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GROWTH RATES OF LOGGERHEAD SEA TURTLES (*CARETTA CARETTA*) FROM THE WESTERN NORTH ATLANTIC

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***Abstract*.—The International Union for Conservation of Nature (IUCN) lists the Loggerhead Sea Turtle (*Caretta caretta*) as an endangered species. Therefore, its protection and recovery requires effective management plans. We assessed the growth of 160 turtles captured in the estuarine waters of North Carolina from 1994 to 2005, and determined that Loggerhead Sea Turtles take an average of 17.4 yr (95% CI: 15.6-19.4 yr) to grow from 50 to 80 cm SCL (standard straight-line carapace length), a size range that encompasses most of their juvenile neritic life stage. Animals in this study had slower mean growth rates than those used for earlier population models. In addition, analyses of these data revealed high variability in growth rate both among individuals in the population and annually for a given individual. These findings suggest that recovery of the population may take longer than indicated by earlier modeling exercises, and that age and SCL in Loggerhead Sea Turtles may not be clearly related. Future investigators should consider these results when formulating models used to calculate estimates of stage duration and age at sexual maturity so that effective management plans can be formulated.**

Key Words.—*Caretta caretta*; demography; growth rate; Loggerhead Sea Turtle; recapture interval; stage duration.

INTRODUCTION

Loggerhead Sea Turtles (*Caretta caretta*), which are considered an endangered species (IUCN [International Union for Conservation of Nature]. 2006. IUCN Redlist of Threatened Species. The Conservation Union, Cambridge. Available at: http://www.redlist.org. Last Accessed: 22 November 2008), require management plans that will successfully provide for their protection and recovery. The development of effective conservation management practices for a given sea turtle population requires knowledge of specific demographic parameters, including the average age at which each life stage is initiated, and the duration of that stage (Zug et al. 1986; Parham and Zug 1997). The life history of Loggerhead Sea Turtles is complex and includes a number of ontogenetic shifts. Small juveniles occur in the open ocean; whereas, larger juveniles and adults typically reside in neritic environments (Bolten, 2003; Hopkins-Murphy et al. 2003). Recent satellite telemetry data, however, suggest that the transition from oceanic to neritic habitat is not a discrete ontogenetic niche shift, and for some individuals is reversible (McClellan and Read 2007).

Because determination of a sea turtle's age is difficult, most investigators use indirect methods such as length-frequency analysis, skeletochronology, and growth rates (Chaloupka and Musick 1997) to estimate life stage durations. While all methods have strengths and weaknesses, mark-recapture studies ultimately yield growth-rate data that better reflect the time required by wild turtles to transition through an ontogenetic stage (Zug et al. 1986; Zug and Glor 1998).

Initially, stage-based population models for Loggerhead Sea Turtles used 22 yr as the age to sexual maturity and assumed average size at maturity to be 87 cm straight-line carapace length (SCL) (Crouse et al. 1987; Crowder et al. 1994). Growth data used to estimate the previously reported neritic stage durations were obtained from early mark-recapture studies (Frazer 1983), which were hampered by small sample sizes and recapture intervals of < 1 yr. Thus, estimates of life stage durations and age to maturity obtained from these data may not accurately reflect inter- and intra-individual

