

Flexible parametric modeling of survival from age at death data: A mixed linear regression framework

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Abstract

Many long-lived vertebrate species are under threat in the Anthropocene, but their conservation is hampered by a lack of demographic information to assess population long-term viability. When longitudinal studies (e.g., Capture-Mark-Recapture design) are not feasible, the only available data may be cross-sectional, for example, stranding for marine mammals. Survival analysis deals with age at death (i.e., time to event) data and allows to estimate survivorship and hazard rates assuming that the cross-sectional sample is representative. Accommodating a bathtub-shaped hazard, as expected in wild populations, was historically difficult and required specific models. We identified a simple linear regression model with individual frailty that can fit a bathtub-shaped hazard, take into account covariates, allow goodness-of-fit assessments and give accurate estimates of survivorship in realistic settings. We first conducted a Monte Carlo study and simulated age at death data to assess the accuracy of estimates with respect to sample size. Secondly, we applied this framework on a handful of case studies from published studies on marine mammals, a group with many threatened and data-deficient species. We found that our framework is flexible and accurate to estimate survivorship with a sample size of 300. This approach is promising for obtaining important demographic information on data-poor species.

KEYWORDS

age at death, Monte Carlo study, regression, survival analysis, survivorship

1 | INTRODUCTION

The protection and conservation of wildlife is a salient challenge in the Anthropocene, where human-induced pressures are both far-reaching in their geographic and temporal scope, and acute in their impact on biodiversity (Bongaarts, 2019). Long-lived species are particularly sensitive to these pressures: they can act as sentinel species for whole ecosystems (Heithaus, Frid, Wirsing, & Worm, 2008). Their demographic trajectory (e.g., extinction) can also affect the functioning of ecosystems, especially in the case of top predators (Beschta &

Ripple, 2009; Ritchie et al., 2012). Assessing the demographic viability of long-lived species in the face of current and future pressures is required for their proactive conservation; but such an endeavor may be hampered in practice because of logistical challenges in monitoring and collecting relevant data at the relevant spatiotemporal scales.

The classical way to assess a populations viability is to first construct a static life-table where mortality and fecundity rates for a cohort of individuals are tallied at each age/stage of their life cycle (Caughley, 1966). Knowledge of mortality at each age/stage allows to

investigate the associated hazards, estimate vital rates, such as (cumulative) survival; and to project the population trajectory forward in time using matrix models (Caswell, 2001; Leslie, 1945). Historically, the age at death data used to construct life-tables were cross-sectional (e.g., Gompertz, 1825): a sample of the population is taken at a specific time and the observed age structure is assumed similar to that of a cohort of individuals had we been able to monitor them from birth to death. This cross-sectional design allows for a rapid demographic assessment (Boyd, Bowen, & Iverson, 2010; Margules & Austin, 1990, pp. 126–127) whose accuracy however hinges on the assumption that the cross-sectional design approximates well a longitudinal one.

Longitudinal designs, whereby an individual is monitored from birth to death are, in wildlife ecology, a byproduct of capture-recapture studies. The initial motivation for the latter was the accurate estimation of abundance in open populations when detectability is less than perfect (Cormack, 1964; Jolly, 1965; Seber, 1965). Models (e.g., the Cormack-Jolly-Seber model) tailored for these life history data can provide accurate estimates of survival that can be fed into matrix population models (e.g., Fujiwara & Caswell, 2001). Since the 1980s, the emphasis of capture-recapture studies in wildlife ecology shifted from abundance to survival estimation (Lebreton, Burnham, Clobert, & Anderson, 1992) and the inclusion of individual-level covariates, which paved the way for a better understanding of evolution and natural selection in the wild (Cam, 2009). Concomitant with this change in focus was the less frequent reporting of life-tables in publications, an omission partly mitigated by the rise of open online databases such as COMADRE/COMPADRE (Salguero-Gómez et al., 2015; Salguero-Gómez et al., 2016). From an applied perspective in conservation, the obvious drawback of capture-recapture studies is the time and manpower required to collect data, especially for long-lived species. White, Nagy, and Gruber (2014) recently proposed a new development that aims to avoid birth to death monitor. From both juvenile mortality and fecundity, it is possible to infer adult mortality. However, it requires monitoring the juvenile part of the whole population in order to model the overall population dynamics. The mismatch between the necessary delay in data acquisition and the urgency of mitigation on conservation decisions can be acute, suggesting interest for cross-sectional data that have the additional benefit of being applicable on species where the identification of individuals is difficult (Williams, Nichols, & Conroy, 2002). One alternative to species identification, for vital rates estimation, is the use of count data. This approach may involve the building of an N-mixture model relying on the individual-state knowledge. Zipkin et al. (2014) proposed

a development that allows taking into account data even if the individual stage is unknown. Another way to obtain vital rates with count data, as time-series, is to conduct an inverse modeling approach: this method also presents the advantage to consider individual-level state data (González, Martorell, & Bolker, 2016). Even if these approaches are promising for hard to monitor species, they remain difficult to apply on some species, especially very mobile ones.

Assuming that cross-sectional data on age at death are available and representative, conservationists now face some further choices, such as non-parametric (e.g., Kaplan–Meier survivorship curves; Clark, Bradburn, Love, & Altman, 2003; Kaplan & Meier, 1958) versus parametric modeling. The latter presents the advantage to provide smoothing and to summarize the data in a handful of parameters. This is small sample attractive: non-parametric approaches such as the Kaplan–Meier estimators (also known as Product Limit Estimators) for survivorship is piecewise constant with discontinuities at the time of death of individuals in the sample. While assumption-lean, this estimator may yield from small samples rough survivorship curves shaped like staircases that can be difficult to compare. Even with little sample size (i.e., few age at death data regarding the overall time series length), parametric modeling aims to estimate smooth survivorship and allow the statistical comparison of parameters values (Kleinbaum & Klein, 2010). It is important to notice that the estimation hinges on the correct specification of the underlying model. More realistically, the challenge is to find a parsimonious model that will nevertheless accommodate the available data without shoehorning the analysis into a convenient, but not necessarily realistic, template. For long-lived animal species, a realistic model should provide the so-called bathtub-shaped curve whereby there is a high juvenile mortality, followed by a lower and rather constant adult mortality and, finally, a late increase due to senescence (Choquet, Viallefont, Rouan, Gaanoun, & Gaillard, 2011; Siler, 1979). Although there are models to accommodate this bathtub pattern (Heligman & Pollard, 1980; Siler, 1979), they can be difficult to fit (but see Saavedra, 2018), their goodness of fit can be hard to measure; and they usually do not allow for the inclusion of individual-level covariates such as sex.

Our aims are to investigate a parametric approach for the construction of life-tables in a data-poor context, with long-lived vertebrate species in mind. We will first present a simple regression modeling framework for the analysis of age at death data (with or without right-censoring) that can accommodate mortality patterns such as constant, increasing/decreasing, unimodal or bathtub-shaped. Importantly, this framework allows the seamless inclusion

of individual-level covariates. We then conduct a Monte Carlo simulation study with five biological scenarios to assess our framework, focusing on the accurate estimation of survivorship and mortality. Finally, we illustrate our methodology on a handful of real case studies, with a focus on marine mammals. This group includes many elusive and long-lived species that are threatened (Avila, Kaschner, & Dormann, 2018), data-deficient (Parsons, 2016) and difficult to study with a longitudinal approach. The most common age at death data for marine mammals are obtained from strandings (i.e., cross-sectional monitoring) which may be associated to selection biases. However, stranding samples are a source of age data from which it is possible to obtain vital rates.

