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Growth of captive leatherback turtles, *Dermochelys coriacea*, with inferences on growth in the wild: Implications for population decline and recovery

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ABSTRACT

Leatherback turtles (*Dermochelys coriacea*) are endangered, and declining population trends suggest that they are vulnerable to becoming extinct in the Pacific Ocean. Population recovery depends on strong conservation measures (e.g., nest protection, reduction of bycatch, and foraging habitat preservation) and on how fast leatherbacks grow and reach maturity, making the latter of grave concern. The research reported here marks the first time that several leatherback turtles have been maintained in captivity for nearly 2 years, from hatchlings (6.31 ± 0.13 cm straight carapace length (SCL) and 46.0 ± 1 g) to juveniles (largest, 72.0 cm SCL and 42.65 kg). Leatherbacks maintained an average growth rate of 31.9 ± 2.8 cm year^{-1} in SCL throughout the study period. A length–mass relationship of the form, mass (kg) = 0.000214 * SCL (cm) 2.86, fitted our data and data from four other captive studies, 11 wild juveniles, and five studies of adult leatherbacks. Von Bertalanffy, Gompertz and logistic growth functions predicted age-at-maturity for leatherbacks of 16.1, 8.7 and 6.8 years, respectively. The accuracy of these age-at-maturity estimates is discussed in the light of skeletochronological studies as well as estimates obtained from conservation and genetic studies. Our data, in combination with data from sightings, suggest that leatherbacks spend their early years (0 to 5 years of age) growing in the warmer waters of the tropical and subtropical seas before entering cooler temperate waters. Information obtained from turtles incidentally captured in fisheries, supplemented with growth curve data, indicates that leatherbacks are vulnerable to entanglement or hooking in various pelagic gear types, such as drift gill nets and longline within 3 years from nest emergence. Consequently, leatherbacks are exposed to threats from marine fisheries for >80% of their early life before carapace length characteristic of reproductive maturity is attained.

1. Introduction

Growth rate may be the single most important parameter in aiding our understanding of marine turtle demography. Growth rates are crucial for understanding life history aspects such as age-at-maturity, the temporal duration of various life history stages, longevity and life stage specific mortality factors. Most studies of marine turtle growth have focused on cheloniid species (see Chaloupka and Musick, 1997, for review), with few investigating growth in leatherback turtles (*Dermochelys coriacea*) (Rhodin, 1985; Rhodin et al., 1996; Zug and Parham, 1996; Price et al., 2004; Avens et al., 2009). This is not surprising considering the almost exclusive oceanic–pelagic lifestyle of leatherbacks (only females go on land for nesting) and the extreme difficulty of maintaining them in captivity (Birkenmeier, 1971; Jones et al., 2000). Growth rate estimates are of concern with regards to leatherback conservation, as the species is endangered (United States Endangered Species Act of 1973) and may be nearing extinction in the Pacific Ocean (Spotila et al., 1996, 2000; Kaplan, 2005).

Leatherbacks are the largest of the marine turtles (Buskirk and Crowder, 1994) and perhaps the fastest growing (Rhodin, 1985; Rhodin et al., 1996). There are three studies on growth rates of adult leatherbacks (Zug and Parham, 1996; Price et al., 2004; Avens et al., 2009), yet growth rate data for juvenile leatherbacks in nature are unavailable as their oceanic distribution is largely unknown, making mark–recapture or use of drift rate (Hays and Marsh, 1997) methods impossible. Mark–recapture data from other marine turtles have shown that loggerhead (*Caretta caretta*) and green turtles (*Chelonia mydas*) reach sexual maturity at ≥15 years and ≥20 years, respectively (Chaloupka and Musick, 1997). Other studies using new or refined techniques extend the age-at-maturity to 30–40 years for various populations of loggerheads and greens (Zug et al., 2002; Heppell et al., 2003), and >40 years for green turtles in Hawaii (Balazs and Chaloupka, 2004). Extremely rapid growth rates in captive leatherbacks have led to the speculation that these animals reach sexual maturity within 2–3 years (Frayr, 1970; Spoczynska, 1970; Birkenmeier, 1971; Foster and Chapman, 1975; Phillips,

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1977; Witham, 1977). However, many of these studies are based on a sample size of a single individual (from >2 months of age) and take no account of the possibility that growth rate declines with age.

Rhodin (1985) predicted a leatherback age-at-maturity of 3–6 years based on chondro-osseous (cartilage and bone) morphology. However, skeletochronological analyses suggest that leatherbacks could take as long as 13–14 years to sexually mature (Zug and Parham, 1996). Dutton et al. (2005) suggested that leatherbacks reach maturity in 12–14 years, based on greatly increased returns at a nesting beach (St. Croix) after intensive beach protection and nest relocation that increased hatchling production by an order of magnitude in the next decade. Genetic analysis from the same site suggested that first-time nesters are related, and possibly the genetic offspring of leatherbacks nesting in the 1980s, pointing to an age-at-maturity estimate of <20 years. In the most recent study on leatherback growth and age-at-maturity, Avens et al. (2009) suggested that leatherbacks of the western North Atlantic Ocean reach sexual maturity in 25–29 years, based on skeletochronolgy analysis of the slericle ossicles and the use of a von Bertalanffy Growth Function (VBGF) to determine growth rates and age-at-maturity. However, it should be noted that there is inherent error in skeletochronology estimates of age at length, as algorithms are used to determine how much bone has been absorbed prior to sampling.

Given the paucity of data and the large range in age-at-maturity estimates, more robust growth rate data are needed, with rearing studies probably presenting the only option to clarify important aspects of leatherback life history. Maintaining leatherbacks in captivity, however, is difficult. Due to the leatherback's completely pelagic lifestyle this species never adapts to the confines of a tank, resulting in animals injuring themselves against obstructions such as the tank walls and bottom (Birkenmeier, 1971; Foster and Chapman, 1975; Phillips, 1977; Witham, 1977; Bels et al., 1988; Chan, 1988). The resulting skin abrasions become infected and generally lead to the death of the animal (Birkenmeier, 1971; Jones et al., 2000). Previous captivity studies were unable to rear leatherbacks beyond 100 days, as a result of infections or complications thereof (Deraniyagala, 1939; Frayr, 1970; Spoczynska, 1970; Birkenmeier, 1971; Witham, 1977; Bels et al., 1988; Jones et al., 2000). Maintaining high water quality and finding an acceptable diet for the obligate jelly feeders presents additional challenges to rearing leatherbacks (Birkenmeier, 1971; Jones et al., 2000).

The objectives of the study, using captive reared leatherbacks, were to: 1) describe the approach used in rearing juvenile leatherbacks in captivity for more than 2 years; 2) compare the length–mass relationships of our captive animals with other captive leatherbacks, wild juveniles, and adults; 3) describe the growth rate of leatherbacks during the initial two years; 4) estimate parameters of the von Bertalanffy (VBGF; von Bertalanffy, 1938), Gompertz and logistic growth functions (Ricklefs, 1967) for growth in leatherbacks, based on juvenile captive stock and adult skeletochronological data; and 5) compare the growth curves to determine the biological relevance.