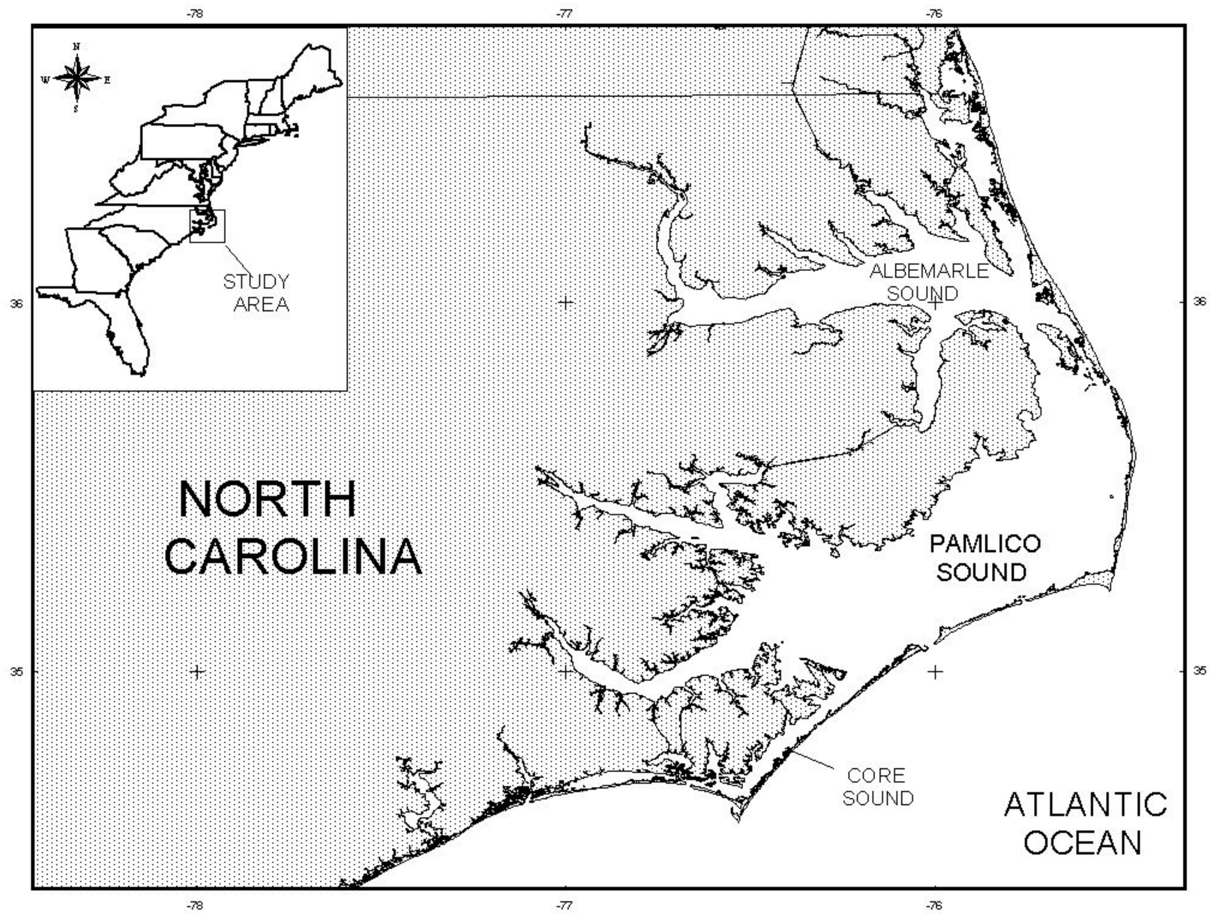

FIGURE 1. Most of the Loggerhead Sea Turtles (*Caretta caretta*) were captured in pound nets set in Core and Pamlico Sounds, North Carolina, a part of the Pamlico-Albemarle estuarine complex, the largest estuarine system (6630 sq km) in the southeastern United States. Inset shows position of main figure within the east coast of the USA.

growth patterns of the larger population, nor the important demographic parameters based upon them.

We assessed the growth rates of a population of recaptured juvenile Loggerhead Sea Turtles inhabiting Pamlico and Core Sounds, North Carolina, USA over a 12 yr period. These estuarine waters provide important foraging and developmental habitat for Loggerhead and other immature species of sea turtles (Epperly et al. 1995a, b, 2007). We estimated the mean duration of the majority of their neritic juvenile stage (50-80 cm; Carr 1987; Bjorndal et al. 2000a) and measured the variability in Loggerhead Sea Turtle growth rates.

