CARIBBEAN HAWKSBILL TURTLE MORPHOMETRICS

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ABSTRACT

Body size measurements were obtained from 53 hatchlings and 276 juvenile to adult hawksbill turtles (*Eretmochelys imbricata*) at Mona Island, Puerto Rico. Allometric change in the size of body structures were examined by regression analysis. Turtle heads underwent the greatest proportional change, with larger turtles presenting a significantly decreased head width to carapace length ratio. The proportion of carapace width to length remained constant for hawksbill turtles throughout the size range examined. Sexual dimorphism in tail size was observed from 68.2 cm straight-line carapace length. Australian and southern African turtles differ from Caribbean hawksbill turtles in having significantly greater carapace width in proportion to carapace length. .

Body size and shape have important physiological, evolutionary and ecological implications for marine turtles. Empirical relationships with turtle body size have been established for diverse properties such as body temperature (Spotila and Standora, 1985), metabolic rate (Prange and Jackson, 1976), evaporative water loss (Smith et al., 1986), growth rate (Bjorndal and Bolten, 1988), and clutch size (Witzell, 1985). Data on body form and the size-mass relationships in marine turtles form key elements to the modeling of swimming (Prange, 1976) and thermal energetics (Spotila and Standora, 1985), and may be used to define the degree of differentiation of distant populations (Hirth, 1982; Figueroa and Alvarado, 1990).

Turtles are particularly suited for morphometric analysis because the rigidity of principal body structures such as shell and skull facilitates the taking of precise measurements (Bookstein et al., 1985). Short term fluctuations in general health and nutritional condition introduce only minor variation in these measurements. Although standard measurements and reference points in marine turtles are generally well defined (Pritchard et al., 1983), the variety of measurement techniques used in different field studies of the hawksbill turtle (*Eretmochelys imbricata*) has impeded the direct comparison of size data. As formulas for the conversion of measurement data can only be applied to turtles sharing the same morphology, the extent of regional differences in hawksbill turtle body form needs to be examined (Limpus and Miller, 1990).

Limited information is available on morphometrics of hawksbill turtles in the Caribbean. Because studies of the species in the region have tended to focus on aspects of nesting, existing morphometric data concerns mainly the hatchling and adult female lifestages. Yet morphometric information covering a wide range of hawksbill turtle sizes is available for populations in Australia (Limpus, 1992) and south-east Africa (Hughes, 1974). In this study we attempt to redress the deficiency of size-related data on hawksbill turtles in the Caribbean by examining hawksbill turtles found on the nesting beaches (hatchlings) and foraging grounds (juvenile to adult turtles) of Mona Island, Puerto Rico. Because the population of hawksbill turtles residing on the Mona foraging grounds is composed of turtles originating from diverse rookeries throughout the Caribbean (Bowen et al., 1996), the morphometric descriptions presented here should apply to a large proportion of Caribbean hawksbill turtles.

METHODS

Morphometric data were recorded from 1992 to 1996 for hawksbill turtles collected on the nesting beaches and captured in the waters surrounding Mona Island, Puerto Rico (18°05'N, 67°55'W). A total of 53 live hatchlings were obtained and measured from five partially emerged nests. Size measurements including straight-line carapace lengths, maximum carapace width, straight-line plastron length, maximum body depth and maximum head width were determined to the nearest 0.01 cm using a vernier caliper (see Figure 1 for measurement reference points). Hatchling body mass was measured to 0.5 g with a Pesola 100 × 1 g spring scale.

Hand capture at sea yielded 276 individual juvenile to adult hawksbill turtles. Turtles were brought aboard a small boat and/or taken ashore for tagging and measurement. Each turtle was subjected to 19 measurements: straight-line and over-the-curve nuchal notch to posteriormost marginal tip carapace lengths (SCL_{nt} and CCL_{nt}, respectively), straight-line and over-the-curve nuchal notch to intermarginal notch carapace lengths (SCL_{nn} and CCL_{nn}), straight-line and over-the-curve maximum carapace lengths (SCL_{max} and CCL_{max}), straight-line and over-the-curve maximum carapace widths (SCW and CCW), straight-line and over-the-curve plastron lengths (SPL and CPL), straight-line maximum head width (HW), straight-line maximum body depth (BD), over-the-curve plastron to cloaca tail length (TL_{pc}), over-the-curve plastron to tail tip length (TL_{pt}), over-the-curve left and right anterior costal scute widths (CSWl and CSWr), over-the-curve anterior and posterior vertebral scute widths (VSW_a and VSW_p), and body mass. Straight-line measurements under 40 cm except head width were taken to 0.1 cm with a 40 cm Haglof tree caliper, those over 40 cm with a 127 cm Haglof tree caliper. Width of tree caliper teeth was 0.5 cm. Maximum head width was measured using a vernier caliper to the nearest 0.01 cm. All curved measurements were made with metric fiberglass tape measures, reading to 0.1 cm. Tape measure condition was checked regularly against the large tree caliper; a tape considered to be in satisfactory condition if deviating less than 0.2 cm over the 120 cm span when stretched along the caliper scale using normal tape tension.

