

AN ABSTRACT OF THE THESIS OF

Jason R. Vaughan for the degree of Master of Science in Fisheries Science presented on December 14, 2009.

Title: Evaluation of Length Distributions and Growth Variance to Improve Assessment of the Loggerhead Sea Turtle, (*Caretta caretta*)

Abstract approved:

Selina S. Heppell

Nest counts from the largest subpopulation of the loggerhead sea turtle (*Caretta caretta*) in the Atlantic, peninsular Florida, have been declining since 1998. Analyzing trends of nests and adult females is insufficient to determine the overall status of a sea turtle population, due to variation in nesting frequency and a 25 – 35 year time lag between hatching and maturation. While nest numbers of this threatened species have declined by 50% since 1998, catches of juvenile turtles in many areas have increased. Better assessment of population status and diagnosis of the causes of population trends are possible if we examine existing data on changes in abundance and size distribution from in-water surveys of juvenile and subadult turtles as well as adults. I have plotted the length frequency data and catch rates of neritic turtles (juvenile, subadult and adult turtles that inhabit nearshore waters) collected from 1980 – 2007 at 4 in-water sites ranging from North Carolina to Florida (N=10,486). I also examined the length distributions recorded from strandings of dead turtles found on

beaches in the Gulf of Mexico (N=4,308) and along the U.S. east coast (N=10,918) from 1990 – 2005. I found a similar pattern in length distribution shifts over time, which provides compelling evidence that the data are revealing true population change. The data suggest an increase in the overall abundance of juvenile turtles in the southeast U.S. since the late 1990s and an increase in the median size of neritic juveniles (40 – 90 cm) since 1990. There has also been a reduction in the number and proportion of small (<55 cm) juveniles since 2000 in some areas; these are considered “recruits” to the neritic feeding areas on the continental shelf. The shift in median size of juveniles coupled with the increased abundance in North Carolina and Florida indicate that there may be a large cohort or group of similar sized turtles that should reach maturity in the next decade. Changes in length frequency through time could indicate changes in recruitment, survival rates, or behavior, and translating length to age requires a good estimate of variance in growth rates. I developed an individual-based growth model using variance estimated through a new technique that measures growth using increments measured in cross sections of the humerus bone of stranded turtles. The technique permits a reconstruction of the growth history of individual turtles. While the growth patterns are clearly not a smooth, asymptotic function over length and time, there is some consistency among individuals. My re-sampling analysis of growth from 92 turtles provided an estimate of 30.74 years (95% CI = 23.82 – 37.66) required for a U.S. loggerhead turtle to grow from 20 cm (age 1 or 2) to 90 cm. This analysis will improve our estimates of the mean and variance in the length of time loggerheads are spending in various habitats and life stages, and

improve future demographic models to determine population status. My analyses incorporate multiple data sets and techniques to improve our understanding of how the whole loggerhead population is changing through time, leading to more accurate diagnosis and predictions about population trends.

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Evaluation of Length Distributions and Growth Variance to Improve Assessment of
the Loggerhead Sea Turtle, (*Caretta caretta*)

by
Jason R. Vaughan

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I understand that my thesis will become part of the permanent collection of Oregon State University libraries. My signature below authorizes release of my thesis to any reader upon request.

Jason R. Vaughan, Author

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DEDICATION

To my family: Mom, Dad, Stacey, my beautiful wife, Joy, and our two pups, Niko and Kaya, for always supporting my dreams, being by my side and encouraging me throughout my graduate work. Thank you for being there for me.

Evaluation of Length Distributions and Growth Variance to Improve Assessment of
the Loggerhead Sea Turtle, (*Caretta caretta*)

CHAPTER 1: INTRODUCTION

General Background

The loggerhead sea turtle (*Caretta caretta*) is listed as threatened under the U.S. Endangered Species Act (ESA) and endangered on the IUCN Red List which covers its entire international range (MTSG 1996). Both of these designations require that management and recovery plans be established to curtail the decline and eventually recover the species. Under the ESA, the loggerhead is protected by both state and federal laws and jurisdiction is determined by where the turtle is at any given time. Management of the loggerhead in the U.S. is the responsibility of both the United States Fish and Wildlife Service (USFWS) and the National Marine Fisheries Service (NMFS). Individual state agencies where the loggerhead occurs and the USFWS are responsible for protection and enforcement of laws on the nesting beaches and NMFS is responsible for protection while the turtles are in the water.

The loggerhead sea turtle is one of six extant species from the family Cheloniidae (Bowen 2003). The species diverged from the ridley and hawksbill turtles approximately 10 million years ago, which indicates a long history of independent evolution and adaptation (Bowen 2003). Loggerheads found in the Atlantic Ocean are genetically distinct and separated from loggerheads in the Pacific and Indian Oceans during the Pliocene (Bowen 2003). They are the only turtle that is known to nest extensively outside the tropics. Nests have been identified on all continents except Antarctica (Ehrhart et al. 2003). This large spatial nesting area

coupled with the long migratory pathways of the loggerheads between foraging and nesting grounds makes them a truly global species.

The Western North Atlantic population of loggerhead sea turtles is divided into five distinct subpopulations:

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

The peninsular Florida subpopulation is the largest nesting aggregation in the Atlantic and one of the two largest in the world (TEWG 2009). Production from the peninsular Florida subpopulation has accounted for as much as 80% of nesting and 90% of hatchling production in recent decades (TEWG 2009). Every one of these five subpopulations has experienced declines in nesting but the current trend in the peninsular Florida subpopulation is the most troubling. This subpopulation, which was increasing from the late 1980s through the late 1990s, has experienced a decline since its peak in 1998 (TEWG 2009). The status of the Western North Atlantic population is critical to the persistence of the global population of the species.

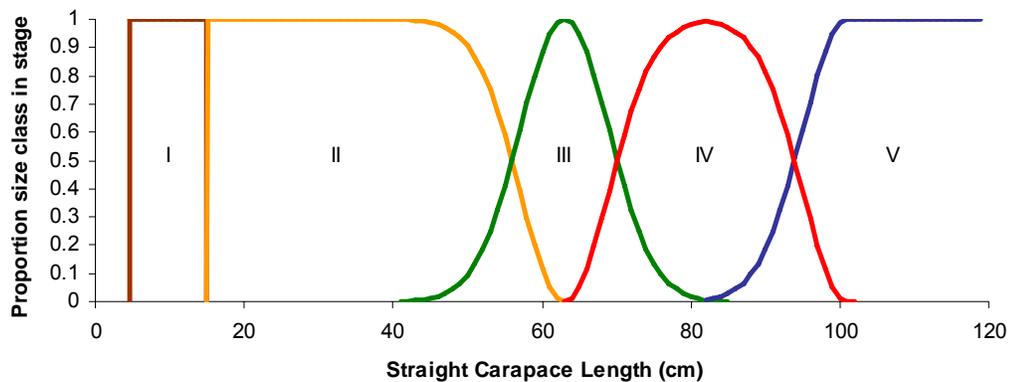
Life History

Loggerhead life history is divided into five stages that are based on habitat used during that stage and overlapping distributions of body size (straight carapace

length, SCL) (Figure 1.1; TEWG 2009). This life history model is an update from those used in previous population models and assessments (e.g., Crouse et al. 1987, Crowder et al. 1994) that incorporates some variability in growth and stage length:

- I. Year One, terrestrial to oceanic, size range 4.6–15 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 greater than 82 cm SCL

Figure 1.1: Conceptual model of size distributions for each life stage of the loggerhead sea turtle (reproduced from TEWG 2009).



Immediately after emerging from the nest, stages I and II are thought to be primarily oceanic while stages III, IV and V may occur in both pelagic and neritic environments (McClellan and Read 2007). Hatchlings from the Western North Atlantic population leave their natal beaches and enter the “swim frenzy” stage which enables them to reach the North Atlantic gyre (Wyneken and Salmon 1992). Stage II

is considered to be mostly oceanic with small juveniles commonly found as far away as the eastern Atlantic (Bolten 2003). After several years in the pelagic zone, most turtles are thought to undergo an ontogenetic shift back to inlets, bays and estuaries in the neritic zone (stage III and IV). Nearshore foraging areas vary seasonally but extend southward from the northeastern U.S., reaching around Florida into the Gulf of Mexico and parts of the Caribbean (Hopkins-Murphy et al. 2003). Many loggerheads will remain in the neritic foraging areas continuously from the large juvenile stage to adulthood while some continue making trips back offshore (McClellan and Read 2007). During the five life stages there are only two opportunities to observe loggerheads in a terrestrial environment: immediately after emerging from the nest (hatchling stage) and when females come back to nest on the beach roughly 25 – 35 years later (adult stage). As a result, the majority of data used to assess population status is based on nesting beach trends.

Threats

Anthropogenic threats to loggerheads are numerous and affect the turtles differently during each stage of their lives. Terrestrial threats, which impact eggs, hatchlings and nesting females, include nesting beach degradation and loss. Some examples of these impacts include beach renourishment, coastal armoring, light pollution and direct harvest of eggs and/or adult females (NMFS & USFWS 2008). However, the single greatest threat to loggerhead sea turtles is direct and indirect interaction with fisheries (NRC 1990). In the neritic zone, the shrimp trawl fisheries

along the south Atlantic coast and in the Gulf of Mexico have been the most destructive historically and led to the greatest single source of human-related mortality. In 1990 the National Academy of Sciences estimated that the U.S. shrimp fishery in the region was responsible for up to 50,000 deaths annually from the NW Atlantic population (NRC 1990). Most of the loggerheads that are affected by this fishery are large juveniles and adults, which are the most critical life stages with regard to recovery of the population (Crowder et al. 1994). Other nearshore fisheries that impact loggerheads include the scallop dredge fishery, fixed net fisheries and the coastal bottom longline fishery for sharks which operates off the Atlantic coast (NMFS & USFWS 2008). In the pelagic zone, the longline fishery, drift gillnets and other fisheries are responsible for the largest proportion of mortality (NMFS & USFWS 2008).

Assessment

The successful management and recovery of this population requires a more complete understanding of loggerhead population dynamics. Our ability to properly assess the species and specifically the Western North Atlantic population is hindered by the fact that demographic data are limited. It is impractical to rely upon a 20-year census of a small fraction of the population (nests or nesting females) to make statements about population level change. Our understanding of key demographic parameters is better now than in the past but we are still lacking critical pieces of information, such as growth variability and stage-specific survival rates (TEWG 2000,

2009). Relying on deterministic population models, parameterized using demographic rates with high levels of uncertainty, may not be in the best interest of managers. Even though we may not have the best data available and the time series are still relatively short there is more that can be done with the existing information. The following chapters introduce two examples of what can be done using existing data by applying techniques that have not been used previously for loggerhead sea turtles. In Chapter 2, I analyze in-water length distributions for juveniles and adults. In Chapter 3, I develop a stochastic growth curve based on skeletochronological analysis of the humerus to incorporate growth variability. These advances in analysis techniques, which incorporate standard methods used in fisheries assessment, will help us gain a better perspective of the population's status. While neither of these techniques will answer all of the questions or find the definitive cause behind the decline of nesters in Florida, they can both be looked at as a step forward for sea turtle assessment. We have shown through years of assessment and management that we may not be doing all that is necessary to recover the population, in part because of a lack of data and in part because of a lack of assessment tools. By borrowing techniques from fisheries assessment and applying them to the sea turtle data that we do have, we can make progress without waiting for decades of expensive research. This thesis demonstrates that we can learn more with what we already have to improve the future of sea turtle assessment.

