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Age and Growth of Juvenile Loggerheads (Caretta caretta), from Chesapeake Bay

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AGE AND GROWTH OF JUVENILE LOGGERHEADS, (*Caretta caretta*), FROM CHESAPEAKE BAY

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by

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APPROVAL SHEET

This thesis is submitted in partial fulfillment of

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DEDICATION

This thesis is dedicated to my parents, Rev. and Mrs. Woodrow J. Klinger, who provided an unending amount of encouragement, support and faith.

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ABSTRACT

Juvenile loggerhead (Caretta caretta) sea turtles in Chesapeake Bay were tagged with tetracycline to establish a chronology for deposition of bone growth rings. Seven recaptures, encompassing intervals of one to three years demonstrated that one growth ring was deposited in humeri during each period of reduced winter growth. Growth rings were deposited on an annual basis, at least during the juvenile life history stage. Between six and ten growth rings were observed in 88 stranded juveniles. However, up to eight additional rings may have been absorbed into the bone medullary cavity (core) during growth, as estimated from back calculated lengths of juvenile humeri. Alternately, rings may not be deposited during the first few years of life, when loggerhead juveniles are believed to inhabit the warm North Atlantic gyre. In either case, seven to fifteen years may be a more accurate estimate for age of juvenile loggerheads in Chesapeake Bay. The Von Bertalanffy growth equation provided a satisfactory fit to this data, and yielded an estimated age at maturity of 20 - 30 years.

AGE AND GROWTH OF JUVENILE LOGGERHEADS (*Caretta caretta*) FROM CHESAPEAKE BAY

INTRODUCTION

Life history parameters of marine turtles are difficult to estimate due largely to logistic aspects of studying migratory marine animals. Only when sexually mature females return to nest on shore do large numbers of them become accessible for analysis. Through most of the life cycle, sufficient numbers have not been available to determine population characteristics. This inability to produce demographic profiles for marine turtle species has impeded our understanding and management of these endangered animals.

Available evidence indicates that chelonid turtles are long lived, slow growing animals (Carr, 1967). However, age at sexual maturity remains a matter of debate, despite predictions from captive loggerheads, *Caretta caretta*, (Caldwell, 1962 (6-7 years); Uchida, 1967 (6-7 years); Frazer and Swartz, 1984 (22 years)) and captive hawksbills, *Eretmochelys imbricata*, (Witzell, 1980 (3.5 years); Brown, et al., 1982 (6 years)). Growth curves have been established for green turtles, *Chelonia mydas*, and loggerheads based on the distribution of carapace lengths among sexually mature females (Hendrickson, 1958; Le Toquoin, et al., 1980; Frazer and Ladner, 1985). Juvenile growth rates have also been estimated for recaptured green turtles (Carr and Goodman, 1970; Balazs, 1979; Limpus and Walter, 1980; Mendonca, 1981; Frazer and Ehrhart, 1985), hawksbills (Limpus, 1979) and loggerheads (Limpus, 1979; Mendonca, 1981; Zug et al., 1984; Frazer and Ehrhart, 1985).

Hard part determinants of growth have been important in demographic research in amphibians and reptiles (Klenenberg and Smirna, 1969; Hemlaar and Van Gelder, 1980; Smirna, 1974, Castanet, et al., 1977; Buffrenil, 1980), in bony fishes (NOAA Technical Report, 1983; Bagenal, 1973) and, more recently, in elasmobranchs (Gruber and Stout, 1983) and mammals (Klenezal, 1973; Hohn and Frazer, 1980). Mattox (1935) first suggested the possibility of periodic growth rings in terrestrial turtles, but the accuracy of growth rings to indicate age in reptiles has been debated (Cagle, 1954; Sexton, 1959; Legler, 1960; Suzuki, 1963; Hammer, 1969; Dobie, 1971; Graham and Doyle, 1977). Castanet and Cheylan (1979) examined the humeri and femurs of two temperate tortoise species, (Testudo humani and Testudo graeca), concluding that osteological ring growth was annular.

Since 1979 researchers at the Virginia Institute of Marine Science (VIMS) have monitored the sea turtles which seasonally inhabit Chesapeake Bay (Musick et al., 1984; Lutcavage and Musick, 1985). Ninety percent of stranded turtles are loggerheads. Kemp's ridleys (Lepidocheyls kempi), leatherbacks (Dermocheyls coriacea), and green turtles comprised the other ten percent. Most strandings occurred in late May to late June when turtles enter seasonal feeding areas in Chesapeake Bay. At this time the size ranges for all species is narrowly limited. Over eighty percent of loggerheads examined were between 50 cm and 80 cm carapace length (Fig. 1), well below size at maturity. The dominance of this size class in Chesapeake Bay provided an unusual opportunity to study large numbers of juvenile loggerheads.

In this study I hypothesize that growth rings deposited in juvenile loggerhead humeri are annular. To test this hypothesis a known time label, oxytetracycline, was applied to the juveniles. Tetracycline has proven effective for this purpose in other vertebrates (Weber and Ridgeway, 1967; Smirna, 1972; Castanet, et al, 1974; Castanet, et al. 1978; Gruber and Stout, 1983). It is deposited in growing bone at time of injection and will subsequently fluoresce under ultraviolet light (Harris, 1960). Tetracycline has already proven to be an effective in vivo mark for captive farm-reared green turtles (Frazier, 1985). However, growth rates in captivity probably differ from growth rates in the wild. In this study the time label was applied to turtles in a wild population. When a marked turtle was recovered, the rate and type of bone deposition during a known time interval could be observed. Once the depositional rate was established, observed rings could determine whether growth was annular. Thus, this study could validate growth rings or laminae as the product of alternate periods of slow winter growth and rapid summer growth. If so, a correlation of carapace length to ring number could be used to establish an accurate growth curve.

METHODS

Humeri were removed from one or both foreflippers of deceased loggerheads examined by VIMS personnel between 1983 and 1985. The following measurements were taken whenever possible (see Fig. 2 for description):

Carapace Length Straight Line (CLS)
Carapace Width Straight Line (CWS)
Carapace Length Curved (CLC)
Carapace Width Curved (CWC)
Head Length (HL)
Head Width (HW)
Plastron Length (PL)
Plastron Width (PW)
Plastron Width with Bridge (PWB)
Weight (WT)

Bones were stripped of muscle tissue and air dried. Humeri were measured by methods described by Zug et al. (1984) (Fig. 3):

Maximum Length (ML)
Longitudinal Length (LL)
Ulnar Process length (UPL)
Proximal Length (PL)
Proximal Width (PW)
Radial Process Length (RPL)
Deltopectoral Crest Width (DpCW)
Medial Width (MW)
Distal Width (DW)
Maximum Head Diameter (MaxHD)
Minimum Depth (MinDepth)
Weight

Dry humeri were initially cut with a Raytech rock saw just below the deltopectoral crest. The sectioned bone was cut into thin (one to three mm) wedges with a Buehler

Isomet 11-1180 low speed saw and 11-4244 high concentration diamond wafering blade. Sections were decalcified with an eight percent formic-hydrochloric acid solution. A five percent ammonium oxalate - five percent ammonium hydroxide solution determined the endpoint of decalcification (David Zwerner, pers. comm.). Dehydration, clearing and impregnation of paraffin (56^{o} C melting point) into the tissue were completed with an autotechnicon over 24 hours. After infiltration in a paraffin dispenser and vacuum treatment for 15 minutes, tissues were set in paraffin blocks. Seven micron sections were cut on an AO 820 microtome (033 inch heavy duty thick AO blades). Slides were stained with Harris hematoxylin and eosin-y. Rings were counted during three independent trials with a light microscope at 10X magnification. Whenever possible, rings were counted from the medullary cavity (core of spongy cancellous bone) to the periosteum (outer hard compact bone) both on the short and long axis. Minimum and maximum counts for both axes were recorded and means for each set of measurement trials were calculated. In addition, distances were measured with a monostat micrometer from the focus (center) of the medullary cavity to each winter ring and periosteum (radius length). Regression between CLS and radius length provided back calculations of length at age using the

Fraser-Lee formula:

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

where, L' = length at first growth ring
C = correction factor related to the y intercept
S' = radius length from the focus to the first ring
S = total radius length
L = length at capture

Regressions between body measurements, humeri measurements and mean ring number were calculated with the BMDP package available from the Statistical Analysis Systems (SAS, Incorporated, 1985).

During the period 1983 - 1987, over 200 live loggerheads (caught in pound nets by Chesapeake Bay fishermen) were examined. These animals were measured, tagged with monel tags on both foreflippers, and injected with 25 mg/kg oxytetracycline (LA-200 Liquamyacin, Pfizer). The injection was given intramuscularly on the ventral shoulder of either foreflipper. Turtles usually were released immediately after tagging.

Healthy recaptures were placed in holding tanks at VIMS until a bone biopsy could be conducted for removal of a humeral plug taken below the deltopectoral crest. Undecalcified sections were processed with methyl methracrylate for 48 hours and polymerized at 37^{o} C (John Tarpley, personal communication). Eukitt medium was used for mounting 50 to 70 micron sections on slides. A fluorescent ring could be observed with an ultraviolet light under a binocular microscope at 10X. Measurements were taken from the fluorescent ring to the periosteum and from the fluorescent ring to the bone medullary cavity. Decalcified sections were histologically prepared so that growth rings could be visualized under transmited light. Since fluorescent tetracycline rings must be observed under ultraviolet light and growth rings must be observed under transmitted white light, these two ring types were measured separately. Measurements were taken from both the (external) periosteum and the (interior) medullary cavity, providing an accurate comparison of ring positions. Total growth was measured from the medullary cavity to periosteum to observe possible stretching of tissue during histological processing.

Several different carapace length measurements were correlated with humeri lengths from 88 stranded loggerheads, to determine if r values were sufficient for direct carapace/ring count estimation. Mean age and mean growth rate were calculated for each ten cm size class of CLS and CLC. A Kruskal-Wallis nonparametric test for ranked data was used to determine significance between size classes. Nonparametric multiple pairwise comparisons were tested for significance between pairs of size classes (Zar, 1984). Nonlinear regression (NLIN) procedures from the SAS computer systems was used to estimate parameters of the Von Bertalanffy growth equation:

$$L_t = L_\infty (1 - e^{-k(t-t_o)})$$

and logistic growth equation:

$$L_t = \frac{L_\infty}{(1 - e^{-k(t-t_o)})}$$

where, L_t = carapace length at time t
L_∞ = asymptotic length
e = natural logarithm
k = intrinsic rate of growth
t = ring count or age
t_o = theoretical age at time zero

L_∞, k and t_o were estimated in an analysis of variance for nonlinearity between straight carapace length and ring count (age). Curved carapace length and ring count were also compared. Back calculated lengths at age one were linearly regressed against length at capture to determine if rings were being absorbed into the medullary cavity. The number of resorbed rings, calculated by the regression equation and based on the smallest radius length, was added to observed ring number to yield an alternate (and possibly more accurate) estimate of age.

