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INDIVIDUAL GROWTH AND ALLOMETRY OF YOUNG GREEN TURTLES (*CHELONIA MYDAS* L.)

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ABSTRACT

Twelve young green turtles (*Chelonia mydas* L.) varied considerably in growth rate when fed satiation rations (mean specific growth rate ranged from 0.01045-0.01462), but individual animals had constant specific growth rates. The following mean morphometric relationships were found: $\log y = -3.42 + 2.94 \log x$ (where y = live weight (g) and x = carapace length mm)); $\log y = 0.069 + 0.93 \log x$ (where y = carapace width (mm) and x = carapace length (mm)); $\log y = -0.115 + 1.01 \log x$ (where y = plastron length (mm) and x = carapace length (mm)); $\log y = -0.417 + 2.04 \log x$ (where y = plastron area (mm^2) and x = plastron length (mm)). Growth was isometric throughout the period of study. There was no significant relationship between the allometric coefficients of the individual turtles and their specific growth rates or between carapace length/width ratios and specific growth rates. No turtle shape, or pattern of shape/weight change is associated with high or low rates of specific growth. The plastral scute patterns of green turtles are stable over time and are individually identifiable. Carapace scutes grow asymmetrically, with little posterior or medial growth, most scutal growth taking place anteriorly and laterally. Photocopying of the plastron and scute patterns as a growth/identity technique was shown to be effective and inexpensive.

INTRODUCTION

This paper reports part of an investigation of individuality of growth and nutrition in young green turtles *Chelonia mydas* L. Much study of the physiology and biochemistry of animals, including reptiles, has been concerned with the estimation of average responses, using statistical techniques to eliminate obscuring variability. This approach has been enormously valuable, but there are circumstances in which study of individual variability may answer questions which are not easily answered by the usual techniques of pooling results and calculating means. A proponent of the study of individuality of response in marine biology has been J.C. Aldrich of Trinity College, Dublin (e.g. Aldrich, 1975, 1986; Aldrich & Regnault 1990).

Experience with previous nutritional studies on young green turtles (Davenport & Oxford, 1984; Davenport *et al.*, 1989) led to the suspicion that there was substantial variation in inherent growth rate amongst turtles, even though there seemed to be no dominance hierarchy of the sort that affects growth in crocodiles (e.g. Davenport *et al.*, 1990), and the animals were well fed. However, although satiation rations were sometimes used in these earlier studies, they were not supplied continuously to the animals, so it remained possible that larger turtles took a disproportionate amount of available food on some occasions, thereby suppressing the growth of smaller animals and exaggerating variability. It was decided that a group of young turtles should be studied intensively and individually during a period of several months when they would always be fed to satiation. The objectives were (1) to determine the degree of variability in growth rate and allometric relationships; (2) to find out whether there were any morphometric differences between 'good' and 'poor' growers; (3) to establish whether there were correlations between growth rate, appetite, metabolic rate and assimilation of nutrients. This communication addresses objectives (1) and (2); the third objective will be discussed in a later paper.

MATERIALS AND METHODS

COLLECTION, MAINTENANCE AND FEEDING

Twelve hatchling green turtles (of unknown but certainly mixed parentage and unknown sex) were sent from the Lara Reserve, Cyprus to the U.K. on 21st October 1989. At this stage they were 40-60 days posthatching. On arrival in the U.K. they were identified by placing hoops of coloured bell wire (four colours available) around the roots of the foreflippers. They were held in a large plastic aquarium (Fastank; 6m x 1m x 1m) filled with sea water (33‰) at a temperature of 25±1°C. The sea water was gradually replaced by a trickle supply; the contents of the tank were circulated through a biological filter at a flow rate of about 5 l min^{-1}. Throughout the experimental period the animals were fed daily on trout pellets. Great care was taken to ensure that the trout pellets were always offered in satiation amounts (i.e. that the animals were always given more food than they could eat), and that no feeding hierarchy could develop to interfere with feeding. The latter objective was achieved by offering trout pellets on large trays suspended a few centimetres below the water surface in the holding tank. The pellets were spread out over a large area so that each animal could feed in undisturbed fashion. Antagonistic behaviour between the turtles during feeding sessions was rare and did not seem to be related to body size; small turtles were as likely to bite bigger animals as the latter were to be the aggressors.

