Current Biology

Report

Decreasing body lengths in North Atlantic right whales

Highlights

- Whales with severe entanglements in fishing gear are stunted
- Whales whose mothers were entangled while nursing are stunted
- Body lengths have been decreasing since 1981
- Cumulative impacts in addition to entanglements may contribute to stunted growth

Authors

Joshua D. Stewart, John W. Durban,
Amy R. Knowlton, ...,
Wayne L. Perryman, Carolyn A. Miller,
Michael J. Moore

Correspondence

joshua.stewart@noaa.gov

In brief

Stewart et al. examine trends in body lengths in endangered North Atlantic right whales using aerial photogrammetry. They show that whales that have experienced severe entanglements in fishing gear are shorter than whales with no documented entanglements, and that body lengths of right whales have been decreasing over the past four decades.

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Report

Decreasing body lengths in North Atlantic right whales

Joshua D. Stewart,[1,7,8,*] John W. Durban,[2,3] Amy R. Knowlton,[4] Morgan S. Lynn,[2] Holly Fearnbach,[5] Jacob Barbaro,[2] Wayne L. Perryman,[2] Carolyn A. Miller,[6] and Michael J. Moore[6]
[1]National Research Council Postdoctoral Fellow for Marine Mammal and Turtle Division, Southwest Fisheries Science Center, National Marine Fisheries Service, National Oceanic and Atmospheric Administration, La Jolla Shores Drive, La Jolla, CA, 92037, USA
[2]Marine Mammal and Turtle Division, Southwest Fisheries Science Center, National Marine Fisheries Service, National Oceanic and Atmospheric Administration, La Jolla Shores Drive, La Jolla, CA, 92037, USA
[3]Southall Environmental Associates, Inc., Soquel Dr., Aptos, CA, 95003, USA
[4]Anderson Cabot Center for Ocean Life, New England Aquarium, Boston, MA, 02110, USA
[5]Marine Mammal Research Program, SR3, SeaLife Response, Rehabilitation and Research, S 216th St., Des Moines, WA, 98198, USA
[6]Department of Biology, Woods Hole Oceanographic Institution, Woods Hole Rd., Woods Hole, MA, 02543, USA
[7]Twitter: @NOAAFish_WCRO
[8]Lead contact
*Correspondence: joshua.stewart@noaa.gov

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SUMMARY

Whales are now largely protected from direct harvest, leading to partial recoveries in many previously depleted species.[1] However, most populations remain far below their historical abundances and incidental human impacts, especially vessel strikes and entanglement in fishing gear, are increasingly recognized as key threats.[2] In addition, climate-driven changes to prey dynamics are impacting the seasonal foraging grounds of many baleen whales.[2] In many cases these impacts result directly in mortality. But it is less clear how widespread and increasing sub-lethal impacts are affecting life history, individual fitness, and population viability. We evaluated changes in body lengths of North Atlantic right whales (NARW) using aerial photogrammetry measurements collected from crewed aircraft and remotely operated drones over a 20-year period (Figure 1). NARW have been monitored consistently since the 1980s and have been declining in abundance since 2011 due primarily to deaths associated with entanglements in active fishing gear and vessel strikes.[3] High rates of sub-lethal injuries and individual-level information on age, size and observed entanglements make this an ideal population to evaluate the effects that these widespread stressors may have on individual fitness. We find that entanglements in fishing gear are associated with shorter whales, and that body lengths have been decreasing since 1981. Arrested growth may lead to reduced reproductive success[4,5] and increased probability of lethal gear entanglements.[6] These results show that sub-lethal stressors threaten the recoveries of vulnerable whale populations even in the absence of direct harvest.

RESULTS AND DISCUSSION

We combined age and length data collected from crewed aircraft in 2000–2002 and from remotely operated drones in 2016-2019 in a growth model mirroring a previous analysis of the 2000–2002 data.[7] We modified the 2-phase Gompertz growth equation to include model-estimated effects on asymptotic length for: (a) birth year, (b) duration of entanglements with attached fishing gear, (c) whether a whale's mother experienced a severe entanglement injury while nursing that whale, and (d) the number of lactation events a female whale experienced, which is known to be one of the most significant energetic expenditures for right whales.[8] We considered the cumulative effects of covariates from birth until age 10 (or until the time of measurement if it occurred prior to age 10), as the expected length at age 10 is more than 95% of the estimated asymptotic length and constraints to growth after that point would be unlikely to measurably affect whale lengths.

