Abstract—The Sea Turtle Stranding and Salvage Network, coordinated by the National Marine Fisheries Service through a network of state coordinators, archives data on sea turtles that strand along the U.S. coast. We conducted length-frequency analyses, using MULTIFAN software, to generate somatic growth functions for loggerhead sea turtles, *Caretta caretta*, that stranded along the Atlantic coast of Florida (n=1234) and along the U.S. coast of the Gulf of Mexico (n=570) between 1988 and 1995. In both regions, the size range of loggerhead sea turtles between the size at which they begin to recruit in substantial numbers from pelagic to neritic habitats (46 cm curved carapace length [CCL]) and minimum size at sexual maturity (87 cm CCL) was composed of 20 year classes and had similar von Bertalanffy growth functions. Our estimates of 20 year classes fall within the range of estimates calculated from previous studies (9 to 29 years) for this life stage. Because survivorship in this size range has been identified as critical for population recovery, an accurate estimate of life stage is essential for developing effective management plans.

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Somatic growth function for immature loggerhead sea turtles, *Caretta caretta*, in southeastern U.S. waters

Karen A. Bjorndal

Alan B. Bolten

Archie Carr Center for Sea Turtle Research and Department of Zoology
University of Florida
P.O.Box 118525
Gainesville, Florida 32611
E-mail address (for K. A. Bjorndal): kab@zoo.ufl.edu

Bruce Koike

Aquarium of the Americas
1 Canal Street
New Orleans, Louisiana 70130

Barbara A. Schroeder

Office of Protected Resources,
National Marine Fisheries Service, NOAA
1315 East West Highway
Silver Spring, Maryland 20910

Donna J. Shaver

Biological Resources Division
U.S. Geological Survey—Padre Island National Seashore
P.O. Box 181300
Corpus Christi, Texas 78480

Wendy G. Teas

Wayne N. Witzell

Southeast Fisheries Science Center
National Marine Fisheries Service, NOAA
75 Virginia Beach Drive
Miami, Florida 33149

Somatic growth functions are critical parameters for understanding the life history of a species and for developing management plans for wild populations. Substantial effort has been invested in—and considerable information on growth rates has been gained from—mark-recapture studies of sea turtle populations (Chaloupka and Limpus, 1997; Chaloupka and Musick, 1997; Limpus and Chaloupka, 1997; Bjorndal et al., 2000). Although growth studies based on mark and recapture of individual animals yield direct measures of growth rates, sea turtles have characteristics that make them relatively poor candidates for mark-recapture studies. Sea turtles are relatively slow growing; consequently mark-recapture studies are long-term labor-intensive efforts. The probability of recapturing marked individuals is low in many populations because of the long-range movements and obscure migratory patterns in some lifestages (e.g. posthatchlings in a pelagic habitat), high natural mortality in young lifestages, and high human-induced mortality in juvenile and adult lifestages.

Length-frequency analysis has been used for many years to estimate growth rates, age structure, and mortality in marine fish and invertebrate populations (Ricker, 1975; Pauly and Morgan, 1987; Hilborn and Walters, 1992). More recently, length-frequency analyses have been used to evaluate somatic growth rates in sea turtles. The accuracy of four length-frequency analysis programs (ELEFAN I, [Holden and Bravington, 1992] Shepherd's length composition analysis [SLCA, Holden and Bravington, 1992], projection matrix method [Holden and Bravington, 1992], and MULTIFAN) for predicting growth rates was tested in a population of green turtles, *Chelonia mydas*, in the southern Bahamas for which growth rates had been measured in a long-term mark and recapture study (Bjorndal and Bolten, 1995; Bjorndal et al., 1995). MULTIFAN successfully estimated growth rates in this population, SLCA was partially successful, and ELEFAN I and the projection matrix method were not successful. In young, pelagic-stage loggerhead sea turtles (*Caretta caretta*), estimates of growth rates generated by MULTIFAN were consistent with results from recaptures of tagged turtles (Bjorndal et al., 2000).