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CHAPTER 2: ANALYSIS OF LOGGERHEAD SEA TURTLE LENGTH DISTRIBUTIONS OVER TIME: COMBINING DATA SETS TO IDENTIFY PATTERNS OF POPULATION CHANGE

Introduction

The loggerhead sea turtle (*Caretta caretta*) was listed under the U.S. Endangered Species Act (ESA) as threatened in 1978. Since that time, loggerheads have been the focus of intense research and conservation efforts to try and recover the population (TEWG 1998, TEWG 2000, NMFS-SEFSC 2001, TEWG 2009). Sea turtles are long-lived, late maturing species that spend the majority of their lives at sea, thus providing a unique challenge when attempting to assess the population. The loggerhead sea turtle's life history is complex and includes several distinct stages that inhabit vastly different habitats. Loggerheads are the most diverse sea turtle with respect to foraging and nesting; through their life history, U.S. Atlantic-hatched loggerheads utilize most of the northern Atlantic Ocean including both pelagic and neritic (nearshore) environments. Wide-ranging movement and life history-specific habitat shifts require us to consider many different mortality sources, both natural and anthropogenic, that affect population dynamics and potential recovery rates.

The life history of loggerhead turtles presents a critical problem in population assessment. Most population trend estimates for the U.S. loggerheads are based on the most easily observed life stages, nests and nesting females (Heppell 2005). Nest counts may vary due to environmental effects on nesting frequency (Saba et al. 2007,

Hawkes et al. 2007, Chaloupka et al. 2008), and even nesting female counts do not give us an accurate picture of the overall population trend. Due to delayed maturity, 25 – 35 years, (NMFS–SEFSC 2001) the adults represent a small proportion of the population and their abundance and trends may not reflect those of the juvenile life stages. Perturbations that affect survival rates of smaller size classes will take a long time to be observed on the nesting beaches (NMFS–SEFSC 2001, Snover et al. 2007, Braun–McNeill 2008).

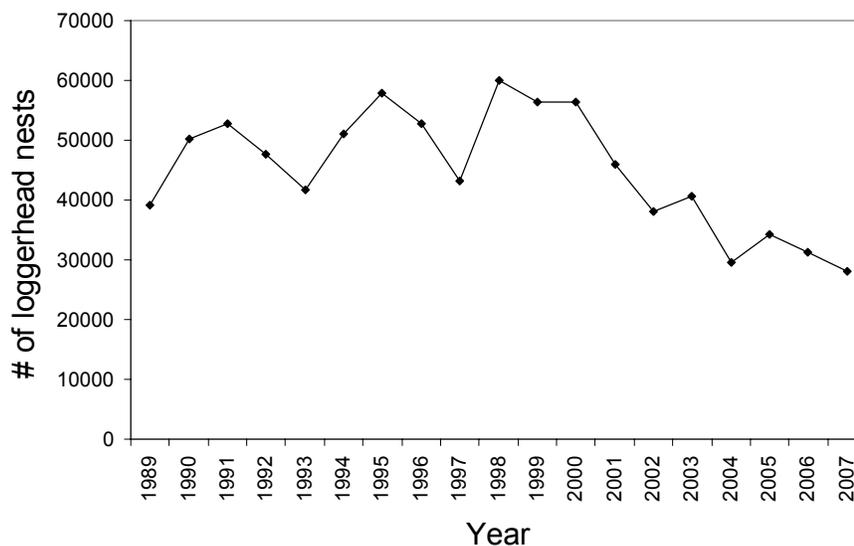
Because of the late age at sexual maturity, even the longest existing data sets are insufficient to follow entire cohorts. Previous models have assumed a stable age distribution in order to use the nesting data to identify trends and responses to perturbations for the whole population (Frazer 1983, Crouse et al. 1987, Crowder et al. 1994, NMFS-SEFSC 2001, Snover 2002, Heppell et al. 2003). This can only be true if the population exhibits stable vital rates (survival, reproduction, and growth) over at least two to three generations (Caswell 2001). This assumption is violated by the simple fact that we have attempted to mitigate for anthropogenic mortality sources, such as interactions with fisheries, by instituting management actions like the Turtle Excluder Devices (TEDs) used on shrimp trawls. Therefore, it is impractical to try to explain the precipitous decline in peninsular Florida nests from 1998 – 2007 with nesting data that spans 20 years, less than one generation.

As in fisheries stock assessment modeling, shifts in the length distributions of loggerheads may help us diagnose changes in abundance and to assess overall population status more completely than a simple trend analysis of nest counts. Length

distribution analyses have been a frequently used and successful tool in fisheries management to obtain estimates of growth, mortality, selection and recruitment in fishes (Gulland and Rosenberg 1992). There are a variety of data sources available for loggerheads that can be coupled with age-length keys to examine changes in age structure through time, but have not been used in sea turtle assessments to date.

Peninsular Florida has the largest current nesting aggregation in the Atlantic Ocean, representing as much as 80% of all nesting in the Western North Atlantic, and is one of the two largest nesting aggregations in the world (TEWG 2009). The Turtle Expert Working Group (TEWG) in 2000 reported a nesting trend for Florida that was increasing at about 4% per year for the period from 1989 – 1998 on the 28 Florida Index Nesting Beaches, which represent roughly 70% of all nests in Florida. The annual numbers of nests from this subpopulation have decreased 37% from 1989 through 2007 and 49% since 1998 (Witherington et al. 2009) (Florida Fish and Wildlife Conservation Commission; <http://research.myfwc.com>) (Figure 2.1). The current decline in nesting could be the result of past perturbations, such as intensive trawl fishery bycatch in the 1970s and 1980s, or more recent ones, such as an increase in pelagic juvenile mortality due to longline fisheries. Because more than 80% of U.S. loggerheads nest on the coast of Florida, this trend is of concern for the entire U.S. population. The northern nesting subpopulation (Georgia and the Carolinas) is already depleted (NMFS-SEFSC 2001, TEWG 2009), so further declines of Florida nests could lead to grave problems for the Western North Atlantic population.

Figure 2.1: Number of loggerhead nests on the 28 Core Index Nesting Beach Survey areas of the Peninsular Florida subpopulation from 1989 through 2007 (Florida Fish and Wildlife Conservation Commission).



To evaluate changes in population composition and gain a better understanding of the entire population, I compiled length data from juvenile and adult-sized turtles captured in the water as well as stranded turtles from Atlantic and Gulf of Mexico beaches to look for patterns that may indicate changes in the Western North Atlantic population size or vital rates for different life stages. I used data from a variety of sources to compare shifts in length distributions across both space and time. This analysis is the first attempt to look at broad scale changes in length distributions of juvenile and subadult loggerheads, and should allow us to eliminate at least some alternative hypotheses for the causes of decline in Florida nesters as well as provide some prediction of change for the future.

Methods

Abundance and size data for U.S. Atlantic and Gulf of Mexico loggerhead turtles were compiled from several sources collected between 1980 and 2007 and encompass a significant proportion of the loggerhead's coastal foraging areas along the eastern United States and Gulf of Mexico.

Listed in order of length of survey the data sources are (see citations referenced below for details on sampling methodologies at each site):

St. Lucie Power Plant (STLPP) – Florida Power and Light has operated their nuclear power plant on Hutchinson Island, Florida since the late 1970s. 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) but I only used measurements collected after 1980 because effort was constant from that point forward. 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.

Indian River, Florida (IRL) – Entanglement nets have been set to monitor the sea turtle population in the Indian River Lagoon since 1982 (Ehrhart et al. 2007). 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. Details of the methodology are described in Ehrhart et al. (2007).

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. In 1989, SEAMAP was standardized to a stratified design, sampling from Cape Hatteras, NC to Cape Canaveral, FL (SCMRI 2000) and, since 1990, it has been conducted exclusively during daylight hours. The region is surveyed seasonally, in spring, summer, and fall. Morphometric data were obtained from all turtles captured and the animals were tagged before being released.

Pamlico–Albemarle Estuarine Complex, North Carolina (NC) – 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). During this study the lengths of all of the turtles were recorded.

Sea Turtle Stranding and Salvage Network (STSSN) – 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. For all regions, it is unclear if we are observing a representative sample of turtles in the area in the STSSN data set and, in the southeast and Gulf of Mexico, length data may be confounded by changing Turtle Excluder Device (TED) regulations over the period examined (Epperly and Teas 2002). I used length data from 1990 – 2005 because prior to that time effort was not consistent.

Table 2.1: Summary of data used in length distribution analysis from four southeastern U.S. study sites: St. Lucie Power Plant, FL (STLPP), Indian River Lagoon, FL (IRL), Cape Canaveral, FL to Cape Hatteras, NC (SEAMAP), Pamlico-Albemarle Estuarine Complex (NC) and strandings data (STSSN) separated into two groups, Gulf of Mexico (GOM) and the East Coast (EC).

Source		Years	N	Size Range
STLPP		1980 – 2007	6,598	40.9 – 109.9
IRL		1982 – 2007	736	41.5 – 103.0
SEAMAP		1990 – 2007	354	41.6 – 106.7
NC		1990 – 2007	2,798	41.4 – 103.4
STSSN	GOM	1990 – 2005	4,308	40.0 – 113.0
	EC		10,918	40.0 – 118.7

Length distributions from the data provided are assumed to be representative of the true length frequencies of loggerhead sea turtles within the sampling area. I report the catch from each of the sites but have not assessed the selectivity of the different sampling methods. I plotted the frequency of turtles within each 5 cm size bin over the time series of each data set. All length measurements are reported as standard straight carapace length (SCL_{std}) which is measured from the notch at the anterior of the carapace to the tip of the last posterior marginal scute. If this measurement was not taken I used the simple linear regression equations of morphometric relationships ($R^2 = 0.9974$) published in TEWG (2009) to convert to SCL_{std} . Size classes examined in this analysis included turtles ranging from 40 cm to 120 cm. I report the median size of juvenile turtles and the proportion of turtles 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. I chose 90 cm as the estimated size at sexual maturity to be consistent with the 2001 stock assessment (NMFS-SEFSC 2001). Data were binned into half-decades except for 2005 – 2007.

Results

Changes in length frequencies of loggerheads from different data sources:

Figure 2.2: Frequency of turtles within each 5 cm size bin over the time series of the dataset from the St. Lucie power plant, FL.

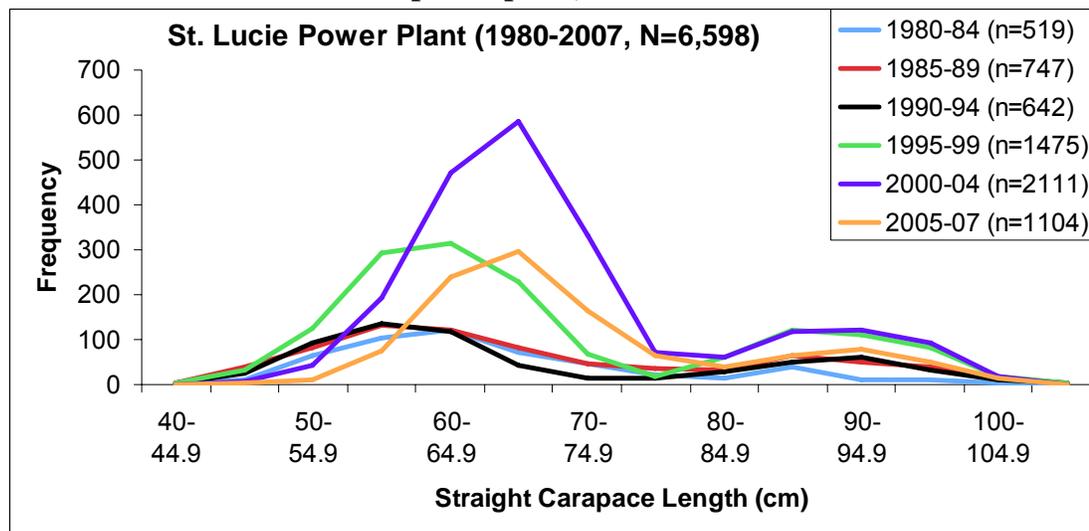


Figure 2.3: Frequency of turtles within each 5 cm size bin over the time series of the dataset from the Indian River Lagoon, FL.

