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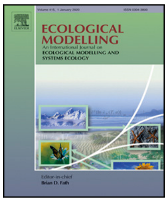

A state-space model for estimating pinniped pup production from serial counts at breeding colonies

Eiren K. Jacobson [a,b,*], Mia R. Goldman [c,b], Len Thomas [a,b], Debbie J.F. Russell [c,b]

[a] School of Mathematics and Statistics, University of St Andrews, St Andrews, Scotland, United Kingdom
[b] Centre for Research into Ecological and Environmental Modelling, University of St Andrews, St Andrews, Scotland, United Kingdom
[c] Sea Mammal Research Unit, School of Biology, University of St Andrews, St Andrews, Scotland, United Kingdom

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ABSTRACT

Estimating pinniped abundance is difficult because they are highly mobile and widely distributed, and spend the majority of time at sea. Abundance estimates are typically based on counts on land or ice. In species that breed colonially, such as the grey seal (*Halichoerus grypus*), monitoring is largely focused on the breeding season, and pup production (number of pups born in a season) is used as an index of the total population size. At any one colony, grey seals give birth over several months, so not all pups are present at the colony at any one time. Pups are born white and moult into an adult-like coat before leaving the colony. At most key UK breeding colonies, over the course of a breeding season, a series of digital photographic aerial surveys are conducted and analysts count the numbers of white and moulted seal pups photographed. We developed a flexible state-space model to estimate pup production using these count data. The model is comprised of a deterministic process model for birth, moult, and leaving, and a stochastic observation model that allows for imperfect detection and classification. We implemented this model in Template Model Builder (TMB) and fit it using maximum likelihood. We show that our model performs well on simulated and real datasets. This model could be applied to other taxa for which successive counts of different life stages are collected, and used to investigate key ecological questions including, for example, the impact of climate change on phenology.

1. Introduction

Estimates of the abundance and trend of animal populations are necessary for effective conservation and management. One component of these estimates can be the number of offspring produced per year. It is challenging to obtain this information for many marine vertebrates, which spend most or all of their time at sea, where they are difficult to observe. It can be particularly hard to obtain information about how many individuals are recruited into a population. However, some species congregate on land or ice during certain life stages. For example, seabirds and pinnipeds congregate at breeding colonies where they reproduce and rear young. For most species, these processes are not precisely synchronous, and for some species there is no one point at which a total count of young-of-the-year can be made: earlier in the breeding season individuals are still to be born, while later in the season some young-of-the-year will have departed the colony.

Grey seals *(Halichoerus grypus)* aggregate on land or ice to give birth at breeding colonies. In the UK, most pups are born between September and December, with colonies in the southwest pupping earliest. Colonies pup progressively later in a clockwise cline around the UK (Kovacs and Lavigne, 1986; Radford et al., 1978). The temporal distribution of births within colonies tends to be right-skewed, with a relatively rapid onset of births followed by a long right tail (Coulson and Hickling, 1964). Adult females give birth to a single pup, which they nurse for 15–21 days (Pomeroy et al., 1999). Around weaning the adult females go into oestrus and leave their pup. The pup undergoes a post-weaning fast before leaving the colony at around 31.5 days of age (Wyile, 1988). Pups are born with white coats (an evolutionary holdover of ice-breeding ancestors Boehme et al., 2012); pups complete their moult into adult-like coats (pelage) at around 23 days of age (Wyile, 1988; Radford et al., 1978). Because this process is not perfectly synchronous within or between colonies (Radford et al., 1978; Russell et al., 2019), there is no time at which all pups are present at the colonies and available to be counted.

To estimate the total number of pups born at key colonies in Scotland and eastern England, the Sea Mammal Research Unit (University of St Andrews) conduct multiple aerial photographic surveys throughout a survey season (usually 4 or 5). For details of survey methods, see Russell et al. (2019). Counts of white and fully moulted pups are

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[*] Correspondence to: The Observatory, Buchanan Gardens, St Andrews, Scotland, KY16 9LX, United Kingdom.
E-mail address: eiren.jacobson@st-andrews.ac.uk (E.K. Jacobson).

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derived from resulting high-resolution photographs. Individual pups cannot be tracked through aerial surveys, so mark-recapture methods are not applicable. The separate counts of white and moulted pups can be used to estimate the timing of birth and moult curves (i.e., the probability of being born on different days of the season, or of moulting at different ages). White and moulted pups are counted separately and imperfectly. The counts are affected by two types of observation error: detection error (i.e., some pups are not counted) and classification error (i.e., white pups being counted as moulted pups and vice versa). False positives (e.g., a rock being mistaken for a seal pup) are thought to be rare.

The pup moulting process and the resulting counts of animals in different stages is somewhat analogous to bird moulting processes, which have been modelled previously (Underhill and Zucchini, 1986; Underhill, 1993; Erni et al., 2013). However, these Underhill-type models are not applicable in the case of grey seal pup production because the number of pups available to be surveyed is not a closed population: animals are entering (by being born) and leaving (by leaving the colony) the population (colony) over the course of the study period. A previous model has been used to estimate pup production (Russell et al., 2019), but it does not allow for the desired flexibility or extensibility to a hierarchical, multi-colony model.

Here, we develop a state-space version of the above model to estimate the total number of pups born at a breeding colony given serial counts of white and moulted pups. We describe the model framework and demonstrate its application to simulated and real data. In the discussion we consider how this model differs from the previous model and how it might be extended in the future.