2. Materials and methods

Twenty leatherback hatchlings (emergence July 2, 2005) were transported by air from Tortola, British Virgin Islands (BVI) to the Animal Care Center, Department of Zoology, University of British Columbia, under Canada CITES Import permit CA05CWIM0039 and British Virgin Islands CITES Export certificate CFD062005. These animals were housed and maintained for research purposes in accordance with animal care standards of the Canadian Council for Animal Care (CCAC) and the UBC Animal Care Committee (UBC Animal Care Protocol: A04-0323).

2.1. Animal husbandry

The three main constraints on rearing leatherbacks are: (a) their oceanic–pelagic nature with no recognition of barriers, (b) water quality, and (c) designing a food capable of replacing their largely gelatinous diet in the wild.

a) Oceanic–pelagic lifestyle: As leatherbacks are oceanic–pelagic animals that swim continuously and do not recognize vertical and horizontal barriers (tank walls and bottom), they were tethered to PVC™ pipes secured across the top of the holding tanks. Animals <10 kg were attached to the pipes by a tether of monofilament fishing line with swivels. Velcro™ coupling patches were used, one tied to the end of the fishing line while the complementary patch was glued to the posterior portion of the carapace. Each hatchling could swim or dive in any direction, but was unable to contact other turtles or the bottom and walls of the tank. Juveniles $=10$ kg or greater were secured to the tether with a harness made of Tygon™ tubing. The harness circled each shoulder like the straps of a backpack, and an additional piece of tubing connected to each shoulder strap looped around the caudal peduncle to hold the harness from moving anteriorly.
b) Water quality: Turtles were maintained in large oval tanks (5 m long × 1.5 m wide × 0.3 m deep) containing ~2500 l of recirculated/filtered salt water. Once a week, the tanks were drained and scrubbed with Quatricide® PV (Pharmacal Research Laboratories Inc., Naugatuck, CT USA) a fungicide, bactericide, and virucide. The tanks were refilled with new water delivered from the Vancouver Aquarium and Marine Science Center, having a zero coliform bacterial count on arrival. As the turtles grew in size, extra tanks were plumbed in that doubled or tripled the volume of filtered water per turtle. The water temperature was maintained at 24 ± 1 °C. Four fluorescent fixtures (40 W UVA/B; Repti-Glow® 8) suspended 0.5 m above each tank provided full spectrum radiation for 12 h/day; each tank was also exposed to ambient light. Water quality was maintained between the following levels: pH $= 8.0$–8.3; salinity $= 28$–33 ppt; and ammonia ion <0.1 mg l^{-1}. Water quality for each tank was controlled by four systems: (i) a biological/mechanical filter (built by UBC-Zoology Workshop staff) containing bio-balls™ and fiberglass matting; (ii) a protein skimmer (Red Sea Berlin XL Turbo Skimmer, Houston TX, USA); (iii) a sand filter (TRITON® II TR 100; Pentair Pool Products™, Sanford, North Carolina, USA) designed for large volumes of water; and (iv) an ultraviolet filter (Aqua Ultraviolet™ 114 W UV water sterilizer, CA USA).
c) Diet: It was necessary to prepare food of the proper texture and consistency, since the diet of leatherbacks in nature consists solely of gelatinous zooplankton (e.g., jellyfish). Furthermore, feeding leatherbacks a diet of non soft-bodied marine organisms, such as fish, has been shown to cause gut impaction and death (Foster and Chapman, 1975; Witham, 1977). A diet of squid and agar was successfully used by Chan (1988) and our diet consisted of squid (Pacific Ocean squid *Loligo* sp.; mantle and head including arms and tentacles), vitamins (Reptavite™), and calcium (Rep-Cal™), blended with unflavored gelatin liquefied in hot water. The molten food was poured into trays lined with waxed paper and refrigerated until solid. The solidified food was cut into strips. Turtles were hand fed three to five times daily to satiation up to the first 2 months of age, and three times daily to satiation when >2 months of age.

2.2. Data collection and analysis

The turtles were weighed and measured on emergence, at 3 days of age, at 7 days of age, and then weekly. Straight carapace length (SCL), the distance from the center of the nuchal notch to the caudal peduncle (posterior of the carapace), was determined with a digital caliper to the nearest 0.1 mm. The turtles were weighed using an Ek-1200 A scale from hatching to body mass of 1.2 kg (± 0.001 kg), and an ADAM CPW-60 scale (Dynamic Scales, 1466 South 8th Street, Terre Haute, IN 47802) for mass >1.2 kg (± 0.02 kg). All averages are given with one standard deviation (SD).

For purposes of comparison with other growth studies, all cited studies using curved carapace length (CCL) were converted to SCL using the equation of Tucker and Frazer (1991):

$$SCL = \left(\frac{CCL}{1.04}\right) - 2.04 \qquad (1)$$

We made comparisons of the length–mass (L–M) data in this study and with other captive turtles (Deraniyagala, 1939; Birkenmeier, 1971; Frayr, 1970; Phillips, 1977; Bels et al., 1988), wild juveniles (Deraniyagala, 1939; Grant, 1994; Prince, 2004; M. Conti, pers. comm.; J. Wyneken, pers. comm.; NOAA/NMFS/PIFSC), and adult leatherbacks (Deraniyagala, 1939; Eckert et al., 1989; Boulon et al., 1996; James et al., 2005; Georges and Fossette, 2006; Wallace, pers. comm.) by fitting a power form of the allometric growth equation:

$$M = a \cdot L^{b} \qquad (2)$$

where M is body mass (kg), L is SCL (cm), a is the proportionality coefficient and b is the body mass exponent.

Growth rate of captive animals was determined as $\Delta L/\Delta t$ or $(L_j - L_i)/(t_j - t_i)$, where t = time in years at time i and j, and given as the growth rate for the mid-length of the starting and ending carapace length $(L_i + L_j)/2$. The growth rates and corresponding mid-length were then divided up into 10 cm length bins, i.e., <10 cm SCL, 10 to 20 cm SCL, etc., and an average growth rate and mid-length were computed for each bin.

Length-at-age data from this study and skeletochronological studies on adults (Zug and Parham, 1996; Avens et al., 2009) were analyzed using the von Bertalanffy (Eq. (3), Gompertz (Eq. (4), and logistic (Eq. (5) growth functions with the form:

$$L_t = L_\infty \left(1 - e^{-k(t - t_0)}\right) \qquad (3)$$

$$L_t = L_\infty \left(e^{-e^{-k(t - t_0)}}\right) \qquad (4)$$

$$L_t = \left(\frac{L_\infty}{1 + e^{-k(t - t_0)}}\right) \qquad (5)$$

in which L_t is the predicted length at age t, L_∞ is the mean SCL that all adults in the population would reach if they grew indefinitely, k is a growth parameter (not a growth rate) of dimension time^{-1}, and t_0 is the hypothetical age when length is zero (VBGF only).