MATERIALS AND METHODS

Since 1988, we have conducted a long-term mark-recapture study of Loggerhead Sea Turtles incidentally captured in pound nets in Core and Pamlico Sounds, North Carolina, U.S.A (Fig. 1). We assessed the growth rates of turtles recaptured from 1994-2005. We tagged all turtles in North Carolina except for three that others had tagged in South Carolina, Florida, and Virginia. We captured all turtles from North Carolina that were used in this study. We double-tagged sea turtles with Inconel Style 681 tags (National Band and Tag Company, Newport, Kentucky, USA) applied to the trailing edge of each rear flipper. Beginning in 1995, we additionally tagged all turtles with 125 kHz unencrypted Passive Integrated Transponder (PIT) tags (Destron-Fearing Corp., South St. Paul, Minnesota, USA), injected subcutaneously above the second-most proximal scale of the trailing margin of the left front flipper to ensure identification of the turtle in the event that both Inconel tags were lost.

We measured standard (notch-to-tip) SCL and recorded measurements to the nearest 0.1 cm. Because more than one trained observer took measurements throughout the course of the study, we determined observer measurement precision by comparing observer measurements of turtles that had recapture intervals of 14 days or less (N = 71). The mean of the absolute measurement errors for the 71 recaptures was 0.35 ±

TABLE 1.—Mean annual growth rates of juvenile Loggerhead Sea Turtles (*Caretta caretta*) using straight-line carapace length. The 95% Confidence Interval is in parentheses. Sample sizes for each size class using recapture intervals ≥ 0.9 yr and recapture intervals in multiples of one year (± 0.1 y). We estimated mean and 95% confidence intervals (CI) from the transformed data and the results back-transformed to the original units.

Recapture Intervals	All Intervals ≥ 0.9 yr		Multiples of one year (± 0.1 yr)	
Size Class (cm)	N	Growth Rate (cm/yr)	N	Growth Rate (cm/yr)
50-59	44	1.58 (1.17-2.04)	25	1.03 (0.61-1.53)
60-69	122	1.82 (1.59-2.05)	55	1.69 (0.75-1.35)
70-79	43	1.63 (1.25-2.05)	21	1.72 (1.20-2.32)
Total	214[a]	1.72 (1.54-1.92)	104[b]	1.52 (1.29-1.78)

[a] Includes one < 50 cm and four > 80 cm growth rates
[b] Includes one < 50 cm and two > 80 cm growth rates

0.40 cm. We calculated individual annual growth rate as (SCL_{final} − $SCL_{initial}$) / recapture interval in years. We only analyzed growth rates in those turtles whose recapture intervals were ≥ 0.9 yr (Chaloupka and Musick 1997).

We tested the distribution of the growth rate data for normality using the Shapiro-Wilk test (Shapiro and Wilk 1965; Zar 1999), and the data were not normally distributed (W = 0.9523, P < 0.005; Fig. 2). Hence, we transformed the data to $\log(x_i+2)$, which resulted in an approximate normal distribution (W = 0.989, P = 0.103). Mean and 95% confidence intervals (CI) were estimated from the transformed data and the results back-transformed to the original units (Zar 1999).

We analyzed patterns of intra- and inter-individual growth rates using three methods. First, we used growth rates for individual turtles as a response variable in a generalized additive model (GAM) to determine whether there were significant effects on individual growth rates of size (average SCL = (SCL_{final} + $SCL_{initial}$) / 2 for each individual turtle), sex (Braun-McNeill et al. 2007), or recapture interval. We used a mixed longitudinal sampling design (Chaloupka and Musick 1997) with 24% of individual Loggerhead Sea Turtles recaptured two or more times. We tested for both linear and non-linear effects of size and recapture interval; sex entered the model as a binary variable (male or female). Second, we estimated the amount of time Loggerheads required to grow from 50 (L_i = initial length) to 80 (L_r = recapture length) cm SCL, the size range of most of the turtles in our study. We calculated this estimate as (80-50)/mean growth rate. To ascertain if growth rates changed throughout the year (i.e., turtles growing faster during warmer months and slower during colder months or during migrations), thus exhibiting a seasonal component, we also calculated this time estimate by only using growth rates of turtles that had recapture intervals of one year (± 0.1 yr), or multiples thereof, to calculate our mean growth rate. Third, we examined how annual growth rates of individuals recaptured two or more times varied over time.