2. Methods

2.1. Overview

We developed a state-space model to estimate the number of grey seals born at a colony using aerial photographic counts of white and moulted pups. The model consists of a deterministic process model and a stochastic observation model (Fig. 1). Time is discretized to day. The parameters (quantities to be estimated) are the total number of pups born N, the mean birth day μ_b, its standard deviation σ_b, and the shape of the skew normal birth curve α_b (note that a full list of symbols used is provided in Appendix A). We evaluated model performance by fitting the model to simulated and real data. All data and code to implement these analyses are available at https://github.com/eirenjacobson/HgPupProdModel.

2.2. State-space model

2.2.1. Process model

At the core of the process model is a discretized, truncated skew normal distribution of birth days. Following Russell et al. (2015), pup birth dates at breeding colonies tend to be right-skewed, with a relatively rapid rise in birth numbers to a peak, followed by a longer decline. The distribution is discretized because we model births per day and truncated because in this example it is assumed that no births occur before October 1st (which we denote as day 0) or after day $D-1$, where D is the maximum length (in days) of the birthing season. In practice, births start a few days after day 0 and finish before D so the amount of truncation is minimal.

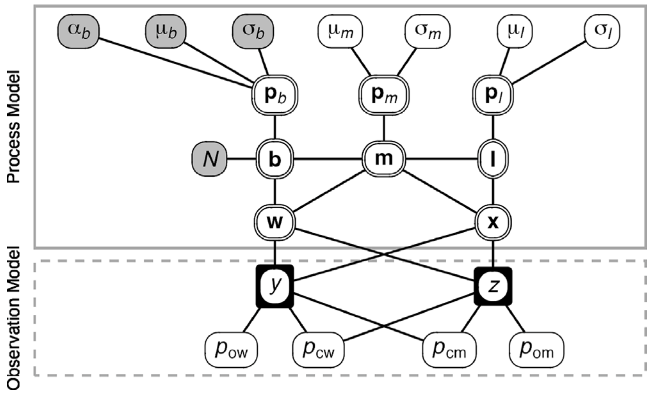

Fig. 1. Schematic of the state-space pup production model. Nodes with single outlines indicate scalars while nodes in bold with double lines represent vectors. Parameters to be estimated by the model are indicated by grey shading. Data are indicated by an outer black box. The upper box delineates the process model, while the lower dashed box delineates the observation model. Symbols are defined in Appendix A.

Let $F(x;\mu,\sigma,\alpha)$ denote the cumulative distribution function (CDF) of the skew normal distribution with mean μ, standard deviation σ, and shape α, evaluated at x. (Note that the skew normal distribution is typically parameterized in terms of location, shape and scale (as per O'Hagan and Leonard, 1976); the relationship between these parameters and the mean, standard deviation, and skewness δ is given in Appendix B.) When $\alpha > 0$ the distribution is right-skewed. Let $F_l^u(x;\mu,\sigma,\alpha)$ denote the CDF of the corresponding truncated distribution with lower and upper truncation l and u respectively, so that

$$F_l^u(x;\mu,\sigma,\alpha) = \frac{F(x;\mu,\sigma,\alpha) - F(l;\mu,\sigma,\alpha)}{F(u;\mu,\sigma,\alpha) - F(l;\mu,\sigma,\alpha)}. \tag{1}$$

Then, the probability that a pup is born on day d (where $0 \le d \le D-1$), given that it is born at some point in the breeding season, is

$$p_b(d) = F_0^{D-1}(d+1;\mu_b,\sigma_b,\alpha_b) - F_0^{D-1}(d;\mu_b,\sigma_b,\alpha_b), \tag{2}$$

where μ_b is the mean birth day parameter, σ_b is the standard deviation of birth day parameter, and α_b is the birth day shape parameter. If there are N pups born over the breeding season, then the number born on day d is

$$b(d) = N p_b(d). \tag{3}$$

Note that $b(d)$ is a continuous-valued function—in other words, we allow for fractional pups to be born. This is an approximation necessary for implementation (see Implementation, below), but it does not cause problems in practice because we model the observed number of pups using a normal distribution (see Observation Model, below).

Pups are assumed to moult and leave the colony according to their age, irrespective of day, up to (but not including) a maximum age A. Therefore, we model the distribution of times to moult and to leave using truncated normal distributions, determined by the age (in days) of the pup rather than the calendar day. Let $\Phi(x;\mu,\sigma)$ denote the CDF of the normal distribution with mean μ and standard deviation σ, evaluated at x, and let $\Phi_l^u(x;\mu,\sigma)$ denote the corresponding truncated normal CDF with lower and upper limits l and u. The probability of a pup moulting at age a is given by

$$p_m(a) = \Phi_0^{A-1}(a+1;\mu_m,\sigma_m) - \Phi_0^{A-1}(a;\mu_m,\sigma_m), \tag{4}$$

where A is the maximum age that a pup can moult, μ_m is the mean moult age parameter, and σ_m is the standard deviation of moult age parameter. The probability of a pup moulting at age a or earlier is

$$p_m(0:a) = \sum_{i=0}^{a} p_m(a) = \Phi_0^{A-1}(a;\mu_m,\sigma_m). \tag{5}$$

Similarly, the probability of a pup leaving the colony at age a is given by

$$p_l(a) = \Phi_0^{A-1}(a+1;\mu_l,\sigma_l) - \Phi_0^{A-1}(a;\mu_l,\sigma_l), \tag{6}$$

where A is the maximum age that a pup leaves (assumed to be the same as the maximum age at moult), μ_l is the mean leaving age parameter, and σ_l is the standard deviation of leaving age parameter. The probability of leaving at age a or earlier is

$$p_l(0:a) = \Phi_0^{A-1}(a;\mu_l,\sigma_l). \tag{7}$$

Given these definitions, the number of white pups present on the colony at the end of day d (where $0 \le d < D + A$) is

$$w(d) = \sum_{i=0}^{d} \Big(b(i)\left[1 - p_m(0:d)\right]\left[1 - p_l(0:d)\right] \Big) \tag{8}$$

and the number of moulted pups is

$$m(d) = \sum_{i=0}^{d} \Big(b(i)p_m(0:d)\left[1 - p_l(0:d)\right] \Big). \tag{9}$$

In the implementation described here, we assume that the process model parameters D, μ_m, σ_m, μ_l, and σ_l are known (see Table 2).