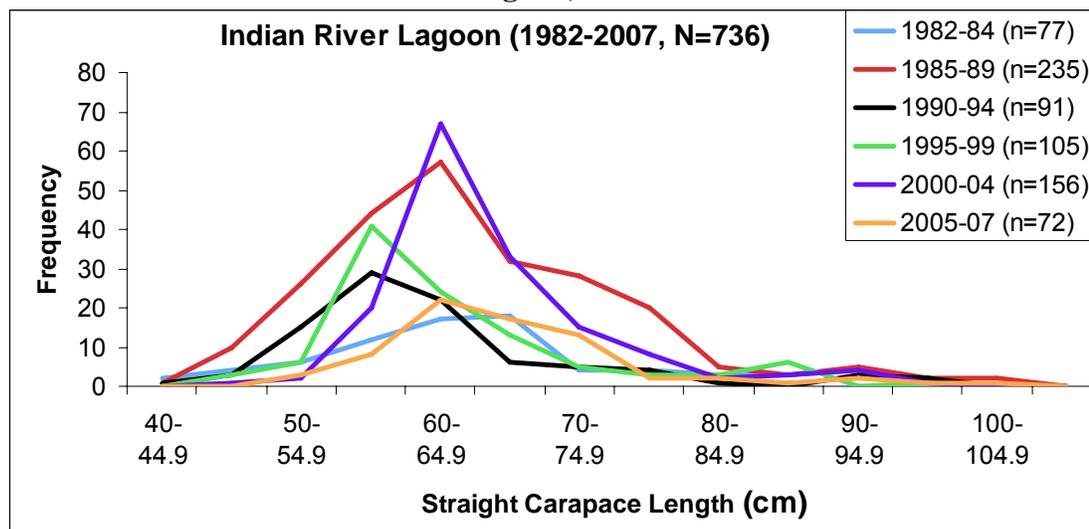


Figure 2.4: Frequency of turtles within each 5 cm size bin over the time series of the dataset from the SEAMAP trawl survey, NC - FL.

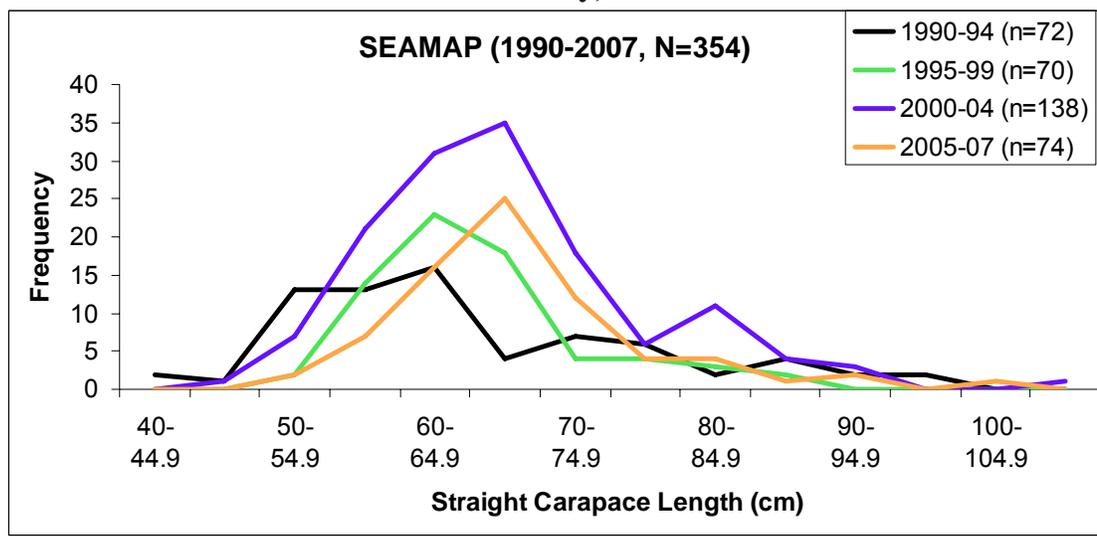


Figure 2.5: Frequency of turtles within each 5 cm size bin over the time series of the dataset from North Carolina.

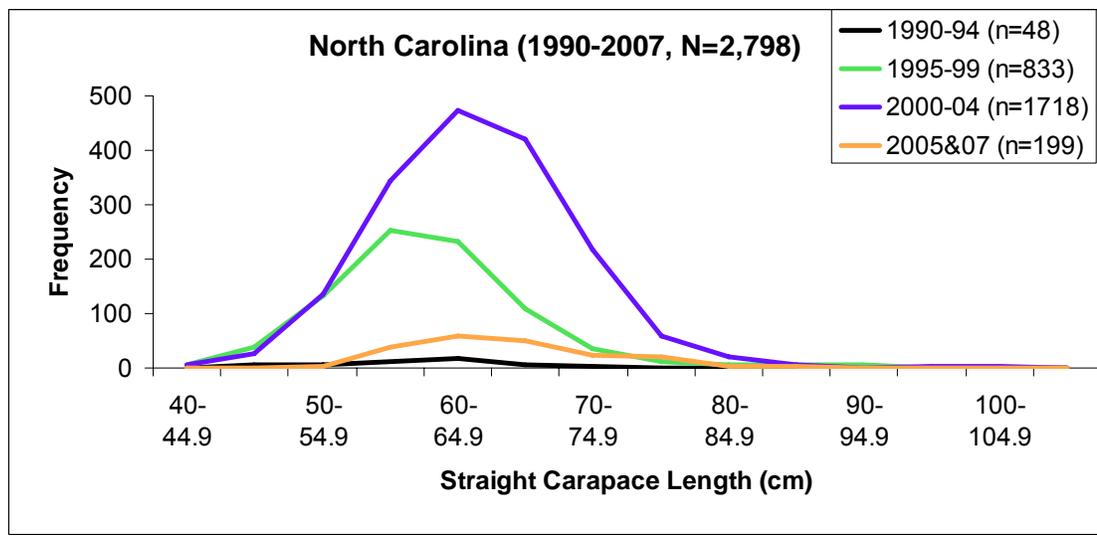


Figure 2.6: Frequency of turtles within each 5 cm size bin over the time series of the dataset from the east coast strandings.

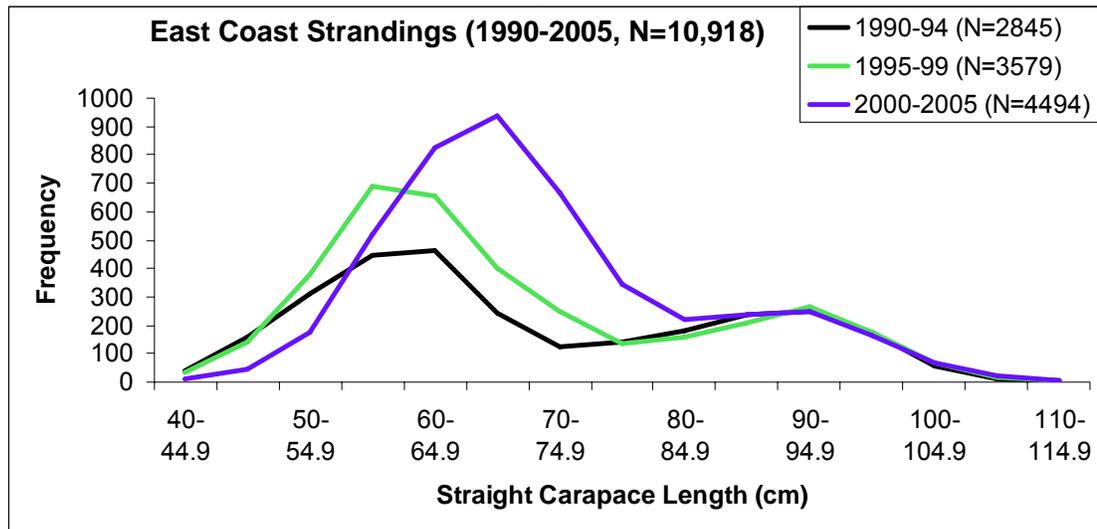
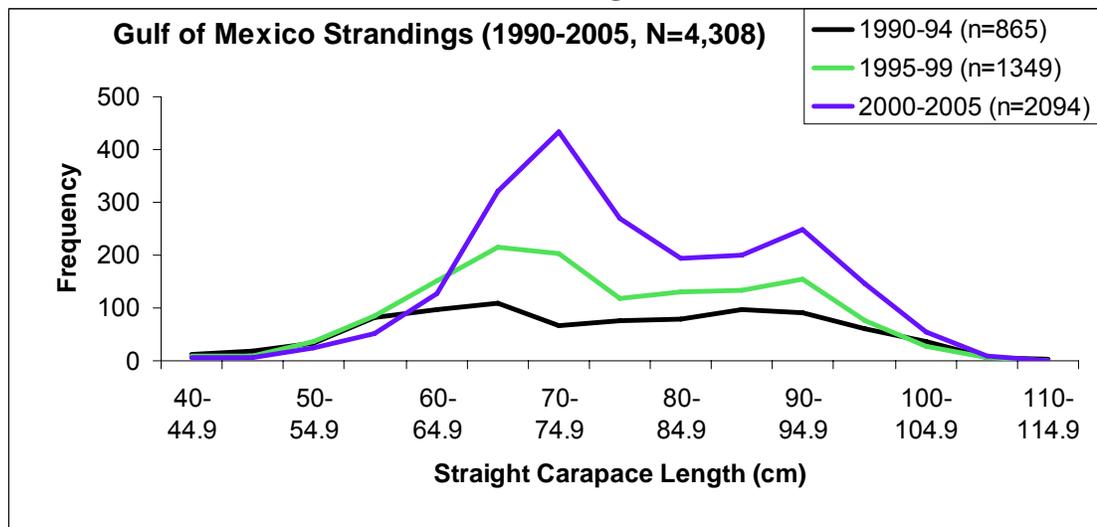


Figure 2.7: Frequency of turtles within each 5 cm size bin over the time series of the dataset from the Gulf of Mexico strandings.



The length frequency distribution from all loggerhead turtles entrained in the St. Lucie Power Plant canal (1980 – 2007, N=6,598) shows several interesting patterns (Figure 2.2). The shifting of the main peak of the distribution to the right through time indicates an overall increase in the median size of juveniles. It also suggests that a cohort or several cohorts of juveniles may be growing and moving through the distribution. From 1990 – 1994 the median size of a juvenile in the sample was 59.3 cm and this increased during each subsequent time bin up to 66.7 cm in 2005 – 2007 (Figure 2.8). 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 2.9). In 1990 – 1994 the smallest neritic juveniles made up 19% of the catch at the power plant and now from 2005 – 2007 they only represent 1% of the total catch. 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 increase in the median size of juveniles and the apparent decrease in proportion of the smallest juveniles (Figure 2.3). One key difference is the lack of large turtles found in the sample. From 1990 – 1994 up to the most recent sampling period the median size of juveniles has increased from 59.2 cm to 65.4 cm (Figure 2.8). 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 and has decreased from 21% of catch down to 4% from 1990 – 2007 (Figure 2.9).

