# A System-of-Equations Growth Function for Southern Great Barrier Reef Green Sea Turtles

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ABSTRACT. – A system-of-equations growth model was used to describe and summarize sex-specific growth for green sea turtles (*Chelonia mydas*) resident in Australia's southern Great Barrier Reef (sGBR) foraging grounds. Each sex-specific growth function in this system has a Weibull-type nonlinear functional form that accounts for a wide range of size-at-age growth behaviors including skew-symmetric or asymmetric monophasic growth. An extension to accommodate polyphasic growth in a systems approach is straight-forward. The system-of-equations model was estimated using nonlinear seemingly unrelated regression (nonlinear SUR) that accounts for contemporaneous correlated error structure as well as allowing for the sharing of parameters across equations in the system. The system-of-Weibull-equations model used here was a good fit to the sex-specific spline growth curves derived from actual measurements of the sGBR green sea turtle stock. An advantage of a parametric growth function over the empirical spline function is that it can be used to derive simple analytic forms of time-specific growth rate functions useful for comparative demographic studies and development of growth state theory. Therefore time-dependent growth derivatives of the Weibull-type function are also provided.

### KEY WORDS. – Reptilia; Testudines; Cheloniidae; *Chelonia mydas*; sea turtle; growth; growth modelling; Weibull function; system-of-equations; demographic modelling; Great Barrier Reef; Australia

Two key demographic processes affecting population growth and abundance are somatic growth and maturation (Roff, 1992; McNamara and Houston, 1996) yet the growth dynamics of marine turtles is not well understood (Chaloupka and Musick, 1997). The size-specific growth dynamics of green turtles (Chelonia mydas) resident in Australia's southern Great Barrier Reef (sGBR) waters was described recently but the age-specific growth behavior was not as well described (Chaloupka and Limpus, 1996; Limpus and Chaloupka, 1997). The purpose of this study was to derive a parametric age-at-size growth function that fits well the empirically derived size-specific growth curves for sGBR green turtles (Limpus and Chaloupka, 1997). Such parametric growth functions are then useful for a range of purposes including comparative life history and demographic modelling as suggested previously by Chaloupka and Musick (1997).

#### MATERIALS AND METHODS

Data Set and Empirical Spline Curves. — This study considers only the benthic growth phase for green turtles resident in sGBR foraging grounds. Immature greens recruit to a benthic habitat in sGBR waters at ca. 40 cm CCL after a pelagic development phase in the Pacific Ocean. Pelagic green turtle stage duration is estimated at ca. 5-6 yrs (Limpus and Chaloupka, 1997; Zug and Glor, 1998). The original data set comprised 1037 growth records for 537 green turtles from the sGBR stock that were tagged with titanium tags in the sGBR foraging grounds between 1974 and 1991 (Limpus and Chaloupka, 1997). Individuals ranged from ca. 40 cm CCL to 116 cm CCL and spanned the entire post-recruitment size range of turtles resident in the foraging grounds. Sex and maturity status of each turtle was derived from visual examination of gonads using laparoscopy (Limpus and Chaloupka, 1997).

Size-at-age functions were derived from size-specific growth rate functions estimated from the time-specific growth observations recorded for the 537 individual turtles (Limpus and Chaloupka, 1997). These size-specific growth rate functions for each sex were estimated using a robust nonparametric regression modelling approach (Limpus and Chaloupka, 1997). The mean size-specific growth rate function for each sex was then extracted as a cubic smoothing spline and integrated numerically to derive the mean size-at-age growth functions (*integrated spline curves*; see Limpus and Chaloupka, 1997). More details on the robust statistical modelling approach and use of numerical integration for growth curve modelling can be found in Chaloupka and Limpus (1997), Limpus and Chaloupka (1997), and Bjorndal et al., (2000).

