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Age and Growth of Wild Kemp's Ridley Turtles (*Lepidochelys kempi*): Cumulative Results of Tagging Studies in Florida

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ABSTRACT. – Subadult Kemp's ridley turtles (*Lepidochelys kempi*) were captured and tagged at Cape Canaveral, Florida, from 1986 to 1991 ($n = 113$) and at Cedar Key, Florida, from 1986 to 1995 ($n = 251$). Subsequent recapture data at Cape Canaveral ($n = 12$) and Cedar Key ($n = 24$) were combined and von Bertalanffy growth equations were fitted with respect to recapture interval duration. Asymptotic carapace length was either underestimated (Cape Canaveral) or overestimated (Cedar Key) for each source database when compared to the known mean length of nesting females. Differences in asymptotic length estimates were attributed to differences in intrinsic growth rates and the inverse correlation of these two parameters. The von Bertalanffy equation for all recaptures in the combined database yielded age to maturity estimates between 8 and 13 years, based on the minimum and mean carapace lengths of nesting Kemp's ridley turtles. A duration of approximately 8–9 years was calculated for the coastal-benthic, subadult stage of development. Recapture data for adult-size turtles are needed to increase the precision of Kemp's ridley turtle growth models.

KEY WORDS. – Reptilia; Testudines; Cheloniidae; *Lepidochelys kempi*; sea turtle; demography; growth; age; maturity; growth models; Florida; USA

Age and growth are important parameters when constructing demographic models of protected species. Unfortunately, marine turtle biologists have been hindered by their inability to accurately estimate turtle growth because of the lack of verifiable aging techniques. Fabens (1965) helped resolve the problem by developing a method of fitting tag and recapture data to the nonlinear von Bertalanffy growth model. This method has been used successfully for fish (Ricker, 1975) and was first applied to marine turtle growth by Witzell (1980). Since then, von Bertalanffy models have been developed for captive loggerhead turtles, *Caretta caretta*, (Frazer and Schwartz, 1984), as well as wild green, *Chelonia mydas*, and loggerhead turtles (Frazer and Ehrhart, 1985; Frazer and Ladner, 1986; Bjorndal and Bolten, 1988a, 1988b; Boulon and Frazer, 1990; Schmid, 1995), and head-started Kemp's ridley turtles, *Lepidochelys kempi*, after release (Caillouet et al., 1995). Studies comparing marine turtle growth models have indicated that the von Bertalanffy equation provides a better fit than the logistic or Gompertz equations (Frazer and Ehrhart, 1985; Bjorndal and Bolten, 1988a, 1988b; Caillouet et al., 1995). Growth models have also been developed using skeletochronological data derived from wild Kemp's ridleys (Zug and Kalb, 1989; Zug, 1990; Zug et al., 1997), loggerhead turtles (Klinger and Musick, 1995), and from length-frequency analysis of green turtles (Bjorndal et al., 1995).

There is little published information concerning the population dynamics of the critically endangered Kemp's ridley turtle. Conservation efforts have focused on females nesting at Rancho Nuevo, Mexico, and an apparent increase in number of nests has been observed during recent years (Márquez et al., 1996). There are also indications that coastal aggregations of subadult turtles may be increasing as a result of nesting beach protection (Ogren, 1989; Schmid, in press). Important demographic parameters such as growth rate and age at maturity remain unresolved, however, and have been identified as high research priorities necessary to recover the severely threatened ridley population (National Research Council, 1990; U.S. Fish and Wildlife Service and National Marine Fisheries Service, 1992). Mean annual growth rates of Kemp's ridley turtles have been analyzed with respect to recapture interval duration, seasonal variation, and size classes (Schmid, 1995; in press). The von Bertalanffy growth equation has been used to estimate age to maturity for other species of marine turtles (Frazer and Ehrhart, 1985; Frazer and Ladner, 1986). Zug and Kalb (1989), Zug (1990), and Schmid (1995; in press) prepared von Bertalanffy growth models for wild, subadult Kemp's ridley turtles, but the range of carapace lengths and sample sizes for these studies were insufficient to accurately describe growth parameters. Zug et al. (1997) recently refined their skeletochronological growth model by increasing the sample and the size range of turtles. Caillouet et al. (1995) provided a growth model for head-started Kemp's ridley turtles released off the Texas coast and subsequently recaptured in the Gulf of Mexico. The present paper summarizes the results of von Bertalanffy growth models for Kemp's ridley turtles using the combined data from Schmid's tagging studies on the east and west coasts of Florida.