RESULTS

Recapture and biopsy of loggerhead turtles tagged with tetracycline demonstrated discrete growth intervals and indicated growth rings in juveniles are deposited on an annual basis (Table 1). In 1985 three marked loggerheads were recaptured and biopsied. All three had overwintered in the wild after tetracycline injection. Only one of these turtles, MT-120-84 showed a fluorescent ring. A biopsy was performed 393 days (1.08 years) after injection. Total growth measurements were very similar for both tissue types in all recaptures, such that tissue stretching was considered negligable. In the undecalcified section, the tetracycline ring was visible on the short axis 0.041 mm from the periosteum. On the decalcified section, the first and second winter rings were 0.022 mm and 0.052 mm from the periosteum, respectively. Thus, the tetracycline ring was observed between the two winter rings, strongly suggesting annular deposition.

No tetracycline tagged loggerheads were recaptured in 1986. In 1987, Biopsy plugs were recovered from six tetracycline marked loggerheads. Five produced fluorecent rings. Of these five, time at large was one year for three recaptures, two years for one recapture and three years for one recapture (Table 2). Two of the loggerheads recaptured after one year, MT-30-86 (Fig.4) and MT-36-86 revealed one ring beyond the tetracycline mark. In the other single year recapture, the fluorescent ring and the outermost decalcified ring were too close to the edge to determine their respective positions. The specimen MT-42-85 (K4033;K4034) recaptured after two years had two outer winter rings which measured 0.012 and 0.021 mm from the periosteum. The tetracycline ring was observed at 0.022 mm from the periosteum. Humeri from a three year recapture, MT-122-84 had a total of eight growth rings in the decalcified section. The four outer rings were 0.004 mm, 0.010 mm, 0.015 mm and 0.067 mm from the periosteum. The tetracycline ring, 0.018 mm from the periosteum, was between the third and fourth winter growth rings (Fig. 5).

Linear regression between straight carapace length (CLS), curved carapace length (CLC) and humerus length was high (0.96; Appendix, Fig. 1 and 2). Based on this correlation and the results of the tetracycline data, ring counts were used to estimate age for 88 stranded loggerheads. Since rings on the long humeral axis were often unreadable, short axis readings were used for further analysis. Seventy eight percent of examined turtles had between six and ten growth rings (Fig. 6).

Mean growth rate and mean age were ranked by 10 cm increments of CLS. A nonparametric Kruskal-Wallis test was used to show significance for growth rate (X^2=20.33, df=6, P>0.0024) and age (X^2=26.96, df=6, P>0.0001) among the different size classes. The size classes for CLC also were significant (growth rate: X^2=21.22, df=6, P>0.0017; age: X^2=30.45, df=6, P>0.0001). To determine which size class had significantly different growth rates, multiple pairwise comparison tests were used. The CLS growth rate of size class 90.0 - 99.9 was significantly slower than 60.0 - 69.9 size class (Q=3.20, df=7, P>0.05)(Table 3). Age for size class 40.0 - 49.9 was significantly younger (df=7, P>0.05) than 60.0 - 69.9 (Q=3.05), 70.0 - 79.9 (Q=3.60) and 100.0 - 110.0 (Q=3.78) size classes (Table 4). Mean growth rate (CLC) of size class 100.0 - 110.0 was significantly lower (df=7, P>0.05) from 50.0 - 59.9 (Q=3.06) and 60.0 - 69.9 (Q=3.27) size classes (Appendix, Table 3). The largest size class was also significantly older than 40.0 - 49.9 (Q=3.55), 50.0 - 59.9 (Q=4.44) and 60.0 - 69.9 (Q=3.54) size class (Appendix, Table 5). See Appendix, Tables 1, 2, 4, and 6 for pairwise comparisons.

These pairwise comparisons depend on the difference in rank means over the standard error (SE):

$$SE = \sqrt{((N(N+1)/12) - (\{T/12(N-1))(1/n_a))+(1/n_b)}$$

where, N = total number observations

$\{T$ = sum of number of tied ranks = $\{(t^3 - t)$

n_a = number of observations in sample a

n_b = number of observations in sample b

If sample size or {T is low, then SE will be high and resultant Q test will be lower than table value. The largest size class (100.0 - 110.0) had a small sample size (n = 2) which probably prevented finding significance with that class size and other ranges. The sample size and difference in pairwise mean ranks were high enough for 60.0 - 69.9 and 90.0 - 99.9 comparison to show significance. There was no significant difference in growth rate among the other size classes, suggesting a relatively homogeneous (linear) rate of growth throughout the juvenile life history stage. This homogeneous growth rate for 50 - 80 cm turtles is similar to Zug's estimate for turtles in the 60 - 80 cm CLC range, and is consistent with the Von Bertalanffy curve. However, my estimate of growth rate (0.64 - 8.99 cm/yr) was slightly lower (but not significantly) than that of Zug, et al. (1.2 - 19.8 cm/yr). Individual growth rate for each sex was not calculated due to the low numbers of males availabe for analysis.

This data indicates that growth rate significantly decreases near sexual maturity. While growth may be nearly linear within specific life stages, a nonlinear growth equation is likely to provide the best general model for loggerhead populations. Dunham (1978) suggested that the appropriate model for a given data set had the lowest residual mean square. Analysis of variance for nonlinear regression of Von Bertalanffy and logistic growth curves were calculated with both CLS and CLC (Appendix, Tables 7 and 8). By Dunham's criteria, the Von Bertalanffy equation provides a slightly better fit than the logistic growth equation for both types of carapace measurement. However, with the growth curve generated by direct ring counts (as indicators of age), estimated length at time zero (hatchling) is about 37 cm (Fig. 7). Despite this inaccuracy, the curve is similar to a Von Bertalanffy curve generated by Frazer and Ehrhart (1985) over the upper size range in this study. To correlate actual ring count with age, back calculations were used to estimate length at time of first growth ring. Log linear regression of bone radius length against carapace length was significant (r^2=0.51, F=31.74, P>0.001). Length at the first growth ring calculated with the Fraser-Lee equation was linearly regressed with length at capture (Fig. 8). Since the correlation was significant (r^2=0.72), that is, larger lengths at capture had larger estimated lengths at ring one, ring loss into the medullary cavity is probably occurring on a continual basis. Estimates of ring loss were determined with a log linear regression of radius length against observed ring number (Fig. 9) (Ketchen, 1975). The smallest loggerhead (40.5 cm CLS), with a medullary cavity diameter of 1.02 mm, was used as a reference or point of no ring loss. The difference in core diameter from larger turtles were used in the regression equation to calculate number of missing rings. Once the number of "lost rings" was added to observed ring number, the Von Bertalanffy equation provide more realistic estimates of growth parameters. The adjusted age growth curve was also in close agreement with Frazer and Ehrhart (1985), especially in the juvenile life stages (Fig. 10). See Appendix, Tables 9 and 10 for analysis of variance for nonlinear regression of Von Bertalanffy and logistic (CLS and CLC) for adjusted ages. Logistic growth curves for observed and adjusted ages are depicted in Appendix, Fig. 3, 4 and 5.

DISCUSSION

The temporal pattern of ring deposition must be established in order to use growth rings from skeletal hard parts for age determination (Beamish and McFarlane, 1983; Brothers, 1987). In the case of juvenile loggerheads sampled in Chesapeake Bay, annular deposition of bone rings allows a greater understanding of growth rates and age at maturity.

Size classes in Chesapeake Bay encompass a range of seven years or more. Many factors are probably responsible for this range, including differences in feeding success, age at recruitment onto feeding grounds, post hatchling environment, and climatic variables. Although these turtles have access to the same feeding areas, individuals grow at different rates (Wood and Wood, 1977; Nuitja and Uchida, 1982). In diamond-back terrapins, (*Malaclemys terrapin*) Hildebrand (1932) demonstrated a four year range of age at sexual maturity within a single clutch.

Most tetracylined marked turtles had fluorescent rings observable under ultraviolet light. The cases that did not may reflect to an insufficient amount of tetracycline at the time of injection, position of biopsy plug when removed (transverse removal produces a blurred or unreadable band), or degradation of the outer edge of the bone during histological preparation.

In the cases where a fluorescent tag was visible, growth ring number was consistent with annular deposition. However, it is possible that annular growth rings are not deposited in all life history stages. If hatchlings inhabit a tropical pelagic habitat, as is widely believed, growth at that stage may be of a continuous (noncyclic) type. Alternately, more than one ring may be deposited per year in hatchlings, due to patchiness in food availability. Growth rate in hatchlings may vary greatly among individuals in the wild. However, this data indicates annular growth rings are established after juveniles recruit to seasonal feeding grounds. Linear regression of back calculated lengths against length at capture strongly suggest the first few growth rings in juveniles are obscured or absorbed by subsequent expansion of the medullary core. This reabsorption process probably continues throughout life.

It was not possible to determine if smaller loggerheads (< 40 cm CLS) also absorb growth rings since no specimens in this study were less than 40.5 cm. Back calculations were based on the smallest turtle, which (for the purposes of this analysis) was assumed to be the point of initial ring loss. It is not implied that ring loss does not occur below 40 cm, but the smallest turtle (40.5 cm) provided the best reference point in this data set. Capture of smaller turtles might demonstrate that ring loss occurs at earlier stages. Therefore, further analysis of turtles in the 10 to 40 cm size range is needed to completely understand loggerhead growth.

Estimates for age at maturity are subjective because individuals probably reach sexual maturity over a broad size range. Mature specimens in the western Atlantic vary in size from 75 - 109 cm CLC on Melbourne Beach, FL (Bjorndal, et al., 1983) to 78 - 142 cm CLC for Little Cumberland Island, GA (T. Richardson, personal communication). Zug estimated age at maturity (based on a mean size of 86.0 CLC) at 13 - 15 years. Mendonca (1981) estimated maturity at 10 - 15 years, based on minimum size of nesting females at Merritt Island, FL (75.0 CLS). Because growth rate is extremely slow in adults, Frazer and Ehrhart (1985) suggested that mean size of nesting females is the best indicator of average age at maturity. They reported an average size of 92.2 cm CLS (for loggerheads nesting on Merritt Island, FL), and reported an age at maturity of 30 years. Since Virginia is at the northermost edge of the loggerhead nesting range, averaging two nests per year (Musick, et al., 1984), Chesapeake Bay juveniles that survive to maturity must nest further south. Therefore, a meaningful estimate of size at maturity must be based on data from rookeries at Cape Romain, SC (Baldwin and Loften, 1959), Little Cumberland Island, GA (T. Richardson, personal communication) and Florida (Stoneburner, 1980), where minimum size at maturity is estimated at 90 cm CLS.

