

ECOLOGY

Extreme longevity may be the rule not the exception in Balaenid whales

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We fit ongoing 40+–year mark-recapture databases from the thriving southern right whale (SRW), *Eubalaena australis*, and highly endangered North Atlantic right whale (NARW), *Eubalaena glacialis*, to candidate survival models to estimate their life spans. Median life span for SRW was 73.4 years, with 10% of individuals surviving past 131.8 years. NARW life spans were likely anthropogenically shortened, with a median life span of just 22.3 years, and 10% of individuals living past 47.2 years. In the context of extreme longevity recently documented in other whale species, we suggest that all balaenid and perhaps most great whales have an unrecognized potential for great longevity that has been masked by the demographic disruptions of industrial whaling. This unrecognized longevity has profound implication for basic biology and conservation of whales.

INTRODUCTION

The first observations documenting the extraordinary longevity of whales were from the counts of annual ear plug lamina of fin whales (*Balaenoptera physalus*) and blue whales (*Balaenoptera musculus*) taken by Japanese whalers (1). Although most individuals had fewer than 20 lamina, a few specimens had more than 100 annual growth layers. From these data, the oldest blue and fin whales were documented to be at least 110 and 114 years, respectively. At the time, these were the oldest documented nonhuman mammals.

Corroborating these ages is more recent evidence of great longevity in bowhead whales (*Balaena mysticetus*). Archaeological artifacts recovered from the blubber of bowheads taken in the modern Indigenous subsistence hunt include several stone or metal and ivory harpoon points last used in the 1880s (2). In 2007, a whale was taken in the traditional hunt and found to have an explosive Yankee Whaler harpoon tip embedded in its blubber last manufactured in 1885. These artifacts suggested that bowhead whales lived at least 130 years. After the recovery of these artifacts, George *et al.* (3) used aspartic acid racemization (AAR) of the eye lens and then a new aging method to estimate the ages of whales taken in the subsistence hunt. In one instance, an individual's AAR-estimated age of 133 years corresponded closely to the 120-year-old whaling artifact recovered from its blubber, validating extraordinary AAR-estimated ages (2). AAR estimated ages of several individuals exceeded 150 years, and one individual, otherwise healthy, was estimated to be 211 years old. This was older than the documented ages of fin and blue whales by a century and would have likely been considered a laboratory error in the absence of the corroborating archaeological evidence.

From the standpoint of physiological scaling, these superannuated ages should not be unexpected. Whales are the largest living animals, and body size is highly correlated with longevity. In log-log space, the mass-longevity relationship has a slope of ~ 0.13 for terrestrial mammals (excluding bats) (4), and the 110- and 114-year

maximum life spans of blue and fin whales fall approximately along this line. Bowhead whales, however, fall considerably above this prediction but below the prediction for flying mammals and birds, which have a much steeper mass to longevity slope of ~ 0.25 (4). Whether or not either of these relationships is appropriate for whales is subject to a potentially larger problem that representative age data for most whale populations, particularly baleen whales, do not exist.

There are three confounding issues in current whale age estimation, and all likely result in considerable downward bias on expected life span at the species level. First, although most toothed whales and some baleen whales have tissues with countable annular growth layers, many do not or, if they do, the archives are incomplete or difficult to count in very old individuals because of tissue remodeling, tooth wear, and/or thinning of the oldest annual layers. This almost always results in an under count of growth layers, especially in older individuals, and ages estimated from counting laminated tissues are usually considered minimum ages (5, 6).

Second, assuming that whales are capable of surviving to 150, as has been definitively demonstrated for bowhead whales and is also likely in fin whales (7), it is unclear whether we could detect superannuated individuals in most whale populations today. Industrial whaling, which for most species ended only 60 years ago, would have required any individuals now aged over 100 years to have survived at least 40 years of intense whaling, and any individual over 150 would have had to survive 90 years of that same intense hunt. Given that many whale species were reduced to less than 10% of their original population size, and the population minima for most species were reached in the mid-20th century, that degree of whaling would have rendered superannuated individuals extremely rare or completely absent from the age structures of most populations. Consequently, extremely old whales may not be part of the demographic makeup of current whale populations, even if they historically existed.

