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Age and Growth in Leatherback Turtles, *Dermochelys coriacea* (Testudines: Dermochelyidae): A Skeletochronological Analysis

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ABSTRACT. – **Leatherbacks are the largest living turtles and grow faster than the smaller, hard-shelled sea turtles (Cheloniidae). Age estimates derived from a skeletochronological analysis of sclerotic ossicles from 15 adult leatherbacks and two juveniles ranged between 8.8 and 22.9 years for the adults, and less than a year and slightly over a year old for the juveniles. These age estimates analyzed by the von Bertalanffy growth model predict maturity on the average at 13–14 years for females, a minimum age at maturity of 5–6 years, and juvenile growth rates ranging between 8.6 to 39.4 cm per year. For conservation management purposes, 9 years is a likely minimum age for maturity based on the youngest adult in the sample.**

KEY WORDS. – **Reptilia; Testudines; Dermochelyidae; *Dermochelys coriacea*; sea turtle; age; skeletochronology; growth curves; growth rates; sexual maturity; morphometrics; conservation; Peru**

Leatherback turtles (*Dermochelys coriacea*) are the largest extant turtles and, in average adult weight, may be the largest living reptiles, having a reported body mass to 916 kg (Eckert and Luginbuhl, 1988). Carapace lengths are typically 130–170 cm (SCL, straight-line carapace length) and mass commonly less than 500 kg. Hatchlings emerge from eggs at lengths of 5.0–6.5 cm SCL and mass of 40–55 g. From hatching to adulthood, leatherbacks increase their length about thirty-fold and mass about 6000-fold. Such growth is an amazing phenomenon, yet the duration of the interval between hatching and adulthood is unknown. If linear growth in leatherback matches the fastest rates of the wild hard-shelled sea turtles (Cheloniidae), a minimum of 25 years would be necessary for a leatherback female to attain a minimum nesting size of about 130 cm. A few growth rates have been proposed for wild leatherbacks (Deraniyagala, 1939; Birkenmeier, 1971; Rhodin, 1985); however, these rates are speculative, and the recent National Academy of Sciences report (1990) presented age and growth data for all USA sea turtles except leatherbacks.

Because it has been impossible to mark hatchling sea turtles so that they still can be recognized individually as adults, there are no longitudinal growth data for the entire juvenile growth phase of any individual sea turtle. For leatherbacks, knowledge of juvenile growth derives solely from individuals raised in captivity (e.g., Deraniyagala, 1939; Birkenmeier, 1971; Bels et al., 1988). In captivity, hatchling leatherbacks experience high mortality (usually living less than 100 days), resulting in growth data that exist mainly for the smallest and earliest growth stages. A few researchers have been able to rear one or two individuals for longer periods (662 days, Deraniyagala, 1939; 1200 days, Bels et al., 1988). Whether for a month or a year, most captive data show extremely rapid growth, even in individuals dying from captivity factors (e.g., fungal and bacterial infections, stress). Thus, these data have led to speculations that leatherbacks might reach sexual maturity as quickly as 2 to 3 years from hatching (Deraniyagala, 1939; Birkenmeier, 1971). Rhodin (1985) re-examined this hypothesis of early maturity and provided evidence that the mammal-like rapid growth pattern of leatherback limb bones supported rapid growth to early maturity. He hypothesized from these data that maturity probably occurred at 3 to 6 years.

Such rapid growth for any turtle seems an incredible hypothesis, but the hypothesis has remained untested in leatherbacks owing to the inability to obtain growth or age data from free-living individuals. Skeletochronology has offered a possible methodology, but the distinct growth pattern of the humerus and femur in leatherbacks has eliminated these skeletal elements of proven usefulness in cheloniid skeletochronology (Zug et al., 1986; Parham and Zug, in press). Zug (1990) recognized the possibility of using sclerotic ossicles (the ring of bony elements within the sclera of the eyeball and encircling the pupil) to examine cyclic growth patterns in leatherbacks and reported that layering was evident and measurable in these ossicles. However, there was no analytical protocol available for reliably estimating layers lost by remodeling. Recently, Parham and Zug (in press) modified and tested several protocols used in fish skeletochronology for sea turtles. One protocol proved especially reliable and is applicable to the layering seen in the sclerotic ossicles, allowing us to estimate age in leatherbacks. We present our results and interpretation below.