Across all years we collected 202 length measurements of 129 individual whales: 133 measurements from crewed aircraft and 69 from remotely operated drones. 76 whales were measured once, 36 twice (in separate years), 14 three times, and 3 four times. The ages of measured whales ranged from <1 to 37 years old, including whales born from 1981 to 2019. Eleven whales in our dataset were observed with attached gear; 8 of those whales were measured once, 2 were measured twice, and 1 was measured four times. Gear entanglement durations (midpoints) ranged from 65 to 334 days. Seven measured whales had known severe maternal entanglement injuries; 1 of those whales was measured twice. No whales in our dataset had both a maternal entanglement injury and an entanglement with attached gear. Nine measured whales had one lactation event, and 1 whale had two lactation events prior to age 10.

Birth year had the greatest effect on the estimated asymptotic length of NARW (99.8% of posterior distribution <0). The estimated

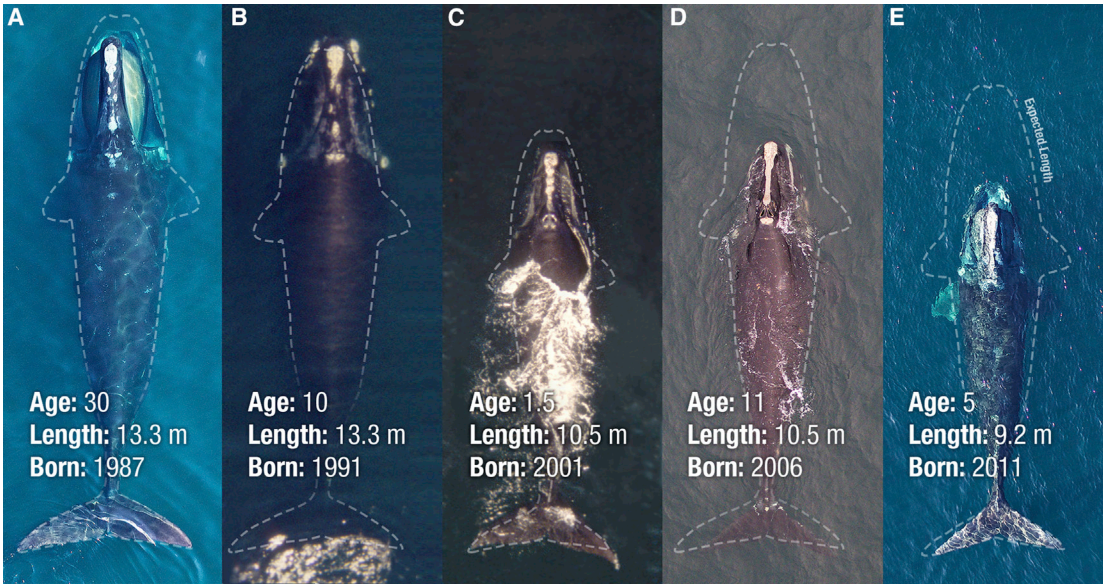

Figure 1. Stunted North Atlantic right whales

A scaled photo illustration comparing the body lengths of (A) Whale 1703, imaged in 2017 at age 30 using a remotely operated drone, (B) Whale 2145, imaged in 2001 at age 10 from a crewed aircraft, (C) Whale 3180, imaged in 2002 at age 1.5 from a crewed aircraft, (D) Whale 3617, imaged in 2017 at age 11 using a drone, and (E) Whale 4130, imaged in 2016 at age 5 using a drone. The dashed outline in each panel represents the median model-estimated body length for a whale of the same age born in 1981 with no history of entanglements or maternal entanglements. Note the entanglement scarring around the caudal peduncle in (D). Figure design by Madeline Wukusick.

