



# Larger females have more calves: influence of maternal body length on fecundity in North Atlantic right whales

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**ABSTRACT:** North Atlantic right whales (NARW) are critically endangered and have been declining in abundance since 2011. In the past decade, human-caused mortalities from vessel strikes and entanglements have been increasing, while birth rates in the population are at a 40 yr low. In addition to declining abundance, recent studies have shown that NARW length-at-age is decreasing due to the energetic impacts of sub-lethal entanglements, and that the body condition of the population is poorer than closely related southern right whales. We examined whether shorter body lengths are associated with reduced fecundity in female NARW. We compared age-corrected, modeled metrics of body length with 3 metrics of fecundity: age at first reproduction, average inter-birth interval, and the number of calves produced per potential reproductive year. We found that body length is significantly related to birth interval and calves produced per reproductive year, but not age at first reproduction. Larger whales had shorter inter-birth intervals and produced more calves per potential reproductive year. Larger whales also had higher lifetime calf production, but this was a result of larger whales having longer potential reproductive spans, as body lengths have generally been declining over the past 40 yr. Declining body sizes are a potential contributor to low birth rates over the past decade. Efforts to reduce entanglements and vessel strikes could help maintain population viability by increasing fecundity and improving resiliency of the population to other anthropogenic and climate impacts.

**KEY WORDS:** Photogrammetry · Cetacean · Reproduction · Anthropogenic impacts

## 1. INTRODUCTION

North Atlantic right whales *Eubalaena glacialis* (NARW) are listed under the Endangered Species Act

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in the USA (National Marine Fisheries Service 2008), the Species at Risk Act in Canada (COSEWIC 2013), and considered Critically Endangered by the International Union for Conservation of Nature (Cooke © H.F., P.K.H., A.R.K., C.A.M., M.J.M., and outside the USA, The U.S. Government 2022. Open Access under Creative Commons by Attribution Licence. Use, distribution and reproduction are unrestricted. Authors and original publication must be credited.

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2020). Following a relatively slow but sustained 20 yr increase in abundance, the NARW population has been in decline since 2011, dropping from an estimated 481 whales in 2011 to an estimated 368 whales in 2019 (Pace 2021). Entanglements in fishing gear and vessel strikes are thought to be the leading sources of mortality in the NARW population (Moore et al. 2021). While a spike in mortalities in the past decade has contributed to the decline in abundance, birth rates in the NARW population have also been unusually low since 2012 (Pettis et al. 2021).

Previous studies have linked NARW fecundity to climate-associated fluctuations in *Calanus finmarchicus*, a key copepod prey species for NARW on their summer foraging grounds in the Gulf of Maine (Meyer-Gutbrod & Greene 2014, Meyer-Gutbrod et al. 2021). During periods of low *C. finmarchicus* abundance in the 1990s and early 2010s, birth rates dropped well below rates in the 1980s and the 2000s when *C. finmarchicus* abundance was higher, suggesting that prey availability is likely a major driver of fecundity in NARW (Meyer-Gutbrod et al. 2021).

Sub-lethal entanglements in fishing gear are energetically costly (van der Hoop et al. 2017) and an increasing rate of serious entanglements (i.e. those with attached gear or severe injuries; Knowlton et al. 2012) is likely to directly contribute to reduced birth rates by diverting energy away from reproduction and reducing fecundity or reproductive success. In addition, Stewart et al. (2021) showed that NARW body lengths have been decreasing since the 1980s, with entanglements explaining a portion of restricted growth rates. Maternal body size and condition in baleen whales are associated with calf growth rates and body sizes (Best & R  ther 1992, Christiansen et al. 2016, 2018), and Stewart et al. (2021) hypothesized that the shorter body lengths in NARW could also contribute to reduced fecundity by delaying first calving events and reducing reproductive success. Here, we build on the results of that study to investigate whether shorter body lengths in NARW are associated with reduced fecundity in females.

## 2. MATERIALS AND METHODS

Aerial photogrammetry measurements were collected from free-ranging NARW under NOAA National Marine Fisheries Service permits 21371, 17355, and 17355-01. From 2000 to 2002, we used a fixed-winged, crewed airplane to collect aerial images of NARW in the Bay of Fundy, Canada (Fortune et al. 2012). A 126 mm format military recon-