2.2.2. Observation model

The timing of observations is measured in terms of days since October 1st of each year. There are two types of observation error that need to be accounted for in the model: detection error and classification error. Let the probability of detecting white pups be p_{ow}, the probability of detecting moulted pups be p_{om}, the probability of correctly classifying white pups as white be p_{cw}, and the probability of correctly classifying moulted pups as moulted be p_{cm}. Then

$$E(y_w(d)) = w(d)p_{\mathrm{ow}}p_{\mathrm{cw}} + m(d)p_{\mathrm{om}}(1 - p_{\mathrm{cm}}) \tag{10}$$

$$E(y_m(d)) = w(d)p_{\mathrm{ow}}(1 - p_{\mathrm{cw}}) + m(d)p_{\mathrm{om}}p_{\mathrm{cm}} \tag{11}$$

where $y_w(d)$ and $y_m(d)$ are observations of the number of white and moulted pups on day d and $E()$ denotes expectation. Here, the observation model parameters p_{ow}, p_{om}, p_{cw} and p_{om} are assumed known (see Table 2).

We model the observations as being normally distributed around these expectations, with variances σ_w^2 and σ_m^2. To derive the variances, we assume that both the detection and the classification process are binomial (i.e., that each detection and classification event is an independent Bernoulli trial), which leads to

$$\sigma_w^2 = w(d)p_{\mathrm{ow}}p_{\mathrm{cw}}(1 - p_{\mathrm{ow}}p_{\mathrm{cw}}) + m(d)p_{\mathrm{om}}(1 - p_{\mathrm{cm}})(1 - p_{\mathrm{om}}(1 - p_{\mathrm{cm}})) \tag{12}$$

$$\sigma_m^2 = w(d)p_{\mathrm{ow}}(1 - p_{\mathrm{cw}})(1 - (1 - p_{\mathrm{cw}})) + m(d)p_{\mathrm{om}}p_{\mathrm{cm}}(1 - p_{\mathrm{om}}p_{\mathrm{cm}}). \tag{13}$$

This observation model assumes that misclassified pups are detected according to their true class; i.e., moulted pups are always detected with probability p_{om} regardless of whether they are classified as white or moulted.

2.2.3. Likelihood

Let O represent the set of days on which observations take place, and o represent one of these days. For each observation day o, the likelihood of the observed number of white pups y_o and moulted pups z_o is evaluated using normal distributions with means w_o and x_o and standard deviations σ_w and σ_x from Eqs. (12) and (13). Assuming independence between observations, the likelihood $\mathcal{L}$ of the parameters of the model, N, μ_b, σ_b, and α_b, given the data and fixed model parameters θ is

$$\mathcal{L}(N,\mu_b,\sigma_b,S|\underline{y},\underline{z},\theta) = \prod_{o\in O} \phi(y_o;w_o,\sigma_w)\phi(z_o;x_o,\sigma_x) \tag{14}$$

where $\underline{y}$ and $\underline{z}$ are vectors of observed white and moulted pups, θ is a vector of parameters that were fixed (see Table 2), and $\phi(x;\mu,\sigma)$ is the PDF of a normal distribution with mean μ and standard deviation σ evaluated at x.

Table 1
Upper and lower bounds for parameters to be estimated by the model.

Parameter	Lower	Upper
N	$\max(\underline{y}+\underline{z})$	$\max(\underline{y}+\underline{z})\times 5$
μ_b	30	70
σ_b	1	20
α_b	1	10

2.3. Model fitting

2.3.1. Implementation

We implemented the model in Template Model Builder (TMB). TMB uses automatic differentiation to evaluate the Laplace approximation of the marginal likelihood and its gradient. This approach requires all latent random variables (in our case, the numbers of white and moulted pups) to be continuous. The model code is written in C++ but is compiled and run using the R package TMB (Kristensen et al., 2016). We fit the model with maximum likelihood estimation (MLE) using a multi-stage approach to prevent the optimization from converging at local (rather than global) minima. First, the TMB model was constructed with the default values of all parameters (N, μ_b, σ_b, and α_b). Default starting values were the mean of the lower and upper limits (Table 1) for each parameter. Then, the model function was evaluated at 10,000 sets of gridded initial values and 10,000 sets of randomly selected initial values. The default values, the best five value sets from the grid search, and the five best value sets from the random search were used as initial values for a limited-memory box-constrained Broyden–Fletcher–Goldfarb–Shanno (L-BFGS-B) optimization in the R package optimx (Nash, 2014). The resulting best-fit (minimum negative log-likelihood) set of parameters was chosen and the model was updated accordingly.

2.3.2. Data simulation

To test the model, we simulated data to mimic the serial grey seal pup count data that are collected via photographic aerial surveys. We simulated data according to the model formulation, with probability of being born on each day as described in Eq. (2) and moulting and leaving processes according to Eqs. (4) and (5). We simulated a normal observation process, where simulated pups were counted and classified according to the probabilities in Table 2 with binomial variance (Eqs. (12) and (13)). We generated test datasets with values of N from 100 to 1000 in intervals of 100, fixing $\mu_b = 50$, $\sigma_b = 10$, and $\alpha_b = 5$ for all simulations.

