	Immature foragers	35
Michael Coyne	seaturtle.org	Bald Head Island, North Carolina	Post-nesting adult females	16
Brendan Godley	University of Exeter			
Mathew Godfrey	NCWRC			
DuBose Griffin	SCDNR	Cape Island, South Carolina	Post-nesting adult females	15
Sally Murphy	SCDNR (ret.)			
Mike Arendt	SCDNR	South Carolina; Cape Canaveral, Florida	Immature foragers; adult males	64
Mark Dodd	GADNR	Georgia nesting beaches	Post-nesting adult females	24
Mike Frick	Caretta Research Project	Wassaw Island, Georgia	Post-nesting adult females	5
Tony Tucker	Mote Marine Lab	Florida, west coast	Post-nesting adult females	33
Mark Nicholas	Gulf Islands National Seashore	Florida, Pan Handle	Post-nesting adult females	3
Jo Anne Williams	NOAA, Galveston	Galveston, Texas; Gulf of Mexico	Immature foragers	7

From: Keinath 1993; Renaud and Carpenter 1994; Morreale and Standora 1998; Mansfield 2006; Hawkes et al. 2007; McClellan and Read 2007; National Aquarium unpub. data, M. Arendt SCDNR unpub. data; D. Griffin SCDNR unpub. data; M. Frick Caretta Research Project unpub. data, Tucker 2008; J. Williams NOAA/NMFS unpub. data; T. Tucker Mote Marine Lab unpub. data; M. Nichols Gulf Islands NWR unpub. data.

Table 9: Parameter settings for the Douglas Filter program run for loggerhead satellite telemetry data. All data were filtered to exclude aberrant locations with a filtering algorithm for PC-SAS-Version 9.0 created by David C. Douglas (U.S.G.S.): <http://alaska.usgs.gov/science/biology/spatial/douglas.html>.

<i>Variable</i>	<i>Value</i>	<i>Rationale</i>	<i>Variable explanation</i>
<i>minoffh</i>	0.0001	This is the suggested value when using <i>Pickday</i> = 1 (which we used).	Minimum time likely to go without a transmission
<i>maxredun</i>	5	This was the value used in the leatherback TEWG analysis. We kept this same value because loggerhead <i>maxredun</i> should not likely be greater than leatherback and should not likely be less than 5 km; 5 km is a relatively small distance in relation to the magnitude of known movement throughout a track line.	Distance (km), less than which consecutive points would be retained
<i>minrate</i>	4.5	This value is slightly larger than recorded average swimming speeds (Lutz and Musick 1997), which we expect could be attained between two consecutive location records if the turtle was aided by favorable tides or currents.	Reasonable rate of movement (km/hr) that animal may sustain over a period of hours or days
<i>ratecoef</i>	25	Kept default for mammals and reptiles.	Coefficient to evaluate angle between three consecutive points
<i>gmtoffst</i>	0	Kept default to remain in GMT.	Deviation (hrs) from GMT
<i>latmin</i>	0	Represents the broad north Atlantic.	Geocoordinate restraint
<i>latmax</i>	60	Represents the broad north Atlantic.	Geocoordinate restraint
<i>lonmin</i>	-110	Represents the broad north Atlantic.	Geocoordinate restraint
<i>lonmax</i>	30	Represents the broad north Atlantic.	Geocoordinate restraint
<i>r_only</i>	0	Kept the default of using rate and angle.	
<i>r_or_a</i>	1	Kept the default of using rate and angle.	
<i>keep_lc</i>	1	Kept all LC3 (best), LC2, and LC1, therefore location error of up to approximately 1km.	Minimum Argos location code that never would be filtered out
<i>keeplast</i>	0	Because we usually do not have any more confidence in the last location than we have for prior locations, we did not keep last location unless it passed the filter.	Last record is filtered out if it exceeds MAXREDUN from the previous location
<i>pickday</i>	1	We are not using any of the output files related to <i>pickday</i> , so this parameter is essentially irrelevant for our purposes. A value needs to be chosen for the program to run. We chose 1 because we will be using data with various duty-cycles and we are ultimately interested in one location per day for the hex-bin composites	Best Argos location is selected on 24 hr period, not transmitter duty-cycle
<i>skiploc</i>	0	“B” should be considered in next triplet, even if “B” is filtered (removed). We chose this so that removing “B” would not increase the likelihood of removing surrounding points.	A previously filtered point is considered in the next evaluation of three consecutive points
<i>xmigrate</i>	1	We set this to 1 so that all DAR points that passed the MRD filter would pass this test for a migration event and be further evaluated for inclusion in the hybrid filter.	A coefficient of MAXREDUN used to evaluate distance during a “migration event”
<i>xoverrun</i>	3.0	We chose this value based on calculations from sample datasets plus evaluation of MRD, DAR, and best hybrid output run under a variety of <i>xoverrun</i> values. We increased this value from	A coefficient of MAXREDUN used to evaluate DAR vector during a “migration event”

		the default so that many of the DAR points that passed the MRD filter would pass this test for a migration event and be further evaluated for inclusion in the hybrid filter.	
<i>xdirect</i>	70	This value was based on the expected asymptote, given that some reasonable distances in a sample dataset were > 100 km.	Used to evaluate azimuth in a direction test of the combined MRD and DAR filter
<i>xangle</i>	45	We decreased this angle from the default value based on calculations from sample datasets plus evaluation of MRD, DAR, and best hybrid output run under a variety of <i>xangle</i> values.	Used to evaluate angle between 3 consecutive points in an angle test of the combined MRD and DAR filter
<i>xpercent</i>	50	We increased this value from the default based on calculations from sample datasets plus evaluation of MRD, DAR, and best hybrid output run under a variety of <i>xpercent</i> values.	Amount of wander allowed by an animal in the combined MRD and DAR filter
<i>testp_0a</i>	1	For location classes “A” and “0”, a location only needs to pass 1 of the 3 related angle tests (direct, angle, percent) to pass this portion of the filter. We chose this option because we think many of the locations accepted by the DAR filter are accurate points, and we want many of the reasonable DAR locations to pass the hybrid filter	The previous “testpass” variable (the number direct, angle, percent tests for the combined MRD and DAR filter that must be passed) has been partitioned into two parts: 1) cases where the location in question is an LC=Z or LC=B; and 2) cases where the location in question was an LC=A, LC=0, or better.
<i>testp_bz</i>	2	For location classes “B” and “Z”, a location only needs to pass 2 of the 3 related angle tests (direct, angle, percent) to pass this portion of the filter. We chose this option because we want to be a little more conservative with this class of locations.	See testp_0a (above).
<i>crossval</i>	1	Because sea turtles are not “slow moving animals” we chose the previous default of 1.	When CROSSVAL = 1, the program attempts to cross-validate its initial choice between the 2 solutions by evaluating the pair of locations from the subsequent overpass. Until program version 7.03, the condition was always CROSSVAL = 1 (internal default).
<i>unixdata</i>	0	We will not be using Unix-formatted SAS datasets, so we set to 0.	Set to 1 if using UNIX-formatted SAS datasets of Argos data.

Figure 4. Movements and habitat use of all loggerhead sea turtles (n=248 animals; 24,535 tracked days). Days tracked from release state are indicated within respective state borders. Florida split into east and west coast release locations. Bathymetric contour line=200 m. There are two hexes per degree; each hex represents approximately 2,686 km². The longitudes are based on 360', starting at 0 from the Prime Meridian moving east.

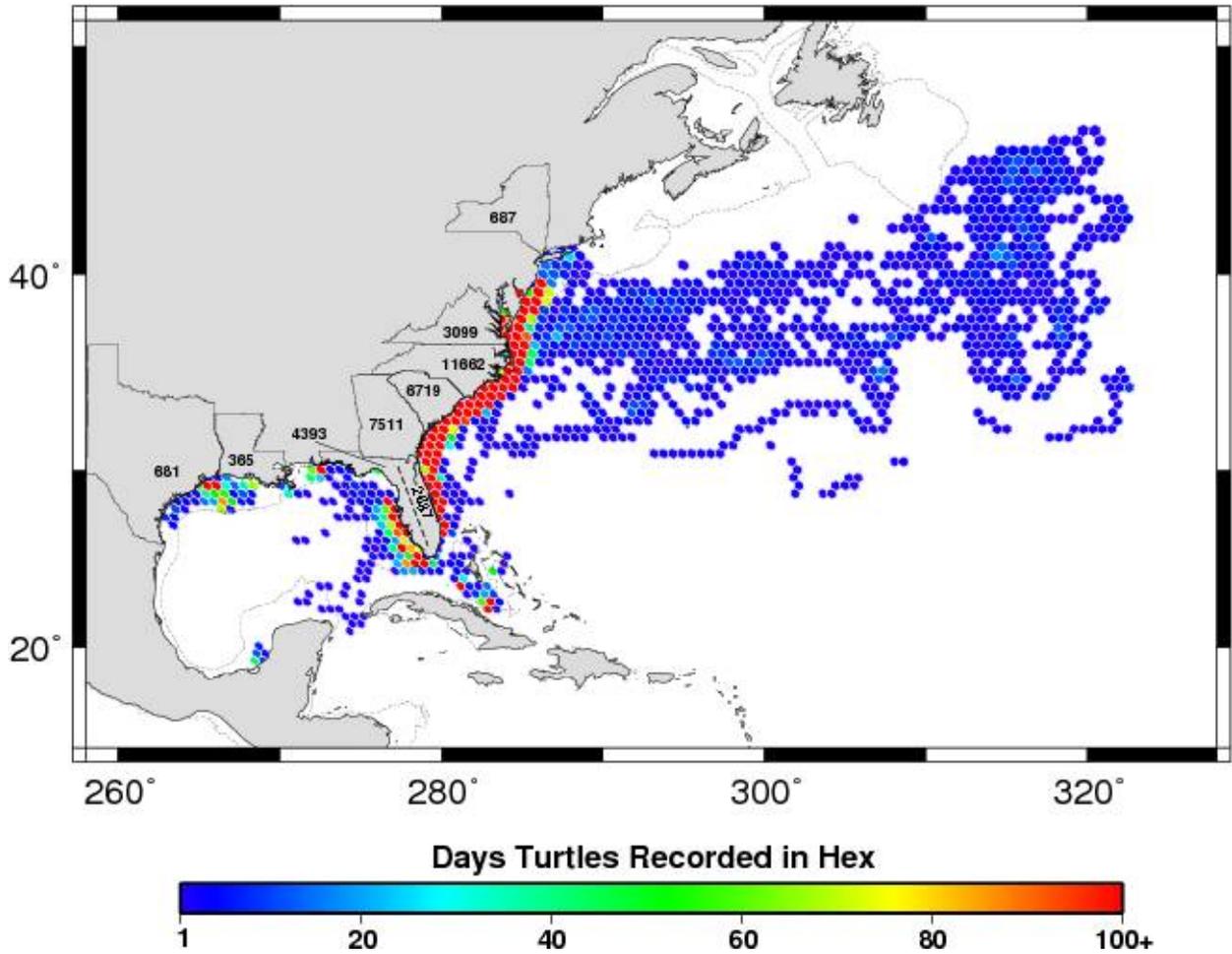
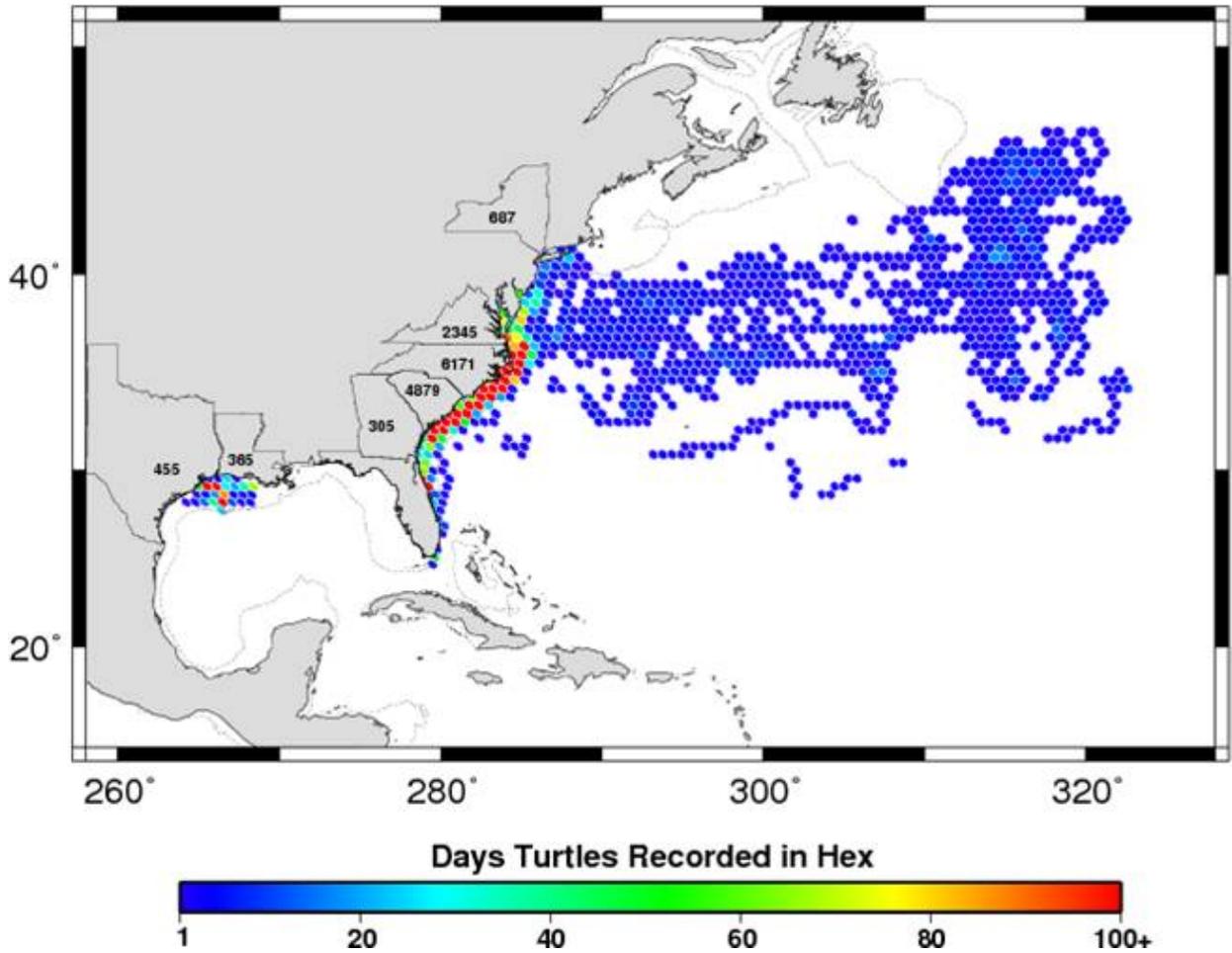


Figure 5. Movements and habitat use of all juvenile loggerhead sea turtles (n=108 animals; 9,833 days). Days tracked from release state are indicated within respective state borders. Bathymetric contour line=200 m. There are two hexes per degree; each hex represents approximately 2,686 km². The longitudes are based on 360°, starting at 0 from the Prime Meridian moving east.



Figures 6A-D. Seasonal movements and coastal habitat use of all juvenile loggerhead sea turtles (n=108 animals; 9,833 days). (A) Winter, January through March (n=61 animals; 2,291 days). (B) Spring, April through June (n=71 animals; 2,325 days). (C) Summer, July through September (n=64 animals; 1,610 days). (D) Fall, October through December (n=87 animals; 3,607 days). Bathymetric contour line=200 m. There are four hexes per degree; each hex represents approximately 669 km². The longitudes are based on 360', starting at 0 from the Prime Meridian moving east.

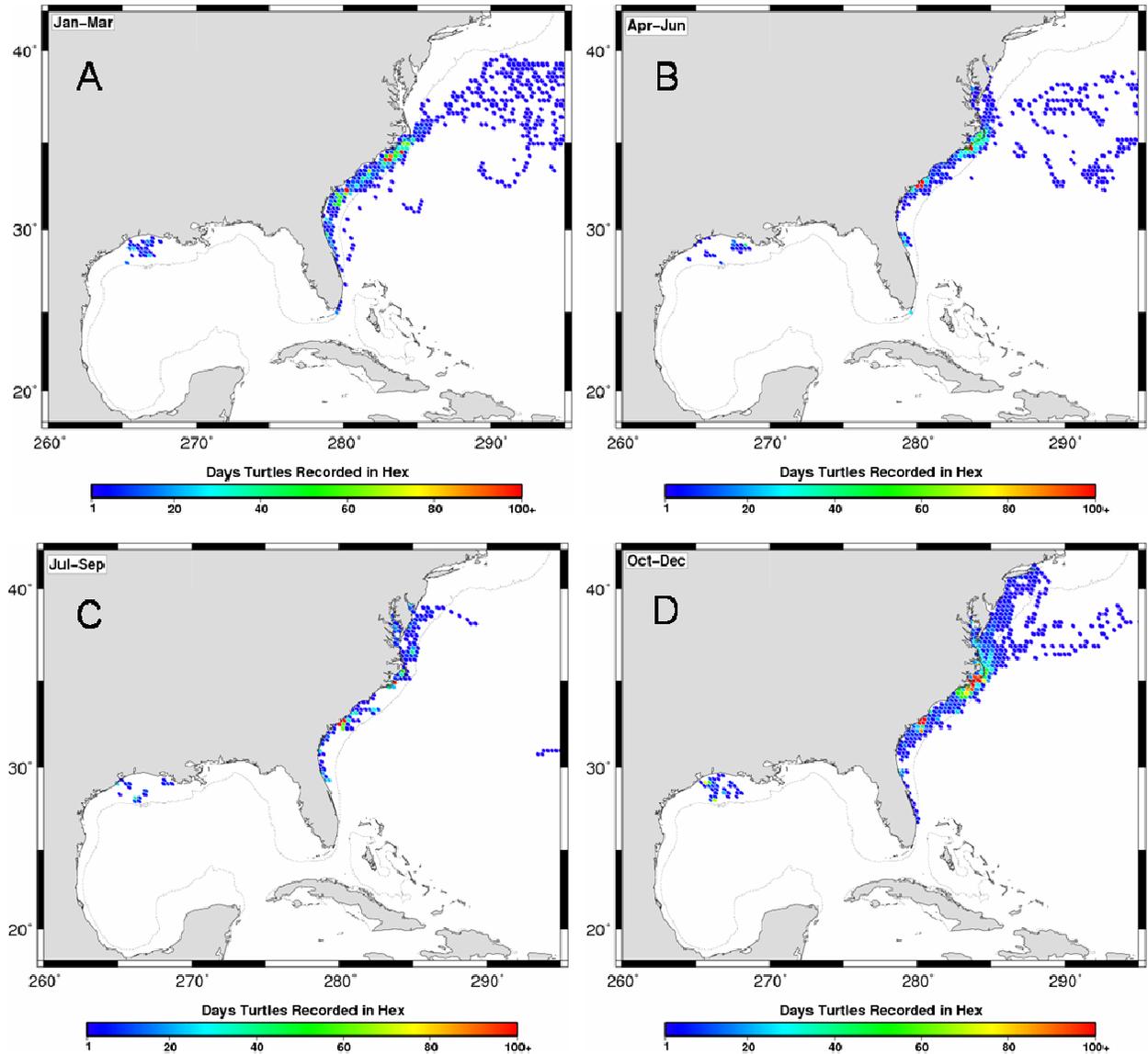
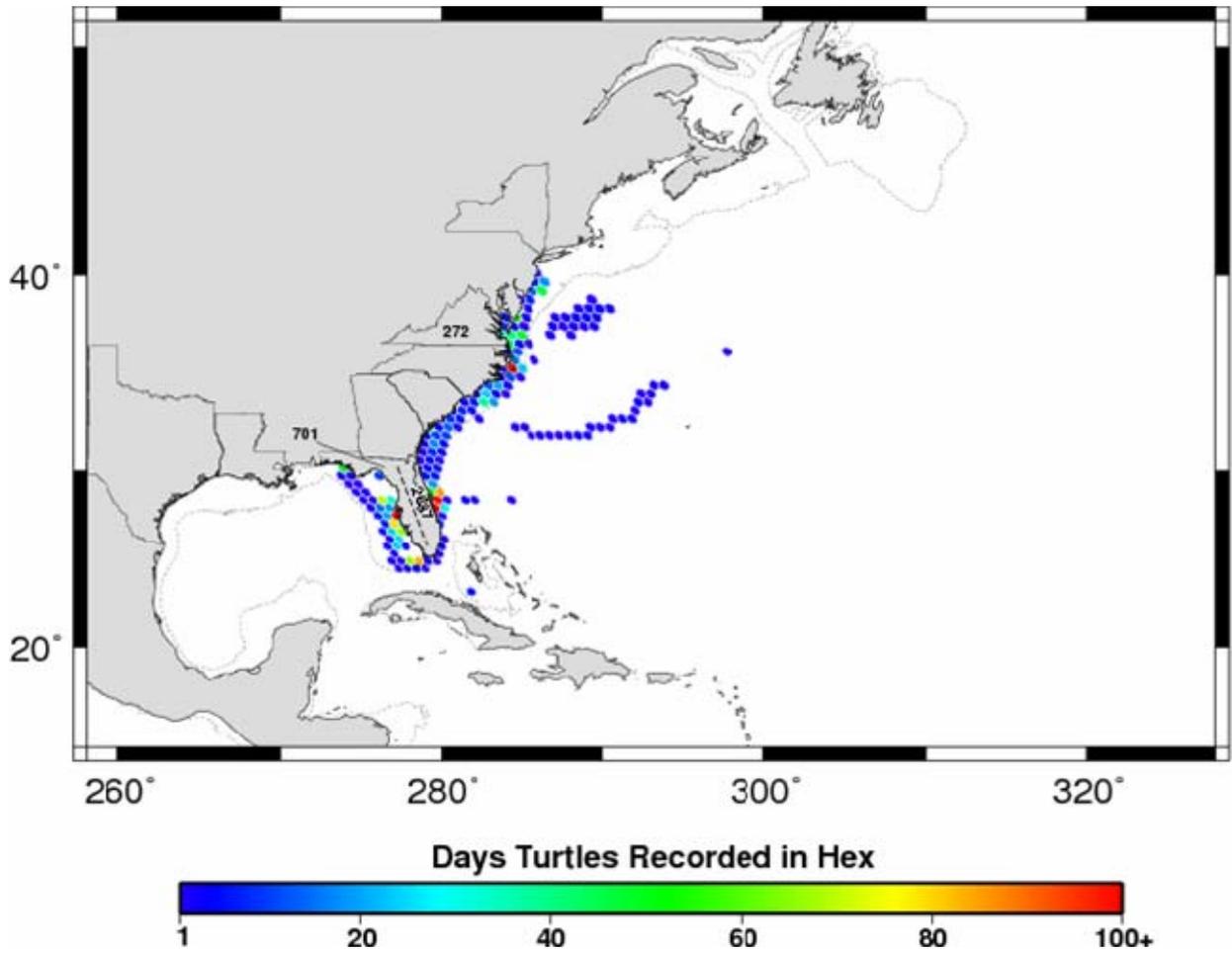


Figure 7. Movements and habitat use of all male loggerhead sea turtles (n=36 animals; 2,612 days). Days tracked from release state are indicated within respective state borders. Florida split into east and west coast release locations. Bathymetric contour line=200 m. There are two hexes per degree; each hex represents approximately 2,686 km². The longitudes are based on 360°, starting at 0 from the Prime Meridian moving east.



Figures 8A-D. Seasonal movements and coastal habitat use of all male loggerhead sea turtles (n=36 animals; 2,612 days). Maps are zoomed to coastal region. (A) Winter, January through March (n=7 animals; 189 days). (B) Spring, April through June (n=36 animals; 1,448 days). (C) Summer, July through September (n=24 animals; 702 days). (D) Fall, October through December (n=9 animals; 273 days). Bathymetric contour line=200 m. There are four hexes per degree; each hex represents approximately 669 km². The longitudes are based on 360°, starting at 0 from the Prime Meridian moving east.

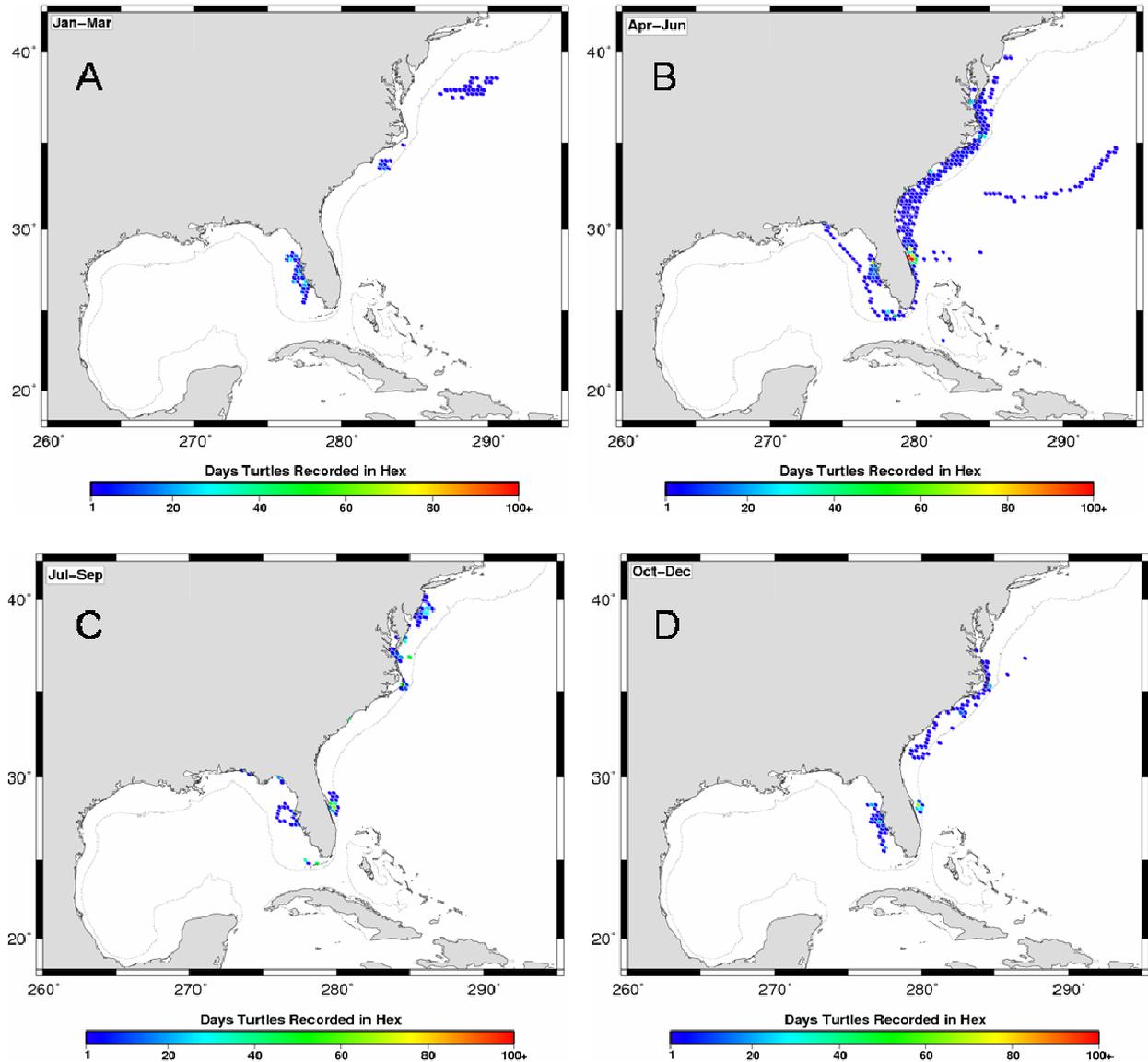
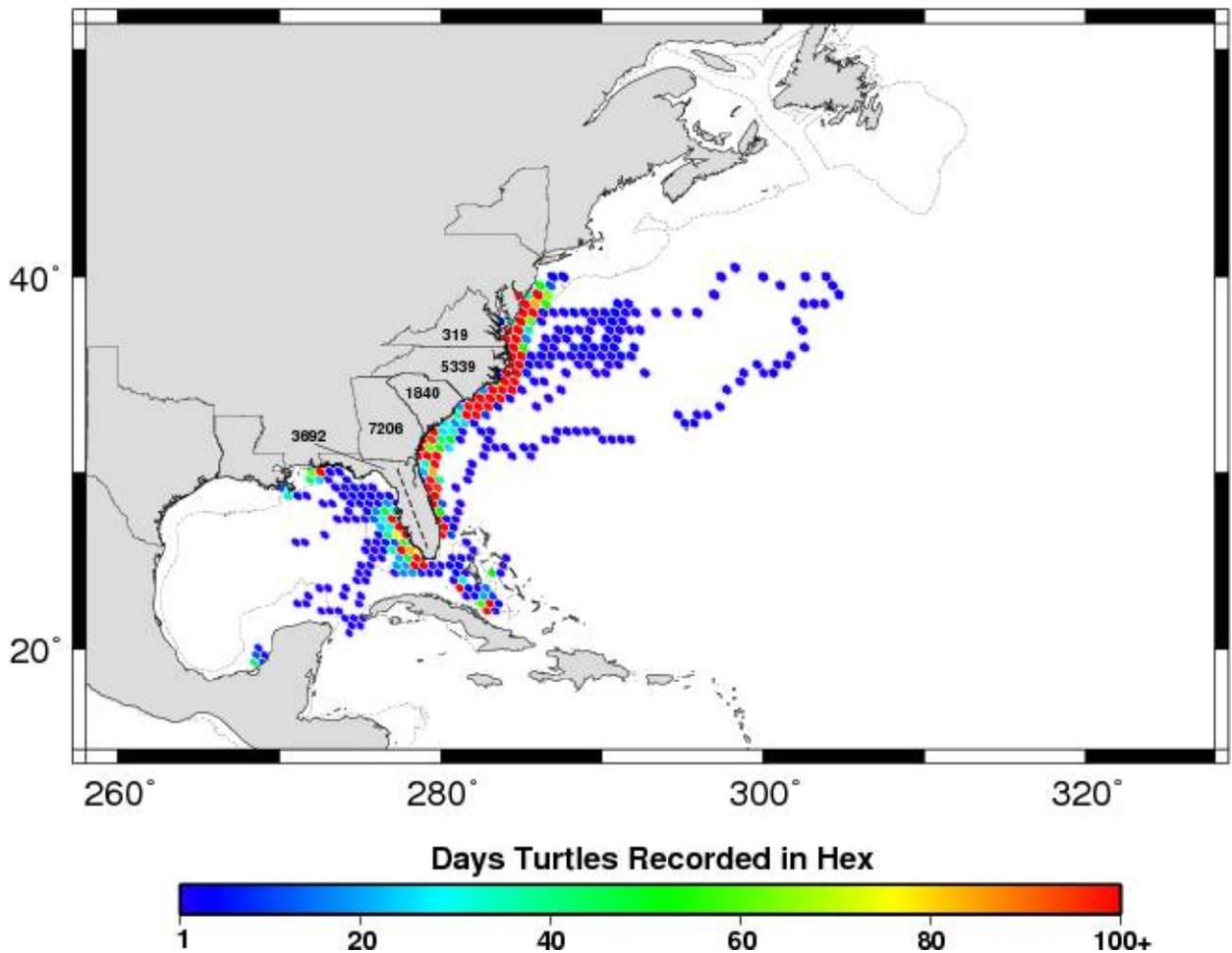
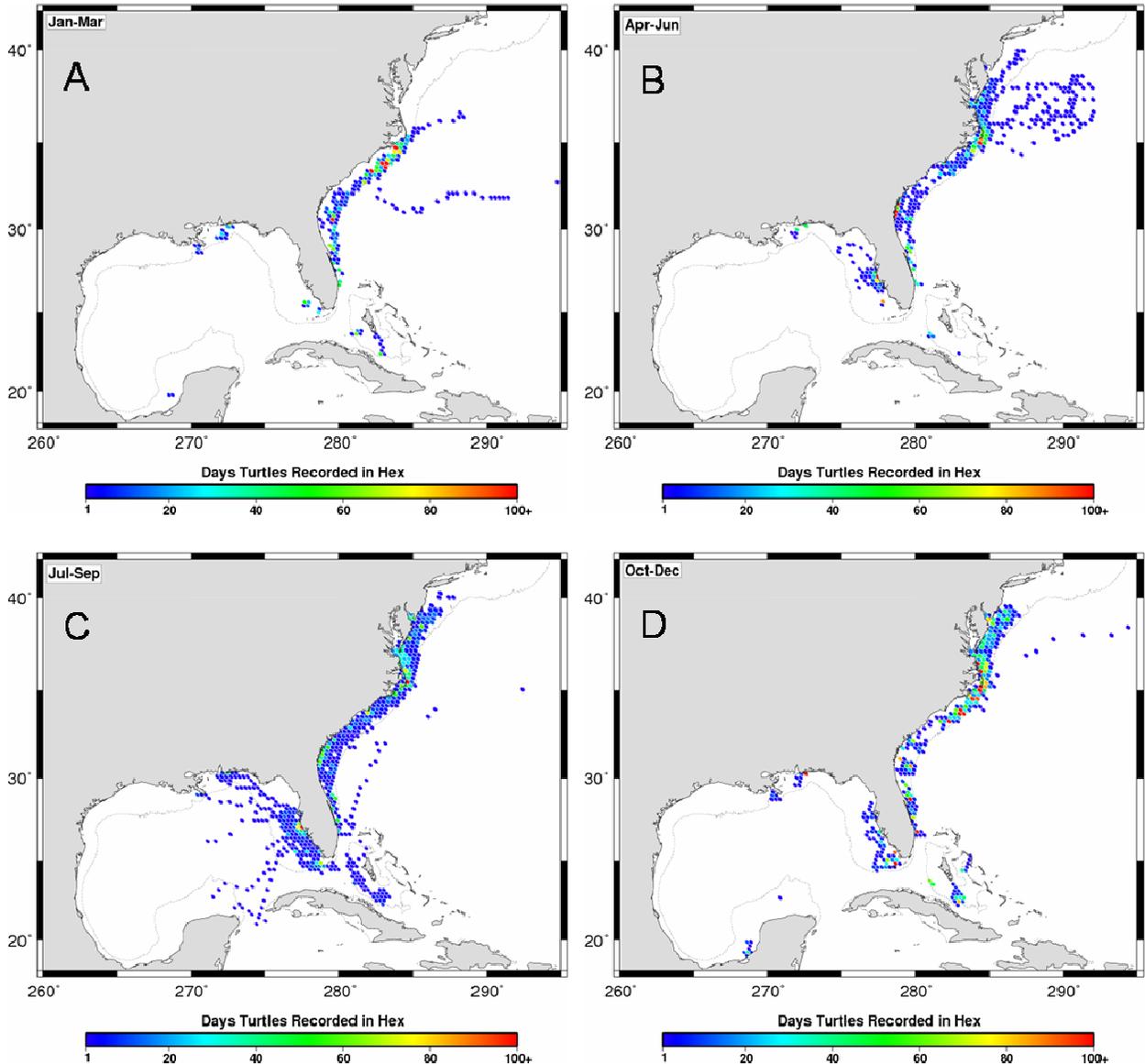


