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Modelling pinniped abundance and distribution by combining counts at terrestrial sites and in-water sightings

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ABSTRACT

Pinnipeds are commonly monitored using aerial photographic surveys at land- or ice-based sites, where animals come ashore for resting, pupping, molting, and to avoid predators. Although these counts form the basis for monitoring population change over time, they do not provide information regarding where animals occur in the water, which is often of management and conservation interest. In this study, we developed a hierarchical model that links counts of pinnipeds at terrestrial sites to sightings-at-sea and estimates abundance, spatial distribution, and the proportion of time spent on land (attendance probability). The structure of the model also allows for the inclusion of predictors that may explain variation in ecological and observation processes. We applied the model to Steller sea lions (*Eumetopias jubatus*) in Glacier Bay, Alaska using counts of sea lions from aerial photographic surveys and opportunistic in-water sightings from vessel surveys. Glacier Bay provided an ideal test and application of the model because data are available on attendance probability based on long-term monitoring. We found that occurrence in the water was positively related to proximity to terrestrial sites, as would be expected for a species that engages in central-place foraging. The proportion of sea lions in attendance at terrestrial sites and overall abundance estimates were consistent with reports from the literature and monitoring programs. The model we describe has benefit and utility for park managers who wish to better understand the overlap between pinnipeds and visitors, and the framework that we present has potential for application across a variety of study systems and taxa.

1. Introduction

Characterizing the abundance and spatial distribution of animal populations is a fundamental challenge in ecology (Scott et al., 2002; Krebs, 2009). The task typically involves fitting a model that relates counts or detections of animals to environmental variables to make inferences about the state of a population and the location of individuals belonging to the population (Hegel et al., 2010). Unfortunately, there are common sources of sampling bias that can produce inaccurate inferences from this basic model, including nondetection of animals that are actually present in the survey area (Gu and Swihart, 2004; Kellner and Swihart, 2014), and temporary emigration of animals during periods of assumed geographic closure (Valente et al., 2017; Yamaura and Royle, 2017). Accounting for nondetection and temporary emigration is particularly important for species that are cryptic or highly mobile within the study area (MacKenzie et al., 2002; Chandler et al., 2011).

Pinnipeds are a group of animals that typify these sampling-related challenges. These species are difficult to study because they are highly mobile and occupy the boundary between marine and terrestrial environments. Locating and enumerating animals while in the water is often considered infeasible; thus, population monitoring is generally carried out by counting animals at terrestrial or ice sites where animals come ashore for resting, pupping, molting, and to avoid predators (Boyd et al., 2010). Although counts at locations on ice platforms and on land are sufficient for monitoring broad-scale population change (Small et al., 2003; Mathews et al., 2011), they communicate no information about the distribution of animals in the water. For the cases in which in-water sighting or remote tracking data are available, they are often analyzed separately from spatially implicit count data gathered at fixed sites (Herr et al., 2009; Himes Boor and Small, 2012; Vincent et al., 2017). The ability to assess factors that influence the in-

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water distribution of pinnipeds is especially relevant to management and conservation because of the potential for interactions between pinnipeds and fishery operations (Read, 2008; Kovacs et al., 2012).

Many of the challenges associated with surveying pinnipeds and synthesizing information from different data sources can be addressed by adopting a hierarchical modelling approach (Ver Hoef and Frost, 2003; Ver Hoef et al., 2014; Williams et al., 2017). Hierarchical models represent ecological processes as latent state variables and the data obtained from surveys as a function of the true state and an incomplete and potentially misleading observation process (Royle and Dorazio, 2008; Kery and Schaub, 2011). This approach allows parameters to be separately related to predictor variables (e.g., sampling effort, environmental attributes), and facilitates the integration of multiple sources of data into a single model (Kery and Royle, 2015). Integrated models use different sources of information to inform a shared set of parameters, which can improve the precision of estimates, fill important gaps in information, and more realistically represent ecological processes (Schaub et al., 2007; Abadi et al., 2010; Cole and McCrea, 2016). Previous developments in integrated modelling have focused on estimating demographic rates from survey and mark-recapture data (Buckland et al., 2004; Besbeas et al., 2009), but there has also been recent progress in the development of models that incorporate different types of spatially explicit data (Chandler and Clark, 2014; Nadeem et al., 2016).

The objective of this paper is to develop a hierarchical model for pinnipeds and similar species and to use this model to broadly characterize the abundance and distribution of Steller sea lions (*Eumetopias jubatus*) in Glacier Bay National Park in southeastern Alaska. Our approach integrates counts from aerial photographic surveys at terrestrial sites and in-water sightings from vessel surveys, and combines elements of N-mixture models (Royle, 2004; Dail and Madsen, 2011) and models that use unstructured sampling approaches (Thompson et al., 2012; Russell et al., 2012; Broekhuis and Gopalaswamy, 2016). Replicated counts of sea lions at terrestrial sites inform estimates of site-level abundance and the probability that an individual is out of the water, which we term "probability of attendance". In-water sightings and abundance parameters are then used to estimate sighting intensity and the spatial distribution of animals.

We fit the model to counts from aerial photographic surveys at a terrestrial haul-out site (Womble et al., 2005, 2009; Mathews et al., 2011), and in-water sightings gathered opportunistically during vessels surveys for humpback whales (*Megaptera novaeangliae*; Gabriele and Lewis, 2012; Keller et al., 2016). We evaluated the performance of the model using a simple sensitivity analysis and by comparing model predictions of abundance and attendance to those reported by monitoring programs and from results derived using different methods (e.g., tagged animals) reported in the scientific literature. This model is intended to form part of a larger decision tool for managing wildlife and visitor restrictions within Glacier Bay National Park.

2. Methods

Our model is composed of two sub-models that describe the abundance of pinnipeds at particular terrestrial sites and their distribution in the water, based on sightings from vessels. The first sub-model, which we term the "count portion" informs several key parameters: (1) overall abundance of pinnipeds in the study area and (2) the probability that an animal is out of the water, and thus available to be counted. The second sub-model, which we refer to as the "sighting portion" uses sightings of pinnipeds in the water to describe their spatial distribution while accounting for imperfect detection and non-uniform survey effort. The model assumes that pinnipeds not available to be counted at terrestrial sites during aerial surveys, are in the water. The number of individuals in the water at a given time is derived from the count model and combined with data on in-water sightings to make inferences about spatial distribution. In the following sections we outline the data sets involved in the Steller sea lion case study, then define the structure of the model and its attributes. Finally, we describe our procedures for fitting the model and evaluating its performance.

2.1. Steller sea lions in Glacier Bay National Park

Steller sea lions are distributed along the North Pacific rim from Japan to California, USA (Loughlin et al., 1987). The species exhibits central-place foraging behavior and typically aggregates at rocky sites and islands, from which they radiate and feed primarily on marine fishes and invertebrates (Womble and Sigler, 2006; Fritz et al., 2015). Sites may be occupied throughout the year or seasonally (Sease and York, 2003), with seasonal movements driven by life-history events (e.g., pupping, breeding) and shifts in prey resources (Womble et al., 2005, 2009). In Alaska, Steller sea lions give birth to pups from mid-June to early July. Steller sea lions have garnered considerable conservation attention in the last several decades due to population declines (Trites and Donnelly, 2003). The species occurs in two distinct population segments: the western distinct population segment, west of 144 °W, which is listed as endangered and the eastern distinct population segment, which was delisted in 2013 (National Marine Fisheries Service, 2013; Allen and Angliss, 2015). The Glacier Bay region represents a mixing zone between the endangered western Distinct Population Segment (wDPS) of Steller sea lions and the recently delisted eastern Distinct Population Segment (eDPS; Jemison et al., 2013; O'Corry-Crowe et al. (2014); Rehberg et al., 2018).