RESULTS

We recaptured 160 Loggerhead Sea Turtles after recapture intervals of ≥ 0.9 yr and there were 54 multiple recaptures (we recaptured 25 turtles twice, 10 turtles three times, and three turtles four times), which resulted in 214 growth-rate measurements. Initial SCLs ranged from 45.1 to 81.6 cm. Recapture intervals ranged from 0.9 to 7.0 yr (mean = 2.0 ± 1.2; median = 1.7). Mean growth rate calculated from all recapture intervals (N = 214) was 1.72 cm/yr (95% CI: 1.54 to 1.92); mean growth rate calculated from recapture intervals of one year (± 0.1 yr; N = 104) was 1.52 cm/yr (95% CI: 1.29 to 1.78; Table 1). Individual growth rates ranged from -1.0 to 7.3 cm/yr.

There was no significant effect on growth based on size (average of SCL at release and at recapture), length of recapture interval, or sex as determined from non-linear or linear regressions in the generalized additive model (Table 2). Therefore, we used the measurements of mean growth for all individuals to estimate the duration of time Loggerhead Sea Turtles require to grow from 50-80 cm, which represents the range of most turtles we encountered. We estimated 17.4 yr (95% CI: 15.6 to 19.4 yr) to be the average time turtles required to grow from 50 (L_i = initial length) to 80 (L_r = recapture length) cm SCL when using all recapture intervals, and 19.7 yr (95% CI: 16.8 to 23.3 yr) when using recapture intervals of one year (± 0.1 yr), or multiples thereof. Growth rates varied widely, both among all turtles in the

TABLE 2. Results from generalized additive model (GAM) tests for effects of size (average SCL), recapture interval (days), and sex on growth rates of individual Loggerhead Sea Turtles (*Caretta caretta*) with recapture intervals greater than 0.9 years.

Model Parameter	**Linear Estimate**	**Linear *t*-value**	**Linear *P*-value**	**Non-linear *F*-value**	**Non-linear *P*-value**
Average SCL	0.0001	0.4568	0.6484	1.101	0.3499
Recapture interval	-0.0220	-1.2965	0.1965	0.8266	0.4808
Sex	-0.0658	-0.5614	0.5452		

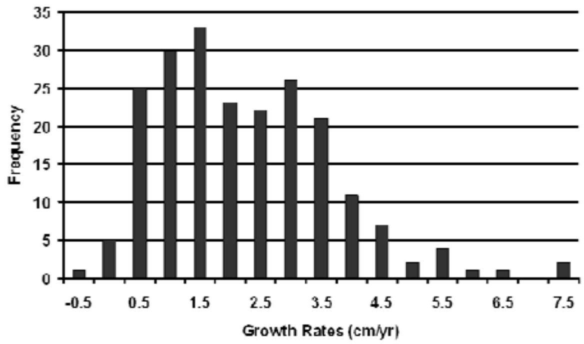

FIGURE 2. Distribution of growth rates of Loggerhead Sea Turtles (*Caretta caretta*) prior to log transformation.

study (from -1.0 to 7.3 cm/y; Fig. 3) and within individual turtles (N = 38; Fig. 4). Some individuals displayed increasing, some decreasing, and others variable growth rates over time (Fig 4).

