

A polyphasic growth function for the endangered Kemp's ridley sea turtle, *Lepidochelys kempii*

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The Kemp's ridley, *Lepidochelys kempii*, is the smallest of the seven extant species of sea turtle (Marquez, 1994) and is endemic to the Gulf of Mexico and Atlantic coast of the United States (Pritchard, 1989). It has been subject to extensive human exploitation and is the most endangered sea turtle species in the world (Marquez, 1994). Seasonal trawl and pound-net fisheries are major hazards, posing a serious risk to the long-term population viability of the Kemp's ridley (Epperly et al., 1995; Caillouet et al., 1996). Although the Kemp's ridley sea turtle is endangered, the somatic growth and population dynamics of this species are not well known (Chaloupka and Musick, 1997) despite several important growth studies that have been carried out for captive or head-started stocks (Caillouet et al., 1986; Caillouet et al., 1995b). We propose a new growth model for the endangered Kemp's ridley sea turtle that is based on a skeletochronological data set derived recently by Zug et al. (1997) from wild stock sea turtles stranded along the Atlantic Bight and Gulf coasts of the United States. The growth model presented provides a basis for improving our understanding of sea turtle growth dy-

namics in general and for modeling Kemp's ridley population viability.

Materials and methods

Data set

The data set used here comprised 70 size-at-age records for Kemp's ridley sea turtles—69 records from stranded turtles plus the inclusion of known mean hatchling size (see Marquez, 1994). The data set ($n=70$) also comprised growth records spanning the postnatal development phase (from 4 to 72 cm straight carapace length, SCL) and including the mature adult phase, but the records were not distributed evenly over this size range. The age estimates were derived from a skeletochronological analysis of wild Kemp's ridley sea turtles stranded along the Atlantic coast of the United States and in the Gulf of Mexico (see Zug et al., 1997). Straight carapace length (SCL) was measured to 0.1 cm and age to 0.1 yr. The original sample of stranded turtles comprised 73 individuals, but age estimates for 4 individuals were not possible because of either 1) a lack of discernible growth rings or 2) uninterpretable irregular

growth. Records for these 4 individuals were discarded, yielding the 69 individual turtles used in this study.

The data set also included stranding location, with 79% of the sample comprising turtles stranded on the Atlantic coast. Sex was recorded for 37% of the strandings; no proportional difference was evident between the Atlantic and Gulf of Mexico subsamples. Further details of the strandings data set and the skeletochronological methods used for age estimation can be found in Zug et al. (1997).

The limitations of skeletochronological ageing techniques and the need for caution in interpreting such age estimates for sea turtles have been well discussed elsewhere (Zug et al., 1986; Zug, 1990; Zug et al., 1997). Chaloupka and Musick (1997) have also provided a critical review of sea turtle skeletochronological studies and have discussed the limitations of such studies in terms of age validation, length back-calculation, growth estimation, layer loss adjustment protocols, and implications of the specific time-dependent sampling design implicit in the data set. For instance, the implicit sampling design in the current study was mixed cross-sectional because only the terminal age-size estimate was available for each of the 69 stranded turtles. This sampling design confounds age and cohort effects and thus only an expected or mean growth function can be estimated (see Chaloupka and Musick, 1997).

Statistical modeling approach

The functional relation between size (cm SCL) and estimated age for the 70 Kemp's ridley sea turtles was modeled with a two-stage approach: 1) exploratory data visualization including nonparametric smoothing (see Cleveland, 1993) to

evaluate the implicit functional form of the growth model without having to specify an explicit and perhaps invalid nonlinear function; and 2) a polyphasic parametric growth function fitted to the size-at-age data on the basis of the functional form implied by the nonparametric smooth. Polyphasic growth means that there is more than one growth phase or cycle in postnatal development, suggesting ontogenetic shifts in growth rates manifested by at least two growth spurts between birth and the onset of adult maturity (see Gasser et al., 1984). The polyphasic growth function used in our study was the Peil and Helwin (1981) parameterization comprising a summation of logistic functions as follows:

$$y_t = \sum_{i=1}^j \left\{ \alpha_i \left[1 + \tanh(\beta_i(t - \delta_i)) \right] \right\} + \varepsilon_{ti} \quad (1)$$

