



AGE AND GROWTH IN WILD KEMP'S RIDLEY SEATURTLES *Lepidochelys kempii* FROM SKELETOCHRONOLOGICAL DATA

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Abstract

*Skeletochronological analysis provides age estimates, not actual ages, for sea turtles. Unlike age and growth data from captive and headstart turtles, these estimates predict the actual patterns of age and growth in free-living turtles. A moderate-sized sample of 69 *Lepidochelys kempii*, salvaged from the Atlantic and Gulf coasts of the USA, had straight-line carapace lengths (SCL) of 188–720 mm and age-estimates of 2–15 years. The von Bertalanffy growth model provides the best fit for the age-estimate and size data and predicts maturity between 11 and 16 years, depending upon the body size selected to represent sexual maturity. The logistic growth model suggests later maturity of 13–19 years. Comparison of the Atlantic and Gulf components of the sample suggests a faster growth rate for ridleys in the Gulf of Mexico, although the sizes of the subsamples are too small for this interpretation to be reliable without additional data. Our age and growth estimates indicate that some members of the early cohorts of headstart ridleys are mature and may have nested already. © 1997 Elsevier Science Ltd. All rights reserved*

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INTRODUCTION

The Kemp's ridley sea turtle is the most endangered of the world's seven species of sea turtles. As recently as 1947, an estimated 40,000 females nested on the beach at Rancho Nuevo in Tamaulipas, Mexico (Carr, 1963; Hildebrand, 1963). There are no other major nesting aggregations for the Kemp's ridley, although a few individuals nest occasionally on other beaches of the Mexican Gulf Coast. Since the late 1970s, the Rancho Nuevo nesting population has numbered no more than 1000 females (Marquez-M., 1994). Much effort has gone

into efforts to stop and reverse the population decline (Fletcher, 1989; Marquez-M. *et al.*, 1989; Woody, 1989). The success of this effort remains uncertain, but fortunately the decline in the population of nesting females has plateaued recently (Marquez-M., 1994).

The geographic range of the Kemp's ridley is small compared to most other sea turtles. Adults are largely confined to the Gulf of Mexico. Juveniles feed each summer in the estuaries of eastern North America from Cape Cod southward to Cape Hatteras, and along the coast of the Gulf of Mexico. Some juveniles are occasionally found along the coast of Europe and northern Africa. It is unclear whether these juveniles are waifs or whether some individuals regularly ride the North Atlantic Gyre.

Kemp's ridleys experience high mortality in all life history stages owing to numerous natural biotic/abiotic factors and high levels of commercial trawling and netting along the Atlantic and Gulf coasts. Conservation efforts have long strived to reduce this mortality and to increase the number of hatchlings reaching the sea to begin their journey to adulthood. However, conservation managers have lacked realistic estimates on the length of time from the hatchlings' entry into the sea to their return to the nesting beach as mature, sexually active adults.

In 1972, Marquez estimated 5–6 years to attain sexual maturity based on the captive growth of hatchlings and the growth rates of nesting females. This estimate of maturity has persisted (e.g., USA National Research Council 1990), even though such youthful estimates for other sea turtles have proven incorrect and are typically more than 25 years (Bjorndal & Zug, 1995). Recent work with headstart turtles (i.e. captive-raised for first year and then released) yields an estimate of 10 years (Caillouet *et al.*, 1995). Even this estimate seems too low, because more than a decade passed from the initiation of strong protection of the nesting Kemp's ridley and their eggs at Rancho Nuevo and the cessation of the population decline of nesting females.

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Although the strandings of dead ridleys on USA beaches is bad news for the conservation of this species, stranded turtles give us an opportunity to examine the pattern of growth and age at sexual maturity of free-living (wild) individuals. Further skeletochronological age estimates for wild *Lepidochelys kempii* provide age data to develop demographic models for management plans and give realistic time-interval data to assess protection and other conservation efforts.

MATERIALS AND METHODS

Kemp's ridleys stranded on the coast of the United States from Long Island, New York, to Padres Island, Texas, were retrieved by members of the seaturtle stranding network. Our sample ($n=69$) of stranded ridleys consists mainly of turtles from Long Island (New York; salvaged 1987), the mouth of the Chesapeake Bay and adjacent Atlantic Coast (Virginia; 1979–81 & 1987–88), and Cumberland Island (Georgia; 1979–82, 1987–88). A smaller component (salvaged 1987–91) is from both the east and west coasts of central Florida, and a few other specimens come from a scattering of localities along the USA Gulf Coast.

