Article:

Ellis, Sam, Croft, Darren P., Nielsen, Mia Lybkær Kronborg et al. (2 more authors) (2025) Bayesian inference of toothed whale lifespans. Biological Journal of the Linnean Society. blaf022. ISSN 0024-4066

https://doi.org/10.1093/biolinnean/blaf022

Biological Journal of the Linnean Society, 2025, **144**, blaf022
https://doi.org/10.1093/biolinnean/blaf022
Advance access publication 27 May 2025
Original Article

Original Article

Bayesian inference of toothed whale lifespans

Samuel Ellis[1,*], Darren P. Croft[1,†], Mia Lybkær Kronborg Nielsen[1,2,†], Daniel W. Franks[3,‡] and Michael N. Weiss[1,4,‡]

[1]Centre for Research in Animal Behaviour, Department of Psychology, University of Exeter, Exeter, United Kingdom
[2]Department of Ecoscience, Aarhus University, C. F. Møllers Allé 3, 8000 Aarhus C, Denmark
[3]Department of Biology, University of York, York, United Kingdom
[4]Centre for Whale Research, Friday Harbor, Washington State, United States

†These authors contributed equally to this work.
‡These authors contributed equally to this work.

[*]Corresponding author. Centre for Research in Animal Behaviour, Department of Psychology, University of Exeter, Exeter, United Kingdom. E-mail: s.ellis@exeter.ac.uk

ABSTRACT

Accurate measures of lifespan and age-specific mortality are important both for understanding life-history evolution and for informing conservation and population management strategies. The most accurate data to estimate lifespan are from longitudinal studies, but for many species (especially those, such as toothed whales, that are wide ranging and inhabit environments that are difficult to access) these longitudinal data are not available. However, other forms of age-structured data, such as data from mass strandings, are available for many toothed species, and using these data to infer patterns of age-specific mortality and lifespan remains an important outstanding challenge. We developed and tested a Bayesian mortality model to derive parameters of a mortality function from age-structured data while accounting for potential error introduced by mistakes in age estimation, sampling biases, and population growth. We then searched the literature to assemble a database of 269 published age-structured toothed whale datasets. We applied our mortality model to derive lifespan estimates for 32 species of female and 33 species of male toothed whale. We also used our model to characterize sex differences in lifespan in toothed whales. Our mortality model allowed us to curate the most complete and accurate collection of toothed whale lifespans to date.

Keywords: toothed wales; odontocetes; lifespan; life history

INTRODUCTION

Quantifying age-specific mortality risk (i.e. the hazard of an individual dying given their age) is fundamental to the study of life-history evolution (Shefferson *et al.* 2017) and is vital to informing conservation and population management strategies (Wade 2018). Data from longitudinal studies of individually identified individuals are the benchmark for calculating age-specific mortality risk. Tracking individuals from birth to death can give an unbiased measure of age-specific mortality risk over the time period when the observations were conducted (Caughley 1966, Hamlin *et al.* 2000, Nuñez *et al.* 2008, Gaillard *et al.* 2017). Although the number of species for which these data are available is increasing (e.g. Salguero-Gómez *et al.* 2016, Lemaître *et al.* 2020) they are still rare and hard to collect, especially for long-lived species and those that are difficult to study in the wild.

Toothed whales (Odontocetes) are difficult to follow longitudinally through their life owing to both their wide-ranging habits in marine habitats and, in at least some species, their extreme longevity. Addressing this challenge is crucial, because characterizing age-specific mortality of toothed whale species is important to inform conservation efforts. Toothed whale populations are subject to a variety of stressors, including fisheries bycatch (Lewison *et al.* 2004), whaling (Clapham *et al.* 2007), pollution (Reijnders *et al.* 2018), anthropogenic noise (National Research Council 2005), and a changing climate (van Weelden *et al.* 2021, Kebke *et al.* 2022). Lifespan and age-specific mortality are important variables when modelling how populations will react to stressors. In addition to conservation implications, toothed whales represent a scientifically important case study of the links between sociality and life history, particularly given that they exhibit a diversity of social systems and life histories (Connor *et al.* 1998, Whitehead and Mann 2000, Gowans *et al.* 2007, Weiss *et al.* 2021), including being the only mammalian taxa in which menopause has evolved multiple times (Ellis *et*

Received 29 July 2024; revised 17 February 2025; accepted 23 March 2025

al. 2018a, b, 2024). It is therefore important to develop robust measures of lifespan that can be applied to toothed whales.

Although long-term longitudinal mortality data are rare in toothed whales, age-structured data are relatively common. The ages of individual toothed whales can be estimated by counting the growth rings in a cross-section of a tooth (Perrin and Myrick 1980, Read *et al.* 2018). This characteristic, along with a tradition of collecting detailed anatomical data from deceased whales (e.g. from mass-strandings or fisheries bycatch), has resulted in the widespread publication of age distributions of samples of toothed whales. However, reporting the ages of calves and younger whales is less common and less systematic than the reporting of adults. For this reason, throughout this study we focus on lifespan from age at maturity. Anatomical and age-distribution data from deceased whales have been an important (and, in many species, the only) source of information on demography, life history, and behaviour in toothed whales. However, because the data are cross-sectional, they have the potential to be biased as a measure of lifespan. In particular, three sources of error in cross-sectional mortality data have been identified: population growth or shrinkage, sample biases, and age-estimation error (Caughley 1966, Hamlin *et al.* 2000, Nuñez *et al.* 2008, Gaillard *et al.* 2017). Population change (growth or reduction) will affect the realized age distribution of a sample independently of patterns of mortality. For example, when a population is increasing, younger individuals will be over-represented in a given sample. Conversely, if a population is shrinking, older individuals will be over-represented. Sample biases might be introduced into the reported age distribution of whales both at the point of mortality (e.g. if younger individuals are more likely to be caught as fisheries bycatch) and during the sample (e.g. if larger, older, whales are preferentially selected for anatomical sampling). Likewise, and as with any data-collection methodology, errors in age estimation might be introduced during the process of counting growth rings in the teeth. Any method using age-structured data to derive age-specific mortality requires a mechanism to propagate error through to the final mortality parameter estimates.

In this study, we develop, test, and apply a method that uses age-structured data to derive estimates of age-specific mortality for toothed whale species. Specifically, we develop a Bayesian mortality model to estimate the parameters of a mortality function from age-structured data, while capturing variation in these values introduced by population growth, sampling biases, and age-estimation errors. We then use large-scale simulation to test our mortality model. Finally, we collate a database of age-structured toothed whale data from the literature and apply our methods to obtain estimates of age-specific mortality for as many toothed whale species as possible. We also use our models to compare male and female lifespans across our sample. Throughout this study, we focus on lifespan as a tractable and biologically relevant property of cumulative age-specific mortality.

MATERIALS AND METHODS

Mortality model

The number of whales of age i in a sample will depend on four key variables (Nuñez *et al.* 2008, Gaillard *et al.* 2017): (i) the probability of a whale surviving to age i; (ii) the population growth rate (positive or negative); (iii) biases in sampling; and (iv) error in age estimation. The aim of our model is to obtain a distribution of potential parameter values for a mortality model (i) given the unknown magnitude and influence of the other effects (ii–iv). Our model, therefore, does not aim to obtain a single 'best estimate' for the lifespan of each species, but rather to generate a distribution of potential lifespans given the observed data and the other processes that might be influencing the observed data. Subsequently, the model is not designed to estimate the effects of (ii–iv) and in fact when fitted, the posteriors of parameters relating to (ii–iv) do not usually differ from their priors. The presence of these parameters in the model, however, means that the derived distribution of mortality parameters (i) are those most consistent with the data, given the unknown effects (ii–iv).

In this section, we initially describe the case of the model applied to a single dataset. We then move on to describe how this single-dataset model can be generalized to combine data from multiple datasets, sexes, and populations of the same species into a single model.

We consider the count, c, of whales of a given age, AGE, in a sample to be drawn from a multinomial distribution, with probability θ over N individuals, where θ_i is a function of: survival to age AGE_i, L_i; the effect of population growth, R_i; and sampling biases at that age S_i (equation 1). Throughout this section AGE refers to age adjusted to age at maturity, such that age 0 is species- and sex-specific age at maturity.

$$\begin{aligned} c &\sim \text{Multinomial}(\theta,\ N) \\ \theta_i &= \frac{L_i R_i S_i}{\sum L_i R_i S_i} \end{aligned} \tag{1}$$

Survival

We model the underlying probability of an individual surviving to age i as the survival curve (equation 2) derived from the Gompertz mortality model (Gompertz 1825):

$$l(i) = e^{-(\alpha/\beta)\left(e^{\beta \times AGE_i}-1\right)} \tag{2}$$

where α is the baseline mortality and β is the increasing probability of mortality with age (ageing). Given that we are modelling survival only from age at maturity, we do not use the Makeham/bathtub form of the Gompertz equation. We chose the Gompertz mortality model because it has few parameters, is widely used in studies of mammal senescence (Gaillard *et al.* 2017), and was recently found to be the most parsimonious mortality model in several killer whale populations (Nielsen *et al.* 2021).

The probability that a sampled individual is of age i, L_i, is drawn from the probability density function of the survival equation. Hence:

$$L_i = \frac{e^{-(\alpha/\beta)\left(e^{\beta \times AGE_i}-1\right)}}{\sum_{j=0}^{n} e^{-(\alpha/\beta)\left(e^{\beta \times AGE_j}-1\right)}} \tag{3}$$

where n is the maximum possible age; here, we use n = 150 for all species.

Given that both Gompertz parameters are bounded between zero and one, we set up priors on α and β drawn from Beta distributions:

$$\begin{aligned} \alpha \quad &\sim \quad \mathrm{Beta}\left(p\alpha_1, \quad p\alpha_2\right) \\ \beta \quad &\sim \quad \mathrm{Beta}\left(p\beta_1, \quad p\beta_2\right) \end{aligned} \tag{4}$$

For this study, $p\alpha_1 = 6.79$, $p\alpha_2 = 166.31$, $p\beta_1 = 9.91$, and $p\beta_2 = 37.93$. These priors are centred on the mean of published Gompertz *alpha* and *beta* values for Artiodactyla, with a variance double that of the published data (Gaillard *et al.* 2004, Toïgo *et al.* 2007, Foote 2008).

Population growth rate

We model the increased probability of individuals of age i being observed owing to population growth R_i as:

$$\begin{aligned} R_i &= (1-\rho)^{AGE_i} \\ \rho &= \frac{r}{{}^{1}/_{2} \times \max\left(\mathrm{o}\right)} \end{aligned} \tag{5}$$

where r is the population growth parameter, with $r = 0$ representing a stable population, $r > 0$ a growing population, and $r < 0$ a shrinking population. For simplicity, we assume that the population growth rate is constant, or averages to a constant value, over the whole length of the study: r, therefore, represents annual population growth in any year of the study. The parameter ρ is the growth parameter scaled to the maximum observed lifespan of the species, max(o), such that the value of r can be compared directly between species and given a sensible and consistent prior. For example, $r = 0.1$ means that the population will increase by 10% over half the maximum species lifespan. Max(o) is calculated from the raw data.

We use priors that allow us to leverage any data that might exist on the given population:

$$r \ \in [-0.5, \ 0.5] \ \sim \begin{cases} \mathrm{Normal}\left(-0.25, \ 0.2\right) & pr = 1 \\ \mathrm{Normal}\left(0, \ 1\right) & pr = 0 \\ \mathrm{Normal}\left(0.25, \ 0.2\right) & pr = -1 \end{cases} \tag{6}$$

where $pr = 1$ indicates that there is strong evidence the population is growing, $pr = -1$ that there is strong evidence that the population is shrinking, and $pr = 0$ that the population growth status of the population is unknown. Priors are moderately informative and are limited between the population halving and doubling over half the maximum species lifetime.

Sampling bias

We model sampling biases as an increased or decreased probability that whales within a given window, W, are under- or over-sampled. The sampling bias age window, W, is a predetermined input into the model. Within the range a sampling bias effect s is applied, thus:

$$S_i \sim \begin{cases} s+1 & AGE_i \in W \\ 1 & AGE_i \notin W \end{cases} \tag{7}$$

where $s > 1$ indicates that ages within range W are more likely to be sampled, $s < 0$ that they are less likely to be sampled, and $s = 0$ means no differences within and outside the range.

The prior used for s in a given sample depends on whether the ages within the range are known to be over-sampled ($ps = 1$), under-sampled ($ps = -1$), or whether the direction is unknown ($ps = 0$).

$$s \ \in [-1, \ 2] \sim \begin{cases} \mathrm{Normal}\left(1, \ 0.5\right) & ps = 1 \\ \mathrm{Normal}\left(0, \ 2\right) & ps = 0 \\ \mathrm{Normal}\left(-1, \ 0.5\right) & ps = \ -1 \end{cases} \tag{8}$$

Age-estimation error

We consider the true age of each whale j in the sample, τ_j, to be drawn from a Gaussian distribution around the observed age o_j with standard deviation ε_j, where B is species–sex specific age at maturity; adding B therefore corrects between the real observed age of the sample and the model age (where age at maturity is age 0).

$$\begin{aligned} \tau_j &\sim \ \mathrm{Normal}\left(o_j, \ \varepsilon_j\right) \\ \varepsilon_j &= \frac{1}{20}\left(o_j + B\right) \end{aligned} \tag{9}$$

We selected a Gaussian distribution because it allows observed ages to be both over- and under-estimates of the true and allows assumptions around different ageing errors with age pattern to be explored.

We assume that the error is additive such that ε is 5% of the observed age, and therefore that there is a greater error around older samples than younger samples. The value of 5% was chosen to reflect a reasonable error rate in counting tooth rings, but changing this variable within reasonable bounds does not affect the model outcomes qualitatively. The outcome of this is that for a sample with an observed age of 10 years, the model assumes that there is a 90% probability that the true age is between 9 and 11 years, and for a whale of observed age 50 years there is a 90% chance the sample is between 45 and 55 years.

We use estimated true ages, rounded to the nearest integer (notation: $\lfloor x \rceil$), of all the whales in the sample (N) to calculate the counts c of whales of a given age i in each sample used for the rest of the model.

$$c_i = \sum_{k=1}^{N} \left[\ \lfloor \tau_k \rceil = AGE_i \right] \tag{10}$$

We combine these parts into a single model per species. Furthermore, we design the model such that we run one model per species, combining multiple datasets and both sexes (where available). We estimate mortality parameters (α and β) for each sex with data from multiple datasets. Where multiple datasets are derived from the same population (most commonly, one for each sex), we estimate a single population growth parameter for these datasets. We calculate a separate sampling bias metric for each dataset. The complete model is shown below (notation key in Table 1):

$$c \ \sim \mathrm{Multinomial}\left(\theta, \ N\right)$$

$$\theta_{d,i} = \frac{L_{d,i} R_{d,i} S_{d,i}}{\sum L_{d,i} R_{d,i} S_{d,i}}$$

Table 1. Explanation of symbols used in equation (1–11).

