Fisheries and Oceans Canada | Pêches et Océans Canada
Ecosystems and Oceans Science | Sciences des écosystèmes et des océans

Canadian Science Advisory Secretariat (CSAS)

Research Document 2023/052

Quebec Region

A Bayesian birth distribution model for grey seals and an evaluation of timing of the harvest

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September 2023

Canada

Foreword

This series documents the scientific basis for the evaluation of aquatic resources and ecosystems in Canada. As such, it addresses the issues of the day in the time frames required and the documents it contains are not intended as definitive statements on the subjects addressed but rather as progress reports on ongoing investigations.

Published by:

Fisheries and Oceans Canada
Canadian Science Advisory Secretariat
200 Kent Street
Ottawa ON K1A 0E6

http://www.dfo-mpo.gc.ca/csas-sccs/
csas-sccs@dfo-mpo.gc.ca

ISSN 1919-5044
ISBN 978-0-660-49987-1 Cat. No. Fs70-5/2023-052E-PDF

Correct citation for this publication:

Mosnier, A., den Heyer, C.E., Stenson, G.B., and Hammill, M.O. 2023. A Bayesian birth distribution model for grey seals and an evaluation of the timing of harvest. Can. Sci. Advis. Sec. Res. Doc. 2023/052. iv + 34 p.

Aussi disponible en français :

Mosnier, A., den Heyer, C.E., Stenson, G.B., et Hammill, M.O. 2023. Modélisation bayésienne de la distribution des naissances de phoques gris et évaluation du moment de la récolte. Secr. can. des avis sci. du MPO. Doc. de rech. 2023/052. iv + 39 p.

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ABSTRACT

Aerial surveys were completed to estimate northwest Atlantic grey seal (*Halichoerus grypus*) pup production in eastern Canada during December 2020 to February 2021. These surveys underestimate pup production if animals are born after the surveys are flown or if pups leave the breeding site before it is surveyed. Past assessments have modelled the distribution of births to correct this bias by fitting the proportion of animals in different morphometrically defined stages of fixed duration to a gamma or Weibull distribution (Myers Birth Distribution [MBD] Model). A new Bayesian modelling approach was developed and compared with the MBD model to examine how this approach impacts our understanding of the timing of births. Assuming that animals are weaned at 20 days of age, the model was also applied to determine the proportion of animals that were weaned and thus available to harvesters at different colonies.

The MBD and Bayesian models showed similar estimates when applied to the data rich dataset acquired on Sable Island. At other breeding sites, the Bayesian model tended to estimate a slightly shorter period of births compared to the MBD model, resulting in a higher estimated proportion of animals born on the aerial survey date, and thus a smaller adjustment of counts. The weaning date estimated with the Bayesian model showed a general trend starting off the Nova Scotia coast then moving into the Gulf of St. Lawrence. The model estimated that 50% of the grey seal pups were weaned by January 6, 2021 on the southwestern Nova Scotia Islands, and on January 24 in the southern Gulf. Application of the Bayesian model to staging data acquired at several colonies in previous years showed that the date when 50% of the pups are weaned has advanced by approximately one day each year since the early 2000s in the Gulf. This trend was less clear outside the Gulf, but the timing of births in 2021 was also estimated to be earlier than in previous years.

The Bayesian model provides an approach to consider several sources of uncertainty not previously taken into account. These include uncertainty associated with the date of first birth, the development stage duration, and variability in classification of stages by the various observers. By updating priors, the model can make use of new information as it is collected. The use of the Bayesian model should lead to improved estimates of population size.

Key words: grey seal births, pupping, pupping season, Bayesian model, birth distribution.

INTRODUCTION

Aerial surveys are often used to estimate wildlife abundance and there is a large body of literature dedicated to sampling design and method development using strip and line transect methods (e.g., Bowen et al. 1987; Buckland et al. 2001; Nielson et al. 2013; Crum et al. 2021). An important assumption is that all animals are available to be counted and all available animals are detected. Although many large vertebrates are widely dispersed for much of the year, some species are highly aggregated at certain stages in their annual life cycle (e.g., pupping and/or breeding seasons), over a period of days or weeks and hence provide an opportunity to be enumerated more easily. For pinnipeds, aerial surveys have been used successfully to count pups on the ice or on terrestrial breeding colonies (e.g., Sergeant 1991; Stenson et al. 1993, 2002, 2003; Bowen et al. 2003; Russell et al. 2019).

The grey seal (*Halichoerus grypus*) is a relatively large sexually dimorphic seal found throughout the north Atlantic (Mansfield and Beck 1977; Lesage and Hammill 2001). The northwest Atlantic population occurs along the east coast of Canada and the United States (Mansfield and Beck 1977; Boskovik et al. 1996; Cammen et al. 2018; den Heyer et al. 2020). Grey seals were once abundant in Atlantic Canada, but declined significantly during the 19th century and were considered rare well into the first half of the 20th century (Lavigueur and Hammill 1993; Lesage and Hammill 2001). Beginning in the second half of the 20th century, grey seal pup production increased, with the population showing remarkable recovery over the last 50 years or so (Hammill et al. 2017; den Heyer et al. 2020). In Canada, the first pups are born in early December on Sable Island and the southwest Nova Scotia area; pupping continues until mid-late February in the Gulf of St Lawrence (Gulf; den Heyer et al. 2020). Nursing lasts 16–22 days (Baker et al. 1995; Lesage and Hammill 2001; Noren et al. 2008; Lang et al. 2009). On Sable Island, animals remain on the island for an additional 9–31 days (mean = 21 ± 1.1 d) after weaning (Noren et al. 2008).

Grey seal pup production can be estimated from counts of live pups photographed during aerial surveys. However, in addition to correcting for pups missed in the review of imagery, aerial survey counts must be corrected for animals that have died or left the breeding site prior to the surveys and those born after surveys were flown. In earlier studies, the temporal distribution of birth was estimated from transition models fitted to the change over time in the proportion of pups in different development stages. Previous assessments of grey seal pup production at Gulf and Scotian Shelf colonies used a transition model based on a frequentist approach, making certain assumptions on the start date of pupping and distribution of births and considered fixed estimates for duration of the different development stages estimated by daily observations of known-age pups (Bowen et al. 1987; Myers and Bowen 1989). The method also assumed there is no pup mortality and that no pups leave the colony prior to the survey. The latter assumption may be justified when surveys are flown well before weaning, but the potential emigration or movement of pups to areas where they are not available to be counted might lead to biased results when surveys are conducted later or there are adjacent areas that are not surveyed. This model, that we refer to as the “Myers Birth Distribution” model (or MBD model), has been applied in Canadian assessments to estimate pup production of harp, hooded and grey seals (Bowen et al. 1987; Myers and Bowen 1989; den Heyer et al. 2020). However, the types of data collected during the assessment also lend themselves to a Bayesian approach, where the modeling of parameters such as the start date of pupping, the distribution of births, stage duration and emigration of animals from the breeding site, can be approximated based on prior information, updating the estimates when new data are presented to the model.

Here we propose a new transition model using a Bayesian model approach which incorporates information from previous studies explicitly through the use of prior probability distributions, and makes inferences accounting for uncertainties associated with the information provided to the model. We first tested this model using the data rich case of Sable Island grey seals, and compared the Bayesian model results with the MBD model results. Then, we carried out a simulation study to examine the impact of changes in stage survey frequency and timing on the Bayesian model predictions.

We then applied the new model results to adjust pup production estimates obtained from aerial surveys conducted during the winter of 2020–2021 (see den Heyer et al. 2023) and addressed a request for advice on the timing of births and the distribution of time at weaning for specific colonies along coastal Nova scotia and in the Gulf of St. Lawrence. This information will assist managers in setting the opening times for the commercial seal harvests in these areas.

METHODS

DATA

The temporal distribution of births is modelled from a transition model of known-age pups and the change over time in the proportion of each developmental stage in the population. Grey seal pups are classified into five developmental stages based on pelage colour and body shape (Radford et al. 1978; Kovacs and Lavigne 1986; Bowen et al. 2003; Appendix 1).

On Sable Island, animals are marked and can be monitored daily from birth to stage 5 to obtain information on the duration of each of the first four developmental stages (Appendix 2). In 2021, 47 pups were observed daily from birth, 42 of which achieved stage five before they were lost or observations stopped (Appendix 1). A single experienced observer collected the stage duration information. In previous years the daily pup observations were completed by different experienced observers.

To estimate how the proportion of pups in each developmental stage changes over time, pup stages along transects were recorded weekly (between December 17and January 27) throughout the colony. During winter 2020–2021 a total of 98 transects (14 unique transects repeated for seven weeks) were completed by the same observer that conducted the daily known-age pup observations (den Heyer et al. 2023).

For the Gulf colonies and the coastal colonies on the Scotian Shelf, it is not possible to mark and follow individuals. Instead, the stage duration estimates for stages 1 through 4 were based on multiple assessments completed on Sable Island (Appendix 2; surveys completed in 1997, 2007 and 2010), which were combined to provide a global mean duration for each of the four stages.

At these colonies, data regarding the proportion of the different developmental stages are collected from a low flying helicopter (≤ 60 m). Data collection varies between sites depending on environmental conditions and habitat. For the coastal colonies on the Scotian Shelf, parallel transects are flown over the barren islands at a speed of approximately 30–50 knots and data are collected on the stage of the pups observed along the transect. For the Gulf colonies, where the whelping area is limited to beaches, the helicopter flies along the beach at 30–50 knots and the stages of animals are recorded as they pass under or beside the aircraft.

MODEL

The Bayesian model considered seven stages, including stage 0 corresponding to the birth period, five development stages (stages 1 to 5) until full moult, and a final unobserved absorbing stage (stage 6) representing the animals that moved to location where they are not available to be counted because they have left the site and entered the water, or they have left the pupping beach and moved to an area where they are not normally detected from the air, e.g., in a forest. Gamma distributions were used to represent respectively the temporal distribution of births ($Birth$, s = 0; Eq. 1a) and the duration (D_s) of each stage of development (s = 1 to 5; Eq. 1b). For the births distribution, shape and rate were chosen to allow the model to test a wide range of values. With the current parametrization (Eq. 1a), the corresponding gamma distribution (Γ) has a median of 4.4 days with a 95%CI of 0.3–87 days.

For $s = 0$,

$$Birth \sim \Gamma(\alpha_0, \beta_0) \tag{1a}$$

with $\alpha_0 \sim U(1, 30)$

and $\beta_0 \sim U(0.001, 7)$

To reduce the number of parameters to be considered in the model, all the Gamma distributions representing the duration of the development stages share the same shape parameter (α) but each stage has a specific rate parameter (β_s).

For $s = 1$ to 5,

$$D_s \sim \Gamma(\alpha, \beta_s) \tag{1b}$$

with $\alpha \sim \Gamma\left(\frac{(\alpha_{mean})^2}{\alpha_{var}}, \frac{\alpha_{mean}}{\alpha_{var}}\right)$

and $\beta_s \sim \Gamma\left(\frac{\left(\beta_{s_{mean}}\right)^2}{\beta_{s_{var}}}, \frac{\beta_{s_{mean}}}{\beta_{s_{var}}}\right)$

Priors for α and β_s corresponding to the stages 1 to 4 were based on den Heyer et al. (2017) (Appendix 2) and considered as Gamma distributions with variance equal to two. It should be noted, that the 2021 stage duration survey resulted in values quite different from the previous years. Considering that only one person contributed to the 2021 staging survey while the previous values were collected over several years and several observers, the latter values were deemed more representative of the actual variability. In the model, the duration of stage 5 corresponds to the time (days) before stage 5 pups leave the colony or become unavailable to be counted. No recent information was available about this time delay, but Noren et al. (2008) identified an average age of departure of 40 days (range 26 to > 49 days) for grey seals born on Sable Island. Taking this into account, we chose a distribution for the rate parameter (β_s) so that the stage 5 duration prior has a mean of 15.7 days (95% CI 9.4–23.7), resulting, when combined with the other priors, in a mean age of departure of 40 days (95% CI 31–50). Animals leaving stage 5 were then considered as stage 6 individuals.

In addition to the prior on each stage duration, a prior corresponding to the sum of the durations from stages 1 to 3 was also included to constrain the model. We considered this sum, with a mean of 18.7 (95% CI 13.4–24.9), as a proxy for the lactation period (Noren et al. 2008; Lowe et al. 2017).

Transitions between the different development stages were described as the sum of the Gamma distributions representing successively the temporal distribution of births and duration of each stage. The sum of the Gamma distributions is also Gamma distributed, and the parameters of this distribution were estimated using the Welch-Satterthwaite approximation (Satterthwaite 1946; Welch 1947; Eq. 2).

For $s = 1$ to 5,

$$T_{s\ to\ s+1} \sim \sum_{i=0}^{s} \Gamma(\alpha, \beta_s) \approx \Gamma(\alpha_t, \beta_t) \tag{2}$$

with $\alpha_t = \frac{\left(\sum_{i=0}^{s} \frac{1}{\beta_i} \times \alpha\right)^2}{\left(\sum_{i=0}^{s} \left(\frac{1}{\beta_i}\right)^2 \times \alpha\right)}$

and $\beta_t = \frac{\left(\sum_{i=0}^{s} \frac{1}{\beta_i} \times \alpha\right)}{\alpha_t}$

Based on these transitions, the model is able to generate the proportion of pups in each development stage over time. A Dirichlet-Multinomial link (Eq. 3) is used to fit the time series produced by the model to the observations obtained from surveys (i.e., counts of animal in each development stage on several surveys dates). The Dirichlet-Multinomial is well-fitted when used with composition count data potentially presenting overdispersion (Stedinger et al. 1965; De Valpine and Harmon-Threatt 2013). In our case, this would account for the observers' variability in stage classification.

