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Body growth of North Atlantic right whales (*Eubalaena glacialis*) revisited

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Abstract

Knowing size-at-age is important for determining food requirements and making inferences about the nutritional status of individuals and their populations. Accurate growth curves are also needed to quantify drug dosages to treat wounded or entangled animals. However, body sizes are often based on small numbers of measured animals that must be improved as new data become available. We updated an existing body growth model for North Atlantic right whales (NARWs) using new data from dead animals and from older individuals. Our models indicate that NARWs attain mean lengths and weights of 4.3 m and 1.0 mt at birth, and 13.1 m and 31.7 mt when sexually mature. Calves more than double their length and attain nearly three-quarters of their asymptotic adult size during their first year of life. Overall, our length estimates agreed well with previous estimates, but our mass-at-age values were considerably higher. These differences revealed that necropsy data used alone in allometric models underestimate mass due possibly to several of the stranded animals in the database having been chronically entangled and in poor body condition. Augmenting the database with healthier individuals, such as harvested North Pacific right whales, yielded mass predictions that reflect both healthy and unhealthy individuals.

KEYWORDS

body size, *Eubalaena glacialis*, growth models, length, mass, morphometry, photogrammetry

1 | INTRODUCTION

Body size is related to sexual maturity, longevity, reproductive strategies, metabolic needs, and abundance, and is arguably the most important trait of individual animals (Kenagy & Trombulak, 1986; Laws, 1956; Speakman, 2005; White, Ernest, Kerkhoff, & Enquist, 2007). Because body mass is largely linked to age at sexual maturity, fast growing species reach maturity sooner than slower growing species. Such is the case for cetacean species that are expected to attain sexual maturity after reaching ~85% of their maximum length (Laws, 1956). Rates of body growth thus influence reproductive output and population dynamics, while body mass affects metabolic rates, energy expenditure, and food requirements (Brodie, 1975). Overall, body size is important when it comes to several aspects of the biology, ecology, and management of species.

Growth curves for North Atlantic right whales (*Eubalaena glacialis*) have been derived from small numbers of opportunistic measurements of dead animals collected by different institutions and individuals over many years (Moore, Knowlton, Kraus, McLellan, & Bonde, 2004; Sharp et al., 2019). This database has evolved and grown with time as errors were corrected and new information became available. Given the importance of having accurate growth curves to determine food requirements and make inferences about the reproductive and nutritional status of populations, or to set drug dosages of sedatives and antibiotics to treat injured whales (Barratclough et al., 2014; Moore et al., 2010), it is important to periodically review the existing morphometric database and update the published growth curves as necessary.

The most recent growth curve for North Atlantic right whales was published in 2012 (Fortune et al., 2012) using measures of length and mass from necropsied animals (Moore et al., 2004), and photogrammetric measurements from live animals (Perryman & Lynn, 2002). Since then, new body size data were added to the database (including animals >22 years old, the upper limit for the previous growth curve), and some of the morphometric measurements included in the North Atlantic Right Whale Consortium Necropsy Database were removed when discovered to have had been estimated rather than measured (North Atlantic Right Whale Consortium, 2018). As a result of these shortcomings, the existing body growth curves for North Atlantic right whales need to be corrected and updated.

Our goal was to use recently acquired data to improve the existing growth models for right whales and generate more robust estimates of body size at age to allow better predications of food requirements to be made, as well as drug dosages to be determined. We also sought to better understand the rapid growth of nursing calves and decelerated growth of juveniles and adults.

2 | MATERIALS AND METHODS

2.1 | Length

We modeled the relationship between length and age for North Atlantic right whales using data obtained during necropsies (lengths were measured directly from dead animals) and from photogrammetry (lengths were obtained from photographs of live animals at-sea). Photogrammetric measurements (n = 133) were taken from 94 unique individuals in the Bay of Fundy between 2000 and 2002 as described by Fortune et al. (2012). Aerial images of individual right whales were collected from a Twin Otter aircraft equipped with a KA-76A United States military reconnaissance camera that was mounted over an 18-in. camera port located in the hull of the aircraft. The majority of the photogrammetric data were obtained using a fixed focal length 126-mm lens with Kodak Aerial Ektachrome film. The aircraft altitude and ground speed of the aircraft were used to determine the camera cycle rate, whereby adjacent frames overlapped by 60%–80%. The goal of the rapid cycle rate was to permit each whale to be photographed on 3–4 frames during a single photo pass. For each image taken, location (global positioning system) and altitude (radar altimeter) data were simultaneously recorded. Prior to each field season, the radar altimeter bias was determined by collecting a series of images of a floating target of known size and conducting a regression analysis. The altimeter bias was subsequently used to correct the altitude for each image used for photogrammetric measurements (Perryman & Lynn, 2002).

Body lengths were measured during necropsies of 29 known-age individuals between 1970 and 2017 and represented the straight-line distance from the snout to the fluke notch. The straight-line distance was determined by laying a measuring tape parallel to the animal on the ground and measuring the distance from the tip of the rostrum to the fluke notch. Measurement errors can be attributed to the many individuals who took these body length measurements, as well as the difficulty associated with placing the tape measure at the precise location that is perpendicular to the snout tip and fluke notch. Body lengths of necropsied individuals that were mechanically hauled onto the beach prior to measurement were corrected for potential stretching (~9% body length; George, Zeh, Suydam, & Clarkm, 2004).

