Estimating Northern Fur Seal Pup Production: A case study of batch mark abundance estimation

Devin S. Johnson[1] Alaska Fisheries Science Center, NOAA Fisheries, Seattle, Washington, USA

Rodney G. Towell Alaska Fisheries Science Center, NOAA Fisheries, Seattle, Washington, USA

Jason B. Baker Pacific Islands Science Center, NOAA Fisheries, Honolulu, Hawaii, USA

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Abstract

We describe a hierarchical N-mixture model for estimating northern fur seal pup production from batch mark-resight data. Our goal was to improve upon a traditional design-based estimation method used for over 50 years. To this end, we propose a hierarchical N-mixture model to account for differences in animal availability for resighting and observer detection probabilities. A Bayesian approach is used for inference with three separate methods proposed for necessary computations. First a straightforward posterior sample is drawn using MCMC. This was considered the gold standard for this analysis. However, we also consider an approximate model based on Gaussian approximation of the Poisson and binomial distributions used in the exact hierarchical model. By using the Gaussian approximations, analytic integration can be used to marginalize over latent components. Inference can then be made by maximizing the posterior to find the mode. Following this we investigate both delta-method and parametric bootstrap approaches for calculating abundance and the associated standard errors. Each of the three methods produced nearly identical estimates and standard errors, providing support for using Gaussian approximations in other latent abundance models where the abundance is relatively large.

[1]Corresponding author: devin.johnson@noaa.gov

Introduction

Estimation of pup production has been the cornerstone for population and management decisions for the Pribilof Islands herd of northern fur seals (*Callorhinus ursinus*; NFS) for over 50 years. The design-based method of estimating production has remained largely unchanged since the late 1960s. Here we consider a modern hierarchical modeling approach for abundance estimation that allows for day-to-day differences in the proportion of pups that are available to be counted, as well as different rates of detection among observers. Although we do not make use of it here, the model-based version allows for use of covariates might be helpful in the future for modeling differences in parameters like detection probabilities or allow for addition of prior information on the proportion of animals that are marked. Although this method was designed and applied to NFS pup abundance, it is a general mark-resight modelling approach that could be used for many other species.

Since the mid-1960s, estimation of NFS pup production in the Pribilof, Is., Alaska has been accomplished using a design-based mark-resight method where pups are batch marked and resighted on at least 2 later dates. Chapman and Johnson (1968), York and Towell (1996), and Towell et al. (2016) provide detailed descriptions of the marking, resight, and current production estimation methods. In the first half of August, pups are batch marked by shearing the guard hairs on top of the head to make the light underfur conspicuous to observers. The light colored underfur represents the mark. The goal of shearing is to mark approximately 10% of the pups on each rookery. The 10% is based on the previous estimate of pup production for the sample rookeries (typically 2 years prior). Shear marks are allocated proportionally on each rookery by section according to the fraction of the total number of breeding males counted in each section. Thus, the marks are spatially allocated to roughly match spatial abundance of pups. Marked and unmarked pups on each rookery are counted by two observers scanning (with the aid of binoculars when necessary) on at least two occasions.

Here we briefly describe the current design-based method of estimation. It is based on the cluster sampling method outlined by Chapman and Johnson (1968), however, the cluster

groups are kept fixed at 25 pups, therefore the estimator formulas can be reduced to those below. In the current method, each resight day is considered an independent replicate. For each replicate $j = 1, 2$, a mark-frequency estimate is calculated, $\hat{f}_j$ (total marks counted / total pups observed), the frequency of marked pups to total pups counted on the jth occasion. From this frequency estimate the occasion specific estimate of the number of pups alive at the time of shearing is estimated as,

$$\hat{A}_j = M/\hat{f}_j.$$

where M is the total number of pups marked. Note that this occasion specific estimate is identical to the classic Lincoln-Petersen estimator (Lincoln 1930). However, the sampling procedure is different with pups often being counted twice by the two different observers, thus, a different standard error (SE) method is used. The full estimate is calculated by $\hat{A} = mean(\hat{A}_j)$. The standard error of this estimate can be estimated using the fact that $var(\bar{x}) = var(x)/n$. Thus, for 2 resight occasions, this becomes

$$SE(\hat{A}) = |\hat{A}_1 - \hat{A}_2|/2.$$

Because the $SE(\hat{A})$ is based on only two replicated samples the estimate can become unstable, often producing estimates that are unreasonably small. See the Results section for example.

In addition to mark-resight methods that are applied to live pups, dead pups are counted on a sample of rookeries. Each sampled rookery is completely examined and the number of dead pups are recorded. For these sampled rookeries, the number of dead pups is added to obtain the pup production estimate $\hat{N} = \hat{A} + D$. For those rookeries $SE(\hat{N}) = SE(\hat{A})$. However, for rookeries without dead pup samples, $\hat{N} = \hat{A} + \hat{D}$ where the number of dead pups is estimated using a ratio estimate (Cochran 1977) based on the number of dead pups on sampled rookeries relative to the number of territorial bulls previously counted on the rookery. York and Kozloff (1987) describe the ratio estimation procedure. The $SE(\hat{N})$ for

these rookeries is then calculated as

$$SE(\hat{N}) = \sqrt{var(\hat{A}) + var(\hat{D})}$$

In this paper we propose an updated, model-based, methodology for analyzing the same batch mark data that is currently collected. The model-based approach is similar in spirit to the open N-mixture batch sampling models of Cowen et al. (2017) but we consider the populations to be closed over the study, however, different proportions of the population are unavailable for sampling in each resight occasion. Thus, abundance does not follow the open population models of Dail and Madsen (2011), but rather in each resight occasion animals have a probability of not being detectable at all. This may occur if they are in the water or out of site from sampling positions. In addition to availability, the model-based approach also allows explicit modeling of different detection rates between observers. Finally, with the model based approach we can directly model neonate mortality simultaneously with the mark-resight data without the need to use the additional bull count data to separately estimate dead pup numbers. Although we do not explore it here, by explicitly modeling neonate mortality we also introduce the possibility of modeling this parameter with environmental covariates that may be useful in determining what conditions lead to increased (or decreased) neonate mortality.