effect of birth year was an asymptotic length 0.025 m (95% credible intervals 0.01–0.04) shorter than the baseline asymptotic length per year born after 1981. With the maximum effect of birth year applied, a whale born in 2019 is expected to reach a maximum length approximately 1 m shorter than a whale born in 1981 (Figure 2). This corresponds to a 7.3% decline in maximum body length. Known entanglements of a whale with attached gear (97.4% of posterior distribution <0) and entanglements of its mother during nursing (99.7% of posterior distribution <0) also had negative effects on expected maximum length, of approximately −0.64 m (4.7% length reduction) and −0.69 m (5.0% length reduction), respectively. The effect of entanglement with attached gear was applied as a continuous effect, so a whale with an entanglement duration that is half the maximum duration is expected to experience half of that negative effect on asymptotic length, or an expected asymptotic length 0.32 m shorter than baseline. There was no significant effect of the number of lactation events (61.2% of posterior distribution >0) on expected maximum length of right whales (Figure 3). The estimates of error around the model-estimated mean length-at-age were different across altimeter types. GPS altimeter measurements had the highest error (median 0.63, 95% CI 0.26–1.01 m), followed by laser altimeter measurements (0.52, 0.19–0.77 m) and radar altimeter measurements (0.27, 0.01–0.48 m).

Our results demonstrate that NARW born in recent years have experienced stunted growth, and over the same period that we detected this effect they have experienced increasing rates of entanglement.[3] As a result, NARW appear to have less energy to devote to early growth. A portion of the estimated length reduction was directly attributable to entanglements, but the effect size of entanglements was smaller than the effect size of birth year. We posit that the birth year effects on asymptotic length represent the cumulative effects of dynamic and hard-to-observe impacts on individual NARW that may include unrecorded entanglements, shifting prey seascapes, vessel strikes, and foraging interference from vessel traffic (Figure 4). For example, entanglements of NARW are imperfectly observed, and many whales have evidence of entanglement injuries without direct observations of attached gear; in these scar-only cases it is impossible to determine the duration of those entanglements.[9] Even direct observations of attached gear events have only approximate entanglement durations (we considered the midpoint between minimum and maximum possible duration of each entanglement) and there is almost certainly a large amount of noise introduced into our analyses as a result of these imperfect observations. Consequently, while our analyses detected a negative effect of entanglements on whale length, we cannot rule out a larger true effect size than our estimate; for example, if entanglements that were not recorded in our dataset contributed to restricted growth that was instead reflected in birth year effects.

The abundance of *Calanus finmarchicus*, a primary copepod prey item for NARW, has fluctuated in the Gulf of Maine over the past 40 years (Figure 4), apparently driving reproductive output in the NARW population.[11] *C. finmarchicus* is a subarctic species, and its distribution is expected to shift poleward as the North Atlantic warms,[12] leading to projected abundance declines in the Gulf of Maine.[13] There has not been a steady decline in *C. finmarchicus* abundance coincident with the decreasing NARW body lengths reported here. However, in the past decade, sighting rates of NARW on their typical foraging grounds have declined, and the timing and geographic distribution of peak

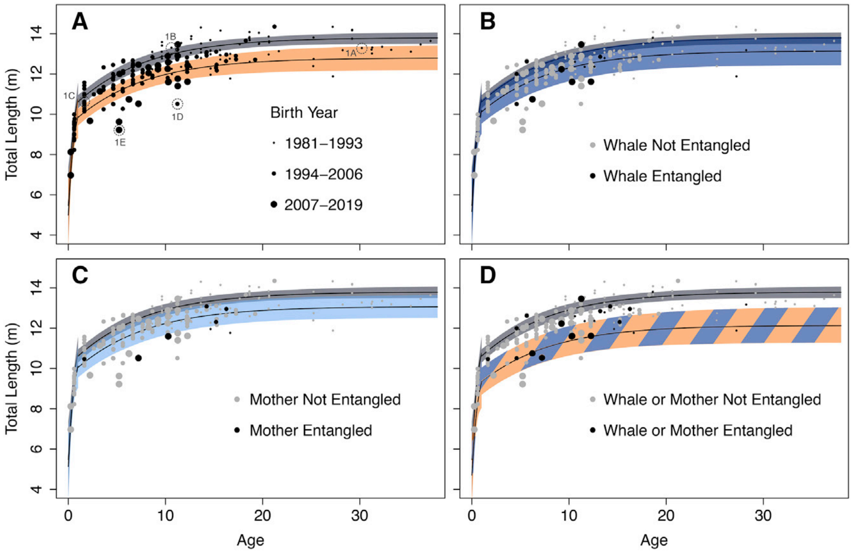

Figure 2. Growth curves for North Atlantic right whales

The gray curve in each panel represents the expected length at age for a typical NARW born in 1981 that experiences no entanglements and does not have an entangled mother while nursing. Solid lines represent median estimates and colored curves represent 95% Bayesian credible intervals for the mean length at age of whales with covariate effects applied.