Body mass of turtles up to 20 kg was measured with a Pesola spring scale (20 kg × 200 g). Hawksbill turtles from 20 to 90 kg were weighed with either a Hanson Heavy Duty spring scale (90 kg × 1 kg) or Pesola spring scales (50 kg × 0.5 kg, 100 kg × 1 kg). Turtles were frequently measured aboard a small boat where instability due to wave action reduced body mass measurement accuracy to an estimated three times scale resolution. Hawksbill turtle epibiota (primarily algae and barnacles) interfering with measurement procedure were either removed or the resulting data excluded from analysis. Plastic and stainless steel flipper tags and injectable passive integrated transponders were used for turtle identification. Measurement data from recaptured turtles and from one animal with a severe carapace deformity (kyphosis) were not included in this study.

To assess size relationships between the various body structures measured and to detect changes in body form with increasing turtle size, measurement data of juvenile to adult hawksbill turtles was fitted to the power function $Y = a\,X^b$. SCL_{nt} was chosen as the reference body size measurement (variable X). Equation parameters (a and b) were calculated for 16 body measurements by linear regression against SCL_{nt} of log transformed data. Regressions met with the assumptions of homogeneous variance around the regression line and normally distributed residuals. Departure from isometry was examined by testing for difference in the populational means (parameter b) and unity using a two-sided t-test with significance set at $P < 0.05$.

RESULTS AND DISCUSSION

Scaling of the measurements taken of hatchling turtles was not attempted due to the limited variance in the data set. Hatchlings measured 4.00 ± 0.02 cm (mean SCL_{nt} ± SE, range 3.47 to 4.26, n = 53). Juvenile to adult hawksbill turtles ranged from 20.0 to 91.8 cm SCL_{nt} (Fig. 2). Small juveniles were best represented in the sample. The allometric equations between body measurements and SCL_{nt} for the non-hatchlings (Table 1) provide a good fit for the measurement data, as evidenced by high correlation coefficients ($r^2 > 0.96$).

