

Evaluating Models of Population Process in a Threatened Population of Steller's Eiders: A Retrospective Approach

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By Kylee Dunham and James B. Grand

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Conversion Factors

International System of Units to U.S. customary units

Multiply	By	To obtain
	Area	
square kilometer (km ²)	247.1	acre
square kilometer (km ²)	0.3861	square mile (mi ²)

Abbreviations

ACP	Arctic Coastal Plain
MCMC	Markov chain Monte Carlo method
NSE	North Slope eider
pdf	probability distribution function
SIS	sequential importance sampling method
SISR	sequential importance sampling with resampling method
SSM	state-space model

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By Kylee Dunham¹ and James B. Grand²

Abstract

The Alaskan breeding population of Steller's eiders (*Polysticta stelleri*) was listed as threatened under the Endangered Species Act in 1997 in response to perceived declines in abundance throughout their breeding and nesting range. Aerial surveys suggest the breeding population is small and highly variable in number, with zero birds counted in 5 of the last 25 years. Research was conducted to evaluate competing population process models of Alaskan-breeding Steller's eiders through comparison of model projections to aerial survey data. To evaluate model efficacy and estimate demographic parameters, a Bayesian state-space modeling framework was used and each model was fit to counts from the annual aerial surveys, using sequential importance sampling and resampling. The results strongly support that the Alaskan breeding population experiences population level nonbreeding events and is open to exchange with the larger Russian-Pacific breeding population. Current recovery criteria for the Alaskan breeding population rely heavily on the ability to estimate population viability. The results of this investigation provide an informative model of the population process that can be used to examine future population states and assess the population in terms of the current recovery and reclassification criteria.

1 Introduction

Steller's eiders (*Polysticta stelleri*) are small sea ducks that inhabit the Arctic and subarctic regions in Russia and Alaska (Fredrickson, 2001; Pearce and others, 2005). The Alaskan breeding population was listed as threatened under the Endangered Species Act in 1997 in response to a perceived decline in abundance throughout their breeding and nesting range (U.S. Fish and Wildlife Service, 1997). The recovery plan identified a critical need to estimate and reduce the

extinction risk of this breeding population (U.S. Fish and Wildlife Service, 2002). Assessing extinction risk requires a comprehensive understanding of population dynamics and underlying population processes, as well as the associated uncertainty. Sufficient information on a threatened species is particularly difficult to obtain, specifically for Steller's eiders, because the remote nature of their nesting, breeding, wintering, and molting sites makes this species especially difficult to observe (Fredrickson, 2001). The lack of observability makes it challenging to accurately estimate demographic processes or population size and trend. Furthermore, there is additional uncertainty regarding how the Alaskan breeding population relates to the larger global population of Steller's eiders. The interaction between the global population and the much smaller Alaskan breeding population may have serious implications for population viability.

There are three geographically distinct breeding populations of Steller's eiders: the Russian-Atlantic population, Russian-Pacific population, and the Alaskan population (U.S. Fish and Wildlife Service, 2002; Pearce and others, 2005). The Russian-Atlantic population nests in northern Norway and west of the Taimyr Peninsula in northern Russia, and winters in the Barents and Baltic Seas (Nygård and others, 1988, 1995; Pearce and others, 2005; Petersen and others, 2006). The largest breeding population of Steller's eiders is the Russian-Pacific population, which nests east of the Taimyr Peninsula in Siberia (Pearce and others, 2005). The smallest of the three breeding populations is the Alaskan population, which may contain fewer than 600 individuals (Stehn and Platte, 2009). This small breeding population nests on the Arctic Coastal Plain (ACP) of Alaska, along the northern coast of Alaska, primarily near the town of Barrow. Both the Russian-Pacific and Alaskan breeding populations congregate on the same molting and wintering areas along the Alaskan Peninsula (U.S. Fish and Wildlife Service, 2002; Martin and others, 2015). Individuals from both breeding populations exhibit high rates of fidelity to specific molting areas in Alaska and pair bonding occurs on the wintering grounds (Flint and Herzog, 1999). Alternative hypotheses have been made regarding closure between the Russian-Pacific and Alaskan breeding populations. Movement

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between these two populations could have serious implications for assessing extinction risk and recovery (Martin and others, 2015). Determining if the Alaskan breeding population is open or closed to movement is a critical component to better understand the processes that govern this population.

Planning for the conservation and recovery of an imperiled species requires an assessment of population status. Like many threatened or endangered species, the Alaskan breeding population of Steller's eiders is monitored annually. Road-based and transect surveys for breeding pairs are conducted by the U.S. Fish and Wildlife Service Ecological Services Fairbanks Field Office and the North Slope Borough Department of Wildlife Management near the town of Barrow, Alaska (Obritschkewitsch and others, 2001; Safine, 2013; Stehn and others, 2013). Additionally, aerial surveys have been flown annually since 1989 along the ACP (Obritschkewitsch and others, 2001; Safine, 2013; Stehn and others, 2013). These surveys indicate that the Alaskan breeding population is present in low and highly variable numbers (Stehn and others, 2013). On the basis of 25 years of aerial survey data from the ACP, the number of birds counted ranged from zero (in 5 years) up to 635 (standard error ± 405) birds (Stehn and others, 2013). These variable counts make it particularly difficult to characterize a reliable population trend and the risk of extinction. Typically, the results of these annual surveys can be used to develop models and estimate population viability; however, highly variable counts, zero count years, and the large amount of uncertainty surrounding these counts make it particularly challenging to quantify viability. Additionally, there is uncertainty regarding demographic rates. Survival rates have been estimated for this species using birds marked on the molting grounds (Flint, Petersen, and others, 2000; Reynolds, 2007; Frost and others, 2013). These studies typically included a large portion of nonbreeding birds and birds from both the Russian-Pacific and Alaskan breeding populations. Although these studies provide a foundation for understanding survival rates for this species, demographic rates of the Alaskan breeding population are likely to differ from the birds studied on the molting sites.