naissance camera captured images on film from approximately 250 m altitude. Aircraft trim was monitored by scientists with bubble levels mounted at 2 sites in the back of the aircraft. During each pass over a whale, scientists communicated with the pilots to ensure the aircraft was in proper trim with the camera facing 90° downward off the vertical plane as the images were collected. A high precision paired transducer radar altimeter was used to collect altitude data during photo passes. Accuracy of the altimeter system was determined by photographing targets of known size and comparing altitudes calculated from measurements with those recorded from the altimeter (Perryman & Lynn 2002). From 2016 to 2019, we flew a remotely controlled hexacopter drone at altitudes of approximately 50 m to collect images of NARW in Cape Cod Bay, USA (Christiansen et al. 2020, Stewart et al. 2021), taking digital images using a 25 mm lens on an Olympus camera with micro 4/3 sensor (Durban et al. 2015), mounted in an electronic gimbal that maintained a 90° downward angle (Durban et al. 2022). We collected altitude measurements using drone GPS in 2016 (Christiansen et al. 2020) and a laser altimeter (Dawson et al. 2017) mounted on the vertical gimbal of the drone camera in 2017 to 2019 (Durban et al. 2021). The laser altimeter recorded altitude at a sampling rate of 16 measurements per second, and we selected the median altitude measurement from the same second that images were captured.

We calculated total lengths of whales using measured aircraft altitude, camera sensor/film size, and lens focal length to convert image sensor measurements to measurements on the real scale (Fortune et al. 2012, Durban et al. 2015). Images were filtered for those of measurement quality, such that the focus and clarity were sufficient to delineate the rostrum and tail for total length measurements. 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 <5% (Perryman & Lynn 1993, Miller et al. 2012, Durban et al. 2016) and in some cases approximately 1% (Dawson et al. 2017). 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 measure-

ment of each whale in cases of multiple measurements of an individual within a single sampling season (Perryman & Lynn 1993, 2002, Fortune et al. 2012).

We developed a 2-phase Gompertz growth equation (modified from Fortune et al. 2012, 2021) with model-estimated covariate effects of birth year, fishing gear entanglements, and maternal entanglements applied to asymptotic length, as described by Stewart et al. (2021). Covariate values were summed across the first 10 yr of life, as growth rates slow considerably after age 10 (Fortune et al. 2021). The Gompertz growth model uses 2 main parameters to define individual growth trajectories: asymptotic length and growth rate. 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 (Kato 1988, Moran et al. 2015), which also supported our decision to apply 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 growth length to unaffected whales. In other words, we assume that the length a whale reaches by age 10 to 15 is likely to be close to the maximum size that whale can achieve (Fortune et al. 2021). In the growth model described by Stewart et al. (2021), we estimated separate observation error terms for measurements taken with the 3 different altimeter types (radar, GPS, and laser). Measurements taken using GPS altimeters had the highest estimated observation error (median 0.63 m, 95% CI 0.26–1.01 m), followed by laser altimeter measurements (0.52 m, 0.19–0.77 m) and radar altimeter measurements (0.27 m, 0.01–0.48 m). These observation errors were estimated within, and therefore explicitly included in, the growth model, propagating the resulting uncertainty into estimates of growth parameters, including in the estimates of asymptotic length used in the present study. Data collection, analysis, and model development and diagnostics are reported in further detail by Stewart et al. (2021).

For the analyses presented in this study, we examined a subset of the measured whales from Stewart et al. (2021). We only included female whales that were 6 yr or older at the time of measurement, which is the minimum reproductive age for the species (with one exception of parturition at 5 yr, see Hamilton et al. 1998). The reproductive histories of these whales

were determined using the North Atlantic Right Whale Consortium identification database (North Atlantic Right Whale Consortium 2020). Measurements of individual whales were taken at different ages and across a 20 yr period. To standardize whale lengths on a common scale in order to evaluate relationships between size and fecundity, we used the asymptotic lengths of each whale estimated by the growth model of Stewart et al. (2021). The asymptotic lengths are the projected lengths that each whale would reach after infinite years, based on the model-estimated growth parameters and observed length-at-age of each whale (Fig. 1). This allows us to remove confounding effects of age on measured lengths, and produce a single relative size value that can be compared to lifetime metrics of fecundity. We considered the median of the Bayesian posterior distribution for model-estimated asymptotic length as our relative size metric for each whale, and included the uncertainty associated with the growth model estimates of asymptotic length in our analyses, as described below.