We denote:

$n_s(d_x)$: Number of pups in stage $s = 1$ to 5 in sample x on day d.

$N(d_x)$: Total number of pups in sample x on day d.

$p_s^u(d)$: Unobserved / expected proportion of pups actually in stage s on day d.

w_{d_x}: A weighting parameter affecting the variance from the Dirichlet distribution (i.e., model the noise within the data; larger values induce less variation; see Appendix 3).

$$p(d_x) \sim Dirichlet(p'^u(d_x)) \tag{3}$$

with $p'^u_s(d_x) = p_s^u(d) * w_{d_x}$

and $w_{d_x} \sim Truncated\ Gamma(1, 0.001),\ L = 0.001$

$n_s(d_x) \sim Multi(N(d_x)\ , p(d_x))$

The date of first birth anchors the start date for the transition model. However, the actual date of first birth is not observed in the surveyed populations and instead, a "guesstimate" is often used based on the stage of the oldest pups. In order to consider the uncertainty around this date, a date-shift parameter allowed the model to estimate the most likely date. This parameter was sampled from a normal distribution centered on zero with a standard deviation of 2.5, resulting in a range of dates centered on the "guesstimate", minus five to plus five days.

The harvest is directed towards weaned animals. The duration of nursing is variable and can last for 16–22 days (Baker et al. 1995; Lesage and Hammill 2001; Noren et al. 2008; Lang et al.

2009). For the purpose of defining the proportion of animals weaned, we used a lactation duration of 20 days in this study.

The model was run using R statistical software (R Core Team 2021). We obtained posterior estimates of all the parameters using a Gibbs sampler algorithm implemented in JAGS (Plummer 2003). Results were examined using the R packages R2jags (Su and Yajima 2021) and coda (Plummer et al. 2006). Each model run included five chains of 20,000 iterations in which we kept one sample every 10 iterations after a burn in phase of 10,000 iterations. This resulted in a final set of 5,000 samples (1,000 samples per chain). We evaluated model convergence by graphical examination of trace plots and by ensuring that Gelman-Rubin convergence diagnostic (R-hat) was < 1.1 for all fitted model parameters.

MODEL TEST AND COMPARISON USING THE SABLE ISLAND WINTER 2020–2021 STAGING DATASET

The Bayesian and the MBD model were fit to the 2021 Sable Island staging data (Appendix 4). The estimated birth curves were compared in monitoring the date of first birth, the dates predicted for reaching 1%, 50% and 95% of births, and the estimated proportion of births on the date the aerial photographic survey was flown to determine the total pup production.

The Bayesian model was first fit to this dataset directly, considering each transect as an independent measurement of the proportions of animals in each development stage. Then it was fit to the dataset aggregated by day, corresponding to the approach used when applying the MBD model, and to the type of data obtained from the surveys of the other colonies (i.e., only one set of proportion per stage per observation day).

Using the same dataset, a sensitivity test was performed to assess the impact of the stage duration priors on the Bayesian model results by doubling the variance around the α and β_s parameters from the gamma distributions representing these stage durations (Eq. 1), resulting in much less informative priors. In addition, while the original Bayesian model used a common α parameter for all gamma distributions, we also tested a model version in which each gamma distribution representing the stage duration was parametrized with a independent α parameter.

The behaviour of the original Bayesian model was then examined using a simulation approach where surveys from the Sable Island dataset were excluded from the analysis and the model was rerun using the reduced dataset. Since the non–Sable Island colonies often have fewer surveys, the objective was to evaluate how the model estimates of the proportion of the pups born might change as the number and the temporal distribution of sampling surveys was altered. We investigated five scenarios:

1. splitting the dataset in two parts, one before and one after the peak of stage 3,
2. using three observation dates separated by one week and conducted before/during/after the peak of stage 3,
3. using two observation dates separated by one week and different timing covering the whole survey period,
4. using observations collected every two weeks over the whole period of development, and finally,
5. using two observations separated by two weeks and conducted before/during/after the peak of stage 3.

APPLICATION TO THE OTHER GREY SEAL COLONIES

The Bayesian model was then fit to the 2021 staging survey data obtained from six other grey seal colonies located in the Gulf of St. Lawrence and on the Scotian Shelf (Table 2; Appendices 5 and 6) to estimate the temporal distribution of birth at these breeding sites. As for the previous tests, the first birth date, and the dates at which 1%, 50%, 95% of the animals were born were extracted from the output of the model and compared among colonies.

For comparison, the dates at which 1%, 50%, and 95% of the animals were born were also estimated from the MBD model (Tables 2a and 2b).

The variability in the birth distribution over the last two decades was estimated by fitting the Bayesian model to the staging data acquired on Pictou Island (2007–2021; 9 surveys), Henry Island (2004–2021; 5 surveys), Saddle Island (2010–2021; 7 surveys), Hay Island (2000–2021; 6 surveys), Mud, Noddy, Flat and Round Islands (2016–2021; 2 surveys). Staging data were only considered when at least three dates were available for a specific year (with the exception of 2016 data from the southern Nova Scotia Islands [Mud, Noddy, Flat and Round Islands] which represents the only year with data other than 2021). The date corresponding to an estimated 50% of pups born (and 50% pups weaned considering 20 days between birth and weaning), was tracked over years with available data to show temporal evolution in the timing of birth.

RESULTS

MODEL TEST AND COMPARISON – SABLE ISLAND DATASET

In the first trial, the Bayesian model was fitted to the Sable Island dataset considering each transect (n = 14) as an independent measure of the proportion of the pups in each development stage. The output suggested a good fit to the data (Figure 1a) and estimated that 1% of the pups were born on Dec. 13 (Figure 1b; Table 1), 50% on Dec. 24, and 95% on Jan. 4. It also estimated that 99.2% of the pups were born by the survey date (Jan. 11, 2021). Moreover, while the “guesstimate” date provided for the first birth was Dec. 3, the model provided a better fit to the data if pupping started on Dec. 5 (Table 1). However, the guesstimate date was still in the 95% credible interval estimated by the model (Nov. 30–Dec. 7). The model output also shows a strong update of the stage duration priors, suggesting a shorter stage duration for stages 1, 3 and 4 (mean prior *versus* mean posterior; 1.53 *vs* 3.22, 9.15 *vs* 11.80 and 3.20 *vs* 5.64 days respectively) and a much longer duration for stage 2 (mean = 7.30 *vs* 3.67 days).

In a second trial, the Sable Island dataset was aggregated by day, summing the counts over all the transects. The Bayesian model predictions for the evolution of the proportion of pups in each stage were very similar to the first trial (Figure 2a *vs* Figure 1a; Table 1; Appendix 2). However, the estimated birth curve was slightly different from the previous trial, predicting 1% births occurred three days earlier (Dec. 11), reaching 50% births on Dec. 21, and 95% of births on Jan. 3. The proportion of pups born on the survey date was similar to the previous results with 99.3 % *vs* 99.2%. Stage duration priors were updated in the same way as before, with shorter duration for stages 1, 3 and 4 and longer duration for stage 2. However, the posteriors were different with mean stage durations of 2.37, 8.52, 9.12 and 3.5 days for stages 1 to 4, respectively.

The sensitivity test involving less informative priors for the stage durations and the alternative version of the model allowing for independent α parameters for each gamma distribution representing the stage duration priors, both resulted in predictions very similar to those obtained with the original settings (figures not shown), with at most a one-day change in estimated dates for the first birth, 1%, 50%, and 95% births, demonstrating the robustness of the Bayesian model results.

To compare the Bayesian model to the MBD model, the latter was also parametrized using stage durations based on previous years (1997–2010; Appendix 2). However when fitted to the 2021 Sable Island dataset, it did not converge. To avoid this problem, both models were then parametrized with the stage durations obtained in 2021 (Appendix 2). The Bayesian model estimated values very similar to those obtained with the 1997–2010 priors (see second trial above; Table 1). The estimated birth curve predicted that 1% of the pups were born on Dec. 10, 50% on Dec. 20, and 95% on Jan. 3. The model estimated that 99.3% of the pups were born on the aerial survey date, but it also suggested that at this time a mean of 5.8% (median = 5.5, 95% CI 0.8–12.8) of the pups had left the island. While the stage duration priors used in this trial (based on 2021 stage duration estimates) differed significantly from the 2007–2010 priors used elsewhere (i.e., 2021 priors means = 2.96, 4.45, 9.79 and 11.53 *vs* 2007–2010 priors means = 3.22, 3.67, 11.79 and 5.64 for stages 1 to 4, respectively), a strong update resulted in similar posterior distributions (mean = 2.53, 7.67, 8.9 and 4.24 for stages 1 to 4). The MBD model predicted that 1% of the pups were born on Dec. 7 (95% CI Dec. 3–10), 50% on Dec. 21 (95% CI Dec. 16–27) and 95% on Jan. 7 (95% CI Dec. 30–Jan. 17). At the survey date, it estimated that 97.1% (95% CI 96.3–97.9) of pups were born (Table 1).

IMPACTS OF TIMING AND NUMBER OF SURVEYS ON MODEL ESTIMATES

When fitted to the first half of the dataset (i.e., before the peak in the proportion of Stage 3 individuals), the model predictions were very close to the estimates obtained with the full dataset (Table 1). The estimated dates for the first birth, 1% and 95% births were one day earlier, but the date for 50% births was the same (Dec. 20). Similarly, the proportion of births at the aerial survey date were close; 99.5 *vs* 99.3%, but the 95% credible interval was slightly larger (97.9–99.9), encompassing the prediction and the credible interval obtained with the full dataset (98.2–99.8). The trial that was fitted to the second part of the data (i.e., after the peak in the proportion of Stage 3 individuals) had a larger effect on the model output. In this trial, there was less updating of the stage duration priors (not shown). While the estimate for the first birth was equal to the one obtained when fitting to the full dataset, the estimated birth curve showed a lower slope, with 1% occurring two days earlier, 50% one day later (Dec. 21) and the 95% occurring four days later. As a result, the estimated proportion of births on the aerial survey date was also lower (97.2%). The corresponding 95% credible interval (94.9–98.7) included the value predicted with the full dataset, but not its entire 95% credible interval.

Model outputs based on the fit to three observations separated by one week collected in the beginning, the middle, or the end of the development period were relatively close to the prediction obtained with the full dataset. The dates for first birth, 1%, and 50% births were estimated to be slightly earlier (-1 to -2 days). The estimated birth curves predicted an earlier date (-2 days) for reaching 95% of births when fitted to the data collected before the peak in proportion of Stage 3 individuals. In contrast the estimated date was two to three days later when data was collected during or after the peak. The later the samples were collected, the lower the estimated proportion of pups born before the aerial survey date. All the 95% credible intervals around each of the estimates included the value obtained when fitting the whole dataset, and most of them were close or included their 95% credible intervals (Table 1).

With only two observations separated by one week, we could see a gradient of effects on the model output. At the extreme, when the timing of the two observations was at the beginning or at the end of the pupping season, very little information was provided to the model about the transitions among stages (two or three stages have proportions close to zero). As a result, the model output showed large 95% credible intervals, particularly when considering the two observations at the beginning of the pupping season (Table 1). While the estimate for the first birth date stayed relatively close to that obtained with the full dataset, only two days earlier (Dec. 2), the 50% and 95% births dates differed, with estimates of Dec. 31 versus Dec. 21 and Jan. 22 versus Jan. 3, respectively. The estimated proportion of births on the aerial survey date was also lower (81.7%), but with a very wide 95% credible interval covering all the proportions from 0.4 to 100%. The effect on the estimates was less important for the trial that considered two stage survey points obtained at the end of the pupping season, with an estimated date for 50% births two days earlier and a proportion born on the aerial survey date of 97.5% (95% CI 92.2–99.5) vs 99.3% (95% CI 98.4–99.7) for the entire dataset. For the intermediate cases, as samples are taken from the beginning to the end of the development period, the model estimated a birth curve with a lower slope, resulting in a date for 50% births shifting from Dec. 21 (for early samples), to Dec. 27 (for late samples), and the proportion of births completed on the aerial survey date declining from 100% to 98.1%. However, the 95% CI for the first birth date, 1%, 50%, 95%, and the proportion born on the aerial survey date generally included the predicted dates obtained with the full dataset. Only the output obtained from the fitting to two observations collected both before the peak of the proportion of stage 3 individuals showed intervals excluding the predicted date for 95% births and the proportion of animal born at the aerial survey date obtained from the fitting on the full dataset.

Limiting the fitted dataset to observations separated by two weeks over the entire pupping period (N = 4) still allowed the model to converge to estimates close to those obtained when fitting the full dataset. Predicted values were all within one day of the original values. Moreover, the estimated proportion of individuals born on the date of the aerial survey was nearly identical (99% *vs* 99.3%, with a 95% credible interval even smaller than in the results obtained with the full dataset; Table 1).