In our study, we generated a growth model for immature loggerhead sea turtles in southeastern U.S. waters between the size at which they begin to recruit in substantial numbers to neritic habitats (46 cm curved carapace length [CCL]) and minimum size at sexual maturity (87 cm CCL). The duration of the growth interval between 46 and 87 cm CCL is critical information for developing management plans and demographic models for this sea turtle, which is listed as a threatened species in the U.S. Endangered Species Act of 1973. This size range includes the large juvenile and subadult lifestages defined in the stage-based population model developed for North Atlantic loggerhead sea turtles (Crouse et al., 1987; Crowder et al., 1994). This stage-based population model has identified survivorship in the large juvenile lifestage as the most critical for population recovery. We based our length-frequency analyses on data collected from hundreds of loggerhead sea turtle carcasses that were measured by the Sea Turtle Stranding and Salvage Network from Florida, Alabama, Mississippi, Louisiana, and Texas between 1988 and 1995.

Methods

Length-frequency data

The Sea Turtle Stranding and Salvage Network (STSSN) is an organized network of individuals who monitor the shoreline and record data on each stranded sea turtle, including date and location of stranding, species, and carapace length (curved or straight carapace length, or both). Carapace length is measured from the anterior point at midline (nuchal scute) to the posterior tip of the supracaudals. The stranding data are compiled and verified by state coordinators and archived at the Southeast Fisheries Science Center (SEFSC) Miami Laboratory (Teas, 1993). We received data on stranded turtles for 1988 through 1995 for Alabama, Mississippi, Louisiana, and Texas from SEFSC and data for 1988 through 1995 for Florida from the Florida Department of Environmental Protection, Florida Marine Research Institute. All turtles known to have been "head-started" (that is, raised in captivity before being released into the wild) were excluded from the analyses because growth rates in captivity, and therefore length-at-age, may be quite different for head-started turtles. We divided the data into two geographic regions: the Atlantic coast of Florida and the U.S. coast of the Gulf of Mexico (Florida, Alabama, Mississippi, Louisiana, and Texas). The Florida coast was divided between Atlantic and Gulf by the STSSN at 80.5°W.

Because most of the data on carapace length were over-the-curve measurements, straight carapace lengths (SCL) were converted to curved carapace lengths (CCL) by using the conversion equation (n=932, r^2=0.97, P<0.001) in Teas (1993)

$$SCL = (0.948 \cdot CCL) - 1.442.$$

After conversions were completed, all CCL data were rounded to the nearest cm.

We wanted to limit our analyses to the subadult, neritic lifestage that inhabits the coastal waters of the southeastern U.S.; therefore we limited the size range of loggerhead sea turtles from 46 to 87 cm CCL. The lower value was based on length-frequency distributions (Bolten et al., 1993; Bjorndal et al., 2000) that indicated that 46 cm CCL is the size at which these sea turtles begin to recruit to neritic habitats in substantial numbers. The largest subadult size was taken as 87 cm CCL based on Witherington (1986), who reported that 88 cm CCL was the size of the smallest nesting loggerhead sea turtle at Melbourne Beach, Florida. This value is a very conservative division between subadults and adults; many with CCLs greater than 87 cm are still immature. For length-frequency analyses, however, it is better to exclude some subadults than to include many adult animals. Any factor that acts to obscure the modal structure of the sample—such as cessation or near-cessation of growth in older age classes—will decrease the potential for successful length-frequency analysis. If older age classes cannot be distinguished, K (intrinsic growth rate) will be overestimated and the number of age classes underestimated (Terceiro et al., 1992). Because loggerheads essentially stop growing at sexual maturity and because they attain sexual maturity at a range of sizes (Frazer and Ehrhart, 1985), the age classes—or modes—above the minimum size at sexual maturity are obscured and cannot be distinguished in length-frequency analyses.

Kolmogorov-Smirnov analyses were conducted with SPSS software (version 9.0 SPSS, 1996).