*Parametric Growth Function.*—The parametric growth function used here to describe and summarize the integrated empirical spline curves was a Weibull-type growth curve (Yang et al., 1978). The Weibull-type model form used here was based on the reparameterization proposed by Ratkowsky (1990:142, Equation 5.4.17) as follows —

where the parameters are interpreted as follows: (1)  $y_{it}$  = mean size (cm CCL) at age t for *i*th sex; (2)  $\alpha_t$  = asymptotic mean size of  $y_t$  for *i*th sex; (3)  $\beta_t$  = mean size range (or  $\alpha_t - y_t$ 

intercept) for *i*th sex; (4)  $\gamma_l$  = growth coefficient for *i*th sex; (5)  $\delta_l$  = dimensionless shape parameter for *i*th sex; (6)  $\varepsilon_{il}$  = an appropriate random error structure.

The Weibull-type function (Equation 1) is regarded as both conceptually and statistically sound with broad applicability (Yang et al., 1978; Reid, 1978; Ratkowsky, 1983, 1990; Gille and Salomon, 1995). This model is a flexible shape equation with sound statistical properties and expected-value forms are available (Ratkowsky, 1990). The shape parameter enables the equation to fit either skewsymmetric or asymmetric functions. For instance, if the shape parameter  $\delta = 1$ , then the function is an asymptotic regression function indicating a monotone decreasing agespecific growth rate function — a von Bertalanffy growth function (VBGF). If the shape parameter  $\delta = 2$ , then the function is a skew-symmetric or logistic curve indicating a nonmonotone age-specific growth rate function. Other Weibull-type growth function parameterizations are possible (Yang et al., 1978; Reid, 1978), including the so-called Janoschek curve (Gille and Salomon, 1995), but these are all related to Equation 1, which is an improved reparameterization (see Ratkowsky, 1990).

Other flexible growth functions that have been used in growth studies include the generalized VBGF or so-called Chapman-Richards function (Yang et al., 1978) and the generalized logistic or so-called Richards-Nelder function (Buis, 1993). Ehrhardt and Witham (1992) applied the Chapman-Richards function to model headstarted green turtle growth but the function did not fit well because the data set comprised only juveniles. The Chapman-Richards function as commonly used requires reparameterization for reliable model estimation (Ratkowsky, 1990). Furthermore, any growth curve must be fitted to a data set that spans the entire ontogenetic range that the curve is intended to fit (see discussion in Chaloupka and Musick, 1997). Most references in the literature to a Richards function refer to the Richards-Nelder function, which has poor conceptual and statistical properties (Yang et al., 1978, Ratkowsky, 1990) and is one reason why Ratkowsky (1990) advocated strongly for its discontinuance. A comprehensive review of the use of parametric functions for sea turtle growth studies is in Chaloupka and Musick (1997).

Weibull System-of-Equations Estimation. — The Ratkowsky form of the Weibull-type growth function (Equation 1) was estimated for each sex as a set of simultaneous nonlinear equations with contemporaneous random error structure that can also include autocorrelation for each sexspecific equation as well as cross-equation correlation. Moreover, the estimable parameters can be unique to each equation or common across equations in the set. The system comprised 8 parameters and 2 sex-specific size-at-age growth equations, each in the form of (Equation 1), that was estimated by maximum likelihood based nonlinear seemingly unrelated regression (SUR) (Judge et al., 1985) and implemented using program SHAZAM (White, 1997). The random error structure in this model of Equation 1 is multivariate normal (see Judge et al., 1985). This system-of-equations model was fitted to the sexspecific integrated spline functions. It is more efficient and informative to estimate the 2 sex-specific growth equations jointly for the following reasons — (1) the growth behavior of both sexes would be affected by contemporaneous factors including measurement error since both sexes resided in the same study area at the same time, and (2) joint estimation enables common parameters to be imposed if appropriate and for the testing of parameter commonality. Applicability of this nonlinear SUR approach was evaluated by testing for the presence of contemporaneous correlation in the error structure of the 2-equations growth model using the Breusch-Pagan Lagrange multiplier test (see Judge et al., 1985).