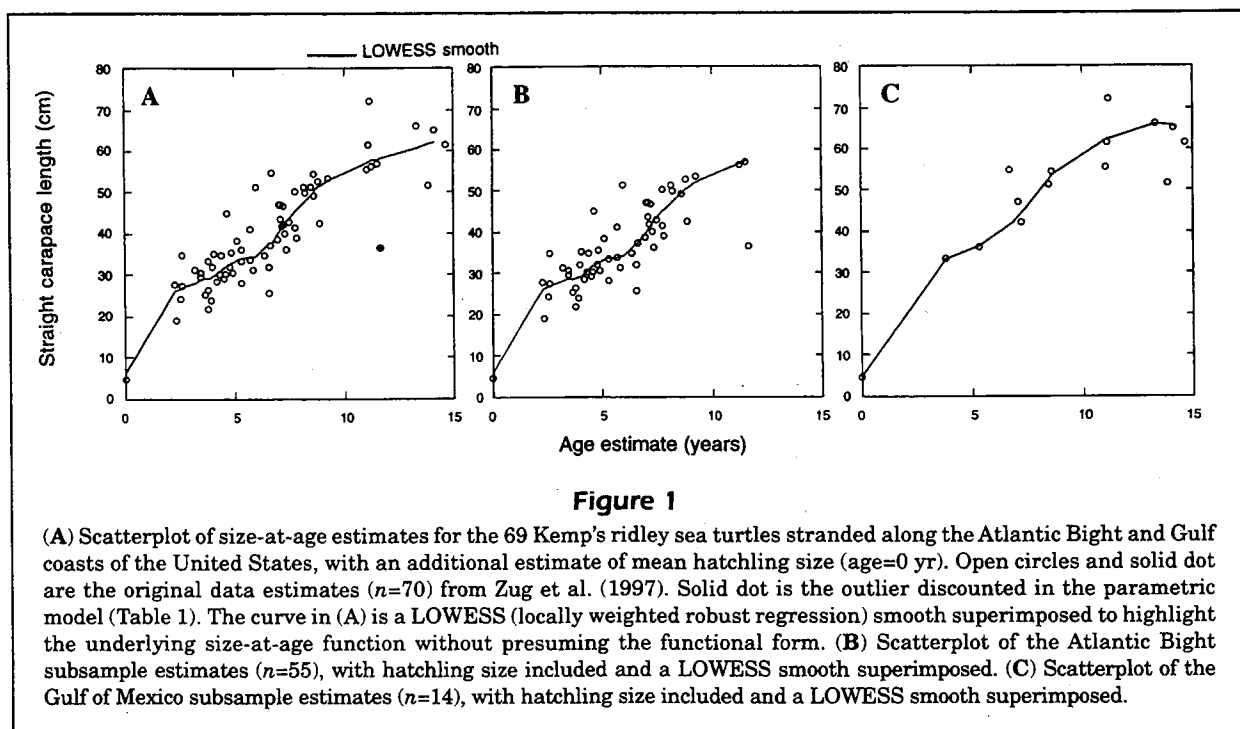
where y_t = mean length at age t ;
 α_i = (asymptotic mean)/ j length in phase i ;
 β_i = growth coefficient in phase i ;
 δ_i = age at the inflection point of phase i ;
 $\tanh(z) = (e^z - e^{-z})/(e^z + e^{-z})$ and $z = (\beta_i(t - \delta_i))$;
 j = number of growth phases; and
 ε_{ti} = an appropriate random error structure.

Parameters of the standard logistic function (monophasic with skewed symmetric inflexion and suggesting one growth spurt) are well known to have excellent statistical properties (Ratkowsky, 1990). It was

assumed that the polyphasic form (Eq. 1) used here also has sound statistical properties. In principle, Equation 1 was fitted by heteroscedasticity-robust nonlinear least-squares (HRNLS) with a heteroscedasticity-consistent covariance matrix estimator (HCCME) to account for growth variability and measurement error (see Davidson and MacKinnon, 1993). In practice, Equation 1 was fitted with RATS (Doan, 1992), which implements HRNLS with White's HCCME. Otherwise, the generalized method of moments (GMM) approach can be used for robust nonlinear regression estimation (Davidson and MacKinnon, 1993). The age-specific growth-rate function for the Kemp's ridley sea turtle was derived analytically by taking the first derivative of the fitted Equation 1 with the software program MATHEMATICA (Wolfram Research, 1993).