Symbol	Explanation
i	Model variable. Index through possible ages (see AGE).
d	Model variable. Index through datasets.
j	Model variable. Index through samples.
p	Model variable. Index through populations.
n	Model variable. Total number of possible ages.
N	Model variable. Total number of samples.
$c_{d,i}$	Model variable. Count of samples in dataset *d* of age *i*.
L_i	Model variable. Probability of surviving to age *i*.
$R_{d,i}$	Model variable. Change in probability of finding a whale of age *i* given population growth in dataset *d*.
$S_{d,i}$	Model variable. Change in probability of finding a whale of age *i* in dataset *d* owing to sampling bias.
ρ_d	Model variable. Change in population size over half the maximum lifespan of the whales in dataset *d*.
ε_j	Model variable. Standard deviation around the observed age of sample *j*.
o_j	Data. Observed age of sample *j*.
SEX_d	Data. Sex of whales in dataset *d*.
AGE	Data. Vector of possible ages of whales in the sample. Here 0–150 (where 0 = age at maturity).
POP_d	Data. Population to which dataset *d* belongs.
$DSET_j$	Data. Dataset sample *j* is drawn from.
W_d	Data. Window of ages with potential sampling bias in dataset *d*.
B_d	Data. Each at maturity of individuals in sample *d*.
pr_p	Data. Prior belief in the direction of population growth in population *p*.
ps_d	Data. Prior belief in the direction of bias for samples in W_d.
$p\alpha_{1\text{-}2}$	Data. Shape parameters (1 and 2) describing the prior expectation for Gompertz α values derived from the literature. Here: $p\alpha_1 = 6.79, p\alpha_2 = 166.31$.
$p\beta_{1\text{-}2}$	Data. Shape parameters (1 and 2) describing the prior expectation for Gompertz β values derived from the literature. Here: $p\beta_1 = 9.91, p\beta_2 = 37.93$.
$\alpha_{1\text{-}2}$	Parameter. Gompertz mortality model baseline mortality for females [1] and males [2].
$\beta_{1\text{-}2}$	Parameter. Gompertz mortality model ageing for females [1] and males [2].
τ_j	Parameter. True age of sample *j*.
r_p	Parameter. Population growth of population *p*.
s_d	Parameter. Sampling bias towards samples in window W_d.

$$L_i = \frac{e^{-\left({}^{\alpha_{SEX_d}}/{}_{\beta_{SEX_d}}\right)\left(e^{\beta_{SEX_d}\times AGE_{d,i}}-1\right)}}{\sum_{k=0}^{n} e^{-\left({}^{\alpha_{SEX_d}}/{}_{\beta_{SEX_d}}\right)\left(e^{\beta_{SEX_d}\times AGE_{d,k}}-1\right)}}$$

$$R_{d,i} = (1-\rho_d)^{AGE_{d,i}}$$

$$\rho_d = \frac{r_{POP_d}}{{}^1/_2 \times \max\left(o_{DSET_{SEX=\ SEX_d}}\right)} \tag{11}$$

$$S_{d,i} \sim \begin{cases} s_d + 1 & AGE_{d,i} \in W_d \\ 1 & AGE_{d,i} \notin W_d \end{cases}$$

$$\tau_j \sim \text{Normal}\left(o_j,\ \varepsilon_j\right)$$

$$\varepsilon_j = \frac{1}{20}\left(o_j + B\right)$$

$$c_{d,i} = \sum_{k=1}^{N} \left[\ \lfloor \tau_k \rceil = AGE_i,\ DSET = d\right]$$

$$\alpha \sim \text{Beta}\left(p\alpha_1,\quad p\alpha_2\right)$$

$$\beta \sim \text{Beta}\left(p\beta_1,\quad p\beta_2\right)$$

$$r_p \in [-0.5,\ 0.5] \sim \begin{cases} \text{Normal}\left(-0.25,\ 0.2\right) & pr_p = 1 \\ \text{Normal}\left(0,\ 1\right) & pr_p = 0 \\ \text{Normal}\left(0.25,\ 0.2\right) & pr_p = -1 \end{cases}$$

$$s_d \in [-1,\ 2] \sim \begin{cases} \text{Normal}\left(1,\ 0.5\right) & ps_d = 1 \\ \text{Normal}\left(0,\ 2\right) & ps_d = 0 \\ \text{Normal}\left(-1,\ 0.5\right) & ps_d = \ -1 \end{cases}$$

The model was implemented in STAN and R using functionality from the RSTAN, CMDSTANR and RETHINKING packages (McElreath 2023, Gabry *et al.* 2024, Stan Development Team 2024, R Development Core Team 2021). The model has been built into an R package [MARINESURVIVAL (github.com/samellisq/marinesurvival)] that includes all R and STAN code necessary to implement the models.

Testing the model

We performed two analyses to test the ability of the model to estimate toothed whale age-specific mortality.

First, we tested the ability of the model to recover the known input parameters. To do this, we generated 100 simulated datasets of each combination of seven sample sizes ($N = 10, 20, 35, 50, 75, 100, 200$) and seven population growth rates ($r = -0.25, -0.1, -0.05, 0, 0.05, 0.1, 0.25$), giving a total of 4900 simulated datasets. Rather than selecting mortality parameters α and β at random, we chose the parameters to represent a plausible range of odontocete adult lifespans. For each 5-year age window between 0 and 50 years, we generated 500 paired α and β parameters, resulting in lifespans within that window by selecting at random from a systematic analysis of the $\alpha \times \beta$ parameter space. For each simulation, we selected α and β parameters from these 7500 pairs. The result of this was an equal probability of the population in any simulation having an (adult) lifespan in any 5-year age window between 0 and 50 years. All other model parameters were chosen at random for each simulation. We applied the mortality model to each simulation and generated a posterior distribution of ordinary maximum lifespans (see section 'Calculating lifespan') predicted by the model. Models that did not converge were not included in any further analysis. As our metric of model accuracy, we used the minimum credible interval width from the posterior distribution of maximum lifespans required to capture the true maximum lifespan. An accuracy of zero would indicate that the median of the posterior matches the true maximum lifespan, whereas an accuracy of 0.52 would mean that the true lifespan is captured by the 52% credible interval of the posterior. We focused on the accuracy of the model in relationship to sample size, population growth, and whale lifespan as those parameters most likely to bias our measures of lifespan systematically with real data. This approach was functionally similar to a simulation-based calibration approach (Modrák *et al.* 2023).

Second, we compared the lifespan estimates from our mortality model with well-characterized lifespan estimates derived from longitudinal data in a well-studied toothed whale population. Southern-resident killer whales inhabiting the north-east Pacific ocean are regularly observed in inland waters in the Salish Sea (Bigg *et al.* 1990). The population has been studied intensively for 50 years, and all births (of whales surviving their first year) and deaths in the population have been collated by the Center for Whale Research since 1976 (details, including age estimate for whales born before 1976, are given by Nielsen *et al.* 2021). A previous study has used these detailed demographic records in conjunction with established Bayesian mark–recapture mortality modelling to estimate age-specific mortality in this population (Nielsen *et al.* 2021). Mark–recapture mortality models derive parameters for a mortality function given known dates of birth and death, incorporating sightings data to improve parameter estimation and estimate unknown years of birth (for further details, see Colchero *et al.* 2012, Nielsen *et al.* 2021). We rescaled the published age-specific survival estimates to apply only to adults by dividing all post-maturity survival estimates by the estimated survival to maturity. From these adult survival curves, we could derive a credible interval of ordinary maximum lifespans (hereafter, longitudinal lifespan). We tested our model by comparing the longitudinal lifespans with estimates derived from our model applied to data from the same population. We used a single year of southern-resident killer whale demographic data (the equivalent of a situation where the whole population of whales in a single year were sampled, sexed, and aged) as the datasets input into the model. We used the year 1992, when the southern-residents population size peaked (1976–2015); the samples consisted of 45 adult females and 16 adult males present in the population in that year.

Literature search

We performed a systematic and opportunistic search of the literature in May–September 2021 to identify and extract all published age-structured toothed whale data. Age-structured data are data where the ages of individuals of known age and sex can be collected or inferred from published results. For each of the 75 species of toothed whale (IWC 2021), we searched the Web of Science database (webofscience.com) with the species name plus, separately, each of 'life history', 'lifespan', and 'age structure'. We repeated this sequence with the currently accepted species name, any previously used species names, and all widely used common names for the species. In addition, limiting searches to publications in English can bias datasets in systematic reviews and meta-analyses (Konno *et al.* 2020); therefore, for each species we repeated the database query, replacing the English search terms with the same terms translated into major languages commonly spoken around the species distribution. However, there is still likely to be some bias, especially against languages not written in the Latin alphabet. We also performed an opportunistic search by consulting the relevant chapters in the *Handbook of Marine Mammals*, Volumes 4–7 (Ridgway and Harrison 1989, 1994, 1999) and the *Encyclopaedia of Marine Mammals*, third edition (Würsig *et al.* 2018) and identifying potential data sources referenced in these chapters, in addition to searching backwards and forwards through the citation network of identified papers.

We extracted age-structured datasets from these publications to create a database of odontocete age-structured data. Where possible, each dataset in the database represents data from a single population collected at a single time; however, in some systems and publications this is not possible, and a single dataset represents data from multiple populations or is collected over a longer time scale. Each dataset represents only whales of a single known sex, and whales of unknown sex are not included in the datasets. In each publication, age data are extracted from the table or figure giving the largest and most complete sample. Where a single publication contains information from multiple populations, we extracted data from each publication as a separate dataset, if possible. Where the same dataset is presented in multiple publications, we used the original publication unless later publications present a larger sample. Data were extracted from figures using WEBPLOTDIGITIZER (Rohatgi 2020). Data were extracted and included in the database if they contained more than three adult samples of a given sex. For each species and sex, we define the age at maturity based on expert consensus (Ridgway and Harrison 1989, 1994, 1999, Würsig *et al.* 2018). The complete database contains 269 datasets from 118 publications, with data from 44 species (Table 2; Fig. 1; Supporting Information, Appendix S1). The database has been built into an R package: MARINELIFEHISTDATA (github.com/samellisq/marinelifehistdata).

Table 2. Details of the age-structured samples identified in this study.

Common name	Species name	Sex	Number of datasets	Number of whales	References
Atlantic spotted dolphin	*Stenella frontalis*	F	1	3	Siciliano *et al.* (2007)
Atlantic spotted dolphin	*Stenella frontalis*	M	1	1	Siciliano *et al.* (2007)
Atlantic white-sided dolphin	*Lagenorhynchus acutus*	F	4	45	Sergeant *et al.* (1980), Addink *et al.* (1997), Rogan *et al.* (1997), Tuerk *et al.* (2005)
Atlantic white-sided dolphin	*Lagenorhynchus acutus*	M	4	32	Sergeant *et al.* (1980), Addink *et al.* (1997), Rogan *et al.* (1997), Tuerk *et al.* (2005)
Baiji	*Lipotes vexillifer*	F	1	17	Gao and Zhou (1992)
Baiji	*Lipotes vexillifer*	M	1	11	Gao and Zhou (1992)
Baird's beaked whale	*Berardius bairdii*	F	2	24	Balcomb (1989), Kasuya *et al.* (1997a)
Baird's beaked whale	*Berardius bairdii*	M	3	84	Balcomb (1989), Kasuya *et al.* (1997a), Urbán *et al.* (2007)
Beluga whale	*Delphinapterus leucas*	F	8	757	Lensink (1961), Burns and Seaman (1986), Heide-Jørgensen and Lockyer (2001), Stewart *et al.* (2006), Suydam (2009), Ferguson *et al.* (2020), Vos *et al.* (2020)
Beluga whale	*Delphinapterus leucas*	M	5	321	Lensink (1961), Burns and Seaman (1986), Heide-Jørgensen and Lockyer (2001), Suydam (2009), Vos *et al.* (2020)
Chilean dolphin	*Cephalorhynchus eutropia*	F	1	9	Molina and Reyes (1996)
Chilean dolphin	*Cephalorhynchus eutropia*	M	1	5	Molina and Reyes (1996)
Commerson's dolphin	*Cephalorhynchus commersonii*	F	2	24	Collet and Robineau (1988), Cáceres-Saez *et al.* (2015)
Commerson's dolphin	*Cephalorhynchus commersonii*	M	2	38	Collet and Robineau (1988), Cáceres-Saez *et al.* (2015)
Common bottlenose dolphin	*Tursiops truncatus*	F	10	423	Read *et al.* (1993), Kasuya *et al.* (1997b), Stolen and Barlow (2003), Mattson *et al.* (2006), Butti *et al.* (2007), Siciliano *et al.* (2007), Neuenhoff (2013), Gol'din and Gladilina (2015), Venuto *et al.* (2020)
Common bottlenose dolphin	*Tursiops truncatus*	M	10	307	Read *et al.* (1993), Kasuya *et al.* (1997b), Stolen and Barlow (2003), Mattson *et al.* (2006), Butti *et al.* (2007), Siciliano *et al.* (2007), Neuenhoff (2013), Gol'din and Gladilina (2015), Venuto *et al.* (2020)
Common dolphin	*Delphinus delphis*	F	6	628	Perrin and Myrick (1980), Van Utrecht (1981), Ferrero and Walker (1995), Danil and Chivers (2007), Viricel *et al.* (2008), Murphy *et al.* (2009)
Common dolphin	*Delphinus delphis*	M	3	44	Van Utrecht (1981), Ferrero and Walker (1995), Durante *et al.* (2016)
Cuvier's beaked whale	*Ziphius cavirostris*	F	1	8	Perrin and Myrick (1980)
Cuvier's beaked whale	*Ziphius cavirostris*	M	1	10	Perrin and Myrick (1980)
Dall's porpoise	*Phocoenoides dalli*	F	4	854	Kasuya (1978), Newby (1982), Kasuya and Shiraga (1985), Ferrero and Walker (1999)
Dall's porpoise	*Phocoenoides dalli*	M	4	456	Kasuya (1978), Newby (1982), Kasuya and Shiraga (1985), Ferrero and Walker (1999)