DISCUSSION

Life stage durations.—The estimate of time for Loggerhead Sea Turtles from North Carolina to grow from 50 to 80 cm SCL ranged from 16 to 23 yr, depending upon whether we used all recaptures or only recaptures based on whole year intervals. The former includes turtles with an unequal number of summer (growing) and winter (non-growing) seasons; more had a greater number of growing seasons. Although the difference in the two estimates is not significant, the range does imply a seasonal component in the growth of these turtles. Therefore, 20 yrs may be a more accurate estimate because it is based on recapture intervals of whole years, which include only full annual cycles of growth. This duration is comparable to that estimated by Bjorndal et al. (2001) using length-frequency analysis (16 yr), but much greater than that estimated by Snover (2002) at 10 yr and Parham and Zug (1997) at 11 yr using skeletochronology. One possible explanation for the greater duration estimates from length-frequency and mark-recapture analyses is the occurrence of zero growth rates. These can obscure the modal structure of length-frequency analysis data (Bjorndal et al. 2001) and may reduce the mean growth rate for mark-recapture data, but are difficult to detect in skeletochronology data (Zug and Glor 1998).

Assuming a mean size at neritic settlement of 49 cm SCL, Bjorndal et al. (2000a) estimated that the oceanic stage duration averages 8.2 yr (range 7-12 y). Adding this duration to the estimates of time (derived from the three different methodologies: mark-recapture, length-frequency analysis, and skeletochronology) for neritic juvenile Loggerhead Sea Turtles to grow from 50-80 cm gives an estimated average age of 24-31 yr (mark-recapture), 24 yr (length-frequency analysis) and 18 yr (skeletochronolgy) for an 80 cm SCL loggerhead, which is about 10 cm smaller than the average size of first-time nesters (TEWG [Turtle Expert Working Group] 1998; NMFS SEFSC [National Marine Fisheries Service, Southeast Fisheries Science Center] 2001). Therefore, the previously accepted projection of 22 yr to attain 87 cm SCL, the age of sexual maturity used in early population models (Crouse et al. 1987; Crowder et al. 1994), is likely an underestimate.

More recent population models have used our

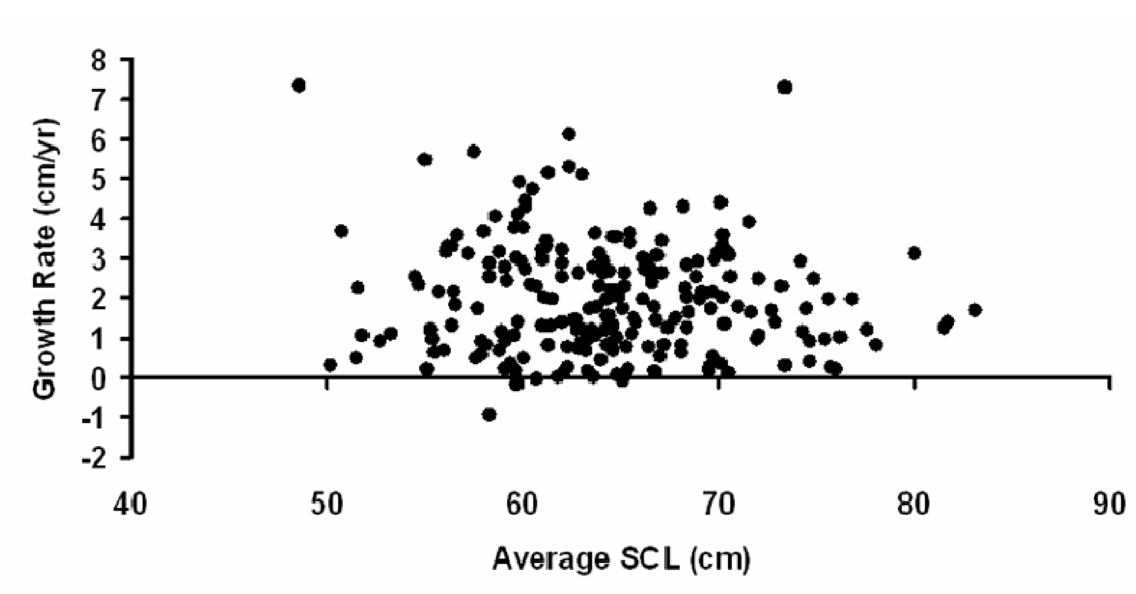

FIGURE 3. Individual growth rates (cm/yr) of Loggerhead Sea Turtles (*Caretta caretta*) as a function of the average of initial and recapture standard carapace lengths (SCL).