We restricted our analysis of count data to terrestrial sites in the inside waters of Glacier Bay that were occupied consistently from May through September and where aerial photographic surveys were conducted regularly. This resulted in the inclusion of South Marble Island, a haulout site that is occupied by sea lions during May through September which coincides with the main tourist season in the Glacier Bay. Sites that were excluded were Graves Rocks, a rookery along the outer coast of Glacier Bay, and several sites (Tarr Inlet, Gloomy Knob, Harbor Point, Cape Fairweather, and Point Carolus) that are typically occupied during other times or year or for briefer time periods, (Fig. 1). South Marble Island was initially colonized by sea lions around 1985 and was initially occupied only seasonally; however, since approximately 2001 Steller sea lions have been present at South Marble Island throughout the year (Womble et al., 2005, 2009; Mathews et al., 2011). From 2001–2004, the number of Steller sea lions at terrestrial sites in Glacier Bay were monitored during monthly aerial photographic surveys (Womble et al., 2005, 2009). Beginning in 2005, sea lions were only monitored during June and August in conjunction with harbor seal aerial photographic surveys (Womble et al., 2009). We assembled the aerial photographic counts data set by compiling 101 observations made by National Park Service personnel with 5 observations from the National Marine Fisheries Service - Marine Mammal Laboratory Steller Sea Lion Count Database (2009–2013; Fritz et al., 2015). The data set included counts of non-pup Steller sea lions from aerial photographic surveys from 2001 to 2017, with the exception of 2006 (Fig. 2).

Aerial surveys coincided with opportunistic sightings of Steller sea lions recorded during vessel surveys for humpback whales, which occurred in the Park annually from April through October. During these surveys, a small vessel (4.9–6.7 m) actively searched for whales using prior knowledge of preferred habitat, and visual and auditory signals from whales (e.g., breaching and spouting). The protocol for recording sightings of non-target marine mammal species during surveys has remained relatively consistent through time (Gabriele and Lewis, 2000, 2012; Keller et al., 2016. Observers recorded the location and estimated group size of marine mammals that pass within 100 m of the survey vessel and make efforts to avoid double counting. The study area for the spatial component of our analysis encompassed a 1332 km^2 area, including the entirety of Glacier Bay and extending slightly into Icy Strait to the south (Fig. 3). We compiled sighting and track point data from 610 survey days that occurred between May and September,

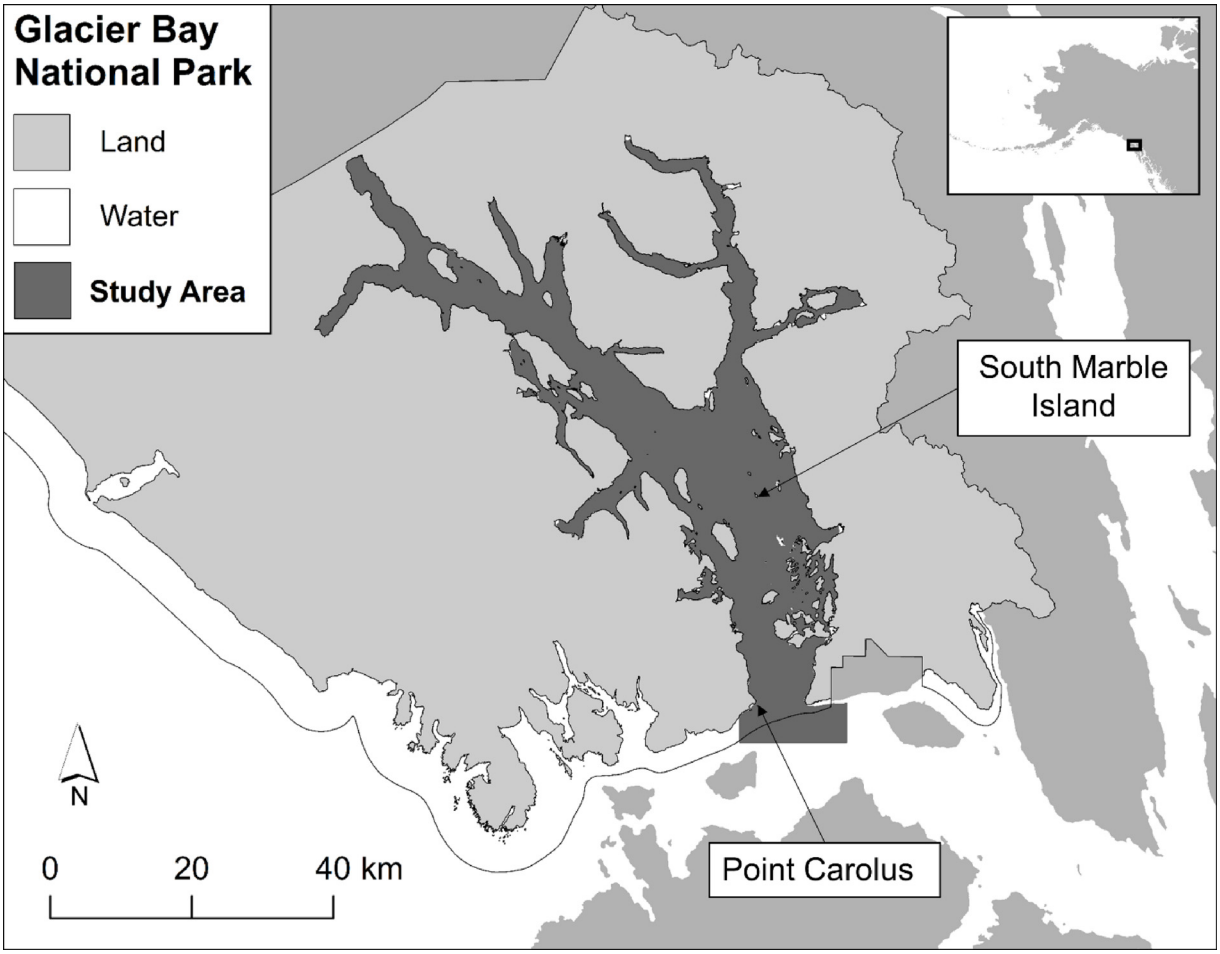

Fig. 1. Study area in the vicinity of Glacier Bay National Park, Alaska.

2006–2016 (Fig. 3). The lack of temporal overlap between this data set and that of the aerial counts did not pose a problem, because the in-water sighting data set still included 10 years and our specific objective was to estimate the average in-water distribution of sea lions. We omitted sightings of sea lions with > 20 individuals, due to concerns about miscounting; these sightings accounted for ~0.4 % of the total.