Table 2. Continued

Common name	Species name	Sex	Number of datasets	Number of whales	References
Dusky dolphin	*Lagenorhynchus obscurus*	M	1	6	Cipriano (1992)
Dwarf sperm whale	*Kogia sima*	F	1	15	Plön (2004)
Dwarf sperm whale	*Kogia sima*	M	1	19	Plön (2004)
False killer whale	*Pseudorca crassidens*	F	2	100	Kasuya (1986), Ferreira *et al.* (2014)
False killer whale	*Pseudorca crassidens*	M	2	42	Kasuya (1986), Ferreira *et al.* (2014)
Franciscana	*Pontoporia blainvillei*	F	7	228	Kasuya and Brownell (1979), Barreto and Rosas (2006), Botta *et al.* (2010), Negri *et al.* (2016), Denuncio *et al.* (2018), Conversani *et al.* (2021)
Franciscana	*Pontoporia blainvillei*	M	7	262	Kasuya and Brownell (1979), Barreto and Rosas (2006), Botta *et al.* (2010), Negri *et al.* (2016), Denuncio *et al.* (2018), Conversani *et al.* (2021)
Fraser's dolphin	*Lagenodelphis hosei*	F	3	39	Van Bree *et al.* (1986), Amano *et al.* (1996), Siciliano *et al.* (2007)
Fraser's dolphin	*Lagenodelphis hosei*	M	4	41	Van Bree *et al.* (1986), Amano *et al.* (1996), Siciliano *et al.* (2007), Durante *et al.* (2016)
Ganges river dolphin	*Platanista gangetica*	M	1	3	Kasuya (1972)
Guiana dolphin	*Sotalia guianensis*	F	6	49	Van Utrecht (1981), Rosas *et al.* (2003), Santos *et al.* (2003), Lima *et al.* (2016), Conversani *et al.* (2021)
Guiana dolphin	*Sotalia guianensis*	M	6	62	Van Utrecht (1981), Rosas *et al.* (2003), Santos *et al.* (2003), Lima *et al.* (2016), Conversani *et al.* (2021)
Harbour porpoise	*Phocoena phocoena*	F	12	643	Read and Tolley (1997), Lockyer *et al.* (2001), Gol'din (2004), Learmonth *et al.* (2014), Kesselring *et al.* (2018), Murphy *et al.* (2020)
Harbour porpoise	*Phocoena phocoena*	M	10	355	Read and Tolley (1997), Lockyer *et al.* (2001), Gol'din (2004), Learmonth *et al.* (2014), Murphy *et al.* (2020)
Hector's dolphin	*Cephalorhynchus hectori*	F	1	7	Slooten (1991)
Hector's dolphin	*Cephalorhynchus hectori*	M	1	9	Slooten (1991)
Indian Ocean humpback dolphin	*Sousa plumbea*	F	1	8	Nolte (2014)
Indian Ocean humpback dolphin	*Sousa plumbea*	M	1	21	Nolte (2014)
Indo-Pacific bottlenose dolphin	*Tursiops aduncus*	F	2	75	Cockcroft and Ross (1990), Kemper *et al.* (2019)
Indo-Pacific bottlenose dolphin	*Tursiops aduncus*	M	2	59	Cockcroft and Ross (1990), Kemper *et al.* (2014)
Indo-Pacific finless porpoise	*Neophocaena phocaenoides*	F	1	11	Jefferson *et al.* (2002)
Indo-Pacific finless porpoise	*Neophocaena phocaenoides*	M	1	8	Jefferson *et al.* (2002)

Table 2. Continued

Common name	Species name	Sex	Number of datasets	Number of whales	References
Indo-Pacific humpback dolphin	*Sousa chinensis*	F	2	20	Jefferson *et al.* (2012), Guo *et al.* (2020)
Indo-Pacific humpback dolphin	*Sousa chinensis*	M	2	22	Jefferson *et al.* (2012), Guo *et al.* (2020)
Killer whale	*Orcinus orca*	F	6	112	Christensen (1984), Herman *et al.* (2008), Best *et al.* (2010), Amano *et al.* (2011), Ellis *et al.* (2017)
Killer whale	*Orcinus orca*	M	5	75	Christensen (1984), Herman *et al.* (2008), Best *et al.* (2010), Ellis *et al.* (2017)
Long-finned pilot whale	*Globicephala melas*	F	3	1170	Martin *et al.* (1987), Bloch *et al.* (1993), Betty (2019)
Long-finned pilot whale	*Globicephala melas*	M	3	460	Martin *et al.* (1987), Bloch *et al.* (1993), Betty (2019)
Melon-headed whale	*Peponocephala electra*	F	4	90	Miyazaki *et al.* (1998), Amano *et al.* (2014), Kurihara *et al.* (2016)
Melon-headed whale	*Peponocephala electra*	M	4	52	Miyazaki *et al.* (1998), Amano *et al.* (2014), Kurihara *et al.* 2016)
Narrow-ridged finless porpoise	*Neophocaena asiaeorientalis*	F	6	96	Gao and Zhou (1993), Shirakihara *et al.* (1993), Kasuya (1999), Mei *et al.* (2012), Lee *et al.* (2013)
Narrow-ridged finless porpoise	*Neophocaena asiaeorientalis*	M	6	104	Gao and Zhou (1993), Shirakihara *et al.* (1993), Kasuya (1999), Mei *et al.* (2012), Lee *et al.* (2013)
Narwhal	*Monodon monoceros*	F	3	100	Garde *et al.* (2015), Watt *et al.* (2020)
Narwhal	*Monodon monoceros*	M	3	85	Hay (1984), Garde *et al.* (2015)
Northern bottlenose whale	*Hyperoodon ampullatus*	F	1	26	Christensen (1973)
Northern bottlenose whale	*Hyperoodon ampullatus*	M	1	52	Christensen (1973)
Northern right whale dolphin	*Lissodelphis borealis*	F	2	105	Ferrero and Walker (1993), Iwasaki and Kasuya (1997)
Northern right whale dolphin	*Lissodelphis borealis*	M	2	50	Ferrero and Walker (1993), Iwasaki and Kasuya (1997)
Pacific white-sided dolphin	*Lagenorhynchus obliquidens*	F	3	73	Walker *et al.* (1986), Ferrero and Walker (1996), Iwasaki and Kasuya (1997)
Pacific white-sided dolphin	*Lagenorhynchus obliquidens*	M	3	65	Walker *et al.* (1986), Ferrero and Walker (1996), Iwasaki and Kasuya (1997)
Pantropical spotted dolphin	*Stenella attenuata*	F	8	1039	Barlow and Hohn (1984), Kasuya (1985)
Pantropical spotted dolphin	*Stenella attenuata*	M	2	499	Barlow and Hohn (1984), Kasuya (1985)
Peale's dolphin	*Lagenorhynchus australis*	F	1	3	Boy *et al.* (2011)

Table 2. Continued

Common name	Species name	Sex	Number of datasets	Number of whales	References
Peale’s dolphin	*Lagenorhynchus australis*	M	1	1	Boy *et al.* (2011)
Pygmy sperm whale	*Kogia breviceps*	F	3	26	Van Utrecht (1981), Plön (2004)
Pygmy sperm whale	*Kogia breviceps*	M	2	18	Van Utrecht (1981), Plön (2004)
Risso’s dolphin	*Grampus griseus*	F	4	51	Amano and Miyazaki (2004), Bloch *et al.* (2012), Evacitas *et al.* (2017), Plön *et al.* (2020)
Risso’s dolphin	*Grampus griseus*	M	4	17	Amano and Miyazaki (2004), Bloch *et al.* (2012), Evacitas *et al.* (2017), Plön *et al.* (2020)
Rough-toothed dolphin	*Steno bredanensis*	F	2	10	Miyazaki (1978), Siciliano *et al.* (2007)
Rough-toothed dolphin	*Steno bredanensis*	M	2	27	Miyazaki (1978), Siciliano *et al.* (2007)
Short-finned pilot whale	*Globicephala macrorhynchus*	F	3	505	Perrin and Myrick (1980), Kasuya and Marsh (1984), Kasuya and Tai (1993)
Short-finned pilot whale	*Globicephala macrorhynchus*	M	3	171	Perrin and Myrick (1980), Kasuya and Marsh (1984), Kasuya and Tai (1993)
Sperm whale	*Physeter macrocephalus*	F	5	2932	Ohsumi (1966), Best *et al.* (1984), Rice *et al.* (1986), Evans and Hindell (2004), Clarke *et al.* (2013)
Sperm whale	*Physeter macrocephalus*	M	5	2451	Ohsumi (1966), Mitchell and Kozicki (1984), Rice *et al.* 1986, Kasuya 1991)
Spinner dolphin	*Stenella longirostris*	F	2	1420	Larese and Chivers (2009)
Spinner dolphin	*Stenella longirostris*	M	2	158	Perrin *et al.* (1977), Perrin and Henderson (1984)
Stejneger’s beaked whale	*Mesoplodon stejnegeri*	M	1	6	Arai *et al.* (2004)
Striped dolphin	*Stenella coeruleoalba*	F	2	913	Miyazaki (1984), Marsili *et al.* (1997)
Striped dolphin	*Stenella coeruleoalba*	M	2	680	Miyazaki (1984), Marsili *et al.* (1997)
Vaquita	*Phocoena sinus*	F	1	11	Hohn *et al.* (1996)
Vaquita	*Phocoena sinus*	M	1	10	Hohn *et al.* (1996)
White-beaked dolphin	*Lagenorhynchus albirostris*	F	3	51	Van Utrecht (1981), Dong *et al.* (1996), Galatius *et al.* (2013)
White-beaked dolphin	*Lagenorhynchus albirostris*	M	3	29	Van Utrecht (1981), Dong *et al.* (1996), Galatius *et al.* (2013)

Note that although all datasets and species where data were identified are included here, we analyse species-sex in further analysis only if it exceeded sample size and sampling intensity conditions (see Materials and Methods: calculating lifespan). Abbreviations: F, female; M, male.

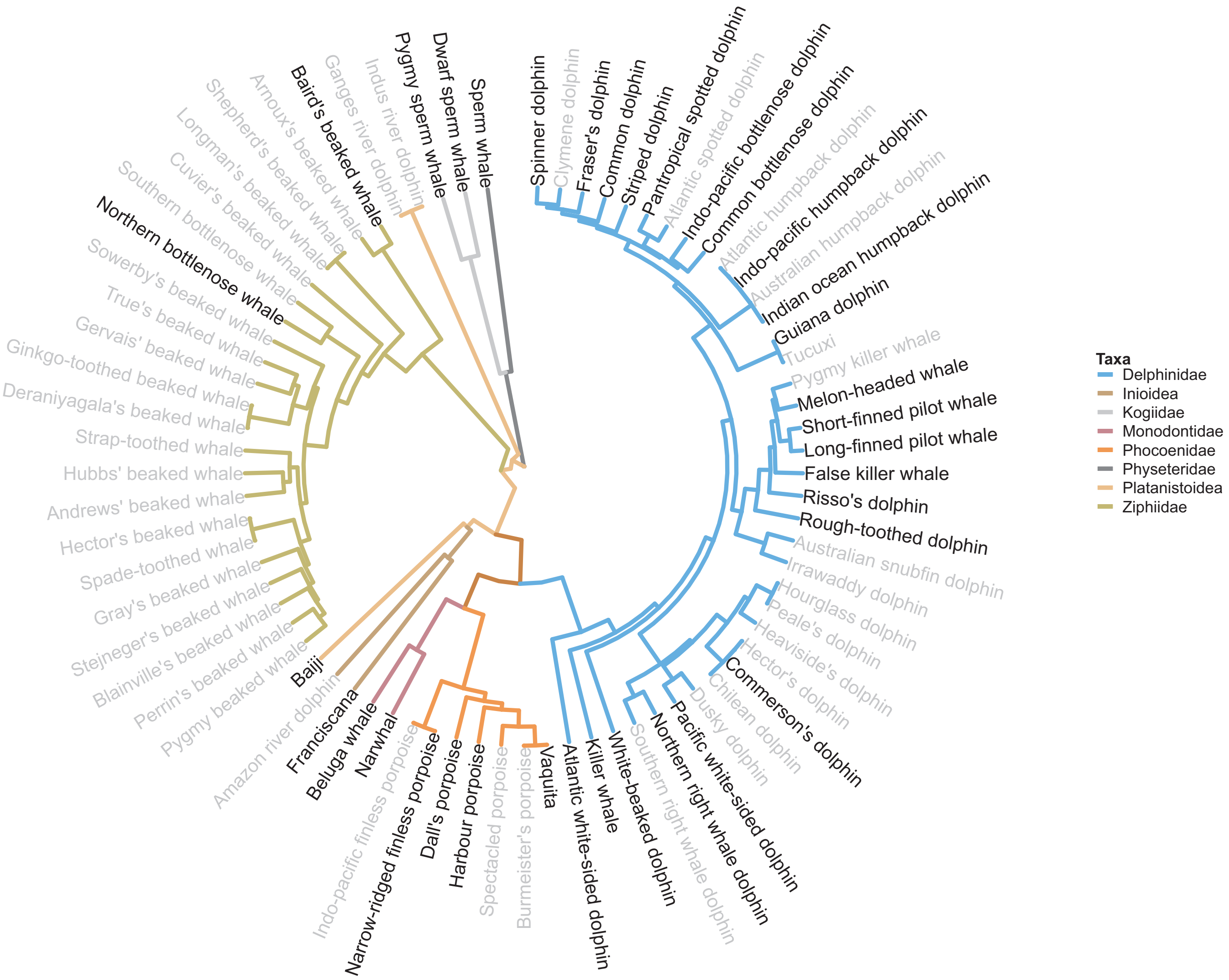


Figure 1. Toothed whale phylogeny (data adapted from McGowen *et al.* 2020). Data are available to apply our model and estimate age-specific mortality for at least one sex in 35 species (black text; grey text = no data). Branch colours correspond to taxonomic family.

We also parametrize the mortality model with dataset-specific information on population growth, sampling biases, and age estimation error. We base our population change prior on necessarily coarse assumptions on the source of the data. Where datasets are derived from bycatch (usually resulting from large-scale bycatch in commercial fisheries, such as the Pacific gillnet fishery; $N = 72$) or whaling/drive fisheries ($N = 50$), we assume that the population is decreasing ($pr = -1$). Where datasets are from Harvest ('Aboriginal Subsistence Whaling' as defined by the International Whaling Commission; $N = 20$), we assume that there is no population change based on the monitoring and management to which the populations are subject. For all other data sources, we assume that the population could be increasing or decreasing ($pr = 0$). Datasets are assumed to have no systematic sampling biases unless noted by the authors of the original study (or subsequent publications analysing the same dataset). Where biased sampling is present, we define the bias window, W, using the information provided by the authors. Unless the ages in a dataset were derived from long-term observations ($N = 8$) or aspartic acid racemization ($N = 6$), they were assumed to have additive age estimation error as defined by the model (above).

