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Polyphasic Growth in Pelagic Loggerhead Sea Turtles

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Zug et al. (1995) presented size-at-age data for 12 pelagic loggerheads caught in the North Pacific drift-net fishery. Size was recorded as straight (SCL cm) and curved (CCL cm) carapace length. Age was estimated using skeletochronology. They found that the pelagic phase for loggerheads spans 10 or more years. The pelagic phase is a major but little known part of sea turtle life history so that this dataset is of great importance despite the small sample size.

Zug et al. (1995) concluded that a von Bertalanffy growth function (VBGF) was sufficient to describe age-specific pelagic growth. This conclusion implies that growth was monophasic, comprising a single growth phase and no growth spurts (see Chaloupka and Musick, 1997; Chaloupka and Zug, 1997). However, a reanalysis of these data given below suggests that an alternative interpretation of pelagic growth is worthy of consideration.

But first the limitation of this dataset must be recognized. Skeletochronological age estimation for sea turtles is a developing methodology (Zug, 1990) with some unresolved validation issues (Chaloupka and Musick, 1997). Also, growth is a time-dependent process with confounded age, year, and cohort effects (Chaloupka and Musick, 1997). The Zug et al. (1995) dataset was derived from cross-sectional sampling so that the age and cohort effects were confounded. Furthermore, the sample was drawn from a single year; thus, there was no way to account for interannual variability in growth (year effect). Moreover, the sample is small (n = 13). It is important to recognize that this dataset can only support a limited insight into the dynamic growth process—no matter how it is reanalyzed.

The reanalysis comprises two stages: (1) exploratory data visualization (Cleveland, 1993) to evaluate the implicit functional form of the growth function without having to specify an explicit nonlinear function; and (2) a polyphasic parametric growth function fitted to the size-at-age data based on the functional form implied by the exploratory analysis.

Figure 1 is a scatterplot matrix (Cleveland, 1993) of the 12 size-age growth data presented in Zug et al. (1995), plus hatchling size to give a total sample size of n = 13. The panels along the diagonal show the density distribution for each variable. The curve in each off-diagonal panel is a distance weighted least squares (DWLS) nonparametric regression estimate (Cleveland, 1993) of the implicit relationship between the various age-age or size-age combinations.

Recall that Zug et al. (1995) assumed that a monophasic VBGF provided a good fit to the data. Yet the DWLS curves (see for example Fig. 1C) reveal that the implicit functional form possibly comprises two growth cycles indicated by a growth curve that rises rapidly from hatchling size, levels off, then rises rapidly again before leveling off again. This type of trajectory is known as polyphasic growth because it comprises more than one growth phase reflecting multiple growth spurts (Chaloupka and Zug, 1997). The polyphasic pattern is apparent regardless of the age or size metric used because there is a strong linear relationship between the different age or size metrics (Fig. 1A,F). Thus the same conclusions apply regardless of the size-age combination used in Figure 1.

The parametric curve proposed to match the form implied in Figure 1C comprises two logistic growth functions, one for each of the two inferred growth phases. The specific double logistic parameterization was the Peil-Helwin model (Chaloupka and Zug, 1997):

$$y_t = \sum_{i=1}^{2} \{\alpha_i[1 + \tanh(\beta_i(t - \delta_i))]\} + \epsilon_{ti} \quad (1)$$

where the parameters are interpreted as follows: (1) y_t = mean length at age t; (2) α_i = (asymptotic mean)/2 length in phase i; (3) β_i = growth coefficient in phase i; (4) δ_i = age at the inflexion point of phase i; (5) $\tanh(z) = (e^z - e^{-z})/(e^z + e^{-z})$ and $z = (\beta_i(t - \delta_i)$; and (6) ϵ_{ti} = a normal random error structure.

Equation (1) was estimated using robust nonlinear least squares (Chaloupka and Zug 1997). The statistical fit of equation (1) to the data is shown in Table 1. The polyphasic logistic model fits the data extremely well with small residual variance (σ^2 = 0.32), significant parameter estimates with small standard errors, and no aberrant residual behavior (for a discussion of nonlinear regression goodness-of-fit criteria, see Ratkowsky, 1990).

The data and the fitted equation (1) are shown in Figure 2A. The mean age-specific growth rate function shown in Figure 2B was derived by taking the first derivative of equation

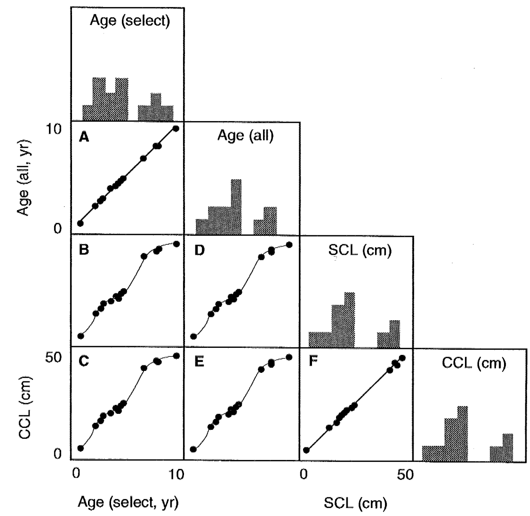

Fig. 1. Half-casement scatterplot matrix of the age and size estimates for pelagic loggerheads recorded in table 2 of Zug et al. (1995) with the addition of estimated hatchling size (n =1 3). Solid dots in the off-diagonal panels indicate growth data, whereas curves show a distance weighted least squares (DWLS) curve fit for each age–age or size–age bivariate plot.