We were interested in investigating how survey parameters (number and timing of surveys) would affect model performance. Therefore, we simulated first survey days occurring from days 25 to 50 in intervals of 5 days and with survey intervals of 1, 5, 10, 15, and 20 days and a total number survey days between 1 and 5. Other parameters were fixed according to the values in Table 2. To understand how the model would perform on existing data, we subsequently subset the simulated datasets to include only those with 4 or 5 surveys in intervals of 15 or 20 days.

2.3.3. Application to real data

To demonstrate model operability on real data, we fitted the model to data collected at six colonies of varying size (maximum pup count: 34-3795; East Scotland: Craigleith, Fast Castle, Inchkeith, Isle of May; Southeast England: Blakeney Point and Horsey) in 2018. Data collection methods are described in Russell et al. (2019), and we compared our results to estimates from the pup production model used by Russell et al. (2019). Note that this is not a validation, as the true numbers of pups (and parameters of the birth curve) are not known.

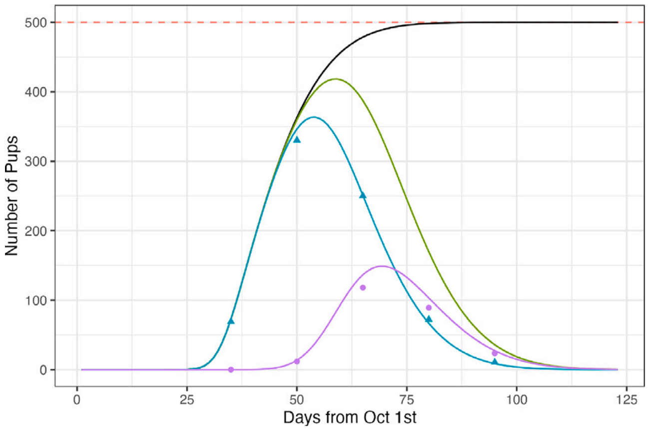

Fig. 2. Example of one simulated dataset. In this example, 500 pups were born over the course of the season (red dashed line). The black line indicates the cumulative number of pups (vertical axis) born by each day (horizontal axis). The blue and purple lines represent the number of white and moulted pups present on each day, while the blue and purple points (triangles and circles, respectively) represent the number of white and moulted pups counted on each of six hypothetical survey days. The green line indicates the total number of pups on the beach on each day.

Table 2
Values of variables that were fixed in both the simulation and the model fitting.

Variable	Value
D	125
μ_m	23
σ_m	5
μ_l	31.5
σ_l	7
p_{ow}	0.95
p_{om}	0.95
p_{cw}	1
p_{cm}	0.91

2.3.4. Model evaluation

For both simulated and real datasets, we used the model-estimated standard error (SE) to calculate log-normal confidence intervals for the number of pups N. For the simulated datasets we also calculated the relative error of estimates of N, μ_{b}, σ_{b}, and α_{b}.

3. Results

3.1. Simulated data

We simulated 1500 datasets with varying values of N, survey start day, and survey interval (see Fig. 2 for one example simulation). The model failed to converge on one simulated dataset, and the Hessian of fixed effects was not positive definite (indicating that the model may not have converged and/or that the parameter estimates may be unreliable) for an additional 203 simulated datasets. Most (133) of these were simulated datasets with only one simulated survey day. We excluded these 204 simulated datasets from further analysis.

The accuracy in model estimates of the total number of pups N varied with number and timing of simulated surveys, but not with the simulated number of pups (Fig. 3). In general, simulated surveys with later first survey days, a greater number of surveys, and a greater interval between surveys (for a given number of surveys) performed best.

After filtering for simulated datasets with 4 or 5 simulated survey days and survey intervals of 15 or 20 days, we were left with 239 simulated datasets. We used this subset of simulations to evaluate model performance given expected characteristics of existing data.

Table 3
Model estimates of the number of pups born at each of six colonies, with 2.5% and 95% confidence intervals (LCI and UCI, respectively).

Colony	Estimate	LCI	UCI
Craigleith	44.59	41.89	47.47
Fast Castle	4317.99	4291.19	4344.96
Inchkeith	756.38	744.67	768.29
Isle of May	1971.27	1952.13	1990.60
Blakeney Point	4763.11	4732.71	4793.72
Horsey	2173.03	2151.81	2194.46

Resulting estimates of the birth curve parameters are shown in Fig. 4. The model-estimated mean birthday ranged from 49.00 to 50.60 (−2% to +1% relative error) with a median of 50.00. The model-estimated standard deviation of the birth curve ranged from 8.86 to 11.00 (−11% to +10% relative error), with a median of 9.96. The model-estimated skew of the birth curve ranged from 2.33 to 10 (−53% to +100% relative error) with a median of 4.64. The estimates of the mean birthday, standard deviation of the birth curve, and skew of the birth curve were approximately unbiased (mean relative error $< 1\%$). The resulting model-estimated birth curves were generally similar in shape to the simulated birth curve (Fig. 5).

The model estimates of N corresponded to the simulated number of pups born (Fig. 6) with CVs ranging from 0.01 to 0.03. The 95% confidence intervals included the true simulated value in 95.8% of simulations.

3.2. Application to real data

Each of the six colonies were surveyed 4–5 times over the course of the 2018 season. The mean interval between surveys was 16 days (range 12–21 days). When applied to the resulting count data from these surveys, the model converged and provided estimates of total number of pups born (Table 3) that mostly agreed with previously published estimates for the same data (see Appendix C). The model-expected numbers of white and moulted pups corresponded well with observations (Fig. 7).

4. Discussion

We developed a state-space model to estimate grey seal pup production given serial counts of white and moulted pups at breeding colonies, and demonstrated the model's performance when applied to simulated and real data. The model recovered simulated life-history parameters (mean, standard deviation, and skew of the birth curve) and total pup production across a range of colony sizes and survey scenarios. When applied to real data, the model provided pup production estimates for six colonies ranging in size from 10s to 1000s of individuals.

