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Investigation of Growth Phases for Bottlenose Dolphins using a Bayesian Modeling Approach

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ABSTRACT

The Gompertz function is the most commonly used growth function for cetacean studies. However, this function cannot represent multiple phases of growth. In this study, we present a Bayesian framework fitting parameters of a triple-logistic growth function to describe multiple phases of growth for bottlenose dolphins (*Tursiops truncatus*), simultaneously fitting and comparing all growth parameters between South Carolina (SC), Mississippi Sound (MSS), and Indian River Lagoon (IRL) cohorts. The fitted functions indicated a preliminary early, rapid growth phase, followed by a second phase of slower growth, and then a moderate growth

spurt later in life. Growth parameters between geographic cohorts did not show obvious differences, although asymptotic length for SC dolphins was lower than MSS and IRL dolphins and significantly lower between females from SC and the IRL. Growth rate velocities between the sexes showed females exceed males initially (<1 yr), followed by males gaining an advantage around the ages of 3–4 yr until the age of around 15 yr when growth rates for both sexes approached zero (asymptotic length). This study demonstrates age-related changes in growth rates between bottlenose dolphin sexes and evidence of at least some differences (*i.e.*, asymptotic length) across geographic cohorts.

Mathematical functions are often applied to describe growth dynamics for a species, allowing researchers to study and compare patterns in growth and development. A number of functional forms have been suggested for vertebrate species, including the Logistic, von Bertalanffy, Gompertz, and Brody (Brody 1945) functions, with the Gompertz function being the most commonly used for cetacean studies (Read *et al.* 1993, Fernandez and Hohn 1998, Stolen *et al.* 2002). The Gompertz growth function was first introduced to describe the growth of solid tumors and assumes that the growth rate declines as mass/length increases. Although the Gompertz function has the advantage of few parameters with relatively straightforward inter-pretations, it limits growth rate to a monotonically decreasing function and cannot represent multiple phases of growth. The need for multiple growth phases and the limitation of the Gompertz function to represent spurts in growth was previously identified in studies of white-sided (*Lagenorhynchus acutus*) (Ferrero and Walker 1996) and bottlenose dolphins (*Tursiops truncatus*) (Mattson *et al.* 2006), as well as for the pantropical spotted dolphin (*Stenella attenuata*) (Perrin *et al*. 1976). The two for-mer studies address the issue by combining two Gompertz functions in a piecewise fashion, fitting the first up to a predetermined age and then fitting the second Gom-pertz to account for a growth spurt. The fixed point for initiating the change in growth rate was determined using estimated age of sexual maturity. Perrin *et al*. (1976) simultaneously fit separate equations for the two phases of growth and de-termined the convergence point for the two phases using an iterative least-squares method. Males and females were combined for the juvenile growth phase with the assumption that growth rates and the convergence point for the second phase are the same for males and females.

More flexible functional forms based on the summation of two or more logistic functions have been applied to modeling multiphasic growth in other species (Bock and Thissen 1976, Koops 1986, Koops *et al.* 1987). The advantage of these models is that the multiple phases of growth are combined in a single functional form and the ages at which growth rate changes are estimated from the empirical data. This is informative for examining growth phases but also provides sufficient flexibility for comparing growth phases between cohorts.

Comparative analyses of growth parameters in bottlenose dolphins have been limited to asymptotic length, girth, and mass. Read *et al*. (1993) examined sex-related differences in asymptotic length, girth, and mass from a single population of wild bottlenose dolphins. Stolen *et al*. (2002) compared asymptotic lengths derived from different studies of dolphins on the east and west coast of Florida. However, no studies to date have quantitatively examined differences in other parameters that describe the phases of growth between various cohorts. In this study, we present

a Bayesian framework fitting parameters of a triple-logistic growth function to describe multiple phases of growth for bottlenose dolphins, simultaneously fitting and comparing all growth parameters between multiple cohorts. We use age and length data from stranded bottlenose dolphins along the South Carolina coast, but also include previously published data on cohorts from Mississippi Sound (Mattson *et al.* 2006), and the Indian River Lagoon (Stolen *et al.* 2002). We explore sexual dimorphism for growth patterns including the magnitude and timing of growth phases and examine differences in growth patterns among geographically distinct populations.

<center>Mᴇᴛʜᴏᴅs</center>

Age Determination

Teeth were collected from bottlenose dolphin carcasses along the South Carolina (SC) coast by the South Carolina Marine Mammal Stranding Network (National Ocean Service, South Carolina Department of Natural Resources, Coastal Carolina University, volunteers) from 1992 to 2005. Only teeth from stranded carcasses were used to reduce total length measurement bias that may occur with free-ranging, captured dolphins. At least four teeth were collected from the left lower mandible (generally teeth positioned at numbers 13–16 in the row), stored in 10% neutral-buffered formalin for up to 48 h, rinsed in tap water, and archived in 70% ethyl alcohol. Teeth were then prepared for sectioning using standard procedures (Myrick *et al.* 1983, Hohn *et al.* 1989). A 1–2-mm-thick section (slab) was taken from each tooth of dolphins >140 cm total body length. For dolphins with a total body length of <140 cm, a slab was not taken, but rather decalcified whole and then thin sectioned. Total body lengths of dolphins were taken from the tip of the upper jaw to the fluke notch in a straight line (Norris 1961). The slabs were cut using a diamond wafer blade mounted on a Buehler Isomet low speed saw (Emerson Industrial Automation, Lake Bluff, IL). The slabs were rinsed in tap water for approximately 6 h and then decalcified in RDO (rapid decalcifying agent of acids; Apex Engineering Products Corporation, Aurora, IL) for 6–12 h based on the thickness of the slab. The slabs were rinsed overnight and thin-sectioned on a Leica SM2000R sledge microtome (Leica, Inc., Nussloch, Germany) attached to a Physitemp freezing stage (Physitemp, Inc., Clifton, NJ). Thin sections were stained in Mayer's hematoxylin, blued for 30 s in a weak ammonia solution, dried on a slide, and mounted in 100% glycerin.

Sections were read three times by the author using a Leica Zoom 2000 stereomicroscope (Leica, Inc., Nussloch, Germany) or a Nikon SMZ1500 stereomicroscope (Nikon Instruments, Inc., Lewisville, TX). At least 1 wk elapsed between readings to eliminate bias. Teeth were aged based on Hohn *et al.* (1989). If two of the three readings were the same, this was used as the age estimate. If differences between readings were <2 growth layer groups (GLGs), a fourth reading was made. Differences >2 GLGs required another tooth to be sectioned and the process repeated. Age estimates <1 GLG were rounded to the nearest 0.25 GLG while others >1 GLG were rounded to 0.50 GLG. Most teeth >5 GLGs were estimated to the last GLG.