MATERIALS AND METHODS

Our skeletochronological sample ($n = 16$) of sclerotic ossicles showing growth layers or marks of skeletal growth (MSGs) derives from 15 presumed adults (132.5–160.0 cm CCL [curved carapace length], mean = 145.3 cm) salvaged from a fisherman's dump in coastal Peru and a juvenile (42.7 cm CCL) caught on a longline in American Samoa (Grant, 1994). In addition, we examined sclerotic ossicles from a juvenile (21.6 cm CCL, USNM 337799) stranded on the

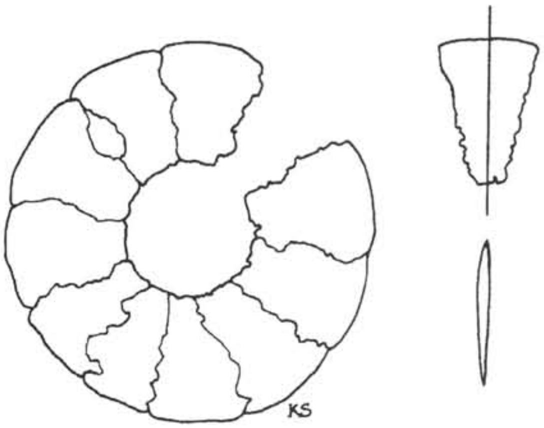

Figure 1. Diagrammatic representation of a sclerotic ossicle ring with an ossicle removed. The vertical line through the ossicle shows the location of the longitudinal section, an outline of which is depicted below the ossicle.

Florida east coast, two captive-raised juveniles (15.0 cm CCL, USNM 222562; 12.0 cm CCL, UF 57866), and two hatchlings (6.0 cm CCL, USNM 313600; 6.5 cm CCL, USNM 222574).

We prepared the ossicles by standard paraffin histotechnique (Zug et al., 1986) and sectioned them (8-12 μm) longitudinally (Fig. 1). We recorded all counts and measurements (by an ocular micrometer, accurate to .001 mm) in the middle of each ossicle.

Skeletochronological studies of sea turtles must inevitably address bone resorption and remodeling, because all skeletal elements, including sclerotic ossicles, show evidence of remodeling. Resorption eliminates the innermost MSGs, the number of which must be estimated in order to estimate age. The correction-factor protocol (Parham and Zug, in press) calculates the number of resorbed MSGs based on the observation that the innermost MSGs are the widest. Our data and interpretation assume each MSG represents an annual growth cycle, and the correction-factor age-estimate is the sum of the estimated resorbed MSGs and the observed MSGs. Vital dye studies in wild loggerheads (Klinger and Musick, 1992) and Kemp's ridley turtles (J. Musick, *pers. comm.*) show the deposition of one periosteal layer in limb bones each year. Nonetheless, there are no data from leatherbacks to confirm or deny this assumption, and other internal or external factors could produce less or more than one growth layer each year, with MSGs representing dietary rather than temporal cycles.