2.2. Model description

2.2.1. Basic structure

The abundance of sea lions during year i were assumed to be Poisson distributed with mean and variance (λ_i)

$$N_i \sim Pois(\lambda_i).$$

We modeled λ_i as a log-linear function of the annual site abundance parameters (α_i)

$$\log(\lambda_i) = \alpha_i$$

which were treated as fixed effects in the model (i.e., log abundance for each year was estimated separately). We linked counts of sea lions to abundance with a binomial distribution:

$$C_{it} \sim Bin(N_i,\ \gamma_{it}),$$

where γ_{it} is the probability of a sea lion being in attendance at the terrestrial site on day t of year i (Fig. 4). By adopting this parameterization, we assumed that variation in counts at sites was driven solely by changes in attendance probability, and that the probability of detecting an individual sea lion given presence was equal to one. We believed this assumption to be reasonable because counts were determined by scrutinizing aerial photographs rather than counting from plane or water (Snyder et al., 2001; Boyd et al., 2010). We used abundance and attendance probabilities to derive the expected number of sea lions not in attendance at the terrestrial site, and therefore present in the water on a given day (W_{it}):

$$W_{it} = \lambda_i \bullet (1 - \gamma_{it}).$$

We assumed that the population of animals in the water at a given time were distributed across J non-overlaping sections, each with probability of occurrence π_j ($\sum_{j=1}^{J} \pi_j = 1$). We partitioned the study area into 60 non-overlapping sections, by overlaying a 500 m grid on the study area, and then merging cells with an area less than 12.5 km^2 with their neighbors. Eleven of the sections were not visited by the whale survey vessel and included areas that are closed to vessels from May 1 to September 15 (Beardslee Islands, Hugh Miller Inlet, Rendu Inlet, and Adams Inlet), and areas in the East and upper West Arms of Glacier Bay.

Finally, we assumed that in-water sightings of sea lions in each section were linked to the expected in-water abundance by a Poisson distribution:

$$S_{ijtr} \sim Pois(W_{it} \bullet \pi_j \bullet P_{ijtr}),$$

where S_{ijtr} is the number of sea lions sighted in year i, in section j, on day t, and during time-interval r ; P_{ijtr} is the probability of detecting an individual sea lion. We include the subscript r to signify that sections could be, and often were, visited multiple times in a day. We represented sightings as a Poisson process because they are rare events that occur with a frequency proportional to the expected number of sea lions present and that detection probability was tied to a measure of survey effort. Sea lions are highly mobile within the study area and

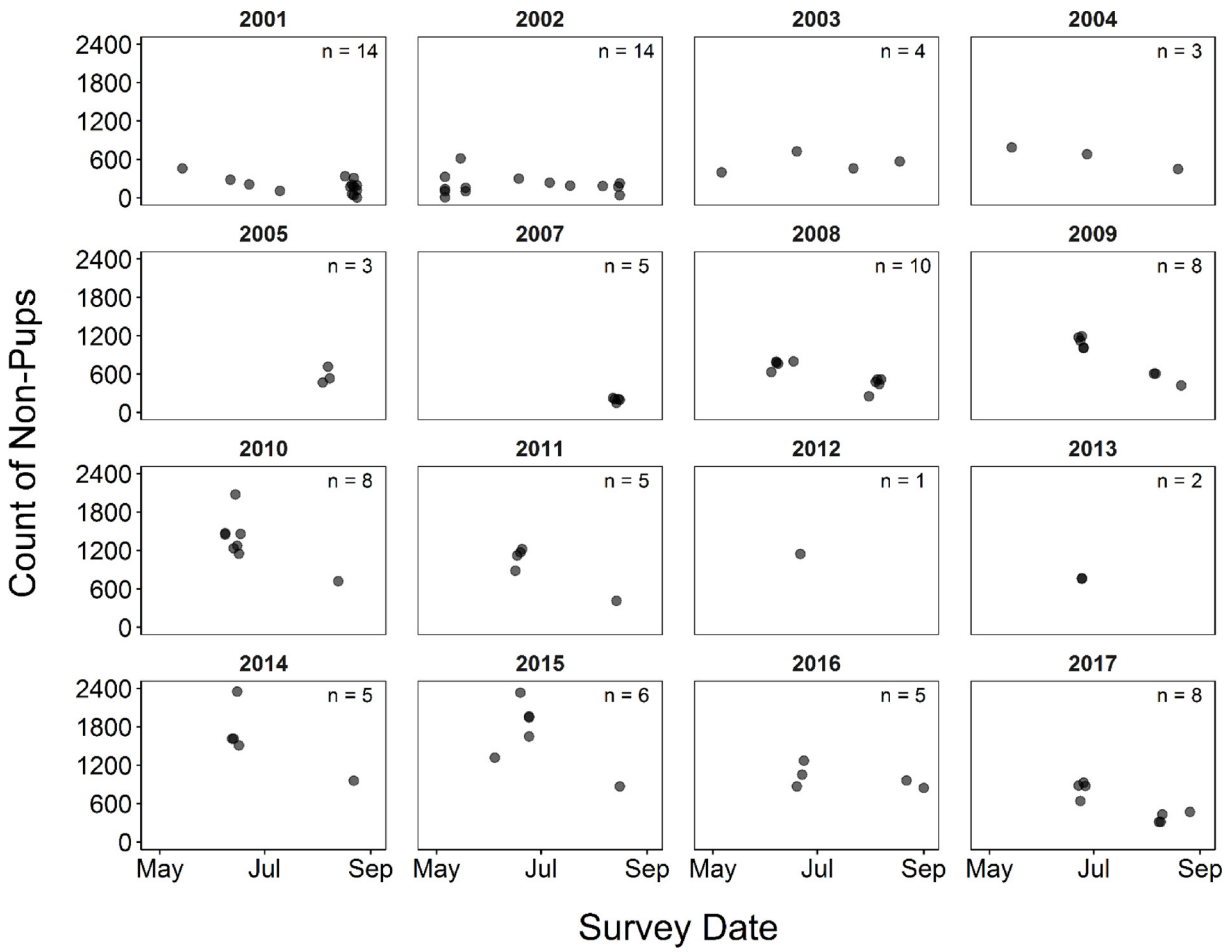

Fig. 2. Counts of non-pup Steller sea lions at South Marble Island in Glacier Bay National Park, Alaska, from aerial photographic surveys. Sample size is displayed in the upper right corner of each panel.

constantly transitioning between land and water, thus modelling sightings in terms of a rate of encounter was more suitable than, for example, apportioning the in-water population at a given time across all sections using a multinomial distribution.

2.2.2. Incorporating predictor variables

The basic model structure provided a framework for evaluating relevant predictors of ecological and observation processes. Additional information was included by defining parameters using linear combinations of predictors and applying appropriate link functions. All linear predictors may also contain random error terms (random effects) at different levels, however, care should be taken to ensure that chosen combinations of error terms and parameters are identifiable (Cole and McCrea, 2016). We defined mean annual abundance using fixed effects via a log link function, however, many alternative parameterizations for mean abundance are also possible. For example, it would be relatively simple to represent mean abundance using a trend line or random intercept terms, as in a formal N-mixture model.