WEIGHING AND MEASURING

Weighing and measuring required handling of the turtles. This was thought to be stressful to a certain extent, so weighing (the least time-consuming procedure) was carried out most frequently (at intervals of roughly seven days). Animals were weighed on top-loading balances (to the nearest 0.1 g).

At intervals of 3-4 weeks the animals were measured in the following manner. Firstly, the plastron surface appearance of each turtle was recorded by photocopying the animal, ventral surface down, on a photocopier (the eyes were shielded during this process). Photocopies are not exactly the same size as the original, but the difference (about 1-2%) is consistent for a given machine; pieces of graph paper were also photocopied to allow precise measurement of plastron length and plastron area. Plastron areas were estimated (to the nearest 5 mm^2) by use of a planimeter (accuracy ca. 1%).

Next, the animals were photographed from above by a Pentax 35 mm camera fitted with a macro lens and mounted on a tripod. The field of view included a scale. Measurements of carapace length were made by inspecting negatives under a binocular microscope fitted with an eyepiece graticule; outlines of carapace scute patterns were traced under a *camera lucida* attached to the microscope. Linear dimensions were recorded in mm (to the nearest 0.1 mm). Ideally shell height would have been measured too. However, young green turtles change their shell heights to some extent when breathing (the shell is flexible) and a stress-free technique applicable to the full size range studied could not be devised.

RESULTS

Growth Rates

Fig. 1 shows the patterns of growth in the 12 turtles over a period of 176 days. Clearly, at this early state of their development, turtles fed a satiation ration exhibit an accelerating (exponential - see Fig. 2) weight increase, with no hint of tailing off. It is also clear that there is considerable variation in growth rate. To investigate this variation further, specific growth rates (g) were calculated as follows:

$$g = \frac{\ln (Wt/Wo)}{t}$$

where g = specific growth rate, t = elapsed time between weight measurements, Wo = initial weight, Wt = weight after time t.