(A) The expected length at age for a typical whale born in 2019 that experiences no entanglements and does not have an entangled mother while nursing (orange curve). Black points are observed lengths of known-age whales, with point size indicating the birth year of the whale (in three ranges for clarity; all panels). The dashed circles and corresponding labels indicate the whales pictured in Figure 1 panels A–E.

(B) The expected length at age for a typical whale born in 1981 that experiences a severe attached-gear entanglement (maximum effect size of a 334-day entanglement duration applied; dark blue curve). Light gray points are whales with no observed attached-gear entanglements; black points are whales with observed attached-gear entanglements. Note that duration of entanglement is not indicated.

(C) The expected length at age for a typical whale born in 1981 whose mother is entangled while that whale is nursing (light blue curve). Black points are whales whose mothers were detected with a severe entanglement injury while the measured whale was a nursing calf.

(D) The expected length at age for a typical whale born in 2019 that experiences a severe entanglement (maximum effect size; orange and blue striped curve). In other words, the cumulative effects of birth year and entanglements. Black points are whales with observed attached-gear entanglements or whales whose mother was known to have a severe entanglement injury while the measured whale was nursing, as these effect sizes were comparable. See model diagnostics in Figures S1–S3.

C. finmarchicus densities have been shifting.[14] These changes may indicate a deteriorating foraging environment in the Gulf of Maine. Given that NARW are dependent on hyper-dense patches of copepods to maximize foraging efficiency,[15] coarse regional indices of *C. finmarchicus* abundance (e.g., Figure 4) may not adequately represent foraging conditions that could affect growth rates. Other anthropogenic factors such as increasing vessel noise could also be interfering with foraging behavior and restricting NARW growth[16] (Figure 4).

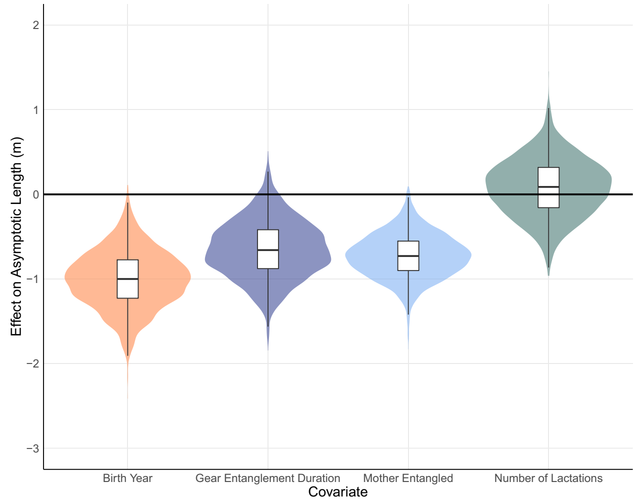

Figure 3. Covariate effects on asymptotic length of North Atlantic right whales

Violin plots represent the Bayesian posterior distributions of the estimated effect (in meters) of each covariate on the asymptotic length parameter in the 2-phase Gompertz growth equation. The interior boxplots represent the median effect size (horizontal black line), the 50% posterior density intervals (white box) and the 95% credible intervals (vertical black line). The effects of birth year, gear entanglement duration, maternal entanglement, and number of lactations are scaled to the maximum effect size as the minimum covariate values for each of these is zero. We considered an effect significant if >95% of posterior draws were below (or above) zero.