Results

The size and estimated age data for the 70 Kemp's ridley sea turtles presented in Zug et al. (in press) are shown in Figure 1A with a locally weighted regression smoothing known as LOWESS (see Cleveland, 1993) superimposed to reveal the implicit functional form. The LOWESS procedure can be implemented by using S software (Becker et al., 1988). The nonparametric smooth (Fig. 1A) implies a polyphasic function with two sequential growth phases, with the first decelerating around 30 cm SCL and the second



at ≥ 60 cm SCL. It is proposed that a polyphasic growth model might be a better mathematical description of growth than the monophasic (monotonic) von Bertalanffy (Caillouet et al., 1995b; Schmid, 1995; Zug et al., 1997) or the monophasic (non-monotonic) Gompertz functions (Caillouet et al., 1986) proposed for this species. A similar polyphasic growth function comprising two phases is also evident for the Atlantic Bight subsample (Fig. 1B) and is suggested for the Gulf subsample (Fig. 1C) despite a very sparse data field in the latter case.

Figure 1 also highlights the considerable variability (heterogeneity) inherent in sea turtle growth and why heteroscedasticity-robust estimation procedures (e.g. HCCME, GMM) should be used to derive regression parameter estimates for growth model fits. There is also a major outlier in Figure 1A indicated by a solid dot—this value was discounted in the explicit parametric model f^+ because no parametric model could be as robust in respect to this outlier as the nonparametric smooth displayed in Figure 1A. Growth variability in sea turtle studies is a complex function of demographic (sex, maturity status) and geographic factors as well as a function of the time-dependent nature of the implicit sampling design (confounding year and cohorts effects) and instrumental measurement error. For instance, Caillouet et al. (1986) have shown conclusive evidence of somatic growth variability due to cohort (year-class) effects for captive reared Kemp's ridley sea turtles. The small sample size, mixed cross-sectional sampling design, and insufficient data on demographic and geographic covariates precluded any reliable estimate of these additional sources of growth record variability in the current study.

The parametric growth curve proposed here to match the nonparametric smooth (Fig. 1A) for the Kemp's ridley data comprises separate logistic growth functions for each of the two inferred growth phases integrated into a single explicit polyphasic function—Equation 1. The statistical fit of this function to the growth data (Fig. 1A) is shown in Table 1. The growth model with robust estimation and with elimination of the extreme outlier (see Fig. 1A) fitted the data well with significant parameter estimates even allowing for family-wise error-rate adjustment, small parameter estimate standard errors, and no aberrant residual behavior (see Judge et al., 1985, or Ratkowsky, 1990, for a discussion of nonlinear regression fitting and goodness-of-fit criteria). Despite the good fit, significant growth variability, probably due to instrumental measurement error and confounding of year and cohort sampling effects, was not accounted for by the model (residual variance: $\sigma^2=29.1$).

Table 1

Parameter estimates for the polyphasic logistic growth function (Eq. 1) fitted to the Kemp's ridley sea turtle size-at-age growth data in Zug et al. (1997). See Equation 1 for definitions of parameters.

Parameter	Estimate	Asymptotic		Inference
		standard error	<i>t</i> -ratio	
α_1	13.6467	2.7463	4.97	$P < 0.001$
β_1	0.7901	0.2989	2.64	$P < 0.008$
δ_1	1.1169	0.4303	2.59	$P < 0.009$
α_2	17.6595	3.9288	4.49	$P < 0.001$
β_2	0.3059	0.1274	2.40	$P < 0.016$
δ_2	7.6361	0.5407	14.12	$P < 0.001$