A central problem in conserving a threatened or endangered species is the difficulty in properly quantifying the uncertainty. For Steller's eiders, uncertainty in population process hinders the ability to accurately assess the population's extinction risk, which, for the Alaskan breeding population, must be less than 1 percent over 100 years to meet one of the criteria for down listing an endangered species (U.S. Fish and Wildlife Service, 2002). A principal objective outlined in the recovery plan for this population was to gain a more comprehensive understanding of the dynamics of the Alaskan breeding population and use this information to estimate the past, current, and future breeding population status (U.S. Fish and Wildlife Service, 2002). The objective of this research was to develop and identify explicit models of population processes to evaluate the status of the Alaskan breeding population. Bayesian state-space models (SSM) were used to formally account for the multiple sources of uncertainty associated with

the observation process, parameters, and population closure. Bayesian state-space models provided a flexible framework to explicitly account for uncertainty, which is particularly important when modeling a threatened species (e.g., Buckland and others, 2004; Thomas and others, 2005; Newman and Lindley, 2006; Newman and others, 2006; Buckland and others, 2007; Newman and others, 2009; Dunham and Grand, 2016).

It is vital to adequately account for uncertainty when making management and policy decisions for species of conservation concern. State-space models provide a convenient framework to explicitly acknowledge uncertainty in population and observation processes while simultaneously modeling biologically plausible population processes and estimating key demographic parameters (Buckland and others, 2004; Thomas and others, 2005; Dunham and Grand, 2016). This approach allowed for the direct comparison of multiple models of population process and fit each model to the available observation data from the aerial surveys. The sequential nature of the aerial survey data provided a convenient opportunity to employ sequential Monte Carlo methods and, more particularly, sequential importance sampling with resampling (SISR) to fit process models to observation data. This method was appropriate for analyzing sequential data and provided posterior estimates of demographic rates and population state at each time step (Newman and others, 2009). Therefore, we were able to incorporate time-varying or hierarchical parameters and estimate posterior distributions for each parameter after each time step (Newman and others, 2009). This was particularly important for this modeling effort because it allowed us to account for movement between the Russian-Pacific and Alaskan breeding populations. Additionally, we directly compared the results from each process model, after each time step, to determine which model of population process best fit the observational data. This approach allowed us to explicitly account for process uncertainty, observation uncertainty, and model uncertainty, while simultaneously providing estimates of demographic rates and identifying the most appropriate population process model.

We developed four competing models to reflect alternative hypotheses and uncertainty in the underlying population processes. Our primary objective was to evaluate support, based on count data, for competing models that represent hypotheses for the population dynamics of the Alaskan breeding population of Steller's eiders. Additionally, because we used SISR, we also were able to estimate underlying demographic rates.

2 Methods

2.1 Survey Methods

Given the importance of the ACP for breeding waterfowl, the U.S. Fish and Wildlife Service Division of Migratory Bird Management conducted aerial surveys for roughly

60,000 square kilometers (km²) in the ACP to monitor the distribution, abundance, and trend of bird species. The original ACP surveys were flown from 1986 to 2006, and many avian species in the area were monitored. Following the listing of the spectacled eider (*Somateria fischeri*) in 1992, the North Slope eider (NSE) survey was established and flown through 2006 to monitor primarily spectacled and Steller's eiders. In 2007, the ACP and NSE surveys were merged. Stehn and others (2013) conducted analyses to combine the datasets from all surveys from 1986 to 2013 and determine population trends of the monitored species. The aerial survey data used in our research to evaluate population process models were taken from the combined survey results in Stehn and others (2013). The dataset used in our analysis of population process models used the number of indicated breeding Steller's eiders estimated each year from 1989 to 2013. Stehn and others (2013) estimated the number of indicated breeding birds as

$$\left((2 * \text{number of single birds}) + (2 * \text{number of pairs}) \right).$$

The number of single birds is doubled under the assumption that only pairs are present on the surveyed area. This number was corrected using an adjustment ratio according to timing of the survey, the percentage of the area sampled, and the stratum to account for the average relative difference between observed densities among the different survey types. Differences included seasonal chronology, survey timing, weather conditions, movement of birds, and observers (Stehn and others, 2013). The adjustment ratio converted aerial index densities observed on the ACP survey as if they had been observed on the NSE survey (Stehn and others, 2013). Therefore, the dataset used in our analysis to evaluate models of population process corresponds to the time while eiders are in breeding pairs, before the males depart, consequently corresponding to a pre-breeding census and is treated as such in our models and analysis. The adjustment ratios used to combine the results from the surveys are not indicative of detection probability, which was accounted for in our model as described below. Additional information on timing, stratification, sampling, and analysis of these surveys and the data collected are available in Stehn and others (2013).

2.2 State-Space Model Formulation

Bayesian state-space models provide a flexible modeling framework to account for multiple sources of uncertainty (Brooks and others, 2004). State-space models account for uncertainty through a state and observation process which link time series of counts to the underlying processes that affect the population state (Buckland and others, 2004; Thomas and others, 2005; Newman, 1998). We used a SSM framework and developed four competing state process models to examine the possibilities of Steller's eider population dynamics. The

general Bayesian state-space modeling framework consists of four probability distribution functions (pdfs):

$$\begin{aligned} \text{Initial state pdf:} & \quad g_0(N_0 | \theta) \\ \text{State process pdf:} & \quad g_t(N_t | N_{0:t-1}, \theta) \\ \text{Observation process pdf:} & \quad f_t(c_t | N_t, \theta) \\ \text{Prior pdf:} & \quad g_0(\theta) \end{aligned}$$

where $t = 1, 2, \dots, T$ and θ is a vector of model parameters. Using this information, we can make inferences about both N_t and θ , conditional on the observed data.

The full state process model is defined as

$$\begin{bmatrix} N_{jf} \\ N_{af} \\ N_{jm} \\ N_{am} \end{bmatrix}_t = \begin{bmatrix} 0 & f_f & 0 & 0 \\ S_{jf} & S_{af} & 0 & 0 \\ 0 & f_m & 0 & 0 \\ 0 & 0 & S_{jm} & S_{am} \end{bmatrix}_{t-1} \begin{bmatrix} N_{jf} \\ N_{af} \\ N_{jm} \\ N_{am} \end{bmatrix}_{t-1} + \begin{bmatrix} 0 \\ I_{af} \\ 0 \\ I_{am} \end{bmatrix}_t$$

where N_t represents the number of individuals in each age-sex class, S_t is the age-sex specific survival rate, f is the sex-specific fertility, and I is the sex-specific number of adult immigrants added to the breeding population at time t . Immigration, I_t was treated as a random effect or time-varying parameter. At each time step, the number of immigrants was modeled using a zero-inflated uniform distribution parameterized as

$$\begin{cases} 0, \text{ with probability } \sim 0.5 \\ \text{Uniform}(1, 3000) \text{ with probability } \sim 0.5 \end{cases}$$

The number of immigrants estimated at time step t was added to the population size at time step t and became part of the state space at that time because they were available to be counted but did not contribute to the population previously. In addition, we assumed that immigrants only moved into the population as breeding adults, and the estimated number of immigrants was added to the adult male and female class assuming equal sex ratios. Immigration was only included in the two open population models and was excluded from the two closed population models, as described in detail below.

