

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 lifespans. Median lifespan for SRW was 73.4 years, with 10% of individuals surviving past 131.8 years. NARW lifespans were likely anthropogenically shortened, with a median lifespan 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 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). Though most individuals had fewer than 20 lamina, a few specimens had over 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 non-human 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 1880's (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 bowhead whales lived at least 130 years. After the recovery of these artifacts, (3) used aspartic acid racemization (AAR) of the eye lens, 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 & 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, does not exist.

There are three confounding issues in current whale age estimation, and all likely result in considerable downward bias on expected lifespan 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 remodelling, 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).

Secondly, assuming 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 if 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 currently 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.

Finally, 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 were collected from individuals taken by Japanese whalers. The currently 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 by American scientists). Ear plug lamination counts were only discovered as a method of aging in the 1950's (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 though 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 it reasonable to hypothesize that currently estimated baleen whale lifespans 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. Importantly, 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 data sets collected from North Atlantic right whales (NARW, *Eubalaena glacialis*) and southern right whales (SRW,

Eubalaena australis) using the methods described in (10, 11). Importantly, this approach does not require a population to be at a stable age distribution to estimate expected longevity, nor does it require 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 (see SI for methodological details). 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 lifespans are both around 70-75 years (12). Our results suggest that *median* life span of SRW is around 74 years, and a significant fraction live past 130 years, while NARW are currently living remarkably short lives, with median lifespans of only 22 years, and only a small fraction surviving past age 45.

Results & Discussion

For both the SRW and NARW mark-recapture time series, all 10 candidate parametric survival models converged. Except for the exponential fits, 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. 1a & 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 & 2).

The estimated longevitys of female NARW and SRW differed markedly. Median lifespan for SRW was 73.4 years (95% 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 lifespan 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. 1a,b). These different lifespans result in dramatically 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 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 the model-estimated credible intervals are too narrow. Similar to 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 longevities estimated for both NARW and SRW are representative.

We thus conclude SRW have the potential to live over 130 years, which exceeds the current longevity estimate of 70-80 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 striking difference in estimated longevities to represent an intrinsic difference in respective life histories, and expect NARW are physiologically capable of longevity equal to SRW.

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). NARW experience their lowest annual mortality hazard in their 5th year of life. In that

year they have an expected 2.56% chance of dying. By comparison, SRW hazard in the 5th 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 are their identical age at first reproduction, a trait highly correlated with longevity across mammalian taxa (16). NARW are somewhat larger (~35%) than SRW, but that should confer relatively longer and not shorter lifespans (4).

The short lifespans 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 unsurprising. If NARW lifespans are normally as long as SRW, such longevity would impart a degree of robustness, at both the individual and population levels, to resource disruptions. With a long lifespan, individuals can delay age at first reproduction or lengthen calving intervals to defer reproductive effort until conditions are favorable (17). Animals with short lifespans 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 lifespans, which is more evidence that current short lifespans 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 source for a deeper discussion of their conservation challenges.

Extreme longevity in right, bowhead, and other whales. Although the longevity we estimated for SRW is much longer than conventionally understood, we believe our estimates are accurate. These estimates should not be surprising 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, centuries-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). And finally, 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 finally demonstrated that single annual layers are deposited, all previous estimated ages using these method had to be doubled (21, 23–25).

Interestingly, 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 as importantly, 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 currently 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 wouldn't 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 currently tend to underestimate the age of the oldest individuals (27, 28).

Conservation & management implications & conclusions. For most marine mammals, population models are usually central to assessment regardless of the degree 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). Lifespan is usually among these, and even where a hard cap on lifespan 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 lifespans 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, it 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 lifespans to be shorter than the true maximum (see simulation analyses in the SI).

Similarly, it is difficult to evaluate how negative density dependence might impact mortality and potential longevity as populations recover following industrial whaling. Whaling reduced populations to sizes where density-dependence was non-existent. However, we expect that maximum longevity to be minimally or not impacted by density dependence as these populations return to their historical pre-whaling sizes. In most long-live mammals, as populations approach K , adult mortality is often minimally or not affected (30, 31). More typically, and we expect this should be the case for many large whale populations, as populations approach K , the vital rates that would be impacted 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 impacted if there is a major overshoot of K or drastic 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, adults 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 prior to industrial whaling when whale populations world wide were likely close to K , whales may have reproduced much less frequently. Whales may have deferred reproduction during unproductive phases of decade 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 whale may have evolved shorter, faster, life history strategies than right and bowhead whales (35).