The expected polyphasic size-at-age function is shown in Figure 2A (age=skeletochronological age estimate) and presented numerically in Table 2 for comparative purposes. The explicit size-at-age growth function (Fig. 2A) was then differentiated with respect to estimated age by an analytical solution to Equation 1 to derive the age-specific growth rate function (Fig. 2B). The expected age-specific growth rate function (Fig. 2B) displays an initial posthatchling growth rate >5 cm SCL/year, increasing to 11 cm SCL/year ≥ 1 year of age (Δ_1) or 13 cm SCL, slowing to 2 cm SCL/year by 3–4 years of age (ca. 27 cm SCL), marking the end of the first growth phase (i.e. $2\alpha_1=27.3$ in Table 1; mid-curve asymptote in Figs. 1A and 2A). The growth rate then rises to 6 cm SCL/year near 8 years of age (δ_2) or to 46 cm SCL before declining slowly to negligible growth approaching adulthood ≥ 15 years of age at a size ≥ 62 cm SCL, marking the end of the second growth phase (i.e. $2(\alpha_1+\alpha_2)=62.6$ in Table 1; upper asymptote in Figs. 1A and 2A).

Discussion

Monophasic von Bertalanffy growth functions have been proposed for the Kemp's ridley sea turtle by Caillouet et al. (1995b), Schmid (1995), Zug et al., (1997), and others (Marquez, 1994, and references therein). With the von Bertalanffy growth function, however, a monotonic decreasing growth-rate function is implied and hence no growth spurt at any age or size. The statistical validity of that function fitted to a limited data span and of the Fabens mark-recapture analogue used by Schmid (1995) and Zug et al. (1997) has been reviewed critically by Chaloupka and Musick (1997). It is questionable whether a monophasic von Bertalanffy function fits the mean growth profile for the complete postnatal

Table 2

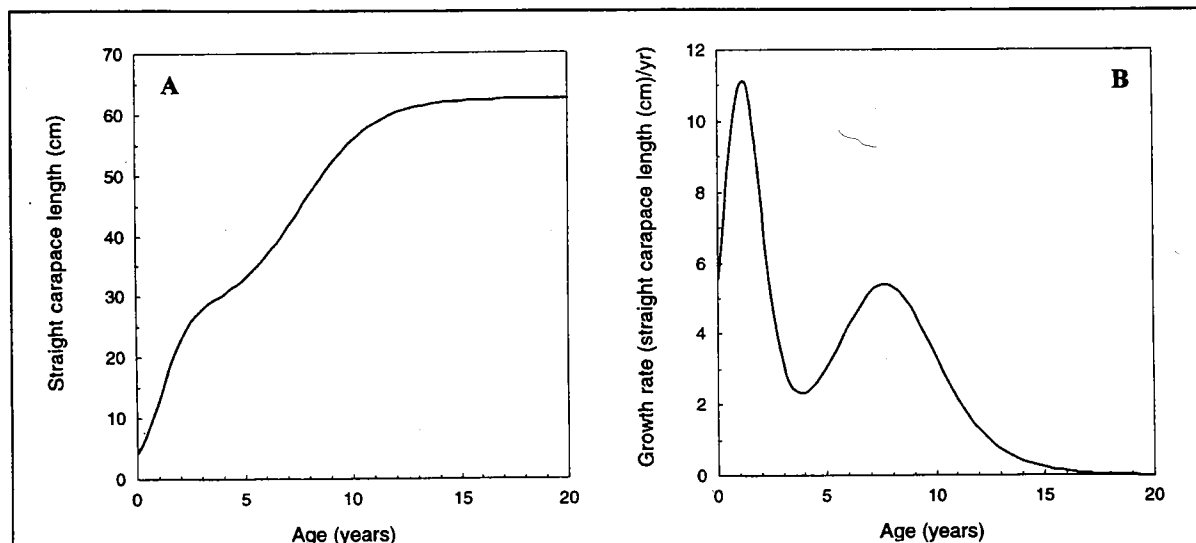
Comparison of size-at-age growth functions for three Kemp's ridley sea turtle growth models. Age = known age for the Caillouet et al. (1995b) model, whereas age = skeletochronological age estimate for the Zug et al. (1997) model and the polyphasic model presented here. SCL = straight carapace length.

