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Growth and rapid early development of North Atlantic right whales (*Eubalaena glacialis*)

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Body growth of North Atlantic right whales (*Eubalaena glacialis*) was described from measurements of known-age live and dead individuals to gain insights into the nutritional needs and life-history strategies of this endangered species. Body lengths from 154 individuals revealed that calves more than doubled in size and attained three-fourths of asymptotic adult size by the time they had weaned at 12 months. Calves gained on average ~1.7 cm and ~34 kg per day while nursing during this extremely rapid growth phase. Mean predicted lengths and body mass were 4.2 m and 1.1 metric tons (mt) at birth, 10.3 m and 13.5 mt at weaning, and 13.6 m and 29.6 mt when fully grown. Growth of right whales was best described using a 2-phased Gompertz growth model and could not be fit using any of the single continuous growth models commonly used for other mammals. Rapid growth during dependency may minimize the risk of predation and maximize calf survival. Rapid calf growth also may maximize development of the mouth and baleen to optimize foraging efficiency of juveniles at the time of weaning, as well as improve reproductive fitness by reducing the age at which sexual maturity is attained. However, transferring the amount of energy needed to support the rapid postnatal growth of North Atlantic right whales may ultimately affect the intervals between pregnancies (>3 years) of mature females.

Key words: *Eubalaena glacialis*, growth models, length, mass, reproductive costs, right whale

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Growth models that describe body size have been widely applied to address questions pertaining to species biology, ecology, physiology, and conservation. Growth models have been integrated into bioenergetic models to determine the total energetic requirements of fish species (e.g., Hufnagl and Peck 2011; Juncos et al. 2011; Thomas et al. 2011), as well as into multispecies (e.g., Rochet et al. 2011) and ecosystem (e.g., Xu et al. 2011) models to determine the flow of energy through predator–prey interactions. Growth models also have been used to compare changes in body size over time to make inferences about the nutritional and reproductive status of populations (e.g., Calkins et al. 1998; Fearnbach et al. 2011; Perryman and Lynn 2002). Growth models even have been used to establish appropriate drug dosages for sedatives and antibiotics of animals of different sizes and consequently of different ages (e.g., Woods et al. 1989).

Various techniques have been used to obtain the data needed to describe body growth. Growth of small aquatic animals can be easily studied with field and laboratory studies. For example, fish can be easily live captured for weighing and measuring (e.g., Barkman and Bengtson 1987; Beamish and McFarlane 1983; Brouwer and Griffiths 2004; Koch et al. 2011), or sampled and aged using dead individuals (e.g., Mercier et al. 2011). Data from larger species, such as marine mammals, have traditionally come from dead animals (e.g., Trites and Bigg 1996; Winship et al. 2001) and sometimes from live-caught (e.g., Crawley 1975; Iverson et al. 1993) or captive (e.g., Jones et al. 2011; Liu et al. 2011) animals.

However, large aquatic animals such as cetaceans present logistical challenges and have typically been measured after being harvested (e.g., Frazer and Huggett 1973; George et al. 1999; Lockyer 1981; Lockyer and Waters 1986; Markussen et al. 1992), stranded, or unintentionally caught in fishing gear (e.g., Agusa et al. 2011; Perrin et al. 1976; Read and Tolley 1997). Growth models for cetaceans have therefore been typically constructed from few measurements.

The majority of data available to describe the size-at-age of cetaceans have been collected from whaling ships and whaling stations, and were collected to assist in the management of exploited and depleted stocks. These historic studies (e.g., Laws 1959; Mackintosh and Wheeler 1929; Nishiwaki and Hayashi 1950) laid the foundation for what is presently known about cetacean growth. More recently, growth studies have been conducted using data sets from stranding events and fisheries bycatch (e.g., Agusa et al. 2011; Read and Tolley 1997). Growth models thus exist for many commercially exploited and bycaught species, but are largely unavailable for species such as North Atlantic right whales (*Eubalaena glacialis*) that were commercially extinct (Reeves et al. 2007) before standardized data collection and aging procedures were implemented (e.g., Norris 1961).

In 1935, North Atlantic right whales were deemed overexploited and placed under international legal protection by the League of Nations (Kraus and Rolland 2007). Unfortunately, the few morphometric measurements taken during the historical right whale hunt were inaccurate (body mass) or inconsistent (lengths) according to the Smithsonian Institution's National Museum of Natural History (C.W. Potter, Smithsonian Institution's National Museum of Natural History, pers. comm., 2009). Growth of right whales thus remained undescribed until morphometric measurements from beached carcasses (1970–2002, $n = 23$ individuals) were analyzed (Moore et al. 2004). This small data set from necropsied whales included animals that were pulled onto the shore and likely stretched prior to measurement. It also contained calves of uncertain ages (estimated in decimal years), which prevented modeling the growth of dependent young.

A means to improve the existing crude model of North Atlantic right whale growth (Moore et al. 2004) is to increase the sample size of morphometric measurements. This can be done using measurements of living animals estimated by aerial photogrammetry (e.g., Perryman and Lynn 2002). Photogrammetric techniques have been widely established to collect noninvasive morphological measurements of various cetacean species (Fearnbach et al. 2011; Webster et al. 2010).

Refining the existing body growth model for North Atlantic right whales can allow questions to be better answered about food requirements, age at sexual maturation, and appropriate doses of medications. Researchers have long hypothesized that the poor recovery of North Atlantic right whales is partially attributed to nutritional stress (Kraus et al. 2007; Miller et al. 2011; Reeves et al. 2001; Rolland et al. 2007) and direct anthropogenic mortality from ship strikes and entanglement in fishing gear (Caswell et al. 1999; Kraus et al. 2005; Moore et al. 2004). Researchers also have hypothesized that delayed ages at sexual maturation (5–21 years) may reflect reproductive failure through neonatal and perinatal loss, but are uncertain about the age at sexual maturation (Browning et al. 2010). A growth model would contribute to testing the nutritional stress hypothesis (e.g., by constructing a bioenergetics model) and could be used to confirm or refine present estimates of the mean age at sexual maturation (9 years). It could even be used to assist in determining effective doses of antibiotics to administer to wounded animals and doses of sedatives for entangled animals of different sizes (Moore et al. 2010).

The goal of our study was to describe North Atlantic right whale growth using linear and nonlinear models fit to measurements from live (remotely measured through photogrammetry) and dead (physically measured during necropsy) whales. We modeled growth in length and mass using standard growth functions that have been previously applied to fish and mammals, and tested the use of 2-phased models to account for differential growth of immature and mature right whales. We also described growth in maximum body width and fluke width using linear mixed-effects models, to enable field biologists to determine approximate age and length of stranded animals that cannot be accurately measured due to decomposition. Our results describe the body growth of the North Atlantic right whale and provide new insights into the reproductive strategy and energetic investment employed by this large cetacean.