The size measures chosen for this analysis correspond to those commonly taken of marine turtles. Two types are represented: "landmark" measures (here SCL_{nt}, CCL_{nt}, SCL_{nn}, CCL_{nn}, SPL, CPL, CSW_l, CSW_r, VSW_a, VSW_p, TL_{pc} and TL_{pt}) corresponding with distances between precisely definable points (landmarks) on the carapace, plastron and tail, and "extremal" measures (SCL_{max}, CCL_{max}, SCW, CCW, BD and HW) representing the maximum dimension of body structures in a prescribed direction. Because turtles were not "mapped," i.e., the relative po-
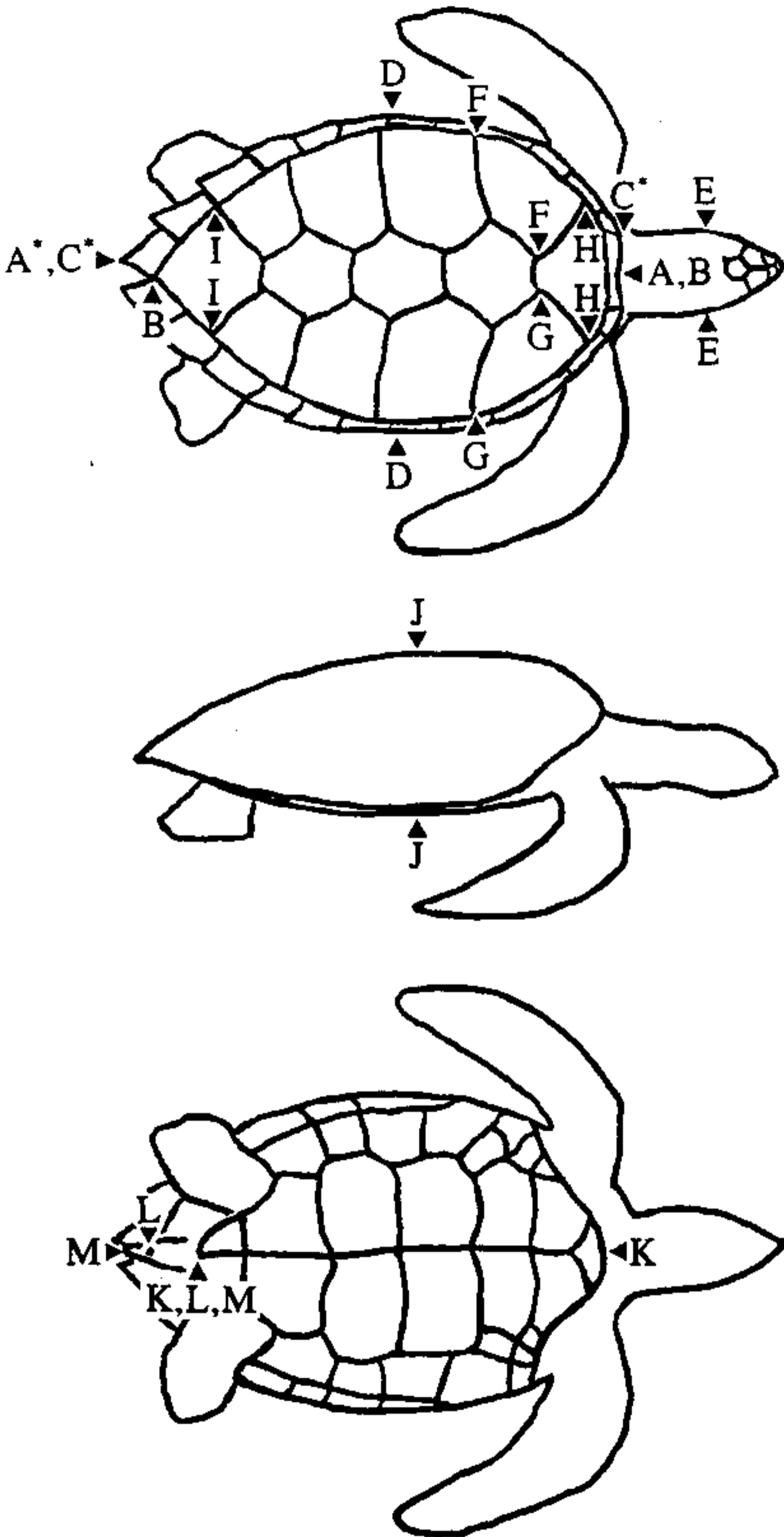
Figure 1.   Diagrams of reference point locations used in hawksbill turtle size measurement. Points marked by an asterisk were taken on the side (left or right) yielding the greatest measurement value. A: nuchal notch to posteriormost marginal tip carapace length, B: nuchal notch to posterior marginal notch carapace length, C: maximum carapace length, D: maximum carapace width, E: maximum head width, F,G: costal scute widths, H,I: vertebral scute widths, J: maximum body depth, K: plastron length, L: tail length to cloaca, M: tail length to tip. Body features are not drawn to scale.
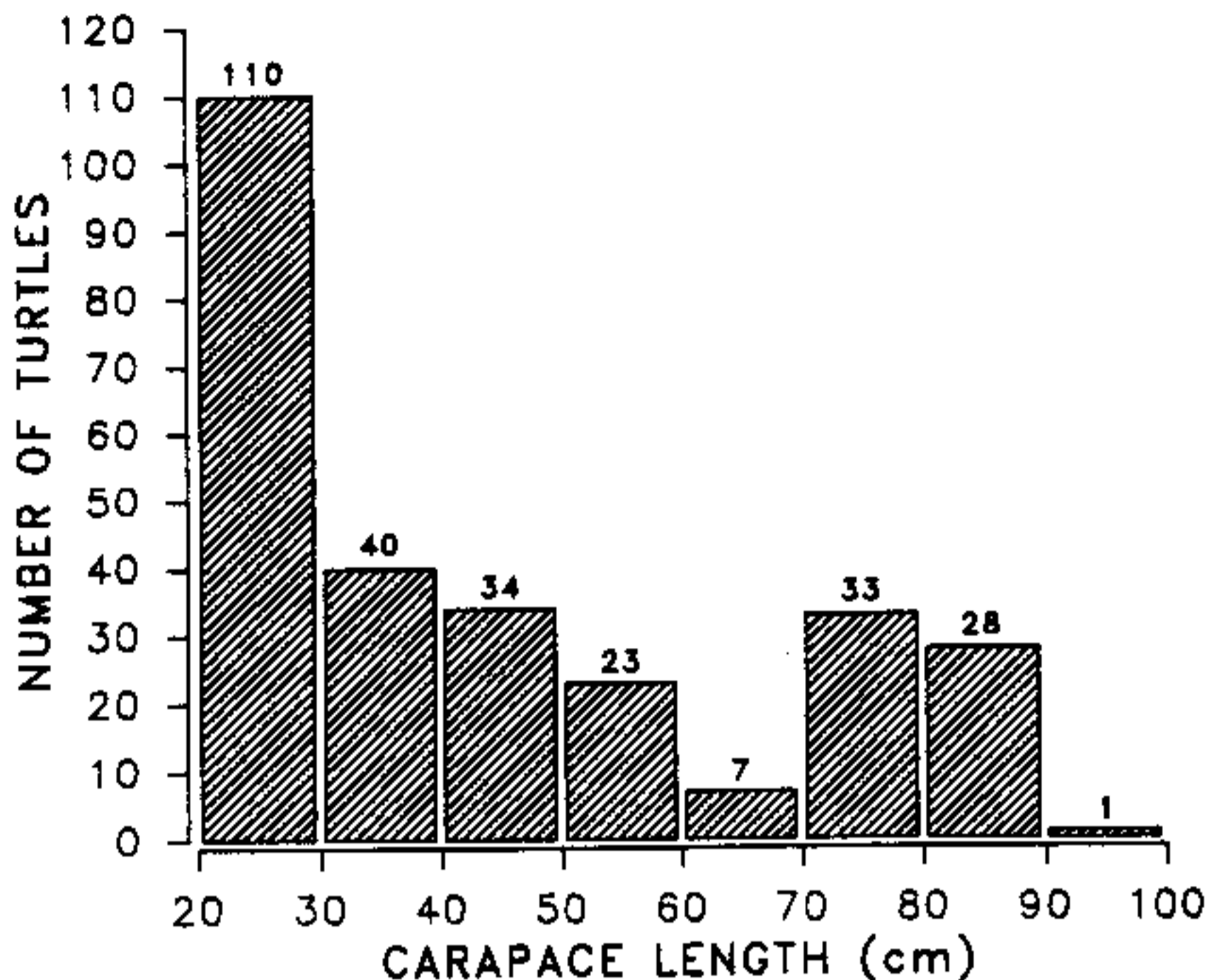
Figure 2.   Distribution by straight-line carapace length (SCL_{nt}) of 276 non-hatchling hawksbill turtles studied.