Length-frequency analysis

We used MULTIFAN (version 32(f), Otter Research Ltd., 1992) modified to include 30 age classes by Fournier (Otter Research Ltd., 1992). MULTIFAN simultaneously analyzes multiple samples of length-frequency data (Otter Research Ltd., 1992) and uses nonlinear statistical modeling and robust parameter estimation to estimate the parameters of the von Bertalanffy growth function (Fournier et al., 1990, 1991). Log-likelihood objective functions are compared by using maximum likelihood analyses to identify the parameter set for the von Bertalanffy model with the best fit.

The form of the von Bertalanffy equation that was used in the MULTIFAN program is

$$\mu_{j\alpha} = m_1 + (m_N - m_l)\left(\frac{1-\rho^{j+(m(\alpha)-1)/12}}{1-\rho^{Nj}}\right),$$

where $\mu_{j\alpha}$ = the mean length of the age class j turtles in the αth length frequency data vset;

m_1 = the mean length of the first age class;

m_N = the mean length of the last age class;

ρ = the Brody growth coefficient;

$m(\alpha) - 1$ = the number of months after the presumed birth month of the turtle in the αth length-frquency data set; and

N_j = the number of age classes in the data set.

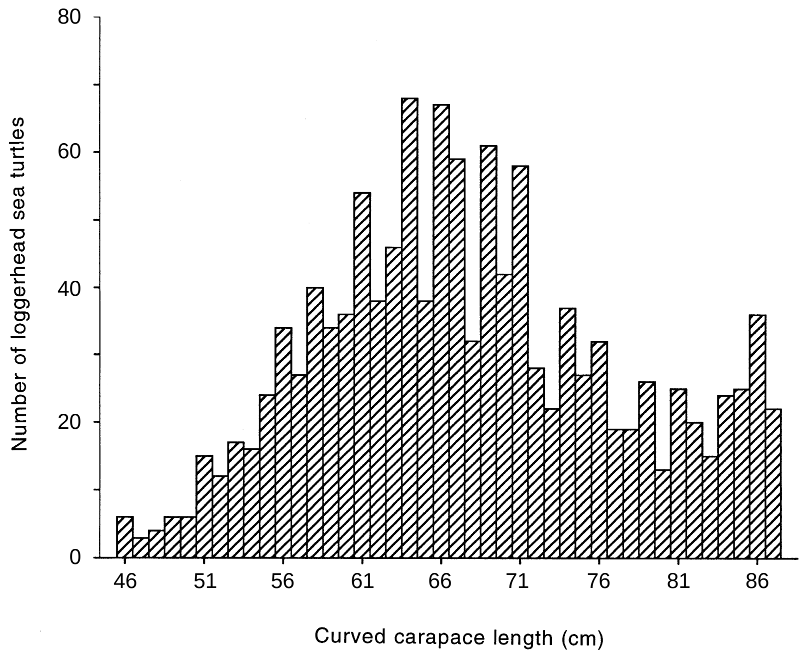

Figure 1

Length-frequency distribution of loggerhead sea turtles stranded along the Atlantic coast of Florida from 1988 through 1995 within the size range of 46 to 87 cm curved carapace length (n=1234).

This parameterization of the von Bertalanffy growth equation is derived in Schnute and Fournier (1980).

The MULTIFAN length-frequency program has the following assumptions: 1) growth is described by a von Bertalanffy growth curve; 2) samples represent the structure of the population; 3) recruitment occurs in seasonal pulses, 4) the lengths of animals in each age class are normally distributed; and 5) the standard deviations of the lengths are a simple function of the mean length-at-age.