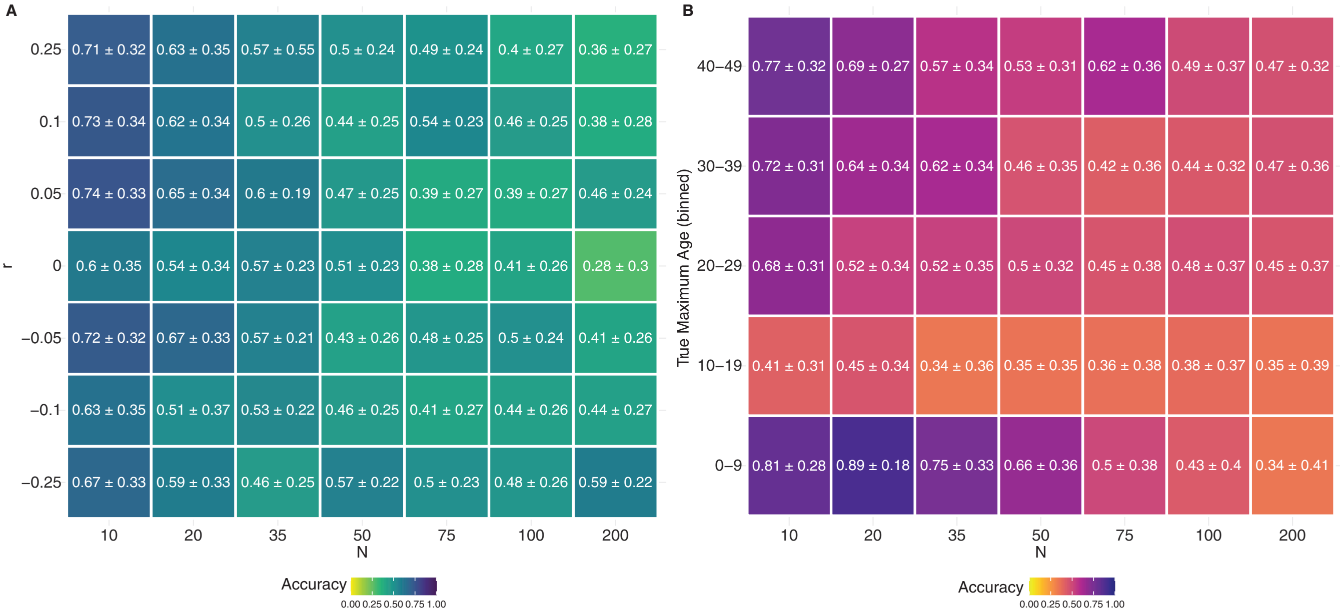
Calculating lifespan

We filtered the database before analysis. For each dataset, we calculate the number of samples and the sampling rate (total samples/maximum observed age observed across all species–sex datasets). We analyse species and sexes only where at least one dataset has >10 samples and a sampling rate of >0.5.

We applied the mortality model to each species as described above (Supporting Information, Appendix S1). We obtained estimates of lifespan for each species and sex using Gompertz α and β parameters. Specifically, we calculated the age at which X proportion of species–sex life years have been lived via:

$$\text{age } X = \min_{x \in [0:150]} \left(\{ l(x) \ \leq (1 - X) \} \right) \tag{12}$$

Here, we used $X = 0.9$ as 'ordinary maximum lifespan' (or age Z) as our measure of species–sex lifespan (Ronget and Gaillard 2020).



A

r \ N	10	20	35	50	75	100	200
0.25	0.71 ± 0.32	0.63 ± 0.35	0.57 ± 0.55	0.5 ± 0.24	0.49 ± 0.24	0.4 ± 0.27	0.36 ± 0.27
0.1	0.73 ± 0.34	0.62 ± 0.34	0.5 ± 0.26	0.44 ± 0.25	0.54 ± 0.23	0.46 ± 0.25	0.38 ± 0.28
0.05	0.74 ± 0.33	0.65 ± 0.34	0.6 ± 0.19	0.47 ± 0.25	0.39 ± 0.27	0.39 ± 0.27	0.46 ± 0.24
0	0.6 ± 0.35	0.54 ± 0.34	0.57 ± 0.23	0.51 ± 0.23	0.38 ± 0.28	0.41 ± 0.26	0.28 ± 0.3
−0.05	0.72 ± 0.32	0.67 ± 0.33	0.57 ± 0.21	0.43 ± 0.26	0.48 ± 0.25	0.5 ± 0.24	0.41 ± 0.26
−0.1	0.63 ± 0.35	0.51 ± 0.37	0.53 ± 0.22	0.46 ± 0.25	0.41 ± 0.27	0.44 ± 0.26	0.44 ± 0.27
−0.25	0.67 ± 0.33	0.59 ± 0.33	0.46 ± 0.25	0.57 ± 0.22	0.5 ± 0.23	0.48 ± 0.26	0.59 ± 0.22

B

Tue Maximum Age (binned) \ N	10	20	35	50	75	100	200
40–49	0.77 ± 0.32	0.69 ± 0.27	0.57 ± 0.34	0.53 ± 0.31	0.62 ± 0.36	0.49 ± 0.37	0.47 ± 0.32
30–39	0.72 ± 0.31	0.64 ± 0.34	0.62 ± 0.34	0.46 ± 0.35	0.42 ± 0.36	0.44 ± 0.32	0.47 ± 0.36
20–29	0.68 ± 0.31	0.52 ± 0.34	0.52 ± 0.35	0.5 ± 0.32	0.45 ± 0.38	0.48 ± 0.37	0.45 ± 0.37
10–19	0.41 ± 0.31	0.45 ± 0.34	0.34 ± 0.36	0.35 ± 0.35	0.36 ± 0.38	0.38 ± 0.37	0.35 ± 0.39
0–9	0.81 ± 0.28	0.89 ± 0.18	0.75 ± 0.33	0.66 ± 0.36	0.5 ± 0.38	0.43 ± 0.4	0.34 ± 0.41

Figure 2. Results from simulations testing the accuracy of the mortality model to detect the true maximum lifespan of a population under a range of sample sizes (*N*) × population growth rates (*r*) (A) and sample sizes × true maximum lifespans (B). Each cell shows the mean ± SD of accuracy over models in each scenario. Cell colour shows the mean accuracy, with lighter colours and smaller values indicating greater accuracy. Accuracy is measured as the minimum credible interval width from the posterior distribution of maximum lifespans required to capture the true maximum lifespan. An accuracy of zero would indicate that the median of the posterior matches the true maximum lifespan, and an accuracy of 0.5 would mean that the true lifespan is captured by the 50% credible interval of the posterior. One hundred models were run for each population growth × sample size scenario, resulting in a total of 4900 fitted models. B is based on the same 4900 fitted models, true maximum lifespans, and has a uniform probability of being selected, but the number of models applied in each cell will vary. Note that neither sample size nor population growth rate is a regular sequence.

We calculated the ordinary maximum lifespan from each of the 40 000 posterior draws of the fitted Bayesian model, resulting in a distribution of age *Z* values for each species–sex.

We also performed a series of additional analyses to explore the robustness and implications of our models. Specifically we: (i) explored the robustness of our model to systematic misageing of older individuals (Barratclough *et al.* 2023; Supporting Information, Appendix S2); (ii) established whether changing the ageing methodologies through time has led to different observed age distributions (Read *et al.* 2018; Supporting Information, Appendix S3); (iii) investigated the sensitivity of our model to our population change assumptions (Supporting Information, Appendix S4); (iv) reformulated and tested our model as an age-at-death model (Supporting Information, Appendix S5); (v) evaluated evidence for phylogenetic signal in toothed whale lifespan evolution (Supporting Information, Appendix S6); and (vi) explored the impact of alternative age estimation error structures on inference of lifespan (Supporting Information, Appendix S7).

RESULTS

Testing the model

Our first set of analyses explored the consistency and accuracy of the model across a realistic range of population growth rates and whale adult lifespans (Fig. 2). There was a trend for increased accuracy with larger sample sizes. With larger sample sizes, the posterior median was closer to the true lifespan (Fig. 2). However, the increase in accuracy was relatively modest and variable; for example, in stable populations ($r = 0$) the mean minimal credible interval required to capture the true lifespan was 60% ± 35% (± SD) for a sample size of 10 and 27% ± 37% for a sample size of 200 (Fig. 2; see also Vaupel 2003). There were no clear trends for increased accuracy for either shorter lifespans or more stable populations (Fig. 2). The model accuracy was maintained across these scenarios because credible intervals were wider under small sample sizes and for long-lived whales: in short, the model became less certain with more unsure information (Supporting Information, Appendix S8). Under all scenarios, the largest mean minimum credible interval needed to capture the true value was 77% ($N = 10$, true age 40–49 years), suggesting that as long as measures of error are carried through subsequent analyses the model is likely to capture the true lifespan.

In our second analysis, we compared the mortality estimates from our model with those derived from longitudinal data when applied to the southern-resident killer whales. The longitudinally derived adult lifespan of female and male southern-resident killer whales was, respectively, 69 (62–79) years [mean (95% credible interval)] and 44 (40–51) years (derived from Nielsen *et al.* 2021). Our model applied to the southern-resident killer whale population in 1992 estimated lifespans of 76 (65–88) years for females and 44 (38–53) years for males. For both males and females, there was considerable credible interval overlap between estimates derived from the two models.

Toothed whale lifespans

Applying our mortality model to the real odontocete age-structured data allowed us to generate adult lifespan estimates

Table 3. Estimated female ordinary maximum adult lifespan for 32 species of toothed whale.

Common name	Age at maturity	Median	lCI50	uCI50	lCI95	uCI95	Posterior mean	Posterior SD
Atlantic white-sided dolphin	9	21	20	21	19	23	20.88	0.97
Baiji	6	22.5	21	24	20	27	22.71	1.85
Baird's beaked whale	13	52	50	55	46	62	52.76	4.09
Beluga whale	10	54	53	55	52	56	53.85	1.15
Commerson's dolphin	5	17	17	18	15	20	17.48	1.32
Common bottlenose dolphin	9	40	39	40	38	41	39.76	0.82
Common dolphin	7	25	25	25	24	26	25.04	0.42
Dall's porpoise	5	13	13	13	12	13	12.88	0.32
Dwarf sperm whale	4	20	19	22	17	25	20.53	1.92
False killer whale	10	67	66	69	62	74	67.51	2.84
Franciscana	2	13	13	13	12	14	13.14	0.55
Fraser's dolphin	6	20	20	21	18	23	20.38	1.22
Guiana dolphin	6	33	32	35	30	38	33.45	2.09
Harbour porpoise	3	17	17	18	17	18	17.3	0.5
Indo-Pacific bottlenose dolphin	12	37	36	38	34	41	36.92	1.85
Indo-Pacific humpback dolphin	9	38	36	40	34	45	38.55	3
Killer whale	13	60	58	62	54	66	59.81	3.31
Long-finned pilot whale	8	45	45	46	44	46	45.17	0.68
Melon-headed whale	7	41	40	42	38	45	41.35	1.83
Narrow-ridged finless porpoise	5	23	23	24	21	25	23.24	1.11
Narwhal	8	77	74	80	69	86	76.81	4.4
Northern bottlenose whale	10	27	26	28	24	31	26.92	1.69
Northern right whale dolphin	9	28	28	29	26	31	28.5	1.15
Pacific white-sided dolphin	9	40	39	42	37	45	40.5	1.98
Pantropical spotted dolphin	10	35	35	35	34	36	35.09	0.47
Pygmy sperm whale	5	22	21	24	20	26	22.58	1.73
Risso's dolphin	9	34	32	35	31	38	33.74	1.82
Short-finned pilot whale	9	56	55	57	54	58	55.81	1.14
Sperm whale	9	49	48	49	48	50	48.7	0.61
Spinner dolphin	8	23	23	23	23	24	23.07	0.26
Striped dolphin	9	31	31	31	30	32	31.11	0.51
Vaquita	5	23	22	24	20	28	23.16	2.24
White-beaked dolphin	8	36	34	37	32	40	35.74	2.03

Here, ordinary maximum lifespan is defined as the age at which 90% of adult life years have been lived. All metrics describe the distribution of the posterior derived from the Bayesian mortality model (see the Materials and Methods). Each metric (apart from SD) is the adult lifespan estimated by the model plus the age at maturity to give the expected maximum lifespan for females who reach maturity (age at maturity). Abbreviations: lCI and uCI represent the lower and upper bounds, respectively, of the 50% (l/uCI50) and 95% (l/uCI95) credible intervals.

for 32 female and 33 male toothed whale species (Tables 3 and 4; Figs 1, 3). The estimates for each species–sex were based on a median of 75 whales (first quartile = 39; third quartile = 355). The phylogenetic spread of samples was broad, with all the major odontocete clades represented (Fig. 1).

Male Baird's beaked whales had the longest lifespan in our sample, with an ordinary maximum lifespan of 84–90 years (50% credible interval). The longest-lived females in our sample were Narwhals, with an ordinary maximum lifespan of 74–80 years (50% credible interval). The shortest-lived species in our sample were female Dall's porpoises and Franciscana of both sexes, all of which had a median ordinary maximum lifespan of 13 years. Our additional analyses demonstrated that the ordinary maximum lifespans derived from the model were largely robust to differences in potential systematic errors in ageing of older whales (Supporting Information, Appendix S2), changing ageing methodologies through time (Supporting Information, Appendix S3), our population change assumptions (Supporting

Table 4. Estimated male ordinary maximum adult lifespan for 33 species of toothed whale.

Common name	Age at maturity	Median	lCI50	uCI50	lCI95	uCI95	Posterior mean	Posterior SD
Atlantic white-sided dolphin	9	22	21	23	20	25	22.21	1.2
Baiji	6	20	19	22	18	25	20.48	1.93
Baird's beaked whale	13	87	84	90	78	97	87.31	4.91
Beluga whale	10	49	48	50	46	52	48.72	1.67
Commerson's dolphin	5	22	21	23	19	25	21.78	1.39
Common bottlenose dolphin	9	37	36	38	35	39	36.89	0.99
Common dolphin	7	25	24	26	23	28	25.32	1.46
Dall's porpoise	5	14	14	14	13	14	13.96	0.26
Dwarf sperm whale	4	20	19	21	17	24	20.12	1.75
False killer whale	10	55	53	58	49	63	55.54	3.52
Franciscana	2	13	12	13	12	13	12.55	0.55
Fraser's dolphin	6	19	18	19	17	21	18.62	1.06
Guiana dolphin	6	28	27	29	25	31	27.64	1.61
Harbour porpoise	3	16	16	17	15	17	16.28	0.51
Indian Ocean humpback dolphin	10	26	25	27	23	30	25.99	1.65
Indo-Pacific bottlenose dolphin	12	36	35	37	33	39	35.83	1.73
Indo-Pacific humpback dolphin	9	29	27	30	25	33	28.75	1.96
Killer whale	13	38	37	39	35	42	38.13	1.73
Long-finned pilot whale	8	35	35	36	34	37	35.45	0.84
Melon-headed whale	7	35	34	37	32	40	35.57	1.97
Narrow-ridged finless porpoise	5	23	22	23	21	25	22.64	0.99
Narwhal	8	66	63	69	58	75	66.27	4.28
Northern bottlenose whale	10	36	35	37	32	40	35.89	1.93
Northern right whale dolphin	9	24	23	25	22	26	23.93	1.2
Pacific white-sided dolphin	9	38	37	39	34	42	37.88	1.92
Pantropical spotted dolphin	10	32	31	32	31	33	31.76	0.58
Rough-toothed dolphin	10	30	29	32	27	35	30.63	1.91
Short-finned pilot whale	9	37	36	38	34	39	36.64	1.31
Sperm whale	9	53	52	53	51	54	52.5	0.63
Spinner dolphin	8	19	19	20	18	20	19.3	0.56
Striped dolphin	9	30	30	31	29	31	30.12	0.68
Vaquita	5	21	20	23	18	27	21.63	2.32
White-beaked dolphin	8	29	28	31	26	34	29.52	2.08

Here, ordinary maximum lifespan is defined as the age at which 90% of adult life years have been lived. All metrics describe the distribution of the posterior derived from the Bayesian mortality model (see the Materials and Methods). Each metric (apart from SD) is the adult lifespan estimated by the model plus the age at maturity to give the expected maximum lifespan for males who reach maturity (age at maturity). Abbreviations: lCI and uCI represent the lower and upper bounds, respectively, of the 50% (l/uCI50) and 95% (l/uCI95) credible intervals.