Last and closely related to the previous point, most methods of aging whales require lethal sampling (5). For most baleen whales, the only sizable sample of age data was collected from individuals taken by Japanese whalers. The now oldest documented ages for almost every great whale species were reported by Japanese scientists sampling hunted whales (bowhead whales being the major exception, and, in that case, ages of traditionally hunted whales were reported

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by American scientists). Ear plug lamination counts were only discovered as a method of aging in the 1950s (8), and all age data were collected from individuals hunted in the mid-20th Century, at the very end of industrial whaling. Thus, the age records that are still used as the basis of the expected longevity of most whale species were collected when the demographic makeup of those populations was most disturbed. Additional age samples do occasionally come available from stranded individuals, but, because ear plugs and eye lens are extremely sensitive to decay and must be collected fresh and because they require considerable technical skill to collect and read, ages from stranded whales are not commonly estimated. Moreover, as the causes of death of most stranded animals are anthropogenic and not natural senescence, their utility for assessing a species' potential maximum longevity is limited.

Most whale populations have recovered or are recovering from industrial whaling, and although the populations are healthy, they have been growing for the past 60 years and are thus composed almost exclusively of individuals born after 1965. To detect very old individuals today using laminated tissues, AAR, or new molecular clock aging methods (9) would still require extremely large sample sizes before detecting a single superannuated individual. Consequently, we believe that it is reasonable to hypothesize that now estimated baleen whale life spans are biased low. We set out to test this hypothesis by analyzing mark-recapture data collected from two great whale species closely related to bowhead whales. Our estimation approach does not rely on directly aging individuals using AAR, laminated tissues, or DNA methylation.

Instead, we fit survival functions to the 40+-year mark-recapture datasets collected from North Atlantic right whales (NARWs; *Eubalaena glacialis*) and southern right whales (SRWs; *Eubalaena australis*) using the methods described in (10, 11). This approach does not require a population to be at a stable age distribution to estimate expected longevity, nor does it require that we have samples from extremely old individuals to infer that such individuals likely exist. Instead, the approach estimates the rate at which marked individuals disappear from an observed population and the shape of the survival curve describing the age-specific probability of disappearance. From the fitted curves, we can estimate the fraction of a population surviving to a given age and potential longevity. NARW and SRW are phylogenetically very closely related and have essentially identical life histories. Their currently believed maximum life spans are both around 70 to 75 years (12). Our results suggest that median life span of SRW is around 74 years, and more than 10% live past 130 years, while NARW are living short lives, with median life spans of only 22 years, and only a small fraction surviving past age 45.

RESULTS AND DISCUSSION

For both the SRW and NARW mark-recapture time series, all 10 candidate parametric survival models converged. Except for the exponential model, which fit very poorly, all fitted models yielded similar survival and hazard functions and were generally in agreement about patterns of longevity and senescence for both species (Fig. 1, A and B). The Gompertz function fit best in both cases, with SRW best fit by an unmodified Gompertz and NARW best fit by a Gompertz function with bathtub modification (Tables 1 and 2; figs. S2 and S3 for parameter posteriors).

The estimated longevity of female NARW and SRW differed markedly. Median life span for SRW was 73.4 years {95% credible