Figure 9. Movements and habitat use of all adult female loggerhead sea turtles (n=99 animals; 11,863 days). Days tracked from release state are indicated within respective state borders. Florida is split into east and west coast release locations. Bathymetric contour line=200 m. Note that 38 nesting Florida females not included in these analyses are represented in **Figure 12**. There are two hexes per degree; each hex represents approximately 2,686 km². The longitudes are based on 360', starting at 0 from the Prime Meridian moving east.



Figures 10A-D. Seasonal movements and coastal habitat use of all adult female loggerhead sea turtles (n=99 animals; 11,863 days). (A) Winter, January through March (n=54 animals; 1,895 days). (B) Spring, April through June (n=74 animals; 2,456 days). (C) Summer, July through September (n=99 animals; 3,279 days). (D) Fall, October through December (n=74 animals; 4,233 days). Bathymetric contour line=200 m. Note that 38 nesting Florida females not included in these analyses are represented in **Figure 12**. There are four hexes per degree; each hex represents approximately 669 km². The longitudes are based on 360', starting at 0 from the Prime Meridian moving east.



Figures 11A-C. Seasonal movements and habitat use of all nesting female loggerhead sea turtles by subpopulation (n=99 animals; 11,863 days). Maps are zoomed to coastal region. (A) Northern U.S. Subpopulation (n=67 animals; 9,425 days). (B) Peninsular Florida Subpopulation (n=29 animals; 1,938 days). (C) Northern Gulf of Mexico Subpopulation (n=3 animals; 500 days). Bathymetric contour line=200 m. Note that 38 nesting Florida females not included in these analyses are represented in **Figure 12**. There are four hexes per degree; each hex represents approximately 669 km². The longitudes are based on 360', starting at 0 from the Prime Meridian moving east.

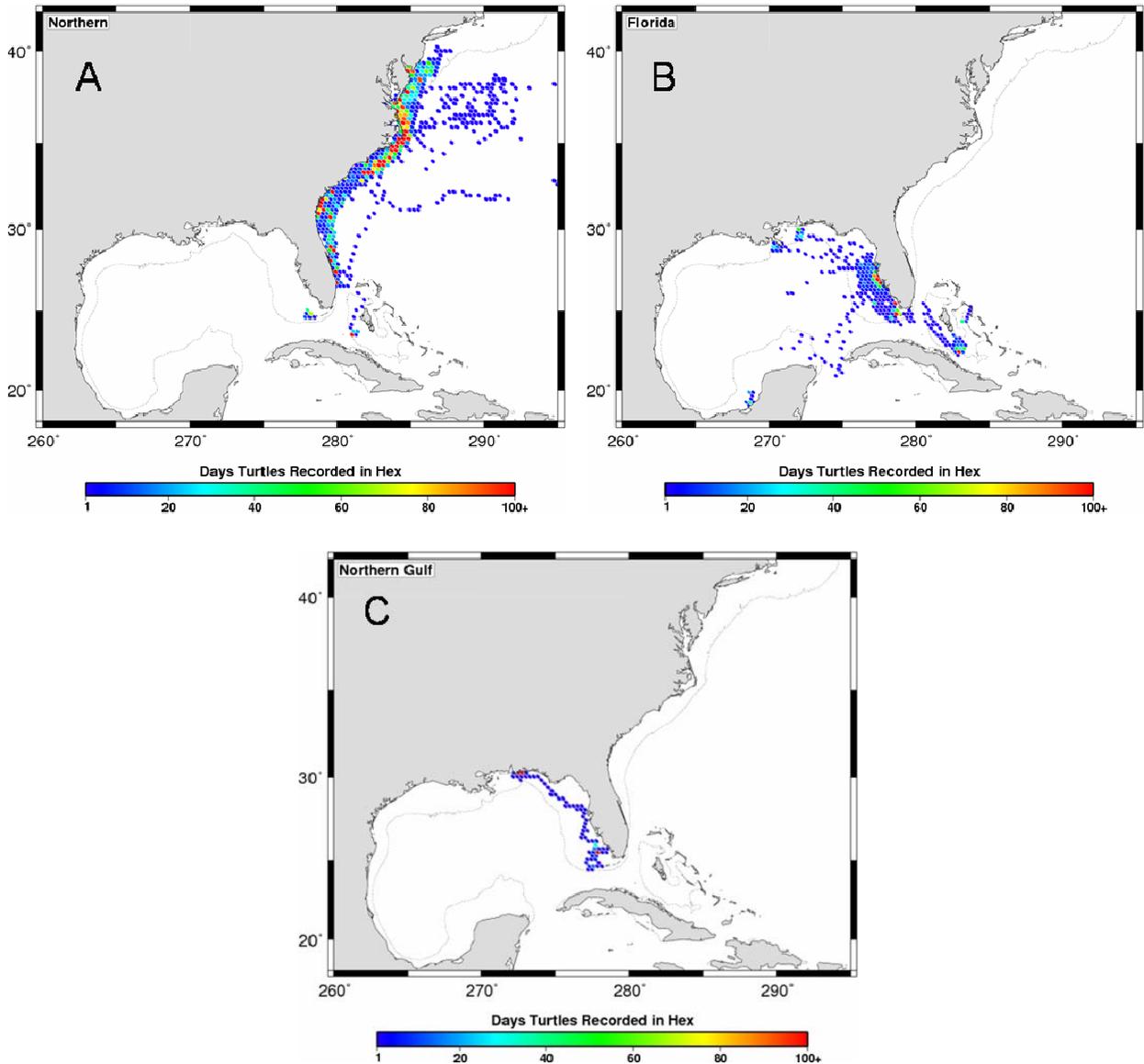
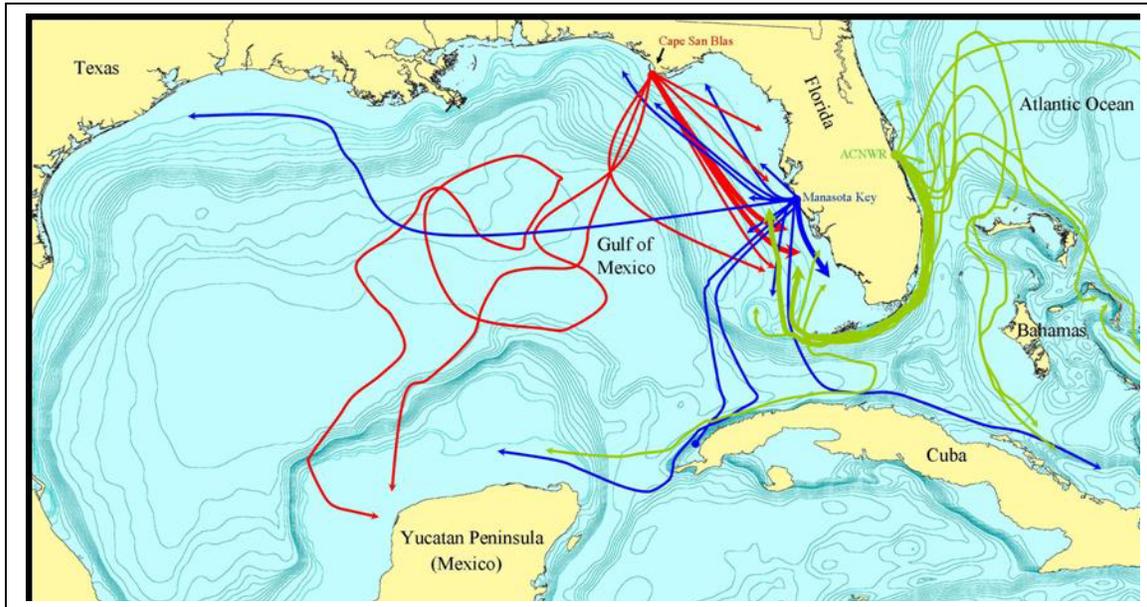


Figure 12. Post-nesting migrations of loggerhead turtles from three Florida nesting beaches: green = Archie Carr NWR; blue = Manasota Key; red = Cape San Blas. Arrowheads represent the termination of post-nesting migrations and the location of resident areas. Only one turtle was still apparently migrating when transmissions ceased (line ending in a blue circle off the northwest coast of Cuba). Thicker lines represent two or more turtles following similar migratory pathways (from Foley et al. 2008).



Aerial Survey and Shipboard Surveys

Aerial and shipboard surveys are another method to assess the in-water distribution of sea turtles within a defined study range. To identify loggerhead sea turtle distributions along the east coast of the United States and Gulf of Mexico, we used aerial and shipboard survey data that were incorporated into NOAA Fisheries Atlantic and Gulf Strategy GIS (U.S. Dept. Commerce 2001). These data originated from a variety of survey sources spanning from the late 1970s to 2002 including:

- * Department of Navy, Continental Shelf Associates
- * Minerals Management Service, Southeast Fisheries Science Center
- * North Atlantic Right Whale Consortium, which includes the following:
 - Associated Scientists at Woods Hole
 - Center for Coastal Studies
 - Cetacean and Turtle Assessment Program
 - Continental Shelf Associates
 - East Coast Ecosystems
 - Florida Marine Research Institute
 - Georgia Dept. of Natural Resources

- International Fund for Animal Welfare
- New England Aquarium
- National Marine Fisheries Service
- University of North Carolina at Wilmington
- University of Rhode Island
- Wildlife Trust

* Northeast Fisheries Science Center

* Southeast Fisheries Science Center

In general, the survey effort for these combined datasets spanned from the eastern continental shelf of North America, from Nova Scotia south to Mexico and into the Caribbean, mainly in the vicinity of Puerto Rico and the U.S. Virgin Islands. Most of the effort was concentrated along the U.S. Atlantic coastline, however, some effort and sightings did occur beyond the U.S. Exclusive Economic Zone (Figures 13-16).

The majority of these data were derived from aerial surveys, with nearly 100,000 records included in this analysis. Transect lines and loggerhead sightings data were binned by season and plotted. Winter was defined as January through March; Spring as April through June; Summer as July through September; and Fall as October through December. In addition to loggerhead sightings, we included sightings of unidentified sea turtles because it is likely many were loggerhead turtles.

Results

The majority of sightings occurred along the continental shelf approximately out to the 200 m bathymetric contour line (Figures 13B-16B). Seasonal composites (Figures 13B-16B) indicate few to no turtles occurring coastally north of 36° N, or just north of Cape Hatteras, N.C. during Winter (Figure 16B). By the Spring and Summer, turtles were found to occur in nearshore coastal waters north of Cape Hatteras, N.C., with sightings occurring frequently as far north as Cape Cod during Summer (Figures 14B, 15B). There were few turtles north of Cape Cod; some turtles were observed beyond the continental shelf, ranging as far east as approximately 60° W and between 30° N to 45° N (Figure 15B). Generally, loggerhead turtles were sighted in the northeast region south of Cape Cod during the Summer wherever there was effort, but had more restricted northern distributions during the other seasons.

Nearshore coastal surveys were infrequently conducted throughout the Gulf of Mexico; most surveys were farther offshore. When surveys did cover the nearshore areas, sightings usually were reported. This was especially true during Fall surveys off the west coast of Florida (Figure 16A), indicating a high density of loggerheads sighted during those surveys (Figure 16B).

The primary concerns associated with existing aerial survey datasets are: (1) survey consistency over time and space; (2) lack of standardization among surveys (*e.g.*, altitude, speed, methods); and (3) sea turtle detectability biases associated with seasonal diving behavior (particularly within the more temperate regions – see Nelson 1996 and Mansfield 2006). Similar issues apply to shipboard surveys where the area searched is relatively small and sea turtles are not often sighted due to their size and their detectability.

Despite these concerns, the survey data provide very broad-scale information related to sea turtle distributions along the U.S. coastline. Observed seasonal sightings are very similar to the distributions of sea turtles tracked using satellite telemetry. Although the conclusions of the aerial survey and shipboard surveys could be biased, overall these data show a similar shelf-constrained distribution (see Satellite Telemetry section, satellite Figure 13) as well as similar seasonal distributions, particularly during the winter months in the northeast (see Satellite Telemetry section, Figures 6A and 10A).

Seasonal differences in surfacing behavior may heavily bias aerial observations. Surfacing behavior may be influenced by an animal's behavior (migrating vs. foraging) or by environmental conditions (*e.g.* water temperature, particularly the vertical distribution of temperatures within the water column) (Mansfield 2006). Table 10 summarizes existing evidence obtained along the east coast of the U.S. and the Gulf of Mexico supporting this potential detectability bias.

Table 10. Summary of loggerhead surfacing behavior derived from radio tracking data and other sources. Adapted from Nelson (1996).

Location	Months	Water T	N	% t near surface	% t mid-depths	% t Bottom	Source
Canaveral, Fl.	Sept	not reported	6	3.78 (~1-2 m)			Kemmerer et al. 1983
Canaveral, Fl.	Mar-Apr	16.5 to 23.6	8	12.7 (<5 m)	22.7	64.7	Standora et al. 1997a
Canaveral, Fl.	July-Aug	19.1 to 30.7	23	26.0 (<5 m)	33.7	40.2	Standora et al. 1997b; excludes 4am-8am time interval; 21 adults, 2 subadults; 25 2-hour monitoring periods
Canaveral, Fl.	Sept	25.9 to 28.2	12	4.3 (<3 m)	12.5	83.2	Nelson and Shafer 1995
Savannah, Ga.	April-May	12.5 to 18.2	2	48.6 (<3 m)	36.9	14.6	Keinath et al. 1995
Savannah, Ga.	Oct-Nov	15.6 to 23.4	9	14.9 (<3 m)	36.9	48.2	Keinath et al. 1995
St. Marys, Ga.	April-May	18.0 to 22.3	4	38.6 (<3 m)	17.8	43.7	Nelson 1996
St. Marys, Ga.	July-Aug	27.4 to 28.3	9	24.1 (<3 m)	13.7	62.3	Nelson 1996
St. Marys, Ga.	Oct-Nov	18.6 to 23.7	6	9.6 (<3 m)	21.1	68.9	Nelson 1996
Charleston, S.C.	May-June	19 to 25	4	8.5 (<3 m)	39.3	52.3	Keinath et al. 1995
Charleston, S.C.	Sept-Oct	22.1 to 27.8	5	6.7 (<3 m)	18.7	74.5	Keinath et al. 1995
Chesapeake Bay Mouth	May-mid-July	18.0 to 25.0	4	9.9 (<2 m)		91.1	Mansfield 2006; % bottom incl. all t below 2 m; 2002
Chesapeake Bay Mouth	June-July	9.0 to 26.0	2	25.0 (<2 m)		75	Mansfield 2006; % bottom incl. all t below 2 m
Chesapeake Bay Mouth	July	19.0 to 26.0	1	12.3 (<2 m)		83.7	Mansfield 2006; % bottom incl. all t below 2 m
Western Chesapeake Bay	June-Oct	Warm/well mixed	14	5.3% (<2 m)		94.7	Byles 1988; % bottom inc. all t below 1-2 m
Other:							
Region	Season	Activity		% t at surface	% t submerged		Source
Gulf of Mexico	Winter				< summer		Renaud and Carpenter 1994
Gulf of Mexico	Summer				> winter		Renaud and Carpenter 1994
Mid-Atlantic	Fall	Migration		6% to 20%			Keinath 1993; satellite telemetry only

Figure 13A-B. Winter (January-March) loggerhead sea turtle sightings from aerial and shipboard surveys. (A) transect lines flown are depicted in blue; (B) observed loggerhead sightings (purple) and unidentified sea turtles (green). Bathymetric contour line = 200 m.

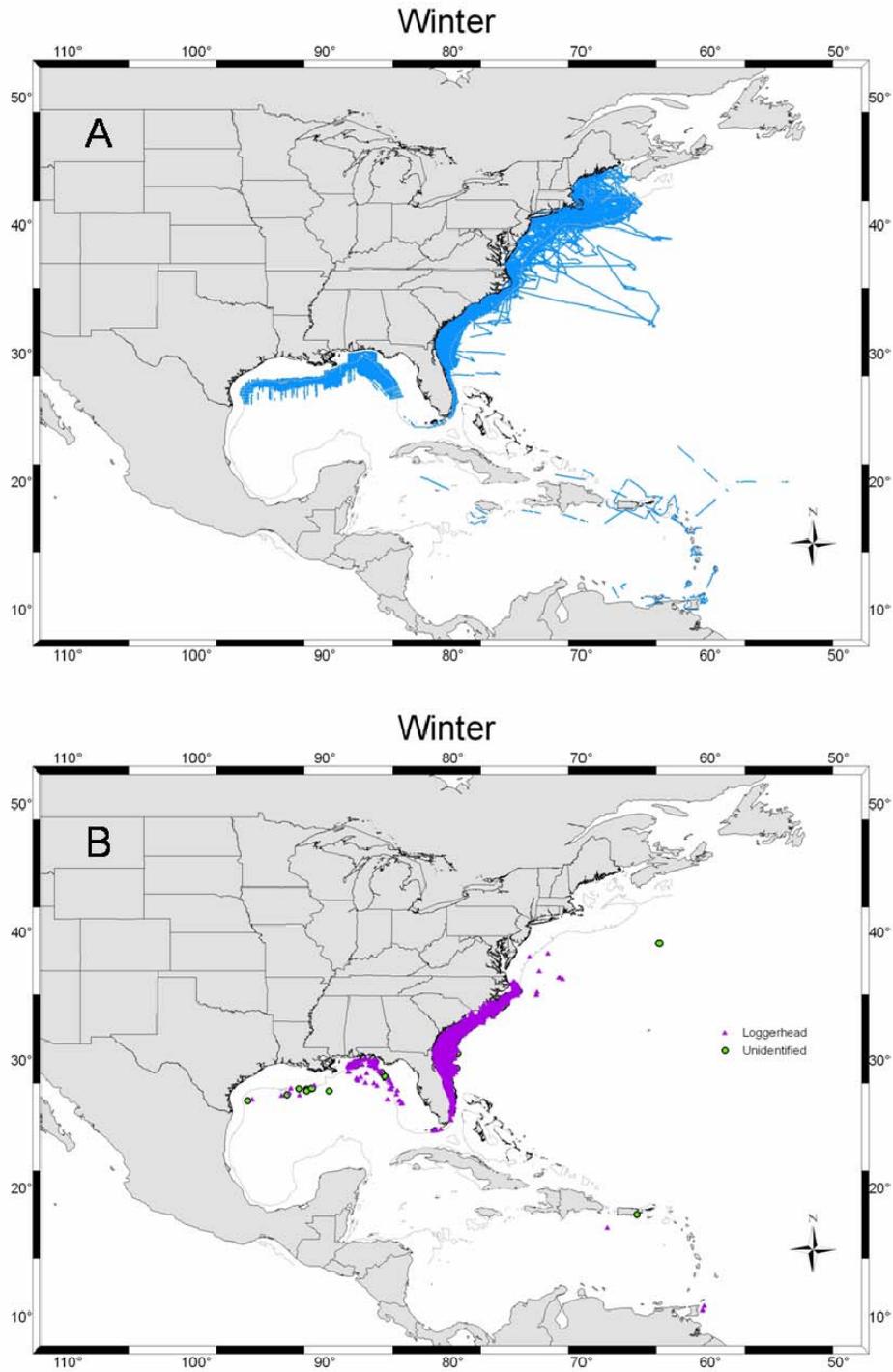


Figure 14A-B. Spring (April-June) loggerhead sea turtle sightings from aerial and shipboard surveys. (A) transect lines flown are depicted in blue; (B) observed loggerhead sightings (purple) and unidentified sea turtles (green). Bathymetric contour line = 200 m.

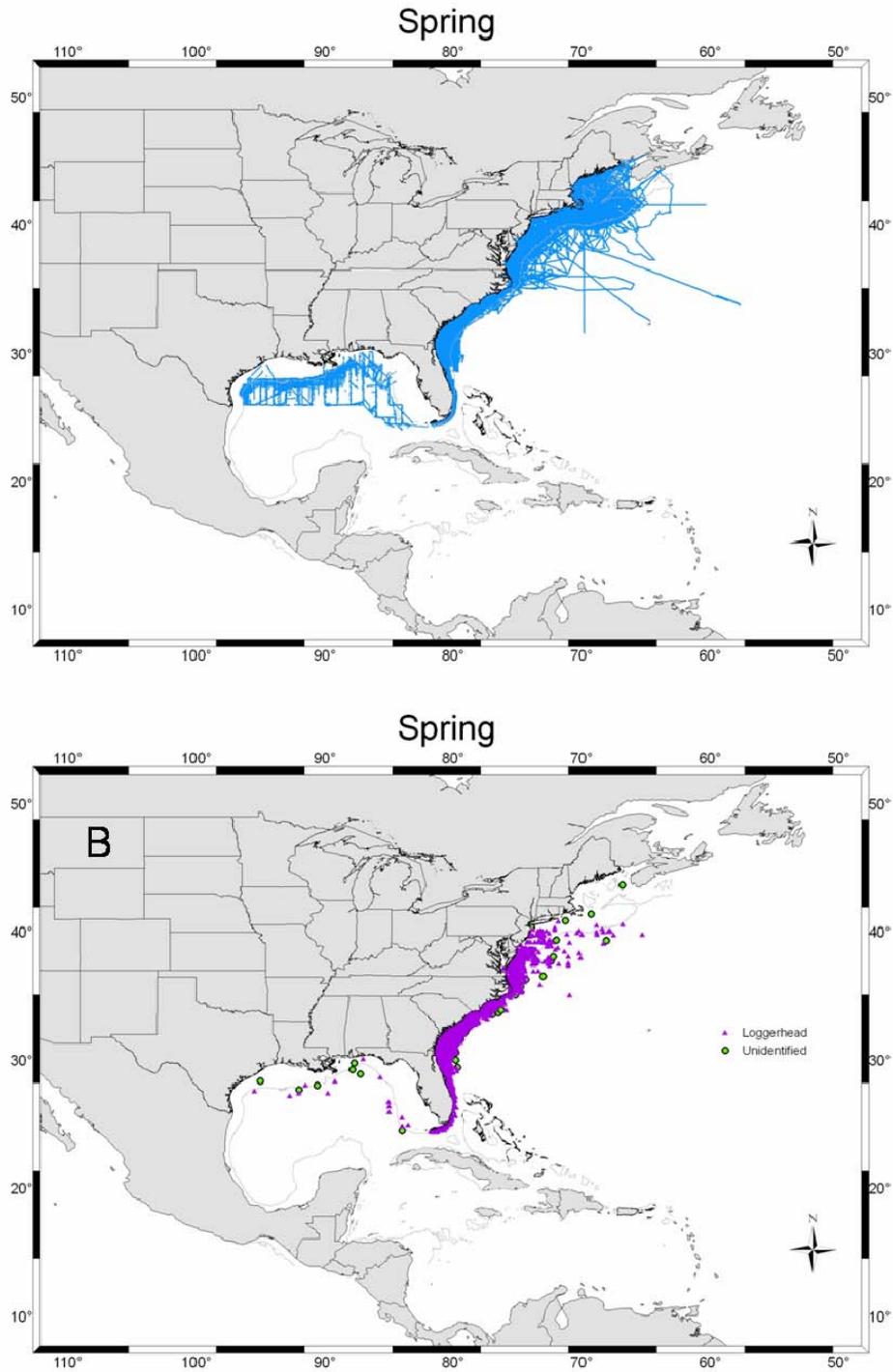


Figure 15A-B. Summer (July-September) loggerhead sea turtle sightings from aerial and shipboard surveys. (A) transect lines flown are depicted in blue; (B) observed loggerhead sightings (purple) and unidentified sea turtles (green). Bathymetric contour line = 200 m.