Information, Appendix S4), and the structure of our model (Supporting Information, Appendix S7).

There was good evidence in 10 species that females have a longer adult lifespan than males (proportion of posterior where female − male lifespan is greater than 0 = 0.97; Fig. 4). However, in four species (Baird's beaked whales, Commerson's dolphin, northern bottlenose whales, and sperm whales) the opposite is true and there is clear evidence that males live longer as adults than females (proportion of posterior female − male lifespan is less than 0 = 0.975; Fig. 4). In the remaining species, there was no clear evidence that the sexes have different lifespans. Combining all species, female toothed whales live a median of 10% longer than males (female − male lifespan/female lifespan), but overall there is no clear evidence of a sex difference in lifespan (proportion of posterior female − male lifespan > 0 = 0.66).

DISCUSSION

Here, we have developed and applied a method to estimate lifespan parameters from age-structured cross-sectional samples. Simulations demonstrate that the models can capture true lifespan given population growth, sampling error, and age-estimation error with a realistic range of sample sizes and species maximum lifespans. Applying the model to data collected from the literature provides adult lifespan estimates for females of 32 and males of 33 species of toothed whale.

We find that there is almost an order of magnitude difference between the ordinary maximum lifespan of the shortest-lived and longest-lived toothed whales. This variation is particularly remarkable given that many other aspects of toothed whale life history do not differ between species. For example, all toothed whales: (i) give birth to a single offspring per breeding event;

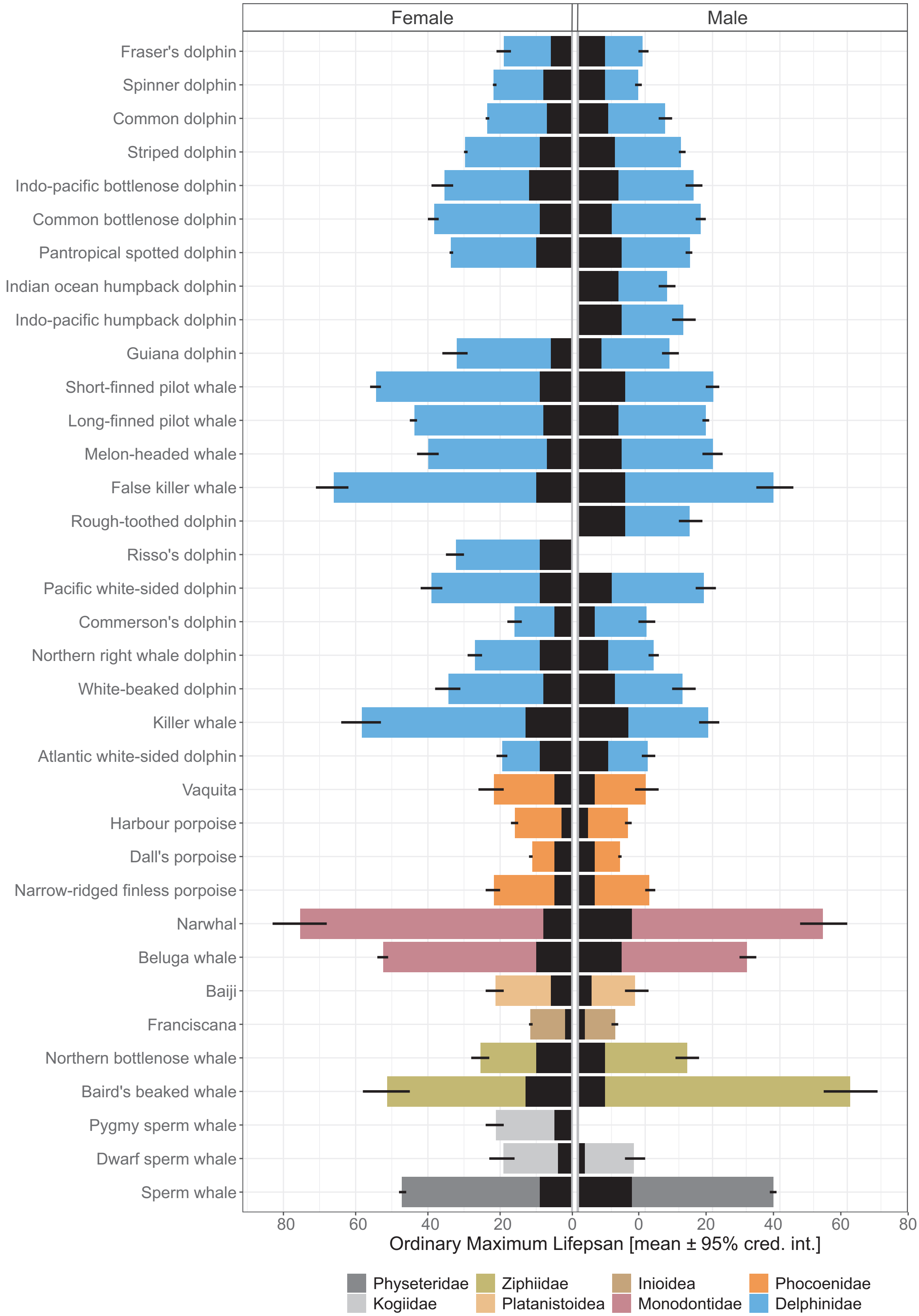


Figure 3. Adult lifespans of female (left panel) and male (right panel) toothed whales estimated by our mortality model. Bars show a mean estimate of the ordinary maximum lifespan (the age by which 90% of adult life years have been lived) derived from our mortality model. Error bars show the 95% credible interval of lifespan estimates. Black areas show the juvenile years not estimated by our model. Ordinary maximum lifespan, therefore, represents lifespan given survival to maturity. Species order and bar colours reflect phylogeny (Figure 1). For some species, data were available for only one sex, resulting in an empty bar.

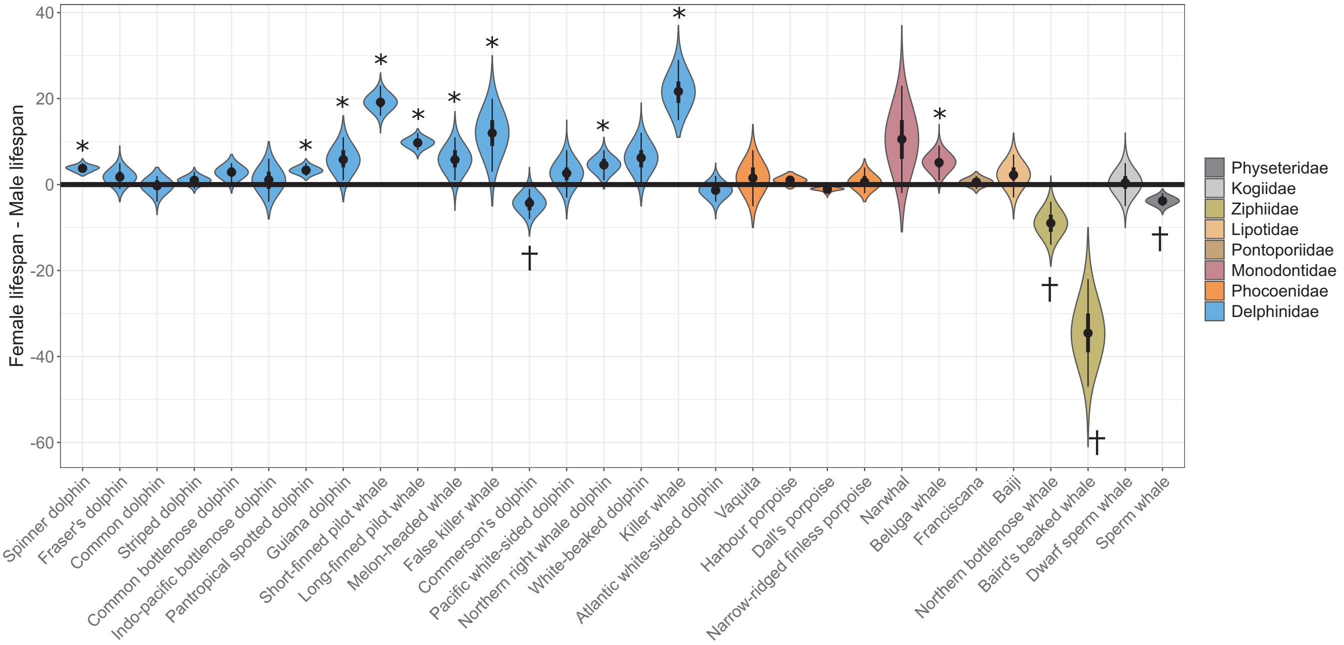


Figure 4. Comparing female and male adult lifespan in toothed whales. Violins show the posterior distribution of female − male lifespan derived from our mortality models. Both sexes are assessed in the same model in order that the posterior lifespan of each sex at each draw can be compared directly. *Species where there is good evidence that females live longer than males (proportion of posterior greater than 0 = 0.975). †Species where there is good evidence that males live longer than females (proportion of posterior less than 0 = 0.975). Species order and violin colour reflect phylogeny (Figure 1).

Table 5. Comparison of adult ordinary maximum lifespan estimates derived from the method developed and applied here (species estimate, dataset estimate) with other methods (published estimate).

Species	Sex	Species estimate (95% CI)	Dataset estimate (95% CI)	Published estimate	Published method used (reference)
Common bottlenose dolphin	F	38–41	33–42	30	Age-at-death Siler model (Stolen and Barlow 2003)
Common bottlenose dolphin	M	35–39	29–37	26	Age-at-death Siler model (Stolen and Barlow 2003)
Killer whale	F	54–66	65–88	62–79 (95% CI)	Mark–recapture (Nielsen *et al.* 2021)
Killer whale	M	35–42	38–53	40–51 (95% CI)	Mark–recapture (Nielsen *et al.* 2021)
Pantropical spotted dolphin	F	34–36	32–34	31	Scaled mammal (Barlow and Hohn 1984)
Pantropical spotted dolphin	M	31–33	34–36	32	Scaled mammal (Barlow and Hohn 1984)

'Published estimates' are sex-specific estimates of age-specific mortality that have been converted into adult ordinary maximum lifespan for comparison with our model. 'Species estimate' is the ordinary maximum lifespan as reported in Tables 3 and 4 using all the data available for a particular species and sex. 'Dataset estimate' is the ordinary maximum lifespan derived by applying our mortality model only to the datasets used to derive the Published estimate. Both species and dataset estimate are reported as a 95% credible interval. Published methods are a Siler model applied to age-at-death data, 'mark–recapture' from a longitudinal study (see main text), and a 'scaled mammal' estimate derived by rescaling a known mammal life history to fit the toothed whale data. Abbreviations: CI, credible interval; F, female; M, male.

(ii) provide several years of maternal year to their dependent offspring; and (iii) exhibit a polygynous mating system, with no evidence of paternal care (Chivers 2018, Whitehead and Mann 2000). At the broadest level, toothed whale species also share a similar ecological niche, all are aquatic carnivores, and most live and often hunt in social groupings. Despite these similarities here, we have shown that lifespan can vary considerably between species. This variation highlights the importance of toothed whales as a model of life-history evolution. Future work using toothed whales to understand how ecological and social factors predict lifespan evolution has the potential to provide important fundamental insights.

We found that in 10 species of toothed whale there is good evidence that females live longer as adults than males, and overall female toothed whales live 10% longer than males. Longer-lived females are the general pattern in mammals; for example, a recent analysis of 101 mammal species, including four toothed whales, found that female mammals live a mean of 18.6% longer than males (Lemaître *et al.* 2020). The evolutionary drivers of sex differences in adult lifespan in mammals remain unresolved, but both genetic conflict and life-history trade-offs have been implicated (Lemaître *et al.* 2020). However, in toothed whales we found that there are exceptions to this pattern. Perhaps most notably, in Baird's beaked whales the males live considerably longer than females: the median predicted ordinary maximum lifespan of females is 52 years, compared with 87 years for males. In Baird's beaked whales, this sex difference in lifespan leads to heavily male-biased adult populations, but the evolutionary reasons for the extreme lifespan differences in this species remain unknown (Kasuya *et al.* 1997a).

In contrast, the comparative rarity of sex differences in toothed whale adult lifespan we find here is also evidence in favour of the argument that sex differences in mammals have been overstated. For example, a recent broad-scale analysis of mammals found that, contrary to established wisdom, only 45% of mammals demonstrate male-biased sexual size dimorphism (Tombak *et al.* 2024). Likewise, although Lemaître *et al.* (2020) found that, on average, female mammals live longer than males, the pattern was, in fact, very variable between species. Reflecting this, we found evidence of sex differences in lifespan in only 53% of toothed whale species in our sample. Overall, there is considerable variability in the presence, direction, and size of sex differences in adult lifespan in these taxa, making toothed whales an important taxonomic group in which to test theories investigating the presence and absence of sex differences in lifespans.

This result of analysis of sex differences highlights a strength of our modelling approach, because rather than simply comparing the final realized maximum lifespans we can compare female and male lifespans at each posterior model draw. More generally, by taking a Bayesian approach we can embrace the uncertainty inherent in age-structured data and still draw useful inferences from uncertain data. The important implication of this is that this analysis aims to capture a distribution of plausible values of lifespan for toothed whale species, rather than to define a single 'best-guess' point estimate. Any future studies using these lifespan estimates should take this into account by carrying error through their analysis and not simply relying on a point estimate of lifespan (e.g. Supporting Information, Appendix S6; Ellis *et al.* 2024). It is also important to note that although throughout this study we have focused on lifespan as our metric of species survival, our methods could also be used to derive distributions of other measures of age-specific mortality (e.g. measures of mortality shape; Healy *et al.* 2019) that might be more relevant for answering some questions.

Our approach builds upon and generalizes concepts and methods that have been used to estimate toothed whale lifespans from age-structured data. Conceptually, our Bayesian approach, which uses priors from other species, has similarities to earlier methods based on scaling known 'model' life tables from other species to toothed whales (Barlow and Boveng 1991, Caswell *et al.* 1998). Unlike previous Bayesian approaches to using age-structured data to estimate toothed whale life history, we aim to capture the distribution of mortality parameters consistent with the data and the unknown effects of population growth and sampling bias, rather than explicitly estimating populating growth and sampling bias parameters (Moore and Read 2008, Saavedra 2018, Rouby *et al.* 2021). As a consequence, our approach can estimate usefully narrow distributions of life-history parameters based on relatively smaller sample sizes than previous methods, but (unlike those methods) is not suited in its present form to calculating growth rates or the demographic consequences of human-induced mortality in a given population.