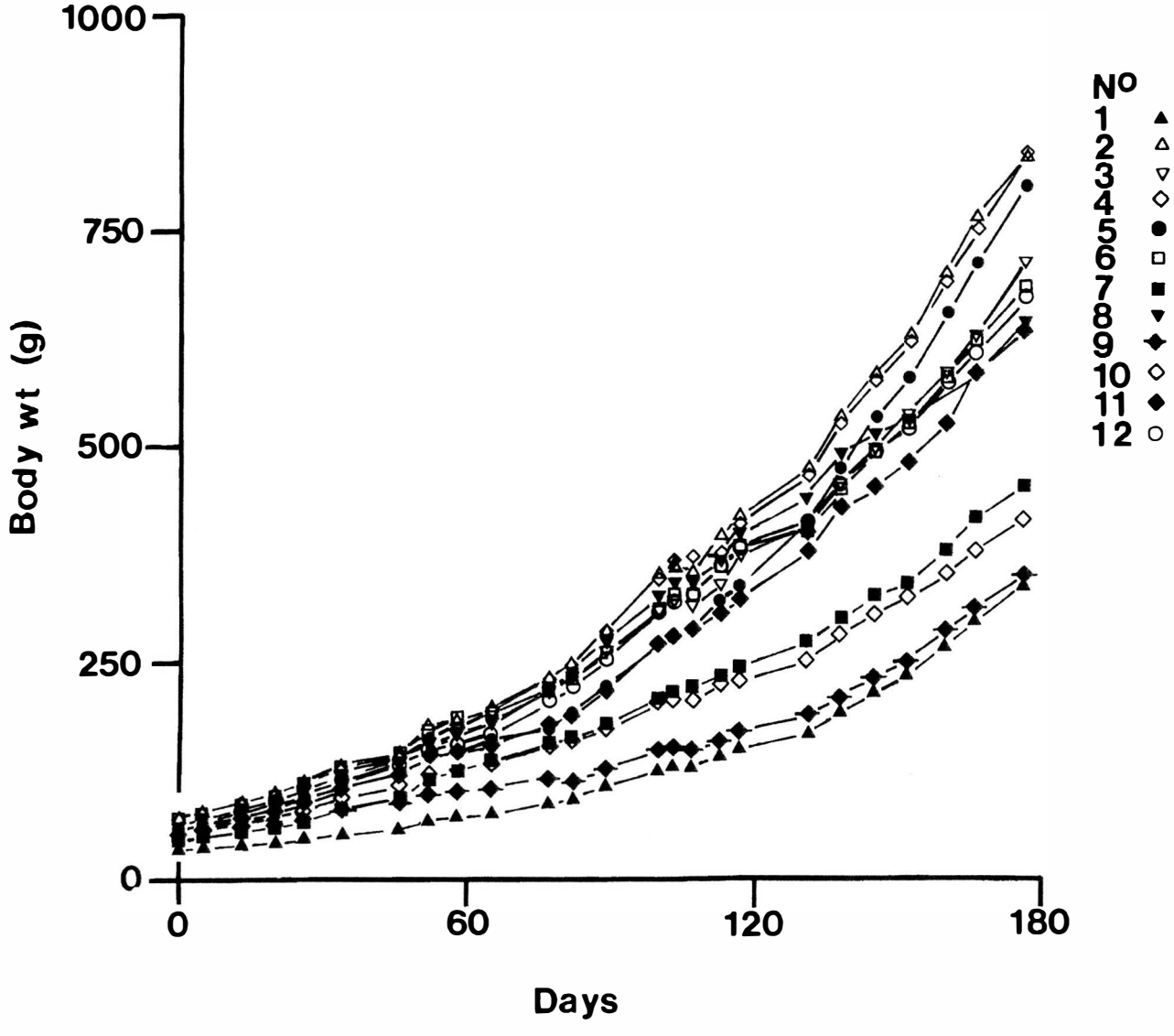

Fig. 1.Growth of 12 specimens of *Chelonia mydas* during the period of study. Symbols identify individual animals.