Materials and Methods

Length.—We modeled length-at-age relationships using measurements from dead North Atlantic right whales and from live animals photographed during aerial surveys. All measurements were collected in accordance with guidelines approved by the American Society of Mammalogists (Sikes et al. 2011). Photogrammetric measurements ($n = 133$) were taken of 94 unique individuals in the Bay of Fundy between 2000 and 2002, following the methods of Perryman and Lynn (2002). Some of these 94 individuals (17 calves, 39 juveniles, and 38 adults) were seen and measured in more than 1 year. This included 9 juveniles and 10 adults that were measured twice, and 8 juveniles and 2 adults that were measured in 3 different years. Calves represented individuals between 0 and 1 year; juveniles consisted of individuals >1 and < 9 years; and adults included those ≥ 9 years. We further increased our sample size of measurements by including 21 necropsy length measurements collected from known individuals between 1970 and 2009. Age classes of all measured animals were determined for individual whales by matching photographs of their unique callosity patterns ((large elevated patches of roughened skin—Kraus et al. 1986) using the *North Atlantic Right Whale Consortium Identification Database* (Right Whale Consortium 2010).

The aerial photographs were taken by National Oceanic and Atmospheric Association Southwest Fisheries Science Centre personnel using a KA-76A United States military reconnaissance camera mounted over an 18-inch camera port in the hull of a Twin Otter aircraft (Chicago Aerial Industries, Ltd., Barrington, Illinois, and de Havilland Aircraft of Canada, Ltd., Toronto, Ontario, Canada). The camera had a fixed-focal-length 126-mm lens and used Kodak Aerial Ektachrome film (SO-397 Eastman Kodak Company, Rochester, New York) for the majority of the images. Cycle rate for the camera was determined based on a combination of aircraft altitude and ground speed to ensure that adjacent frames overlapped by 60–80%. This rapid cycle rate allowed each animal to be captured on 3 or 4 frames during each photo pass. Position (based on global positioning system) and altitude (radar altimeter; Honeywell AA-300 series Honeywell Corp., Phoenix, Arizona) were recorded automatically each time the camera fired. Bias in radar altimetry data was estimated each field season from regression analysis of a photographed series of floating targets. This calculated bias was used to correct recorded altitude for each frame from which length measurements were made. More detailed explanation of these techniques can be found in Perryman and Lynn (2002).

Necropsy length measurements ($n = 21$) consisted of a straight-line distance from the tip of the snout to the fluke notch. The straight-line distance usually is measured by laying the tape measure on the beach parallel to the body and measuring from the tip of the rostrum to the fluke notch. However, there is some degree of variation associated with the person making the measurement and from the difficulty of placing the tape measure at the exact spot that is perpendicular to the rostrum tip and fluke notch. Necropsy measurements were adjusted to correct for the assumed effects of stretching (while animals were mechanically maneuvered on the beach) by subtracting 9% of the total body length for individuals that were hauled before they were measured. In the absence of pre- and posthauling length measurements for North Atlantic right whales, we assumed that length was overestimated by 9%, based on the finding by George et al. (2004) that bowhead whales (*Balaena mysticetus*) stretched by this amount during the postharvest hauling process.

Age.—Lengths were available for calves of unknown ages (≤ 1 year) and for juveniles and adults of known ages. We estimated the ages of the dead calves based on when they stranded and the estimated median date of birth for North Atlantic right whales, which we assumed was the median day of 1st sighting of 154 individual calves on the calving grounds off the southeastern United States, using identification data from 1991 to 2007 (Right Whale Consortium 2010). All juveniles and adults were observed within their 1st year of life and were aged in decimal years using the assumed median birth date and the year and day they were measured. We compared calculated ages with length measurements for 78 females and 73 males (3 measurements were of unknown sex) and between data sets (133 photogrammetric and 21 necropsy measurements) to identify outliers or possible errors in measurements and estimates.

Growth curves.—We attempted to fit 4 commonly used growth functions to the length-at-age data. These included the Putter (equation 1—Ricker 1979; von Bertalanffy 1938), von Bertalanffy (equation 2—Ricker 1979; von Bertalanffy 1938), Gompertz (equation 3—Gompertz 1825; Zach et al. 1984), and logistic (equation 4—Ricker 1979) equations:

$$\mathrm{S}_t = \mathrm{A}\left(1 - e^{-k(t-t_0)}\right), \tag{1}$$

$$\mathrm{S}_t = \mathrm{A}\left(1 - e^{-k(t-t_0)}\right)^3, \tag{2}$$

$$\mathrm{S}_t = \mathrm{A}e^{-ce^{-kt}}, \tag{3}$$

and

$$\mathrm{S}_t = \frac{\mathrm{A}}{1 + e^{-k(t-t_0)}}, \tag{4}$$

where S is size at age t for males and females, A is asymptotic size, t_0 is time at which size is zero, c is the constant of integration (Zach et al. 1984), and k is indicative of growth rate (Ricker 1979). These parameters have slightly different properties between models, but are generally comparable within models.

We fit the growth models using a 2-phased approach with nonlinear, least squares regression (nls package) in the statistical program R (R Development Core Team 2009), and were unable to apply nonlinear mixed-effects models to the limited duplicate measurements (i.e., few animals were measured 3 times). Phase 1 represented calves that experienced a rapid growth period and phase 2 represented both juvenile and adult animals that experienced decelerated growth. The inflection point between phase 1 and phase 2 was defined as the age at which the difference between the predicted length of the phase 1 and phase 2 models was zero. We used the Akaike information criterion (AIC) to measure the relative fit of each model and selected the model with the smallest AIC value as having the lowest relative expected Kullback–Leibler distance and maximized log-likelihood (Burnham and Anderson 2002). To account for repeated measures (i.e., some whales were seen in more than 1 year and were photogrammetrically measured as many as 3 times), we generated a set of 10,000 data sets from the 154 measurements with randomly selected duplicate length measurements removed. We then bootstrapped these samples with replacement and fit the growth function to the data. We extracted mean model parameters from the bootstrap replicates and defined these coefficients as the "best model." We then generated confidence intervals by sorting the bootstrap replicates into 95% quartiles (by ordering bootstrap replicates into the 2.5% and 97.5% quartiles).

We tested for sexual dimorphism by comparing mean length-at-age measurements for males and females aged 9–22 years using a repeated-measures analysis of variance (ANOVA). We then fit sex-specific growth curves to the data using the above methods.