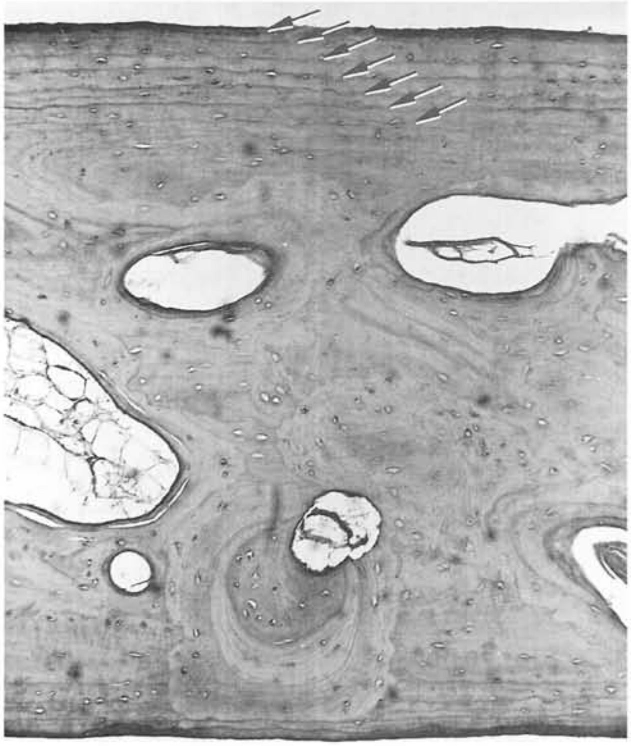

Figure 2. A cross-section of a sclerotic ossicle of *Dermochelys coriacea* (USNM 317614, 146.5 cm CCL) showing seven MSGs (marks of skeletal growth). Arrows point to LAGs (lines of arrested growth). This individual is estimated to have been 16.3 yr old at the time of its death.

Protocol calculations require radial width measurements of: 1) the resorption cores; 2) the ossicles at the end of each growth phase (i.e., each MSG); and 3) a hatchling's ossicle. Because growth and remodeling are asymmetrical, the growth center (also the center of resorption) of an ossicle is not in the middle of the ossicle (Fig. 2). As a result, the number of visible MSGs often differ on opposites sides. To determine the center, we use a proportion based on the total widths of the complementary MSGs of the two sides. We were unable to measure accurately the radius of the hatchling ossicles, so we substituted the radius of the presumed 1-yr old (i.e., possessing one MSG) Samoan specimen for the hatchling radius and adjusted the correction-factor appropriately. The estimated number of lost MSGs plus one is the total number of resorbed MSGs, because a 1-yr old was used instead of a hatchling.

The relationship between the estimated ages and the recorded sizes are examined by three growth models (von Bertanlanffy, Gompertz, and Logistic). These growth models allow inferences about growth rates as well as permit us to predict both a minimum and an average age for sexual maturity. The growth models also allow comparison to the captive growth data. Analyses were performed by the NONLIN module of SYSTAT 5.03 (Wilkinson, 1990).

RESULTS AND DISCUSSION

Age Estimates. — The sclerotic ossicles of the larger specimens from Peru have 3–9 (mean = 5.6) MSGs and the 42 cm wild juvenile a single MSG (see Appendix). There is no linear association ($r^2 = 0.043$, $P = 0.456$) between the observed MSGs and carapace length for the Peru sample, and this association is slight but not significant with the inclusion of the juvenile ($r^2 = 0.237$, $P = 0.056$).

The 22 cm CCL wild juvenile, the captive-raised juveniles (12 and 15 cm CCL), and the hatchlings show no lines of arrested growth (LAGs), hence no layering or MSGs in their ossicles. We interpret the absence of a LAG in the wild juvenile to indicate that it died prior to the completion of its first growth cycle and was, therefore, probably less than one year old at death. The alternative interpretation is continuous growth possibly beyond one year. The fine structure of its ossicle is identical to that of the captive-raised juveniles, suggesting continuous growth in this wild individual. Because the Samoan juvenile (42 cm) had a distinct LAG near the outer periphery of its ossicle and no recognizable resorption core, we considered it to have started its second growth cycle prior to death. It was identified as a 1-year old in our data set, although it probably had at least one month of growth subsequent to its first growth arrest, judging from the thickness of the periosteal layer external to its LAG.

The correction-factor protocol yields age estimates of 8.8 to 22.9 yr (Fig. 3; Appendix) for the adult specimens. There is no linear association of estimated age and carapace length ($r^2 = 0.136$, $P = 0.177$). The absence of correlation between size and age in leatherback adults is not unexpected. Sea turtles and other turtles commonly show no direct correlation between adult size and age (e.g., *Caretta caretta*, Dodd, 1988, Table 7; *Chelonia mydas*, Bjorndal, 1980; *Emydoidea blandingii*, Congdon and van Lobel Sels, 1993; *Geochelone gigantea*, Swingland and Coe, 1979; *Trachemys scripta*, Gibbons et al., 1981). In turtles and other reptiles as well as in most mammals including man, individuals within the same cohort attain maturity at different body sizes, and these size differences persist among the adults.