2 | MATERIALS AND METHODS

2.1 | Definitions

Survival analysis deals with the analysis of the timing of death (Clark et al., 2003; Kaplan & Meier, 1958; Lesaffre & Lawson, 2012; Tanner & Wong, 1984). We assume data $y \geq 0$ to be time-to-event data, for example longevity, survival time or age at death data. Such data can be collected from stranding of animals (that is marine animals that are washed ashore), or any recovery of dead specimens (e.g., *Lepus europaeus*, Pallas 1778; *Ovis dalli*, Nelson 1884) when aging is possible (e.g., from teeth growth layers). Let the index i denotes the i^{th} individual, and N the sample size. The equation $y_i \sim \mathcal{D}(\theta)$ reads as datum y_i follows statistical distribution \mathcal{D} of parameters θ and with probability density function $f(y; \theta)$ and cumulative density function $F(y; \theta) = \Pr(y \leq t) = \int_0^t f(y; \theta) dy$.

The survival function $S(t; \theta)$ gives the probability of being alive at time t , that is $\Pr(y > t) = 1 - \Pr(y \leq t) = 1 - F(y; \theta)$. At the population level, this quantity correspond to the fraction of the population that is still alive at age t , that is cumulative survival or simply survivorship. The hazard rate, or age-specific mortality rate, is the instantaneous probability of dying at time $t + dt$ given that and individual i has survived until time t .

$$h(t) = \lim_{dt \rightarrow 0} \frac{\Pr(t \leq y_i < t + dt; y_i > t)}{dt} \quad (1)$$

With parametric models, the hazard rate can be expressed in terms of the probability density and survivorship functions:

$$h(t; \theta) = \frac{f(t; \theta)}{S(t; \theta)}, \text{ with } S(t; \theta) > 0 \quad (2)$$

Estimation of the hazard rate function is the goal of parametric survival analysis (Lesaffre & Lawson, 2012).

2.2 | Data simulation scenarios

We considered five biological scenarios corresponding to different patterns in survivorship and the underlying hazard (Figure 1, see Text S1):

1. A unimodal distribution of age at death corresponding to a unimodal hazard, whereby mortality risk increases in early ages, peaks and decreases in late life.
2. A mixture of two hazards corresponding to either a unimodal (a) or bimodal (b) distribution of age at death.
3. A bathtub-shaped hazard due to individual frailty, that is individual-specific risk of mortality.
4. A bathtub-shaped hazard with an additional bump in early life due, for example, to an additional source of mortality.

Each scenario is associated to survivorship and hazard functions (Figure 1).

2.3 | Statistical analysis of age at death data

We used parametric models \mathcal{M} of age at death data y to estimate hazard and survivorship rates (see Data S1 for model code): the latter are especially of interest to conservationists. We assumed that the exact timing of death is available, but our framework can easily accommodate censoring (that is cases when death is known to have occurred before or after measurement). Our framework consists in modeling the logarithmic transform of y_i in a regression framework (location-scale model):

$$\log y_i = \mu + \sigma \times \varepsilon_i - \frac{Z_i}{\beta} \quad (3)$$

where μ is a location parameter; σ and $\frac{1}{\beta}$ are (positive) scale parameters; and Z_i are independent standard exponential deviates. The parameter $\frac{1}{\beta}$ quantifies individual frailty (Kannisto, 1991; Reed, 2011) or persistent demographic heterogeneity sensu Cam, Aubry, and Authier (2016). The choice of the statistical distribution for the residuals ε_i determines the shape of the underlying hazard rate. We considered three different choices, each corresponding to a model (see Text S2 for the associated survivorship and hazard functions).

- \mathcal{M}_1 : $\varepsilon_i \sim \mathcal{N}(0, 1)$ and $\frac{1}{\beta} = 0$ ($\beta = +\infty$)

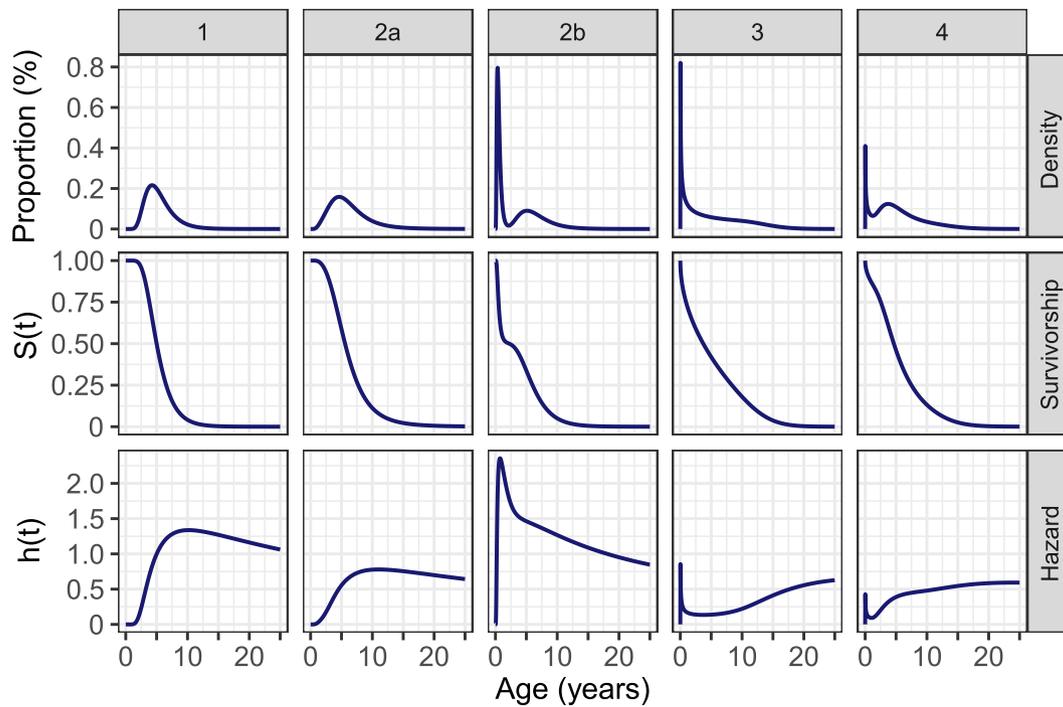


FIGURE 1 The five biological scenarios considered in the Monte Carlo simulation study. Scenario 1 corresponds to a low juvenile mortality, a high adult mortality and no senescence. Scenario 2a corresponds to a low juvenile mortality and a higher adult mortality plateau. Scenario 2b corresponds to a high juvenile mortality and a lower adult mortality that decreases in a linear fashion. Scenario 3 corresponds to a high juvenile mortality, a lower adult mortality and senescence (bathtub shaped hazard). Finally, Scenario 4 corresponds to a high juvenile mortality and a high adult mortality, with a transient dip in mortality risk between these two life-stages [Color figure can be viewed at wileyonlinelibrary.com]

This model assumes a log-normal distribution for y_i , which corresponds to a unimodal hazard curve.

- \mathcal{M}_2 : $\varepsilon_i \sim \mathcal{G}(0, 1)$ and $\frac{1}{\beta} = 0$ ($\beta = +\infty$)

This model assumes a Gumbel distribution for the residuals ε_i , which corresponds to a Weibull distribution for y_i . It is known as the Accelerated Failure Model. The hazard rate is monotonic: it can be constant, increasing or decreasing depending on the value of σ .