We begin development in the following section describing the model pieces in a hierarchical version of an N-mixture model (Royle 2004) that accounts for differential availability of animals during each resight occasion. Next, we propose two different methods of Bayesian estimation for abundance and model parameters. The first is a straightforward implementation in the Markov chain Monte Carlo (MCMC) software `JAGS` (Hornik, Leisch, and Zeileis 2003). In the second approach we consider an asymptotic approximation similar to Brintz, Fuentes, and Madsen (2018) where the latent discrete components of the model are treated as continuous valued and modeled with a multivariate normal distribution (Normal). This is motivated by the fact that the unknown abundance is large and little is lost empirically but much is gained analytically by this approximation. The unobserved discrete components can be marginalized out of the model to improve numerical procedures

of estimation. In addition, one can also use automatic differentiation based software such as `stan` (Gelman, Lee, and Guo 2015) and Template Model Builder (`TMB`; Kristensen et al. 2016) which cannot fit models with discrete latent components directly. Both of these approaches are used to fit data collected in 2016 by the National Marine Fisheries Service as part of the biannual monitoring survey of Pribilof NFS pup production.

Methods

Pup production, N, is defined as the combined total of the number of pups alive at the time of the marking study, A, as well as, the number of pups that have died before marking, D. The notation for the descriptions in this section are summarized in Table 1 for further reference. Notably, i indexes a rookery (or site), j indexes a resight occasion, and k indexes an observer. The number of pups batch marked at each rookery is M_i, the unobserved total number of unmarked pups is U_i, and the number of pups that died before the survey is D_i, thus, pup production is $N_i = M_i + U_i + D_i$. For all rookeries M_i is known and for *some* rookeries D_i is observed via dead pup counts that take place after the resighting occasions. While this likely does not represent the full number of dead pups it helps to account for neonatal death in the final estimate (it is usually on the order of 2–5% of N). The number of marked and unmarked pups counted by the kth observer on the jth occasion is m_{ijk} and u_{ijk} respectively.

A hierarchical N-mixture approach

The model-based approach we develop here seeks to improve on the design-based method of the last section by accounting for variability in the detection process, as well as, differing availability of animals to be observed between resighting occasions. This latent availability induces positive correlation between observers on any single occasion.

Table 1: Glossary of terms for the mark-resighting of northern fur seals.

Notation	Description
i	Rookery (site) index ($i = 1, \ldots, I$)
j	Resight occassion index ($j = 1, \ldots, J$)
k	Observer within occasion index ($k = 1, \ldots, K$)
N_i	Total pup production ($N_i = M_i + U_i + D_i$)
D_i	Number of pups that died before marking
M_i	Number of pups batched marked
U_i	Number of pups that are unmarked
A_i	Number of pups alive at marking ($A_i = M_i + U_i$)
M_{ij}	The number of marked pups available for resight on jth occassion
U_{ij}	The number of unmarked pups available for resight on jth occasion
m_{ijk}	Number of marked pups counted on resight effort j by the kth observer
u_{ijk}	Number of unmarked pups counted on resight effort j by the kth observer
ξ_i	Probability that a pup dies before batch marking
τ_i	Probability that a pup is marked given it is alive when marking occurs
α_{ij}	Probability that a pup can be observed at a resight occasion by an observer (*e.g.*, not in the water or hidden from view)
δ_{ijk}	Probability that a visible pup is counted at a rookery by an observer

The top level of the hierarchical model begins with the usual N-mixture model choice of

$$[N_i|\lambda_i] = \text{Poisson}(\cdot|\lambda_i)$$

for the pup production model, where λ_i is a rate hyperparameter. In all the description herein, we use the notation "$[x]$" and $[x|y]$" to represent the probability density function (PDF) of x and the conditional PDF of x given y. We do not necessarily have to use this model, but it can make it sufficiently uninformative (see following section).

The second level of the model partitions the N_i pups born into three categories: (1) those that died before the survey, D_i, (2) those that were marked at the start of the survey, M_i,

and finally, all those pups that were not marked, U_i. Assuming that each pup is independently placed in 1 of the 3 categories, we can integrate over the unobserved N_i to obtain the model

$$[D_i, M_i, U_i|\tau_i, \lambda_i] = \text{Poisson}(D_i|\xi_i\lambda_i) \cdot \text{Poisson}(M_i|(1-\xi_i)\tau_i\lambda_i) \cdot \text{Poisson}(U_i|(1-\xi_i)(1-\tau_i)\lambda_i)$$

where ξ is the neonate mortality probability, and τ_i is the probability that a pup is marked given it was alive at the start of the survey. Notice that we actually do not need to estimate N_i as a parameter, because M_i is known, we only need estimates of U_i and any unobserved D_i to estimate pup production.

Now that we have defined a model for (M_i, U_i, D_i) we can examine the next level of the model which is the availability process for how many pups are available to be observed on subsequent resights. On occasion j the number of pups from each subpopulation that are observable (i.e., in the open and not in the water) is modeled by

$$[M_{ij}, U_{ij}|M_i, U_i, \alpha_{ij}] = \text{Binomial}(M_{ij}|M_i, \alpha_{ij}) \times \text{Binomial}(U_{ij}|U_i, \alpha_{ij})$$

that is, each individual pup is randomly available for observation on each occasion. Given the number of pups available from each subpopulation, each observer randomly detects each pup in their counts. Thus for observer k on occasion j the data models for the observed counts are

$$[m_{ijk}, u_{ijk}|M_{ij}, U_{ij}, \delta_{ijk}] = \text{Binomial}(m_{ijk}|M_{ij}, \delta_{ijk}) \times \text{Binomial}(u_{ijk}|U_{ij}, \delta_{ijk}).$$