In baleen whales, larger maternal size and body condition are associated with faster calf growth rates and larger calves.[4,5] Decreasing body size may therefore be associated with smaller calves and lower calf survivorship, or potentially delayed first calving and lower reproductive success in females. NARW exhibit generally poor body condition compared to other populations of right whales,[17,18] which could contribute to synergistic negative effects where females in poor condition produce smaller calves that ultimately reach smaller maximum sizes, further contributing to reduced calf growth and declining calf condition. In addition, our results suggest that sub-lethal entanglements constrain overall body size in NARW, which may in turn make them less resilient to future entanglements by reducing their absolute energetic reserves and increasing the probability of a lethal entanglement.[6]

Mortality from vessel strikes and entanglements in fishing gear are thought to be a major driver of the current NARW population decline,[3] but the observed changes in body lengths also indicate a troubling trend that may have further negative effects on population viability in this critically endangered species, with chronic sub-lethal health effects slowing growth and potentially reducing reproductive success. Changes in body size can also be a leading indicator of population collapse,[19–21] further highlighting the ongoing and compounding threats to the NARW population. Implementing solutions to reduce entanglements and other anthropogenic impacts could give North Atlantic right whales increased

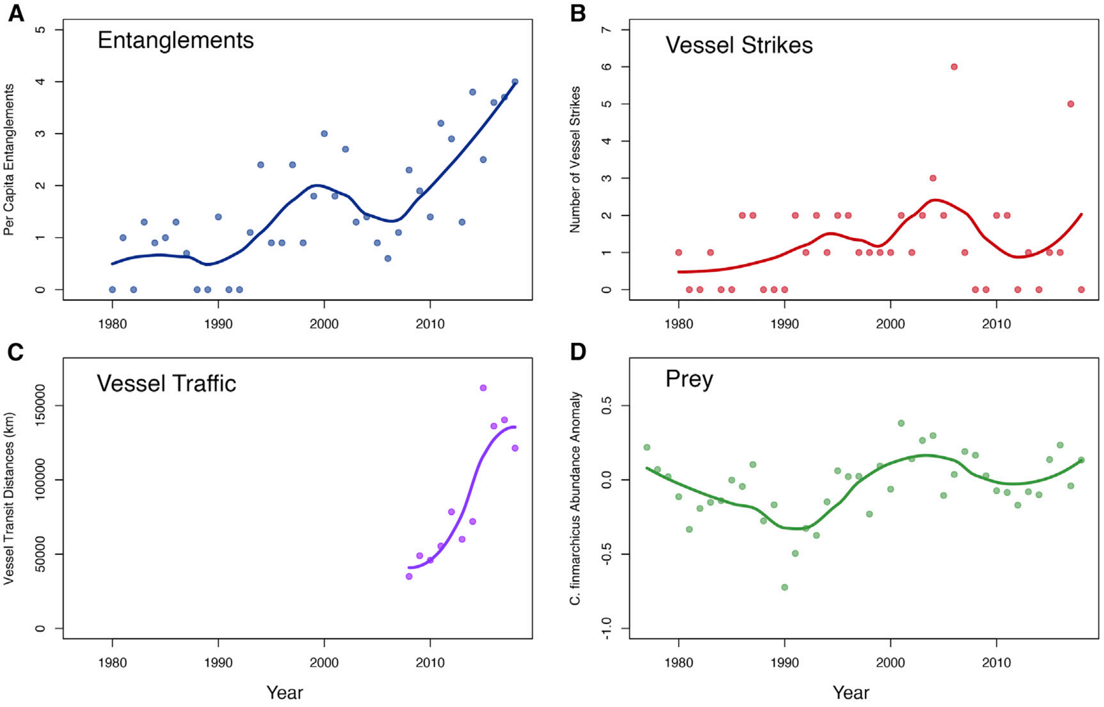

Figure 4. Possible cumulative impacts affecting right whale growth

Time series of potential stressors that could affect right whale energy budgets and foraging success.

(A) Number of new serious entanglements (attached gear or severe injuries) observed each year, standardized by the number of individual whales observed during field surveys; source ref.[9]

(B) Number of vessel strikes resulting in blunt trauma or deep lacerations observed each year. Note that vessel strikes are raw counts and not per capita rates; source ref.[10]

(C) Cumulative vessel transit distances (in kilometers) within three special management areas that are NARW foraging hotspots: Cape Cod Bay, Race Point, and Great South Channel; source NMFS Right Whale Vessel Speed Rule Assessment, June 2020.