Reproduction in NARW is complex, with previous studies highlighting prey availability as a major driving factor of the timing of reproduction (Meyer-

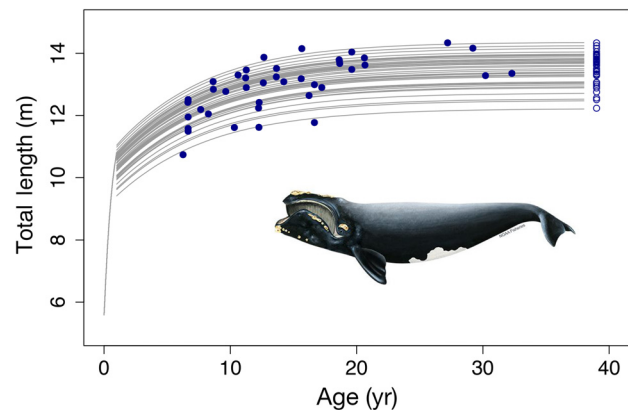


Fig. 1. Measured lengths and projected asymptotic lengths of North Atlantic right whale *Eubalaena glacialis* reproductive females. (●) Photogrammetry-based measurements of total lengths of whales with known ages; gray curves: median of the Bayesian posterior distribution for the model-estimated growth trajectory (from Stewart et al. 2021) for each of the 41 measured female whales in the present study, i.e. the most likely estimated growth trajectory associated with a length-at-age measurement after accounting for anthropogenic impacts on growth using the 2-phase growth model specified by Stewart et al. (2021) (see Section 2). Note that measured total lengths are not expected to fall directly on the growth trajectories, as the lines are the median estimates, and the growth model assumes observation error. In cases where a female was measured in more than 1 year, we show the length measurement associated with the oldest age. (○) Median model-estimated asymptotic lengths, each corresponding to a measured whale

Gutbrod et al. 2021). Other factors such as female body condition are likely to affect reproductive timing and success (Miller et al. 2011, 2012, Christiansen et al. 2016, 2018). With this complexity in mind, our analyses are not intended to predict reproductive output in females. Instead, we use simple linear models to make inferences about the direction of the relationship (if any) between body lengths and metrics of fecundity, acknowledging the existence of many additional contributing factors.

We considered 4 metrics of fecundity to compare to estimated whale lengths. (1) Age at first reproduction, which we calculated as the number of years between the birth year of a whale and the year it was first observed with a dependent calf. We excluded females with zero births. (2) Average birth interval, which we calculated as the mean of the number of years between recorded births for an individual whale. For whales with only 2 recorded births, the average birth interval was the single recorded birth interval between the 2 births. We excluded females with zero or 1 recorded birth. (3) The total number of recorded births for each female whale, although this metric is severely confounded by maternal birth year (see next paragraph). (4) Births per reproductive year, which we calculated as the total number of recorded births divided by the potential reproductive span for each female whale. We calculated the potential reproductive span as the number of years between age 7 (the minimum age at first reproduction in our subset of female whales) and the year of the last recorded sighting of each whale.

While we accounted for the confounding effects of age at the time of measurement by using estimated asymptotic lengths rather than measured lengths, there are additional potentially confounding effects of age on some metrics of fecundity. Stewart et al. (2021) identified a declining linear trend in body length by birth year, where whales born in more recent years are stunted compared to older whales. Whales born more recently have, with few exceptions, the smallest estimated asymptotic lengths, and at the same time have had less time to reproduce than older whales, which could make it challenging to differentiate the effects of size versus potential reproductive span on fecundity (Fig. 2). For example, the maximum possible reproductive span for a whale declines linearly with its birth year (Fig. 2a). Similarly, the oldest observable age at first reproduction declines linearly with birth year (Fig. 2b). As the potential reproductive span of a whale increases, its total potential reproductive output predictably increases as well (Fig. 2c), meaning that older whales

in general have produced more total offspring and are also generally the largest females. We addressed this by standardizing the total number of births by potential reproductive span to remove the correlation between birth year and reproductive output (Fig. 2d). In addition, average birth interval did not have a clear relationship with birth year, although no whales born after 2001 had enough births to calculate a birth interval (Fig. 2e).

To evaluate the relationships between fecundity and estimated whale length we used modified Bayesian linear regressions, fit using Markov chain Monte Carlo (MCMC) sampling implemented using JAGS (Plummer 2003) in R v4.1.2 (R Core Team 2021). In our analyses, the independent variable (estimated asymptotic length of a female) is derived from the growth model described by Stewart et al. (2021) with associated uncertainty (Fig. S1 in the Supplement at [www.int-res.com/articles/suppl/m689p179\\_supp.pdf](http://www.int-res.com/articles/suppl/m689p179_supp.pdf)). To account for this uncertainty, we included an observation process in our regression models, such that:

$$\text{Est.}A_i \sim N(A_i, \sigma_i) \quad (1)$$

where Est.*A* is the estimated asymptotic length for individual *i* from the growth model, which is normally distributed around *A*, the latent or ‘true’ asymptotic length of individual *i* estimated by the regression model, with standard deviation  $\sigma$ , which is the standard deviation of the posterior distribution of the estimated asymptotic length for individual *i* from the growth model. We specified *A* with uninformative, uniform priors spanning 0 to 20. The regression model is then defined based on *A*, such that:

$$\mu_i = \beta_1 + \beta_2 \times A_i \quad (2)$$

where  $\mu$  is the expected response for individual *i*,  $\beta_1$  is the intercept for the regression,  $\beta_2$  is the slope term, and *A* is the model-estimated true asymptotic length of individual *i*, as in Eq. (1). We specified both the slope and intercept terms using uninformative, normally distributed priors with mean 0 and standard deviation 10. For the analysis of total births, which are effectively count data, we modeled births as Poisson distributed around the mean linear relationship, such that:

$$\text{Obs}_i \sim \text{Poisson}(\mu_i) \quad (3)$$

where Obs is the observed fecundity metric (in this case total births) of individual *i*, which is Poisson

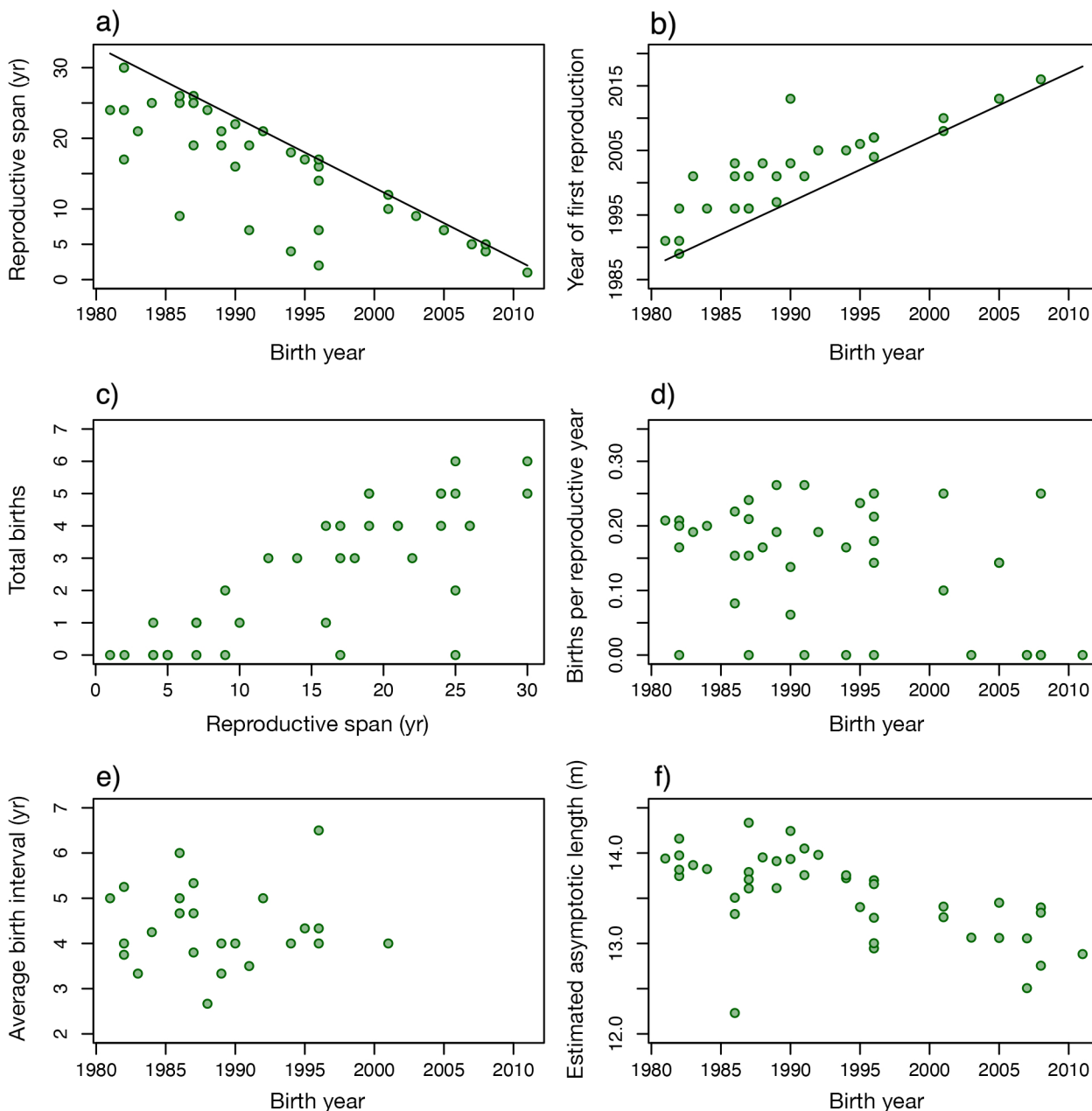


Fig. 2. Potentially confounding effects of birth year on metrics of fecundity in female North Atlantic right whales. (a) Potential reproductive span (defined here as the number of years between age 7 and the most recent sighting of an individual whale) of whales related to their birth year. Solid black line: maximum possible reproductive span for a whale based on its birth year. (b) Year of first observed reproduction related to birth year. Solid black line: earliest possible year of first reproduction for a whale born in a given year, using the minimum age at first reproduction of 7 in our subset of females. (c) Total recorded births for each female as related to their potential reproductive span. (d) Births per reproductive year (calculated as the number of recorded births for each female divided by their potential reproductive span for that female) by birth year. (e) Average birth interval for each whale by birth year. (f) Model-estimated asymptotic length and birth year of each female

distributed with mean  $\mu$ , the expected response for individual  $i$ . For average birth interval, age at first reproduction, and births per reproductive year, we modeled the response variables as normally distributed around the mean linear relationship, such that:

$$Obs_i \sim N(\mu_i, \sigma) \tag{4}$$

where  $Obs$  is the observed fecundity metric (in this case average birth interval, age at first reproduction, or births per reproductive year) of individual  $i$ , which is normally distributed with mean  $\mu$  and standard



deviation  $\sigma$ . We specified  $\sigma$  with uninformative, uniform priors spanning 0 to 5. For each model, we ran 3 chains of 200 000 iterations with a burn-in of 100 000 and a thinning interval of 200, resulting in 1500 draws from the posterior distribution. We evaluated convergence of the regression models based on visual inspection of chains and  $\hat{R}$  values  $<1.01$ , which indicates that an infinite number of iterations would lead to potential reduction of posterior intervals by less than 1% (Gelman & Rubin 1992).