sitions in three dimensions of landmarks were not quantified, interpretation of the resulting data in terms of shape change with increasing size is subject to some limitations. However, at least general trends of constancy and change in body form can be discerned from the parameter values of the allometric equations (factors a and exponents b in Table 1). Factors provide information on the prevalent proportion of body structures with the reference measure, here SCL_{nt}, whereas exponents deviating from unity are indicative of size-related body form change. Turtle body form may become different due to (1) disproportional variation in the size of certain body parts (expressed by exponents relating straight-line measures) and (2) change in the degree of body structure curvature (as reflected by over-the-curve measure exponents).

CARAPACE AND PLASTRON FORM CHANGE. The power function exponents in Table 1 concerning carapace measurements of juvenile to adult turtles show variation around the value one, indicating minor but for several measures significant departure from the isometric condition. Over-the-curve measures, particularly carapace width, appear to increase disproportionately, denoting greater carapace curvature or "doming" in larger animals. Straight-line measures with the exception of nuchal notch to posterior marginal notch carapace length (SCL_{nn}) indicate the width to length ratio remains relatively constant.

The computed exponent for SCL_{nn} is significantly less than one, which is unexpected because SCL_{nn} and the reference measure SCL_{nt} differ only in the length of the posteriormost marginal scute. However, the low SCL_{nn} exponent may be an artifact due to measurement procedure. The teeth of the aluminum calipers used in straight-line carapace measurement are 0.5 cm wide. Because the V-notch between the posterior marginal scutes used as a reference point in the SCL_{nn} measures is frequently narrow, a caliper inserted into the notch does not always reach the scute junction. This may result in a biased measurement of SCL_{nn}, the

Table 1. Allometric relationship of 15 hawksbill turtle size measurements against nuchal notch to posteriormost marginal tip straight-line carapace length (SCL_{nt}). Estimated parameters ($\pm SE$) of $Y = a \times SCL_{nt}{}^b$ were calculated through linear regressions of log transformed data. Bold parameters b indicate significant departure from isometry (two-sided t-test, $P < 0.05$). All measurements are in cm. Data were obtained from hawksbill turtles in the size range of 20.0 to 91.8 cm SCL_{nt}. See text for abbreviations.

Y	a $\pm$ SE	b $\pm$ SE	r^2	n
CCL_{nt}	1.0534 $\pm$ 0.0065	0.9986 $\pm$ 0.0017	0.9992	272
SCL_{nn}	1.0217 $\pm$ 0.0087	**0.9876** $\pm$ 0.0023	0.9985	275
CCL_{nn}	1.0402 $\pm$ 0.0108	**0.9940** $\pm$ 0.0028	0.9979	271
SCL_{max}	1.0124 $\pm$ 0.0037	0.9989 $\pm$ 0.0010	0.9997	276
CCL_{max}	1.0314 $\pm$ 0.0073	**1.0068** $\pm$ 0.0019	0.9990	272
SCW	0.7215 $\pm$ 0.0124	0.9981 $\pm$ 0.0046	0.9942	276
CCW	0.8274 $\pm$ 0.0136	**1.0192** $\pm$ 0.0044	0.9950	271
SPL	0.8288 $\pm$ 0.0122	**0.9779** $\pm$ 0.0040	0.9955	276
CPL	0.8725 $\pm$ 0.0144	**0.9731** $\pm$ 0.0044	0.9944	275
BD	0.5302 $\pm$ 0.0144	**0.9090** $\pm$ 0.0073	0.9827	274
HW	0.3534 $\pm$ 0.0123	**0.7833** $\pm$ 0.0093	0.9624	276
CSW_1	0.2163 $\pm$ 0.0056	**1.1326** $\pm$ 0.0069	0.9899	274
CSW_r	0.2269 $\pm$ 0.0059	**1.1185** $\pm$ 0.0070	0.9895	272
VSW_a	0.3427 $\pm$ 0.0110	**0.9812** $\pm$ 0.0086	0.9796	273
VSW_p	0.2176 $\pm$ 0.0105	**1.0590** $\pm$ 0.0130	0.9607	274

effect of which would be greatest in small turtles that have only a small gap between marginal scutes.