(D) *Calanus finmarchicus* abundance anomalies for the Gulf of Maine; source NOAA Ecosystem Dynamics and Assessment Branch ecodata. The lines in each panel are a loess smooth to the annual data.

resilience to adapt to changing prey dynamics and other climate-related impacts while maintaining population viability.

Changes to life history traits, such as growth rates and age or size at maturity, are well documented in heavily exploited species (in particular fishes).[22] Body size changes in mammals (both positive and negative) are also expected under changing climate conditions.[23,24] Our results suggest that humans are impacting the demographic characteristics of endangered and protected marine mammals through indirect and incidental pressures on vulnerable populations. Entanglements in fishing gear are a growing problem for migratory baleen whale species and a wide variety of marine mammals.[25] Extensive survey effort for the NARW population allowed the sub-lethal effects of entanglements to be directly (if imperfectly) estimated, but it is likely that other marine mammal species that experience chronic entanglements are being similarly affected.

STAR★METHODS

Detailed methods are provided in the online version of this paper and include the following:

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SUPPLEMENTAL INFORMATION

Supplemental information can be found online at https://doi.org/10.1016/j.cub.2021.04.067.

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AUTHOR CONTRIBUTIONS

J.D.S., J.W.D., and M.J.M. conceived the analysis; J.W.D., M.J.M., and H.F. conceived the study; J.W.D., M.J.M., A.R.K., H.F., and W.L.P. obtained funding for data collection; J.W.D., M.S.L., M.J.M., H.F., J.B., A.R.K., C.A.M., and W.L.P. collected and processed data; J.D.S. analyzed data and drafted the manuscript; all authors edited and revised the manuscript.

DECLARATION OF INTERESTS

The authors declare no competing interests.

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STAR★METHODS

KEY RESOURCES TABLE

REAGENT or RESOURCE	SOURCE	IDENTIFIER
Software and algorithms		
R	The R Project for Statistical Computing	V4.0.0
Just Another Gibbs Sampler (JAGS)	Plummer 2013	V4.2.0
Other		
126mm Reconnaissance Camera	Chicago Aerial	KA-76A
Remotely Operated Hexacopter	Aerial Imaging Solutions	APH-22
Digital Camera System	Olympus	E-PM2; 25mm Zuiko Lens

RESOURCE AVAILABILITY

Lead Contact

Further information and requests for resources should be directed to and will be fulfilled by the lead contact, Joshua Stewart (joshua.stewart@noaa.gov)

Materials Availability

This study did not generate new unique reagents

Data and Code Availability

All data and R code to replicate these analyses are available at http://github.com/stewart6/NARW-Growth.

EXPERIMENTAL MODEL AND SUBJECT DETAILS

Aerial photogrammetry measurements were collected from free-ranging North Atlantic Right Whales under NOAA National Marine Fisheries Service permits 21371, 17355 and 17355-01.

METHOD DETAILS

From 2000-2002, we used a fixed-winged, crewed airplane to collect aerial images of North Atlantic right whales (NARW) in the Bay of Fundy, Canada.[7] A 126mm format military reconnaissance camera captured images on film from approximately 250 m altitude. From 2016-2019 we flew a remotely controlled hexacopter drone at altitudes of approximately 50 m to collect images of NARW in Cape Cod Bay, U.S.A,[17] taking digital images using a 25mm lens mounted on an Olympus camera with micro 4/3 sensor.[26] Both methods achieved flat images that were undistorted across the entire frame. We collected altitude measurements using radar altimeters in 2000-2002,[7] drone GPS in 2016[17] and a laser altimeter[27] mounted on the vertical gimbal of the drone camera in 2017-2019. We established length estimates from image measurements by using altimetry data to convert image sensor distances to distances on the real scale.[7,26] We only selected images for use in length measurements when a whale was fully visible and appeared to be in flat orientation parallel to the water surface. In general, variability in repeated-measurements of total lengths of cetaceans is low, with average coefficients of variation typically ranging from approximately 1%–3%.[27–29] While altimeter inaccuracies can lead to both positive and negative length measurement errors, any movement or curvature of an animal will result in the animal appearing shorter from above than it actually is. To minimize this negative bias, and following previous studies using aerial photogrammetry to estimate cetacean lengths, we selected the longest measurement of each whale in cases of multiple measurements of an individual within a single sampling season[7,28,30]