As noted above, birth year and estimated asymptotic length are highly correlated (correlation coefficient  $-0.63$ ; or  $-0.79$  if we exclude Whale 1608, born in 1986 with estimated asymptotic length 12.23, see Fig. 2f). This multicollinearity precluded us from using multivariate analyses with both estimated asymptotic length and birth year as explanatory variables for fecundity, as the estimated regression coefficients from multivariate regressions were similarly correlated.

### 3. RESULTS

Our subset of reproductive females included 41 whales, measured between 2000 and 2019 at ages ranging from 6 to 32 (Fig. 1). Of these, 21 whales were measured in only 1 year, 13 were measured in 2 years, 5 were measured in 3 years, and 2 were measured in 4 years. The ages of those whales at the time of their last sighting ranged from 8 to 37 yr old, and the time gap between the year of measurement and the year of last sighting in the photo-identification database ranged from 0 to 20 yr (median 8 yr). The median number of total calves born to each whale was 3 (range 0–6). A total of 11 whales (26.8%) did not reproduce, 6 whales (14.6%) reproduced only once, and 24 whales (58.5%) reproduced at least twice, allowing us to calculate reproductive intervals for this subset of females. To evaluate the statistical significance of linear regression slope coefficients, we calculated the proportion of the Bayesian posterior MCMC samples that were greater than (or less than) zero, which corresponds to the probability that the slope coefficient is positive or negative. If more than 95% of the posterior draws were greater than or less than zero, we considered the regression to be statistically significant. If more than 90% of posterior draws were greater than or less than zero, we considered the regression to be marginally significant. As expected, we found a significant positive relationship between length and total births (99.5% of posterior draws  $>0$ ), which illustrates the correlation between

maternal length, birth year, and reproductive span, and should not be interpreted as a biologically meaningful result. We found a significant positive relationship between length and births per reproductive year (97.8% of posterior draws  $>0$ ); a marginally significant negative relationship between estimated asymptotic length and average birth interval (92.9%  $<0$ ; Fig. 3); and a marginally significant positive relationship between length and age at first reproduction (92.0%  $>0$ ). To evaluate the leverage of the smallest female in our dataset (Whale 1608) on the analyses, we ran the regression models both including and excluding this whale. With Whale 1608 excluded, the linear relationship between estimated asymptotic length and average birth interval was not significant (63.5% of posterior draws  $<0$ ), the relationship between age at first reproduction and estimated asymptotic length was significant (96.9%  $>0$ ), and the relationship between births per reproductive year and estimated asymptotic length remained significant (96.9%  $>0$ ; see Fig. S2). In all of the linear regressions,  $>95\%$  of the observations were within the 95% posterior prediction intervals of the regressions, indicating that the regressions were correctly specified to the distributions of the observed data (Fig. S3).