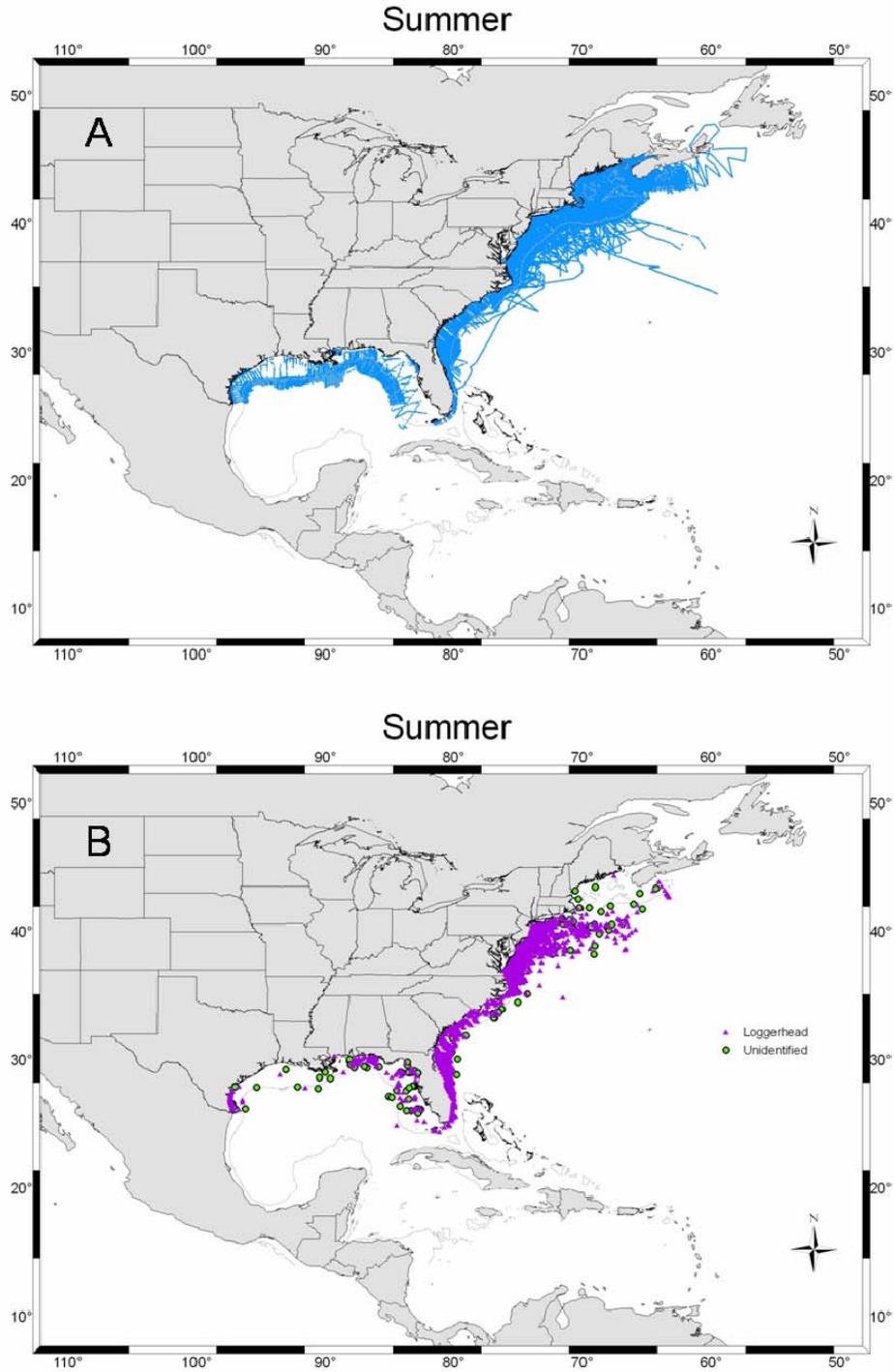
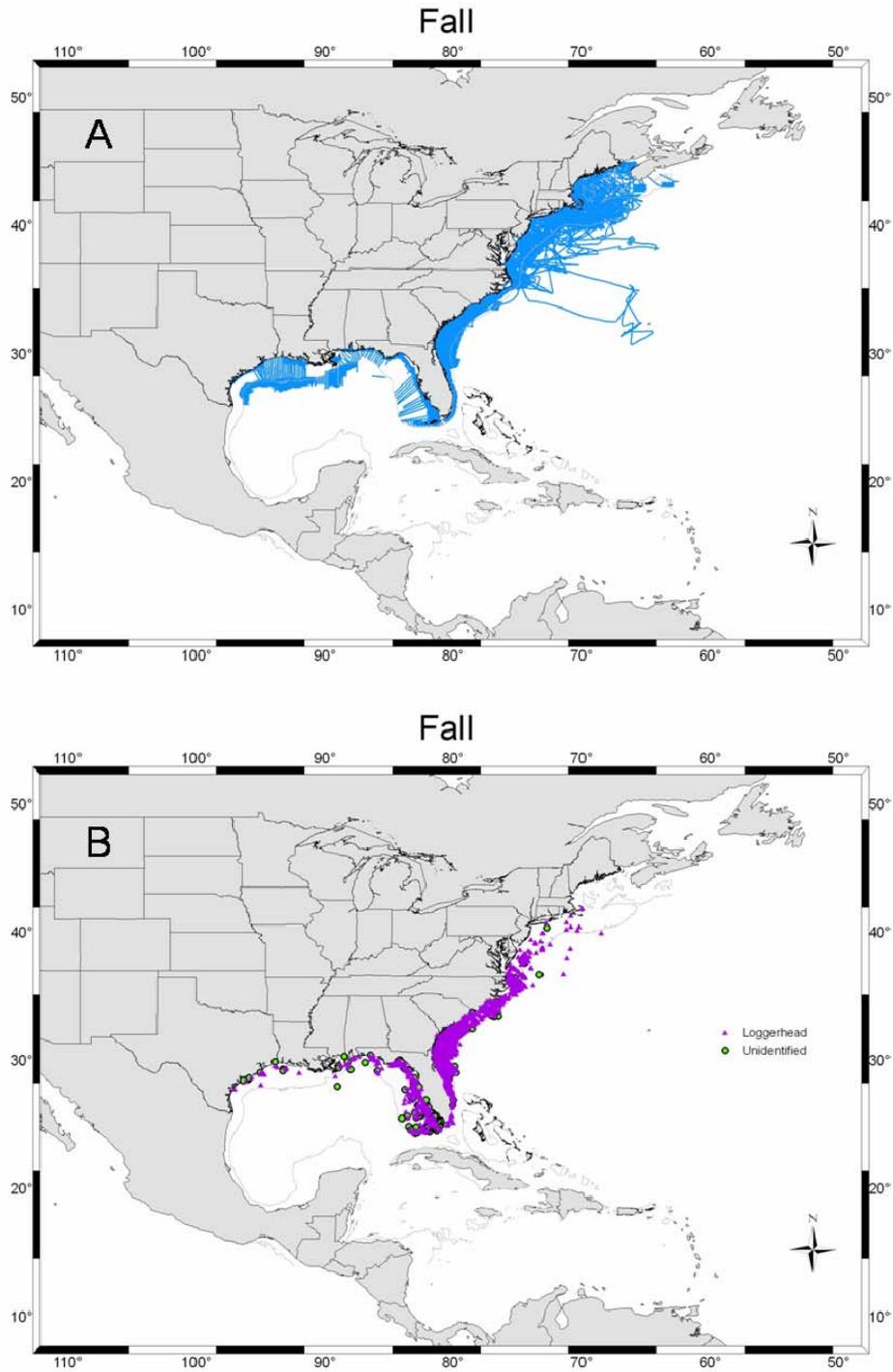


Figure 16A-B. Fall (October-December) loggerhead sea turtle sightings from aerial and shipboard surveys. (A) transect lines flown are depicted in blue; (B) observed loggerhead sightings (purple) and unidentified sea turtles (green). Bathymetric contour line = 200 m.



Overall conclusions

Despite the drawbacks associated with the different types of datasets (conventional tagging, satellite telemetry, and aerial/ship surveys), there is substantial agreement in the patterns borne out of each dataset. For instance, turtles captured and tagged within the Gulf of Mexico region likely remain within the Gulf of Mexico or more southern geographic regions (Mexico, the Caribbean) and appear less likely to range into the more northern regions along the east coast of the U.S. Seasonal residents found in waters north of Cape Hatteras, North Carolina will migrate either south of Virginia or offshore in the fall to escape the colder, winter temperatures (Lutcavage and Musick 1985; Bellmund et al. 1987; Keinath et al. 1987; Byles 1988; Keinath 1993; Morreale and Standora 1998; Mansfield 2006; see Figure 8). The analyses presented in this report support these prior studies and observations. Juveniles found within the northern region genetically represent several stocks (Rankin-Baransky et al. 2001; Bass et al. 2004; Bowen et al. 2005; Norrgard 1996).

The mid-Atlantic Bight, particularly the coastal waters off of North Carolina north to New Jersey provide important seasonal habitat to juvenile loggerheads and adult females from the Northern U.S. Subpopulation (Lutcavage and Musick 1985; Byles 1988; Keinath 1993; Mansfield 2006; Hawkes et al. 2007; McClellan and Read 2007). The shelf waters along the eastern U.S. provide important migratory habitat, particularly within the more northern temperate waters north and south of Cape Hatteras, N.C. (Shoop and Kenney 1992; Keinath 1993; Plotkin and Spotila 2002; Morreale and Standora 1998; Mansfield 2006; McClellan and Read 2007). The shelf off southwestern Florida provides important habitat for females from both the Peninsular Florida and the Northern Gulf of Mexico subpopulations.

PART II. SUBPOPULATION NESTING TRENDS

Loggerheads in the Western North Atlantic originate from many different, often widely separated, nesting beaches (Bowen et al. 2004). The reproductive output of all of these subpopulations influences the numbers of loggerheads found in this part of the world. An overall assessment of the status of loggerheads in the Western North Atlantic must consider trends in the annual numbers of nests of each of the contributing subpopulations (Table 11).

There are five loggerhead nesting subpopulations in the Atlantic and two in the Mediterranean that are known to produce more than 1,000 nests per season (Ehrhart et al. 2007a; Margaritoulis et al. 2003; Canbolat 2004). Two of these are found on beaches in the U.S. (Peninsular Florida and Northern U.S.), and one each is found in the Eastern Atlantic (primarily Cape Verde), Brazil, the greater Caribbean (primarily Mexico), Greece, and Turkey. Two smaller (< 1000 nests per year) loggerhead nesting subpopulations that have been identified in the U.S. are found in the Northern Gulf of Mexico (primarily in northwest Florida, otherwise known as the Florida Panhandle; Encalada et al. 1998) and in the Dry Tortugas (Florida) and Cay Sal Bank (Bahamas) (Francisco Pearce 2001; Bolten and Bjorndal unpubl. data). All of these nesting aggregations contribute to a greater (in the case of nesting subpopulations in the U.S., Caribbean, and possibly Cape Verde) or lesser (in the case of the subpopulations in the Mediterranean and Brazil) extent to loggerhead foraging areas of the Western North Atlantic (Bowen et al. 2004).

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For subpopulations in the Western North Atlantic, we used both simple linear regression and Bayesian state-space modeling approaches to estimate population trends based on nest census data. For each subpopulation included in these analyses, the data were from a subset of all the surveyed beaches and included only those beaches that were most consistently surveyed. Often (but not always), these beaches represented a majority of all nesting activity for each subpopulation. A description of these surveys and their percent representation of the whole subpopulation are given in the following subsections.

In the first (frequentist) approach, nest count data from these beaches were log-transformed and plotted against time. The estimated slope of the regression, β , through these data represented the natural log of the geometric growth rate of the population. We set up the null hypothesis, $H_0: \beta \geq 0$, and the alternative hypothesis, $H_0: \beta < 0$, to test if the populations declines were statistically significant. 95% confidence intervals around the estimate for population growth rates were computed using the Student's t distribution with $T-2$ degrees of freedom, where T is the length of the time series (yr). Due to the high level of interannual variability in nest census data, it can be difficult to detect statistically significant trends using this approach to trend analysis; the 95% confidence intervals for population trends based on nest census data often span from decreasing to increasing, making it difficult to state with any kind of certainty whether the trend of a given population is increasing, decreasing or stable.

To better address the uncertainties caused by interannual variability, we also estimated the annual population growth rates and the probability that nesting aggregations were declining using a Bayesian state-space modeling approach (TEWG 2007). With Bayesian methods,

uncertainty is measured in probabilities, making statements regarding uncertainty much more transparent than is possible with frequentist approaches. We followed the approach used in TEWG (2007) where the results were stated in terms of actual probability, such as ‘the average annual population growth is less than one (declining) with probability y .’ The interpretation of these results is then subjective: is a 50% probability that a population is declining cause for concern? Obviously the higher the probability, the greater is the cause for concern. In spite of the inherent subjectivity, it is often more useful to be able to report this probability than to report a trend that is not statistically different from stable.

Both approaches were applied to nest census data from the Peninsular Florida, Northern U.S., Northern Gulf of Mexico, Dry Tortugas/Cay Sal Bank, and Greater Caribbean Subpopulations. The mathematical details and assumptions for the Bayesian state-space model can be found on pages 47-48 and Appendices 1 and 2 in TEWG (2007). Matlab and winBUGs code for the model were provided by Tomo Eguchi (NMFS, Southwest Fisheries Science Center). Convergence of Markov chains for each dataset was confirmed using the convergence statistics of Gelman et al. (2004), using S-plus code from Smith (2005).

Peninsular Florida Subpopulation

Peninsular Florida hosts the largest loggerhead nesting aggregation in the Atlantic (Table 11) and one of the two largest in the world (Ehrhart et al. 2007a). Originally, loggerheads nesting in northeast Florida (north of 29° latitude) were included as a part of the subpopulation that also nests from Georgia through North Carolina (Northern Subpopulation; TEWG 1998). However, the most recent recovery plan (National Marine Fisheries Service and U.S. Fish and Wildlife Service 2008) delineates the Peninsular Florida Subpopulation as using beaches from the Florida/Georgia border to the central west coast of Florida.

A coordinated network of sea turtle nesting beach surveys in Florida began in 1979. By the mid-1990’s, these surveys included almost all of the sea turtle nesting beaches in Florida. This Statewide Nesting Beach Survey program (SNBS) provides the best data for determining the overall extent of loggerhead nesting, the beginning and ending of the nesting season, the distribution of nesting effort, and the overall number of nests. However, because of variations in survey areas and survey times, the SNBS methodology is not well suited for determining trends in the annual number of nests.

A nesting beach survey program in Florida that was intended to provide nest trend data by standardizing nesting beach survey effort began in 1989. This program, the Index Nesting Beach Survey Program (INBS), involves standardized surveys on a subset of Florida’s nesting beaches each day from May 15 through August 31. Twenty-eight nesting beach survey areas have been consistently surveyed as a part of this program since 1989. The exact methodology used by this program including efforts to assure high quality data are described in Witherington et al. (2009).

Although the beaches surveyed for the INBS program constitute only about 25% of the area where loggerheads nest in Florida, they represent an average of almost 70% of the total number of loggerhead nests in Florida each year. The number of loggerhead nests documented on these

INBS beaches each year from 1989 through 2007 is given in Figure 17. Loggerhead nesting documented annually by this program was found to have decreased from 28-31% between 1989 and 2007 and to have declined from 43-44% between 1998 and 2007 (Witherington et al. 2009). In 2008, there were 38,064 nests in 2008 on those index nesting beaches (FFWCC).

There is no indication from the SNBS data that the decrease in the annual numbers of loggerhead nests on the INBS beaches has been due to a shift of loggerhead nesting from the INBS beaches to other beaches in Florida or due to an increasing amount of loggerhead nesting before or after the INBS survey period (Witherington et al. 2009). Furthermore, the same INBS surveys in Florida that have documented declines in the annual numbers of loggerhead nests have documented substantial increases in the annual numbers of green turtle and leatherback nests over the same period of time (Witherington et al. 2009).

Results from both of our trend analyses on the INBS data also present strong evidence that this aggregation is declining in terms of the number of nests per year. In the trend analyses, we used the time series from 1989–2007 and 1998–2007 to estimate population growth rates (Table 12). The entire 19-year dataset for this subpopulation indicated an overall decline at a rate of 1.4 to 2.6 % per year. If only the last 10 years of data are considered, the data suggest a more rapid decline (6.4 to 9.1 % per year with a probability of 0.88).

Northern U.S. Subpopulation

The Northern U.S. Subpopulation nests on beaches from Georgia through North Carolina and represents the third largest loggerhead nesting aggregation in the Atlantic and the second largest in the Western North Atlantic (Table 11). Some of the nesting beach surveys in this area began in the 1960's but much of the survey effort here has been variable and cannot be used to assess trends in the annual numbers of loggerhead nests. However, a subset of eleven nesting beaches within this region has been surveyed more consistently since 1983. The number of loggerhead nests on these beaches each year during 1983-2006 is given in Figure 18. The nest total from these 11 beaches represented approximately 30% of the total loggerhead nesting for the subpopulation in 2005. A log-linear regression with an autoregressive error correction to account for temporal correlation in annual nest totals shows a significant ($P < 0.05$) declining trend of 1.6 % annually in loggerhead nesting on these beaches (GDNR unpubl. data). There were 1,159 nests in 2007 and 1,854 nests in 2008 for the Northern U.S. subpopulation which makes 2008 one of the highest counts on record.

In our analyses of the data from the 11 most consistently surveyed beaches during 1983-2005, the simple log-transformed regression and the Bayesian state-space model resulted in similar estimates for mean and median population growth rates suggesting a decline of 1.4 to 1.7% per year (Table 12). While the simple log-transformed regression was not quite significant ($P=0.062$), results of the Bayesian state-space model suggest that the decline was likely with a probability of 0.92 (Table 12).

Northern Gulf of Mexico Subpopulation

The loggerhead nesting aggregation in the Northern Gulf of Mexico is one of the smallest in the Atlantic and the second smallest in the Western North Atlantic (Table 11). Nesting in this area is concentrated in the Florida Panhandle (1995-2005 mean of 955 nests/year) with a consistent but small amount of nesting (< 50 nests) in other Gulf States, mostly Alabama. As in the rest of Florida, some nesting surveys began in the Florida Panhandle as early as 1979 and by the mid-1990's included almost all of the nesting beaches. There are three INBS beaches in the Florida Panhandle and these have been consistently surveyed since 1997.

The number of loggerhead nests documented on the three INBS beaches in the Florida Panhandle each year during 1997-2007 is shown in Figure 19. Both of the trend analyses presented here indicated a very likely decline in numbers of nests per year for these three beaches (Table 12). However, the three INBS beaches in the Florida Panhandle represented a relatively small fraction (about 17%) of the overall loggerhead nesting in this area and may not be a true indicator of the overall trend. Nevertheless, the annual numbers of loggerhead nests determined by the SNBS for the entire Florida Panhandle during the period of 1997 through 2006 indicated a similar decline (from a high of 1,212 nests in 1999 to a low of 587 nests in 2006) (FFWCC unpubl. data).

Dry Tortugas/Cay Sal Bank Subpopulation

The loggerhead subpopulation that nests in the Dry Tortugas and Cay Sal Bank is the smallest recognized here (Table 11). A survey of sea turtle nesting was conducted in the Dry Tortugas each year from 1995 to 2004, excluding 2002 (Van Houton and Pimm 2006; FFWCC unpubl. data). The range of loggerhead nests counted was 134 to 242. The annual numbers of loggerhead nests documented in the Dry Tortugas each year during this time period are given in Figure 20. Both of the trend analyses we conducted indicated a high likelihood of a declining annual number of nests in the Dry Tortugas (Table 12). Nesting on Cay Sal Bank was estimated to be between 500 and 600 nests each year as extrapolated from partial surveys conducted during 1995 and 1996 (Addison 1996; Addison and Morford 1997). No data to discern trends in annual numbers of loggerhead nests were available for Cay Sal Bank.

Greater Caribbean Subpopulation

The majority of the loggerhead nesting in the Greater Caribbean occurs in Quintana Roo, Mexico (Ehrhart et al. 2003). The loggerhead nesting aggregation in Quintana Roo is the third largest in the Western North Atlantic (Table 11). Sea turtle nesting beach surveys began here in 1984. By the early 1990's, almost all beaches in Quintana Roo where loggerhead nesting occurred were being surveyed. Eighty-five percent of loggerhead nesting is along the central coast from Punta Venado (just south of Playa Del Carmen) south to Punta Allen. There are eight nesting beach survey areas along this coast that have been consistently surveyed since 1989. These nesting beach surveys were conducted daily and encompassed the entire loggerhead nesting season, beginning on May 1 and ending on October 31. These eight beaches included only about 10% of the overall area where loggerheads nest in Quintana Roo but contained an average of almost 65% of all the loggerhead nests documented in Quintana Roo.

The total number of loggerhead nests on these beaches each year from 1989 to 2006 is shown in Figure 21. In our trend analyses of nesting numbers on the eight most consistently surveyed beaches, the log-transform regression for the entire time series indicated no trend. However, over the same time period, the Bayesian state-space model indicated that the population was declining at a rate of ~3.8% per year with a probability of 0.9589 (Table 12). For the time period from 1995-2006, both of the trend analyses indicated a steep decline of >5% per year. For the log-transform regression this was significant and the Bayesian state-space model indicated a 99.1% probability that the population was declining (Table 12).

As in the Peninsular Florida Subpopulation, there was no indication that loggerhead nesting shifted from the eleven beaches used to indicate annual trends in the numbers of nests to other beaches. The total number of loggerhead nests documented each year in Quintana Roo showed a similar type of trend as that of the eight most consistently surveyed beaches during the period of 1989-2006. The annual numbers of nests on all of the beaches increased from an average of 1,407 during 1989 through 1993 to an average of 2,121 during 1995 through 1999, and then decreased to an average of 1,404 during 2002 through 2006. In 2007 there were 1,535 and in 2008 there were 2,137 nests. Also, as in Peninsular Florida, the same beaches that have documented a recent decline in the annual numbers of loggerhead nests have also documented an increase in the annual numbers of green turtle nests (J. Zurita unpubl. data).

Other Atlantic and Mediterranean Subpopulations –Allen Foley

Eastern North Atlantic

Loggerhead nesting in the Eastern North Atlantic is concentrated in the Cape Verde Archipelago (López-Jurado et al. 2000; Cruz et al. 2007; Loureiro, 2008). On mainland Africa, there is minor nesting on the coast from Mauritania and Senegal (Brongersma 1982; Arvy et al. 2000). Earlier reports of loggerhead nesting in Morocco and Western Sahara (Marquez M. 1990) have not been confirmed in recent years (Tiwari et al. 2001). Nesting has not been reported from Macaronesia (Azores, Madeira Archipelago, The Selvagens Islands, and the Canary Islands), other than in the Cape Verde Archipelago (Brongersma 1982).

Cape Verde Subpopulation

The Republic of Cape Verde is an archipelago of ten main islands and several islets situated about 500 km off the coast of Senegal. Loggerhead nesting occurs primarily on the easternmost islands of Boa Vista, Sal, and Maio with some nesting also known from Santa Luzia, São Vicente, and Santiago (López-Jurado et al. 2000; Cruz et al. 2007, Loureiro 2008, N. Varo-Cruz pers. comm.). Regular nesting surveys have only been conducted on Boa Vista. These surveys have been conducted since 2001 on only 3.1 km of the approximately 55 km of suitable nesting beach on that island (Cruz et al. 2007, N. Varo-Cruz pers. comm.). During the period of 2001-2004, an annual average of 1,771 loggerhead nests was documented on this stretch of beach. The highest annual total was 2,728 loggerhead nests during 2004 (N. Varo-Cruz pers. comm.).

Intermittent surveys conducted recently on other beaches in Cape Verde indicate that the total number of loggerhead nests each year on all the beaches of Boa Vista could be as high as 10,000

and that the number of loggerhead nests on the other islands each year could be as high as 5,000 (N. Varo-Cruz pers. comm.). Based on these observations, we more conservatively estimate that the number of loggerhead nests each year in the Republic of Cape Verde during 2001 through 2004 was about 10,000. If more consistent and comprehensive future nesting beach surveys validate this estimate (or show it to be a likely underestimate), the Republic of Cape Verde will be recognized as hosting the second largest loggerhead nesting aggregation in the Atlantic (Table 11). No data were available to discern trends in the annual numbers of loggerhead nests in Cape Verde.

Western South Atlantic

Nesting in the Western South Atlantic occurs primarily along the mainland coast of Brazil from Sergipe south to Rio de Janeiro, with peak concentrations in northern Bahia, Espírito Santo and northern Rio de Janeiro (Marcovaldi and Chaloupka 2007). In the Eastern South Atlantic diffuse nesting may occur along the mainland coast of Africa (Fretey 2001), with >200 loggerhead nests reported for Rio Longa beach in central Angola in 2005 (Brian 2007). However, other researchers have been unable to confirm nesting by loggerheads in the last decade anywhere along the South Atlantic coast of Africa, including Angola (Fretey 2001; Weir et al. 2007). There is the possibility that reports of nesting by loggerheads from Angola and Namibia (Márquez M. 1990; Brian 2007) may have been misidentified nesting by olive ridley turtles (Brongersma 1982; Fretey 2001). At the current time, it is not possible to confirm that regular nesting of loggerheads occurs along the Atlantic coast of Africa south of the equator.

Brazil Subpopulation

The loggerhead nesting subpopulation in Brazil is relatively large (Table 11) but probably contributes only a few individuals to the Western North Atlantic foraging grounds (Bowen et al. 2004). Nesting beach surveys in Brazil began on the major loggerhead nesting beach at Praia do Forte in the state of Bahia in 1982, but comprehensive nesting surveys along the entire coast of Brazil did not begin until the 2002/2003 nesting season. Since 1988, there have been consistent nesting beach surveys on 22 beaches in the states of Bahia and Espírito Santo (Marcovaldi and Chaloupka 2007). These beaches cover only about 23% of the available loggerhead nesting beaches in Brazil but contain more than 75% of the loggerhead nesting there. The numbers of loggerhead nests made each year on the consistently surveyed nesting beaches in Bahia and Espírito Santo have increased during the period of 1988-2004, with >4,800 nests total laid per year (Marcovaldi and Chaloupka 2007).

Mediterranean Sea

Nesting occurs throughout the central and eastern Mediterranean, on the shores of Italy, Greece, Cyprus, Turkey, Syria, Lebanon, Israel, the Sinai, Egypt, Libya, and Tunisia (Sternberg 1981; Margaritoulis et al. 2003; SWOT 2007). Sporadic nesting also has been reported in the Western Mediterranean, on Corsica (Delaugerre and Cesarini 2004), southwestern Italy (Bentivegna et al. 2005) and on the Spanish Mediterranean coast (Tomás et al. 2003). Most (>80%) of the loggerhead nesting in the Mediterranean occurs in Greece and Turkey (Margaritoulis et al. 2003).

Greece Subpopulation

In Greece, about 60-65% of the loggerhead nesting occurs on beaches in Laganas Bay (annual mean of 1,294 nests) or Kyparissia Bay (annual mean of 580 nests) (Margaritoulis and Rees 2001; Margaritoulis et al. 2003; Margaritoulis 2005). Consistent nesting beach surveys have been conducted at both sites since 1984. No overall increase or decrease in the annual numbers of loggerhead nests have been detected in either area (Margaritoulis and Rees 2001; Margaritoulis 2005). In contrast, the annual number of loggerhead nests laid at Rethymno Beach on the Island of Crete is 387 (accounting for about 10% of loggerhead nesting in Greece), and recently is reported to be declining (Margaritoulis et al. 2009).

Turkey Subpopulation

Loggerhead nesting in Turkey is somewhat evenly spread across 14 known nesting areas, with an annual average of 1,366 nests (Margaritoulis et al. 2003). Intermittent nesting surveys have been conducted in Turkey since the 1970's but more consistent surveys on some of the beaches have only been conducted since the 1990's (Margaritoulis et al. 2003). At Fethiye, the annual number of loggerhead nests has declined over the 12-year period from 1993 through 2004 (Ilgaz et al. 2007). Loggerhead nesting at Fethiye represents about 10% of the overall nesting in Turkey (Margaritoulis et al. 2003).

Summary

The three largest nesting subpopulations responsible for most of the production in the Western North Atlantic - Peninsular Florida, Northern U.S. and Mexico (Quintana Roo) - are all known to be decreasing since the late 1990's or longer (Table 11 and 12). The relationship between the trends on these beaches is striking (Table 13). The strong correlation between these beaches suggests that a similar mechanism is driving the trends on these beaches. The other smaller nesting subpopulations in the Western North Atlantic are also decreasing but the time series are shorter so it is difficult to discern a meaningful trend. Cape Verde may in fact be a large nesting subpopulation, but lack of consistent monitoring leaves many unknowns and does not allow us to perform any trend analyses. Brazil, in the Southern Atlantic, is the only rookery where an increasing trend is noted but this is based on a short time series and this rookery contributes very little to the Western North Atlantic.

Based on the overall trend that is correlated among all of the beaches in the Western North Atlantic, the decline is likely real and should not be ignored. The only drawback to these nesting surveys is that none of them cover even one generation time for the loggerhead, ~50 years. Therefore, it is tough to make statements about the status of loggerheads in the North Atlantic by only examining nesting beach trends. Even with these short time series we have witnessed drastic declines in the number of nests and the cause of this is still unknown. Furthermore, because we have now experienced a period of ten years of declines in nesting we can be sure that we will see another cycle of decreased nesting as the hatchlings from this time period reach sexual maturity in roughly thirty years.

One source of supplemental information is available that could help us understand these trends more completely. The in-water data that is presented in the next section can provide insight into a greater proportion of the whole population and allow us to see cycles coming far earlier than we would if we just observed nesting females. By continuing nesting beach monitoring and combining it with all other supplementary sources of trend data for juveniles we will gain a better understanding of Western North Atlantic loggerhead.

Table 11. Overall loggerhead nesting numbers and trends in the annual numbers of nests at each of the nine rookeries likely to contribute individuals to the Western North Atlantic.

Data used to determine the total number of nests for a given subpopulation were from all nesting surveys. Data used to determine trends for each subpopulation were from a consistently surveyed subsample of all the nesting beach survey areas for each subpopulation. See text for more details. Data for Peninsular Florida, the Florida Panhandle, and the Dry Tortugas were from the Florida Fish and Wildlife Conservation Commission (unpubl. data). Data for the Northern U.S. were from the Georgia and South Carolina Departments of Natural Resources and the North Carolina Wildlife Resources Commission (unpubl. data). Data for Cay Sal Bank were from Addison and Morford (1996) and Addison (1997). Data for Mexico were from J. Zurita (unpubl. data). Data for Cape Verde were from López-Jurado et al. (2000) and N. Varo-Cruz (pers. comm.). Data for Brazil were from Marcovaldi and Chaloupka (2007). Data for Greece were from Margaritoulis and Rees (2001), Margaritoulis (2005), and Margaritoulis et al. (2009). Data for Turkey were from Ilgaz et al. (2007) and Margaritoulis et al. (2003).

Nesting subpopulation	Total number of nests	Trend in annual # of nests
Peninsular Florida	65,460 (1989-2006 mean)	Decreasing
Northern U.S.	5,151 (1989-2005 mean)	Decreasing
Northern Gulf of Mexico	1,000 (1995-2005 estimated mean)	Decreasing (from data in the Florida Panhandle)
Dry Tortugas/Cay Sal Bank	700 (1995-2004 estimated mean)	Decreasing (from data in Dry Tortugas)
Mexico (Quintana Roo)	1,674 (1989-2005 mean)	Decreasing
Cape Verde	10,000 (1998-2004 estimated mean)	Unknown
Brazil	4,535 (2003-2004 mean)	Increasing
Greece	3,000 (recently estimated mean)	Stable or decreasing
Turkey	2,000 (1979-2000 estimated mean)	Decreasing

Table 12. Results of the log-transformed regression analyses and the Bayesian state-space model for estimating annual population growth rate (λ). The nest census data used in these analyses were from a consistently surveyed subsample of all the nesting beach survey areas for each subpopulation. See text for more details. For the log-transformed regressions, mean and 95% confidence intervals (C.I.) are presented along with the P value for the regression ($P < 0.05$ indicates the reported population growth rate is statistically significantly less than one). Median and 95% prediction intervals for the posterior distribution (P.I.) of λ are reported as well as the probability that the population is increasing, $\text{Pr}(\lambda > 1.0)$. All trends were based on numbers of nests per year.

Subpopulation	Duration of data	Log-transformed regression		Bayesian state-space Model	
		Mean λ [95% C.I.]	P $H_A = \lambda < 1$	Median λ [95% P.I.]	$\text{Pr}(\lambda < 1.0)$
Northern U.S. (11 beaches from Georgia to North Carolina)	1983 – 2005; 23 yr	0.983 [0.962, 1.005]	0.062	0.986 [0.968, 1.007]	0.922
Peninsular Florida (Core Index Beaches)	1989-2007; 19 yr	0.974 [0.957, 0.991]	0.003	0.984 [0.969, 1.050]	0.766
Peninsular Florida (Core Index Beaches)	1998-2007; 10 yr	0.913 [0.894, 0.932]	< 0.001	0.938 [0.908, 1.010]	0.908
Northern Gulf of Mexico (Florida Panhandle Index Beaches)	1997-2007; 11 yr	0.937 [0.901, 0.975]	0.002	0.899 [0.852, 0.973]	0.991
Dry Tortugas/Cay Sal Bank (Dry Tortugas)	1995 – 2004; 9 yr*	0.951 [0.921, 0.982]	0.003	0.929 [0.883, 1.009]	0.963
Mexico (Quintana Roo)	1989-2006; 18 yr	0.988 [0.967, 1.008]	0.114	0.961 [0.941, 1.014]	0.947
Mexico (Quintana Roo)	1995-2006; 12 yr	0.943 [0.917, 0.970]	<0.001	0.927 [0.884, 1.010]	0.991

*Data missing for 2002; data point estimated as the mean of the data for 2001 and 2003 for the purpose of the trend analyses.