Although the time series of data from the SEAMAP trawl surveys is shorter and the sample size is smaller (1990 – 2007, N=354) than the two previously discussed nearshore sites, this trawl survey represented similar patterns, including an increase through time in the median size of juveniles (Figure 2.4). Over the entire time series of data collected during the trawl surveys the median size of juveniles increased from 63.0 cm up to 68.1 cm (Figure 2.8). The pattern observed in the longer time series from the 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 from 22% in the earliest time bin to 3% most recently (Figure 2.9).

The data from North Carolina's Pamlico–Albemarle Sound Estuarine Complex (1990 – 2007, N=2,806) also show a similar trends to those observed at the three other sampling sites but large turtles are absent in this data set (Figure 2.5). The median juvenile size has increased through the sampling period, beginning in 1990 at 60.3 cm and increasing to 65.1 cm during the last sampling period (Figure 2.8). The proportion of small juveniles also followed the same pattern as the other three sampling sites dropping from 21% of total catch down to 3% by the end of the time series (Figure 2.9).

Length distributions collected from strandings in states along the eastern U.S. (CT, DE, FL, GA, MD, ME, NC, NJ, NY, RI) from 1990 – 2005 show a similar pattern to the four in–water sampling sites in the same area (Figure 2.6). Over the

time period sampled the median length of juveniles increased from 62.1 cm in the first time bin up to 67.1 cm (Figure 2.8). The proportion of small turtles, 40 – 55 cm, also decreased in the strandings from 18% to 5% over the time series (Figure 2.9).

The length distribution of strandings from the states that border the Gulf of Mexico (AL, FL, LA, MS, TX) show some of the same patterns observed along the east coast but also exhibit some slightly different trends (Figure 2.7). The median size of juveniles did increase in the Gulf of Mexico over the time series from 68.8 cm up to 73.0 cm. Note that the trend was the same, increasing, but the starting median size is larger than the final median size for any of the other sites (Figure 2.8). The decreasing proportion of small juveniles was also apparent in the Gulf of Mexico but once again showed a slight difference from the pattern observed on the Atlantic coast. The proportion from the beginning to the end of the time series decreased from 7% to 2% but the starting proportion was much smaller to begin with than the other four in-water sites and east coast strandings (Figure 2.9). Once the differences in consistency were noted with regard to the other in-water sampling sites and the strandings data from the eastern U.S., I examined some other trends more thoroughly.

Figure 2.8: Median length of juvenile loggerhead sea turtles (40-90 cm SCL) at four southeastern U.S. study sites: St. Lucie Power Plant, FL (STLPP), Indian River Lagoon, FL (IRL), Cape Canaveral, FL to Cape Hatteras, NC (SEAMAP), and Pamlico-Albemarle Estuarine Complex (NC) and strandings data separated into two groups, Gulf of Mexico (GOM) and the East Coast. Note the IRL time series does not include data prior to 1982.

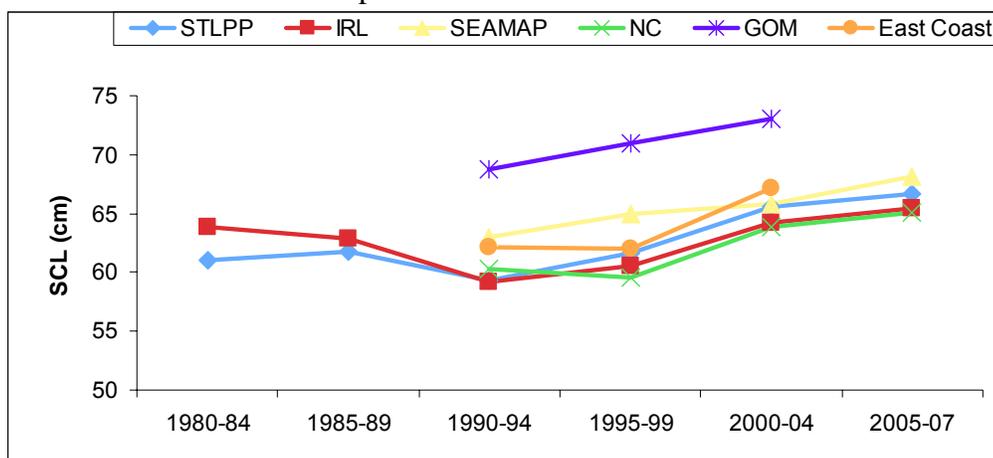
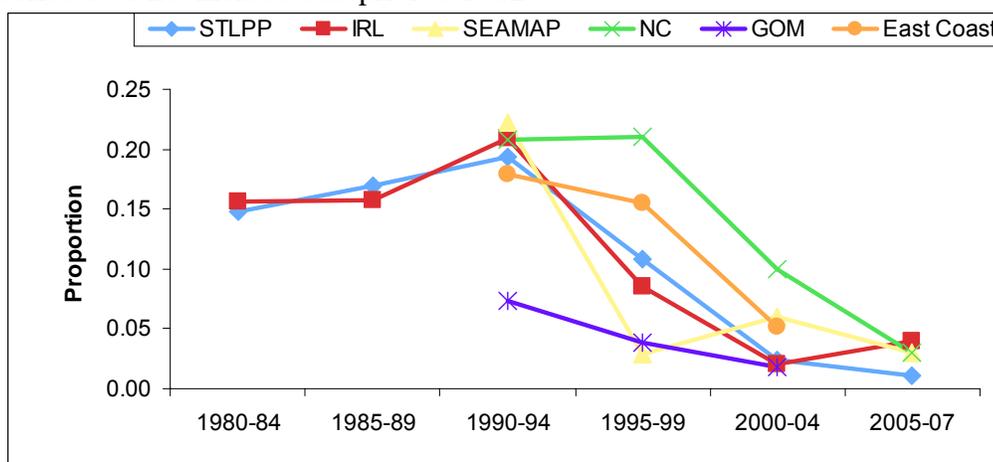


Figure 2.9: Proportion of small (40-55 cm SCL) juvenile loggerhead sea turtles at four southeastern U.S. study sites: St. Lucie Power Plant, FL (STLPP), Indian River Lagoon, FL (IRL), Cape Canaveral, FL to Cape Hatteras, NC (SEAMAP), and Pamlico-Albemarle Estuarine Complex (NC) and strandings data separated into two groups, Gulf of Mexico (GOM) and the East Coast. Note the IRL time series does not include data prior to 1982.



Based on the strandings data the larger size classes of loggerheads seem to be using the Gulf of Mexico. The proportion of adult sized turtles, greater than 90 cm, versus immature turtles was compared for all of the sites. The four in–water sampling sites showed quite different proportions of large, potentially mature, turtles than the strandings data sets (Table 2.2). The in–water sampling sites caught the lowest proportion, 7% from 1980 – 2007, while the strandings in the Gulf of Mexico contained 21% adult sized turtles from 1990 – 2005.

Table 2.2: Proportion of turtles < and > 90 cm from the four in–water sampling sites and the strandings data.

	In–Water Sites (N=10,496)	Strandings East Coast (N=10,918)	Strandings GOM (N=4,308)
Proportion <90	0.93	0.86	0.79
Proportion >90	0.07	0.14	0.21

The strandings on the east coast and in the Gulf of Mexico both show increasing trends during the time period sampled (Figure 2.10). When the number of strandings of turtles larger than 90 cm is plotted a difference between the areas is apparent (Figure 2.11). The number of strandings of adult sized turtles on the east coast has remained fairly constant from 1990 – 2005 while the number of adults stranding in the Gulf of Mexico has continually increased with time. In the most recent time bin the number of adult sized turtles that strand in the Gulf is almost equal to the number that strand along the east coast when it was closer to 50% in the past.

Figure 2.10: Number of strandings at east coast and Gulf of Mexico sites from 1990 – 2005.

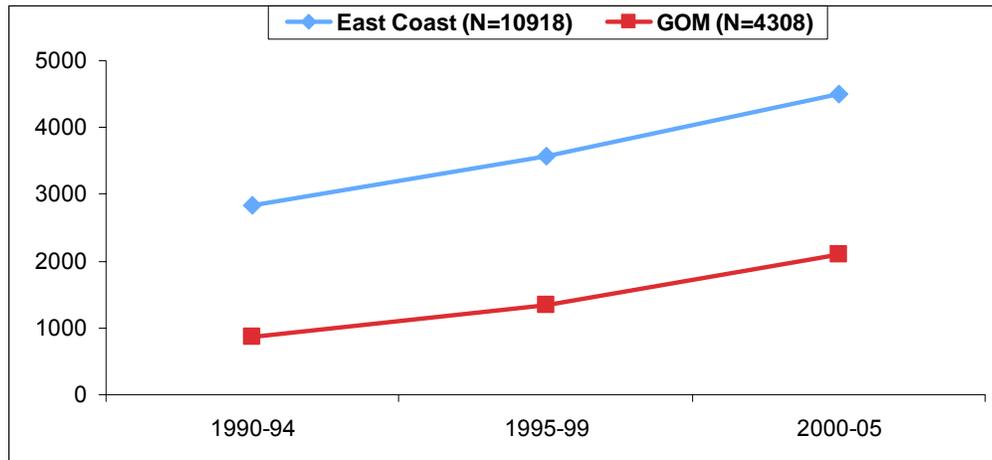
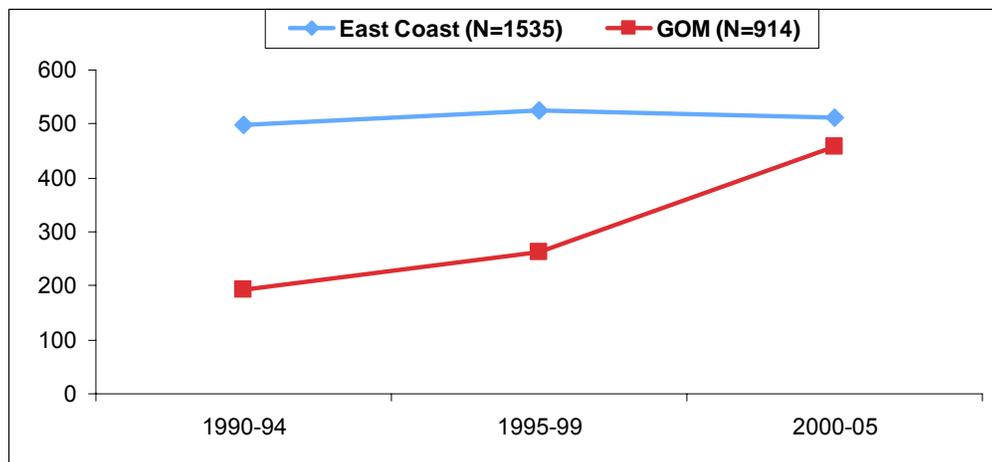


Figure 2.11: Number of mature sized, >90 cm, strandings at east coast and Gulf of Mexico sites from 1990 – 2005.