Using only two observations separated by two weeks resulted in a similar trend as observed when fitting to only two observations separated by one week. When data considered were collected later in the development period, the model estimated a longer duration for the birth period. Thus, while the date for 1% births remained the same (Dec. 10–11; Table 1), the estimated date for 95% births shifted from Jan. 1 when considering early data, to Jan. 8 when late data were used. Similarly, the proportion of births completed on the aerial survey date changed from 99.7% to 96.9%. The estimated date for the 50% births also changed, but did not follow a similar trend (Dec. 20, early data; Dec. 25 middle data, Dec. 24 late data). In all cases, the 95%CI of each estimate (first birth, 1%, 50%, 95%, and proportion born on the aerial survey date) encompassed the median value predicted with the full dataset.

TEMPORAL DISTRIBUTION OF BIRTHS

Based on Bayesian modelling, the uncertainty associated with the date of first pupping and in the distribution of pupping resulted in overlap between the colonies (Tables 1, 2a). On the Scotian Shelf, pupping started in the southern portion of the colonies distribution, at Sable Island on Dec. 5, followed by the southwest Nova Scotia islands of Mud, Round, Noddy and Flat Islands (Dec. 8), which, being only 28 nautical miles south of Sable Island, are essentially at the same latitude. Pupping began about a week later on Hay Island (Dec. 14), which lies approximately 61 nautical miles to the north of Sable Island off the north east coast of Cape Breton. In the Gulf, pupping was estimated to have started later than on the Scotian Shelf, but dates varied by colony, starting in the Northumberland Strait on Pictou Island (Dec. 16), then successively on Brion Island (Dec. 19), Henry Island (Dec. 20) and finally Saddle Island (Dec. 21). The model estimated that 50% of the births were completed on Dec. 17at Mud, Round, Noddy and Flat Islands, Dec. 20 on Sable Island and Dec. 27on Hay Island. In the Gulf, Brion Island reached this proportion on Dec. 29, Henry Island on Jan. 1and both Pictou and

Saddle Islands on Jan.4. Finally, most of the births (95%) were completed by Jan. 3 on Sable Island, Jan. 4 on the Mud, Round, Noddy and Flat Islands, and by Jan. 10 on Hay Island. In the Gulf, pupping ended slightly later on Brion Island (Jan. 13) and 5 to 6 days later on Henry and Saddle Islands, respectively. Pictou Island, which was estimated to be the first area of pupping in the Gulf in 2021, was also predicted to be the last to reach the 95% of birth completed. It has to be noted that in most cases, the 95% credible intervals of each of these estimates (Tables 1 and 2) encompassed the median values predicted in the other areas, the only exception being the Mud, Round, Noddy and Flat Islands which clearly showed an earlier timing in the birth distribution compared to Hay Island and the Gulf colonies.

Based on the distribution curves estimated by the Bayesian model, 95% of the births were generally completed within 17 days on most islands (Sable, Hay, Henry, Saddle). However, this period was estimated to have been shorter on the Mud-Round-Noddy-Flat and Brion Islands (15 and 16 days, respectively), and longer on Pictou Island (19 days).

The MBD model applied to these colonies always estimated a wider birth distribution curve (Table 2a, b), with a smaller percentage of animals estimated to be born at the survey date and thus a larger adjustment to the counts resulting in a higher pup production estimate (Table 3).

TEMPORAL DISTRIBUTION OF WEANED ANIMALS

The grey seal harvest is directed towards weaned animals, and weaning was assumed to occur at 20 days post partum. Colonies located along the Nova Scotia coast were the first to see weaned animals with a south to north trend beginning on the Mud-Round-Noddy-Flat Islands (Dec. 30), Sable Island (Dec. 30) then Hay Island (Jan. 9) (Table 4a). In the Gulf, it started first on Brion Island (Jan. 9) and Pictou Island (Dec. 9), then Henry Island (Jan. 11), and finally Saddle Island (Jan. 13) (Table 4b). An estimated 50% of the seals on the colony were weaned by Jan. 6 on the Mud-Round-Noddy-Flat Islands, Jan. 10 on Sable Island, Jan. 18 on Hay Island, Jan. 18 on Brion Island, Jan. 21 on Henry Island and Jan. 24 on Saddle and Pictou Islands. On the Nova Scotia coast, most of animals (95%) were estimated to be weaned by the end of January, early February (Sable Island Jan. 23, Mud-Round-Noddy-Flat Islands Jan. 24, Hay Island Feb. 2) and in the Gulf in the first half of February, Brion Island (Feb. 2), Henry Island (Feb. 7), Saddle Island (Feb. 8) and Pictou Island (Feb. 13) (Tables 4a,b).

TEMPORAL EVOLUTION OF THE BREEDING SEASON OVER YEARS

A dataset of 9, 7 and 5 years of surveys was used to study the temporal evolution of the birth distribution on Pictou, Saddle and Henry Islands, respectively (Figure 3a). The time series started in 2003 for Henry, 2007 for Pictou and 2010 for Saddle Islands. Even with the uncertainties around the estimates provided by the Bayesian model, the results described a trend that shows an advancement of the breeding season by one day per year over the last 10 to 15 years.

On Hay Island, this shift in the breeding season date was not visible for the period 2000–2018 (Figure 3b), although, the model did estimate an earlier date for 2021. For the Islands located in the southern Nova Scotia, staging data were only available for 2016 and 2021. While the Bayesian model suggested a large uncertainty around the 2016 estimate, the date at which 50% pups were born in 2021 was estimated to be significantly earlier than in 2016 (median date Dec. 17 *vs* Dec. 29 respectively).

DISCUSSION

The assessment of the northwest Atlantic grey seal population in eastern Canada is based on the count of pups at the time of whelping obtained from a photographic survey. This count must be adjusted for several factors including individuals photographed but missed by the reader (detectability bias), as well as pups not available to be photographed (availability bias). There are three main reasons for the latter; individuals may have died before the survey, pups may have already left the colony or, some animals were born after the survey flight.

Given the high-quality imagery available, detectability bias is small. Mortality rates at the breeding site are also considered to be low (~5%; den Heyer et al. 2017). Ideally, aerial surveys are timed to occur after peak pupping, but before the pups begin to leave the colony. To account for births occurring after the photographic survey has been flown, it is necessary to estimate the overall temporal distribution of births. This is done by means of a transition model that fits to proportion of pups at each stage from a series of surveys completed throughout the breeding season. Correcting for pups that may have left the breeding colonies is more difficult and further work in this area is needed.

In the previous assessments, the MBD model was used to estimate the grey seal birth distribution for several of the largest colonies. This model assumed the date of first birth is known, represented duration of each stage as a Gamma distribution with a separate or common shape parameter considered as fixed, and fitted the birth distribution as either another Gamma distribution or a Weibull distribution. Since pupping often starts before observers are in the field, this start date is normally based on observer experience, and the approximate age of animals seen on the first survey day. In addition, the uncertainty in the stage duration in MBD is assumed to be known without error, which may be problematic when applied to other colonies as the stage assessments may vary among observers and between platforms (see Stenson and Myers 1988 for such variability in hooded seals staging surveys). Grey seal stage durations have been estimated by different observers assessing known-age pups from birth to stage 5 on Sable Island (den Heyer et al. 2023). Here we present an alternative model based on a Bayesian framework that incorporates information on our prior understanding of first birth date and stage duration but allows these estimates to be updated by information in the stage surveys. The Bayesian approach used to fit this model allows both the information and uncertainties associated with the priors and the data to be combined and propagated in the results without any additional procedure. This differs from the MBD model, which applies a jackknife method post-hoc to the stage survey data to estimate the uncertainty.

The MBD model offered the possibility to use different family of statistical distributions (Weibull or Gamma) to describe the birth distribution. While the different parametrizations of the Gamma distribution already offered a wide range of shapes to represent both the stage duration and the birth distributions, the Weibull distribution was even more flexible. However, this distribution was not used in the Bayesian model as the calculation of the sum of multiple Weibull distributions is much more complex to implement than the sum of Gamma distributions (Nadarajah 2008; Garcia et al. 2021). Moreover, the sum of Gamma distributions is also Gamma distributed, and there is an efficient method for approximating the parameters of this distribution (Welch-Satterthwaite approximation; Satterthwaite 1946; Welch 1947). Finally, while the MBD model was based on a multinomial distribution (i.e., a generalization of the binomial distribution) to link the model predictions to the number of animals observed in each stage, the Bayesian model used a Dirichlet-multinomial distribution corresponding to a multivariate beta distribution. The latter can be seen as an overdispersed multinomial distribution, allowing in our case to account for some of the variability in the classification of animals between the different stages that can occur within successive observations by the same observer or between observations by different observers.

The comparison between the MBD and the Bayesian models when both were fitted to the data-rich case of Sable Island showed similar estimates for the first birth date, and the dates at which 1%, 50% and 95% of pups were born. The Bayesian model tended to estimate a birth curve predicting a slightly shorter period of births, leading to a higher estimated proportion of animals born on the aerial survey date compared to estimates from the MBD model and thus produced a smaller adjustment to the count. The Bayesian model also updated the stage duration estimates for all stages, with a much longer stage 2 than is estimated by observation of known-age animals, suggesting that these priors might need to be revised, or that a bias in the data in the classification among stages may render it not totally comparable to the stage classification used when the stage duration surveys were conducted. Further work is needed to explain these discrepancies. The application of both models over the other colonies showed the same trends.

The effect of the timing and number of stage surveys on the estimates of the Bayesian model was examined by subsetting the Sable Island dataset. Apart from extreme cases involving a lower number of surveys conducted at the very beginning or at the end of the pup development period, the model results were relatively stable, and generally, credible intervals included the estimates obtained when fitting to the full dataset. At least three stage surveys separated by one or two weeks ensured an output close to the result obtained when the full dataset was considered. However, the tests showed that the estimated proportion of births on the aerial survey date declined if the stage surveys were only completed late in the pupping season. This trend was even more pronounced when the number of surveys was low (< 3). The model fitted to late survey data also did not update the stage duration priors (in particular for stages 1 and 2) as much as the model fitted to survey data that included surveys conducted early in the pupping season, suggesting it is important to distribute the survey effort throughout the pupping season.

The Bayesian model estimation of the birth distribution on eastern Canada's largest grey seal colonies showed a general trend starting off the Nova Scotia coast then moving into the Gulf of St. Lawrence. However, apart from the Mud-Round-Noddy-Flat Islands and Sable Island that presented an earlier distribution of birth, the timing of births on the other colonies was not significantly different (i.e., the 95% credible intervals around the predicted dates overlap). In some seal species (harbour seals [spp.], California sea lions [spp.]; Temte 1993; Temte et al. 1991) a relationship between birth timing and latitude was observed and attributed to a link with the photoperiod. However, in the North Atlantic, grey seals breeding dates show an irregular geographical distribution and do not support the existence of such a relationship (Coulson 1981). Coulson (1981) suggested that sea temperature could be the main environmental factor involved, acting on the termination of the suspended development of the embryo and thus, delaying the birthing day in areas of lower sea temperature. The trend in sea surface temperature in the study area corresponds to the sequence of births described above from the southern Nova Scotia colonies to Brion Island in the Gulf, but the islands located in southern Gulf which have later birthing periods than Brion Island, generally featured higher sea temperatures. Bowen et al. (2020) showed a high degree of individual repeatability in parturition dates and an inter-annual variability limited to 1–3 days between breeding seasons. However, they also estimated that pupping on Sable Island has advanced by 15 days over the past 30 years. The application of the Bayesian model on staging data acquired over the last 15 years at several islands from southern Gulf suggested a similar advancement of the breeding season by approximately 10–15 days compared to 15 years ago. These inter-annual, inter-colony discrepancies demonstrates that, to provide advice on the timing of harvest, it will be necessary to monitor birth distribution at the colonies where harvests occur.

The Bayesian model was developed to estimate the temporal distribution of births, providing information needed to adjust aerial survey estimates for the proportion of pups not born when the surveys are flown. However, this new model also provides means to include new information as it is collected, by updating the priors, and can thus be used as a tool to evaluate factors that may be affecting the temporal distribution of births across colonies and years. Moreover, this Bayesian model allows unobserved states to be quantified, so that the date of first pupping, and the proportion of animals that may have left the surveyed area at the survey date can be estimated (Appendix 7). While some additional validation work is needed, this information will lead to improvements in understanding the temporal distribution of pupping, a better adjustment of the count, and improved estimates of population size.

ACKNOWLEDGMENTS

We thank Damian Lidgard for completing the stage duration and staging surveys on Sable Island, and Susan Heaslip, Warren Joyce, Megan Wilson for staging surveys in southwest Nova Scotia. Priyanka Varkey and Pierre Rivard as readers of the large number of aerial photos collected during the 2020–2021 winter surveys, and Harrison MacRae, Colin Lavalee, Malte Dehler, Per Klattenhoff with Canadian Coast Guard, for help during the surveys.