Length of the plastron (PL) is reduced in proportion to SCL_{nt} in larger turtles (straight-line and over-the-curve exponents are significantly smaller than one, see Table 1). This reduction is not attributable to changes in plastron curvature as is evident when we examine the direct relationship between CPL and SPL through transformation of the plastron length equations in Table 1. In the resulting formula $CPL = 1.047 \cdot SPL^{0.9951}$, the two plastron length measures are isometrically related, indicating insignificant change in plastron curvature (Table 2).

Comparison of measured hatchling dimensions with those predicted by the allometric equations reveals that hatchling carapace width to length ratio conforms with that of larger hawksbill turtles. Measured hatchling SCW (mean SCW $\pm$ SE = 2.88 $\pm$ 0.02 cm, range 2.51 to 3.21, n = 53) coincides with the value (2.88) predicted by extrapolation of the SCW against SCL_{nt} relationship to hatchling dimensions. Hatchling plastrons (mean SPL $\pm$ SE = 3.05 $\pm$ 0.03 cm, range 2.56 to 3.42, n = 53), however, are significantly shorter than predicted (3.22 cm; two-sided t-test, $P < 0.05$). A low value for hatchling SPL may be largely due to the

Table 2. Proportional size and curvature changes with increasing size measured in Caribbean hawksbill turtles. Based on allometric relationship of body size measures with carapace length (SCL_{nt}) in juvenile to adult turtles and comparison of observed hatchling dimensions with values obtained through extrapolation of allometric equations. n.s.c. = no significant change.

	Hatchling size	Juveniles to adults	
		Size	Curvature
Carapace length			n.s.c.
Carapace width	n.s.c.	n.s.c.	increase
Plastron length	increase	decrease	n.s.c.
Body depth	decrease	decrease	
Head width	decrease	decrease	

yet incomplete transition by hatchlings from the folded body form while within the egg shell (with the plastron flexible and concave) towards a more rigid state.

BODY DEPTH. The exponent in the equation relating body depth to SCL_{nt} is indicative of a strongly flatter body form with increasing turtle size. Considering that carapace curvature increased concurrently, the implication is that hawksbill turtles adopt a more box-like shape as they become larger. In part this compression of the carapace may be due to the disappearance of keels in the vertebral scutes that are prominent in juvenile hawksbill turtles. Carapaces of adults are frequently flat for a large part of the area covered by the anteriormost four vertebral scutes (RvD and CED, pers. obs.). Body depth of hatchlings (mean BD $\pm$ SE = 1.85 $\pm$ 0.02 cm, range 1.44 to 1.96, n = 53) is not significantly different from the value (1.87 cm; two-sided t-test, P > 0.05)) obtained by extrapolation of the body depth against SCL_{nt} relationship to hatchling dimensions. Hatchling body depth therefore decreases in equal proportion to carapace length as occurs in larger turtles (Table 2).

HEAD WIDTH. Maximum head width undergoes the greatest proportional change of all the measures examined. Heads of 20 cm SCL_{nt} juvenile hawksbill turtles are proportionally 38% wider than the heads of 90 cm adults. Measured hatchling head width (mean HW $\pm$ SE = 1.40 $\pm$ 0.01 cm, range 1.29 to 1.49, n = 53) is significantly greater (two-sided t-test, P < 0.05) than the 1.05 cm predicted through extrapolation of the already strongly negative allometric relationship of head width versus SCL_{nt}. Hawksbill turtles undergo a pronounced decrease in relative head size with greater carapace length throughout the size range examined (Table 2).

BODY MASS. The scaling formula determined for body mass (kg) against SCL_{nt} (cm) of juvenile to adult hawksbill turtles is:

$$\text{Body mass} = 1.20 \times 10^{-4} \times SCL_{nt}^{3.002}$$

with r^2 = 0.9957, n = 270, SE_{factor} = 1.1 $\times$ 10^{-5}, $SE_{exponent}$ = 1.2 $\times$ 10^{-2}. The exponent in the equation is not significantly different from three, implying that the observed morphological changes from the juvenile to adult stage do not have a net effect on total tissue mass. Differential growth of the body structures therefore must cause the distribution of tissue mass to be altered. Mass gained through development of reproductive organs may offset the relative loss caused by a deceleration in head growth, for example. Hatchling body mass (mean body mass $\pm$ SE = 14.8 $\pm$ 0.21 g, range 12.5 to 17.0, n = 35), however, is significantly greater than the value predicted by extrapolation of the body mass equation to hatchling dimensions (7.7 g; two-sided t-test, P < 0.05). The disproportionately large head and substantial yolk mass that is resorbed by hatchlings shortly before leaving the nest are likely to contribute to the higher than predicted hatchling body mass.

TAIL LENGTH. Mature hawksbill turtles have sexually dimorphic tails whereby males feature substantially larger tails than do females. Although tail size is not a sound criterion for identifying adult females (Limpus, 1992), hawksbill turtles with tails extending well beyond the carapace can be reliably classified as adult males. The tail length plots of 276 hawksbill turtles against SCL_{nt} (Fig. 3) illustrates this tail dimorphism, with a bifurcation in data points starting at 68.2 cm carapace length, the size of the smallest observed adult male. The lack of turtles with tails of intermediate size in our sample suggests rapid tail development in maturing males.