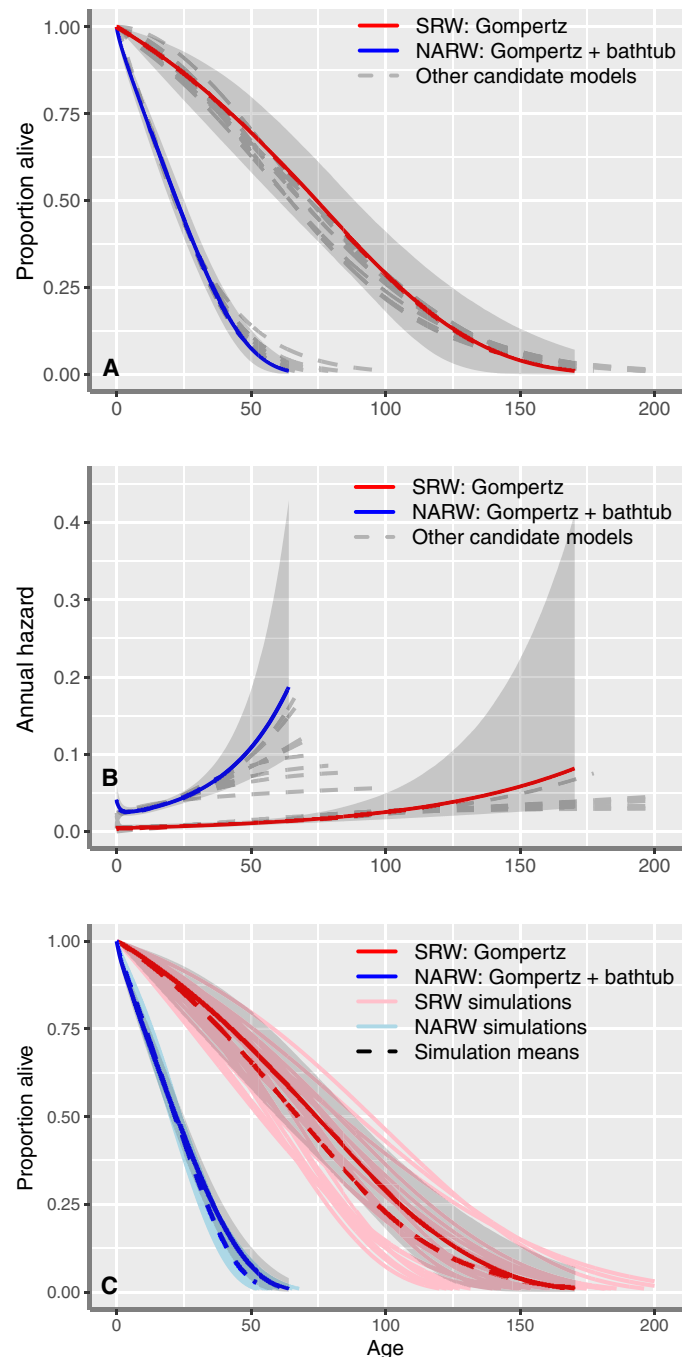


Fig. 1. Fitted SRW and NARW survival and hazard curves, and validation simulations. (A) Survival functions for each of the 10 models fitted. Colored lines with gray 95% credible interval (CI) uncertainty region show the best fitting model for each species, while gray dashed lines show the models that were not selected (except for exponential, which fit very poorly and is not shown). (B) Hazard functions for the 10 models fitted. Dashed gray lines show model fits that were not selected, while colored lines with gray uncertainty regions show the selected candidate model. (C) Validation simulations. Solid colors and gray uncertainty regions show the original best-fit models' fit to empirical data, pastel colors show fits to 24 different simulated data realizations generated from survival parameters estimated from real data, and dashed colored lines show the average of all fits to simulated data.

Table 1. Model rankings based on DIC, ranking highest to lowest. NA, not applicable; DIC, Deviance Information Criterion.

Model	Adjustment	<i>k</i>	DIC	ΔDIC
North Atlantic right whale				
Gompertz	Bathtub	6	6,148	–
Gompertz	Makeham	4	6,159	10
Gompertz	Unmodified	3	6,164	16
Logistic	Bathtub	7	6,177	29
Weibull	Bathtub	6	6,198	49
Weibull	Makeham	4	6,201	60
Logistic	Makeham	5	6,250	109
Logistic	Unmodified	4	6,300	152
Weibull	Unmodified	3	6,420	271
Exponential	NA	2	6,607	459
Southern right whale				
Gompertz	Unmodified	3	9,155	–
Gompertz	Bathtub	6	9,190	35
Weibull	Bathtub	6	9,254	99
Logistic	Makeham	5	9,289	134
Gompertz	Makeham	4	9,292	137
Weibull	Unmodified	3	9,314	159
Logistic	Unmodified	4	9,323	168
Weibull	Makeham	4	9,356	201
Logistic	Bathtub	7	9,419	264
Exponential	NA	2	10,220	1065

Table 2. Estimated parameters for best fitting model for each species. See figs. S2 and S3 for posterior distribution density plots. CI, credible interval.