Hatchlings emerge from nest when t is zero; therefore t_0 represents embryonic growth duration in the egg. For the Gompertz and logistic growth functions 't_0' is simply a right/left curve shift and does not hold a biological meaning. To estimate age-at-maturity from our growth functions, we defined maturity as the time when 97.5% of L_∞ is obtained. The asymptote (L_∞) represents mean maximum length and as marine turtles have near zero growth rates after first nesting (Frazer and Ehrhart, 1985; Price et al., 2004), then 'L_∞' also represents mean population nesting length. However, 'L_∞' is the asymptotic length; therefore, the best-fit curve approaches but never attains 'L_∞', thus a point near the asymptote equals mature length (Witzell, 1980). While 95.0 to 99.9% of the asymptote has been used in longevity studies of fish (Cailliet et al., 2006), we chose 97.5% as a conservative measure (N.B. the full range of maturity estimates are given in the results).

2.3. Statistical analysis

Each individual turtle, both from our study as well as from data obtained from the literature, contributed one measurement (the final measurement taken when the animal was in good health) to the length–mass relationships and the growth functions to avoid complications of pseudo-replication or nonindependence of data points.

Length–mass relationships (in the form of Eq. (2) for this study, data from other captive studies (Deraniyagala, 1939; Birkenmeier, 1971; Frayr, 1970; Phillips, 1977; Bels et al., 1988), as well as juveniles caught in the wild (Deraniyagala, 1939; Grant, 1994; Prince, 2004; M. Conti, pers. comm., J. Wyneken, pers. comm., NOAA/NMFS/PIFSC) and adult data (Deraniyagala, 1939; Eckert et al., 1989; Boulon et al., 1996; James et al., 2005; Georges and Fossette, 2006; Wallace, pers. comm.) were compared using Student's t test to determine if the slopes (b) and intercepts (a) were significantly different. The test statistic was $t = (b_1 - b_2)/(S_{b1-b2})$ where 'b' is the slope for the two regressions and 'S_{b1-b2}' is the standard error between regression coefficients. If no difference was found between the slopes, the elevations (y-intercept) were then compared where the test statistic was $t = \frac{(\overline{Y}_1 - \overline{Y}_2) - b_c(\overline{X}_1 - \overline{X}_2)}{\sqrt{(s^2_{y \cdot x})_c \left[\frac{1}{n_1} + \frac{1}{n_2} + \frac{(\overline{X}_1 - \overline{X}_2)^2}{A_c}\right]}}$ and 'A_c', 'b_c', and $(s^2{}_{y.x})_c$ are the common sum of squares, common slope, and common mean square residual, respectively.

Growth rates of the captive animals were compared using a one-way ANOVA and a Tukey–Kramer post-hoc test to determine where significant differences lay. In all statistical analyses, alpha was set to 0.05. Student's t tests were performed by hand calculations following Biostatistical Analysis by Zar (1999). Growth rate analyses were conducted on JMP® 4 statistical software program (SAS Institute INC., 2001).

The von Bertalanffy, Gompertz and logistic growth functions were fit to the data using nonlinear least squares (NLLS) regression (SigmaPlot® 10.0, Systat Software Inc., 2006). Initial parameter limitations were set for k (>0), and t_0 (<0). Mean square residual (MS_{res}) and the adjusted coefficient of determination (R^2) were compared between the three growth functions in an attempt to determine the best model to represent leatherback growth.

Ninety-five percent confidence and prediction bands are given for both the length–mass relationships and the growth curve. The confidence bands show how well the curve fits the data (i.e., 95% confidence that the true best-fit curve is within the bands). The prediction bands show the scatter of the data (i.e., if more data points were collected, 95% of them would be expected to fall within the prediction bands) (Motulsky and Christopolous, 2004).

3. Results

The hatchlings averaged 6.31 ± 0.13 cm SCL and 46 ± 1 g body mass at emergence from the nest (Table 1). All hatchlings began feeding on the formulated squid gelatin by 3–5 days after emergence. One turtle lived for 815 days obtaining a mass of 42.65 kg and a length of 72.0 cm SCL. Weekly length and mass measurements taken during the life span of all 20 hatchlings are given in Table 1.

3.1. Length–mass relationships

The length–mass relationship was $M = 0.000288 \cdot L^{2.78}$ for our study (Fig. 1A, data from Table 2). These parameter estimates were similar to leatherbacks from the wild $M = 0.000234 \cdot L^{2.84}$ (Fig. 1B, data from Table 3), and showed no significant difference ($p > 0.05$) in slope ($t = 0.7099$) or y-intercept ($p = 0.084$). Furthermore, there was no significant difference ($p > 0.05$) in the slope ($t = 1.824$) or y-intercept ($p = 0.1325$) of length–mass data from four other captive studies (Table 2), wild juveniles (Table 3), five adult studies (Deraniyagala, 1939; Eckert et al., 1989; Boulon et al., 1996; James et al., 2005; Georges and Fossette, 2006; Wallace, pers. comm.) and our study. The relationship for leatherback turtles was $M = 0.000214 \cdot L^{2.86}$after pooling the data (Fig. 1C).

Table 1
Weekly measurements of straight carapace length (SCL) and mass of 20 leatherback turtles raised in captivity. n = number of turtles measured at corresponding age. n decreases with age as a result of mortality, but some weeks have smaller sample sizes as a result of the turtles being used in other experiments. *Final SCL and mass at death of last remaining turtle, these data were not used as the turtle was on antibiotics and had not eaten for many days.