The two measures used to assess tail length, the over-the-curve distance from plastron to tail tip (TL_{pt}) and from plastron to cloaca (TL_{pc}), make it is possible
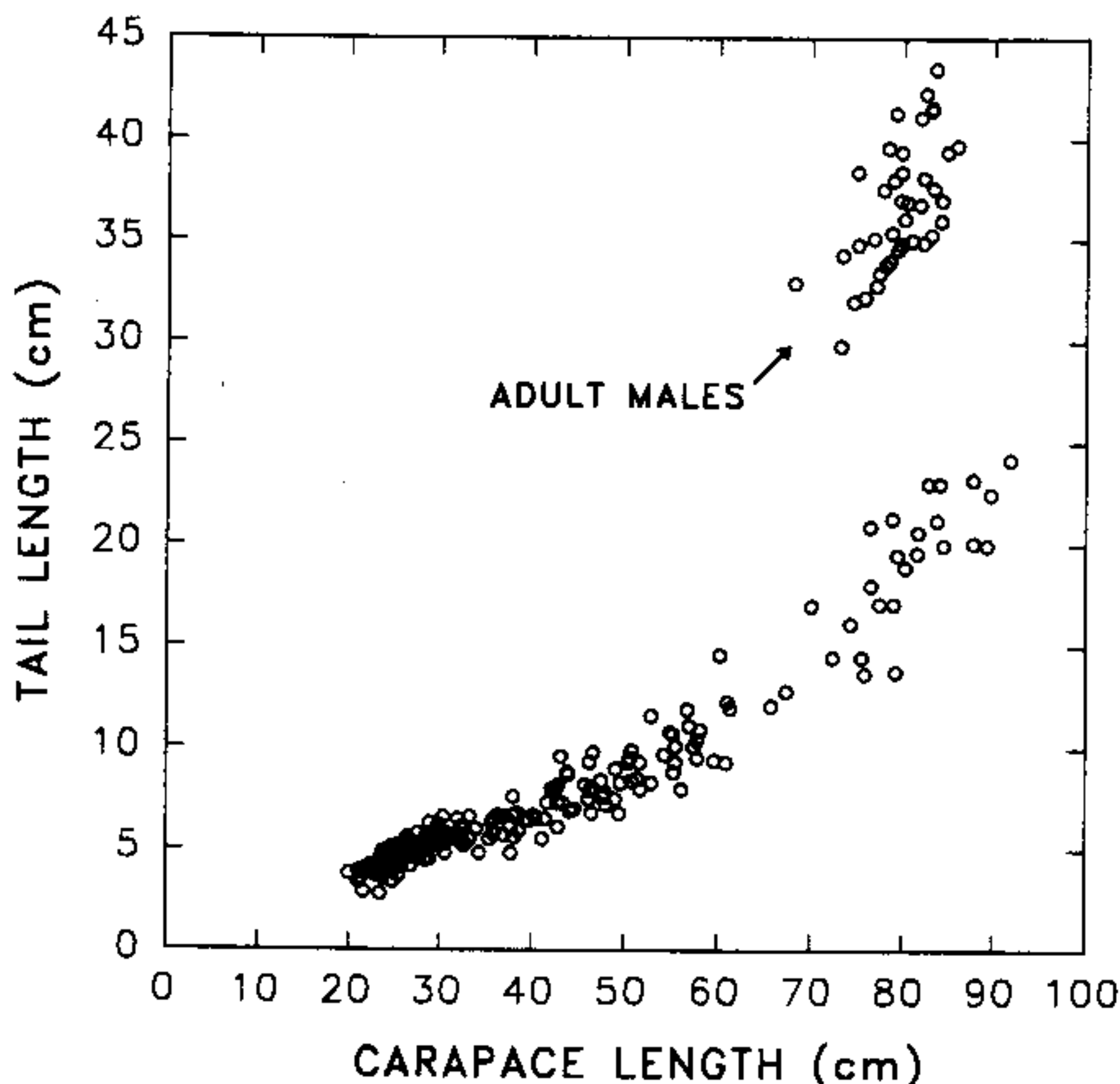
Figure 3. Plastron to tail tip length development in hawksbill turtles (n = 276). Note the bifurcation in tail length of turtles from 68.2 cm SCL_{nt}, corresponding with the appearance of external sexual characteristics in males.

to examine changes in cloaca position relative to tail size. Linear regression of log-transformed tail length data yields the relationship:

$$Tl_{pc} = 0.617 \cdot TL_{pt}^{1.068},$$

with $r^2 = 0.9897$, n = 276, $SE_{factor} = 0.050$, $SE_{exponent} = 0.007$. With increasing turtle size tail length becomes greater (Fig. 3) and relative cloaca position is shifted towards the tail tip. The cloaca, which is perhaps the most functional attribute of marine turtle tails, may be positioned further outwards in larger turtles as an adaptation to facilitate mating.