The pup production model was implemented in TMB and fitted using MLE, which allows us to obtain parameter estimates within a frequentist framework. TMB uses automatic differentiation to evaluate the Laplace approximation of the marginal likelihood, which enables relatively fast computation of the gradient of the marginal likelihood with respect to model parameters. This model improves on the model presented by Russell et al. (2019) (also see Appendix C) by allowing for misclassification of white pups and by establishing a state-space framework that can be extended in future work.

Understanding the assumptions underlying the pup production model is crucial for interpreting its results and assessing its applicability. The model relies on several key assumptions.

First, the model assumes that pups transition instantaneously between two distinct life stages: white (approx. 0–22 days of age) and moulted pups (approx. 23–32 days of age; Reilly, 1991). In reality,

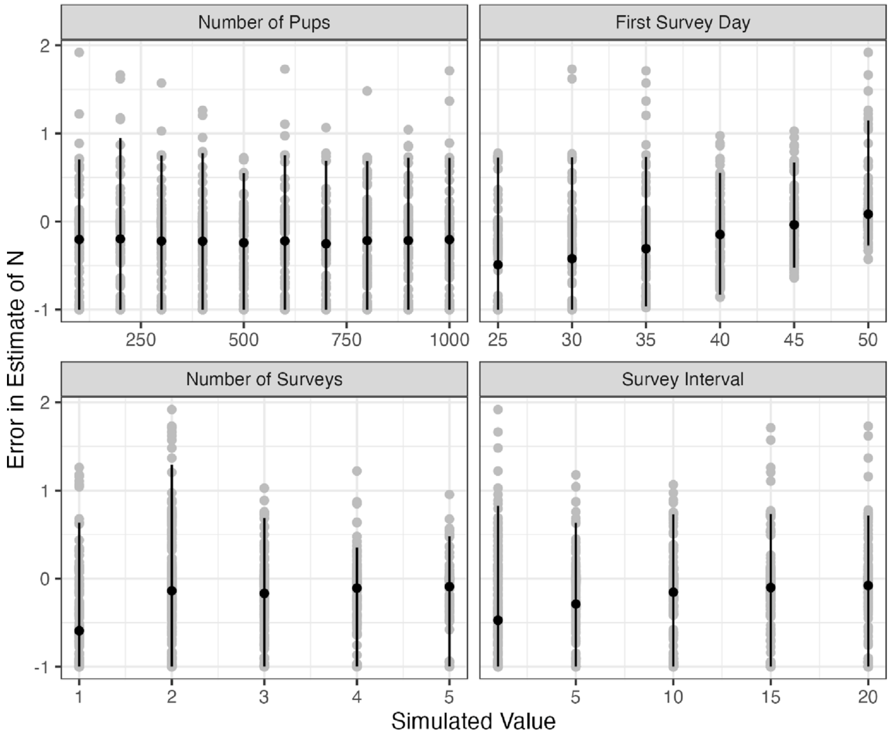

Fig. 3. Marginal plots of simulated values (horizontal axis) versus error in model estimates of the number of pups N for simulated number of pups (first panel) and survey properties (first survey day, number of surveys, and survey interval; remaining panels) across 1500 simulated datasets. Grey points indicate relative error in the estimate of number of pups from individual simulations, while the black points are the median and the black bars span the 2.5% to 95% quantiles of relative error across all simulations.

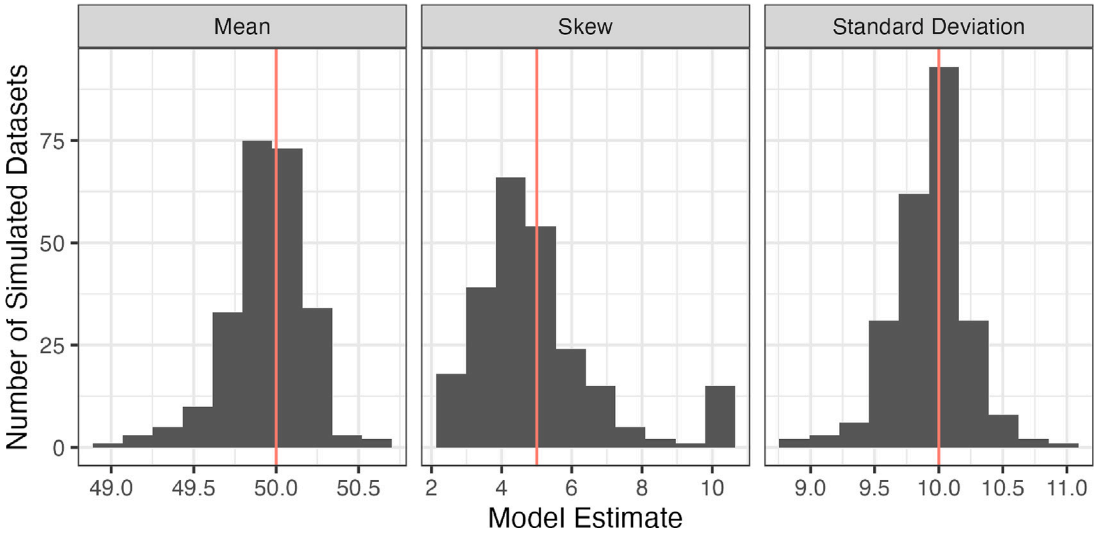

Fig. 4. Model-estimated mean birthday and skew and standard deviation of the birth curve (horizontal axis) for 239 simulated datasets. The red vertical lines show the true simulated values.

moulting is a continuous process that takes place over the course of 6–8 days (approx. 16–23 days of age), during which time the pups are considered to be moulting. The counts of white pups are therefore comprised of both white and moulting pups. This moulting process has previously been described as a separate stage (Davies, 1949; Radford et al., 1978; Bowen et al., 2003). Misclassification of pups is most likely to occur during this intermediate stage between white and fully moulted; i.e., pups in this stage might be correctly classified as white pups or misclassified as moulted pups. Therefore, better representation of the moulting process in the model may allow us to better understand misclassification errors, and ultimately improve precision and accuracy of parameter estimates.