Other Data Sources

Previously published age-length data were obtained for stranded bottlenose dolphins from the Indian River Lagoon (IRL), Florida (Stolen *et al.* 2002) and from the Mississippi Sound region (MSS) of the Gulf of Mexico (Mattson *et al.* 2006). Data

from the IRL included ages and lengths for 199 dolphins (118 males, 72 females, 9 of unknown sex). Data from MSS included ages and lengths for 111 dolphins (69 males, 42 females).

Previous interlaboratory comparisons had been conducted between the McFee and Stolen laboratories, validating that data generated for the IRL and SC studies were comparable. A subset of 22 teeth from the IRL and SC were read twice by co-authors McFee and Stolen and the mean of the two reads from each researcher was calculated as the final age estimate. The final estimates from the two researchers were compared and a Pearson's correlation coefficient (r) as well as a coefficient of accuracy (C_a) was calculated (Lin and Torbeck 1998). The correlation coefficient represents the precision of the data measuring how far the paired observations deviate from the best-fit regression line, while the coefficient of accuracy represents the accuracy of the paired data compared to the ideal $45°$ line. Age estimates ranged from 0.75 to 36 GLGs. The calculated r was 0.995 and the C_a was 0.994, indicating excellent agreement between the two researchers.

No interlaboratory comparisons have been conducted between the SC and MSS laboratories. However, the original slide sections were obtained from the MSS study and a random subset of 27 teeth were selected to be read by McFee to ensure that no large discrepancies would be seen in age estimates. Two readings were performed by McFee and the mean of the two readings was used as the final age estimate. The protocols for the MSS study differed from the other two studies in that dolphins that were considered nonneonates <1 yr of age were pooled with neonates and assigned age zero (Mattson *et al*. 2006). This is in contrast to the SC and IRL studies for which the age of nonneonates <1 yr was estimated by comparing the width of the forming GLG with that of the prenatal dentine. For this reason, all of the randomly selected teeth were estimated to be at least 1 yr of age, the oldest estimated age was 26 GLGs. The calculated correlation coefficient between the age estimates from the two researchers was 0.980 and the C_a was 0.993, again indicating good agreement.

Statistical Analysis

Several growth curves were considered for this analysis with primary focus on the double and triple logistic forms (Bock and Thissen 1976). Initial attempts to fit the double logistic form exhibited unsatisfactory residual error plots (Fig. 1). In the double logistic model, the first logistic function is fixed to have its peak growth rate at 0, leaving the second to explain any remaining growth spurt. Our analysis indicated that the positioning of this second spurt that best fit the data was also at very young ages and tended to fit the early, gradually decreasing growth rate (to about 8 yr). However, prior dolphin growth analyses (Ferrero and Walker 1996, Mattson *et al*. 2006) have suggested a growth spurt near age of sexual maturity, which could not be represented with the double logistic model without forcing the elimination of the identified fluctuation in younger years. We therefore chose to focus on the triple logistic form which would allow for an additional fluctuation in growth rate. The model is described as follows. Length for animal of sex s, from location l, at age a is described by the following model:

$$L(a) = \frac{\mu}{1 + \exp(-\beta_0 a)} + \frac{\Delta\mu_1}{1 + \exp(-\beta_1(a - t_1))} + \frac{\Delta\mu_2}{1 + \exp(-\beta_2(a - (t_1 + t_2)))}$$
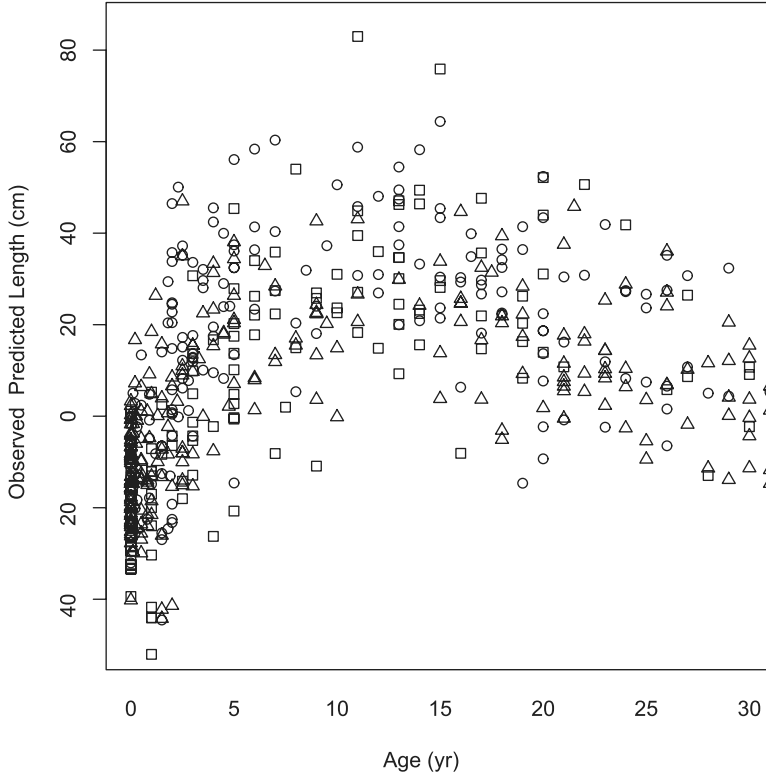$$= C_0 + C_1 + C_2$$

Figure 1. Residual errors for the double logistic model including SC (Δ, $n = 263$), MSS ($\square$, $n = 111$), and IRL ($\circ$, $n = 199$). Residual prediction error using point estimates of the model parameters and a double logistic model indicated age-dependent error, as illustrated by the notable age-related pattern in the scatter plot. The double logistic model was abandoned in favor of a triple logistic model.

where

$\quad a$ is the animal's age in years

$\quad \mu$ is the contribution to total length due to the first growth phase

$\Delta\mu_1$ is the contribution to total length due to the second growth phase

$\Delta\mu_2$ is the contribution to total length due to the third growth phase

$\quad \beta_0$ is the growth rate during the first growth phase

$\quad \beta_1$ is the growth rate during the second growth phase

$\quad \beta_2$ is the growth rate during the third growth phase

$\quad t_1$ is the time at maximal growth rate during the second growth phase, and