Skeletochronology is analogous to dendrochronology with the distinct difference that tree-rings are not resorbed as the tree grows larger and older. In seaturtles, resorption and remodeling is a major feature of bone growth, and skeletochronological techniques must address the progressive loss of earlier bony growth layers (reptiles have periosteal growth). We (Zug & Kalb, 1989; Parham & Zug, in press) have developed several protocols for estimating the loss of periosteal layers and the estimation of the age of individual turtles. The following analysis will use two estimation protocols: ranking (Zug, 1990) and correction-factor (Parham & Zug, in press).

A third analytical technique, the back-calculation protocol, does not estimate the number of lost layers or an individual's age, but predicts a growth curve by using Fabens' method of estimating a von Bertalanffy growth equation for time-interval and size data (see Frazer *et al.*, 1990 for a detailed explanation). The size data derive from back-calculated carapace lengths (CL) at the innermost LAG (periosteal line of arrested growth) and the outermost LAG for each individuals. The back-calculated CLs use the equation

$$L' - C = (S'/S)(L - C)$$

where C is a correction factor; L' and L are CLs at time₀ and time₁, respectively; and S' and S are humerus diameters at the preceding times (detailed explanation in Parham & Zug, in press).

Operationally, the back-calculation/Fabens protocol uses a rearrangement (1) of the standard van Bertalanffy equation.

$$L_o = (A - L_i)e^{-kd} \quad (1)$$

where L_o is the CL back-calculated from the outermost LAG; L_i , CL back-calculated from innermost LAG; A , asymptotic CL; e , base of natural logarithm; k , intrinsic growth rate; and d , duration (year) or number of growth intervals (MSGs) between LAG_i and LAG_o. Since eqn 1 lacks the growth constant (B), this constant is estimated by another rearrangement (Frazer *et al.*, 1990) of the von Bertalanffy equation,

$$B = e^{-k}(1 - L_h/A) \quad (2)$$

where L_h is mean hatchling carapace length (43.5 mm; Marquez-M., 1994) of *L. kempii*. The estimated asymptote (A), intrinsic growth rate (k), and growth constant (B) can then be substituted into the standard van Bertalanffy equation.

$$L = A(1 - Be^{-kAge}) \quad (3)$$

Setting L at the mean CL (650 mm SCL; Marquez-M., 1994) for females nesting at Rancho Neuvo and rearranging the equation

$$Age = \ln |(A - L)/AB| - k \quad (4)$$

yields an estimate of the 'average' age of nesting females and sexual maturity in *L. kempii*.

Our skeletochronological data is derived from bone sections (0.5–0.8 mm thick) cut transversely from the middle of the diaphysis, just distal to the deltopectoral crest, of the right humerus. These sections are examined and stored in a glycerine ethanol solution (4:6). For each section, a series of long (ab- to adaxial) axis measurements record the diameter of the resorption core and each subsequent humeral growth diameter to the last diameter (i.e. outside of the bone). These diameters provide the data set for the aforementioned estimation protocols.

Some ($n=19$) of the skeletochronological specimens had curved (CCL), but not straight (SCL) carapace lengths. SCL is the preferred size measurement for comparison among population and species of seaturtles. Thus, we converted CCL data to SCL by the equation: $SCL = 0.712 + 0.946 CCL$. These estimated SCLs were substituted only for those specimens without SCLs recorded at time of salvage. This regression equation derives from a sample of wild ridleys (headstart and captive-raised individuals are excluded; some individuals are included that are not in the skeletochronological sample); the regression statistics are $n=33$, adjusted $r^2=0.99$, slope significantly different from zero $P=0.80$.

RESULTS

Age estimates

The size range of our sample is 188–720 mm SCL, with the majority of the specimens from 300–550 mm SCL

(Fig. 1). The ranking age-estimation protocol yields an age range of 1–12 years. The estimated one-year-old (188 mm SCL) is the smallest individual in our sample, but the 12-year-old (615 mm SCL) is not the largest.