### 4. DISCUSSION

Our findings add to a growing body of evidence demonstrating that maternal size and nutritive condition in baleen whales influence fecundity through a variety of mechanisms. Larger and more robust females produce larger and more robust calves (Best & Rüther 1992, Perryman & Lynn 2002, Christiansen et al. 2016, 2018), which may influence calf survival rates. We show that smaller females produce fewer calves per reproductive year, possibly because the average interval between births is greater in shorter whales. Late gestation and lactation are costly energetic phases for female whales (Villegas-Amtmann et al. 2015, van der Hoop et al. 2017), with female body condition declining as calves increase in size prior to weaning (Miller et al. 2011, 2012, Christiansen et al. 2016, 2018). The degree to which the energetic reserves of females are depleted during lactation may govern the length of the resting period between successful pregnancies (Miller et al. 2011, Marón et al. 2015). The total energetic reserves of a female whale should be dependent on body volume, which is a combination of both body length and nutritive condition (Christiansen et al. 2018). Shorter whales would therefore be inherently limited in their

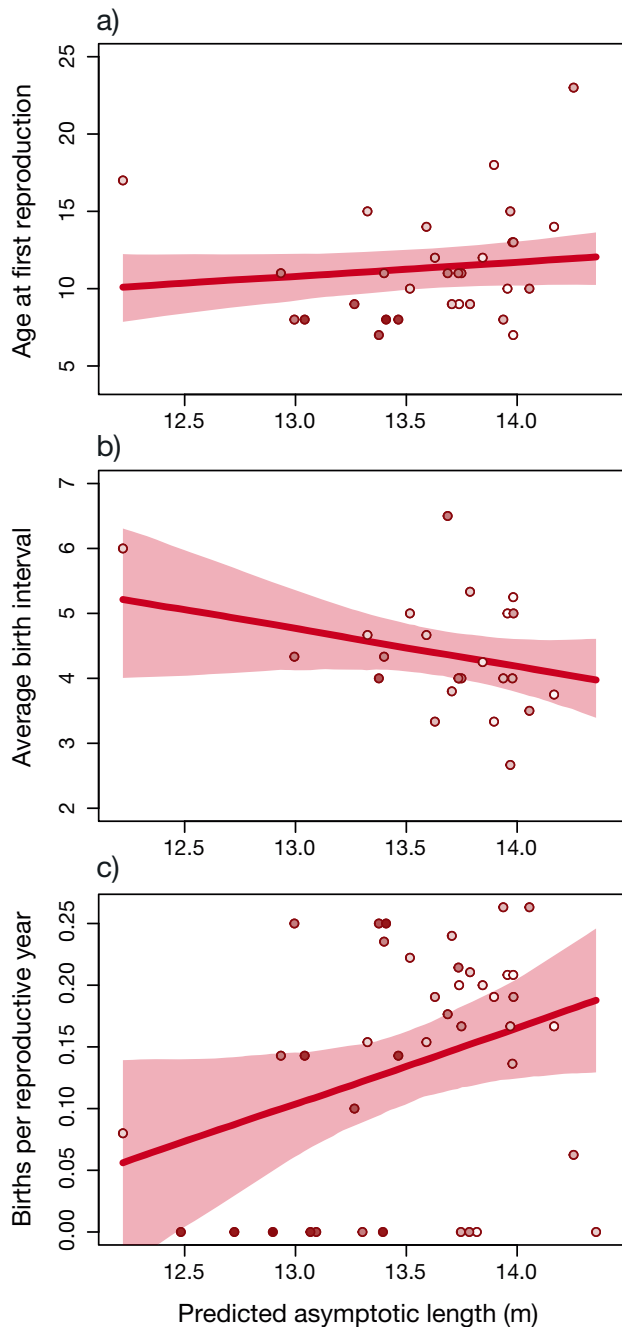


Fig. 3. Relationships between fecundity and the estimated asymptotic length of female North Atlantic right whales. **Dark red line:** median estimate of the Bayesian posterior distribution; **light red polygon:** 95% Bayesian credible interval for the linear regressions between: (a) estimated asymptotic lengths and the observed age at first reproduction; (b) estimated asymptotic lengths and average birth intervals; and (c) estimated asymptotic lengths and the number of observed births per reproductive year. In all panels, point colors represent the birth year of a given whale, with lighter colors representing whales born in earlier years and darker colors representing whales born in later years (range 1981–2011). Note Whale 1608 (born in 1986) had the smallest predicted asymptotic length of any whale in the dataset (leftmost point in all panels)

maximum energetic reserves compared to longer whales, even if they attain similar nutritive condition and blubber thickness, and may require a longer recovery period between births.