*Model Evaluation.* — Several reduced parameter forms of Equation 1 were then also fitted to derive a system-of-equations growth model that not only fitted the original spline curves well but did so with as few parameters as possible to ensure parsimony. For instance, if the shape of the size-at-age growth curve was the same for both sexes then a common shape parameter could be used in the 2-equation model to reduce the number of estimable parameters from 8 to 7. Model selection was based on analysis-of-deviance (McCullagh and Nelder, 1989) and use of the Akaike Information Criterion (AIC: Anderson et al., 1998).

Maximum likelihood parameter estimates were then derived from the Weibull system-of-equations model that fitted the integrated spline curves well but with fewer parameters. The sex-specific Weibull growth curves were then plotted for visual comparison with the integrated spline curves. It is common practice in growth studies to use r<sup>2</sup> as a goodness-of-fit measure but this metric is invalid for nonlinear models (see Ratkowsky, 1990, and references therein). Weibull model evaluation was done here using residual variance and standard error estimates coupled with examination of residual patterns and other related diagnostic tests applicable to both linear and nonlinear regression models (Draper and Smith, 1981; McCullagh and Nelder, 1989; Ratkowsky, 1990). Model evaluation was further enhanced using a Tukey mean-difference plot approach for residual assessment (Cleveland, 1993).

### RESULTS

System-of-Equations Fit. — The best fit Weibull system-of-equations growth model was Model 3 (Table 1) that comprises sex-specific parameters ( $\alpha_i$ ,  $\beta_i$ ,  $\delta_i$ ) but a common growth coefficient ( $\gamma$ ). There was significant contemporaneous correlation in the error structure for Model 3 (Breusch-Pagan LM test:  $\chi^2_{0.05} = 40.4$ , df = 1, p < 0.001) supporting a SUR approach to estimate the sex-specific Weibull-type growth functions jointly as a system-of-equations.

The Weibull-type growth curves derived from Model 3 approximated the empirically derived spline curves well for both sexes (Table 2, Figs. 1a,b). Nonetheless, residual deviations revealed some interesting differences (Tukey meandifference plots: Figs. 1 c,d) that were related to changes in

**Table 1.** Summary of Weibull system-of-equations growth model fitted for 4 sex-specific combinations of the growth coefficient ( $\gamma$ ) and shape parameter ( $\delta$ ). Adequacy of model fit was assessed using residual variances and residual assessment. Comparative model fit was assessed using analysis-of-deviance and AIC. LLF = loglikelihood function, df = degrees of freedom, np = number of model parameters, AIC = Akaike Information Criterion. Best fit model shown by bold AIC, which was Model 3.

	Weibull model parameters		residual variance						
Model	growth $(\gamma)$	shape $(\delta)$	female	male	LLF	df	np	AIC	
1 2 3 4	sex-specific sex-specific common common	sex-specific common sex-specific common	18.152 0.154 0.148 1.044	4.542 0.539 0.429 4.522	-240.76 -12.26 -8.02 -149.32	118 119 119 120	8 7 7 6	497.52 38.52 <b>30.04</b> 310.64	

the spline curves at (1) ca. 55 to 65 cm CCL reflecting the juvenile growth spurt (Limpus and Chaloupka, 1997) and (2) ca. 95 to 105 cm CCL reflecting a growth deceleration phase approaching onset of sexual and physical maturation (Limpus and Chaloupka, 1997). The Weibull-type curves overestimate growth in length at these 2 points for both sexes but the deviations are negligible, especially considering the issue of measurement error of the spline growth curve that is not included here (see Fig. 2 in Limpus and Chaloupka, 1997).

There was no significant sex-specific difference in the growth coefficient ( $\gamma$ ) so it was a common parameter in Model 3, thereby reducing the number of parameters from 8 to 7 compared to Model 1 (Table 1). The common growth coefficient ( $\gamma$ ) means that sGBR female and male greens approach the sex-specific asymptotic mean size ( $\alpha$ ) at the same rate even though mean female size is larger than mean male size at all lengths from ca. 65 cm CCL or all ages from ca. 10–12 years of age (see Limpus and Chaloupka, 1997).

