Growth and development of North Pacific gray whales (*Eschrichtius robustus*)

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Understanding variability in growth patterns of marine mammals provides insights into the health of individuals and status of populations. Body growth of gray whales (*Eschrichtius robustus*) has been described for particular life stages, but has not been quantified across all ages. We derived a comprehensive growth equation for gray whales by fitting a two-phased growth model to age-specific length data of eastern North Pacific gray whales that were captured, stranded, or harvested between 1926 and 1997. To predict mass-at-age, we used the allometric relationship between mass and length. We found that on average (± *SD*), calves were 4.6 ± 0.043 m and 972 ± 26 kg at birth, and reached 8.5 ± 0.095 m and 6,019 ± 196 kg by the end of their first year of life (*n* = 118). Thus, calves almost double (2×) in length and octuple (8×) in mass while nursing, and are effectively about two-thirds of their asymptotic adult length and one-third of their maximum mass when weaned. The large sample of aged individuals (*n* = 730) indicates that gray whales live up to ~48 years and have a life expectancy of < 30 years. Adult females attain a mean (± *SD*) asymptotic size of 13.1 ± 0.048 m and 20,758 ± 222 kg, while the smaller males average 12.6 ± 0.048 m and 19,938 ± 222 kg at ~40 years of age. Females are thereby ~4% longer and heavier than males. These age-specific estimates of body size can be used to estimate food requirements and assess nutritional status of individuals.

Key words: eastern gray whale, growth curves, length, life expectancy, longevity, mass, morphometrics, Putter model, sexual dimorphism

Body growth of gray whales (*Eschrichtius robustus*) has been extensively studied, but there are no comprehensive models that describe growth over their entire life span. A number of studies have quantified growth for different life stages, such as fetal growth (Rice 1983; Sumich et al. 2013), postnatal growth patterns of calves and juveniles (Rice and Wolman 1971; Blokhin and Tiupeleyev 1987; Sumich et al. 2013), and sexually mature adults (Zimushko 1970; Rice and Wolman 1971; Zimushko and Ivashin 1980). In addition, there is detailed information on the growth rates of two captive gray whale calves (named Gigi and JJ) during their first year before release (Sumich 1986; Sumich et al. 2001, 2013). Unfortunately, additional information on growth rates of calves and juvenile gray whales less than 5 years old is sparse. While existing data sets on body-size measurements have been used to construct separate growth models per life stage, they never have been compiled to derive a comprehensive growth model.

Models describing the growth of marine mammals have been used to determine and understand variability in sizes among individuals and populations (Stevick 1999; Winship et al. 2001; Fortune et al. 2013). They also have been important tools to assess the health of individuals and derive the age structure of populations (Shotwell et al. 2010). However, age-specific estimates of body size are not available for all marine mammals (Stevick 1999) and are incomplete for gray whales.

The objective of our study was to quantitatively determine how gray whale growth varies across all age-classes. We therefore mathematically describe the growth of eastern North

Pacific gray whales using all available age-associated observations of body lengths. We also derive a length–mass relationship to describe changes in body mass with age using the few available sets of mass and length measurements. The comprehensive growth model and mass estimates we derive can be used to model energetics, estimate food requirements, and estimate drug dosages where gray whales may need rehabilitation, veterinary care, or humane euthanasia (e.g., Wahrenbrock et al. 1974; Sumich et al. 2001; Gulland et al. 2005).

MATERIALS AND METHODS

We conducted a review of published literature on eastern North Pacific gray whale lengths and compiled all reported measurements from 1926 to 1997 (n = 999) into a single data set. The data set was compiled from a collection of US scientific surveys and studies (Gilmore 1960, 1961; Rice and Wolman 1971; Norris and Gentry 1974; Wahrenbrock et al. 1974; White and Griese 1978; Rice 1983; Sumich 1986; Sumich et al. 2001, 2013; Perryman and Lynn 2002). The data set also included data from the Norwegian Whalers Association (Risting 1928), and Russian research reports to the International Whaling Commission (IWC) on the Chukotkan Indigenous fishery (Zenkovich 1937; Zimushko 1970; Zimushko and Ivashin 1980; Blokhin 1982, 1984, 1985, 1986, 1987; Yablokov and Bogoslovskaya 1984). Reported body lengths were standard lengths measured as a straight-line distance from the tip of the rostrum to the fluke notch (Lockyer 1976).

We estimated age from published data on: (1) counts of adjacent light and dark ear plug layers, known as growth layer groups (GLGs), each representing 1 year of life (Rice and Wolman 1971; Blokhin and Tiupeleyev 1987); and (2) counts of *corpora albicantia* and *corpora lutea* found in the ovaries of female gray whales (Rice and Wolman 1971). Two studies describe methods of estimating ages of gray whales: Rice and Wolman (1971) and Blokhin and Tiupeleyev (1987). Rice and Wolman (1971) assumed that the first year was represented by two GLGs based on their observation that the smallest whales in their data set had a minimum of 2 GLGs. Using this method, the estimated age at sexual maturation is ~8 years based on a count of 9 GLGs. This was later challenged by Blokhin and Tiupeleyev (1987) who observed fewer than 2 GLGs during the first year of growth. Blokhin and Tiupeleyev (1987) also presented additional data showing the average age of sexual maturation occurs slightly earlier, at ~7 years of age. We chose to use the method described by Blokhin and Tiupeleyev (1987) to estimate age from GLG counts and age at sexual maturation. We further assumed that gray whales reproduce once every 2 years on average as concluded by others (Rice and Wolman 1971; Blokhin and Tiupeleyev 1987).

Where *corpora* counts were available, we used the estimate of age at sexual maturation from Blokhin and Tiupeleyev (1987) to calculate age estimates for late pregnant or postpartum females. We did so by multiplying the number of *corpora* (*albicantia* and *lutea*) in the ovaries (n) by 2 years to account for the reproductive cycle and added 7 years to account for age at sexual maturation. As this method applies only to

sexually mature females, all male gray whales in the data set were aged using the GLG method.

We fit four commonly used mathematical growth functions to the gray whale length-at-age data (Table 1). We then used the Akaike Information Criterion (AIC) to determine which model best described gray whale growth (Winship et al. 2001; Fortune et al. 2012). Only observations that had both length and age data (n = 730) were used to fit the length-at-age growth models (Risting 1928; Zimushko 1970; Rice and Wolman 1971; Zimushko and Ivashin 1980; Blokhin 1982, 1984, 1985, 1986, 1987; Rice 1983; Rice et al. 1984; Yablokov and Bogoslovskaya 1984; Sumich 1986; Sumich et al. 2001, 2013; Perryman and Lynn 2002). Repeated measures from captive gray whale calves Gigi and JJ (Sumich et al. 2001, 2013) were not included in the analysis. Instead, only one length measurement from each whale (i.e., Gigi and JJ) was included in the analysis (i.e., their lengths at 1 year, just before they were returned to their natural habitat and presumably at their healthiest while in captivity). We fit each of the growth models to the length-at-age data using nonlinear least squares regression from the nls2 package of the statistical program R (Grothendieck 2013; R Core Team 2018), and compared the relative fits of each model using AIC. The model with lowest AIC value was selected as the "best model" (Akaike 1974; Burnham and Anderson 2002).