Each state process model was linked to the count data from the ACP surveys through an observation process model. The aerial survey was conducted on the breeding grounds, prior to nesting; therefore, the survey only detected adult birds (age 2+) (Quakenbush and others, 1995; Fredrickson, 2001). The observation process model for each state process model is

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$$\begin{bmatrix} c_{jf} \\ c_{af} \\ c_{jm} \\ c_{am} \end{bmatrix}_t = \begin{bmatrix} p_{jf} & p_{af} & p_{jm} & p_{am} \end{bmatrix}_t \begin{bmatrix} N_{jf} \\ N_{af} \\ N_{jm} \\ N_{am} \end{bmatrix}_t$$

where c_t represents the number of individuals counted in each age-sex class, and p_t is the detection probability of individuals. Only adult birds were detected on surveys; thus, the probability of detecting juveniles is zero; therefore, $p_{jf,jm} = 0$ and $c_{jf,jm} = 0$. Otherwise, detection probability, p_t , was modeled using a beta distribution with $\mu = 0.3$ and $\sigma = 0.02$ to reflect additional uncertainty in detection probability (table 1). We assumed detection probability was approximately 30 percent for adult Steller's eiders on the ACP aerial surveys and that detection was relatively constant across years (Stehn and Platte, 2009).

The population models were based on a two-sex, two-age structured matrix population model. Juveniles were 1 year old and annual juvenile survival rate ($S_{jf,jm}$) was the probability of the individual surviving from 1 year old to 2 years old. Juvenile survival of Steller's eiders was estimated to be relatively high, and we chose a prior distribution based on expert opinion, previous studies, and data on spectacled eiders to reflect the range of values that we believed to be likely (Flint, Grand, and others, 2000; J. Runge, Colorado Division of Wildlife, written commun., 2004). In addition, we assumed juvenile survival was equal between the sexes to reduce model complexity and thus parameter redundancy (Bailey and others, 2010; Dunham and Grand, 2016). Survival of eiders prior to 1 year of age (that is, duckling and immature survival) was accounted for in the estimate of fertility ($f_{f,m}$). Expert opinion and data on the Steller's eiders that nest near Barrow suggest that fertility was low, which is typical of a long-lived sea duck (Quakenbush and Suydam, 1999; Quakenbush and others, 1995; Quakenbush and others, 2004; Safine, 2013). The estimate of fertility was assumed to produce an equal sex ratio and was therefore set equal between the sexes. Adult survival was the annual survival rate ($S_{af,am}$) of birds 2 years and older. Adult male survival is characteristically high, with average annual estimates from previous studies reported to range between 0.77 and 0.87 (Flint, Petersen, and others, 2000; Reynolds, 2007; Frost and others, 2013). We assumed adult female survival would be lower and more variable than male survival due to the increased energetic costs and increased predation risk associated with nesting (Williams, 1966; Stearns, 1976; Erikstad and others, 1998; Flint, Petersen, and others, 2000; Ghalambor and Martin, 2001). However, average annual survival rates of adult females from previous studies ranged from 0.81 to 0.90 (Flint, Petersen, and others, 2000; Reynolds, 2007; Frost and others, 2013). Higher survival of females than males is uncommon in ducks species, and we believe these rates may have been higher because the studies were conducted on the molting grounds including only non-breeding

females. Additional uncertainty was incorporated into each of the parameter values to account for additional sampling and process variance (fig. 1; table 1).

Four models were formulated to represent competing hypotheses about the dynamics of the Alaskan breeding population of Steller's eiders. Each model used the general state process model framework defined above. Due to the timing of the aerial surveys and the treatment of model parameters, the differences in the competing models originated in the interpretations of the observed data. The interpretations of zero count years were particularly important for Steller's eiders. For birds to be detected they must arrive at the grounds to breed; however, there were alternative hypotheses about the reason for zero count years. Models 1 and 2 assumed that the population was closed to immigration and emigration between the Alaskan breeding population and the Russian-Pacific breeding population. Models 3 and 4 assumed an open population and included the hierarchical time-varying parameter (I_t), corresponding to immigration.

Model 1 assumed a closed population with no probability of a population level nonbreeding event. Therefore, the only circumstance in which there could be zero birds observed was a catastrophic event causing the population to collapse. The observation model for state process Model 1 was the observation model described above, however, in zero count years $c_t = 0$ and $N_t = 0$. Model 2 also assumed a closed population; however, we assumed that years in which zero birds were counted represented a population level nonbreeding event. Therefore, the expected count, c_t , was allowed to equal zero in years for which zero birds were observed. However, unlike Model 1, a zero count year strictly represented a nonbreeding event and not a population collapse. In the zero count years, the parameters (θ) were not updated because of the lack of data. It follows that survival in the zero count year was equal to the survival rates estimated in the previous time step, and fertility was set to zero to indicate nonbreeding. The number of individuals in the population (N_t) was the number of individuals expected to survive the nonbreeding year.

Model 3 was reflective of a more transient population, which assumed population level emigration events corresponding with the zero count years. This was modeled using the assumption that in the zero count years, the Alaskan breeding population emigrated and joined the Russian-Pacific population. In these zero count years, $c_t = 0$ and $N_t = 0$. Therefore, in years following these zero counts, N_t was entirely made up of immigrants, I_t . Years in which there were successive nonzero counts are representative of breeding birds that exhibit breeding area fidelity and constitute the Alaskan breeding population. However, in any zero count years these birds emigrated from the breeding population, resulting in $N_t = 0$. The estimated number of immigrant birds was added to N_t during the pre-breeding census period and, therefore, were accounted for in the estimated count in any nonzero count year. If $c_t = 0$, both N_t and I_t were zero because there were zero birds present. Immigration was treated as a random effect; therefore, it was not defined through a Markov

Table 1. Prior mean, standard deviation, and distribution for the parameters used to initialize each candidate model. Posterior mean and standard deviation are reported for the final time step (year 2013) from Model 4.