Mass.—Growth in mass-at-age was modeled using the allometric relationship of length and body mass derived from dead whales (Table 1; Moore et al. 2004; Right Whale Consortium 2010) to predict mass-at-age from the length-at-age models. Body masses from the 15 individuals were collected by using either a vessel travel lift while the animal

TABLE 1.—North Atlantic right whale (*Eubalaena glacialis*) necropsy and Pacific right whale (*Eubalaena japonica*) whaling data used in the allometric mass models. An individual (case 14) was excluded from analysis because the recorded values were estimates rather than direct measurements and were considerably lower than what would be predicted based on the individual's age. U = unknown sex; F = female; M = male.

Species	Sex	Length (cm)	Mass (kg)	Case
Atlantic	U	600	700	14
Atlantic	F	455	1,130	42
Atlantic	F	473	1,134	29
Atlantic	F	478	1,151	34
Atlantic	M	412	1,227	21
Atlantic	M	495	1,586	80
Atlantic	M	417	2,000	40
Atlantic	M	581	2,041	28
Atlantic	M	1,030	9,055	32
Atlantic	F	910	11,045	49
Atlantic	F	1,005	15,000	26
Atlantic	F	1,360	29,700	27
Atlantic	F	1,370	52,640	44
Atlantic	M	365	749	73
Atlantic	F	1,229	14,785	45
Pacific	M	1,470	52,870	
Pacific	M	1,510	55,250	
Pacific	M	1,520	48,250	
Pacific	M	1,610	67,770	
Pacific	M	1,640	78,500	
Pacific	M	1,700	65,760	
Pacific	M	1,710	67,240	
Pacific	M	1,240	22,250	
Pacific	M	1,710	63,490	
Pacific	F	1,170	22,870	
Pacific	F	1,630	58,590	
Pacific	F	1,660	63,130	
Pacific	F	1,710	63,490	
Pacific	F	1,740	106,500	
Pacific	F	1,260	28,920	
Pacific	M	1,410	47,560	

was removed from the water, individually weighing dismantled body parts (flesh and bones) and adding 6.8% to account for fluid loss (Lockyer 1976), or weighing the individual at a weigh station on a flatbed truck (McLellan et al. 2002; Moore et al. 2004). Additionally, 16 length and body mass measurements from North Pacific right whale (*Eubalaena japonica*) whaling records (Omura et al. 1969) were compared to the North Atlantic measurements for possible inclusion in length and body mass models to increase the sample size.

Body mass was estimated using Schultz's (1938) allometric model to predict mass based on body length:

$$\mathrm{W} = a\mathrm{L}^{b}, \tag{5}$$

where W is mass in kilograms, L is length in centimeters, a is a constant factor, and b is an exponential constant. This length and mass model may be expressed in its logarithmic form as:

$$\log_{10}\mathrm{W} = b\log_{10}\mathrm{L} + \log_{10}a. \tag{6}$$

We fit linear regressions to both North Atlantic and North Pacific right whale data. A 2-tailed Student's t-test (Zar 1996) compared the allometric regressions for North Atlantic and North Pacific right whales by testing for significance in the difference of the slopes.

We generated mass-at-age estimates by substituting predicted lengths-at-age into the allometric model once we had solved for the a and b parameters. Uncertainty was incorporated into the mass-at-age estimates by 1st bootstrapping the allometric model and generating 10,000 fitted parameters, and then by using predicted length-at-age estimates from 10,000 bootstrap replicates.

Width.—We used photogrammetric measurements of fluke and maximum body width to model the relationship between width and total body length. The analysis of fluke width included 130 measurements of both sexes of 83 unique individuals, and 94 measurements of 65 unique individuals for maximum body width. The relationship between width (maximum body and fluke width) and total body length was tested with linear mixed-effects models using the lme statistical package in R (R Development Core Team 2009) to address violations of independence (Pinheiro and Bates 2000). These models accounted for repeated measures and were fit by maximum likelihood (Pinheiro and Bates 2000). Multiple linear regressions were fit to the data to test for differences between sexes and age classes and were compared using ANOVA. Because body width is likely to be confounded by body length, we tested for significant adult width-to-length ratio differences between sexes using a repeated-measures ANOVA.

RESULTS

Age.—One-half of all North Atlantic right whale calves observed on the calving grounds during intensive aerial surveys (1991–2007) were seen for the 1st time by 5 January (Fig. 1). The day with the greatest number of 1st sightings—9 calves (Fig. 1)—also was 5 January. First sightings of right whale calves were most frequent between November and March, thereby suggesting that the estimated median birth date of 5 January had an associated uncertainty of approximately ±2 months.

We used the 5 January birth date to estimate the decimal ages of all animals. Individuals less than 1 year old represented 25% of the total sampled body-length measurements (Fig. 2a), suggesting that the data were skewed toward immature animals. In comparison, 40% of female and 33% of male body-length measurements were from animals aged 9–22 years old (Fig. 2a). As a general trend, the frequency of measurements decreased with age for both sexes. Comparisons of age-frequency data by category (Fig. 2b) also showed that the majority of necropsy measurements (67%) were from individuals aged 0–1 year, and that relatively few were from noncalves (33%).

Length.—Of the 4 growth models we tested (equations 1–4), the 2-phased Gompertz curve yielded the lowest AIC scores and was judged to be the best descriptor of growth for males and females combined (Fig. 3; Table 2). However, AIC scores for the von Bertalanffy model also were very low. We

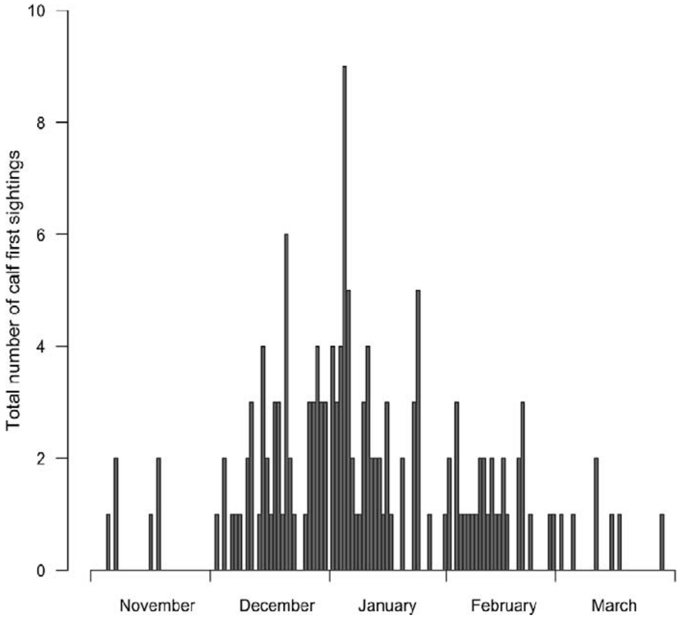

Fig. 1.—Frequency distribution of 1st sightings of uniquely identified North Atlantic right whale (*Eubalaena glacialis*) calves in the southeastern United States (Florida and Georgia) collected between November and March 1991–2007. Each tick mark represents the 1st day of each month. The median day of 1st sighting is 5 January.