Age (years)	SCL (cm)	SD	Mass (kg)	SD	*n*	Age (years)	SCL (cm)	SD	Mass (kg)	SD	*n*
0.003	6.31	0.13	0.046	0.001	20	0.83	34.30	0.65	5.49	0.63	5
0.01	6.53	0.18	0.05	0.002	19	0.85	35.21	0.90	5.92	0.74	5
0.03	7.22	0.21	0.06	0.003	20	0.87	35.36	0.94	6.15	0.75	5
0.05	7.81	0.34	0.08	0.005	20	0.89	36.21	1.12	6.61	0.87	5
0.07	8.31	0.36	0.10	0.01	20	0.91	36.81	1.11	6.75	0.87	5
0.08	8.91	0.30	0.12	0.01	20	0.93	38.26	0.78	7.55	0.70	4
0.10	9.59	0.38	0.15	0.01	20	0.95	39.06	0.93	8.00	0.66	4
0.12	10.28	0.42	0.18	0.02	20	0.97	39.75	0.97	8.40	0.79	4
0.14	10.76	0.41	0.21	0.02	20	0.99	40.44	1.00	8.76	0.78	4
0.16	11.33	0.43	0.24	0.02	20	1.01	41.28	1.28	9.12	1.00	4
0.18	12.10	0.46	0.28	0.03	16	1.02	42.61	1.47	9.68	1.21	4
0.20	12.77	0.53	0.32	0.03	19	1.04	42.53	1.18	9.89	1.18	4
0.22	13.20	0.60	0.37	0.04	18	1.06	43.21	1.00	10.57	1.29	4
0.24	13.64	0.63	0.41	0.05	18	1.08	43.75	0.76	11.30	1.42	4
0.26	14.35	0.50	0.45	0.04	17	1.10	44.97	1.59	11.53	1.52	4
0.28	14.92	0.63	0.51	0.06	16	1.12	45.46	1.68	11.63	1.62	4
0.30	15.49	0.77	0.56	0.07	16	1.14	46.02	1.98	12.26	1.97	4
0.32	16.04	0.91	0.62	0.09	16	1.16	46.08	1.72	11.89	1.57	4
0.33	16.49	1.12	0.68	0.12	16	1.18	46.34	1.95	12.05	1.82	4
0.35	17.50	0.73	0.82	0.08	12	1.22	47.36	2.08	12.87	2.22	4
0.37	18.23	0.58	0.91	0.08	11	1.24	47.57	2.00	12.79	2.09	4
0.39	18.88	0.66	1.01	0.09	11	1.25	47.86	2.43	13.23	2.05	4
0.41	19.41	0.67	1.10	0.10	11	1.31	50.30	2.63	15.44	2.94	3
0.43	20.10	0.81	1.21	0.12	11	1.33	52.00	2.26	17.26	2.46	2
0.45	20.55	0.87	1.28	0.13	10	1.35	53.10	2.26	17.99	3.01	2
0.47	21.19	1.01	1.39	0.15	10	1.37	53.90	2.12	18.68	2.38	2
0.49	22.04	1.09	1.51	0.18	10	1.39	52.60	–	17.28	–	1
0.51	22.61	1.19	1.68	0.21	10	1.45	54.50	–	18.76	–	1
0.53	23.68	0.92	1.87	0.16	9	1.47	55.45	–	18.72	–	1
0.55	24.40	0.98	2.03	0.17	9	1.49	56.30	–	19.88	–	1
0.56	25.14	0.93	2.28	0.17	9	1.51	56.10	–	20.20	–	1
0.58	25.82	1.17	2.40	0.22	9	1.53	56.70	–	20.02	–	1
0.60	26.27	1.22	2.63	0.25	9	1.55	57.10	–	20.28	–	1
0.62	27.57	0.67	2.81	0.15	7	1.56	57.70	–	21.14	–	1
0.64	28.10	0.56	3.03	0.15	7	1.59	58.20	–	23.06	–	1
0.66	28.61	0.57	3.20	0.18	7	1.60	58.70	–	22.92	–	1
0.68	29.31	0.60	3.47	0.19	7	1.62	59.50	–	23.56	–	1
0.70	30.21	0.48	3.77	0.28	6	1.67	61.50	–	25.60	–	1
0.72	30.92	0.45	4.15	0.26	6	1.69	60.20	–	25.38	–	1
0.74	31.74	0.53	4.30	0.28	6	1.72	62.50	–	27.20	–	1
0.76	32.29	0.49	4.51	0.30	6	1.85	67.00	–	31.96	–	1
0.78	32.89	0.53	4.85	0.43	6	1.93	69.00	–	34.84	–	1
0.79	33.36	0.61	5.10	0.56	6	2.23*	72.00	–	42.65	–	1
0.81	33.86	0.67	5.28	0.55	6						

3.2. Growth

Growth rate averaged 31.9 ± 2.8 cm year^{-1} throughout the study period of 1.93 years from emergence (6.31 ± 0.13 cm SCL) through to a juvenile length of 70 cm SCL (Table 4). Statistical analysis showed that growth rate slowed significantly at 10 to 20 cm SCL (by 7%) and 40 to 50 cm SCL (by 16%), compensatory growth was not observed after the slow growth phases.

Length-at-age data (Table 2) combined with adult length-at-age data from skeletochronology studies (Zug and Parham 1996, Avens et al. 2009) fitted by NLLS regression gave the following von Bertalanffy, Gompertz, and logistic growth functions for length respectively, $L_t = 143\cdot(1-e^{-0.226\cdot(t+0.17)})$, $L_t = 141\cdot(e^{-e^{-0.511(t-1.86)}})$, $L_t = \left(\frac{140}{1+e^{-0.883(t-2.6)}}\right)$ (Figs. 2A, B, C, respectively). Table 5 shows the fitted parameters for all three growth functions with standard errors. The VBGF had the lowest MS$_{\mathrm{res}}$. The von Bertalanffy, Gompertz and logistic growth functions predicted an age-at-maturity of 16.1, 8.7, and 6.8 years with a minimum SCL at that age ($L_{\min}$) of 121, 117 and 116 cm SCL, respectively ($L_{\min}$ is given by the lower limit of the 95% prediction band at 97.5% L_∞). A range of age-at-maturity estimates are given by taking the age at 95–99% of L_∞ for the growth functions, e.g., 13.1–20.2 (VBGF), 7.7–10.9 (Gompertz) and 5.9–7.8 years (logistic).