We also assume that pups do not move between colonies during the breeding season. However, when colonies are close to each other, pups may be born at one colony and, upon leaving for sea (or being swept to sea by weather events), haul out at another nearby colony (Boyd et al., 1961) to complete the post-weaning fast. Movement between colonies during the breeding season has been demonstrated in other pinniped pups as well (Goldsworthy et al., 2021). If there is not an equal exchange of pups between colonies, this movement could lead to misleading counts if a pup is recorded in one survey at its birth colony

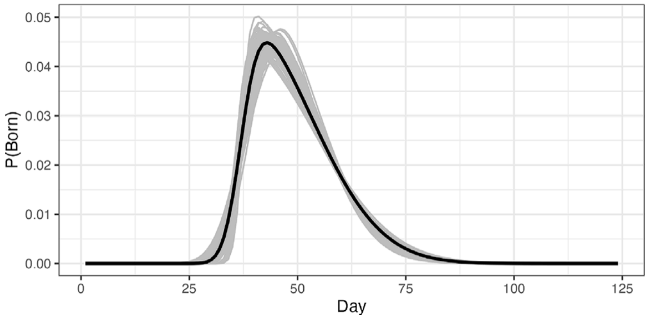

Fig. 5. Simulated (black line) and model fitted (grey lines) birth curves from 239 simulated datasets indicating the probability of being born (vertical axis) on each day of the season (horizontal axis).

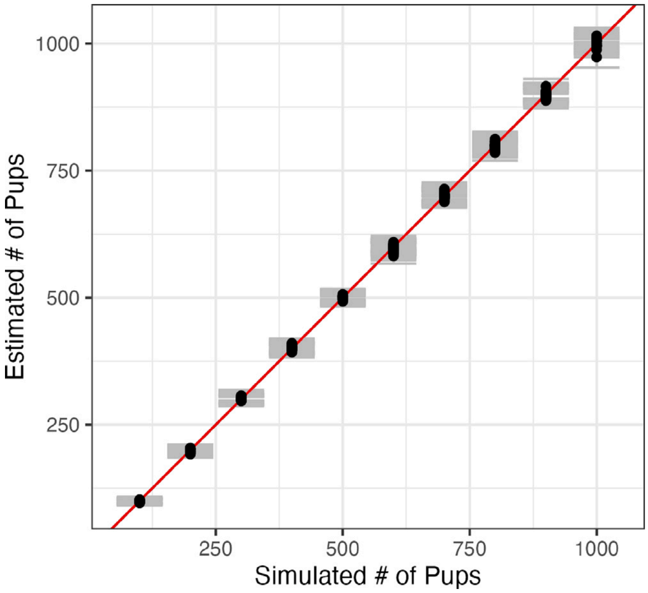

Fig. 6. Simulated (horizontal axis) versus model-estimated (vertical axis) number of pups for 239 simulated datasets. Each individual simulation is shown by a black point with grey 95% confidence intervals. The red line indicates 1:1.

and in a subsequent survey at a different colony, potentially resulting in biased estimate of pup production and mean birth date.

Since moulting and leaving are modelled as independent processes, our approach assumes that pups can leave the colony before completing the moult process. Pups that do leave before completing the moult process are most likely to move to other colonies or become a mortality (i.e., be swept to sea and not survive; Russell et al., 2019). For the majority of pups, departure for the sea occurs after the moult is complete. If our assumption is incorrect, and pups never leave before completing the moult, total pup production could be overestimated. If we were certain that pups could not leave the colony before completing the moult process, we could reformulate the process model so that leaving the colony would be conditional on moulting.

We assume that all pups, regardless of their birth day within the season, progress through life stages at the same rate. It is possible, though, that pups born later in the season experience different developmental timelines (Coulson and Hickling, 1964). For instance, the post-weaning fast for these late-born pups might be triggered sooner compared to those born early in or at the peak of the season. Consequently, their moult period may be shorter, and they may depart for the sea at younger ages. Our assumption of fixed life-history parameters could misrepresent the timing of transitions and departures, leading to biased estimates of total pup production. It may be more realistic to allow life-history parameters to vary over the course of the season (de Valpine et al., 2014). However, this would likely require substantially more data and may not impact pup production estimates, since pups born towards the end of the season would only be surveyed as white pups.

The model assumes that all pups remain alive from birth until they leave for the sea, with deceased pups being absorbed into the white pup class in the data. The process model therefore effectively implies there is no mortality, which, if carcasses are observable for substantially longer than the white phase, could lead to overestimation of pup production by counting deceased pups as though they are alive. Accounting for mortality in the model is challenging due to several factors. Mortality rates may vary over the course of the season and by colony. On some colonies, pups that are born earlier in the season have a higher survival rate than pups born later in the season due to overcrowding during the peak of births (Coulson and Hickling, 1964). Depending on the colony and time of season, mortality rates can vary by up to 20% (Coulson and Hickling, 1964; Boyd and Campbell, 1971; Twiss et al., 2003; Quaggiotto et al., 2018). Variability in geographic and environmental conditions across colonies influences the duration carcasses remain visible, with pups close to the shore being washed out to sea more quickly than those further inland. Explicitly modelling dead pups and removing them from the white pup count would likely lead to more accurate population estimates. However, this refinement would also introduce additional parameters (i.e., mortality rate and carcass persistence rate) and complexity into the model.