Age classes of all measured animals were determined for individual whales by matching photographs of their unique callosity patterns (Kraus et al., 1986) using the North Atlantic Right Whale Consortium Identification Database (North Atlantic Right Whale Consortium, 2018). We also estimated the ages of individuals (in decimal years) based on when they stranded or were photogrammetrically measured, and their estimated median date of birth of January 5 (Fortune et al., 2012). Detailed descriptions of how ages were estimated, and how necropsies and aerial photogrammetry were conducted are contained in Fortune et al., (2012).

2.2 | Growth curves

We fit four standard growth functions to the length-at-age data, including the Putter (Equation 1; von Bertalanffy, 1938; Ricker, 1979), von Bertalanffy (Equation 2; von Bertalanffy, 1938; Ricker, 1979), Gompertz (Equation 3; Gompertz, 1825; Zach, Liner, Rigby, & Mayoh, 1984), and logistic equation (Equation 4; Ricker, 1979):

$$S_t = A\left(1-e^{-k(t-t_0)}\right) \quad (1)$$

$$S_t = A\left(1-e^{-k(t-t_0)}\right)^3 \quad (2)$$

$$S_t = Ae^{-ce^{-kt}} \quad (3)$$

$$S_t = \frac{A}{1+e^{-k(t-t_0)}} \quad (4)$$

where S is length at age t for males and females, A is asymptotic size, t_0 is time at which size is theoretically zero, c is the constant of integration (Zach et al., 1984) and k is indicative of growth rate (Ricker, 1979).

We fit length-at-age models as per Fortune et al. (2012) in a 2-phased approach with nonlinear least squares regression. We fit standard growth functions to length-at-age data for individuals aged 0–1.65 years (*Phase 1*) and older animals aged 1.65–30.5 years (*Phase 2*). We used the statistical program R (nls package; R Development Core Team, 2016) for analysis. *Phase 1* represented rapid calf growth and *Phase 2* represented decelerated growth of juveniles and adults. The inflection point between models was determined based on the age where the difference between predicted lengths of *Phase 1* and *2* models was equal to zero. Model selection was made by observing the Akaike information criterion (AIC) and selecting the model with the lowest AIC and greatest weight. Since some photogrammetrically measured animals were seen in more than 1 year and were measured as many as three times, we created (i.e., bootstrapped) 10,000 data sets from the 162 measurements by randomly selecting duplicate length measurements to be removed. Resampling was done to avoid issues related to nonindependence of observations whereby one length-at-age measurement per individual per model simulation was selected randomly. Growth curves were fit to the bootstrapped samples and mean model parameters were extrapolated from the bootstrap replicates to define the "best model." Confidence intervals (95%) were subsequently calculated by ordering bootstrap replicates into the 2.5% and 97.5% quartiles.

We used a linear mixed-effects model and a repeated-measures analysis of variance (ANOVA) to test for sexual dimorphism through comparison of mean length-at-age measurements for adult (9–30 years) male and female right whales. This analysis accounted for violations of independence by including animal ID as a random factor as there were duplicate length measurements for photogrammetrically measured individuals.

2.3 | Mass

Mass-at-age was derived from the allometric relationship of length and mass determined from 13 dead whales (North Atlantic Right Whale Consortium, 2018; Moore et al., 2004; Sharp et al., 2019) as described by Fortune et al. (2012). We linearized Schultz's (1938) allometric model:

$$W = aL^b \tag{5}$$

to predict mass based from body length:

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

where W is mass in kilograms, L is length in centimeters, a is a constant factor, and b is an exponential constant. We tested the significance of coefficients using a two-tailed Student's t-test (Zar, 1996). Model uncertainty was incorporated by bootstrapping the allometric model 10,000 times to generate a distribution of predicted masses for given lengths. We also compared the relationship derived for North Atlantic right whales to that derived for 16 North Pacific right whales (*Eubalaena japonica*) (Omura, Oshumi, Nemoto, Nasu, & Kasuya, 1969).