MULTIFAN requires that initial values for the following parameters be designated as starting points for the iterations: expected number of age classes; expected initial K values; mean length of the mode representing the youngest age class; standard deviation of a distinct mode; and month in which youngest animals recruit to the population. We estimated initial values for expected number of age classes as varying between 2 and 30 years, and for K as 0.01, 0.05, 0.1, and 0.5/yr. The initial estimate for mean length of the youngest age class was 47 cm, and the initial standard deviation of mode width was estimated as 1.5 cm. Because there was a significant trend in standard deviation of length-at-age with increasing length, this parameter was included in the models reported here. April was designated as the month in which youngest turtles recruit into the population because the April samples had the smallest individuals. The CCL data were combined among years by month so that samples were sufficiently large for length-frequency analyses.

Results

The length-frequency distributions of loggerhead sea turtles within the size range of 46 to 87 cm CCL that stranded from 1988 through 1995 along the Atlantic coast of Florida (n=1234) and along the U.S. coast of the Gulf of Mexico (Gulf coast of Florida, Alabama, Mississippi, Louisiana, and Texas, n=570) are shown in Figures 1 and 2, respectively. The two distributions are significantly different (Kolmogorov-Smirnov test, Z=3.934, P<0.001), although the relative patterns are similar. We assumed that the length-frequency distributions of stranded sea turtles are representative of the length-frequency distributions of sea turtles in the two regions, although there is potential for sampling bias from incidental capture in commercial fisheries.

For loggerhead sea turtles in both the Florida Atlantic and the Gulf of Mexico, the MULTIFAN analysis estimated that the 46 to 87 cm CCL size range comprises 20 year classes (Table 1, Fig. 3). For both geographic regions, visual inspection revealed that the models fit the length-frequency data well (an example is shown in Fig. 4). We were unable to assess annual variation because we combined data for each month from different years owing to small sample sizes. Also, combining data among years

Table 1

Number of age classes (years) in Atlantic loggerhead sea turtle populations within the size range of 46 to 87 cm curved carapace length. Estimates were calculated from von Bertalanffy growth models presented in the referenced studies. Method is type of data (SC=skeletochronology, MR=mark-recapture, LF=length frequency); *n* = sample size.

Location	Number of age classes	*n*	Method	Reference
Chesapeake Bay	13	83	SC	Klinger and Musick, 1995
Cumberland Island, Georgia	11[1]	25[1]	SC	Parham and Zug, 1997
	9[2]	26[2]	SC	Parham and Zug, 1997
Cape Canaveral, Florida	29[3]	51[3]	MR	Schmid, 1995
	26[4]	17[4]	MR	Schmid, 1995
Mosquito Lagoon, Florida	15	28	MR	Frazer and Ehrhart, 1985
Florida, Atlantic Coast	20	1234	LF	This study
Gulf of Mexico	20	570	LF	This study

[1] Based on “1979-new” data set in which correction-factor protocol was used (Parham and Zug, 1997).
[2] Based on “1980” data set in which correction-factor protocol was used (Parham and Zug, 1997).
[3] Based on “all recaptures” data set (Schmid, 1995).
[4] Based on “contract vessel” data set (Schmid, 1995).

could have obscured age-class modes, but because MULTIFAN was able to distinguish modes and the models fitted the data well, this procedure was apparently not a problem.

The von Bertalanffy parameter estimates generated by MULTIFAN for asymptotic length (L_∞) and intrinsic growth rate (K) for the Florida Atlantic were L_∞=118.5 ±0.7 cm and K=0.044 ±0.001/yr and for the Gulf of Mexico were L_∞=113.0 ±0.4 cm and K=0.051 ±0.001/yr. The maximum CCL value recorded for loggerheads nesting in the southeastern United States is 124 cm (Dodd, 1988); therefore the estimates of asymptotic length are reasonable.