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TABLES

Table 1. Estimated date at which specific proportion of births was reached on Sable Island in 2021 using the Bayesian birth distribution model fitted to all the 2021 stage survey transects treated independently or aggregated by day. Many different subsets of the transect data were fitted to explore the performance of the model in situations with more limited data. The Bayesian model was also fitted with priors on stage duration based on stage durations from 2021, and for comparison, results from the MDB model are indicated on the last portion of the table. Results are shown as median date and 95% credible interval. The last column shows the proportion of births, along with its 95% credible interval, on the photographic survey date (Jan. 11, 2021).

Transect data as independent measures (2007–2010 priors)

Dataset considered	Start Date (95% CI)	1% births (95% CI)	50% births (95% CI)	95% births (95% CI)	Prop. births Jan. 11
Complete dataset	Dec. 05 (Nov. 30– Dec. 07)	Dec. 13 (Dec. 11–15)	Dec. 24 (Dec. 22–26)	Jan. 04(Jan. 03–06)	99.2 (98.6–99.6)
First half	Dec. 04 (Dec. 01–09)	Dec. 11 (Dec. 07–14)	Dec. 23 (Dec. 19–26)	Jan. 07(Jan. 04–11)	97.9 (94.9–99.1)
Second half	Dec. 03 (Nov. 29–Dec. 10)	Dec. 10 (Dec. 06–13)	Dec. 22 (Dec. 17–26)	Jan. 06(Jan. 03–09)	98.2(96.5–99.2)

Transect data aggregated by day (2007–2010 priors)

Dataset considered	Start Date (95% CI)	1% births (95% CI)	50% births (95% CI)	95% births (95% CI)	Prop. births Jan. 11
Complete dataset	Dec. 04 (Nov. 30–Dec. 08)	Dec. 10 (Dec. 07–12)	Dec. 21 (Dec. 17–23)	Jan. 03 (Dec. 31–06 Jan.)	99.3 (98.4–99.7)
First half	Dec. 03 (Nov. 27–Dec. 08)	Dec. 09 (Dec. 06–12)	Dec. 20 (Dec. 17–24)	Jan. 02 (Dec. 29–07 Jan.)	99.5 (97.9–99.9)
Second half	Dec. 04 (Nov. 29–Dec. 08)	Dec. 08 (Dec. 05–12)	Dec. 21 (Dec. 17–25)	Jan. 07 (Jan. 04–11)	97.2 (94.9–98.7)
1 obs./week	Dec. 04 (Nov. 29–Dec. 08)	Dec. 10 (Dec. 07–13)	Dec. 21 (Dec. 17–24)	Jan. 03 (Dec. 30–06 Jan.)	99.3 (98.1–99.8)
1 obs./week – 3 obs. sample – First half	Dec. 02 (Nov. 27–Dec. 07)	Dec. 11 (Dec. 07–14)	Dec. 21 (Dec. 18–24)	Jan. 01 (Dec. 28–05 Jan.)	99.7 (98.7–100)
1 obs./week – 3 obs. sample – Middle	Dec. 02 (Nov. 28–Dec. 07)	Dec. 11 (Dec. 07–15)	Dec. 23 (Dec. 19–27)	Jan. 06 (Jan. 01–10)	98.6 (95.9–99.8)
1 obs./week – 3 obs. sample – Second half	Dec. 03 (Nov. 29–Dec. 08)	Dec. 12 (Dec. 06–16)	Dec. 23 (Dec. 18–27)	Jan. 05 (Jan. 01–10)	98.0 (94.9–99.5)
1 obs./week – 2 obs. sample – 1/6	Dec. 02 (Nov. 27–Dec. 07)	Dec. 13 (Dec. 08–16 Jan.)	Dec. 21 (Dec. 17–21 Feb.)	Jan. 22 (Dec. 26–21 Feb)	81.7 (0.4–100)
1 obs./week – 2 obs. sample – 2/6	Dec. 03 (Nov. 29–Dec. 08)	Dec. 12 (Dec. 10–15)	Dec. 21 (Dec. 18–23)	Dec. 29 (Dec. 25–01 Jan.)	100.0 (99.9–100)
1 obs./week – 2 obs. sample – 3/6	Dec. 02 (Nov. 28–Dec. 07)	Dec. 12 (Dec. 07–16)	Dec. 23 (Dec. 18–26)	Jan. 03 (Dec. 28–09 Jan.)	99.6 (96.9–100)
1 obs./week – 2 obs. sample – 4/6	Dec. 02 (Nov. 27–Dec. 07)	Dec. 12 (Dec. 07 –18)	Dec. 24 (Dec. 20–29)	Jan. 07 (Jan. 03–11)	98.3 (95.4–99.7)
1 obs./week – 2 obs. sample – 5/6	Dec. 03 (Nov. 28–Dec. 08)	Dec. 15 (Dec. 10–20)	Dec. 27 (Dec. 22–30)	Jan. 07 (Jan. 04–11)	98.1 (94.7–99.5)
1 obs./week – 2 obs. sample – 6/6	Dec. 02 (Nov. 27–Dec. 07)	Dec. 06 (Nov. 30–15 Dec.)	Dec. 19 (Dec. 10–28)	Jan. 06 (Dec. 31–15 Jan.)	97.5 (92.2–99.5)
1 obs./2 weeks – 4 obs. sample	Dec. 05 (Nov. 29–Dec. 09)	Dec. 09 (Dec. 06–12)	Dec. 20 (Dec. 15–24)	Jan. 03 (Dec. 30–07 Jan.)	99.0 (97.4–99.7)
1 obs./2 weeks – 2 obs. sample – First half	Dec. 02 (Nov. 28–Dec. 07)	Dec. 10 (Dec. 06–12)	Dec. 20 (Dec. 15–24)	Jan. 01 (Dec. 23–06 Jan.)	99.7 (98.1–100)
1 obs./2 weeks – 2 obs. sample – Middle	Dec. 02 (Nov. 27–Dec. 07)	Dec. 13 (Dec. 07–17)	Dec. 25 (Dec. 20–28)	Jan. 06 (Jan. 02–11)	98.4 (95.2–99.6)
1 obs./2 weeks – 2 obs. sample – Second half	Dec. 03 (Nov. 28–Dec. 08)	Dec. 11 (Dec. 06–16)	Dec. 24 (Dec. 19–29)	Jan. 08 (Jan. 04–13)	96.9 (92.4–99.1)

2021 priors

Dataset considered	Start Date (95% CI)	1% births (95% CI)	50% births (95% CI)	95% births (95% CI)	Prop. births Jan. 11
Aggregated Transect data by day	Dec. 04 (Nov. 29–Dec. 09)	Dec. 10 (Dec. 07–12)	Dec. 20 (Dec. 18–23 Dec.)	Jan. 03 (Dec. 31–Jan. 06)	99.3 (98.2–99.8)
MDB model	Dec. 03 (fixed value)	Dec. 07 (Dec. 03–10)	Dec. 21(Dec. 16–27 Dec.)	Jan. 07 (Dec. 30–Jan. 17)	97.1 (96.3–97.9)

Table 2a. Estimated date at which specific proportions of birthswas reached in winter 2020–2021 at the largest grey seal colonies located along the coast of Nova Scotia and in the Gulf of St Lawrence, using the Bayesian birth distribution model fitted to stage survey data acquired from each of these colonies. Results are shown as median date and 95% credible interval for specific proportions of births.

Coastal Nova Scotia

Location	Start date (95% CI)	1% births (95% CI)	50% births (95% CI)	95% births (95% CI)
Hay Island	Dec. 14 (Dec. 10–19)	Dec. 17 (Dec. 14–21)	Dec. 27 (Jan. 23–31)	Jan. 10 (Jan. 6–15)
Mud, Round, Noddy and Flat Islands	Dec. 8 (Dec. 4–12)	Dec. 9 (Dec. 06–12)	Dec. 17 (Dec. 13–21)	Jan. 4 (Dec. 30–Jan. 10)

Gulf of St. Lawrence

Location	Start date (95% CI)	1% births (95% CI)	50% births (95% CI)	95% births (95% CI)
Brion Island	Dec. 19 (Dec. 15–23)	Dec. 20 (Dec. 17–23)	Dec. 29 (Dec. 25–Jan. 1)	Jan. 13 (Jan. 10–17)
Henry Island	Dec. 20 (Dec. 16–24)	Dec. 22 (Dec. 18–26)	Jan. 1 (Dec. 27–Jan. 6)	Jan. 18 (Jan. 13–23)
Pictou Island	Dec. 16 (Dec. 11–20)	Dec. 20 (Dec. 16–23)	Jan. 4 (Dec. 29–Jan. 8)	Jan. 24 (Jan. 19–30)
Saddle Island	Dec. 21 (Dec. 16–26)	Dec. 24 (Dec. 21–28)	Jan. 4 (Dec. 31–Jan. 8)	Jan. 19 (Jan. 15–24)

Table 2b. Estimated start dates and proportions of grey seal births in winter 2020–2021 at the largest colonies located along the coast of Nova Scotia and in the Gulf of St. Lawrence, using the MBD model fit to stage survey data acquired from each of these colonies.

Sable Island

Location	Model	Start date	1% births (95% CI)	50% births (95% CI)	95% births (95% CI)
Sable Island	Weibull	Dec. 3	6 Dec. (Dec. 6–7)	Dec. 22 (Dec. 21–22)	Jan. 5 (Jan. 5–Jan. 6)

Coastal Nova Scotia

Location	Model	Start date	1% births (95% CI)	50% births (95% CI)	95% births (95% CI)
Hay Island	Gamma	Dec. 14	Dec. 17 (Dec. 15–22)	Dec. 31 (Dec. 21–Jan. 20)	Jan. 23 (Jan. 4–Mar. 1)
Mud, Round, Noddy and Flat Islands	Gamma	Dec. 10	Dec. 11 (Dec. 10–14)	Dec. 20 (Dec. 12–Jan. 14)	Jan. 11 (Dec. 22–Mar. 10)

Gulf of St. Lawrence

Location	Model	Start date	1% births (95% CI)	50% births (95% CI)	95% births (95% CI)
Brion Island	Gamma	Dec. 20	Dec. 21 (Dec. 20–22)	Jan. 1 (Dec. 27–Jan. 9)	Jan. 23 (Jan. 12–Feb. 11)
Henry Island	Gamma	Dec. 21	Dec. 24 (Dec. 22–31)	Jan. 6 (Dec. 27–Jan. 29)	Jan. 26 (Jan. 8–Mar. 9)
Pictou Island	Weibull	Dec. 16	Dec. 24 (Dec. 22–27)	Jan. 14 (Jan. 10–Jan. 19)	Jan. 30 (Jan. 26–Feb. 4)
Saddle Island	Gamma	Dec. 21	Dec. 26 (Dec. 23–Jan. 3)	Jan. 10 (Dec. 31–Jan. 31)	Jan. 29 (Jan. 12–Mar 6)

Table 3. Counts of live pups from aerial survey and the estimated proportion born using the Myers Birth Distribution (MBD) and Bayesian birth distribution models (den Heyer et al. 2021). The estimates from the maximum count are in bold.

Survey location and date	Count	MBD Estimate	MBD Var.	Bayesian Estimate	Bayesian Var.
Sable Island 2021-01-11	**72,209**	**0.987**	**0.001**	**0.993**	**0.000**
Brion Island 2021-01-13	4,987	0.849	0.004	0.939	0.000
Brion Island 2021-01-15	**5,151**	**0.877**	**0.003**	**0.956**	**0.000**
Brion Island 2021-01-20	4,350	0.928	0.002	0.982	0.000
Henry Island 2021-01-05	395	0.460	0.004	0.648	0.010
Henry Island 2021-01-13	1,218	0.756	0.005	0.880	0.002
Henry Island 2021-01-20	1,397	0.895	0.004	0.958	0.000
Henry Island 2021-01-22	**1,447**	**0.918**	**0.003**	**0.969**	**0.000**
Pictou Island 2021-01-16	2,792	0.560	0.061	0.858	0.002
Pictou Island2021-01-21	3,452	0.743	0.064	0.921	0.001
Pictou Island 2021-01-23	**3,604**	**0.804**	**0.055**	**0.938**	**0.001**
Saddle Island 2021-01-13	1,750	0.636	0.018	0.823	0.003
Saddle Island 2021-01-16	2,530	0.736	0.019	0.889	0.002
Saddle Island 2021-01-19	2,873	0.814	0.016	0.933	0.001
Saddle Island 2021-01-23	**3,155**	**0.889**	**0.011**	**0.966**	**0.000**
Hay Island 2021-01-11	1,619	0.821	0.023	0.949	0.001
Hay Island 2021-01-11	1,614	0.821	0.023	0.949	0.001
Hay Island 2021-01-13	**1,705**	**0.855**	**0.019**	**0.966**	**0.000**
Hay Island 2021-01-16	1,702	0.895	0.013	0.982	0.000
Hay Island 2021-01-22	1,637	0.946	0.006	0.995	0.000
Mud, Noddy, Round, Flat Islands 2021-01-16	**1,456**	**0.972**	**0.006**	**0.991**	**0.000**
Mud, Noddy, Round, Flat Islands 2021-01-16	**184**	**0.972**	**0.006**	**0.991**	**0.000**
Mud, Noddy, Round, Flat Islands 2021-01-16	**560**	**0.972**	**0.006**	**0.991**	**0.000**
Mud, Noddy, Round, Flat Islands 2021-01-16	**46**	**0.972**	**0.006**	**0.991**	**0.000**
Scatarie Island 2021-01-13	70	0.855	0.019	0.966	0.000
Scatarie Island 2021-01-16	107	0.895	0.013	0.982	0.000
Scatarie Island 2021-01-22	**121**	**0.946**	**0.006**	**0.995**	**0.000**

Table 4a. Estimated dates in the 2021 breeding season when between 1% and 95% of pups had weaned at colonies located along the coast of Nova Scotia and on the Scotian Shelf. Animals were considered weaned 20 days after birth. The 95% credible intervals are also shown.

