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Allometry in the Loggerhead Turtle, Caretta caretta

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Although many studies have dealt with morphology of the loggerhead turtle, Caretta caretta (e.g., Deraniyagala, 1930, 1933; Carr, 1952; Brongersma, 1972), few studies have involved allometry (Gould, 1966) of this or any other sea turtle species. Uchida (1967) reared loggerhead hatchlings for 4.5 yrs and examined allometry in six characters ---- straight carapace length, straight carapace width, body depth, head length, head width, and body weight. Davenport and Scott (1993) investigated allometry of five characters (straight carapace length, straight carapace width, plastron length, plastron area, and body weight) in the green turtle, Chelonia mydas, based on growth of captive-raised hatchlings for 180 days. Characters employed in these studies are not sufficient to relate changes in external morphology with life stage in a functional way. Sea turtles shift their habitats with changes in their life stage (Carr, 1952). This paper presents the results of an allometric study of 19 meristic characters representing overall body shape,



Figure 1. External measurements of the loggerhead turtle. 1 = standard carapace length along a straight line (CL), 2 = carapace width along a straight line (CW), 3 = nuchal scale width (NSW), 4 = plastron length (PL), 5 = basal forelimb width (BFLW), 6 = basal hindlimb width (BHLW), 7 = forelimb length (FLL), 8 = forelimb width (FLW), 9 = hindlimb length (HLL), 10 = hindlimb width (HLW), 11 = head length (HL), 12 = head width (HW), 13 = interorbital width (IOW), 14 = nostril-orbit length (NOL), 15 = rostrum height (RH), 16 = rostrum-orbit length (ROL), 17 = upper jaw height (UJH), 18 = orbital diameter (OD), 19 = upper jaw length (UJL).

using a wide range of stages from hatchling to adult *C. caretta*. The relationship between allometry in each character and the specific ecology of turtles at each life stage is discussed.

Materials and Methods. — One hundred and seventyfive loggerhead turtles (*Caretta caretta*) were examined, of which 158 originally hatched from eggs collected at several localities in Japan (Yaeyama Islands of the Ryukyu Archipelago, Kii Peninsula, and Atsumi Peninsula) and reared in an aquarium. Straight carapace length increased from 38.4 mm to 835 mm in 9 yrs in one of these individuals. The remaining specimens were 5 females captured accidentally by fishermen and 12 nesting females from Minabe Beach, Kii Peninsula. Carapace lengths of the adults ranged from 762 mm to 960 mm. We did not determine the sex of young animals. Captive individuals were measured once each.

Nineteen measurements (Fig. 1) were taken: 1) standard carapace length along a straight line (CL), 2) carapace width along a straight line (CW), 3) nuchal scale width (NSW), 4) plastron length (PL). 5) basal forelimb width (BFLW), 6) basal hindlimb width (BHLW), 7) forelimb length (FLL), 8) forelimb width (FLW), 9) hindlimb length (HLL), 10) hindlimb width (HLW). 11) head length (HL), 12) head width (HW), 13) interorbital width (IOW), 14) nostrilorbit length (NOL), 15) rostrum height (RH). 16) rostrumorbit length (ROL). 17) upper jaw height (UJH). 18) orbital diameter (OD), 19) upper jaw length (UJL). Usually, paired structures were measured on the left side of the body unless there was a defect or anomaly on that side. All measurements were made using calipers to the nearest 0.1 mm.

On the basis of carapace length, specimens were arbitrarily classified into four categories: hatchling stage class (38.4 to 58.4 mm CL), early pelugic stage class (60.3 to 149 mm), late pelagic stage class (152 to 265 mm), benthic stage class (475 to 960 mm). For each category, CL was taken as the standard dimension (x) against which CW, PL, BFLW, BHLW, HL, HW, FLL, FLW, HLL, HLW, and NSW (y) were compared using a logarithmic scale. Similarly, in order to examine the allometry of the head characters, HL (x) was taken as the standard dimension and HW, IOW, NOL, RH, ROL, UJH, OD, and UJL (y) were plotted against it on a logarithmic scale. The relationship of y to x was expressed by the power function $y = bx^4$ (Huxley, 1932; Sweet, 1980) estimated by the least squares method.

In order to detect differences among classes in each allometric relationship, an analysis of covariance (ANCOVA) procedure was performed using CL or HL as the covariate. Furthermore, an ANCOVA was performed to examine the difference of growth pattern between wild and captive individuals in the benthic stage. All measurements were log-transformed in this procedure.