Once the best model was selected, a visual assessment of the fit revealed that a single growth curve did not adequately describe the data. The single model overestimated body lengths of nursing calves, and underestimated body lengths of weaned juveniles and adults. We therefore used a two-phased approach to fit the length-at-age data, similar to the method used for other cetacean species (Perrin et al. 1976; Danil and Chivers 2007; Larese and Chivers 2009; Fortune et al. 2012). Phase 1 represented the early growth stages of calves before weaning (occuring ≥ 6–7 months—Sumich 1986); Phase 2 represented the decelerated growth phase after weaning. We identified the transition point between the two phases as the point where the difference between predicted lengths of Phase 1 and Phase 2 was zero (Fortune et al. 2012). We incorporated uncertainty into the growth model by running 10,000 Monte Carlo simulations and calculating the 95% confidence interval around the model fit.

Table 1.—Growth models fit to size (S) at age (t) data. Size is measured as standard length (in meters), and age is measured in decimal years. A represents asymptotic size, t_0 is time at which size is zero, c is a constant of integration, and k is a fitted parameter indicative of growth rate. Each parameter, while generally comparable across models, does not necessarily represent the same property in each model.

Model	Equation		Sources
Putter	$S_t = A(1 - e^{-k(t-t_0)})$	(1)	(von Bertalanffy 1938; Ricker 1979)
von Bertalanffy	$S_t = A(1 - e^{-k(t-t_0)})^3$	(2)	(von Bertalanffy 1938; Ricker 1979)
Gompertz	$S_t = Ae^{-ce^{-kt}}$	(3)	(Gompertz 1825; Zach et al. 1984)
Logistic	$S_t = \frac{A}{1+e^{-k(t-t_0)}}$	(4)	(Ricker 1979)

The number of observations for length data at each age was insufficient to determine the exact age at which sexual dimorphism in size becomes significant. However, we calculated the difference in length of males and females for each age cohort: (1) at birth; (2) as calves (0–1 years); (3) as weaned juveniles (> 1–7 years); and (4) as sexually mature adults (7+ years). We calculated statistical significance for sexual differences in length using a Welch two-sample t-test (an adaptation of Student's t-test) from the R *stats* package (R Core Team 2018), and power analyses using the *pwr* R package (Champely 2018) to determine whether the sample sizes for each age were sufficient to detect sexual dimorphism if it did exist. Where evidence for sexual dimorphism was found, we generated sex-specific size correction factors by calculating mean differences between observed lengths and model-predicted lengths (values are shown in Supplementary Data SD2). We then multiplied these values with the predicted lengths from the two-phased Putter growth curves to estimate sex-specific length estimates.

Body mass was estimated using an allometric length–mass relationship (Schultz 1938):

$$W = aL^b \qquad (5)$$

which was linearized in logarithmic form:

$$log_{10}W = log_{10}a + b \cdot log_{10}L \qquad (6)$$

where W represents mass in kg, L represents length in meters, a is a constant factor, and b is an exponential constant. We fit a regression to length and mass data ($n = 15$) to solve for the a and b parameters and calculated gray whale body mass at each age using lengths-at-age predicted by the two-phased growth model (Gilmore 1961; Rice and Wolman 1971; Wahrenbrock et al. 1974; White and Griese 1978; Blokhin 1986; Sumich 1986; Sumich et al. 2013; details in Supplementary Data SD1). To incorporate uncertainty into our mass estimates, we bootstrapped the data by running 10,000 Monte Carlo simulations. Before fitting the model, we examined the data for potential outliers (i.e., biologically improbable measurements). We excluded one animal from our analysis because the reported mass measurement (3,500 kg) was considerably less than what was reasonable for its reported length (9.1 m). It was reported to have died of probable starvation (Sumich 1986), and was therefore considered to be nonrepresentative of a typical individual at that size. Pregnant females also were poorly represented, with only three observations for animals of unknown ages: (1) 12.7 m and 16,360 kg; (2) 13.55 m and 33,846 kg (Rice and Wolman 1971); (3) 13.35 m and 31,466 kg (Zenkovich 1937; Rice and Wolman 1971).

RESULTS

The gray whale data set spans the period 1926–1997 and consists of 999 observations. Of these, 730 were associated with age estimates and used to describe average changes in body lengths. The age-sex frequency distribution of the age-length data set ($n = 730$) shows an imbalanced sex ratio, with a notably high number of females ($n = 73$) between the ages 10 and 15 years (Fig. 1). The majority of the data obtained for calves and juveniles up to 4 years of age were of unknown sex ($n = 195$). There also were notably fewer observations for female calves in the data set. Individuals < 30 years old accounted for ~91% of the data set. The oldest individual in the data set was female, estimated to be 77 years of age from counts of *corpora albicantia* (Rice and Wolman 1971), and the mean age of sampled animals was 11.7 years.

Body lengths.—Mean body lengths of gray whale calves at birth and at 1 year of age were consistent with estimates from prior studies (Table 2; Fig. 2; Sumich et al. 2013). There was no evidence of sexual dimorphism between male and female calves and juveniles within the data set. However, the statistical power for the t-test was very low (power = 0.1 for calves at birth; 0.05 for juveniles), which may have affected our ability to detect a significant difference. We did find evidence of sexual dimorphism when comparing the mean ($\pm$ *SD*) lengths of sexually mature females (12.7 $\pm$ 0.611 m) and males (12.1 $\pm$ 0.705 m) ($t_{250} = 8.94$, $P < 0.001$) assuming that sexual maturation occurs at ~7 years of age on average (Blokhin and Tiupeleyev 1987).

Overall, we found that the two-phased Putter growth model was the best model to describe growth of gray whales (equation 1, Table 1) as it yielded the lowest AIC scores, highest likelihood, and greatest weight of evidence in favor of the model (Table 2; Figs. 3 and 4). The point of inflection between the two growth phases (i.e., the point where the difference between predicted lengths of Phase 1 and 2 was zero) was at 0.8 years (~9.6 months) of age.

Gray whale calves reach up to two-thirds of their adult asymptotic lengths in the first year, growing on average ~1.05 cm per day. Estimated asymptotic lengths ($\bar{X} \pm SD$) were 13.11 $\pm$ 0.048 m for adult females and 12.59 $\pm$ 0.048 m for adult males, which they reach at ~40 years of age (Rice and Wolman 1971). On average, observed lengths of female calves during Phase 1 growth (< 0.8 years) were 1.13% (0.05 m) longer than the lengths predicted by the two-phased Putter model, while male calves were 0.17% (0.01 m) shorter than predicted (Supplementary Data SD2). Similarly, observed lengths of females during Phase 2 growth (> 0.8 years) were 1.91% (0.25 m) longer than predicted, while males were 2.11% (0.26 m) shorter than predicted (Supplementary Data SD2). Due to the paucity of data on differences in body size between female and male gray whales during Phase 1 growth, we applied the adult sex-specific correction factors across all ages to generate comprehensive sex-specific growth curves (Fig. 4).