The methods presented here derive the same or similar estimates of ordinary maximum lifespan estimates as lifespan estimates derived from other methods applied to the same datasets (Table 5). However, these 'single dataset' lifespan measures often differ from the species-level measure derived by applying the model to multiple datasets (Table 5). This highlights the value of our approach; by combining datasets from multiple populations, we can both increase our sample size and derive a more general species lifespan that is less likely to be driven by characteristics of a single population. Lifespan is only one of the traits that contribute to the life history of a species; nevertheless, it is important to quantify and understand in its own right.

Lifespan can be viewed as an emergent property of other processes, such as senescence (Jones *et al.* 2014, Shefferson *et al.* 2017). To understand senescence therefore requires an understanding of species lifespans and shapes of mortality (Ronget and Gaillard 2020), both of which can be derived from the outputs of our model. Lifespan is also hypothesized to have an important role in social evolution (e.g. Silk and Hodgson 2021, Aubier and Kokko 2022). For example, in a number of species (Péron *et al.* 2019), including toothed whales (Foster *et al.* 2012, Nattrass *et al.* 2019), older individuals have been shown to have a positive influence on the fitness of their younger relatives and group mates. In killer whales, one of the mechanisms driving this positive influence is the value of long-term ecological knowledge in allowing older females to lead their group to resources (Brent *et al.* 2015). The first step to understanding how the distribution of ecological knowledge differs across a social group, and how this therefore allows social species to thrive in spatially and temporally complex ecologies, is to understand how long individuals live. Quantifying lifespan is important, therefore, to understanding both social and life-history evolution.

CONCLUSION

It will be decades before longitudinal studies can provide the data necessary to provide estimates of life-history metrics by currently established methods for most toothed whale species. For many species, using age-structured data is the only way we will be able to begin to understand their life histories for the foreseeable future. In this study, we used modern statistical methodology and the power of modern computing to derive age-specific mortality estimates for 44% of extant toothed whale species, representing an important step in understanding the evolution and diversity of odontocete life history.

SUPPLEMENTARY DATA

Supplementary data is available at *Biological Journal of the Linnean Society* online.

ACKNOWLEDGEMENTS

We would like to thank members of the Centre for Research in Animal Behaviour at the University of Exeter for comments throughout the development of this project. We would also like to thank three reviewers and two editors for the constructive and valuable comments on the manuscript.

CONFLICT OF INTEREST

None declared.

FUNDING

This project was funded as part of a Leverhulme Trust Early Career Research Fellowship awarded to S.E. D.P.C., D.W.F., and M.N.W. acknowledge funding from a NERC Standard Grant (no. NE S010327/1), and M.L.K.N. acknowledges funding from a NERC PhD studentship.

DATA AVAILABILITY

The data underlying this article are avalaible in the MARINELIFEHISTDATA R package at github.com/samellisq/marinelifehistdata.

REFERENCES

Addink M, Hartmann MG, Couperus B. A note on life-history parameters of the Atlantic white-sided dolphin (*Lagenorhynchus acutus*) from animals bycaught in the Northeastern Atlantic. *Reports of the International Whaling Commission* 1997;**47**:637–9.

Amano M, Miyazaki N. Composition of a school of Risso's dolphins, *Grampus griseus*. *Marine Mammal Science* 2004;**20**:152–60. https://doi.org/10.1111/j.1748-7692.2004.tb01146.x

Amano M, Miyazaki N, Yanagisawa F. Life history of Fraser's dolphin, *Lagenodelphis hosei*, based on a school captured off the Pacific coast of Japan. *Marine Mammal Science* 1996;**12**:199–214. https://doi.org/10.1111/j.1748-7692.1996.tb00571.x

Amano M, Yamada TK, Brownell RL *et al.* Age determination and reproductive traits of killer whales entrapped in ice off Aidomari, Hokkaido, Japan. *Journal of Mammalogy* 2011;**92**:275–82. https://doi.org/10.1644/10-mamm-a-276.1

Amano M, Yamada TK, Kuramochi T *et al.* Life history and group composition of melon-headed whales based on mass strandings in Japan. *Marine Mammal Science* 2014;**30**:480–93. https://doi.org/10.1111/mms.12050

Arai K, Yamada TK, Takano Y. Age estimation of male Stejneger's beaked whales (*Mesoplodon stejnegeri*) based on counting of growth layers in tooth cementum. *Mammal Study* 2004;**29**:125–36. https://doi.org/10.3106/mammalstudy.29.125

Aubier TG, Kokko H. Volatile social environments can favour investments in quality over quantity of social relationships. *Proceedings of the Royal Society B: Biological Sciences* 2022;**289**:20220281. https://doi.org/10.1098/rspb.2022.0281

Balcomb KC. Baird's beaked whale *Berardius bairdii* Stejneger, 1883: Arnoux's beaked whale *Berardius arnuxii* Duvernoy, 1851. In: Ridgway SH, Harrison R (eds.), *Handbook of Marine Mammals*, Vol. **4**: *River Dolphins and the Larger Toothed Whales*. London: Academic Press, 1989, 261–88.

Barlow J, Boveng P. Modeling age-specific mortality for marine mammal populations. *Marine Mammal Science* 1991;**7**:50–65. https://doi.org/10.1111/j.1748-7692.1991.tb00550.x

Barlow J, Hohn A. *Interpreting Spotted Dolphin Age Distributions*. La Jolla, CA: NOAA Techincal Memoradum NMFS, 1984.

Barratclough A, McFee WE, Stolen M *et al.* How to estimate age of old bottlenose dolphins (*Tursiops truncatus*); by tooth or pectoral flipper? *Frontiers in Marine Science* 2023;**10**:1135521.

Barreto AS, Rosas FCW. Comparative growth analysis of two populations of *Pontoporia blainvillei* on the Brazilian coast. *Marine Mammal Science* 2006;**22**:644–53. https://doi.org/10.1111/j.1748-7692.2006.00040.x

Best PB, Canham PAS, Macleod N. Patterns of reproduction in sperm whales, *Physeter macrocephalus*. *Report of the International Whaling Commission* 1984;**Special Issue 6**:51–80.

Best PB, Meÿer MA, Lockyer C. Killer whales in South African waters—a review of their biology. *African Journal of Marine Science* 2010;**32**:171–86. https://doi.org/10.2989/1814232x.2010.501544

Betty EL. Life history of the long-finned pilot whale (Globicephala melas edwardii); insights from strandings on the New Zealand coast. Ph.D. Thesis, Auckland University of Technology, 2019.

Bigg MA, Olesiuk PF, Ellis GM *et al.* Social organization and genealogy of resident killer whales (*Orcinus orca*) in the coastal waters of British Columbia and Washington State. *Report of the International Whaling Commission, Special* 1990;**Special Issue 12**:383–405.

Bloch D, Lockyer C, Zachariassen M. Age and growth parameters of the long-finned pilot whale off the Faroe Islands. *Report of the International Whaling Commission* 1993;**Special Issue 14**:163–207.

Bloch D, Desportes G, Harvey P *et al.* Life history of Risso's dolphin (*Grampus griseus*) (G. Cuvier, 1812) in the Faroe Islands. *Aquatic Mammals* 2012;**38**:250–66. https://doi.org/10.1578/AM.38.3.2012.250

Botta S, Secchi ER, Muelbert MMC *et al.* Age and growth of franciscana dolphins, *Pontoporia blainvillei* (Cetacea: Pontoporiidae) incidentally caught off southern Brazil and northern Argentina. *Journal of the Marine Biological Association of the United Kingdom* 2010;**90**:1493–500. https://doi.org/10.1017/S0025315410001141

Boy CC, Dellabianca N, Goodall RNP *et al.* Age and growth in Peale's dolphin (*Lagenorhynchus australis*) in subantarctic waters off southern South America. *Mammalian Biology* 2011;**76**:634–9. https://doi.org/10.1016/j.mambio.2011.03.001

Brent LJN, Franks DW, Foster EA *et al.* Ecological knowledge, leadership, and the evolution of menopause in killer whales. *Current Biology: CB* 2015;**25**:746–50. https://doi.org/10.1016/j.cub.2015.01.037

Burns JJ, Seaman GA. Investigations of belukha whales in coastal waters of western and northern Alaska. II. Biology and Ecology. Alaska Department of Fish and Game, Fairbanks, AK, USA, 1986.

Butti C, Corain L, Cozzi B *et al.* Age estimation in the Mediterranean bottlenose dolphin *Tursiops truncatus* (Montagu 1821) by bone density of the thoracic limb. *Journal of Anatomy* 2007;**211**:639–46. https://doi.org/10.1111/j.1469-7580.2007.00805.x

Cáceres-Saez I, Dellabianca NA, Pimper LE *et al.* Sexual dimorphism and morphometric relationships in pelvic bones of Commerson's dolphins (*Cephalorhynchus c. commersonii*) from Tierra del Fuego, Argentina. *Marine Mammal Science* 2015;**31**:734–47. https://doi.org/10.1111/mms.12172

Caswell H, Brault S, Read AJ *et al.* Harbor porpoise and fisheries: an uncertainty analysis of incidental mortality. *Ecological Applications* 1998;**8**:1226–38. https://doi.org/10.2307/2640975

Caughley G. Mortality patterns in mammals. *Ecology* 1966;**47**:906–18. https://doi.org/10.2307/1935638

Chivers SJ. Cetecean life history. In: Würsig B, Thewissen JGM, Kovacs KM (eds.), *Encyclopedia of Marine Mammals*, 3rd edn. London: Academic Press, 2018, 186–7.

Christensen I. Age determination, age distribution and growth of bottlenose whales, *Hyperoodon ampullatus* (Foster) in the Labrador sea. *Norwegian Journal of Zoology* 1973;**21**:331–40.

Christensen I. Growth and reproduction of killer whales, *Orcinus orca*, in Norwegian coastal waters. *Report of the International Whaling Commission* 1984;**Special Issue 6**:253–8.

Cipriano FW. Behavior and occurrence patterns, feeding ecology, and life history of dusky dolphins (Lagenorhynchus obscurus) off Kaikoura, New Zealand. Ph.D. Thesis, University of Arizona, 1992.

Clapham PJ, Childerhouse S, Gales NJ *et al.* The whaling issue: conservation, confusion, and casuistry. *Marine Policy* 2007;**31**:314–9. https://doi.org/10.1016/j.marpol.2006.09.004

Clarke R, Paliza O, Van Waerebeek K. Sperm whales of the Southeast Pacific. Part VII. Reproduction and growth in the female. *Latin American Journal of Aquatic Mammals* 2013;**9**:8–39. https://doi.org/10.5597/lajam00172

Cockcroft VG, Ross GJB. Age, growth, and reproduction of bottlenose dolphins *Tursiops truncatus* from the east coast of Southern Africa. *Fishery Bulletin* 1990;**88**:289–302.

Colchero F, Jones OR, Rebke M. BaSTA: an R package for Bayesian estimation of age-specific survival from incomplete mark–recapture/recovery data with covariates. *Methods in Ecology and Evolution* 2012;**3**:466–70. https://doi.org/10.1111/j.2041-210x.2012.00186.x

Collet A, Robineau D. Data on the genital tract and reproduction of Commerson's dolphin, *Cephalorynchus commersonii* (Lacepede, 1804), from the Kergulen Islands. *Report of the International Whaling Commission* 1988;**Special Issue 9**:119–41.

Connor RC, Mann J, Tyack PL *et al.* Social evolution in toothed whales. *Trends in Ecology & Evolution* 1998;**13**:228–32. https://doi.org/10.1016/s0169-5347(98)01326-3

Conversani VRM, Silva DF, Barbosa RA *et al.* Age and growth of franciscana, *Pontoporia blainvillei*, and Guiana, *Sotalia guianensis*, dolphins from southeastern Brazil. *Marine Mammal Science* 2021;**37**:702–16. https://doi.org/10.1111/mms.12763

Danil K, Chivers SJ. Growth and reproduction of female short-beaked common dolphins, *Delphinus delphis*, in the eastern tropical Pacific. *Canadian Journal of Zoology* 2007;**85**:108–21. https://doi.org/10.1139/z06-188

Denuncio P, Negri MF, Bastida R *et al.* Age and growth of Franciscana dolphins from northern Argentina. *Journal of the Marine Biological Association of the United Kingdom* 2018;**98**:1197–203. https://doi.org/10.1017/s0025315417000765

Dong JH, Lien J, Nelson D *et al.* A contribution to the biology of the white-beaked dolphin, *Lagenorhynchus albirostris*, in waters off Newfoundland. *The Canadian Field-Naturalist* 1996;**110**:278–87.

Durante CA, Santos-Neto EB, Azevedo A *et al.* POPs in the South Latin America: bioaccumulation of DDT, PCB, HCB, HCH and Mirex in blubber of common dolphin (*Delphinus delphis*) and Fraser's dolphin (*Lagenodelphis hosei*) from Argentina. *The Science of the Total Environment* 2016;**572**:352–60. https://doi.org/10.1016/j.scitotenv.2016.07.176

Ellis S, Franks DW, Nattrass S *et al.* Mortality risk and social network position in resident killer whales: sex differences and the importance of resource abundance. *Proceedings of the Royal Society B: Biological Sciences* 2017;**284**:20171313. https://doi.org/10.1098/rspb.2017.1313.

Ellis S, Franks DW, Nattrass S *et al.* Postreproductive lifespans are rare in mammals. *Ecology and Evolution* 2018a;**8**:2482–94. https://doi.org/10.1002/ece3.3856

Ellis S, Franks DW, Nattrass S *et al.* Analyses of ovarian activity reveal repeated evolution of post-reproductive lifespans in toothed whales. *Scientific Reports* 2018b;**8**:12833. https://doi.org/10.1038/s41598-018-31047-8

Ellis S, Franks DW, Nielsen MLK *et al.* The evolution of menopause in toothed whales. *Nature* 2024;**627**:579–85. https://doi.org/10.1038/s41586-024-07159-9

Evacitas FC, Kao WY, Worthy GAJ *et al.* Annual variability in dentin δ^{15}N and δ^{13}C reveal sex differences in weaning age and feeding habits in Risso's dolphins (*Grampus griseus*). *Marine Mammal Science* 2017;**33**:748–70. https://doi.org/10.1111/mms.12396

Evans K, Hindell MA. The age structure and growth of female sperm whales (*Physeter macrocephalus*) in southern Australian waters. *Journal of Zoology* 2004;**263**:237–50. https://doi.org/10.1017/s0952836904005096

Ferguson SH, Willing C, Kelley TC *et al.* Reproductive parameters for female beluga whales (*Delphinapterus leucas*) of Baffin Bay and Hudson Bay, Canada. *Arctic* 2020;**73**:405–20. https://doi.org/10.14430/arctic71435

Ferreira IM, Kasuya T, Marsh H *et al.* False killer whales (*Pseudorca crassidens*) from Japan and South Africa: differences in growth and reproduction. *Marine Mammal Science* 2014;**30**:64–84. https://doi.org/10.1111/mms.12021

Ferrero RC, Walker WA. Growth and reproduction of the northern right whale dolphin *Lissodelphis borealis* in the offshore waters. *Canadian Journal of Zoology* 1993;**71**:2335–44. https://doi.org/10.1139/z93-328

Ferrero RC, Walker WA. Growth and reproduction of the common dolphin, *Delphinus delphis* Linnaeus, in the offshore waters of the North Pacific Ocean. *Fishery Bulletin* 1995;**93**:483–94.