Parameter	Prior μ	Prior σ	Prior Distribution $g_0(\theta)$	Posterior μ	Posterior σ
$f_{f,m}^a$	0.009	0.03	<i>beta</i> (0.085,18.82)	0.0062	0.00015
$S_{jf,jm}^b$	0.75	0.10	<i>beta</i> (13.31,4.43)	0.748	0.011
S_{af}^c	0.80	0.10	<i>beta</i> (12,3)	0.754	0.015
S_{am}^c	0.85	0.075	<i>beta</i> (18.42,3.25)	0.81	0.009
p_i^d	0.30	0.02	<i>beta</i> (157.2,366.8)	–	–

Note: S indicates sex and age specific survival, f indicates sex specific fertility, and p indicates detection rate.

^a Mean fertility was from estimates in Quakenbush and others (1995), Quakenbush and Suydam (1999), Quakenbush and others (2004), Safine (2013), and J. Runge, written commun., Nov. 2004. Additional error was incorporated into the prior standard deviation to account for process and sampling error.

^b Estimated juvenile survival was based on expert opinion.

^c Adult survival was taken from Flint and others (2000), Reynolds (2007), and Frost and others (2013). Additional error was incorporated into the prior standard deviation to account for process and sampling error.

^d Detection rate was assumed to be relatively constant (Stehn and Platte, 2009). Additional error was incorporated to account for process and sampling error.

process and, thus, was not dependent on the estimate of immigrants at any previous time step.

Model 4 also assumed an open population; however, zero count years represented a population level nonbreeding event ($f = 0$). Therefore, when the observation was zero, $c_t = 0$, but the population size N_t remained intact, no immigrants were added ($I_t = 0$) in these years. All other years allowed for immigrants that were added into the resident population at the current time step. These immigrants were incorporated into the population at this time and remained in the population throughout the time series, becoming resident birds under the assumption they were exhibiting breeding area fidelity.

Each model was fit to the available historic observation data from the aerial surveys on the ACP using sequential importance sampling with resampling that simultaneously estimated population size N_t and both time invariant (θ) and time varying (I_t) model parameters.

2.3 Fitting the Population Models

We estimated the demographic parameters, population size, and dynamics that most likely described the observation data from the ACP surveys. Several inferential procedures can be used to estimate both parameters and population size, including but not limited to the sequential Monte

Carlo (Doucet and others, 2001) and Markov chain Monte Carlo (MCMC; Gilks and others, 1996) methods. Newman and others (2009) compared both sequential importance sampling (SIS) and MCMC methods for making inference about unknown states and parameters of Bayesian state-space models for British grey seal (*Halichoerus grypus*) metapopulation and simulated data for a Chinook salmon (*Oncorhynchus tshawytscha*) population. Although MCMC methods are more commonly implemented in deriving inference from SSMs, Newman and others (2009) suggest that both methods are useful for analyzing time-series observation data. Although MCMC methods typically produce results with less Monte Carlo variation, they are also more difficult to implement and, in the case of complex models, may require employing a simpler model. Sequential importance sampling algorithms typically are very easy to implement, are computationally and statistically efficient, and offer the posterior distributions after each intermediate time step, providing a useful diagnostic for model deficiencies.

The SIS algorithm is initialized by generating a large number X of “particles” or samples from the prior distribution on the parameters, $g_0(\theta_0^x)$, and the initial state distribution $g_0(N_0^x | \theta_0^x)$, which generates $g_0(N_0^x, \theta_0^x)$. We chose $X = 500,000$ particles, where $x = 1, \dots, X$. Each particle, x , represents a single realization of the demographic parameters, θ_t^x , combined with a single realization of the

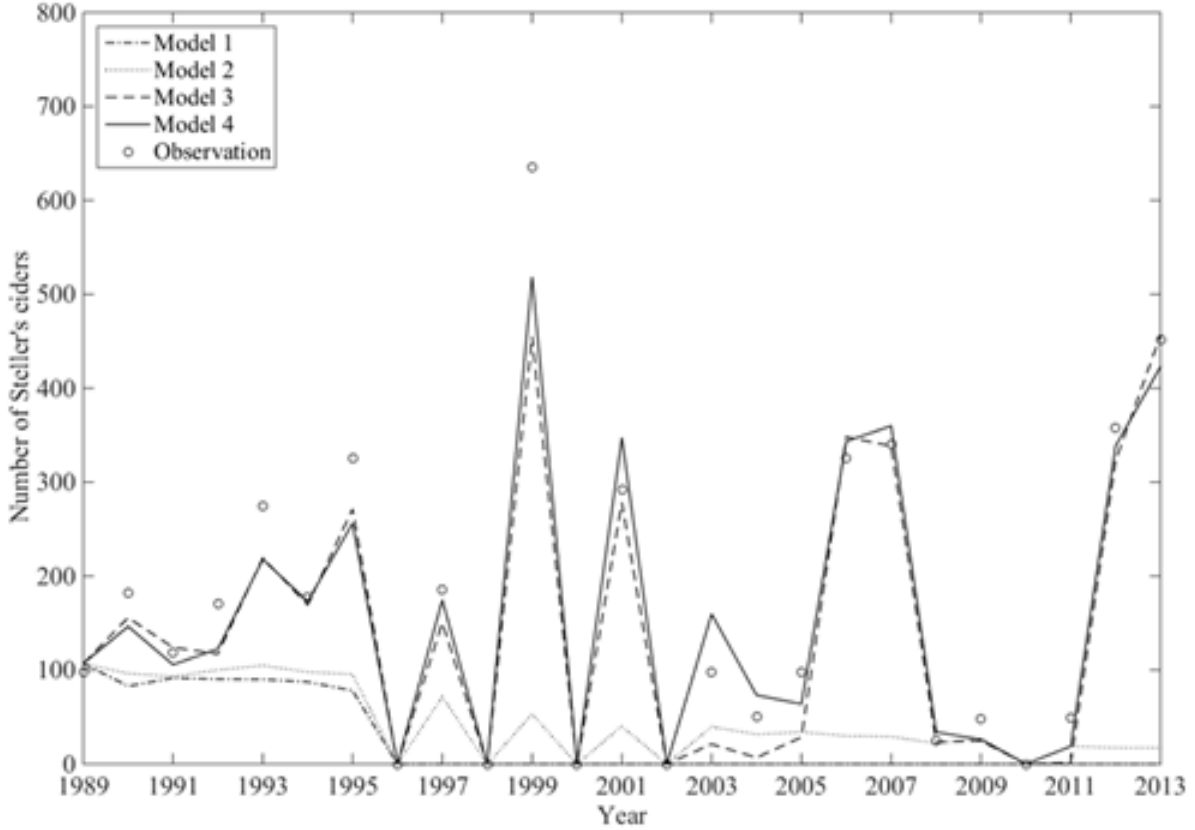


Figure 1. Posterior means of expected counts from sequential importance sampling with resampling (SISR) for four candidate models compared to annual estimated counts from aerial surveys of Steller's eiders on the Arctic Coastal Plain of Alaska from 1989 to 2013. Models 1 and 2 were closed population models and were unable to track with the highly variable observations. Models 3 and 4 were open population models and fit the observed data closely.

