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ARTICLE

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Application of a Bayesian hierarchical model to estimate trends in Atlantic harbor seal (*Phoca vitulina vitulina*) abundance in Maine, U.S.A., 1993–2018

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Abstract

The population of harbor seals (*Phoca vitulina vitulina*) along the coast of Maine, U.S.A., has experienced rapid growth in abundance following passage of the Marine Mammal Protection Act in 1972 but current information on trends in abundance is lacking. In this study, we apply a Bayesian hierarchical model to aerial survey data of nonpups and pups. Prior to 2001, estimates of growth rates from 8-year moving averages reached a high of 2.1% and 9.4% per year with posterior probabilities of positive growth of .97 and >.99 for nonpups and pups, respectively. Between 2001 and 2012, estimated growth rates for nonpups decreased to a low of −1.9% per year with a posterior probability of negative growth of .95. Between 2012 and 2018, posterior estimates of growth were close to zero suggesting little change in abundance of nonpups. Estimates of growth for pups were close to zero between 2001 and 2012 but reached a low of −2.5% per year with a posterior probability of negative growth of 0.94 at the end of the time series suggesting a decrease in pup abundance between 2012 and 2018. The total abundance estimate for 2018 is 61,336 ($CV = 0.08$).

KEYWORDS
Bayesian hierarchical model, harbor seals, informative priors, *P. vitulina vitulina*, trend analysis

1 | INTRODUCTION

Change in a population size over time offers insight to the status of the population and the underlying environment on which it depends. Trends in population abundance may reflect depletion or augmentation of a prey base, ecosystem changes, predation, habitat condition, or disease (Lucas & Stobo, 2000; Matthews & Pendleton, 2006; Taylor et al., 2007). Information from trend estimation can offer important information critical to guiding conservation and management decisions (Taylor et al., 2007; Wade, 2000) and is often a legal requirement for many government agencies (Hovestadt & Nowicki, 2008). For example, under the Marine Mammal Protection Act (MMPA) stock assessment reports must include information on trends and abundance for all species in U.S. waters (Read & Wade, 2000), although federal budget levels preclude this actually happening for many species.

Despite the importance of quantifying and understanding changes in abundance, for many marine mammal populations estimating trends remains an elusive goal due to sparse data and gaps in survey effort (Jewell et al., 2012; Taylor et al., 2007). Many populations are depleted or cryptic; therefore, assessment data are limited (Jewell et al., 2012; Moore & Barlow, 2013). For other populations there are funding limitations which complicate the ability to survey frequently leading to gaps between survey years (Taylor et al., 2007). To address these challenges some studies have adopted a Bayesian hierarchical approach (Johnson & Fritz, 2014; Moore & Barlow, 2013). The hierarchical framework can allow for estimation of missing states as well as the sharing of information across data sets or surveys, which can improve estimation and increase precision (Goodman, 2004; Johnson & Fritz, 2014). Also, the use of prior information can be included when direct information is lacking (Goodman, 1994). Finally, results from Bayesian analyses can be more easily communicated in terms of probabilities and have been shown to be successful in detecting trends when more traditional methods fail (Wade, 2000). Taking advantages of these attributes, a number of studies have been able to estimate trends from sparse data and provide results that are useful to inform management and conservation decisions (Boveng et al., 2018; Moore & Barlow, 2013; Thompson et al., 2005).

For many seal populations, applications of Bayesian approaches have proven to be an invaluable tool in estimating trends (Boveng et al., 2018; Thompson et al., 2005; Ver Hoef & Frost, 2003). For example, using a Bayesian state-space model Thompson et al. (2005) were able to link sparse data with more current data to investigate trends in a harbor seal (*Phoca vitulina vitulina*) population impacted by phocine distemper virus (PDV). Similarly, Boveng et al. (2018) combined prior information and a population dynamics model to investigate trends in a data-poor population of harbor seals in Alaska. Seal populations are particularly amenable to trend analysis using hierarchical methods because the observation process can be modelled directly (Ver Hoef & Frost, 2003) and often there are good sources of prior information when direct information from a survey is missing (Thomas et al., 2019). More generally, data from seal surveys have a much higher power to detect trends than most other species of marine mammals (Taylor et al., 2007). As seal populations continue to experience stress from virus outbreaks (Brasseur et al., 2018), interspecific competition with other seals (Bowen et al., 2003), and threats from climate changes (Johnston et al., 2015), it is necessary to apply robust statistical techniques to existing data sets to provide updated information on current trends even when survey data are sparse.