Patterns in allometric relationships among characters to CL or HL were examined in each stage with reference to the allometric constant (a in $y = bx^{a}$). The values of a were statistically compared with the case of a = 1 in each character for each stage (p < 0.05) and were divided into

Table 1. Results of regression analysis for each character on carpace length (CL). HS = hatchling stage, EPS = early pelagic stage, LPS = late pelagic stage, BS = benthic stage, C = captivity, W = wild: a and b in $y = bx^a$ (x: logCL, in mm), I = isometry, N = negative allometry, P = positive allometry.

Table 2. Results of regression analysis for each character on hea	d
length (HL). Abbreviations as in Table 1.	

Characters	Stage	$\begin{array}{c} \text{Regression} \\ a \pm \text{SE} & b \end{array}$		п	r	Growth type	
CW	HS	1.060 ± 0.166	-0.159	43	0.896	I	
	EPS	0.964 ± 0.045	+0.017	64	0.983	1	
	LPS	1.003 ± 0.052	-0.078	37	0.989	1	
	8.5	0.860 ± 0.123	+0.308	31	0.935	N	
24	HS	0.948 ± 0.141	-0.004	43	0.905	1	
	EPS	1.044 - 0.036	-0.175	64	0.991	Р	
	LPS.	1.083 ± 0.061	-0.271	37	0.987	Р	
	BS	0.841 ± 0.065	+0.348	31	0.980	N	
RFI W	HS	0.787 ± 0.180	-0.017	42	0.814	N	
	EPS	1.045 ± 0.072	-0.475	62	0.966	I	
	LPS	1.001 ± 0.118	-0.377	27	0.962	1	
	BS	1.000 ± 0.233	-0.376	29	0.861	1	
BHLW	HS	0.822 ± 0.182	-0.176	42	0.822	1	
	EPS	1.045 ± 0.049	-0.567	62	0.984	1	
	LPS	1.055 ± 0.079	-0.588	27	0.984	I	
	BS	1.054 ± 0.143	-0.640	28	0.947	I	
HL	HS	0.533 ± 0.120	+0.401	42	0.818	N	
	EPS	0.820 ± 0.040	-0.093	63	0.983	N	
	LPS	0.594 ± 0.093	+0.401	37	0.401	N	
	BS	0.744 ± 0.151	+0.094	29	0.890	N	
HW	HS	0.618 ± 0.145	+0.164	42	0.806	N	
	EPS	0.787 ± 0.035	-0.139	63	0.985	N	
	LPS	0.805 ± 0.071	-0.171	37	0.968	N	
	BS	0.788 ± 0.120	-0.070	30	0.930	N	
FLL	HS	0.850 ± 0.153	+0.110	39	0.880	I	
	EPS	0.948 ± 0.070	-0.044	64	0.960	1	
	LPS	0.836 ± 0.125	+0.197	37	0.916	N	
	BS	0.749 ± 0.171	+0.429	30	0.861	N	
FLW	HS	0.665 ± 0.215	-0.025	40	0.713	N	
	EPS	0.881 ± 0.059	-0.387	64	0.967	N	
	LPS	0.854 ± 0.146	-0.322	37	0.895	N	
	BS(C)	0.055 ± 0.051	-0.514	12	0.879	N	
	BS(W)	1.264 ± 0.047	-1.510	15	0.757	1	
HLL	HS	0.676 ± 0.117	+0.189	40	0.884	N	
	EPS	1.016 ± 0.099	-0.392	57	0.940	1	
	LPS	0.946 ± 0.111	-0.243	36	0.948	I	
	BS	0.845 ± 0.105	+0.040	30	0.952	N	
HLW	HS	0.482 ± 0.179	+0.297	39	0.668	N	
	EPS	0.848 ± 0.069	-0.327	57	0.958	N	
	LPS	0.820 ± 0.103	-0.245	36	0.940	N	
	BS	0.756 ± 0.172	-0.041	28	0.872	N	
NSW	HS	0.417 ± 0.351	+0.330	29	0.425	N	
	EPS	0.903 ± 0.095	-0.506	61	0.928	N	
	LPS	0.891 ± 0.119	-0.438	37	0.932	I	
	BS	0.539 ± 0.253	+0.573	28	0.652	N	

three growth types (Gould, 1966): positive allometry (a > 1, henceforth expressed as P), isometry (a = 1, I), and negative allometry (a < 1, N).

Results. — The allometric relationships of 11 characters to CL and 8 characters to HL are shown in Tables 1 and 2, respectively. In the benthic stage, significant differences (p < 0.05) were recognized in the slopes of regressions (= a) between the wild and captive individuals in FLW to CL and UJH to HL. Therefore, these relationships are indicated apart. Although NOL in the late pelagic stage and UJH of wild individuals in the benthic stage did not correlate with HL, correlations in all the other combinations were statistically significant (p < 0.05).