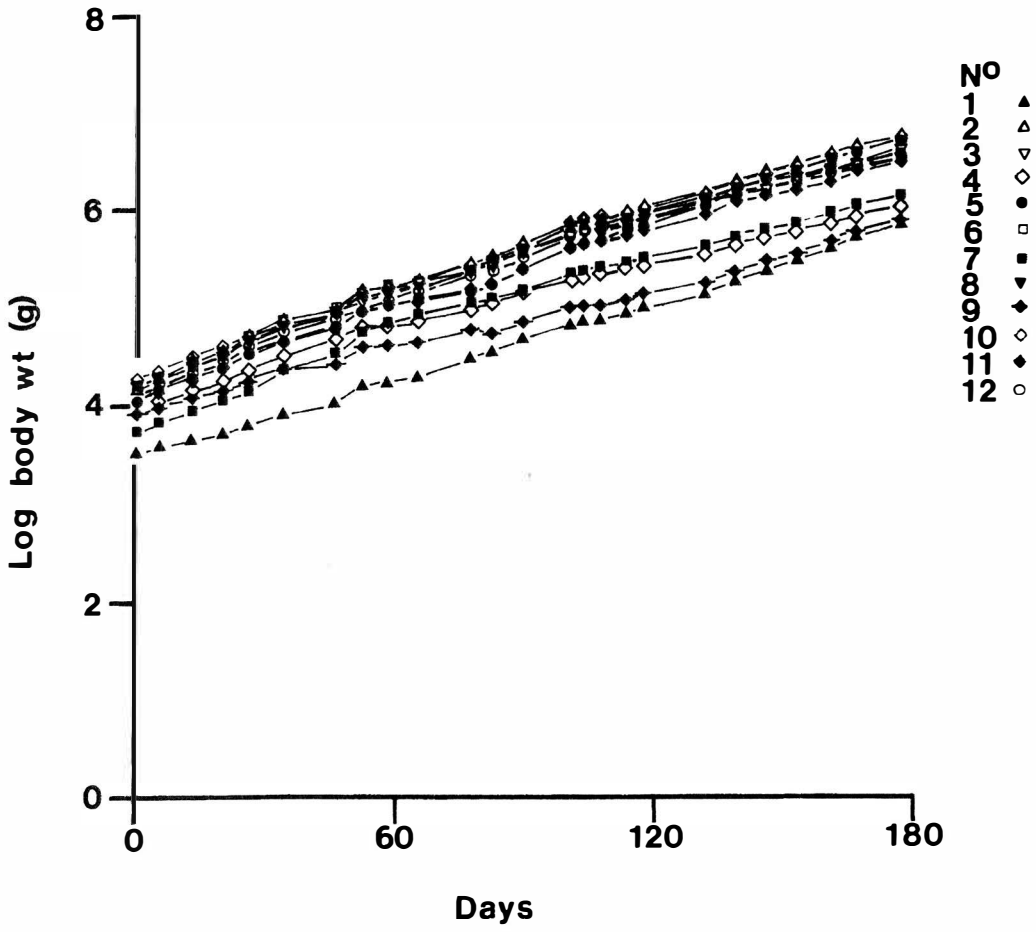

Fig. 2.Growth of 12 specimens of *Chelonia mydas*. Body weights have been logarithmically transformed (ln). Symbols as in Fig. 1.

Values of specific growth were calculated in two ways. Firstly they were calculated for each inter-weighing interval, and then an overall mean value obtained. Secondly, the weights were replotted as ln body weights (Fig. 2) and linear regression carried out upon the data. From Table 1 it may be seen that there is reasonable correspondence between these two approaches.

Although green turtles vary considerably amongst themselves in their growth rates, individual animals have remarkably constant specific growth rates when fed satiation rations (Fig. 2; Table 1); this results in a strong correlation between the rank order of their body weights at the beginning of the experiment and the rank order at the end (Spearman rank correlation coefficient: $r_s = 0.895$; $P<0.002$).

Allometric Relationships

The allometric equation $y=ax^b$ is used in comparisons of proportions of animals (see Gould, 1966; Reiss, 1989 for discussion). This equation can be conveniently rewritten as $\log y = \log a + b \log x$, so that log-transformed data may be plotted graphically to yield straight line relationships. If the proportions of an animal do not change as it grows (isometric growth or geometric similarity) then, if y and x are linear dimensions $b = 1$. If y is an area and x a length $b = 2$. If y is a weight (or volume) and x a length $b = 3$. In each case the b values were compared with the null hypothesis (isometric growth) using a t-test:

$$t = \frac{ß - b}{s/\Sigma(x-\bar{x})^2}$$

where ß = expected slope if growth is isometric; b = actual slope; s = standard deviation of b; $\bar{x}$ = mean of values of x. t values are compared with critical t values for n-2 degrees of freedom.

In recent years there has been some criticism of simple model I regression analysis of this type (see Rayner (1985) for discussion), but if the correlation coefficients for the data are very high (as is the case in this study) there are negligible differences between the b values derived from model 1, model 2 or reduced major axis models. Values of the exponent b in the model 2 regression equations can be found by using the values of r, the correlation coefficient, and b in the model 1 equation (from rb).

The mean carapace length: live weight relationship from the green turtles investigated here was as follows:

$$y = 0.00038\, x^{2.94},\ (r^2 = 0.996;\ n = 9)$$

where y = live weight (g) and x = carapace length (mm).

A t-test against the null hypothesis showed that the b value (2.94; S.D.=0.068) did not differ significantly from 3, so the mean relationship indicates that young green turtles grow isometrically. Table 2 shows the carapace length : live

Turtle No.	Wg (g) (day 0)	Wt (g) (day 217)	Mean specific growth rate (*A*)	Mean specific growth rate (*B*)
1	33.5(12)	338.9(12)	0.01358 (10)	0.01313 (9)
2	65.4(2)	839.3(2)	0.01470 (2)	0.01405 (3)
3	58.9(5)	711.9(4)	0.01444 (3)	0.01382 (5)
4	51.4(9)	415.7(10)	0.01152 (11)	0.01150 (11)
5	56.7(6)	803.8(3)	0.01552 (1)	0.01462 (1)
6	64.7(3)	681.9(5)	0.01407 (7)	0.01302 (10)
7	42.0(11)	454.8(9)	0.01383 (8)	0.01329 (8)
8	64.3(4)	645.2(7)	0.01365 (9)	0.01357 (7)
9	49.9(10)	350.9(11)	0.01100 (12)	0.01045 (12)
10	70.5(1)	840.2(1)	0.01444 (4)	0.01391 (4)
11	52.3(8)	633.2(8)	0.01440 (6)	0.01372 (6)
12	56.6(7)	669.9(6)	0.01441 (5)	0.01413 (2)