In this paper we take a Bayesian approach to investigate trends and update abundance estimates for Atlantic harbor seals in the northeastern United States. Harbor seals are year-round inhabitants of the coastal waters of eastern Canada and Maine and occur seasonally throughout New England and the Mid-Atlantic (Baird, 2001; Desportes et al., 2010). In U.S. waters, harbor seals of different age and sex classes are concentrated in coastal Maine from May to early June for pupping (Gilbert et al., 2005; Waring et al., 2006). Some pupping may occur in areas outside of

Maine, but it is considered to be small and infrequent (Hayes et al., 2019), and branding studies in other regions support strong adult female site fidelity for breeding areas (Härkönen & Harding, 2001). Like many harbor seal populations this population was subject to hunting and bounties up until the 1960s but has since been protected following the passage of the MMPA in 1972. To monitor this population, aerial surveys were conducted intermittently starting in 1981 (see Gilbert et al., 2005 for details). Counts from this survey increased by an average of 22% per year between 1981 and 2001 (Gilbert et al., 2005).

Changes in the Gulf of Maine ecosystem over the past three decades may have influenced the demography in the harbor seal population. For instance, there has been a substantial increase in the gray seal (*Halichoerus grypus*) population (Wood et al., 2020), which are a known to negatively impact harbor seal abundance in other populations (Bowen et al., 2003; Thompson et al., 2019). Also, several mass mortality events or unusual mortality events (UMEs; see Gulland, 2006) have affected this population of seals since 1991, with the most recent occurring in 2018 (https://www.fisheries.noaa.gov/national/marine-life-distress/active-and-closed-unusual-mortality-events#active-umes). Some of these UMEs have been associated with phocine distemper virus (PDV), the same virus that significantly impacted harbor seal populations in Europe in 1988 and 2002 (Dietz et al., 1989; Earle et al., 2011). However, because a formal analysis has never been conducted for this population, trends in abundance are currently considered unknown (Hayes et al., 2019). In addition to trends, there is no abundance estimate for 2018 the most recent year of survey data. The last estimate of abundance was based on a 2012 survey (Waring et al., 2015), and under the MMPA if an estimate of abundance is not updated within 8 years, the abundance of the stock is considered unknown (Moore & Merrick, 2011).

In this study, we analyze data from five aerial surveys conducted between 1993 and 2018 during the pupping season with a Bayesian hierarchical model. Our model includes latent states for unobserved years and unobserved environmental covariates, an informative prior distribution on the proportion of seals hauled out under ideal conditions, and temporal autocorrelation that acts as a nonparametric smoother on the shape of the trend over time. The objectives of our study are (1) to estimate trends in pup and nonpup abundance using a methodological approach that accommodates sparse data; and (2) to provide an estimate of abundance for 2018, which is the most recent survey year.

2 | METHODS

2.1 | Data collection and processing

We utilized data from aerial surveys conducted in 1993, 1997, 2001, 2012, and 2018 along the coast of Maine from the Maine-New Hampshire border to the Canada-United States border (Figure 1). Surveys were flown during the pupping season (Table 1), when most of the population was thought to be concentrated in the region (Gilbert et al., 2005) and timed to coincide with the peak pupping period estimated to be around May 23 (Skinner, 2006). We conducted all surveys within 2 hr of either side of low tide. Surveys conducted before 2012 were described in detail in Gilbert et al. (2005), and the 2012 survey was described in Waring et al. (2015). In 2001 replicate surveys were conducted in different portions of the study area in two time periods: May 16–20, and May 27–June 4. In 2012 not all seal haul-out ledges could be surveyed due to a shortened survey window, so randomly selected regions within the entire study area were surveyed using a probability-based design (Waring et al., 2015). All other years represented a presumed census of all pupping sites in the population.

In 2018, a NOAA Twin Otter aircraft was used to survey the same seal haul-out ledges as those surveyed in all previous years. All ledges of known historic occupancy were surveyed, but if new ledges were occupied, they may have been missed. The Twin Otter surveyed seal haul-out ledges at an altitude of 228 m (750 ft), and oblique photographs were taken from a left-side rear pop-out window using a Canon EOS 7D and fixed 300 mm f:4.5 lens. Digital images were georeferenced, analyzed for overlap, and then pups and nonpups were counted with a paint-dot technique in Adobe Photoshop (version 2015.5) by two readers. Counts were compared and differences were rectified by jointly reviewing the image, otherwise an average of the two total counts was taken.