Age (years)	Size-at-age estimate (cm SCL)			Age (years)	Size-at-age estimate (cm SCL)		
	Caillouet et al. (1995b)	Zug et al. (1997)	This study (Fig. 2A)		Caillouet et al. (1995b)	Zug et al. (1997)	This study (Fig. 2A)
0 (hatchling)	2.79	8.86	4.32	13	61.30	59.49	61.33
1	18.95	14.85	12.99	14	61.57	61.63	61.91
2	30.72	20.39	22.96	15	61.76	63.62	62.23
3	39.29	25.50	27.93	16	61.90	65.45	62.40
4	45.53	30.23	30.46	17	62.00	67.14	62.50
5	50.08	34.60	33.11	18	62.07	68.70	62.55
6	53.39	38.63	36.77	19	62.13	70.15	62.58
7	55.80	42.36	41.56	20	62.17	71.48	62.59
8	57.56	45.81	46.91	21	62.19	72.72	62.60
9	58.84	48.99	51.92	22	62.21	73.86	62.61
10	59.77	51.94	55.88	23	62.23	74.91	62.61
11	60.45	54.65	58.61	24	62.24	75.89	62.61
12	60.94	57.17	60.32	25	62.25	76.79	62.61

development phase of any sea turtle species (see Chaloupka and Limpus, 1997; Chaloupka and Musick, 1997).

On the other hand, the monophasic form of the Gompertz growth function used by Caillouet et al., (1986) in a single cohort growth study (weight gain) of 10 Kemp's ridley sea turtles held in captivity

clearly fitted the data well at least for the observed range (ca. 2–7 years old). In the Gompertz function, a nonmonotonic growth-rate function is assumed with a growth spurt in early development similar to the first growth spurt in our study (see Fig. 2B). Whether growth in Caillouet et al.'s (1986) study might have been better fitted by using a polyphasic

**Figure 2**

(A) Kemp's ridley sea turtle size (SCL cm) plotted as a function of the correction-factor age estimates derived from Zug et al. (1997). Solid curve shows the polyphasic logistic growth Equation 1 fitted to the growth data shown in Figure 1A, excluding the single outlier. (B) The age-specific growth-rate function for the Kemp's ridley sea turtle growth function shown in Panel A represented by the first derivative of Equation 1, which is $y'_{(t)} = \sum (\alpha_i \beta_i \text{sech}^2(\beta_i(t - \delta_i)))$ with the same parameters defined for Equation 1 and with sech (hyperbolic secant) = $(1 - \tanh)$.

function is inconclusive because the data span was incomplete, missing not only the first growth cycle (if it occurred at all) but also the onset of adult maturation. By the end of the study the remaining 8 turtles were still growing and below estimates of adult size (weight) recorded for wild stocks. Moreover, growth in captivity might well bear little similarity to the growth dynamics of wild stock Kemp's ridley sea turtles, which seem to grow much slower at a given size (Caillouet et al., 1986).

The nonparametric smooth shown here in Figure 1A fitted to a more complete age and size range for wild stock Kemp's ridley sea turtles implied that growth comprised two consecutive phases and that an explicit polyphasic model (Table 1; Fig. 2) might be a better parametric description of growth than monophasic models proposed previously for this species. Nonetheless, two major cautions are warranted prior to drawing further conclusions from Figure 2 about Kemp's ridley growth dynamics. These cautions relate to the implications for growth inferences due to 1) data sparsity in the early growth years for this data set and 2) the size composition anomaly between stranding subsamples for this data set.

The data were sparse in the lower region of the first inferred growth spurt (see Fig. 1). The growth-layer loss protocols used in deriving the skeleto-chronological age estimates provided differing coverage of this growth region (see Zug et al., 1997). The age estimates used in our study were based on the correction-factor protocol that was considered more reliable than ranking protocol estimates (Zug et al., 1997) despite providing no coverage of the first growth year except for hatchling size. The model that was fitted (Fig. 2A) interpolated between known hatchling age and the end of the first year on the basis of the explicit form implied by the specified parametric function (Eq. 1). Although the conclusion of the first growth phase completed by ca. 25–30 cm SCL (see Fig. 1A) is firm despite sparse data during early growth, a specific growth spurt ≥ 1 year of age is tenuous. Given the lack of data during the first year, maximum growth might just as feasibly occur immediately following hatching, resulting in a monotonic decreasing age-specific growth-rate function for the first cycle and not the nonmonotonic function seen in Figure 2B. On the other hand, a growth spurt might occur a little later after hatching, resulting in a nonmonotonic age-specific growth-rate function for the first cycle similar to that proposed in Figure 2B but with the spurt occurring at say 3 or 6 months rather than at 12 months of age. Because of a sparsity of data during the early growth years, all these growth scenarios for the first growth cycle are feasible; therefore data for the first 12 months of life

following hatchling dispersal from the nesting beach are essential to resolve this important issue.