ultimately selected the Gompertz model over the von Bertalanffy model for biological reasons because the Gompertz model accounts for somatic and reproductive development, whereas the von Bertalanffy model assumes perfect allocation of resources and only accounts for somatic growth (Neuenhoff et al. 2011). The mean Gompertz model parameters derived from 10,000 bootstrap replicates for phase 1 were 1,082.04 ± 13.719 *SD* for A, 0.95 ± 0.096 for *c*, and –3.02 ± 0.280 for *k*. Phase 2 model coefficients were 1,390.87 ± 30.737 for A, 0.33 ± 0.021 for *c*, and –0.13 ± 0.273 for *k*. Fitting 2 curves was the only way to account for the rapid growth of individuals between ages 0 and 1.05 years old (phase 1; Fig. 3), and the decelerated growth of older animals (1.06–22.00 years old; phase 2; Fig. 3). We found that calves gained an average of 621 cm ± 62 *SD* from birth to weaning. This translates into 1.70 cm per day ± 0.17 *SD*, assuming a constant growth rate. Predicted asymptotic length (~95% of maximum length) occurred at ~12 years of age.

Length measurements differed significantly between adult males and females (repeated-measures ANOVA, $F_{1,38} = 13.22$, $P < 0.001$). Mean lengths at sexual maturity were 1,344 cm ± 61 *SD* for females and 1,287 cm ± 48 *SD* for males, suggesting slight sexual dimorphism (females were 71 cm longer on average than males at maturity).

Mass.—The mass-to-length relationship differed significantly between North Atlantic and North Pacific right whales (2-tailed *t*-test, $t_{28} = 3.04$, $P < 0.01$), and showed North Pacific right whales to be heavier for a given length than North Atlantic right whales (Fig. 4; Table 2). We thus only used North Atlantic right whale data to estimate mass-at-age. We were unable to make additional comparisons between the 2 right whale species due to small sample sizes and missing age information for North Pacific right whales.

North Atlantic right whale calves gained considerable mass during the 12 months that they were assumed to have nursed. Based on the growth curves, the average calf grew ~34 kg per day and had gained ~12.4 metric tons (mt) by the time it had weaned (based on the mean birth mass of 1,101 kg ± 311 *SD* and mean weaning mass of 13,460 ± 1,848 kg; Table 3). Remarkably, calves were ~12 times their birth mass at the assumed onset of independence, and had attained ~40% of their mass at sexual maturity. However, mass accretion decelerated considerably between independence and sexual maturity (~2.8 kg per day).

Width.—There was a positive, linear relationship between maximum body width and body length. The slope (ANOVA, $F_{1,28} = 319.30$, $P < 0.001$) and intercept (ANOVA, $F_{1,64} = 28{,}007.69$, $P < 0.001$) were highly significant for the null model, where both sexes and all age classes were combined (Fig. 5). No significant differences were found between the null model and alternative models that accounted for potential differences between sexes (ANOVA, $F_{1,63} = 0.002$, $P = 0.96$) and age classes (ANOVA, $F_{2,24} = 0.06$, $P = 0.94$). We thus pooled the data because of the similarity among all categories. Similarly, the slope (ANOVA, $F_{1,46} = 360.01$, $P < 0.0001$) and intercept (ANOVA, $F_{1,82} = 38{,}201.77$, $P < 0.0001$) were significant for the fluke width and body length model (Fig. 5). However, sex (ANOVA, $F_{2,80} = 2.86$, $P = 0.06$) and age class (ANOVA, $F_{2,42} = 0.45$, $P = 0.64$) were insignificant. The width-to-length ratio also did not differ significantly between sexes (repeated-measures ANOVA, $F_{1,25} = 3.80$, $P = 0.062$).

DISCUSSION

Data error and model uncertainty.—Combining morphometric measurements collected directly from a dead animal or indirectly using photogrammetry increased the sample sizes but could have introduced unintended errors that biased model predictions. Addressing uncertainty by examining necropsy and photogrammetry data for unusually large or small individuals resulted in removing 1 of 15 mass measurements from necropsied individuals (because it was incorrectly measured).

Measurement precision is nearly impossible to estimate for necropsied animals because individuals are generally only measured once while lying in a single position. However, precision can be estimated from photogrammetric measurements where 3 or more photographs are taken of the same individual. Multiple photogrammetric measurements from individual right whales taken between sampling years suggest that photogrammetry estimates have relatively small coefficients of variation (*CVs*); mean *CV* values for length were 0.0236 (range 0.009–0.047) and 0.022 (0.007–0.0515) for fluke width. *CV* values were not calculable for body width because few duplicate measurements exist. Precision of our photogrammetric measurements are comparable to those of