We modeled attendance probability (γ) via a logit link function, defined as.

$$logit(\eta) = \frac{1}{1 + e^{-(\eta)}},$$

where η is a linear predictor (e.g., $\beta_0 + \beta_1 X$). Hereafter we denote this transformation using the left-hand expression logit(η). To identify an appropriate model for interpretation, we fit and evaluated six alternative linear predictors for attendance probability and used a model selection procedure to identify a top model. Candidate models included combinations linear and quadratic effects for the day of year (DOY), a linear effect for the number of hours before or after the nearest high tide ($TideHour$), as well as a null model. All linear predictor also included a daily normal random error term meant to account for extra-binomial variation (τ_t) which may be the result of behavioral heterogeneity (Dorazio et al., 2013). The global model with the full set of predictors was:

$$\text{logit}(\gamma_{it}) = \beta_0 + \beta_1 DOY_t + \beta_2 DOY_t^2 + \beta_3 TideHour_{it} + \tau_t,$$

$$\tau_t \sim Norm(0, \sigma_{attend}),$$

with β s denoting coefficients. We hypothesized that more sea lions would be attendance at lower tide (i.e., positive relationship with the number of hours to closest high tide), as this would relate to there being more space on land on which to haul out. It should be noted that the $TideHour$ is measured at a finer scale than DOY and known for all aerial counts and all survey intervals indexed by r, thus inclusion of this predictor would result in sub-daily predictions of in-water abundance. Attendance probability was the only parameter for which we compared alternative sets of predictors.

We related the distribution of sea lions across sections to several predictors using a multinomial logit link function (Agresti, 2013; Royle and Converse, 2014), where probability of occurrence for all but one of the sections ($J - 1$) is defined as:

$$\pi_j = \frac{e^{(\theta Z_j)}}{1 + \sum_{j=1}^{J-1} e^{(\theta Z_j)}};\ j = \{1,2,\ 3,...,J - 1\},$$

and π_J serves as a reference category. Section-specific probability of

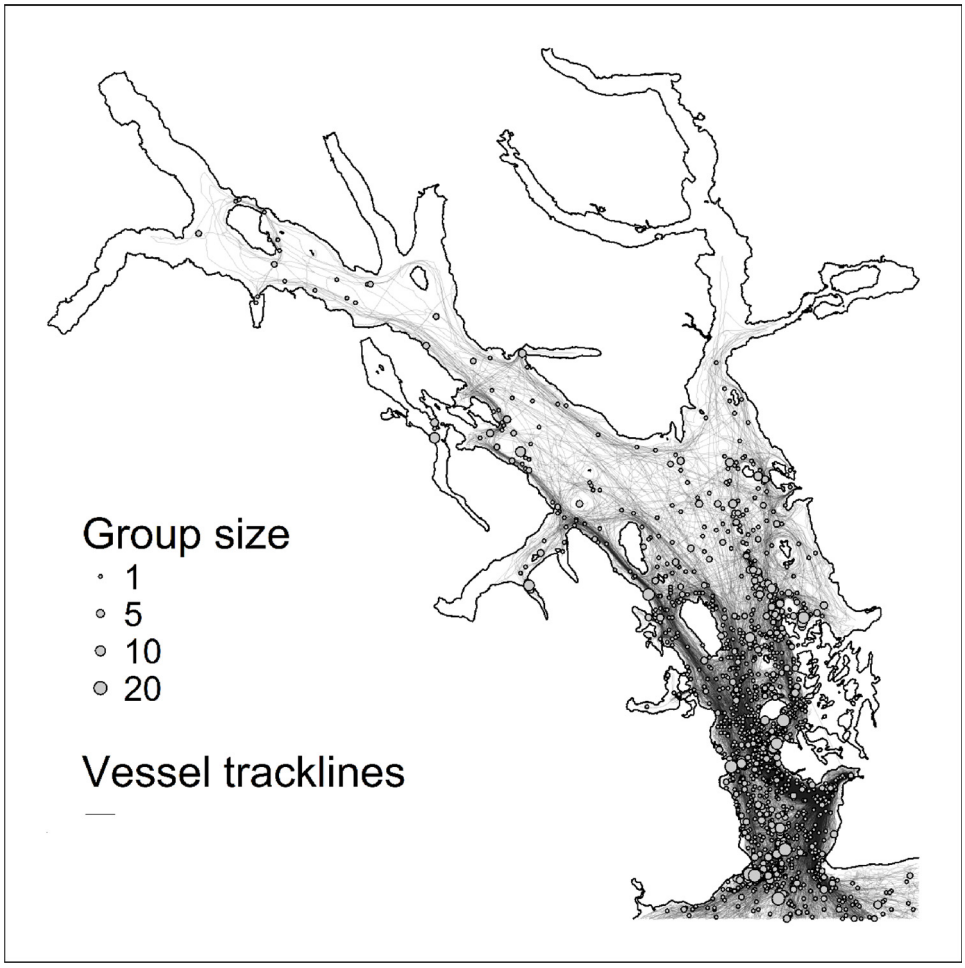

Fig. 3. Steller sea lion sightings recorded during vessel surveys in the vicinity of Glacier Bay National Park, Alaska (2006–2016).

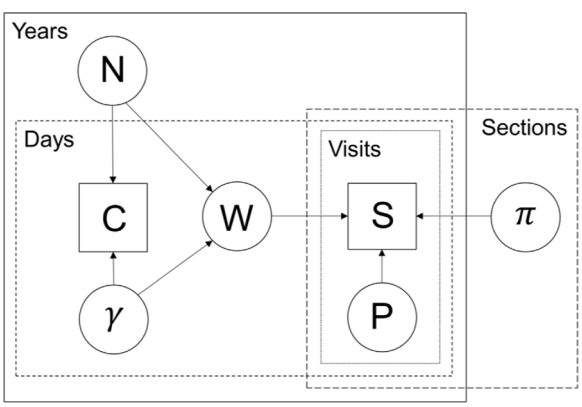

Fig. 4. Directed acyclic graph describing relationships between parameters (circles) and data sources (boxes) in the pinniped abundance and distribution model applied to Steller sea lions in Glacier Bay National Park. The count portion of the model is shown on the left side of the graph with abundance of pinnipeds in the study area denoted by $\boldsymbol{N}$, the probability of attendance at a terrestrial site by $\boldsymbol{\gamma}$, the number of pinnipeds counted at a terrestrial site by C, and the number pinnipeds in the water by $\boldsymbol{W}$. The sighting portion of the model is shown on the right side of the graph, with the probability of occurrence in each survey area denoted by $\boldsymbol{\pi}$, the number of pinnipeds sighted in a section on a given day by S, and the individual probability of detection by P.

occurrence is defined by a linear combination with one or more coefficients (θ) and section-specific variables (Z). Similar to above, we denote this transformation using the left-hand expression $mlogit(\eta_j)$, where η_j is the section-specific linear predictor. Given that Steller sea lions are central-place foragers, we hypothesized that probability of occurrence in the study area was inversely related to the distance to sites where sea lions are known to haul-out of the water. We used distance to South Marble Island as a predictor of probability of occurrence in the water. In addition to including a site that is occupied throughout the year, we included distance to a seasonally occupied terrestrial site at Point Carolus, near the mouth of Glacier Bay (Fig. 2). The function used to describe section-specific occurrence probability (π_j) was as follows:

$$\text{mlogit}(\pi_j) = \theta_1 D(\text{South Marble Island}_j) + \theta_2 D(\text{Point Carolus}_j),$$

where θ s are slope coefficients, and $D()$ is a function that describes the distance, in kilometers, between the centroid of a survey cell and each of the two sites. The section nearest to Point Carolus served as the reference category in the model.