For each rookery, the complete likelihood for the hierarchical model is

$$[\mathbf{y}_i, \mathbf{X}_i|\boldsymbol{\theta}_i] \propto [(D_i, M_i, U_i)|\xi_i, \tau_i, \lambda_i] \times \prod_j \left\{ [M_{ij}, U_{ij}|M, U, \alpha_{ij}] \times \prod_k [m_{ijk}, u_{ijk}|M_{ij}, U_{ij}, \delta_{ijk}] \right\},$$

where $\boldsymbol{\theta}_i$ is used to denote all of the parameters such as δ_{ijk} and α_{ij}, $\mathbf{X}_i$ represents all the latent abundance values (U_i, M_{ij}, and U_{ij}), and $\mathbf{y}_i$ is the observable data (M_i, m_{ijk}, and

u_{ijk}). Note, that for some rookeries, D_i will be included in $\mathbf{X}_i$ and for the others it will be in $\mathbf{y}_i$. Now, we can make inference to the latent quantities and parameters with the full complete-data likelihood,

$$[\mathbf{y}, \mathbf{X}|\boldsymbol{\theta}] = \prod_i [\mathbf{y}_i, \mathbf{X}_i|\boldsymbol{\theta}_i].$$

Bayesian inference

Traditional maximum likelihood estimation is difficult as the appropriate likelihood to maximize would be

$$[\mathbf{y}|\boldsymbol{\theta}] = \sum_{\mathbf{X}} [\mathbf{y}, \mathbf{X}|\boldsymbol{\theta}]$$

where the sum is over all possible values of the high-dimensional, unobserved $\mathbf{X}$. Numerically calculating the integrated likelihood over every iteration of a maximization routine would be daunting. Cowen et al. (2017) illustrate an efficient numerical method for an open population model using a hidden Markov model formulation. However, the latent structure here is not time indexed in a way that makes HMM formulation straightforward.

The most straightforward way of estimating parameters and abundance from the model developed in the previous section is to sample from the posterior distribution using MCMC. The appropriate posterior distribution in this case

$$[\boldsymbol{\theta}, \mathbf{X}|\mathbf{y}] \propto [\mathbf{y}, \mathbf{X}|\boldsymbol{\theta}] \times [\boldsymbol{\theta}]$$

where $[\boldsymbol{\theta}]$ is the prior distribution of the parameters.

For specification of the prior distribution we will begin with λ_i. Link (2013) suggested that N_i, should follow the prior distribution $[N_i] \propto N_i^{-1}$, an improper prior. This can be approximated with the Poisson-gamma mixture

$$\begin{aligned}[N] &= \int_\lambda \text{Poisson}(N|\lambda)\ \text{gamma}(\lambda|a, a)\ d\lambda \\ &\approx N^{-1} \text{ as } a \to 0.\end{aligned}$$

Thus, we suggest $[\lambda_i|a] = \text{gamma}(\lambda_i|a, a)$ with $a =$ 1.0e-6 (or something small). For the

detection and availability parameters, we switch to the logit parameterization

$$\text{logit}(\delta_{ijk}) = \mathbf{x}'_{ijk}\boldsymbol{\beta}_\delta, \quad \text{and} \quad \text{logit}(\alpha_{ij}) = \mathbf{x}'_{ij}\boldsymbol{\beta}_\alpha$$

where $\mathbf{x}$ contains covariates such as weather conditions or observer related variables. They are not necessarily the same between the parameter types. Then a prior would be specified for each $\boldsymbol{\beta}$ such as a multivariate normal distribution. The mortality and marking probabilities, ξ_i and τ_i could also be modeled this way, but for this investigation we leave their parameterization in its natural form and use beta or uniform prior distributions for those parameters.

An approximate hierarchical model

An alternative to working with the model as it stands in the "exact" form presented in the previous section is to analytically integrate over the latent components to produce the appropriate likelihood for the model and data. However, the latent components, U_i, U_{ij}, and M_{ij} are all discrete with infinite upper bounds, thus the marginalization over these components involves many intractable infinite sums. Thus, straight forward maximum likelihood is difficult. The typical approach is to pick fixed upper bounds and execute the sums to those bounds (e.g., Dail and Madsen (2011), Schmidt et al. (2015), Cowen et al. (2017)). With large abundances this is still a monumental task. In the example of the next section the smallest rookery produces approximately 500 pups, so, the sums necessary become quite cumbersome.

In an attempt to overcome the computational issues of large abundances in open N-mixture models Brintz, Fuentes, and Madsen (2018) propose a normal approximation that allows analytic integration to be performed, thus producing an asymptotically approximate integrated likelihood. Maximization of the likelihood can then be accomplished in a fraction of the time MCMC takes to run while still producing comparable results. In this section, we derive an asymptotically approximate likelihood for our batch marking capture-recapture model using the same principles.

The goal of this approach is to allow modeling the same data with an approximation of the general form

$$
\begin{aligned}
[\mathbf{y}_i|\boldsymbol{\theta}] &= \sum_{\mathbf{X}_i}[\mathbf{y}_i, \mathbf{X}_i|\boldsymbol{\theta}] \\
&\approx \text{Normal}(\mathbf{u}_i|\boldsymbol{\mu}_i^{(u)}, \boldsymbol{\Sigma}_i^{(u)}) \times \text{Normal}(\mathbf{m}_i|\boldsymbol{\mu}_i^{(m)}, \boldsymbol{\Sigma}_i^{(m)}, M_i) \\
&\quad \times [M_i|\xi_i, \tau_i, \lambda_i] \times [D_i|\xi_i, \lambda_i].
\end{aligned}
$$

The approximation is accomplished by matching the mean vectors and covariance matrices to that of the marginal distribution of $\mathbf{m}_i$ and $\mathbf{u}_i$ after integrating over the latent components.