Finally, 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 lifespans mean that reaching stable age distributions that include the oldest age classes could still be 50 or 100 years away.

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Tables

Model	Adjustment	k	DIC	Δ DIC
North Atlantic Right Whale				
Gompertz	bathtub	6	6148	-
Gompertz	Makeham	4	6159	10
Gompertz	unmodified	3	6164	16
Logistic	bathtub	7	6177	29
Weibull	bathtub	6	6198	49
Weibull	Makeham	4	6201	60
Logistic	Makeham	5	6250	109
Logistic	unmodified	4	6300	152
Weibull	unmodified	3	6420	271
Exponential	NA	2	6607	459
Southern Right Whale				
Gompertz	unmodified	3	9155	-
Gompertz	bathtub	6	9190	35
Weibull	bathtub	6	9254	99
Logistic	Makeham	5	9289	134
Gompertz	Makeham	4	9292	137
Weibull	unmodified	3	9314	159
Logistic	unmodified	4	9323	168
Weibull	Makeham	4	9356	201
Logistic	bathtub	7	9419	264
Exponential	NA	2	10220	1065

Table 1: Model rankings based on DIC, ranking highest to lowest.

Parameter	Estimate	Lower 95%CI	Upper 95%CI	\hat{r}
North Atlantic Right Whale - Gompertz w/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

Table 2: Estimated parameters for best fitting model for each species.

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%

Table 3: Projected lifetime calves produced by female southern and North Atlantic right whales given estimated lifespans under different average calving intervals. Assumes age at first reproduction is 12 years.

Figures

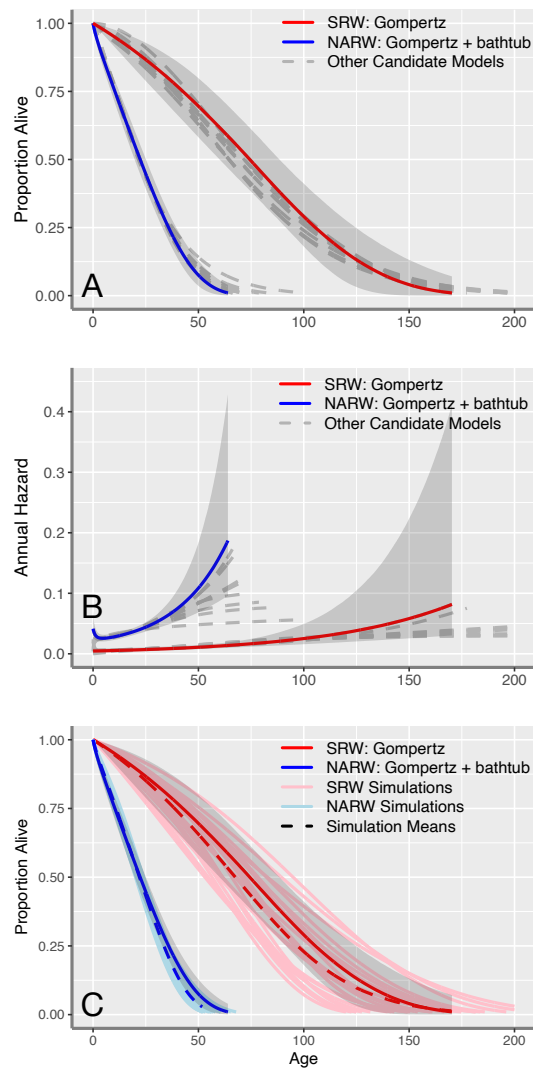


Figure 1: **A)** Survival functions for each of the 10 models fitted. Colored lines with grey 95% CL uncertainty region show the best fitting model for each species, while grey dashed lines show the models that were not selected (except for exponential, which fit very poorly and is not shown). **B)** Hazard functions for the 10 models fitted. Dashed grey lines show model fits that were not selected, while colored lines with grey uncertainty regions show the selected candidate model. **C)** Validation simulations. Solid colors and grey 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 simulated fits.