3 | RESULTS AND DISCUSSION

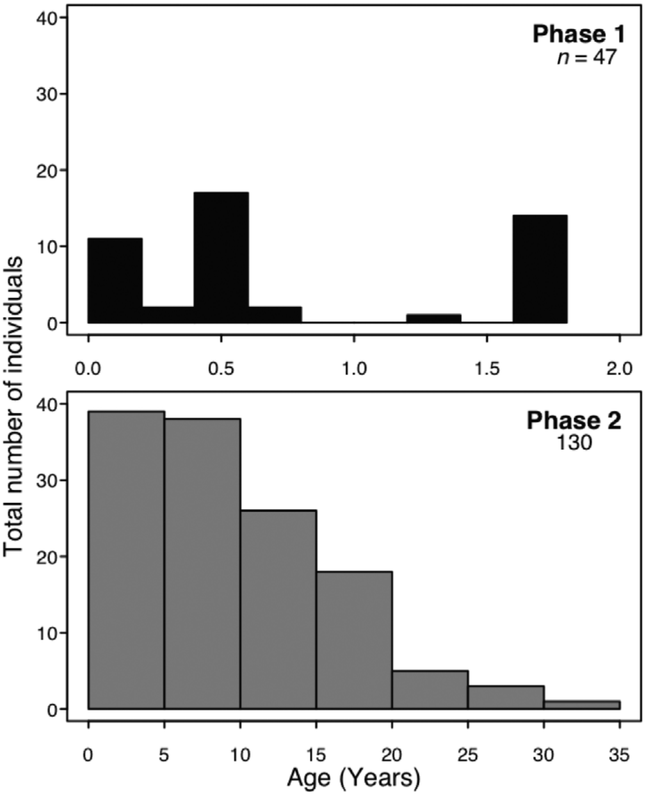
3.1 | Length

The 2-phased Gompertz model best described the growth of North Atlantic right whales (Figure 1, Table 1), although the von Bertalanffy and Putter models presented similar AIC scores and weights suggesting that right whale growth may be adequately described using several growth functions (Anderson, 2008). We nevertheless selected the model with the lowest AIC and greatest weight. Furthermore, we biologically justified using the Gompertz model over the von Bertalanffy model because the Gompertz equation accounted for somatic and reproductive development, while the von Bertalanffy model only accounted for somatic growth (Neuenhoff, Cowan, Whitehead, & Marshall, 2011).

To find a point of inflection where the multiphase growth curves met, we fit two Gompertz growth models to data for younger (0–1.65 years) and older (1.65–30.5 years) animals. Morphometric data were only available for one individual between 0.65 and 1.65 years (1.27 years). We found that the inflection point occurred at 0.79 years and that the average age of individuals used to fit the *Phase 1* was 0.78 ± 0.62 *SD* and 9.70 ± 6.68 *SD* years for *Phase 2* (Figure 1).

The Gompertz growth functions were fit in a two-phased approach whereby *Phase 1* included animals between 0 and 1.65 years and *Phase 2* included whales between 1.27 and 30.5 years and bootstrapping was used to account for model uncertainty. We found that the point of inflection (i.e., where the two-phased growth curves met) occurred at 0.79 years. Since we did not have morphometric data for animals >0.65 and ≤ 1.26 years (*Phase 1*)

FIGURE 1 Distribution of ages for the morphometric measurements used to generate multiphase length-at-age growth curves for North Atlantic right whales calves (*Phase 1* model fit to data spanning birth to 1.65 years) and juveniles and adults (*Phase 2* fit to data >1.28 years). To ensure both models intersected, some of the same measurements for young juveniles were used to fit both phases of the model. After finding the inflection point at 0.79 years, the models were truncated whereby *Phase 1* included animals between 0 and 0.79 years and *Phase 2* included whales between 0.80 and 30.5 years.



and > 0.79 and < 1.27 years (*Phase 2*) length-at-age predictions for these age ranges using the Gompertz equation should be interpreted with caution. Mean (± *SD*) Gompertz model parameters (from 10,000 bootstrap replicates) were: 1,067.19 ± 19.67 for *A*, 0.93 ± 0.08 for *c*, and – 3.11 ± 0.28 for *k* for *Phase 1*; and 1,362.75 ± 22.88 for *A*, 0.37 ± 0.03 for *c*, and – 0.18 ± 0.03 for *k* for *Phase 2*. The average age of individuals used to fit the *Phase 1* was 0.78 ± 0.62 *SD* and 9.70 ± 6.70 *SD* years for *Phase 2* (Figure 1).

The rapid growth of calves occurred between ages 0 and 0.79 years (*Phase 1*; Figure 2; 288.35 days), and the decelerated growth of older animals occurred from 0.80 to 30 years old (*Phase 2*; Figure 2). Calves were estimated to gain an average of 559 cm (± 43 *SD*) from birth to near weaning (0.79 years), representing 1.94 cm per day (± 0.15) if a constant growth rate is assumed.

Right whales attained 90% of their maximum body length (1,362 cm) at 8 years of age—which is about when females become sexually mature (assuming age at first parturition is 9 years and pregnancy lasts ~12 months; Hamilton, Knowlton, Marx, & Kraus, 1998). Sexual dimorphism appears to occur near sexual maturity based on the measured sizes of males and females between 8.0 and 8.9 years (females measured 1,309 cm ± 0.177 *SD*, *n* = 2, on average and males measured 1,197 cm ± 0.183 *SD*, *n* = 4).

Predicted asymptotic length (~95% of maximum length) occurred at 12 years, which follows findings from previous studies (Fortune et al., 2012). Thus, calves were estimated to more than double their length and to attain almost three-quarters of the asymptotic adult length at 1 year old (when weaning is assumed to occur).

Including sex as a fixed factor yielded a better linear mixed-effects model than a null model that did not distinguish between the body length of adult males and females (Log Likelihood ratio test LRT = 9.7, p = .002). Slopes (repeated-measures ANOVA, $F(1,41) = 10.5$, p = .002) and intercepts (repeated-measures ANOVA, $F(1,41) = 22{,}356.3$, p < .0001) of the model for adult males and females (≥9 years old) differed significantly from one

TABLE 1 Parameter estimates (A, k, c, t_0) (± SE) for the 2-phased growth models (Putter, von Bertalanffy, Gompertz, and logistic; Equations 1–4) for North Atlantic right whales (see "Materials and Methods" for model parameters description), 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 are in centimeters and age is in decimal years. AIC values are shown 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 AIC weight was considered to be the "best" model.