The correction-factor estimates yield an age range of 2.3–14.7 years (Fig. 1). Again, the smallest individual has the lowest age estimate and the largest individual is not the oldest turtle. The correction-factor ages were determined by the equation: $\text{Age} = \text{Number of MSGs} + ((\text{Resorption diameter} - 0.8) / 2.065)$. The 0.8 value is the diameter of a hatchling's humerus. The

2.065 value is the average slope of the regression of humerus diameters to the number of complete MSGs (i.e. bony growth layers); the sample ($n=25$) for calculating the average slope contained only individuals < 500 mm SCL with resorption core diameters < 12 mm (see Parham & Zug, in press for explanation of the correction-factor protocol).

The back-calculation/Fabens protocol does not yield individual age-estimates for the turtles. It produces a growth curve from which growth rates and age at sexual maturity can be determined.

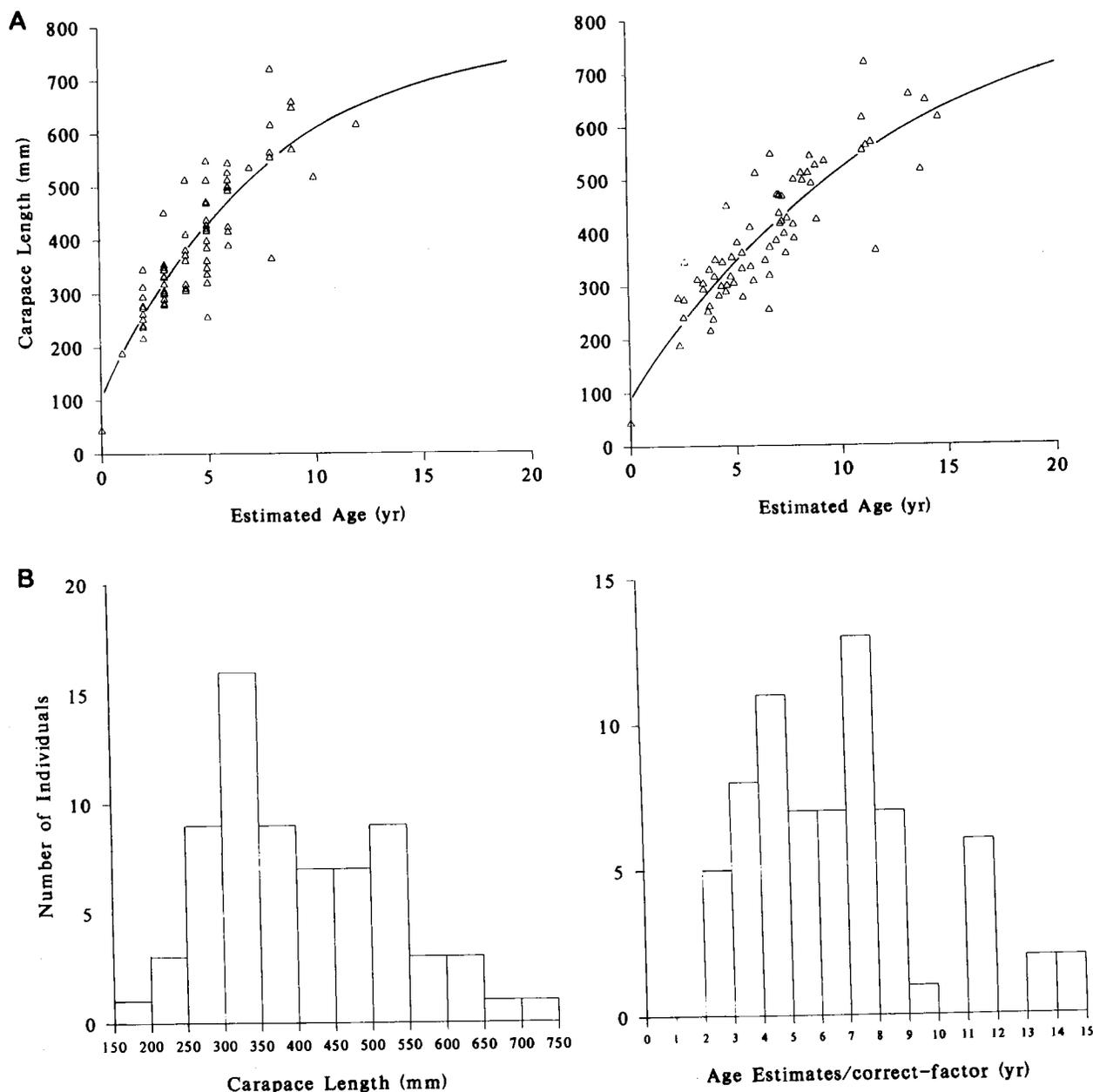


Fig. 1. (a) Comparison of age estimates derived from the ranking protocol (top left) and the correction-factor protocol (top right) for the total *Lepidochelys kempii* sample. Carapace length is a straight-line length (SCL). The solid line in each graph is the von Bertalanffy curve based on the respective age-estimates (Table 2). (b) The bar graphs show the size distribution (bottom left) and the correction-factor age-estimates distribution (bottom right) of the total sample.