We modeled the probability of the survey vessel detecting a sea lion using a logit-linear regression with search time (*Time*) in each section as a predictor

$$\text{logit}(P_{ijtr}) = \delta_0 + \delta_1 \text{Time}_{ijtr} + \varepsilon_{ijtr},$$
$$\varepsilon_{ijtr} \sim \text{Norm}(0, \sigma_{detection})$$

whereδ s are coefficients and ε_{tr} is a random error term meant to account for additional observation error. We computed the time spent in each section by summarizing time-stamped vessel tracking data.

2.3. Model fitting

We fit the model using a likelihood-based approach, which entailed using optimization to identify the set of parameters that jointly maximize the likelihood of the observed data. A Bayesian approach could also be used to estimate parameters, as with all hierarchical models (Cressie et al., 2009). We calculated the joint likelihood for all data and parameters in the integrated model by combining the likelihood contributions of the count and in-water sighting portions of the model into a single objective function. We accomplished this by defining the objective function to be minimized as the sum of the negative log-likelihood contributions of the two portions of the model (ℓ_1 and ℓ_2):

$$\ell_{total} = \ell_1 + \ell_2,$$

where ℓ_{total} is the joint likelihood to be minimized using an optimization procedure. We carried out the analysis in the R statistical platform using the Template Model Builder (TMB) package, a tool that interprets user-defined C++ model templates and uses automatic differentiation to efficiently compute the derivatives of a joint likelihood function while also enabling random effects to be estimated via the Laplace approximation (Kristensen et al., 2015; R Core Team, 2017). For clarity, and because they are integrated out during model fitting, we ignore the random effects in the notation.

To compute the likelihood contribution of the count portion of the model we marginalized over the joint Binomial-Poisson likelihood. This process entailed summing the likelihood values over a wide range of possible abundances for each year in the manner shown below:

$$\ell_1 = -log\left[\prod_{i=1}^{I}\sum_{N_i=\max(C_i)}^{K}\prod_{t=1}^{T_i} Bin(C_{it}N_i, \gamma_t)\bullet Pois(N_i\lambda_i)\right],$$

where ℓ_1 is negative log likelihood component for the count portion of the model, I is the number of years, K is the upper bound used for N, T_i is the number of replicate counts on the i th year. We examined the influence of our choice of K by comparing joint likelihood values and abundance estimates over a range of values, ultimately deciding that a value of 15,000 was suitably large (Dennis et al., 2014). We computed the negative log likelihood component for the in-water sighting portion of the model, more simply, as the product of likelihood of all sighting records assuming a Poisson distribution

$$\ell_2 = -\log\left[\prod_{i=1}^{I}\prod_{j=1}^{J}\prod_{t=1}^{T}\prod_{r=1}^{R} Pois(S_{ijtr}W_{it}\bullet\pi_j\bullet P_{ijtr})\right].$$

Minimization of the objective function, was performed using the base non-linear optimization function nlminb(). To facilitate convergence, we normalized predictor variables for attendance probability and detection effort and estimated σ parameters on the log scale.

2.3.1. Attendance probability (γ) model selection

As noted above, we were interested in identifying a top model or models on which to base inferences about the sea lion population in Glacier Bay. We ranked six different candidate models using Akaike' information criterion (AIC). These models represented six alternative sets of predictors defining attendance probability; all other sets of predictors were held constant. We based our determination of a suitable top model on recommendations of Burnham and Anderson (2002), and we considered models within the 2.0 AIC of the top model as competitive.

2.3.2. Model evaluation

After identifying a top model for interpretation, we evaluated its performance using a simple sensitivity analysis and by comparing model predictions of abundance and attendance probability to those reported in the literature. We were interested in examining the effect that inclusion of sighting data would have on predictions of abundance and attendance, so we compared predictions from the final model with those of a reduced version of the model, in which we omitted in-water sighting data. This comparison enabled us to examine the influence of the in-water sighting data on both the estimated relationships and the precision of estimates. We compared model estimates of abundance to indices of abundance from monitoring surveys. Past studies estimated attendance probabilities by making detailed observations at haulouts or by affixing tags to sea lions, some of which were equipped to record the time spent in the water (Merrick and Loughlin, 1997; Milette, 1999; Rehberg Andrews et al., 2009; Rehberg et al., 2018). Although, many of these studies focused on the foraging behavior primarily from post-partum or lactating females at breeding sites, we assumed that attendance estimates of this age-sex class would provide an indication of the model's realism. The estimated coefficients and associated uncertainty were also used in determining the degree to which the model reasonably reflected abundance, distribution, and sighting processes.

3. Results

We successfully fit the pinniped abundance and distribution model to the Glacier Bay sea lion data to the six different candidate models. Model selection using AIC suggested substantial support for the two models containing quadratic day-of-year effects, including the global model and a model with only a quadratic day-of-year effect (Table 1). We chose to interpret the model ranked second, which described only the quadratic day-of-year effect:

$$\text{logit}(\gamma_{it}) = \beta_0 + \beta_1 DOY_t + \beta_2 DOY_t^2 + \tau_t\ .$$

We based this decision on the recommendation of Burnham and Anderson (2002) that if two competing models differ by one parameter and the difference in likelihoods is minimal, then the model with fewer parameters is preferred. This decision was further justified by the observation that the 95 % confidence interval for the *TideHour* coefficient in the global model overlapped zero and was in the direction opposite that which we had hypothesized.

Our selected model produced parameter estimates that appeared to reasonably describe the population trend at terrestrial sites and in-water distribution of Steller sea lions. The model indicated that sea lion abundance at South Marble Island increased over the study period from 2001 to 2017 (Table 2; Fig. 5). The overall abundance and attendance patterns were similar for the fully integrated model compared to the reduced version that relied solely on aerial counts. Abundance estimates were more precise for the reduced version model; however, the fully integrated model was able to estimate the annual abundance for 2006, based on in-water sighting data alone. Attendance probability predictions were comparable for the models with and without in-water sighting data, although predictions from the fully integrated model were more precise (Fig. 6). Estimated attendance probability began at 30 % in May, peaked at the end of June at 73 %, and then declined to 31 % by the end of August (Fig. 6). There was considerable uncertainty in these estimates, however, with the 95 % confidence interval for attendance probability spanning values from 37 % to 67 % for the entire

Table 1
Ranking of integrated abundance and distribution models for Steller sea lions in Glacier Bay National Park and Preserve, Alaska based on AIC. The selected model, interpreted in the remainder of the analysis, is shown in bold.