MATERIALS AND METHODS

The Kemp's ridley turtle mark-recapture data used in this analysis were collected from two separate surveys located at Cape Canaveral, eastern Florida (Atlantic Ocean) and Cedar Key, western Florida (Gulf of Mexico). Both tagging studies were conducted as part of the NMFS Miami Laboratory Cooperative Marine Turtle Tagging Program. Turtles at Cape Canaveral were captured in standard commercial shrimp trawl nets between 1986 and 1991 (Schmid, 1995). Turtles at Cedar Key were captured in large-mesh tangle nets between 1986 and 1995 (Ogren, 1989; Schmid and Ogren, 1990, 1992; Schmid, in press). All captured turtles were double tagged on the trailing edge of the fore flippers with #681 Inconel cattle ear tags. Tagging information included: tag codes, turtle species, date, location, latitude and longitude, water depth, gear type, standard straight-line carapace length (SCL; nuchal notch to posterior end of postcentral scute; Pritchard et al., 1983), straight-line carapace width, and weight. Length and width were measured to the nearest 0.1 inch with calipers and weight to the nearest 0.25 lbs with a spring scale; measurements were converted to metric units for analysis. The turtles sampled at Cape Canaveral were measured and tagged by the captain of a commercial shrimp vessel, who also measured 10 of the 12 recaptures. The remaining two recaptures were measured by stranding network volunteers. Turtles in the Cedar Key study were measured both initially and upon recapture by JRS.

The Cape Canaveral and Cedar Key populations were compared in terms of mean SCL and length frequency distribution for captured and recaptured turtles. Nonparametric statistical procedures were used when the assumptions of parametric procedures were violated. Regression equations for the carapace width to length

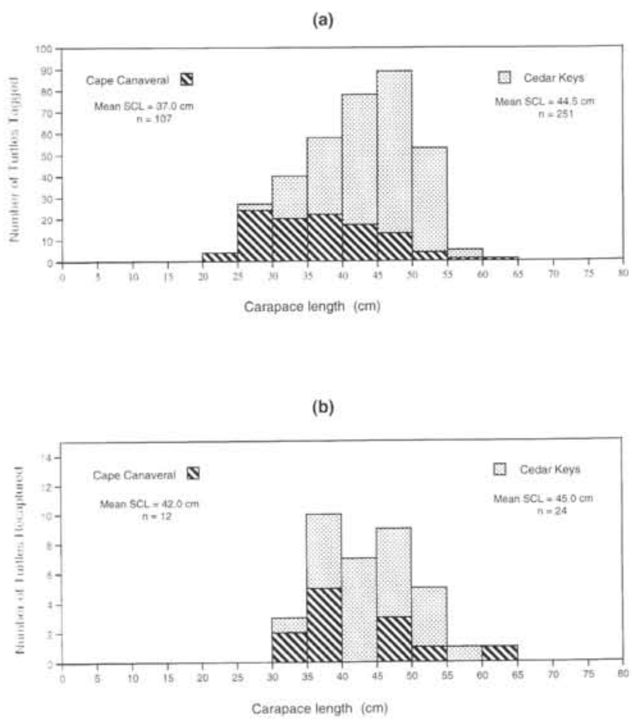


Figure 1. Carapace length frequency distributions of Kemp's ridley turtles at **(a)** initial capture and **(b)** recapture for Cape Canaveral and Cedar Key, Florida.

and weight to length relationships of turtles captured at each location were compared using a single multiple regression model and multiple-partial F tests (Kleinbaum et al., 1988).

The von Bertalanffy growth equation is generally expressed as:

$$\mathbf{L_t = a(1 - be^{-kt})} \qquad [1]$$

where $\mathbf{L_t}$ is length at age t, **a** is asymptotic length, **b** is a parameter related to size at hatching, **k** is the intrinsic growth rate, and **t** is age. The von Bertalanffy growth interval equation was modified by Fabens (1965) in order to estimate growth parameters of animals of unknown age based on recapture data. The Fabens growth equation is:

$$\mathbf{L_r = a - (a - L_c)e^{-kd}} \qquad [2]$$

where $\mathbf{L_r}$ is the length at recapture, **a** is asymptotic length, $\mathbf{L_c}$ is the length at first capture, **k** is the intrinsic growth rate, and **d** is the time interval between captures. The growth interval equation was fitted to the Kemp's ridley turtle recapture data with a non-linear least-squares regression procedure (SAS, 1989). The Fabens equation does not contain an estimate of **b**, which is necessary to complete the von Bertalanffy model. This parameter was estimated using equation 1 simplified to:

$$\mathbf{b = 1 - L_0/a} \qquad [3]$$

where $\mathbf{L_0}$ is the mean hatchling carapace length of 4.4 cm (Márquez, 1994) at age 0 years. Growth models were constructed using different intervals of time between tag and recapture, in order to minimize the effects of measurement errors on short-term recaptures. Samples and subsamples analyzed included: all recapture data combined, all recaptures over 90 days, and all recaptures over 180 days.

Both the minimum and mean carapace lengths of nesting Kemp's ridley turtles were used as estimates of carapace length at maturity. Length data for nesting females at Rancho Nuevo were summarized in Burchfield et al. (1988) in terms of total curved carapace length (TCCL; nuchal tip to postcentral tip). Curved length data were converted to SCL with the following regression equation based on a sample of Kemp's ridley turtles measured by WNW: SCL = 4.0554 + 0.8662 $*$ TCCL ($r^2 = 0.92$; $n = 46$). Using this conversion, a mean SCL of 64.2 cm (range 56.0–72.5 cm; $n = 468$) was calculated for nesting Kemp's ridley turtles.

RESULTS AND DISCUSSION

One hundred and thirteen Kemp's ridley turtles were captured and tagged at Cape Canaveral with 12 turtles measured upon recapture or recovery. Two hundred and fifty-one turtles were captured and tagged at Cedar Key with 24 turtles subsequently recaptured. Mean carapace lengths were significantly different for captured turtles in the two areas ($\chi^2 = 61.51$, df = 1, $p = 0.0001$; Fig. 1a), but not for recaptured turtles ($\chi^2 = 2.28$, df = 1, $p = 0.1307$; Fig. 1b). Tests of coincident regression lines were non-significant for the carapace width to length relationship (F = 1.93, p = 0.1462) and the log-transformed weight to length relationship (F = 1.04, p = 0.3532), indicating that the morphometric relationships for turtles captured at Cape Canaveral and at Cedar Key were similar. The two samples were combined into a single database and regression equations were calculated for carapace width (CW) on length (SCL): CW = –3.0409 + 1.0377 * SCL, $r^2 = 0.99$, $n = 331$; and log-transformed weight (WGHT) on length: ln WGHT = –8.2694 + 2.8418 * ln SCL, $r^2 = 0.99$, $n = 313$.

Using the recapture interval data treatments described earlier, Schmid (1995, in press) provided von Bertalanffy growth parameters for Kemp's ridley turtles at Cape Canaveral and Cedar Key (Table 1). Frazer et al. (1990) suggested that biologically realistic estimates of asymptotic length should be slightly larger than the mean length of the adult population. The asymptotic lengths for the Florida populations were either underestimated (Cape Canaveral) or overestimated (Cedar Key) when compared to the known mean length of nesting females. There were also profound differences in the intrinsic growth rates and the standard error of the estimates between these two data sets (Table 1). These differences can be caused by a variety of factors, both artificial and natural. Small sample sizes with narrow length frequency distributions, combined with possible differences in annual growth within and between sample sets, would certainly affect the growth parameters of the models. Annual growth rates for the recapture data treatments were, in fact, different between the data sets with the Cape Canaveral group ranging from 5.9–8.8 cm/yr and the Cedar Key group ranging from 3.6–5.4 cm/yr. Consequently, all these factors combined may have resulted in inadequate growth models for the individual Cape Canaveral or Cedar Key data sets.