Table 1. Summary of the size (carapace lengths) of nesting female *Dermochelys coriacea* from around the world. Abbreviations: CCL, over-the-curve carapace length; SCL, straight-line carapace length; *n*, sample size; SD, standard deviation. All measurements are in cm. Márquez (1990) did not cite the original source of the data in his tables. Position of carapace measurements are noted as superscripts: 1) along top of dorsal ridge; 2) along top of dorsal ridge, from back of notch; 3) along side of ridge; 4) along side of ridge, front of notch; 5) along side of ridge, back of notch.

Locality	*n*	Range	Mean	SD	Method	Source
Eastern Pacific						
Mexico	85	129-163	145.8	-	SCL	Márquez, 1990
Mexico	52	124-162	144.4	-	SCL	Márquez, 1990
Mexico	395	127-188	144.6	-	SCL	Márquez, 1990
Mexico	85	126-156	143.3	5.7	CCL^2	Nisenbaum, 1983
Mexico	85	130-163	145.6	6.5	CCL^2	Nisenbaum, 1983
Mexico	81	120-148	134.0	5.6	SCL^2	Nisenbaum, 1983
Mexico	49	126-148	136.6	5.1	SCL^2	Nisenbaum, 1983
Mexico	11	137-150	144.9	-	CCL^3	Pritchard and Trebbau, 1984
Mexico	81	131-158	150.0	-	SCL	Reyes et al., 1995
Mexico	81	131-163	158.0	-	CCL	Reyes et al., 1995
Costa Rica	18	128-151	141.0	-	SCL^4	Cornelius, 1976
Western Pacific						
New Guinea	101	145-178	161.0	-	CCL	Starbird and Suarez, 1994
Australia	9	151-175	162.4	-	CCL	Márquez, 1990
Indian Ocean						
Sri Lanka	4	148-165	155.9	-	CCL	Márquez, 1990
South Africa	122	134-178	161.1	7.0	CCL^1	Hughes, 1974
South Africa	8	147-165	154.0	6.4	SCL	Hughes, 1974
Western Atlantic						
Puerto Rico	2	153-160	156.5	3.5	SCL	Márquez, 1990
Costa Rica	176	135-173	152.1	-	SCL	Márquez, 1990
Colombia	16	140-170	153.8	-	CCL	Márquez, 1990
Trinidad	20	125-185	158.0	15.4	CCL^1	Bacon, 1969; Pritchard, 1971
Guyana	3	138-163	150.1	10.3	SCL	Márquez, 1990
Surinam	16	149-170	159.4	6.1	SCL	Pritchard, 1969
French Guiana	834	135-189	167.0	-	SCL^4	Fretey, 1978
French Guiana	192	138-182	158.5	-	CCL^5	Pritchard, 1971

Sexual Maturity. — To predict the average age for sexual maturity in leatherbacks, we follow the recommendation of Frazer and Ehrhart (1985) to use the average carapace length of nesting females. The average size more accurately reflects the average age of maturity for a population, because once attaining maturity, female sea turtles, including leatherbacks (Boulon, 1994b), exhibit little growth between nesting seasons. For convenience, we also include age estimates at a minimum nesting size.

Although numerous nesting leatherbacks have been measured (see summary in Márquez, 1990), the selection of average size is confounded by the variety of measuring techniques used. In addition to the differences between straight and curved carapace lengths, some authors measure along the dorsal ridge (Bacon, 1969), whereas others measure in the trough (Pritchard and Trebbau, 1984), some authors measure from the front of the nuchal notch (Fretey, 1978) and others from the rear (Nisenbaum, 1983). Additionally, most studies do not precisely state the actual method of measurement. Clearly, the different methods hinder exact comparisons of leatherback nesting populations (Table 1).