Model	AIC	ΔAIC	ℓ_{total}	k
$\lambda(t)\,\pi(Distance)\,\gamma(DOY^2 + TideHour)\,P(Time)$	9496.4	0	4721.2	27
$\boldsymbol{\lambda(t)\,\pi(Distance)\,\gamma(DOY^2)\,P(Time)}$	**9496.7**	**0.31**	**4722.3**	**26**
$\lambda(t)\,\pi(Distance)\,\gamma(DOY + TideHour)\,P(Time)$	9538.2	41.85	4743.1	26
$\lambda(t)\,\pi(Distance)\,\gamma(TideHour)\,P(Time)$	9539.7	43.29	4744.8	25
$\lambda(t)\,\pi(Distance)\,\gamma(DOY)\,P(Time)$	9539.9	43.49	4744.9	25
$\lambda(t)\,\pi(Distance)\,\gamma(.)\,P(Time)$	9542.9	46.48	4747.4	24

Table 2
Abundance estimates from an integrated abundance and distribution model for Steller sea lions in the vicinity of Glacier Bay National Park and Preserve, Alaska. LCL and UCL denote the lower and upper 95 % confidence limits, respectively. The asterisk in 2006 denotes the only year for which no aerial count data were available.

Year	Abundance	LCL	UCL
2001	511	465	557
2002	673	630	716
2003	861	648	1,074
2004	1,046	681	1,412
2005	908	622	1,194
2006*	345	133	557
2007	445	270	619
2008	915	806	1,024
2009	1,312	1,178	1,446
2010	2,183	2,062	2,303
2011	1,341	1,193	1,490
2012	1,284	1,079	1,489
2013	865	747	983
2014	2,527	2,273	2,781
2015	2,471	2,277	2,666
2016	1,447	1,192	1,701
2017	1,027	905	1,149

season (May-August). Estimates for attendance coefficients were also more precise for the combined model (Table 2

Time that a survey vessel spent in the section was found to be positively related to the probability of detection of an individual sea lion (Table 2). The coefficient for the effect of search time indicated that odds of sighting an individual sea lion increased by 51 % (32 %, 73 % [95 % LCL, UCL]) for every 30 min that the survey vessel was present. The estimated effect of predictor variables on occurrence and detection probability matched our hypotheses and were consistent with central-place foraging behavior. Coefficients for the effect of distance to South Marble Island and secondary sites were both significantly less than zero, suggesting that the geographic location of the site influenced the in-water distribution of sea lions (Table 2). However, the effect of proximity to Point Carolus was greater and more precisely estimated than at South Marble Island. Interpretation of distribution coefficients is somewhat difficult considering that the two predictor variables are based on the distance to two different sites and are thus non-independent. The clearest possible interpretation of the coefficients comes from computing an odds ratio for the slope terms separately and expressing changes in the odds of occurrence as a percentage ($100\% \times [1 - e^{\theta}]$). Based on this approach, odds of a sea lion being present in a cell diminish by 3.5 % and 5.6 % with every kilometer traveled from South Marble Island and Point Carolus, respectively. The influence of these parameters on prediction is more easily interpretable, however, by examining a map of in-water occurrence probability (π) across the study area (Fig. 7). This map describes the probabilities that a given sea lion in the water would be found in each cell; those not in the water are assumed to be present at South Marble Island Table 3.

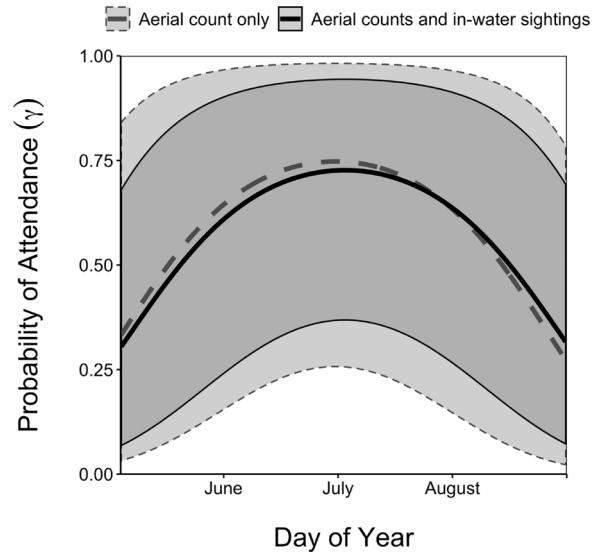

Fig. 6. Predicted probability of attendance for Steller sea lion at South Marble Island in Glacier Bay, Alaska, with 95 % prediction intervals based on models fitted using only an aerial count data set (dashed gray) and both aerial counts and an in-water sighting data set (black).

The abundance and attendance probability estimates were comparable to those reported in the literature. The pattern of increasing abundance at South Marble Island was consistent with the findings of Mathews et al. (2011) during the period when the two studies overlapped; however, there were decreases in estimated abundance in 2016 and 2017 that differed from the trend line reported by Mathews et al. (2011). Attendance probabilities reported in previous studies fell within the range estimated by our model. For example, Merrick and Loughlin (1997); Rehberg et al. (2009), and Milette (1999) reported that female Steller sea lions spent on average 47 %, 52 %, and 59 % of their time on land, respectively. The main discrepancies between our model predictions and previous work were related to seasonal patterns in attendance. Several studies that analyzed counts of Steller sea lions at South Marble Island in the early 2000s described a bimodal pattern with peaks in the spring and fall (Womble et al., 2009; Mathews et al., 2011). In contrast, our model estimated a mid-season peak in attendance (mid-June to mid-July).

4. Discussion

The objective of this study was to develop a pinniped abundance and distribution model for situations in which both in-water sighting information and counts at terrestrial sites are available. We used a hierarchical modelling framework to accomplish this task, which

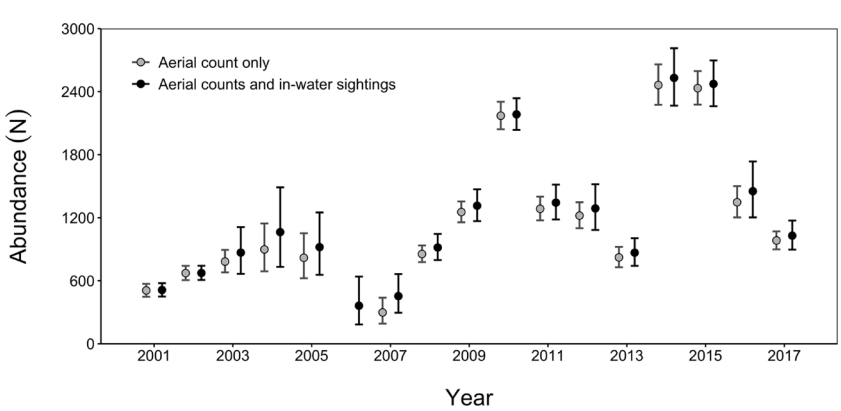

Fig. 5. Estimates of Steller sea lion abundance at South Marble Island in Glacier Bay, Alaska, with 95 % prediction intervals, based on models fitted using only an aerial count data set (gray) and both aerial counts and in-water sighting data set (black). There is no estimate for 2006 because only in-water sighting data were available that year.