As indicated in Tables 1 and 2, the allometric constant (a) varied with characters and among stages. Isometry (a =

Characters	Stage	Regression		n	r	Growth
		$a \pm SE$	b	1215		type
HW	HS	0.855 + 0.258	+0.092	42	0.727	Ĩ
	EPS	0.977 + 0.052	-0.012	63	0.977	N
	LPS	1.163 ± 0.179	-0.374	37	0.913	I
	BS	0.883 ± 0.199	+0.222	29	0.868	I
IOW	HS	0.907 ± 0.409	-0.271	40	0.589	1
	EPS	1.025 ± 0.089	-0.400	63	0.948	I
	LPS	1.041 ± 0.185	-0.433	36	0.890	I
	BS	1.046 ± 0.264	-0.482	29	0.843	I
NOL	HS	0.868 ± 0.351	-0.510	38	0.642	- I
	EPS	0.964 ± 0.067	-0.632	63	0.965	1
	LPS	0.575 ± 0.662	+0.072	36	0.290	¢ _
	BS	0.538 ± 0.536	+0.287	29	0.369	I
RH	HS	1.059 ± 0.319	-0.660	41	0.732	I
	EPS	0.907 ± 0.111	-0.461	63	0.903	I
	LPS	1.300 ± 0.240	-1.108	35	0.887	Р
	BS	1.080 ± 0.253	-0.643	29	0.860	I
ROL	HS	0.958 ± 0.337	-0.511	40	0.683	1
	EPS	1.079 ± 0.060	-0.678	62	0.978	Р
	LPS	1.293 ± 0.172	-1.079	37	0.932	P
	BS	0.920 ± 0.222	-0.248	29	0.853	1
UJH	HS	0.820 ± 0.538	-0.634	40	0.448	1
	EPS	0.860 ± 0.099	-0.665	62	0.914	N
	LPS	1.208 ± 0.244	-1.234	37	0.880	I
	BS(C)	1.492 ± 0.107	-1.824	12	0.963	P
	BS(W)	0.364 ± 0.052	+0.719	16	0.249	¢ _
OD	HS	1.135 ± 0.313	-0.504	40	0.765	I
	EPS	0.817 ± 0.133	-0.055	63	0.845	N
	LPS	1.026 ± 0.222	-0.422	37	0.846	1
	BS	0.673 ± 0.306	+0.299	28	0.663	N
UJL	HS	0.762 ± 0.252	+0.052	41	0.699	I
	EPS	1.052 ± 0.062	-0.339	63	0.975	1
	LPS	1.148 ± 0.128	-0.509	37	0.951	P
	BS	0.747 ± 0.165	+0.334	29	0.873	N

1) was found in 4 characters relative to CL and all variables to HL in the hatchling stage, 5 variables to CL and 4 to HL in the early pelagic stage, 5 variables to CL and 5 to HL in the late pelagic stage, and 3 variables to CL and 5 to HL in the benthic stage. Positive allometry (a > 1) to CL was found in the PL in the early and late pelagic stages and to HL in the ROL in the early pelagic stage and RH, ROL, and UJL in the late pelagic stage, and UJH in the benthic stage of captive individuals.

Results of ANCOVA showed significant differences (p < 0.05) in the slopes of regressions (= a) among the four stages in PL, HL, HLL, HLW, and NSW to CL, and in HW, RH, ROL, UJH, and UJL to HL (Figs. 2 and 3). Results of comparisons of allometric constants (= slopes, a) among stages are shown in Figs. 4 and 5. The pattern of allometry of each character in *C. caretta* was as follows:

Carapace.—CW was isometric to CL in the hatchling, early pelagic, and late pelagic stages, but became negatively allometric in the benthic stage. NSW was negatively allometric to CL in the hatchling, early pelagic, and benthic stages, but was isometric in the late pelagic stage. Allometric constants in the hatchling and benthic stages were extremely low (a = 0.417 and 0.539, respectively).

Plastron. — Growth of PL in relation to CL was isometric in the hatchling stage (a = 0.948), positively



allometric in the early pelagic stage (a = 1.044) and the late pelagic stage (a = 1.083), and negatively allometric in the benthic stage (a = 0.841). BFLW and BHLW were isometric to CL in all stages, except for BFLW in the hatchling stage which was negatively allometric.