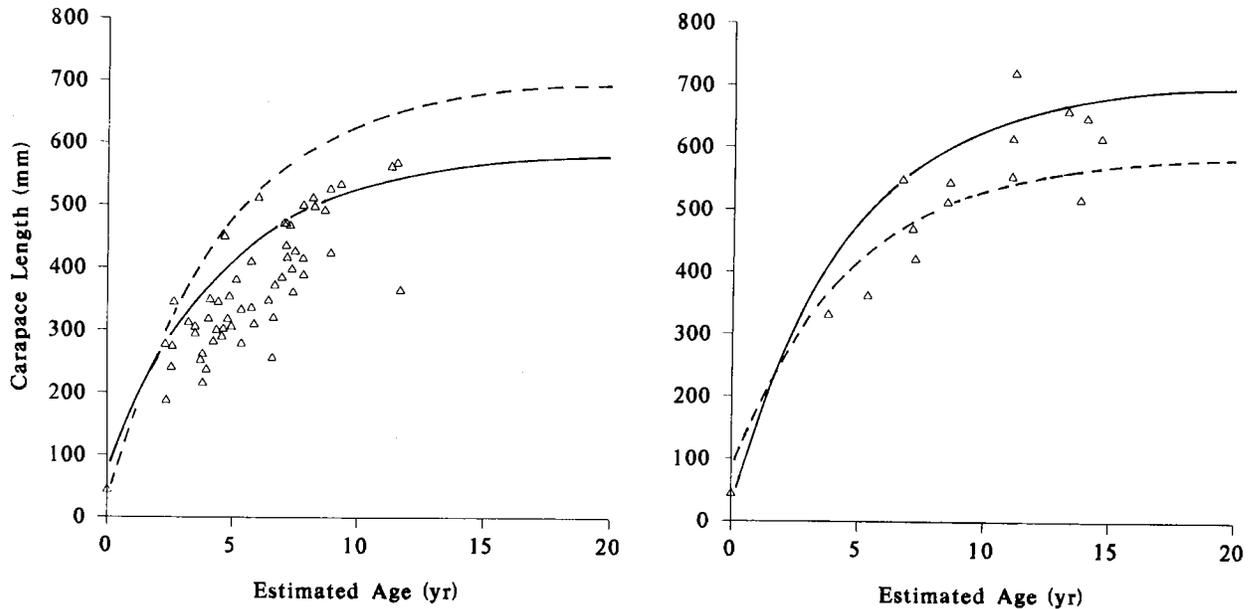


Fig. 2. Comparison of correction-factor age-estimates for the Atlantic (left) and Gulf (right) subsamples of *Lepidochelys kempii*. Carapace length is a straight-line length (SCL). The solid line in each graph is the von Bertalanffy curve based on the respective age-estimates (Table 2); the broken line represents the curve from the opposite graph for comparison.

Table 1. Presumptive growth rates (mm/year) for *Lepidochelys kempii* derived from ranking and correction-factor age-estimates. The growth rate for each age class is the difference between the mean SCL of that age class and the mean SCL of the preceding age class. The statistics are mean \pm standard deviation and range (n) of SCL.

Age class (year)	Ranking statistics	Growth rate	Correction statistics	Growth rate
0	43 ^a		43 ^a	
1	188 (1)	145	—	110
2	270.9 \pm 38.5 216–345 (10)	83	264.8 \pm 57.4 188–345 (5)	110
3	326.0 \pm 45.4 279–450 (13)	55	276.1 \pm 40.3 216–331 (8)	12
4	371.4 \pm 68.0 306–512 (8)	47	328.5 \pm 46.9 282–450 (11)	52
5	414.4 \pm 74.5 256–548 (17)	43	344.4 \pm 44.0 279–410 (7)	16
6	477.8 \pm 54.4 389–544 (9)	64	391.6 \pm 103.9 256–548 (7)	48
7	534 (1)	56	434.1 \pm 39.8 361–500 (13)	42
8	563.4 \pm 129.1 365–720 (5)	29	501.1 \pm 38.2 424–544 (7)	67
9	625.3 \pm 49.1 569–659 (3)	62	534 (1)	33
10	517 (1)	—	—	15 ^b
11	—	—	564.3 \pm 115.5 365–720 (6)	15
12	615 (1)	—	—	12 ^b
13	—	—	588.0 \pm 100.4 517–659 (2)	12
14	—	—	631.5 \pm 23.3 615–648 (2)	43

^aMean hatchling size from Marquez-M. (1994).

