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Prenatal data impacts common bottlenose dolphin (*Tursiops truncatus*) growth parameters estimated by length-at-age curves

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ABSTRACT

Compilation of marine mammal demographic data is central to management efforts. However, marine mammal length-at-age growth curves demonstrate limitations. Physiological growth parameters of terrestrial mammals are typically estimated using curvilinear models fit to size-at-age data along a time series from conception to senescence. The difficulty of collecting and aging prenatal cetaceans is addressed here, and growth parameters of common bottlenose dolphins (*Tursiops truncatus*) along coastal Texas were estimated using length-at-age information from a broader scope of age classes, including late-term fetuses. A Gompertz growth curve fit to pre- and postnatal data underestimated size parameters, but demonstrated similar growth rate constants (k) to an exclusively postnatal model. However, when growth parameters were broken out, the absolute growth rate (G) and rate of growth decay (g) decreased (0.44 from 0.27 and 0.55 from 0.39, respectively), which underscores the importance of reporting k in its expanded form (G/g). Although the Gompertz fits most age classes well, it cannot explain growth in all age classes. We argue that a novel sigmoidal model would be more useful for inference.

Key words: cetacean fetal growth, length-at-age, *Tursiops truncatus*, prenatal age, allometry, Gompertz, von Bertalanffy.

Long-term observations of demographic patterns in large predator populations, such as common bottlenose dolphins (*Tursiops truncatus*, hereafter referred to as bottlenose dolphins), are important to effective management and conservation efforts. Accurate characterization of population demographics including length-at-age and sexual dimorphism is crucial to constructing useful growth models, particularly with respect to growth parameter estimation (Sergeant *et al.* 1973, Cockcroft and Ross 1990*b*, Read *et al.* 1993, Fernandez and Hohn 1998, Stolen *et al.* 2002, Mattson *et al.* 2006). Fluctuations in growth parameters over time may indicate density compensatory responses, ultimately reflecting the population's proximity to its carrying capacity (Chivers and Myrick 1993), an important assessment for population management of long-lived animals.

Population parameters for terrestrial mammals are estimated by characterizing growth as a size-at-age curvilinear function that includes pre- and postnatal life (*e.g.*, Laird 1966*a*). Unfortunately, prenatal data are generally omitted from cetacean length-at-age curves due to the scarcity of embryonic and fetal specimens. For this reason, cetacean growth curves are exclusively postnatal. Parameter estimates must be interpreted with caution if a large proportion of the variation is unexplained, particularly for genetically structured populations (Eveson *et al.* 2007). The typical cetacean length-at-age curve is often displayed such that the scale does not suggest a point of inflection, or the curve lacks any discernible point of inflection, and thus fails to conform to the underlying sigmoidal stipulation of the Gompertz model.

Size-at-age growth curves are anchored by their parameters. In the Gompertz growth model, the point of inflection directs the path of the curve. Ricklefs (1967) assumed that the point of inflection of dynamic growth models occurs at $t = 0$ and L_i (time and length at birth, respectively). This point along the curve is also referred to as the "inflection parameter" (Fitzhugh 1975). Mammalian growth curves can be normalized by setting the inflection parameter to $t = 0$ while the position of the inflection parameter along the ordinate varies (Laird 1966*b*). By convention, the Gompertz model predicts the point of inflection at 37% of the curve, whereas another commonly used growth model, the von Bertalanffy model, predicts the point of inflection at 30% (Zullinger *et al.* 1984). Unfortunately, discussion regarding the manipulation of the point of inflection is often overlooked with respect to marine mammal age and growth.

The inflection parameter along a growth curve represents maximal growth, or the transition from increasing to decreasing growth rate. Laird (1966*a*) examined a number of trends across terrestrial mammalian taxa, but forced maximal growth rate of each subject to pass through $t = 0$. Upon closer inspection, the location of the inflection point among mammalian growth curves was variable, which was likely linked to life history strategy choices in offspring development and parental care (Laird 1966*a*). This hypothesis was later expanded to the size-at-age growth of 69 taxa of eutherian mammals, which were compared using a Chapman-Richards model

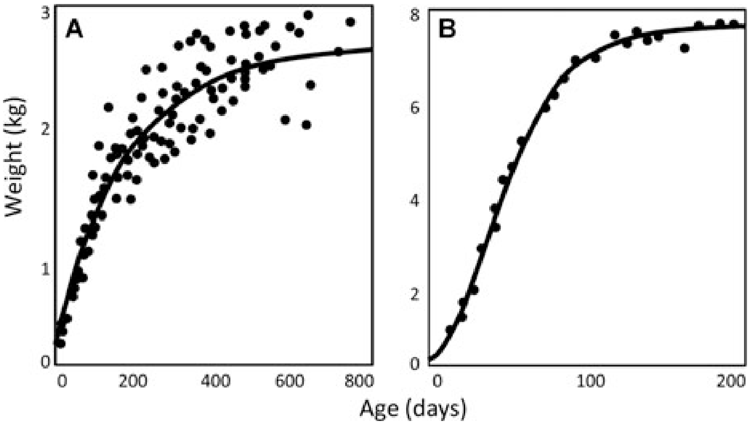

Figure 1. Monomolecular *vs.* Gompertzian growth. Postnatal weight-at-age growth curves for two mammalian species that produce two types of offspring respectively: (A) monomolecular growth pattern of the more precocial offspring of African brush-tailed porcupines (*Atherurus africanus*), and (B) Gompertzian growth of the more altricial offspring of muskrats (*Ondatra zibitheca*, modified from Gaillard *et al.* 1997).

to detect plasticity in growth trends (Gaillard *et al.* 1997). Each mammalian group was assigned a precociality index from 0 to 4 (in order of increasing precociality) based upon a series of developmental and parental strategies that affect neonatal independence: thermoregulation, sensory ability, locomotion, and nutritional requirement (Derrickson 1992, Vaughan *et al.* 2000). Among terrestrial mammals, more precocial offspring tended to exhibit maximal growth rates (point of inflection) before birth, whereas altricial offspring exhibited maximal growth rates after birth. Cetaceans are given a precociality index of three, indicating moderate precociality (Gaillard *et al.* 1997).