Table 13. Pearson correlation coefficients for nesting time series from Western North Atlantic loggerhead subpopulations. The nest census data used in these analyses were from a consistently surveyed subsample of all the nesting beach survey areas for each subpopulation. See text for more details. Bold coefficients are significant at $P < 0.05$. Numbers in parentheses indicate the length of years for each time series for which there was overlapping data.

Subpopulation	Northern U.S. (11 beaches from GA to NC)	Peninsular Florida (Core Index Beaches)	N. Gulf of Mexico (Florida Panhandle Index Beaches)	Dry Tortugas/Cay Sal Bank (Dry Tortugas)	Mexico (Quintana Roo)
Northern U.S. (11 beaches from Georgia to North Carolina)	1 (23)				
Peninsular Florida (Core Index Beaches)	0.531 (17)	1 (19)			
Northern Gulf of Mexico (Florida Panhandle Index Beaches)	0.304 (9)	0.753 (11)	1 (11)		
Dry Tortugas/Cay Sal Bank (Dry Tortugas)	0.397 (10)	0.741 (10)	0.892 (8)	1 (10)	
Mexico (Quintana Roo)	0.046 (17)	0.697 (18)	0.596 (10)	0.841 (10)	1 (18)

Figure 17. Number of loggerhead nests counted in the 28 Core Index Nesting Beach Survey areas of the Peninsular Florida Subpopulation from 1989 through 2007 (Florida Fish and Wildlife Conservation Commission unpubl. data). These beaches represented about 70% of loggerhead nesting in the Florida. Analyses of nesting on these beaches revealed a 28-31% decline from 1989 through 2007 and a 43-44% decline since 1998 (Witherington et al. 2009).

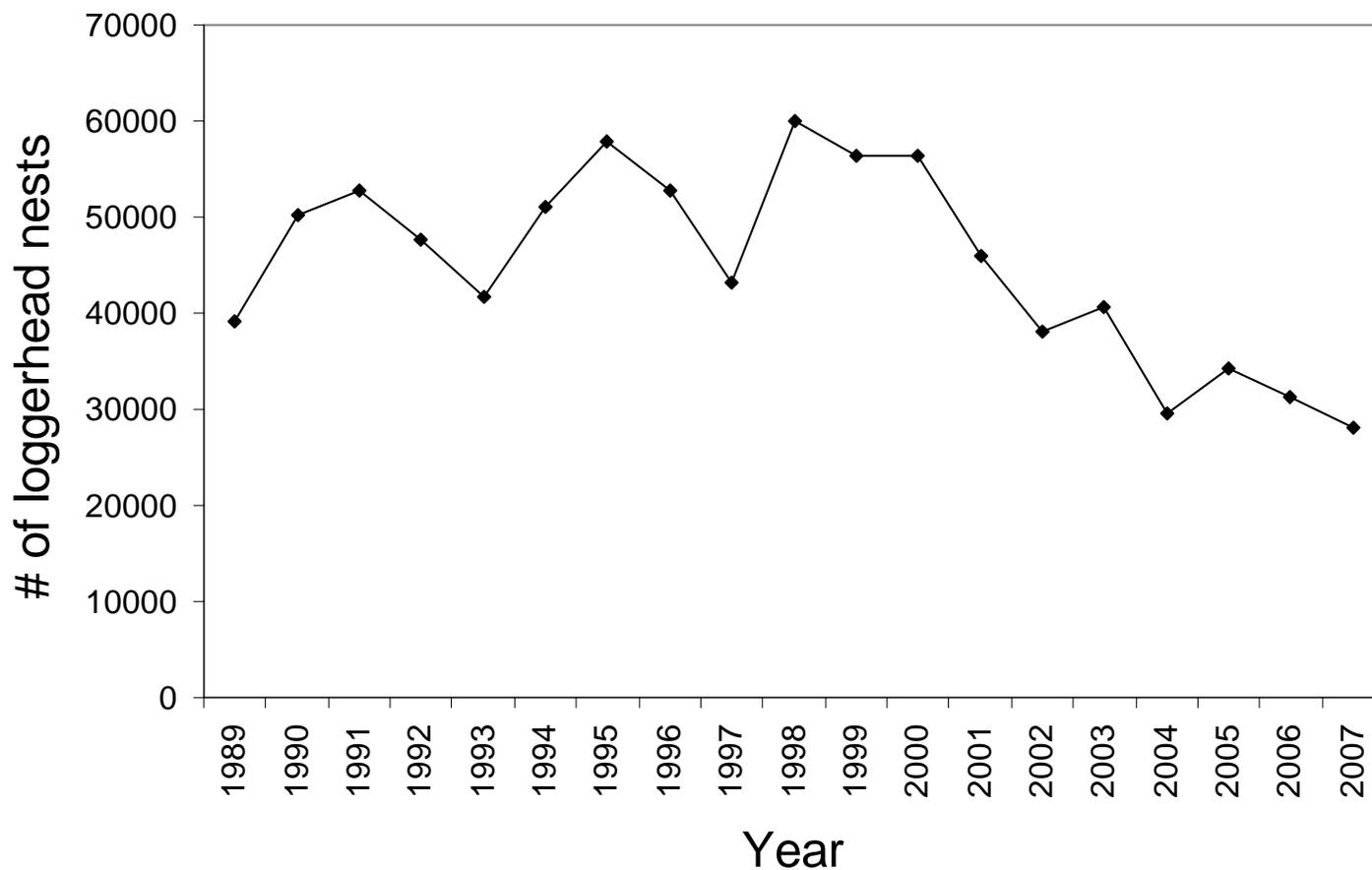


Figure 18. The number of loggerhead nests counted each year on 11 consistently surveyed beaches of the Northern U.S. Subpopulation each year during 1983 through 2006 (Georgia and South Carolina Departments of Natural Resources and North Carolina Wildlife Resources Commission unpubl. data). These beaches represented about 30% of the loggerhead nesting along this coast. The number of nests on these beaches has decreased by 1.6 % annually during this period (Georgia Department of Natural Resources unpubl. data).

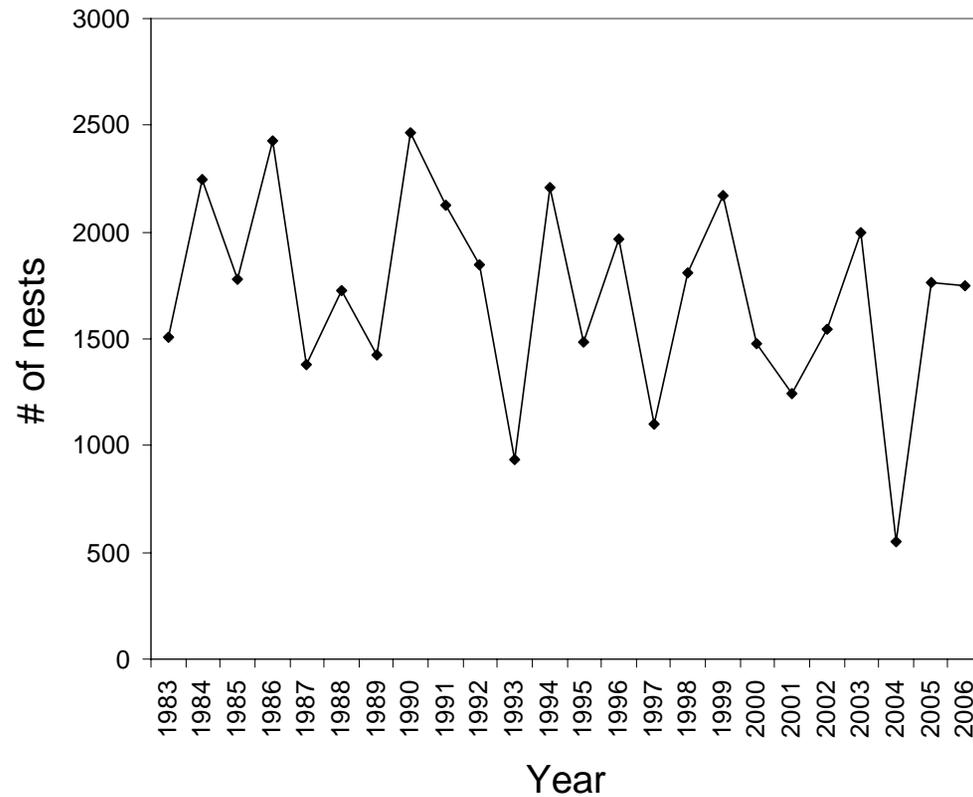


Figure 19. Number of loggerhead nests counted each year from 1997 through 2007 in three Florida Panhandle Index Nesting Beach Survey (INBS) areas (where survey effort was standardized) of the Northern Gulf of Mexico Subpopulation (Florida Fish and Wildlife Conservation Commission unpubl. data). Nesting in the Florida Panhandle represents about 95% of that for the Northern Gulf of Mexico Subpopulation and the three INBS beaches here represented about 17% of loggerhead nesting in the Florida Panhandle.

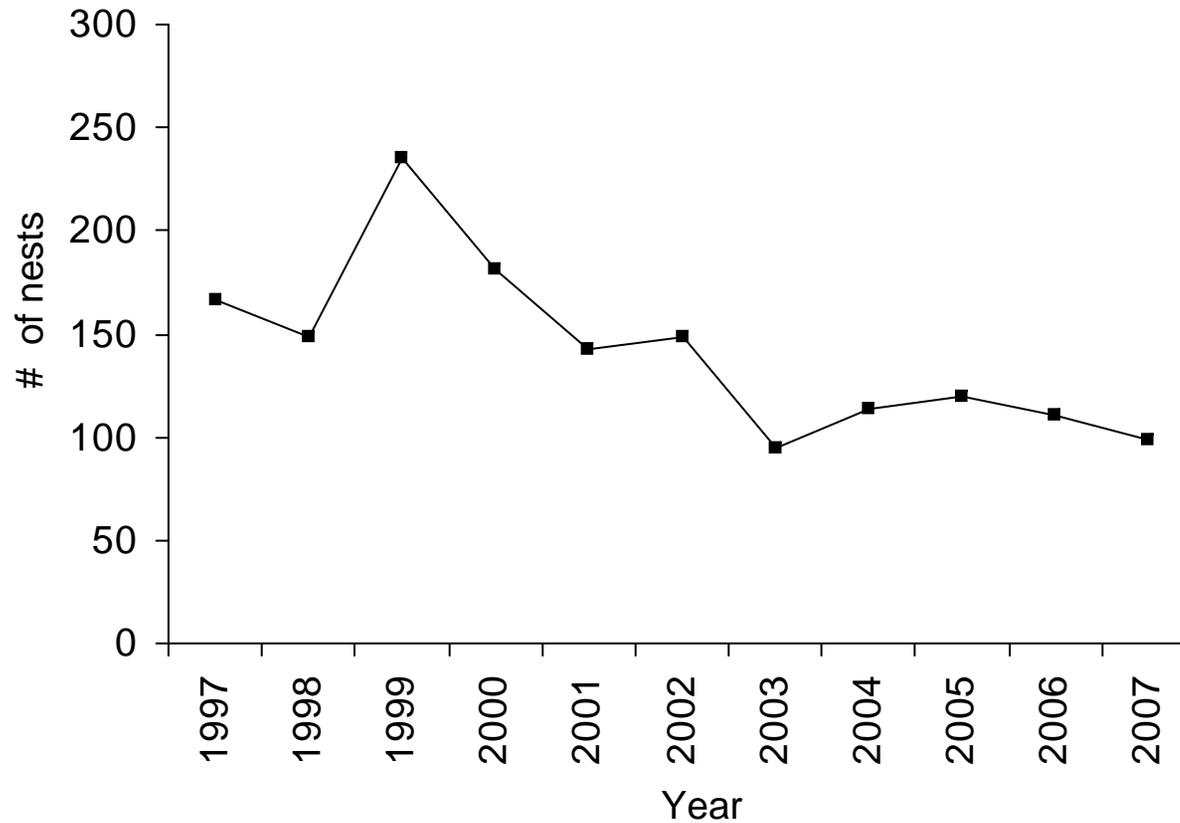


Figure 20. Number of loggerhead nests counted in the Dry Tortugas, a part of the Dry Tortugas/Cay Sal Bank Subpopulation, during 1995 through 2004 (no survey was conducted during 2002) (Florida Fish and Wildlife Conservation Commission unpubl. data).

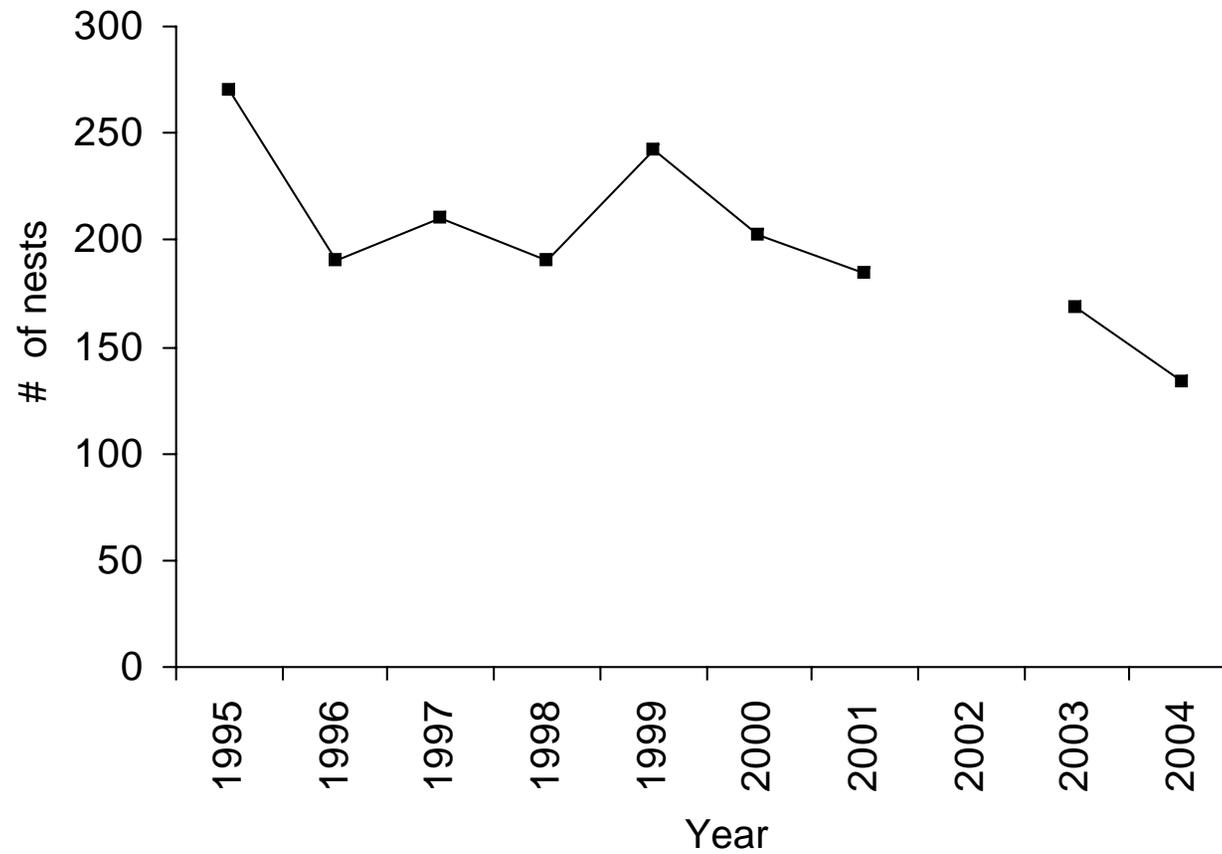


Figure 21. Number of loggerhead nests counted annually on eight beaches in Quintana Roo (Mexico Subpopulation) that were consistently surveyed from 1989 through 2006 (J. Zurita unpubl. data). These beaches represented about 65% of the loggerhead nesting in Quintana Roo.

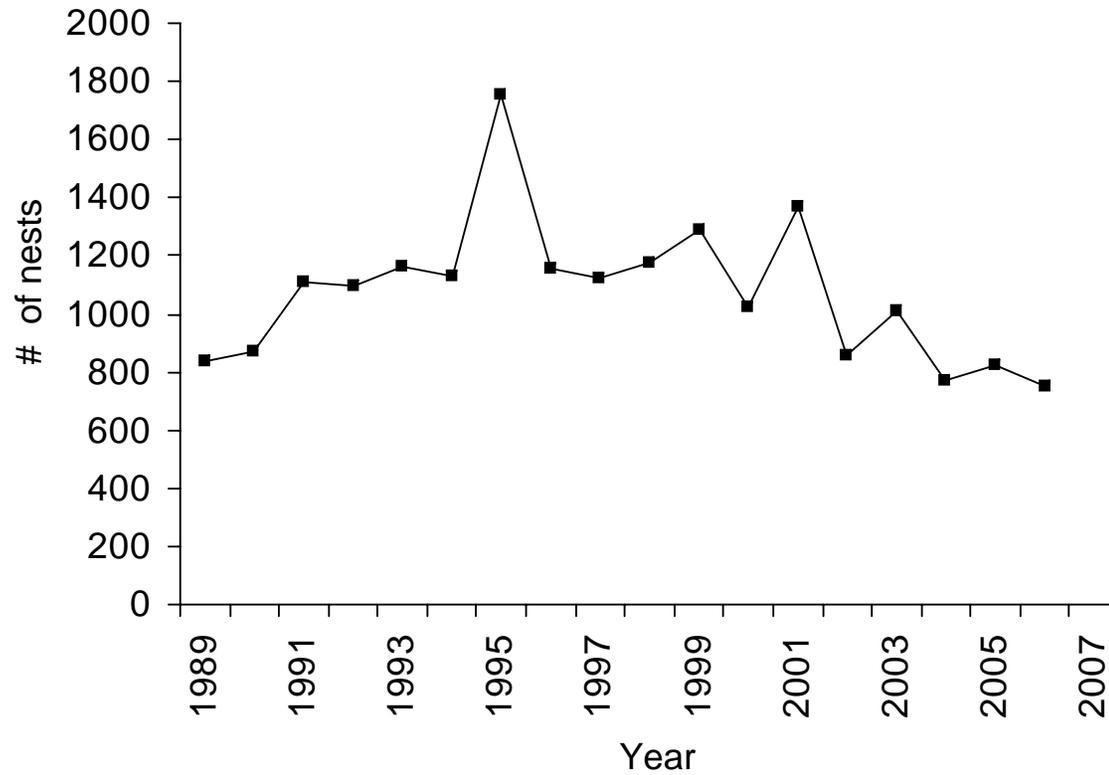
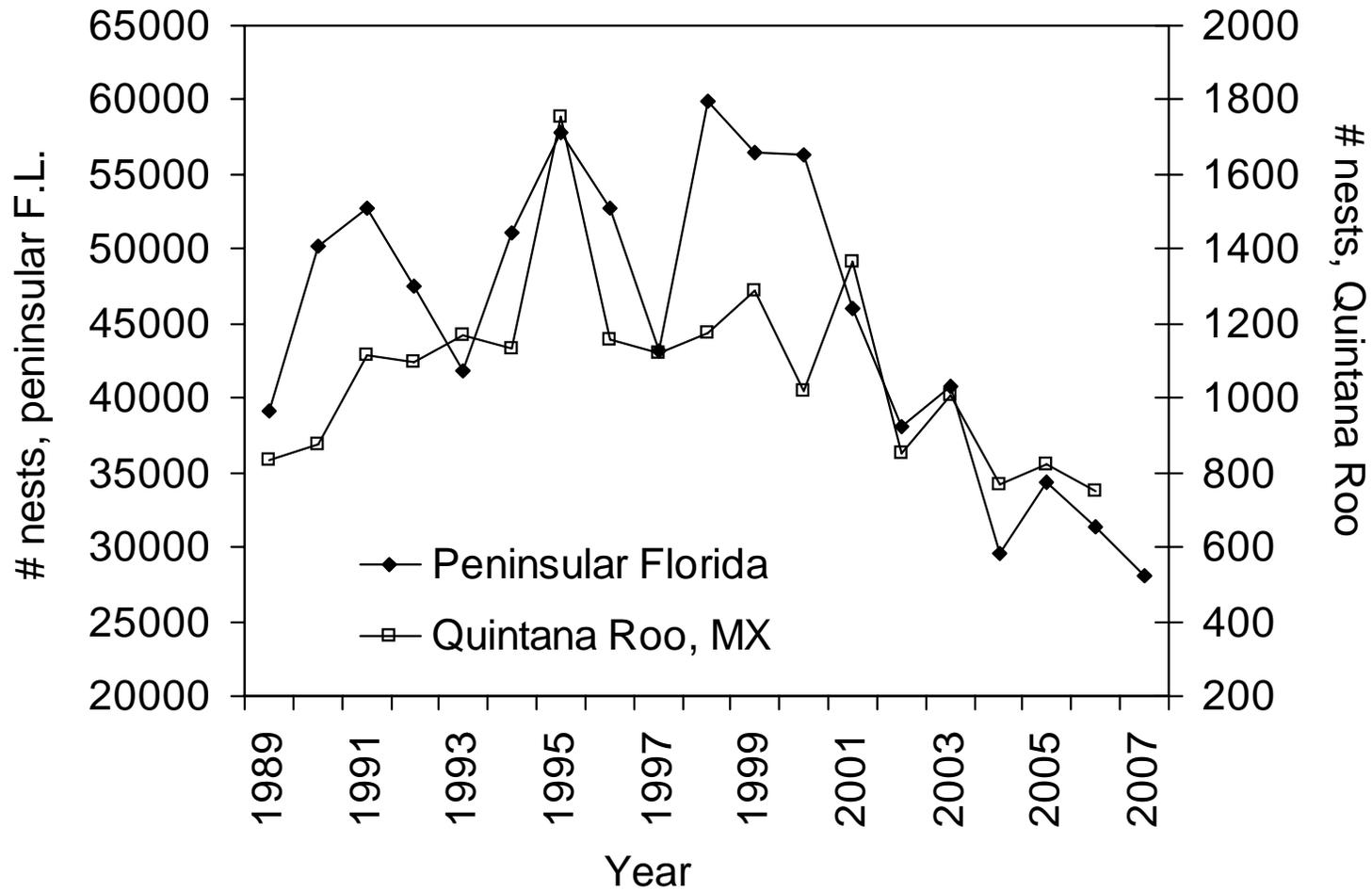


Figure 22. Annual counts of loggerhead nests in the 28 Core Index Nesting Beach survey areas of the Peninsular Florida Subpopulation compared to the annual counts of loggerhead nests on eight consistently surveyed beaches in Quintana Roo (Mexico Subpopulation). The Pearson correlation coefficient for these trends is 0.697 (P = 0.003).



PART III. IN-WATER TRENDS *Sheryan Epperly, Jason Vaughan, and Paul Richards*

We examined data from animals captured in the water as well as strandings data to look for patterns in capture rates that may indicate changes in population size and to determine if there were changes in size distributions which could indicate changes in recruitment and survival rates of the juvenile population as well as in recruitment to the adult population.

From south to north the data sources are (see citations referenced below for details on sampling methodologies):

St. Lucie Power Plant – Florida Power and Light (FP&L) has operated their nuclear power plant on Hutchinson Island, Florida since the late 1970's. Turtles are entrained with cooling water in intake pipes located in the ocean and transported into an enclosed intake canal where they are captured with a net. Records of turtle captures have been maintained since 1976 (Bresette et al. 2003). Flow through the intake pipes is directly related to the number of reactors operating at any given time, and although researchers report a decrease in turtle captures when flow is diminished, a cursory analysis by Ecological Associates, Inc., a contractor to FP&L, indicated that there was no significant relationship between flow and the number of turtles caught (M. Bresette pers. comm.). Morphometric data are collected and turtles are tagged before their release near the plant site. All of the length distribution data used in this analysis is presented as minimum straight carapace length (SCL_{min}). This measurement was not taken prior to 1980 and that is the reason data prior to this was not used in the length frequency analysis. The second unit came online in 1982, which is when we start our trend analysis.

Indian River, Florida – Entanglement nets have been set to monitor the sea turtle population in the Indian River Lagoon since 1982 (Ehrhart et al. 2007b). Effort during the first year was quite small (15 hours over 3 days in late July). Since 1983, effort was expended during May-September and, beginning in 1985, effort was expended throughout the year. A minimum of 10 days were sampled each year. Because the most consistent sampling occurred May-September, it was the period we examined; we did not use the 1982 data in the analysis of CPUE trends. Details of the methodology are described in Ehrhart et al. (2007b). We calculated annual catch rates as the arithmetic mean of each of the daily CPUEs (Ehrhart et al. 2007b calculated catch rates similarly, except that they grouped their data into two year intervals). All of the length distribution data used in this analysis are presented as standard straight carapace length (SCL_{std}).

Southeast Area Monitoring and Assessment Program (SEAMAP) – In 1986, the South Carolina Marine Resources Research Institute teamed with the National Marine Fisheries Service's SEAMAP program to initiate a fishery-independent trawl survey off the southeastern U.S. states. In 1989, it was standardized to a stratified design, sampling from Cape Hatteras to Cape Canaveral (SCMRI 2000) and, since 1990, has been conducted exclusively during daylight hours. The region is surveyed seasonally, in spring, summer, and fall. Annual catch rates for the inshore strata (4-10 m), sampled continuously since 1990, were the number of loggerheads captured divided by the number of tows made (231-234 tows annually during 1990-2000 and 306 annually beginning in 2001). The binomial 95% confidence intervals were estimated using the "Wilson" interval, which has been shown to have a reasonable coverage particularly for extreme probabilities (Brown et al. 2001). Morphometric data were obtained from all turtles captured and

the animals were tagged before being released; SCL_{std} was not recorded prior to 1996. All of the length distribution data used in this analysis is presented as standard straight carapace length (SCL_{std}).

Pamlico-Albemarle Estuarine Complex, North Carolina – In the fall of the year, migrating sea turtles are intercepted by the flounder pound net fishery which operates behind the Outer Banks. Since 1995, NMFS has randomly sampled the fishers to develop an index of abundance for sea turtles. The methodology is described in Epperly et al. (2007). All lengths are reported as standard straight carapace length (SCL_{std}). Beginning in 2007, the State closed the fishery by proclamation on December 1. Hence, beginning in 2007, the index of abundance is based on 11 weeks of sampling, not 13 weeks as described in Epperly et al. (2007).

Chesapeake Bay – Aerial surveys were conducted in the mid-1980s (1982-1987) throughout the lower half of Virginia's Chesapeake Bay, an area of approximately 1,300 km² (Byles 1988; Musick et al. 1985; Keinath 1993). Surveys were conducted in the 2000's (2001 to 2004) in same region, using the same transect lines and methods (Mansfield 2006).

Long Island Sound, New York – Sea turtles in New York waters, primarily the Peconic Bays, were studied in the late 1980's and early 1990's (Morreale and Standora 1998) and work resumed in 2002 (Morreale et al. 2005). The majority of the data are from pound net-captured animals. Recent sampling effort was much lower than in the past decade, but geographically was distributed in the same area. We were provided size data for the live captures during 1988-1995 by the Riverhead Foundation for Marine Research and Preservation (R. DiGiovanni pers. comm.). Lengths are reported as standard straight carapace length (SCL_{std}).

Sea Turtle Stranding and Salvage Network – The STSSN documents dead or injured sea turtles along the coasts of the eastern United States, including the Gulf of Mexico and the U.S. Caribbean (Schroeder 1989; Shaver and Teas 1999). Each animal was identified to species and standard carapace measurements were taken. We did not use the STSSN data to infer trends in abundance because it is not clear there is any relationship between sea turtle abundance and the number of animals stranding. In addition, it is unclear whether size frequency distributions observed in the stranding data are representative of the overall population. In the southeast U.S. and Gulf of Mexico, length data are confounded by changing TED regulations over the period examined (Epperly and Teas 2002). We only used size distribution data available from the STSSN for the northeast; the STSSN and the New York data are the only source of size data we could use for this region. We used STSSN length data from 1987-2007 because prior to that time survey effort was less consistent. All of the length distribution data used in this analysis is presented in straight carapace length standard (SCL_{std}). When necessary, measurements were converted to SCL_{std} (see Appendix B).

Trends in Catches or Catch Rates

Epperly et al. (2007) and Ehrhart et al. (2007b) recently reported their time series for catch rates of loggerhead turtles in North Carolina and Florida, respectively. In the Pamlico-Albermarle Sound Estuarine Complex, loggerhead turtle catch rates during 1995-2003 increased at a rate of 13% per year (Epperly et al. 2007). While there was not a significant trend in the catch rate of

loggerheads in the Indian River Lagoon when the data point for 1982 was included, Ehrhart et al. (2007b) reported an increase in the last 4 yr of their study (catch rates in 2002 and 2005 were about twice those from the earlier time periods). Captures at the St. Lucie Power Plant increased at an average rate of 11% yr⁻¹ from 1988 to 2005 (M. Bresette unpubl. data) and SEAMAP catch rates showed an overall increase from 1990 to 2006 of about 5% per year (SCDNR unpubl. data). Catch rates in 2007 were generally lower than earlier in the decade (Figure 23), but preliminary data indicate that in 2008 the St. Lucie Power Plant loggerhead captures (420) were slightly greater than the catch in 2006, the Indian River Lagoon CPUE (0.84) is comparable to CPUE in 2002, the SEAMAP CPUE (0.10) is among the highest reported in this decade, and the catch of loggerheads in the North Carolina study is more than double the number captured in 2007 (78 in 2006 and 177 in 2007; mean annual CPUE has not yet been calculated).