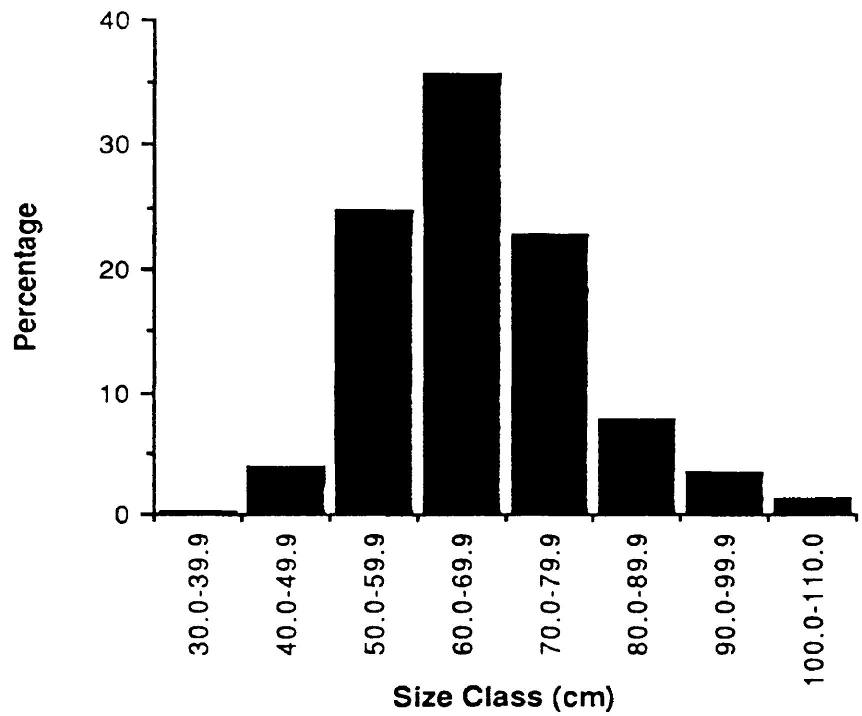
With the age estimates adjusted for ring loss, the Von Bertalanffy growth equation predicts an age at maturity of 20 years (Fig. 10). Von Bertalanffy growth curve for CLC data, once adjusted for back calculated ages, was similar to the CLS curve (Appendix, Fig. 5). This estimate agrees with an age at maturity of 12 - 30 years proposed by Frazer and Ehrhart (1985), based on recaptured loggerheads. However, it is greater than the estimates of Mendonca (1981); 10 - 15 years, and Zug et al. (1984); 13 - 15 years. This discrepancy may be due to different methods of analysis. Mendonca and Zug both used a simple linear regression whereas Frazer and Ehrhart (1984) and I used the nonlinear Von Bertalanffy and logistic growth curves to express growth. Since juveniles grow faster than adults, the nonlinear functions probably better fit the data. The Von Bertalanffy equation gives a better fit to known life history parameters while the logistic growth equation yields a clearly inappropriate estimate of length at younger ages (< 10 years). (Appendix, Fig. 3 and 6). Therefore, data are consistent with Witzell's (1980) statement that the Von Bertalanffy growth curve seems to best describe the type of growth observed in marine turtles.

However, the logistic growth curve adequately fits captive loggerhead growth (Uchida, 1967; Frazer and Schwartz, 1984). Frazer and Ehrhart suggest that a detrimental crowding affect may inhibit captive growth in the first years. This lag phase may not exist in wild populations and could explain why the Von Bertalanffy equation provides the better fit for growth in the wild.

Age estimates for marine turtles are difficult to generate due to long lifespans, slow growth rate, and extensive variation in growth rate among juveniles. Annular growth rings, as demonstrated by tetracycline tagging, can increase our understanding of age and growth in these threatened animals. However, several mediating factors, including ring reabsorption and habitat switching (in successional life stages) must be considered in any analysis of age and growth based on bone ring deposition.

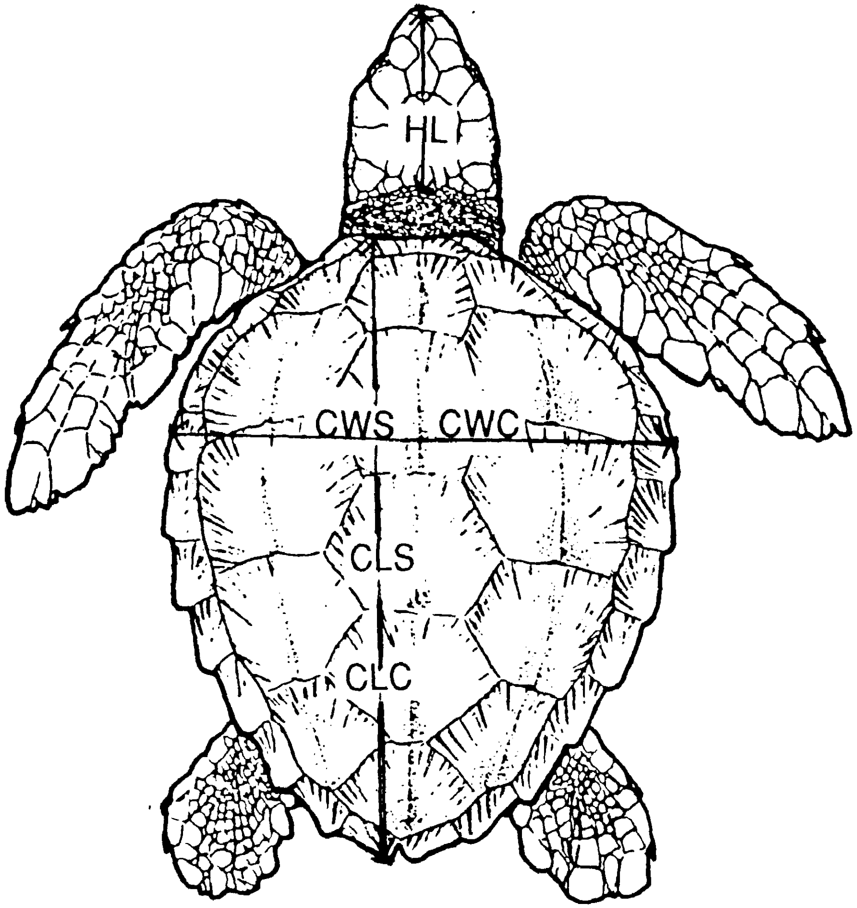
TABLES AND FIGURES

Fig. 1. Frequency distribution of size classes (straight carapace length) for loggerheads examined in Chesapeake Bay, 1979-1985. Data compiled from live and dead stranded individuals (N=454).



Percentage
40
30
20
10
0
30.0-39.9
40.0-49.9
50.0-59.9
60.0-69.9
70.0-79.9
80.0-89.9
90.0-99.9
100.0-110.0
Size Class (cm)

Fig. 2. Diagram of standard carapace and plastron measurements. Abbreviations in text.


HL
CWS
CWC
CLS
CLC

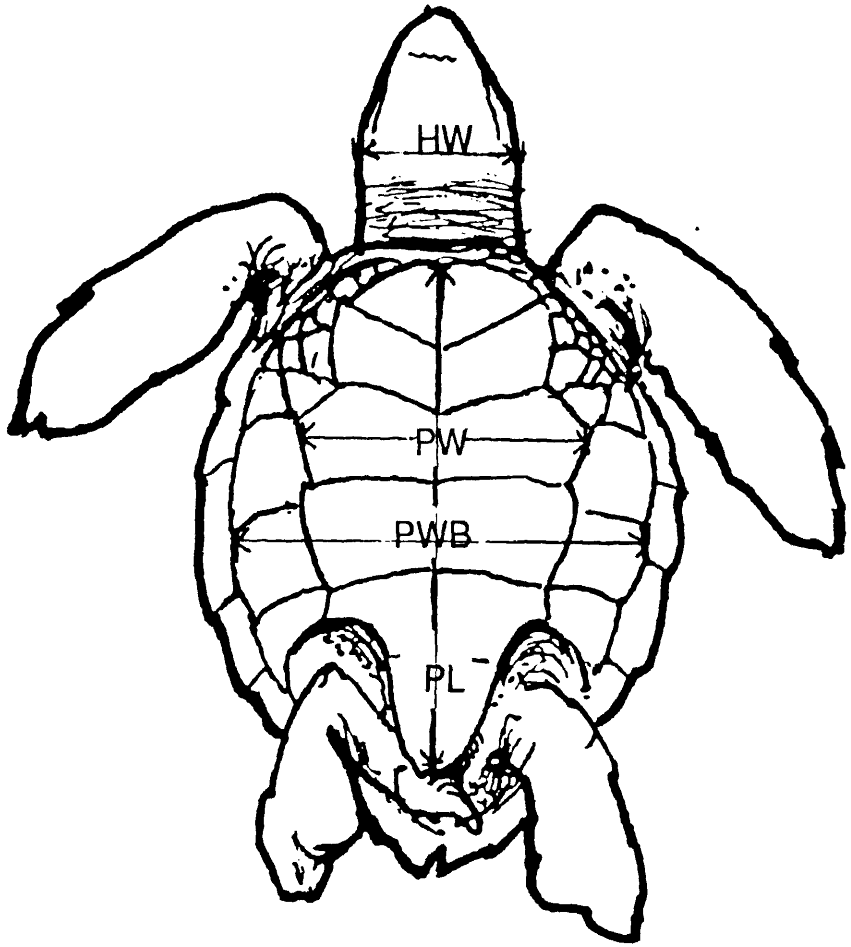
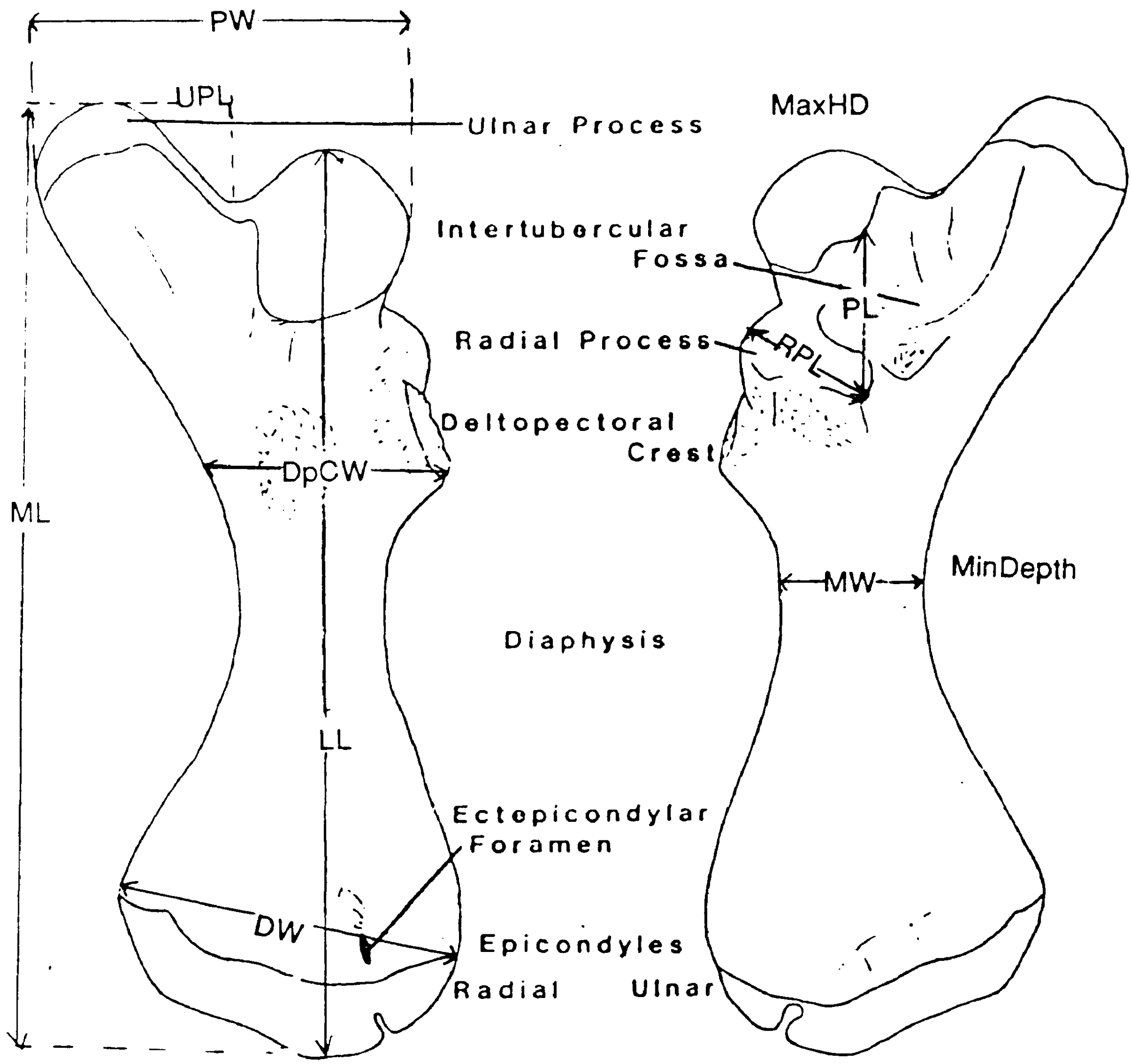