$t_1 + t_2$ is the time at maximal growth rate during the third growth phase

The corresponding growth rate as a function of age is given by

$$V(a) = \frac{\beta_0 C_0 (\mu_0 - C_0)}{\mu} + \frac{\beta_1 C_1 (\Delta\mu_1 - C_1)}{\Delta\mu_1} + \frac{\beta_2 C_2 (\Delta\mu_2 - C_2)}{\Delta\mu_2}.$$
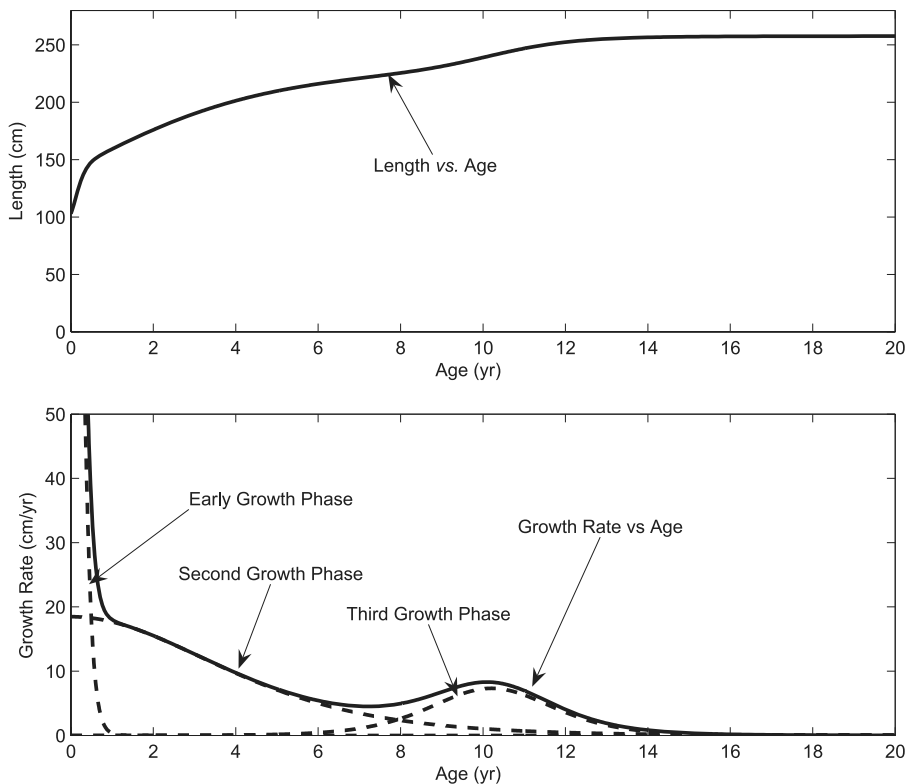
Figure 2. Representative growth curve using triple logistic model. Growth (upper panel) and growth rate (lower panel) curves illustrate the model used in this analysis. The overall growth curve is constructed as three scaled and shifted logistic curves. Dashed lines in the lower panel illustrate the contribution of each of these curves to the overall growth rate. Curves plotted here use point estimates of the parameters determined for male dolphins ($n = 100$) from South Carolina.

Figure 2 illustrates the components of this model showing the total growth curve (upper panel) and the first, second, and third growth rate curves and the total growth rate (lower panel). The early growth phase (lower panel) represents initial high rate of growth with growth rate rapidly decreasing during the animal's initial months of life. The animal then enters a second growth phase where the rate of growth continues to slow but the decrease in the rate is dampened. Finally, a third growth phase represents a "spurt" of increased growth rate, potentially related to sexual maturity, which then decreases and approaches zero (end of growth).

We applied a Bayesian framework for fitting parameters of the triple-logistic growth function, simultaneously fitting and comparing all growth parameters between multiple cohorts. All of the model parameters must be positive; therefore, we defined log-linear functions to represent the eight model parameters of the triple-logistic growth functions. Sex (male/female) and geographic location (SC/MSS/IRL) were defined as potential influential factors for the growth parameters and each of the eight parameters were defined as a function of these factors:

$$\log(\mu_{l,s}) = \mu_0 + \mu_l + \mu_s$$
$$\log(\Delta\mu_{1,l,s}) = \Delta\mu_{1,0} + \Delta\mu_{1,l} + \Delta\mu_{1,s}$$
$$\log(\Delta\mu_{2,l,s}) = \Delta\mu_{2,0} + \Delta\mu_{2,l} + \Delta\mu_{2,s}$$
$$\log(\beta_{0,l,s}) = \beta_{0,0} + \beta_{0,l} + \beta_{0,s}$$
$$\log(\beta_{1,l,s}) = \beta_{1,0} + \beta_{1,l} + \beta_{1,s}$$
$$\log(\beta_{2,l,s}) = \beta_{2,0} + \beta_{2,l} + \beta_{2,s}$$
$$\log(t_{1,l,s}) = t_{1,0} + t_{1,l} + t_{1,s}$$
$$\log(t_{2,l,s}) = t_{2,0} + t_{2,l} + t_{2,s}$$

where l and s indicate, respectively, the location (SC/MSS/IRL) and sex (male/female) of the animal. The proposed formulation requires the estimation of 32 parameters and provides a unified model allowing statistical tests for differences in the eight growth model parameters across locations and sexes. South Carolina males were chosen as the reference group. Therefore, e^{μ_0} would represent the contribution to total length due to the first growth phase for SC males, and $e^{\mu_0 + \mu_{MSS}}$ would represent the same for MSS males. It follows that $e^{\mu_{MSS}}$ represents the factor for decrease (if <1) or increase (if >1) in total length due to the first growth phase for MSS dolphins as compared with SC dolphins.

Applying Bayes theorem, the probability density of the parameters conditioned on the observed data can be written as the product of the density of the observed data conditioned on the parameters, the prior density of the parameters, and an integration constant. To obtain the posterior density of the parameters, the joint density is integrated over the prior densities and the data. When, as in this case, a closed form solution of this integral is not possible, computational methods such as Markov Chain Monte Carlo (MCMC) can be used (Carlin and Louis 2000). Samples taken from the Markov chain using these methods are distributed according to the posterior distribution of the parameter vector. Statistical measures (mean, median, and credible interval) estimated from these samples characterize the parameters of interest in our models. Additionally, statistical measures for functions of these parameters such as the growth curve, growth rate curve, and asymptotic length can also be computed from the posterior density. We use this approach to provide point estimates and credible intervals for growth and growth rate as a function of time. A hierarchical model was developed to describe the joint distribution. For the full model with location and sex factors, the hierarchical model is expressed as

$$\hat{L}_i \sim N\left(L_{l_i,s_i}\left(a_i \left|\begin{array}{c} \mu_0, \mu_{IRL}, \mu_{MSS}, \mu_{sex}, \Delta\mu_{1,0}, \Delta\mu_{1,IRL}, \Delta\mu_{1,MSS}, \Delta\mu_{1,sex}, \\ \Delta\mu_{2,0}, \Delta\mu_{2,IRL}, \Delta\mu_{2,MSS}, \Delta\mu_{2,sex}, \beta_{0,0}, \beta_{0,IRL}, \beta_{0,MSS}, \beta_{0,sex}, \\ \beta_{1,0}, \beta_{1,IRL}, \beta_{1,MSS}, \beta_{1,sex}, \beta_{2,0}, \beta_{2,IRL}, \beta_{2,MSS}, \beta_{2,sex}, \\ t_{1,0}, t_{1,IRL}, t_{1,MSS}, t_{1,sex}, t_{2,0}, t_{2,IRL}, t_{2,MSS}, t_{2,sex} \end{array}\right.\right)\right), \tau_{length}\right)$$

$$a_i = \hat{a}_i \cdot \exp(f_i)$$
$$f_i \sim N(0, 58.37)$$
$$\tau_{length} = \frac{1}{\sigma_{length}^2}$$
$$\sigma_{length} \sim U(0.1, 30)$$

where $\hat{L}_i$ is the observed length for the ith animal, a_i is its true age, and $\hat{a}_i$ is its observed age. The statistical model given above can be interpreted as follows.