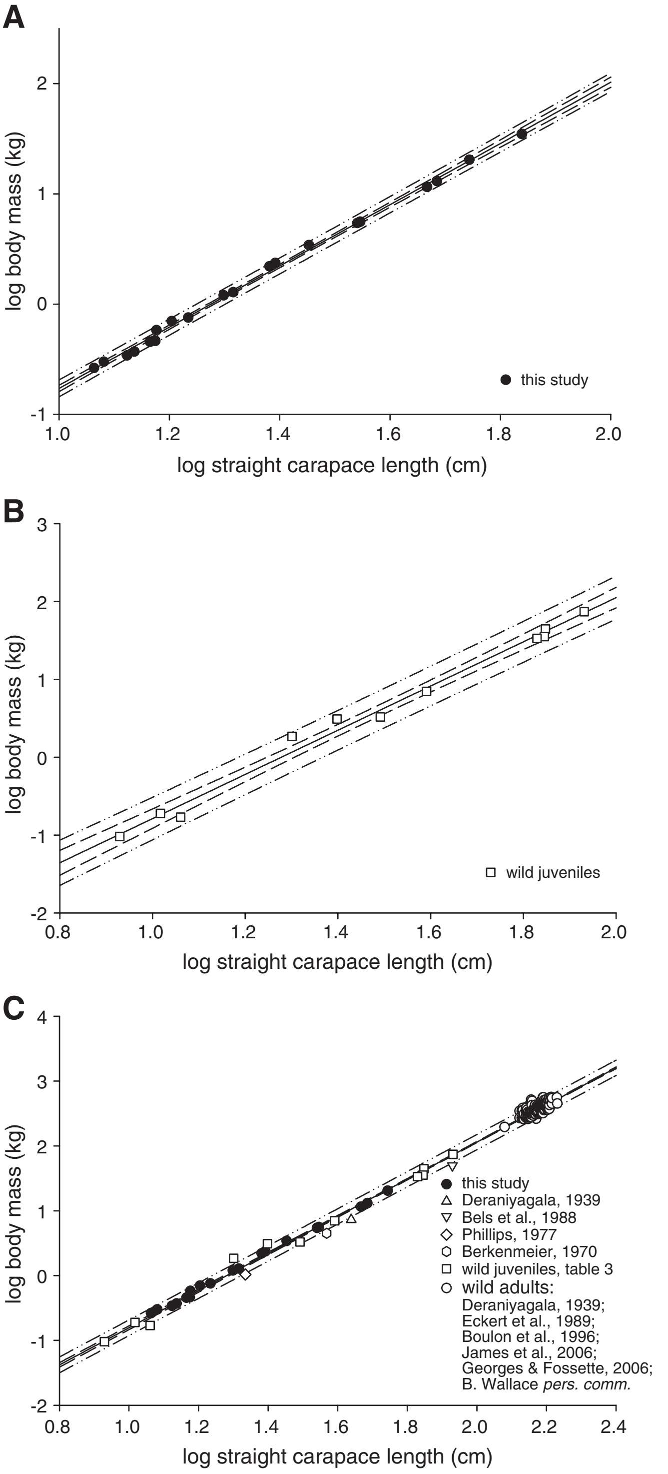

Fig. 1. Log of length–mass relationships (log length–log mass) of leatherback turtles for (A) this study, (B) juveniles from the wild and (C) all available length–mass data pairs. The relationships for A, B, and C are $y = 0.000288(x)^{2.78}$, $y = 0.000234(x)^{2.84}$ and $y = 0.000214(x)^{2.86}$, respectively. The solid black line denotes the best-fit line (as given in the previous equations), the inner medium dashed lines are the 95% confidence bands around the regression and the outer dash–dot–dot lines are the 95% prediction bands for the scatter of data pairs.

Table 2
Straight carapace length (SCL) and mass-at-age of individual turtles raised in captivity.

Turtle id	Age (years)	SCL (cm)	Mass (kg)	Source
1	0.20	13.29	0.34	This study
2	0.43	20.69	1.28	This study
3	1.25	46.45	11.54	This study
4	0.60	24.65	2.36	This study
5	1.31	48.40	13.04	This study
6	0.60	24.06	2.20	This study
7	1.93	69.00	34.84	This study
8	0.33	15.01	0.58	This study
9	0.68	28.38	3.42	This study
10	0.26	14.62	0.46	This study
11	0.18	11.57	0.26	This study
12	1.37	55.40	20.36	This study
13	0.81	34.74	5.44	This study
14	0.24	12.05	0.30	This study
15	0.35	16.00	0.70	This study
16	0.33	17.15	0.75	This study
17	0.91	35.13	5.58	This study
18	0.33	13.69	0.37	This study
19	0.33	14.95	0.46	This study
20	0.51	19.87	1.20	This study
A	1.71	43.50	7.27	Deraniyagala, 1939
C	0.46	16.00	–	Deraniyagala, 1939
1	0.08	5.40	–	Bels et al., 1988
2	0.12	6.60	–	Bels et al., 1988
3	0.12	7.80	–	Bels et al., 1988
4	0.13	7.00	–	Bels et al., 1988
5	0.16	7.80	–	Bels et al., 1988
6	0.21	8.00	–	Bels et al., 1988
7	0.22	8.10	–	Bels et al., 1988
8	3.70	85.00	49.50	Bels et al., 1988
9	0.12	8.10	–	Bels et al., 1988
10	0.17	7.90	–	Bels et al., 1988
11	0.30	8.90	–	Bels et al., 1988
12	0.41	10.40	–	Bels et al., 1988
13	0.41	10.80	–	Bels et al., 1988
14	0.50	14.30	–	Bels et al., 1988
–	0.22	13.20	–	Frayr, 1970
–	0.67	21.6	1.04	Phillips, 1977
1	0.56	37.00	4.50	Birkenmeier, 1971
2	0.27	17.00	–	Birkenmeier, 1971
3	0.23	14.00	–	Birkenmeier, 1971
4	0.19	12.00	–	Birkenmeier, 1971
5	0.13	10.50	–	Birkenmeier, 1971
6	0.12	12.50	–	Birkenmeier, 1971
7	0.13	12.50	–	Birkenmeier, 1971
8	0.13	12.00	–	Birkenmeier, 1971

4. Discussion

4.1. Length–mass relationship

Comparison of our length–mass relationships with wild animals suggests nonsignificant differences in the regression of captive, wild juvenile and adult leatherbacks. Length–mass regressions are commonly used as body condition indices to compare animals of different sizes, where body condition is a term representing the proportion of body tissue carried by an animal in relation to its total length or the length of an arm, wing, snout, etc. (Hayes and Shonkwiler, 2001). Here, we used the length–mass regression to show that for any carapace length our captive animals are carrying the same proportion of body tissue as wild animals. Using wild animals as the model of proper conditioning allows us to infer to the population at large from studies on our captive stock. We do not know, however, if the ratio of the tissues (e.g., fat and lean muscle) is similar to wild animals. While we fed our leatherbacks a diet of blended squid for practical reasons, in natural circumstances leatherbacks feed on gelatinous zooplankton which have low energy density (Doyle et al., 2007). Furthermore, free-living leatherbacks probably feed intermittently, as good quality prey patches are only occasionally found (e.g. Fossette et al., 2010). Therefore, future work may investigate how prey energy density impacts growth rate as well as establish how food availability drives variability in the growth rate of young leatherbacks. Such research would help to elucidate the possible bioenergetic, physiologic, or genetic differences leading to the dichotomy in size, demographics, and conservation status of the eastern Pacific and North Atlantic leatherback populations.

Table 3
Straight carapace length (SCL) and mass of 11 wild individual turtles (stranded or as bycatch). Date, location, and source are shown for each turtle, except one, for which only the SCL and mass are known.