- \mathcal{M}_3 : $\varepsilon_i \sim \mathcal{N}(0, 1)$ and $\frac{1}{\beta} > 0$

This choice leads to assume a normal-Laplace distribution for $\log y_i$, which induces a flexible hazard curve depending on the value of β (Reed, 2011). In particular, the hazard can be a bathtub-shaped, as expected for example for long-lived species of vertebrates in the wild (Choquet et al., 2011).

Our framework given by Equation (3) is a flexible location-scale model and boils down to a generalized linear mixed model (GLMM; Bolker et al., 2009) with a handful of parameters $\theta = (\mu, \sigma, \beta)$ to accommodate a large diversity of survivorship and hazard curves (see Text S2 for equations). One attractive feature of this framework is the seamless incorporation of p individual-level covariates x_{ip} in Equation (3) (Reed, 2011):

$$\log y_i = \mu + \sum_{j=1}^p \gamma_j x_{ip} + \sigma \varepsilon_i - \frac{Z_i}{\beta} \quad (4)$$

An important restriction of our approach is that only time-invariant individual-level covariates can be included. This covers however interesting cases such as sex-differences in survival or differences due to geography (that is comparing different populations of the same species).

2.4 | Monte Carlo study

Our aim is to carry a Monte Carlo study (e.g., Morris, White, & Crowther, 2019) to investigate whether our modeling framework can provide accurate survivorship estimates from age at death data. We considered five biological scenarios to cover a diversity of realistic mortality patterns. For each scenario, we simulated 100 data sets of sample size 100, 200, 300, 400, 500 and 1000 to provide recommendations on the minimum sample size required for accurate estimation. Data simulation was carried out in R version 3.6.0 (R Core Team, 2019) using base

TABLE 1 Design of the Monte Carlo study: model \mathcal{M}_2 acts as a negative control as it was never used to simulate data, hence it should not be selected as the best model as it is misspecified

Model/scenario	1	2a	2b	3	4
\mathcal{M}_1	+	-	-	-	-
\mathcal{M}_2	-	-	-	-	-
\mathcal{M}_3	-	-	-	+	-

Note: Likewise, scenarios 2a, 2b and 4 corresponds to data generated from mixture models not included in the set: they serve as tests of the performance of our framework to obtain accurate estimates with misspecified models. Finally, scenarios 1 and 3 act as positive control as they correspond to data simulated under models \mathcal{M}_1 and \mathcal{M}_3 , respectively.

functions such as `rnorm` and `rexp`. Each simulated data set was then analyzed with our framework that considered three parametric models. Crucially, we considered scenarios for which the true model was not among the set (Table 1). In other words, we assessed the performance of our framework under the possibility that none of the candidate models is correctly specified with respect to the data at hand. For example \mathcal{M}_2 is a Weibull model, which is widely used in survival analysis (Kleinbaum & Klein, 2010) it is biologically unreasonable for marine megafauna and top predators as a model over their entire lifetime because it cannot accommodate the expected bathtub-shape hazard. Model fitting was done with software Stan version 2.18 (Carpenter et al., 2017) called from R via the library `rstan` (Stan Development Team, 2018). Three chains were run with a warm-up of 500 iterations, followed by an additional 1000 iterations. No thinning was performed but the delta parameter of the NUTS algorithm was increased from 0.80 to 0.95 to avoid divergent transitions and the maximum tree depth increased to 15. Parameter convergence was assumed when its \hat{R} statistics was lower than 1.10. Upon convergence, the three chains were pooled to obtain a sample of ≈ 1000 values from the posterior distribution.

Model fit was assessed with the widely applicable information criterion (WAIC, Gelman, Hwang, & Vehtari, 2014), computed with R package `loo` (Vehtari, Gelman, & Gabry, 2017). Survivorship estimates from each model were computed from the posterior distribution of parameters, and visually compared to the true survivorship curve and a non-parametric (Kaplan–Meier) estimate. Because we carried out a simulation study, the true survivorship curve was known and could have been used to compute the root-mean-squared error (RMSE). However, in practice, this is not the case and we chose instead to compute RMSE with respect to the non-parametric Kaplan–Meier survivorship estimates. The latter were thus assumed to represent the best estimates

available to researchers, and the aim was to assess whether a parametric model could provide a fit as good as that from a non-parametric approach.

$$\text{RMSE}_{\mathcal{M}} = \sqrt{\mathbb{E} \left[\left(\hat{S}_{KS}(t) - \hat{S}_{\mathcal{M}}(t) \right)^2 \right]} \quad (5)$$

where $\hat{S}_{KS}(t)$ is the Kaplan–Meier estimate of survivorship at age t , $\hat{S}_{\mathcal{M}}(t)$ is the corresponding estimate from parametric model \mathcal{M} , and the expectation is taken over a sequence of values of t .

In order to assess model selection and model check, it is necessary to determine if the models represent well the data. Conn, Johnson, Williams, Melin, and Hooten (2018) recently reviewed some ways to proceed. We choose to do a prior predictive check to test for adequacy between models and time to event data (Text S3 and Figure S1). We also did a posterior predictive check (Text S3 and Figure S2) to see whereas data simulated through the fitted models are similar to that observed from the Barlow and Hohn (1984) data set. The comparison is done with both the true Kaplan–Meier survivorship curve and the ones from posterior simulated data sets (Text S3).

Our focus was on accurate estimation of survivorship, and thus we assessed goodness-of-fit by comparing the expected mean survivorship under each model to the observed Kaplan–Meier estimates. This focus was in line with downstream use of such estimates in matrix population models: here the salient statistics we want our model to reproduce (Gelman, 2003) is the survivorship function.

Our study design is summarized in Table 1 and Figure 2. It consisted in a comprehensive factorial design crossing (a) sample size (100, 200, 300, 400, 500 and

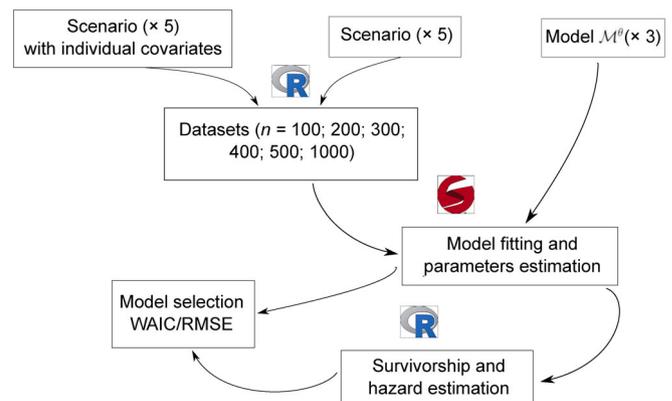


FIGURE 2 Monte Carlo study flowchart. We considered five biological scenarios, six different sample sizes for data, and three models for analysis. For each combination, we assessed model fit and the accuracy of parameter estimates. Model selection is done with Watanabe-Akaike information criterion (WAIC) and root-mean-square error (RMSE) [Color figure can be viewed at wileyonlinelibrary.com]

TABLE 2 Case studies

Data set	Taxon	Species	Sample size	Covariate
Murphy et al. (2012)	Pinniped	Monk seal (<i>Monachus monachus</i> , Hermann 1779)	28	Sex
Slooten (1991)	Cetacean	Hector's dolphin (<i>Cephalorhynchus hectori</i> , Van Beneden 1881)	60	None
Rodríguez-Caro et al. (2019)	Chelonian	Spur-thighed tortoise	154	None
Murphy et al. (2009)	Cetacean	Common dolphin (<i>Delphinus delphis</i> , Linnaeus 1758)	515	None
Kesselring, Viquerat, Brehm, and Siebert (2018)	Cetacean	Harbor porpoise (<i>Phocoena phocoena</i> , Linnaeus 1758)	561	Area
Saavedra (2018)	Cetacean	Delphinidae	579	None
Barlow and Hohn (1984)	Cetacean	Pantropical spotted dolphin (<i>Stenella attenuata</i> , Gray 1846)	1892	Sex

Note: Data sets were selected based on the availability of published (raw) data, species and sample size.