population, N_t^x . Each particle is projected forward to $t = 1$, generating the state pdf $g_1(N_1^x | N_{0:t-1}^x, \theta_1^x)$. The particles are assigned weights proportional to the likelihood of the observation at $t = 1$,

$$w_1^x w_1^x w_1^x \propto \frac{f_1(c_1 | N_1^x, \theta_1^x) * g_1(N_1^x | N_{0:t-1}^x, \theta_1^x)}{g_1(N_1^x | N_{0:t-1}^x, \theta_1^x)}.$$

Each particle is resampled according to its associated weight w_t^x , using a bootstrap filtering technique (Gordon and others, 1993). The parameter distributions are then kernel smoothed using a multivariate normal distribution to mitigate the issue of particle depletion (West, 1993a, b; Newman and Lindley, 2006; Newman and others, 2009; Dunham and Grand, 2016). The parameters are transformed to the real number line, \mathbf{R}^1 , before smoothing and are back transformed afterward. The survival rates were logit-transformed, and the fertility rates were square-root transformed to ensure normality. For each particle, N_t^x is redefined as the weighted resampled state, and the parameters θ_t^x are redefined as the resampled and smoothed values. The resulting particles are used to generate

the prior distribution at the subsequent time step, following a first-order Markov process. This procedure is repeated sequentially through the final time step of available observation data, using the state process distribution to project forward to the next time step, then adjusting the resulting predicted state distribution using the weighted resample according to the observation process, followed by kernel smoothing the parameter distributions. For additional information on the methodology, refer to Doucet and others (2001), Newman and others (2006), Dunham and Grand (2016), and (or) Newman and others (2009) for more detailed descriptions on the sequential importance sampling/resampling algorithm.

2.4 Model Selection

To evaluate which model best fit the aerial survey data, we used Bayesian model weight updating. One of the primary benefits of SISR is the production of posterior estimates at each time step (Newman and others, 2009). This process provides an estimate from each model, for each year, which can then be used to evaluate the fit of the models to each year of available data. Initially, each model was assigned equal weight. Using Bayes' theorem, the model weights were

updated sequentially, given the prediction provided by each model compared to the actual observation from that year:

$$P(model_t^j | data_t) = \frac{P(model_{t-1}^j) * P(data_t | model_t^j)}{\sum_j P(model_{t-1}^j) * P(data_t | model_t^j)}$$

where $P(model_t^j | data_t)$ is the model weight for model j in time step t , $P(model_{t-1}^j)$ is the prior probability of model j , $P(data_t | model_t^j)$ is the likelihood of the data given the model, and $data_t$ is the actual observation from the aerial survey at that time step. This method was used in similar applications by McGowan (2015) to compare multiple competing models of population dynamics using sequential observation data. Additionally, this approach was discussed in Barker and Link (2013) and in Hooten and Hobbs (2015). The models, SISR algorithm, and analysis were coded using MATLAB version 8.4.0.15 (The Mathworks, Inc., Natick, Massachusetts, United States).

3 Results

The expected annual counts from each model indicate that Models 1 and 2, which represented closed systems, did not fit the observations well, likely due to the inability of the closed model predictions to vary enough to capture the variability of the data (fig. 1). Models 3 and 4, which characterized open populations, tracked well with the aerial survey data (fig. 1). Although the annual estimates for Models 3 and 4 both seemed to fit the data, the results of the model weight updating suggested that Model 4 fit the data the best (fig. 2). The combined results of the SISR algorithm and the Bayesian model weight updating strongly support that the Alaskan breeding population is an open population, with movement between the Alaskan and Russian-Pacific breeding populations.

Considering the overwhelming support for Model 4 as the most likely population process model, we focused on the results from Model 4. The posterior results at the final time step for the parameter estimates from Model 4 indicated that adult survival and fertilities may be lower than previously expected (fig. 3; table 1). The posterior on juvenile survival rates remained very similar to the prior distribution. Despite the large distribution from which the algorithm had to choose for each demographic parameter, the posteriors for the time-invariant parameters were similar although more precise than the prior distributions.

Because the time-varying parameter I_t was treated as a random effect and therefore did not evolve over time, we reported the weighted, resampled posterior for three time periods (fig. 4). These three time periods were chosen because they represent the variability in the estimated number of immigrants. The prior distribution on I_t was roughly half non-zero particles over a uniform distribution from 1 to 3,000 individuals (fig. 4). In 1997, which immediately

followed a nonbreeding (that is, zero count) year and a generally stable population, the estimated number of immigrants was very low (<300) with a high probability (approximately 85 percent) of there being zero immigrants (fig. 1). In 1995, the posterior estimate of immigrants suggested there was about a 50 percent probability of zero immigrants, but the remainder of the distribution suggested that there were likely between 300 and 600 immigrants. In 2004, the posterior distribution was heavily skewed toward an immigration event. The probability of zero immigrants was very small (approximately 15 percent), suggesting that the observation from this year (following successive low count years) was most likely the result of a relatively large number of immigrants, approximately 600 to 1,100 individuals.

4 Discussion

To properly and efficiently monitor and manage a population, it is critical to understand the dynamics of the population and, most importantly, the fundamental structure and underlying processes that govern the population. Bayesian state-space models provide a flexible framework to incorporate multiple sources of uncertainty while addressing competing models of population process. For further analysis of population status and trend required for Steller's eiders, an appropriate model of population process is necessary. Previous attempts at estimating population trend and extinction risk suggest that to effectively model population dynamics, one must allow for movement between the larger Russian-Pacific population and the Alaskan population, otherwise predictions from these models will be inaccurate (J. Runge, written commun., Nov. 2004).