Scotian Shelf

Proportion weaned (%)	Sable Island date (95% CI)
1	Dec. 30 (Dec. 27–Jan. 1)
15	Jan. 4 (Dec. 31–Jan. 7)
25	Jan. 6 (Jan. 2–8)
35	Jan. 7 (Jan. 4–10)
45	Jan. 9 (Jan. 5–12)
50	Jan. 10 (Jan. 6–12)
55	Jan. 10 (Jan. 7–13)
65	Jan. 12 (Jan. 9–15)
75	Jan. 14 (Jan. 11–17)
85	Jan. 17 (Jan. 14–20)
95	Jan. 23 (Jan. 20–26)

Coastal Nova Scotia

Proportion weaned (%)	Mud, Round, Noddy Flat Islands date (95% CI)	Hay Island date (95% CI)
1	Dec. 29 (Dec. 26–Jan. 1)	Jan. 6 (Jan. 3–10)
15	Jan. 1 (Dec. 28–Jan. 4)	Jan. 11 (Jan. 6–14)
25	Jan. 2 (Dec. 30–Jan. 6)	Jan. 12 (Jan. 8–16)
35	Jan. 4 (Dec. 31–Jan. 7)	Jan. 14 (Jan. 9–18)
45	Jan. 5 (Jan. 1–9)	Jan. 15 (Jan. 11–19)
50	Jan. 6 (Jan. 2–10)	Jan. 16 (Jan. 12–20)
55	Jan. 7 (Jan. 3–11)	Jan. 17 (Jan. 13–21)
65	Jan. 9 (Jan. 5–13)	Jan. 19 (Jan. 15–22)
75	Jan. 12 (Jan. 8–16)	Jan. 21 (Jan. 17–25)
85	Jan. 16 (Jan. 11–21)	Jan. 24 (Jan. 20–28)
95	Jan. 24 (Jan. 19–30)	Jan. 30 (Jan. 26–Feb. 04)

Table 4b. Estimated dates in the 2021 breeding season when between 1% and 95% of pups had weaned at colonies located in the Gulf of St. Lawrence. Animals were considered weaned 20 days after birth. The 95% credible intervals are also shown.

Proportion weaned (%)	Brion Island date (95% CI)	Henry Island date (95% CI)	Pictou Island date (95% CI)	Saddle Island date (95% CI)
1	Jan. 9 (Jan. 6–12)	Jan. 11 (Jan. 7–15)	Jan. 9 (Jan. 5–12)	Jan. 13 (Jan. 10–17)
15	Jan. 12 (Jan. 9–16)	Jan. 15 (Jan. 10–19)	Jan. 15 (Jan. 10–19)	Jan. 18 (Jan. 14–21)
25	Jan. 14 (Jan. 11–17)	Jan. 16 (Jan. 12–21)	Jan. 18 (Jan. 13–22)	Jan. 20 (Jan. 16–24)
35	Jan. 15 (Jan. 12–19)	Jan. 18 (Jan. 13–23)	Jan. 20 (Jan. 15–24)	Jan. 22 (Jan. 18–25)
45	Jan. 17 (Jan. 13–20)	Jan. 20 (Jan. 15–25)	Jan. 22 (Jan. 17–27)	Jan. 23 (Jan. 19–27)
50	Jan. 18 (Jan. 14–21)	Jan. 21 (Jan. 16–26)	Jan. 24 (Jan. 18–28)	Jan. 24 (Jan. 20–28)
55	Jan. 18 (Jan. 15–22)	Jan. 22 (Jan. 17–27)	Jan. 25 (Jan. 19–29)	Jan. 25 (Jan. 21–29)
65	Jan. 20 (Jan. 17–24)	Jan. 24 (Jan. 19–29)	Jan. 28 (Jan. 22–1 Feb.)	Jan. 27 (Jan. 23–31)
75	Jan. 23 (Jan. 19–26)	Jan. 27 (Jan. 22–Feb. 1)	Jan. 31 (Jan. 26–5 Feb.)	Jan. 30 (Jan. 26–2 Feb.)
85	Jan. 26 (Jan. 23–29)	Jan. 30 (Jan. 26–Feb. 5)	Feb. 5 (Jan. 30–9 Feb.)	Feb. 2 (Jan. 29–6 Feb.)
95	Feb. 2 (Jan. 30–Feb. 6)	Feb. 7 (Feb. 2–12)	Feb. 13 (Feb. 8–19)	Feb. 8 (Feb. 4–13)

FIGURES

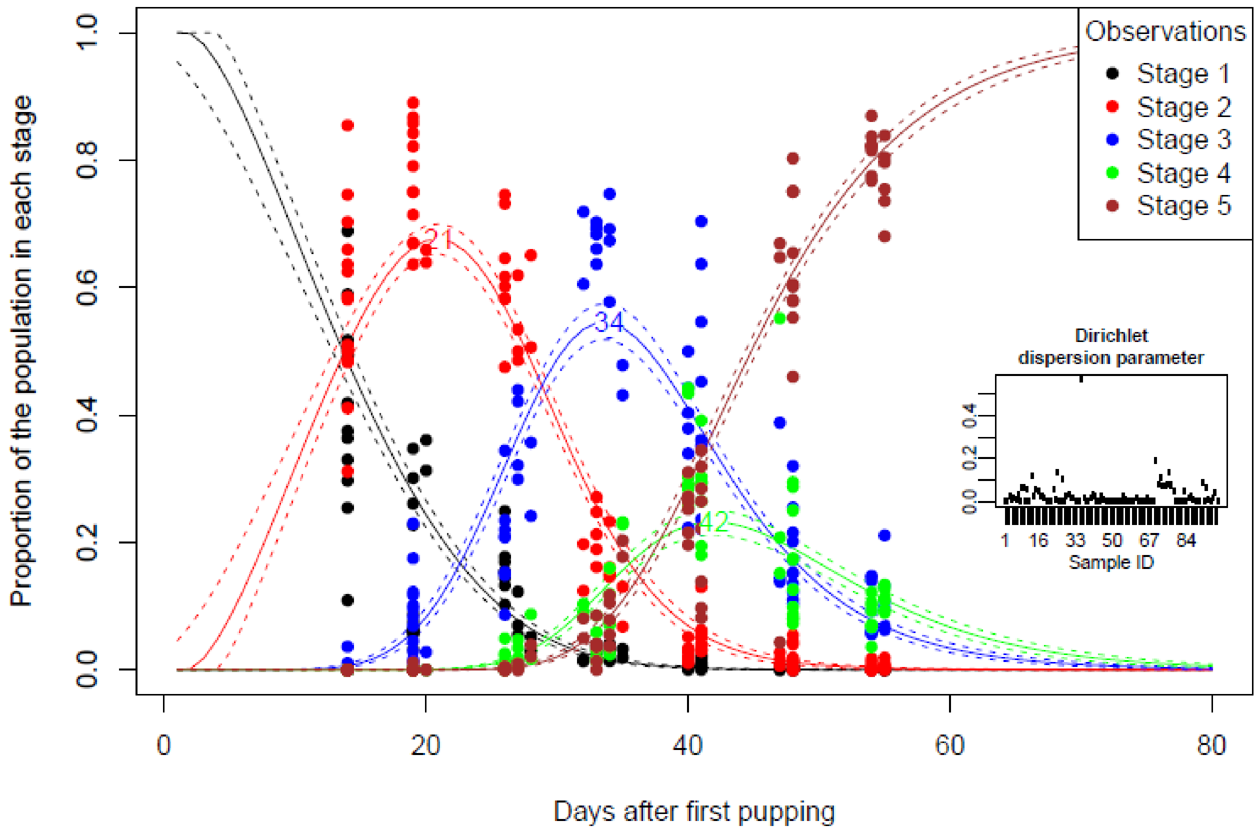


Figure 1a. Output of the Bayesian birth distribution model showing the estimated proportion of grey seal pups in the five development stages over time (black, red, blue, green, brown representing stages 1 to 5, respectively) after fitting to the 2021 Sable Island stage survey data. Plain lines and dotted lines represent the median value and the 95% CI, respectively. Coloured dots show the observed proportions in their corresponding stages over time. An inset graphic shows the inverse of the weighting parameter value controlling the variation among deviates obtained from the Dirichlet distribution for each sample (i.e., $1/w_{d_x}$, larger values suggest more noise in the data, see Eq. 3).

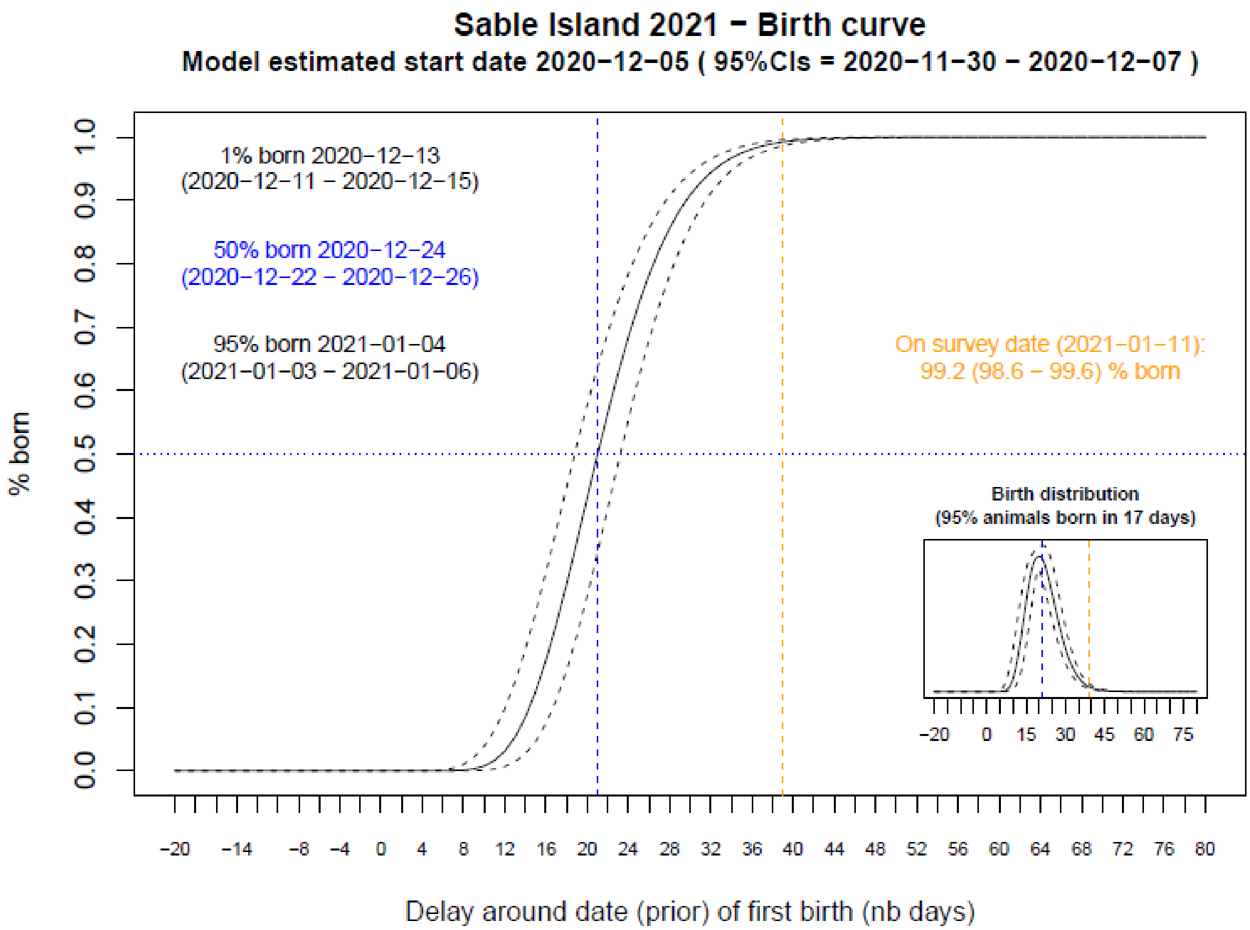


Figure 1b. The predicted birth curve of grey seal pups on Sable Island in 2021 from the Bayesian birth distribution model fitted to the stage survey data. The black plain line and dotted lines correspond respectively to the median and the 95% credible interval of the predicted proportion of pups born depending on delay (in days) around the prior date of first birth. Note that time 0 corresponds to the date provided to the model (i.e., the "guesstimate") but that the model can change it if needed (see Model description in methods). Here, the prior date was Dec. 3 but the model suggested (as indicated in the graph title) that Dec. 5 allowed a better fit to the data. The predicted dates at which 1%, 50% and 95% of the births occurred are indicated (with 95%CIs). The proportion of pups born (and 95% CIs) on survey date is also shown. The inset shows the birth curve as a density function for the indicated period encompassing 95% of the births. Vertical blue and yellow lines indicate the date at which 50% of the births were predicted to occur and the survey date, respectively.