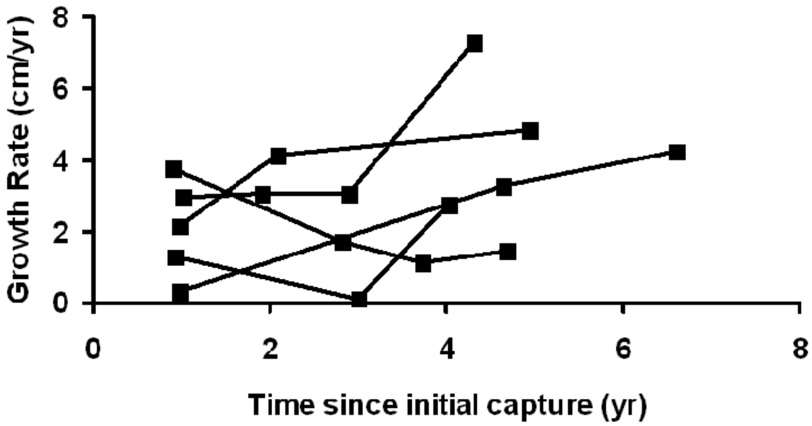

FIGURE 4. Growth rates over time of five Loggerhead Sea Turtles (*Caretta caretta*) having two or more recapture intervals.

preliminary growth data (NMFS, unpubl. data) along with a revised estimate of oceanic juvenile stage duration to estimate age at maturity of 35 yr (Heppell et al. 2003) and 39 yr (NMFS SEFSC 2001). Using back-calculations based on skeletochronology, Snover (2002) more recently estimated the oceanic stage duration at 14 yr. This potential increase in the estimate of the duration of the oceanic stage suggests an even greater time to maturity.

Loggerhead sea turtles occupy various oceanic and neritic habitats during their complex life history (Meylan and Ehrenfeld 2000), and as elucidated by our analyses, are long-lived and slow-growing animals. Consequently, they experience prolonged susceptibility to various sources of human-induced mortality, including pollution, boat strikes, entanglement and ingestion of debris, and incidental capture in fishing gear (Eckert 1995; Lutcavage et al. 1997; Allen 2000; Turtle Expert Working Group 2000; Lewison et al. 2004). If the time spent in life stages prior to reproduction is greater than previously thought, more animals might be expected to die before reaching reproductive age, and recovery of the population may take longer than previous modeling exercises had suggested. Our findings highlight the need to revisit population models, specifically elasticity analyses, to evaluate the potential impact of slower growth rates combined with different sources of mortality on Loggerhead populations.

Variation in growth rates.—Variability in sea turtle growth rates may be contributing to the uncertainty regarding life stage durations (Heppell et al. 2003). Growth rates of juvenile Loggerhead Sea Turtles from North Carolina ranged from -1.0 to 7.3 cm/yr. In contrast, while growth rates of turtles occupying the inshore waters of Mosquito Lagoon, Florida (Mendonça 1981) were in the upper range of our estimate (5.0-7.4 cm/yr, N=13), those inhabiting the nearshore waters of Florida (-0.2-2.3 cm/yr, N = 74) and Chesapeake Bay, Virginia (0.3-3.0 cm/y, N = 18) were in the lower range (Schmid 1995; National Marine Fisheries Service, Southeast Fisheries Science Center, unpubl. data; R. Herren, Quantum Resources, unpubl. data; Klinger and Musick 1995). Calculation of these other Loggerhead growth rates used much smaller sample sizes than did our study, and/or data from those earlier studies were from the summer foraging/growing season. Long-term mark-recapture studies in several different areas along the southeastern United States will help to determine if geographic differences in growth rates exist among Loggerhead Sea Turtles and what proportion of the Atlantic Loggerhead population resides in different geographic areas.