The observed length for the ith animal is assumed to be normally distributed about some average length, L_{l_i, s_i}, that is a function of the animal's true age, a_i, its sex, s_i, and its location, l_i, given the model parameters. The remaining uncertainty due to biological variability and measurement error is represented by the precision, τ_{length}, which is the inverse of the variance, σ_{length}^2. The prior distribution for the unknown square root of the variance (standard deviation σ_{length}) is assumed to be uniformly distributed between 0.1 and 30 cm. The observed age, $\hat{a}_i$, is assumed to be log-normally distributed about the unknown true age and the random variable f_i representing this uncertainty. Its prior distribution is based on an analysis of data from multiple, independent estimates of age from a sample of teeth. Each tooth was read between 3 and 10 times. The mean age, its standard deviation, and coefficient of variation were then computed. The average coefficient of variation across teeth was used to set the precision parameter of the distribution for f_i. We chose to use uniform priors for all of the parameters and chose bounds based on the limits of possible growth rates, lengths, and timing of the later growth phases. The prior distribution and associated rationale for each parameter of the model are given in Table 1.

Parameters were inferred using the WinBUGS program (Lunn *et al.* 2000). The Markov Chain was run for 120,000 iterations following a 50,000 iteration burn-in period. The remaining samples were thinned by a factor of 10 to provide 7,000 samples from which statistics were computed and convergence was assessed by inspection of the sample histories for the inferred parameters.

For parameters representing the difference between sexes or geographic cohorts, credible intervals were examined to assess the probability that a difference exists. For example, if a 95% credible interval for parameter μ_x is determined to be (2,10), this indicates that the posterior probability that μ_x lies in the interval from 2 to 10 is 0.95, and the posterior probability that μ_x is greater than or equal to 2 is 0.975.

RESULTS

A total of 536 bottlenose dolphins were reported stranded in South Carolina from 1992 to 2005. Of these, ages were estimated for 263 (49%) comprising 100 males and 163 females. Figure 3 illustrates a histogram of SC stranded dolphin ages combined with the IRL and MSS dolphins.

Parameter estimates for the triple logistic growth function are summarized in Table 2. Residual plots (Fig. 4) indicated that the age-dependent error identified with the double logistic model (Fig. 1) was eliminated with the addition of the third logistic function, which allowed for an additional growth phase. The fitted functions (Fig. 5–7) indicated a preliminary early, rapid growth phase, followed by a second phase of sustained but slower growth, and then a moderate growth spurt later in life. For the reference group (SC males), the time at maximal growth rate during the second growth phase ($t_{1,0}$, Table 1) occurred at around 6 wk of age ($e^{-2.18} \times 365 = 41.26$ d), while the time at maximal growth rate during the third growth phase ($t_{2,0}$) occurred at around 10 yr of age ($e^{-2.18} + e^{2.31} = 10.19$ yr). There was not strong evidence that the timing of the growth spurts (t_1, t_2) differed between sexes or sample collection sites (Table 1).

Credible intervals around the velocity curves (B in Fig. 5–7), suggested a high degree of uncertainty with regard to the magnitude of the later growth spurt. This uncertainty is in part due to the paucity of samples for this age dolphin, but also is indicative of individual variation in the timing and magnitude of the growth spurt.

Table 1. Prior distributions for parameters of the model.

Parameter	Prior Density	Rationale
μ_0	$U(3, 7)$	Allow broad range (between 100 and 250 cm) for early growth phase giving $\mu_0 \in (4.6, 5.5)$.
$\Delta\mu_{1,0}$	$U(1, 7)$	Anticipate between 100 and 250 cm in late growth phase giving $\Delta\mu_0 \in (4.6, 5.5)$.
$\Delta\mu_{2,0}$	$U(1, 7)$	Anticipate between 100 and 250 cm in late growth phase giving $\Delta\mu_0 \in (4.6, 5.5)$.
$\beta_{0,0}$	$U(-3, 7)$	Allows early phase growth rates between ~1 and ~500 cm per year.
$\beta_{1,0}$	$U(-3, 7)$	Allows late phase growth rates between ~1 and ~500 cm per year.
$\beta_{2,0}$	$U(-3, 7)$	Allows late phase growth rates between ~1 and ~500 cm per year.
$t_{1,0}$	$U(-3, 1.6)$	Allows second phase growth rate peak to occur between years ~0 and ~5.
$t_{2,0}$	$U(\log(5), \log(14))$	Allows late phase growth rate peak to occur between years 5 and 14.
$\mu_{IRL}, \mu_{MSS}, \mu_{Female}, \Delta\mu_{1,IRL}, \Delta\mu_{1,MSS}, \Delta\mu_{1,Female}, \Delta\mu_{2,IRL}, \Delta\mu_{2,MSS}, \Delta\mu_{2,Female}, \beta_{0,IRL}, \beta_{0,MSS}, \beta_{0,Female}, \beta_{1,IRL}, \beta_{1,MSS}, \beta_{1,Female}, \beta_{2,IRL}, \beta_{2,MSS}, \beta_{2,Female}, t_{1,IRL}, t_{1,MSS}, t_{1,Female}, t_{2,Female}$	$U(-1, 1)$	Anticipate equal likelihood of sex- or site-specific increases or decreases. Prior centered at 0 with effects ranging from ~1/3X to ~3X.
$t_{2,IRL}, t_{2,MSS}$	0	No site-dependent shift in location of third growth phase.

Without longitudinal data, the individual variation contributes excessive noise to the growth model that cannot be controlled.