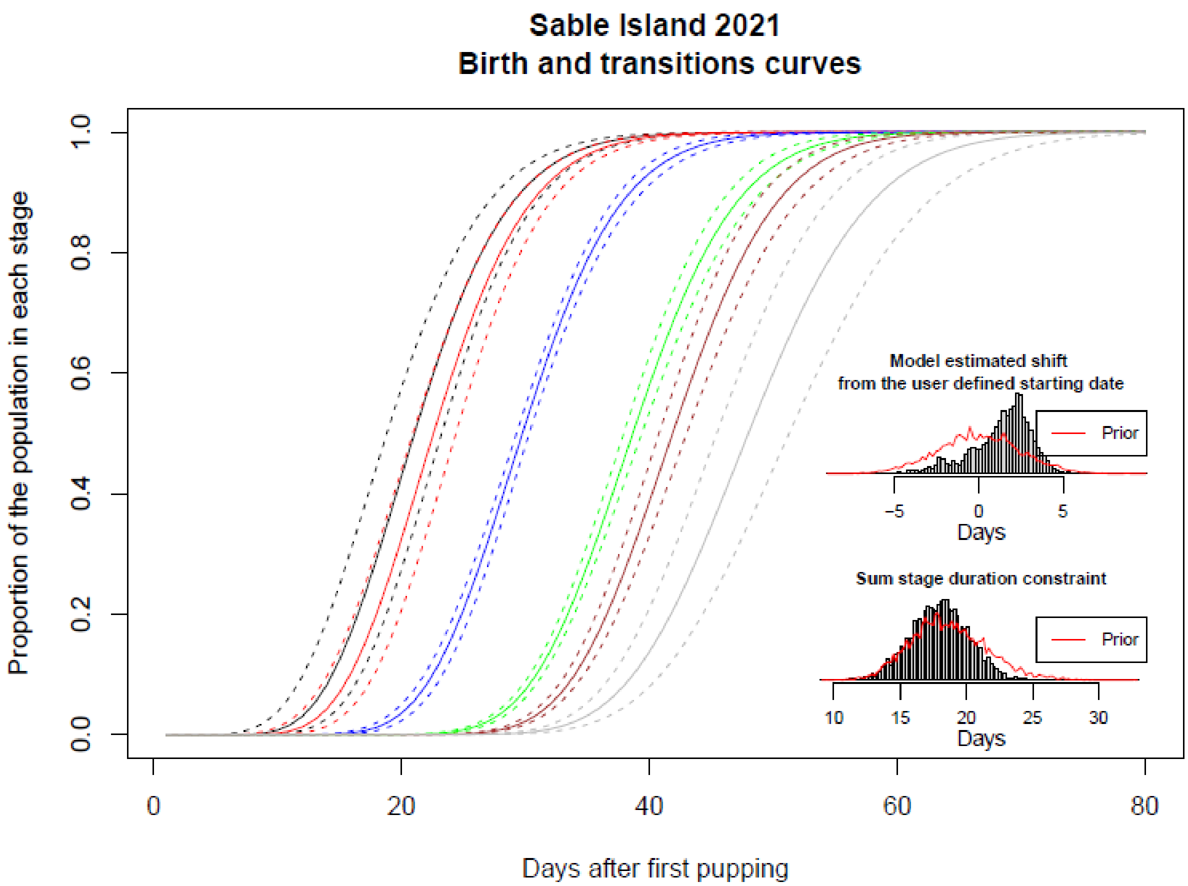


Figure 1c. Output of the Bayesian staging model showing the estimated birth and transition curves among the five development stages over time (black, red, blue, green, brown representing stages 1 to 5, respectively) after fitting to the 2021 Sable Island staging data. A 6th curve (grey) represents the estimated proportion of animals that left the colony. Plain lines and dotted lines represent the median value and the 95%CI, respectively. Two inset graphs show the prior (red line) and the posterior (bar chart) distributions of (1) Upper graph: the potential shift of the date around the prior date provided to the model (i.e., the guesstimate"), (2) Lower graph: the sum of the duration of the stages 1 to 3.

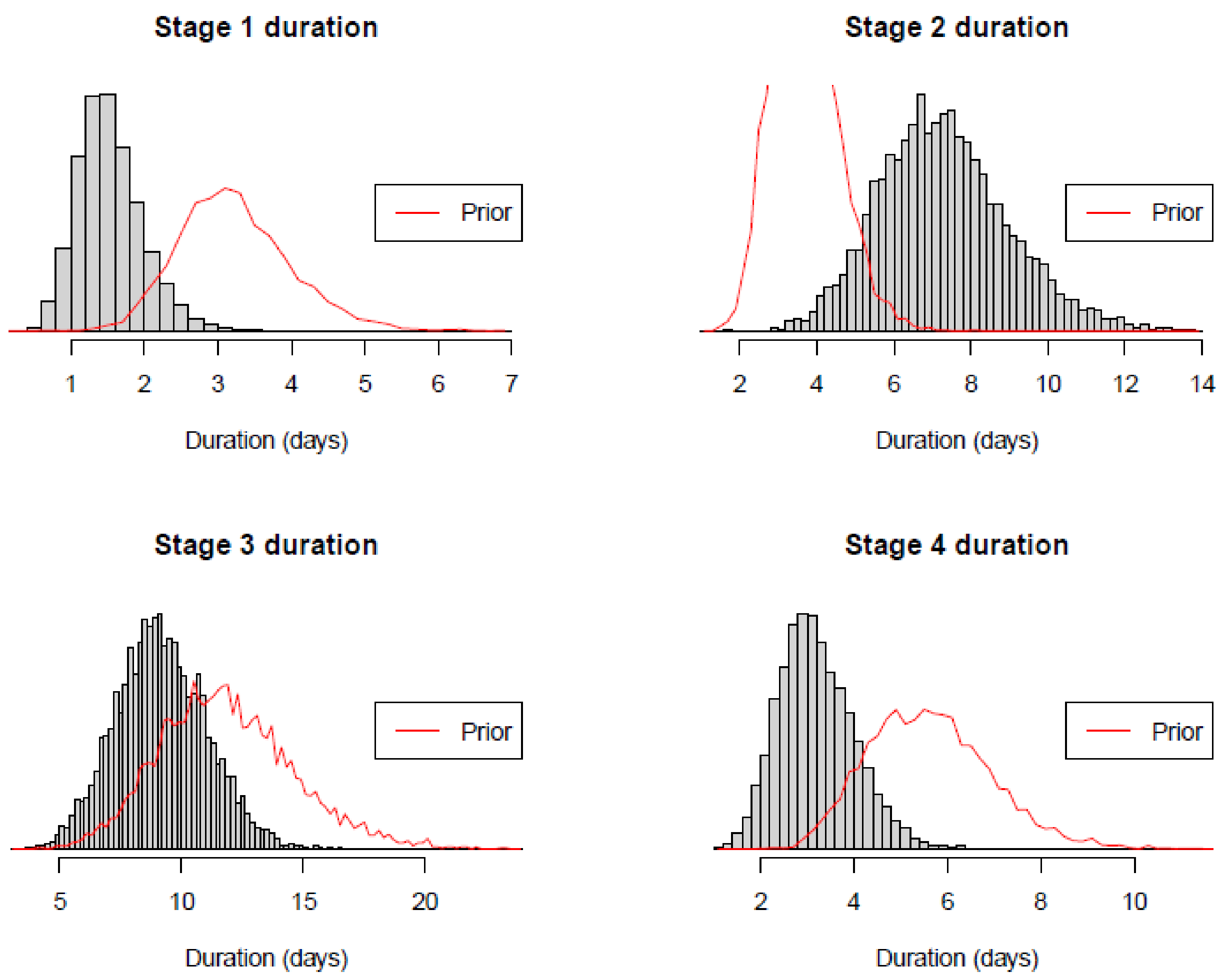


Figure 1d. Output of the Bayesian staging model showing the priors (red lines) and the posteriors (bar charts) of the distributions representing the duration of the development stages 1 to 4 after fitting to the 2021 Sable Island staging data.

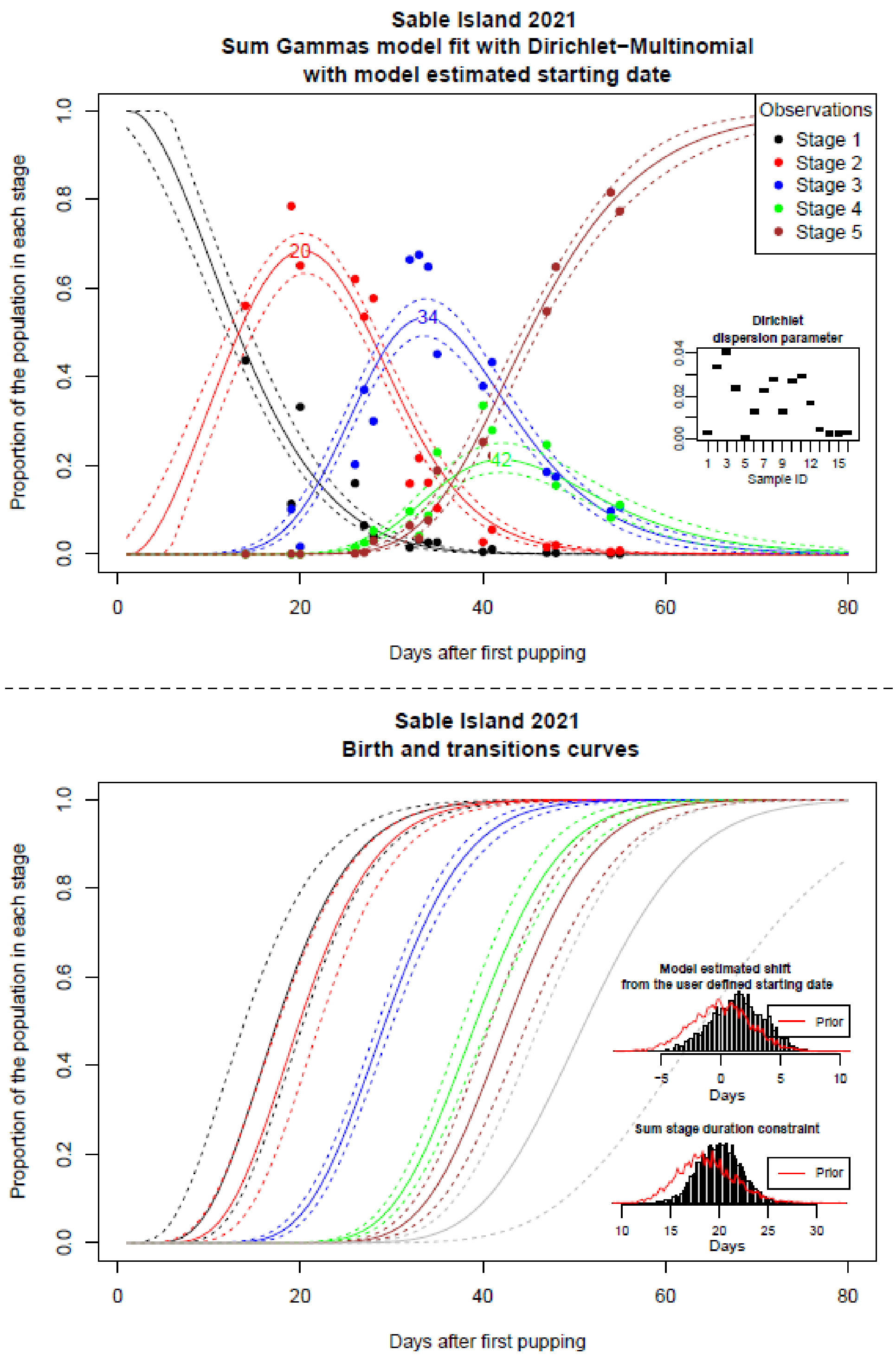


Figure 2a. Output of the Bayesian staging model based on the daily aggregated staging data collected on Sable Island during winter 2020–2021. Part 1/2.