The estimated sex-specific shape parameters (Table 2:  $\delta_{\text{female}}, \delta_{\text{male}}$ ) were significantly > 1 (female Wald  $\chi^2$  test = 4620.7, df = 1, p < 0.001; male Wald  $\chi^2$  test = 6450.5, df = 1, p < 0.001) but significantly < 2 (female Wald  $\chi^2$  test = 21098.1, df = 1, p < 0.001; male Wald  $\chi^2$  test = 17852.3, df 1, p < 0.001). Hence, the size-at-age growth curve for either sex was neither a von Bertalanffy ( $\delta$ = 1) nor a logistic ( $\delta$  = 2) growth function but a form of asymmetric sigmoid type curve well summarized by the Weibull-type function (Equation 1).

Derived Forms of the Weibull Function. — The timederivatives and other derived forms of the Weibull-type growth function (Equation 1) are useful but not readily available so they are presented here for completeness. The following Equations (2 to 4) were derived analytically from Equation 1 using MATHEMATICA (Wolfram Research, 1993). The first derivative (*dy/dt*) of Equation 1 yields the

**Table 2.** Parameter estimates for best fit Model 3 (Table 1) fitted to sex-specific green turtle size-at-age integrated spline curves from Limpus and Chaloupka (1997, their Figs. 3c,f). Parameters shown in Equation 1, ASE = asymptotic standard error.

Parameter	Estimate	ASE	t-ratio	Prob(t)	
$\alpha_{\text{female}}$	106.320	0.0449	2368.4	p < 0.001	
$\beta_{\text{female}}$	65.526	0.1692	387.2	p < 0.001	
$\delta_{\text{female}}$	1.319	0.0047	281.2	p < 0.001	
$\alpha_{\rm male}$	99.419	0.0705	1409.3	p < 0.001	
$\beta_{male}$	57.275	0.2536	225.8	p < 0.001	
$\delta_{ m male}$	1.375	0.0047	294.2	p < 0.001	
$\gamma$ temale, male	4.140	0.0177	233.3	p < 0.001	

age-specific absolute growth rate function as follows with group-specific parameters if used as a system-of-equations model (subscripts not shown) —

The second derivative  $(d^2y/dt^2)$  of Equation 1 yields the agespecific growth acceleration function as follows —

$$y'' = \beta \,\delta \exp(-2\gamma - (t^{\delta}/\exp(\gamma))) t^{\delta-2}(-\exp(\gamma) + \delta \exp(\gamma) - \delta t^{\delta}) \dots (3)$$

Equation 1 can also be solved for t (or age) for a known size (CCL, cm) as follows with parameters specific to each sex —

$$t \rightarrow \left[-\exp(\gamma)\ln[-\{(-\alpha + \text{size})/\beta\}]\right]^{1/2} \dots (4)$$

These 3 derived forms of Equation 1 have broad applicability such as Equations 2 and 3 for growth state theory (Buis, 1993), Equations 2 and 3 for comparative life history modelling (Roff, 1992) and Equation 2 for comparative demographic modelling (Chaloupka and Musick, 1997). Equation 4 is useful for age-from-size back-calculations used for stochastic simulation modelling of sea turtle population dynamics (Chaloupka, in press) or for deriving the age/size composition of stranded turtles (C. Caillouet, *pers. comm.*).

The age-specific absolute growth rate curves for sGBR green turtles derived from Equation 2 using Model 3 parameters (Table 2) are shown in Fig. 2a. The absolute growth rate curve for female greens is a nonmonotonic function. It increases rapidly from ca. 1.2 cm CCL/yr at recruitment to a maximum of ca. 2.1 cm CCL/yr at around 9 or 10 years of age since recruitment, before declining to negligible growth approaching the onset of sexual and physical maturity at ca. 95 to 100 cm CCL or ca. 35 to 37 years since recruitment, based on Equation 4.