Discussion

It is nearly impossible to draw any conclusion about regional abundance and population trends based on data from a single site or size class. However, the fact that the four in-water data sets and strandings records, which cover a large portion of the loggerhead's nearshore habitat off the U.S. Atlantic and Gulf of Mexico coasts, show similar patterns in catch through time and that virtually all sources of data show a similar pattern in length distributions is compelling. By examining the length distributions from the in-water sampling sites and strandings, we are likely to recognize true population level changes before they are realized in the nesting beach surveys. This cohesiveness both temporally and spatially shows how important it is to use information in addition to nesting surveys when making decisions about the status of a population and developing recovery criteria.

All four of the in-water sites and strandings show the same trends in the juvenile size classes: an increase in the median size of juveniles (40 – 90 cm), a decrease in the proportion of 40 – 55 cm juveniles and an increase in catch through the time series. These are all very important factors affecting the whole population that would not be evident if we relied solely on nesting beach surveys for assessment. The increase of the median size of juveniles suggests a large cohort or group of cohorts is moving through the population and will be approaching maturity in the near future. This means that there is potential for recovery, an increase in nest numbers and hatchling production if these large juveniles are able to survive to maturity. The decrease in the proportion of the smallest juveniles seen in the neritic zone is another

important trend that would not have been recognized this early and should be watched closely in the future. At this point it is unclear whether this pattern is a result of a change in behavior, staying in the pelagic zone for a longer period of time, a change in growth rates in the pelagic zone or simply a recruitment failure from the past that is just now showing up in the juvenile length distributions. Regardless of the reason, this trend needs to be monitored because if it continues there could be another severe downturn in nest numbers when this size class should be reaching maturity (Snover 2008).

The results from this analysis of the length distribution data coupled with catch rate data published in (Epperly et al. 2007, Ehrhart et al. 2007, TEWG 2009) provide valuable information about the neritic juvenile size classes. In North Carolina, turtle catch rates during 1995 – 2003 increased at a rate of 13% per year (Epperly et al. 2007). Ehrhart et al. (2007) reported an increase in the last 4 years of their study in the Indian River Lagoon, Florida. Captures at the St. Lucie Power Plant in Florida increased at an average rate of 11% per year from 1988 to 2005 (TEWG 2009) and SEAMAP catch rates showed an increase from 1990 to 2006 of approximately 5% per year (TEWG 2009). Overall, data from these in–water mark-recapture projects show an increasing trend in the abundance of loggerhead sea turtles in the nearshore foraging areas. Also, the loggerhead strandings data from 1990 – 2005 shows an increasing trend in all of the areas that are monitored. The increase in loggerhead sea turtle abundance at in–water sampling sites is not consistent with the more commonly used trends observed in nest counts. However, it is likely the difference in trends

between in–water abundance and nest counts, based on the trend seen in the length distributions, can be attributed to an increase in the number of juveniles that are occurring in the neritic zone. This is further evidence that we need to assess all available data for all size classes before we make statements about population level change or status.

Since the majority of the sites analyzed are located in the southeast U.S. I was concerned that the patterns observed may just be a shift in spatial distribution. However, TEWG (2009) has shown that similar patterns to those observed along the southeastern sites can be seen in more northern sites as well. The strandings data from just the northeastern states, (VA, MD, DE, NJ, NY, CT, RI, MA, ME) were separated and analyzed to attempt to understand if there had been a spatial shift. The number of strandings in this area increased through the length of the time series, 1990 – 2005, similarly to the patterns observed in the southeastern sites. An increasing trend in the median size of 40 – 90 cm animals was observed, increasing from 60.5 cm to 68.4 cm. The consistently decreasing trend in the proportion of small juveniles was also observed with proportions dropping from 25% to 5% (TEWG 2009). Trends from two other in–water study sites in the waters of the northeast U.S. are not as easy to discern but I will address the results qualitatively in an effort to discuss the entire range of turtles along the U.S. east coast. Loggerhead sea turtles found in New York waters are typically smaller than animals to the south with a reported size range of 36.6 – 89.2 cm SCL (Burke et al. 1993, Morreale et al. 1992). From 1988 – 1995 turtles were live captured (N=201) and the overall median was 50.5 cm. From 2002 to present, only 2

loggerheads have been captured, both in 2003 and neither was less than 55 cm.

Although this study was not consistent in effort over the whole time period the pattern of decreasing small juveniles is apparent. New recruits to the neritic zone, juveniles less than 55 cm, used to make up 66% – 90% of the catch during the earlier years of the study and now catch has dropped to near zero (TEWG 2009). Another area that was a highly used traditional foraging ground for neritic juveniles is the Chesapeake Bay. 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. 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, 3) an overall decline in the Atlantic loggerhead population (Mansfield 2006) 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 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. However, the strandings data which has been shown to be consistent with the southeastern in-water sites shows that neritic juveniles are still moving through these areas and simply may not be utilizing them as heavily as they have in the past.

Overall, the same three trends are consistently seen throughout the loggerhead's range along the eastern U.S. but the strandings records from the Gulf of Mexico (GOM) indicate that something different is occurring in that region. The three major patterns can still be observed in the GOM but the median size of juveniles has always been larger (Figure 2.8) and the proportion of small juveniles has always been low (Figure 2.9). This may be due to differential use of the GOM by larger juveniles and adults or differential mortality due to fisheries bycatch (Epperly & Teas 2002). A comprehensive analysis of satellite telemetry data performed by TEWG (2009) showed that the GOM was a "hotspot" for both male and female adults as well as juveniles that were tagged and released as far north as Virginia. Catches of adults, >90 cm, at the in-water study sites was about 7%, whereas the proportion of adults in the east coast strandings was about double that and was triple that in the Gulf of Mexico (Table 2.2). Witherington et al. (2009) hypothesized that the dramatic decrease in nest numbers on Florida beaches was the result of a decrease in the number of mature females due to an increase in mortality during some stage in their lives. Figure 2.11 shows that the number of strandings in the GOM has increased significantly in recent years and is now nearly equal to the number of strandings along the east coast. In the past, strandings in the GOM were typically half the number observed along the east coast. This increasing trend is particularly troublesome due to the fact that these larger individuals have a higher reproductive value and are therefore more important to recovery of the population (Wallace et al. 2008). One reason for the increase in strandings, especially of larger turtles, may be increased interaction

with trawl fisheries in the GOM. Shrimp trawling efforts increased through the mid 1900s and by the late 1970s data showed that thousands of turtles were being killed as bycatch in the fishery (Henwood and Stuntz 1987). The National Research Council performed a separate analysis in 1990 and found that upwards of 50,000 loggerheads were being killed annually. They concluded that this fishery was the single most destructive anthropogenic mortality source in U.S. waters (NRC 1990). Due to this analysis turtle excluder devices (TEDs) were mandated by U.S. law on all trawlers by 1994. Despite this management action to try and reduce the mortality levels on large juveniles and adults in the GOM, strandings have continued to increase and are now at their highest level. This may be due to poor compliance and monitoring of the shrimping vessels (Lewison et al. 2003) or the fact that the TED openings were too small to allow the large juveniles and adults to escape (Epperly and Teas 2002). In 2004 larger TEDs were required but this still has not yet shown to be effective in reducing the number of strandings of mature sized turtles in the GOM.

The good news is that there appears to be increasing trends in catch rates of juvenile loggerheads through 2007 in the southeast U.S. (TEWG 2009). This, coupled with the increase in median size of neritic juveniles, may indicate there is a relatively large cohort or group of cohorts that will be reaching maturity in the near future. Hopefully, this cohort will start to appear on the nesting beaches within a decade, reversing current declines; however, monitoring of those nesters and subadults in nearshore habitats is essential, as there could be an existing or newly emerging source of mortality affecting these size classes.

The decrease in the proportion of the smallest size classes of juveniles in the most recent years raises concern that we may currently be witnessing a recruitment failure from the recent past. I observed the lowest proportion of small juveniles in 2000 – 2007 in all of the data sets. Taking into account the range in duration of the pelagic juvenile stage, these new recruits to the neritic zone would have hatched sometime between the mid 1980s to the late 1990s. During this period there was an increasing trend in nesting on the Peninsular Florida beaches (TEWG 2000). Assuming that hatching and emergence success rates have not changed, one may conclude that there was increased production on the beaches 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 an increase. However, the recent data on catch/catch rates does not support the hypothesis of recruitment failure (TEWG 2009). 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 (Snover 2008). Alternatively, the change in numbers and catch rates observed since the mid 1990s could be related to changing proportions of the juvenile population moving between the pelagic 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.

This analysis using data from the Western North Atlantic loggerhead population serves as an example of how analysis of a greater proportion of available data, especially for juveniles, is useful and necessary when dealing with a long-lived species like the loggerhead sea turtle. With increased in-water monitoring, not just of numbers but of growth rates, sex ratios, survival rates and other demographic parameters, we will be able to make more accurate predictions in the future and possibly anticipate declines in nesting like the one we are currently observing. The length distribution data from these sources suggest that we need to be aware of and pay attention to changes in the overall distribution of size classes other than adult females. This will allow us to be prepared for events similar to the present decline that will occur in the future and we will not be caught off guard.

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CHAPTER 3: DEVELOPMENT OF A STOCHASTIC GROWTH MODEL FOR LOGGERHEAD SEA TURTLES IN THE WESTERN NORTH ATLANTIC

Introduction

Loggerhead sea turtles, which are long-lived and slow growing, exhibit complex life histories and spend the vast majority of their lives at sea. Hatchlings from the Western North Atlantic population begin their juvenile stage in the North Atlantic gyre, followed by several years spent in the pelagic zone before making an ontogenetic shift to neritic foraging grounds along the east coast of the U.S. (Musick and Limpus 1997). This life history strategy makes it very difficult to obtain accurate estimates of vital rates, especially growth rates. Because loggerheads use a variety of habitats and each of these has different mortality rates, it is very important to understand how fast a turtle is growing and how long they may be spending in each habitat type.

Typically, mark-recapture studies have been used to assess growth rates in loggerheads (Mendonca 1981, Frazer and Ehrhart 1985, Henwood 1987, Frazer 1987, Foster 1994, Schmid 1995, NMFS-SEFSC 2001, Braun-McNeil et al. 2008). While these types of studies may provide accurate short-term estimates of growth for those individuals that can be recaptured in neritic habitats, it is nearly impossible to obtain growth data that spans the entire life history of an individual. In many cases, mean growth curves are fit to the available mark-recapture data from multiple turtles (often

with just one or two recaptures per individual) and then extrapolated using the von Bertalanffy growth equation.

The von Bertalanffy growth equation is a simple growth model commonly used in fisheries assessment and can prove to be accurate and useful if you account for and understand its limitations. The problems associated with this technique include extrapolating beyond the range of the data, estimating stage durations, estimating time to size at sexual maturity and it does not allow for incorporation of observed variability (Bjorndal and Bolten 1988, Chaloupka and Musick 1997). Extrapolation can be particularly problematic with regards to estimates of age at sexual maturity (Day and Taylor 1997), a common practice in sea turtle assessment and modeling studies (Frazer 1983, Crouse et al. 1987, Crowder et al. 1994, NMFS–SEFSC 2001, Snover 2002, Heppell et al. 2003). As an alternative to growth curve extrapolation, researchers have combined stage–length estimates from separate studies of particular life stages to estimate time spent in the various stages and time to size at sexual maturity (NMFS–SEFSC 2001, SEFSC 2009). Estimates of growth and pelagic stage duration (Bjorndal et al. 2000) have been combined with estimates of the time it takes juveniles to grow from size at recruitment to the neritic zone to size at maturity in order to obtain estimates of age at sexual maturity (Bjorndal et al. 2001).