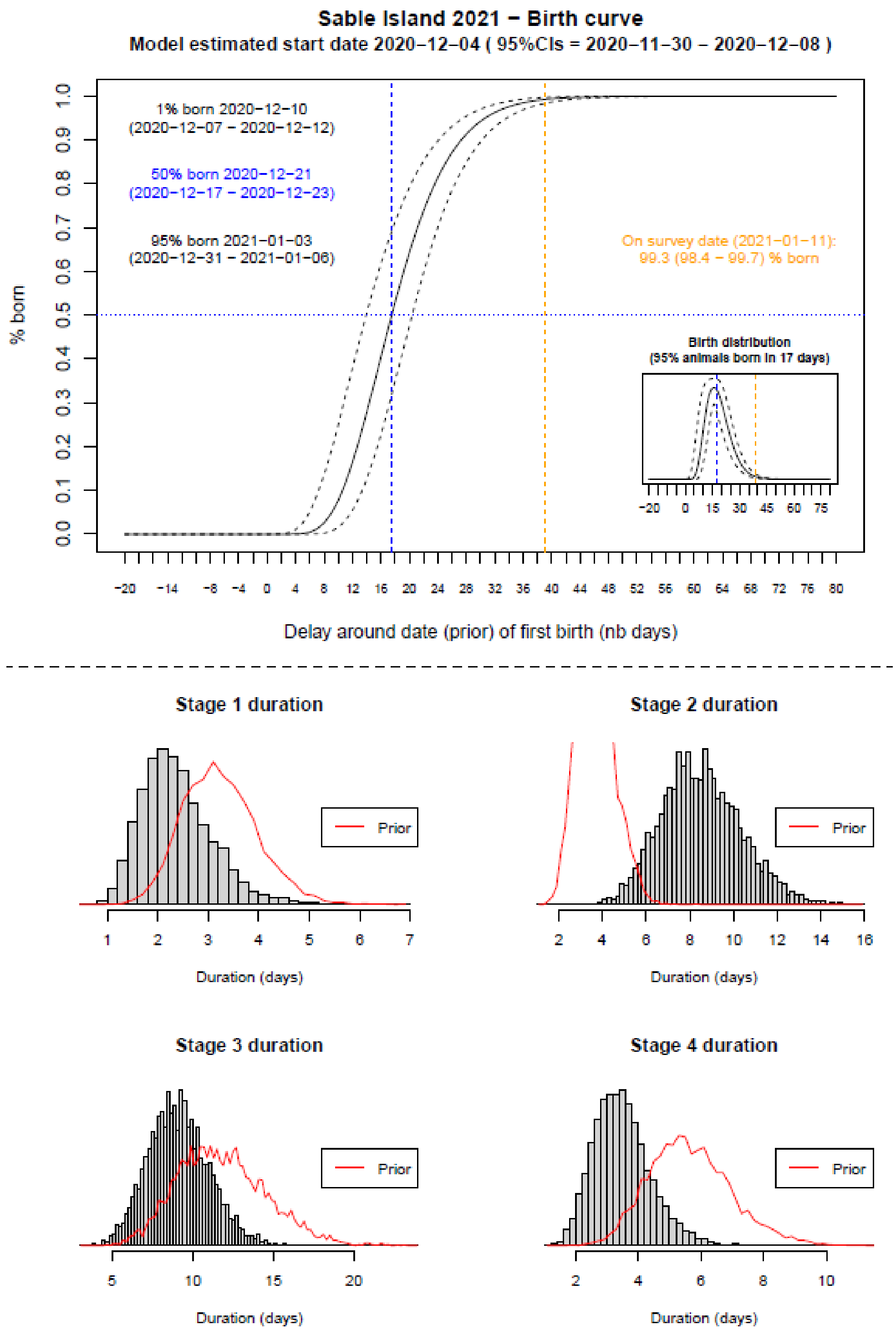


Figure 2b. Output of the Bayesian staging model based on the daily aggregated staging data collected on Sable Island during winter 2020–2021. Part 2/2.

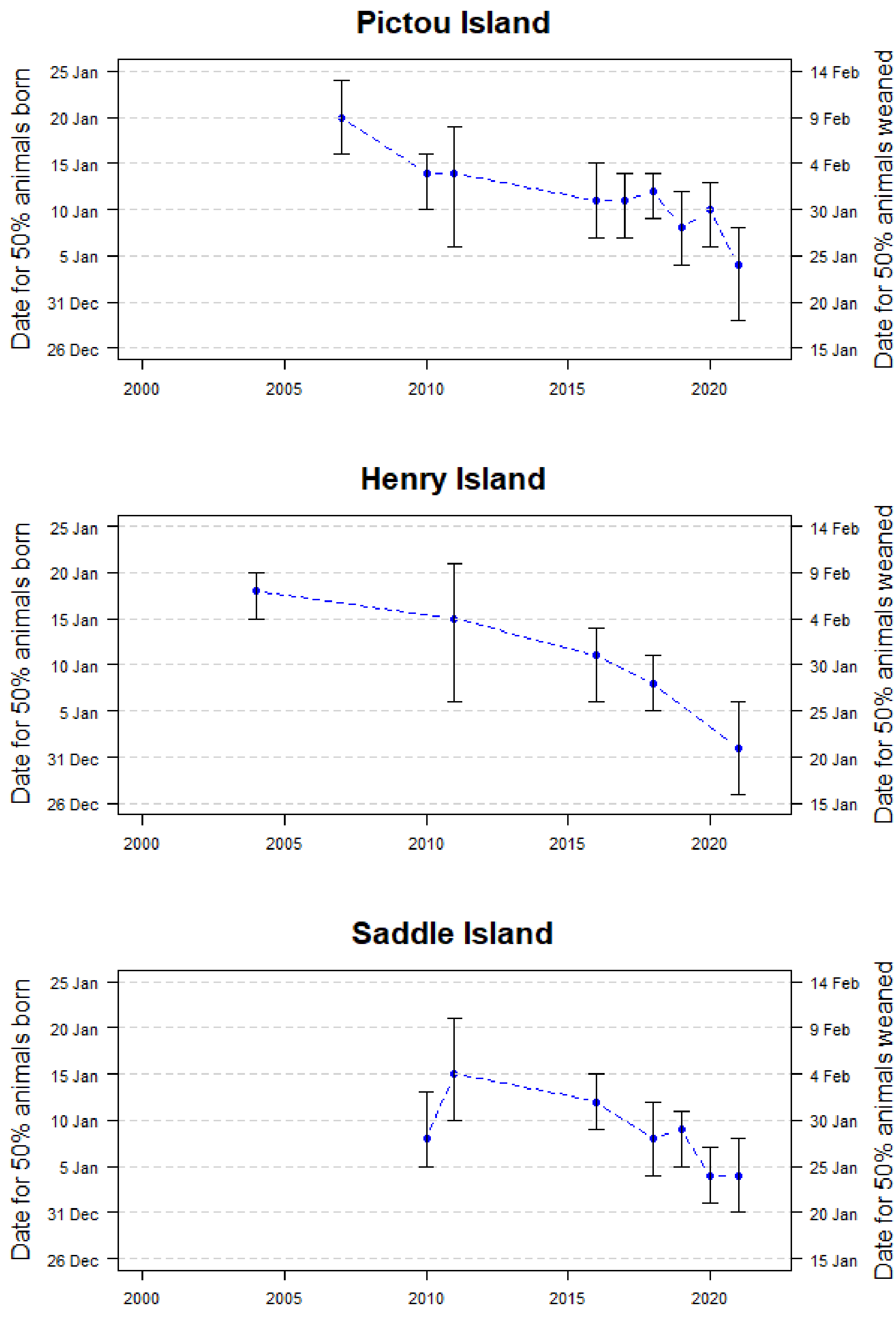
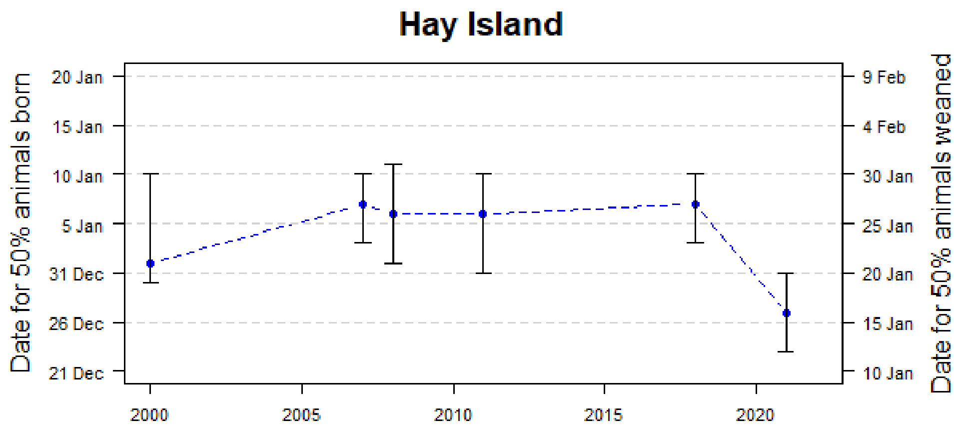


Figure 3a. Estimated dates when 50% of pups were born (left axis) and 50% of pups were weaned (right axis) for three colonies in the Gulf of St. Lawrence (Pictou Island, Saddle Island and Henry Island). Animals were considered weaned 20 days after birth. Also shown are the 95% credible intervals.



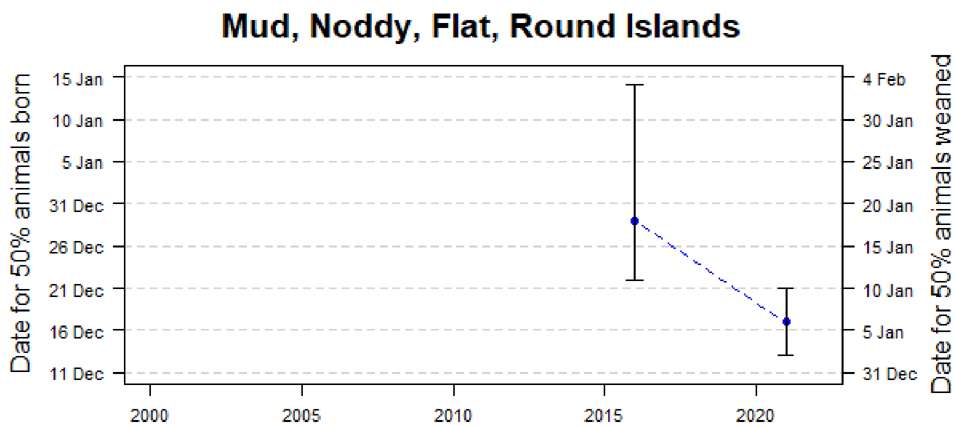


Figure 3b. Estimated dates when 50% of pups were born (left axis) and 50% of pups were weaned (right axis) for southern Nova Scotia Islands (Mud, Noddy, Flat and Round Islands) and Hay Island (northeast Cape Breton). Animals were considered weaned 20 days after birth. Also shown are the 95% credible intervals.

APPENDICES

Appendix 1. Description of the 5 development stages of grey seals pups

Stage 1: animals very thin, movements uncoordinated, and the fur has a yellowish hue from the placental fluids.

Stage 2: animals are thin, although they are beginning to show signs of fattening; a distinct neck is still visible; movements are more coordinated and the pelage no longer has a yellowish hue.

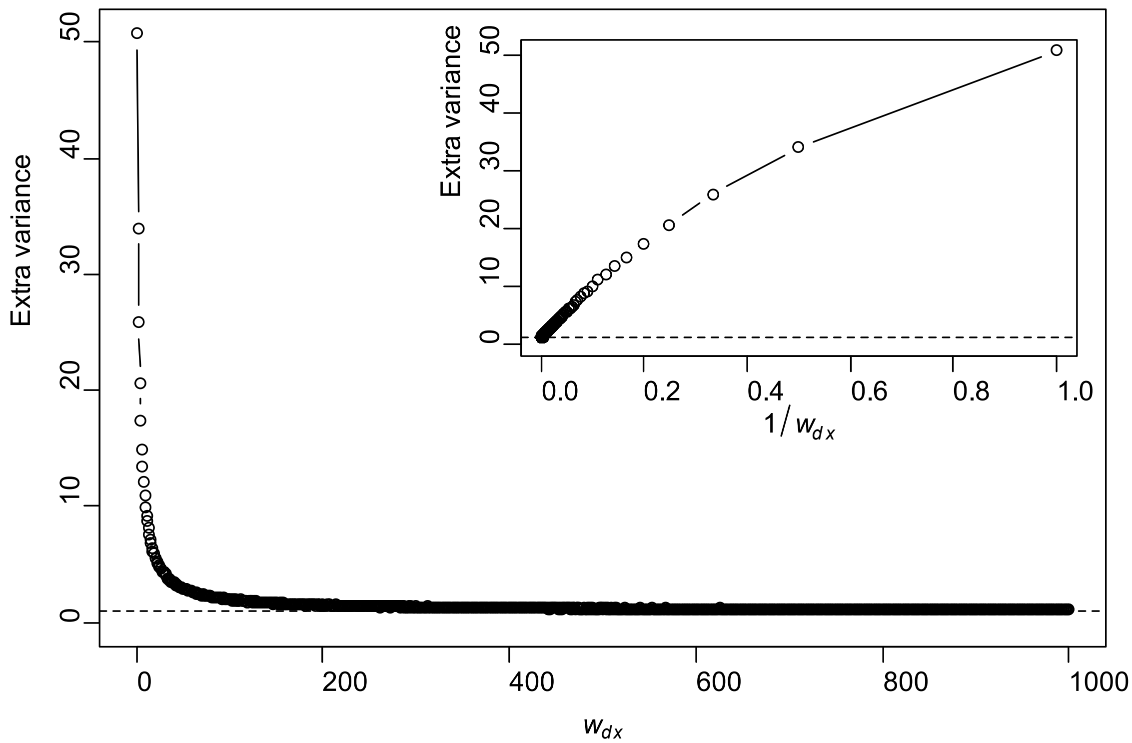
Stage 3: the fur is white in colour and the animals have become so fat that a distinct neck is no longer discernable; no sign of moult.