^bWhen an age class is missing, the difference of the subsequent year with the preceding year is halved.

Segregation of Atlantic and Gulf Coast individuals to examine potential differences in growth yields an Atlantic sample ($n=55$) with age-estimates ranging from 1 to 9 years (ranking protocol) and 2.3 to 11.7 years (correction-factor); for the Gulf sample ($n=14$), these age-estimates are 3–12 and 3.8–14.7 years (Fig. 2).

Growth-rate estimates

Growth rates are available from the various growth equations (see Table 2); however, we examine firstly the rates derived from the differences between the mean carapace sizes of each age class, because these are more comparable to previously published rates. Growth rates (ranking protocol) range from 29 to 145 mm/year (Table 1). These presumptive growth rates do not display a sequential decline with increasing age. The correction-factor growth rates range from 12 to 110 mm/year (Table 1) and show a similar irregular pattern.

The growth equations (Table 2) represent summaries of growth for all individuals in a sample, thus yielding a steady decline of growth rates. For example, the von Bertalanffy curve for the correction-factor age-estimates gives the rates of 105, 55, 51, 47, 44 mm/year for the first 5 years of growth and 29, 28, 25 mm/year for the 10th through the 12th years. Similar estimates of growth for the Atlantic and Gulf subsamples are 138, 79, 64, 51, 42 and 117, 107, 87, 69, 55 mm/year (1st–5th years) and 14, 12, 10 and 18, 15, 12 mm/year (10th–12th years), respectively.

Estimates of age at sexual maturity

Estimates of age at maturity depend upon the size of nesting females. We use the average size (650 mm SCL; Marquez-M., 1994) of nesting females, because that has become the standard among seaturtle biologists (for

rationale, see Frazer & Ehrhart, 1985). We also include in parentheses the estimated age at 600 mm SCL for comparative purposes, as Caillouet *et al.* (1995) considered this value representative of the average size at maturity and we used a comparable size in our preliminary report (Zug & Kalb, 1989). These ages also derive exclusively from the correction-factor age-estimates (for rationale see Parham & Zug, in press).

Direct calculation from the von Bertalanffy equation yields an 'average' age of maturity of 15.7 years (13.2 years) for the total sample and 11.4 years (8.5 years) for the Gulf subsample. Maturity estimates for the Atlantic subsample cannot be calculated because the asymptote (589 mm) is less than the size at maturity. The logistic curve gives maturity at 19.3 years (13.3 years). The back-calculated/Fabens' von Bertalanffy curve predicts maturity at 12.8 years (11.3 years).

DISCUSSION

Comments on skeletochronological data and analysis

As noted previously (e.g. Zug, 1991), skeletochronological data for seaturtles yield age-estimates, not actual ages. Their usefulness is not for the identification of an individual seaturtle's age but in predicting the population's growth pattern and 'average' age of maturity.

The age (or size) composition of the sample determines the reliability of the predicted growth curve. For example, the absence of adults in the Atlantic subsample results in a prediction of an adult size (the asymptote) less than the actual size of maturity of nesting females. The Gulf subsample provides an asymptote within the upper size range of adult female ridleys, but the high residual mean square (Table 2) indicates that

Table 2. A summary of growth model parameters for the total sample ($n=70$, includes one hatchling with age of 0 yr) and Atlantic and Gulf subsamples ($n=56$, 15, respectively) of *Lepidochelys kempii*. Column labels: *B*, growth constant; *k*, intrinsic growth rate; r^2 , corrected coefficient of determination; MS, residual mean square; Hatchling, predicted SCL based on the preceding growth equation parameters