Model	A	k	c	t_0	AIC values	AIC differences	Likelihoods	AIC weights
Phase 1 (0–0.79 years)								
Putter	1,079.037 ± 23.676	0.613 ± 0.025	—	2.336 ± 0.281	540.658	1.748	0.417	0.187
von Bertalanffy	1,071.000 ± 21.260	0.267 ± 0.015	—	2.824 ± 0.301	539.324	0.414	0.813	0.364
Gompertz	1,067.353 ± 20.479	0.923 ± 0.058	−3.075 ± 0.315	—	538.910	0.000	1.000	0.448
Logistic	1,039.574 ± 22.351	—	—	3.328 ± 0.424	551.5023	12.593	0.002	0.001
Phase 2 (0.80–30 years)								
Putter	1,365.000 ± 21.120	0.311 ± 0.017	—	0.149 ± 0.025	1,471.243	0.307	0.858	0.305
von Bertalanffy	1,362.000 ± 20.000	0.114 ± 0.007	—	0.160 ± 0.026	1,471.031	0.095	0.954	0.339
Gompertz	1,360.675 ± 19.501	0.361 ± 0.023	−0.166 ± 0.026	—	1,470.936	0.000	1.000	0.356
Logistic	1,285.664 ± 10.285	—	—	0.639 ± 0.046	1,540.582	69.646	0.000	0.000

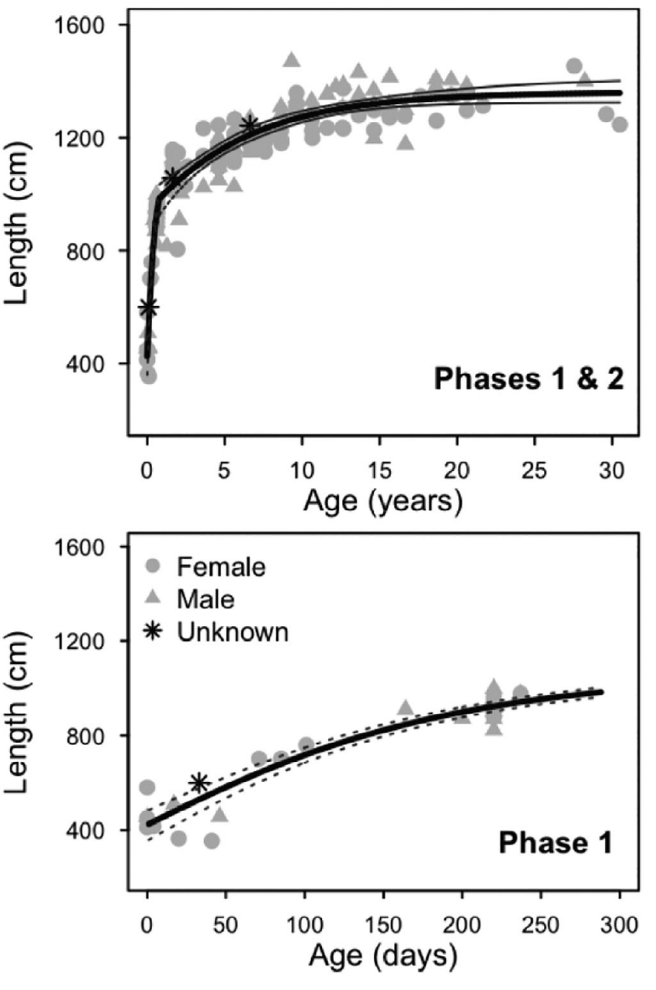


FIGURE 2 Mean 2-phase (*Phase 1* and *2*) and 1-phase Gompertz growth curves for North Atlantic right whales. The 95% confidence intervals (dashed lines) were derived from 10,000 bootstrap replicates. Length-at-age can be calculated using the equations provided in the upper graph with age expressed in years. *Phase 1* includes growth from birth to 0.79 years old, and *Phase 2* describes growth for right whales >0.79 years old. The multiphase Gompertz growth equations based on mean model parameters as determined by bootstrapping were *Phase 1* length = 1,067.35 * exp[−0.923 * exp (−3.08 * Age]) and *Phase 2* length = 1,360.68 * exp[−0.36 * exp (−0.16 * Age)].

another. This was consistent with sexual dimorphism, with adult females (1,345.7 cm ± 61.2 *SD*) being 4% larger on average than adult males (1,291.9 cm ± 56.1 *SD*) (Figure 3).

3.2 | Mass

In terms of body mass, our models show that North Atlantic right whales gain considerable mass during their first year of life, with calves growing an average of ~42 kg/day and weighing over 13 mt after 0.79 years (based on the mean birth mass of 1,022 ± 252 kg and mean inflection mass of 13,206 ± 747 kg; Table 2). Calves near the onset of independence (9.6 months) were 13 times heavier than their birth mass and had attained 47% of the mass of a sexually mature animal. However, this rate of increase in body mass dropped significantly between weaning (~1 year) and sexual maturity (9 years), i.e., ~4.9 kg/day. Mean body mass was an estimated 13.7 mt at weaning, and 28.2 mt when mature.