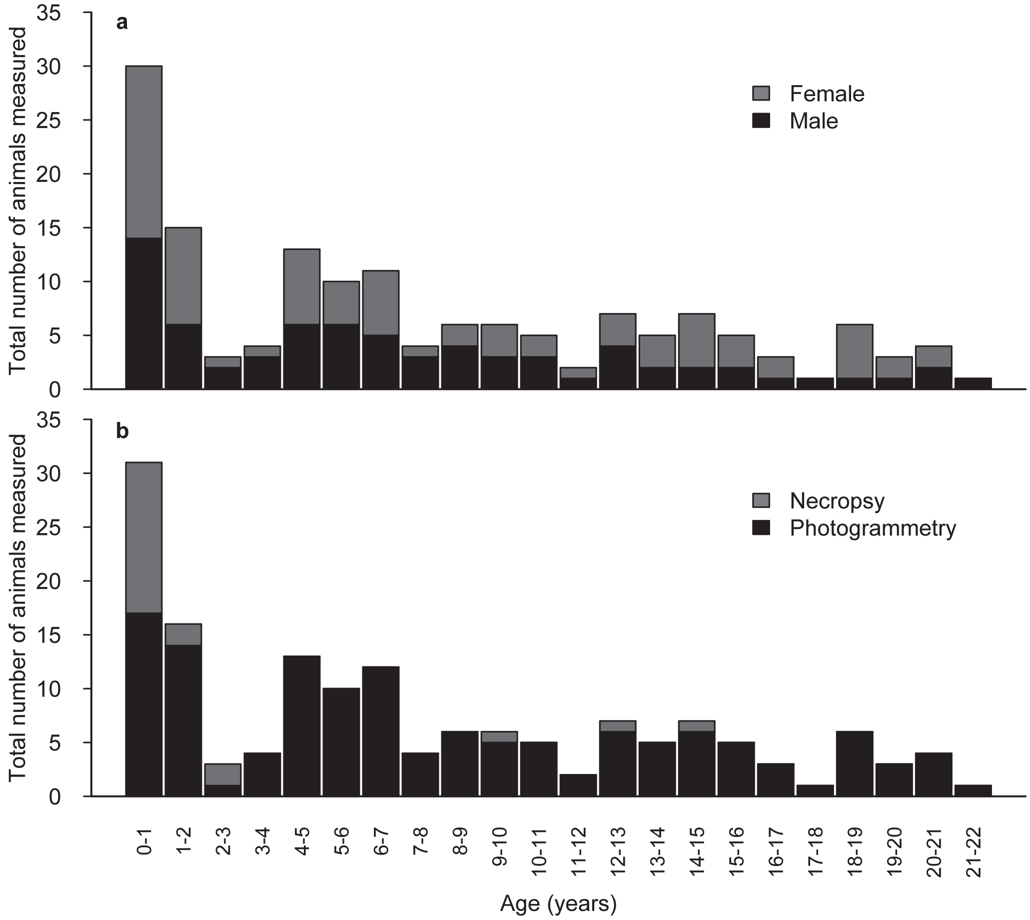

FIG. 2.—Age-frequency distributions of body lengths of North Atlantic right whales (*Eubalaena glacialis*) from the necropsy and photogrammetry databases categorized by a) sex and b) data type.

previous studies of gray whales (*Eschrichtius robustus*), whereby Perryman and Lynn (2002) report *CV* values of 0.020 for body length and 0.030 for fluke width.

Body mass is far more difficult to measure than body length of large cetaceans. Consequently, wide confidence intervals resulting from a small sample size reduced the reliability of our mass estimates. Other studies, however, seem to ignore the uncertainty of length-at-age and mass-at-length predictions when generating confidence intervals for mass-at-age models, and, thus, likely underestimate error in body mass predictions (e.g., George 2009; Lockyer 1981). The inclusion of unhealthy animals (emaciated animals due to fishing gear entanglement and suckling calves in poor nutritive condition) also may have resulted in mass being underestimated relative to age. Our growth curves likely underestimated body mass and should be refined as more data become available. Veterinarians wishing to apply the growth curves should adjust dose levels of antibiotics and sedatives for chronically entangled individuals that are likely to be underweight relative to their body length.

Body mass also is related to girth, and body width can be used as a proxy for girth. Our maximum-width analysis complements a detailed study of North Atlantic right whale dorsal body shape changes in relation to nutritional condition of calves and mature females (Miller et al. 2012). However, we found no significant difference between the widths and width-to-length ratios of males and females, and therefore did not generate sex-specific mass estimates. This lack of difference in widths may reflect our small sample size, lower statistical power, and the underrepresentation of pregnant females—therefore warranting further investigation into body width differences.

Errors in aging also can bias the descriptions of growth and age is particularly challenging to estimate for large cetaceans. Our median birth date method used to estimate age in decimal years introduced ±0.16 years of uncertainty. Using measurements taken from identified individuals with a known birth year greatly reduced the uncertainty of our estimated ages. Growth studies of other species with unidentifiable individuals often use less-accurate techniques to age individuals, such as using aspartic acid racemization (e.g., ±6–35 years uncertainty in age) to age bowhead whales (George et al. 1999).

Unequal size representation within age classes also may have biased the length-at-age estimates, which were positively skewed toward animals between 0 and 1 year. Consequently, model uncertainty was greater in the juvenile and adult model. The lack of data for animals beyond 22 years limits the predictability of our model for older age classes (the oldest known North Atlantic right whale is just over 70 years old [Right Whale Consortium 2010]). However, this is unlikely to

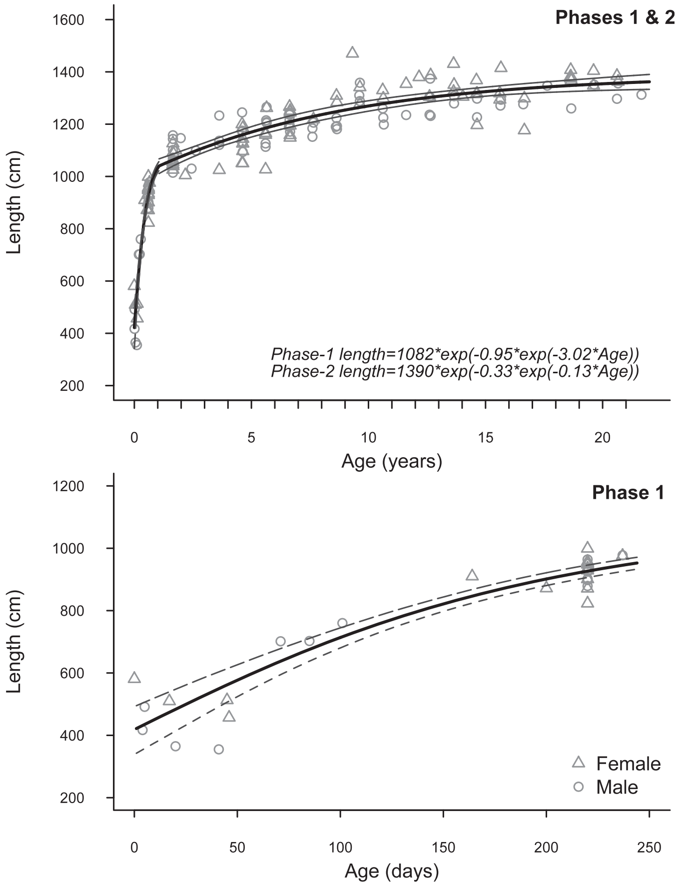

FIG. 3.—Mean 2-phase (phases 1 and 2) and 1-phase (phase 1) Gompertz growth curves for North Atlantic right whales (*Eubalaena glacialis*). Body lengths of necropsied individuals were corrected for potential stretching (~9% body length) and 95% confidence intervals (dashed lines) were derived from 10,000 bootstrap replicates. Length-at-age can be calculated using the equations provided with age expressed in years. Phase 1 includes growth from birth to age 1 year old, and phase 2 describes growth for right whales aged 1+ years old.