1000), (b) mortality patterns (five scenarios), (c) parametric models (three models) and (d) individual covariate inclusion. Two covariates (x_1 , x_2) were generated by sampling from a Bernoulli distribution with probability 0.5. These covariates could represent for example sex or two sub-populations in different geographic areas.

2.5 | Applications

We analyzed real data sets from published case studies (Table 2) within our framework, and compared the estimated parametric survivorship curves with the non-parametric Kaplan–Meier one. All species in Table 2 are marine mammals except the spur-thighed tortoise (*Testudo graeca*, Mertens 1946) which was included to compare our approach with that of Rodríguez-Caro et al. (2019) in a data-poor context for conservation. It is important to precise that data from Rodríguez-Caro et al. (2019) were obtained from live animals, still alive at the time of measurement (Rodríguez-Caro, Graciá, Anadón, & Gimenez, 2013; Sanz-Aguilar et al., 2011). However, we used these data as if they were age at death data and ignored right-censoring.

3 | RESULTS

Across all scenarios and sample size, parameter convergence (assessed with \hat{R}) was not equivalently reached depending on the model and scenario (see Figures S3 and S4a). \mathcal{M}_1 always converged very easily. In contrast, \mathcal{M}_2 and \mathcal{M}_3 were not as good as \mathcal{M}_1 to converge with 1000 iterations (500 as warm up). More precisely, convergence for \mathcal{M}_3 was difficult for β given this configuration (see

Figures S5 to S10). An increased in the number of iterations per chains (here from 1,000 to 2000) solved the problem (Figure 3).

3.1 | Hazard rate estimation

Estimated hazard curves are shown in Figure 4 for each combination of scenario, model and sample size. Models \mathcal{M}_1 and \mathcal{M}_3 were the best fitting ones in the first and third scenarios respectively (i.e., positive control, Table 1): estimates were accurate and precision increased with sample size. For scenarios 2a, 2b and 4, all estimates were biased, and precision increased with sample size (Figure 3). In contrast, model \mathcal{M}_2 never provided accurate hazard estimates (i.e., negative control). The same results were obtained when covariates were included (not shown).

3.2 | Survivorship estimation

Estimated cumulative survival curves are shown in Figure 5 for each combination of scenario, model and sample size. Across all scenarios and sample sizes, estimates from model \mathcal{M}_3 were the most accurate (Figure 5, see Text S4 and Figure S11 for RMSE results). Precision increased with sample size. In particular, survivorship rates estimated with \mathcal{M}_3 were very close to Kaplan–Meier estimates for sample size ≥ 300 . This sampling size also provided a good confidence interval precision with a maximum width of 0.04% while estimating survivorship (Figure S12). Predictive ability, as measured with WAIC, was the greatest for model \mathcal{M}_3 : it was consistently ranked first across each combination of scenario and sample size,

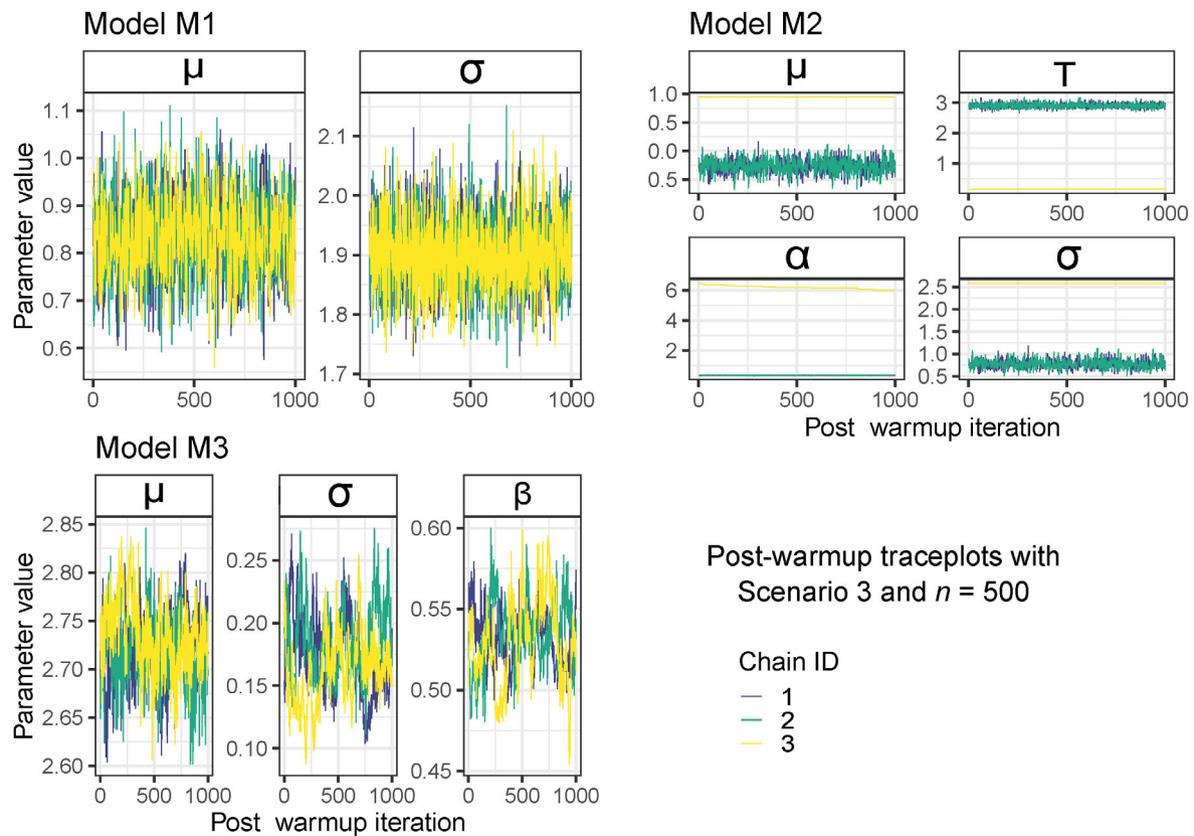


FIGURE 3 Models parameters convergence assessment for each sampling size with $n(\text{warm-up}) = 1000$ iterations and a total of $N = 2000$ iterations [Color figure can be viewed at wileyonlinelibrary.com]

even for scenario 1 where model \mathcal{M}_1 was the true data-generating mechanism (see Text S4 and Figure S13).

3.3 | Covariate effects

Covariate effect estimation is summarized on Figure 6 as a difference between survivorship rates. Model \mathcal{M}_2 could not estimate difference in survivorship. Model \mathcal{M}_1 is only effective for both scenario 1 and 2a. \mathcal{M}_3 could estimate accurately covariate effects when the difference is expressed as an unimodal pattern (i.e., scenario 1, 2a and 3). The precision of the estimated effect increased with sample size for models \mathcal{M}_1 and \mathcal{M}_3 . With small sample size, sign errors on the effect of covariate was possible but disappeared with sample size ≥ 300 .