The mass-to-length relationship did not differ significantly between North Atlantic and North Pacific right whales (two-tailed *t*-test, $t(27) = 2.05$, $p > .05$), although the harvested North Pacific right whales were likely older and bigger animals compared to the North Atlantic right whales in the analyses (Figure 4, Table 3). We found that mass-at-age estimates differed considerably depending on which allometric model was used. For example, mass-at-

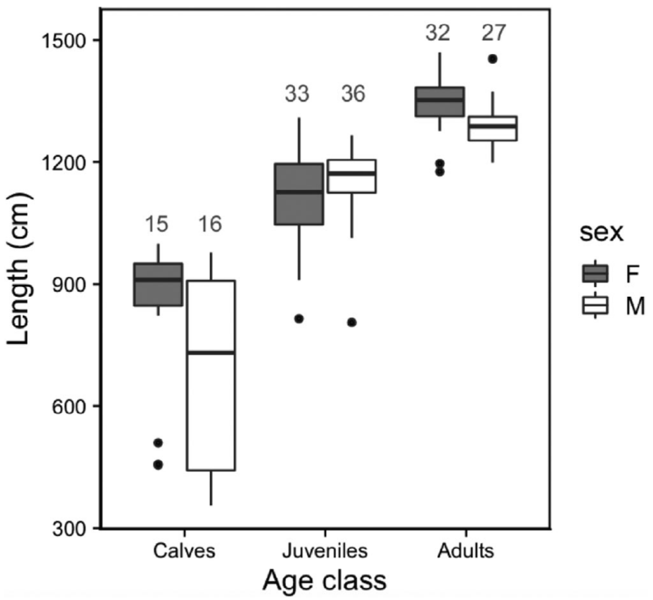


FIGURE 3 Body length (cm) for necropsied and photogrammetrically measured male and female North Atlantic right whales by age class (calves ≤1 year; juveniles >1 and < 9 years; adults ≥9 years). The horizontal black bar represents the medians, the interquartile range is represented by the box, the whiskers indicate nonextreme maximum and minimum values, and outliers are represented by black dots.

age estimates were lower when using an allometric model constructed for North Atlantic right whale necropsy data alone compared to the model that included North Pacific right whale whaling data (Figure 5). Additionally, we found that by increasing the sample size to include North Pacific right whales and adding larger and likely older animals to the data set, we reduced model uncertainty (i.e., smaller 95% confidence limits). Consequently, it appears that including North Pacific right whales results in body mass predictions that are more precise and better represent healthy individuals.

Comparing our new estimates with previous studies (Fortune et al., 2012) shows similar body lengths-at-age whereby updated lengths are 4.6% ± 9.47 *SD* lower than previous estimates on average. However, mass-at-age estimates differ considerably such that updated weights are 12.8% ± 6.03% *SD* heavier on average compared to our earlier predictions. This notable difference in predicted mean body mass is due to excluding masses that were estimated rather than weighed from the North Atlantic right whale necropsy database, the addition of new animals weighed since 2012 and the inclusion of North Pacific right whales that were presumably healthy at their time of death.

In the previous study (Fortune et al., 2012), a significant difference between allometric models for North Pacific and North Atlantic right whales led us to only use North Atlantic right whale weights to predict the age-specific weights of North Atlantic right whales. However, our new allometric model for North Atlantic right whales derived from additional morphometric data (and the removal of estimated weights from the database) did not differ significantly from the North Pacific allometric model. Further support for combining morphometric data from the two species of right whales comes from a recent photogrammetric study that found genetically related *Eubalaena* species share a similar morphology (Christiansen et al., 2020). We consequently combined both data sets into a single model that encompassed a much broader range of ages and sizes of right whales. This new model, built with a more inclusive data set of right whale body sizes and ages, yields estimates that better reflect body weights of healthy right whales.

A second notable difference between our previous and revised growth models for North Atlantic right whales is the placement of the inflection point between *Phase 1* and *Phase 2* growth. Our revised model indicates that it occurs earlier (0.79 years) than we previously estimated (1.05 years), i.e., at 9.6 months rather than at 13 months of age. These differences in length-at-age estimates reflect inclusion of the new data from older animals in our analysis.

TABLE 2 Predicted mean mass and length measurements (± *SD*) for North Atlantic right whales. Daily growth rates in length (cm/day) and mass (kg/day) were calculated using mean model predictions for length-at-age and mass-at-age. Mean allometric model coefficients for *Phase 1* growth were $a = -5.091821 \pm 0.2578327$ and $b = 3.077823 \pm 0.08325852$. Mean parameter estimates for *Phase 2* growth were $a = -5.096379 \pm 0.2592405$ and $b = 3.079408 \pm 0.08360103$.