The variation in individual growth rates observed in this and other sea turtle populations is likely due to a combination of variation in growth among and within individuals, as well as measurement error/variation in the collection of the data. We included several negative growth rates in our analysis. While Loehr et al. (2007) documented negative growth rates in certain populations of tortoises, we suspect that measurement error was the cause of our negative growth rates as there are no documented studies of sea turtle carapaces decreasing in size. Although having multiple data collectors did introduce error into our estimations, we do not believe that our estimated measurement error of 0.35 cm was a significant contributor to the variation of the growth rates. The variance we recorded on the raw data for 10 cm size classes from 50-80 cm ranged from 1.3-1.5, which is comparable to that recorded by studies utilizing one data collector (0.9-1.6) (Bjorndal and Bolten 1988).

Earlier mark-recapture studies only addressed variability in growth rates of Loggerhead Sea Turtles among size classes or individuals (Mendonça 1981; Schmid 1995; Klinger and Musick 1995); however, our numerous (N = 38) multiple-recaptured individuals made it possible to determine intra-individual growth rates over time. Zug and Glor (1998) observed similar individual variation in growth via skeletochronological analysis of humeri of juvenile Green Sea Turtles

(*Chelonia mydas*) obtained from individuals inhabiting the Indian River lagoon system in Florida, manifesting as variable growth mark width. Likewise, oceanic-stage Loggerhead Sea Turtles demonstrated substantial variation in growth rates within individual turtles, attributed to the stochastic environment in which they live (Bjorndal et al 2003). The changing growth patterns exhibited by individual turtles in these studies suggest that the time required to transition through each life stage and to reach maturity may vary considerably among individuals.

Previous studies used GAM analyses to demonstrate the relationships between growth rates and sex, mean size, year, recapture interval, and site (Chaloupka and Limpus 1997; Limpus and Chaloupka 1997; Bjorndal et al. 2000b; Bjorndal et al. 2003; Chaloupka et al. 2004; Balazs and Chaloupka 2004). However, our GAM analysis did not find a significant relationship between growth rate and sex, size, or recapture interval. This lack of significant effect may be due to the narrow size range (~50-80 cm) of the juvenile population inhabiting inshore locations along the U.S. Atlantic coastline (Musick and Limpus 1997), including this study site, or may reflect substantial variability in the growth rates of these turtles.

A number of different factors can influence variability in growth rates both among and within individual turtles. Environmental parameters such as prey abundance, habitat availability (Parmenter 1980; Gibbons et al. 1981; Balazs 1982; Diez and Van Dam 2002) and water temperatures (Parmenter 1980; Gibbons et al. 1981) may concentrate turtles in particular areas, which may result in density-dependent effects on growth rates (Bjorndal et al. 2000b). Furthermore, researchers note that sex (Chaloupka and Limpus 1997; Bjorndal et al. 2000b; Chaloupka et al. 2004) and age (Bjorndal et al. 2003) also affect growth rates of wild turtles.

Growth rates of sea turtles vary depending upon the genetic stock from which they came (Bjorndal et al. 2000*b*). Juvenile turtles occupying feeding grounds (such as those in our study population) comprise a mixture from several different breeding stocks (Bowen et al. 2004). Mixed stock analysis estimated that 80% of Loggerhead Sea Turtles occupying feeding grounds in North Carolina originated from the south Florida rookery, 12% were from the northeast Florida to North Carolina rookery, 6% from the Yucatán, Mexico rookery, and 2% from other nesting populations (Bass et al. 2004); our samples were taken from this same foraging ground. Investigators need to conduct a more comprehensive comparison of growth rates of juvenile Loggerhead Sea Turtles among the various feeding aggregations in conjunction with their respective genetic composition to evaluate a genetic source of variation in growth.