Postnatal size-at-age growth functions fall into one of two categories that are largely influenced by the degree of demonstrative precociality in early life history. These are nonsigmoidal size-at-age functions that take on a "monomolecular" (monotonic concave) pattern, and sigmoidal size-at-age functions that take on a true "Gompertzian" pattern (Fig. 1). Gaillard *et al.* (1997) encouraged workers to consider growth beginning from conception, instead of birth, whenever possible to capture the point of inflection. It follows then that the growth trend of bottlenose dolphins from conception to birth and through adulthood would show a similar sigmoidal pattern exhibited by terrestrial mammals that produce precocial young.

Gestational Aging

A number of methods have been proposed to estimate fetal age (Huggett and Widdas 1951, Frazer and Huggett 1973, Kasuya 1977, Boyde 1980, Lacave *et al.* 2004). Because no validated recording structure exists for stranded fetal bottlenose dolphins, age must be estimated using validated growth relationships, as in this study. Captive studies where reproductive timing and status are strictly controlled are extremely useful in this capacity. Examples can be found in agricultural and bovine literature. Given the phylogenetic proximity of the Order Artiodactyla to the

Order Cetacea, studies of cattle conceived using assisted reproductive technologies (ART, Correa and Zavos 1996) provide a useful model to develop cetacean fetometrics for aging purposes. For instance, crown to rump length (CRL) in fetal cattle is linear with respect to gestational age (Riding *et al.* 2008). The linearity of this growth relationship is not surprising, since cows give birth to relatively precocial offspring (index: 3, Derrickson 1992). Similar underlying relationships are also conserved in cetaceans. Lacave *et al.* (2004) showed that fetal biparietal diameter (BPD), measured from sonograms taken of pregnant bottlenose dolphins, demonstrated linearity with respect to gestational age. It is now common practice among public viewing facilities to estimate parturition dates of bottlenose dolphin mothers using fetal BPD measurements.

In this study, information from salvage material and artificial insemination programs was used to investigate the impact of prenatal data on growth parameter estimates of bottlenose dolphins along the Texas coastline. We hypothesized that a combined pre- and postnatal length and age data set would improve parameter estimates by explaining more variability. The specific objectives were to (1) analyze postnatal growth of bottlenose dolphins using two commonly used length-at-age growth models, the Gompertz (Laird 1966*a*) and the von Bertalanffy growth models (von Bertalanffy 1938); (2) establish a growth curve for males and females using the best fitting model to test sexual dimorphism with respect to length; (3) determine gestational age, and variation of growth patterns in fetal bottlenose dolphins, to test the hypothesis that the allometric relationship (*sensu* Huxley 1936) between BPD and length is a more accurate indicator of gestational age than average length gain per gestational day (*sensu* Kasuya 1977); (4) analyze pre- and postnatal growth of bottlenose dolphins stranded along the Texas coast using the least-squares Gompertz and von Bertalanffy growth model; and (5) compare length at birth values using independent methods.

METHODS

Postnatal Aging

Three hundred and twenty-one teeth were collected by volunteers from the Texas Marine Mammal Stranding Network (TMMSN) and RDN from January 1991 to December 2007, and processed for aging (Fig. 2). Like many regions, the Gulf of Mexico has "inshore" and "offshore" stocks. Recent genetic analyses (2007) indicate that bottlenose dolphins that strand along coastal Texas are of predominantly "inshore" origin.[1] In addition, Turner and Worthy (2003) used cranial morphological criteria to determine that less than 2% of bottlenose dolphins stranded along coastal Texas were "offshore" ecotypes. Total length was measured from the tip of the rostrum to the notch of the tail for all individuals. Teeth were extracted from the left mandibular ramus, and stored in 10% buffered formalin for 24 h. Because there is a possibility that formalin can degrade to formic acid, the principal agent used for acid etching (Hohn *et al.* 1989), teeth were rinsed for an hour, and stored dry immediately after fixation until processing could take place. Teeth were processed using the methodology of Hohn *et al.* (1989). Each tooth was thick-sectioned using a low-speed Buehler Isomet saw (Buehler, Lake Bluff, IL) to obtain a 2 mm section

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[1] Personal observations from HW.

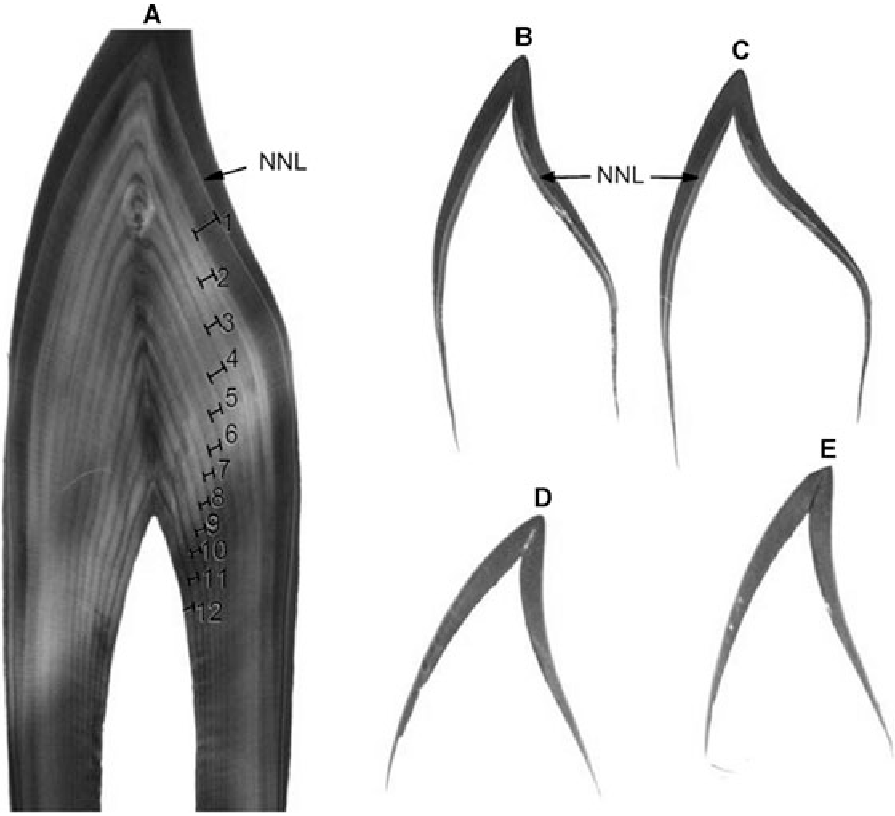

Figure 2. Growth layer group analysis. (A) An adult bottlenose dolphin tooth from a 12-yr-old individual. The thin, lightly stained, neonatal line is also present in a calf tooth (B and C), but not in a fetal tooth (D and E). Subsequent GLG boundaries are marked and labeled by year.