We individually identified whales from aerial images based on their callosity patterns,[31] with known ages and birth years for individual whales provided by the Right Whale Consortium.[32] Directly observed entanglements with attached gear, as well as indirect evidence of entanglements (e.g., scarring) have been recorded for NARW since 1980.[9,32] Scarring patterns can provide approximate information about the severity of an entanglement injury (minor, moderate or severe),[33] but it is impossible to establish the duration of an entanglement based on scarring alone. Entanglements with attached gear provide quantitative—although still imperfect—information about entanglement duration. We estimated the minimum and maximum duration of entanglements with attached gear based on a whale's sighting records.[33] The minimum duration was calculated as the number of days between the date that a whale was first observed with gear attached and the date that a whale was last observed with gear attached. If a whale was first seen with attached gear on the same day that the gear was removed by a disentanglement team or shed by its next sighting, the minimum duration was recorded as one day. The maximum duration was calculated as the number of days between the most recent date that a whale was observed without attached gear prior to the first observation with attached gear, and the first observation without attached gear after the last observation with attached gear. For example, consider a whale that was seen on February 1st with no attached gear, March 10th with attached gear, May 1st with attached gear, and July 10th with no attached gear. The minimum entanglement duration would be March 10th – May 1st (52 days), and the maximum entanglement duration would be February 1st – July 10th (160 days). To account for the uncertainty in true entanglement duration, we used the midpoint between the minimum and maximum durations as our best estimate of entanglement duration. Growth rates in NARW slow considerably after age 10[7], so we used mid-point entanglement durations for any measured whale in our aerial photogrammetry dataset seen with attached gear during the first 10 years of life to represent a cumulative entanglement burden during early growth. If a length measurement was taken prior to age 10, we used the entanglement duration midpoint prior to that measurement. Entanglement duration was included as a continuous effect on asymptotic length (see model description below).

Maternal size and condition have been demonstrated to substantially impact calf growth rates in several populations of baleen whales, including southern hemisphere right whales.[4,5] This suggests that entanglements of a female with a dependent, nursing calf could affect calf growth if maternal energy stores are lost to excess drag from an entanglement.[34] In our dataset of aerial photogrammetry measurements, we had no records of measured whales whose mothers had an observed entanglement with attached gear while the measured whale was a nursing calf. However, there were three records of measured whales whose mothers were seen with attached gear that first appeared while the measured whale was < 1 year old and likely still nursing and eight records of measured whales whose mother was detected with attached gear or severe injuries that may have occurred when the calf was < 1 year old.[32] For measured whales whose mother had evidence of a severe entanglement injury or attached gear known to or likely to have occurred while the measured whale was nursing, we included a fixed effect of maternal entanglement on asymptotic length.

Lactation is an extremely costly life history event for right whales.[8] The energetic burden of supporting dependent calves could in theory reduce the amount of energy a female whale can devote to its own growth. We therefore considered the number of lactation events that a whale experienced[32] prior to age 10 as a continuous effect on the expected asymptotic length of that whale. If a whale was measured prior to age 10, we considered the number of lactation events experienced prior to measurement, similar to our handling of entanglement durations. For entanglement duration and number of lactation events, we scaled the covariate values associated with each measured whale to 1 by dividing the observed covariate by the maximum covariate value.

QUANTIFICATION AND STATISTICAL ANALYSIS

We based our growth model on the two-phase Gompertz growth function that was fit previously to age and length data for North Atlantic right whales collected between 2000 and 2002:[7]

$$S_t = Ae^{-ce^{-kt}}$$

where S is the expected length at age t, A is asymptotic length, c is the constant of integration, and k is the growth rate. This equation is fit separately in two phases to whales < 1 year old (Phase 1) and > 1 year old (Phase 2). We modified this equation to apply covariate effects to asymptotic length, such that:

$$S_{t,i} = A_i e^{-ce^{-kt}}$$

$$A_i = \widehat{A} + O_i$$

$$O_i = \sum_{j=1}^{n} Cov.Eff_{j,i}$$

$$Cov.Eff_{j,i} \sim N[Cov_{j,i} * \beta_j, \sigma_j]$$

where S is the expected length at age t for individual i, A is expected asymptotic length for individual i, $\widehat{A}$ is the asymptotic length shared across all whales before covariate effects are applied, and O is the asymptotic length offset for individual i. Cov is the covariate j (e.g., birth year, entanglement duration, etc.) experienced by whale i, and β is the model-estimated effect of covariate j. We introduce process error by allowing the estimated covariate effect $Cov.Eff$ to vary around the expected covariate effect with an independently estimated standard deviation σ for each covariate j. O is then calculated by summing the covariate effects $Cov.Eff$ for each individual *i.* We chose to apply covariate effects to asymptotic length because growth rate and asymptotic length are typically highly correlated in growth models, making it inappropriate to apply the same covariate to both parameters simultaneously. Whales are expected to have determinate growth due to the fusing of growth plates,[35,36] and we therefore applied covariate effects to asymptotic length rather than growth rate. This was based on the assumption that reduced early growth would lead to a truncated maximum attainable length for an individual, rather than slower growth that could eventually result in a similar maximum length to unaffected whales. In other words, we assume that the length a whale reaches by age 10-15 is likely to be close to the maximum size that whale can achieve. We applied the same model-estimated offset on asymptotic length to both growth phases. Our limited sample size of whales age < 1 (less than 10% of measured whales) contained no whales with attached gear or known maternal entanglements, and all but four measured calves were born in 2001, making the estimation of independent covariate effects for each growth phase impossible.

Previous analyses of NARW growth incorporated lengths from both aerial photogrammetry and necropsies from stranded whales. We excluded necropsied individuals from our analysis because we were investigating potentially small changes in body length as a result of covariate effects. Changes in body length are known to occur in stranded whales that have been towed to shore (stretching), and correction factors for these stretching effects are approximate.[7] As a result, our sample size of whales < 1 year old was smaller than in previous studies, so we applied an informative prior to $\widehat{A}$, *k,* and *c* for both Phase 1 & 2 based on the estimated parameters from the same Gompertz 2-phase growth equation fit using length data from both photogrammetry and necropsies:[7]

$$\widehat{A}_{\mathrm{Phase1}} \sim N[11.93,\ 2.83]$$

$$\widehat{A}_{\mathrm{Phase2}} \sim N[13.82, 0.28]$$

$$k_{Phase1} \sim N[2.325,\ 1.25]$$

$$k_{Phase2} \sim N[0.13,\ 0.03]$$

$$C_{Phase1} \sim N[1.017,\ 0.195]$$

$$\mathrm{C}_{\mathrm{Phase2}} \sim N[0.33,\ 0.02]$$

where each prior is normally distributed around a mean with standard deviation. This allowed parameter estimates to depart from the provided informative priors if there was sufficient information in the data to estimate a different value, but helped align baseline estimates of growth parameters with previous studies if there were insufficient data to produce a new estimate (see Figure S1 & Table S1).

To account for different aerial photogrammetry platforms that used different methods to calculate aircraft altitude (radar altimeter, GPS altimeter, and laser altimeter), we applied three separate model-estimated error terms to individual observations of length data, such that:

$$s_{t,i} \sim N[S_{t,i}, \sigma_{pt,i}]$$

where *s* is the measured length of individual *i* at age *t*, which is normally distributed around the expected length *S* of individual *i* based on its age *t* and applied covariate effects, with a unique standard deviation σ for each photogrammetry platform *p*, which is applied based on the platform used to measure individual *i* at time *t*.

We constructed and fit these models using the JAGS Bayesian modeling software[37] run via R.[38] We ran three chains, each of 100,000 iterations with a burn-in period of 50,000 iterations and a thinning interval of 50, for a total of 3,000 draws from the posterior distribution. Model convergence was determined based on visual inspection of chains and $\widehat{R}$ values < 1.05, which indicates that an infinite number of iterations would lead to potential reduction of posterior intervals by less than 5%.[39] We considered covariate effects to be significant if 95% of posterior draws for the estimated effect were < 0 for negative effects or > 0 for positive effects. To determine whether the model was specified appropriately, we performed posterior predictive checks on all 202 length measurements in our dataset. We applied the model-estimated covariate effects to the recorded covariates for each whale, and sampled from those mean values using the model-estimated observation error terms specific to the platforms used to image each whale. We then compared observed values to the 95% posterior prediction intervals (Figures S2 and S3).