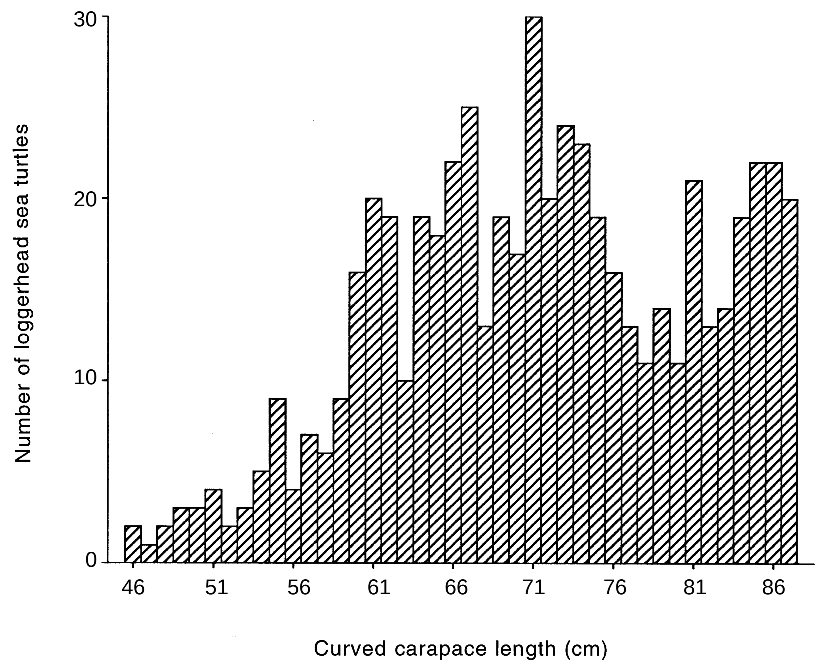

Figure 2

Length-frequency distribution of loggerhead sea turtles stranded along the U.S. coast of the Gulf of Mexico from 1988 through 1995 within the size range of 46 to 87 cm curved carapace length (n=570).

Discussion

Duration of the neritic lifestage

Most loggerhead sea turtles in the North Atlantic recruit to neritic habitats over a size range of 46 to 64 cm CCL (Bjorndal et al., 2000). Size at recruitment will affect duration of the neritic lifestage. From our model, loggerhead sea turtles that recruit at 46 cm CCL will require 20 years to reach 87 cm CCL, whereas those that recruit at 64 cm CCL will require 13 years to grow to 87 cm CCL (Fig. 3). Because loggerhead sea turtles usually remain in neritic habitats after recruiting to these habitats, total duration of the neritic lifestage will include the years subsequent to attaining 87 cm CCL. The demographic ramifications of this variation in size at recruitment should be evaluated.

Other studies have used von Bertalanffy models to evaluate growth in immature loggerhead sea turtles in the Atlantic (Table 1) based on either mark and recapture data (Frazer and Ehrhart, 1985; Schmid, 1995) or skeletochronology data (Klinger and Musick, 1995; Parham and Zug, 1997). Schmid (1995) and Parham and Zug (1997) presented data for a number of data sets and types of calculation. For both studies, the data presented in Table 1 are for the two data sets that Schmid (1995) and Parham and Zug (1997) considered the most representative.

Our estimates of 20 year classes in the size range from 46 to 87 cm CCL fall within the range of values of 9 to 29 years that we calculated from the von Bertalanffy growth equations presented in other studies (Table 1). There is no geographic trend in these estimates.

Von Bertalanffy growth model

MULTIFAN uses a von Bertalanffy growth model as derived by Schnute and Fournier (1980). Concerns about the application of the von Bertalanffy model to sea turtle populations have been discussed elsewhere (Bjorndal and Bolten, 1988; Chaloupka and Musick, 1997). A major concern is the use of the von Bertalanffy model to extrapolate outside the size range of a study (Day and Taylor, 1997), which has been a common practice in estimating age at sexual maturity in sea turtle populations (reviewed in Chaloupka and Musick, 1997). However, within a growth phase that exhibits monotonic decline—that is, for a given size range of a population with similar habitats and diet and that has declining growth rates with increasing body size—the von Bertalanffy model may provide reasonable estimates of growth rates and number of age classes. Green turtles in the southern Bahamas have a monotonic nonlinear declining function for SCL-specific growth rates in a size range of 30 to 70 cm SCL as determined from nonlinear regression of mark-recapture data (Bjorndal et al., 2000). Length-frequency analyses with MULTIFAN yielded the same estimates as the nonlinear regression analysis for growth rates and number of age classes between 30 and 70 cm SCL for that population (Bjorndal et al., 2000). Similar trends of decreasing growth rates with increasing size have been reported from mark-recapture studies in Atlantic loggerhead sea turtles (summarized in Parham and Zug, 1997). In addition, use of the von Bertalanffy model within the studied size range is supported by the similarity between growth rates generated from MULTIFAN and those calculated from recaptures of tagged pelagic-stage loggerhead sea turtles (Bjorndal et al., 2000). As growth data accumulate for sea turtle populations, appropriate growth functions—which may well be polyphasic (Chaloupka and Zug, 1997; Chaloupka, 1998) as a result of habitat shifts—can be incorporated into the length-frequency software.