Body mass.—Parameter values for the allometric relationship between body length and mass (equation 6) were $log_{10}a = 1.0354 \pm 0.1590$ ($a \pm SE$), $b = 2.9509 \pm 0.1963$ ($b \pm SE$), $R^2 = 0.96$, $P < 0.01$ (Fig. 5). Applying this relationship to the length-at-age estimates from the fitted two-phased Putter growth model (Fig. 6) showed that calves attained up to one-third of maximum predicted mass ($\bar{X} \pm SD$) in the first year of growth (females = 6,134 $\pm$ 196 kg; males = 5,892 $\pm$ 196 kg).
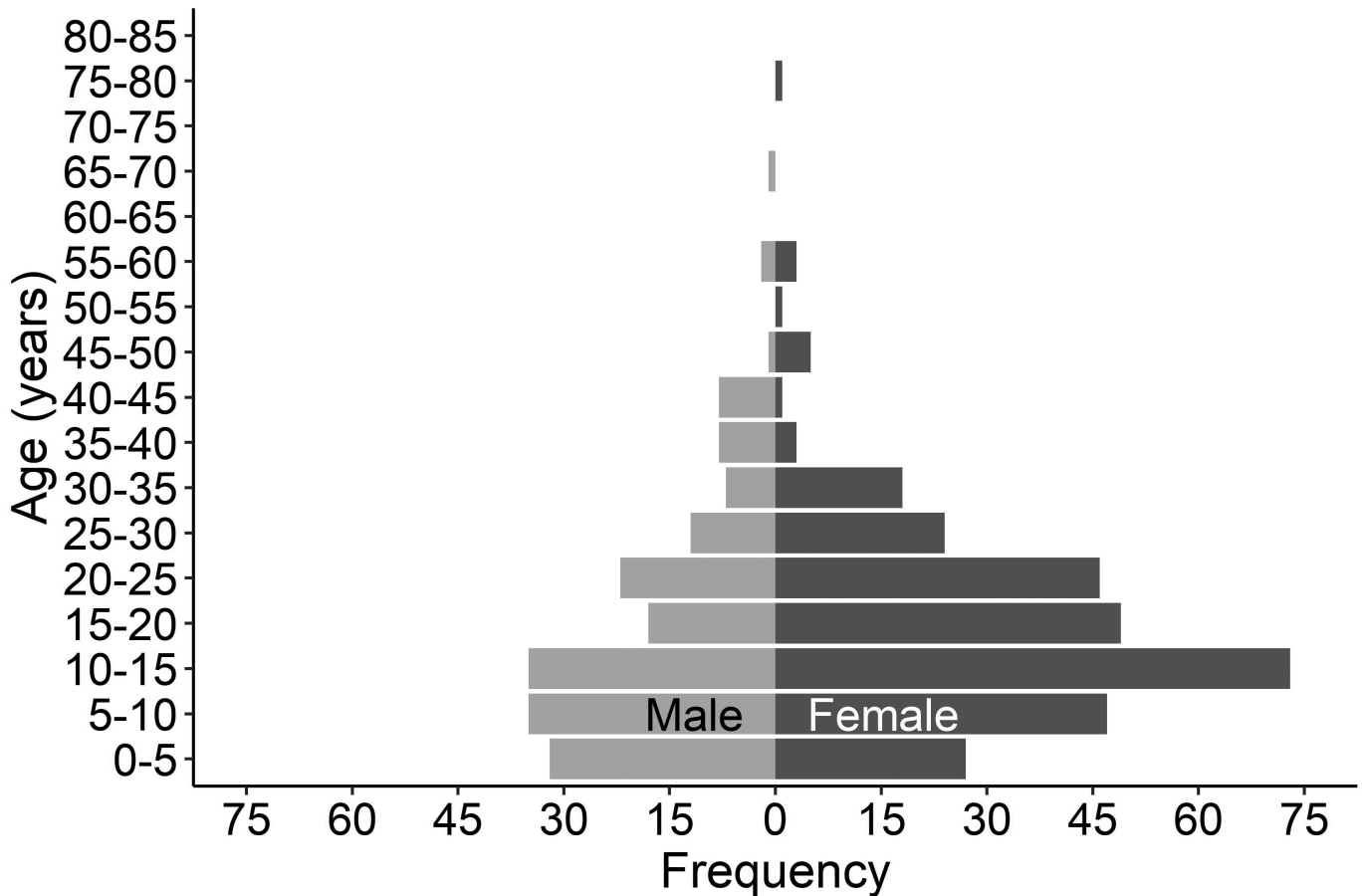
Fig. 1.—Age-frequency distribution of measured gray whales (*Eschrichtius robustus*) by sex (captured or stranded individuals). A portion of the data obtained for calves and juveniles (up to 4 years of age) were of unknown sex (195 individuals). Lighter shaded bars on the left represent male gray whales (*n* = 211) and darker shaded bars on the right represent females (*n* = 324).

It also showed that upon reaching maximum predicted lengths at ~40 years of age, females have a predicted mass of 20,758 ± 222 kg, and males reach a maximum predicted mass of 19,938 ± 222 kg (Fig. 6).

DISCUSSION

Gray whales have two distinct phases of growth. The first is characterized by a rapid growth rate from birth to weaning, while the second represents decelerated growth rate after weaning. The two-phased growth model fit to the body lengths of all known-aged gray whales measured from 1926 to 1997 shows that the average gray whale attains about two-thirds of its maximum body length by the time it weans. Applying the allometric relationship between mass and length further shows that calves attain one-third of their body weight during the first few months while they nurse. Overall, adult males are about 4.2% shorter and 4.3% lighter than adult females.

Confidence in our model predictions are tempered by difficulties apparent in the data set in identifying the sex of younger animals. Similar shortcomings in model confidence are associated with limitations in methods of aging gray whales and measuring whales that were captured, stranded, or harvested. These issues on data error and model uncertainty are addressed below.

Data error and model uncertainty.—Historical data sets of morphometric measures of marine mammals, such as the ones we used for gray whales, typically come from harvested or stranded animals that have recognized errors and uncertainties (Lockyer 1981a; Fortune et al. 2012; Rechsteiner et al. 2013). A large portion of the measurements in our data set were from Russian aboriginal harvests and US strandings, neither of which can be assumed to be a random sample of the population (Stevick 1999). Historical commercial harvest was known to target specific size classes of whales—usually larger whales—depending on the IWC regulations for each species (Stevick 1999), but it is uncertain whether more recent subsistence harvests targeted smaller, more easily handled whales. Some of the stranded animals may have had compromised growth due to poor health and could be a source of error. New noninvasive methods using aerial images to measure living baleen whales have been developed in recent years (Perryman and Lynn 2002; Miller et al. 2012; Christiansen et al. 2016). However, aerial photographs fail to capture age, and need to be linked to a database of birth dates for each photographed animal to describe changes in body size.