of the central-most portion in the buccal-lingual plane. The thick section was decalcified using a rapid commercial decalcifier (RDO, Apex, Aurora, IL). Decalcified teeth were rinsed in tap water, and thin sectioned at 30 μm on a circulating water freezing stage (Physiotemp, Clifton, NJ) attached to a Lipshaw 80A sledge microtome using HistoPrep freezing media (Fisher Scientific, Fair Lawn, NJ). On-center thin-sections were stained in Mayer's hematoxylin for 65 min, then "blued" in dilute (1%) ammonia for 1 min. Sections were floated onto 5% gelatin coated slides, and warmed on low heat for less than a minute to ensure adhesion to the slide. Sections were dehydrated in an alcohol series, cleared in xylene, and coverslipped with Eukitt (Electron Microscopy Sciences, Hatfield, PA). Slides were examined under a Nikon Eclipse E400 light microscope (Nikon Instruments, Inc., Melville, NY).

Postnatal ages were estimated by counting growth layer groups (GLGs) from teeth, according to the methodology of Myrick *et al.* (1983). We assumed dentinal deposition was constant throughout the year, but there is some question whether this assumption is valid (Danil and Chivers 2007). However, many investigators have reduced age-specific variability in length-at-age models by estimating to the

Table 1. Field criteria for determining status (fetal *vs.* nonfetal) of bottlenose dolphins stranded along coastal Texas.

Feature	Developmental timing	Reference
Rostral vibrissae	Apparent in stage 8 (see Sterba *et al.* 2000) *in utero*, diminishes 22 d postnatal	Sterba *et al.* (2000), Cockcroft and Ross (1990*a*)
Teeth erupt	Less than 6 wk postnatal	McBride and Kritzler (1951)
<100 cm long	Based on predicted length at birth of 110 cm	Fernandez and Hohn (1998)
True fetal folds	Diminish 62 d postnatal	Cockcroft and Ross (1990*a*)
Umbilicus	Heals 22 d postnatal	Cockcroft and Ross (1990*a*)

nearest fraction of a year.[2] We adopted a similar methodology to reduce age-specific variability. We estimated age to the nearest tenth of a GLG for animals <20 yr of age, and the nearest half-GLG for animals >20 yr of age. Estimations were made in the blind to the reader (necropsy reports were not reviewed until after age was estimated) to assure consistency and reduce bias. Two readers (RDN and CDM) read each tooth three times. Each respective reading was spaced at least one day apart. If disagreement of a perceived age existed, a fourth reading took place, and the average of the three nearest readings was taken as the actual age. A third reader (Megan Stolen, Hubbs Seaworld Research Institute) read approximately 17% of processed teeth (range: 0–28 GLGs) to validate the aging protocol utilized for this study.

Prenatal Aging

To date, average fetal length gain per gestational day has been used as a rough estimate of odontocete fetal age of deceased individuals (Kasuya 1977). Age prediction is given by the following:

$$\frac{L_0}{365 - t_0}\ (\mathrm{cm/d})$$

(Kasuya 1977), where L_0 is length at birth and t_0 is the first fetal gestational day (for bottlenose dolphins this is approximately 36.5 gestational days). However, no studies to date have validated this method empirically. Therefore, the growth relationship between total length and a validated age structure will help support or refute the hypothesis that total length is an adequate estimator of fetal age.

Salvage Material

Stranded perinates ($n = 10$) were collected during March 2008. The term "perinate" in this study is reserved for carcasses suspected, but not confirmed, to be fetal. Perinates were confirmed fetuses if they met a set of field criteria outlined in Table 1.

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[2] Personal communication from Megan Stolen, Hubbs-Seaworld Research Institute, 3830 South Highway A1A #4-181, Melbourne Beach, FL 32951, 2007.

Figure 3. Radiographs of fetal bottlenose dolphin skulls. Biparietal diameter was measured at the widest point of the skull (indicated by the white bars). Measurements were taken from the outer wall of one parietal bone to the contra-lateral parietal wall. This approach was used to maintain consistency with BPD measurements taken from ultrasound images at Dolphin Quest, Bermuda.

We measured total length, and removed the heads for radiography to measure BPD (Fig. 3). We imaged heads in the horizontal plane at the Texas A&M University College of Veterinary Medicine (Small Animal Clinic Radiology College Station, TX). Biparietal diameter was measured directly from radiographs using Image J 1.40g (http://rsb.info.nih.gov/ij/).

Biparietal diameter and total length from radiographed fetuses were fit to the allometric equation

$$y = bx^{\alpha}$$

(Huxley 1936), where y is a structure of interest (BPD), x is the standard or whole (total length), and b is the growth index or the relationship between the two measurements. It should be noted that due to the small sample size used to fit the equation, we did not carry model error forward for the remainder of the study. Therefore, fetal size variation is not represented in pre- and postnatal models.

Once the allometric equation was fit using BPD and total length from confirmed fetuses, we searched the TMMSN database for length records from stranded individuals that we suspected were fetal (<110 cm). Because none of the fetal records included BPD measurements, we used total length in the fitted allometric equation to estimate biparietal diameter. Age was then estimated based on the best-fit regression equation of BPD-at-known gestational age from a live sample of bottlenose dolphins (*sensu* Lacave *et al.* 2004). We also estimated ages using length as a prenatal age indicator (*sensu* Kasuya 1977). We used an independent two sample *t*-test to determine differences between the two aging methods.

Live Sample

Although captive animals regularly receive superior quality nutrition compared to their wild counterparts, the literature suggests that the fetus would only benefit marginally. Kuzawa (2005) described the phenomenon of "intergenerational phenotypic inertia," in humans, whereby the fetus is unable to utilize a transitory "boon" of nutrition due to genetic constraints. This mechanism also serves to insulate the fetus from habitat poor conditions, whereby the cost to the fetus during resource scarcity is reduced. Similarly, maternal genomic imprinting diminishes the potential benefits of abundance or opportunity to the fetus (see Reik and Walter 2001). Therefore, we deemed it appropriate to use fetal growth data from mothers held in public display facilities despite the mothers' access to superior nutrition.