Model	Asymptote (mm)	<i>B</i>	<i>k</i>	r^2	MS	Hatchling (mm)
Ranking protocol						
von Bert	794.0	0.878	0.130	0.74	4196	97
Gompertz	696.4	1.621	0.242	0.74	4257	138
Logistic	657.8	3.138	0.353	0.74	4297	159
Correction-factor protocol						
von Bert	877.3	0.899	0.079	0.75	4020	89
Gompertz	718.7	1.734	0.171	0.75	4051	127
Logistic	665.0	3.517	0.261	0.75	4070	147
vB-Atlantic	589.0	0.858	0.215	0.68	3541	84
vB-Gulf	705.3	0.962	0.219	0.87	4225	27
Back-calculated/Fabens protocol						
von Bert	1214.1	0.965	0.057	0.81	2577	43
Equations						
von Bert						CL = Asympt $(1 - Be^{-kAge})$
Gompertz						CL = Asympt $(e^{-Be^{-kAge}})$
Logistic						CL = Asympt $(1 + Be^{-kAge})$

Table 3. Growth rates (mm/year) for free-living *Lepidochelys kempii*. These growth rates represent average annual growth for various size (SCL) classes and derive from tables in Marquez-M. (1994) and the von Bertalanffy equation of Caillouet *et al.* (1995). The average rates from Marquez's tables include only individuals with no or positive growth recaptured after an interval of four or more months. The Caillouet rates are for individuals between 250 and 450 mm SCL, which comprised > 90% of the sample used in determining the growth equation. The integer in parentheses is sample size.

SCL class	Growth rate	Type	Source
130–180	106.3 (9)	Headstart	McVey & Wibbel (1984) ^a
250–300	110	Headstart	Caillouet <i>et al.</i> (1995) ^b
300–350	92	Headstart	Caillouet <i>et al.</i> (1995) ^b
350–400	78	Headstart	Caillouet <i>et al.</i> (1995) ^b
400–450	71	Headstart	Caillouet <i>et al.</i> (1995) ^b
600–649	24.4 (5)	Wild	Marquez-M. (1994) ^a
650–700	25.3 (4)	Wild	Marquez-M. (1994) ^a
600–649	28.5 (4)	Wild	Marquez-M. (1994) ^c
650–699	18.9 (7)	Wild	Marquez-M. (1994) ^c
> 699	1.5 (2)	Wild	Marquez-M. (1994) ^c

^aMeans calculated from data in Marquez-M. (1994), Table 15.

^bRates derived from von Bertalanffy equation with an asymptote of 622.7 (Caillouet *et al.*, 1995).

^cMeans calculated from data in Table 14, Marquez-M. (1994).

the predicted growth curve for this sample does not explain the variation of the sample as well as the curves for the total or the Atlantic samples.

Of the two age-estimation protocols, the correction-factor yields a less variable data set (see residual mean squares, Table 2) because it incorporates the actual number of observed growth layers with an objective and repeatable estimate of the resorbed layers (Parham & Zug, in press). The back-calculated/Fabens protocol avoids the estimation of age and is potentially a useful technique for skeletochronological analysis, but our data set encompasses a range predominantly between 200–450 mm SCL, and this narrow range yields an asymptotic value greatly exceeding the maximum adult size.

The preceding comments purposefully highlight the negative aspect of our results and indicate a cautious interpretation. Nonetheless, the similarities of predicted growth patterns (within the 200–500 mm SCL range) within our three protocols and with various nonskeletochronological studies (e.g. Marquez, 1972; Caillouet *et al.*, 1995) show the strength of skeletochronological data.

Age and growth in wild ridleys

The three protocols present different ranges of age and growth estimates for our sample of *L. kempii*. The differences are not unexpected because the bases for estimating the number of lost growth layers or total number of layers is different for each protocol. Even though the age-estimates are different, the actual ranges overlap (rank age, 1–12 years; correction age, 2.3–14.7 years; Fig. 1). The correction-factor ages are consistently older than the rank age and, as noted above, appear to be the most accurate estimates. These ages and the von Bertalanffy growth curves are used in comparing our results with those of other researchers.

Only a few sets of growth rates have been published for free-living Kemp's ridleys, and these require some adjustments for comparison with the skeletochronological ones. One adjustment is the segregation into age-classes and calculation of means for each class; we summed only positive or no-growth rates, thus the rates in Table 3 might overestimate the rate of growth in these samples. Also, we are unable to assign rates to age-classes and will compare the size-class rates with those for age-classes.