3.4 | Case studies

Estimated survivorship curves from published data sets are plotted against the Kaplan–Meier curves in Figure 7 for each model. Model \mathcal{M}_3 was the most flexible: it provided the most accurate estimates for each data set. Uncertainty, as measured with 80% credible intervals

were narrower with model \mathcal{M}_3 , and overlapped most with Kaplan–Meier estimates. Model \mathcal{M}_3 consistently had the lowest WAIC.

In the handful of case studies where covariates were available (Table 2), a similar pattern arose. Including covariate can be expected to account for more variation in the data, and a lower WAIC. For both \mathcal{M}_1 and \mathcal{M}_2 , this was indeed the case. For \mathcal{M}_3 it was only true with the Murphy et al., 2012 data set (see Text S4 and Table S1). The estimated covariate effect for both Barlow and Hohn (1984) and Kesselring et al. (2018) case studies is summarized on Figure 8 (see also Text 5). Models \mathcal{M}_1 and \mathcal{M}_3 both estimated a survivorship difference between each covariate. As it is the case without covariates (Figure 7), the \mathcal{M}_3 curve fits the Kaplan–Meier estimate better. However, there is a discrepancy between both, for each covariate. \mathcal{M}_3 is able to spot a difference depending on covariate, but is not able to perfectly fit the Kaplan–Meier estimate.

4 | DISCUSSION

We assessed the ability of a simple linear mixed model to estimate hazard and survivorship rates with

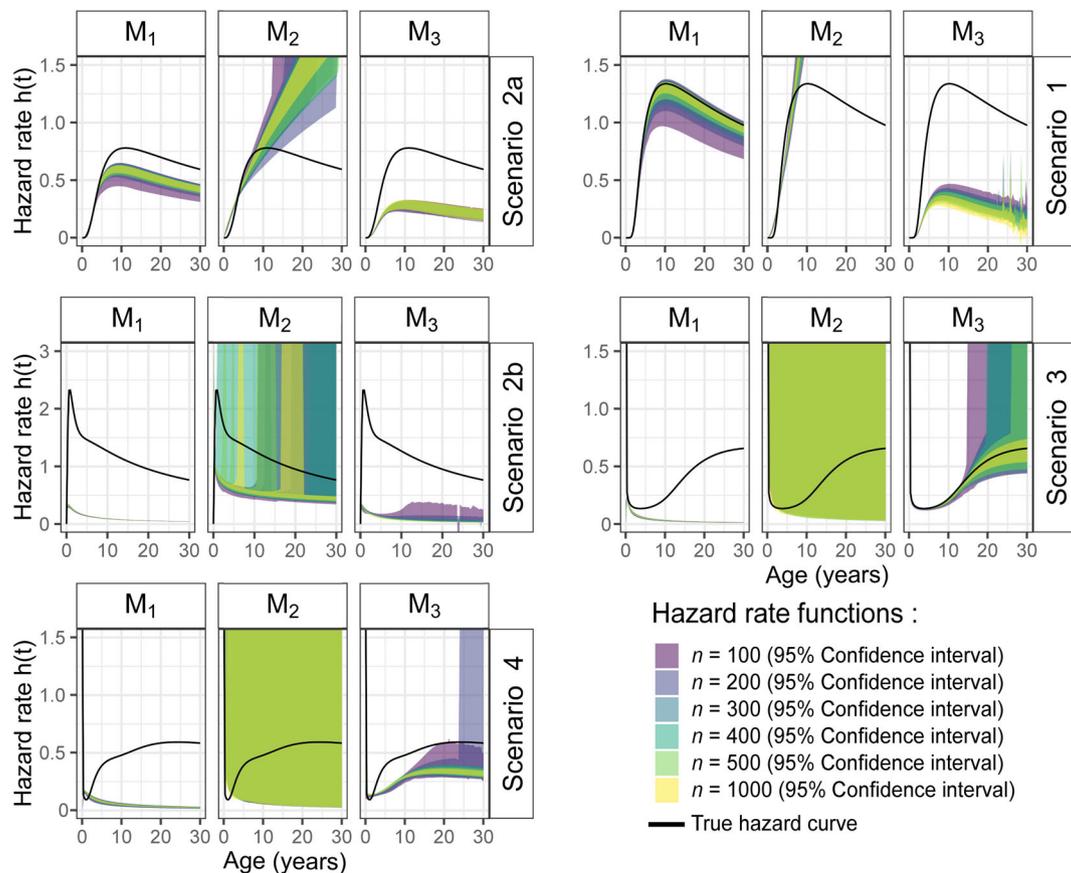


FIGURE 4 Estimated hazard curves confidence intervals for each combination of scenarios (rows), models (columns), and sample size (facets). Estimated confidence intervals are depicted in each panel and compared to the true hazard curves (in black). Even-numbered scenarios (2a, 2b and 4) are on the left, and odd-numbered ones (1 and 3) on the right [Color figure can be viewed at wileyonlinelibrary.com]

cross-sectional age at death data. We used Monte Carlo simulations to investigate the accuracy and precision of estimates across a diversity of mortality patterns and several sample sizes. We contrasted the performance of three different models and found one model, the model \mathcal{M}_3 ; that was consistently better with respect to prediction of survivorship, even when it was misspecified.

4.1 | Age at death data and sampling bias

A crucial but implicit assumption of the cross-sectional approach to survival analysis is that the sample is representative of the larger population, especially with respect to age structure (Caughley, 1966). This assumption is on the data set, not on the modeling. The way of collecting age at death data is therefore determinant to support this assumption. Transversal designs involving, for example, recording of dead carcasses, hunting bags or population census must match the representativity premise. However, it is possible that an implicit process (e.g., bycatch)

shapes the observed age frequency (e.g., from stranded animals). In this case, it is necessary to explore some potentials age-dependent selection biases in the population (Barlow & Hohn, 1984). With stranding data, the stationary age distribution assumption needs to be substantiated with auxiliary data, but ultimately, it is likely to remain a working hypothesis on which any cross-sectional method will lean on. In the case of cetaceans, many species are not amenable to study with a longitudinal design, and strandings remain an important source of information (e.g., Murphy et al., 2009), and demographic information in particular (Ferguson, Stirling, & McLoughlin, 2006; Saavedra, 2018). When longitudinal studies are not possible, there are very limited options to obtain demographic information. In some cases, a comparative approach may be possible where information on species with similar life histories can be leveraged (Caswell, Brault, Read, & Smith, 1998; Hashimoto, Shirakihara, Shirakihara, & Hiramatsu, 2013). This choice relies crucially on the assumption of between-species similarity. Even if comparative data are available,