Nonetheless, other sources of information corroborate the growth profile proposed for the first phase in Figure 2B. First, the polyphasic function described by Equation 1 fitted the growth data well, including an estimated mean adult size (upper asymptote = $2(\alpha_1 + \alpha_2) = 62.6$ cm SCL from Table 1) consistent with empirical estimates of mean nesting female size of 64–65 cm SCL (Marquez, 1994). Moreover, the polyphasic function also predicted a mean hatchling size of 4.3 cm, which is consistent with the empirical estimate of mean hatchling size of 4.4 cm (Marquez, 1994). No other growth model has come close to predicting both the mean upper and lower size asymptotes of the postnatal development phase for the Kemp's ridley sea turtle. It is worth noting here that it is a common misconception in growth studies (particularly sea turtle growth studies) involving more than one animal that the upper asymptote of a parametric growth function estimates maximum adult size rather than the correct interpretation of mean adult size (see Ricker, 1979).

Second, a growth spurt ≥ 12 months of age and a growth phase completed by ca. 27 cm SCL (30–36 months of age) is coincident with developmental changes to the blood oxygen system of the Kemp's ridley sea turtle prior to acquisition of an adult blood system by 28 months of age (see Davis, 1991)—at least this was the case for captive-reared Kemp's ridley sea turtles. Davis (1991) also found that the oxygen capacity of the blood had increased substantially during the first 12 months of growth. The size range and timing of the first growth cycle is also consistent with apparent dietary and habitat shifts around 20 cm SCL (ca. 18 months of age; Fig. 2A; Eq. 1) from a presumed epipelagic habit to a coastal benthic habit (see Shaver 1991; Burke et al., 1994; Musick and Limpus, 1997).

The second major caution relates to a lack of informative cofactors (sex, geographic subsample) being included in the model because of insufficient records or small subsamples. For instance, sex was recorded for only 37% of the strandings, whereas the Atlantic coast subsample (cf. Gulf coast) accounted for 79% of the strandings data (see Fig. 1, B and C). Moreover, the Atlantic subsample comprised a significantly different size composition compared with that of the Gulf of Mexico (see Fig. 3). The apparent size composition anomaly might be due to 1) differential and inadequate spatial sampling of strandings and 2) developmental migration of Kemp's ridley sea turtles ≥ 40 cm SCL from the Atlantic coast to the Gulf of Mexico (see Collard and Ogren, 1990; Morreale et al., 1992; Epperly et al., 1995; Musick and Limpus,

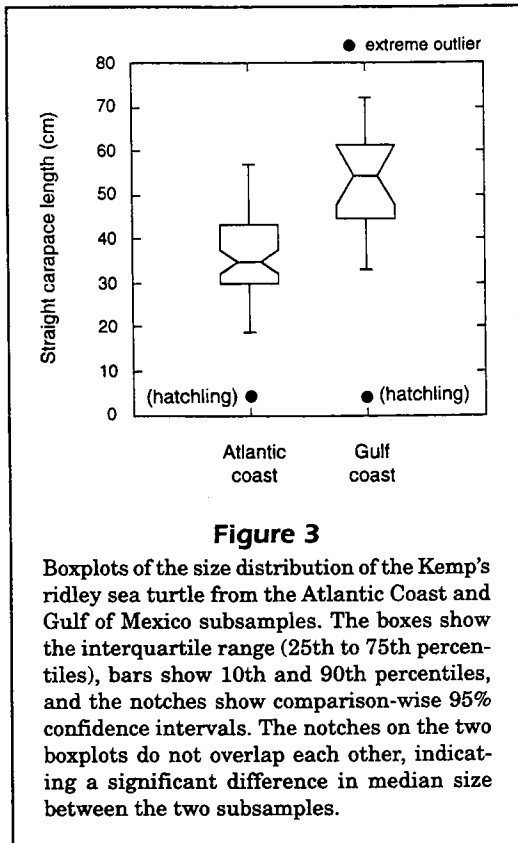


Figure 3

Boxplots of the size distribution of the Kemp's ridley sea turtle from the Atlantic Coast and Gulf of Mexico subsamples. The boxes show the interquartile range (25th to 75th percentiles), bars show 10th and 90th percentiles, and the notches show comparison-wise 95% confidence intervals. The notches on the two boxplots do not overlap each other, indicating a significant difference in median size between the two subsamples.