Age (years)	Mass (kg)	Mass growth (kg/day)	Length (cm)	Length growth (cm/day)
0	1,022 ± 252	0.00	426 ± 33	0.00
0.25	4,553 ± 444	38.70	695 ± 17	2.95
0.5	9,220 ± 594	51.15	875 ± 11	1.97
0.75	12,771 ± 724	38.92	973 ± 10	1.07
0.79	13,206 ± 747	29.79	989 ± 27	1.10
1	13,737 ± 1,270	6.93	996 ± 26	0.25
2	16,026 ± 1,122	6.27	1,048 ± 18	0.14
3	18,236 ± 1,063	6.05	1,093 ± 14	0.12
4	20,319 ± 1,087	5.71	1,132 ± 12	0.11
5	22,244 ± 1,156	5.27	1,167 ± 11	0.10
6	23,994 ± 1,234	4.79	1,194 ± 11	0.08
7	25,564 ± 1,302	4.30	1,218 ± 11	0.07
8	26,959 ± 1,354	3.82	1,239 ± 11	0.05
9	28,187 ± 1,392	3.36	1,256 ± 10	0.05
10	29,262 ± 1,421	2.95	1,272 ± 10	0.04
11	30,197 ± 1,445	2.56	1,285 ± 9	0.04
12	31,007 ± 1,470	2.22	1,296 ± 9	0.03
13	31,707 ± 1,497	1.92	1,306 ± 9	0.03
14	32,310 ± 1,530	1.65	1,315 ± 9	0.02
15	32,829 ± 1,568	1.42	1,322 ± 9	0.02
16	33,274 ± 1,611	1.22	1,328 ± 10	0.02
17	33,656 ± 1,657	1.05	1,333 ± 10	0.01
18	33,983 ± 1,706	0.90	1,338 ± 11	0.01
19	34,263 ± 1,757	0.77	1,342 ± 12	0.01
20	34,504 ± 1,807	0.66	1,345 ± 13	0.01
21	34,709 ± 1,857	0.56	1,348 ± 14	0.01
22	34,885 ± 1,905	0.48	1,351 ± 15	0.01
23	35,036 ± 1,951	0.41	1,353 ± 15	0.01
24	35,166 ± 1,994	0.36	1,355 ± 16	0.01
25	35,277 ± 2,035	0.30	1,357 ± 17	0.01
26	35,372 ± 2,073	0.26	1,358 ± 17	0.00
27	35,453 ± 2,109	0.22	1,359 ± 18	0.00
28	35,523 ± 2,141	0.19	1,360 ± 19	0.00
29	35,584 ± 2,171	0.17	1,361 ± 19	0.00
30	35,635 ± 2,198	0.14	1,362 ± 20	0.00

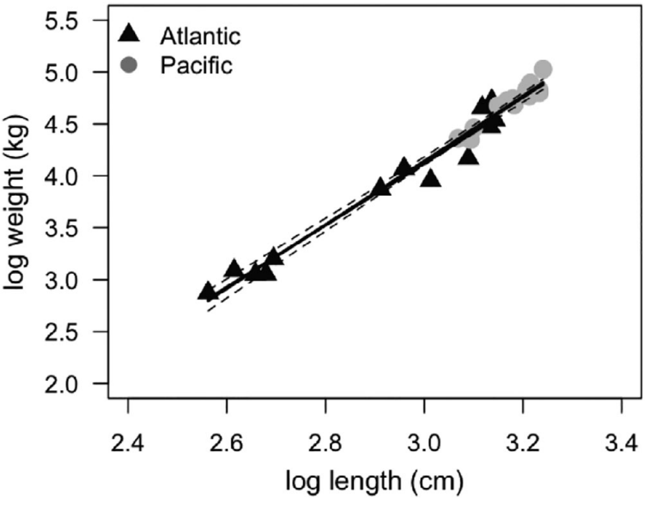


FIGURE 4 Mass-length relationships for North Atlantic (▲) and North Pacific (●) right whales (*Eubalaena glacialis* and *E. japonica*). A linear regression was fit to the log-transformed data for both species: r^2 = 0.98, p < .001. Fitted parameters for North Atlantic and North Pacific right whales (a = 0.000008634158, b = 3.06) were used to model mass-at-age.

3.3 | Biological implications of new growth curves

Our updated growth models indicate that right whales are considerably larger in mass than previously recognized, which means that previously estimated energy requirements have been underestimated for some age-classes on a mass-specific basis. More specifically, sexually mature right whales require more energy per unit body mass than previously thought because their estimated body mass exceeds the upper limits of previous estimates (Fortune et al., 2012). However, the predicted mass of calves and juveniles compare favorably to previous estimates and are within the reported uncertainty. For example, the predicted weights of sexually immature whales (0–8 years) were 8.67% (± 6.91 *SD*) heavier on average than previous estimates. Conversely, sexually mature animals (9–22 years) were 16.3% (± 0.73 *SD*) heavier on average.

Our body mass estimates are also higher than what others have predicted using three-dimensional volumetrics (Christiansen et al., 2019, 2020). For example, Christiansen et al. (2019, 2020) predicted that North Atlantic right whales weighed 940 kg at birth (8% lower than our mean model predictions, but within the 95% CIs). They also predicted that right whales weigh 7,830 kg when weaned, which is 15% lower than our model predictions and outside the 95% CIs (based on a body length of 8.8 m). They further predicted that right whales weigh 20,680 kg at sexual maturity (27% lower than our model predictions and outside the 95% CIs based on the assumption that right whales attain sexual maturity at 9 years of age). Reconciling these differences in predicted mass is challenging because live animals cannot be weighed to validate model predictions and dead animals often include few mature animals and many animals in poor health.

Informative comparisons can be made between model predictions and morphometric measurements obtained from necropsies. For example, our model predictions were just 3% heavier than the weight of a recently born calf (Case number 80; Table 3) that weighed 1,586 kg and measured 495 cm in body length. Another necropsied calf measuring 910 cm weighed 11,772 kg, which was 15% heavier than our mean model predictions (9,984.7 kg), but within the 95% confidence limits. Lastly, an animal approaching sexual maturity measuring 12.29 m and weighing 14,785 kg was considerably underweight compared to our model predictions (24,535 kg). However, this animal was entangled and considerably emaciated at the time of measurement.