To our knowledge, no artificial insemination program exists for Texas coast bottlenose dolphins. However, between 2004 and 2007, three Atlantic common bottlenose dolphins (Dolphin A, B, and C, respectively) gave birth to three calves at a public viewing facility, Dolphin Quest Bermuda. Dolphins A and B were born at the Brookfield Zoo of the Chicago Zoological Society. Dolphin A's parentage originated in the Gulf of Mexico, Mississippi Sound region. Dolphin B's mother also came from the Mississippi Sound, while her father was wild caught in the Florida Keys. Dolphin C was wild caught along coastal Florida and joined Dolphin Quest from a naval program in 1996. Two sires wild caught along the gulf coast of Florida fathered the three calves used in this study. All wild caught animals were acquired from inshore stocks.[3] We used sonograms taken at random intervals during each pregnancy (Fig. 4), to generate a BPD-at-gestational age regression relationship (*sensu* Lacave *et al.* 2004). Animal trainers followed a standardized protocol when imaging fetuses. Trainers recorded straight-line measurements from the inside wall of one parietal bone to the contra-lateral parietal wall. Once an image was captured and BPD measured, the image was sent to a licensed veterinarian to evaluate the plane of the image, and the resulting measurement. Images that were deemed askew in the dorso-ventral aspect were discarded from growth analyses. A one-way ANOVA demonstrated no significant variation among fetal BPD-at-age of each pregnancy, and therefore BPD data generated from each pregnancy were pooled to generate a single regression line for BPD-at-gestational age ($P = 0.01$).

Pre- and Postnatal Length-at-Age

Once pre- and postnatal ages were available, an exclusively postnatal and a pre- and postnatal length-at-age data set were analyzed with two dynamic curvilinear models; the Gompertz:

$$L_t = L_0 \mathrm{e}^{[G/g(1-\exp(-gt))]}$$

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[3] Personal communication from Michelle Campbell, Dolphin Quest Hawaii, 5000 Kahala Avenue, Honolulu, HI 96816-5411, 2009.

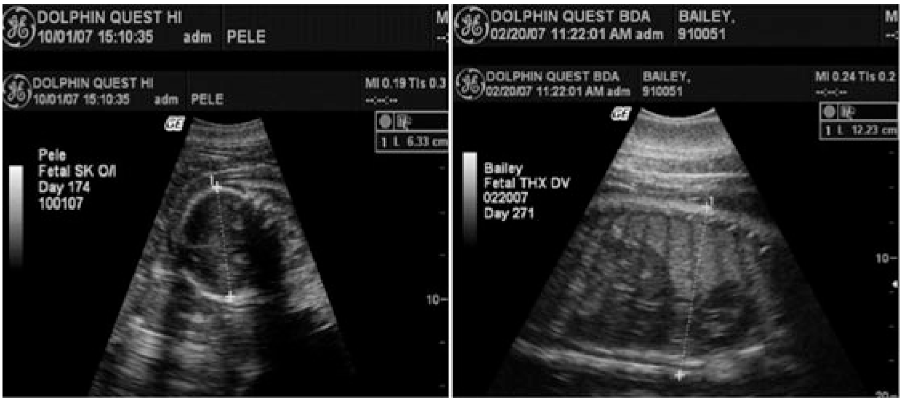

Figure 4. Sonograms. Ultrasound images taken from pregnant females as part of the artificial insemination program at Dolphin Quest, Bermuda. We considered many potential sonogram measurements to quantify allometric relationships (left, fetal biparietal diameter; right, fetal thoracic depth). We chose BPD to maintain consistency with fetometrics in the literature.

(Laird 1966*a*), where L_t is the length at time t, L_0 is the length at birth, G is the absolute growth rate, and g is the rate of growth decay; and the von Bertalanffy model:

$$L_t = L_\infty(1 - \mathrm{e}^{-G/g(t)})$$

(von Bertalanffy 1938), where L_∞ is the asymptotic length. Model fit was determined by the least-squares iteration, and Akaike's Information Criterion (AIC). The model explaining the most variation was used to make inferences regarding growth.

Predicted length at birth values were compared among the best-fitting postnatal and pre- and postnatal models. A logistic curve was fit to the binomial condition of being either fetal or nonfetal as explained by length (*sensu* Danil and Chivers 2007). To create a binomial distribution of fetal and nonfetal individuals, we examined TMMSN records corresponding to the 301 teeth analyzed for aging, and classified individuals as either fetal (absence of the neonatal line in tooth or total length <100 cm) or nonfetal (neonatal line present and total length greater than 100 cm). Binomial data were fit with a logistic model. The inflection point (0.5 probability) along the fitted curve indicated median overlap of fetal and nonfetal conditions, and was used as an alternative measure of length-at-birth.

Gestational ages were calculated using Microsoft Office Excel 2003. Prenatal regression analysis, residual analyses and ANOVAs were conducted using SPSS 14.0 (SPSS, Chicago, IL). Postnatal, and pre- and postnatal growth analyses, and logistic point estimate of length at birth were conducted in R 2.9.2 (R Development Core Team 2009). Because the Gompertz growth model may underestimate the asymptote when data are variable, the asymptotic length for each Gompertz growth model was fit to Ricker's equation

$$L_\infty = L_0\mathrm{e}^k,$$

where L_∞ is the asymptotic length and L_0 is the length at birth predicted by the Gompertz growth model (Ricker 1979).

RESULTS

Two hundred ninety teeth were successfully processed for aging. Three of these could only be estimated to a minimum age. Another 30 were processed and determined to be fetal. This provided a final sample size of 257 postnatal individuals that had both length and age information. The oldest female in the study was estimated to be 38 yr of age ($n = 73$) and the oldest male was estimated to be 44 yr of age ($n = 114$). Overall, the age distribution of bottlenose dolphins was left skewed. Neonates (postnatal individuals confirmed to be less than 1 yr old) made up 23% percent of the postnatal sample. Stranding patterns of near-term and neonatal individuals (<1 GLG) indicated that most calving occurred in March, and began to diffuse in April and May (Fig. 5).