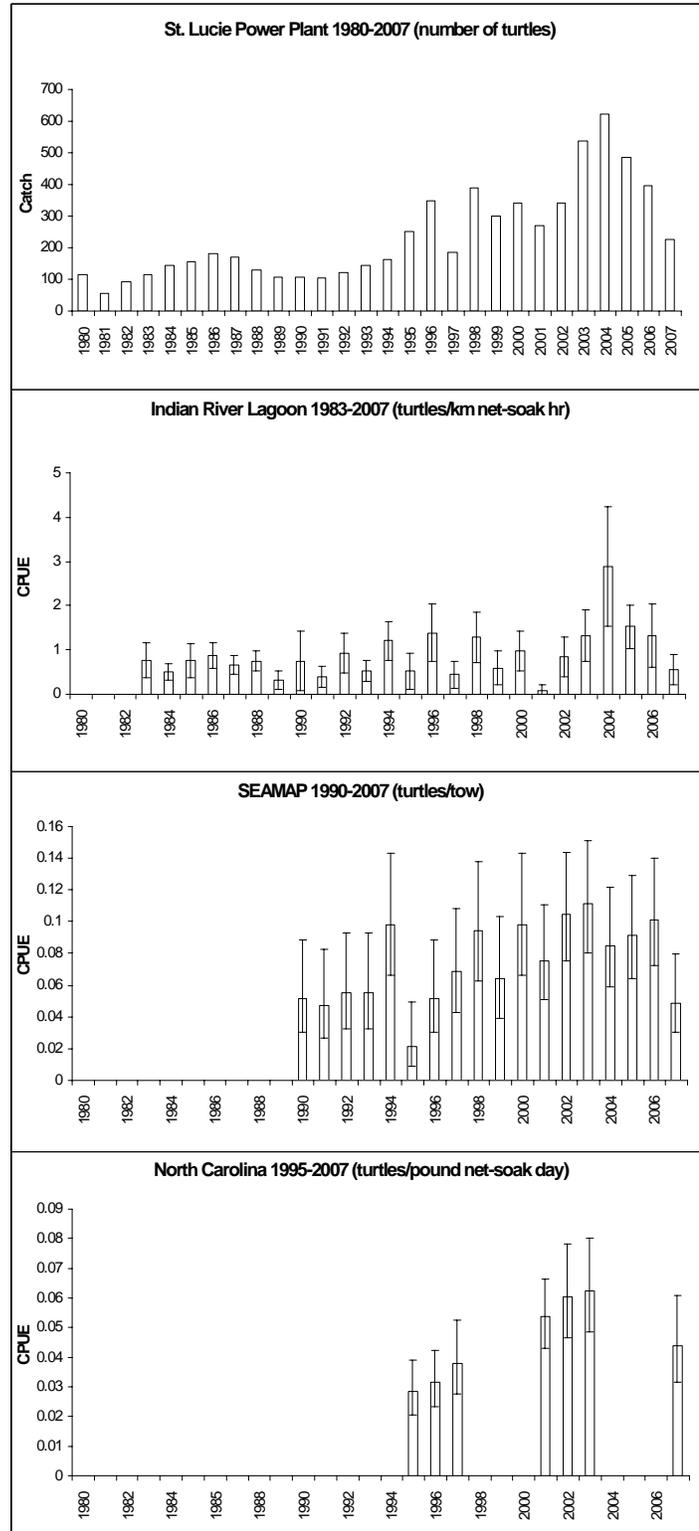
Overall, data from three of the four in-water projects showed an increasing trend in the abundance of loggerhead turtles. However, this trend must be viewed with caution given the limited number and size of studies dedicated to assessing in-water abundance of loggerheads. The increase in loggerhead turtle abundance at in-water sampling sites is not consistent with trends observed in nest counts; however, this discrepancy may be attributed to the fact that the Pamlico-Albemarle Estuarine Complex and SEAMAP studies sample in areas where adult loggerheads are not found or are not seasonally abundant. The difference in trends between in-water abundance and nest counts may also be attributed to an increase in the number of juveniles that are occurring in the neritic zone. This trend can be seen in the size distribution time series that are presented in the following section.

The trends in the waters of the northeast U.S. are not as easy to discern. The studies there were not designed to monitor abundance trends and the effort is very low, but despite these shortcomings we will discuss the results qualitatively.

In Chesapeake Bay, during the aerial surveys in the 1980s, between 122 and 284 turtles were observed annually and mean annual turtle densities ranged between 0.18 turtles/km² (+/- 0.11 turtles/km² SD) to 0.34 turtles/km² (+/- 0.35 turtles/km² SD) (Byles 1988; Mansfield 2006). Fewer turtles were observed during the 2001-2004 surveys. Only 36 to 63 turtles were observed annually and mean turtle densities ranged between 0.05 turtles/km² (+/- 0.03 turtles/km² SD) and 0.09 turtles/km² (+/- 0.29 turtles/km² SD) (Mansfield 2006). Mansfield (2006) compared median densities observed in the 1980s and 2001-2004, suggesting a three-fold reduction of turtles in the lower Chesapeake Bay since the 1980s.

Morreale et al. (2005) reported that the species composition of sea turtles in New York waters had changed, from 59% loggerheads in 1987-1992 to just 4% in 2002-2004. Whereas they captured 144 loggerhead turtles in the earlier sampling period, they caught only 2 in 2003 and none in the other two years. Sampling continued through 2007, but no more loggerheads were caught (K. Durham pers. comm.). The inequity in sampling effort among the two time periods (1978-1992 vs. recent) confounds the interpretation of these results.

Figure 23. Annual catches or catch rates of loggerhead sea turtles at four southeastern U.S. study sites: St. Lucie Power Plant, Indian River Lagoon, Cape Canaveral to Cape Hatteras (SEAMAP), and Pamlico-Albemarle Estuarine Complex (N.C.). Note that the y-axis scale differs among graphs.



Size Distribution of In-water Trends

Length distributions from the data provided are assumed to be representative of the true length frequencies of loggerhead sea turtles within the sampling area. We plotted the proportion of turtles within each 5 cm size class over the time series of each dataset. Unless otherwise noted, standard straight carapace length (SCL) is reported. Size classes examined in this analysis included turtles ranging from 40 cm to 110 cm. We report the median size of juvenile turtles and the proportion of turtles of sizes in the smallest size classes, 40-55 cm. Juveniles were defined as 40-90 cm, but animals in this size range may include some adults, and conversely, some animals greater than 90 cm may not be adults (see Life History section in this TEWG Report). Data were binned into half-decades except for 2005-2007.

The length frequency distribution from all loggerhead turtles entrained in the St. Lucie Power Plant canal (1980-2007, n=6,600) shows several interesting patterns (Figure 24). The shifting of the peak to the right indicates an overall shift in the median size of juveniles (Figure 25). Another pattern observed in the length distributions through the time series is the decrease in the relative proportion of the smallest size classes, 40-55 cm (Figure 26). The proportional decrease of small turtles in the more recent samples may also be contributing to the shift in median size of the juvenile size class.

The length frequency distribution data collected in the Indian River Lagoon (1982-2007, n=736) show similar patterns to the data from the St. Lucie Power Plant: the shift in the median size of juveniles and the apparent decrease in proportion of the smallest juveniles (Figure 25). The trend in the proportion of small, 40-55 cm turtles is consistent with the trend observed in the St. Lucie Power Plant time series (Figure 26).

Although the time series of data from the SEAMAP trawl surveys is shorter and the sample size is smaller (1990-2007, n=354) than in the two previously discussed nearshore sites, this trawl survey represented similar patterns, including a shift through time in the median size of juveniles (Figure 25). The pattern observed in the longer time series of St. Lucie Power Plant and Indian River Lagoon, showing a decrease in the smallest size classes, is also evident in this data set. Although there are few turtles captured that are smaller than 55 cm, the proportion has been decreasing over the time series (Figure 26).

The data from North Carolina's Pamlico-Albemarle Sound Estuarine Complex (1990-2007, n=2,806) also show a similar trend to those observed at the three other sampling sites (Figure 24). The median juvenile size has increased through the sampling period, beginning in 1990 (Figure 25). The proportion of small juveniles also followed the same pattern as the other three sampling sites (Figure 26).

Length frequency data from the northeast STSSN data set (1987-2007, n=3,175) also show similar trends to the four southeastern sites. Throughout the entire time series (1987-2007) we observed an increasing median SCL in the juvenile size classes and also decreasing proportions of the smallest juveniles (Figure 25). The proportion of small juveniles also showed a decreasing trend through the entire time series (Figure 26).

Loggerhead turtles in New York waters apparently are smaller than animals to the south (Figure 27); the reported size range is 36.6-89.2 cm SCL (Burke et al. 1993; Morreale et al. 1992). Live captured animals from 1988-1995 (n=201) ranged in size from 40.3 cm to 65.6 cm; annual median sizes ranged from 47.8 to 52.7 SCL_{std} and overall was 50.5 cm. From 2002 to present, only two loggerheads have been captured, both in 2003 (Morreale et al. 2005; K. Durham pers. comm.): 55.4 cm and 62.6 cm. The proportion of small juveniles observed at this site was much higher than at the southeastern sites and ranged from 0.66 to 0.90 from 1988-1995.

Summary

It is nearly impossible to draw any conclusion about regional abundance and population trends based on a single site. However, the fact that the four southern data sets, which cover a large portion of the loggerhead's nearshore habitat off the southeast U.S. Atlantic coast, show similar patterns in catch/catch rates and that virtually all sources of data show a similar pattern in size distributions is intriguing. Several distinct patterns have emerged from these analyses. Together they indicate there was an increase in abundance and/or catchability of neritic animals in the southeast U.S. through the early part of this decade. In the first ten years of the two longest time series, the median size of 40-90 cm animals was decreasing to a low in 1990-1994 and then began increasing at all sites to a peak in 2005-2007 (Figure 25). The proportion of small juveniles, 40-55 cm, increased to a high in 1990-1994 and then began decreasing to a low in 2005-2007 (Figure 26). The exception to these two trends is seen in the northeast STSSN data. Through that entire time series we observed an increasing trend in the median size of 40-90 cm animals and a consistently decreasing trend in the proportion of small juveniles. Interestingly, the northernmost area (New York), where the foraging population comprised the smallest size classes (Figure 27; Burke et al. 1993; Morreale et al. 1992), has seen a dramatic change, with only two loggerheads being captured over a 6 yr period. This decrease in captures during the most recent sampling is consistent with the lack of small juveniles appearing at the other sampling sites examined further south.

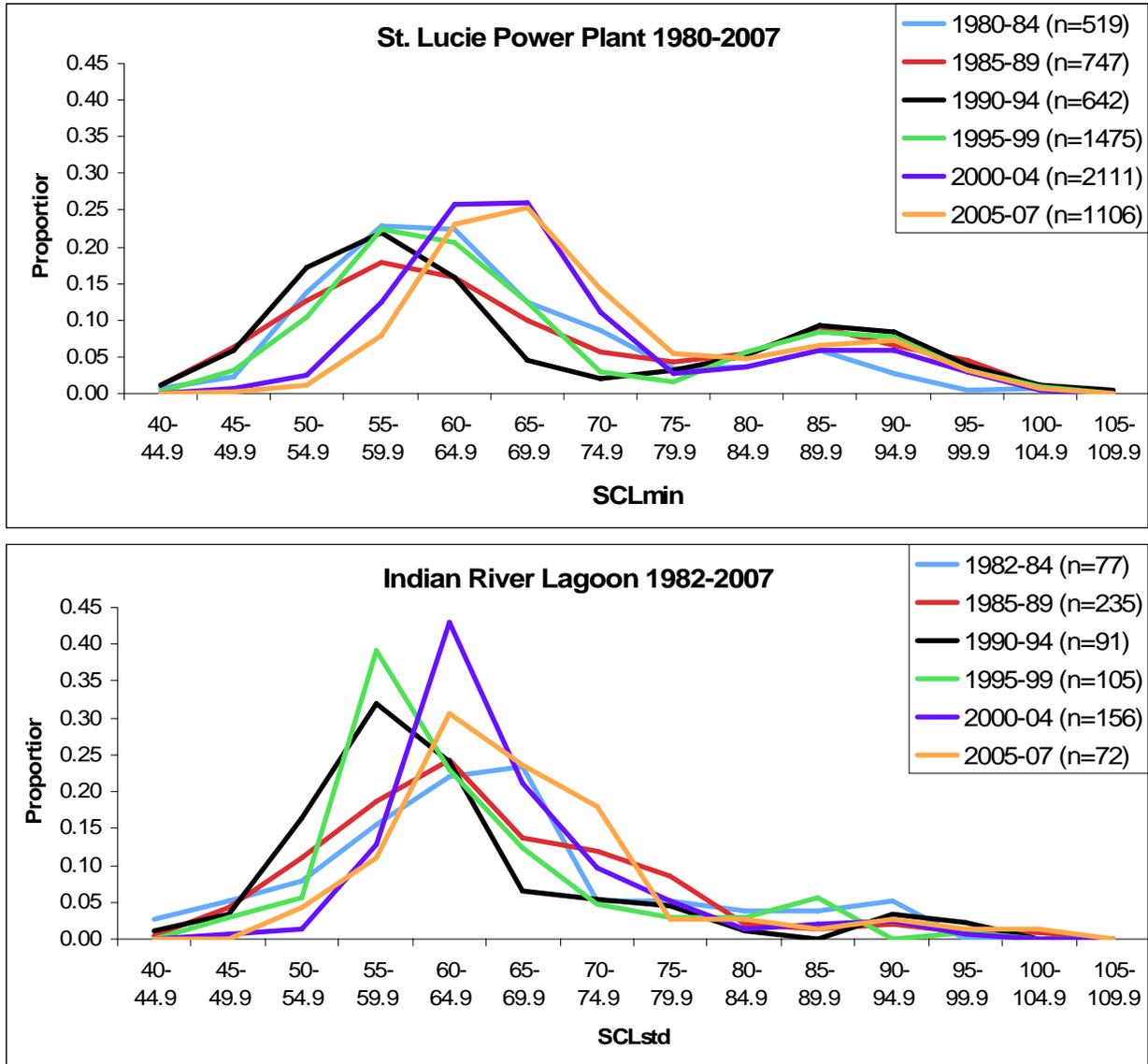
The apparent decline of loggerhead abundance in the northeast, based on aerial surveys in the Chesapeake Bay, and the dearth of captures in New York may be due to 1) fewer turtles migrating north of Cape Hatteras, North Carolina each spring; 2) fewer turtles utilizing the Chesapeake Bay en route to northern foraging grounds (Mansfield 2006), 3) an overall decline in the Atlantic loggerhead population, and/or 4) changes in sighting or capture probabilities in time and space, due to changes in environmental conditions and/or methods across time and space. Morreale et al. (2005) suggested that the reduction in the number of loggerheads caught in New York and the commensurate shift in marine turtle species composition might be indicative of a major shift in foraging grounds. Without additional data, it is not possible to determine the relative significance of the decline in Virginia's or New York's numbers over time.

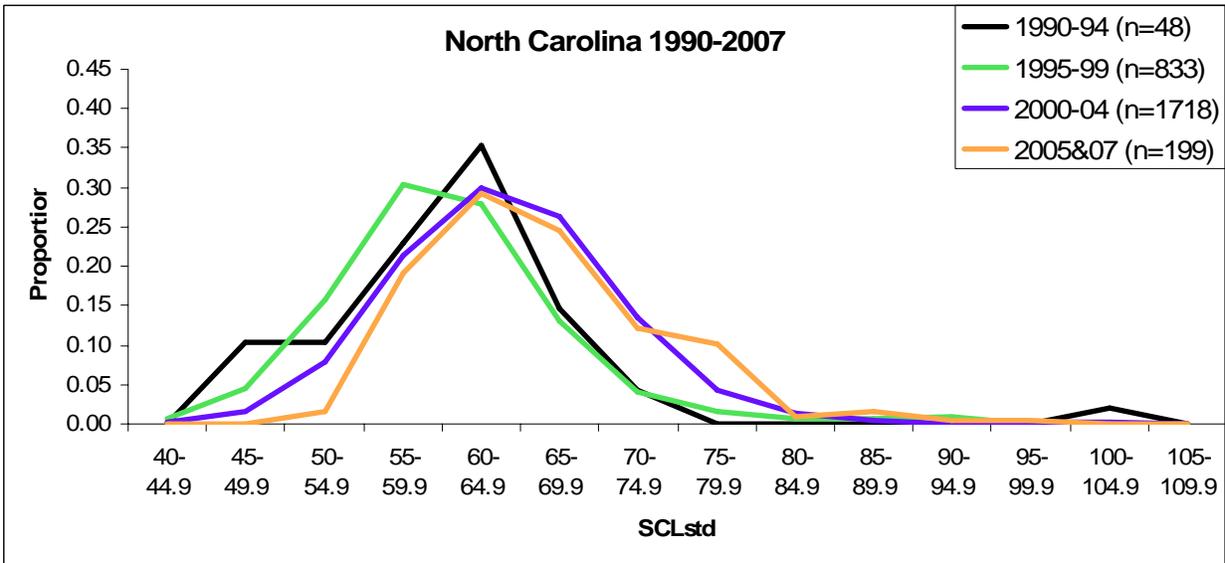
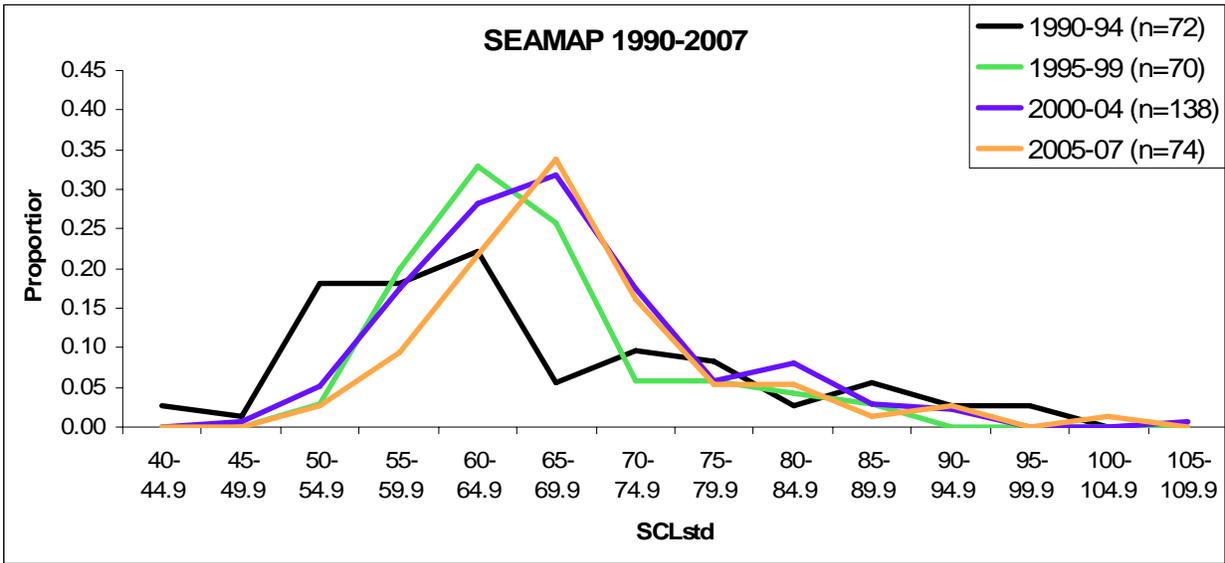
The good news is that there appears to be increasing trends in catch rates through 2008 in the southeast U.S. This, coupled with the shift in median size of neritic juveniles, may indicate there is a relatively large cohort that will be reaching maturity in the near future, assuming there is not an emerging source of mortality on the larger juveniles and adults.

The majority (12,725 of 13,826 turtles, 92%) of the data used in our analyses was from turtles less than 90 cm, and most were from Juvenile Stage III (see Life History Section in this TEWG report). Thus, we are limited in hypothesizing what may be causing the declines on the nesting beaches since the turn of this century is two life stages removed (Stage V). We estimate that the duration of the two juvenile neritic/oceanic stages (III and IV) together is approximately 20 years or longer (see Life History Section in this TEWG report). If we look back 20+ years, to the beginning of the two longest time series, we can see that catch rates were low in the early 1980s. We do not know what they were before the 1980s and cannot determine if immediately prior there was a lull in recruitment to the youngest neritic juvenile stage at that time. Interestingly, it was during the early 1980s that we observed the highest proportions of the smallest juveniles, perhaps indicative of high levels of recruitment from the oceanic stage, and/or, the paucity of larger juveniles.

The decrease in the proportion of the smallest size classes of juveniles in the most recent years raises concern that currently we may be witnessing a recruitment failure or, alternatively, that oceanic animals (Stage II) are moving to the next stage (III) at a larger size (2008). We observed the lowest proportion of small juveniles in 2000-2007. Taking into account the range in duration of the oceanic juvenile stage (II), these new recruits to the neritic zone would have hatched sometime between the mid 1980's to the late 1990's. During this period there was an increasing trend in nesting on the Peninsular Florida beaches (TEWG 2000; see Population Trends section in this TEWG report). Assuming that hatching and emergence success rates have not changed, one may conclude that there was increased production on the beach during that time. If we also assume that the survival rates during the oceanic juvenile stage have not changed, we then would not expect to see a decrease in the proportion of small juveniles, but rather we would expect to observe an increase. Snover (2008) demonstrated that variable environmental conditions could have considerable impacts on the optimal size for the shift from oceanic to neritic habitats, determined as the point that maximizes growth rates and minimizes mortality rates, in loggerhead turtles. She suggests that these environmentally driven increases in size at the shift could be mistaken for loss of recruitment from the oceanic stage and that alternative hypotheses regarding changing growth rates and optimal sizes at habitat shifts need to be considered. Notably, through 2003 we observed an increase in catch/catch rates in the southeast U.S., which appears to be inconsistent with the hypothesis of recruitment failure. However, the recent data on catch/catch rates may support the hypothesis of recruitment failure. One possible explanation is that animals recently may have grown differently in the oceanic environment, achieving a larger size before recruiting onto the neritic foraging grounds. Alternatively, the change in numbers/catch rates we saw since the mid-1990's could be related to changing proportions of the juvenile population moving between the oceanic and neritic environment (McClellan and Read 2007) and not due to an actual increase in the numbers of the juvenile population. This enigma reinforces the need to continue monitoring the juvenile loggerhead foraging grounds to observe whether these patterns continue. With increased in-water monitoring, not just of numbers but of sex ratios, survival rates and other demographic parameters, we will be able to make better predictions for the future and maybe anticipate declines in nesting like the one we are observing now.

Figure 24. Proportion of turtles within each 5 cm size class over the time series of each dataset: St. Lucie Power Plant, Indian River Lagoon, Cape Canaveral to Cape Hatteras (SEAMAP), Pamlico-Albemarle Estuarine Complex (N.C.) and the northeast STSSN.





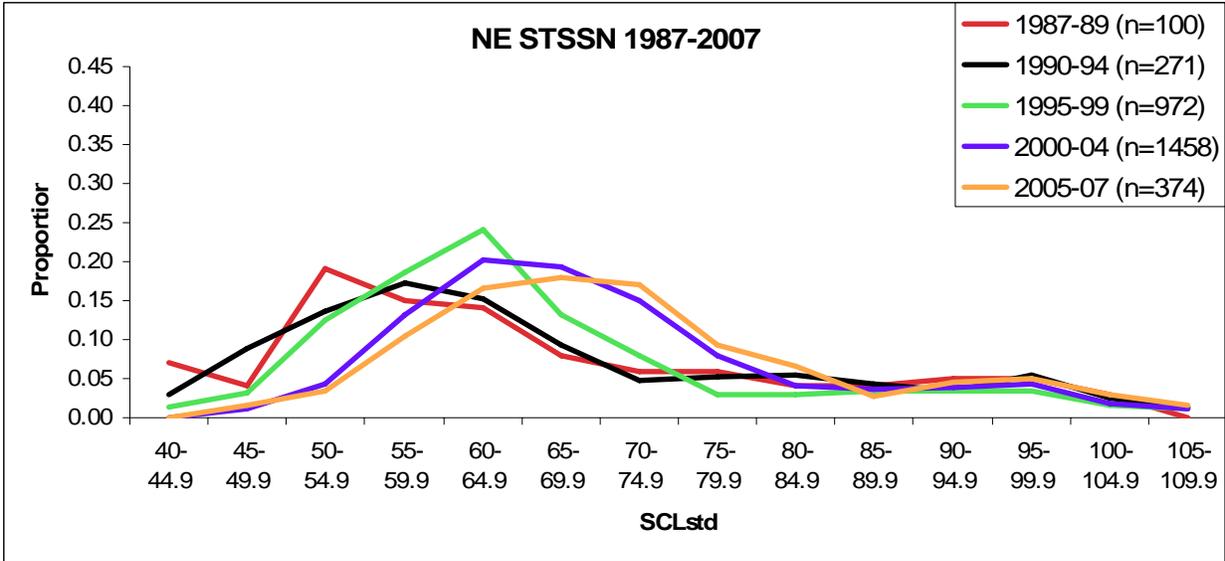


Figure 25. Median length of juvenile loggerhead sea turtles (40-90 cm SCL) at four southeastern U.S. study sites and the Northeast STSSN: St. Lucie Power Plant (STLPP), Indian River Lagoon (IRL), Cape Canaveral to Cape Hatteras (SEAMAP), and Pamlico-Albemarle Estuarine Complex (NC). Note the IRL time series does not include data prior to 1982 and NE STSSN does not include data prior to 1987.

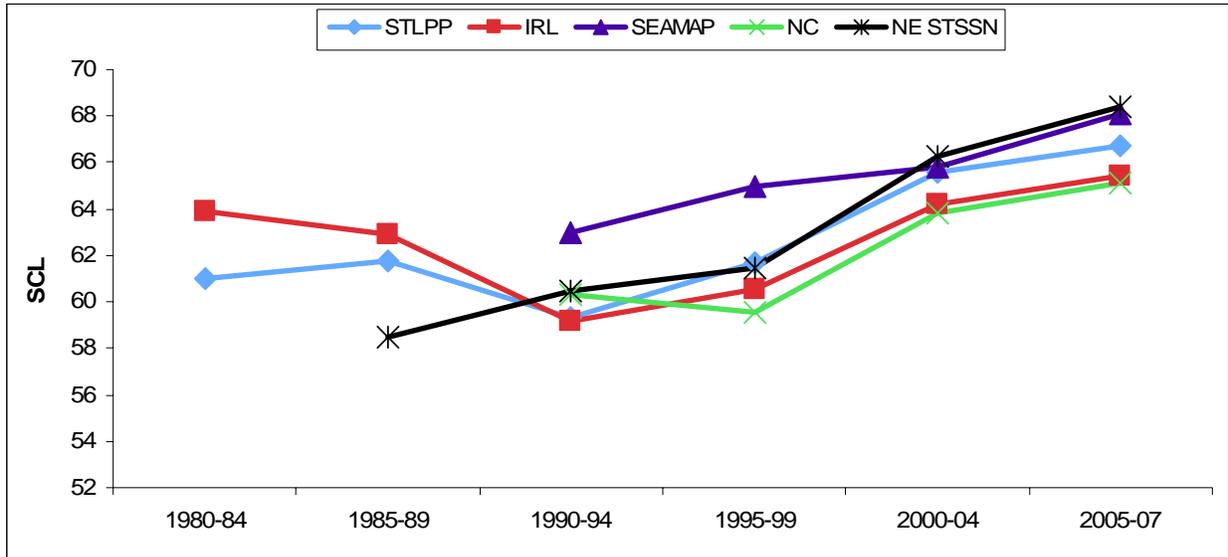


Figure 26. Proportion of small (40-55 cm SCL) juvenile loggerhead sea turtles at four southeastern U.S. study sites and the Northeast STSSN: St. Lucie Power Plant (STLPP), Indian River Lagoon (IRL), Cape Canaveral to Cape Hatteras (SEAMAP), and Pamlico-Albemarle Estuarine Complex (NC). Note the IRL time series does not include data prior to 1982 and NE STSSN does not include data prior to 1987.

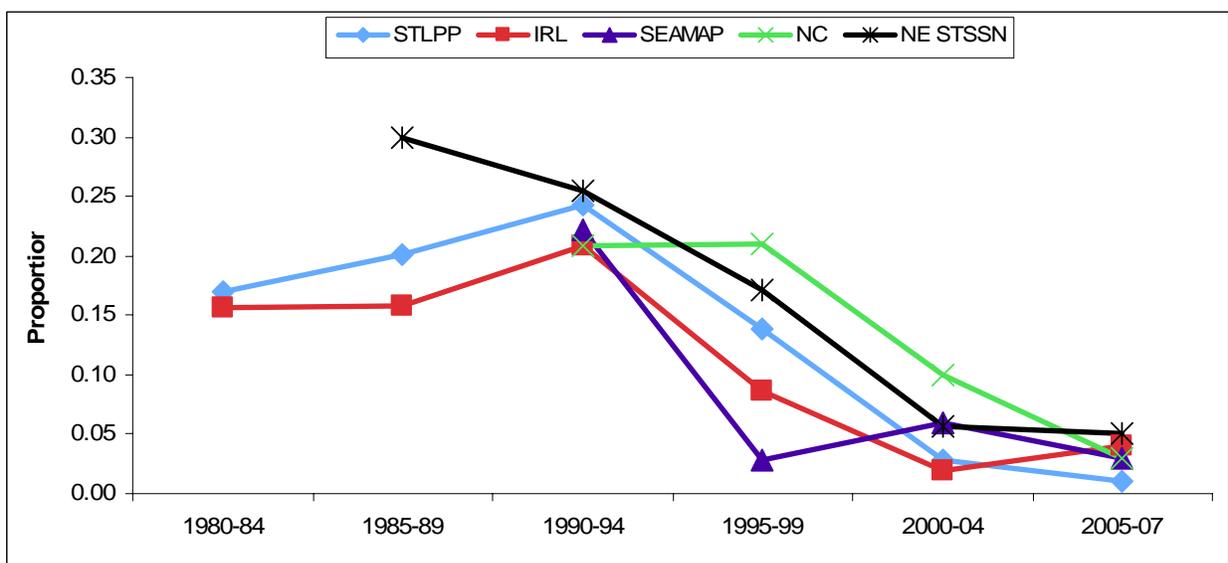
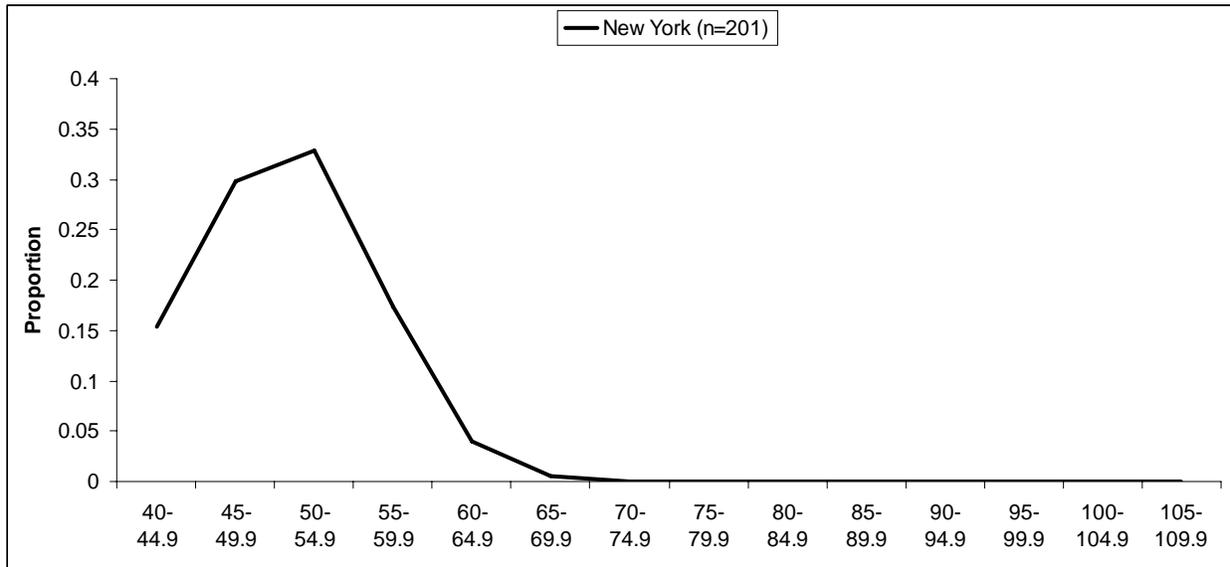


Figure 27. Length frequency data from live-captured animals in Long Island Sound, New York from 1988-1995 (R. DiGiovanni pers. comm.).