SCUTE WIDTHS. Morphometric relationships of anatomical features may be used to estimate sizes of individuals for which only a few remains are recovered. Limpus and Miller (1990) established correlations between the over-the-curve width of selected carapacial scutes and carapace length of Great Barrier Reef hawksbill turtles, thus enabling the reconstruction of the size distribution of harvested animals from scutes found in the "tortoise-shell" trade. The relationships between SCL_{nt} and size of these same scutes in Caribbean turtles are provided with the allometric equation parameters in Table 1. The widths of the left and right front costal scutes of Australian hawksbill turtles are not significantly different in relative size compared with front costal scute widths in Caribbean hawksbill turtles (CCL_{nt} measures in Limpus and Miller (1990) were converted to SCL_{nt} with regressions provided by Limpus (1992); data sets overlap from 36.9 to 84.6 cm SCL_{nt}). However, measured Caribbean hawksbill turtle anterior vertebral scute

width is on average 1.7% greater and posterior vertebral (PV) scute width is a mean 9.2% less than the values reported for Australian turtles with the same SCL_{nt} (means calculated on overlapping data set size range). This scute width disparity may be explained at least in part by differences in measurement procedure. The scute imbrication characteristic of hawksbill turtles frequently conceals the PV scute width measurement reference points (Fig. 1). Limpus and Miller (1990) chipped away overlapping scute edges to expose the margin of the scute to be measured. Because such procedure was not followed in our study, the values obtained for PV scute widths of Caribbean hawksbill turtles are probably lower than those had interfering scute edges been removed.

REGIONAL BODY FORM VARIATION. Carr (1952) proposed a division of *Eretmochelys imbricata* into two subspecies, the Atlantic hawksbill turtle *E. i. imbricata* (Linnaeus) and the hawksbill turtle of the Indo-Pacific *E. i. squamata* (Agassiz), citing regional differences in coloration and carapace morphology. Intrapopulational variation in these features, however, can be significant and cast doubt on the validity of this classification (Frazier, 1971). While our study does not address turtle coloration, the presented morphological data on Caribbean hawksbill turtles permits quantitative comparisons to be made between distinct populations, thus contributing to discussion on subspeciation.

We are aware of only two other studies that have yielded size and body mass information based on substantial samples of hawksbill turtles in a wide range of sizes. These concern hawksbill turtle populations along the southern Great Barrier Reef (Limpus, 1992) and southeast Africa (Hughes, 1974). Although in each of these studies numerous morphometric measures were taken of turtles, the differences in methodology allow only a few to be used for direct comparative purposes. The dissimilar formats of data analysis furthermore impedes comparisons using parametric statistics. However, a graphical presentation of the available regional data for four measures (body mass, straight-line carapace width, straight-line plastron length, head width) in relation to SCL_{nt} illustrates the similarities and differences by region (Figs. 4A–D). As a further example of the morphology of Caribbean hawksbill turtles, the mean values are plotted of measurements reported by Carr et al. (1966) for 65 adult hawksbill turtles in a limited size range (74.9 to 91.4 cm SCL_{nt}) of the eastern Costa Rican coast.

Hawksbill turtle body mass and carapace width relative to SCL_{nt} display the greatest variation by geographic region (Figs. 4A,B). There is a strong difference between the body mass relationship of Caribbean and Australian hawksbill turtles with that reported by Hughes (1974) for south-east African turtles (Fig. 4A). However, the greater body mass of the latter may be attributed to the inclusion of well fed captive specimens in the data set. One hawksbill turtle measured was being kept at the Durban Aquarium and is described as "displaying signs of obesity" (Hughes, 1974). In contrast, regional variation in relative carapace width is substantial (Fig. 4B) and not ostensibly due to sampling design or environmental conditions. In the size range from 33.2 to 82.3 cm SCL_{nt} for which data is available from all three areas, hawksbill turtles of the Australian Great Barrier Reef are on average 26% (range 23 to 33%) wider and those from south-east Africa a mean 17% (range 15 to 20%) greater in width than Caribbean hawksbill turtles of equal carapace length.