Parameter	Estimate	Lower 95% CI	Upper 95% CI	$\hat{\rho}$
North Atlantic right whale: Gompertz with bathtub				
a_0	–3.940	–5.096	–2.990	1.000
a_1	0.870	0.131	2.369	1.001
c	0.008	0.0004	0.019	1.002
b_0	–4.410	–5.312	–3.806	1.016
b_1	0.042	0.024	0.066	1.060
ρ	0.726	0.713	0.738	1.000
Southern right whale: Unmodified Gompertz				
b_0	–5.409	–6.212	–4.772	1.016
b_1	0.017	0.008	0.031	1.015
ρ	0.180	0.173	0.188	1.005

interval (CI) [60.0, 88.3]}, with 10% of individuals expected to survive past 131.8 years (95% CI [110.9, 159.3]). By contrast, median life span of NARW was just 22.3 years (95% CI [19.7, 25.1]), with 10% of individuals expected to live past 47.2 years (95% CI [43.0, 53.3]) (Fig. 1, A and B). These different life spans result in markedly lower potential lifetime calf production for NARW compared to SRW (Table 3).

Fits of survival models to data simulated from the parameters estimated from real data suggest that estimates of longevity for NARW

are accurate and generally unbiased. Although fits to individual simulated data realizations did not perfectly match the fit to real data, most were very close. If anything, the fit slightly overestimated the rate of senescence (Fig. 1C). Fits to simulated SRW survival data generally surrounded the real fit, with nearly equal fits suggesting slower senescence and faster senescence than the fit to the real data. Fits to simulated data tended to fall outside the 95% uncertainty region of empirical fits to a greater degree than would be expected, suggesting that the model-estimated credible intervals are too narrow. Similar to

Table 3. Projected lifetime calves produced by female southern and North Atlantic right whales given estimated life spans under different average calving intervals. Assumed age at first reproduction is 12 years. RW, right whale.

Calving interval	Total lifetime calves	
	Southern RW	North Atlantic RW
3	21.2	4.6
4	15.9	3.4
5	12.7	2.8
6	10.6	2.3
7	9.1	1.9
Juvenile survival	93%	71%

the NARW, fits to data simulated from SRW indicate, if anything, a slight negative bias in longevity estimates (Fig. 1C). Overall, fits to simulated data suggest minimal bias and provide confidence that longevity estimates for both NARW and SRW are representative.

We thus conclude that SRWs have the potential to live over 130 years, which exceeds the current longevity estimate of 70 to 80 years by at least 50 years (12). The only mammal known to live longer is the closely related bowhead whale. Given the close phylogenetic relationship between the three extant right whales [North Atlantic, North Pacific (*Eubalaena japonica*), and southern] and their similar life histories, it is likely all right whales have the potential to live well past 100 years and perhaps approach 150. Our analysis, however, indicates only SRW longevity was extreme. NARW median age at death was just 22, with only 10% reaching age 48, far shorter than conventional estimates. However, we do not attribute the notable difference in estimated longevity to represent an intrinsic difference in respective life histories and expect that NARWs are physiologically capable of longevity equal to SRWs.

Instead, the very short life span of NARW almost certainly results from the well-documented anthropogenic and ecological factors that greatly increase the mortality hazard across age classes (13–15). NARWs experience their lowest annual mortality hazard in their fifth year of life. In that year, they have an expected 2.56% chance of dying. By comparison, SRW hazard in the fifth year of life is only 0.5%, and their annual mortality hazard does not exceed 2.56% until their 102nd year of life. NARW and SRW are very closely related and have otherwise identical life histories. Particularly notable is their identical age at first reproduction, a trait highly correlated with longevity across mammalian taxa (16). NARWs are somewhat larger (~35%) than SRWs, but that should confer relatively longer and not shorter life spans (4).

The short life spans estimated for NARW are of great concern, but given the large number of other studies documenting high mortality and other negative changes to vital rates of this gravely endangered whale, they are expected. If NARW life spans are normally as long as SRW, then such longevity would impart a degree of robustness at both the individual and population levels to resource disruptions. With a long life span, individuals can delay age at first reproduction or lengthen calving intervals to defer reproductive effort until conditions are favorable (17). Animals with short life spans have less flexibility to defer reproduction without sacrificing one of a small number of lifetime reproductive opportunities. NARW life history traits are consistent with much longer life spans, which is

more evidence that current short life spans are due to atypically high mortality. There is extensive discussion of the endangered status of NARW and potential management and conservation actions (13, 18–20), and we direct readers to those sources for a deeper discussion of their conservation challenges.