Measurement errors also can be attributed to the way in which animals are handled, and the way in which they are measured. In contrast to multiple measurements that can be

Table 2.—Mean lengths of gray whales (*Eschrichtius robustus*) for each age cohort. Ages at birth are zero, calves are ≤ 1 year, juveniles are 1–7 years, and adults are sexually mature individuals > 7 years. Data for calves between 0 and 1 year were insufficient to determine sexual dimorphism within that age cohort. SD = standard deviation; n = sample size; t = t-value; $d.f.$ = degrees of freedom; P = P-value; Effect size = Cohen d measure of effect size; Min n for power of 0.8 = minimum sample size to obtain statistical power of 0.8.

Age cohort	Mean Length (m)	SD	n	d.f.	t	P	Effect size	Statistical power	Min n for power of 0.8
At birth									
Female	4.66	0.379	26	48	0.65	0.52	−0.176	0.10	507
Male	4.60	0.305	30						
Unknown	4.59	0.336	62						
Calf (up to 1 year)									
Female	8.87	0.382	2	Sample sizes too low to compare mean lengths					
Male	9.14	0.000	3						
Unknown	7.75	0.650	80						
Juvenile (1–7 years)									
Female	10.40	1.200	36	57	−0.13	0.90	0.0292	0.05	18,462
Male	10.40	0.725	39						
Unknown	8.97	0.633	53						
Adult (7+ years)									
Female	12.70	0.611	260	250	8.94	< 0.001	−0.960	1.00	18
Male	12.07	0.705	139						

taken from aerial images to decrease uncertainty, measurements taken during necropsies tend to only be done once (Fortune et al. 2012). Accurately measuring the straight-line distance from the tip of the nose to tip of the tail for large animals can also be logistically challenging depending on the environment and size of the animal. Measurements taken with the measuring tape stretched along the ground alongside a whale would likely differ from measurements taken with the measuring tape stretched above the whale, because of potential sagging in the measuring tape (Stevick 1999). In addition, lengths of harvested animals when pulled up on shore can be overestimated due to stretching—which can potentially increase the body length of an animal by up to 1 m (J. L. Sumich, Oregon State University, pers. comm.), which is ~7% of an adult's length. This is similar to the 9% increase in lengths reported for stretched bowhead whales (George et al. 2004). This should not be an issue for stranded gray whales on shore that are measured in place. Unfortunately, we were unable to assess measurement error for the data we used because it was unclear from published reports which measurements were from hauled animals.

A second source of possible error in our data set is the accuracy with which the gray whales were aged. The two methods most commonly used for aging gray whales are counting the number of adjacent pairs of light and dark layers, known as GLGs, from ear plugs, and estimating age from counts of *corpora albicantia* and *corpora lutea* in sexually mature females (Zimushko 1970; Rice and Wolman 1971; Blokhin and Tiupeleyev 1987). The majority of age estimates of gray whales in our data set were from GLG counts. Age estimates based on GLG counts depend on the rate of accumulation of age layers, but there are discrepancies regarding whether one or two layers are accrued in the first year (Zimushko 1970; Rice and Wolman 1971; Blokhin and Tiupeleyev 1987). Where GLG counts were available, we assumed that one GLG layer (i.e., a pair of adjacent light and dark bands) was accrued for each year of growth (Blokhin and Tiupeleyev 1987). *Corpora* counts are considered to provide a more reliable estimate of age for sexually reproductive female gray whales than GLG counts, where ovulation is assumed to occur once every 2 years, and sexual maturation is assumed to occur after 7 years of age (Blokhin and Tiupeleyev 1987). However, *corpora* counts were only available for a small fraction (~16%) of the individual gray whales in our analysis.

The gray whales included in our analysis were between 0 and 77 years old and had an average age of 11.7 years. This age range covers the period of significant growth. Our model shows cessation of growth at about 40 years. However, longevity is unknown. Although the oldest gray whale was estimated to be 77 years old based on *corpora* counts (Rice and Wolman 1971), it was an unusually old whale compared to other whales in the data set. It is possible that this whale is a good representative of maximum life span given that individuals of other whale species have been known to reach this age or older (Lockyer 2001). However, based on the age distribution of this particular data set, this age does not reflect average longevity.

A rigorous means to estimate longevity is to use the 99th percentile of the age distribution of a sample of aged animals
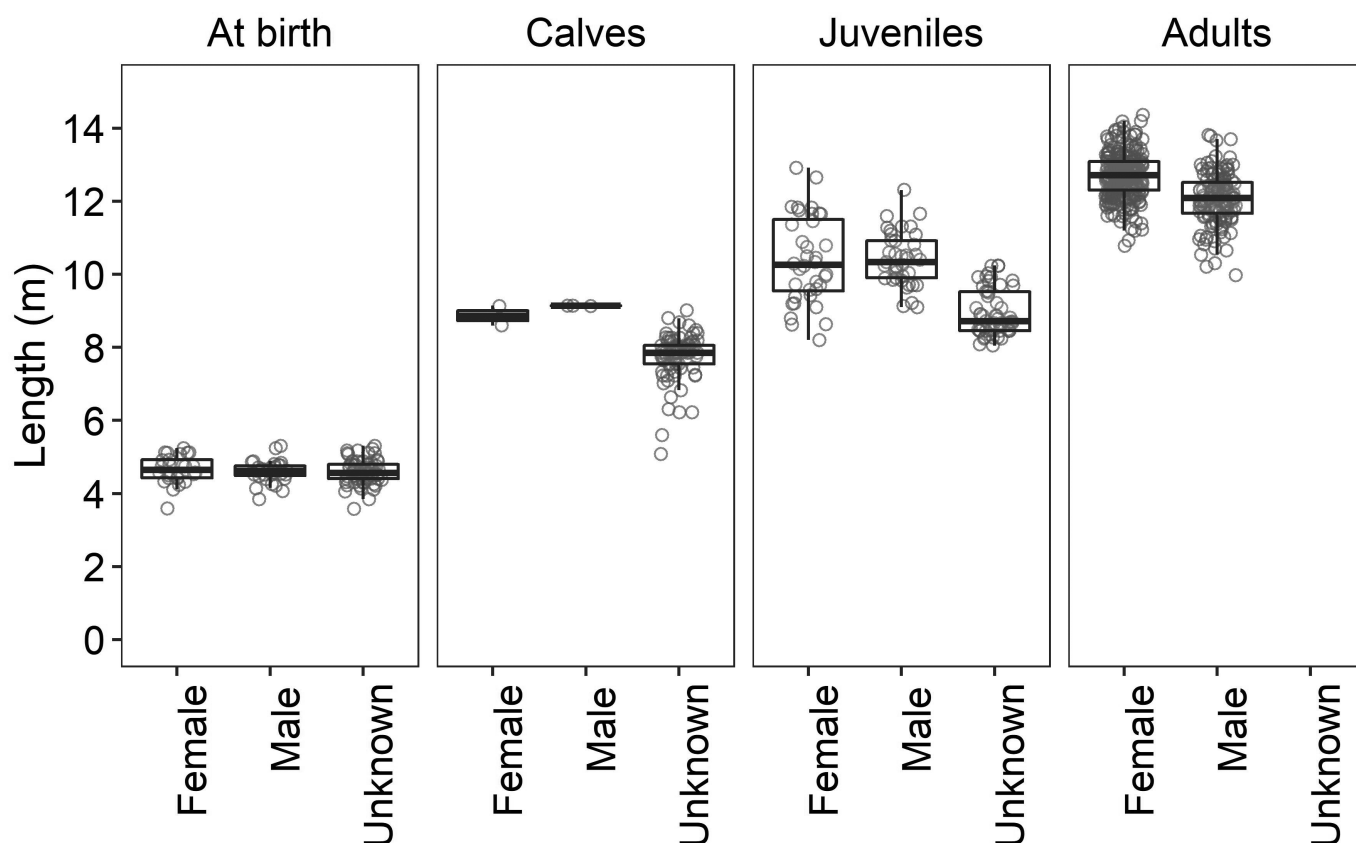
Fig. 2.—Individual measurements (unfilled circles) and distributions (boxplots) of body lengths of gray whales (*Eschrichtius robustus*) by sex and cohort including neonates and newborns (at birth), calves (ages up to 1 year), juveniles (1–7 years old), and adults (sexually mature, 7+ years). The majority of the observations for calves are of unknown sex. Mean values for each cohort are reported in Table 3.