HW
PW
PWB
PL

Fig. 3. Diagram of standard humeri measurements modified from Zug, et al. (1984). Abbreviations defined in text.



- From Zug, 1984

Table 1. Summary of recapture data for tetracycline tagged loggerheads.

Tag Numbers	Tetracycline Date	Biopsy Date	Time Interval (yrs)	Fluorescence Observed
ONE YEAR:				
K4653;K4654	6-15-84	9-25-85	1.28	no
K4636;K4556	8-13-84	9-25-85	1.12	no
K4568;K4569	8-13-84	9-10-85	1.08	yes
K2771;K6421	6-27-86	7-22-87	1.07	yes
K6448;K6449	7-03-86	7-20-87	1.05	yes
G1059;G1060	8-06-86	7-08-87	1.17	yes
K6431;K6432	10-15-86	7-08-87	0.81	no
TWO YEAR:				
K4033;K4034	6-06-85	7-22-87	2.13	yes
THREE YEAR:				
K4640;K4641	8-13-84	7-22-87	2.94	yes

Table 2. Summary of growth ring data from tetracycline tagged loggerheads.

Tag Numbers	Time Interval (yrs)	Growth CLS (cm)	Growth CLC (cm)	Number Rings After Tetracycline
ONE YEAR RECAPTURES				
K2771;K6421	1.07	0.3	0.7	1
G1059;G1060	1.17	0.9*	1.3*	on edge
K6448;K6449	1.05	0.5	1.3	1
K4638;K4639	1.08	0.4	-	1
TWO YEAR RECAPTURES				
K4033;K4034	2.13	3.1	4.0	2
THREE YEAR RECAPTURES				
K4640;K4641	2.94	2.9	3.9	3

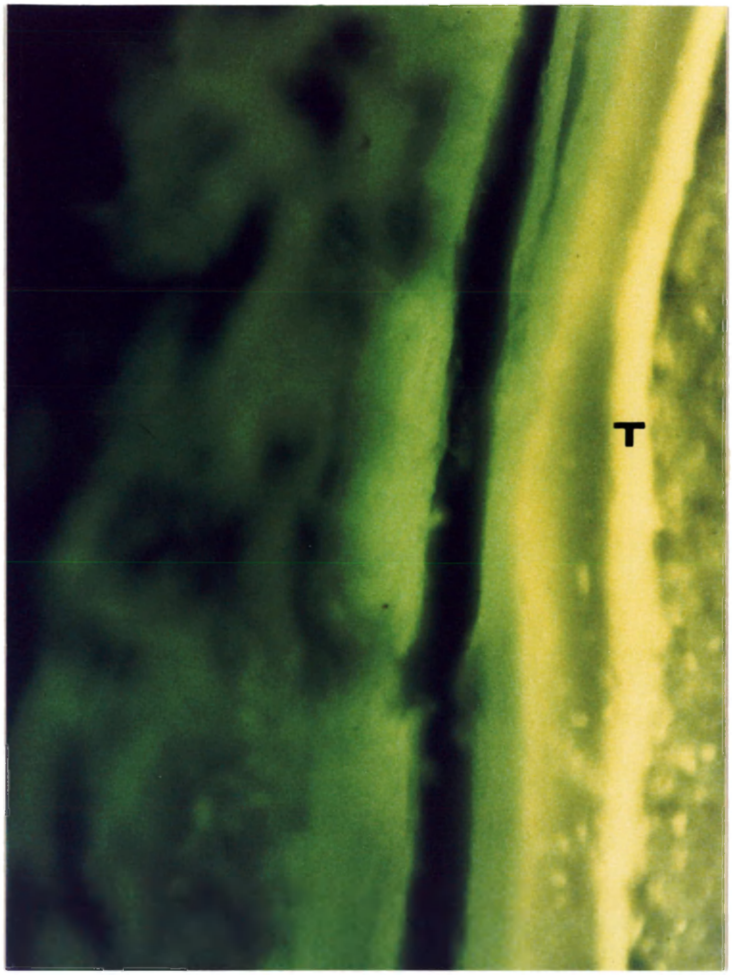
* Carapace width measurements substituted for length measurements due to previous damage to posterior section of carapace, probably the result of shark predation.

Fig. 4. One year recapture (MT-30-86).

a. Tetracycline fluorescence in undecalcified bone section, indicated by T.

b. Bone growth rings in decalcified section as indicated by ring number.

a.



b.

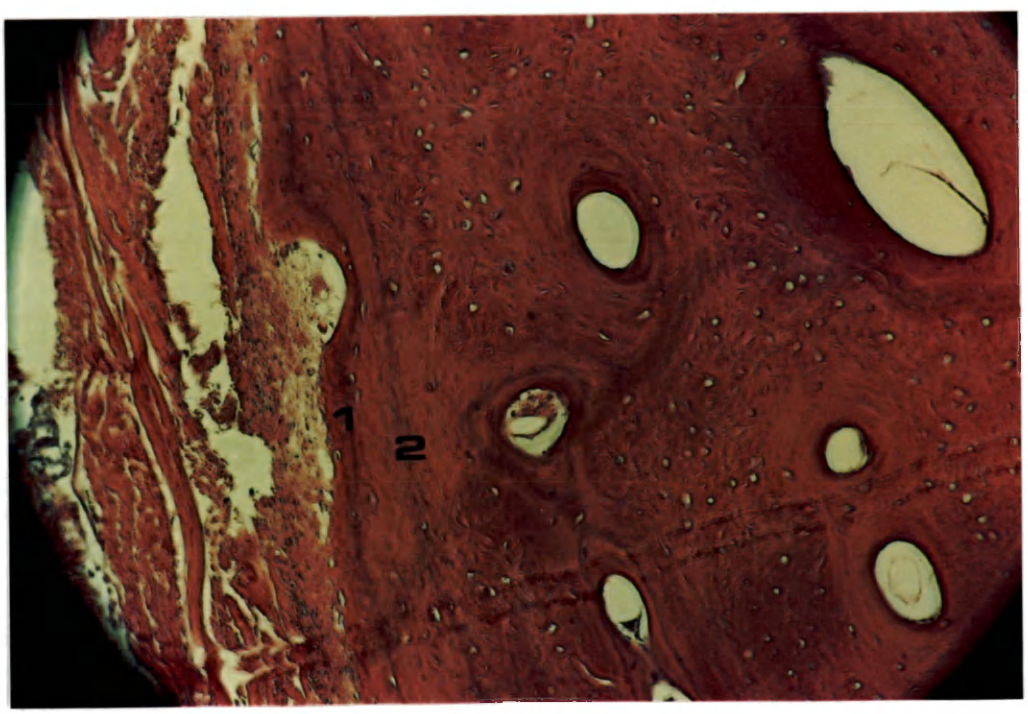
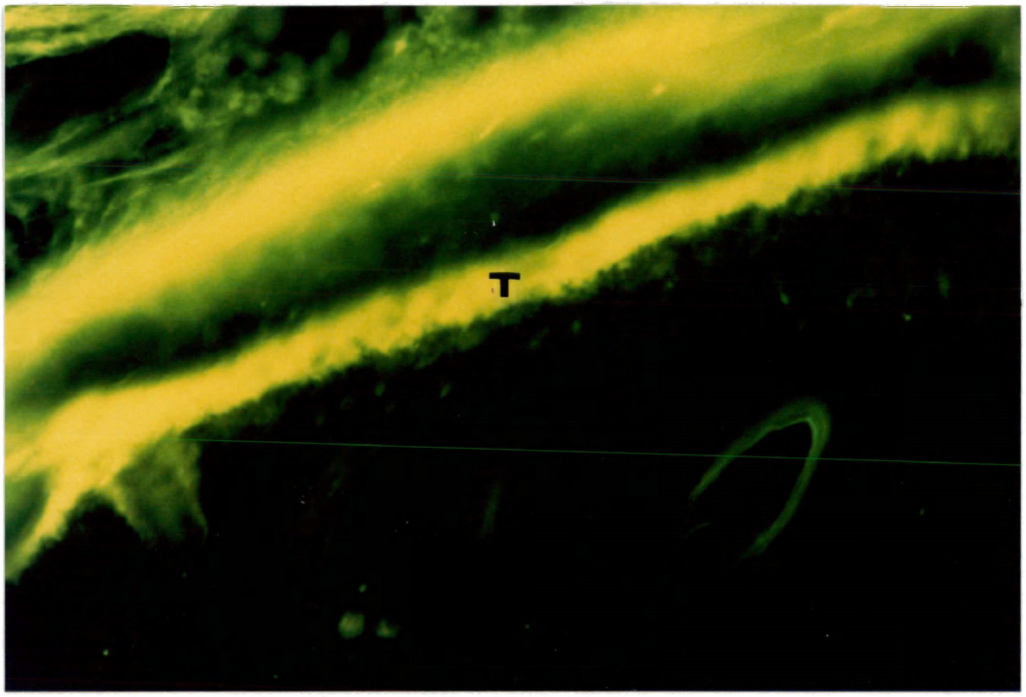


Fig. 5. Three year recapture (MT-122-84).

a. Tetracycline fluorescence in undecalcified bone section, indicated by T.

b. Bone growth rings in decalcified section as indicated by ring number.

a.



b.