Our results indicate that the most likely process model includes both immigration and nonbreeding events; therefore, it will be necessary to include these events in projection models for predicting future population states and estimating extinction risk. In addition, previous studies of the three geographically distinct breeding populations suggest that there is no significant genetic differentiation between the Alaskan and Russian-Pacific breeding populations (Pearce and others, 2005). Although there may not have been sufficient time since de-glaciation for significant genetic differences to evolve, these results are consistent with movement between the two breeding populations, providing additional support for our conclusion that the Alaskan breeding population is open.

This conclusion is evident based on model weight updating after the first 2 years of observation data. At this point, Models 3 and 4 provided the best fit to the data (figs. 1, 2). Following the first set of zero count years in 1996 and 2000, Models 3 and 4 were the only models that were able to fit the observations because they included immigration (fig. 1). This result was expected because a species with such low fertility would be highly unlikely to recover from zero years or successive low count years from recruitment alone. The high

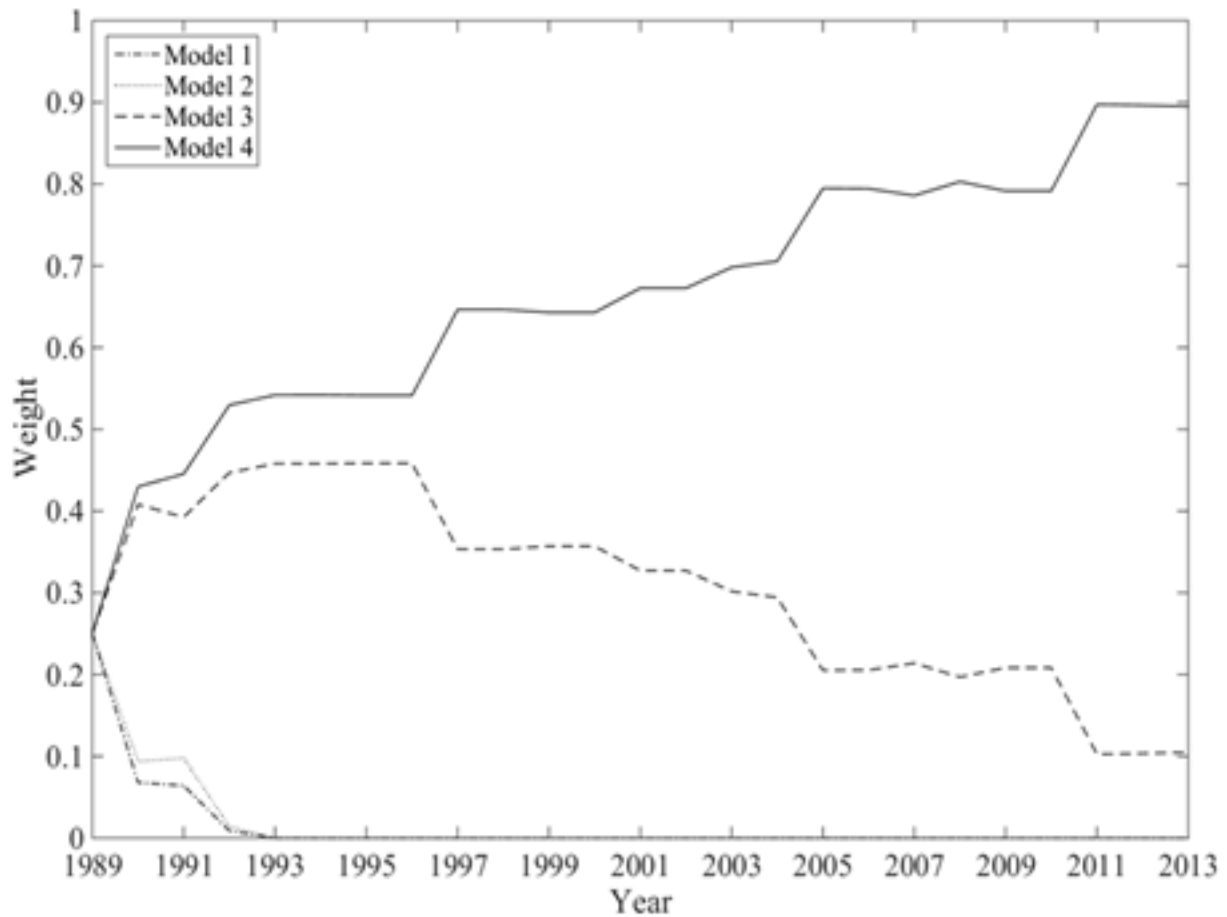


Figure 2. Model weight evolution from Bayesian updating for four candidate models of Steller's eider populations on the Arctic Coastal Plain of Alaska from 1989 to 2013. Although Models 3 and 4 produced reasonable count estimates, Model 4 outperformed all of the other models.