To obtain the multivariate normal means and covariance matrices in the approximation, we will use the same moment matching approach as Brintz, Fuentes, and Madsen (2018). The following means and covariance are derived using the independence of M_i and U_i given the parameters and the law of total covariance. First, the mean vectors, are straightforward to produce;

$$\mu_{ijk}^{(m)} = E[m_{ijk}|M_i, \boldsymbol{\theta}] = M_i\alpha_{ij}\delta_{ijk}$$

and

$$\mu_{ijk}^{(u)} = E[u_{ijk}|\boldsymbol{\theta}] = \lambda_i(1-\xi)(1-\tau_i)\alpha_{ij}\delta_{ijk}$$

The covariance becomes a little more notationally challenging, but they can also be calculated using the standard unconditional variance formula, $Cov(X,Y) = E[Cov(X,Y|Z)] + Cov\{E(X|Z), E(Y|Z)\}$. First we define some terms to make the notation easier to follow. We will use $\omega = (i,j,k)$ to index a specific site, occasion and observer. Next we define the three functions

- $\sigma_i(\omega,\omega') = \alpha_{ij}\alpha_{ij'}\delta_{ijk}\delta_{ij'k'}$ for $i = i'$ and 0 else-wise
- $\sigma_{ij}(\omega,\omega') = \alpha_{ij}(1-\alpha_{ij})\delta_{ijk}\delta_{ijk'}$ for $i = i'$, $j = j'$ and 0 else-wise
- $\sigma_{ijk}(\omega,\omega') = \alpha_{ij}\delta_{ijk}(1-\delta_{ijk})$ for $\omega = \omega'$ and 0 else-wise

Now, the entries of the covariance matrices can be specified as

$$Cov(m_\omega, m_{\omega'}|M_i, \boldsymbol{\theta}) = M_i\{\sigma_{ij}(\omega,\omega') + \sigma_{ijk}(\omega,\omega')\},$$

for $i = i'$, $j = j'$, and 0 else-wise. For the unmarked animals we are also marginalizing over U_i as well, covariances are thus positive over different occasions, that is

$$Cov(u_\omega, u_{\omega'}|\boldsymbol{\theta}) = \lambda_i(1-\xi)(1-\tau_i)\{\sigma_i(\omega,\omega') + \sigma_{ij}(\omega,\omega') + \sigma_{ijk}(\omega,\omega')\},$$

for $i = i'$ and 0 else-wise.

Using this approximation, we can form the marginal posterior distribution,

$$[\boldsymbol{\theta}|\mathbf{y}] = \prod_i [\mathbf{y}_i|\boldsymbol{\theta}] \times [\boldsymbol{\theta}].$$

From this specification we can use MCMC to draw from the posterior distribution or use optimization methods to make simulation free inference. The major numerical argument for this approximation is that it marginalizes over all discrete valued components of the model. Therefore, the remaining parameters are all continuously valued, thus MCMC or optimization can be carried out with software that uses automatic differentiation such as `stan` or `TMB`. In addition, it is often note that marginalizing over some model components can improve posterior sampling or optimization (Van Dyk and Park 2008).

Now that we have integrated $\mathbf{X}_i$ out of the models, it begs the question, how can we now estimate $N_i = M_i + U_i + D_i$ when U_i and some D_i are no longer in the model? There are two approaches we can take, but they are both based on the posterior predictive distribution of the needed quantities. If D_i is unobserved, then we can write down the predictive distribution

$$[U_i, D_i|\mathbf{y}_i] = \int_{\boldsymbol{\theta}} [D_i|\xi_i, \lambda_i]\ [U_i|\xi_i, \tau_i, \lambda_i]\ [\boldsymbol{\theta}|\mathbf{y}_i] d\boldsymbol{\theta}.$$

The obvious first approach for making abundance inference is to sample from these distributions by first drawing a sample from $[\boldsymbol{\theta}|\mathbf{y}_i]$ using, say MCMC, then for each draw, select a D_i and U_i from their respective Poisson distributions. However, we were seeking to produce a MCMC free method which might be computationally inexpensive. So, we can optimize $[\boldsymbol{\theta}|\mathbf{y}_i]$ with respect to $\boldsymbol{\theta}$ to obtain the posterior mode, then using the calculated

posterior Hessian, $\hat{\mathbf{H}}$, further approximate

$$[\boldsymbol{\theta}|\mathbf{y}_i] \approx \text{Normal}\left(\hat{\boldsymbol{\theta}}, -\hat{\mathbf{H}}^{-1}\right)$$

From this approximation one can readily draw thousands of samples in seconds. We will denote this approach as the parametric bootstrap method.

For an alternate fully simulation free approach we can use the same technique as Johnson, Laake, and Ver Hoef (2010). That is, we can use the standard unconditional mean and variance formulas

- $E(X) = E_Y\{E_X(X|Y)\}$
- $Var(X) = Var_Y\{E_X(X|Y)\} + E_Y\{Var_X(X|Y)\}$

to approximate the mean (the optimal predictor) and variance of the predictive distribution for U_i and D_i. That is,

$$\begin{aligned}\hat{N}_i &= E_{\boldsymbol{\theta}}\left\{E(M_i + U_i + D_i|\boldsymbol{\theta})\right\} \\ &\approx M_i + (1-\hat{\xi}_i)(1-\hat{\tau}_i)\hat{\lambda}_i + \hat{\xi}_i\hat{\lambda}_i \\ &= M_i + \hat{U}_i + \hat{D}_i,\end{aligned}$$

where the last term is replaced with D_i if it is observed. The parameter estimates can be obtained by the posterior mode $\hat{\boldsymbol{\theta}}$ found by optimization as before. The prediction variance is calculated by

$$\begin{aligned}Var(\hat{N}_i) &= Var_{\boldsymbol{\theta}}\left\{E(M_i + U_i + D_i|\boldsymbol{\theta})\right\} + E_{\boldsymbol{\theta}}\left\{Var(M_i + U_i + D_i|\boldsymbol{\theta})\right\} \\ &\approx Var_{\boldsymbol{\theta}}\{\hat{U}_i + \hat{D}_i\} + M_i + \hat{U}_i + \hat{D}_i,\end{aligned}$$

Because $\hat{U}_i$ and $\hat{D}_i$ are just nonlinear functions of the parameters we can approximate the variance using the delta method (Dorfman 1938) based on the asymptotic posterior variance, $-\hat{\mathbf{H}}^{-1}$ (Johnson, Laake, and Ver Hoef 2010).