(i.e., the age at which only 1% of the sample is older—Barlow and Boveng 1991; Trites and Pauly 1998). Thus, we estimate the longevity of gray whales is on average ~48 years, and their life expectancy is < 30 years, based on > 90% of the samples being < 30 years old. These estimates represent average longevity and life expectancy for the population from 1926 to 1997, when our data were collected. The gray whale population has been increasing since the data were collected, but experienced unusual mortality events (UMEs) in 1999–2000 and 2019 (Le Boeuf et al. 2000; NOAA Fisheries 2020). Emaciated adults and subadults during these events could reflect the population overshooting carrying capacity. However, it is unknown whether carrying capacity has been relatively constant or is artificially depressed due to changing climatic conditions (Reilly 1992; Le Boeuf et al. 2000; Moore et al. 2001). Whether or not average longevity has changed from before whales were harvested to the time after harvesting ceased and the population began to recover, is unknown in the absence of more data.

Populations may experience decreased growth rates as they approach carrying capacity due to increased competition for food (Scheffer 1955; Eberhardt 1977; Fowler 1987; Trites 1990). Climate change (Cheung et al. 2013; Baudron et al. 2014; Pauly and Cheung 2018) and high levels of exploitation (Allendorf and Hard 2009; McLenahan 2009; Therkildsen et al. 2019) can also reduce body size. However, testing whether

decadal changes had occurred in the body lengths of mature gray whales as the population approached carrying capacity revealed no change in mean sizes (± *SD*) of adult gray whales between the 1970s (12.5 ± 0.727 m) and 1980s (12.5 ± 0.648 m) (t_{133} = −0.65, P = 0.52). Unfortunately, we were unable to assess whether body size has decreased since the 1920s, or remained constant in recent decades, due to limited sample sizes.

In addition to changes in body size, populations at carrying capacity may also experience delayed maturity, resulting in an increase in age at sexual maturation (Eberhardt 1977; Fowler 1987). Inter-calving intervals have increased from 2.1 ± 0.40 years (± *SD*) for the period 1977–1982 to 2.39 ± 0.58 years (± *SD*) for the period 2005–2017 (Swartz and Jones 1983; Swartz et al. 2018). This suggests that age estimations using *corpora* counts (assuming that age at sexual maturation has remained the same, and that one *corpora* is produced every 2 years) may result in underestimating ages of whales in the current population.

The length estimates we calculated from the growth model were derived from a large sample size of body measurements that yielded a good model fit. However, there was a lack of weight measurements available to model changes in body mass due to the logistical difficulties associated with weighing large whales (Lockyer 1976). We therefore calculated mass at age by applying the allometric relationship between mass and length to

Table 3.—Parameter estimates for four different two-phased models (Putter, von Bertalanffy, Gompertz, and logistic; equations 1–4) describing the growth of gray whales (*Eschrichtius robustus*). A = asymptotic size; k = growth rate; c = constant of integration; t_0 = time at which size is zero. Standard lengths are in meters, and time (age) is in decimal years. We selected the best model using the Akaike Information Criterion (AIC). Also reported are the differences in AIC values (ΔAIC) between the model with the lowest AIC value (i.e., Putter; equation 1) and the other fitted models, the likelihoods of each model, and the weight of evidence in favor of each model. The model with the lowest AIC value, greatest likelihood, and greatest AIC weight was considered the "best" model.

| Model	A	c	k	t_0	ΔAIC	Likelihoods	AIC weights
Phase 1 (0–0.8 years)							
Putter	9.47 ± 0.19		1.85 ± 0.15	−0.36 ± 0.02	0.00	1.00	0.44
von Bertalanffy	9.32 ± 0.16		2.24 ± 0.15	−0.70 ± 0.04	0.59	0.74	0.33
Gompertz	9.13 ± 0.07	0.68 ± 0.01	2.56 ± 0.11		85.00	0.00	0.00
Logistic	9.21 ± 0.14		2.64 ± 0.15	−0.51 ± 0.02	1.22	0.54	0.24
Phase 2 (> 0.8 years)							
Putter	12.82 ± 0.06		0.18 ± 0.01	−5.09 ± 0.40	0.00	1.00	0.58
von Bertalanffy	12.85 ± 0.05		0.19 ± 0.01	−9.81 ± 0.60	1.75	0.42	0.24
Gompertz	12.84 ± 0.05	0.49 ± 0.01	0.20 ± 0.01		2.74	0.25	0.15
Logistic	12.82 ± 0.05		0.07 ± 0.00	−2.28 ± 0.25	6.03	0.05	0.03
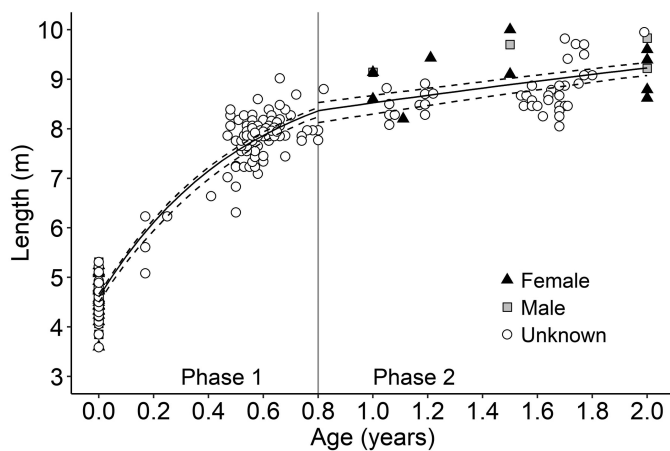
Fig. 3.—The two-phased growth model describing the first 2 years of life for gray whales (*Eschrichtius robustus*; males, females, and individuals of unknown sex have been combined). Phase 1 spans from 0 to 0.8 years and Phase 2 spans from 0.8 years onwards. Length-at-age (meters) can be calculated by inserting age (decimal years) into the following equations: (i) $S_t = 9.47(1 - e^{-1.85(t + 0.36)})$ for Phase 1, and (ii) $S_t = 12.82(1 - e^{-0.18(t + 5.09)})$ for Phase 2. 95% *CI*s (dashed lines) were derived from 10,000 Monte Carlo simulations.

the growth modeled estimates of length at age. Unfortunately, our confidence in our predictions of mass at age are limited by the small sample size of weighed and measured gray whales (n = 15) we used to derive the allometric relationship (the biggest animal reported among the 15 individuals was 12.4 m and ~15 years old). This bias toward smaller whales is presumably due to the relative ease in measuring and weighing smaller animals. This, combined with the small sample size, resulted in increased uncertainty in body mass predictions, particularly for older animals (Fig. 6). Additional mass-at-age measurements, combined with information on fetal growth such as those from Rice (1983) and Sumich et al. (2013), are needed to predict the mass of pregnant gray whales.