Postnatal Growth Analysis

The Gompertz and the von Bertalanffy models were run until they each converged upon the least-squares iteration (Table 2). The von Bertalanffy was rejected based on a high AIC score relative to the Gompertz growth model (AIC: 7,923 and 2,477, respectively). The Gompertz growth model exhibited a lower AIC value in all cases. The overall postnatal data set demonstrated good fit in later life (>2 GLGs) but large variation in early life (<2 GLGs, Fig. 6). The results of least-squares Gompertz growth curves demonstrated good fits to female and male length-at-age data (Fig. 7), but in all cases, residual distribution was nonnormal. Length at birth values were similar between males and females (120 and 115 cm, respectively), as were the growth rate constants (0.70 and 0.74, respectively). Males exhibited a lower absolute growth rate and growth decay rate than females. As a consequence, females were shorter and reached asymptotic length sooner than males. However, this length difference is biologically insignificant.

Prenatal Growth Analysis

Ten collected perinates met most of the criteria outlined in Table 1. However, only six met all criteria and were used in subsequent analysis. The mean allometric growth index (b) was calculated to be 0.05. This value was used to convert stranded fetal length records to estimates of biparietal diameter. The best fitting regression of BPD-at-age measured from sonograms of known age fetuses bred in public viewing facilities is given by the following:

$$\text{Gestational age (days)} = (bx + 0.3774)/0.0376,$$

where b is the relationship between BPD and total length (Fig. 8). A variation of the equation was used to express age in units of 1 yr for the context of the growth model

$$\text{Age} = (365 - (((b \times \text{BPD}_{\text{est}}) - 0.2553)/0.0371))/365.$$

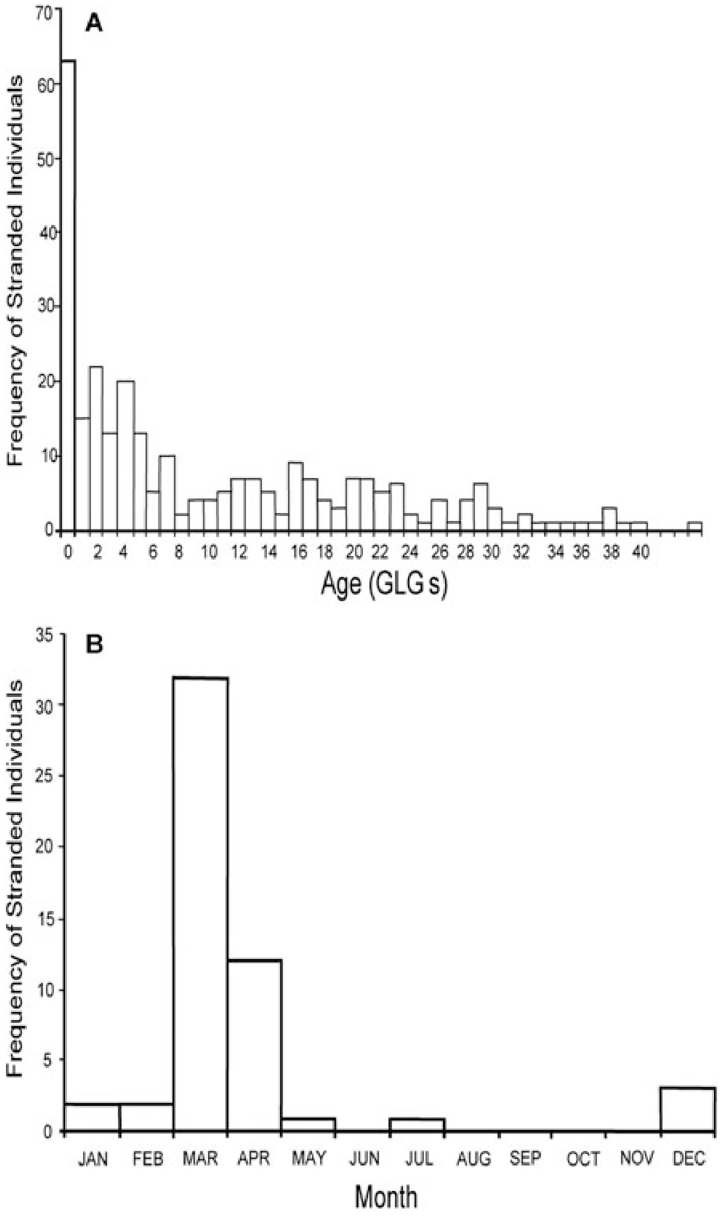

Figure 5. Age and frequency distributions of stranded bottlenose dolphins along coastal Texas. (A) Age distribution of 290 individuals estimated by GLG analysis. (B) neonatal (<1 GLG) stranding frequencies by calendar month.

The ages predicted by allometric growth indices were significantly different from those predicted from average growth per gestational day (*sensu* Kasuya 1977), therefore fetal allometric relationships (BPD/length) were used to estimate gestational age in further analyses.

Table 2. Summary of predicted growth parameters from the Gompertz growth model. The values in parentheses are the refitted asymptotic lengths for the Gompertz growth model.

Model	*n*	Outliers	Final *n*	*G*	*g*	*k*	L_0	L_∞
Postnatal model	258	4	254	0.27	0.39	0.69	118.00	235.80
Female postnatal model	73	3	70	0.31	0.42	0.74	115.00	240.57
Male postnatal model	114	2	112	0.26	0.38	0.68	120.00	237.86
Pre- and postnatal model	660	3	657	0.44	0.55	0.80	106.00	235.91
Female pre- and postnatal model	162	0	162	0.42	0.51	0.82	105.00	239.25
Male pre- and postnatal model	302	1	301	0.43	0.55	0.78	107.00	233.84

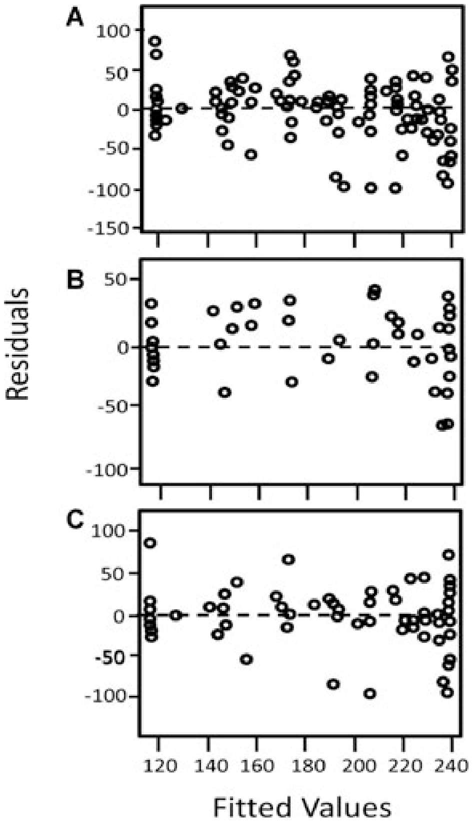

Figure 6. Postnatal Gompertz residual plots. Least squares residual plots for (A) the overall postnatal population, (B) the female postnatal population, and (C) the male postnatal population of bottlenose dolphins along coastal Texas.