Extreme longevity in right, bowhead, and other whales

Although the longevity that we estimated for SRW is much longer than conventionally understood, we believe that our estimates are accurate. These estimates should not be unexpected given the established allometric curves relating body mass and longevity and increasing evidence of great longevity demonstrated in other cetacea (2, 7, 21, 22). The finding of extreme longevity in SRW, in the context of that already demonstrated in bowhead whales and similar overall life histories, suggests the potential for extreme longevity is a trait common to all four members of the Balaenidae.

The potential for extreme longevity, however, may not be limited to this cetacean family, and it may be a common life history trait among other large cetaceans. The 2010 observation of a fin whale in Norway to be at least 120 years and perhaps as old as 140 considerably increased the known maximum age for that species (7). The oldest narwhal (*Monodon monoceros*) found in a relatively small sample of individuals aged by Canadian scientists was reported to be 114 years in 2007 (22), and recent evidence that beluga (*Delphinapterus leucas*) could also exceed 100 years has also emerged (21). These new detections of superannuated individuals may be occurring now due to better aging methods combined with populations of whales that are beginning to recover older age classes after industrial whaling. Earlier estimates, made shortly after or during industrial whaling, were likely biased downward because intense, century-long hunts destroyed the older age classes, leaving only young individuals alive to sample. In addition, contemporary aging methods (counting of laminated tissues, especially teeth and ear plug growth layer groups) are well demonstrated to be biased low, especially for very old individuals (5). Last, it seems that there may have been, or perhaps still is to some degree, an unwillingness to believe that animals could live that long. This is evidenced by the originally long-held belief that two layers of ear wax or tooth growth layers were deposited each year; when it was lastly demonstrated that single annual layers are deposited, all previous estimated ages using these methods had to be doubled (21, 23–25).

All three Arctic endemic cetaceans (beluga, narwhal, and bowhead whales) have had direct observations of very old individuals,

mostly via AAR of the eye lens (21, 22, 26). While it is possible that Arctic species experience selective forces that promote extreme longevity more so than temperate counterparts, it is at least as likely that detecting superannuated individuals is simply a matter of sampling. All three Arctic endemics experienced lower hunting pressure during industrial whaling, and a subset of their populations may have been protected from whaling by sea ice, allowing an older age class to survive that period. At least, all three species are subject to a current high degree of sampling owing to aging of individuals taken in well-regulated Indigenous hunts. AAR is the most precise aging method now available, which requires the removal of the eye lens. This cannot be achieved from live individuals and is generally only possible from freshly dead animals. Such specimens are available for few, if any, temperate cetaceans because they are not hunted. In addition, temperate species would not have had sea ice in which to take refuge from Yankee and Industrial Whalers, and, consequently, fewer or no old individuals would have survived industrial whaling. Thus, even if old individuals historically existed, they likely would not today, and, even if they did, we do not yet have a way to accurately age them without lethal sampling. This may be changing as epigenetic aging methods mature methodologically, but these methods are still imperfect and now tend to underestimate the age of the oldest individuals (27, 28).

Conservation and management implications and conclusions

For most marine mammals, population models are usually central to assessment regardless of the degree that they are threatened by human activities. In most cases, especially in the modeling of whale populations, models are built with a few known parameters and limited data from the population in question, with the lion's share of parameters and assumptions borrowed from other species or systems. Some parameters, often key, are simply assumed (29). Life span is usually among these, and even where a hard cap on life span is not directly imposed, models are conditioned using post-whaling age structures, where even middle-aged individuals are absent or underrepresented. Inference drawn from such models about fitness, potential lifetime reproductive success, population momentum, and robustness to resource disruptions would almost certainly be biased downward where assumed potential life spans are shorter than reality or age structures used to build models are missing older age classes.

Survival analysis can estimate actuarial age-specific survival and potential longevity in populations of mostly young individuals recovering from whaling. However, this approach has some limitations. It requires long, well-observed time series, and few, if any, other whale populations likely have sufficient data. The approach also cannot be used to estimate changes in survival between time points in the time series and assumes that there have been no appreciable changes in mortality over the analyzed period. This assumption has likely been violated in our analysis in the case of NARW, as mortality rates increased around the year 2000, and, consequently, our estimate of a 22-year median longevity is likely optimistic. It may also have been violated in the case of SRW. However, any bias resulting from changes in the mortality over the course of the mark-recapture time series would be conservative with respect to the central question of our analysis, estimating maximum life span. Variance in mortality parameters over time would cause estimates of maximum life spans to be shorter than the true maximum (see simulation analyses in the Supplementary Materials).