The Cape Canaveral and Cedar Key recapture data were subsequently merged and von Bertalanffy growth parameters were calculated for each data treatment (Table 1). With the exception of recaptures greater than 180 days, the resultant estimates of asymptotic length and intrinsic growth rate were intermediate to the source databases. The standard errors for these growth parameters were fairly large, indicating a lack of precision for the estimates. The model for all recaptures combined had the lowest residual mean square error for the combined database (Table 1) and was therefore considered the most appropriate growth model (Dunham, 1978). The fitted von Bertalanffy growth equation for all recaptures combined was:

$$\mathbf{L_t = 80.0\ (1 - 0.9450e^{-0.1292t})} \qquad [4]$$

This model also provided the smallest estimate of asymptotic length (80.0 cm SCL) for the combined database. This value seems rather large when compared to the mean size of nesting Kemp's ridley females. However, since this estimate is only slightly larger than the maximum size observed at Rancho Nuevo, Mexico (72.5 cm converted SCL; Burchfield et al., 1988), it does not appear to be a gross overestimate of the "largest average size" (Knight, 1968; Boulon and Frazer, 1990) attained by this species.

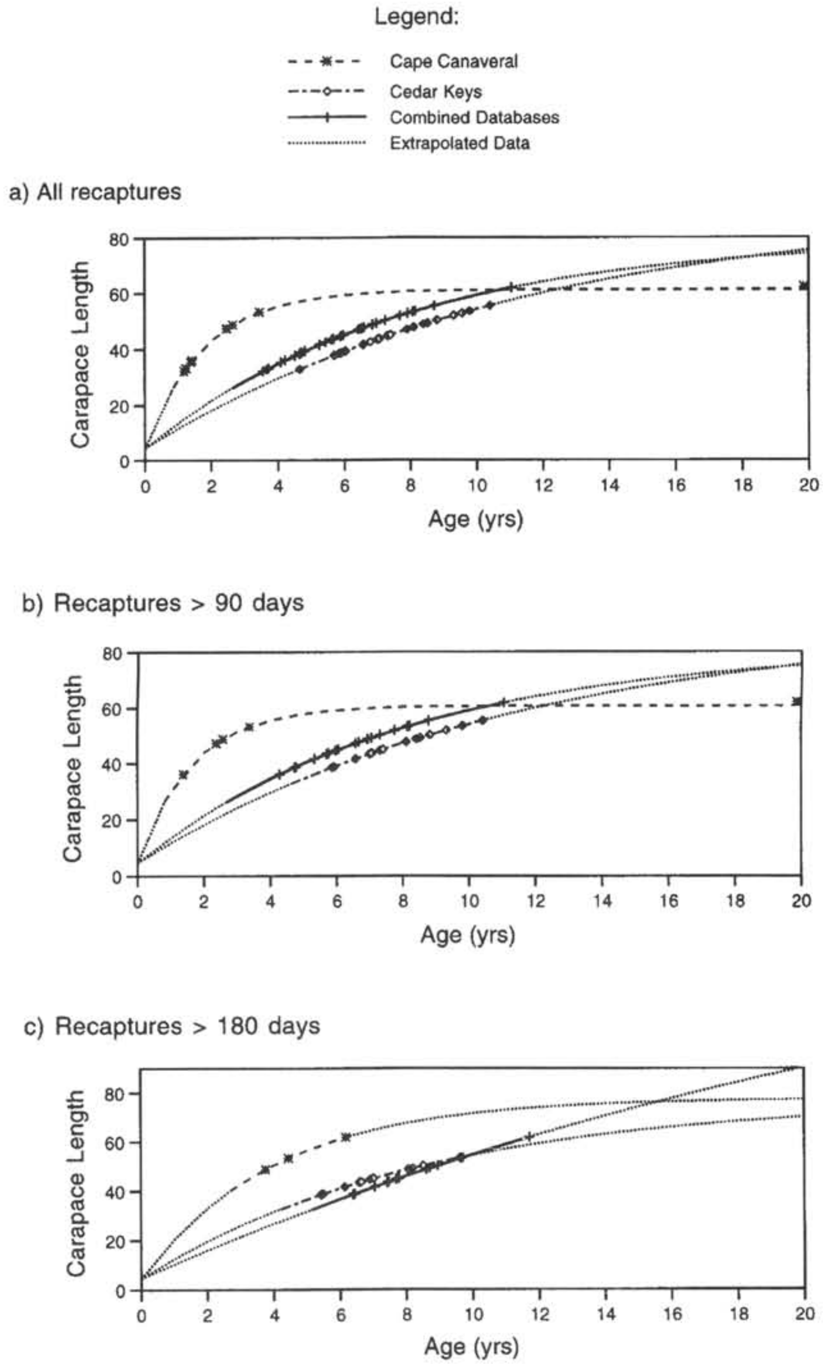
Estimating age to maturity has been the primary application of growth curves derived for marine turtles. Growth curves for each database and data treatment are illustrated in Fig. 2. By using equation 4 and the mean size of nesting females (64.2 cm converted SCL) as the estimated mean length at maturity, it appears that Kemp's ridley turtles may reach sexual maturity at 12–13 years of age. However, this age estimate was derived for a carapace length beyond the size range used to compute the growth equation and extrapolation as such should be avoided. Furthermore, using the mean length of nesting females may have overestimated age to maturity, since smaller turtles are obviously nesting at Rancho Nuevo. By using the minimum length observed for nesting females (56.0 cm converted SCL) as the size at first maturity, some Kemp's ridley turtles may become reproductively active as early as 8–9 years of age. Schmid (1995; in press) and Caillouet et al. (1995) used 60 cm SCL as an estimate of size at sexual maturity, which would result in an age to maturity estimate of 10–11 years.