PART IV. FACTORS POTENTIALLY RESPONSIBLE FOR DECREASING NUMBERS OF NESTS

Incidental Capture -Paul Richards

Loggerhead sea turtles are caught as bycatch in numerous fisheries operating in the Western North Atlantic. Loggerhead sea turtles are also incidentally captured in other ways such as in power plant intake pipes, dredge operations, etc. (see the Loggerhead Recover Plan [National Marine Fisheries Service and U.S. Fish and Wildlife Service 2008] for a full review and subsequent threats analysis). Extrapolated estimates of loggerhead bycatch from selected fisheries are available on the SEFSC website

(<http://www.sefsc.noaa.gov/seaturtlepublications.jsp>; see NMFS SEFSC 2001 for a summary through 2000, see Table 14 for list of reports and publications since 2000); however, the impact of bycatch and other incidental capture on the Western North Atlantic loggerhead population has not been quantitatively evaluated for a number of reasons. First, we have inadequate information to assess the size and status of the loggerhead stock. Second, there are many fisheries and other activities (both U.S. and foreign) that may impact loggerhead turtles in the Western Atlantic (see Lewison et al. 2004), and we have very spotty knowledge of total lethal takes by all of these fisheries and other sources of mortality. For example, in the year 2000, the loggerhead takes from the observed U.S. pelagic longline fishery were estimated to be about 1,256 (Yeung 2001), a tiny fraction of the estimated 150,000 to 200,000 total takes in the Atlantic (Lewison et al. 2004). Furthermore, the total takes of loggerhead sea turtles in all U.S. fisheries (observer based estimates plus other estimates) was about 748,112 annually for the years 2001 to 2005 (SEFSC unpubl. data). Of these, approximately 729,456 were estimated as taken (*e.g.* passing through turtle excluder devices) by shrimp trawls. This leaves about 18,656 takes from all other U.S. fisheries combined, and therefore an even smaller fraction of the total takes by just pelagic longlines in the Atlantic.

In observed U.S. fisheries, loggerhead takes range from moderate sized juveniles (> 40 cm CCL) through adult sized individuals. Mortality is about 20 to 50% (see reports in Table 14). Hatchling and small size classes (< 40 cm CCL) are rarely seen as bycatch in U.S. commercial fisheries. Even within relatively well observed fisheries, the estimates of uncertainty are very high (CVs of 1.0 are common due to sparse data; see longline reports cited below in Table 14). Increased observer coverage in U.S. and other nations' fisheries would improve the precision of and increase confidence in loggerhead bycatch estimates. However, in the absence of a quantitative population estimate, even precise bycatch estimates could not contribute to a stock assessment.

Table 14. List of reports and publications of estimated bycatch of loggerhead sea turtles in U.S. fisheries since 2000.

Fishery	Report
Shrimp trawl	Epperly et al. 2002
Pelagic longline	Garrison 2003a
	Garrison and Richards 2004
	Fairfield-Walsh and Garrison 2006
	Fairfield-Walsh and Garrison 2007
Shark bottom longline	Richards 2007
	Southeast Fisheries Science Center 2007
Gulf of Mexico reef fish	Southeast Fisheries Science Center 2008
	Southeast Fisheries Science Center 2009a
	Southeast Fisheries Science Center 2009b
Shark gillnet	Garrison 2003b
	Garrison 2007
North Carolina inshore gillnet (Pamlico Sound Restricted Gillnet Area)	Price 2004
	Price 2005
	Price 2006
	Price 2007
	Price 2008
	Price 2009
Sea scallop dredge	Murray 2004a, Murray 2004b, Murray 2005, Murray 2007
Sea scallop trawl	Murray 2007
U.S. mid-Atlantic bottom otter trawl	Murray 2008

Adult Female Survival Rates –Christopher Sasso

Annual survival rates were estimated using tagging data from Melbourne Beach, Quintana Roo (Mexico), and Wassaw Island using a multistate conditional Arnason-Schwarz model with separately identifiable survival and capture probabilities (Lebreton et al. 1992; Schwarz and Arnason 1996).

Details on the nesting surveys for Quintana Roo, Mexico and Wassaw Island, Georgia are provided in the description of nesting beach tagging studies earlier in this report. For Melbourne Beach, Florida nesting surveys have been conducted along 21 km of beach in the Archie Carr National Wildlife Refuge since 1982 (Ehrhart et al. 2007a). From 1982 through 1984 they concentrated on tagging turtles. In 1985, their emphasis shifted to primarily marking nests for reproductive studies, and tagging has been secondary; from 2005-2007 their tagging efficiency

has ranged from 2.8% - 4.3% (W. Redfoot pers. comm.). W. Redfoot (pers. comm.) indicated that while an attempt is made to flipper tag each nesting turtle, it is often not possible. These data tagging data were used to estimate adult survival.

Annual survival estimates were generated following the methods of Rivalan et al. (2005) which allowed individuals to transition between an observable breeder state and an unobservable nonbreeder state. Using these methods, individuals could temporarily emigrate, spend multiple years in a nonbreeder state, and transients could be accounted for in the analyses. Transients were accounted for by specifying two groups: one for all individuals marked and never recaptured (transients) and one for individuals recaptured in at least one subsequent year (residents). The number of years spent in the nonbreeder state was constrained by the number of years being tested for the breeding cycle with cycles of 2, 3, 4 and 5 years tested here where the cycle length is defined as the number of years skipped between nesting plus one as a breeder. Models were assessed using the program MSURGE (Chopquet et al. 2005).

The candidate models for each data set were parameterized for varying effects on survival and capture probabilities, different lengths of the breeding cycle, and constant transition between states. Survival was modeled as time dependent (S_t), transients (S_T), interaction between time dependence and transients (S_{t*T}), and additive effects of time dependence and transients (S_{t+T}). Capture could be modeled as time dependent (P_t), trap dependent (P_m), interaction between time dependence and trap dependence (P_{t*m}), and time dependence with additive effects of trap dependence (P_{t+m}). No models of trap dependence only were analyzed for Melbourne Beach due to variability in sampling effort among years. Variability in sampling effort may result in underestimates of parameters. Goodness of fit for the models were assessed following the protocol described in Rivalan et al. (2005)

The best of the candidate models for each nesting area was selected using the quasi-likelihood Akaike Information Criterion adjusted for small sample size (QAIC; Akaike 1973, Lebreton et al. 1992). The survival rates calculated by the model for each group (transients and residents) allow for an unbiased estimate of the proportion of transients in the data using the following equation from Pradel et al. (1997):

$$\text{Proportion of transients} = 1 - \frac{S_{transients}}{S_{residents}}$$

The best model for Melbourne Beach had a four year breeding cycle with a transient effect for survival and time dependent recapture probability ($S_T P_t$). The survival estimate for residents was 0.73 (95% CI 0.71 – 0.76) with 39% of the individuals in the data being transients. The best model for Mexico was also $S_T P_t$ with a four year breeding cycle with resident survival estimated to be 0.85 (95% CI 0.81 – 0.88) and 35% of the individuals in the data being transients. Wassaw Island data were best described by a three year breeding cycle with a transient effect on survival and trap dependent capture probability ($S_T P_m$). The resident survival estimate for Wassaw Island was 0.81 (95% CI 0.77 – 0.84) with 69% of the individuals being transients.

The same methods have been applied to 16 years of data from Bald Head Island, North Carolina (Hedges 2007) with a survival estimate of 0.85 (95% CI 0.78 – 0.93) for residents. On Bald

Head Island, transients represented 67% of individuals in the data. Interestingly, the proportions of transients on the two Northern U.S. Subpopulation beaches (Wassaw and Bald Head Islands) are much greater than for Peninsular Florida and Mexico. This finding is not surprising given these Northern U.S. Subpopulation beaches represent small beaches within a larger matrix of suitable nesting habitat, and suggests these studies may need to monitor nesting at a larger scale to make meaningful conclusions on population trends.

Previous estimates of survival were generated with the Melbourne Beach and Wassaw Island data using a Jolly-Seber model which did not account for emigration or the unobservable nonbreeder state (NMFS SEFSC 2001). Those analyses suggested the best model for survival was time dependent, but only an average over all years was presented with Wassaw Island estimated to be 0.79 and Melbourne Beach estimated to be 0.83. Frazer (1983b) estimated survival to be 0.8091 on Little Cumberland Island, Georgia.

The results generated here suggest that survival may be lower for Melbourne Beach nesters. The foraging grounds for Peninsular Florida nesters do differ from those of Northern U.S. Subpopulation nesters (see Spatial Distribution section in this TEWG report) and it is possible mortality is higher for Peninsular Florida nesters. However, the data from Melbourne Beach do not represent a dedicated mark-recapture study and the interception rate is very low. Hence, the analysis based on these data may be an underestimate of true survival and the estimate is suspect. Further research will be necessary to determine if adult female survival is lower for the Peninsular Florida Subpopulation and a potential cause for the rapid decline in nesting numbers.

In addition to the models presented here, models to assess any change in survival since the implementation of turtle excluder devices (TED) in the shrimp fishery were explored. However, these models were poor compared to those presented above. No TED effect may have been found due to the fact that while TEDs were introduced to the shrimp fishery in 1987, they were not required to be large enough to release turtles the size of nesting females until 2003 (Epperly and Teas 2002) .

Proportion of Putative First-time Nesters –Melissa Snover and Sheryan Epperly

We estimated the proportion of first-time nesters over time on Quintana Roo to determine if there were any changes over time (Table 15). The Florida and Northern U.S. researchers did not believe that they intercepted a sufficient proportion of the females on the nesting beaches to support this type of analysis. Thus, the estimates are for beaches of the Mexican Subpopulation only. Data for the first two years were censored in the first-time nesters analyses to allow the majority of neophyte nesters to be marked during those first two years.

Table 15. Percent first-time nesters by year for Quintana Roo.

Year	Percent of Neophytes on Quintana Roo Beaches
1996	inconel single tagging began this year for all animals
1997	
1998	47.10
1999	43.62
2000	48.51
2001	44.22
2002	46.45
2003	47.45
2004	57.05
2005	59.90
2006	52.71

The trend for Quintana Roo shows a significant increase at a rate of 2.99% per year ($P=0.022$). Thus, Quintana Roo, which has a decreasing trend in nesting activity comparable to the decrease on Florida beaches (see Population Trends in this TEWG report) shows an increase in the proportion of first-time nesters, which indicates a loss of experienced adult females from the population.

Directed Harvest –Matthew Godfrey

Sea turtles in the Western Atlantic, including loggerheads, have been harvested for human consumption for centuries (see McClenachan et al. 2006 for overview). International trade in sea turtles and their products has been strictly controlled by the Convention in International Trade in Endangered Species (CITES) since 1989, when all species and populations were placed on Appendix I, which bans all international trade (Bräutigam 1989). Most nations and territories in the Western Atlantic are parties of CITES; exceptions include Anguilla and the Turks & Caicos Islands (Richardson et al. 2006). All parties are bound by the regulations of CITES, although some countries, such as Cuba, have reservations to certain species on Appendix I and are not bound by a ban on international trade of those species. Currently, no party to CITES has a reservation to loggerhead sea turtles (www.cites.org). In the case of the Western North Atlantic, there is little evidence of widespread international commercial trade based on CITES statistics (Bräutigam and Eckert 2006). However, there has been, and in some cases continues to be, directed take of loggerheads within nations or territories in the Western Atlantic. Of the 42 countries and territories in the Western Atlantic listed in Appendix III of the Recovery Plan for the Western North Atlantic Population of Loggerhead Sea Turtles, 14 allow loggerhead egg and/or whole animal harvest (National Marine Fisheries Service and U.S. Fish and Wildlife Service 2008). For example, in the Cayman Islands, the legal loggerhead harvest has targeted large juveniles or adults (Bell et al. 2006). However, most locations in the Western North Atlantic, where legal harvest of loggerhead turtles or eggs currently occur, are found the Caribbean, where loggerhead density is low (Ehrhart et al. 2007a) and thus actual harvest levels are low (*e.g.* in the Cayman Islands, only three loggerheads were taken in a five year period; Bell

et al. 2006). A notable exception to this pattern is the case of Cuba, where many loggerhead turtles were actively harvested from Cuban waters until the mid 1990's (Moncada Gavilan 2000).

Between the years of 1968 and 1975, the Cuban loggerhead fishery was not actively managed and the mean annual catch was 491 metric tons (Moncada Gavilan 2000). To put this in context, assuming that the mean mass of adult females is 114 kg (LeBuff 1990), the annual catch would represent an annual harvest of 4,307 adult females in these early years of the fishery, although presumably adult males and juveniles were also captured. Moncada Gavilan et al. (2003) report a majority of juveniles represented in incidentally captured loggerheads in other Cuban fisheries, so the actual number of individual turtles captured per year in the targeted loggerhead fishery may have been higher. Between 1967 and 1987, the turtle fishery was restricted between June and August, to protect reproductive animals. Annual catch rates for these years were reduced by 40% to about 300 metric tons (or an equivalent of 2,631 adult females). From 1988 to 1994, the closed seasons were modified and extended to increase protection of reproductive animals. The annual catch rate decreased during this period from initial levels >200 metric tons (or 1,750 adult female equivalents) to <75 metric tons (or 660 adult female equivalents) at the end. Starting in 1995, fishing effort for turtles was limited to two sites (Isle of Pines and Nuevitas) and targeted hawksbills nearly exclusively. Annual catch rates of loggerheads were close to zero by 1996 and onwards. The hawksbill harvest was ended in early 2008, and all species of sea turtle in Cuban waters are now completely protected from directed harvest (www.wwfca.org).

The overall pattern for harvest of loggerheads in Cuba is a three-phase step-down, from a peak in the late 1960s and early 1970s to a relatively low level in the early 1990's. Interestingly, as fewer loggerheads were harvested in Cuban waters in the late 1980s through the late 1990's, there was a concurrent increase in the number of loggerhead nests laid on index beaches in Florida (<http://research.myfwc.com>). When the loggerhead fishery in Cuba ended in 1996, the annual number of nests in Florida was still increasing, with little sign of decline that has characterized recent years. It is unclear whether the harvest of loggerheads in Cuba from the late 1960s through the early 1990's is linked to the present declining trend in number of loggerhead nests laid in Florida, but the current complete protection of loggerheads in Cuban waters is a positive management action that can only contribute to recovery.

Increase in Mortality Due to Disease –Allen Foley

The most common evidence of disease documented in cases of dead or moribund (*i.e.*, stranded) sea turtles is emaciation. Emaciation is usually determined by appraising the overall body condition of a turtle. Typically, only severe cases (*i.e.*, turtles with a distinctly concave plastron and a prominent supraoccipital) are noted as emaciated. Since 1986, both the number and percentage of loggerhead strandings in Florida that were emaciated has increased (Figure 28). Several recent epizootics involving loggerheads have also been documented in Florida during the past decade. Blooms of *Karenia brevis* (commonly referred to as red tide) have been detected every year in southwest Florida since 1995 (FFWCC unpubl. data). At concentrations above 100,000 cells per liter (referred to as a strong red tide), *K. brevis* is considered potentially lethal for manatees (*Trichechus manatus latirostris*, Landsberg 2002). Red tide is also believed to be a mortality factor for loggerheads (Redlow et al. 2003) and we assume that strong red tides could be potentially lethal for loggerheads. From 1995 through 2005, unusually high numbers of

loggerhead strandings were associated with strong red tides in southwestern Florida during seven of those years (1995, 1996, 2000, 2001, 2002, 2003, and 2005; FFWCC unpubl. data). In late 2000 and early 2001, there was a loggerhead epizootic throughout southern Florida accounting for about 150 strandings that was associated with trematode infections (Jacobson et al. 2006). In September and October of 2006, an epizootic involving about 100 loggerheads occurred in northeast Florida (FFWCC unpubl. data).

The annual numbers of loggerhead nests in the Peninsular Florida Subpopulation were increasing during the period of 1989 through 1998 but have since decreased to such a large extent that there has now been an overall decrease in the annual numbers of nests since 1989 (Witherington et al. 2009). Possible reasons for the decline in the annual numbers of nests could be due to increased mortality of adult female loggerheads or to a decrease in the recruitment of large, immature females into the adult population (from increased mortality of that life stage). The recent increases in the incidences of disease in loggerheads in Florida have also been documented for adult (Stage V) and large immature loggerheads (Stage IV; Figure 29) and could have played a role in the recent decrease of loggerhead nesting. However, the magnitude of the mortality of adult and large, immature loggerheads in Florida from disease as represented by strandings of emaciated loggerheads > 81.9 cm SCL has been relatively small (<35 individuals per year) (Figure 29).

Figure 28. The number and percentage of dead or moribund (*i.e.*, stranded) loggerheads that were noted to be emaciated each year in Florida during 1986 through 2008. Both have increased during this period. Trends are best represented by the power regressions models.

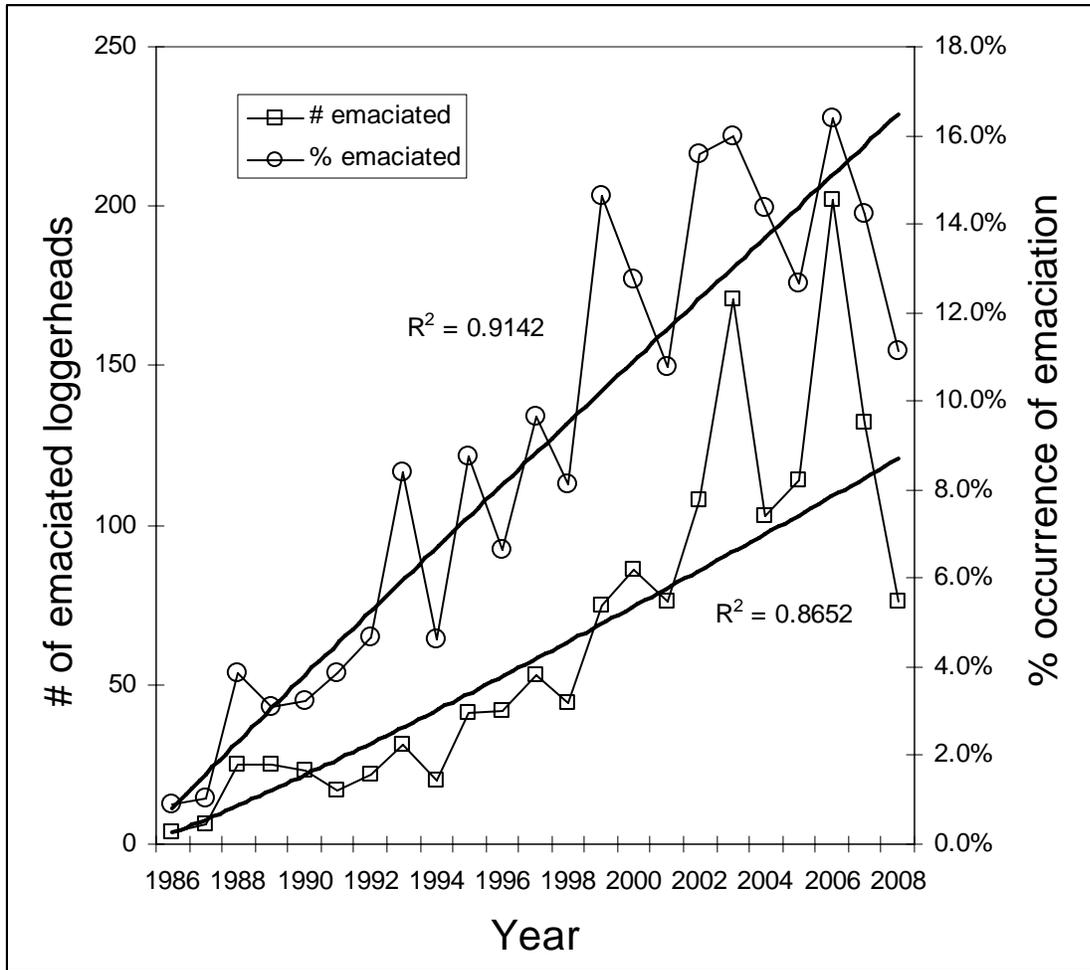
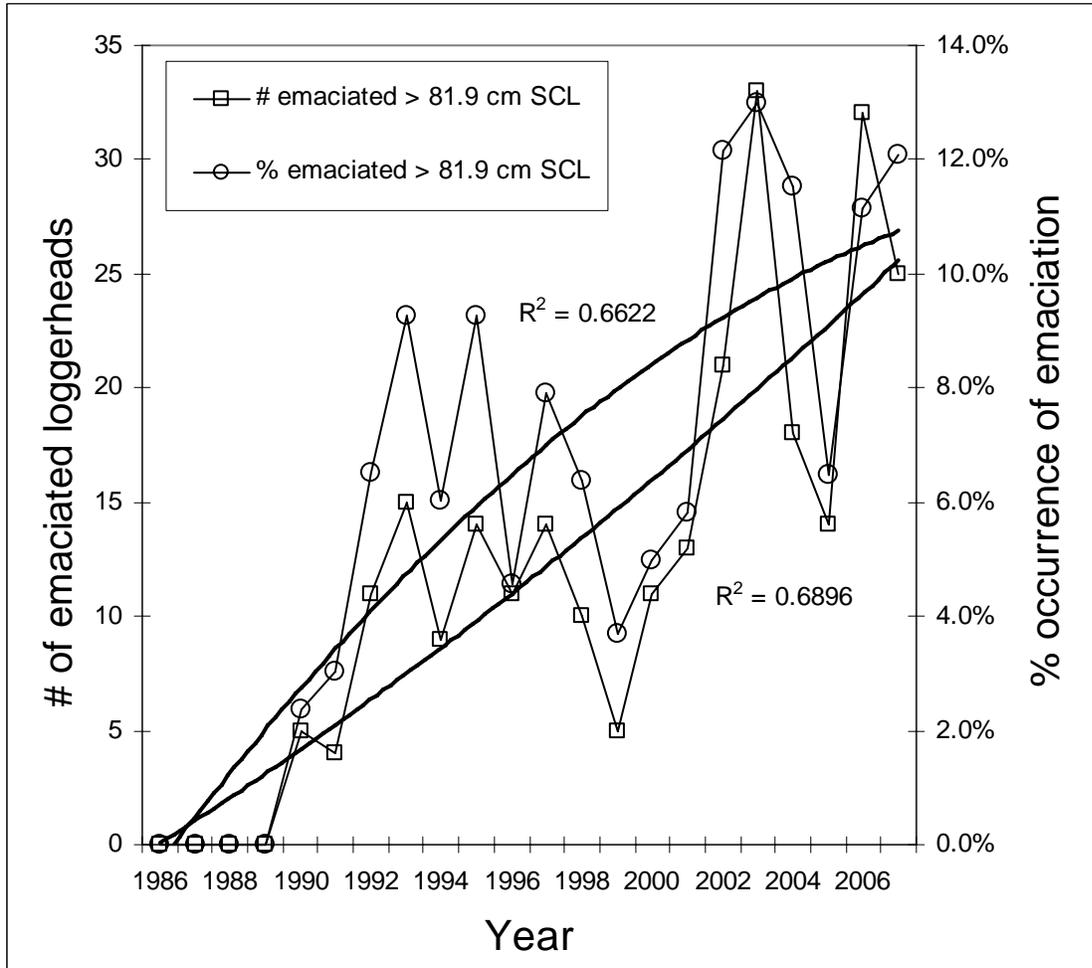


Figure 29. The number and percentage of dead or moribund (*i.e.*, stranded) loggerheads greater than 81.9 cm straight carapace length (measured from the nuchal notch to the posterior marginal tip) that were noted to be emaciated each year in Florida during 1986 through 2007. Both have increased during this period. The trends are best represented by the polynomial regressions that are shown.



PART V. RESEARCH NEEDS AND RECOMMENDATIONS

The most worrisome conclusion this TEWG committee faced was that existing data remain woefully inadequate to determine the cause(s) of the declines in nesting for any of the Western North Atlantic subpopulations, to detect if declines in nesting signal a decline in the adult population. While past TEWGs also note research needs, we point out that meeting such needs require adequate funding to collect essential data, cooperation across agencies including recognition of permitting hurdles, open access agreements to make the data available in a timely manner, and robust quantitative approaches so that the various data lend themselves to stock assessments. Below we summarize the research needs and recommendations.

Population Parameters

Our knowledge of loggerhead population parameters is rudimentary. Additional information on population parameters are needed to enhance our ability to adequately assess this stock. Top priorities need to focus on generating better estimates of abundance, survivorship, stage duration, size-class distribution, and fecundity parameters. Changes in any of these parameter estimates could cause changes in the number of nests, which is currently our main assessment dataset. Mark and recapture studies remain a research need, at all ages and stages.

Better estimates of population abundance and trends and estimates of demographic parameters are needed and can be obtained through in-water, mark-recapture, and satellite studies. To ensure such estimates are robust, the monitoring should include long term, continuous (within the limits of technology) studies and address all life history stages to assess changes in vital rates over time and better understand their natural variability and impact on population trends. Survival rates for life history stages not easily recaptured (*e.g.* oceanic/pelagic juveniles and adult males) can be estimated using satellite telemetry technologies. Smaller size classes should be tracked and robust sample sizes should be used. In-water studies should be coupled with sampling to estimate and monitor other demographics, such as shifts in size distribution, sex ratios, growth rates and age/size at maturity. A network of study sites in foraging areas, particularly those found along the east coast of the U.S., the Gulf of Mexico, Cuba, the Yucatán Peninsula and in oceanic foraging areas should be established to provide estimates of survivorship, growth, recruitment, emigration rates, and populations estimates.

Better estimates of population parameters derived from nesting beaches are also needed and may be obtained through saturation tagging studies on nesting beaches representative of all subpopulations. Sampling should be designed to provide estimates of the following parameters as well as the variability in the estimates: recruitment, fidelity, survivorship, remigration, clutch size, number of clutches, hatching success, emergence success, and primary sex ratio.

Secondary priorities include research on sex ratios and migratory routes. For example, we do not know the operational sex ratios for any subpopulation nor the implications of highly skewed sex ratios. We need to understand the mechanisms that direct sex determination and the variation is response to environmental variables. Similarly we need to understand how and why sex ratios shift with sex-specific behavior or seasonal migrations. Forensics and aerial surveys

of coastal zones (where turtles, fisheries, boating activities, and pollutants are most concentrated) will enhance our understanding of which turtles are where, relative to known risk factors.

Tertiary priorities include quantifying how epizootics and other sub-lethal events affect population parameters. Epizootic events remain poorly studied and may be cryptic when declines in health are slow. Epidemiological approaches are lacking in studies of marine turtle health. Data quantifying sub-lethal effects of disease on condition, reproduction, maturation, ontogenetic migration, or remigration are completely absent.

Strandings data currently provide us with restricted insight into some of these parameters, but without a better understanding of how these samples vary in space and time and how they are biased by behavior, physiology and cause of death, we will remain limited in how we interpret the populations of interest. Added forensic and necropsy parameter collection would allow the strandings data to increase greatly in value and would enable future rigorous analyses to address demographic parameters as well as mortality risks.

Spatial and Temporal Distributions

There is a need to better understand the distribution of turtles in space and time and to relate turtle distribution to environmental parameters and habitat use. In addition to survival rates, mentioned above, the use of satellite telemetry (as well as other tracking modalities where scale-appropriate) can provide distribution data which could be incorporated into state-space models to predict turtle habitat use and spatial distribution. Such research could provide suggestions for how the spatial overlap between turtles and threats could be reduced. Aerial surveys can be used for the same, but in much smaller areas. While there is very limited information on the U.S. subpopulations and more is needed, there is nothing known about the distribution of animals originating in the Caribbean, except where Mexico juveniles have been detected on the northern foraging grounds through genetic analysis.

Behavioral and physiological studies coupled with satellite telemetry will help us understand how loggerheads select habitats. Several rather significant holes exist in our understanding of loggerhead biology that impact how effectively we can interpret declines. The factors that trigger ontogenetic migrations are poorly studied yet may be critical to our understanding of recruitment. How the various age/stage classes differ in their responses to habitat features or cues, what changes in behavior occur in Western North Atlantic loggerheads as they transition from juveniles to reproductive adults, and whether subsets of loggerheads regularly brumate at some or all locales rather than migrate when temperatures drop below thermal thresholds (along with how responses to such cues act) should be addressed.

Additionally, region- and season-specific behavioral/diving studies are needed to interpret detectability or sightability of loggerheads during aerial surveys. Within-season and/or within-region (or environmental condition) comparisons of turtle distributions should reduce the observational bias from seasonal differences in surfacing behavior.

Stock ID

Efforts are needed to define the population structure. Analyses of genetic samples collected continuously throughout the range of loggerheads in the Western North Atlantic are needed to describe the spatial structure. Additional analyses using non-coding regions and microsatellite DNA are needed to determine female relationships and the extent of male-mediated gene flow among all the subpopulations.

The determination of the natal origin of subpopulations represented on the foraging grounds also contributes to our understanding of stock-specific movements and whether differences in their movements might subject them to differential threats.

Effects of Incidental Capture

Research on the effects of bycatch on survival rate and population growth rate remain needed and should be expanded. Fishery bycatch is often implicated as a source of population declines but direct links to such declines must be clear. As this is a domestic and international issue, collaboration among foreign nations in identifying bycatch effects is essential in addressing bycatch issues.

Trophic Changes/ Carrying Capacity

Shifts in diet have been documented in loggerhead turtles but it is unknown whether the phenomenon is just opportunistic feeding on bycatch or reflects shifts in preferred prey. The reasons and impacts of dietary shifts are important because of trophic changes and losses of preferred prey can change the carrying capacity of the habitat and may result in reduced nesting. Where marine turtles undergo dietary shifts, it is important to establish causal relationships so that the source of change, such as environmental change vs. competition with commercial fisheries may be addressed.