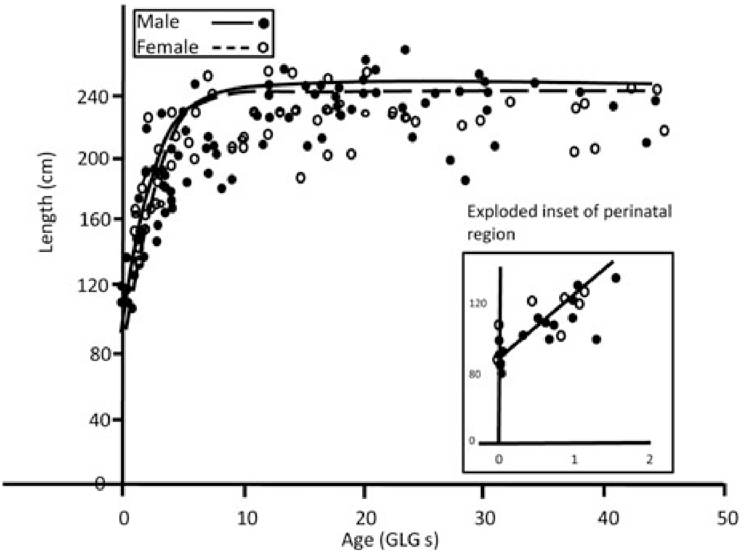

Figure 7. Length-at-age, postnatal growth curves of male (solid line) and female (dashed line) bottlenose dolphins from the Texas coast. Individual males (filled circle) and females (unfilled circle) are also plotted. An inset of perinatal length-at-age (roughly conception to 2 yr of age) is also provided to demonstrate variability.

Pre- and Postnatal Growth Analysis

Fetal and postnatal length-at-ages were fit with a Gompertz growth model (see Table 2). Overall, the model exhibited a reasonable fit to the new length-at-age data, but carried a higher AIC value. However, the pre- and postnatal model predicted

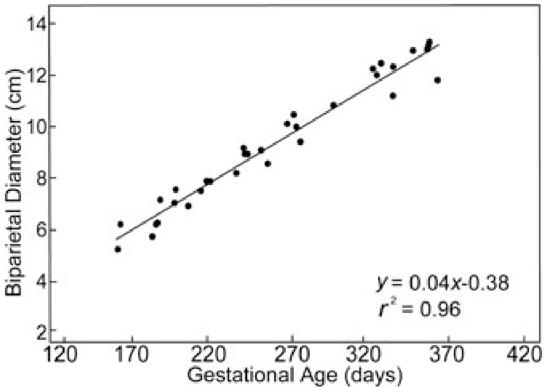

Figure 8. Biparietal diameter regressed against gestational age for fetal Atlantic bottlenose dolphins detected by ultrasound during pregnancies conceived by artificial insemination. Data from three pregnancies were pooled after a one-way ANOVA detected no significant differences between BPD-at-age of each fetus. The best fit equation and coefficient of determination are also given.

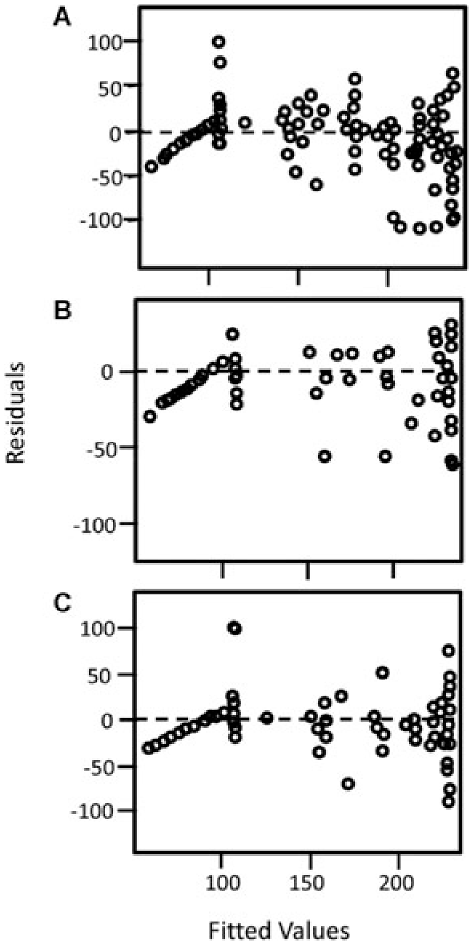

Figure 9. Pre- and postnatal Gompertz residual plots. Least squares residual plots for (A) the overall pre- and postnatal population, (B) the female pre- and postnatal population, and (C) the male pre- and postnatal population of bottlenose dolphins along coastal Texas.

an earlier age at attainment of asymptotic length (yr 6) than the postnatal model (yr 12). Asymptotic length decreased slightly (240 to 236 cm) from the postnatal model. The visual fit of the model was far better at the lower end than the upper end of the growth spectrum. Residual plots also confirm this observation (Fig. 9). Interestingly, the initial growth rate (*G*) and the exponential rate of growth decay (*g*) both increased by nearly 1.5× when fetal data were included. The growth rate constant (*k*) remained similar between both the postnatal and the pre- and postnatal growth curve. Fetal male and female lengths and ages were combined for the fitted curves (Fig. 10) because differences in growth regimes do not manifest until well after birth (Fernandez and Hohn 1998). However, among our sample, sexual dimorphism was minimal. Growth rate parameters, lengths at birth, and asymptotic lengths were within a few centimeters (see Table 2).