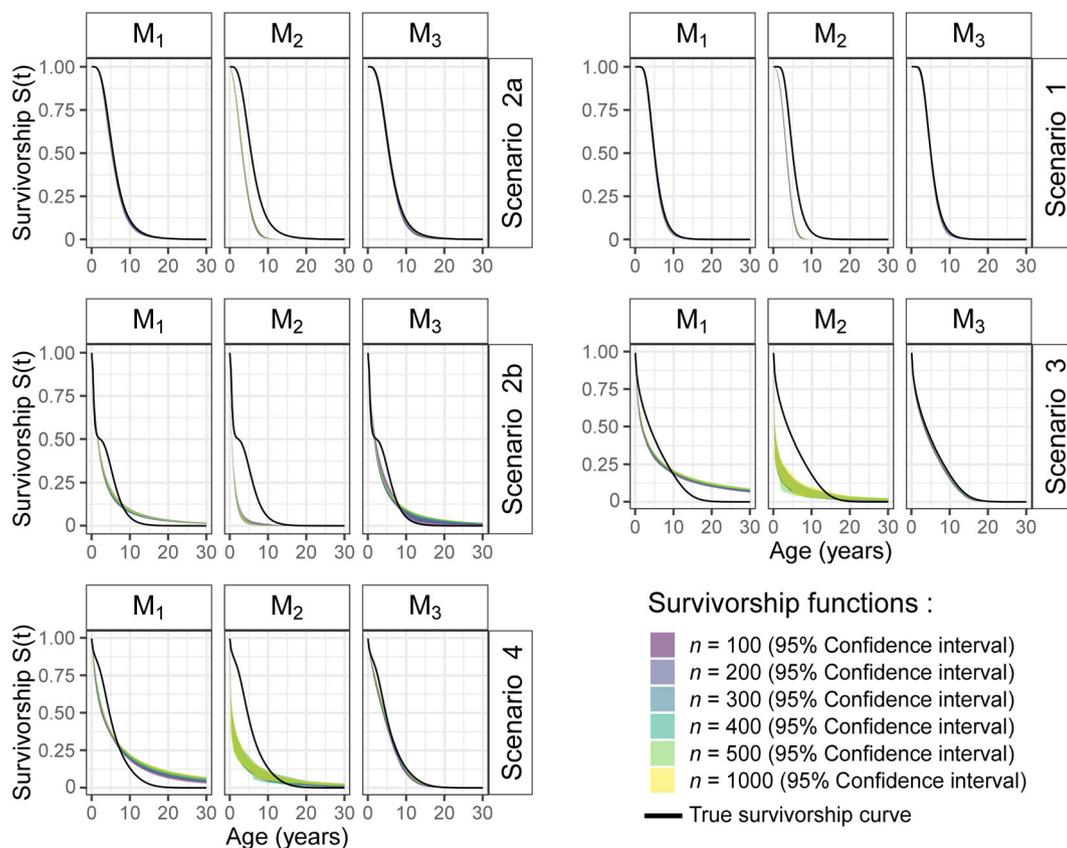


FIGURE 5 Estimated survivorship confidence intervals for each combination of scenarios (rows), models (columns) and sample size (facets). Estimated confidence intervals are depicted in each panel and compared to the truth (in black). Even-numbered scenarios (2a, 2b and 4) are on the left, and odd-numbered ones (1 and 3) on the right [Color figure can be viewed at wileyonlinelibrary.com]

the ecological context may be too different to justify this approach in some instances. Strandings may be the only available source of data, and even if they are suspected to suffer from some selection bias, a pragmatic approach to conservation requires to use them (Boyd et al., 2010), keeping in mind the inherent limitations of these data.

Many conservation instruments specifically requires to use the best available science (e.g., the Marine Strategy Framework Directive EC 2008/56 in Europe). The operative expression “the best available science” may be understood broadly as what lies at the intersection of state-of-the-art methods, good data and accurate knowledge. In practice, there may be a hiatus between the canonical approach that should be, and the pragmatic one that can be pursued at the time conservation actions need to be decided. A conclusion of a species being data-deficient often leads to the doldrums with respect to conservation decisions (Parsons, 2016). Likewise, the many uncertainties that can affect any scientific studies can easily lead to inactions (Ascher, 2004). It is because we are starkly aware of these limitations that we carried out this study to identify a pragmatic approach to estimate survivorship rates from age at death data. Crucially, all the

models we used are conditional of the underlying sample being representative of the population it is taken from. Granting this assumption, we identified a simple model from Reed (2011) to obtain accurate estimates.

4.2 | Prediction accuracy and models' goodness of fit

Traditionally, estimating survivorship rates of marine mammals with cross-sectional data was done with parametric models such as the Siler or Heligman-Pollard models (Heligman & Pollard, 1980; Siler, 1979). These models aim at reproducing a bathtub-shaped hazard curve, but need several parameters to do so. Furthermore, they can be difficult to fit although new tools have been developed to use these models (Saavedra, 2018). A remaining challenge with these models is to assess goodness of fit, to incorporate individual-level covariates and perform model selection. The simple parametric form of Reed (2011) for analyzing the logarithm of age at death data provides a bathtub-shaped hazard with a linear mixed model, the current workhorse of ecologists (Bolker

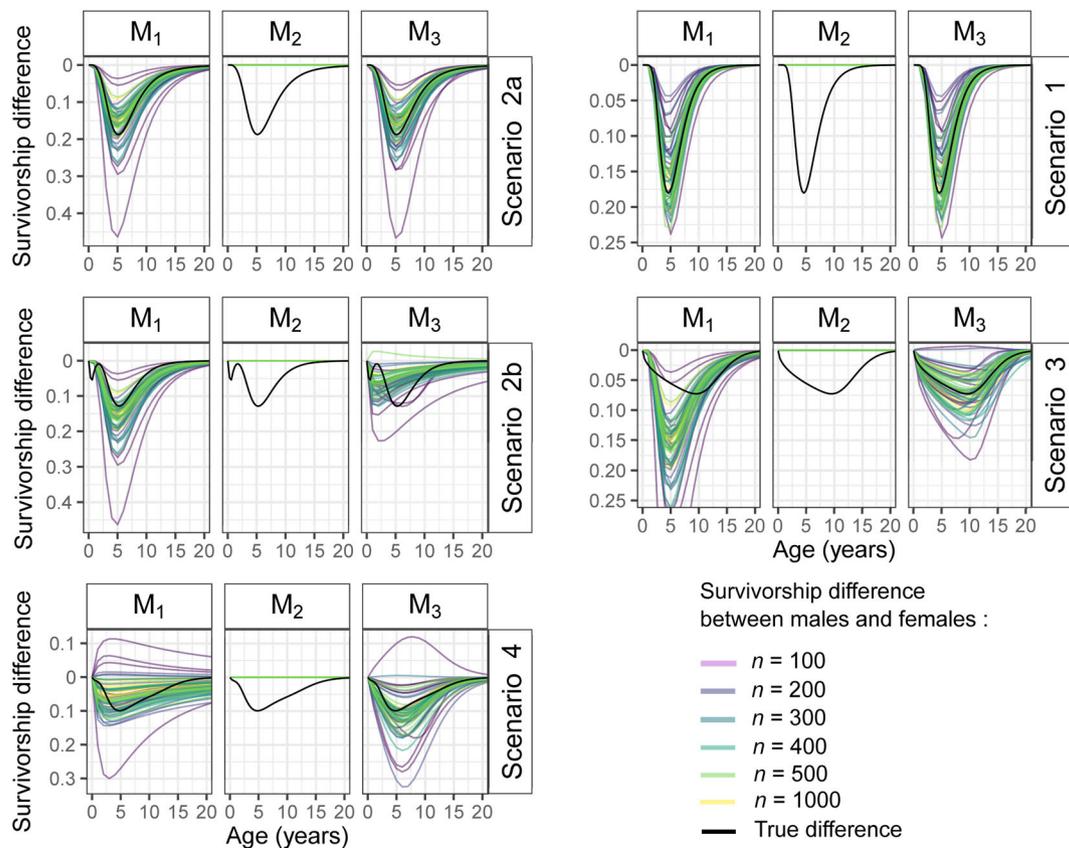


FIGURE 6 Estimated survivorship difference $((\hat{S}_M(t)|x=1) - (\hat{S}_M(t)|x=0))$ under each scenario. The covariate effect could correspond to that of sex (e.g., $x = 1$ for females and $x = 0$ for males). Ten estimated difference curves are depicted in each panel and compared with the truth [Color figure can be viewed at wileyonlinelibrary.com]

et al., 2009). This linear mixed modeling framework allows for a seamless incorporation of covariates, and to use standard tools for model selection and goodness-of-fit assessments. In other words, model \mathcal{M}_3 brings back survival analysis within the comfort zone of ecologists. We harnessed the simplicity of Reed (2011) to conduct our Monte Carlo study, and found that the model suggested by Reed (2011), our model \mathcal{M}_3 , was very accurate in predicting survivorship (i.e., it consistently had the lowest RMSE), even in cases when it was not the true model behind the data (see Text S6 to have details about priors). This result is important as it suggests to start building model of increasing complexity from \mathcal{M}_3 and use tools such as WAIC (Gelman et al., 2014) to balance model complexity with prediction accuracy.