Another limitation is the use of a deterministic process model, which does not capture the inherent stochasticity in biological processes. Adding stochasticity to the process model (both in data generation and in fitting) would likely increase the uncertainty of parameter estimates, including in the estimates of pup production. We used a normal approximation to the binomial distribution in both the simulation and model. This approximation can be negatively biased particularly when the number of pups and/or number of surveys is small; in future a normal approximation with a continuity correction may be more appropriate.

An important piece of future work will be to conduct analyses to assess how sensitive the model results are to changes in fixed parameters. Specifically, the model relies on assumptions about time to moult, time-to-leave (TTL), the probability of observation (Pobs), and the probability of misclassification. Research by Russell (2015) has shown that TTL varies among colonies, and the currently used value of 31.5 days may be too low for many colonies, potentially leading to overestimates of pup production. Collecting more empirical data would enable more accurate estimation of these parameters. Additionally, it has been assumed, based on comparisons between ground and film aerial surveys, that pups are counted with a 95% detection rate (Pobs) for both film and digital surveys (Thompson and Wyile, 1985). However, this value may be too high as it does not account for factors such as the possibility of pups being missed due to being washed out to sea or obscured by geographic features.

We formulated this model with the eventual goal of building a hierarchical model encompassing multiple monitored grey seal colonies in the UK. A hierarchical approach would introduce information sharing across colonies so that parameters and their associated uncertainty could be estimated at a colony or regional level, leveraging information from data-rich colonies and years to improve estimates in data-poor colonies and years. A hierarchical model could also be used to investigate variation and/or change in grey seal breeding phenology over space and time.

We anticipate this model will have applicability to other systems in where multiple, imperfect count surveys are conducted to estimate abundance of open populations. The mechanistic nature of the process model should make it easily adaptable to other systems. This may be particularly useful for certain seabirds, diseases, and other biological and ecological processes with latent stages and imperfect detection.

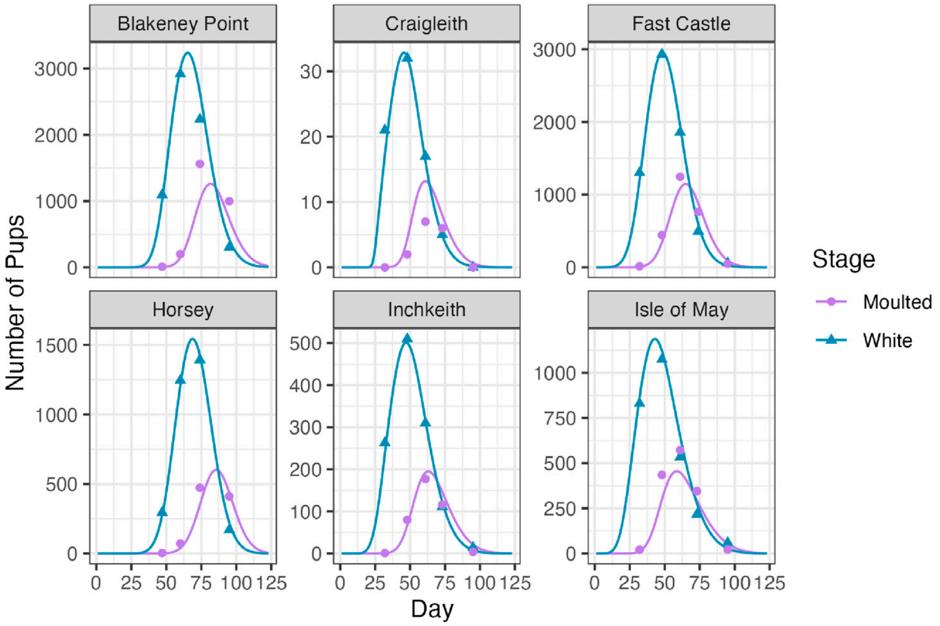

Fig. 7. Model-expected number (vertical axis) of white (blue) and moulted (purple) pups on each day of the season (horizontal axis) at six grey seal colonies (panels). Points (triangles and circles for white and moulted pups, respectively) represent real observations of white and moulted pups.

CRediT authorship contribution statement

Eiren K. Jacobson: Writing – review & editing, Writing – original draft, Visualization, Validation, Software, Methodology, Investigation, Formal analysis. **Mia R. Goldman:** Writing – review & editing, Writing – original draft, Validation, Formal analysis. **Len Thomas:** Writing – review & editing, Supervision, Methodology, Investigation. **Debbie J.F. Russell:** Writing – review & editing, Supervision, Project administration, Methodology, Investigation, Funding acquisition, Formal analysis, Data curation, Conceptualization.

Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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Appendix A. Glossary of symbols used

See Table A.4.

Appendix B. Parameterization of the skew normal distribution

The skew normal distribution was first described by O'Hagan and Leonard (1976). The distribution is typically parameterized in terms of location ξ, scale ω, and shape α. These are related to the mean μ, standard deviation σ, and skewness δ by the following equations.

$$\alpha = \frac{\delta}{\sqrt{1-\delta^2}} \tag{B.1}$$

Table A.4
Glossary of symbols used in the manuscript. Where applicable, units are indicated in parentheses.