Although it is unknown how much weight chronically entangled whales may lose, substantial decreases in blubber thickness have been documented (van der Hoop, Corkeron, & Moore, 2017). Lactating North Atlantic right whale mothers, for example, are believed to lose 25% of their total body weight during the lactation period (Christiansen et al., 2018). As such, the differences between predicted and observed weight values (40% difference in mass) may

TABLE 3 North Atlantic right whale necropsy and Pacific right whale whaling data used in allometric mass models. One animal (No. 27) was weighed without baleen, and others (No. 34, 44, and 49) were weighed in parts and had 6.8% added to their measured mass estimates to account for fluid loss. A fourth animal (No. 45) was likely underweight relative to its body length, and as was entangled in fishing gear, appeared thin to emaciated and was weighed without baleen. Similarly, animals 32 and 120 were also entangled at the time of death and were in poor nutritive condition. Animal No. 80 was also emaciated at the time of necropsy, likely due to the inability to obtain sufficient energy as a nursing calf. Note that the previous analysis (Moore et al., 2007) included body masses for Case No. 28, 29, and 40, which were estimated rather than measured. Furthermore, body masses of Case No. 34, 21, and 32 were corrected after verifying necropsy reports, and Case No. 106, 120, and 139 are new animals that were added to our analysis.

Species	Sex	Length (cm)	Weight (kg)	Case No.	Field ID/EgNo
Atlantic	M	412	1,225	21	MH89-424-Eg
Atlantic	F	1,360	29,700	27	EgNo 1223
Atlantic	M	1,030	9,035	32	EgNo 2366*
Atlantic	F	478	1,136	34	Eg_Jan_02_96 calf
Atlantic	F	455	1,130	42	RKB-1451
Atlantic	F	1,370	52,804	44	EgNo 1014
Atlantic	F	1,229	14,785	45	EgNo2030*
Atlantic	F	910	11,772	49	NY-2680-2001
Atlantic	M	365	749	73	EgNEFL0704
Atlantic	M	495	1,586	80	KLC 022 Eg**
Atlantic	F	1,390	34,600	106	EgNo 2320
Atlantic	F	1,310	45,359	120	MME-16-249Eg*
Atlantic	F	815	7,481	139	IFAW17-182Eg
Pacific	M	1,470	52,870	NA	NA
Pacific	M	1,510	55,250	NA	NA
Pacific	M	1,520	48,250	NA	NA
Pacific	M	1,610	67,770	NA	NA
Pacific	M	1,640	78,500	NA	NA
Pacific	M	1,700	65,760	NA	NA
Pacific	M	1,710	67,240	NA	NA
Pacific	M	1,240	22,250	NA	NA
Pacific	M	1,710	63,490	NA	NA
Pacific	F	1,170	22,870	NA	NA
Pacific	F	1,630	58,590	NA	NA
Pacific	F	1,660	63,130	NA	NA
Pacific	F	1,710	63,490	NA	NA
Pacific	F	1,740	106,500	NA	NA
Pacific	F	1,260	28,920	NA	NA
Pacific	M	1,410	47,560	NA	NA

Note: For reference purposes, animal FieldID/EgNo marked with one asterisk (*) denote animals that were entangled and underweight and animals with two asterisks (**) were not entangled but were underweight at the time of death presumably due to issues with energy acquisition while nursing.

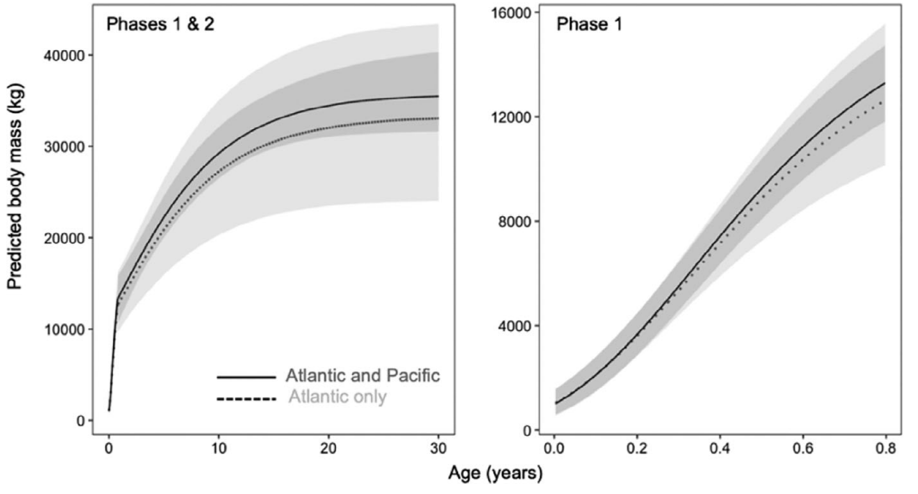


FIGURE 5 Predicted body mass (kg) at age (years) for North Atlantic right whales using the bootstrapped multiphase Gompertz length-at-age predictions (n = 10,000 replicates) and an allometric mass-at-length model that was constructed using (1) North Atlantic right whale necropsy (Atlantic only) data and (2) North Pacific right whale whaling data and North Atlantic right whale data (Atlantic and Pacific). We bootstrapped the model to generate 10,000 predictions of mass-at-age and sorted the predicted values into 95% quartiles by ordering the bootstrap replicates of mass-at-age into 2.5% and 97.5% quartiles. The light gray shaded region represents the 95% confidence limits for the Atlantic only model and the smaller, dark gray region reflects the confidence limits for the Atlantic and Pacific model.

be attributed to compromised body condition caused by lactation, reduced feeding efficiency, and increased energetic costs associated with being entangled (van der Hoop et al., 2017), and may provide insight into the extreme physiological consequences of chronic entanglement.