Date	Location	SCL (cm)	Mass (kg)	Source
Aug-93	American Samoa	39	7.00	MTN (1994; no. 66, p. 3–5)
Sep-34	Ceylon, India	8.5	0.096	Deraniyagala (1939; Ceylon Journal of Science)
Sep-05	Florida, USA	10.4	0.19	J. Wyneken (*pers. comm.*)
Mar-06	Florida, USA	25	3.10	J. Wyneken (*pers. comm.*)
Apr-98	Hawaii, USA	70.4	44.50	NOAA (NMFS/PIFSC)
Apr-99	Hawaii, USA	85.3	74.10	NOAA (NMFS/PIFSC)
Apr-06	Hawaii, USA	70	35.45	NOAA (NMFS/PIFSC)
Jul-06	Hawaii, USA	67.5	33.60	NOAA (NMFS/PIFSC)
Jul-02	W. Australia	20	1.85	MTN (2004; no. 104, p. 3–5)
1983	W. Australia	31	3.30	MTN (2004; no. 104, p. 3–5)
Unknown	Unknown	11.5	0.17	M. Conti (*pers. comm.*)

Table 4
Growth rate $(\Delta L/\Delta t)$ and mid-length $(L_1+L_2)/2$ calculated from leatherback turtle growth data separated into 10 cm SCL data bins. For each data group (length bin) the standard deviations (SD) and total number of measurements (n) are given. *Indicates a significant decline in growth rate. (Tukey–Kramer post-hoc, $p<0.05$).

Length bin	Avg mid-lengths (cm SCL)	SD	Growth rate (cm year^{-1})	SD	n
<10 cm SCL	7.95	1.09	33.28	12.65	130
10 to 20 cm SCL	14.36	2.85	29.62*	11.00	259
20 to 30 cm SCL	24.65	2.88	34.81	10.53	115
30 to 40 cm SCL	34.32	2.74	34.21	13.87	77
40 to 50 cm SCL	44.56	2.49	26.77*	19.45	51
50 to 60 cm SCL	54.67	2.68	31.68	17.30	19
60 to 70 cm SCL	64.42	3.76	32.90	6.28	3

Leatherbacks from different populations, e.g., Atlantic, Pacific, and Indian Oceans, all had data on the same length–mass regression line. Wabnitz and Pauly (2008) have recently shown that the same is true of hard-shelled marine turtles. For instance, Pacific and Atlantic green and loggerhead turtles had a similar length–mass relationship. The values for the proportionality coefficient a (0.00021 and 0.00028, green and loggerhead, respectively) and scaling exponent b (2.89 and 2.82, green and loggerhead, respectively) are similar to our generalized relationship for leatherbacks ($a = 0.00021$, $b = 2.86$), suggesting all marine turtles are constrained by their similar body plans.

4.2. Growth

Our leatherback growth rates averaged 31.98 ± 2.8 cm year^{-1} for lengths of <10 cm SCL to 70 cm SCL and compare favorably with those found by Zug and Parham (1996) of 31.6 cm year^{-1} for juveniles of 8–37 cm SCL (from <10 to 40 cm SCL our growth rates averaged 32.98 ± 2.33 cm year^{-1}). However, their measurements of 23.1 cm year^{-1} for juveniles of 37–65 cm SCL are 21% less than our growth rates over the same length interval (29.22 ± 3.47 cm year^{-1}). While our initial growth rates agree with Zug and Parham (1996) they are nearly 3.5 times greater

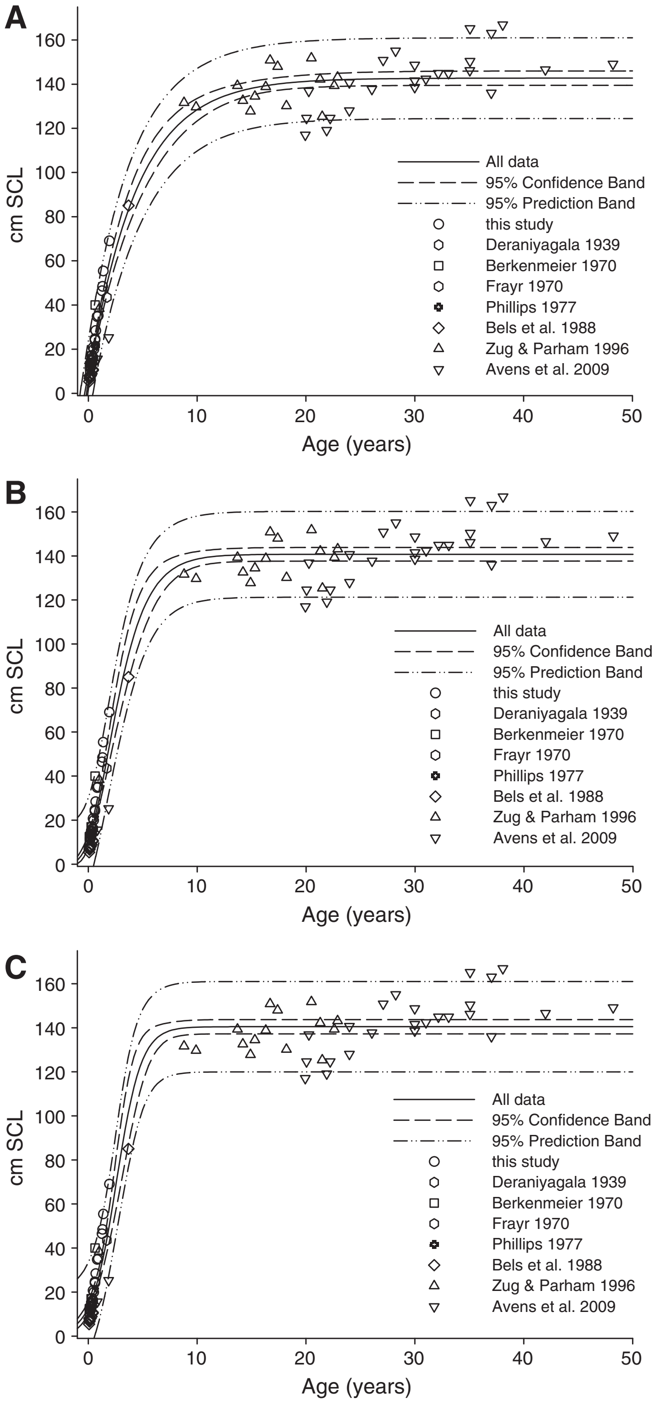

Fig. 2. The (A) von Bertalanffy, (B) Gompertz and (C) logistic growth functions for leatherback turtles: Black line: best-fit curve using nonlinear least squares (NLLS) regression. Medium dashed line: 95% confidence bands around the regression. Dash–dot–dot line: 95% prediction bands for the scatter of data pairs.

Table 5
Parameters from three growth models (von Bertalanffy, Gompertz, and logistic) for the length-at-age data and adult data from skeletochronology studies (Zug and Parham, 1996; Avens et al., 2009). Parameters include the asymptotic length in cm straight carapace length (L_∞), intrinsic growth rate year^{-1} (k), predicted age in years at length = 0 (t_0), adjusted regression coefficient (R^2), residual mean squares (MS_{res}), predicted age-at-maturity in years (age), and minimum length in cm SCL at maturity as given by the 95% prediction band (L_{min}). Standard error (SE).