Geographic Cohorts

The parameter for contribution of length for the early growth phases for the MSS cohort suggested a greater contribution from the second growth phase (median = $e^{0.47} = 1.60$) as compared to SC dolphins. The credible intervals indicated a 95% probability that the contribution of the second growth phase for MSS was between 1.02 and 2.59 times greater than the contribution of the second growth phase for SC. However, this is likely driven by inconsistency in measurement precision between MSS and SC cohorts. In data for the MSS cohort, dolphins that were considered nonneonates under 1 yr of age were pooled with neonates and assigned age zero
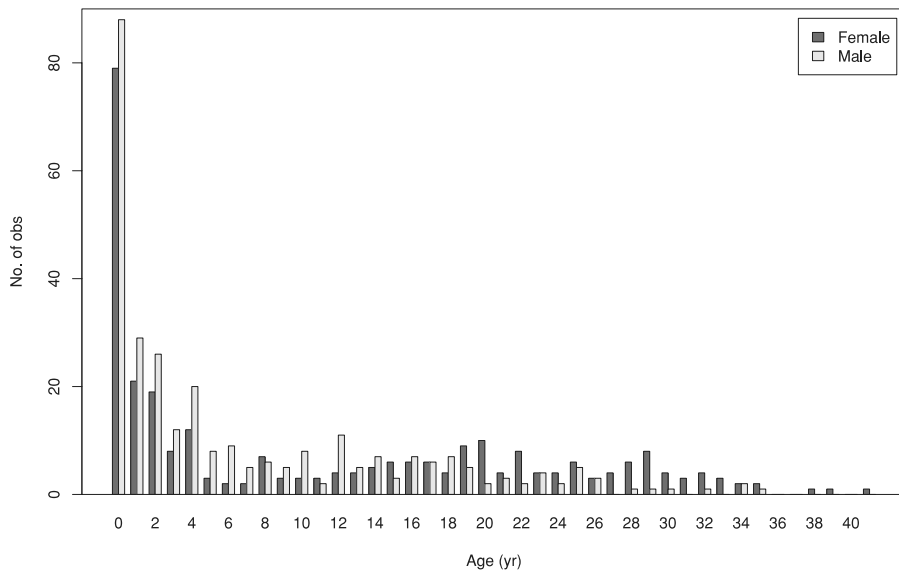
Figure 3. Histogram of frequency of observations (obs) in each age class combining all three sites analyzed (SC, males = 100, females = 163; MSS, males = 69, females = 42; IRL, males = 118, females = 72).

(Mattson *et al*. 2006), while for the SC dolphins, we estimated the age of the nonneonates under 1 yr of age by comparing the width of the forming GLG with that of the prenatal dentine.

Other than this observed difference in early growth phase parameters attributable to measurement bias, growth parameters between geographic cohorts did not show obvious differences (Table 2). Median growth functions for SC dolphins differed from MSS and IRL (Fig. 8), but the differences were generally not substantial and credible intervals around the growth functions (not plotted) had a significant degree of overlap. However, asymptotic lengths (calculated by summing μ, $\Delta\mu_1$, and $\Delta\mu_2$) for SC dolphins was slightly less than lengths for IRL or MSS (Table 3). The distribution of difference in asymptotic lengths (SC–IRL, SC–MSS, stratified by sex) was also computed (Table 4). While the probability distributions suggested a greater likelihood that SC dolphins, both male and female, have slightly lower asymptotic lengths as compared to both IRL and MSS, only the comparison of females between SC and IRL excluded zero from the credible interval.

The computed asymptotic lengths for IRL and MSS cohorts (Table 3) were similar to those previously reported (Stolen *et al*. 2002, Mattson *et al*. 2006). The asymptotic lengths computed using a simple Gompertz growth function was 255 and 246 cm for IRL males and females, respectively (Stolen *et al*. 2002), as compared to 258.5 and 247.2 cm estimated by our model. Similarly, the asymptotic lengths computed using a two-stage Gompertz with a fixed age for growth shift was 255.4 and 249.7 cm for MSS males and females, respectively (Mattson *et al*. 2006), as compared to 257.5 and 247.7 cm computed from our model. The previously reported values from both studies are well within the computed credible intervals for this study (Table 3).

Table 2. Estimates of parameter means, standard deviation, median and 95% credible interval for model using uniform priors for all parameters.

Parameter	Mean	SD	MC error	2.5%	Median	97.5%
μ_0	5.16	0.09	0.0073	4.97	5.16	5.31
μ_{IRL}	0.09	0.08	0.0059	−0.07	0.09	0.26
μ_{MSS}	−0.12	0.12	0.0080	−0.39	−0.11	0.07
μ_{Female}	−0.03	0.05	0.0027	−0.14	−0.03	0.06
$\Delta\mu_{1,0}$	3.95	0.21	0.0182	3.49	3.99	4.30
$\Delta\mu_{1,IRL}$	−0.10	0.28	0.0187	−0.68	−0.09	0.39
$\Delta\mu_{1,MSS}$	0.48	0.24	0.0182	0.02	0.47	0.95
$\Delta\mu_{1,Female}$	−0.01	0.09	0.0037	−0.21	−0.01	0.18
$\Delta\mu_{2,0}$	3.24	0.50	0.0356	1.84	3.38	3.90
$\Delta\mu_{2,IRL}$	−0.39	0.36	0.0144	−0.96	−0.42	0.45
$\Delta\mu_{2,MSS}$	−0.48	0.39	0.0179	−0.98	−0.55	0.48
$\Delta\mu_{2,Female}$	−0.36	0.36	0.0173	−0.94	−0.39	0.54
$\beta_{0,0}$	−0.89	0.26	0.0170	−1.46	−0.86	−0.45
$\beta_{0,IRL}$	0.03	0.20	0.0106	−0.35	0.02	0.44
$\beta_{0,MSS}$	−0.09	0.27	0.0145	−0.56	−0.11	0.54
$\beta_{0,Female}$	0.15	0.18	0.0090	−0.19	0.13	0.54
$\beta_{1,0}$	2.14	0.47	0.0298	1.41	2.08	3.11
$\beta_{1,IRL}$	0.10	0.48	0.0194	−0.87	0.12	0.92
$\beta_{1,MSS}$	0.28	0.47	0.0181	−0.75	0.33	0.96
$\beta_{1,Female}$	−0.34	0.38	0.0101	−0.94	−0.38	0.49
$\beta_{2,0}$	2.17	2.47	0.0807	−1.66	1.78	6.72
$\beta_{2,IRL}$	0.00	0.57	0.0082	−0.94	0.00	0.95
$\beta_{2,MSS}$	0.01	0.57	0.0089	−0.94	0.00	0.95
$\beta_{2,Female}$	0.02	0.57	0.0081	−0.94	0.02	0.95
$t_{1,0}$	−2.16	0.43	0.0254	−2.92	−2.18	−1.26
$t_{1,IRL}$	−0.23	0.44	0.0112	−0.95	−0.26	0.70
$t_{1,MSS}$	0.06	0.49	0.0160	−0.87	0.07	0.90
$t_{1,Female}$	0.24	0.43	0.0169	−0.72	0.29	0.94
$t_{2,0}$	2.30	0.15	0.0052	1.88	2.31	2.56
$t_{2,Female}$	−0.02	0.24	0.0071	−0.71	0.01	0.37