A standardized measuring technique (as well as publication of standard deviations) or the development of conversion factors would eliminate some confusion and allow for more accurate comparisons of populations. For example, Pritchard and Trebbau (1984) noted a possible difference in size between the Atlantic and Pacific populations of leatherbacks; however, they compared Pacific SCL with Atlantic CCL measurements. In spite of this miscomparison, differences in average female size appear to exist among the various nesting populations. A comparison of samples that used the same measurement method (over the dorsal ridge: Table 1) with a *t*-test shows that the east Pacific samples (Nisenbaum, 1983) are significantly smaller than those from the Atlantic (Bacon, 1969) and Indian (Hughes, 1974) oceans ($t = 3.88, 21.07$, respectively, $P < 0.001$). Because our sample is from the east Pacific and measured over the dorsal ridge, we use Nisenbaum's (1983) estimates of the mean (144.5 cm) and minimum (126.0 cm) carapace lengths at sexual maturity.

These mean and minimum sizes were used to estimate age at sexual maturity via three growth models (von Bertalanffy, Gompertz, and Logistic). The parameters of the growth models derive from the estimated ages of the skeletochronology sample including the Samoan juvenile (estimated as 1 yr, 42.7 cm CCL) and one hatchling (0 yr, 6.0 cm CCL). The 6.0 cm CCL value for "average" hatchling carapace length derives from four specimens (USNM 313599–313602) from Michoacan, Mexico, and matches the size data in Márquez (1990).

The Gompertz and Logistic growth models predict a rapid attainment of near asymptotic size (Table 2). The von Bertalanffy growth model, however, provides a better fit (i.e., lower residual mean square and higher r^2 values; Table

Table 2. Growth model parameters for the skeletochronological sample ($n = 16$) of east Pacific *Dermochelys coriacea*, including prediction of age at sexual maturity for three growth models. Abbreviations: B, growth constant; k, intrinsic rate of growth; mean, mean predicted age of maturity at 144.5 cm CCL (Nisenbaum, 1983); min, minimum predicted age at 126 cm CCL (Nisenbaum, 1983); MS, mean square of the residuals; r^2, corrected coefficient of determination. Age in years; asymptotic carapace length in cm.

Growth Model	Asymptote	B	k	r^2	MS	Age	
						min	mean
von Bertalanffy	147.62	0.955	0.286	0.97	64.99	5.7	13.3
Gompertz	145.32	3.110	0.928	0.96	75.45	3.3	6.8
Logistic	145.30	23.216	2.268	0.96	75.60	2.2	3.7

2) and generates a more biologically feasible growth curve (Fig. 3). Using the von Bertalanffy parameters, the average age for maturity is 13 to 14 years (13.3 yr) at the mean size and 5 and 6 years (5.7 yr) at the minimum size of nesting females. In comparison with cheloniid sea turtles, leatherbacks mature much faster. The smallest cheloniid turtle, Kemp's ridley (*Lepidochelys kempii*) matures in 11–16 yr (Zug et al., in press) and at about half the size of the smallest known mature leatherback. Green and loggerhead turtles mature at 90–110 cm SCL (Table 3), and most require twice as long as leatherbacks.

Table 3. Selected age estimates for the attainment of sexual maturity in 4 species of cheloniid sea turtles. Age and size data are usually presented for the mean size of nesting females; if the published data are for the minimum size of nesting females, the data are marked with an asterisk (*). Age in years; size, SCL in cm.

Sexual Maturity Age	Size	Location	Source
Caretta caretta			
22	–	Georgia, USA	Frazer, 1983
22	92.5	Virginia, USA	Klinger and Musick, 1995
20–24	92.4	Georgia, USA	Parham and Zug, in press
Chelonia mydas			
27	99.0	Florida, USA	Frazer and Ehrhart, 1985
19*–24	–	Atlantic Ocean	Ehrhardt and Witham, 1992
Eretmochelys imbricata			
19+	88.7	Bahamas and Virgin Islands	Boulon, 1994a
31+	83.0	Australia	Limpus, 1992
Lepidochelys kempii			
10*	60.0	Gulf of Mexico	Caillouet et al., 1995
11	65.0	Gulf of Mexico	Zug et al., in press
16	65.0	Atlantic Ocean	Zug et al., in press