TABLE 1. Mean specific growth rates of individual young green turtles *Chelonia mydas*). Calculated either as mean value estimated from growth rates calculated for each interweighing interval (*A*), or from linear regression analysis of all weights recorded during the period of observation (*B*). Figures in parentheses represent rank orders of weight and growth rate, with 1 being highest and 12 lowest.

weight relationships for the twelve individual animals. In no case was there any statistically significant deviation from isometric growth, although 11 out of the 12 animals showed *b* values slightly below 3, suggesting that a longer study might eventually reveal slight negative allometric change in body weight, with weight increasing a little more slowly than carapace length.The mean carapace length: mean maximum carapace width relationship was as follows:

$$y = 1.72\, x^{0.930},\ (r^2 = 0.997;\ n = 9)$$

where y = carapace width (mm) and x = carapace length (mm).

The *b* value (0.93; S.D.=0.019) does not differ significantly from 1 (t=1.466; P>0.1) so from regression analysis it is evident that there is no statistically significant deviation from isometry. However, 11 out of 12 turtles showed an increased carapace length: carapace width ratio during the course of the study. The mean initial (1.16) and final (1.23) ratios differ significantly (P<0.001; t-test preceded by F-test for comparability of variance). Taken together, these findings indicate that a more prolonged study (or possibly a study involving more turtles) would reveal a positive allometric relationship, with carapace length increasing faster than carapace width (this is compatible with the slight tendency to decreased weight with increasing carapace length indicated above).

The relationship between carapace length and plastron length was as follows:

$$y = 0.767\, x^{1.01},\ (r^2 = 0.992;\ n = 8)$$

where y = plastron length (mm) and x = carapace length (mm).

In this case the *b* value (1.01; S.D.=0.034) is very close to 1 (t=0.125, P>0.05), so the relationship between plastron length and carapace length is isometric. There was no statistically significant difference between the mean carapace length : plastron length ratios measured at the start and finish of the course of the study (1.22 on Day 0; 1.21 on Day 217). Plastron area was related to plastron length by the following equation and again confirms isometry as the *b* value (2.04; S.D.=0.035) is not significantly different from 2:

$$y = 0.383\, x^{2.04},\ (r^2 = 0.998;\ n = 9)$$

where y = plastron area (mm^2) and x = plastron length (mm).

Regression analysis was performed to determine whether there was any relationship between the allometric coefficients of the individual turtles and their specific growth rates, and between carapace length/width ratios and specific growth rates. No significant relationships were revealed (r^2 values were very

Turtle No.	Equation	r^2	t	significance
1	$\log y = -3.42 + 2.92 \log x$	0.994	0.367	NS
2	$\log y = -3.42 + 2.94 \log x$	0.992	0.239	NS
3	$\log y = -3.32 + 2.88 \log x$	0.995	0.610	NS
4	$\log y = -3.25 + 2.84 \log x$	0.995	0.682	NS
5	$\log y = -3.34 + 2.91 \log x$	0.995	0.480	NS
6	$\log y = -3.54 + 2.99 \log x$	0.995	0.037	NS
7	$\log y = -3.77 + 3.10 \log x$	0.995	0.377	NS
8	$\log y = -3.29 + 2.88 \log x$	0.995	0.607	NS
9	$\log y = -3.55 + 2.96 \log x$	0.990	0.103	NS
10	$\log y = -3.12 + 2.82 \log x$	0.993	0.854	NS
11	$\log y = -3.17 + 2.81 \log x$	0.993	0.833	NS
12	$\log y = -3.32 + 2.89 \log x$	0.995	0.555	NS

TABLE 2. Carapace length (x, mm) and live weight (y, g) relationships in young green turtles (*Chelonia mydas*). Critical t at P<0.05) is 2.365 (7 d.f.)