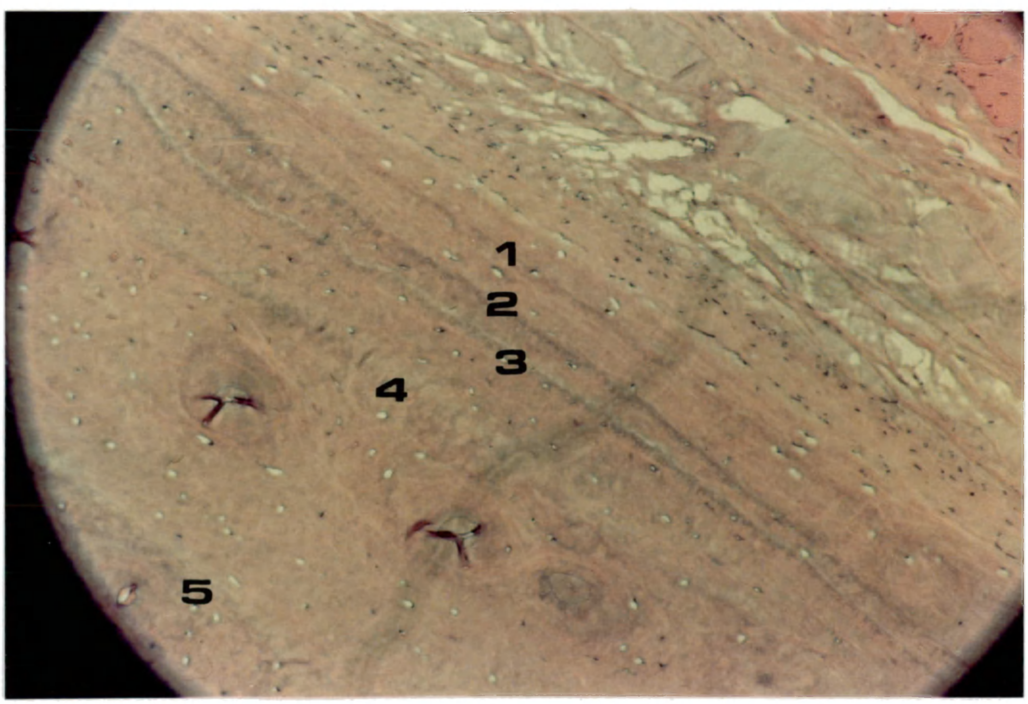


Table 3. Mean growth rate (cm/yr) in 10 cm (straight carapace length) size classes (N=83).

CLS (cm)	N	MEAN GROWTH RATE (cm/yr)	SD	RANGE
40.0 - 49.9	6	5.28	2.75	2.76 - 8.99
50.0 - 59.9	13	5.29	1.44	3.23 - 7.94
60.0 - 69.9	29	5.27	1.60	2.44 - 8.59
70.0 - 79.9	24	4.35	2.00	1.33 - 8.64
80.0 - 89.9	2	3.08	1.17	2.25 - 3.91
90.0 - 99.9	7	2.87	0.85	1.86 - 4.02 *
100.0 - 110.0	2	0.66	0.02	0.64 - 0.67

* Denotes significance with nonparametric multiple pairwise comparison tests. Size class 90.0 - 99.9 is significantly different from 60.0 - 69.9 size class ($Q=3.20$, $df=7$, $P>0.05$). See Appendix, Table 1 for calculations.

Table 4. Mean age in 10 cm (straight carapace length) size classes (N=92).

CLS (cm)	N	MEAN AGE	SD	RANGE
40.0 - 49.9	6	5.17	1.33	4.00 - 7.00 *
50.0 - 59.9	16	7.31	2.75	2.00 - 15.00
60.0 - 69.9	30	8.43	2.44	4.00 - 17.00
70.0 - 79.9	26	8.73	1.69	6.00 - 13.00
80.0 - 89.9	5	9.00	2.83	7.00 - 14.00
90.0 - 99.9	7	10.43	2.51	7.00 - 14.00
100.0 - 110.0	2	29.00	9.90	22.00 - 36.00

* Denotes significance with nonparametric multiple pairwise comparison tests. Size class 40.0 - 49.9 is significantly different from 60.0 - 69.9 (Q=3.05), 70.0 - 79.9 (Q-=3.60) and 100.0 - 110.0 (Q=3.78) size classes (df=7, P>0.05). See Appendix, Table 2 for calculations.

Fig. 6. Frequency distribution of growth rings observed in 88 stranded loggerheads.

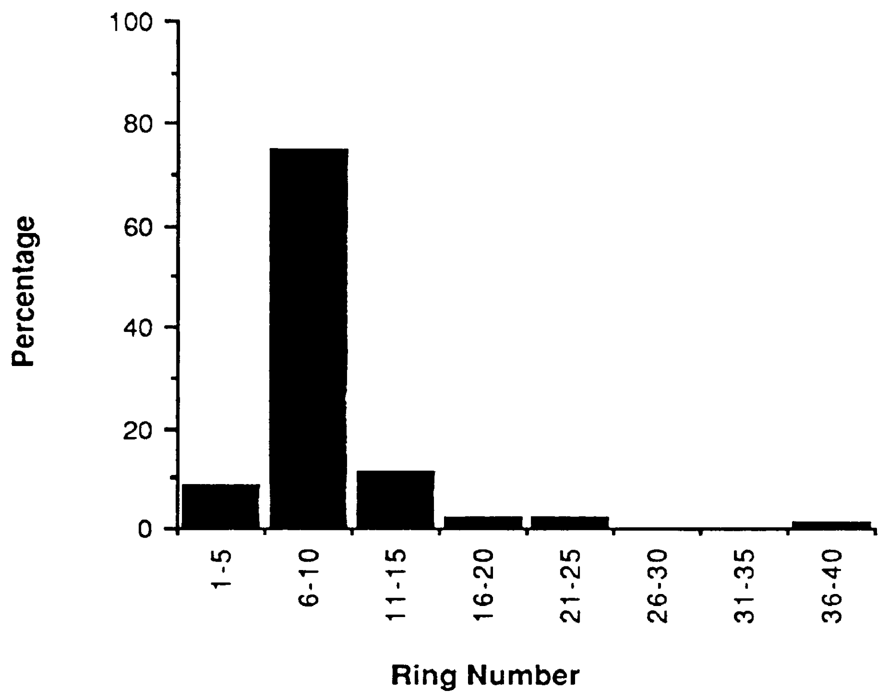
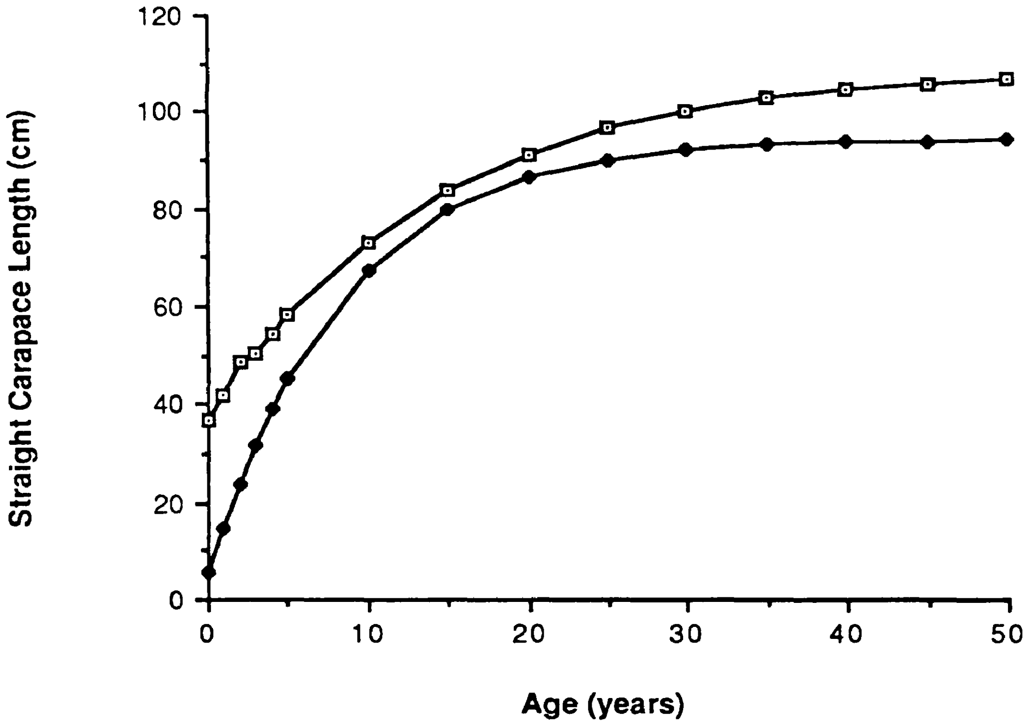

100
80
60
40
20
0
Percentage
1-5
6-10
11-15
16-20
21-25
26-30
31-35
36-40
Ring Number

Fig. 7. Von Bertalanffy growth curve (straight carapace length) for stranded loggerheads (N=88), based on observed number of growth rings. Growth curved from Frazer and Ehrhart (1985) included for comparison. See Appendix, Table 7 for ANOVA calculations.