Similarly, it is difficult to evaluate how negative density dependence might affect mortality and potential longevity as populations recover following industrial whaling. Whaling reduced populations to sizes where density dependence was nonexistent. However, we expect maximum longevity to be minimally or not affected by density dependence as these populations return to their historical pre-whaling sizes. In most long-live mammals, as populations approach carrying capacity (K), adult mortality is minimally or not affected (30, 31). More typically, and we expect that this should be the case for many large whale populations, as populations approach K , the vital rates that would be affected to slow growth and reduce population size are age at first reproduction, calving interval, and juvenile mortality (31, 32). As populations feel density dependence, fewer calves are born, and, of those born, fewer reach adulthood. Adults, by contrast, are superior competitors so can acquire enough resources to survive, even during resource disruptions, and can conserve energy expenditure by deferring reproduction, especially if they have long life spans.

Adult survival could be affected if there is a major overshoot of K or marked change in the environmental conditions that reduces K considerably. However, adult whales are likely very well equipped to weather mild to moderate environmental variation or disruptions in ocean productivity, as their large size allows them to take advantage of intense bursts of ocean productivity by storing energy in the blubber and relying on those stores for many months or even years. The large size also affords very low mass-specific metabolic rates, so they can both store extraordinary amounts of energy and use those stores very economically. It also limits potential predators to essentially only killer whales. However, adult great whales may be even be too large for killer whales, and predation-related mortality of adults is likely near zero as killer whales usually (but not always) target calves (33, 34). This collection of traits may be key in the evolution of extreme longevity, and before industrial whaling when whale populations worldwide were likely close to K , whales may have reproduced much less frequently. Whales may have deferred reproduction during unproductive phases of decadal oscillations, waiting until productive phases. Such an extremely slow pace of life would require great potential longevity to work, and it may not be the life history strategy of every large whale. Species such as minke and gray whales may have evolved shorter, faster, life history strategies than right and bowhead whales (35).

Last, although we validated our analysis by simulation, it will not be possible to validate the longevity estimate for SRW with directly measured ages for decades to come. Few, if any, extremely old individuals could have survived whaling, and there has not been time for animals born after whaling to achieve great age. While many whale populations may have ecologically recovered from whaling, extreme life spans mean that reaching stable age distributions that include the oldest age classes could still be 50 or 100 years away.

MATERIALS AND METHODS

Mark-resight data

From 1979 to 2021, SRWs were annually surveyed in October by helicopter between Nature's Valley and Muizenberg, False Bay, along the south coast of South Africa. All individuals sighted were noted, and callosity patterns of females with calves were carefully photographed for identification purposes. Photos were compared to a long-running photo-identification catalog and matched. Over the

42-year period, this resulted in a mark-recapture dataset of 2476 unique females, of which 139 have known birth years. Survey methods and photo-identification details are available in (36, 37).

Mark-recapture records for NARW spanned approximately the same period. Starting in the mid-1970s, a photographic catalog of all NARWs began, and the observation effort intensified and became more organized in the 1980s. Unlike the SRW mark-recapture data, observations for NARW are assembled by a large group of collaborating scientists working across the species' entire range. The photographic catalog and data are maintained by the North Atlantic Right Whale Consortium, who made the mark-recapture records of females available for this analysis. All NARWs encountered by members of the consortium any time during the year and in any geographic region, were photographed. These photos are compared to the master catalog maintained by the consortium and matched to individuals on file. This much more intense survey effort results in many observations per year for most individuals. Here, we analyze only observations from females.

Following (38), these multiple detections per year were reduced so that the detection period was simply annual, and individuals in a given year were either detected (1) or not detected (0). In total, this dataset spanned 1974 to 2020 and included 328 unique females, of which 205 had known birth years. Further details on data collection and the photo-identification catalog can be found in (38, 39).