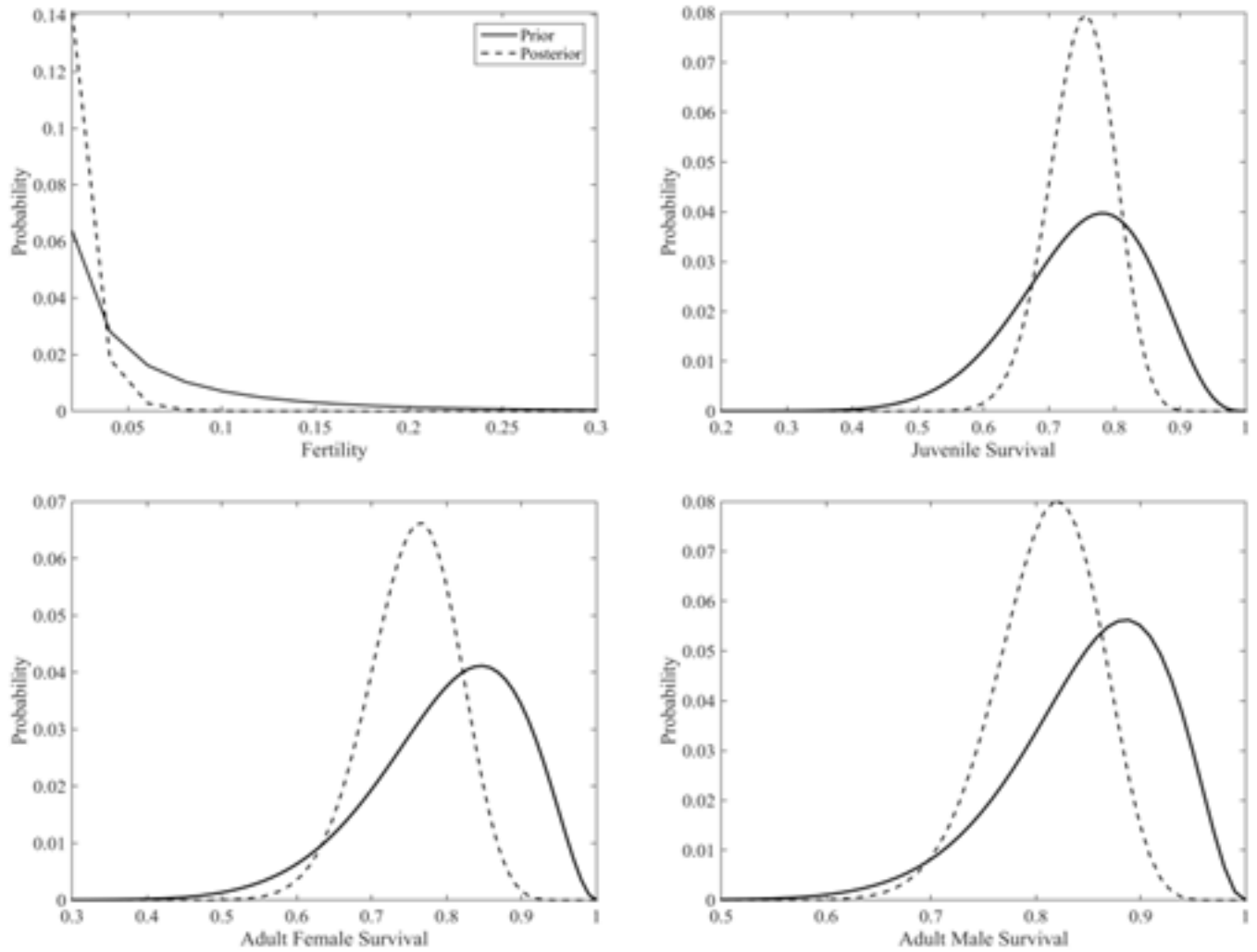


Figure 3. Prior and posterior distributions for fertility and survival rates. Posterior distributions are from the final time step (year 2013) from Model 4. Posterior means were lower and more precise than priors for each parameter.

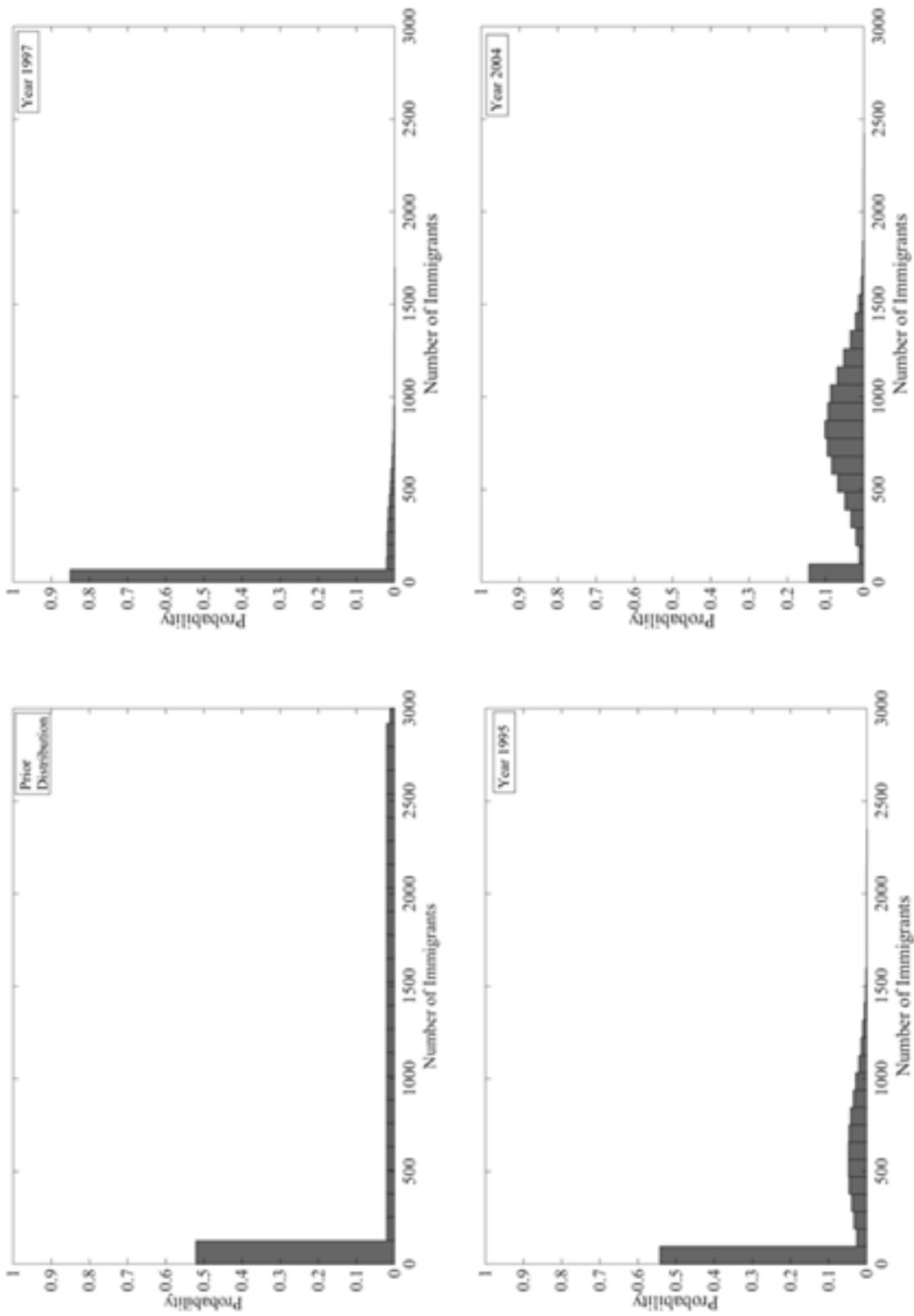


Figure 4. Prior and three posterior distributions for immigration (I_t) from Model 4. The prior distribution is a zero inflated uniform distribution, and the posterior distributions are representative of years with low (1997), medium (1995), and high (2004) probability of immigrants.

variability in the number of observed birds, combined with the extremely low fertility rates of this species, points to frequent supplementation to the Alaskan population through immigration from the Russian-Pacific population.