There are benefits to both the bootstrap and delta method approaches. For the parametric bootstrap approach, the main benefit is the ease in which estimates of derived parameters can be calculated. As with the full MCMC one must only calculate the derived parameters

for all the sample draws and one has a posterior sample of the derived parameter. In the next section, for example, we examine total pup production for each island. The delta method approach maintains the benefit that the calculations are quick and free of simulation issues such as choice of sample size, etc. In the following section we examine how each of these approximate approaches compare to the "exact" MCMC approach, as well as, the traditional design-based estimates.

Pup production in 2016

Here we analyze the northern fur seal pup production data obtained in 2016 for monitoring pup production in the Pribilof Islands, Alaska (Figure 1). There are 19 separate rookeries on the two main islands in the archipelago, St. Paul Island in the north and St. George Island to the south. The rookeries on St. Paul I. produce approximately 80% of the pups and contains the majority of the rookeries. The 2016 data is fully described by Testa (2018). We built an R (R Core Team 2019) package called `mbpp`[2] that contains the model estimation procedures presented in the previous section and the data analyzed herein. We use the MCMC software `JAGS` (Hornik, Leisch, and Zeileis 2003) through the `R` package `R2jags` (Su and Yajima 2015) to sample from the exact hierarchical model and the R package `TMB` (Kristensen et al. 2016) to optimize the integrated posterior distribution for the approximate model bootstrap and delta approaches.

For each of the rookeries ($I = 19$) in 2016, there were 2 observers ($J = 2$) who visited each rookery twice ($K = 2$) after shear-marking to count marked and unmarked pups. Each of the 3 model fitting methods presented in the previous sections was used to estimate pup production. Parmeterizations and prior distributions are summarized in Table 2 for reference. For this analysis we used the previously suggested gamma distributions for each rookery to approximate a scale prior distribution for N_i. Neonate mortality was modeled as constant within each island so the number of dead pups at unsampled rookeries could be predicted. The proportion of shear-marked pups (τ_i) was separately modeled for each rookery with a

[2]This package is available at https://github.com/dsjohnson/mbpp and can be directly installed using the devtools package. The github page provides instructions for installation.

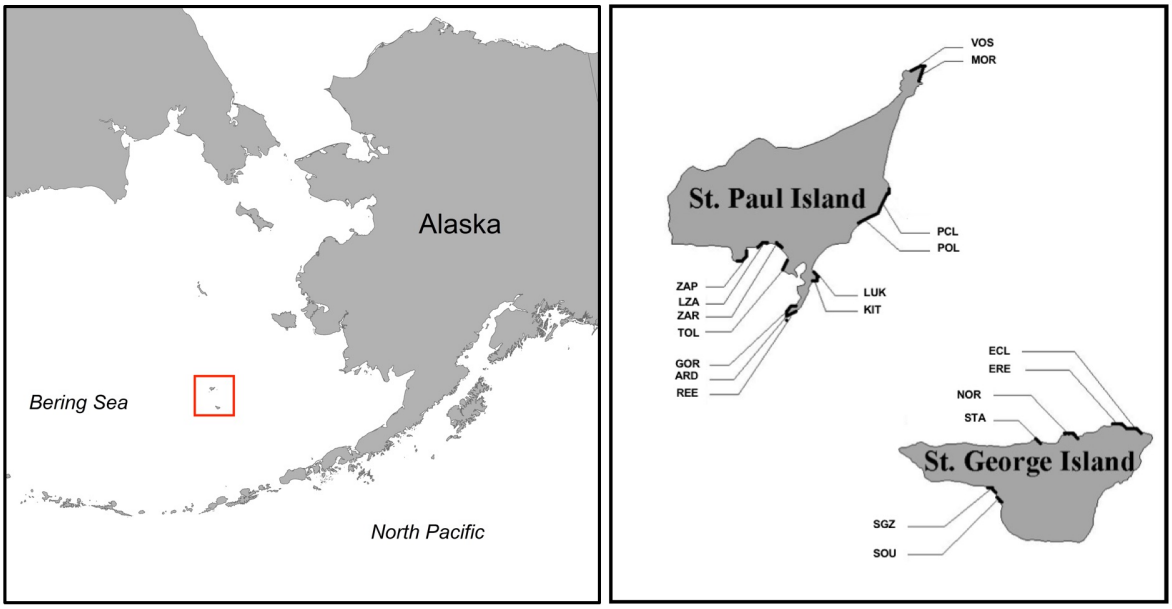

Figure 1: Map of northern fur seal rookeries in the Pribilof Isalands, Alaska. The Pribilof Islands are an archipelago in the Bering Sea off the coast of Alaska. The main islands are St. Paul Island, to the north, and St. George Island, to the south. Note, the distance between the islands is not to scale in the right-hand figure. The rookeries are each labeled by their 3-letter NOAA Fisheries rookery code.

Table 2: Parameter formulation and prior distribution specification. The 'Model' column uses R notation to specify variation in the parameters over rookeries, occasions, and observers. Pup production was estimated separately for each island, therefore an intercept only model (~ 1) would mean that the parameter is constant within each island.