One notable difference between the NARW and SRW mark-recapture time series is the size and trajectory of the respective populations that were observed. As the SRW population is large and growing, new individuals have steadily been incorporated into the SRW dataset since the study's inception, most of which do not have known birth years. Individuals with unknown birth year detected after 1990 also have short observation periods (relative to life span) and thus provide minimal information about the shape of the survival function. Therefore, we limited the analysis of SRW data to individuals with known birth year or individuals first observed (but without a known birth year) before 1985. The resulting SRW dataset included 361 individuals: 139 with known birth year and 222 with unknown birth year but observation periods > 35 years. Similar subsampling was not required for NARW because most of the individuals in the dataset have known birth year and nearly all individuals added to the mark-recapture database without known birth year were added before 1990 and thus have long observation periods relative to their life spans. Both the SRW and NARW mark-recapture datasets have had relatively steady observation effort over their respective time series with no missing observation years. Thus, the analyzed samples for SRW and NARW were of similar size, length, and quality and, as they both included hundreds of individuals, were more than adequate for estimation of longevity; data are publicly available at the Dryad repository (<https://doi.org/10.5061/dryad.np5hqc01m>).

Survival modeling

Mark-recapture data were fit with parametric survival models using the R package "BaSTA" (10, 11). This survival modeling framework is specifically designed for, and relatively robust to, both left truncation (unknown birth year) and right censoring (individuals surviving past the study period). Four basic mortality functions were fit. These included an exponential mortality function (40), with constant, age-independent mortality specified as

$$\mu(x|b) = b; b > 0 \quad (1)$$

where μ is the instantaneous mortality rate, b is the shape parameter, and x is age.

The Gompertz mortality function (41, 42)

$$\mu(x|\theta) = e^{b_0+b_1x}; -\infty < b_0, b_1 < \infty \quad (2)$$

where b_0 is age-independent shape parameter and b_1 is the age-specific shape parameter, and θ represents the parameter vector; in this case, $\theta = [b_0, b_1]$.

The Weibull mortality function (43)

$$\mu(x|\theta) = b_0 b_1^{b_0} x^{b_0-1}; b_0, b_1 > 0 \quad (3)$$

where both b_0 and b_1 are age-specific shape parameters.

In addition, the logistic mortality function (42)

$$\mu(x|\theta) = \frac{e^{b_0+b_1x}}{1 + b_2 e^{b_0}/b_1 (e^{b_1x} - 1)}; b_0, b_1, b_2 > 0 \quad (4)$$

where b_0 and b_2 are the age-independent shape parameters and b_1 is the age-specific shape parameter.

Except for the exponential mortality function, to the basic model shapes, we further considered the "Makeham" adjustment (42), which adds a constant value c to the base mortality function

$$\mu_0(x|\theta, c) = \mu(x|\theta) + c \quad (5)$$

and the "bathtub" adjustment (44), which adds both a concave shape to the mortality curve (to accommodate high juvenile mortality) as well as a constant

$$\mu(x|\theta, a_0, a_1, c) = \mu(x|\theta) + e^{a_0 - a_1 x} + c \quad (6)$$

where $-\infty < a_0 < -\infty, a_1 \geq 0$ and $c \geq [e^{a_0 - a_1 x_{\min}} + \mu(x_{\min}|\theta)]$; x_{\min} is the age at which Eq. 6 takes its lowest value.

Thus, in total, we fit 10 different survival models. The first nine models include the Gompertz, logistic, and Weibull models fit without adjustments, those same three models fit with the Makeham adjustment, and again with the bathtub adjustment. The 10th model was the exponential, which, as an age-independent constant parameter model, the Makeham and bathtub adjustments are not sensible and thus not included.

Models were fit in a Bayesian framework using a Reversible Jump Markov chain Monte Carlo (MCMC) simulation with Metropolis-within-Gibbs sampling specifically designed to sample mark-recapture data (10), running two chains for 2,000,000 updates, with a burn in of 1,000,000 and a thin of 250. Convergence was assessed by visual inspection of chains and Gelman-Rubin statistic ($\hat{\tau}$) values below 1.1 for all parameters. Candidate model fit was evaluated using the Deviance Information Criterion statistic (DIC), and models with the lowest DIC were considered best fitting.

Estimation of lifetime reproductive output

Our analysis was primarily focused on establishing expected and maximum life spans of SRW and NARW. However, to understand how different life spans might affect lifetime reproductive output and the potential long-term persistence of the two species analyzed, we estimated the total number of calves an average female would produce in their lifetimes. To do this, we integrated the survival curves and multiplied the integrals by a range of typical calving intervals (every 3 to every 7 years). This produced the estimates shown in Table 3.