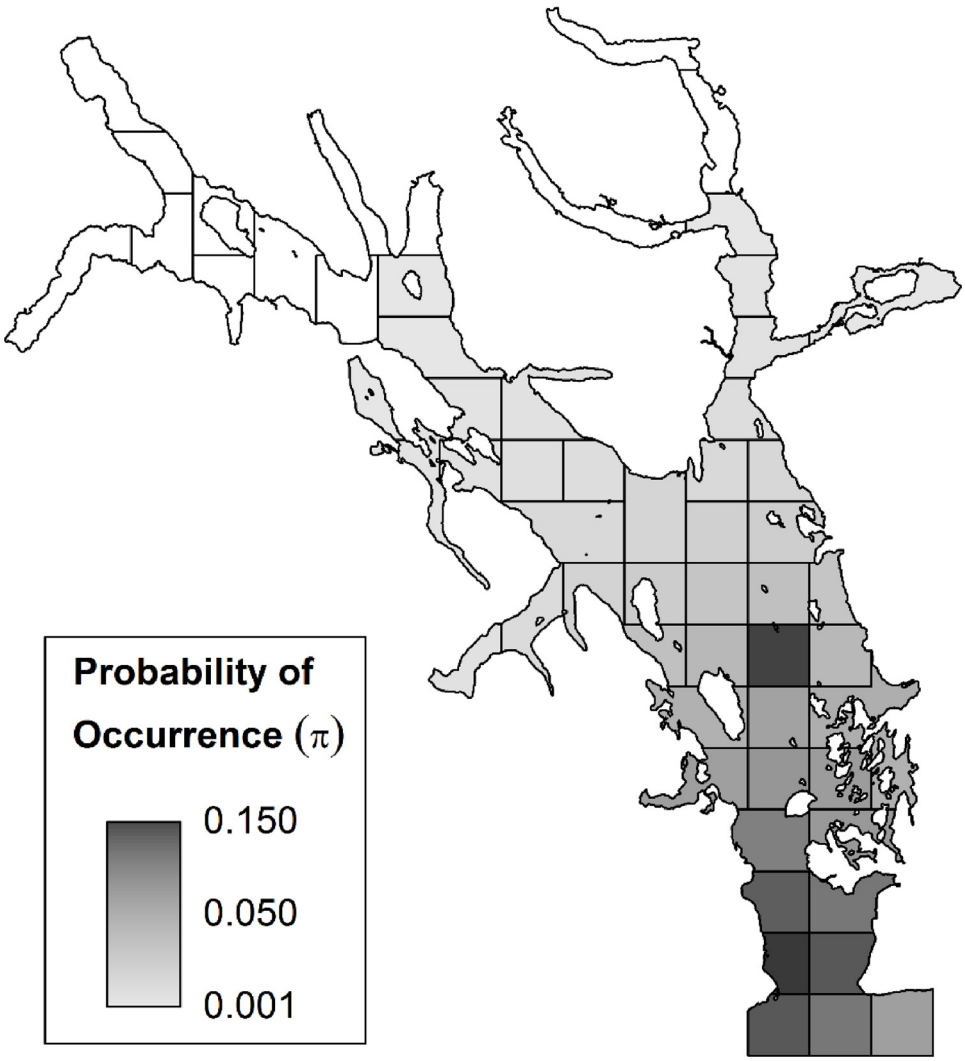

Fig. 7. Estimated Steller sea lion occurrence probability in the vicinity of Glacier Bay National Park. Probabilities of occurrence sum to 1 and are interpreted as the probability that a given sea lion in the water is contained within a cell; sea lions that are out of the water are assumed to be present at South Marble Island.

Table 3
Selected parameter estimates from an integrated abundance and distribution model for Steller sea lions in the vicinity of Glacier Bay National Park and Preserve, Alaska. LCL and UCL denote the lower and upper 95 % confidence limits, respectively.

Parameter	Description	Estimate	Standard Error	LCL	UCL
Integrated Model					
Attendance (γ)					
β_0	Intercept	1.04	0.17	0.71	1.38
β_1	Day of year linear effect	−0.37	0.09	−0.56	−0.19
β_2	Day of year quadratic effect	−0.70	0.10	−0.90	−0.50
σ_{attend}	Attendance standard deviation	0.88	0.06	0.76	1.00
Occurrence (π)					
θ_1	Distance South Marble Island	−0.035	0.010	−0.055	−0.016
θ_2	Distance to Point Carolus	−0.058	0.007	−0.072	−0.044
Detection (P)					
δ_0	Intercept	−10.5	0.165	−10.9	−10.2
δ_1	Time in area	0.29	0.07	0.15	0.42
$\sigma_{detection}$	Detection standard deviation	6.78	0.30	6.20	7.37
Reduced Model (Aerial counts only)					
Attendance (γ)					
β_0	Intercept	1.36	0.22	0.92	1.79
β_1	Day of year linear effect	−0.59	0.13	−0.85	−0.32
β_2	Day of year quadratic effect	−0.86	0.15	−1.16	−0.56
σ_{attend}	Attendance standard deviation	1.27	0.12	1.04	1.49

consisted of separating ecological and sampling-related processes into separate tiers of a model and then specifying intuitive connections between data sets and a shared set of parameters (Royle and Dorazio, 2008; Cressie et al., 2009). The key assumption linking these data sets was that attendance at a terrestrial site and availability to be sighted in the water were mutually exclusive states. We demonstrated the utility of this framework by applying it to Steller sea lions in Glacier Bay, Alaska. The clearest benefits of our approach were improved precision in attendance predictions, the ability to estimate abundance for 2006 in lieu of any aerial count data, and the ability to characterize in-water density of sea lions in the bay over the course of the spring and summer.

Model predictions of abundance and attendance probabilities showed general agreement with the range of estimates reported in the literature. It bears mentioning, however, that the attendance probability estimates to which we compared our model outputs were obtained from studies that took place at different times of year, different geographic areas, and a limited sex and age range of sea lions (Merrick and Loughlin, 1997; Milette, 1999; Rehberg et al., 2009). The greatest inconsistency between our findings and previous research was with respect to seasonal attendance patterns at South Marble Island (Womble et al., 2009; Mathews et al., 2011). Our model identified a convex seasonal attendance relationship for the time span from 2001 to 2017, whereas these other studies described patterns with relatively low mid-season attendance at the same location from 2001 to 2004. The inconsistency was somewhat surprising considering that all analyses shared at least some of the same aerial count data. We did not regard the difference between our model and these other studies as indicative of poor performance, considering that our model included counts from thirteen additional years. It is possible that the attendance pattern identified for the early 2000s has since shifted and that our model instead detected a prevailing pattern with a mid-season peak. A shift to a mid-season peak in attendance is reasonable considering that it would coincide with the onset of pupping, a period when both males and females would be expected to spend more time ashore.