The comparatively low predicted body weights previously estimated for mature North Atlantic right whales were likely due to biases in the source data used to establish the earlier allometric relationship between body length and mass. Several of these data came from underweight North Atlantic right whales that were emaciated and in poor overall health due to entanglement in fishing gear (Sharp et al., 2019). Supplementing this database with lengths and weights of North Pacific right whales recorded during commercial whaling provided a more comprehensive set of measurements of healthy-sized individuals.

Bigger body sizes require more energy for growth and maintenance of mass. In our case, our revised growth model has little consequence for the energy needs of young animals (e.g., predicted mean mass gains were 33.9 kg/day for previous models and are 34.8 kg/day for the updated equations between 0 and 1 year). However, the considerably greater body mass of adult right whales suggests they have higher metabolic demands. It appears, for example, that sexually mature right whales (9 years) require 12.9% (or 82.53 MJ) greater food intake per day to meet their basal metabolic costs. Assuming the costs associated with swimming (or active metabolism) are twice maintenance costs, the energy needed to meet active and basal metabolism for a 9-year-old animal will be 25.8% higher in total than previously predicted. In contrast, the basal metabolisms of older individuals between 20 and 22 years are 12% higher than previously estimated (i.e., 760.13 MJ/day for a 22-year-old animal based on the new model using an average mass of 34,885 kg compared with 662.03 MJ/day using the previous model assuming a mean mass of 26,639 kg). Consequently, the new predictions of body mass result in elevated metabolic rates, lending further support to certain ages of right whales being more vulnerable to nutritional stress than others. This is particularly important for reproductively mature females, who may be able to withstand short periods of reduced feeding if they can replenish their blubber reserves during the postlactation period (Christiansen et al., 2018; Miller et al., 2011).

Improved estimates of body mass models contribute to the care and conservation of North Atlantic right whales. Ship strikes (Kite-Powell, Knowlton & Brown, 2007; Vanderlaan & Taggart, 2007) and fishing gear entanglements (Caswell, Fujiwara, & Brault, 1999; Clapham, Young, & Brownell, 1999; Hamilton & Kraus, 2019; Johnson et al., 2005) are the leading causes of mortality for this endangered species. Consequently, accurate estimates of right whale mass are needed to help mitigate anthropogenic mortality. As an example, an adult right whale 9 years old, weighing 23.4 tons, and not emaciated due to chronic entanglement (Barratclough et al., 2014) would require 2.34 kg (i.e., 0.1 mg/kg; van der Hoop et al., 2014) of anesthetic (butorphanol and midazolam) to facilitate disentanglement by reducing swimming speed and evasiveness (Noren, 2011). Conversely, we predict that a whale of the same age, that is 16.9% heavier (28,187 kg) than previously predicted, would require 2.82 kg of sedation. These revised mass estimates will enable more accurate drug dosages to be determined and administered to animals prior to disentanglement.

A limitation of our earlier growth equations was that veterinarians needed to extrapolate beyond the upper age-limits of the model (i.e., 22 years). However, the additional data used to derive the updated growth curves means that dosages can now be determined with greater confidence for older animals (between 22 and 30 years). Overall, our updated mass-at-age predictions will assist in determining the correct dosages of medication for right whales that need to be sedated or treated for infections caused by entanglement and ship strike wounds.

3.4 | Conclusions

Adding new body size data, correcting errors in some of the previous records, and using an improved allometric model to predict mass that includes North Pacific right whale measurements from whaling records has yielded better models of body growth for North Atlantic right whales. The new models show that right whales are on average larger than originally predicted and that the inflection point in their 2-phased growth occurs earlier in development than previously thought (i.e., at ~10 months compared with 13 months; Fortune et al., 2012). This suggests that calves experience a deceleration in growth prior to weaning (assuming whales wean after 12 months). The revised growth models show that right whale calves experience rapid growth between 0 and 9.6 months, and decelerated growth between 9.7 months and 9 years.

Our revised growth models have implications for the conservation and management of North Atlantic right whales. Most notably, they indicate that energetic requirements associated with basal and active metabolism are likely higher than previously believed—particularly for adult animals (9 years) and juveniles that are approaching sexual maturity. These are important findings because juveniles and lactating North Atlantic right whales have the highest predicted daily energy needs, and may experience periods of food shortage based on comparisons with prey ingestion (Fortune, Trites, Mayo, Rosen, & Hamilton, 2013). Consequently, the energy deficit incurred by these demographic groups may be greater than originally thought. They also indicate that higher dosages of sedatives and antibiotics than originally predicted should be used to treat wounded animals that are not emaciated due to chronic entanglement.

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AUTHOR CONTRIBUTIONS

Sarah Fortune: Conceptualization; formal analysis; investigation; methodology; project administration; visualization; writing-original draft; writing-review and editing. **Michael Moore:** Data curation; funding acquisition; methodology; project administration; writing-review and editing. **Wayne Perryman:** Conceptualization; data curation; funding acquisition; methodology; writing-review and editing. **Andrew Trites:** Investigation; resources; supervision; writing-review and editing.

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