Symbol	Definition
N	Total number of pups born at a colony within a season
μ_b	Mean birth day (days)
σ_b	Standard deviation of birth day (days)
α_b	Skew of birth day (days)
μ_m	Mean age at moulting (days)
σ_m	Standard deviation of age at moulting (days)
μ_l	Mean age at leaving (days)
σ_l	Standard deviation of age at leaving (days)
p_b	Probability of being born on each day of the season
p_m	Probability of moulting at each age
p_l	Probability of leaving at each age
b	Number of pups born on each day of the season
m	Number of pups moulting on each day of the season
l	Number of pups leaving the colony on each day of the season
w	Number of white pups present on the colony on each day of the season
x	Number of moulted pups present on the colony on each day of the season
y	Number of white pups observed on each survey day
z	Number of moulted pups observed on each survey day
p_{ow}	Probability of observing white pups
p_{cw}	Probability of correctly classifying white pups
p_{om}	Probability of observing moulted pups
p_{cm}	Probability of correctly classifying moulted pups
d	Day of the season
D	Maximum length of season (days)
a	Age (days)
A	Maximum pup age (days)

$$\omega = \frac{\sigma}{\sqrt{1-(2\delta^2/\pi)}} \tag{B.2}$$

$$\xi = \mu - \omega\delta\sqrt{\frac{2}{\pi}} \tag{B.3}$$

Appendix C. Comparison to model from Russell et al. 2019

A model to estimate grey seal pup production in Scotland from serial counts of pups at breeding colonies was developed c. 30 years ago by Lex Hiby, and first documented in a peer-reviewed publication by Russell et al. Russell et al. (2019). We refer to this model as

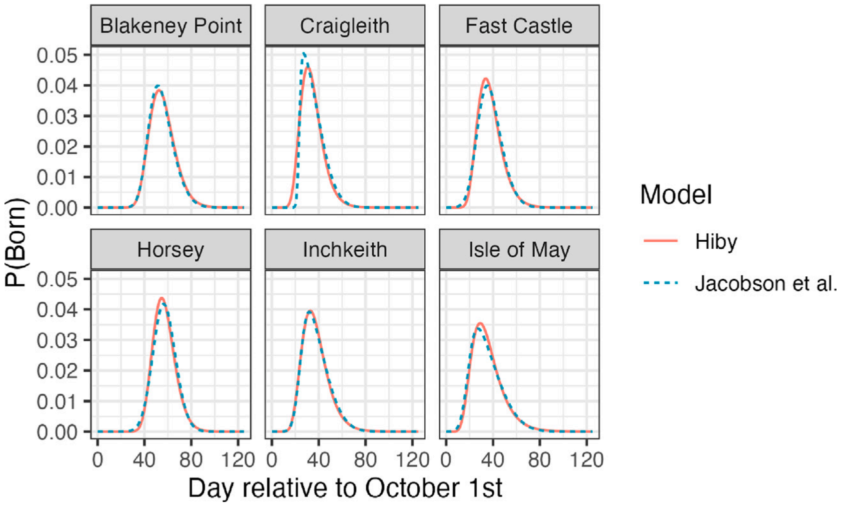

Fig. C.8. Estimated birth curves from the model presented in the main body of the manuscript (blue dashed lines) and from the Hiby model (red lines) when applied to data from six grey seal colonies.

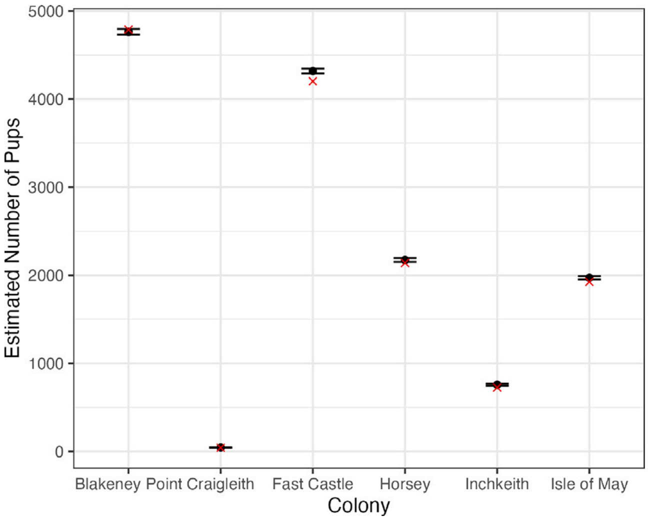

Fig. C.9. Point estimates and 95% CIs of total pup production at six colonies using the model presented in the main body of the manuscript (black dots and lines) with the Hiby model estimate of pup production (red crosses).

the ‘Hiby model’. The Hiby model has been replicated in R and is fitted using maximum likelihood estimation (MLE; Russell et al., 2019; SCOS, 2024). Since the Hiby model was developed, other studies have increased our understanding of the pup production and survey processes. For example, the Hiby model assumes that white pups cannot be misclassified as moulted pups. However, white pups are sometimes misclassified as moulted pups. Therefore, an additional model parameter is required. Incorporating these more complex mechanisms of observation error requires an age-specific model and cannot be encompassed within the Hiby model framework.

We expect the version of the model presented in the main body of the manuscript to produce results similar to those of the Hiby model when parameters are set at the same values. To evaluate this, we compared the performance of the Hiby model to that of the model presented in the main body of the manuscript when presented with real data.

One major difference between the Hiby model and the model presented in this manuscript is that the former uses a log-normal birth curve, while the latter uses a skew-normal. Therefore, the parameters of the birth curve estimated by the two models are slightly different.

We ran both models on the same data as presented in the main text of the manuscript. We found that the estimated birth curves were visually similar between the two models (Fig. C.8) and the Hiby model estimates fell within the 95% CIs of the new model estimates for 5/6 colonies (Fig. C.9).

Data availability

As per the methods section of the manuscript, all data and code to implement these analyses is available at https://github.com/eirenjacobson/HgPupProdModel.

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