Sexual Dimorphism in Growth Patterns

The average of the differences between male and female lengths (Fig. 9A) and growth rates (Fig. 9B) were plotted to examine sexual dimorphism in growth patterns. The model suggested that males had a greater expected length at birth (age 0) as compared with females (Fig. 9A), but growth rate for females quickly exceeded that for males in the very early (<1 yr) growth period (Fig. 9B). The female advantage in growth rate diminished and by the age of 3–4 yr, the growth rates were more similar with males holding a slight advantage until around 15 yr of age when growth rate for both sexes approached zero (asymptotic length reached). Uncertainty in the growth rate was particularly high around the age of 3–4 yr when male growth rate surpassed female growth rate, and also around the age of 10 yr when a second growth spurt purportedly occurs. Still, growth rates between the sexes did differ significantly for at least some period during the early growth phase (<1 yr) and for all but a brief period between the ages of 7–15 yr, as indicated by 95% credible intervals around the difference in growth rate that do not include zero.
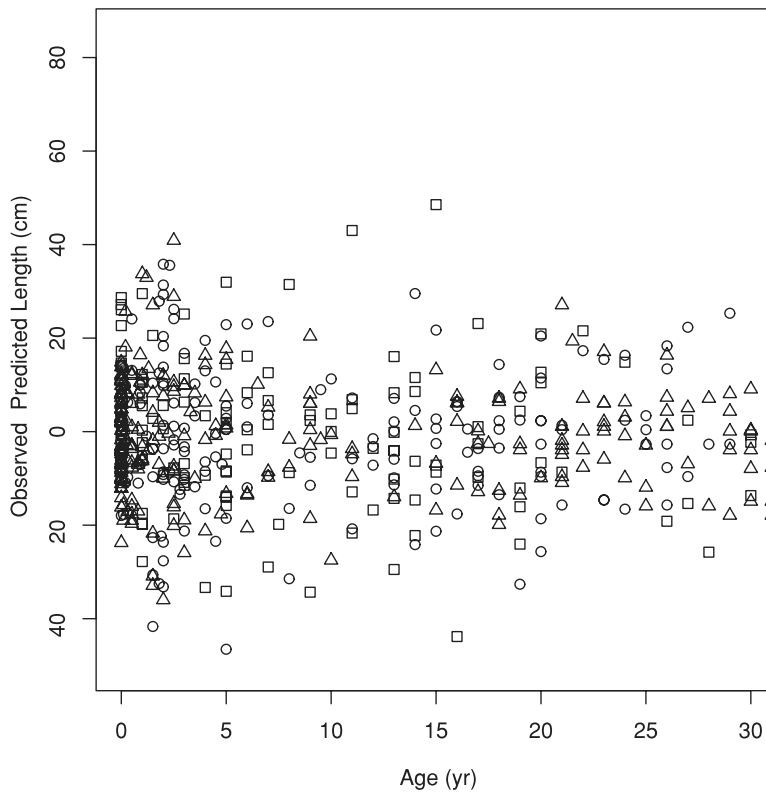
Figure 4. Residual errors for the triple logistic model including SC (△, *n* = 263), MSS (□, *n* = 111), and IRL (○, *n* = 199).

DISCUSSION

Fitting mechanistic growth models such as the double or triple logistic growth functions to observations of dolphin length and age data allow for the examination of potential growth phases. Our model supported the existence of multiple growth phases for bottlenose dolphins, indicating an early period of rapid growth, followed by a decrease in growth velocity and a period of sustained but slower growth, and then a rapid increase in growth at around the age of sexual maturity. A growth spurt around the age of sexual maturity has been suggested by other studies (Perrin *et al.* 1976, Cockroft and Ross 1990, Cheal and Gales 1992, Ferrero and Walker 1996) based on observations of plotted age *vs.* length data points. The slowing of growth prior to sexual maturity has been suggested to occur as dolphins shift their investment from growth in length to growth or weight of reproductive organs (Rosas *et al.* 2003). This could explain the second growth phase observed in this study where we have a period of sustained but slower growth. This is followed by the growth spurt seen around the age at sexual maturation which Bryden (1986) suggests may be related to social maturity. Still other studies suggest that this growth spurt is confined only to males (Cheal and Gales 1992, Reynolds *et al.* 2000, Rosas *et al.*
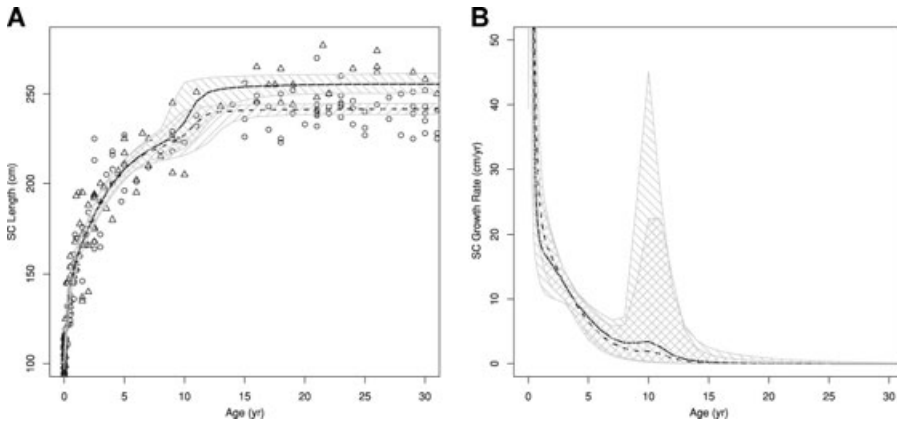
Figure 5. South Carolina growth and rate curves. (A). Median male (solid line) and female (dashed line) growth curves, 95% credible intervals for the growth curves (hashed area) and data for samples (Δ males, $n = 100$; ○ females, $n = 163$) from South Carolina. (B) Median male (solid line) and female (dashed line) growth rate curves and 95% credible intervals (hashed area).
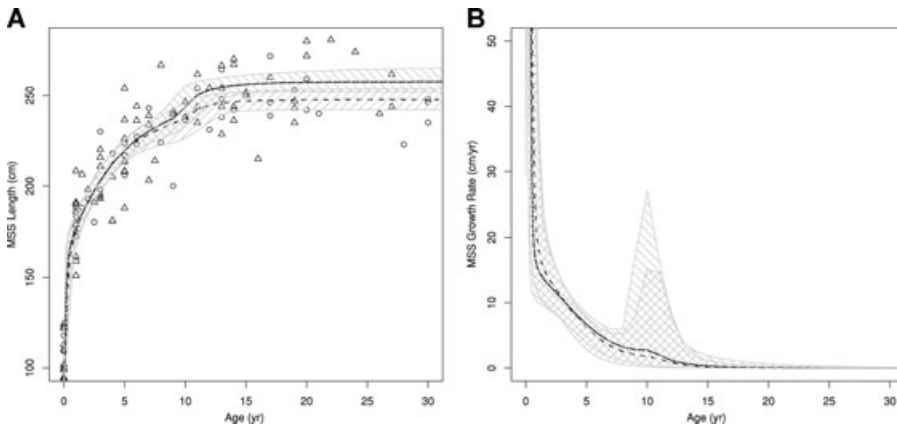

Figure 6. Mississippi Sound growth and rate curves. (A). Median male (solid line) and female (dashed line) growth curves, 95% credible intervals for the growth curves (hashed area) and data for samples (Δ males, $n = 69$; ○ females, $n = 42$) from Mississippi Sound. (B) Median male (solid line) and female (dashed line) growth rate curves and 95% credible intervals (hashed area).