The results of our growth model analysis of Kemp's ridley turtles are comparable to those of earlier investigations. Skeletochronological age estimates derived by Zug and Kalb (1989) indicated that it took more than 10 years for

Table 1. Estimated values of asymptotic straight-line carapace length (a, in cm) and intrinsic growth rate (k) from non-linear regression of von Bertalanffy growth interval equation for Kemp's ridley turtles, *Lepidochelys kempi* (± one standard error [S.E.] and residual mean square error [RMSE]). Known mean nesting length = 64.2 cm converted SCL.

Data treatment	n	a	S.E.	k	S.E.	RMSE
1) Cape Canaveral database						
All recaptures	12	61.1	5.4	0.5774	0.2176	3.4359
All recaptures > 90 days	6	60.7	8.0	0.6037	0.3549	8.2325
All recaptures > 180 days	3	77.9	21.1	0.2466	0.1771	1.1478
2) Cedar Key database						
All recaptures	24	91.4	41.9	0.0852	0.0720	1.3872
All recaptures > 90 days	16	90.9	51.1	0.0858	0.0892	2.1179
All recaptures > 180 days	13	77.3	29.2	0.1167	0.0957	2.0085
3) Both databases combined						
All recaptures	36	80.0	30.5	0.1292	0.1060	3.8900
All recaptures > 90 days	22	81.4	42.7	0.1241	0.1370	6.4870
All recaptures > 180 days	16	178.0	424.0	0.0343	0.1072	4.2265

Figure 2. Kemp's ridley turtle growth curves for the Cape Canaveral, Cedar Key, and combined databases using the data treatments: **(a)** all recaptures, **(b)** recaptures greater than 90 days duration, and **(c)** recaptures greater than 180 days duration. Estimated ages for recaptured turtles are plotted on the corresponding growth curves.



specimens collected along the Atlantic coast to reach sexual maturity. However, the asymptotic length used in this preliminary analysis was underestimated as a result of the limited range of carapace lengths in the database. Zug (1990) added larger specimens to the sample but the asymptotic length for the resulting von Bertalanffy equation was still less than the mean size of nesting females. Age estimates from this model suggested that at least 11–12 years were required to reach the minimum size of nesting females. Zug et al. (1997) further refined their growth model by adding specimens collected in the Gulf of Mexico and by increasing the sample size and range of carapace lengths for turtles collected along the Atlantic coast. The asymptotic length derived from the total sample was sufficiently large to estimate an "average" age to maturity of 15–16 years. Caillouet et al. (1995) produced a von Bertalanffy growth model using recapture data from released head-started Kemp's ridley turtles, but the asymptotic length from this analysis was also underestimated. The authors acknowledged that the paucity of data from larger specimens had biased their analyses and concluded that it took approximately 10 years to reach their estimated size at maturity (60 cm SCL). We concur with these researchers that a full range of specimens is needed to derive realistic growth parameters for Kemp's ridley turtles and our own analysis undoubtedly suffers similar problems.