1997). If the Atlantic and Gulf coast subsamples in the Zug et al., (1997) data set represent two discrete populations with population-specific growth behaviors, then the growth model here (Table 1; Fig. 2) is applicable to the Atlantic group only although a similar polyphasic model is apparent for both subsamples despite a sparsity of data for the ≥ 50 cm SCL group of the Atlantic subsample (Fig. 1B) and ≤ 40 cm SCL group of the Gulf subsample (Fig. 1C). The inclusion of the Gulf subsample serves to provide sufficient data to derive the upper asymptote for estimating mean adult size (see Fig. 1C). The Atlantic subsample comprised only immature Kemp's ridley sea turtles consistent with recorded size distributions for populations resident in various habitats along the US Atlantic coast (see Burke et al., 1994, Epperly et al., 1995; Schmid, 1995).

If the Zug et al. (1997) data set is representative of a single panmictic interbreeding stock displaying some form of staged developmental migration, then the model presented here is a reasonable approximation of the growth dynamics of the endangered Kemp's ridley sea turtle. There is compelling support for this view given current knowledge of Kemp's ridley sea turtle movement patterns (Musick and Limpus, 1997). Further support comes from the dis-

covery of a Kemp's ridley sea turtle (70 cm CCL, 67 cm SCL) nesting at Rancho Nuevo in 1996 (116 eggs laid) that had been tagged as a juvenile (51 cm CCL, 49 cm SCL) seven years earlier in Chesapeake Bay (Musick¹). Growth for this nesting ridley was consistent with the polyphasic growth function (Fig. 2A) although clearly a single record is not sufficient to provide conclusive evidence. Nonetheless, if the Atlantic and Gulf subsamples represent a single panmictic interbreeding stock, then a juvenile growth spurt at 46 cm SCL (ca. 8 years old, Fig. 2B) would indicate an ontogenetic shift associated with developmental migration from juvenile foraging habitats in the South Atlantic Bight (Musick and Limpus, 1997) and from within the Gulf of Mexico (Collard and Ogren, 1990) to foraging grounds in habitats along the Gulf coast prior to the onset of sexual maturity.

It is also conceivable, given the dispersal scenarios proposed by Collard and Ogren (1990), that the Kemp's ridley sea turtle is a single panmictic interbreeding stock that comprises two distinct post-hatchling developmental groups. One group remains within the Gulf of Mexico displaying relatively rapid growth owing to the warmer water (see Caillouet et al., 1995b). The second group represents the posthatchlings swept from the Gulf of Mexico that settle as juveniles (ca. 20 cm SCL) in the inshore developmental habitats of the mid-Atlantic (Morreale et al., 1992; Burke et al., 1994) and South Atlantic Bights (Epperly et al., 1995; Schmid, 1995). In this case the polyphasic growth model presented here (Table 1; Fig. 2) would be applicable to describing the mean stochastic growth dynamics of the cohorts swept each year from the Gulf of Mexico and undergoing growth in the Atlantic Bights prior to migrating back to the Gulf of Mexico. A separate growth model would need to be derived for the Gulf of Mexico developmental group although polyphasic growth behavior is also apparent for that subsample in our study (see Fig. 1C).

Clearly, a better understanding of the dispersal and developmental dynamics of the Kemp's ridley sea turtle based on a mark-recapture program with a high recapture likelihood is needed to resolve these complex issues. Although several local tagging programs have been undertaken (e.g. Caillouet et al., 1995a; Schmid, 1995; Burke et al., 1994, and references therein) a more comprehensive spatial and sampling-intensive program spanning the distributional range of this species is needed.

¹ Musick, J. 1997. Virginia Institute of Marine Science, College of William and Mary, Gloucester Point, VA. Personal commun.