Even though our growth model predicts average maturity at a mean of 13–14 yr, not all individuals will mature at this age; some will mature sooner and others later. Possibly all members of our Peruvian sample were adults at the time of their deaths, but we cannot confirm either their sex or their maturity because they were collected as eviscerated, mummified carcasses. If we accept the maturity of the entire sample because the sizes of all individuals lie within the size range of females nesting in the east Pacific, then 8–9 yr represents the youngest possible age of maturity of this sample, based on a 139 cm CCL, 8.8 yr old individual. An even smaller individual (132.5 cm) was estimated as 21.5 yr, and because of its age is assumed to be mature, even though it could have been immature or just maturing. Although we have no means of defining the actual age range for maturing individuals from our data and analysis, the average age of maturity of 13–14 yr predicted by the growth model seems a robust conclusion based on the low variation about the growth-model curve.

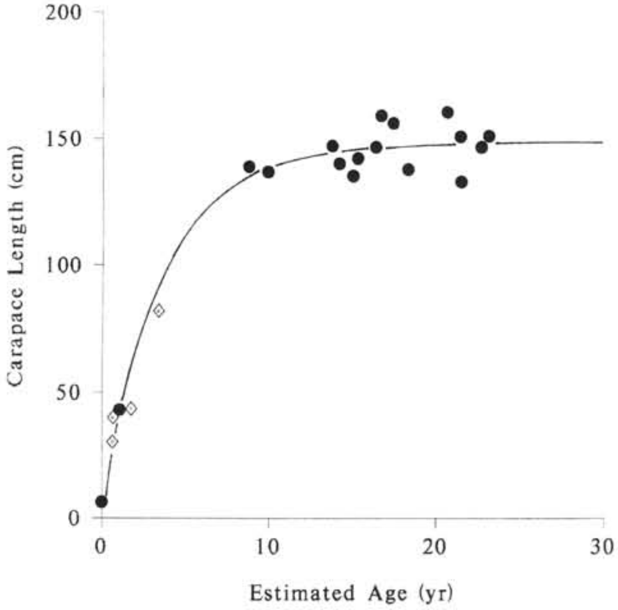

Figure 3. The growth pattern of *Dermochelys coriacea* based on skeletochronological age estimates. The solid line is the von Bertalanffy growth curve (Table 2) based on the age estimates of 15 presumed adults, one wild juvenile, and one hatchling. These wild individuals are shown as solid circles; captive-growth records are shown as open diamonds (82.0 cm, 3.3 yr; 30.2 cm, 0.6 yr; 40.0 cm, 0.63 yr; and 43.5 cm, 1.7 yr; from Bels et al. (1988), Birkenmeier (1971) 2 specimens, and Deraniyagala (1939), respectively).

We suggest a tentative acceptance (for conservation management) of 9 years as the minimum age of maturity. This minimum age and the variation in age and size (Fig. 3) of our adult sample are not unexpected even if the sample derived from first-time nesting females. Similarly, the ranges are realistic because the sample represents a set of individuals harvested from a population of migratory, nonreproductive leatherbacks, some of which might have been near or had just attained maturity and others that might have already nested one or more times.

Growth Rates. — At average juvenile growth rates exceeding 8.5 cm/yr (Table 4), *Dermochelys* has the fastest growth of living turtles. Rapid juvenile growth is regularly observed in hatchling leatherbacks held in captivity for the first months of their lives. It is this initial rapid growth that yielded the hypotheses that *Dermochelys* attains sexual maturity in 2–3 or 3–6 yr (Deraniyagala, 1939; Birkenmeier, 1971; Rhodin, 1985). These authors apparently considered growth to be linear prior to maturity and did not account for the common phenomenon of declining growth rates as organisms approach maturity (Peters, 1983). This slowing of growth is evident in the individual maintained in captivity for the longest time (Bels et al., 1988, Fig. 12). At 3.3 yr (1200 days), this individual was 82 cm SCL — well below the size of the smallest nesting female (Table 1).