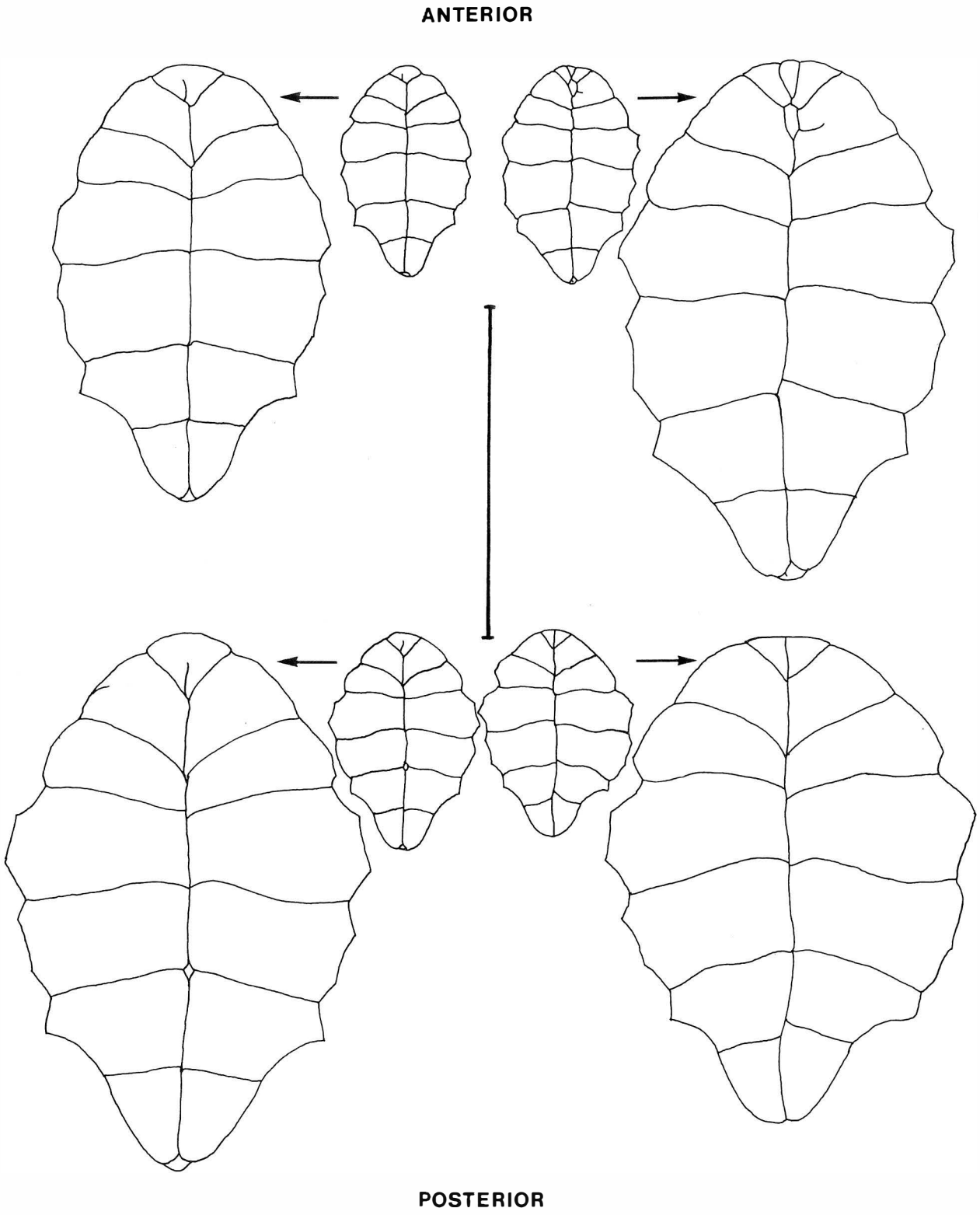

Fig. 3.Comparison of plastral scute patterns recorded from animals on 21-11-89 and 18-6-90. Vertical line has a length of 100 mm.

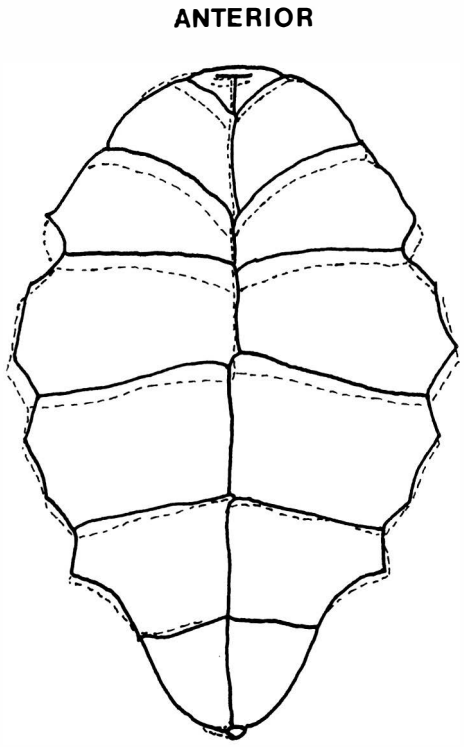

Fig. 4. Comparison of plastral scute patterns of turtle no. 3 recorded on 21-11-89 (solid line) and 18-6-90 (dotted line). The pattern recorded on 21-11-89 has been enlarged to match the plastral length recorded on 18-6-90.

low (<0.1) in all cases); it is clear that no turtle shape, or pattern of shape/weight change is associated with high or low rates of specific growth.