The growth rates for the smaller size-classes (130–180 and 250–300 mm SCL; Table 3) match closely the skeletochronological rates for the first year of growth. The larger juvenile (300–450 mm) rates, in contrast, are about 1.5 times greater than those of the 2–4 year old ridleys (total sample), but nearly the same as those of the Gulf ridleys. The growth rates from the nesting females (classes > 600 mm SCL, Table 3) are similar to the 10–12-year-old ridleys (total sample) but somewhat greater than those for the Atlantic and Gulf subsamples.

The degrees of differences and similarities between the growth rates of the recapture-data samples and our skeletochronological sample show more concordance than discordance. We believe the differences derive largely from the small sample sizes and/or poor representation in some of the age- and size-classes. Relative to our data, the high and low asymptotic values (i.e. lying outside the range of adult body size) result from inadequate representation of ridleys > 550 mm SCL in our sample. Our samples are dominated by 300–500 mm SCL turtles, and the least-square fitting of growth curves generates the best fit for curve through this cluster and the few larger and smaller individuals have only a minor effect on the position of the curve, thus the upper (asymptote) and lower (y -intercept + hatchling size) ends of the curve are poor fits to reality.

Caillouet *et al.* (1995) suggest that ridleys in the Gulf of Mexico grow faster than those from the Atlantic coast of North America. The growth rates of our two subsamples match their prediction and can be interpreted as confirmatory. Although warmer water temperatures and longer growing seasons do result in faster growth rates in turtles (Gibbons *et al.*, 1981), the difference in the size representation within our Atlantic and Gulf samples also can produce the differences observed in the rates and slopes of the growth curves. Thus, our analysis is inconclusive on this presumed difference in rates of growth.

Maturity in wild ridleys

The age of maturity for all species of seaturtles derives from extrapolations of growth models. No cohort (or even one individual) of seaturtles has been tracked from hatching to their return to a nesting beach. For Kemp's ridleys, only our data set and that of Caillouet *et al.* (1995) provide growth models based on free-living individuals. As for the growth rates, the similarities in the growth models (von Bertalanffy) are greater than the differences, although our interpretations of the 'average' age of sexual maturity diverge.

Our growth models predict maturity between 11 and 16 years based on a mature size of 650 mm SCL. Caillouet *et al.* (1995) estimate maturity at 10 years using 600 mm SCL; our data yields 9–13 years for this smaller size. We advocate the use of the mean size of nesting females as a more accurate predictor of the average age of maturity for a population than the minimum size of nesting females. Data from other turtles (*Chrysemys*, Mitchell, 1988; *Emydoidea*, Congdon & van Loben Sels, 1991; Sels, 1993; *Trachemys*, Dunham & Gibbons, 1990), which have had long-term population monitoring, show that often the fastest growing individuals mature at larger sizes and earlier than the slower growing individuals. Indeed, individuals maturing at the smallest sizes are often the oldest and slowest growing individuals in the population (Congdon & van Loben Sels, 1993). These data support Frazer's and Ehrhart's (1985) argument that the mean size of nesting females is the most reliable predictor for estimating the average age of maturity for seaturtle populations.

Observations from conservation activities

The single, major nesting beach (Rancho Nuevo, Tamaulipas) has received enhanced protection since 1978 concurrently with an attempt to headstart Kemp's ridleys and to establish an auxiliary nesting beach (Padre Island, Texas) in a USA wildlife reserve. The number of nesting females at Rancho Nuevo continued to decline to a low of 658 females in 1986, plateaued for a few years, and began a modest increase in 1990 (Marquez-M., 1994). Since the annual densities of nesting females are notoriously erratic (Schulz, 1975), the modest increase might be only a stochastic phenomenon, but it also might reflect the beginning

of maturation of the cohorts receiving enhanced protection.

The headstart program released over 21,000 juvenile ridleys between 1978 and 1992. With a minimum maturity of 11 years, Kemp's ridley females should have begun nesting on Padre Island if beach imprinting occurred for that beach. There has been no increase above the normal irregular occurrence of 1–2 solitary nesting females (Shaver, 1995; although four females nested by mid-June 1995). If imprinting is necessary to locate natal nesting beaches but does not occur as supposed, the maturing headstart ridleys might be unable to locate their natal beach and begin nesting elsewhere. Bowen *et al.* (1994) suggested that nesting in Florida in 1989 and the 1992 nestings in North and South Carolina were headstart ridleys. The skeletochronological age-estimates for maturity support this hypothesis of disoriented headstart females.

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