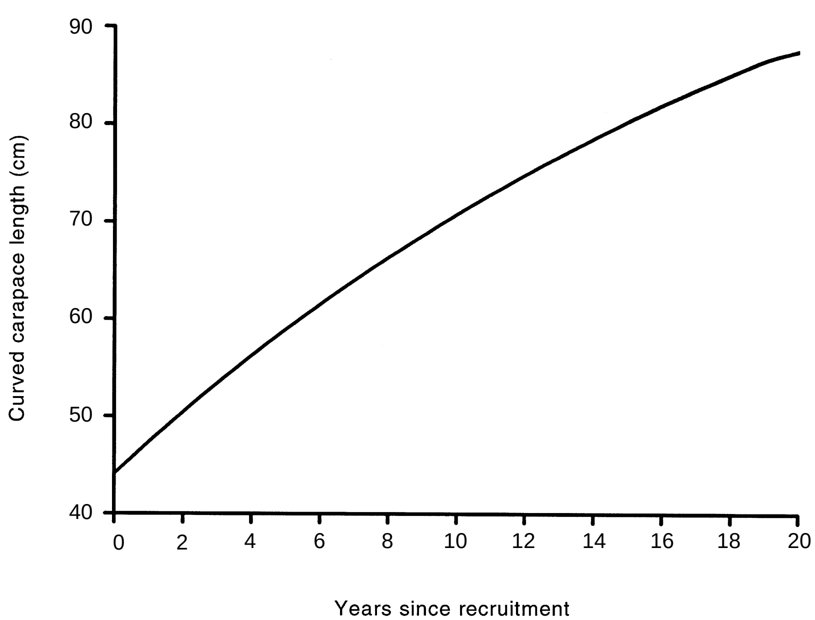

Figure 3

Age-specific von Bertalanffy growth model generated by MULTIFAN for loggerhead sea turtles stranded along the Atlantic coast of Florida from 1988 through 1995 within the size range of 46 to 87-cm curved carapace length. The growth curve for loggerhead sea turtles stranded in the Gulf of Mexico is not plotted because it is indistinguishable from the line plotted for the Atlantic coast of Florida. Age is defined as years since recruitment to neritic habitats at a size of 46 cm curved carapace length.

Age at sexual maturity

An estimate of the number of years to grow to 87 cm CCL may be generated by combining our results (20 year classes between 46 and 87 cm CCL) with those from a growth study in pelagic-stage loggerhead sea turtles in the North Atlantic (Bjorndal et al., 2000). In that study, based on length-frequency analyses and mark-recapture data, the age of loggerheads with a CCL of 46 cm was estimated to be 6.5 years. Therefore, an 87-cm loggerhead sea turtle would be approximately 26.5 years old.

This estimate of 26.5 years at 87 cm CCL should not be used as an estimate of age at sexual maturity. Although we used 87 cm CCL to represent the largest subadult in our study, as explained above, we used a conservative estimate to exclude almost all adults from the sample to avoid obscured modes in the length-frequency distributions. Many loggerhead sea turtles will reach sexual maturity at lengths much greater than 87 cm CCL, and because growth rates are slow in these large subadults, the average age at sexual maturity would be substantially greater than the average age at 87 cm CCL.