We have greater confidence in our estimates of body length than in the estimates of body mass. Although this limitation

in confidence in estimated body masses should be considered when using our models, our mass-at-age estimates are an improvement over prior estimates because of the improvement in length estimates.

Sexual dimorphism.—As with prior studies, we found sexual dimorphism in length among adults, but not for calves and juveniles (Rice and Wolman 1971; Sumich 1986). However, our data also show that observed lengths for female calves are longer on average than predicted, while observed lengths for male calves are shorter than predicted at a given age. It is therefore possible that sexual dimorphism starts at birth (and even before), such that young females should be ~4% longer and heavier than males—similar to the difference in body size observed among adult males and females. Other dimorphic species such as northern fur seals (*Callorhinus ursinus*) with large sample sizes exhibit sexual dimorphism starting at the fetal stage (e.g., Trites 1991; Trites and Bigg 1996). Rice and Wolman (1971) found no significant difference in the lengths of as many as 30 male and 25 female near-term fetuses, but they did find statistically significant differences for other factors in postnatal individuals (e.g., as many as 167 males had longer flippers and shorter tails compared to 147 females). Our sample sizes for the younger age-classes of gray whales were relatively small and the variability between the sizes of individual whales of any given age was too large to detect such a relatively small difference in sizes of young males and females.

There were notably few measurements of young females, and many measurements from individuals of unknown sex (Fig. 1). One possible explanation for the bias in reported sexes could be the relative ease in definitively identifying males versus females. Sighting a penis clearly indicates that an animal is male, whereas not sighting a penis does not necessarily indicate that the animal is female, because the penis may be hidden or contracted. In the case of observations from gray whales of unknown sex, it is unclear whether the sex of the individuals was not identified, or if the associated sex information simply was not reported.

Even if all 195 gray whales of unknown sex (aged 0–4 years) in our study had been identified as male or female, it is unlikely
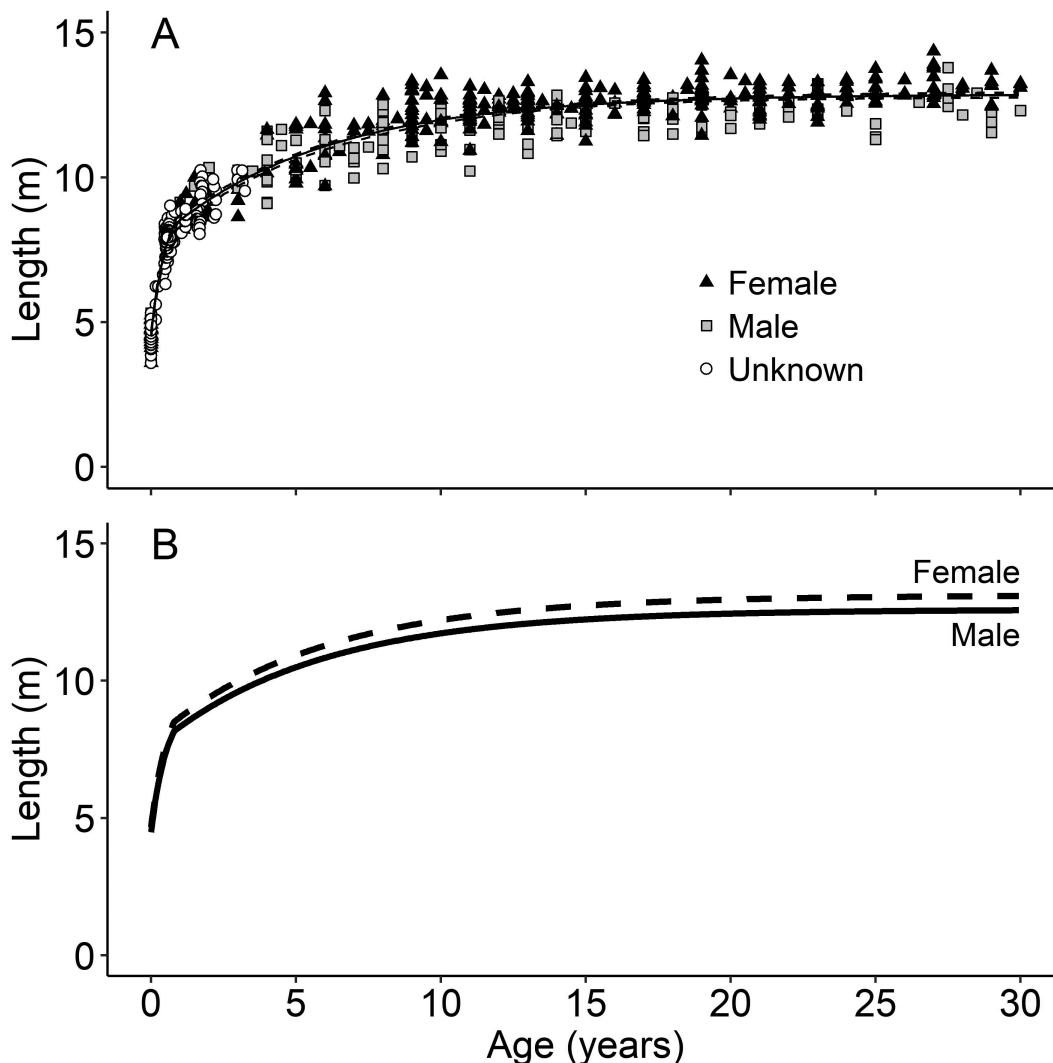
Fig. 4.—Comprehensive two-phased growth model (panel A) for gray whales (*Eschrichtius robustus*), showing Phase 1 (0–0.8 years) and Phase 2 (> 0.8–30 years). 95% *CI*s (dashed lines) were derived from 10,000 Monte Carlo simulations. Length-at-age (meters) can be calculated by inserting age (decimal years) into the following equations: (i) $S_t = 9.47(1 - e^{-1.85(t + 0.36)})$ for Phase 1, and (ii) $S_t = 12.82(1 - e^{-0.18(t + 5.09)})$ for Phase 2. Length-at-age estimates (panel B) after sex-specific correction factors (females: +1.91%; males: −2.11%) were applied to the estimates from the two-phased Putter growth model. The dashed line represents female gray whales, and the solid line represents males.

that the sample size would have been sufficient to detect sexual dimorphism. Results from a power analysis (Table 4) indicates that > 500 young whales would be needed to detect sexual dimorphism at birth, and over 18,000 whales would be required to conclusively demonstrate sexual dimorphism in gray whale calves and juveniles with these sample sizes. However, our data show patterns indicating that sexual dimorphism observed in adults may indeed start at conception. We therefore generated comprehensive growth curves under the assumption that sexual dimorphism begins at birth in addition to the general growth curves presented here.