Scute Patterns

Fig. 3 shows plastral scute patterns for some of the young turtles. These show that scute patterns are stable over time and are individually identifiable, at least amongst fairly small numbers of turtles. Although the plastron photocopies allowed easy recognition of individuals amongst an experimental group, slight differences in scute proportions did take place during growth over periods of several months (Fig. 4). Scute patterns are therefore unlikely to be useful for long term identification of individual turtles until they have reached maturity.

Zangerl (1969) considered scute growth in relation to the embryonic scutes present at hatching, noting that the scutes of the diamondback terrapin *Malaclemys* grew symmetrically around the embryonic scutes, while the scutes of the box turtle *Terrapene* grew wholly anteriorly and laterally to the embryonic structure. Inspection of photographs of the carapaces of all of the juveniles studied here showed that the scutes of *Chelonia mydas* also grow asymmetrically, with little posterior or medial growth, most scutal growth taking place anteriorly and laterally.

DISCUSSION

Growth in green turtles is extremely variable amongst individuals, even when large quantities of high quality food are available; the specific growth rate (which includes a logarithmic component) of the fastest growing animal in this study (no. 5) was 41 % higher than that of the slowest (no. 9). On the other hand, individual specific growth rates are stable, indicating that each turtle has a different maximum growth rate programmed by its characteristic physiology/biochemistry. The wide range in growth rate is to some extent surprising: it has long been postulated that the life history strategy of sea turtles involves rapid growth to a size where likelihood of predation is substantially reduced. Given this strategy, it would seem probable that there would be substantial selection pressure in favour of uniformly high growth rates. Yet of the 12 animals studied, two (nos. 1 and 9) grew so slowly that they weighed less than 400 g even when nine months old, and were much less than half the weight of the largest animals. It is difficult to accept that these animals would ever survive to maturity in the wild where their growth would be even slower (as they would have to expend energy in foraging for food of lower quality than the trout pellets supplied in this study). Quality of offspring is a concept that clearly merits further study in sea turtles, particularly as the results of this investigation indicate that quality in terms of specific growth rate may be estimated reliably within a few weeks on a satiation diet.

The finding that young green turtles grow isometrically (individually as well as on average) during the first few months of life is not too surprising. As Alexander (1971) points out, animals with external shells (e.g. crabs, snails) tend to grow isometrically, whereas animals with internal skeletons (e.g. fish, lizards, mammals) usually grow in negative allometric fashion. Turtles effectively have both internal and external skeletal elements. The chelonians investigated by Meek (1982) all showed b values for the length:weight relationship which were very close to 3, again indicating isometry for this group which is so constrained by its shelled nature. However, the isometry of growth in these animals means that they are tending to lose "the struggle to increase surface [area] in proportion to volume" (Haldane, 1928), and presumably have to accept/counteract reductions in the efficiency of transport processes as they grow. Despite these findings, in all chelonian species, including *Chelonia mydas*, it is quite easy to distinguish a well-grown juvenile animal from a hatchling, even from photographs which do not include a scale. The reason for this discrepancy between the indications of simple allometric measurements and the reality of an animal's appearance, is that proportions of structures such as the eyes, nostrils, claws, neck and pectoral musculature (plus fine details of skin and scute surfaces) do change during growth, but are less easy and more stressful to quantify in live animals than weight, length, breadth and area of shell.

As a by-product of the study, the use of photocopying of the plastron and scute patterns as a growth recording technique was shown to be simple and considerably less expensive than photography; it is also less stressful in sea turtles which will not stay still on their backs unless exhausted. Because modern photocopiers allow the ready scaling up and scaling down of images, the photocopier has considerable potential as a tool for allometric studies on animals with rigid shells.

ACKNOWLEDGEMENTS

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