The growth rate curve for males is similar until the growth rate peak at ca. 9 to 10 years before declining faster at all ages than the female curve to negligible growth approaching sexual maturity at a smaller size < 95 cm CCL, estimated using Equation 4 at ca. 32 to 35 years since recruitment. These growth rate functions (Fig. 2) are monophasic rather than polyphasic functions (see Chaloupka and Zug, 1997; Chaloupka, 1998) displaying a single growth cycle with a juvenile growth spurt for either sex ca. 9 to 10 years since recruitment to the benthic habitat or ca. 60 cm CCL. These sex-specific growth rate characteristics are consistent with the size- and age-specific growth rate func-



Figure 1. Plots of the empirical size-at-age spline function sourced from Limpus and Chaloupka (1997) and the Weibull growth function fitted here for (a) female and (b) male sGBR green sea turtles. Tukey mean-difference plot showing the Weibull curve deviation (residuals) from the empirical spline curve on a common scale for (c) females and (d) males derived from comparison of the two curves in (a) and (b).

tions derived from the empirical spline growth models in Limpus and Chaloupka (1997).

The age-specific growth acceleration curves for each sex derived from Equation 3 (Table 2) are shown in Fig. 2b, which show 3 distinct growth phases — (1) a rapidly decelerating juvenile growth phase approaching the juvenile growth spurt ca. 9 years, then (2) a slower decelerating immature growth phase reaching a minimum ca. 20 years, followed by (3) a slowly accelerating subadult growth phase approaching the onset of sexual and physical maturity.

#### DISCUSSION

Growth Modelling. — The Weibull-type parametric growth function fitted the empirically derived spline growth curves well for both female and male green turtles resident in sGBR waters. The size related parameter estimates ( $\alpha$ ,  $\beta$ ) were consistent with empirical estimates of mean adult (ca.  $\alpha$ ) and juvenile recruitment size (ca.  $\alpha - \beta$ ) and the juvenile sex-specific growth spurts at ca. 60 to 62 cm CCL (see Limpus and Chaloupka, 1997). The asymptotic mean size for sGBR female greens estimated from Model 3 was ca. 106.3 cm CCL ( $\alpha_{female}$ , Table 2) and for males ca. 99.4 cm CCL ( $\alpha_{male}$ , Table 2). Estimated asymptotic mean size was consistent with actual measurements for green sea turtles resident in sGBR waters (Limpus, 1993), with mean adult female size estimated at ca. 107 cm CCL (95% CI: 97–117 cm) and mean adult male size at ca. 100 cm CCL (95% CI: 92–109 cm). Estimated recruitment size ( $\alpha - \beta$ : Table 2) was ca. 41 to 42 cm CCL with no meaningful sex-specific difference. Estimated mean recruitment size was consistent with empirical estimates of sGBR green turtle recruitment size at ca. 44 cm CCL (95% CI: 43–45 cm; Limpus and Chaloupka, 1997).

A variety of other parametric growth functions have been used to study turtle growth dynamics (Chaloupka and Musick, 1997). Most sea turtle growth studies have used size-based analogues of age-specific parametric growth functions since age was unknown. It is easy to derive sizebased analogues, including for Equation 1, but this approach has many shortcomings for modelling growth dynamics that were discussed in detail elsewhere (Chaloupka and Limpus, 1997; Chaloupka and Musick, 1997; Limpus and Chaloupka, 1997). When age is unknown a useful means for studying growth dynamics is a 2-stage modelling approach comprising the following (see details in Chaloupka and Limpus, 1997; Limpus and Chaloupka, 1997) — (1) a statistical model of growth rates for turtles of unknown age to derive the expected size-specific growth rate function (size-specific growth rate spline curve) for each sex conditioned on informative covariates and sampling design constraints, then followed by (2) numerical integration of the sizespecific growth rate functions to derive an estimate of the expected size-at-age growth functions for each sex (size-atage spline curve).