Stage 4: the fur has become discoloured, assuming a grey tinge, and lanugo is lost, beginning around the head and flippers. When the amount of fur loss exceeds approximately the equivalent of 1 hand on the back, or has progressed beyond the head, the animal is considered a stage 4.

Stage 5: the final stage, all lanugo has been lost. Animals begin leaving the colony during this stage.

Appendix 2. Estimates of stage durations, assuming gamma distributions with common shape parameter across stages, from daily records of Sable Island pups followed from birth to stage 5 in 1997 (n = 47), 2007 (n = 52), 2010 (n = 54), and 2021 (n = 47) fitted individually and combined.

Year	Stage	Shape	Rate	Mean	Variance
2021	1	12.86291	4.341684	3.0	0.7
2021	2	12.86291	2.891907	4.4	1.5
2021	3	12.86291	1.313669	9.8	7.5
2021	4	12.86291	1.115495	11.5	10.3
2010	1	21.48996	7.683241	2.8	0.4
2010	2	21.48996	5.482523	3.9	0.7
2010	3	21.48996	1.64196	13.1	8.0
2010	4	21.48996	4.748541	4.5	1.0
2007	1	25.1543	8.494021	3.0	0.3
2007	2	25.1543	8.267426	3.0	0.4
2007	3	25.1543	2.111281	11.9	5.6
2007	4	25.1543	4.764856	5.3	1.1
1997	1	21.19984	5.4541	3.9	0.7
1997	2	21.19984	5.265707	4.0	0.8
1997	3	21.19984	2.016769	10.5	5.2
1997	4	21.19984	3.00928	7.0	2.3
1997_2010	1	18.77814	5.823208	3.2	0.6
1997_2010	2	18.77814	5.120926	3.7	0.7
1997_2010	3	18.77814	1.592576	11.8	7.4
1997_2010	4	18.77814	3.329191	5.6	1.7
All	1	16.93842	5.35995	3.2	0.6
All	2	16.93842	4.40333	3.8	0.9
All	3	16.93842	1.495801	11.3	7.6
All	4	16.93842	2.631148	6.4	2.4



Appendix 3. Effect of the weighting parameter (w_{d_x}) value on the extra variance obtained from the Dirichlet distribution. Simulations assumed a population of 100 animals distributed into 5 classes. The extra variance was calculated as the ratio between the variance obtained from the Dirichlet distribution and the variance obtained from the Multinomial distribution. The variance obtained from the Dirichlet was evaluated for a range of w_{d_x} values comprised between 1 and 1,000. Results are presented as Extra variance versus w_{d_x}, but also, in the inset, as Extra variance versus $1/w_{d_x}$ because this value is used in some graphs showing the results of the staging model (e.g., Figure 1a). The dotted line represents a ratio of 1 (i.e., no extra variance).

Appendix 4. Staging data from Sable Island based on transect ground surveys conducted in winter 2021–2022.

Date	Transect	Stage 1	Stage 2	Stage 3	Stage 4	Stage 5	Total
2020-12-17	1	39	55	0	0	0	94
2020-12-17	2	54	56	0	0	0	110
2020-12-17	3	89	83	0	0	0	172
2020-12-17	4	89	62	0	0	0	151
2020-12-17	5	30	71	0	0	0	101
2020-12-17	6	31	62	1	0	0	94
2020-12-17	7	56	53	0	0	0	109
2020-12-17	8	48	80	0	0	0	128
2020-12-17	9	20	35	0	0	0	55
2020-12-17	10	15	44	0	0	0	59
2020-12-17	11	18	25	0	0	0	43
2020-12-17	12	42	19	0	0	0	61
2020-12-17	13	11	11	0	0	0	22
2020-12-17	14	6	47	2	0	0	55
2020-12-22	1	6	163	19	0	0	188
2020-12-22	2	10	145	14	0	0	169
2020-12-22	3	13	175	25	0	0	213
2020-12-22	4	11	140	45	0	0	196
2020-12-22	5	12	120	28	0	0	160
2020-12-22	6	9	123	14	0	0	146
2020-12-22	7	13	178	9	0	0	200
2020-12-22	8	15	136	21	0	0	172
2020-12-22	9	31	69	3	0	0	103
2020-12-22	10	30	77	8	0	0	115
2020-12-22	11	42	77	2	0	0	121
2020-12-22	12	20	66	1	0	1	88
2020-12-23	13	44	78	0	0	0	122
2020-12-23	14	56	118	5	0	0	179
2020-12-29	7	39	161	19	1	0	220
2020-12-29	8	34	105	76	5	1	221
2020-12-29	9	55	133	33	0	0	221
2020-12-29	10	38	154	58	13	1	264
2020-12-29	11	30	146	47	3	0	226
2020-12-29	12	42	153	52	1	0	248
2020-12-29	13	22	161	33	0	0	216
2020-12-29	14	42	159	64	7	1	273
2020-12-30	1	15	105	91	4	1	216
2020-12-30	2	12	135	70	1	0	218
2020-12-30	3	3	107	94	10	0	214
2020-12-30	6	25	109	61	7	2	204
2020-12-31	4	12	151	56	4	9	232
2020-12-31	5	7	122	86	21	5	241
2021-01-04	7	4	30	174	22	12	242
2021-01-04	8	3	44	135	23	18	223
2021-01-05	10	7	36	142	19	19	223
2021-01-05	11	8	54	149	4	3	218
2021-01-05	12	6	47	146	13	9	221
2021-01-05	13	5	61	156	3	0	225

Date	Transect	Stage 1	Stage 2	Stage 3	Stage 4	Stage 5	Total
2021-01-05	14	9	42	156	7	8	222
2021-01-06	1	6	25	123	34	25	213
2021-01-06	2	3	51	116	26	23	219
2021-01-06	5	8	37	175	19	14	253
2021-01-06	6	4	39	163	17	19	242
2021-01-06	9	10	37	183	6	9	245
2021-01-07	3	4	14	99	48	42	207
2021-01-07	4	9	36	119	63	49	276
2021-01-12	1	1	5	54	107	75	242
2021-01-12	2	0	3	90	115	57	265
2021-01-12	5	1	3	102	58	40	204
2021-01-12	6	2	8	124	72	74	280
2021-01-12	7	2	8	96	72	60	238
2021-01-12	8	2	14	103	79	74	272
2021-01-13	3	1	11	61	108	95	276
2021-01-13	4	3	33	60	77	81	254
2021-01-13	9	4	8	130	63	33	238
2021-01-13	10	0	7	104	68	51	230
2021-01-13	11	1	7	164	42	19	233
2021-01-13	12	2	15	84	70	68	239
2021-01-13	13	5	12	151	46	23	237
2021-01-13	14	5	12	75	61	55	208
2021-01-19	6	2	7	37	39	172	257
2021-01-19	7	0	2	38	57	178	275
2021-01-19	8	0	2	45	64	5	116
2021-01-20	1	0	1	38	16	166	221
2021-01-20	2	0	0	24	19	175	218
2021-01-20	3	1	3	33	24	183	244
2021-01-20	4	3	13	48	30	144	238
2021-01-20	5	0	3	28	66	133	230
2021-01-20	9	0	0	24	68	139	231
2021-01-20	10	0	4	36	59	137	236
2021-01-20	11	1	3	53	36	115	208
2021-01-20	12	0	5	40	21	199	265
2021-01-20	13	1	8	64	35	92	200
2021-01-20	14	1	11	53	20	161	246
2021-01-26	1	0	0	11	24	162	197
2021-01-26	2	0	3	13	24	187	227
2021-01-26	3	0	1	35	9	206	251
2021-01-26	4	0	4	33	15	172	224
2021-01-26	5	0	0	22	22	194	238
2021-01-26	6	0	0	14	16	200	230
2021-01-26	7	0	2	35	17	186	240
2021-01-26	8	0	0	14	23	190	227
2021-01-27	9	0	2	15	28	176	221
2021-01-27	10	0	1	25	31	175	232
2021-01-27	11	0	1	23	22	189	235
2021-01-27	12	0	2	14	20	187	223
2021-01-27	13	0	0	31	16	100	147
2021-01-27	14	0	4	28	24	156	212

Appendix 5. Staging data from Coastal Nova Scotia based on aerial surveys conducted in winter 2020–2021

Southwest Nova Scotia

Location and survey date	Stage 1	Stage 2	Stage 3	Stage 4	Stage 5	Total
Round Island 2020-12-20	11	51	7	0	0	69
Round Island 2021-01-09	2	18	123	15	41	199
Round Island 2021-01-13	0	6	31	25	93	155
Round Island 2021-01-27	0	0	2	6	90	98
Mud Island 2020-12-20	20	56	24	0	0	100
Mud Island 2021-01-09	13	27	356	11	29	436
Mud Island 2021-01-13	0	2	46	55	155	258
Mud Island 2021-01-27	0	2	19	16	275	312
Mud Island 2021-01-12	0	15	67	6	0	88
Mud Island 2021-01-19	0	4	41	28	10	83
Noddy Island 2021-01-09	4	27	15	4	13	63
Noddy Island 2021-01-13	0	13	21	15	13	62
Noddy Island 2021-01-27	0	1	1	1	59	62

Eastern Nova Scotia

Location and survey date	Stage 1	Stage 2	Stage 3	Stage 4	Stage 5	Total
Hay Island 2021-01-11	2	166	345	22	14	549
Hay Island 2021-01-16	3	138	409	150	112	812
Hay Island 2021-01-22	2	57	408	204	491	1,162
Hay Island 2021-02-09	0	0	35	27	263	325
Scatarie Island 2021-01-13	0	31	31	1	0	63
Scatarie Island 2021-01-16	1	24	35	3	1	64
Scatarie Island 2021-01-22	0	24	58	12	6	100
Scatarie Island 2021-02-09	0	2	11	6	26	45
Red Island 2021-01-13	0	17	18	1	0	36
Red Island 2021-01-16	0	11	40	2	1	54
Red Island 2021-01-22	2	5	45	7	4	63
Bowen's Ledge 2021-01-16	0	1	1	0	0	2
Basque Island 2021-01-13	0	8	0	0	0	8

Appendix 6. Staging data from the Gulf of St. Lawrence region based on aerial surveys conducted in winter 2020–2021.

Gulf Centre

Location and survey date	Stage 1	Stage 2	Stage 3	Stage 4	Stage 5	Total
Brion Island 2021-01-11	62	415	1,010	83	21	1,591
Brion Island 2021-01-15	30	467	1,249	203	93	2,042
Brion Island 2021-01-18	19	285	1,726	439	473	2,942
Brion Island 2021-01-20	8	151	1,054	345	431	1,989
Brion Island 2021-02-01	7	68	212	245	880	1,412
Deadman Island 2021-01-15	1	17	2	2	1	23

Gulf Southern Coast

Location and survey date	Stage 1	Stage 2	Stage 3	Stage 4	Stage 5	Total
Pictou Island 2021-01-05	43	450	13	1	0	507
Pictou Island 2021-01-12	29	650	232	1	0	912
Pictou Island 2021-01-19	58	681	643	46	14	1,442
Pictou Island 2021-01-21	39	1,314	1,338	141	61	2,893
Pictou Island 2021-01-23	52	393	923	224	68	1,660
Pictou Island 2021-02-01	22	530	821	242	377	1,992
Pictou Island 2021-02-09	1	66	468	184	523	1,242
Henry Island 2021-01-05	22	258	84	0	0	364
Henry Island 2021-01-13	17	379	232	6	1	635
Henry Island 2021-01-20	14	159	490	110	32	805
Henry Island 2021-01-22	1	191	665	148	123	1,128
Henry Island 2021-02-01	4	36	283	181	531	1,035
Henry Island 2021-02-09	0	6	85	34	303	428
Saddle Island 2021-01-05	54	202	2	0	0	258
Saddle Island 2021-01-12	36	453	360	4	0	853
Saddle Island 2021-01-19	42	535	899	54	23	1,553
Saddle Island 2021-01-23	31	318	508	95	58	1,010
Saddle Island 2021-01-29	0	154	818	216	326	1,514
Purdy Island 2021-01-19	4	58	54	3	0	119
Margaree Island 2021-01-13	0	10	2	0	0	12

Appendix 7. Estimated proportion of animals in stage 6 on the aerial survey date at the main grey seal colonies. Stage 6 represents the animals that moved to location where they are not available to be counted because they have left the site and entered the water, or they have left the pupping beach and moved to an area where they are not normally detected from the air, e.g., in a forest.

Location	Prop. born on date of survey (%)	Proportion Stage 6 (%)
Sable Island	99.3 (98.2–99.8)	5.5 (0.8–12.9)
Mud, Round, Noddy, and Flat Islands	99.1 (97.4–100)	11.1 (0–63.0)
Hay Island	94.9 (88.4–98.0)	1.1 (0.2–3.0)
Brion Island	95.5 (92.6–97.8)	0.3 (0–3.4)
Henry Island	96.7 (93.2–99.0)	0.1 (0–2.5)
Pictou Island	93.4 (87.6–96.9)	0.1 (0–1.4)
Saddle Island	96.6 (92.6–98.5)	0.1 (0–1.9)