The abundance and distribution model that we describe in this paper combines elements from several modelling approaches, specifically N-mixture and spatial capture-recapture models and may be applied to other taxa. The count portion of the model broadly resembles an N-mixture model in that counts at terrestrial sites are viewed as a binomial random variable and a function of the underlying abundance parameter. The traditional N-mixture model uses replicated counts to simultaneously estimate detection probability and abundance, assuming that nondetection is the sole explanation for the variation in observed counts. In contrast, our model assumes perfect detection and attributes variation in counts to changes in the availability of individuals to be counted by an aerial survey (i.e., temporary emigration). Availability and its compliment, temporary emigration, are sometimes viewed as nuisance parameters in hierarchical models because they can be used to account for transitions of individuals into unobservable states (Kendall and Nichols, 2002; Kery and Royle, 2015). We thought it more appropriate to apply the term “attendance probability” for this model because transitions occur between two observable states, water and land, and the term “attendance” is commonly used in the pinniped literature to refer to occurrence at a terrestrial site (Milette and Trites, 2003; Meise et al., 2014). Although this study focuses on developing a model for monitoring pinnipeds, this or a similar framework could also be applied to other species. Seabird species are one such candidate for this type of model, because they aggregate at terrestrial breeding colony sites, where they may be easily counted, but are also sightable from vessels during foraging trips at-sea.

Although our model uses only counts of unmarked (unidentifiable) individuals, the sighting portion of the model bears some resemblance to spatial capture-recapture models. Spatial capture recapture models relate observations of animals to their distance from an estimated activity center, and derive abundance estimates by summing the number of such centers in the study area (Royle et al., 2013; Royle and Converse, 2014). The sighting portion of the pinniped model can be parameterized in a manner that is conceptually similar, specifically when distance to the terrestrial site is used as a predictor of distribution in water. In this case, the location of activity centers is fixed at terrestrial sites rather than estimated, and the number of such centers is also informed by the count sub-model. Another way in which our model broadly relates to spatial capture-recapture approaches is in its reliance on unstructured spatial sampling, in which surveyors roam the study area recording animal sightings or scats (Thompson et al., 2012; Broekhuis and Gopalaswamy, 2016). Some models that rely on unstructured surveys are also defined using spatial capture-recapture terminology, even referring to grid cells as “conceptual traps” (Russell et al., 2012). Our approach does not build individual encounter histories from sightings in cells as these models do, but instead uses replicate visits and measures of effort within grid cells to provide information regarding detection and occurrence probability.

The realism and utility of the model that we describe is predicated on assumptions regarding latent ecological and data collection processes, many of which it inherits from the approaches that we discussed above. The most significant assumption of the model is that the population remains closed during each season and that variation in counts only reflects changes in attendance probability and not, for example, imperfect detection or movement of individuals among sites (Dénes et al., 2015). Violation of this assumption is likely to result in additional heterogeneity in the attendance parameter, which could obscure relevant patterns in the attendance process and lead to positive bias in abundance estimates (Barker et al., 2017; Duarte et al., 2018). Another key assumption of the model is that the spatial extent of the study area encompasses the home range within which pinnipeds travel during each season and does not overlap with the home ranges of populations at other terrestrial sites. If the second assumption is violated, then estimates of individual detection probability will be affected as well as abundance estimates. The sighting portion of the model assumes that counts of animals in cells are independent after adjusting for covariate effects, the pinniped species is not miscounted or misidentified by surveyors, and that pinnipeds are neither avoidant of nor attracted to the survey vessel. An additional assumption of unstructured sampling approaches is that survey routes are independent of the density (Thompson et al., 2012).

The data used in the Steller sea lion case study satisfied the model assumptions reasonably well, considering our objective of broadly characterizing trends in abundance and spatial distribution. There are several important aspects of sea lion ecology, however, that are not captured by the model, and some assumptions could not be assessed. We could not readily assess the geographic closure assumptions because of the paucity of detailed movement or demographic information on the South Marble Island population over the study period; however, some degree of within-season movement among nearby sites was likely, based on previous studies (Jemison et al., 2013, 2018; Rehberg et al., 2018). We also assumed that sightings of individuals were independent although Steller sea lions are known to forage and are sighted in groups (Fiscus and Baines, 1966; Gende et al., 2001; Sigler et al., 2004). The greater estimated effect of proximity to Point Carolus relative to that of South Marble Island was another unexpected result from the model. This was surprising considering that substantially fewer sea lions have been observed hauled-out at Point Carolus, relative to South Marble Island. The most likely explanation is that distance to Point Carolus is correlated with a latent variable that also predicts the in-water occurrence of sea lions, most likely having to do with prey availability and productive foraging conditions in this region near the mouth of Glacier Bay. Sea lions have been observed in the vicinity Point Carolus in late summer and autumn, which coincides with the migration of Pacific salmon (*Oncorhynchus* spp.) through Cross Sound and Icy Strait from the Gulf of Alaska (Womble et al., 2009). In addition, a shallow glacial sill at the mouth of Glacier Bay promotes localized upwelling and increased productivity in the Sitkaday Narrows, an area of intense tidal

currents and mixing (Etherington et al., 2007). In addition, most of the water that is entrained into Glacier Bay comes in on the west side of the mouth, producing a headland wake system that has been positively related to quality of foraging habitat for whales (Chenoweth et al., 2011), and fish schools and groups of sea lions are commonly observed near Point Carolus during aerial surveys (Jamie Womble, personal observation).

A major advantage of hierarchical models is that there are a number of extensions to the model that can be made to improve estimates and confront potential assumption violations. With respect to the sea lion case study, there are additional sources of information that could be leveraged to improve the model. For example, uncertainties regarding inter-seasonal movement among sites could be reduced by incorporating transition probability estimates obtained via telemetry (Rehberg et al., 2018) or mark-resight studies (Jemison et al., 2013). The precision of the model could also be improved by incorporating additional types of data, including counts of pups or observations gathered using more error-prone methods (e.g., counts from vessels), provided that an additional detection parameter be included in the model. The issue of non-independent sightings could be addressed by directly modelling the process that determines group size (Martin et al., 2011; Schmidt and Rattenbury, 2018).

This study illustrates the value of a hierarchical modelling approach for characterizing abundance and spatial distribution when multiple data sources are available. This approach is particularly useful for pinniped monitoring programs because of the behavioral complexity of these animals and the expense and logistical challenges associated with conducting population surveys (Ver Hoef and Frost, 2003; Boyd et al., 2010). The modelling framework presented in this paper, provides a method for supplementing these surveys with spatially explicit in-water sighting data and for creating model-based predictions that provide a full accounting of where populations of pinnipeds occur on land and in the water. Without the integrated model for Steller sea lion in Glacier Bay it would not have been possible abundance estimate for 2006 or to have identified a seasonal attendance pattern that will be instrumental for reconstructing in-water density patterns across all study years. Another possible management application for this type of model would be for estimating the degree of overlap between pinnipeds and commercial fishing operations, based on the location and occupancy status at terrestrial haul-out sites. Furthermore, species with similar ecology and types of monitoring data available (e.g., sea birds) may also benefit from the application of this framework.

CRediT authorship contribution statement

Steven L. Whitlock: Conceptualization, Methodology, Formal analysis, Writing - original draft, Visualization, Writing - review & editing. **Jamie N. Womble:** Conceptualization, Investigation, Validation, Writing - review & editing. **James T. Peterson:** Conceptualization, Supervision, Writing - review & editing.

Declaration of Competing Interest

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

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