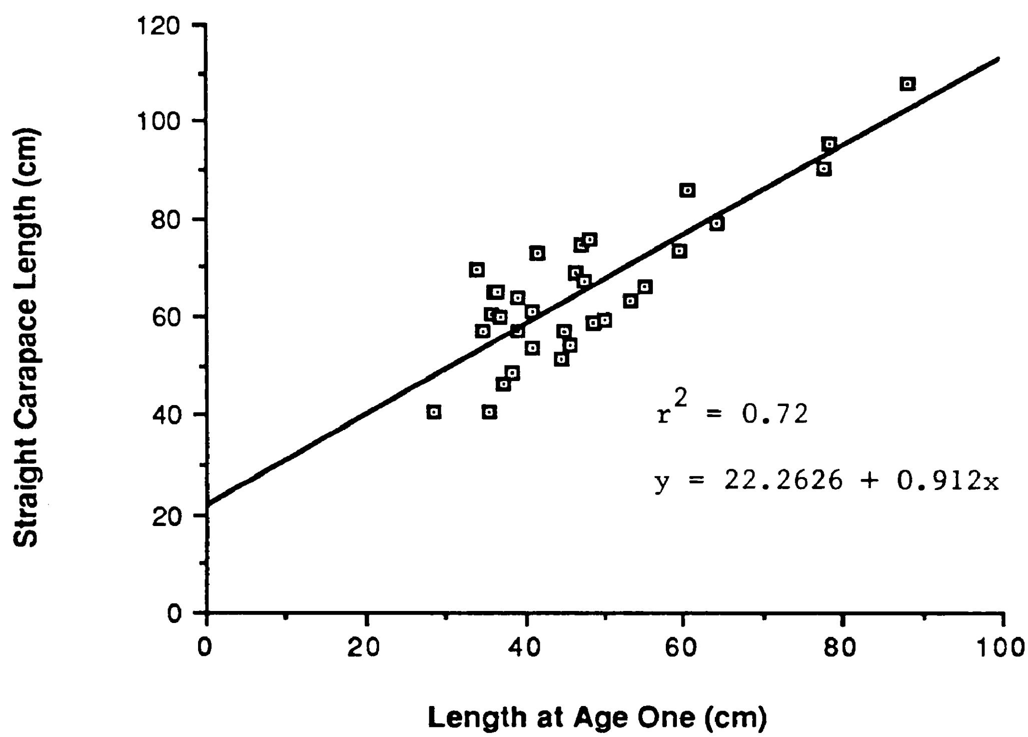
VON BERTALANFFY GROWTH CURVES (CLS)



Klinger: $L_t = 108.9(1-e^{-0.071(t+5.84)})$

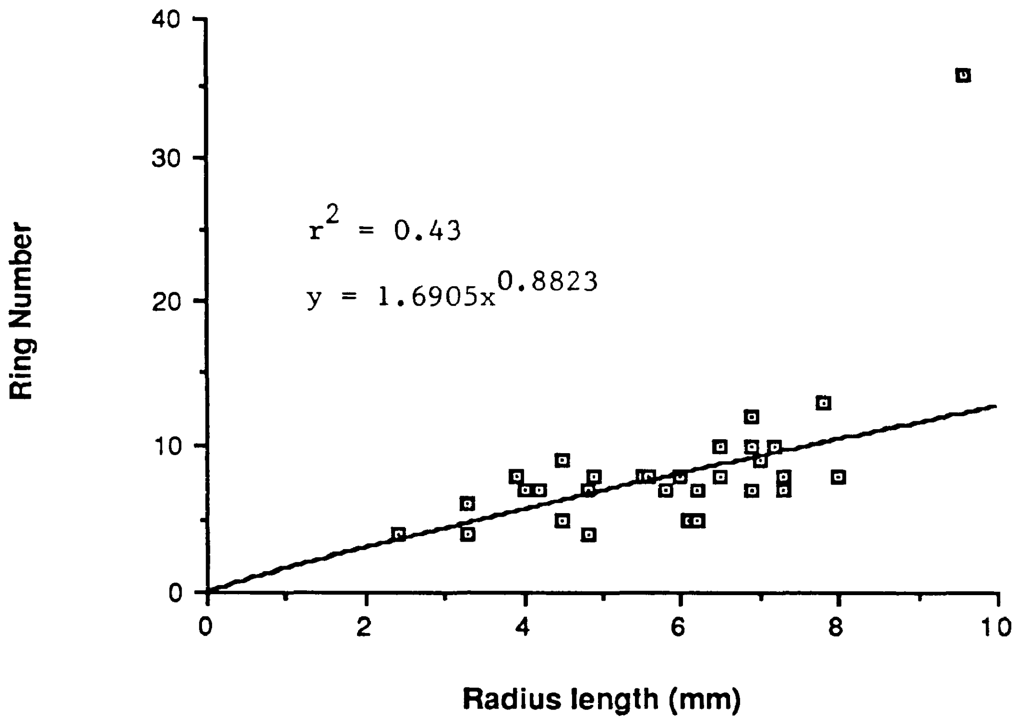
Frazer & Ehrhart (1985): $L_t = 94.6(1-0.952e^{-120t})$

Fig. 8. Linear regression of straight carapace length against back calculated lengths at age one (N=32).



Straight Carapace Length (cm)
Length at Age One (cm)
0
20
40
60
80
100
120
0
20
40
60
80
100
r2 = 0.72
y = 22.2626 + 0.912x

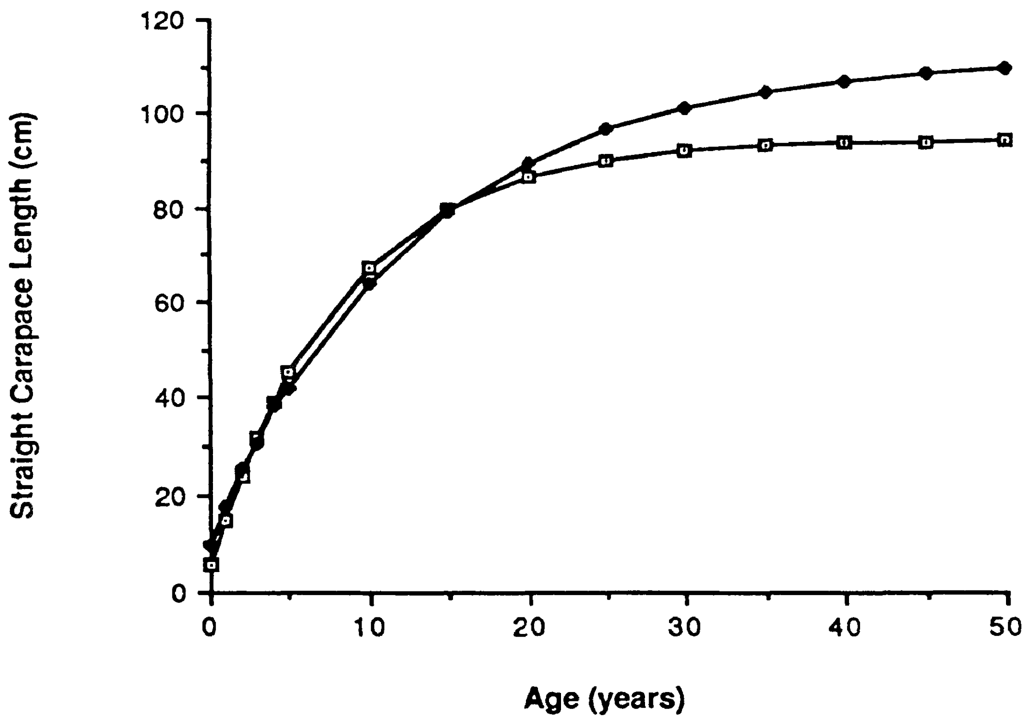
Fig. 9. Log linear regression of bone radius length against growth ring number for back calculation of radius length at age one (N=32).



Ring Number
40
30
20
10
0
0
2
4
6
8
10
r^2 = 0.43
y = 1.6905x^0.8823
Radius length (mm)

Fig. 10. Von Bertalanffy growth curve (straight carapace length) with age estimates adjusted for ring loss (N=32). Frazer and Ehrhart (1985) included for comparison. See Appendix, Table 8 for ANOVA calculations.

VON BERTALANFFY GROWTH CURVES



Klinger: $L_t = 111.9(1-e^{-0.076(t+1.16)})$

Frazer & Ehrhart (1985): $L_t = 94.6(1-0.952e^{-120t})$

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APPENDIX

LIST OF TABLES

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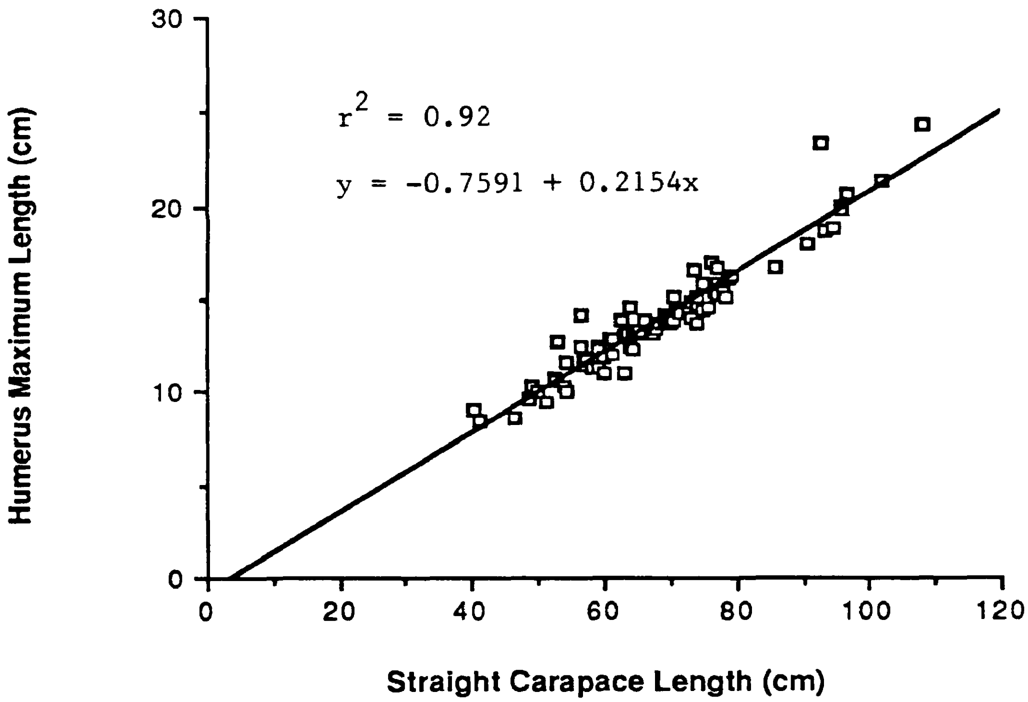
Fig. 1. Linear regression of straight carapace length against humerus maximum length (N=87).



30
20
10
0
0
20
40
60
80
100
120
r² = 0.92
y = -0.7591 + 0.2154x
Humerus Maximum Length (cm)
Straight Carapace Length (cm)

Fig. 2. Linear regression of curved carapace length against humerus maximum length (N=78).