Gray whale growth models.—Among the four models we tested, the one that best fit the data was the Putter equation (equation 1). As expected, gray whales grow extremely rapidly in their first year, but their growth rates decrease considerably

following weaning until they are ~40 years old. This is consistent with observed growth patterns of other cetaceans, such as North Atlantic right whales (*Eubalaena glacialis*—Fortune et al. 2012), humpback whales (*Megaptera novaeangliae*—Stevick 1999), whitebelly spinner dolphins (*Stenella longirostris*—Larese and Chivers 2009), short-beaked common dolphins (*Delphinus delphis*—Danil and Chivers 2007), and the spotted dolphin (*Stenella attenuata*—Perrin et al. 1976). Calves attain about two-thirds of their asymptotic adult length and one-third of their maximum mass within the first year of growth. This is slower than the reported growth rates of North Atlantic right whales, which attain up to three-quarters of their asymptotic adult mass in the first year (Fortune et al. 2012).

Large aquatic mammals are known to rely on size for energy and thermoregulation (Rice and Wolman 1971). Calves that grow large and fat earlier in life have the thermoregulatory
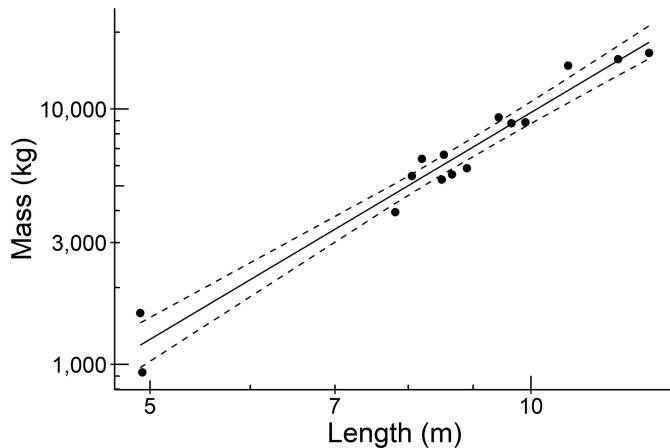
Fig. 5.—Length–mass allometric regression for gray whales (*Eschrichtius robustus*) where $\log_{10}$ Mass (kg) = $2.9509 \cdot \log_{10}$ Length (m) + 1.0354, $R^2 = 0.96$, $P < 0.01$. Dashed lines represent the 95% *CI*. Data are contained in Supplementary Data SD1.

benefit of a lower surface area to volume ratio (Christiansen et al. 2018) with larger blubber reserves adding insulation and an energetic buffer while they learn to forage independently (Lockyer 2007). In addition, rapid growth rates may help prepare calves for transitioning between nursing and consuming solid food in the Chukchi and Bering Seas. Juvenile baleen whales allocate resources toward rapid growth and expansion of the head and jaw regions (Lockyer 1981b), and calves with bigger jaws or thicker baleen may have the advantage of an increased filtering surface area for foraging. As a result, larger gray whale calves likely have lower risks of starvation and predation from killer whales (*Orcinus orca*), and ultimately better chances of surviving during migration (Rice and Wolman 1971; Fortune et al. 2012).

Our model shows a decrease in the rate of growth at ~9.6 months (0.8 years), which is 2–3 months later than the ~7 months age at weaning reported by others (Rice and Wolman 1971; Sumich 1986). This could mean that while weaning may
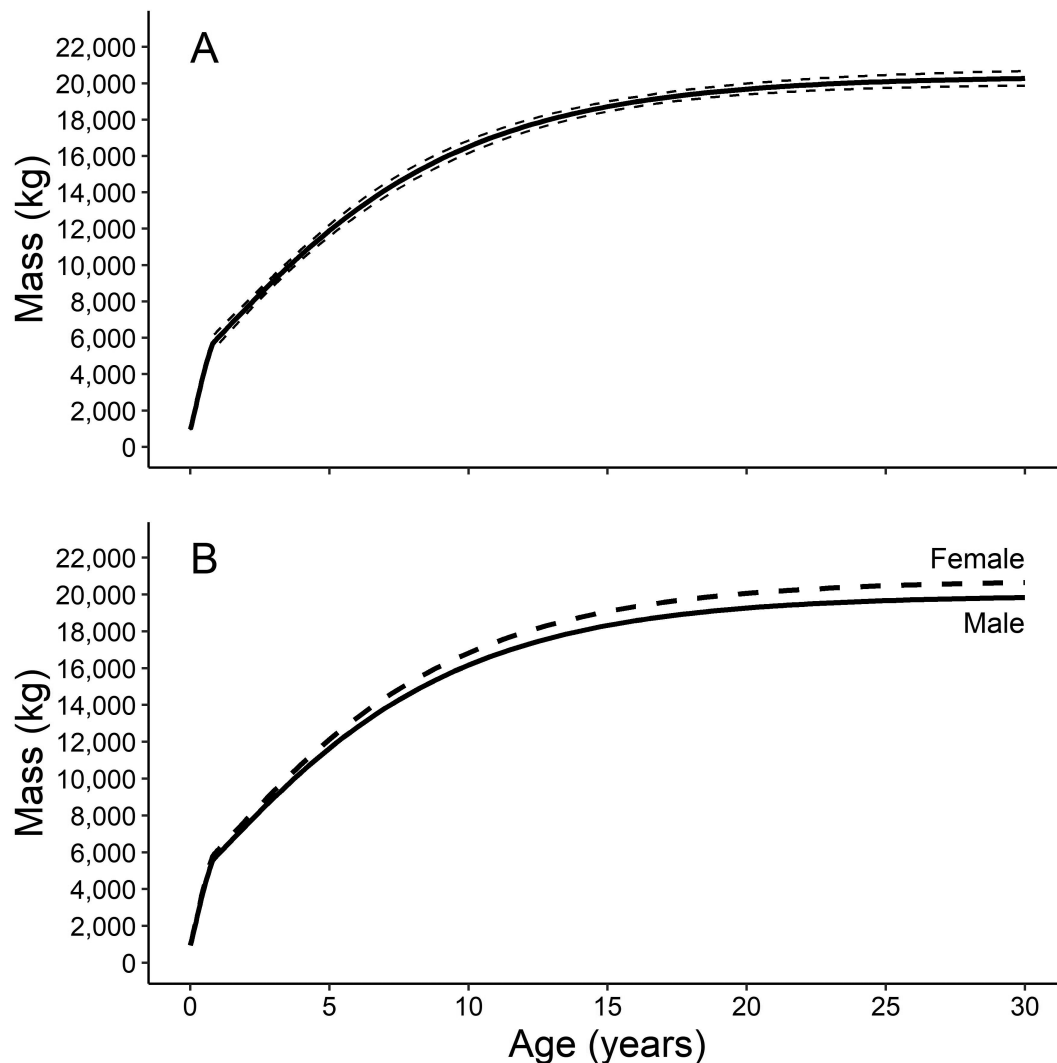

Fig. 6.—Estimated mass-at-age (kg) for gray whales (*Eschrichtius robustus*) calculated using length-at-age estimates from the two-phased Putter growth model (equation 1, Phase 1 and 2), sex-specific correction factors (females: +1.91%; males: −2.11%), and a length–mass allometric relationship (equation 6). Panel (A) shows mass estimates from the general two-phased Putter model (dashed lines = 95% *CI* calculated from 10,000 Monte Carlo simulations). Panel (B) shows sex-specific mass estimates (females = dashed line; males = solid line).