2003). Our study shows that females also display a growth spurt although not as pronounced as the males.

In our model, the age of the final growth spurt was fit as a model parameter and estimated to be 10.19 yr (CI = 6.769–13.12 yr). However, there was significant uncertainty in the magnitude of this growth spurt. Unfortunately, the timing of the final growth spurt coincides with the age period when the least number of samples are available (Fig. 1). This is primarily due to the fact that availability of stranded carcasses is strongly biased by the age-dependent survivorship of the
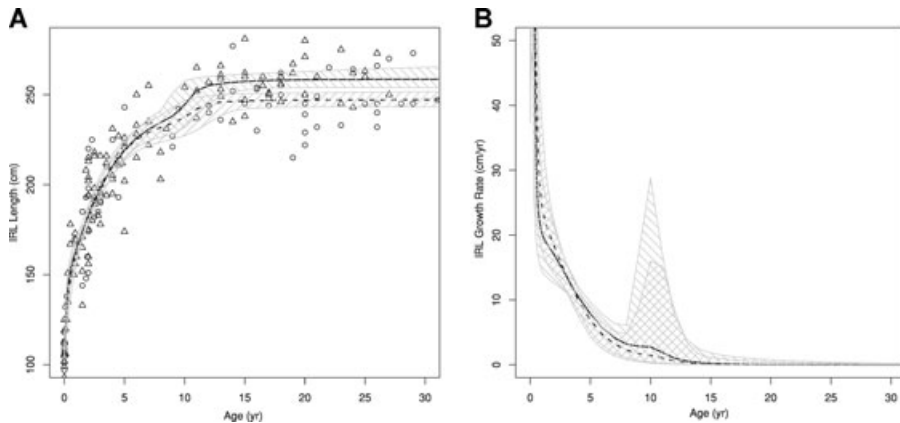
Figure 7. Indian River Lagoon growth and rate curves. (A). Median male (solid line) and female (dashed line) growth curves, 95% credible intervals for the growth curves (hashed area) and data for samples (Δ males, $n = 118$; ○ females, $n = 72$) from Indian River Lagoon. (B) Median male (solid line) and female (dashed line) growth rate curves and 95% credible intervals (hashed area).
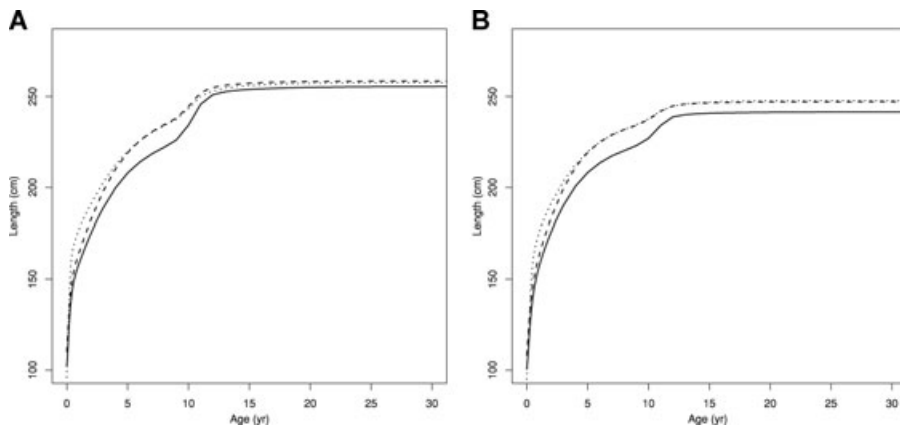

Figure 8. Comparison of computed growth curves from SC (solid line), IRL (dashed line) and MSS (dotted line) males (A; SC = 100, IRL = 118, MSS = 69) and females (B; SC = 163, IRL = 72, MSS = 42).

species. Bottlenose dolphins have been shown to exhibit age-dependent survivorship similar to other mammalian species (Stolen and Barlow 2003, Lane 2007). Their mortality risk is highest just following birth, declining rapidly as the calf ages. The risk then becomes constant throughout most of their lifespan until an age of senescence when risk of mortality again increases. Given this varying mortality risk, it is expected that the greatest number of carcasses will be very young dolphins that represent the largest age cohort in a stable population and that have the highest risk of mortality. The fewest samples are likely from young adult dolphins that have the lowest risk of mortality. This bias in carcass availability makes it difficult to estimate accurately the magnitude of the final growth spurt, which occurs in the middle

Table 3. Estimates of asymptotic lengths (means, medians, and credible intervals) for each of the locations and sexes. Abbreviations for locations are South Carolina (SC), Indian River Lagoon (IRL), Mississippi Sound (MSS). Lengths are in centimeters. Uncertainty (SD and credible interval) apply to the population mean.

	Mean	SD	MC error	2.5%	Median	97.5%
SC, Males	255.7	2.9	0.0711	250.3	255.5	261.8
SC, Females	241.6	1.6	0.0315	238.5	241.5	244.7
IRL, Males	258.9	3.4	0.1390	254.0	258.5	266.8
IRL, Females	247.3	2.4	0.0668	243.2	247.2	251.9
MSS, Males	257.9	3.5	0.0951	252.0	257.5	265.7
MSS, Females	247.8	3.1	0.0569	242.1	247.7	254.1

Table 4. Comparison of asymptotic lengths for South Carolina and other sites shows generally smaller animals in South Carolina (both males and females). Only the comparison of South Carolina and Indian River Lagoon females excludes 0 from the credible interval.