Validation by simulation

The methods used here were well vetted and validated by simulation by (10) when initially introduced and have been subsequently used in numerous analyses to accurately estimate animal longevities from mark-recapture data identical in structure to ours (45–49). The nature of the data that we analyzed, however, is extreme relative to other published examples, and it is unclear that our time series of observations is long enough to estimate longevity, particularly for SRW. Therefore, to evaluate whether the life spans that we estimated were potentially inaccurate or biased, for both NARW and SRW, we simulated a population of life spans from the fitted survival model parameters. To this simulated population of life spans, we further simulated the observation process using the estimated mark-recapture detection probabilities. These simulated mark-recapture time series were then fit using the BaSTA package exactly as the real data had been originally fit to see how well they recovered the survival curves.

Our main concern in assessing the potential for bias was the relatively short observation periods (45 years) relative to the long life spans that we estimated (>100 years). Therefore, we simulated datasets that were identical to ours, which included the same number of individuals with known and unknown birth year. For individuals with known birth years, we used the same known birth years, and, for those without known birth year, we used the same year of their first record in the real mark-recapture database.

For each simulated individual, we began populating their mark-recapture record by drawing a random age at death from the survival curve fit to the real data. For individuals with known birth year, we added the age at death to the birth year to establish a year of death. For individuals without known birth year, we also simulated the age at which that individual was first observed from a uniform distribution that ranged between age 5 and $0.9 \times (\text{age at death})$. For these individuals, the year of death was established by adding the year that they were first detected to the number of years left in their life given their age when first observed.

Note that we bound the above uniform distribution on age of first observation for those without known birth year for the following reasons. Individuals younger than age 5 would have an inferred birth year based on morphology during their first observation in the real data. Elderly individuals are likely reproductively senescent, and individuals without calves were not recorded in the SRW data. Thus, a simulated individual's age at first observation was always between age 5 and before it reached 90% of their age at death.

To simulate the observation process, we drew from a Bernoulli distribution with a probability p (the detection probability estimated from the real data) for all years between first observation and death that coincided with the years' mark-recapture surveys were conducted (1974 to 2020 for NARW and 1979 to 2021 for SRW). This produced a mark-recapture time series for each individual and an overall simulated dataset with exactly the same structure, years of first observation, and duration as the real NARW and SRW datasets. However, for these simulated whales, we know the age of death of every individual as well as the true population longevity and senescence curves because we simulated from those known parameters.

Once generated, simulated datasets were fit with BaSTA assuming a Gompertz mortality function without modification (SRW) and with a bathtub modification (NARW) as these were the respective best fitting survival models to the real data. For both SRW and NARW, 24 simulated datasets were fit to evaluate any systematic bias

of the survival functions fit to simulated datasets relative to the fit to real observations from which those data were generated.

Effect of changes in mortality during the mark-recapture time series

In addition to validating that models could recover parameters from simulated data without bias, we also evaluated how a key assumption violation might affect estimates. The models that we fit assumed that the survival parameters associated with each survival function were stationary and did not change during the period data were observed. This is ecologically unlikely in most situations and especially unlikely over the very long time spans from which observations were made for this analysis.

To assess how a violation of this assumption might affect estimates of longevity, we used the same simulation approach as described above, except that we generated the data by mixing two survival curves. The first 21 years of the simulated time series (1979 to 2000) were simulated using the survival function estimated from the real SRW data, with maximum longevities of about 135 years. After 2000, we set the mortality to increase markedly, so that maximum longevity dropped to ~65 years. This was accomplished by increasing the b_0 parameter of the Gompertz function from -5.409 to -4.00 .

The mark-recapture observation process was then simulated as described above, and these simulated data were fit using the simple Gompertz survival function to see whether the resulting mixtures would be biased in unexpected ways. We found, as expected, that changes in the mortality during the time series resulted in survival curves that were intermediate between the two being mixed (fig. S1). This means that, with respect to the question being asked in this analysis, the bias introduced is conservative. Violation of the stationarity assumption in survival parameters does not result in overestimates of maximum longevity. On the contrary, maximum longevity estimates will be biased low, if the time series includes periods of elevated mortality due to harmful anthropogenic interactions such as entanglements or periods of harsh ecological conditions. If anything, the maximum potential longevities of SRW fitted in our analyses are underestimated.

Supplementary Materials

This PDF file includes:

Figs. S1 to S3

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