Knight (1968) identified the difficulty of fitting a von Bertalanffy growth curve to a truncated dataset and extrapolating meaningful estimates of asymptotic length. Asymptotic length and intrinsic growth rate are inversely correlated, such that asymptotic length may become a function of growth rate in the absence of data for larger individuals. Frazer et al. (1990) examined the effects of truncated data on von Bertalanffy estimates by systematically omitting small or large individuals from a known-age dataset for freshwater slider turtles, *Trachemys scripta*. The authors concluded that the omission of small turtles resulted in little change in estimated values, while the omission of large turtles could result in underestimation, overestimation, or reasonable estimation of asymptotic length, depending upon the variability in growth rates. This later relationship is readily apparent for the Kemp's ridley turtle databases used in the present analysis (Table 1). Data treatments with high growth rates (all recaptures and recaptures > 90 days at Cape Canaveral) exhibited low estimates of asymptotic length and treatments with lower growth rates (all recaptures and recaptures > 90 days at Cedar Key) exhibited higher estimates of asymptotic length. Combining these databases resulted in intermediate estimates of asymptotic length and intrinsic growth rate.

Bjorndal et al. (1995) recently applied the von Bertalanffy model to estimate the number of years required for subadult green turtles to grow within the size range of their data. Similarly, equation 4 could be used to estimate the age of Kemp's ridley turtles within the size range of the combined database, assuming the asymptotic length and intrinsic growth rate are reasonable estimates of the entire population. Carapace lengths ranged from 26.3 cm SCL for the smallest initial capture to 61.8 cm SCL for the largest recapture. This size range encompasses the coastal-benthic subadult stage of development (Ogren, 1989) commonly found stranded on Florida beaches (Teas, 1993). The estimated age for the smallest turtle is 2.6 years, which is in agreement with the skeletochronological age estimate of 2 years (Zug and Kalb, 1989; Zug, 1990; Zug et al., 1997) for post-pelagic Kemp's ridley turtles (20–25 cm; Ogren, 1989). The age estimate for the largest turtle is 11.0 years, which may be the approximate age at which Kemp's ridley turtles mature and recruit to the Gulf of Mexico breeding population. The duration of the coastal-benthic subadult stage would therefore be approximately 8 to 9 years.

The von Bertalanffy growth models presented in this paper are based on the most extensive tag and recapture database to date for wild, subadult Kemp's ridley turtles. It is anticipated that the models will improve as more long-term tag returns are accumulated. Recently, two Kemp's ridley turtles tagged as subadults in the Cape Canaveral study were observed nesting at Rancho Nuevo (WNW, *pers. obs.*). The recapture measurements for these turtles were converted (62.1 cm and 63.8 cm SCL) and added to the combined database of all recaptures. The resultant fitted von Bertalanffy growth equation was:

$$\mathbf{L_t = 72.5\ (1 - 0.9393e^{-0.1721t})} \qquad [5]$$

The addition of the two nesting females increased the residual mean square error (4.1210) of the growth model when compared to that of equation 4. However, the estimate of asymptotic length decreased to 72.5 cm SCL, which is equal to the maximum converted SCL observed for nesting females (Burchfield et al., 1988) and may be more biologically realistic when compared to the mean SCL of nesting females as suggested by Frazer et al. (1990). Growth data for larger (> 65 cm SCL) adult turtles are clearly needed to increase the precision of von Bertalanffy estimates for Kemp's ridley turtles. Furthermore, thorough identification of carapace measurement techniques and accurate conversions between these techniques are needed to reduce measurement errors associated with recapture information.

The von Bertalanffy equation assumes a steadily decreasing growth rate with increasing size and age. However, there is recent evidence that Kemp's ridley turtles exhibit seasonal, geographic, and, possibly, ontogenetic variation in growth rates. Schmid (in press) suggested that the mean annual growth rate for turtles recaptured during the summer was significantly greater than that of turtles recaptured after the winter. Caillouet et al. (1995) indicated that growth of released head-started turtles in the Gulf of Mexico appeared to be faster than in the Atlantic Ocean. Zug et al. (1997) also observed faster growth for wild turtles found stranded in the Gulf, but cautioned on the difference in size ranges for the two areas. Furthermore, Zug et al. (1997) indicated that the growth rates of Kemp's ridley turtles do not exhibit a sequential decline with increasing age. Subsequently, Chaloupka and Zug (1997) have proposed a polyphasic growth model for the skeletochronological data set of Zug et al. (1997). These factors, and statistical problems outlined by Chaloupka and Musick (1997), have raised concerns about the use of the von Bertalanffy equation for marine turtle growth analyses. Nonetheless, until alternative growth models have been developed and thoroughly tested, the von Bertalanffy equation provides estimates of demographic parameters that are required for the management of the critically endangered Kemp's ridley turtle.

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