Energetic costs associated with migrations may influence growth rates as well (Klinger and Musick 1995). Turtles in our study area, while occupying similar habitats during the spring and summer, inhabit different areas after leaving the sounds. We estimate that 21-25% of turtles are residents, returning in subsequent years to their original capture location (Avens et al. 2003; Sasso et al. 2006). As water temperatures cool in the autumn, juvenile turtles begin migrating to three general over-wintering areas: Florida, offshore North Carolina, and the North Atlantic via the Gulf Stream (McClellan and Read 2007; Mansfield 2006). Depending on the water temperatures and prey availability experienced by turtles at these locations, each over-wintering area may incur different costs and/or benefits, thus affecting growth rates.

***Conclusions*.—**Using the average growth rate of recaptured Loggerhead Sea Turtles, we estimate that growth from 50-80 cm SCL takes an average of 16-23 yr, comparable to the 16 yr estimated from length-frequency analyses (Bjorndal et al 2001) but greater than the 10-11 yr estimated from skeletochronology (Parham and Zug 1997; Snover 2002). Our results suggest that researchers underestimated the age to sexual maturity used in early Loggerhead growth models (22 years; Crouse et al. 1987; Crowder et al. 1994) and for recovery plans. Furthermore, the variability in growth rates described herein suggests that there is not a clear relationship between the age of sea turtles and their carapace length. Consequently, the derivation of accurate growth rates and life stage durations requires a better understanding of the influences of environmental factors (e.g., prey selection, prey availability), and individual behavior (e.g., foraging or migration strategies) on growth.

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Erratum corrected 5 December 2008

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SHERYAN EPPERLY is a Research Fishery Biologist for the National Marine Fisheries Service, Southeast Fisheries Science Center where she leads NMFS' sea turtle research program in the southeastern U.S. and U.S. Caribbean. She received her B.S. in Biological Sciences from Marshall University and her M.S. in Marine Sciences from the University of South Florida. She currently works on sea turtle population biology and fisheries-sea turtle interactions, such as trawling and longlining. She is an active member of the International Sea Turtle Society and has served on their Executive Board as Secretary. Sherry is pictured in the Boundary Waters Canoe Area Wilderness. Photographed by Alexander Chester.

LARISA AVENS is currently a Research Fishery Biologist with the National Marine Fisheries Service and is the lead researcher for the agency's National Sea Turtle Aging Laboratory in Beaufort, North Carolina. She received her Ph.D. from the University of North Carolina – Chapel Hill in 2003, where her research was on homing behavior, navigation, and orientation in juvenile sea turtles. She currently uses skeletochronology to study the age, growth, and stage duration of sea turtles. She also collaborates on in-water sea turtle research in North Carolina to study population demographics and health status. Larisa is pictured removing a satellite tag from a loggerhead. Photographed by Lisa Goshe.

MELISSA SNOVER is a Research Fishery Biologist with the National Marine Fisheries Service Pacific Islands Fisheries Science Center in Honolulu, HI. She has worked in marine turtle research for over 10 years. Currently, her research focuses on growth, life history, and population dynamics in sea turtle populations in the Pacific, including Green, Hawksbill, Olive Ridley, Loggerhead, and Leatherback turtles. She has a Ph.D. in Ecology from Duke University where her research focused on growth and ontogenetic habitat shifts in Loggerhead and Kemp's Ridley Sea Turtles. Photographed by Larisa Avens.

CHRIS TAYLOR is a Research Ecologist for the National Ocean Service, Center for Coastal Fisheries and Habitat Research. He received his B.S. in Biology from University of Wisconsin-Stevens Point and his M.S. and Ph.D. in Zoology from North Carolina State University. His current research includes developing video and sonar sampling techniques for distribution and behavioral research of estuarine and marine fauna, modeling environment-organism interactions, and life-history studies of marine organisms. Photographed by Larisa Avens.