Meanwhile, it is common practice to use somatic growth functions to estimate mean age at sexual maturity. The difficulty in using growth functions for this purpose is that there are no conclusive growth criteria to indicate onset of sexual maturity. Minimum or mean female nesting size, or an arbitrary size set slightly below mean nesting size, is a commonly used criterion. Using an arbitrary size criterion based on reasonable biological considerations, Caillouet et al., (1995b) proposed that head-started Kemp's ridley sea turtles irrespective of sex, took 10 years to reach sexual maturity at ca. 60 cm SCL. Zug et al. (1997) estimated 11–16 years for age-at-maturity for wild stock Kemp's ridley sea turtles on the basis of mean female nesting size. The upper asymptote of a parametric growth function is the correct estimate of mean adult size, if the correct growth function was used (see Ricker, 1979). By using the upper asymptote metric, it is then apparent that sexual maturity could be reached at ≥ 20 years of age for the current study (see Fig. 2B; Table 2) compared with 30 years of age for the Caillouet et al. (1995b) growth function (see Table 2).

But as Caillouet et al., (1995b) point out, mean adult size (nesting females) is a questionable criterion for estimating age at sexual maturity. That is why Caillouet et al. (1995b) defined an arbitrary size criterion to estimate age-at-maturity. However, the correct function for estimating mean age at maturity is an age-specific maturity-rate function conditioned on time-varying age, year, and cohort effects derived from a mixed longitudinal sampling study (see Chaloupka and Musick, 1997, for time-dependent demographic sampling issues). In the absence of such a complex function, a useful growth criterion for estimating age-at-maturity might be negligible growth derived from the age-specific growth-rate function indicating the onset of maturity. It is increasingly apparent that growth for sea turtles becomes negligible approaching the onset of sexual maturity (see Chaloupka and Limpus, 1997). Although this is a study-dependent and subjective metric, it is clear that negligible growth in the current study occurs ≥ 15 years of age or ≤ 0.25 cm SCL/year (see Fig. 2B and Table 2). Growth was imperceptible by 21 years of age (Table 2); thus the age range of 15–20 years appears to be a reasonable interval estimate of expected age at sexual maturity for the Kemp's ridley sea turtle.

It is therefore noteworthy that the Kemp's ridley sea turtle tagged in Chesapeake Bay as a juvenile (ca. 49 cm SCL) and discovered nesting seven years later at Rancho Nuevo (see "Discussion" above) was estimated by reference to Figure 2 to be about 9 years old when tagged and therefore 16 years old at the

first recorded nesting. The nesting turtle was ca. 67 cm SCL, which is larger than the estimated upper asymptote of ca. 63 cm SCL (Table 1: $2(\alpha_1 + \alpha_2)$ cm SCL). Recall, however, that the upper asymptote here represents mean adult size (or mean nesting size, assuming growth is not sex-specific); therefore 50% of a random sample of adult or nesting Kemp's ridley sea turtles would be >63 cm SCL, whereas 50% of the sample would be smaller.

Despite sampling design constraints, cautions about skeletochronological methods, small sample size, and perhaps nonequivalent geographic subsamples, the data set presented in Zug et al. (1997) is of considerable importance for helping to improve our understanding of the growth dynamics of the endangered Kemp's ridley sea turtle. The re-analysis of these data with exploratory nonparametric smoothing suggested that expected age-specific growth for the Kemp's ridley sea turtle was polyphasic and could be modeled with a sequence of parametric curves. A parametric model comprising a summation of logistic functions fitted the data well, implying growth spurts at ≥ 1 year of age (mean size=13 cm SCL) and ca. 8 years of age (mean size=46 cm SCL) followed by negligible growth approaching the onset of maturity ca. 15–20 years of age (mean size=63 cm SCL). Polyphasic growth behavior is therefore one of many reasons why a monophasic growth function cannot fit the entire postnatal developmental phase of the Kemp's ridley sea turtle, let alone for any other sea turtle species (see Chaloupka and Musick, 1997).

Acknowledgments

We thank members of the USA sea turtle stranding network for collection of skeletal material and Heather Kalb and Stephen Luzar for processing skeletochronological data. We are grateful for the Smithsonian Research Opportunities Fund that provided support of the skeletochronological work being undertaken by George Zug. We thank Charles Caillouet, Col Limpus, Jack Musick, and the anonymous referees for helpful comments on the manuscript.

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