Table 4.—Predicted length-at-age for gray whales (*Eschrichtius robustus*) in meters ($\bar{X} \pm SD$) generated from the two-phased Putter growth curves (Phase 1: 0–0.8 years; Phase 2: > 0.8–40 years), and mass-at-age estimates in kilograms ($\bar{X} \pm SD$) generated from a length–mass allometric relationship (equation 6). These values are average sizes of males and females. Sex-specific correction factors (females: +1.91%; males: −2.11%) can be applied to these values to derive average lengths-at-age for males and females. *SD* values listed are the standard deviations of 10,000 Monte Carlo bootstrap estimates of mean lengths and mass for each age.

Age (years)	Length (m)	Mass (kg)
0	4.59 ± 0.043	972 ± 26
0.1	5.41 ± 0.046	1,583 ± 39
0.2	6.09 ± 0.057	2,248 ± 61
0.3	6.66 ± 0.062	2,924 ± 80
0.4	7.13 ± 0.060	3,577 ± 88
0.5	7.52 ± 0.056	4,187 ± 92
0.6	7.85 ± 0.052	4,743 ± 91
0.7	8.12 ± 0.048	5,240 ± 90
0.8	8.34 ± 0.048	5,679 ± 96
0.9	8.43 ± 0.099	5,858 ± 200
1	8.51 ± 0.095	6,019 ± 196
2	9.22 ± 0.066	7,618 ± 158
3	9.81 ± 0.053	9,155 ± 143
4	10.31 ± 0.049	10,590 ± 148
5	10.72 ± 0.050	11,901 ± 162
6	11.07 ± 0.051	13,077 ± 176
7	11.36 ± 0.051	14,119 ± 184
8	11.60 ± 0.049	15,033 ± 186
9	11.81 ± 0.047	15,828 ± 184
10	11.98 ± 0.044	16,515 ± 177
11	12.12 ± 0.041	17,105 ± 168
12	12.24 ± 0.038	17,611 ± 160
13	12.34 ± 0.035	18,042 ± 151
14	12.43 ± 0.033	18,408 ± 144
15	12.50 ± 0.032	18,719 ± 140
16	12.56 ± 0.032	18,982 ± 138
17	12.61 ± 0.031	19,205 ± 140
18	12.65 ± 0.032	19,393 ± 143
19	12.69 ± 0.033	19,551 ± 147
20	12.71 ± 0.034	19,685 ± 153
25	12.80 ± 0.040	20,094 ± 183
30	12.84 ± 0.044	20,266 ± 204
35	12.86 ± 0.047	20,338 ± 216
40	12.86 ± 0.048	20,368 ± 222

begin at ~7 months, calf nutrition likely is supplemented with energy rich milk for another 2 months. The decrease in growth rate at 9.6 months may therefore be the combined effect of weaning and decreased prey availability in the late summer or early fall (Highsmith and Coyle 1990). The 7-month estimate for age of weaning was based on stomach contents of calves (Rice and Wolman 1971). However, calves have been observed mimicking adult feeding behavior—diving and filtering mud and sand through their baleen while still nursing (Swartz 1986). Stomach contents of calves may therefore contain benthic invertebrate prey before weaning is complete.

Ultimately, our model agrees with the general premise that calves are weaned by the end of their first year, and our descriptions of calf and neonate growth are consistent with prior estimates derived with the Gompertz model (Sumich 1986; Sumich et al. 2001, 2013). Our descriptions of growth after weaning also are consistent with prior estimates from von Bertalanffy models (Rice and Wolman 1971; Zimushko and Ivashin 1980; Blokhin and Tiupeleyev 1987). Overall, we generated robust predictions of length-at-age by combining morphometric data for gray whales obtained off the coasts of Chukotka and Alaska, and further south to Mexico. This consolidated comprehensive data set for the eastern North Pacific population provides better descriptions of gray whale growth patterns than has been previously available. Our growth model can be applied to western North Pacific gray whales as well, assuming that the two populations are indeed morphometrically similar (Yablokov and Bogoslovskaya 1984).

Improvements to our model estimates likely will come as sample sizes are increased. Most valuable would be obtaining more weight measurements from whales > 12 m to refine the allometric relationship between mass and length. Another improvement would be to estimate the body mass of pregnant females by including fetal growth (from Sumich et al. 2013), and including mass of tissue growth during pregnancy. Similarly, increasing sample sizes of young animals would substantiate our assumption that sexual dimorphism begins at birth.

Prior efforts in modeling mass at age determined that adding girth to allometric models allows for differences between lean and fat body conditions to be accounted for, and can yield better model fits (Lockyer and Waters 1986; Vikingsson et al. 1988; Sumich et al. 2013). Girth therefore significantly improves mass estimates for individual whales (pregnant females in particular), but does not improve mass estimates across age and length classes. Length also has been found to have a greater effect than girth on mass estimates for gray whales, fin whales, and sei whales (Sumich et al. 2013). To effectively incorporate the variability in girth for every age and size class, there would ideally be girth measurements from multiple individuals for every length and age-class measured. In light of this and the paucity of published age-associated girth measurements ($n = 9$), we only used length and mass measurements to derive the allometric relationship.

The growth curves we derived describe length-at-age and mass-at-age for male and nonpregnant female gray whales over their entire age spectrum. Our resulting estimates can be used to estimate food requirements, assess health and body condition, and model bioenergetic requirements for gray whales throughout the North Pacific.

ACKNOWLEDGMENTS

SUPPLEMENTARY DATA

Supplementary data are available at *Journal of Mammalogy* online.

Supplementary Data SD1.—Gray whale (*Eschrichtius robustus*) length and mass data used in the allometric model. We excluded pregnant individuals and one individual of length 9.1 m and mass of 3,500 kg from the analysis because the reported mass measurement was considerably less than expected for its reported size. This individual was noted to have died of probable starvation (Sumich 1986), and was not likely representative of a typical individual at that size.

Supplementary Data SD2.—Mean percent differences between observed and predicted lengths for female and male gray whales (*Eschrichtius robustus*) in Phase 1 (0–0.8 years) and Phase 2 (> 0.8–30 years). The observations available from individuals in Phase 1 were insufficient to calculate phase- and sex-specific correction factors. We therefore applied Phase 2 sex correction factors (percent differences) to both growth phases of the fitted Putter growth model to generate comprehensive sex-specific growth curves (Fig. 4).

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