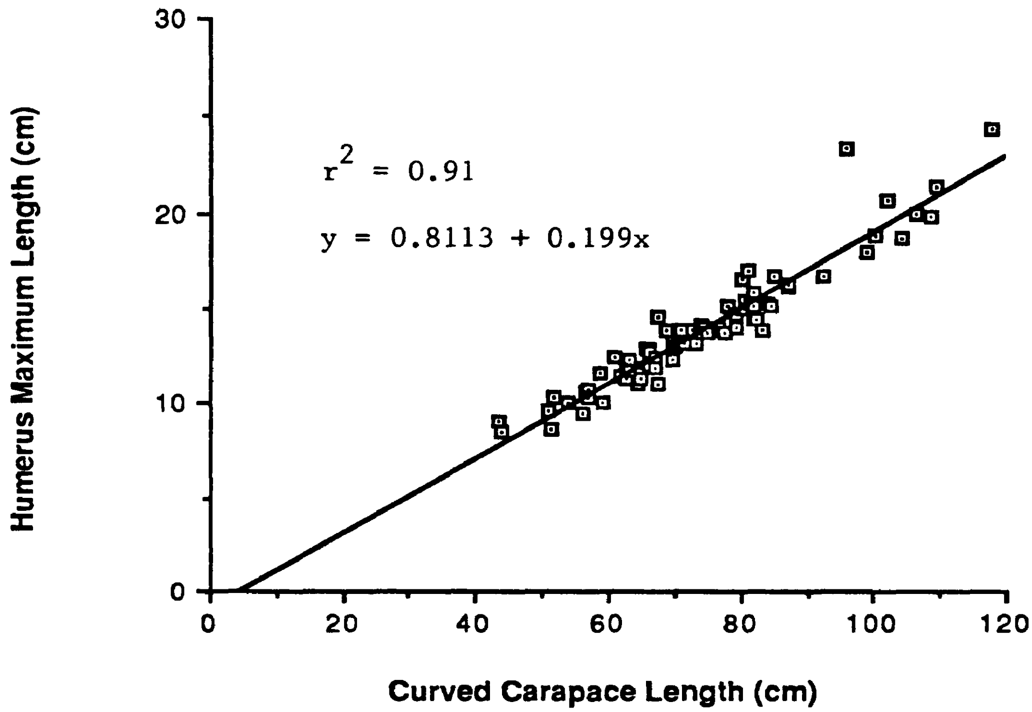

r^2 = 0.91
y = 0.8113 + 0.199x
Humerus Maximum Length (cm)
Curved Carapace Length (cm)
0
10
20
30
0
20
40
60
80
100
120

Table 1. Nonparametric multiple pairwise comparison tests of ranked mean growth rates (N=83) in 10 cm (straight carapace length) size classes.

Samples ranked by rank means	10	9	8	7	4	6	5
Rank sums	3	125	42	914.5	277	1459.5	665
Sample sizes	2	7	2	24	6	29	13
Rank means	1.50	17.86	21.00	38.10	46.17	50.33	51.15

Pairwise Comparison	Difference in mean ranks	SE	Q	Q(0.05,df=7)	Significance (*)
5 vs 10	49.65	18.30	2.71	3.038	
5 vs 9	33.29	11.30	2.95	3.038	
5 vs 8	Do not test				
5 vs 7	Do not test				
5 vs 4	Do not test				
5 vs 6	Do not test				
6 vs 10	48.83	17.62	2.77	3.038	
6 vs 9	32.47	10.15	3.20	3.038	*
6 vs 8	29.33	17.60	1.67	3.038	
6 vs 7	Do not test				
6 vs 4	Do not test				
4 vs 9	23.31	13.41	2.11	3.038	
4 vs 10	44.67	19.68	2.27	3.038	
4 vs 8	Do not test				
4 vs 7	Do not test				

Table 2. Nonparametric multiple pairwise comparison tests of ranked mean ages (N=92) in 10 cm (straight carapace length) size classes.

Samples ranked by mean ranks	4	5	6	8	7	9	10
Rank Sums	60.5	546.5	1382.5	253	1381	471.5	183
Sample Size	6	16	30	5	26	7	2
Rank Means	10.08	34.16	46.08	50.60	53.12	67.36	91.50

Pairwise Comparison	Difference in mean ranks	SE	Q	Q(0.05,df=7)	Significance (*)
10 vs 4	81.42	21.53	3.78	3.038	*
10 vs 5	57.34	19.78	2.90	3.038	
10 vs 6	45.42	19.26	2.36	3.038	
10 vs 8	Do not test				
10 vs 7	Do not test				
10 vs 9	Do not test				
9 vs 4	57.28	21.5	2.66	3.038	
9 vs 5	Do not test				
9 vs 6	Do not test				
9 vs 8	Do not test				
9 vs 7	Do not test				
7 vs 4	43.02	11.94	3.60	3.038	*
7 vs 5	18.96	8.38	2.26	3.038	
7 vs 6	Do not test				
7 vs 8	Do not test				
8 vs 4	40.52	15.97	2.54	3.038	
8 vs 5	Do not test				
8 vs 6	Do not test				
6 vs 4	36.00	11.79	3.05	3.038	*
6 vs 5	13.92	7.46	1.86	3.038	

Table 3. Mean growth rate (cm/yr) in 10 cm (curved carapace length) size classes (N=94).

CLC (cm)	N	MEAN GROWTH RATE (cm/yr)	SD	RANGE
40.0 - 49.9	2	4.74	1.17	3.91 - 5.57
50.0 - 59.9	9	6.35	2.70	2.95 - 9.88
60.0 - 69.9	20	5.64	1.46	2.62 - 8.15
70.0 - 79.	18	5.36	2.10	1.48 - 9.57
80.0 - 89	15	4.27	1.62	2.13 - 8.43
90.0 - 99.9	3	2.42	0.36	2.06 - 2.77
100.0 - 110.0	7	2.67	1.59	0.70 - 4.54 *

Denotes significance with nonparametric multiple pairwise comparison tests. Size class 100.0 - 110.0 is significantly different from 50.0 - 59.9 (Q=3.06) and 60.0 - 69.9 (Q=3.27) size classes. See Appendix, Table 4 for calculations.

Table 4. Nonparametric multiple pairwise comparison tests of ranked mean growth rates (N=94) in 10 cm (curved carapace length) size classes.

Samples ranked by mean ranks	9	10	8	4	7	6	5
Rank sums	26.5	108	446	73	759	925.5	437
Sample size	3	7	15	2	18	20	9
Rank means	8.83	15.43	29.73	36.50	42.17	46.27	48.56

Pairwise Comparison	Difference in rank means	SE	Q	Q(0.05,df=7)	Significance (*)
5 vs 9	39.73	14.34	2.77	3.038	
5 vs 10	33.13	10.84	3.06	3.038	*
5 vs 8	18.83	9.07	2.08	3.038	
5 vs 4	Do not test				
5 vs 7	Do not test				
5 vs 6	Do not test				
6 vs 9	37.44	13.32	2.81	3.038	
6 vs 10	30.84	9.44	3.27	3.038	*
6 vs 8	16.54	7.34	2.25	3.038	
6 vs 4	Do not test				
6 vs 7	Do not test				
7 vs 9	33.34	13.41	2.49	3.038	
7 vs 10	26.74	9.58	2.79	3.038	
7 vs 8	Do not test				
7 vs 4	Do not test				

Table 5. Mean age in 10 cm (curved carapace length) size classes (N=83).

CLC (cm)	N	MEAN AGE	SD	RANGE
40.0 - 49.9	2	4.00	0.00	4.00
50.0 - 59.9	10	6.00	2.21	2.00 - 10.00
60.0 - 69.9	22	7.86	2.45	4.00 - 17.00
70.0 - 79.9	21	8.81	1.57	7.00 - 12.00 *
80.0 - 89.9	16	8.62	1.54	7.00 - 12.00
90.0 - 99.9	5	9.60	2.88	7.00 - 14.00
100.0 - 110.0	7	16.14	9.87	8.00 - 36.00 *

* Denotes significance with nonparametric multiple pairwise comparison tests. Size class 100.0 - 110.0 is significantly different from 40.0 - 49.9 (Q=3.55), 50.0 - 59.9 (Q=4.44), and 60.0 - 69.9 (Q=3.54) size classes.

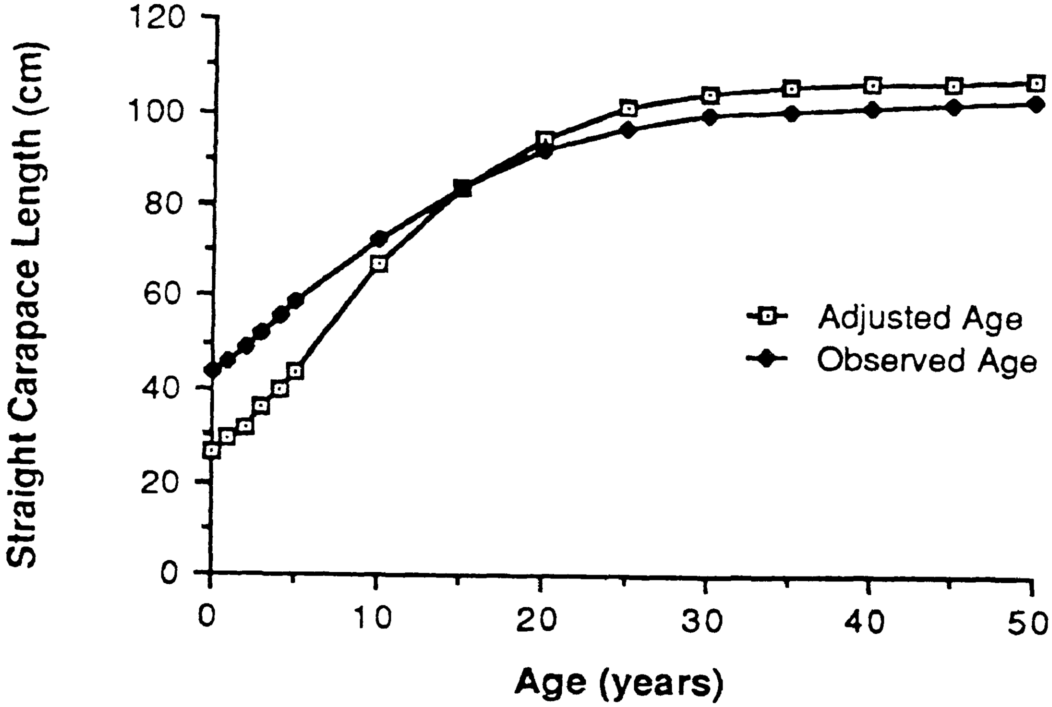
Size class 70.0 - 79.9 is significantly different from 50.0 - 59.9 (Q=3.27) size class.

Table 6. Nonparametric multiple pairwise comparison tests of ranked mean age in 10 cm (curved carapace length) size classes (N=83).

Samples ranked by rank means	4	5	6	8	7	9	10
Rank sums	7	191	761	744	1027	258.5	497.5
Sample size	2	10	22	16	21	5	7
Rank means	3.50	19.10	34.59	46.50	48.90	51.70	71.07

Pairwise Comparison	Difference in rank means	SE	Q	Q(0.05,df=7)	Significance (*)
10 vs 4	67.57	19.02	3.55	3.038	*
10 vs 5	51.97	11.69	4.44	3.038	*
10 vs 6	36.48	10.29	3.54	3.038	*
10 vs 8	24.57	10.75	2.28	3.038	
10 vs 7	Do not test				
10 vs 9	Do not test				
9 vs 4	48.23	19.84	2.42	3.038	
9 vs 5	32.64	12.99	2.50	3.038	
9 vs 6	Do not test				
9 vs 8	Do not test				
9 vs 7	Do not test				
7 vs 4	45.42	17.55	2.58	3.038	
7 vs 5	29.81	9.11	3.27	3.038	*
7 vs 6	14.31	7.24	1.98	3.038	
7 vs 8	Do not test				
8 vs 4	27.43	9.56	2.87	3.038	
8 vs 5	Do not test				
8 vs 6	Do not test				

Fig. 3. Logistic growth curves (straight carapace length) for stranded loggerheads based on observed (N=87) and adjusted (N=32) ages. See Appendix, Tables 7 and 8 for ANOVA calculations.



$$L_t = \frac{107.0}{(1+e^{-0.15(t-7.49)})}$$

$$L_t = \frac{103.2}{(1+e^{-0.12(t-2.73)})}$$

Table 7. Analysis of variance for nonlinear regression of Von Bertalanffy and logistic growth equations for observed age (straight carapace length).