	Mean difference	SD	MC error	2.5%	Median difference	97.5%
SC *vs.* IRL, Males	−3.2	3.8	0.1308	−10.8	−3.1	3.7
SC *vs.* MSS, Males	−2.2	3.9	0.0983	−9.9	−2.1	5.2
SC *vs.* IRL, Females	−5.7	2.6	0.0706	−10.9	−5.7	−1.0
SC *vs.* MSS, Females	−6.3	3.3	0.0635	−12.7	−6.2	0.1

range of ages. However, even given the limited data set, our model supported such a growth spurt. The increase in growth velocity around the age of 10 yr was consistent across data sets (SC, MSS, and IRL), lending support that the observed growth spurt is genuine. Furthermore, our attempt to fit a reduced model (double logistic), which did not allow for the later growth spurt, indicated age-related error. This error was eliminated by the expansion of the model to a triple logistic function, allowing for the inclusion of the later growth spurt (Fig. 1). Future efforts could include age and length measurements from carcasses obtained through bycatch or live animals
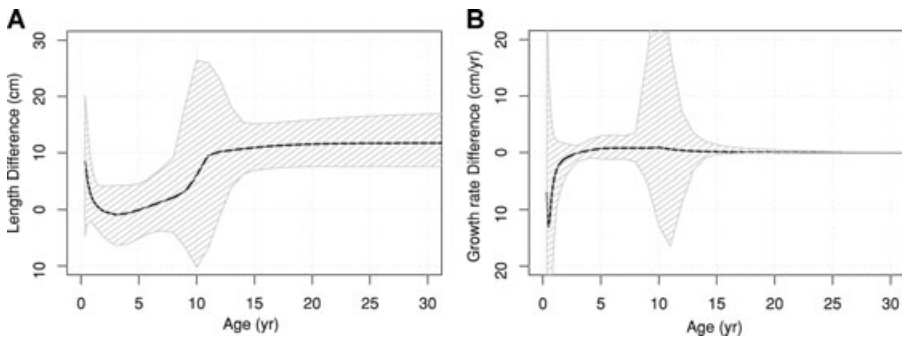

Figure 9. Differences (male minus female) in length (A) and growth rate (B) as a function of age.

that are caught and then released for tagging or health assessment. These additional samples could improve the precision in estimates for the later growth spurt.

With data collected from stranded dolphins along the southeast U.S. coast, we explored sexual dimorphism in growth phases. Our model results suggest that female dolphins grow at an increased rate very early in life (<1 yr) but at around the age of independence (5–6 yr of age, Wells 1991), males surpass females in growth velocity and likely maintain this advantage throughout the remaining growth period. Ferrero and Walker (1995) describe a similar occurrence in common dolphins (*Delphinus delphis*) in which female growth is more rapid until about the age of two. In a long-term study of bottlenose dolphins in Sarasota, Florida, Reynolds *et al.* (2000) suggest that as females reach their age of sexual maturity considerable energy is devoted to the anticipation of fetal development and lactation and diverted from growth in length. These divergent reproductive strategies of sex could explain male growth rate surpassing females since female bottlenose dolphins attain sexual maturity earlier than males (Cockroft and Ross 1990, Read *et al.* 1993). In contrast, male growth velocity, while slower than females at an earlier age, continues to surpass females after onset of puberty possibly as a result of increased food intake for investment in greater social activity than females as seen in captive bottlenose dolphins (*Tursiops aduncus*) (Connor 1990, Cheal and Gales 1992).

Differences in growth patterns between the geographic cohorts were not as obvious. There was one noted difference in the contribution of the first growth phase for MSS dolphins, but this is likely attributable to the aging protocol employed by the MSS study and emphasizes the need for inter-study standardization.

The lack of findings showing significant differences among geographic cohorts should not be taken as definitive proof that growth phases do not differ. There is a considerable loss of power to detect differences when cross-sectional (multiple individuals measured at a snapshot in time) *vs.* longitudinal (same individual measured repeatedly over time) data are used. There is considerable variation in growth between individuals and this is reflected in wide credible intervals around the reported parameter values. However, even with this considered, for model parameters representing site-specific differences the probability masses for the posterior densities were generally concentrated around zero, providing no indication that there are significant differences in growth model parameters among geographic cohorts.

Although growth function parameters did not differ, the computed asymptotic lengths for SC animals were lower than those computed for IRL and MSS, and the difference between SC and IRL female asymptotic lengths was statistically significant. The reason(s) for this discrepancy is unclear. Differing energy requirements may partially explain the discrepancy and has been linked to body size (Hammill *et al.* 1995). South Carolina dolphins are at a higher latitude (32–33°N) than the MSS (30°N) and IRL (27°N) dolphins, but experience a wider fluctuation in seasonal water temperatures than the IRL, though similar to MSS. This wider fluctuation in seasonal water temperatures may impart more energy expenditure for travel rather than growth as seen in bottlenose dolphins from Spencer Gulf, Australia (Ross and Cockroft 1990). There is also strong evidence to suggest that at least a portion of the dolphins in SC are seasonally migratory in nature and may range as far north as Cape Lookout, North Carolina (Zolman 2002, McFee *et al.* 2006).

It is plausible that habitat differences may be a governing factor in size differences. The IRL is a semi-closed estuary whereas the SC coastline consists of numerous open estuaries including narrow tidal creeks and barrier islands in the south and a long sandy beach in the north. Dolphins may simply be optimizing their body size to

maximize their reproductive output based on energy requirements, or anthropogenic, environmental, and predator stressors (Kleiber 1975, Schmidt and Jensen 2003).

Our proposed modeling framework allows for the comparison of patterns of growth among cohorts, providing credible intervals not only for model parameters but also for other calculated functions of interest. This ability to compute functions with associated credible intervals from the posterior distributions is a significant advantage of the Bayesian framework. The computed functions, such as asymptotic length, age of growth spurts, and growth velocity or difference in length or growth velocity as a function of age, are often of greater interest than the model parameters themselves. With appropriate data sets, the proposed modeling framework could be applied to compare growth phases between cohorts to explore relationships between environmental variables (*e.g.*, climate, ecosystem productivity, habitat pressures) and timing and/or magnitude of growth phases. Growth has long been considered an indicator of health in humans and analyses to explore differences in growth patterns have been applied extensively for human cohorts (Hauspie 1989, Milani 2000). However, comparison of growth phases across cohorts for humans or even agricultural species generally utilize longitudinal measurements over time (Marubini and Milani 1986). For wildlife species and particularly for marine species such as cetaceans for which longitudinal measures are difficult, cross-sectional measurements of size and estimated age from stranded carcasses are often the only option. We are only aware of one cetacean study which has utilized longitudinal data (Read *et al.* 1993), and it was necessarily limited in the number of sampling points for each individual and could not include samples from very young calves (<1 yr), which would exhibit the highest growth velocities. While fitting of growth functions from sampling of random individuals of differing age certainly limits the power to detect underlying differences in growth phases, the approach may still be applicable. At least one human study has used a cross-sectional design to determine the relationship of environmental quality and gene flow on timing and magnitude of growth phases (Khongsdier and Mukherjee 2003). With our model, we demonstrate the potential for dolphins, showing age-related changes in growth velocities between males and females and evidence of at least some differences (*i.e.*, asymptotic length) across geographic cohorts. The utility of this approach will be greatly strengthened if data sets from multiple studies can be combined. It follows that standardized protocols for morphometric measurements and inter-laboratory and/or inter-technique comparisons for dentinal layer age estimates are critically important to ensure comparability of data and to eliminate, or at least quantify, potential biases across studies.

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