Limbs.—FLL was isometric to CL in the hatchling and early pelagic stages, but was negatively allometric in the late pelagic and benthic stages. On the other hand, FLW was negatively allometric in the hatchling, early pelagic, and late pelagic stages. In the benthic stage FLW of captive individuals was negative, though in one of the wild individuals it was isometric. Negative allometry of the forelimb to CL was shown by FLL in the benthic stage and FLW in the hatchling stage, and each presented low allometric constants (0.749 and 0.665, respectively).

In the hindlimb HLL in the hatchling and benthic stages and HLW in all stages showed negative allometry to CL, though HLL in the early and late pelagic stages was isometric. The degree of negative allometry in HLW in the hatchling stage was very strong with an allometric constant as small as 0.482.

Head.—HL and HW were negatively allometric to CL in all stages and especially prominent (a = 0.533 and 0.618, respectively) in the hatchling stage. Head characters that were positively allometric to HL were as follows: RH in the late pelagic stage, ROL in the early and late pelagic stages, and UJL in the late pelagic stage. The following characters were negatively allometric to HL: HW and UJH in the early pelagic stage, OD in the early pelagic and benthic stages, and UJL in the benthic stage. On the other hand, UJH of captive individuals in the benthic stage was positively



allometric. All the remaining characters showed an isometric relationship to HL. Positive allometry in RH, ROL, and UJL of the late pelagic stage indicated strong growth of the rostrum at this stage.

Discussion. — Patterns of allometry among the four stages of loggerhead turtles were significantly different in most of the characters examined. Habitats of sea turtles shift as they grow (Carr. 1987) and changes in growth pattern therefore may be related to associated ecological, ethological, and physiological (e.g., habitat, food, and reproduction) shifts.

After C. caretta hatchlings emerge from the nest, they enter the sea and drift with sea weeds or algae in the surface water (Caldwell, 1968). During this period hatchlings alter their neonatal morphology, which was adapted for hatching from the egg, emerging from the nest, and moving to the sea. Measurements for BFLW, HL, HW, FLW, HLL, HLW, and NSW were negatively allometric to CL in the hatchling stage, and allometric constants, except for BFLW, were smaller than 0.7. These results suggest that the sizes of head and limb characterss relative to CL become much smaller during this period. On the other hand, FLL was isometric in relation to CL; juveniles of C. caretta are known to use their forelimbs to manipulate their food (Davenport and Clough, 1985) and the isometric growth of forelimbs may highlight their relative importance in foraging behavior during the juvenile stage.

Negatively allometric growth of the flipper has been observed after birth in some cetacean species, e.g., Dall's porpoise, *Phocoenoides dalli* (Amano and Miyazaki, 1993)



Figure 4. Comparisons of allometric constants to CL among various stages. Closed circles = PL, open circles = HL, closed triangles = HLL, open triangles = HLW, closed squares = NSW. See text for abbreviations.



Figure 5. Comparisons of allometric constants to HL among various stages. Closed circles = HW, open circles = RH, closed triangles = ROL, open triangles = UJH, closed squares = UJL. UJH in the BS was from captive individuals [BS(C)]. See text for abbreviations.

and the long-finned pilot whale, *Globicephala melas* (Sergeant, 1962). Amano and Miyazaki (1993) considered that the development of relatively larger appendages before birth ensured that newborn calves were able to swim. Relatively long forelimbs in the hatchling also may be an adaptation for swimming. Moreover, these forelimbs fit easily into the egg, whereas a larger shell would require a much larger egg with associated energy costs and effects in reproductive fitness.

When turtles are between 39 and 53 mm in CL, CW has been reported to be positively allometric to CL (a = 1.4189; Uchida, 1967). However, in the present study we found isometry (a = 1.060) between CW and CL in the hatchling stage. Differences are derived in part from the differences in origin of our respective specimens. The regression line given by Uchida (1967) was calculated from measurements of 14 captive individuals originally hatched from a single clutch and are genetically homogeneous, at least maternally. By contrast, our results are based on measurements of specimens from mixed localities that are genetically far more heterogeneous.

On the other hand, Davenport and Scott (1993) obtained allometric constants of 0.930 in CW and 1.01 in PL against CL for 12 captive-reared hatchlings of the green turtle, *Chelonia mydas*. These values are judged

to be isometric and concurred with the results of the present study.

In the early pelagic stage, ROL was unique among characters of the head region because it showed an a = 1.079 and was positively allometric to HL in the early and late pelagic stages. This pattern of growth implies an elongation of the rostrum and seems to be an adaptation for foraging. Although foraging ecology in the wild has not yet been observed in turtles of the juvenile stage, they are thought to feed on macroplanktons, particularly coelenterates (van Nierop and den Hartog, 1984; Dodd, 1988). A pointed rostrum might be particularly useful in this feeding behavior.