From our simulations, we can recommend a sample size of at least 300 individuals to obtain accurate and precise estimates of survivorship, from which age-specific survival estimates can be derived (see Figure S14 for parameters estimates). This sample size recommendation is practical and realistic (e.g., Kesselring et al., 2018; Mannocci et al., 2012; Murphy et al., 2009). This recommendation is mostly to obtain precise estimates, but may

be relaxed in some cases where only sparse data may be available (data-poor context hereafter). Estimates from a simple linear model with an individual frailty term, were accurate, if imprecise, with a sample size as small as 100. The possibility to use sparse data is critical as it can help conservation of marine mammals, many of which being classified as data-deficient (Parsons, 2016; Schipper et al., 2008). Some of the cases studies presented in this paper support this statement, although, with so few data, including covariates in the model will be difficult or will require great care (see, e.g., Cox, Authier, Orgeret, Weimerskirch, and Guinet (2020)). Rodríguez-Caro et al. (2019) recently provided an approach to estimate survival in data-poor settings using inverse modeling, also to obtain accurate estimates of demographic rates. With the latter, population matrix models can then be used to assess population dynamics and the fate of populations over time (Caswell, 2001).

5 | HAZARD AND FRAILTY

A linear mixed model can fit age at death data very well: this ability comes for the individual frailty term, which

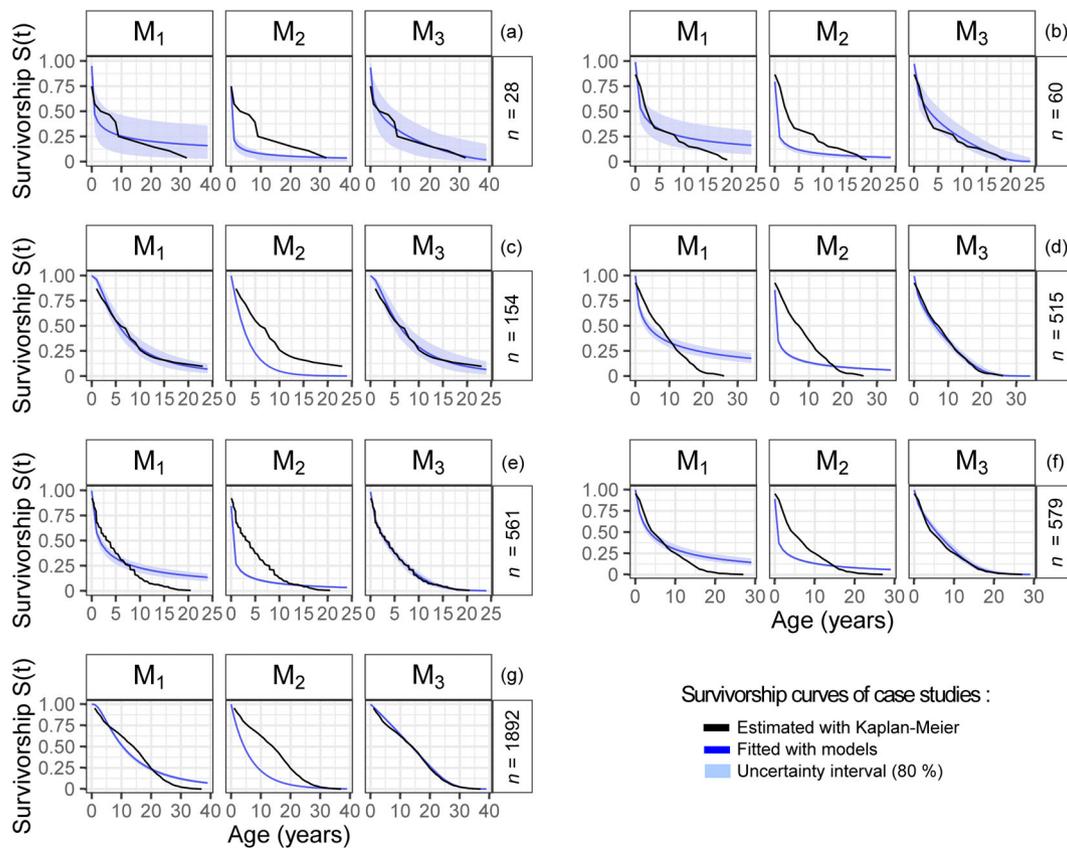


FIGURE 7 Survivorship curves estimated from published data sets. Each subpanel corresponds to a case studies in Table 2. Data set size is represented horizontally. Panels are associated to the following data sets: (a) Murphy et al., (2012); (b) Slooten, (1991); (c) Rodriguez-Caro et al., (2019); (d) Murphy et al., (2009); (e) Kesslerling et al., (2018); (f) Saavedra, (2018); (g) Barlow and Hohn, (1984) [Color figure can be viewed at wileyonlinelibrary.com]

corresponds to an individual random effect in the mixed modeling framework. Individual frailty in statistical models translate the empirical observation that two similar individuals (with respect to observable features of their phenotypes) can nevertheless differ markedly in their longevity (Cam et al., 2016; Kannisto, 1991). The parametric form (i.e., exponential) for individual frailty gives extra flexibility to the model, and can accommodate a bathtub-shaped hazard curve (Reed, 2011). However, in our simulations, we found that estimating hazard rates was more difficult than estimating survivorship rates (Figures 3 and 4). Thus, even though we identified a model (\mathcal{M}_3) for reliable and accurate estimation of survivorship, the same model was less reliable with respect to hazard. In other words, the individual frailty term in our model \mathcal{M}_3 should not be over-interpreted, and is probably best seen as a statistical device for robust estimation. Hazard estimation is a difficult statistical problem (Watson & Leadbetter, 1964), for which there are better tools available, especially non-parametric ones (see, e.g., Hanson & Jara, 2013), than the simple parametric approach we considered in this study. Non-parametric approaches to infer

the shape of the hazard curve are data-hungry: Hanson and Jara (2013) using Bayesian non-parametric, which is better described as a model with a massive number of parameters (Hoff, 2013). The traditional Kaplan-Meier approach is truly a non-parametric approach but it does not give access to the underlying hazard, and give rough (i.e., non-smooth; Figure 5) survivorship rates with small sample size. In data-poor settings, parametric modeling remains attractive because it has interpretable parameters (e.g., individual frailty) and because these parameters can smooth out noise in data, yielding more precise estimates if the model is at least approximately correct, or more pragmatically, if it is grounded in theory (e.g., bathtub-shaped hazard for natural populations) and cannot be rejected from a goodness-of-fit test. It is precisely in this data-poor setting that we envision our parametric modeling approach to be most useful. Because the approach boils down to linear mixed effects modeling, great flexibility in model specification of additional random effects (e.g., year effects, sex-specific frailties) is possible provided there are enough data to offset the increase in complexity.