**Figure 2.** Plots of the (a) age-specific growth rate function (see Equation 2) derived from the Weibull-type function (see Equation 1) for each sex and (b) the age-specific acceleration function (see Equation 3) derived from the Weibull-type function (Equation 1) for each sex.

This was the approach adopted here with the main purpose being to develop an age-specific parametric approximation to the sex-specific growth curves derived empirically from step (2) of the 2-stage process. The Weibulltype model used here for this purpose is a simple parametric form that is well able to describe and summarize sex-specific growth dynamics for green turtles resident in sGBR foraging grounds. The advantage of using one parametric growth function such as the Weibull-type (Equation 1) and its time derivative forms (Equations 2, 3) is that it would enable comparison of sex-specific growth functions among the stocks or substocks comprising a metapopulation in terms of the same ecologically relevant growth parameters.

For instance, the sGBR green turtle stock occupies widely separated foraging grounds linked by adult mixing during reproductive dispersal to a single stock-specific breeding ground in sGBR waters. Therefore, the Weibull-type model provides a means for estimating foraging ground specific growth dynamics for the sGBR metapopulation that can be expressed in simple summary form as (1) mean adult size ( $\alpha$ ), (2) mean size at recruitment to the benthic habitat ( $\alpha$ - $\beta$ ), (3) growth coefficient ( $\gamma$ ), and (4) the intrinsic growth function shape parameter ( $\delta$ ). More generally, these 4 parameters coupled with estimated mean age at sexual maturity provide a quantitative basis for comparative populationor stock-specific demographic modelling. The system-of-equations growth model used here can be readily extended in the following two ways. Firstly, measurement error was not included here but can be accounted for by either direct model estimation if the study was based on known age turtles or indirectly when age is unknown by including instrumental variables that are some form of variance estimates of the empirically derived mean growth curve. Secondly, the monophasic equation form in the system-of-equations model can be replaced by suitable polyphasic functions to account for multiple growth cycles, if applicable (see Chaloupka and Zug, 1997; Chaloupka, 1998).

Demographic Modelling. — The main approaches used for summarizing life history dynamics irrespective of whether environmental effects are constant or stochastic are based on either age-specific (Roff, 1992) or state-dependent demography (McNamara and Houston, 1996). The demographic structure of the sGBR green sea turtle stock is best summarized using a state-dependent approach with the states defined here by a combination of both size and reproductive status based on developmental stages (Chaloupka and Limpus, 1996). The mean duration of these stages can be estimated using Equation 4 in conjunction with sizespecific growth functions presented in Limpus and Chaloupka (1997).

The demography of green turtles resident in sGBR foraging grounds comprises four fundamental developmental states once turtles have recruited from a pelagic developmental phase to a benthic habitat in sGBR waters — (1) benthic juveniles (40–62 cm CCL), (2) subadults (62–91 cm CCL), (3) maturing adults (< 97 cm CCL), and (4) mature adults (>90 cm CCL). The upper bound of the subadult stage and the identification of both maturing and mature adults depends not only on size considerations but also assessment of reproductive and maturity status by visual examination of the gonads using laparoscopy (Limpus and Chaloupka, 1997).

Given these considerations, the mean juvenile stage duration for sGBR green turtles resident in sGBR foraging grounds is estimated at ca. 11 yrs, with mean subadult duration ca. 19 yrs. Therefore, the immature developmental phase comprising benthic juveniles and subadults has a mean duration of ca. 30 yrs. The maturing adult duration is estimated to be ca. 5 yrs so that on average an adult female or male sGBR green turtle resident in the sGBR foraging grounds is ca. 35 yrs of age since recruitment to the benthic habitat. It is important to note that these size- and agespecific growth characteristics are not necessarily the same for other foraging ground populations comprising the sGBR green sea turtle metapopulation but these foraging ground specific findings will be presented in detail elsewhere.

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