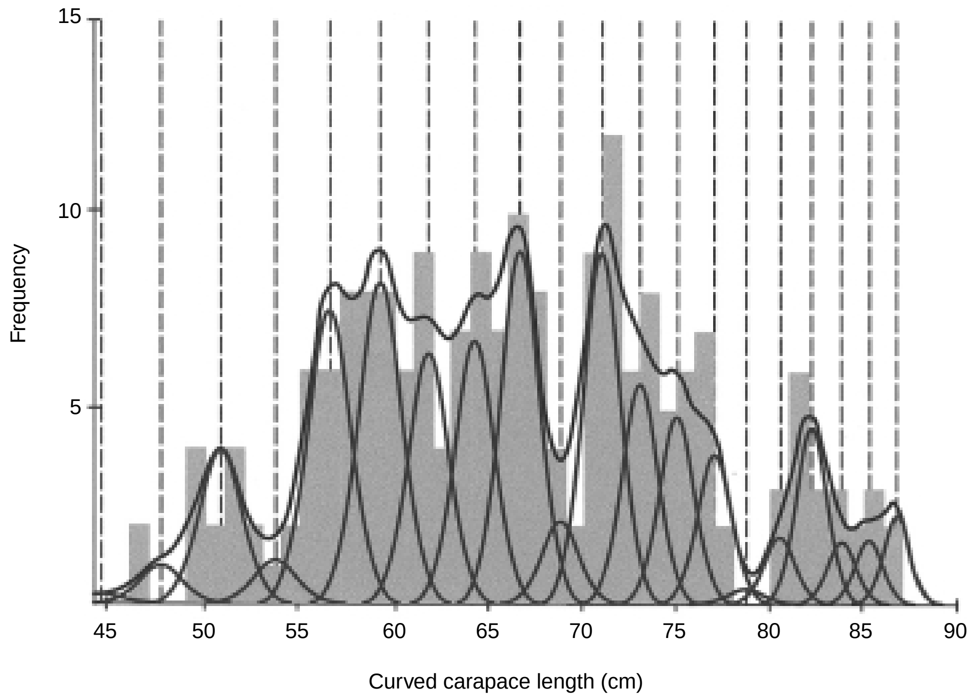

Figure 4

Fit of model to length-frequency data for loggerhead sea turtles stranded along the Atlantic coast of Florida in May (n=203). The dashed vertical lines represent estimated mean lengths-at-age. Both the estimated aggregate (upper line) and the estimated length distribution for each age class are shown. Histogram represents length-frequency data.

Conclusion

With length-frequency analyses, we estimated that growth from 46 to 87 cm CCL in Atlantic loggerhead sea turtles requires 20 years. This estimate falls within the range of estimates of 9 to 29 years that we calculated from other studies based on mark-recapture and skeletochronology. Because survivorship in this size class has been identified as a critical parameter for population recovery (Crouse et al., 1987; Crowder et al., 1994), accurate estimates for the duration of the stage are essential for developing successful management plans. Research must be continued to refine this estimate.

Conservation of loggerhead sea turtles that spend an extended period of time in nearshore habitats prior to reaching sexual maturity is compromised. Numerous and significant threats—including incidental capture in commercial fishing operations, collisions with motorized vessels, dredging operations, exposure to pollutants and biotoxins, and habitat degradation—are present in nearshore developmental habitats. There is a high probability that these turtles will encounter one or more of these threats during their maturation period (National Research Council, 1990; Eckert, 1995; Lutcavage et al., 1997). To be successful, recovery activities must be sustained for long periods of time, and long-term monitoring programs to assess the status of populations of juvenile loggerhead sea turtles in U.S. waters must be established. Because current loggerhead population assessments depend upon the numbers of nesting females or nests, two or more decades must pass before results of recovery activities aimed at the earliest age classes in nearshore waters can be evaluated.

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