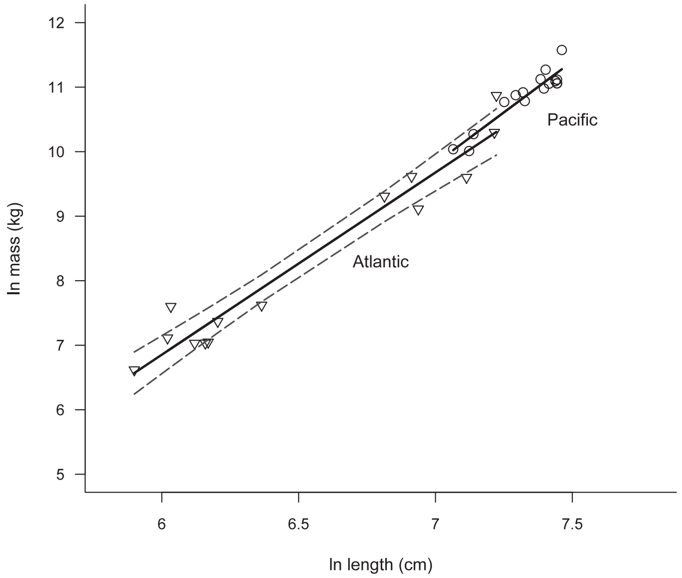

FIG. 4.—Mass–length relationships for North Atlantic (Δ) and North Pacific ($\circ$) right whales (*Eubalaena glacialis* and *Eubalaena australis*). Log-transformed data were fit separately with linear regressions: North Atlantic, $y = -10.095x + 2.825$, $r^2 = 0.94$, $P < 0.001$; North Pacific, $y = -12.286x + 3.158$, $r^2 = 0.88$, $P < 0.001$. Fitted parameters for North Atlantic ($a = 0.000041298$, $b = 2.825$) and North Pacific ($a = 0.000004616$, $b = 3.158$) right whales were used to model mass-at-age.

have any meaningful consequence because the growth rate of adult animals is small and asymptotic length is likely achieved by ~12 years of age. Overall, we consider any biases in age estimation to be minimal, and have similar confidence in the estimates of body length.

The large data set that resulted from combining measurements of dead and living whales revealed several interesting aspects about right whale growth. Most notably, the morphological measurements showed that like southern right whales (*Eubalaena australis*—Best and Ruther 1992), North Atlantic right whale calves grow extremely fast compared to other cetacean species because they attain more than three-fourths of

TABLE 2.—Two-phased parameter estimates (± *SE*) for growth models (Putter, von Bertalanffy, Gompertz, and logistic; equations 1–4) where A is asymptotic size, *k* is indicative of growth rate, *c* is the constant of integration, and t_0 is time at which size is zero. Length measurements were in centimeters and age was measured in decimal years. Model selection was conducted using the Akaike information criterion (AIC). AIC values are provided along with the difference in AIC values between fitted models, the likelihood of each model, and the weight of each model (i.e., the weight of evidence in favor of each model). The model with the greatest weight was considered to be the "best" model.

Model	A	*k*	*c*	t_0	AIC values	AIC differences	Likelihoods	AIC weights
Phase 1 (0–1.05 years)								
Putter	1,658.975 ± 1,246.92	0.739 ± 0.18		0.858 ± 1.171	357.839	0.536	0.765	0.282
von Bertalanffy	1,277.000 ± 405.70	0.303 ± 0.06		1.829 ± 1.221	357.480	0.177	0.915	0.337
Gompertz	1,193.126 ± 283.42	2.325 ± 1.25	−1.017 ± 0.195		357.303	0.000	1.000	0.368
Logistic	966.771 ± 70.16			4.447 ± 1.789	363.914	6.612	0.037	0.013
Phase 2 (1.06–22 years)								
Putter	1,392.00 ± 32.35	0.29 ± 0.01		0.11 ± 0.02	1,368.597	0.348	0.840	0.302
von Bertalanffy	1,386.00 ± 29.57	0.10 ±0.01		0.12 ± 0.03	1,368.362	0.113	0.945	0.339
Gompertz	1,382.87 ± 28.37	0.13 ± 0.03	−0.33 ± 0.02		1,368.249	0.000	1.000	0.359
Logistic	1,269.00 ± 9.45		0.79 ± 0.06	1,461.731	93.481	0.000	0.000	

TABLE 3.—Predicted mean mass and length measurements (± *SD*) for North Atlantic right whales (*Eubalaena glacialis*). Mean allometric model coefficients for phase 2 growth were $a = -10.072 \pm 1.368$ and $b = 2.820 \pm 0.211$. Mean parameter estimates for phase 1 were $a = -10.085 \pm 1.358$ and $b = 2.822 \pm 0.210$.

Age (years)	Mass (kg)	Length (cm)
0	1,101 ± 311	422 ± 40
0.25	4,332 ± 506	691 ± 18
0.5	8,449 ± 996	876 ± 11
0.75	11,582 ± 1,510	978 ± 9
1	13,460 ± 1,848	1,032 ± 9
2	15,147 ± 2,168	1,076 ± 11
3	16,577 ± 2,445	1,111 ± 9
4	17,936 ± 2,729	1,142 ± 10
5	19,213 ± 3,005	1,170 ± 10
6	20,402 ± 3,268	1,195 ± 11
7	21,501 ± 3,513	1,217 ± 11
8	22,510 ± 3,738	1,237 ± 11
9	23,430 ± 3,943	1,254 ± 11
10	24,267 ± 4,131	1,270 ± 10
11	25,025 ± 4,301	1,284 ± 10
12	25,708 ± 4,456	1,296 ± 9
13	26,324 ± 4,598	1,307 ± 9
14	26,876 ± 4,726	1,316 ± 9
15	27,372 ± 4,844	1,325 ± 9
16	27,815 ± 4,131	1,332 ± 9
17	28,212 ± 5,051	1,339 ± 10
18	28,566 ± 5,142	1,345 ± 11
19	28,882 ± 5,225	1,350 ± 12
20	29,163 ± 5,302	1,354 ± 13
21	29,415 ± 5,372	1,358 ± 14
22	29,639 ± 5,438	1,362 ± 15

their asymptotic size upon weaning. Furthermore, the growth rate decreased sharply following the onset of independence.

Single- versus 2-phased growth.—Commonly used continuous growth equations yielded poor model fits because the growth rates of young right whales differed markedly before and after weaning. Had we fit a continuous growth function, we would have overestimated juvenile growth and underestimated the asymptotic length of adults. Growth functions (equations 1–4) commonly used to describe increases in animal lengths and masses were developed for fish and other species that have different life-history strategies and growth patterns. All growth functions have fixed inflection points that are a proportion of adult length (Ricker 1979), which when fit to the right whale data would have resulted in calves reaching the point of inflection at ~37% of their maximum adult length prenatally. However, right whale calves are only ~31% of their maximum length at birth. Applying a continuous Gompertz model would have incorrectly assumed that a larger proportion of growth was achieved prenatally.