Whereas Hughes (1974) reports that hawksbill turtles occur around the Cape of Good Hope, which suggests a mixing of Atlantic and Indian Ocean stocks, the effects of such turtle movements on interocean gene flow may be minimal. In the Caribbean, it is possible to recognize several genetically distinct breeding populations (Bass et al., 1996), yet hawksbill turtles on the foraging grounds at Mona
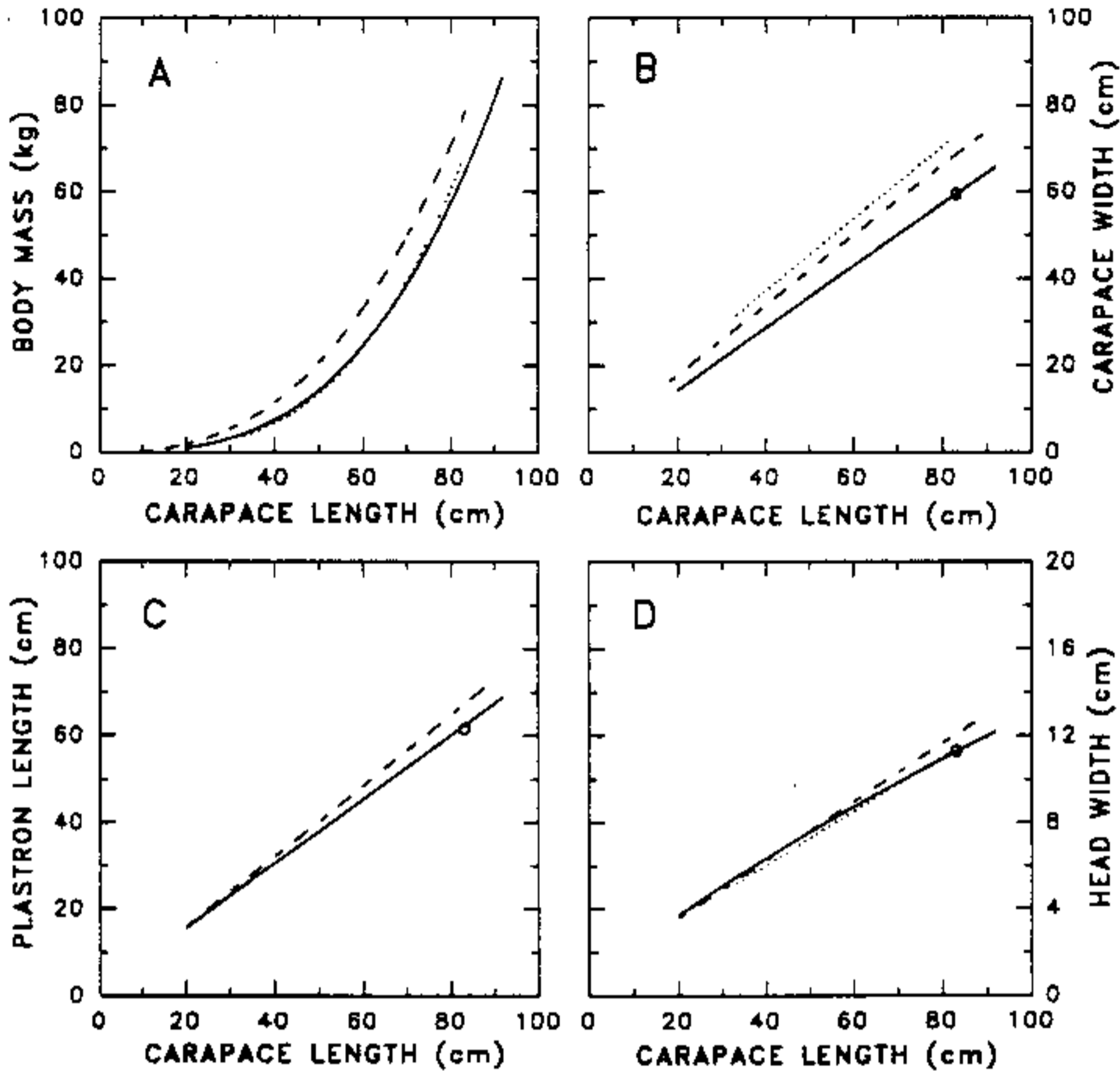
Figure 4. Comparison of hawksbill turtle morphometrics as measured in populations of Mona Island (solid line; this study), south-east Africa (dashed line; Hughes, 1974), and the Great Barrier Reef, Australia (dotted line; Limpus, 1992). Open circles represent mean measurement values of 65 mature hawksbill turtles from the Caribbean coast of Costa Rica as reported by Carr et al. (1966). Carapace length is SCL_m.

Island are of mixed Caribbean breeding stock (Bowen et al, 1996) and may remigrate to their place of origin for reproduction. If gene flow between hawksbill turtle rookeries only a few thousand kilometers apart is insignificant, as suggested by Broderick et al. (1994) and Bass et al. (1996), then a high degree of genetic isolation between Atlantic, Indian and Pacific Ocean stocks is to be expected. The observed divergence in regional hawksbill turtle morphologies is likely to be a phenotypical expression of such stock isolation.

CONCLUSIONS

Caribbean hawksbill turtles undergo substantial change in body form from the juvenile stage to adulthood. Most significant are the decrease in body depth and head width in proportion to carapace length. In hatchlings, measured head width and body mass are substantially greater than predicted from the allometric relationships established for larger turtles. Supplemental morphometric data is needed for turtles of the size range not covered by this study, i.e., of Carr's (1967) "lost year" post-hatchlings, to reach a fuller understanding of hawksbill turtle body form change. For measurement data covering in a wide size range of turtles, the use of the power function is recommended for assessing allometric change in body structures (Gould, 1966).

Substantial differences exist in the shape of hawksbill turtles belonging to geographically distant populations, and are most markedly perceived in the ratio of carapace width to length. The carapaces of Caribbean hawksbill turtles are relatively much narrower than those of Indo-Pacific turtles. Additional and more detailed morphometric characterizations of hawksbill turtle populations are required (in particular for Central and Eastern Pacific hawksbill turtles) to supplement the information becoming available from genetic studies (e.g., Broderick et al., 1994; Bass et al., 1996) and in conjunction provide a solid basis for further evaluations of subspeciation in *Eretmochelys*.

ACKNOWLEDGMENTS

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