Growth model	L_∞	SE	k	SE	t_0	SE	R^2	MS_{res}	age	L_{min}
VBGF	142.7	1.64	0.2262	0.021	−0.17	0.07	0.98	81.73	16.1	121
Gompertz	140.8	1.56	0.511	0.201	1.86	0.14	0.98	93.42	8.7	117
Logistic	140.4	1.63	0.883	0.121	2.6	0.2	0.97	103.71	6.8	116

than initial growth rates of loggerhead post-hatchlings determined from transit time in the North Atlantic (Hays and Marsh, 1997) and 4 to 11 times greater than juvenile (30 to 70 cm SCL) green and loggerheads from neritic foraging grounds (Mendonca, 1981). Leatherbacks are thought to be strictly oceanic–pelagic as juveniles (Bolten, 2003), eating a readily available diet of gelatinous zooplankton (Bjorndal, 1997; Salmon et al., 2004), and possibly stay in warmer equatorial waters (Eckert, 2002), thus, the dichotomy in growth rate between leatherbacks and cheloniidae is not surprising. While gelatinous zooplankton have low energy densities as prey items (Doyle et al., 2007), the high assimilation efficiency of jellyfish (80%; Wallace et al., 2006, Hatase and Tsukamoto, 2008) compared with crustaceans (65%; Zwarts and Blomert, 1990) and seagrass (34–69%; Bjorndal, 1997) may allow a greater energy turnover in leatherbacks versus pelagic and benthic cheloniidae. The coupling of higher assimilation efficiencies with warmer habitat would lead to higher growth rates of leatherbacks during early development (Avery et al., 1993), thus, allowing early attainment of sexual maturity at a large size. If leatherbacks were to maintain growth rates of 31.98 ± 2.8 cm year^{-1} they could attain the mean minimum nesting length (124 cm SCL, Stewart et al., 2007), found across all populations, in 4 years. This same approach led to an estimate that leatherbacks could attain sexual maturity in as little as 2–3 years. For instance, growth rates from captive turtles have been measured at 22 cm year^{-1} (Deraniyagala, 1939) to 52 cm year^{-1} (Birkenmeier, 1971). Adult growth rates have been measured at 0.2 cm year^{-1} (Price et al., 2004), thus juvenile growth rates either slowly decline with age or maintain themselves (linearly) until adulthood is reached and then drastically decline after the first nesting episode. Unfortunately, there are no measured growth rates for leatherbacks between 80 and 120 cm SCL.

Growth functions can be used from multiple data sets to fill gaps in our understanding of leatherback growth. Data were combined from our and other captive studies with adult skeletochronology length-at-age estimates in order to fit von Bertalanffy, Gompertz and logistic growth functions. Based on the combined length-at-age data set for leatherback growth the VBGF, Gompertz and logistic growth functions estimated that leatherbacks take 16.1, 8.7 and 6.8 years to attain mean nesting length, respectively. The estimates from the Gompertz and logistic functions are in agreement with the early attainment of sexually mature length from the extrapolation of early growth rates of captive turtles and corroborate the estimate of 6 years by Rhodin (1985) and Rhodin et al. (1996) based on the chondro-osseous (cartilage and bone) morphology of leatherbacks. The Gompertz growth function predicted linear growth from 20 cm SCL to nearly 120 cm SCL, and the logistic growth function predicted linear growth until mature nesting length is attained. Neither the Gompertz nor logistic function fit the initial growth data well, however, leading to high MS_{res}. The logistic function also gives the lowest L_∞ value, nearly 2.5 cm less than the VBGF. Furthermore, the Gompertz and logistic growth functions give L_{min} values of 117 and 116 cm SCL, which are within recorded measurements of nesting females but still near the smallest recorded (Stewart et al., 2007). Studies by Rhodin (1985) and Rhodin et al. (1996) suggest rapid growth in leatherbacks but chondro-osseous morphology is not an aging or growth rate technique.

The VBGF estimated 16.1 years for age-at-maturity, the highest of the three growth functions. The VBGF also resulted in the lowest MS_{res} and the highest L_∞ (142.7 cm SCL) and L_{min} (121 cm SCL) estimates, which corroborate a recent study by Stewart et al. (2007), suggesting a mean length for nesting leatherback populations worldwide (Atlantic, Pacific and Indian Oceans) of 147 cm SCL and an average minimum nesting length worldwide of 124 cm SCL (both SCL measurements converted from CCL). Our VBGF estimates are similar to Zug and Parham (1996), where k equals 0.226 and 0.286, respectively, and our age-at-maturity is slightly older (16.1 and 13.3 years, respectively). Furthermore, age-at-maturity estimates of 13–16 years corroborate those of Dutton et al. (2005) who estimated that leatherbacks take 12–14 years to mature, based on large increases in numbers of nesting females after intensive conservation efforts produced an order of magnitude increase in hatchling production on St. Croix, U.S. Virgin Islands. A long-term DNA finger-printing study of the same turtles suggested that recent first-time nesters were the genetic offspring of turtles sampled in the 1980s, again suggesting age-at-maturity estimates <20 years (Dutton et al., 2005). Our data are at the lower end of the spectrum of the Avens et al. study (2009), which suggests leatherbacks could reach lengths characteristic of sexual maturity in 16–22 years; however, the median age-at-maturity was estimated at 24.5–29 years. This discrepancy may result from the available data sets and estimated parameters in the growth functions. In light of (i) the MS_{res}, L_∞ and L_{min} estimates, (ii) the corroboration of skeletochronology-growth function studies (Zug and Parham, 1996), (iii) conservation based and genetic (Dutton et al., 2005) aging studies, and (iv) the unlikelihood of linear growth from hatching to 120 cm SCL, we suggest the VBGF provides a more biologically relevant age-at-maturity estimate of 16.1 years. Furthermore, the VBGF fit the data much better than the Gompertz and logistic models, considering the distribution of residuals.

Table 6
SCL of leatherback turtle bycatch in artisanal, drift gill net (DGN) and longline fisheries of the Pacific Ocean. CA–OR is used as abbreviation for the DGN fishery off California and Oregon, USA. This list of leatherbacks represents only those animals that were measured and not the total number of bycatch incidents.