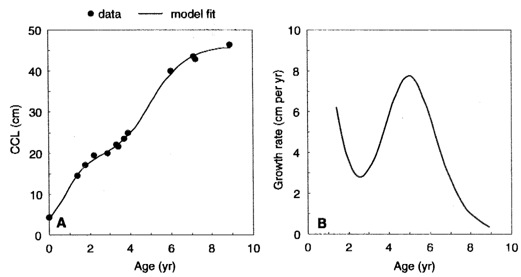

Fig. 2. (A) Pelagic loggerhead size (CCL cm) plotted as a function of estimated age (select age metric) sourced from Zug et al. (1995) with the addition of estimated hatchling size. Solid curve shows the polyphasic logistic growth function fitted to the growth data indicated by solid dots (n = 13). (B) Time derivative of the polyphasic size-at-age growth function shown in (A) indicating the age-specific growth function.

(1) (Chaloupka and Zug, 1997). Unlike the VBGF, this age-specific growth function is nonmonotonic and polyphasic with initial growth > 8 cm CCL year^{-1}, slowing to 3 cm CCL year^{-1} by year 3 or 18 cm CCL ($2\alpha_1$ in Table 1). Growth then rises to 8 cm CCL year^{-1} by year 5 (δ_2) or 46 cm CCL [$2(\alpha_1 + \alpha_2)$ in Table 1] before declining to 0.1 cm CCL year^{-1} by year 10 (Table 2).

The data suggest that pelagic growth for North Pacific loggerheads is apparently polyphasic comprising at least two growth spurts around < 1 year of age and 5 years. This small dataset does not span the entire pelagic phase; thus, additional phases could also occur prior to recruitment in coastal waters. However, a larger dataset might not support a conclusion of polyphasic growth for pelagic loggerheads. Nonetheless, nonmonotonic (but not polyphasic) growth was suggested for pelagic loggerheads recorded in a mark-recapture program operating off the Canary Islands (Bjorndal et al., 1994). The incidental growth rates recorded for those Atlantic pelagic loggerheads (Bjorndal et al., 1994) are inconsistent with a VBGF but consistent with the polyphasic age-specific growth rate function shown in Figure 2B.

Polyphasic growth behavior is one reason why a monophasic function cannot be presumed to fit the entire postnatal development period of sea turtle species (Chaloupka and Musick, 1997). In fact, polyphasic growth has been shown to be a good description of the entire

TABLE 1. PARAMETER ESTIMATES FOR THE POLYPHASIC LOGISTIC GROWTH FUNCTION (1) FITTED TO THE PELAGIC LOGGERHEAD SIZE-AT-AGE GROWTH DATA IN ZUG ET AL. (1995).

Parameter	Estimate	Asymptotic standard error	t-ratio	Inference
α_1	9.1609	0.6307	14.53	$P < 0.001$
β_1	0.9269	0.1184	7.83	$P < 0.001$
δ_1	0.6952	0.1152	6.04	$P < 0.001$
α_2	13.8950	0.8359	16.62	$P < 0.001$
β_2	0.5609	0.0640	8.76	$P < 0.001$
δ_2	4.9794	0.1335	37.30	$P < 0.001$

TABLE 2. COMPARISON OF AGE-SPECIFIC GROWTH RATES ESTIMATED FROM THE PELAGIC LOGGERHEAD GROWTH DATA IN ZUG ET AL. (1995).

Estimated age (years)	Age-specific growth rates (cm year^{-1})	
	This study (Fig. 2B)	Zug et al. (1995)
1	8.20	5.09
2	3.58	4.87
3	3.21	4.65
4	5.92	4.45
5	7.80	4.27
6	5.71	4.07
7	2.65	3.89
8	0.98	3.72
9	0.34	3.55
10	0.11	3.40

postnatal growth behavior of the endangered Kemp's ridley sea turtle (Chaloupka and Zug, 1997).

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LITERATURE CITED

BJORNDAL, K. A., A. B. BOLTEN, J. GORDON, AND J. A. CAMINAS. 1994. *Caretta caretta* (loggerhead): growth and pelagic movement. Herpetol. Rev. 25:23–24.

CHALOUPKA, M. Y., AND J. A. MUSICK. 1997. Age, growth and population dynamics, p. 233–276. *In:* The biology of sea turtles. P. L. Lutz and J. A. Musick (eds.). CRC Marine Science Series. CRC Press, Inc., Boca Raton, FL.

———, AND G. R. ZUG. 1997. A polyphasic growth function for the endangered Kemp's ridley sea turtle *Lepidochelys kempii*. Fish. Bull. 95:849–856.

CLEVELAND, W. S. 1993. Visualizing data. Hobart Press, Summit, NJ.

RATKOWSKY, D. A. 1990. Handbook of nonlinear regression models. Marcel Dekker, New York.

ZUG, G. R. 1990. Age determination of long-lived reptiles: some techniques for sea turtles. Ann. Sci. Nat. Zool. Paris 13e Ser. 11: 219–222.

———, G. H. BALAZS, AND J. A. WETHERALL. 1995. Growth in juvenile loggerhead seaturtles (*Caretta caretta*) in the north Pacific pelagic habitat. Copeia 1995:484–487.

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