Modeling exercises and approaches should be advanced that integrate new biotic data and allow for predictive assessment. Similarly, retrospective techniques should remain as integral parts of the analyses examinations but with the recognition that the many data gaps this TEWG faced should not persist.

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APPENDIX A. Sex Ratios of Stranded Turtles –*Jeanette Wyneken*

The U.S. Sea Turtle Stranding and Salvage Network (STSSN) collects information on and documents strandings of marine turtles along the U.S. Atlantic and Gulf of Mexico coasts, and infrequently, from the U.S. Caribbean. The reliability, standardization, and magnitude of STSSN participation have increased since the early 1980s (the STSSN was formally established in 1980). The steepest increase in STSSN effort was likely between 1980 and 1985, though some increases in effort continued past 1985. Currently, the network encompasses the coastal areas of the 18 states from Maine through Texas, and includes portions of the U.S. Caribbean. Data are compiled through the efforts of network participants who document marine turtle strandings in their respective areas and contribute those data to the centralized STSSN database (posted at <http://www.sefsc.noaa.gov/seaturtleSTSSN.jsp>). The database is composed primarily of strandings, including cold-stunned turtles, and also contains some reports of incidental captures and distressed turtles. The wide participation allowed the STSSN to accumulate approximately 40,000 loggerhead records; only a small proportion of the records include the sex of the stranded animal. For our analyses, we did not include data from animals whose sex was listed as indeterminate or unknown.

The gender of each turtle in the most inclusive data sets analyzed was based on one or more of the following criteria:

- (a) in adult sized animals, the tail including the cloacal opening extended beyond the caudal margin of the carapace (male) or the tail was short and the cloacal opening did not extend beyond the caudal-most carapace margin (female);
- (b) the turtle carcass was opened and reproductive organs inspected so gender was based on internal morphology;
- (c) if laparoscopy was performed on the turtle at an earlier stage and the gender was assigned, or
- (d) the turtle was tagged previously while nesting (mature females).

In all cases we used in our analysis, the sex of the turtles analyzed was categorized as male (M) or female (F). We examined sex ratios in stranded turtles using several subsets from the STSSN database. First, we analyzed ~5,800 records from 1987 through 2004; data prior to 1987 were omitted because of variable effort in data collection and a lack of rigorous data-checking. We excluded any records for which species was coded as “probable” or “unsure.” Because nearly all records (99.99%) were from the continental U.S., we limited our analyses to this geographic range. We excluded records for which straight carapace length (SCL) > 120 cm or the curved carapace length (CCL) > 128.1 cm, because we were uncertain that these unusually large sizes were correct or were loggerheads. Because CCL was the more commonly reported metric, when necessary we converted all straight carapace lengths (SCL) into estimated CCL values using the morphometric relationships reported in Appendix B.

Second, we analyzed data from 1998-2004. These records have undergone the most rigorous data checking. However, this time series is short and is less likely to detect temporal changes in stranding sex ratios. The sample sizes for different analyses varied depending on whether records contained all variables of interest.

Finally, we analyzed two additional subsets of the data designated as “verified sex”: all records of animals for which the sex of the carcass was verified from necropsy or by previous laparoscopy from (i) 1987-2004 and (ii) 1998-2004. They are smaller data subsets and are probably biased in excluding males because carcasses with a long tail are less likely to be necropsied. These data subsets do not include nesting females that died on the nesting beach. The sample sizes for different analyses varied depending on whether records contained all variables of interest.

Below we defined several stage-identifying categorical variables to use in the sex ratio analysis of the strandings. The size distributions of the turtles in the categories are described by the median CCL in cm and the upper and lower 2.5th percentiles of the distribution of all turtles in the 1987-2004 data subset. The rationale for the size cutoffs is discussed in the Life Stages section of this TEWG report.

- Immatures: turtles with CCL >10 and ≤ 80 cm. The median size of these animals was 67.1 cm CCL; the lower 2.5th percentile was 42.0 cm CCL and the upper 97.5th percentile was 79.2 cm CCL.
- Mixed adults and immatures: turtles with CCL > 80 cm and ≤ 98.45. These data were excluded from analyses, except where all strandings in the time series subsets were considered regardless of stage.
- Adults: turtles with CCL >98.45 cm, the mean size of putative first-time nesters (see Table 3 of this report). While this size class is mostly adults, we could not say unequivocally that a few large immature turtles might also be included in the subset. The median size of these animals was 102.2 cm CCL; the lower 2.5th percentile was 98.6 cm CCL and the upper 97.5th percentile was 109.0 cm CCL.
- Large adults: turtles with CCL >109.3cm. The median size of these animals was 112.3 cm CCL; the lower 2.5th percentile was 109.5 cm CCL and the upper 97.5th percentile was 126.5 cm CCL.

Because of the preponderance of moderately to strongly female-biased hatchling sex ratios (Tables 4 and 5 of this report), variations from a female bias by later stages are potentially informative about trends in size class related death rates.

We compared sex ratios in strandings by latitude, state, and region and tested for differences using chi-square or Fisher-exact tests ($\alpha = 0.05$). Regions were distinguished by climate, ecology, behavioral areas (*e.g.* areas where turtles are feeding vs. an area used for mating), gross fisheries similarities (*e.g.* TED regulations), or combinations of these. The Gulf of Mexico region (GoM) was defined as Florida’s west coast and the coastlines of Alabama, Mississippi, Louisiana, and Texas. The Southeast U.S. Atlantic region (SE) was defined as the Florida east coast through North Carolina, and the Northeast U.S. Atlantic region (NE) was defined as Virginia through Maine. The months of May through August were defined as the main nesting season.

Using the stranding database within the limits defined above, we outlined a series of assumptions, framed questions and then formulated hypotheses to query the four data subsets for sex ratio information. We address these below.

Assumption: The strandings reflect the same trends in sex ratio as the live turtle assemblages from which they came.

Question 1: What are the baseline sex ratios in the immature, adult and large adult strandings, respectively, and do they differ?

H₀: Sex ratio does not differ between immature and mature turtles.

We reject the null hypothesis that sex ratios within stranded loggerheads are the same in immature vs. either subset of mature turtles. The differences are manifested in each of the 4 data subsets examined (Figure A-1, Table A-1). In all cases, about 70% of the immature turtles were females and the percent females decreased between the immature and the mature stages. These changes suggest that mortality rates and/or the probabilities of stranding are not uniform for both sexes by stage (length classes). Interestingly, the data category that most rigorously met the criteria for data checking and sex identification (1998-2004 verified sex) showed a lower percent females (proportionately more males) compared with the percentage characterizing immature stages in spite of its exclusion of some adult males. The much lower female sex ratios in the large adult categories probably underestimate the percentage of males in strandings (Table A-1) and point to sex specific changes in death rates (or stranding rates) with age, with the caveat that we are comparing samples that differ greatly in n. Sample sizes for immatures are one to two orders of magnitude greater than those for adult and large adult categories.

The observed stage-specific sex ratio shifts in strandings may have a variety of nonexclusive explanations, including (i) there is sex-specific mortality so that the sex ratio changes from ~2:1 to 1:1 or 1:2 with increasing age class, (ii) proportionately more males wash ashore once they reach adulthood than when they are immature, (iii) the likelihood that a carcass will be cast up on a beach (and thus observed by the stranding network) differ by age class and sex, (iv) there are sex-specific differences in distribution and risk of mortality by stage, and/or (v) primary sex ratios shifted across time so that conditions that 3-8 decades ago produced the nearly even or male-biased sex ratios found in mature turtles that hatched 3-8 decades ago differ from those that produced the immature turtles sex ratios, which hatched 1-3 decades ago.

We also note that there was a decrease in the percent female when adults and large adults sex ratios are compared in the data subsets that include both verified and unverified sex turtles. However, this difference in the two mature sizes was not significant when the verified sex data subsets were analyzed.

Figure A-1. Sex ratios of immature and mature loggerhead strandings by size category including all seasons and regions. Sex ratios differed between immature and mature size classes. Mature size classes (adults and large adults) did not differ from one another in sex ratios. Numbers over each bar are the number of female strandings in each category. Detailed data and analyses are found in Table A-1.

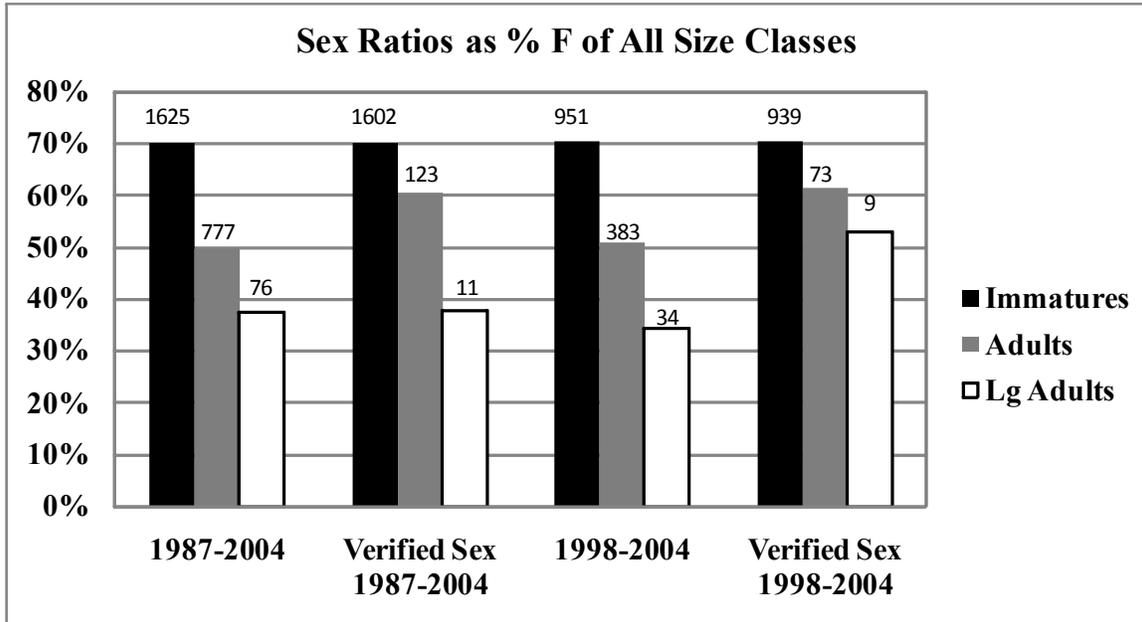


Table A-1. Sex ratios of all immature and mature loggerhead strandings in all seasons and regions. Parenthetical numbers are the number of strandings in each category. Comparisons of numbers if males and females were made by Chi-square tests for equal proportions (1 df). F = females; M = males; I = immatures; A = Adult; LgA = large adults

Size classes	% Females 1987-2004	% Females Verified Sex 1987-2004	% Females 1998-2004	% Females Verified Sex 1998-2004
Immatures	70.13% (2317)	70.20% (2282)	70.39% (1351)	70.55% (1331)
Adults	49.74% (1562)	60.59% (203)	51.00% (751)	61.34% (119)
Lg Adults	37.44% (203)	37.93% (18)	34.34% (99)	52.94% (17)
Chi-Square FxMxIxA	$X^2 = 165.0$, 1 df, $P < 0.001$	$X^2 = 8.11$, 1 df, $P = 0.004$	$X^2 = 73.8$, 1 df, $P < 0.001$	$X^2 = 4.39$, 1 df, $P = 0.036$
Chi-Square FxMxIxLgA	$X^2 = 91.0$, 1 df, $P < 0.001$	$X^2 = 14.0$, 1 df, $P < 0.001$	$X^2 = 55.0$, 1 df, $P < 0.001$	$X^2 = 4.81$, 1 df, $P = 0.028$
Chi-Square FxMxAxLgA	$X^2 = 11.8$, 1 df, $P = 0.001$	$X^2 = 0.002$, 1 df, $P = 0.965$	$X^2 = 9.71$, 1 df, $P = 0.002$	$X^2 = 1.33$, 1 df, $P = 0.249$

Assumption: Shifts in strandings sex ratios by stage, over time, can reflect losses of large proportions of reproductive turtles or of immature turtles from subsequent life stage categories .

Question 2. Have sex ratios of stranded loggerheads changed over time.

H₀: Sex ratios do not change with time within size classes.

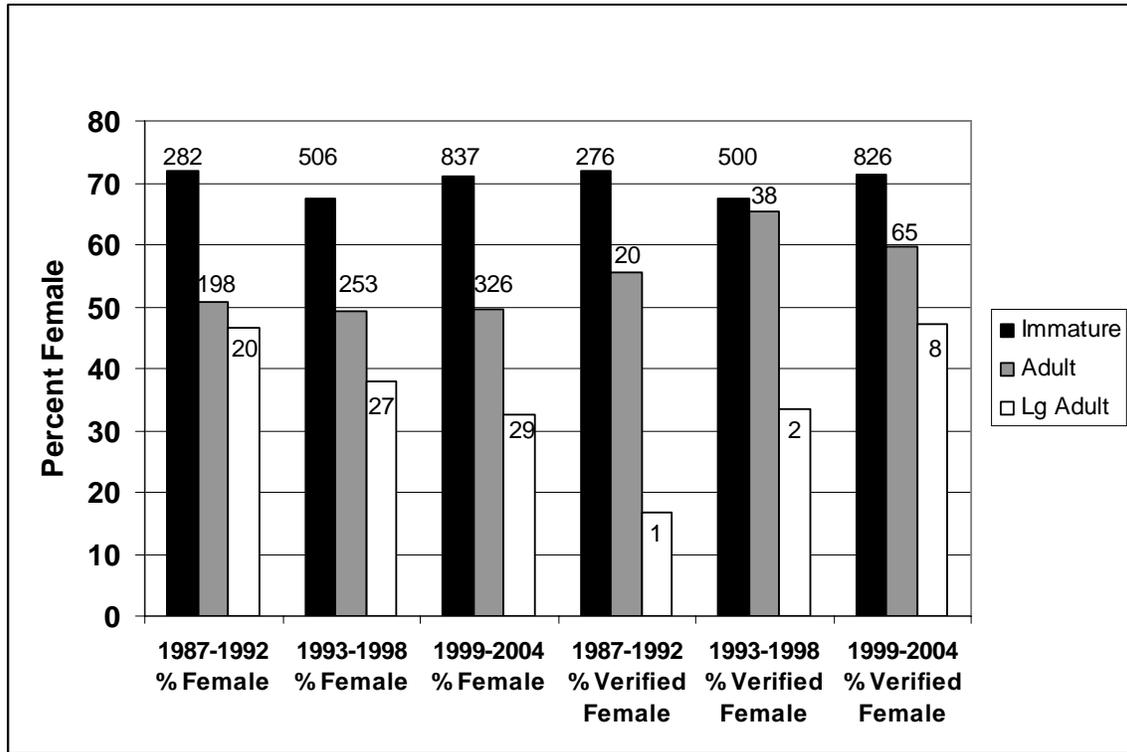
We considered the data for all regions together but calculated the sex ratios separately for the 4 subsets of data. We tested the hypothesis separately within immature turtles, adults, and large adults over time, with counts of males and females parsed in three bins (1987-92, 1993-98, 1999-2004). We compared sex ratios within stages using 3x2 Chi-square analyses or, where sample sizes were small, Fisher exact test (Table A-2, Figure A-2,).

We were unable to reject the null hypothesis of no change in sex ratio from 1987-2004 within immatures and within either subset of mature turtles. When we restricted our analysis to only those records of verified sex data, we found similar results. We did not detect large changes in sex ratios over time in two sets of years surveyed. Because multiple year classes contribute to each stage class, and loggerhead turtles are late maturing animals, several more decades of sufficient data collection will be needed to detect sex ratio shifts over time and only if such a shift persists for a biologically sufficient period to resolve such changes.

Table A-2. Sex ratios as percent of females by stage over time. Comparisons were made of male and female counts by stage and time bin. Numbers of total stranding in each category are given parenthetically. There were no differences in sex ratio over time within the immatures and within adults.

Size classes	1987-1992	1993-1998	1999-2004	1987- 1992 Verified Sex	1993-1998 Verified Sex	1999-2004 Verified Sex
Immatures	71.9 % (392)	67.6% (749)	71.2% (1176)	71.9% (384)	67.6% (740)	71.3% (1158)
	$X^2 = 3.62, 2 \text{ df}, P=0.164$			$X^2 = 3.67, 2 \text{ df}, P = 0.159 \text{ ns}$		
Adults	50.8 % (390)	49.3% (513)	49.5% (659)	55.6% (26)	65.5% (58)	59.6% (109)
	$X^2 = 0.22, 2 \text{ df}, P=0.895$			$X^2 = 1.01, 2 \text{ df}, P = 0.602 \text{ ns}$		
Lg Adults	46.5 % (43)	38.0% (71)	32.6% (89)	16.7% (6)	33.3% (6)	47.0% (17)
	$X^2 = 2.42, 2 \text{ df}, P=0.229$			Fisher Exact Prob = 2 df, P = 0.063 ns		

Figure A-2. Sex ratios as percent of females by stage over time. Comparisons were made of male and female strandings across time bins by stages. No significant differences were found within size classes in any of the data subsets. Numbers over, or in, each bar are the number of female strandings in each category. Details of the analyses and samples are found in Table A-2.



Assumption: If stage-specific turtle mortality is uniform across time for large areas, then sex ratios should remain relatively constant. Deviations in sex ratio by regions could identify high risk and low risk areas. We explored regional sex ratios for the Northeast U.S., Southeast U.S. and Gulf of Mexico) with all seasons were considered together.

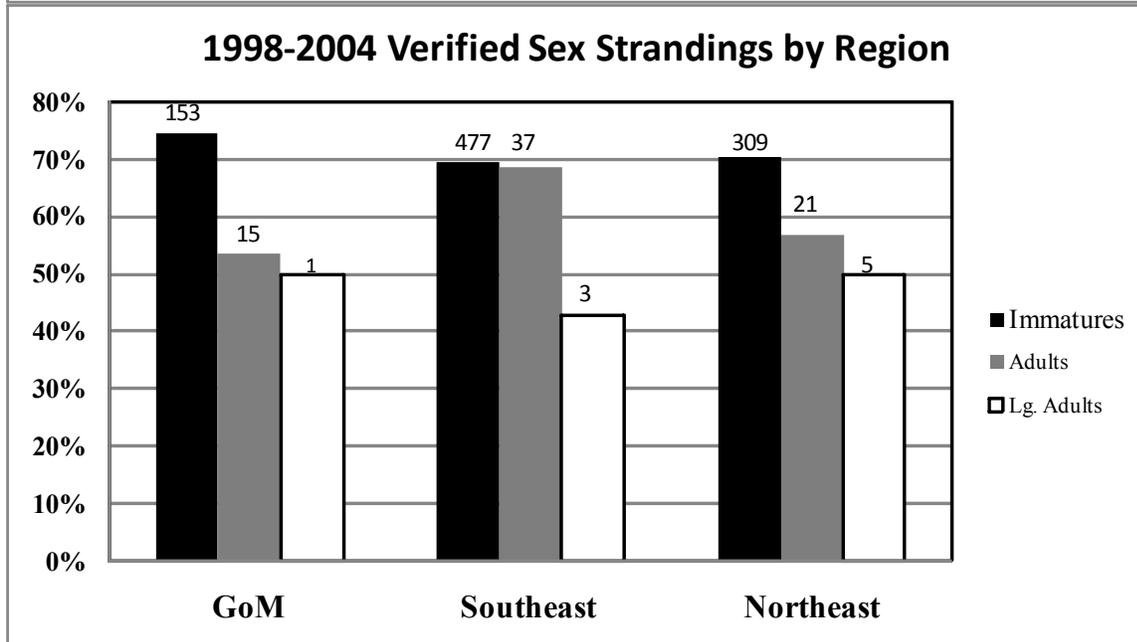
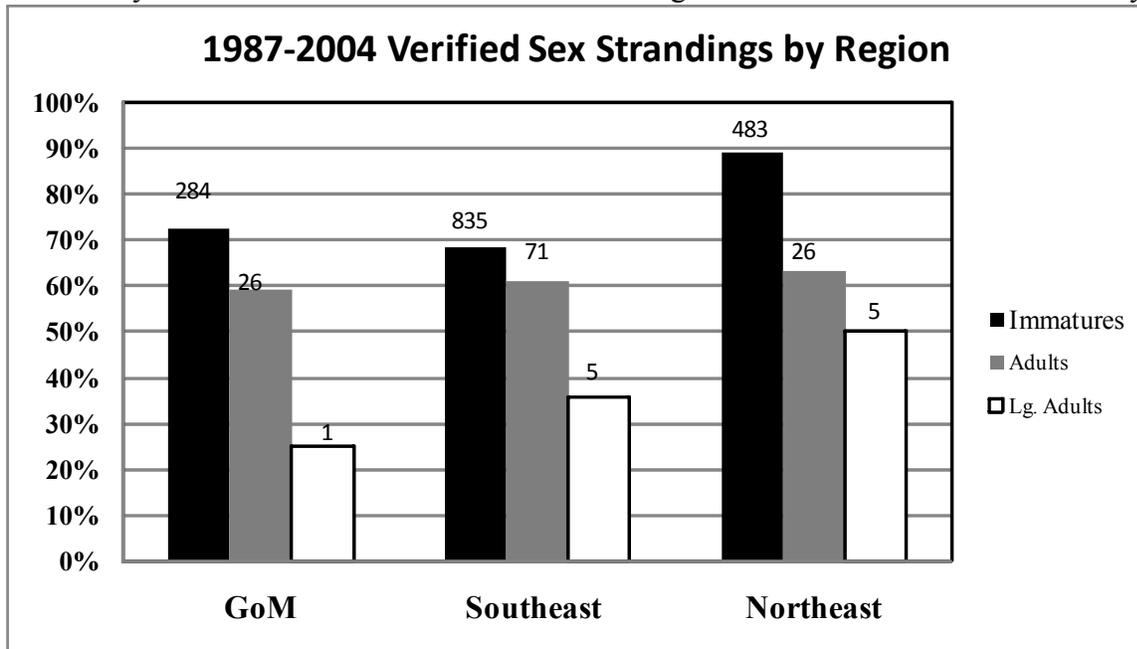
Question 3. Are there high risk vs. low risk regions of coast?

H_0 : Sex ratios of the three size classes are similar across regions.

We failed to reject the null hypotheses that sex ratios were similar across regions within all immature turtles, adults of verified sex, and all large adults; (Figures A-3a, A-3b, Table A-3) but reject the null hypothesis when adults from the 1987-2004 and 1998-2004 subsets were compared across regions (Figures A-3c, A-3d, Table A-3). While the sex ratios of immature turtles were female-biased in all regions, the sex ratios of mature turtles tended to be even or slightly male biased across most regions. We note that our analyses failed to detect the predicted mature female bias in any region in spite of a known lack of adult male necropsies. Within the adults, proportionally fewer females stranded in the Gulf of Mexico than along in the southeast Atlantic coastline (Figures A-3a, A-3b, Table A-3). No sex ratio differences were detected in the

Verified Sex subsets, with the caveat that the adult sample sizes for the Northern and Gulf of Mexico regions are small and probably lack sufficient resolution.

Figures A-3a and A-3b. Sex ratios by stage and region across all seasons based on 1987-2004 verified and 1998-2004 verified sex subsets. Numbers over the bars are total females by category. Northeast region strandings occurred north of the North Carolina-Virginia state lines. Southeast strandings occurred between North Carolina and Florida’s east coast, and Gulf of Mexico (GoM) turtles were defined as those stranding along Florida’s west coast through the coasts of Alabama, Mississippi, Louisiana, and Texas. There were no differences across regions in the sex ratios by size class. Sex ratios shifted from strongly female biased immature turtles to moderately female biased adults and male biased large adults. Table A-3 details the analyses.



Figures A-3c and A-3d. Sex ratios by region across the three size categories for 1987-2006 and 1998-2004 subsets. The only significant differences among regions in sex ratios by size class were in the Adult stages of the verified sex subsets (Table A-3). Those differences may reflect different sources of mortality by regions (for example various TED implementations in the GoM vs. the Southeast and Northeast U.S.). The immature turtle strandings sex ratio in the Southeast U.S. is less strongly female biased that in the GoM or the Northeast; the empirical data to explain this difference. Sex ratios in GoM large adults are not informative because of small numbers. Data groupings, format and comparisons are described in Figure A-3a.

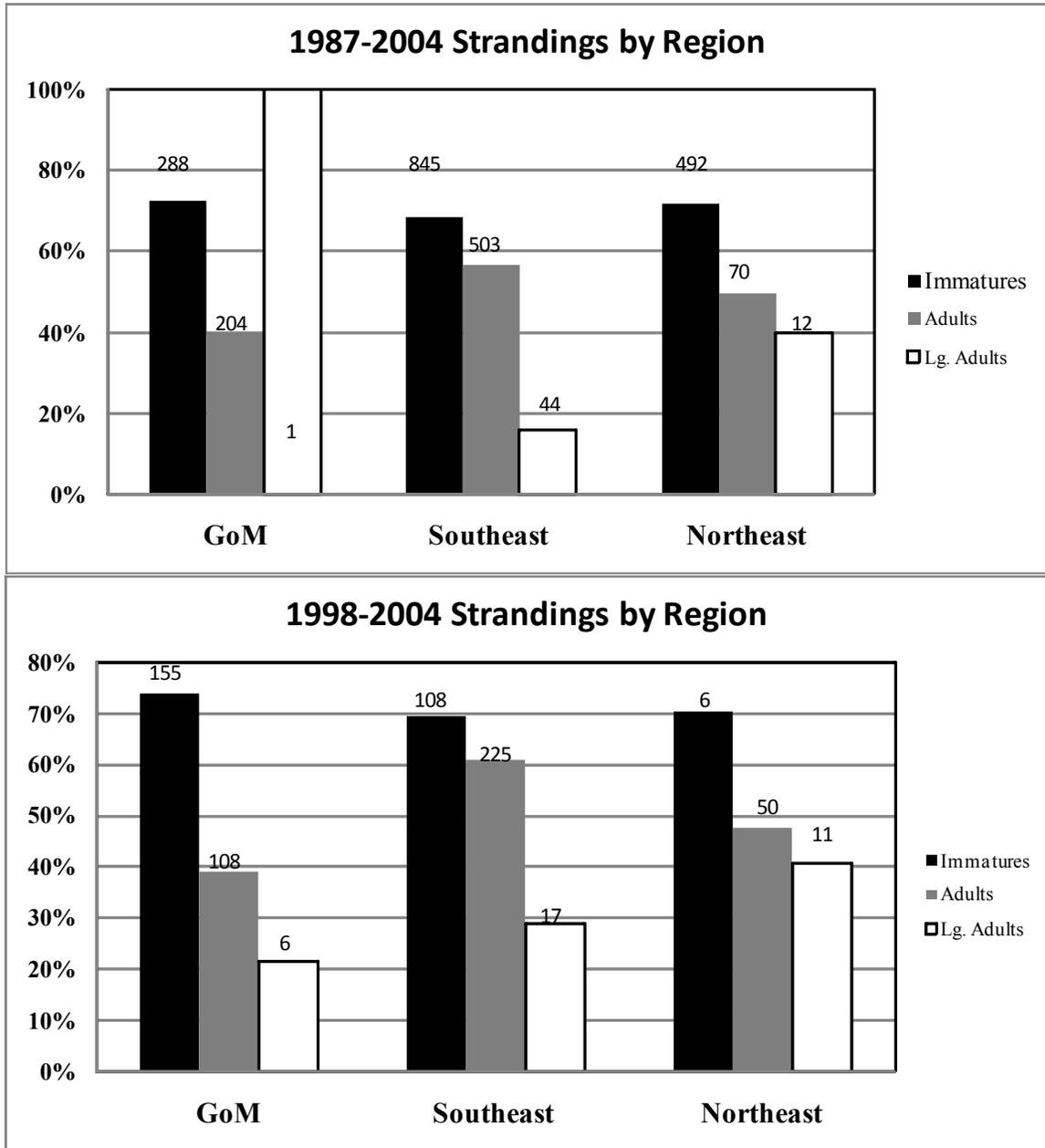


Table A-3. Sex ratios of loggerhead strandings by stage and region as described above.
The 3x2 Chi-square or Fisher Exact test analyses were run within a stage for each of the 4 data subsets.

Stage by Region	% Females 1987-2004	% Females 1987-2004 Verified Sex	% Females 1998-2004	% Females 1998-2004 Verified Sex
Northeast immature	71.82 (685)	71.88 (672)	70.40 (446)	70.39 (439)
Southeast immature	68.48 (1234)	68.56 (1218)	69.35 (695)	69.53 (686)
GoM immature	72.36 (398)	72.45 (392)	73.81 (210)	74.27 (206)
	X ² = 2.62, 2 df, P=0.27, ns	X ² = 3.42, 2 df, P=0.180, ns	X ² = 1.54, 2 df, P=0.464, ns	X ² = 1.72, 2 df, P=0.423, ns
Northeast adult	49.65 (141)	60.47 (43)	47.62 (105)	56.76 (37)
Southeast adult	56.73 (911)	61.21 (116)	60.98 (369)	68.52 (54)
GoM adult	40.00 (508)	59.09 (44)	38.99 (277)	53.57 (28)
	X ² = 30.3, 2 df, P<0.001	X ² = 2.73, 2 df, P=0.255, ns	X ² = 31.20, 2 df, P<0.001	X ² = 2.21, 2 df, P=0.332, ns
Northeast large adult	40.00 (30)	45.45 (11)	40.74 (27)	50.00 (10)
Southeast large adult	15.79 (108)	35.71 (14)	38.64 (44)	42.86 (7)
GoM large adult	16.67 (6)	25.00 (4)	21.43 (28)	50.00 (2)
	X ² = 1.38, 2 df, P=0.502, ns	Fisher Exact Prob. =0.10 ns	X ² = 2.92, 2 df, P=0.232, ns	Fisher Exact Prob. =0.20 ns

Assumptions and background: Because mortality risks in nearshore coastal waters may vary by location, we grouped states in which the turtles' natural history is likely to be the most similar and whose waters shared similarity in TED regulations in the past. Our groupings of states ignored coastline length and are based on large scale differences in ecology, many of which reflect seasonal changes: (i) the Northeast (NE) states (Maine through Virginia) that have turtles in their near coastal waters to feed during warmer water months but do not host significant nesting; those turtles migrate away when temperatures cool and day lengths shorten; (ii) Turtles utilize the nearshore waters off North Carolina through Georgia, and some breeding and nesting occurs on their shores; the subpopulation differs from that nesting on the east and southwest coasts of Florida. Like those loggerheads in NE states, they tend to leave the nearshore waters in the fall and winter, except in Raleigh Bay (Epperly et al. 1995); (iii) Florida's Atlantic coast and nearshore waters host significant feeding, breeding and nesting; turtles reside in its coastal waters year round, and much of the coastal environment is influenced by the Gulf Stream current and its eddies; (iv) Florida's West coast, and the coasts of the Florida Panhandle, Mississippi, and Alabama and the nearshore waters are treated as part of the eastern Gulf of Mexico coast which hosts feeding and some significant nesting in the southwestern Florida; nesting elsewhere is limited. Fewer turtles reside in the shallow, coastal waters of the eastern Gulf during cooler months, and the coastal environment is somewhat more temperate, at least to the north; (v) States bordering the Western of the Gulf of Mexico (Louisiana, and Texas) do not host significant

nesting numbers of loggerhead turtles, but turtles use their nearshore waters seasonally. Until 2003, TED regulations differed between the Atlantic and Gulf regions, with smaller escape openings allowed in the Gulf of Mexico. As of August 2003 the regulations were similar and both areas are required to use openings much larger than required in the past. There were no TED requirements in the Northeast U.S. until 1992 when the summer flounder fishery was required to use TEDs, but only as far north as Cape Charles, Virginia. Note also that until 1994, the TED regulations for the shrimp fishery were seasonal and that tow times were allowed to be used in lieu of TEDs in inshore waters; as of December 1992 TEDs were required at all times in all areas for the shrimp fishery (Epperly 2003).