To our knowledge, baleen whale growth has never been described using this 2-phased approach. However, there is evidence that cetacean growth in general is poorly described by continuous functions and that applying single-equation growth models may result in poor model predictions and confound interspecies comparisons. Dolphin and porpoise growth, for example, appears to slow after weaning and increase near sexual maturation, and has been mathematically described using 2-phased Laird's models to account for secondary growth spurts (Danil and Chivers 2007; Larese and Chivers 2009; Perrin et al. 1976). Consequently, future cetacean growth studies should consider using 2-phased models instead of continuous growth functions.

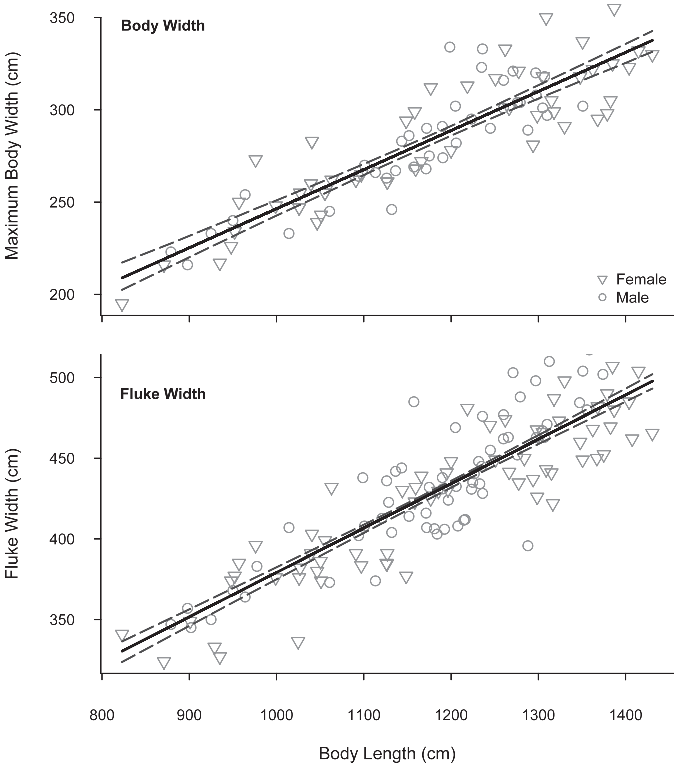

FIG. 5.—Linear mixed effects models fit to maximum body width, fluke width, and length data for North Atlantic right whale (*Eubalaena glacialis*) calves, juveniles, and adults of both sexes. The 95% confidence intervals (dashed lines) were estimated by bootstrapping the residuals 1,000 times fit to width and length data for calves, juveniles, and adults of both sexes. Body width is predicted by $y = 38.63x + 0.21$, $P = 0.006$, and fluke width is predicted by $y = 103.96x + 0.28$, $P < 0.0001$, where x is body length in centimeters.

Calf growth.—Overall, the 2-phased model captured the precocious exponential growth of calves. Applying the 2-phased growth model showed that right whales more than double in length and are ~12 times heavier upon weaning than at birth. Furthermore, right whales are predicted to be 422 ± 40 cm at birth, which is similar to the mean length of perinatal (near-birth) animals measured in the field (i.e., 446 ± 31 cm, $n = 3$). By the time they wean at 1 year, right whales are 1,032 ± 9 cm long and 76% of their asymptotic length. However, in terms of weaned mass, yearlings attain a mere 47% of their asymptotic mass, suggesting that a large increase in mass occurs later in life.

The rapid growth of dependent young is consistent with what has been described for other baleen species. For example, the daily growth rate of nursing blue whales (*Balaenoptera musculus*) and fin whales (*Balaenoptera physalus*) was estimated to be 3.45 cm and 2.40 cm, respectively (over a 7-

month nursing period—Lockyer 1981). However, North Atlantic right whales attain a greater proportion of their maximum size at weaning (~76%) compared to the ~70% attained by blue and fin whales (estimated from Lockyer [1981]). Furthermore, right whales grow an average of ~2.6 cm per day when only the first 7 months of nursing are considered. Some of the apparent difference between calf growth rates of blue, fin, and right whale species may be explained by the duration of the lactation period (which is 5 months longer for right whales) and length-based whaling regulations that may have led to falsified measurements, such as those made on whaling vessels (Gilpatrick and Perryman 2008). However, neither the possibility of erroneous measurements or different ages at weaning negates the fact that baleen whales appear to employ a similar growth strategy that invests heavily in the physical development of calves.

The length-at-age model predicts that North Atlantic right whale calves grow faster than those of the closely related bowhead whale. Although both species have a similar weaning age of 12 months (Nerini et al. 1984), bowhead whale calves gain a mere 1.1 cm per day while nursing (George 2009), which is slower than the estimate for right whales (1.7 cm per day). Furthermore, bowhead calves attain a smaller proportion of their maximum body length after 1 year (~52%, estimated from George [2009]) compared to 76% for right whales. This faster postnatal growth suggests that right whales may be more precocial than bowheads and that maternal investment is likely greater for right whales (Gaillard et al. 1997; Pontier et al. 1993).

Juvenile and adult growth model.—The 2-phased model shows an apparent pause or deceleration of growth at weaning. This decreased growth rate of yearlings corresponds with the 12-month nursing period, and may reflect reduced energy acquisition during the transition from dependency to independency. Although uncertainty exists in the age of weaning (age of weaning has varied from 8 months to >12 months), 12 months appears to be the most reasonable estimate given visual observations of mother–calf association times (Hamilton and Cooper 2010; Hamilton et al. 1995). Whether the reduced growth reflects decreased caloric intake associated with the transition from milk to zooplankton or foraging inexperience is unknown. However, delayed growth at weaning is consistent with current understanding of North Atlantic right whale life history and also agrees with what has been reported for other precocious mammals, including other cetacean species (e.g., Lockyer 1981).

North Atlantic right whale growth slowed markedly after sexual maturity. Our growth model shows that right whales attain ~92% of their maximum length at the mean age at sexual maturation ($\bar{X} = 9$ years, range = 5–21 years) and ~95% at 12 years. However, cetaceans are generally thought to reach sexual maturity after attaining 86% of their maximum length (Laws 1956), which would have occurred for right whales when 5 years old. The early attainment of maximum length agrees with observations of 1st parturition in females beginning as early as 5 years (Kraus et al. 2007), and supports the hypothesis of Browning et al. (2010) that extended age at which right whales are believed to 1st give birth may simply be a function of reproductive dysfunction (i.e., undetected perinatal and neonatal mortality). The adult and juvenile growth model is thus consistent with the current understanding of right whale reproduction and conforms to assumptions about the importance of size in determining the age of 1st parturition.