Parameter	Model	Prior Distributions
λ_i	$\sim$ rookery	$[\lambda_i] = \text{Gamma}(1.0e^{-6}, 1.0e^{-6})$
τ_i	$\sim$ rookery	$[\tau_i] = \text{Uniform}(0, 1)$
ξ_i	~ 1	$[\xi] = \text{Uniform}(0, 1)$
logit α_{ij}	$\sim$ rookery	$[\boldsymbol{\beta}_{\alpha,\text{term}}] = \text{Normal}(\mathbf{0}, \sigma^2_{\text{term}}\mathbf{I})^*$
logit δ_{ijk}	$\sim$ rookery * occasion * observer	$[\boldsymbol{\beta}_{\delta,\text{term}}] = \text{Normal}(\mathbf{0}, \gamma^2_{\text{term}}\mathbf{I})^*$
σ_{term}	~ 1	$[\sigma_{\text{term}}] = \text{Exponential}(1)$
γ_{term}	~ 1	$[\gamma_{\text{term}}] = \text{Exponential}(1)$

* The index 'term' is used to represent each term in the model specification, e.g., intercept, rookery main effects, rookery*occasion interaction, etc.

uniform prior. For the availability (α_{ij}) and detection (δ_{ijk}) we used a logistic regression parameterization to model rookery, occasion, and observer differences. The coefficients for each term were treated as normal random effects. So, for each term in the model, a variance component was estimated. This allows for regularization of the coefficients to be used for model selection (Hooten and Hobbs 2015). An exponential prior distribution was used for each of the variance parameters to penalize complexity (Simpson et al. 2017).

For each island, the MCMC algorithm was run for 100,000 iterations following a burnin of 10,000 iterations. Every 100th iteration was retained to obtain a final sample of 1,000 posterior draws. In order to fit the approximate model we used Laplace approximation functionality in `TMB` to numerically integrate over the random coefficients and maximize the marginal likelihood. Then we used the delta-method and parametric bootstrap approaches for inference.

Results

The overall conclusion of the separate analysis of the shear sampling data using the 3 proposed methods in this paper revealed very little difference in the results between the

model-based estimates. Certainly, there were no qualitative or management-level differences between the three estimation procedures considered here (Figure 2). In addition, there was no appreciable difference in execution time. All three methods finished in a little less than 2 seconds. However, this data set is relatively small, so there may be a larger differences with larger data sets.

There were some differences between the design-based and model-based point estimates, for example ZAR and LUK (Figure 2). However, these differences are not significant in terms of possible management decisions. There were some noticeable differences in uncertainty estimates. The production estimate coefficients of variation ranged from 2.5–9.5% for the model-based estimates, but 0.0–12.5% for the design-based estimates. The design-based estimates of uncertainty were more volatile using the design-based method with some standard error estimates unreasonably small. For example production at PCL was estimated to be on the order of 7,000 pups, but the design-based SE was estimated to be 0.5! The model-based estimators produced an SE around 215 for PCL, much more reasonable.

To examine whether we might see differences between the bootstrap method versus the MCMC sample for estimating derived parameters we also estimated total pup production for each island. These island total estimates are the pup production quantities typically reported by NOAA Fisheries for management decisions. We only compared the bootstrap and MCMC methods because they are both sample based methods which allow straightforward estimates of derived parameters. Both methods produced very similar point and interval estimates (Table 3). In addition, the distribution of the island total samples were also very similar (Figure 3). So, in this instance, the bootstrap approach seems to produce a nearly identical posterior sample compared to MCMC sampling of the exact hierarchical model. The model-based methods produced very similar point estimates when compared to the design-based method. The SE estimate was slightly higher for the model-based estimates due to the fact that the design-based SE was unreasonably small for some rookeries. However, the overall difference was not great (Table 3).