Model 4 gained the majority of the weight following updates based on data from 1997 because the high count in 1999 was better explained by a resident population and a large influx of immigrants. Model 3 was representative of a population that was predominantly transient; the algorithm was unable to provide an adequate estimate of the 1999 count based entirely on immigrants. Biologically, an entirely transient population is relatively unlikely, specifically in waterfowl which typically exhibit high breeding area fidelity (Anderson and others, 1992). The support for Model 4 over Model 3 provides further evidence for breeding area fidelity by the Alaskan breeding population. Although there is some evidence for this behavior (D. Safine, USFWS, oral commun., 2016) and it is typical in sea duck species (Phillips and Powell, 2006; Mallory, 2015), the low and highly variable breeding numbers and difficulty associated with tracking these birds over multiple years has made it extremely challenging to estimate breeding area fidelity for this population.

Periodic nonbreeding has been observed in Steller's eiders near Barrow (Quakenbush and others, 2004) and in Russia on the Lena River (Solovieva, 1999) as well as in common eiders (*Somateria mollissima*) in Northumberland (Coulson, 1984, 2010), making it an important parameter to incorporate into population models. However, in some years when zero birds were counted on the ACP survey, some birds were present and bred near Barrow (Safine, 2013). The number and distribution appear to have been very limited and would not be sufficient to explain the large number of breeding birds present in subsequent years. Thus, our conclusions would be unaffected. Speculation regarding the factors influencing these nonbreeding events in Steller's eiders include associations with high densities of lemmings, nesting pomarine jaegers (*Stercorarius pomarinus*), and snowy owls (*Bubo scandiacus*) (Quakenbush and others, 2004). The correlation of nonbreeding birds with low lemming density is based on the hypotheses that, in years with high lemming density, the lemmings provide an alternative food source for predators of eiders (Quakenbush and others, 2004). Nonbreeding in correlation with high density of nesting pomarine jaegers and snowy owls has been suggested because these species are highly territorial of their nests and may provide protection for neighboring Steller's eiders (Quakenbush and others, 2004). Additional explanations for nonbreeding events in eiders may be related to food availability, climate change impacts, and (or) oceanic regime shifts, in which nonbreeding may be a strategy to reduce the risk of mortality associated with poor breeding conditions (Coulson, 1984, 2010). Cross-seasonal effects of nutrient availability and storage have been shown to affect breeding success in common eiders (Lehikoinen and others, 2006; Descamps and others, 2010), and oceanic regime shifts have been shown to be correlated with population changes in eider species (Coulson, 2010; Flint, 2013). It is

possible that oceanic conditions and relative seasonal climate may have strong effects on the overall body condition and, therefore, breeding probability of Steller's eiders because they are inextricably linked to the ocean for the majority of their food resources (Fredrickson, 2001; Flint, 2013). The cross-seasonal and carryover effects of climate, regime shifts, and resource availability on breeding are extremely complex and vary among species and location (Flint, 2013; Alisaukas and Devink, 2015). These effects could be important ecological mechanisms behind the nonbreeding events of this population, and additional studies regarding these effects on breeding of this population would be invaluable to the greater understanding of the dynamics of the population. Although it remains difficult to say with any certainty what ultimately causes periodic nonbreeding, the results of this modeling effort are supportive of periodic population level nonbreeding.

This species is characteristically long-lived, with high adult survival and low fertility (Fredrickson, 2001). Previous studies and expert opinion informed the prior distributions on the demographic rates, therefore providing reasonable estimates and relative uncertainty in these rates (Flint, Petersen, and others, 2000; Reynolds, 2007; Frost and others, 2013). However, survival estimates for adults were based on studies that included largely nonbreeding adults at Izembek Lagoon, Alaska (Flint, Petersen, and others, 2000; Reynolds, 2007; Frost and others, 2013). We would expect lower survival rates for breeding adults because of the relative costs associated with reproduction (Williams, 1966). Posterior estimates of mean adult survival of both sexes were significantly lower than values estimated from previous studies (table 1) (Flint, Petersen, and others, 2000; Reynolds, 2007; Frost and others, 2013). These low survival rates may indicate that the studies conducted on the molting grounds are not truly representative of the Alaskan breeding population and that this population has considerably lower survival rates than the larger Russian-Pacific population. The mean posterior estimate for fertility was also lower than expected (table 1). Although low fertility is common among long-lived sea ducks, these results are surprising because predator control, primarily fox control, was implemented in 2005 to increase fertility and adult female survival (Savory and others, 2009, 2010). This may indicate that fox control either did not affect the demographic rates, or the effect was not substantial enough to detect through the observed data. There could also be an unidentified relation with the removal of foxes and an increase in nest predation from avian predators which would offset any positive effect on nest survival. Additional explanations for lower demographic rates could be attributed to a population breeding on the periphery of its range. Öst and others (2016) found that a population of common eiders breeding along the eastern edge of their range had substantially lower reproductive success than a population breeding in the core of their range. Low fertility may be the result of negative impacts on the survival of immature birds once they leave the breeding grounds (birds younger than 1 year old). Local climate issues on breeding and wintering sites may not only affect nonbreeding behavior but

also negatively impact survival of young birds, which could lead to reduced fertility rates (Mallory, 2015). It is difficult to point to one specific cause of low fertility; it may be caused by a combination of factors that exacerbate the overall effects of predation and climate on fertility.

Current recovery criteria for the Alaskan breeding population rely heavily on the ability to estimate population viability in the future (U.S. Fish and Wildlife Service, 2002). This modeling effort provides an informative model of population process that can be used to examine future population trends and assess the population in terms of the current recovery and reclassification criteria. Previous attempts to quantify population viability and trend concluded that the Alaskan breeding population was declining (Stehn and others, 2013; J. Runge, written commun., Nov. 2004). However, J. Runge (written commun., Nov. 2004) suggested that, without accounting for dispersal from the larger Russian-Pacific population, these results were likely an inaccurate representation of the population. The results of this modeling effort demonstrate that immigration and periodic nonbreeding are necessary to explain the observations and, therefore, should be included in any predictive modeling of this population to obtain accurate estimates of population viability.

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