Questions 4: Are there shifts in sex ratio found at scales that integrate both natural history and management-specific mortality risks?

H₀: Sex ratios do not vary by regions in which loggerheads share similar natural history and TED history.

We rejected the null hypothesis that strandings shared similar sex ratio across ecologically similar state-groups in our examinations of both large data subsets, and failed to reject the null hypothesis when we tested the two verified sex data subsets. The significant differences were found in the adult sizes (Table A-4).

The 1987-2007 and 1998-2004 Verified Sex subset showed different trends (Tables A-4) than the other subsets. That implies that either the assignments of sex for the turtles which were not necropsied are highly prone to error, or that the verified sex datasets are biased in some ways other than what is found in the unverified subsets. Using the Verified sex data subsets (datasets that are presumed to underestimate mature males), we found female bias is common in all state-groups. The absolute number of stranded female turtles shows that there is significant female mortality that removes future recruits and mature turtles from the population at all locations.

Strandings from locations where adult and large adult turtles share grossly similar ecology tended to differ in sex ratio. For example, Florida Atlantic and Gulf coasts strandings tended to suggest either coast-specific differences in the standing stock sex ratios, the sex-specific mortality differed in rates on the two coasts, or some combination of these factors. The sex ratios tended to be slightly female-biased or not biased in sex ratios on the Atlantic coast but show male bias on the Gulf coast based on the two larger data subsets.

Because many more immature than mature turtles are found in all the data subsets, the sex ratios are driven by those immature turtles. The 1987-2007 shows ~1:1 sex ratios along Florida's Atlantic coast and male biased sex ratio along the northeastern Gulf of Mexico coast (Tables A-4). Elsewhere the trend is for sex ratios to be moderately female biased. These subsets likely include immature males that were not necropsied and that may be misidentified as females in all samples, it is possible that female biases are somewhat less than what we detected. Thus, in this analysis the strandings data may underestimate male presence in nearshore waters.

Table A-4. Sex ratios of all stranded loggerhead turtles (all stages combined) as percent female across all seasons, by state groups. Chi-square (2 x 5, 4 df) comparisons were made among state groups comparing numbers of males and females in each state-group. Expected numbers were based upon standard rows and columns calculations and did not for a 1:1 expectation.

State-groups:	Northeast States: Maine-Virginia	North Carolina – Georgia	Florida Atlantic	Eastern Gulf of Mexico	Western Gulf of Mexico
1987-2004	70.90% (1066)	64.44% (2013)	54.47% (1202)	42.74% (1088)	65.21% (470)
$X^2=130.0, 4df, p<0.001$					
1987-2004 Verified Sex	71.99% (714)	67.37% (1143)	68.78% (205)	66.38% (116)	71.34% (328)
$X^2=5.56, 4df, P=0.23$					
1998-2004	64.88% (578)	67.43% (832)	59.06% (276)	43.06% (360)	73.55% (155)
$X^2=77.2, 4 df, p <0.001$					
1998-2004 Verified Sex	68.93% (486)	69.81% (636)	65.77% (111)	68.29% (82)	73.38% (154)
$X^2=1.98 4df, p=0.74, ns$					

Assumption: Theoretically, the percentage of adult females should increase during breeding season along shorelines that serve as major rookeries. Because mating precedes nesting, we also expect that adult males may increase in proportion in these same waters just before or early in the nesting season. Mating is often a high-risk activity and strandings of both sexes should increase during nesting season. This assumption was supported by comparison of strandings numbers during the nesting and non-nesting seasons (Table A-5a, and A-5b).

Question 5. Do sex ratios of strandings differ between breeding (nesting) and non-breeding (non-nesting) seasons?

H₀: Strandings sex ratios do not differ between breeding and nonbreeding seasons.

We compared sex ratios of strandings during nesting and non-nesting seasons. First we compared the groupings of strandings used in Table A-4 and next, to explore nesting beach effects more specifically, we separately grouped strandings sex ratios by shoreline regions with significant nesting vs. those with little or no nesting and tested the null hypothesis by shoreline.

(i) *We rejected the null hypothesis of similar sex ratios across all shorelines during the nesting (May – September) and non-nesting (October–April) seasons.* Based on the 1987-2004 data, the strandings numbers tended change between nesting season and non-nesting seasons, and the sex ratios were not uniform among shoreline groups in which the turtles should share similar

behavior within either the nesting season or outside of it (Table A-5a); this difference was largely driven by a shift to a stronger female bias in southeastern Florida. We then compared sex ratios between nesting and non-nesting seasons using the within regions 1987-2004 Verified Sex totals. We could not draw the same conclusion as we found no overall shifting sex ratio between nesting and non-nesting seasons (Table A-5b).

Shoreline-specific comparisons: Data were split into numbers of nesting and non-nesting season strandings and were compared along shorelines that hosted appreciable nesting and shores that did not. This set of comparisons addressed the assumption that breeding season affects behavior and so could subject turtles to differing mortality risks. We examined sex ratio of strandings of all size classes grouped in order to explore the data for shoreline aggregations represented by all size classes and then we also analyzed the available data subsets for each size (or stage) class.

(ii) We rejected the null hypothesis that strandings sex ratios do not differ between breeding and nonbreeding seasons when we analyzed the 1987-2004 data set (Table A-5c). We found that sex ratios shifted from female-biased during the nesting season to male-biased outside of the nesting season in regions that host loggerhead nesting. When we analyzed the other three data subsets, no significant differences were found and the null hypothesis could not be rejected.

In all data subsets, the numbers of females were highest in the nesting season, but the generally female-biased sex ratios differed little between nesting and non-nesting seasons. Because immature turtles stranding tend to be the most numerous of all size classes, they most influenced sex ratio trends. These immature sizes are not known to migrate to waters off nesting beaches.

We found that in most cases there were no differences in sex ratios between nesting and non-nesting seasons (Tables A-5c-d). *Based on the 1987-2004 subset we cannot reject the null hypothesis. The notable exceptions in which we reject the null hypothesis are when we examined adult sex ratios for turtles stranding on nesting beaches. During nesting season the sex ratio was usually female biased along shores that host nesting while nesting tended to be male biased during the non-nesting season for the same areas. The large adult sex ratios tended to be male biased (Tables A-5d), perhaps implying that the largest turtles tend to be males.*

When we restricted our comparisons of strandings sex ratios in the nesting and non-nesting seasons and regions using the most rigorously data-checked subset (1998-2004 verified sex) and again tested the null hypothesis. We found no significant changes in sex ratios between seasons in either region (Tables A-5c).

Table A-5a. Strandings sex ratios (1987-2004) during the nesting and non-nesting season by regions as outlined in Tables A-4. SFla: Florida Atlantic coast; CG: (Carolinas and Georgia); NE: Northeast States; GoM East: Eastern Gulf of Mexico; GoM West: Western Gulf of Mexico; ns: not significant.. All size classes are combined. Total strandings by shoreline groups are given in columns 2 and 3. A Chi-Square comparisons of standing numbers by nesting and non-nesting season is given in the bottom row. Comparisons in numbers of males and females by nesting and non-nesting season are compared by Chi-Square tests summarized in the last column.

Strandings by Shoreline Groups	Non-Nesting Season	Nesting Season	N	Females Non-Nesting Season	Males Non-Nesting Season	Females Nesting Season	Males Nesting Season	Chi-Square, df, p
SFla	331	336	667	156	175	214	122	18.5, 1 df, p <0.001
GoM East	346	278	624	142	204	126	152	1.15, 1 df, p=0.283 ns
GoM West	214	120	334	149	65	89	31	0.77, 1 df, p <0.379 ns
CG	400	1186	1586	249	151	773	413	0.03, 1 df, p =0.85 ns
NE	265	606	871	180	85	400	206	0.31, 1 df, p=0.58 ns
Totals	1556	2526	4082	876	680	1602	924	20.51, 1df, p <0.001
Chi Sq = 346.0, 4 df, p , <0.001								

Table A-5b. Strandings sex ratios assessed in the 1987-2004 verified-sex data subset; regions as outlined in Tables A-4. All size classes are combined. Format as in Table A-5a

Strandings by Shoreline Groups	Non-nesting Season	Nesting Season	N	Females Non-nesting Season	Males Non-nesting Season	Females Nesting Season	Males Nesting Season	Chi Sq, df, p
SFla	122	83	205	79	43	62	21	1.84, 1 df, p =0.175 ns
GoM East	162	53	215	116	46	36	17	23.59, 1 df, p <0.001
GoM West	207	118	325	145	62	89	29	0.83, 1 df, p=0.36 ns
CG	197	845	1042	123	74	572	273	1.76, 1 df, p=0.18 ns
NE	208	518	726	149	59	365	153	0.05, 1 df, p =0.82 ns
Totals	896	1617	2513	612	284	1124	493	0.34, 1 df, p =0.56 ns
Chi Sq: 453.0, 4 df, p <0.001								

Table A-5c. Comparisons of sex ratios in strandings between nesting and non-nesting season on shoreline with and without appreciable nesting. All size classes are combined. Strandings for each state were combined for the states that hosted significant nesting and separately combined for states without significant nesting. Parenthetical numbers are the total numbers of strandings by category. Chi-Square comparisons were made using stranding numbers, not percentages.

	Nesting Shoreline <i>Nesting Season</i>	Nesting Shoreline <i>Non-nesting Season</i>	Chi-Square
1987-2004	59.00% (2610)	45.58% (1673)	X ² =35.5, 1 df, p <0.001
1987-2004 Verified Sex	68.94% (1201)	66.77% (641)	ns
1998-2004	70.90% (653)	68.11% (370)	ns
1998-2004 Verified Sex	54.43% (660)	58.43% (372)	ns
	Nonnesting Shoreline <i>Nesting Season</i>	Nonnesting Shoreline <i>Non-nesting Season</i>	Chi-Square
1987-2004	66.67% (930)	70.50% (617)	ns
1987-2004 Verified Sex	70.51% (790)	72.76% (525)	ns
1998-2004	70.68% (556)	69.96% (253)	ns
1998-2004 Verified Sex	45.88% (561)	41.57% (258)	ns

Table A-5d. Comparisons of strandings sex ratios by size class across nesting vs. non-nesting season at shorelines with and without appreciable nesting. Parenthetical numbers are the total strandings by category. Comb. Stages reflect the immatures, adults and large adults together. Comparisons of 1998-2004 verified sex by stage were limited to total strandings because a detailed breakdown was not available.

1987-2004	Nesting Season	Non-nesting Season	Chi-Square
Shorelines with Nesting			
Immatures	69.13% (881)	68.94% (425)	ns
Adults	56.74% (816)	39.42% (586)	40.9, 1 df, p <0.001
Large adults	36.73% (98)	35.59% (59)	ns
Comb. stages	61.73% (1795)	50.93% (1070)	35.3, 1 df, P < 0.001
Shoreline without Nesting			
Immatures	71.69% (604)	71.96% (403)	ns
Adults	49.06% (106)	57.41% (54)	ns
Large adults	42.86% (21)	40.00% (25)	ns
Comb. stages	67.58% (731)	68.67% (482)	ns
1987-2004 Verified Sex			
Shorelines with Nesting			
Immatures	68.46% (837)	66.79% (280)	ns
Adults	71.25% (80)	38.89% (36)	11.0, 1 df, P < 0.001
Large adults	36.36% (11)	25.00% (4)	ns
Comb. stages	68.32% (928)	63.32% (347)	ns
Shoreline without Nesting			
Immatures	72.52% (626)	72.12% (538)	ns
Adults	60.00% (55)	59.38% (32)	ns
Large adults	37.50% (6)	42.86% (7)	ns
Comb. stages	70.83% (672)	71.06% (577)	ns
1998-2004			
Shorelines with Nesting			
Immatures	70.89% (474)	68.91% (178)	ns
Adults	66.67% (57)	50.00% (22)	Fisher Exact test p = 0.059
Large adults	42.86% (5)	50.00% (2)	ns
Comb. stages	70.07% (538)	67.35% (202)	ns
Shoreline without Nesting			
Immatures	71.60% (412)	69.66% (267)	ns
Adults	67.74% (31)	33.33% (9)	ns
Large adults	40.00% (5)	60.00% (5)	ns
Comb. stages	70.98% (448)	67.71% (281)	ns
1998-2004 Verified Sex			
Shorelines with Nesting			
All stages	54.12% (660)	58.43% (372)	ns
Shoreline without Nesting			
All stages	45.88% (561)	41.57% (258)	ns

While the breeding season, per se, should not attract immature turtles to nesting areas, some of the same environmental factors associated with the onset of breeding seasons also trigger other kinds of turtle migrations (*e.g.* feeding migrations, seasonal warming of temperate waters, and transit through breeding areas by immature as well nonbreeding mature turtles). Changes including day length and water temperature are associated with feeding migrations of immature loggerheads shoreward from the edges of the Gulf Stream and coastal migrations to and from summer feeding grounds.

Interestingly, the numbers of adult male turtles stranding tend to be high, in spite of perceived sampling biases that should produce female biased sex ratios (because adult males are often excluded from necropsy). The observed trend in the strandings data probably reflects differences in the behavior of the sexes and their vulnerabilities. For example, while males and females are both attracted to coastlines that host nesting, the females go to the site because it is appropriate and safe for nesting. While mating occurs along the coastline near nesting beaches, it could theoretically occur elsewhere. In contrast, males arrive in these waters to intercept females and mate. The male-biased sex ratios or less-pronounced female bias undoubtedly includes the impacts of the greater risks males face while mating and searching for mates (*e.g.* boat strikes, predation, attack and injury by other male turtles). Males are not particularly maneuverable when mating and tend to be closer to the surface and vulnerable to boat strikes when mating. The importance of these sex ratio changes with class provide clues to change, but we lack sufficient understanding of sampling biases to link those changes to production directly.

If we accept the assumption that these data subsets accurately reflect the sex ratio trends for the stranded turtles during breeding and nonbreeding seasons, then increases in stranding numbers during nesting season (which includes both large numbers of immature turtles and adult turtles) contributes losses in potential productivity. It is the trends in changes in the sex ratios between the immature and adult size classes that herald such. The roughly 65-70% female-bias found in the immature turtles tends to be of lesser magnitude in the adult stage subsamples (or in some subsamples, shifts to male bias). The loss of recruits to the adult stages and loss of mature turtles from important rookeries during the breeding season should be considered as particularly important source of lost of productivity.

Among the potential indicators of shifts in life history is change in size of sexually mature animals. In declining populations, for which breeding sites are not limiting, breeding may commence at a smaller size than in previous generations.

Question 6. Is there any indication of a shift or shifts in the sizes of stranded mature animals (*e.g.*, “Adults”)?

Ho: There is no detectable change in the sizes of stranded adult loggerheads between 1987 and 2004.

We failed to reject the null hypothesis. While our size cutoffs may have excluded the very smallest individuals and undoubtedly missed some smaller but mature animals, we found no significant shift in the median sizes of either sex of stranded adult loggerheads (Table A-6). We

note that it is possible that the time range covered may not be sufficient to detect selection for breeding at a smaller size.

Table A-6. Sizes of stranded turtles over time. F is female, M is male, FV and MV are females and males verified through necropsy or other confirming data.

Median	Min	Max	N	Years	Sex
102.60	98.50	127.00	302	1987-95	F
102.85	98.50	127.42	416	1996-2004	F
103.50	98.50	128.00	318	1987-95	M
104.00	98.50	127.00	497	1996-2004	M
101.80	98.60	114.00	36	1987-95	FV
103.00	98.50	123.00	98	1996-2004	FV
103.00	98.50	119.00	38	1987-95	MV
104.90	98.60	122.00	60	1996-2004	MV

Conclusions

Our understanding of loggerhead sex ratios remains rudimentary despite nearly 25 years of study. From the egg to the reproductive adult, the sources of sex ratio variation and their implications are still poorly understood. The physiological mechanisms that select which signals direct embryonic gonads to be male or female are not yet understood. Temperature interacts with the embryo, but the mechanisms of how temperature directs sex and what other factors modify sex determination are still key unanswered questions. How much loggerhead sex ratios vary spatially and temporally has not been addressed systematically or across sufficient numbers of years to establish a measure of variability. Such measures are necessary baselines.

How and why sex ratios differ among hatchlings, immature stages, and adult turtles remain intriguing. The contributions of mixed stocks and multiple year classes undoubtedly dampen oscillations in sex ratios, but also make it challenging to recognize if sex ratios of different cohorts have changed. Understanding the mating systems of loggerheads from the physiological, behavioral, and ecological perspectives are key to understanding how changes in populations and sex ratios may impact productivity. Yet, we know little of the details of loggerhead mating systems.

Based on strandings data, the lack of female bias in mature sized turtles across analyses is worth noting and may reflect long-term reductions or losses of females from the population. However, we cannot rule out other explanations including sex-specific differences in remigration intervals and distributions or the possibility of sex-specific vulnerabilities.

Strandings sex ratio data remain intriguing and in some cases alarming, particularly in the absolute numbers and proportions of adult females lost from the breeding population. Immature, adult, and large adult sex ratios all reflect the integration of many year classes. Hence, discerning the causes(s) of the shift away from a strong female bias in the older (adult or large

adult) stages cannot be specifically interpreted without further data such as necropsy results or better understanding of sex-specific movements and risks. However, one can hypothesize that because of the large numbers of immature females that strand in all regions, there is loss in recruitment to reproductive stages that we are now detecting in the strandings. We cannot discount the possibility that the high proportion of stranded immature turtles reflects losses of large proportions of females from mixed stocks that feed in or migrate through U.S. coastal waters. There is evidence for sex-specific dispersal differences of immature turtles (Casale et al. 2002 using Mediterranean strandings, Dellinger 2007 for wild-caught immature turtles in the eastern Atlantic), however, differences in behavior, while a possible explanation, cannot be tested with the strandings data base in the absence of stock assignments.

APPENDIX B Description of Loggerhead Morphometric Relationships –*Heather Haas*

Sea turtle researchers do not always obtain the same suite of morphometric measurements, and even in cases when they do, some measurements may have missing or erroneous data. Hence, it is useful to be able to use one morphometric measurement to convert to another. There are several well-documented loggerhead morphometric analyses (Frazer and Ehrhart 1983; Teas 1993; Coles 1999; Epperly and Teas 2002; Byrd et al. 2005). Although these studies are very useful for specific purposes, each is limited in spatial extent, size classes represented, sample size, or morphometric measurements considered. In this analysis, we create a dataset with broad spatial extent, wide representation of size classes, and a large sample size in order to parameterize equations to describe the relationship between all the typical carapace measurements of loggerhead sea turtles.

Data Sources

We compiled morphometric information (Table B1) from over 11 thousand loggerhead sea turtles. We deleted all records with a measurement of zero because we assume these were used to represent missing data rather than true zeroes. Potential outliers were not removed unless directly suggested by the data suppliers (as described below). The final dataset that was used in the morphometric analysis contained records from the following sources: Sea Turtle Stranding and Salvage Network (STSSN, n=6602), Northeast Fisheries Observer Program (NEFOP, n=297), SEFSC in-water research in North Carolina (n=3253), SEFSC sea turtle life history database (n=544), Casey Key and Manasota Key nesting data (n=241), and Keywadin Island nesting data (n=81)(See Part I of this report for information on the nesting data). Although the full dataset contains loggerheads from a wide range of size classes (CCL_{std} ranged from less than 10 cm to greater than 110 cm), the majority of the turtles had CCL_{std} measurements between 60 and 80 cm (90% between 50.8 and 101.4 cm, and 50% between 62.2 and 78.5 cm).

STSSN

The United States Sea Turtle Stranding and Salvage Network (STSSN, <http://www.sefsc.noaa.gov/seaturtleSTSSN.jsp>) supplied morphometric information from stranded loggerhead sea turtles along the U.S. Gulf of Mexico and Atlantic coasts from 1987 through 2005. The data were supplied by STSSN coordinator, Wendy Teas, and the following data quality controls were implemented. We used only those records from the Gulf, Northeast, and Southeast regions with the highest reliability code. We only used records from 1987 onward because stranding data prior to 1987 were not ever verified or edit-checked. Only live and fresh dead loggerheads were included so that turtles with bloating or other decomposition processes would not bias the results. At the suggestion of STSSN coordinator, we deleted curved carapace length measurements (CCL) over 128.1 cm and straight carapace length measurements (SCL) over 120.0 cm.

NEFOP

We obtained morphometric data for loggerhead turtles from the Northeast Fisheries Observer Program (NEFOP) of the Northeast Fisheries Science Center (NEFSC). The data were obtained from turtles bycaught in commercial fisheries from 1990-2007 from Maine through North Carolina. Loggerheads that were described as “Dead, Condition Unknown”, “Dead, Moderately

Decomposed”, “Dead, Severely Decomposed”, or “Dead, Seen by Capt/Crew Only” were not included in the dataset.

Nesting:

We used data from loggerheads nesting at Casey Key and Manasota Key (2002-2006) and Keywadin Island (2002-2005). As a quality-control measure, we deleted all CCL measurements (notch to notch and notch to tip) that were less than 70 cm. Both of these datasets are described elsewhere in this TEWG document.

North Carolina

We used data from SEFSC Beaufort Laboratory from their North Carolina in-water work, 1986-2006 (J. Braun-McNeill pers. comm.).

SEFSC

We obtained morphometric data for loggerhead turtles from the Southeast Fisheries Science Center (SEFSC) sea turtle life history database, 1999-2007 (L. Stokes pers. comm.). The primary source of turtles is from their observer database for Highly Migratory Species programs, but other sources include animals from their pelagic longline experiments, shark observer programs (bottom longline and drift gill net), resource assessment cruises (NOAA vessels), and more recently, reef fish observer program. Our database does not include records from the SEFSC shrimp observer program because they do not record multiple size measurements per turtle.

Analytic Approach

Because we wanted to use the simplest model that was statistically appropriate, we started the modeling process with a simple model to estimate one morphometric measurement from another, and we iteratively explored whether more complex models were necessary. There was a more uniform distribution of observations across size-classes, whether to transform the raw data, and whether to use model II regression techniques (to address measurement error). Rather than revisiting these issues for every pair of morphometric variables, we chose to explore these issues using CCW (as Y) and CCL_{std} (as X) because these were the two variables with the most number of observations. We ultimately decided to use a very simple approach of Model I (simple linear) regression techniques with no intercept term and unfiltered and untransformed data.

We chose a regression model with no-intercept term because this simple model appears to be theoretically justified. A model with no intercept term (where the intercept is set to zero) is theoretically justified when one morphometric measurement is zero the corresponding measurements should also be zero. There is no reasonable biological scenario where a turtle would have a CCL of zero and a positive value for CCW. To explore whether a model with no intercept term is empirically justified in addition to being theoretically justified, we performed simple linear regression analysis with and without an intercept term. Although the model with the intercept has a lower AIC value and an intercept parameter estimate that was statistically different than zero, we were concerned that this model was biased high for smaller turtles (< 40 cm CCL). We compared the average residual value at sizes related to the transition between Stage I (15 cm, no intercept = 0.5, intercept = -3.6), the division between Stage II and Stage IV at the peak of Stage III (63 cm, no intercept = 1.5, intercept = 0.7) and the division between

Stage III and Stage V at the peak of Stage 4 (82 cm, no intercept = -0.4, intercept = 0.1). The maximum residual value for both models was similar (~ 24 cm). We decided against using the intercept model because it had larger residual values at smaller sizes, which likely exceed measurement error. The no intercept model had average residual values that are likely close to or within measurement error. We strongly caution that none of these models should be used outside of the range of our data (Figure B1), especially at the lower end. The no-intercept model assumes the relationship between the lowest observed values and zero are the same as in the rest of the dataset, and we can not address this assumption given our data. Hence, these models should generally not be applied to loggerheads less than about 15 cm CCL_{std} .

We chose to keep all data rather than remove (filter) data in order to obtain a more uniform distribution of observations across size-classes. Filtering data would be justified if the risk of bias due to uneven distribution of samples across size classes outweighs the risks associated with reducing the sample size and disregarding potentially useful data. We explored these issues by creating a heavily filtered dataset (with approximately a tenth of the original observations and a nearly uniform distribution of observations across size classes), and we then compared regression diagnostics and results between the filtered and unfiltered data when using CCL_{std} to estimate CCW.

Filtering the data does not appear to be necessary. Based on plots of raw data and residuals from the regression analyses, there was no evidence that the relationship between CCW and CCL_{std} changes across size classes or is unduly influenced by a particular size class. Even a drastic reduction in sample size (keeping only about a tenth of the data) only slightly changed the slope of the regression line (full dataset = 0.9341; filtered dataset = 0.9257) and the R^2 values (full dataset = 0.9974; filtered dataset = 0.9969). If we filtered the data rather than using the full dataset, our estimates of CCW from CCL_{std} would only differ by about 1%, which is likely inside of the range of possible measurement error and not biologically significant for the purposes of most sea turtle researchers. Hence, although we do not think it would be inappropriate to filter the data, we chose the simple approach of keeping all data because there does not appear to be a strong and biologically meaningful reason to filter the data.

We chose to use raw rather than transformed data. Biological data are often transformed to address assumptions of the analysis which can not be otherwise met. The most common transformation is the logarithmic transformation (Sokal and Rohlf 1995). If greater means are accompanied by greater variances, the logarithmic transformation can often remedy the situation. We have an *a priori* concern that this situation could be true with morphometric data because there could be larger variation in larger turtles. We examined this issue by examining whether the residuals (from both the full and filtered datasets) increased with increasing CCL_{std} . Although the absolute value of the residuals from both the full and filtered datasets is slightly smaller between 10 and 20 cm CCW than they are for turtles greater than 20 cm, the magnitude of the residuals appears fairly well-distributed across the range of turtle sizes. Because the departure from homogeneity of variance is minimal and the consequences of moderate heterogeneity of variances are not too serious for the overall test of significance (Sokal and Rohlf 1995) and because our focus is describing the relationship between X and Y (rather than testing hypotheses or creating confidence intervals for parameter estimates), we do not feel it is necessary to transform the raw data.

We chose to use Model I simple linear regression models rather than using more complex Model II regression techniques to address measurement error. Model I regression techniques assume (among other things) that the independent X variables are measured without error (Sokal and Rohlf 1995). Many biological analyses do not meet the assumptions of Model I regression, and we do not expect this morphometric analysis will meet the assumption that X variables are measured without error because all our measurements (X and Y) are likely made with some error. Although there is debate on how to appropriately model X variables measured with error, if the regression equation is being fitted primarily for prediction purposes (rather than for an examination of the functional relationship), then simple linear regression techniques are generally applied (Sokal and Rohlf 1995). Simple linear regression (Model I) techniques are further justified in this case because there is a definite causality relation between the X and Y variables and because our X and Y variables are of similar dimensions, sizes, and units. Sokal and Rohlf (1995) do caution that when X is measured with error, X should only be used to predict Y, and Y should not be used to predict X. Although we expect it would not be problematic in our particular analysis, we do present all pertinent regression equations so that Y never has to be used to predict X.

Results

Each morphometric measurement under consideration was a suitable predictor of every other measurement (Table B2). All p-values were less than 0.0001; all coefficients of determination (R-square values) were greater than 0.9900, and all sample sizes were greater than 4,000.

Table B1. Explanation of variables used in the morphometric analysis.

Abbreviation	Explanation
CCW	Curved carapace width
CCL _{std}	Curved carapace length, standard, notch to tip
CCL _{min}	Curved carapace length, minimum, notch to notch
SCW	Straight carapace width
SCL _{std}	Straight carapace length, standard, notch to tip
SCL _{min}	Straight carapace length, minimum, notch to notch

Table B2. Summary of simple linear regression equations of morphometric relationships.

The X variables are listed in the first column and are used as row headers. The Y variables are listed in columns 2-7 and are used as column headings. Each regression equation uses the form $Y=X*B$, where B=the regression parameter estimate. For each regression equation, three statistics are listed (in order): parameter estimate (B), R-Square value, and N (sample size).

	Y Variables					
	CCW	CCL _{std}	CCL _{min}	SCW	SCL _{std}	SCL _{min}
CCW	-	1.0678 0.9974 8938.0	1.0447 0.9974 4819.0	0.7997 0.9971 6124.0	0.9858 0.9974 5977.0	0.9640 0.9974 4734.0
CCL _{std}	0.9341 0.9974 8938.0	-	0.9820 0.9994 4824.0	0.7504 0.9960 5990.0	0.9264 0.9994 6002.0	0.9086 0.9993 4747.0
CCL _{min}	0.9547 0.9974 4819.0	1.0178 0.9994 4824.0	-	0.7622 0.9961 4253.0	0.9423 0.9992 4258.0	0.9247 0.9991 4264.0
SCW	1.2468 0.9971 6124.0	1.3273 0.9960 5990.0	1.3069 0.9961 4253.0	-	1.2282 0.9957 6830.0	1.2026 0.9960 5026.0
SCL _{std}	1.0118 0.9974 5977.0	1.0788 0.9994 6002.0	1.0604 0.9992 4258.0	0.8107 0.9957 6830.0	-	0.9811 0.9998 5033.0
SCL _{min}	1.0347 0.9974 4734.0	1.0999 0.9993 4747.0	1.0805 0.9991 4264.0	0.8282 0.9960 5026.0	1.0191 0.9998 5033.0	-

Note that because we used no intercept models, SAS has calculated the R-Square values based on uncorrected (for the mean) sums of squares (Uyar and Erdem 1990).

Figure B1. Histogram of standard curved carapace length (CCL_{std} in cm) by percent frequency in each 10 cm size class. $N=9,062$.