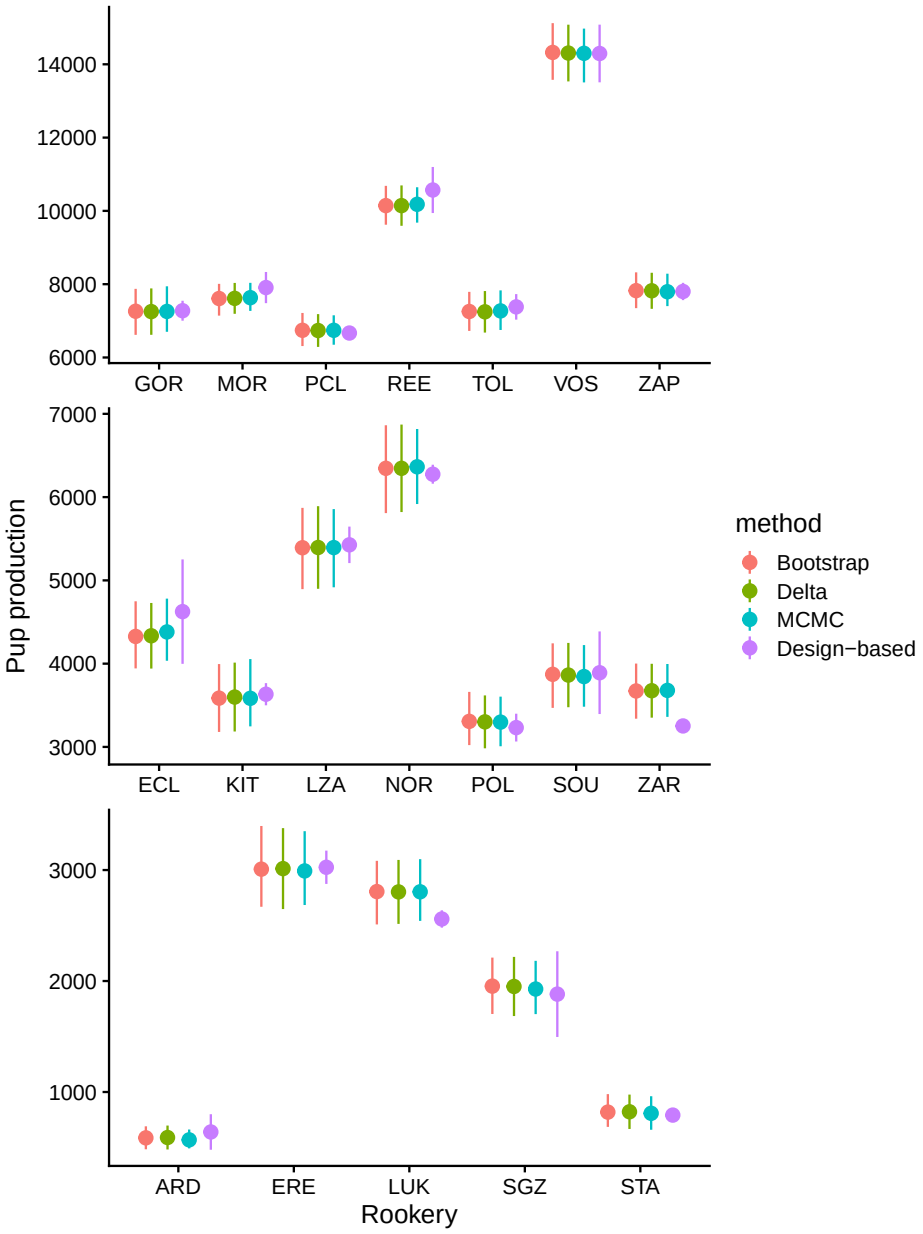

Figure 2: Estimated northern fur seal pup production. Each color represents a different model fitting method. Blue is a full MCMC sampling of the hierarchical model, red in the asymptotic normal approximation fitted with Template Model Builder using Laplace approximation, green in the asymptotic normal approximation with estimation based on a Gaussian parametric bootstrap, and purple is the traditional design-based estimator. The figure is divided into general rookery size classes for presentation.

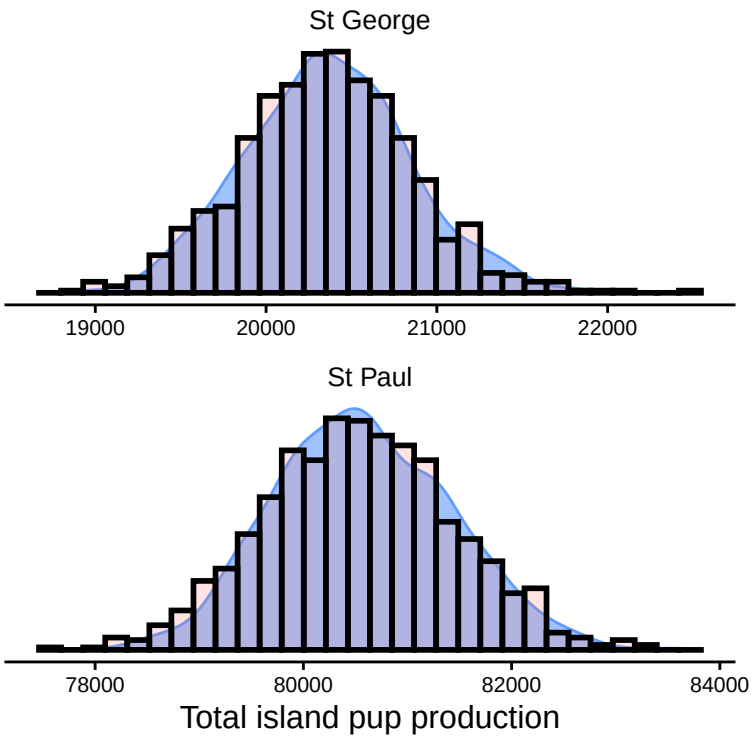

Figure 3: Estimated island-wide total northern fur seal pup production. The histogram represents the parametric bootstrap sample using the asymptotic approximation model. The density plot comes from the MCMC sample drawn from the exact hierarchical model using ‘JAGS‘.

Table 3: Estimates of total pup production for each island using MCMC sampling of the exact hierarchical model, parametric bootstrap samples from the approximate model, and the traditional design-based estimator.

Method	N	SE	CI
St George			
MCMC	20,356	485	[19,449 – 21,359]
Bootstrap	20,354	494	[19,398 – 21,309]
Design-based[1]	20,490	454	[19,395 – 21,646]
St Paul			
MCMC	80,533	852	[79,044 – 82,263]
Bootstrap	80,526	906	[78,816 – 82,269]
Design-based[1]	80,641	717	[79,135 – 82,176]

[1] Design-based estimates taken from Testa (2018) "Population assessment of northern fur seals on the Pribilof Islands, 2015–2016."

Discussion

Here we considered a model-based approach to estimating pup production for the Pribilof Islands population of northern fur seals. In the end, the model-based version produced similar point estimates, but more stable standard error estimates. With the model-based approach there is also a floor on the uncertainty estimation of U_i, even if τ_i and ξ are perfectly known, there is still binomial variation present in the model for U_i. Therefore, unlike the design-based method, $SE(\hat{N}_i)$ will never be zero because it is the prediction variance for an unobserved variable. Thus, producing realistic uncertainty assessment for each rookery.

Although there were not great computational savings, it was quite encouraging that the continuous-value approximate hierarchical model produced very similar results to the MCMC sampling of the exact model. Brintz, Fuentes, and Madsen (2018) also noticed little difference in approximating the count data of open N-mixture models with a continuous valued multivariate normal distribution. This might form a blueprint for use of continuous approximation for open-population batch mark models such as those considered by Cowen et al. (2017) or the known-fate assisted N-mixture models proposed by Schmidt et al. (2015). In general, using mean and covariance matched Gaussian distributions may prove to be a

useful approach for modeling latent discrete-valued variables in automatic differentiation based software such as `TMB` and `stan`. These models are ubiquitous in abundance estimation.

In addition to improvements over the design-based methods, the model-based method adds room for improvement for other ecologically interesting questions. As mentioned previously, we might choose to model α_{ij} in some interesting way. For example a temporal trend to reflect the increasing proportion of animals that are entering the water or moving around as they age or using weather related covariates might indicate a relationship between conditions and pup avaialbility. The detection parameters, δ_{ij} might be similarly modeled with, for example, weather or visibility covariates or effort. Further, separate estimates can be linked through time and space in a model-based coherent framework. Currently this is often accomplished with a two-stage approach where production is estimated with the design-based method, then separate estimates are modeled through space and time using a weighted regression model (Towell, Ream, and York 2006; Johnson et al. 2013). Under the model-based framework, all of the λ_i could be liked with a space-time model. Or, they could be linked using the two-stage version fitting procedure for hierarchical models proposed by Hooten, Johnson, and Brost (2019).