Ferrero RC, Walker WA. Age, growth, and reproductive patterns of the Pacific white-sided dolphin (*Lagenorhynchus obliquidens*) taken in high seas drift nets in the central North Pacific Ocean. *Canadian Journal of Zoology* 1996;**74**:1673–87. https://doi.org/10.1139/z96-185

Ferrero RC, Walker A. Age, growth, and reproductive patterns of Dall's porpoise (*Phocoenoides dalli*) in the Central North Pacific Ocean. *Marine Mammal Science* 1999;**15**:273–313. https://doi.org/10.1111/j.1748-7692.1999.tb00803.x

Foote AD. Mortality rate acceleration and post-reproductive lifespan in matrilineal whale species. *Biology Letters* 2008;**4**:189–91. https://doi.org/10.1098/rsbl.2008.0006

Foster EA, Franks DW, Mazzi S *et al.* Adaptative prolonged postreproductive life span in killer whales. *Science* 2012;**337**:1313. https://doi.org/10.1126/science.1224198

Gabry J, Češnovar R, Johnson A *et al. CmdStanR: the R interface to CmdStan*, 2024. https://mc-stan.org/cmdstanr/ (February 2025, date last accessed).

Gaillard J-M, Viallefont A, Loison A *et al.* Assessing senescence patterns in populations of large mammals. *Animal Biodiversity and Conservation* 2004;**27**:47–58.

Gaillard J-M, Garratt M, Lemaitre JF. Senescence in mammalian life history traits. In: Shefferson RP, Jones OR, Salguero-Gómez R (eds.), *The Evolution of Senescence in the Tree of Life*. Cambridge: Cambridge University Press, 2017;126–55.

Galatius A, Jansen OE, Kinze CC. Parameters of growth and reproduction of white-beaked dolphins (*Lagenorhynchus albirostris*) from the North Sea. *Marine Mammal Science* 2013;**29**:348–55. https://doi.org/10.1111/j.1748-7692.2012.00568.x

Gao A, Zhou K. Sexual dimorphism in the baiji, *Lipotes vexillifer*. *Canadian Journal of Zoology* 1992;**70**:1484–93. https://doi.org/10.1139/z92-205

Gao A, Zhou K. Growth and reproduction of three populations of finless porpoise (*Neophocaena phocaenoides*) in Chinese waters. *Aquatic Mammals* 1993;**19**:3–12.

Garde E, Hansen SH, Ditlevsen S *et al.* Life history parameters of narwhals (*Monodon monoceros*) from Greenland. *Journal of Mammalogy* 2015;**96**:866–79. https://doi.org/10.1093/jmammal/gyv110

Gol'din P. Growth and body size of the Harbour Porpoise, *Phocoena phocoena* (Cetacea, Phocoenidae), in the Sea of Azov and the Black Sea. *Vestnik Zoologii* 2004;**38**:59–73.

Gol'din P, Gladilina E. Small dolphins in a small sea: age, growth and life-history aspects of the black sea common bottlenose dolphin *Tursiops truncatus*. *Aquatic Biology* 2015;**23**:159–66. https://doi.org/10.3354/ab00617

Gompertz B. On the nature of the function expressive of the law of human mortality, and on a new mode of determinng the value of life contingencies. *Philosophical Transactions of the Royal Society* 1825;**115**:513–83.

Gowans S, Würsig B, Karczmarski L. The social structure and strategies of delphinids: predictions based on an ecological framework. *Advances in Marine Biology* 2007;**53**:195–294. https://doi.org/10.1016/S0065-2881(07)53003-8

Guo L, Lin W, Zeng C *et al.* Investigating the age composition of Indo-Pacific humpback dolphins in the Pearl River Estuary based on their pigmentation pattern. *Marine Biology* 2020;**167**:50. https://doi.org/10.1007/s00227-020-3650-x

Hamlin KL, Pac DF, Sime CA *et al.* Evaluating the accuracy of ages obtained by two methods for montana ungulates. *The Journal of Wildlife Management* 2000;**64**:441–9. https://doi.org/10.2307/3803242

Hay KA. The life history of the narwal (Mondon monoceros L.) in the Eastern Canadian Arctic. PhD Thesis, McGill University, 1984.

Healy K, Ezard THG, Jones OR *et al*. Animal life history is shaped by the pace of life and the distribution of age-specific mortality and reproduction. *Nature Ecology & Evolution* 2019;**3**:1217–24. https://doi.org/10.1038/s41559-019-0938-7

Heide-Jørgensen MP, Lockyer C. Age and sex distributions in the catches of belugas, *Delphinapterus leucas*, in West Greenland and in western Russia. *Mammalian Biology* 2001;**66**:215–27.

Herman DP, Matkin CO, Ylitalo GM *et al*. Assessing age distributions of killer whale *Orcinus orca* populations from the composition of endogenous fatty acids in their outer blubber layers. *Marine Ecology Progress Series* 2008;**372**:289–302. https://doi.org/10.3354/meps07709

Hohn AA, Read AJ, Fernandez S *et al*. Life history of the vaquita, *Phocoena sinus* (Phocoenidae, Cetacea). *Journal of Zoology* 1996;**239**:235–51. https://doi.org/10.1111/j.1469-7998.1996.tb05450.x

Iwasaki T, Kasuya T. Life-history and catch bias of Pacific white-sided (*Lagenorhynchus obliquidens*) and Northern right whale dolphins (*Lissodelphis borealis*) incidentally taken by the Japanese high seas squid driftnet fisher. *Report of the International Whaling Commission* 1997;**47**:683–92.

IWC. Taxonomy: classification of Cetacea. In: *International Whaling Commission/About Whales*, 2021. https://iwc.int/about-whales/cetacea (May 2021, date last accessed).

Jefferson TA, Robertson KM, Wang JY. Growth and reproduction of the finless porpoise in southern China. *Raffles Bulletin of Zoology* 2002;**10**:105–13.

Jefferson TA, Hung SK, Robertson KM *et al*. Life history of the Indo-Pacific humpback dolphin in the Pearl River Estuary, southern China. *Marine Mammal Science* 2012;**28**:84–104. https://doi.org/10.1111/j.1748-7692.2010.00462.x

Jones OR, Scheuerlein A, Salguero-Gómez R *et al*. Diversity of ageing across the tree of life. *Nature* 2014;**505**:169–73. https://doi.org/10.1038/nature12789

Kasuya T. Some informations on the growth of the Ganges dolphin with a comment on the Indus dolphin. *Scientific Reports of the Whales Research Institute* 1972;**24**:87–108.

Kasuya T. The life history of Dall's porpoise with special reference to the stock off the Pacific coast of Japan. *Scientific Reports of the Whales Research Institute* 1978;**29**:1–63.

Kasuya T. Effect of exploitation on reproductive parameters of the spotted and striped dolphins off the Pacific coast of Japan. *Scientific Reports of the Whales Research Institute* 1985;**36**:107–38.

Kasuya T. False killer whales. In: Tamura T, Ohsumi S, Arai S (eds.), *Report of the Investigation in Search of Solution for Dolphin Fishery Conflict in the Iki Island*. Japan: Japan Fisheries Agency, 1986, 178–87.

Kasuya T. Density dependent growth in North Pacific sperm whales. *Marine Mammal Science* 1991;**7**:230–57. https://doi.org/10.1111/j.1748-7692.1991.tb00100.x

Kasuya T. Finless porpoise *Neophocaena phocaenoides* (G. Cuvier, 1829). In: Ridgway SH, Harrison R (eds.), *Handbook of Marine Mammals*, Vol. **6**: *The Second Book of Dolphins and the Porpoises*. London: Academic Press, 1999, 411–42.

Kasuya T, Brownell RLJ. Age determination, reproduction, and growth of the Franciscana dolphin *Pontoporia blainvillei*. *Scientific Reports of the Whales Research Institute Tokyo* 1979;**31**:45–67.

Kasuya T, Marsh H. Life history and reproductive biology of the short-finned pilot whale, *Globicephala macrorhynchus*, off the Pacific coast of Japan. *Report of the International Whaling Commission* 1984;**Special Issue 6**:259–310.

Kasuya T, Shiraga S. Growth of Dall's porpoise in the western North Pacific and suggested geographical growth differentiation. *Scientific Reports of the Whales Research Institute* 1985;**36**:139–52.

Kasuya T, Tai S. Life history of short-finned pilot whale stocks off Japan and a description of the fishery. *Report of the International Whaling Commission* 1993;**Special Issue 14**:35.

Kasuya T, Brownell RL Jr, Balcomb KC. Life history of Baird's beaked whales. *Report of the International Whaling Commission* 1997a;**47**:969–79.

Kasuya T, Izumisawa Y, Komyo Y *et al*. Life history parameters bottlenose dolphins off Japan. *IBI Reports* 1997b;**7**:71–107.

Kebke A, Samarra F, Derous D. Climate change and cetacean health: impacts and future directions. *Philosophical Transactions of the Royal Society B: Biological Sciences* 2022;**377**:20210249. https://doi.org/10.1098/rstb.2021.0249

Kemper CM, Trentin E, Tomo I. Sexual maturity in male Indo-Pacific bottlenose dolphins (*Tursiops aduncus*): evidence for regressed/pathological adults. *Journal of Mammalogy* 2014;**95**:357–68. https://doi.org/10.1644/13-mamm-a-007.1

Kemper C, Talamonti M, Bossley M *et al*. Sexual maturity and estimated fecundity in female Indo-Pacific bottlenose dolphins (*Tursiops aduncus*) from South Australia: combining field observations and postmortem results. *Marine Mammal Science* 2019;**35**:40–57. https://doi.org/10.1111/mms.12509

Kesselring T, Viquerat S, Brehm R *et al*. Coming of age: - do female harbour porpoises (*Phocoena phocoena*) from the North Sea and Baltic Sea have sufficient time to reproduce in a human influenced environment? *PLoS One* 2018;**13**:e0199633. https://doi.org/10.1371/journal.pone.0199633

Konno K, Akasaka M, Koshida C *et al*. Ignoring non-English-language studies may bias ecological meta-analyses. *Ecology and Evolution* 2020;**10**:6373–84. https://doi.org/10.1002/ece3.6368

Kurihara N, Amano M, Yamada TK. Decrease in tooth count in melon-headed whales. *Journal of Zoology* 2016;**300**:8–17. https://doi.org/10.1111/jzo.12363

Larese JP, Chivers SJ. Growth and reproduction of female eastern and whitebelly spinner dolphins incidentally killed in the eastern tropical Pacific tuna purse-seine fishery. *Canadian Journal of Zoology* 2009;**87**:537–52. https://doi.org/10.1139/z09-038

Learmonth JA, Murphy S, Luque PL *et al*. Life history of harbor porpoises (*Phocoena phocoena*) in Scottish (UK) waters. *Marine Mammal Science* 2014;**30**:1427–55. https://doi.org/10.1111/mms.12130

Lee YR, An YR, Park KJ *et al*. Age and reproduction of the finless porpoises, *Neophocaena asiaeorientalis*, in the Yellow Sea, Korea. *Animal Cells and Systems* 2013;**17**:366–73. https://doi.org/10.1080/19768354.2013.851116

Lemaître JF, Ronget V, Tidière M *et al*. Sex differences in adult lifespan and aging rates of mortality across wild mammals. *Proceedings of the National Academy of Sciences of the United States of America* 2020;**117**:8546–53. https://doi.org/10.1073/pnas.1911999117

Lensink CJ. Status report: beluga studies. Juneau, AL: Division of Biological Research, Alaska Department of Fish and Game, 1961.

Lewison RL, Crowder LB, Read AJ *et al*. Understanding impacts of fisheries bycatch on marine megafauna. *Trends in Ecology & Evolution* 2004;**19**:598–604. https://doi.org/10.1016/j.tree.2004.09.004

Lima JY, Carvalho APM, Azevedo CT *et al*. Variation of age and total length in *Sotalia guianensis* (Van Bénéden, 1864) (Cetacea, Delphinidae), on the coast of Espírito Santo state, Brazil. *Brazilian Journal of Biology* 2016;**77**:437–43. https://doi.org/10.1590/1519-6984.13215

Lockyer C, Heide-Jørgensen MP, Jensen J *et al*. Age, length and reproductive parameters of harbour porpoises *Phocoena phocoena* (L.) from West Greenland. *ICES Journal of Marine Science* 2001;**58**:154–62. https://doi.org/10.1006/jmsc.2000.0998

Marsili L, Casini C, Marini L *et al*. Age, growth and organochlorines (HCB, DDTs and PCBs) in Mediterranean striped dolphins *Stenella coeruleoalba* stranded in 1988-1994 on the coasts of Italy. *Marine Ecology Progress Series* 1997;**151**:273–82. https://doi.org/10.3354/meps151273

Martin AR, Reynolds P, Richardson MG. Aspects of the biology of pilot whales (*Globicephala melaena*) in recent mass strandings on the British coast. *Journal of Zoology* 1987;**211**:11–23. https://doi.org/10.1111/j.1469-7998.1987.tb07449.x

Mattson MC, Mullin KD, Ingram GW *et al*. Age structure and growth of the bottlenose dolphin (*Tursiops truncatus*) from strandings in the Mississippi sound region of the north-central Gulf of Mexico from 1986 to 2003. *Marine Mammal Science* 2006;**22**:654–66. https://doi.org/10.1111/j.1748-7692.2006.00057.x

McElreath R. *Rethinking: Statistical Rethinking Book Package*, version number 2.31. 2023. https://github.com/rmcelreath/rethinking (Feb 2025, date last accessed).

McGowen MR, Tsagkogeorga G, Álvarez-Carretero S *et al.* Phylogenomic resolution of the cetacean tree of life using target sequence capture. *Systematic Biology* 2020;**69**:479–501. https://doi.org/10.1093/sysbio/syz068

Mei Z, Huang SL, Hao Y *et al.* Accelerating population decline of Yangtze finless porpoise (*Neophocaena asiaeorientalis asiaeorientalis*). *Biological Conservation* 2012;**153**:192–200. https://doi.org/10.1016/j.biocon.2012.04.029

Mitchell E, Kozicki M. Reproductive condition of male sperm whales, *Physeter macrocephalus*, taken off Nova Scotia. *Reports of the International Whaling Commission* 1984:243–52.

Miyazaki N. Preliminary note on age determination and growth of the rough-toothed dolphin, *Steno bredanensis*, off the Pacific coast of Japan. *Report of the International Whaling Commission* 1978;**Special Issue 3**:171–80.

Miyazaki N. Further analyses of reproduction in the striped dolphin, *Stenella coeruleoalba*, off the Pacific coast of Japan. *Reports of the International Whaling Commission* 1984;**Special Issue 6**:343–53.