There are undoubtedly many other factors influencing reproduction and fecundity in NARW beyond female body lengths, including prey availability (Meyer-Gutbrod et al. 2021), maternal health (Rolland et al. 2016), and individual nutritive condition (Miller et al. 2011, 2012). Reduced prey availability in the 1990s and early 2010s was associated with a reduction in birth rates throughout the NARW population (Meyer-Gutbrod et al. 2021). Some of the shortest whales in our dataset were born in the early 2000s and would have reached sexual maturity during this recent period of reduced prey availability, which may be confounding the effects of maternal body length on fecundity. Indeed, 5 out of 10 females in our dataset born between 2001 and 2008 have not yet reproduced despite reaching ages ranging from 11 to 16, and it is challenging to determine how maternal length, prey availability, and the truncated observation windows due to the later birth years of these whales are each influencing the recorded reproductive output in this recent cohort of females. We note that the prediction intervals of our linear regressions, in particular the relationship between estimated asymptotic length and births per reproductive year, are wide (Fig. S3). This highlights that our analyses are most useful for inferring the direction of relationships between size and fecundity, and not for predicting the reproductive output of a female based solely on her estimated asymptotic length. A more complete accounting of the many potential drivers of reproductive output in NARW would help evaluate the relative contributions of these drivers to the depressed birth rates in recent years. For example, the multi-state model developed by Meyer-Gutbrod et al. (2021) could be extended to include maternal body length, health (e.g. Rolland et al. 2016), and nutritive condition in addition to prey availability, in order to explicitly account for these effects and their interactions. Nevertheless, while the effects of prey availability on fecundity almost certainly add noise to our analyses, our observations span periods of both high and low prey abundance, which should mitigate the confounding influence of prey availability on our inferences of the direction of the relationships between maternal body length and fecundity.

Maternal age at the time of reproduction may have important effects on calf fitness related to maternal body size and nutritive condition. For example,

Whale 1608 had the shortest estimated asymptotic length (~12 m) of any female in our dataset and was a clear outlier among females born prior to 2000 (Fig. 2f). Her mother, Whale 1163, was entangled with attached gear while nursing 1608, which has a reported negative effect on calf growth (Stewart et al. 2021). In addition, the birth of Whale 1608 to Whale 1163 at age 5 is the youngest recorded age at first reproduction in the population (Hamilton et al. 1998). While maternal age was not explored as a potential effect on NARW growth rates by Stewart et al. (2021), it is likely that this reflects the pattern reported previously in several cetacean species of smaller female whales producing smaller calves (Best & Rüther 1992, Perryman & Lynn 2002, Christiansen et al. 2016). At 5 yr, Whale 1163 would be substantially smaller than most reproductive females and would likely be devoting considerable energy to her own continued growth, in addition to the added drag of attached gear, which may have contributed to the reduced growth of Whale 1608. In turn, Whale 1608 had one of the lower reproductive rates among females in our dataset (Fig. 3).

Almost all female whales with an estimated asymptotic length below 13 m in our dataset produced 0 or 1 calves within our study period, excluding them from our analyses of average birth interval. The 1 exception was Whale 1608, which, as noted above, was anomalously small for her cohort, most likely due to the age and entanglement status of her mother at her time of birth. When Whale 1608 is excluded from our analysis of average birth interval, the negative regression slope changes from moderately significant (92.5% of posterior draws <0) to not significant (63.5% <0). One possible explanation for this pattern is that average birth interval is not, in fact, related to the estimated asymptotic length of a female, and that the long birth interval recorded in Whale 1608 is an outlier. However, when Whale 1608 is excluded from the analysis of births per reproductive year, the positive regression slope remains significant (96.9% >0). Presumably, birth interval is the mechanism driving the number of calves a female produces per reproductive year, as a longer average birth interval would result in fewer calves produced within a given reproductive span. As such, our analysis of births per reproductive year is similar to our analysis of average birth interval, with the primary difference that we can include females that have produced 0 or 1 calves. Given that the regression analysis of births per reproductive year remains largely unchanged with or without the inclusion of Whale 1608, we posit that a more likely explanation is that

our analysis of average birth interval is heavily impacted by our limited sample size, especially of younger females with shorter estimated asymptotic lengths. As these younger females extend their reproductive spans in coming years and produce more calves, it should be possible to determine whether the average birth interval of Whale 1608 is anomalous or indicative of the true influence of maternal length on birth intervals.