Counter to expectations, the growth models did not detect a statistical difference in the growth rates of male and female right whales, although mean lengths of adult females (≥9 years old) were significantly greater than those of males (by ~4% on average). Although slight sexual dimorphism was detected in mean lengths, small sample sizes may have prevented differentiating sex-specific growth curves. The difference between mean lengths of adults was consistent with what has been observed for other baleen species (e.g., George et al. 1999; Lockyer 1981). Greater female size may equate with greater energy reserves that could increase reproductive fitness by partially offsetting the physiological costs of reproduction and reducing offspring mortality (Blanckenhorn 2005; Gittleman and Thompson 1988; Gordon 1989).

Why rapid calf growth?—The rapid growth of calves implies that females invest heavily in the growth of their offspring (Hall et al. 2001; Huang et al. 2009; McMahon et al. 2000). North Atlantic right whales provision their young using energy from stored blubber and are known to have significantly more blubber than other species (Lockyer 1976). Right whales are thus only likely to be able to meet the high costs of lactation by catabolizing their stored lipids. Trade-offs between maternal investment, offspring mortality, and adult survival expectancy are common among mammals (Gittleman and Thompson 1988; Glazier 1999; Gordon 1989; Huang et al. 2009; Oftedal 1997; Pontier et al. 1993). Consequently, the potential benefits of rapid postnatal growth in right whales may include reduced starvation and predation of offspring, and improved foraging efficiency and reproductive fitness of progeny.

Right whale mothers may disproportionately transfer energy to maximize the body condition, growth, and survival of their offspring. Such a strategy could offset the challenges that an otherwise recently weaned and inexperienced right whale calf would have in locating sufficient prey patches, which are highly spatially and temporally variable (Baumgartner et al. 2003; Baumgartner and Mate 2003; DeLorenzo Costa et al. 2006; Greene and Pershing 2000; Greene et al. 2003; Hlista et al. 2009; Jiang et al. 2007; Kenney 2001). Yearlings are known to catabolize a significant proportion of their energy stores shortly after independence (1.7-cm reduction in blubber from calf to yearling [Miller et al. 2011]), and are known to be significantly thinner during years of low prey availability compared to years of improved prey availability (Miller et al. 2011). Rapid growth while nursing may thus be an evolutionary adaptation to maximize an offspring's energy stores and enable inexperienced yearlings to better cope with nutritional stress and the ephemeral nature of their prey.

Fast postnatal growth also may optimize foraging success by maximizing baleen development and mouth size. In other words, right whales may need to attain a critical size at weaning if they are to optimally feed. Morphological studies have found that cetaceans invest the greatest growth in expansion of the head and that larger jaws can accommodate a bigger feeding apparatus (Armfield et al. 2011; Lockyer 1981). This pattern of growth may thus reflect the high energy needs of independent whales (Lockyer 1981). Furthermore, baleen growth is rapid during the 1st year of life and slows during adulthood for bowhead whales (George 2009). Although little is known about North Atlantic right whale baleen and head development in relation to body length, it is possible that rapid growth maximizes the efficiency of the filter-feeding apparatus to capture prey. Rapid growth may thus be used to improve offspring foraging efficiency and survival.

Increased body size at time of weaning also may reduce the probability of being eaten by a killer whale (*Orcinus orca*) or white shark (*Carcharodon carcharias*—Huang et al. 2011). Right whales are thought to employ active physical defense while in the presence of predators because they are slow swimmers and are unable to flee their predator (Ford and Reeves 2008). As such, right whales have evolved to fight with their strong tailstock and dry accretions of dead skin (callosities—Ford and Reeves 2008). Killer whale predation, however, does not appear to be a significant threat to the population today because only 9% of North Atlantic right whales have scars from predatory attacks from killer whales and few attacks have been confirmed (Hamilton and Knowlton 2010; Kraus 1990). However, recent observations of white shark attacks on right whale calves have been made (Taylor et al. 2012). Thus, the evolutionary presence of predators may be enough to warrant such adaptations (Ford and Reeves 2008; Lima 1998; Lima and Dill 1990; Sih 1985).

The heavy investment made by lactating females may increase the probability of their offspring reproducing at younger ages (i.e., increased reproductive fitness—Lockyer 1981; Read and Gaskin 1990) given that faster-growing mammals mature earlier than slower growing species (Ferrero and Walker 1999; Greene and Rothstein 1991). This is consistent with North Atlantic right whales attaining a comparatively larger size at weaning and a younger age at maturity compared with bowhead whales (George 2009). High maternal investment may therefore maximize fitness by optimizing the size at weaning and juvenile survival rate, and lowering the age of 1st birth (Pontier et al. 1993).

Adults may exhibit a reduced life span through long-lasting phenotypic effects (Metcalfe and Monaghan 2003) as a consequence of rapid postnatal growth. Reduced life spans may result from increased investment in growth and decreased investment in prevention or repair of molecular damage (Cichon 1997; Metcalfe and Monaghan 2003). However, little is known about the longevity of right whales (Hamilton et al. 1998). Calves may thus undergo rapid growth while nursing to minimize the time to reach sexual maturity, but adults may incur long-term consequences.

The reproductive rate of North Atlantic right whales may be adversely affected by the high maternal investment required to support rapid postnatal growth. Mammals with rapid growth trajectories are often not food limited. However, they are susceptible to starvation during food shortages (Blanckenhorn 2000; Metcalfe and Monaghan 2003). Species that undergo rapid growth are generally considered to have high metabolic rates and are poorly equipped to adapt to prey shortages (Arendt 1997). Birth rates of right whales are known to fluctuate wildly from one year to the next (from 1 to 39 calves born per year [Kraus et al. 2007; Waring et al. 2011]) and have been correlated with oceanographic anomalies thought to influence the quality and quantity of prey (Greene and Pershing 2004; Hlista et al. 2009). This suggests that reproductively mature females may forgo reproduction during years of sparse prey abundance because they cannot meet the rapid postnatal growth strategy. In this way, females may have evolved to physiologically select offspring quality over quantity (Greene and Rothstein 1991).

Conclusions.—North Atlantic right whales employ a growth strategy that favors rapid development of dependent animals and decelerated growth of larger juveniles. Such a growth trajectory does not conform to continuous-growth functions, and is mathematically best described using a 2-phased approach. Rapid growth may increase reproductive fitness by maximizing foraging efficiency and minimizing predation risk at the time of weaning, and could result in right whales reaching sexual maturity at younger ages than other species of baleen whales. However, this growth strategy likely comes at a cost (i.e., variability in calving interval). The possible costs and benefits of mothers investing so heavily in the growth of their calves have significant implications for the ecology, population dynamics, and management of North Atlantic right whales.

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