Miyazaki N, Fujise Y, Iwata K. Biological analysis of a mass stranding of melon-headed whales (*Peponocephala electra*) at Aoshima, Japan. *Bulletin of the National Science Museum Tokyo, Japan Series A* 1998;**24**:31–60.

Modrák M, Moon AH, Kim S *et al.* Simulation-based calibration checking for Bayesian computation: the choice of test quantities shapes sensitivity. *Bayesian Analysis* 2023;**1**:1–50. https://doi.org/10.1214/23-BA1404

Molina DM, Reyes JC. Determinación de edad en el delfín chileno *Cephalorhynchus eutropia* (Cetacea: Delphinidae). *Revista Chilena de Historia Natural* 1996;**69**:183–91.

Moore JE, Read AJ. A Bayesian uncertainty analysis of cetacean demography and bycatch mortality using age-at-death data. *Ecological Applications* 2008;**18**:1914–31. https://doi.org/10.1890/07-0862.1

Murphy S, Winship A, Dabin W *et al.* Importance of biological parameters in assessing the status of *Delphinus delphis*. *Marine Ecology Progress Series* 2009;**388**:273–91. https://doi.org/10.3354/meps08129

Murphy S, Petitguyot MAC, Jepson PD *et al.* Spatio-temporal variability of harbor porpoise life history parameters in the North-East Atlantic. *Frontiers in Marine Science* 2020;**7**:1–19. https://doi.org/10.3389/fmars.2020.502352

National Research Council (ed.). *Marine Mammal Populations and Ocean Noise: Determining When Noise Causes Biologically Significant Effects*. Washington, DC: National Academies Press, 2005.

Nattrass S, Croft DP, Ellis S *et al.* Postreproductive killer whale grandmothers improve the survival of their grandoffspring. *Proceedings of the National Academy of Sciences of the United States of America* 2019;**116**:26669–73. https://doi.org/10.1073/pnas.1903844116

Negri MF, Panebianco MV, Denuncio P *et al.* Biological parameters of franciscana dolphins, *Pontoporia blainvillei*, by-caught in artisanal fisheries off southern Buenos Aires, Argentina. *Journal of the Marine Biological Association of the United Kingdom* 2016;**96**:821–9. https://doi.org/10.1017/S0025315414000393

Neuenhoff RD. Age, growth, and population dynamics of common bottlenose dolphin (Tursiops truncatus) along coastal Texas. Master of Science Thesis, Texas A&M University, 2013.

Newby TC. Life history of Dall's porpoise (Phocoenoides dalli, True 1885) incidentally taken by the Japanese high seas salmon mothership fishery in the northwestern North Pacific and western Bering Sea, 1978 and 1980. Ph.D. Thesis, Univeristy of Washington, 1982.

Nielsen MLK, Ellis S, Towers JR *et al.* A long postreproductive life span is a shared trait among genetically distinct killer whale populations. *Ecology and Evolution* 2021;**11**:9123–36. https://doi.org/10.1002/ece3.7756

Nolte Z. The natural history of the humpback dolphin, Sousa chinensis, in KwaZulu-Natal, South Africa: age, growth and reproduction. M.Sc. Thesis, Rhodes University, 2014.

Nuñez CMV, Coulson T, Festa-Bianchet M *et al.* Measuring senescence in wild animal populations: towards a longitudinal approach. *Functional Ecology* 2008;**22**:393–406. https://doi.org/10.1111/j.1365-2435.2008.01408.x

Ohsumi S. Sexual segregation of the sperm whale in the North Pacific. *Scientific Reports of the Whales Research Institute* 1966;**20**:1–16.

Péron G, Bonenfant C, Lemaitre JF *et al.* Does grandparental care select for a longer lifespan in non-human mammals? *Biological Journal of the Linnean Society* 2019;**128**:360–72. https://doi.org/10.1093/biolinnean/blz078

Perrin WF, Henderson JR. Growth and reproductive rates in two populations of spinner dolphins, *Stenella longirostris*, with different histories of exploitation. *Report of the International Whaling Commission* 1984;**Special Issue 6**:417–30.

Perrin WF, Myrick AC. *Age Determination of Toothed Whales and Sirenians: Report of the Workshop*, Report of the International Whaling Commission 1980;Special Issue 3.

Perrin WF, Holts DB, Miller RB. Growth and reproduction of the eastern spinner dolphin, a geographical form of *Stenella longirostris* in the eastern tropical Pacific. *Fishery Bulletin* 1977;**75**:725–50.

Plön S. The status and natural history of pygmy (Kogia breviceps) and dwarf (K. sima) sperm whales off Southern Africa. Ph.D. Thesis, Department of Zoology & Entomology, Rhodes University, 2004.

Plön S, Heyns-Veale ER, Smale MJ *et al.* Life history parameters and diet of Risso's dolphins, *Grampus griseus*, from southeastern South Africa. *Marine Mammal Science* 2020;**36**:786–801. https://doi.org/10.1111/mms.12675

R Development Core Team. *R: A language and Environment for Statistical Computing*. Vienna: R Foundation for Statistical Computing, 2021.

Read AJ, Tolley KA. Postnatal growth and allometry of harbour porpoises from the Bay of Fundy. *Canadian Journal of Zoology* 1997;**75**:122–30. https://doi.org/10.1139/z97-016

Read AJ, Wells RS, Hohn AA *et al.* Patterns of growth in wild bottlenose dolphins, *Tursiops truncatus*. *Journal of Zoology* 1993;**231**:107–23. https://doi.org/10.1111/j.1469-7998.1993.tb05356.x

Read FL, Hohn AA, Lockyer CH. A review of age estimation methods in marine mammals with special reference to monodontids. *NAMMCO Scientific Publications* 2018;**10**:1–67. https://doi.org/10.7557/3.4474

Reijnders PJH, Borrell A, van Franeker JA, Aguilar A. Pollution. In: Würsig B, Thewissen JGM, Kovacs KM (eds.), *Encyclopedia of Marine Mammals*, 3rd edn. London: Academic Press, 2018, 746–53.

Rice DW, Wolman AA, Mate BR *et al.* A mass stranding of sperm whales in Oregon: sex and age composition of the school. *Marine Mammal Science* 1986;**2**:64–9. https://doi.org/10.1111/j.1748-7692.1986.tb00027.x

Ridgway SH, Harrison RJ (eds.). *Handbook of Marine Mammals*, Vol. **4**: *River Dolphins and the Larger Toothed Whales*. London: Academic Press, 1989.

Ridgway SH, Harrison RJ (eds.). *Handbook of Marine Mammals*, Vol. **5**: *The First Book of Dolphins*. London: Academic Press, 1994.

Ridgway SH, Harrison RJ (eds.) *Handbook of Marine Mammals*, Vol. **6**: *The Second Book of Dolphins and the Porpoises*. London: Academic Press, 1999.

Rogan E, Baker JR, Jepson PD *et al.* A mass stranding of white-sided dolphins (*Lagenorhynchus acutus*) in Ireland: biological and pathological studies. *Journal of Zoology* 1997;**242**:217–27. https://doi.org/10.1111/j.1469-7998.1997.tb05798.x

Rohatgi A. *WebPlotDigitizer*, Version 4.0. 2020. https://apps.automeris.io/wpd4/ (November 2021, date last accessed).

Ronget V, Gaillard J-M. Assessing ageing patterns for comparative analyses of mortality curves: going beyond the use of maximum longevity. *Functional Ecology* 2020;**34**:65–75. https://doi.org/10.1111/1365-2435.13474

Rosas FCW, Barreto AS, Monteiro-Filho ELdA. Age and growth of the estuarine dolphin (*Sotalia guianensis*) (Cetacea, Delphinidae) on the Paraná coast, southern Brazil. *Fishery Bulletin* 2003;**101**:377–83.

Rouby E, Ridoux V, Authier M. Flexible parametric modeling of survival from age at death data: a mixed linear regression framework. *Population Ecology* 2021;**63**:108–22. https://doi.org/10.1002/1438-390x.12069

Saavedra C. strandCet: R package for estimating natural and non-natural mortality-at-age of cetaceans from age-structured strandings. *PeerJ* 2018;**6**:e5768. https://doi.org/10.7717/peerj.5768

Salguero-Gómez R, Jones OR, Archer CR *et al.* COMADRE: a global data base of animal demography. *Journal of Animal Ecology* 2016;**85**:371–84. https://doi.org/10.1111/1365-2656.12482

Santos MCO, Rosso S, Ramos RMA. Age estimation of marine tucuxi dolphins (*Sotalia fluviatilis*) in south-eastern Brazil. *Journal of the Marine Biological Association of the United Kingdom* 2003;**83**:233–6. https://doi.org/10.1017/s0025315403007021h

Sergeant DE, St.Aubin DJ, Geraci JR. Life history and Northwest Atlantic status of the Atlantic white-sided dolphin, Lagenorhynchus acutus. *Cetology* 1980;**37**:1–12.

Shefferson RP, Jones OR, Salguero-Gómez R (eds.) *The Evolution of Senescence in the Tree of Life*. Cambridge: Cambridge University Press, 2017.

Shirakihara M, Takemura A, Shirakihara K. Age, growth, and reproduction of the finless porpoise, *Neophocaena phocaenoides*, in the coastal waters of western Kyushu, Japan. *Marine Mammal Science* 1993;**9**:392–406. https://doi.org/10.1111/j.1748-7692.1993.tb00472.x

Siciliano S, Ramos RMA, Di Beneditto APM *et al.* Age and growth of some delphinids in south-eastern Brazil. *Journal of the Marine Biological Association of the United Kingdom* 2007;**87**:293–303. https://doi.org/10.1017/s0025315407053398

Silk MJ, Hodgson DJ. Differentiated social relationships and the pace-of-life-history. *Trends in Ecology & Evolution* 2021;**36**:498–506. https://doi.org/10.1016/j.tree.2021.02.007

Slooten E. Age, growth, and reproduction in Hector's dolphins. *Canadian Journal of Zoology* 1991;**69**:1689–700. https://doi.org/10.1139/z91-234

Stan Development Team. *Rstan: the R Interface to Stan*, Version 2.32.6. 2024. http://mc-stan.org/ (February 2025, date last accessed).

Stewart REA, Campana SE, Jones CM *et al.* Bomb radiocarbon dating calibrates beluga (*Delphinapterus leucas*) age estimates. *Canadian Journal of Zoology* 2006;**84**:1840–52. https://doi.org/10.1139/z06-182

Stolen MK, Barlow J. A model life table for bottlenose dolphins (*Tursiops truncatus*) from the Indian River Lagoon system, Florida, U.S.A. *Marine Mammal Science* 2003;**19**:630–49. https://doi.org/10.1111/j.1748-7692.2003.tb01121.x

Suydam RS. Age, growth, reproduction, and movements of beluga whales (*Delphinapterus leucas*) from the Eastern Chukchi Sea. Ph.D. Thesis, University of Washington, 2009.

Toïgo C, Gaillard JM, Festa-Bianchet M *et al.* Sex- and age-specific survival of the highly dimorphic Alpine ibex: evidence for a conservative life-history tactic. *Journal of Animal Ecology* 2007;**76**:679–86. https://doi.org/10.1111/j.1365-2656.2007.01254.x

Tombak KJ, Hex SB, Rubenstein DI. New estimates indicate that males are not larger than females in most mammal species. *Nature Communications* 2024;**15**:1872.

Tuerk KJS, Kucklick JR, McFee WE *et al.* Factors influencing persistent organic pollutant concentrations in the Atlantic white-sided dolphin (*Lagenorhynchus acutus*). *Environmental Toxicology and Chemistry* 2005;**24**:1079–87. https://doi.org/10.1897/04-120r.1

Urbán JR, Cárdenas-Hinojosa G, Gómez-Gallardo UA *et al.* Mass stranding of Baird's beaked whales at San Jose Island, Gulf of California, Mexico. *Latin American Journal of Aquatic Mammals* 2007;**6**:83–8. https://doi.org/10.5597/lajam00111

Van Bree PJH, Collet A, Desportes G *et al.* Le dauphin de Fraser, *Lagenodephis hosei* (Cetecea, Odontoceti), espèce nouvelle pour la faune d'Europe. *Mammalia* 1986;**50**:57–86.

Van Utrecht WL. Comparison of accumulation patterns in leyered dentinal tissue of some odontocety and corresponding patterns in baleen plates and ear plugs of Balaenopteridae. *Beaufortia* 1981;**31**:111–22.

van Weelden C, Towers JR, Bosker T. Impacts of climate change on cetacean distribution, habitat and migration. *Climate Change Ecology* 2021;**1**:100009. https://doi.org/10.1016/j.ecochg.2021.100009

Vaupel JW. Post-Darwinian longevity. *Population and Development Review* 2003;**29**:258–69.

Venuto R, Botta S, Barreto AS *et al.* Age structure of strandings and growth of Lahille's bottlenose dolphin (*Tursiops truncatus gephyreus*). *Marine Mammal Science* 2020;**36**:813–27. https://doi.org/10.1111/mms.12683

Viricel A, Strand AE, Rosel PE *et al.* Insights on common dolphin (*Delphinus delphis*) social organization from genetic analysis of a mass-stranded pod. *Behavioral Ecology and Sociobiology* 2008;**63**:173–85. https://doi.org/10.1007/s00265-008-0648-7

Vos DJ, Shelden KEW, Friday NA *et al.* Age and growth analyses for the endangered belugas in Cook Inlet, Alaska. *Marine Mammal Science* 2020;**36**:293–304. https://doi.org/10.1111/mms.12630

Wade PR. Population dynamics. In: Würsug B, Thewissen JGM, Kovacs KM (eds.), *Encyclopedia of Marine Mammals*, 3rd edn. London: Academic Press, 2018, 763–70.

Walker WA, Leatherwood JS, Goodrich KR *et al.* Geographical variation and biology of the Pacific white-sided dolphin, *Lagenorhynchus obliquidens, in the north-eastern Pacific*. In: Bryden MM, Harrison R (eds.), *Research on Dolphins*. Oxford: Oxford University Press, 1986, 441–465.

Watt CA, Stewart BE, Loseto L *et al.* Estimating narwhal (*Monodon monoceros*) age using tooth layers and aspartic acid racemization of eye lens nuclei. *Marine Mammal Science* 2020;**36**:103–15. https://doi.org/10.1111/mms.12623

Weiss MN, Ellis S, Croft DP. Diversity and consequences of social network structure in toothed whales. *Frontiers in Marine Science* 2021;**8**:688842.

Whitehead H, Mann J. Female reproductive strategies of ceteceans: life histories and calf care. In: Mann J, Connor RC, Tyack PL, Whitehead H (eds.), *Cetacean Societies: Field Studies of Whales and Dolphins*. Chicago and London: The University of Chicago Press, 2000, 219–46.

Würsig B, Thewissen JGM, Kovacs KM (eds.). *Encyclopedia of Marine Mammals*, 3rd edn. London: Academic Press, 2018.