Current growth models based on mark-recapture analysis fail to cover the wide spatial and temporal range of loggerheads. The high variability in the published von Bertalanffy growth curves for turtles from different studies is evident in the loggerhead stock assessment; estimates of the time that it takes a turtle to grow from

49 cm to 90 cm are 20 – 36 years (NMFS–SEFSC 2001). The manager or modeler must choose one of these mean growth curves and use that to determine stage durations. Because all of the limitations of the von Bertalanffy growth model have not been accounted for in previous studies it is necessary to use a different technique to assess growth and compare estimates of stage duration and growth rates.

Increment analysis is a much different technique that has been used to estimate annual growth rates for both plants and animals but has not yet been applied to sea turtles. In growth studies of fish, annual rings deposited on the otoliths or other hard parts are used to estimate age and growth rates (Summerfelt and Hall 1987, Francis 1990, Secor and Dean 1992, Chambers and Miller 1995, Labropoulou and Papaconstantinou 2000, Campana and Thorrold 2001, Doering–Arjes 2008). When a relationship between otolith diameter and fish length can be determined, the width of the increments between rings can provide a growth history for an individual. A similar methodology is employed by dendrochronologists who use rings in the trunks of trees to develop growth curves (Lieberman and Lieberman 1985, Worbes et al. 2003, Brienen and Zuidema 2006). Lieberman and Lieberman (1985) simulated a growth trajectory for a tree by allowing it to grow in the model using size–specific growth increments obtained from the data. Similar techniques are possible for sea turtles, using increments measured from the growth rings on the humerus bone (Zug and Parham 1996, Parham and Zug 1997, Zug et al. 1997, Snover 2002, Bjorndal et al. 2003).

Skeletochronology, using growth marks or lines of arrested growth (LAGs), in skeletal structures is becoming a more commonly used standard for assessing individual growth trajectories in sea turtles (Bjorndal 2003, Snover et al. 2007). Snover and Hohn (2004) validated that the LAGs in loggerhead humeri are deposited annually using known-age animals. The annual periodicity of LAG deposition combined with the strong correlation between humerus diameter and straight carapace length (SCL) can therefore provide back-calculated lengths and accurate estimates of annual growth (Snover and Hohn 2004). Snover et al. (2007) showed that incremental analysis of the loggerhead's humeri using skeletochronology can be used to back-calculate lengths within a very reasonable margin of error, 0.2 – 0.3 cm. This level of error is comparable to estimates of measurement error, 0.2 cm, for experienced observers (Bresette and Gorham 2001). LAGs are annuli, similar to the lines found on the otoliths of fish, and the difference between adjacent LAGs provides the change in diameter from t to $t+1$ of the humerus. This distance between annually deposited LAGs is proportional to the change in straight carapace length. It is possible to back-calculate from the diameter of the humerus at a particular LAG to determine the turtle's straight carapace length at that time, reconstructing an individual growth history that can be incorporated into a stochastic growth model.

Using incremental analysis of the humerus allows for construction of a growth model where each turtle is not growing along a mean growth curve and the variability in observed growth is maintained. This can provide several useful outputs including: duration of the pelagic stage, duration of the neritic stage, and time to size at sexual

maturity. A model of this form is necessary to include an accurate estimate of growth variability. Accurate estimates of stage lengths are crucial if we are going to continue to expand our knowledge of loggerhead sea turtle demographics and use this knowledge to better inform the population models used for conservation and management.

Methods

Analysis of skeletochronology data:

Humeri were collected from 92 dead stranded loggerheads ranging in length at death from 45 – 90 cm, straight carapace length (SCL). The humeri were collected from the coastal mid-Atlantic region of the U.S. (North Carolina; n = 72, Virginia; n = 14, Maryland; n = 6), between 1996 and 2002 and were presented and analyzed in Snover (2002). Methodology for preparation of the humeri and reading of the LAGs is described in Snover (2002), Snover and Hohn (2004) and Snover et al. (2007). Using an equation from Snover et al. (2007), it is possible to back-calculate the SCL from the measured LAG diameters and determine the length of the turtle when each of the LAGs was deposited.

$$L = L_{op} + b (D - D_{op})^c$$

Where L is the carapace length of the turtle, D is the diameter of the humerus, L_{op} is the carapace length of the turtle at hatching, D_{op} is the diameter of the humerus at hatching, c is the allometric proportionality and b is the slope of the relationship. I

used the parameter values from Snover et al. (2007) which were: $L_{op} = 4.6$ cm (SE= 0.1 cm), $D_{op} = 1.9$ mm (SE= 0.1 mm), $b = 4.25$ (SE= 0.26) and $c = 0.85$ (SE= 0.02).

Using the back-calculated lengths I was able to construct an individual growth trajectory for each turtle. I used the Ljung-Box test to test the 92 growth trajectories for autocorrelation. The Ljung-Box test is based on the autocorrelation plot. However, instead of testing randomness at each distinct lag, it tests the "overall" randomness of the entire series. The null hypothesis for this test is that the data are random. The test statistic varied for each trajectory but the mean significance value was 0.17, so the growth rate in year $t+1$ is not dependant on the previous year.

I subtracted predicted SCL_t from predicted SCL_{t-1} to obtain a total of 532 annual growth rates for 92 individuals of estimated body lengths spanning 20 – 90 cm SCL. After back-calculating all of the LAGs to carapace lengths I was able to construct a growth trajectory for each turtle over the span of years of readable LAGs and size-specific annual growth rates for a range of years from 1982 – 2002.

I arranged the 532 annual growth rates that I had previously calculated in order by initial length, (SCL) of each individual trajectory. This allowed me to separate the growth rates into 10 cm size bins and quantify the variability within each of these smaller intervals. I used 10 cm bins to preserve the true growth rates and variability observed within that size class since the rates did change as the turtles grew through the size range. After determining the mean and standard deviation of the annual growth rates within each of these 10 cm bins I plotted frequency histograms to see how the growth rates were distributed over each 10 cm range. Using the

Kolmogorov–Smirnov Lilliefors test I analyzed the distributions of annual growth rates within each of the seven bins for normality (Zar 1998). I found each of the distributions to be normally distributed except the last bin, 80 – 90 cm, which showed a pattern of decreasing increment width with size that would be expected for turtles reaching sexual maturity (Table 3.1).

Table 3.1: Results from Kolmogorov–Smirnov Lilliefors test for normality on each of the 10 cm bins. Each of the bins was found to be normally distributed except the last bin.

	Kolmogorov-Smirnov	
	Statistic	Significance
20-29	.140	.200
30-39	.169	.102
40-49	.147	.200
50-59	.153	.195
60-69	.137	.200
70-79	.118	.200
80-89	.371	.000

Growth Model Fitting:

Using the back-calculated lengths from the 92 stranded turtles I fit the interval form of the von Bertalanffy growth equation (Fabens 1965).

$$L_1 = L_\infty - (L_\infty - L_2) * e^{(-k)}$$

Where L_1 = predicted straight carapace length according to the outermost LAG and L_2 = predicted straight carapace length for the 2nd to last LAG, L_∞ = mean maximum length and k = growth rate constant. I then minimized the residual sums of

squares between the observed and predicted lengths using Solver in Microsoft Excel to estimate the parameters L_{∞} and k . I plotted the growth curve using these parameter values and set the initial SCL to 49 cm to directly compare the growth curve to those which had been previously examined in the 2001 loggerhead stock assessment.

Stochastic Growth Model:

Fitting growth curves to increment data is a common technique for evaluating growth variability within and among individuals. To generate a series of loggerhead growth curves that accounted for the observed variance in individual growth rates, I created an individual-based simulation to create a growth trajectory based on random draws from the observed annual growth rates in each 10 cm size class. All of the within size-class growth rate distributions were truncated at zero because negative growth rates were not observed in the raw data. For the last size-class, 80 – 90 cm, I also truncated the values at zero. The positive portion of the truncated normal distribution fit the observed distribution of growth rates well even though the entire distribution was not normally distributed. I then ran a Monte Carlo simulation to step each simulated turtle through time and generate its own growth trajectory using the PopTools add-in for Microsoft Excel (Hood 2006). I used a starting length of 20 cm SCL, because that was the lower end of the range of data from this study, and added the appropriate randomly drawn growth rate to the previous year's length. Each simulated turtle "grew" through the range of distributions in this manner until it reached the final distribution, 80 – 90 cm. At this point, the model will continue to

draw annual growth rates from this last distribution until it has run for the specified number of years. Using this growth model I ran a Monte Carlo simulation, using the PopTools add-in for Microsoft Excel, to generate 10,000 new individual growth trajectories. Using these trajectories I was able to calculate the mean time spent in each 10 cm length bin, mean time to grow from 20 – 90 cm and the error associated with these estimates. This same procedure can be used to calculate any stage duration or the length of time to reach the predicted size at sexual maturity, 90 cm SCL (NMFS–SEFSC 2001).

Results

The von Bertalanffy growth parameters I calculated using this skeletochronology data are within the range of the previously published L_{∞} and k values that were derived from mark-recapture studies, (Table 3.2). The fact that the L_{∞} and k parameters derived from these data are within the range of other published parameters will allow for direct comparison of stage length estimates and time to size at sexual maturity.

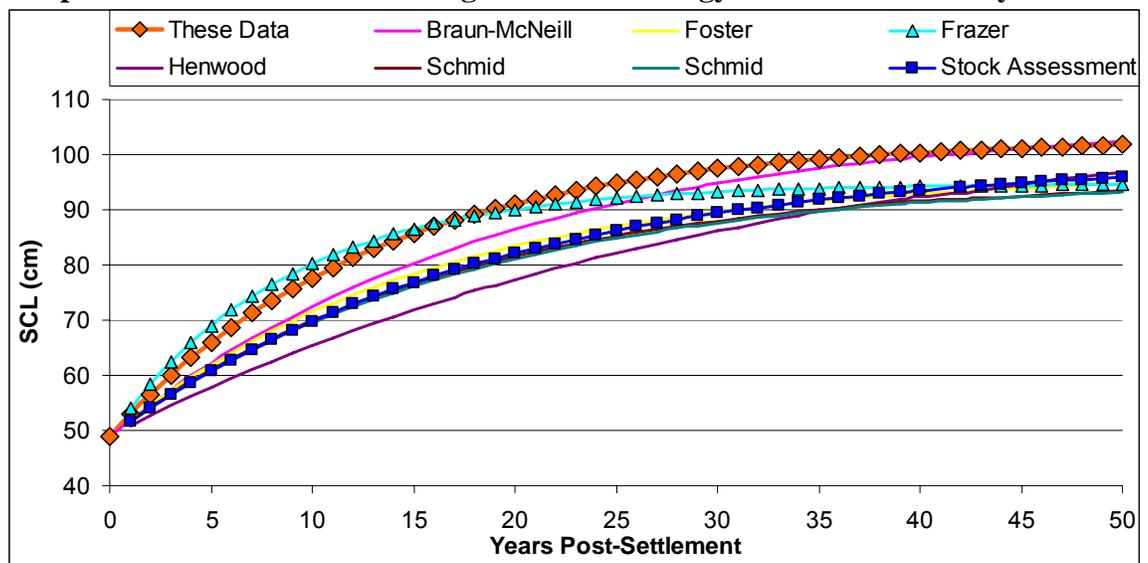
Table 3.2: Published von Bertalanffy growth parameters for North Atlantic loggerhead sea turtles taken from (NMFS-SEFSC 2001: all derived from mark-recapture studies). The bottom row of this table represent the parameters derived using these skeletochronology data. The last column shows the number of years it would take a turtle to grow from 49 cm (mean size at settlement, Bjorndal 2000) to 90 cm (mean size at sexual maturity, NMFS-SEFSC 2001).