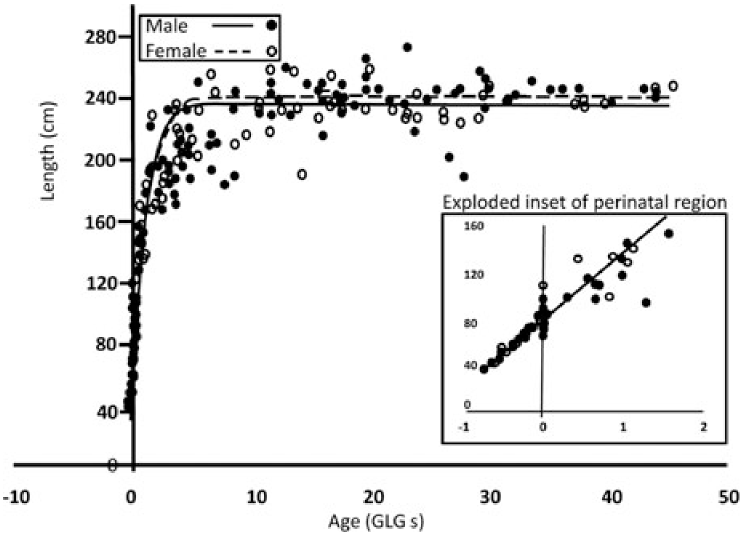

Figure 10. Pre- and postnatal male (solid line) and female (dashed line) Gompertz growth models for bottlenose dolphins along coastal Texas. Individual male (filled circle) and female (unfilled circle) are also plotted. An inset of perinatal length-at-age (roughly conception to 2 yr of age) is also provided to demonstrate variability.

Length at birth decreased markedly with the inclusion of prenatal data, from 118 to 106 cm. The results of a logistic model fit to a binomial distribution demonstrated observable overlap, and the fitted mean probability (0.5) indicated that the point estimate of length-at-birth was approximately 114.7 cm (Fig. 11). This estimate was closest to the Gompertz postnatal model prediction of 118 cm.

DISCUSSION

The Gompertz growth model explained more postnatal length-at-age variation than the von Bertalanffy growth model, and the parameters predicted from the least-squares Gompertz growth model are consistent with parameters predicted for other coastal regions along in the southeastern United States (Table 3). Although length is a poor estimator of age, it is useful to describe growth processes, which may be of greater management concern than age prediction. Deviations from baseline growth parameters may indicate population perturbations. For example, a trend toward early sexual maturation at smaller size is associated with increased adult mortality. Similar size outcomes related to life history plasticity have been thoroughly summarized by Stearns and Koella (1986).

The postnatal growth rate constant in this study (0.69) is consistent with previous estimations. Parameter values reported by Turner *et al.* (2006) and Fernandez and Hohn (1998) represent length-at-age curves generated for coastal Texas, and are similar for values reported for the Indian River Lagoon (Stolen *et al.* 2002). Bottlenose dolphin sexual dimorphism did not manifest in early life. Male and female growth parameters in these cases reflect low variation between the sexes at birth (Fernandez and Hohn 1998). In the postnatal length-at-age model, sexual dimorphism was

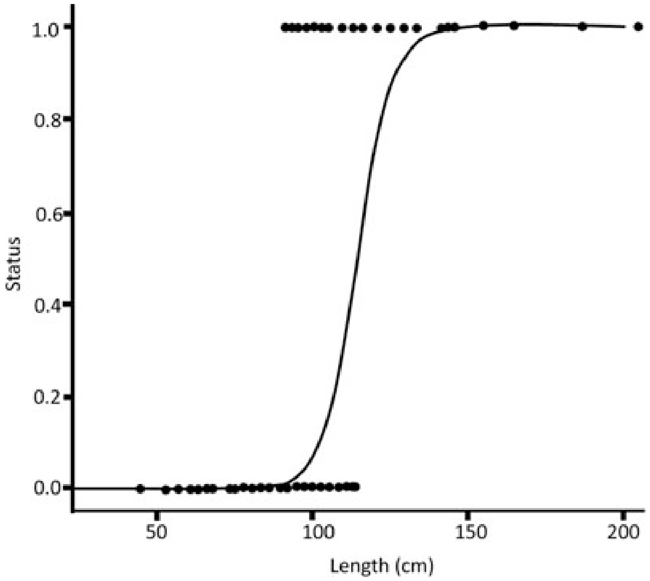

Figure 11. Logistic fit for length at birth for bottlenose dolphins along coastal Texas. The *y* axis represents the probability that an observed individual stranded bottlenose dolphin will be fetal or nonfetal dependent upon length. Only bottlenose dolphins stranded along coastal Texas are represented in this analysis.

evident in male and female rates of growth decay. Females demonstrated a higher rate of growth decay, which could potentially drive size dimorphism in adulthood, specifically, length accretion. Size differences may be related in part, to reproductive strategies (Read *et al.* 1993), which undoubtedly would place demands on the instantaneous growth rate. For example, females along the coast of northeast Florida typically achieve sexual maturity approximately 2 yr before males (Sergeant *et al.* 1973), and the asymmetry in growth may be related to an earlier onset of sexual maturity.

Table 3. Summary of postnatal Gompertz growth rate constants of bottlenose dolphin populations. The following represents a compilation of growth rate constants calculated for additional populations of bottlenose dolphins (*T. truncatus*, *T. aduncus*).

Male	Female	Model	*n*	Species	Reference
0.16[a]	0.16[a]	Gompertz	36	*T. truncatus*	Siciliano *et al.* (2007)
0.73	0.77	Gompertz	36	*T. truncatus*	Turner *et al.* (2006)
0.72	0.77	Gompertz	199	*T. truncatus*	Stolen *et al.* (2002)
0.10	0.17	von Bertalanffy	174	*T. aduncus*	Cockcroft and Ross (1990*b*)
0.76	0.79	Gompertz	205	*T. truncatus*	Fernandez and Hohn (1998)
0.07	0.12	Gompertz	96	*T. truncatus*	Read *et al.* (1993)
0.68	0.74	Gompertz	232	*T. truncatus*	Present study

[a] *k* reported as combined value for males and females.

We observed pronounced seasonality in our sample, based on the frequency distribution of neonates. Typically, populations that experience predictable, seasonal food shortages will reproduce seasonally. Females begin to store or divert resources in preparation for reproductive activities at select times of the year (Vaughan *et al.* 2000). In bottlenose dolphins, storage is related to the timing of lactation rather than conception or gestation (Kastelein *et al.* 2002). The generalist diet of bottlenose dolphins makes it difficult to predict which seasonal food abundances are the most important relative to lactational effort. The concept of seasonal food availability warrants more investigation, particularly since bottlenose dolphin populations at similar latitudes exhibit vastly dissimilar breeding seasons (Urian *et al.* 1996), perhaps in response to regionally diverse prey abundances.