	LOGISTIC			VON BERTALANFFY		
Parameters:	L	K	t	L	K	t
	103.2	0.12	2.73	108.9	0.71	-5.84

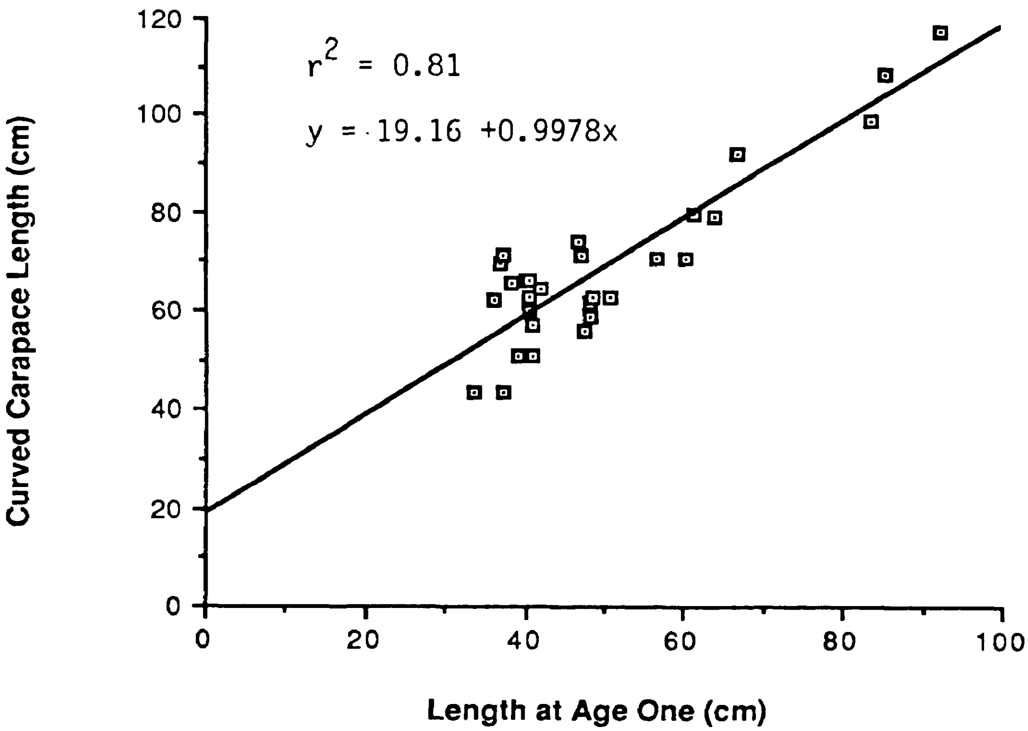
	LOGISTIC			VON BERTALANFFY		
Source:	DF	SS	MS	DF	SS	MS
Regression	3	416,897.3	138,965.8	3	417,020.2	139,006.7
Residual	84	10,313.6	122.8	84	10,190.7	121.3
Uncorrected total	87	427,210.9		87	427,210.9	
(Corrected total)	86	16,020.6		86	16,020.6	

Table 8. Analysis of variance for nonlinear regression of Von Bertalanffy and logistic growth equations for adjusted ages (straight carapace length).

	LOGISTIC			VON BERTALANFFY		
Parameters:	L	K	t	L	K	t
	107.0	0.15	7.49	111.9	0.076	-1.16

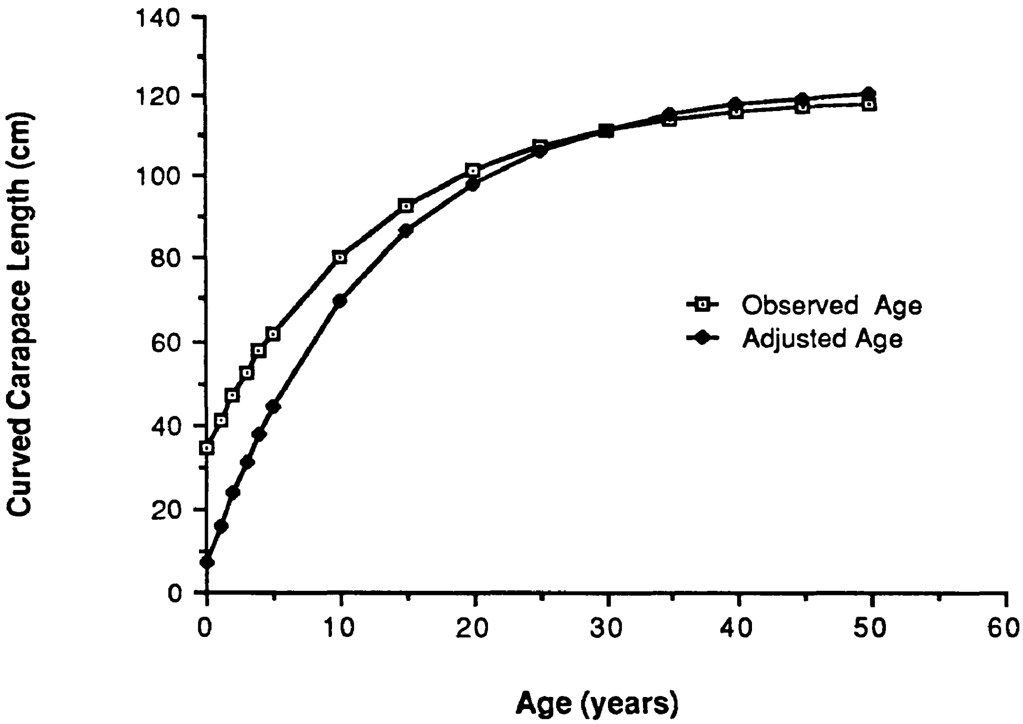
Source	DF	SS	MS	DF	SS	MS
Regression	3	134,805.1	44,935.0	3	134,812.3	44,937.4
Residual	27	1,871.8	69.3	27	1,864.6	69.0
Uncorrected total	30	136,676.8		30	136,676.8	
(Corrected total)	29	6,998.1		29	6,998.1	

Fig. 4. Linear regression of curved carapace length against back calculated lengths at age one (N=27).



r^2 = 0.81
y = 19.16 +0.9978x
Curved Carapace Length (cm)
Length at Age One (cm)
0
20
40
60
80
100
120

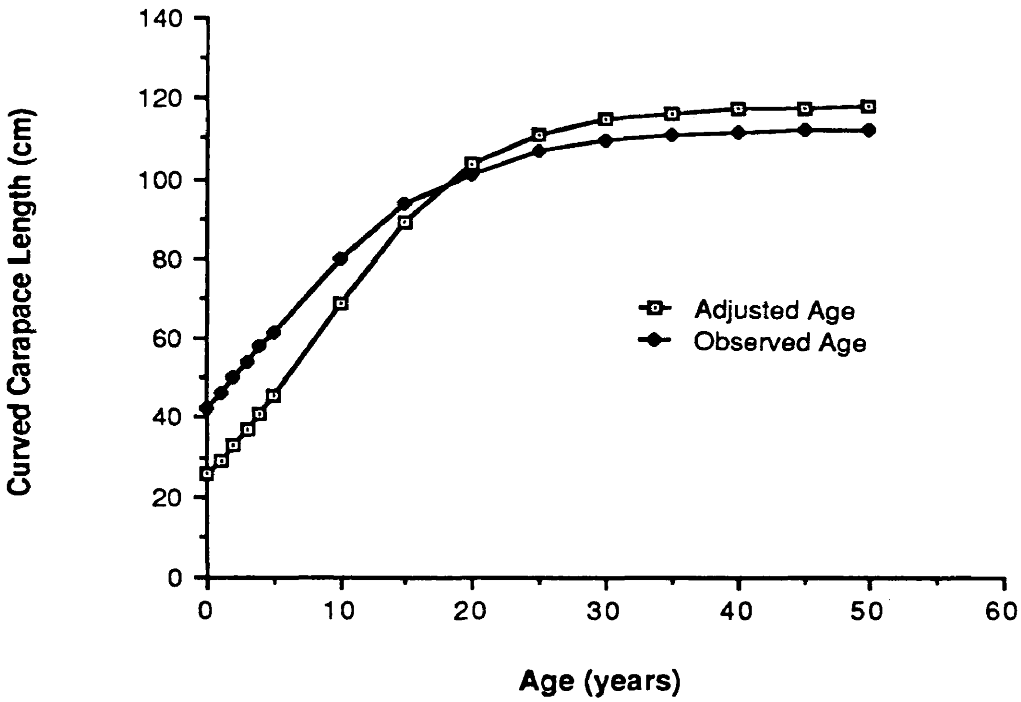
Fig. 5. Von Bertalanffy growth curves (curved carapace length) for stranded loggerheads based on observed (N=83) and adjusted (N=27) ages. See Appendix, Table 8 and 10 for ANOVA calculations.



$L_t = 120.1(1-e^{-0.077(t+4.43)})$ (open squares)

$L_t = 123.1(1-e^{-0.077(t+0.789)})$ (filled diamonds)

Fig. 6. Logistic growth curves (curved carapace length) for stranded loggerheads based on observed (N=83) and adjusted (N=27) ages. See Appendix, Tables 8 and 10 for ANOVA calculations.



$$L_t = \frac{112.3}{(1+e^{-0.143(t-3.52)})}$$

$$L_t = \frac{118.0}{(1+e^{-0.160(t-7.96)})}$$

Table 9. Analysis of variance for nonlinear regression of Von Bertalanffy and logistic growth equations for observed age (curved carapace length).

	LOGISTIC			VON BERTALANFFY		
Parameters:	L	K	t	L	K	t
	112.3	0.143	3.52	120.1	0.077	-4.43

Source:	DF	SS	MS	DF	SS	MS
Regression	3	445,678.9	148,559.6	3	471,400.4	157,133.5
Residual	76	10,892.4	143.3	80	11,031.2	137.9
Uncorrected total	79	456,571.4		83	482,431.6	
(Corrected total)	78	18,503.8		82	18,895.6	

Table 10. Analysis of variance for nonlinear regression of Von Bertalanffy and logistic growth equations on adjusted age (curved carapace length).

	LOGISTIC			VON BERTALANFFY		
Parameters:	L	K	t	L	K	t
	118.0	0.160	7.96	123.1	0.077	-0.789

Source:	DF	SS	MS	DF	SS	MS
Regression	3	140,078.0	46,692.7	3	140,010.6	46,670.2
Residual	24	2,354.2	98.1	24	2,421.6	100.9
Uncorrected total	27	142,432.2		27	142,432.2	
(Corrected total)	26	8,629.9		26	8,629.9	