After drifting on oceanic currents for several years, C. caretta leaves the pelagic environment and moves to the coastal zone which has been identified as the developmental habitat for the benthic stage (Carr, 1987). Developmental habitats for the Japanese breeding population range from the North Pacific to the vicinity of Baja California (Bowen et al., 1995). In the late pelagic stage, FLL was negatively allometric to CL, although it was isometric in the hatchling stage and the early pelagic stage. The decreased growth rate of the forelimb may be related to a shift to the vicinity of Baja California as the permanent habitat (Carr, 1987). Furthermore, RH and UJL, isometric to HL in the younger stages, became positively allometric to HL in the late pelagic stage. These allometric features may be affected by a change in foraging ecology. Hatchling and juvenile C. caretta probably feed on macroplankton species that accumulate in drift lines in the open ocean (Carr, 1987), although subadults and adults feed on a wide variety of benthic hard-shelled invertebrates (Dodd, 1988; Plotkin et al., 1993; Plotkin, 1996). To crush them, enlarged jaw musculature and hard jaws are required. Intensive growth of RH and UJL relative to HL in this stage allows the morphological changes necessary for crushing such hard organisms. The result of the modest growth of FLL relative to CL, as discussed above, also is thought to be a morphological adaptation in the feeding behavior of subadults and adults in which the forelimbs are not used. Furthermore, in the benthic stage UJH did not correlate with HL in wild individuals, although one of captive individuals was positively allometric. This may be affected by foraging on hard-shelled organisms in the wild.

Our report is the first study of relative growth in head and limb sizes in Testudines. None of the previous studies of such characters (e.g., Mosimann, 1956; Meek, 1982) discussed relative growth. We suspect that the pattern of relative growth of the head and limbs of *C. caretta* may be related to functional adaptations to an oceanic existence. In order to test this hypothesis, future comparisons with other species of turtles are indispensable.

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Incidental Capture of Sea Turtles in Shrimp Trawls With and Without TEDs in U.S. Atlantic and Gulf Waters

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Five species of endangered or threatened sea turtles inhabit the Gulf of Mexico and Atlantic Ocean. These are the loggerhead (Caretta caretta), green (Chelonia mydas), Kemp's ridley (Lepidochelys kempii), hawksbill (Eretmochelys imbricata), and leatherback (Dermochelys coriacea). The olive ridley (L. olivacea) occasionally occurs in the Atlantic. All are legally protected by the United States Endangered Species Act of 1973. Sea turtles are caught incidentally in shrimp trawls, and these captures have been identified as the major source of sea turtle mortality in the Gulf of Mexico and along the U.S. Atlantic coast (Magnuson et al., 1990). In these areas. Henwood and Stuntz (1987) estimated turtle capture and mortality rates for loggerheads. Kemp's ridleys, and green turtles from a variety of shrimp trawl data collected between 1973 and 1984. Turtle mortality was estimated at 9874 per year for loggerheads, 767 per year for Kemp's ridleys, and 229 per year for greens. Overall capture rates per year for these species were approximately four times higher than their mortality rate. Magnuson et al. (1990) considered the mortality of turtles in shrimp trawls to range from 5000 to 50,000 per year for loggerheads and 500 to 5000 per year for Kemp's ridleys. Information on actual observed captures and catch rates of sea turtles remains relatively scarce, especially regarding incidental catches in trawls equipped with a TED (Trawling Efficiency Device or Turtle Excluder Device) or BRD (Bycatch Reduction Device). The intent of this note is to estimate catch rates of turtles in shrimp trawls, excluding try nets, with and without TEDs in U.S. waters.

Methods. — The National Marine Fisheries Service (NMFS) has conducted two shrimp trawling studies since 1988 in which sea turtles were captured incidentally. The first study (TED study), from March 1988 through September 1990, compared the effects of TEDs on shrimp catch by commercial shrimp trawlers in the southern North Atlantic and Gulf of Mexico (Renaud et al., 1993). Typically, vessels pulled 2 or 4 standard nets (TED-less nets) for 2–6 hrs and intermittently sampled with a smaller try net. Try nets were not equipped with TEDs. Observers recorded shrimp catch during trawling operations. Gear specialists modified the standard nets so that shrimp catch among the nets was nearly equivalent. Then TEDs were installed into half of the standard nets and adjusted to have the least impact, if any, on