This study provided an opportunity to examine neonatal size variation, demonstrated by estimations of lengths at birth using fits from three models. The prenatal model is dependent upon well-established allometric growth relationships, and predictions of length at birth are likely more conservative. The postnatal model is more heavily weighted by the postnatal growth regime, and predicts a longer length at birth. Birth length estimated using a logistic fit to binomial data likely provides a realistic compromise between the two methods, so long as fetal and neonatal conditions are accurately assigned based on validated morphologic indicators. The range of the three estimates demonstrates the considerable variability and size overlap of near-term fetuses and early neonates. This problem is commonly mentioned in bottlenose dolphin length-at-age studies, and is ascribed a number of explanations (see Mattson *et al*. 2006, Stolen *et al.* 2002, Fernandez and Hohn 1998, Read *et al*. 1993). Regardless of the precise reason for size variation at birth, it is evident from prior studies (Riding *et al.* 2008, Kuzawa 2005, Lacave *et al.* 2004), and the present one, that birth size is largely determined by growth constraints established sooner rather than later in fetal development.

Model Choice

The Gompertz growth model was chosen in favor of the von Bertalanffy growth model for the postnatal, and the pre- and postnatal data set due to superior fit in both cases (Table 2). The addition of fetal information influenced the absolute growth rate (G) and the rate of growth decay (g). The comprehensive growth curve indicated that the absolute growth rate (G) for bottlenose dolphins may be significantly higher than previously reported. This is to be expected since absolute growth is not constrained by growth decay until postpartum. However, the overall change in the growth rate constant k was relatively minor since G and g fluctuated in constant proportions to one another. The commonly reported growth parameter k is somewhat misleading because it provides no information about the absolute growth rate (G), or the growth rate decline (g), at time x, and these parameters become masked in the context of population comparison. For instance, the growth rate constant for postnatal individuals in this study was predicted by the model to be 0.69, but when fetal data was included, the growth rate constant increased to 0.80. This suggests a slight growth discrepancy but it does not indicate in which aspects. Despite the variance in growth rate constants across geographic regions (Table 3), the absolute growth rate and rate of decay were similar to values previously reported by Fernandez and Hohn (1998). In summary, the sensitivity of the growth rate constant to small changes limits its use in practical management. Expressing the constant as G/g instead of k

is far more informative for growth assessments. This is particularly important when summarizing life history traits that may be influenced to some degree by intrinsic growth rates and survival strategies.

The von Bertalanffy model has been successfully used to simulate growth in a number of marine species (Espinosa *et al.* 2008, Hughes *et al.* 2008, Hwang *et al.* 2008, Leaf *et al.* 2008, Liu *et al.* 2009, Paul and Horn 2009, Robillard *et al.* 2009, Tovar-Avila *et al.* 2009). It is interesting to note that the fit of the von Bertalanffy declined with the pre- and postnatal data set, and failed to explain growth early in life. In large measure, this is due to the high weight given to larger individuals. The theory of von Bertalanffy's growth is based on the assumption of perfect allocation, or the supposition that anabolism is equal to catabolism, and all nutrition is optimally assimilated for somatic growth (von Bertalanffy 1938). In reality, mammalian growth regimes change at sexual maturity, and at best, von Bertalanffy growth is an optimality model (Czarnoleski and Kozlowski 1998). The Gompertz growth model is advantageous for mammalian size-at-age data because it is anchored by a "size at birth" parameter, and it accounts for resource allocation for reproduction. As growth rate decay increases, so does the inversely proportional impact to somatic growth. Recall the Gompertz and the von Bertalanffy growth equations:

$$L_t = L_0 \mathrm{e}^{[G/g(1-\exp(-gt))]} \quad \text{(Laird 1966b)}$$

$$L_t = L_\infty(1 - \mathrm{e}^{-G/g(t-t_0)}) \quad \text{(von Bertalanffy 1938).}$$

Each equation contains a growth penalty for increasing size. As age and the rate of growth decay (g) become larger, so does the cost to the growth rate constant (G/g). In the Gompertz model, length from birth (L_0) only increases by some factor of assimilation ($\mathrm{e}^{[G/g(1-\exp(-gt))]}$). In contrast, von Bertalanffy's model implies that length at time t should be equal to some proportion of asymptotic length *assuming* that all energy is expended for somatic increase throughout life. Many mammalian species face a tradeoff between size and reproduction (Czarnoleski and Kozlowski 1998). For this reason, western Atlantic common bottlenose dolphin growth is better described by a Gompertz rather than a von Bertalanffy growth model.

Both curves demonstrated variation in length at birth, but neither model fully explained variation at all life stages along the growth curve. For instance, the length at birth was validated using three independent methodologies: a fetal model, a pre- and postnatal Gompertz model, and a logistic model fit to binomial data. All three models predicted a length at birth between 106 and 120 cm (116.5, 106.2, and 114 cm, respectively). It is possible that some teeth that were aged as neonatal were in fact fetal. However, it is more likely that no single growth model explains variation in early life well, particularly given the great length variability observed in neonates. Recently, more flexible, multistage models have been explored to model growth in delphinids. A two-stage Laird-Gompertz has been used to incorporate a pubertal growth spurt that precedes reproductive maturity in short-beaked common dolphins (*Delphinus delphis*; Danil and Chivers 2007). The advantage to using a multistage model is that it accounts for quickly changing growth regimes. Workers have argued that there is no evidence of a pubertal growth spurt with respect to length in bottlenose dolphins (Read *et al.* 1993), but these studies may be limited by small sample size. More recently, investigators have employed unique models that may suggest multiple growth spurts in bottlenose dolphin life history (McFee *et al.* 2010). Studies such as this one will help corroborate dynamic growth trends observed in multiple life history stages.

In summary, the authors make the following suggestions: Growth rate estimates should always be expressed in expanded form; G/g rather than k in order to capture a realistic depiction of growth dynamics. For example, the growth rate constant estimate in this study exhibited a slight increase from the postnatal to the pre- and postnatal model, while at the same time the absolute growth rate and rate of growth decay increased dramatically. Second, the entire life cycle of bottlenose dolphins should be explained by a model framework that allows greater flexibility of model parameters. Lastly, parameters that affect length accretion (*i.e.*, absolute growth rate), should carry greater weight in prenatal and early postnatal life, and parameters that promote social and sexual dimorphism (*i.e.*, growth rate decay) should have increasing influence near the onset of reproductive maturity and adulthood.

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