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References

Brintz, Ben, Claudio Fuentes, and Lisa Madsen. 2018. "An Asymptotic Approximation to the N-Mixture Model for the Estimation of Disease Prevalence." *Biometrics* 74 (4): 1512–8.

Chapman, D. G., and A. M. Johnson. 1968. "Estimation of Fur Seal Pup Populations by Randomized Sampling." *Transactions of the American Fisheries Society* 97 (3): 264–70.

Cochran, William Gemmell. 1977. *Sampling Techniques: 3d Ed.* Wiley New York.

Cowen, Laura LE, Panagiotis Besbeas, Byron JT Morgan, and Carl J Schwarz. 2017. "Hidden Markov Models for Extended Batch Data." *Biometrics* 73 (4): 1321–31.

Dail, D, and L Madsen. 2011. "Models for Estimating Abundance from Repeated Counts of an Open Metapopulation." *Biometrics* 67 (2). Wiley Online Library: 577–87.

Dorfman, Robert. 1938. "A Note on the Delta-Method for Finding Variance Formulae." *The Biometric Bulletin* 1: 129–37.

Gelman, Andrew, Daniel Lee, and Jiqiang Guo. 2015. "Stan: A Probabilistic Programming Language for Bayesian Inference and Optimization." *Journal of Educational and Behavioral Statistics* 40 (5). Sage Publications Sage CA: Los Angeles, CA: 530–43.

Hooten, Mevin B, and N Thompson Hobbs. 2015. "A Guide to Bayesian Model Selection for Ecologists." *Ecological Monographs* 85 (1): 3–28.

Hooten, Mevin B, Devin S Johnson, and Brian M Brost. 2019. "Making Recursive Bayesian Inference Accessible." *The American Statistician* To appear.

Hornik, Kurt, Friedrich Leisch, and Achim Zeileis. 2003. "JAGS: A Program for Analysis of Bayesian Graphical Models Using Gibbs Sampling." In *Proceedings of Dsc*. Vol. 2. 1.

Johnson, Devin S, Jeffrey L Laake, and Jay M Ver Hoef. 2010. "A Model-Based Approach for Making Ecological Inference from Distance Sampling Data." *Biometrics* 66 (1): 310–18.

Johnson, D. S., Rolf R. Ream, Rodney G. Towell, Michael T. Williams, and Juan D. Leon Guerrero. 2013. "Bayesian Clustering of Animal Abundance Trends for Inference and Dimension Reduction." *Journal of Agricultural Biological and Environmental Statistics* 18 (3): 299–313.

Kristensen, Kasper, Anders Nielsen, Casper W Berg, Hans Skaug, and Brad Bell. 2016.

"TMB: Automatic Differentiation and Laplace Approximation." *Journal of Statistical Software* 70 (1): 1–21.

Lincoln, F. C. 1930. "Calculating Waterfowl Abundance on the Basis of Banding Returns." Circular 118. United States Department of Agriculture.

Link, William A. 2013. "A Cautionary Note on the Discrete Uniform Prior for the Binomial *N*." *Ecology* 94 (10): 2173–9.

R Core Team. 2019. *R: A Language and Environment for Statistical Computing*. Vienna, Austria: R Foundation for Statistical Computing. https://www.R-project.org/.

Royle, J Andrew. 2004. "N-Mixture Models for Estimating Population Size from Spatially Replicated Counts." *Biometrics* 60 (1): 108–15.

Schmidt, Joshua H, Devin S Johnson, Mark S Lindberg, and Layne G Adams. 2015. "Estimating Demographic Parameters Using a Combination of Known-Fate and Open N-Mixture Models." *Ecology* 96 (10): 2583–9.

Simpson, Daniel P, H Rue, Andrea Riebler, Thiago G Martins, and SH Sørbye. 2017. "Penalising Model Component Complexity: A Principled, Practical Approach to Constructing Priors." *Statistical Science* 32: 1–28.

Su, Yu-Sung, and Masanao Yajima. 2015. *R2jags: Using R to Run 'Jags'*. https://CRAN.R-project.org/package=R2jags.

Testa, J. W., ed. 2018. *Fur Seal Investigations, 2015-2016*. NMFS-AFSC-375, 107 p. U.S. Dep. Commer., NOAA Tech. Memo. NMFS-AFSC-375, 107 p.

Towell, R. G., Rolf R. Ream, Jeremy T. Sterling, John L. Bengtson, and Michael Williams. 2016. "Demographic Studies of Northern Fur Seals on the Pribilof Islands, Alaska, 2013-2014." In *Fur Seal Investigations, 2013-2014*, edited by J. W. Testa. U.S. Dept. of Commer., NOAA Tech. Memo. NMFS-AFSC-316, 124 p.

Towell, RG, RR Ream, and AE York. 2006. "Decline in Northern Fur Seal (*Callorhinus Ursinus*) Pup Production on the Pribilof Islands." *Marine Mammal Science* 22 (2):

486–91.

Van Dyk, David A, and Taeyoung Park. 2008. "Partially Collapsed Gibbs Samplers: Theory and Methods." *Journal of the American Statistical Association* 103 (482): 790–96.

York, AE, and P Kozloff. 1987. "On the Estimation of the Numbers of Northern Fur Seal, *Callorhinus Ursinus*, Pups Born on St. Paul Island, 1980-86." *Fisheries Bulletin* 85: 367–75.

York, AE, and RG Towell. 1996. "A New Sampling Design for Estimating Numbers of Fur Seal Pups." In *Fur Seal Investigations, 1994*, edited by E. H. Sinclair. U.S. Dept. of Commer., NOAA Tech. Memo. NMFS-AFSC-69, 144 p.