Our estimates of growth rates (Table 4) are taken directly from the von Bertalanffy growth model. As they are based on data from free-living turtles, they represent wild growth rates. These rates (Table 4) range from 8.6 to 34.9 cm/yr. We and others (Balazs, 1980; Frazer, 1983) have noted that it is inappropriate to equate captive and wild growth rates. Yet in leatherbacks, the early captive growth pattern closely matches the growth curve of wild individuals predicted by the von Bertalanffy growth model (Fig. 3). All four individuals which survived in captivity for more than half a year lie on or immediately adjacent to the predicted growth curve. Thus, wild leatherbacks might be able to match the growth rates of similarly aged juveniles in captivity.

Faster growth implies a higher metabolism, digestive efficiency, and assimilation than in other turtles. A study of hatchling energetics (Lutcavage and Lutz, 1986) showed that leatherbacks have a metabolic rate 3x that of green and loggerhead hatchlings. At least some of this difference can be explained by the activity of the specimens during testing. Leatherback hatchlings swam constantly, whereas cheloniid sea turtles did not. Cheloniid turtles match leatherback metabolic rates only when struggling and only for brief periods, whereas leatherbacks maintain their rate and activity for hours.

Maintenance of a high metabolic rate requires an enhanced dietary intake and energy conversion. There are no data on the natural diet of hatchlings, nor are data available on digestive efficiency and assimilation. We can only speculate that the diet of leatherbacks contains potentially more energy than that of the cheloniid turtles and that they ingest more and are better at extracting and converting this energy.

Adult leatherbacks are inertial endotherms (Paladino et al., 1990). Their high level of activity, oily subcutaneous insulation, counter-current circulation in limbs, and high mass permit them to maintain elevated body temperatures in temperate and subarctic waters. The high juvenile metabolism indicates the potential for such a physiological future as adults, although the high surface area to mass ratio likely precludes significantly elevated body temperature in juveniles and might force them to remain in warm or tropical waters. The size and age at which leatherbacks shift to inertial endothermy (gigantothermy) and how this shift affects growth rate are only a few of the intriguing and unknown aspects of leatherback life history.

Table 4. Predicted growth rates for *Dermochelys coriacea*, based on the von Bertalanffy model and skeletochronological age estimates (Table 2). The growth rates are for 30 cm curved carapace length intervals.

Size (CCL cm)	Age (yr)	Growth Rate (cm/yr)
10	0.08	34.9
40	0.94	26.1
70	2.09	17.5
100	3.80	8.6
130	7.27	

Significance of Age-Estimates for Conservation. — Most of the major nesting populations of leatherbacks have experienced a precipitious decline during the last decade (Eckert, 1991; Spotila et al., 1996). A decline in the numbers of nesting females has been noted since the late 1970s as a result of intense egg-collecting; on some beaches nearly 100% of the eggs laid have been harvested (Eckert, 1996). Conservation efforts such as egg hatcheries might have lessened the abruptness of the decline, but during the last decade, adult mortality has increased significantly through accidental capture and death in the driftnet and longline fisheries (Eckert, 1996; Spotila et al., 1996). The loss of the long-lived adults and the lack of recruitment by elimination of the annual influx of hatchlings into the population through egg-harvesting has caused the sharp decline. The relatively short maturation time of leatherbacks offers some hope for their survival if we can greatly reduce the harvest of their eggs and the accidental and intentional capture and killing of large juveniles and adults.

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APPENDIX

Skeletochronological data for the east Pacific sample of *Dermochelys coriacea*. MSGs = marks of skeletal growth.

Carapace Length (cm)	Number of MSGs		Estimated Age (yrs)
	Observed	Estimated	
21.6	0	0.0	<1.0
42.0	1	0.0	1.0
132.5	10	11.5	21.5
135.0	9	5.9	14.9
137.0	7	2.9	9.9
137.5	5	13.2	18.2
139.0	4	4.8	8.8
140.0	4	10.2	14.2
142.0	6	9.3	15.3
146.5	7	9.3	16.3
147.0	4	18.6	22.6
147.0	5	8.7	13.7
150.0	3	18.3	21.3
151.0	4	18.9	22.9
156.0	8	9.4	17.4
159.0	6	10.7	16.7
160.0	5	15.5	20.5

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