Source	k L_{∞}	N	Range of Samples (SCL)	Predicted number of years to grow from 49 - 90 cm
Braun-McNeill	0.0521 106.90	57	45-76 cm	24
Foster	0.0637 96.74	54	62-104 cm	31
Frazer	0.1150 94.70	41	n/a	20
Henwood	0.0313 110.00	118	n/a	36
Schmid	0.0586 96.08	51	38-110 cm	35
Schmid	0.0573 96.10	19	n/a	36
Stock Assessment	0.0530 99.70	n/a	n/a	32
These Data	0.0759 102.98	92	40-90 cm	19

Figure 3.1 shows the resulting growth curves from all of the published von Bertalanffy growth parameters and the ones derived from this skeletochronology data set. All of the curves begin at mean size of recruitment back to the neritic zone, 49 cm SCL, as defined in (Bjorndal et al. 2000). Bjorndal et al. (2000) found that 49 cm SCL was the mean size that loggerheads began their ontogenetic shift back to the nearshore foraging sites. Therefore, it is crucial to understand how long the turtle may

be spending in the nearshore waters before it reaches maturity and is able to reproduce. Note the large spread of possible ages at a given SCL, especially at a critical point like estimated size at sexual maturity (90 cm SCL), from 19 years to 36 years. The aqua line with the triangles is the growth curve that was used to estimate stage durations in early assessments and the blue line with squares is what has been used more recently.

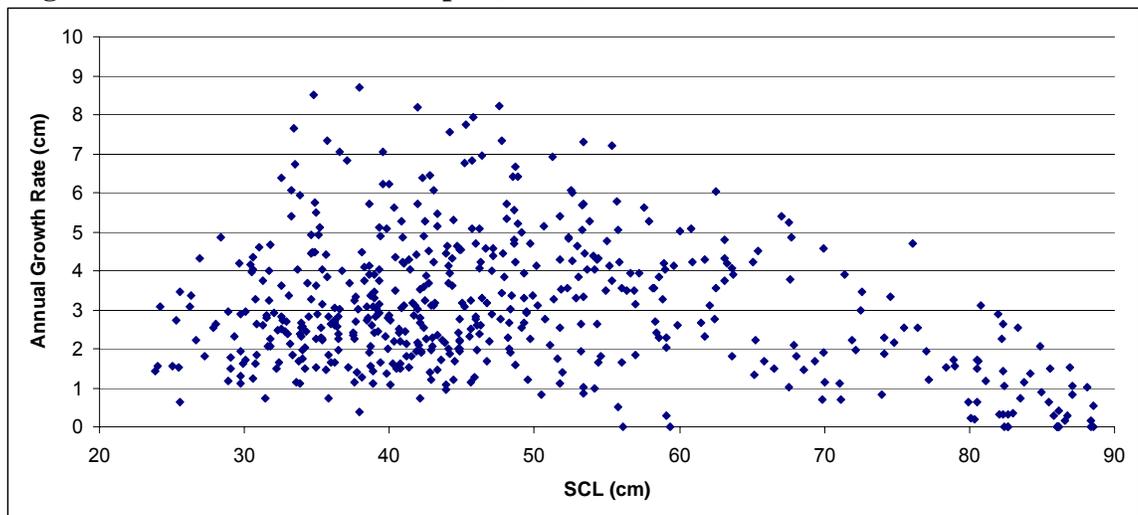
Figure 3.1: von Bertalanffy growth curves from published estimates using mark–recapture data and the curve using skeletochronology data from this study.



The individual growth rates calculated from the visible LAGs within the humeri of the 92 samples (532 annual growth rate estimates) are highly variable throughout the entire range of sizes but the variability does decrease with increased length, (Figure 3.2). There is an expected trend toward lower growth rates in the largest animals, but the range of estimated annual growth rates in the smallest turtles is

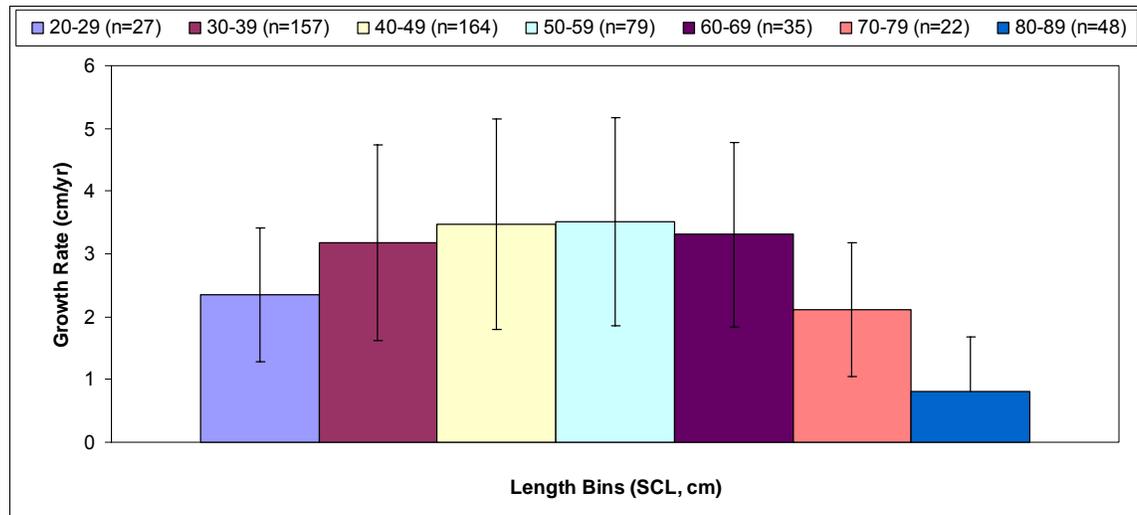
very broad, suggesting a wide range of possible growth trajectories that may be due to environment (temperature, food availability or location).

Figure 3.2: Each of the 532 annual growth rates calculated over the range of lengths for the turtles in the sample (N=92).



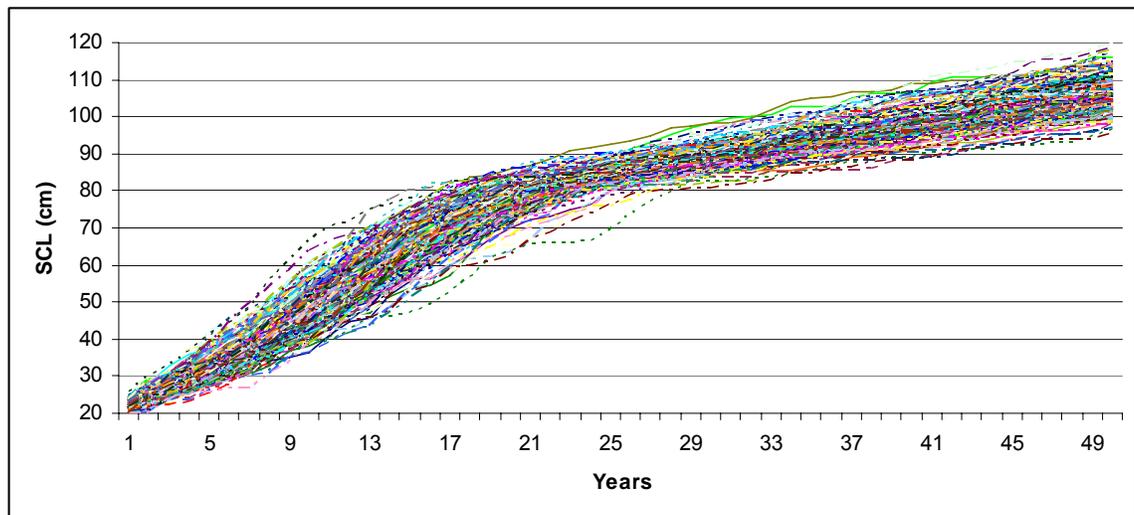
In this study based on a limited sample size of loggerheads from one geographic area, growth rates from 532 annual growth increments varied from, 0 – 8.7 cm yr^{-1} , for turtles ranging in length from 20 – 90 cm SCL. Annual growth rate means and variances calculated for the smallest size class, 20 – 29 cm, were slightly lower than the intermediate size classes, 30 – 69 cm SCL, but then growth began to slow once the turtles reached a length of 70 cm SCL (Figure 3.3). The last bin, 80 – 89, had the lowest annual growth rate, as expected because loggerheads begin to reach the minimum size at maturity around this length and somatic growth is slowing as they invest more of their resources towards reproduction.

Figure 3.3: Mean annual growth rates calculated for each of the 10 cm bins for the range of the data. The error bars represent one standard deviation and the samples sizes for each bin can be seen in the legend.



The truncated normal distributions of annual growth rates for each of the bins, which are based on the sample means and standard deviations, provide the backbone necessary for the stochastic growth model to function correctly and incorporate all of the observed variability. Each new run of the growth model produces a new growth trajectory for that individual “turtle” (Figure 3.4). Each simulated turtle plotted in Figure 3.4 was started at 20 cm SCL and allowed to grow for 50 years. Notice the spread of possible growth trajectories and the potential range of ages at critical points such as mean length at recruitment back to the neritic zone, 49 cm SCL, and size at sexual maturity, 90 cm SCL.

Figure 3.4: An example of 250 individual “turtle” growth trajectories generated from the growth model when they are started at 20 cm and allowed to grow for 50 years.



The model can be run for however many iterations are deemed necessary using a Monte Carlo simulation and will produce results like those seen in Table 3.3. Using these growth trajectories produced by the model it is then possible to estimate mean time spent in each stage plus the corresponding standard deviation for each estimate. The estimate of the mean number of years that it would take a turtle to grow from 20 – 90 cm is 30.74 years (95% CI = 23.82 – 37.66) and the mean number of years it would take to grow from 50 – 90 cm is 20.65 years (95% CI = 14.32 – 26.97). The estimate to grow from 50 – 90 cm is towards the lower end of the estimates derived from mark–recapture studies (Table 3.2) but the estimate of time to grow from 20 – 90 cm is within the range of previously published values (NMFS–SEFSC 2001). The benefit of the stochastic growth model is the variance in stage durations is more clearly delineated with this analysis.