Interestingly, the relationship between female length and the age at first reproduction was opposite to the expectations of Stewart et al. (2021), who hypothesized that shorter females may need to delay first reproduction. Age at first reproduction was positively related to estimated asymptotic length, either at the marginal significance level (92% >0) or the full significance level (96.9% >0), depending on whether Whale 1608 was included or excluded in the analysis, respectively. The average age at first reproduction for female right whales is 9.6 (Hamilton et al. 1998), and almost half of the females in our dataset produced their first calf before age 10. This suggests that most female NARW produce their first calf before they have reached their expected maximum length (Fortune et al. 2021), and that the length of a female may not have a strong influence on when she first reproduces, as exemplified by Whale 1163, who had her first calving event at age 5. Instead, it is possible that the positive relationship between age at first reproduction and estimated asymptotic length we report here is indicative of the effect that delaying first reproduction can have on early growth in females. For example, females delaying first reproduction until after age 10 may devote the energy that would otherwise be used on parturition and lactation towards their own growth. However, we note that Stewart et al. (2021) explicitly included the number of calves produced before age 10 as an explanatory covariate for estimated asymptotic length, and found no significant effect. As such, we caution the over-interpretation of this result and emphasize that our sample sizes in the age at first reproduction analysis are constrained only to whales that have reproduced, which excludes many of the smallest whales in our dataset, similar to our average birth interval analysis.

In our analyses, we considered the number of calves produced by each female to be known. However, the NARW population is not fully censused each year, and between 1990 and 2018, 86 calves were born that were observed with their mothers but could not be photo-identified (Hamilton et al. 2022, P. K. Hamilton unpubl.). From 1991 to 2018,



105 whales with unknown birth years were added to the NARW photo identification database (P. K. Hamilton unpubl.). This implies that a minimum of 19 births were not recorded; more if some proportion of the 86 unidentified calves died and were not part of the 105 whales with unknown birth years. The reported reproductive histories of females in our dataset may therefore be incomplete in some cases, although we note that the minimum of 19 missing births would be applied to all reproductive females in the population, which is at least 4 times as large as our sample of 41 females analyzed here. If a calf were missing from the recorded reproductive history of a female, it would lead to an inflation of her average birth interval and an underestimate of fecundity (total births and births per reproductive year). If her first birth were missed, it could also affect the reported age at first reproduction. If every female in the dataset shares the same probability of having an unobserved calf, then we would expect these observation errors to produce a minimal effect on our analyses, especially at the scale of an expected approximately 5 missing calves from our dataset. However, if an observation bias exists, it is more likely that older females would have unobserved calving events, as survey effort for NARW at both their foraging grounds and calving grounds has increased over the past 40 yr. If the fecundity of older females is higher than reported here, we would expect the linear relationships between asymptotic length and fecundity to be even stronger than our results suggest, as older females are generally the largest individuals in our dataset. The one exception to this expectation is in the case of Whale 1608. If Whale 1608 had an unobserved calving event, then her average birth interval would likely be substantially lower, which would affect the significance of our birth interval analysis, as noted above.

Given the recently described declining trend in NARW body lengths by birth year (Stewart et al. 2021), the relationships we present here between body length and fecundity may be contributing to depressed birth rates in the population, and may be an early indicator of reduced birth rates for NARW in the future if the adult female size structure continues to decline. We did not examine the effects of body condition on birth rates as we typically have only 1 to 2 body condition measurements per female, and body condition fluctuates interannually depending on prey availability and individual energetic demands, making it impossible to compare annual body condition measurements with lifetime fecundity metrics. However, the overall body condition of

the NARW population is poor compared to southern right whale populations (Miller et al. 2011, Christiansen et al. 2020). Body condition fluctuates substantially throughout the reproductive cycle of right whales, with the greatest blubber thickness observed in females shortly before the initiation of pregnancies, the thinnest blubber in lactating whales, and increasing blubber thickness post-weaning (Miller et al. 2011). The poor body condition observed in the NARW population may therefore be an indicator that females have insufficient energetic reserves to maintain a similar reproductive rate to southern right whales (1.98% population growth rate for NARW, 5.34–7.21% for southern right whales; Corkeron et al. 2018). The cumulative impacts of rapidly changing ocean conditions in the North Atlantic, repeated and worsening entanglements (Knowlton et al. 2012), and increasing vessel traffic and ship strikes may all be partially driving body length and condition declines in NARW (Corkeron et al. 2018, Christiansen et al. 2020, Stewart et al. 2021), which may have contributed to depressed birth rates in the past decade. Entanglements are energetically costly (van der Hoop et al. 2017), and there is a detectable negative effect of entanglements in fishing gear on whale lengths (Stewart et al. 2021). Reducing entanglements in fishing gear could help arrest the observed decline in body lengths in the NARW population as well as improve individual body condition, which may in turn help maintain population viability by increasing fecundity and improving resiliency to other anthropogenic and climate impacts.

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