SCL (cm)	Location/fishery	Source
39	American Samoa/Longline	MTN (1994; no 66, p. 3–5)
50	Hawaii/Longline Observer data	NOAA (NMFS/PIFSC)
64.5	Hawaii/Longline Observer data	NOAA (NMFS/PIFSC)
67.5	Hawaii/Longline Observer data	NOAA (NMFS/PIFSC)
70	Hawaii/Longline Observer data	NOAA (NMFS/PIFSC)
70.4	Hawaii/Longline	Fish. Bull. (2002; no 100, p. 876–880)
71	Hawaii/Longline Observer data	NOAA (NMFS/PIFSC)
80	Hawaii/Longline Observer data	NOAA (NMFS/PIFSC)
85.3	Hawaii/Longline	Fish. Bull. (2002; no 100, p. 876–880)
87.5	Hawaii/Longline Observer data	NOAA (NMFS/PIFSC)
130	Hawaii/Longline Observer data	NOAA (NMFS/PIFSC)
98–123	Peru/Artisanal	CCB (2007; no 6, p. 129–134)
111–165	Peru/unknown	CCB (2007; no 6, p. 129–134)
113–160	Gulf of California/Longline	CCB (2007; no 6, p. 137–141)
132	CA–OR/DGN	NOAA (NMFS/SWFSC)
136	CA–OR/DGN	NOAA (NMFS/SWFSC)
155.5	CA–OR/DGN	NOAA (NMFS/SWFSC)
160	CA–OR/DGN	NOAA (NMFS/SWFSC)
Mean (SD)		
74 (23)	Hawaii/Longline	NOAA (NMFS/PIFSC)
113 (12)	Peru/Artisanal	CCB (2007; no 6, p. 129–134)
137 (6)	Peru/unknown	CCB (2007; no 6, p. 129–134)
139 (12)	Gulf of California/Longline	CCB (2007; no 6, p. 137–141)
146 (14)	CA–OR/DGN	NOAA (NMFS/SWFSC)

Analysis of our data suggests that leatherbacks mature at a younger age than cheloniid turtles, and they do so at a larger length. For example, loggerhead and green turtles take 15 to 40 years to reach a sexually mature length of ~90–100 cm SCL, respectively, with green turtles spending nearly 20 years as juveniles (Limpus and Walter, 1980; Mendoca, 1981; Frazer and Ehrhart, 1985; Frazer and Ladner, 1986; Bjorndal and Bolten, 1988; Seminoff et al., 2002). This suggests that while the early reports of Rhodin (1985) and Rhodin et al. (1996) of 3–6 years for maturity in leatherbacks are incorrect, their suggestion that leatherbacks have fast growth rates is undoubtedly correct. Indeed, leatherbacks attain substantially longer mean nesting lengths (147 cm SCL, Stewart et al., 2007) in considerably less time than any other marine turtle.

Unlike leatherbacks, most hard-shelled turtles experience marked habitat shifts through ontogeny and concomitant changes in diet (e.g., Bjorndal and Bolten, 1988). Such transitions may be reflected in different growth patterns during those life stages (Chaloupka and Musick, 1997). Leatherbacks, however, are oceanic–pelagic animals throughout their life history (Bolten, 2003) and have no known diet shifts after hatching. Their diet consists solely of gelatinous zooplankton (Bjorndal, 1997; Salmon et al., 2004). While tracking studies have shown prolonged coastal foraging by leatherbacks (e.g., Houghton et al., 2006; James et al., 2007), direct observations have confirmed that even in these habitats leatherbacks are feeding on pelagic jellyfish prey (James and Herman 2001; Houghton et al. 2006). This further justifies applying the monotonic VBGF to leatherback growth data.

Data on leatherback bycatch in longline and drift gillnet (DGN) fisheries in the Pacific Ocean (Table 6; Work and Balazs, 2002; Seminoff and Dutton, 2007) show a dichotomy in the length range of the animals caught by the two types of fishery. These differences probably reflect different leatherback length class assemblages in the zones in which the fisheries operate, with smaller turtles typically being caught in warmer waters. All leatherbacks <90 cm SCL (mean 74 ± 23 cm SCL; Table 6) were caught in warmer equatorial waters off American Samoa and Hawaii (sea surface temperature (SST) range: 21.7–28.9 °C; NDOC 2008). Conversely, data for the DGN fishery in the cooler waters off California and Oregon (SST range: 5.6–20 °C; NDOC 2008) report only adult leatherbacks (mean 146 ± 14 cm SCL; Table 6). The artisanal fisheries of Peru, operating in relatively stable sea temperatures (SST range: 16–20.5 °C; Coker, 1918) caused by the Humboldt Current, entangle subadult leatherbacks (mean 113 ± 12 cm SCL; Table 6). The trend of larger leatherbacks being caught in colder waters is corroborated by recent studies in the North Atlantic showing a latitudinal gradient in body size with smaller turtles excluded from higher latitude foraging grounds (James et al., 2007; Witt et al., 2007). Furthermore, Eckert (2002) reported that leatherbacks do not move above ~30°N until they are >100 cm SCL. The difference in SCL with water temperature is probably a reflection of the thermoregulatory capabilities of larger leatherbacks allowing them to exploit colder, more productive foraging grounds (Bostrom and Jones, 2007). A 100 cm SCL corresponds to an age of 5.2 years and a mass of 96 kg, given our VBGF and length–mass relationships. This may be the size at which leatherbacks's thermoregulatory capabilities allow them to move into colder waters where they can exploit different assemblages and perhaps a greater abundance of gelatinous zooplankton.

The smallest leatherbacks interacting with fisheries are ~70 cm SCL which may represent the length at which leatherbacks are large enough to entangle, foul hook, or ingest baits from fishing gear. Alternatively, this may represent the life history stage at which leatherbacks are congregating in fishery zones where greater abundance of gelatinous prey may be found. While the reason for the increasing number of interactions after 70 cm SCL (2.8 years of age based on our VBGF) remains unknown, it places a greater human-induced mortality on leatherbacks earlier in their life history. Assuming that VBGF accurately depicts growth, leatherbacks require 16.1 years to reach mean nesting length, and >80% of their juvenile and their entire adult life finds them in jeopardy of fishery induced mortality. All studies on early growth in leatherbacks suggest that 70 cm SCL is attained rapidly, i.e., within 3 years, therefore, regardless of what growth function or age estimate is used, leatherbacks spend the majority of their lives at risk of marine fishery interactions. While attaining a large mass quickly decreases natural mortality from predation, it unfortunately puts leatherbacks at a greater risk of fishery interactions from an early (juvenile) life history stage.

Decades of intense egg harvesting and widespread incidental bycatch from fisheries have led to drastic declines in leatherback populations, especially in the Pacific Ocean (Spotila et al., 2000; Alfaro-Shigueto et al., 2007; Sarti-Martinez et al., 2007). Although our data confirm the vulnerability of leatherbacks to capture and incidental mortality in various types of fishing gear to occur for the majority of their life, our results also suggest that their growth rate, which allows them to reach mean nesting length after only 16.1 years, offers potential for relatively rapid population recovery, as indicated by Dutton et al. (2005). Such recovery, however, depends on the continued protection of nesting females and nests to ensure the greatest recruitment of hatchlings and implementation of effective fishing regulations to minimize mortality of primarily adult leatherback turtles that are critical to prevent population extinction (Congdon et al., 1993).

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