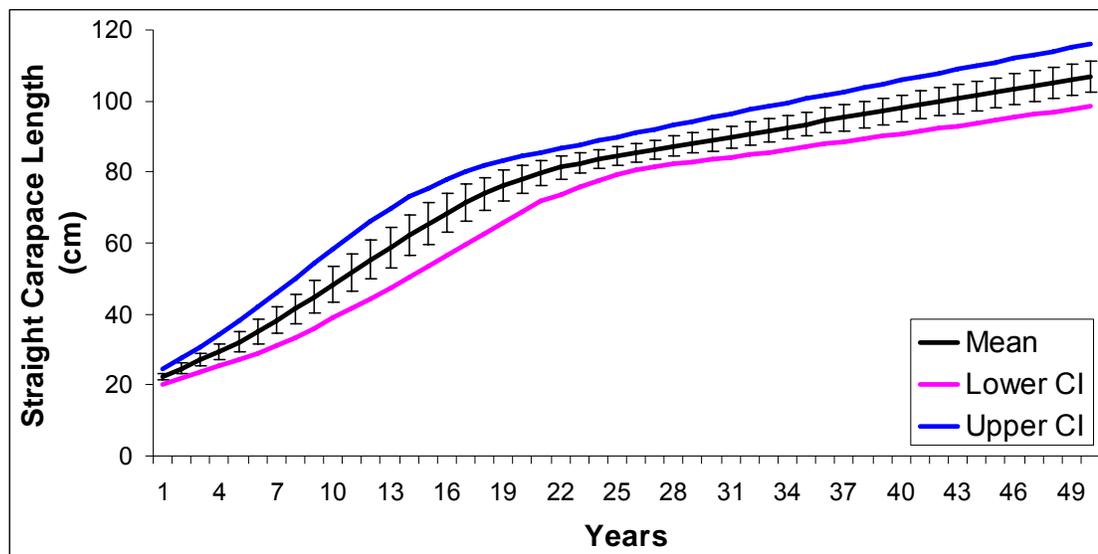
Table 3.3: Mean number of years required for simulated turtles to grow through each 10 cm size class, based on randomly drawn growth increments from observed distributions (Figure 3.3) and standard deviations for each 10 cm bin over the entire data range. These estimates were derived from the growth model after running it 10,000 times with each turtle beginning at an initial length of 20 cm, SCL.

Size Class (SCL, cm)	Mean Years to grow through size class	Standard Deviation	95% Confidence Interval
20-29.9	3.85	0.98	1.92 – 5.78
30-39.9	3.30	0.92	1.49 – 5.10
40-49.9	2.92	0.91	1.14 – 4.70
50-59.9	2.84	0.89	1.09 – 4.59
60-69.9	2.98	0.88	1.25 – 4.70
70-79.9	4.39	1.21	2.02 – 6.76
80-89.9	10.45	2.88	4.81 – 16.09

Using the results from 10,000 runs of the model which generated 10,000 individual growth trajectories, it was then possible to estimate durations of the pelagic juvenile stage, neritic juvenile stage and time to reach size at sexual maturity (Figure 3.5). The pelagic stage, which I've identified as hatchling to 49 cm, so it is consistent with previous studies, is estimated to be 13.2 years (SD=1.67). This estimate falls within the range of two previous studies; 8.2 years (Bjorndal et al. 2000) and 14.8 years (SD=3.3) (Snover 2002). The estimate derived from this growth model used the same data presented in Snover (2002) so it is expected that we will see similar estimates of stage durations. The neritic stage which I defined as 50 – 90 cm is estimated to be 20.7 (SD=3.19). This estimate is comparable to the estimate of 17 years to grow from 49 – 90 cm (Snover 2002). Bjorndal et al. (2001) estimated it would take 20 years for turtles to grow from 42 – 81 cm SCL and Braun-McNeill et al.

(2008) estimated it would take 17.4 years (95% CI = 15.6 – 19.4) to grow from 50 – 80 cm. Each of these estimates was for a slightly smaller size interval but are similar to the estimate of 20.7 years I estimated it would take a turtle to grow from 50 – 90 cm. The last duration I calculated using this growth model was duration to size at sexual maturity; which I defined as 90 cm based on estimates from the loggerhead stock assessment (NMFS–SEFSC 2001). I estimated 33.9 years (SD=3.6) and this was comparable to the estimate of 30.8 years from (Snover 2002) but is much longer than the early estimate of 22 years from (Frazer 1983) which was used in the early stage–based population models (Crouse et al. 1987, Crowder et al. 1994).

Figure 3.5: Mean growth curve calculated from 10,000 model runs. Each turtle was started at 20 cm and allowed to grow for 50 years. The 95% confidence intervals are shown for the mean growth trajectory and the error bars represent \pm one standard deviation.



Discussion

Obtaining current and accurate growth rates is critical in the development of quantitative demographic models used in management and recovery plans for the loggerhead sea turtle. Variability in growth rates throughout their lives is high and is a likely factor driving the uncertainty of life stage durations (Heppell et al. 2003). This is a critical issue for analyses that attempt to relate size to age. Based on 10,000 runs of the stochastic growth model the estimate of years that it could take a turtle to grow from 20 cm to 90 cm is 30.74 years (95% CI = 23.82 – 37.66). Because the turtle's true age is difficult to determine due to their long life span and resorption of growth marks from the interior of the humerus (Snover and Hohn 2004), many different methodologies have been used to quantify and understand growth in loggerheads, including mark–recapture, length frequency analysis and skeletochronology. This is the first attempt to quantify growth rate variability over the life span of individual turtles, as opposed to growth curve extrapolation from measurements of turtles from particular size classes. The variability observed in these trajectories calls into question the use of fixed stage durations in demographic models.

All of the population models that have been prepared up to this point have used fixed stage durations based on a single mean growth curve. Most of these analyses have used mark–recapture data and fit the von Bertalanffy growth model to these data. One major problem with using the published von Bertalanffy growth curves is that all of them were derived from a truncated range of sizes and then the curve was extrapolated beyond this range (Bjorndal and Bolten 1988, Chaloupka and Musick

1997, Day and Taylor 1997). Use of a mean von Bertalanffy growth curve to step turtles through matrix models is not optimal because it does not incorporate the high levels of observed variability of growth rates in the wild. Incorporating a growth model like the one presented in this chapter, which draws an annual growth rate from a distribution of possible growth rates, would more closely mimic the way turtles actually grow within the range of available data. Accurate estimates of time spent in both the pelagic and neritic stages are absolutely necessary for development of successful management plans. Each of these environments pose different threats to the juvenile loggerheads and understanding how long they are exposed to each is critical. Neritic sized juveniles, approximately 50 – 90 cm SCL, and especially the largest in that stage, 70 – 90 cm SCL, have been identified as having the highest elasticity values which means this is a very important stage to understand (Crouse et al. 1987). Miscalculations of time spent in this stage could alter population growth rates significantly. Over a period of twenty years there have been several updates to the original stage-based population model developed by Crouse et al. in 1987. Crouse et al. (1987) and Crowder et al. (1994) both used stage durations derived from the life tables constructed by Frazer (1983) and used a time to size at sexual maturity of 22 years. In later models the estimate of time to size at sexual maturity was increased to between 23 – 39 years (NMFS–SEFSC 2001, Snover 2002, Heppell et al. 2003). A change in the time to sexual maturity of this magnitude can have significant impacts on population growth rates and recovery times. Allowing stage durations and time to

size at sexual maturity to vary within the range of observed values is a more appropriate way of dealing with uncertainty rather than just ignoring it.

Although this method can improve how we determine stage durations and time to size at sexual maturity it is still not a perfect answer. One reason is that it still does not include growth rate estimates from the loggerhead's entire size range. However, it does span the range from 20 – 90 cm SCL, which covers most of the critical periods with which we are concerned. The lower range of values in this dataset comes very close to the estimate of a 1-year old turtle according to TEWG (2009) which is 15 cm SCL. Therefore, it is possible to start the turtles at that size in the growth model and then add one year to obtain estimates such as time to size at sexual maturity. The upper range of this dataset is coincidentally the same as the estimated size at sexual maturity published in the loggerhead stock assessment (NMFS–SEFSC 2001). Because these data span that range I can be confident in estimates of the pelagic stage (hatchling – 49 cm), the neritic stage (50 – 90 cm) and estimated time to size at sexual maturity (90 cm).

The only way that we are going to be able to understand loggerhead growth and stage durations more completely is by combining growth estimates for the entire size range into a framework like this stochastic growth model. We can only make progress by incorporating the uncertainty into the population models used for assessment instead of ignoring the variability and progressing as we have in this data poor situation. Mark–recapture may not be the best method to use if we want to fill in the data gaps quickly. It is possible to gain as much or more information using

incremental analysis of one humerus collected from a dead stranded turtle than you could obtain from many years of mark–recapture work. Since so much potential growth information can be obtained by using skeletochronology and now that it has been validated and accepted as a proper aging technique we need to concentrate on expanding the breadth of our samples to include the full range of sizes. If we are able to obtain humeri from the smallest strandings or fisheries bycatch it is likely that we will be able to calculate growth rates for the smallest size classes. Filling in the larger end of the size spectrum should not be too difficult since there are turtles in this size class stranding on the beaches and being taken by interactions with fisheries. The larger growth rates could also be supplemented by mark–recapture data from ongoing projects that already have tags on turtles. Starting a catalogue of humeri from more strandings, especially in size ranges where the sample sizes are lower, will lead to the best available growth model for the loggerhead.

Since most methods used to this point for developing conservation and recovery strategies have relied on deterministic matrix models I believe that it is crucial to update these models to allow for the variable and stochastic growth that we know is occurring in wild loggerheads. The past models have used fixed stage durations and have not allowed movement through life stages to vary. Decisions have to be made, usually by combining information from several studies, as to what the lengths of these stages are going to be. By incorporating a simple stochastic growth model like the one presented in this chapter we can step turtles through the matrices in a more stochastic fashion that will ultimately lead to more biologically realistic results

and projections. Beissinger and Westphal (1998) caution that the outputs from deterministic population models for endangered species may be unreliable due to poor demographic parameter estimates and the exclusion of the variability associated with these rates. By building a more appropriate matrix model and validating it by comparing it with analyses such as the length distribution analysis presented in chapter 2 we can come closer to being able to perform a proper stock assessment and understand the population fluctuations and cycles that this population is going to encounter in the future. Sea turtle assessment is lagging behind fisheries modeling and assessment and only when we incorporate methods they have been using for years and start to do more than count nests will we begin to better understand sea turtle population dynamics. Then we can start to anticipate cycles and test our hypotheses by using a combination of matrix projections and comparing and validating these outputs to the length distributions of juveniles from in-water studies. If this is what we work towards, a better understanding of sea turtle demography, then we won't be caught off guard the next time we have a decade long decline in nesting numbers. Our data sets are becoming more robust and long enough that we are soon going to be able to gain a better understanding of how past perturbations have affected the population and how what we are still doing might impact the production of hatchlings, recruitment of juveniles back to the neritic zone, and numbers of nesting females which all ultimately determine the population's growth rate and recovery potential.

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CHAPTER 4: CONCLUSION

My work shows that we can learn much from the existing data on loggerhead sea turtles by applying previously unused techniques. I have been able to identify trends in the juvenile size classes that would not have been apparent on the nesting beaches for many more years and have demonstrated a new technique to model the highly variable growth of loggerheads. Our current understanding of loggerhead population dynamics is not sufficient to reliably model the population or make predictions about the current or future status of the population. Using methods such as the stochastic growth model presented in chapter 3 will ultimately improve our understanding of sea turtle growth and the associated variability. This will lead to a clearer understanding of stage durations and the time it takes to reach sexual maturity, which in turn will improve the current population models. Improving estimates of demographic parameters and improving model structure by incorporating uncertainty will aid in our ability to make more accurate predictions and develop potential hypotheses about the current decline of the species. It will then be possible to use these improved population models to test hypotheses and validate projections using length distribution data from in-water studies similar to those discussed in chapter 2. By combining length distribution analyses, nesting beach trends and population models we are immediately assessing a greater proportion of the population and coming closer to understanding true population level changes and trends.

Use of the techniques discussed in this thesis can only improve our ability to successfully manage the loggerhead sea turtle. We will no longer have to rely on questionable trend estimates or population projections and will be able to identify potential problems much earlier than we would have in the past if we relied solely on nesting beach surveys. This expansion of our assessment toolbox will provide more accurate information to managers who are tasked with making the important policy decisions necessary to recover the loggerhead sea turtle.

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