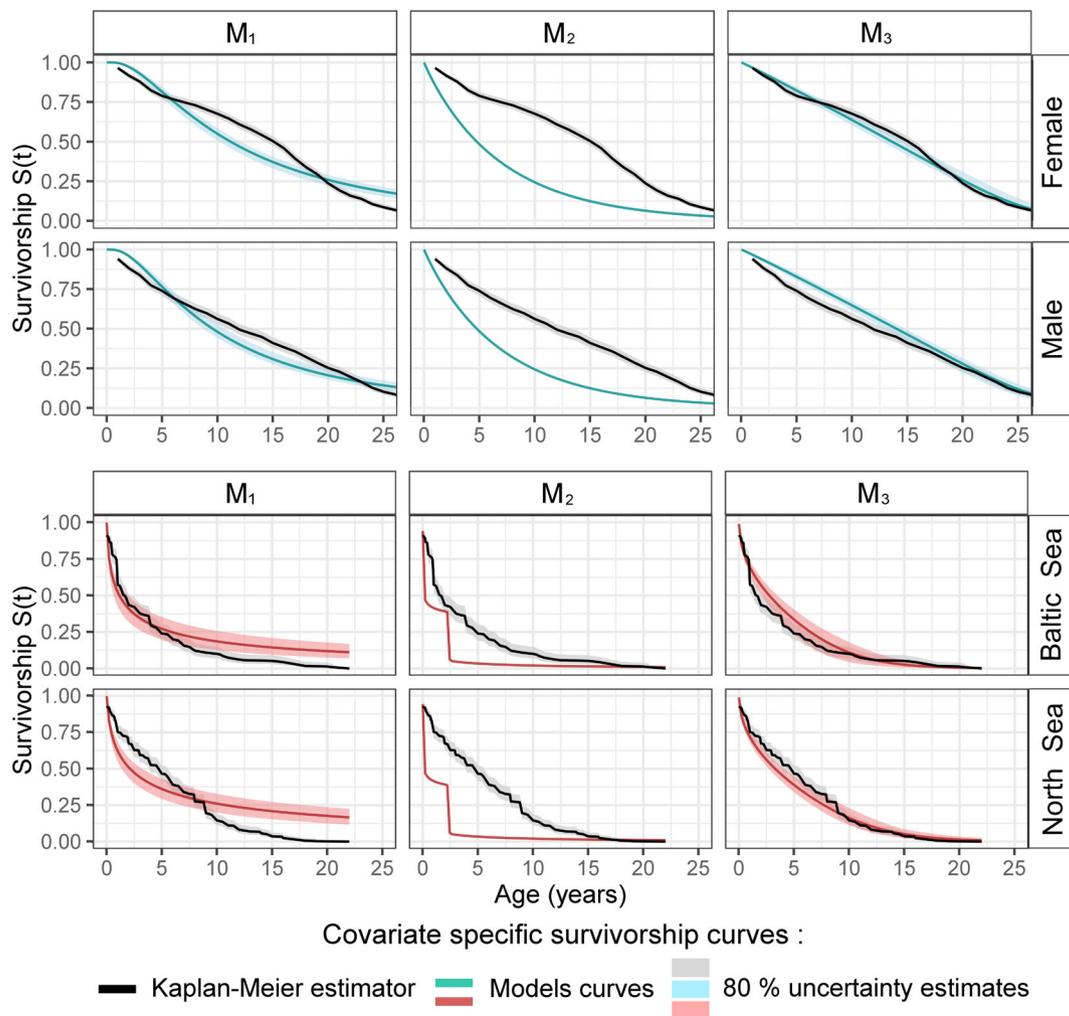


FIGURE 8 Estimated survivorship difference ($(\hat{S}_{\mathcal{M}}(t)|x=1) - (\hat{S}_{\mathcal{M}}(t)|x=0)$) for both case studies [Color figure can be viewed at wileyonlinelibrary.com]

6 | BENEFITS AND LIMITS

We believe our approach is very valuable to estimate survivorship from sparse data but may be inadequate for bimodal age at death data distribution. A bimodal distribution of age at death data may be a sign of selection in data collection Barlow & Hohn, 1984. Rather than consider the sampling as biased, our approach can accommodate the selection phenomenon through two ways. Firstly, it is possible to consider the selection bias as a covariate in the study if one such covariate is available (e.g., Bycatch index). If no such covariate is available, it may be possible to build a mixture of two models (e.g., \mathcal{M}_1 and \mathcal{M}_3) in order to take into account an additional mortality on some age classes. However, such a development requires to conduct its own simulation study which is beyond the scope of this study. Since our approach is based on linear regression, it is straightforward to expand the model (e.g., random year effects, mixtures) while using familiar and well-established methods

for model selection (e.g., WAIC) and assessment of model fit (e.g., posterior predictive checks, R^2 statistics). These features are assets, and suggest that our approach is complementary to existing ones (e.g., Heligman & Pollard, 1980; Saavedra, 2018; Siler, 1979) to estimate vital rates in some data-poor species.

7 | CONCLUSION

Survivorship and hazard estimation are the goals of survival analysis but they remain difficult to achieve, even for some long-lived and charismatic vertebrate species such as cetaceans. User-friendly modeling methods are of primary interest to leverage the demographic information available in sparse, but previous, data that field ecologists have collected. We think that our framework can facilitate the difficult statistical problem of survival analysis in data-poor context by providing ecologists with a flexible method to obtain accurate survivorship estimates from

age at death data. A simple linear mixed-model can accommodate various mortality patterns without drastically increasing the number of estimated model parameters. All the methods developed to assess fit quality within models can be applied since our framework is based on a mixed linear regression approach. This framework is also very convenient to deal with small sample size. With as few as 100 data points, survivorship may be estimated to conduct exploratory analysis. With 300 data points, survivorship estimates can be precise enough to build life-tables and project populations trajectories taking into account covariates. Covariate inclusion can allow to distinguish different causes of mortality (e.g., pathology, bycatch, collision and so on) and to quantify their respective influence on survival. This is valuable when the studied population is under various pressures as it may allow to identify the most threatening ones, and to design efficient and relevant conservation policies accordingly.

ACKNOWLEDGMENTS

We would like to thank Pr. Elisabeth Slooten, Dr. Aleta Hohn, Dr. Ursula Siebert, Dr. Sinéad Murphy, Pr. Jay Barlow, Dr. Leszek Karczmarski and Dr. Camilo Saavedra for sharing their data. Also, we would like to thank the two anonymous reviewers for their critical comments that led to many improvements in the manuscript.

AUTHOR CONTRIBUTIONS

Matthieu Authier, Vincent Ridoux and Etienne Rouby conceived the ideas; Matthieu Authier and Etienne Rouby chose the methodology; Etienne Rouby carried out the analyses; Etienne Rouby and Matthieu Authier led the writing of the manuscript. All authors contributed critically to the drafts and gave final approval for publication.

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SUPPORTING INFORMATION

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How to cite this article: 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: 108–122. <https://doi.org/10.1002/1438-390X.12069>