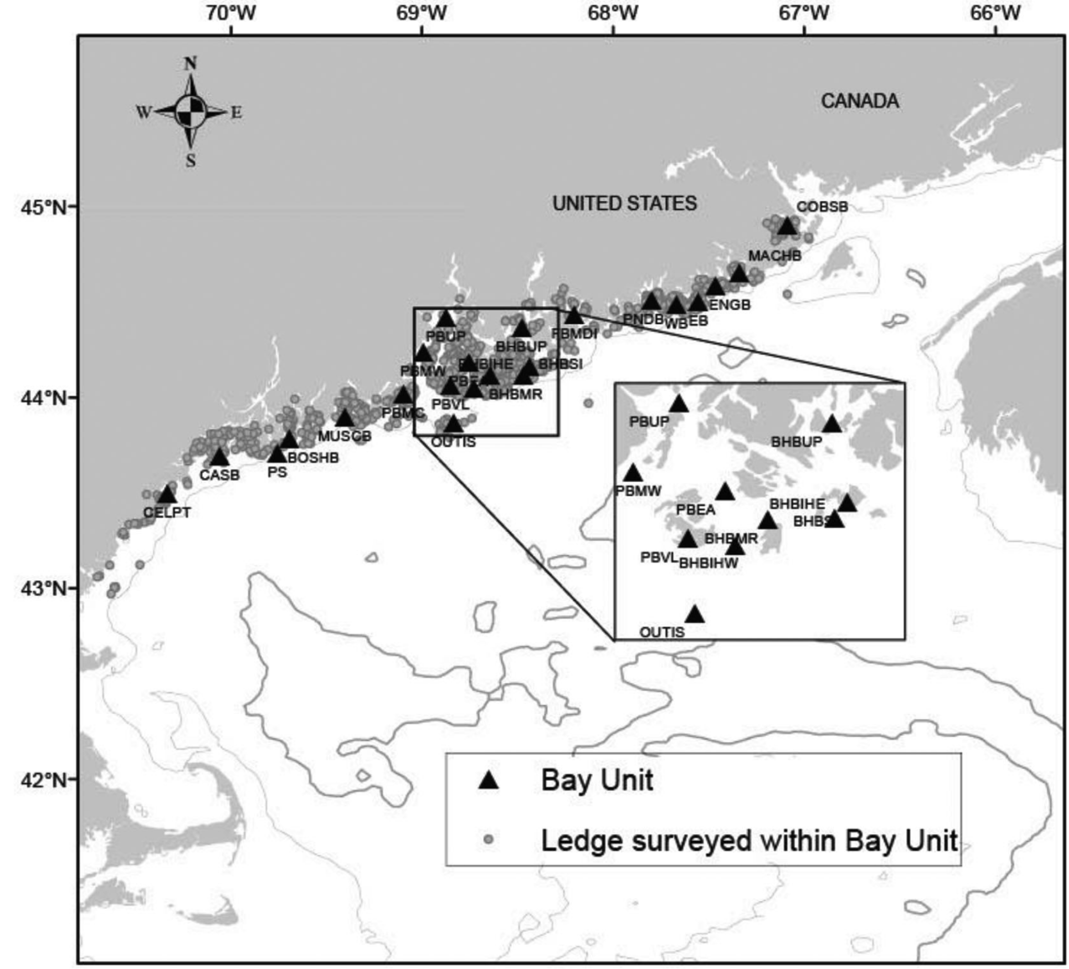

FIGURE 1 Atlantic harbor seal survey sites for coastal Maine. Individual haul-out ledges (gray dots) were surveyed and then aggregated into larger bay units (triangles) to model trends in abundance.

We surveyed a total of 990 ledges. We initially analyzed the data at the ledge level but found models were extremely slow to converge. Therefore, we grouped ledges into 25 bay units that were the same as, or divisions of, the units used for previous analyses of harbor seal abundance (Gilbert et al., 2005; Waring et al., 2015). For the 2001 survey, we used the replicate with the highest count as the observation for that year and bay unit. We assumed the general random movement among individuals in all bay units prevented any bias in counts.

2.2 | Statistical model

To model the number of observed seals in each bay unit in each surveyed year we assumed counts of seals follow a Poisson process:

$$y_{i,t} \sim \text{Poisson}(\lambda_{i,t}),$$

TABLE 1 Year and date range for each bay unit surveyed for harbor seal abundance from 1993–2018.

Bay unit	1993	1997	2001	2012	2018
BHBIHE	May 31–June 3	June 4	May 17–June 1	June 1	May 22–23
BHBIHW	June 3–4	May 29–June 4	May 17–June 1	June 1	May 23
BHBMR	June 3	May 29–June 4	May 17–31	May 31–June 1	May 22
BHBSI	June 3	June 4	May 17–June 1	June 1	May 22
BHBUP	June 3	June 4	May 17–31	May 30	May 22
BOSHB	June 9–11	May 28–30	May 17–June 4	NS	May 21–25
CASB	June 11	May 30	May 18–29	May 28	May 21–25
CASBE	June 11	May 30	May 17–29	May 28	May 21–25
CELPT	June 11	May 30–31	May 18–29	NS	May 23
COBSB	May 28	June 2	May 27–30	NS	May 24
EB	May 28–31	June 2	May 18–30	May 27	May 24
ENGB	May 28	June 2	May 18–27	NS	May 24
FBMDI	May 31	June 3–4	May 17–June 1	May 27	May 22–23
MACHB	May 28	June 2	May 18–30	May 27	May 24
MUSCB	June 4–11	May 28	May 16–June 4	May 28	May 21–25
OUTIS	June 9	May 27–28	May 17–June 4	NS	May 19–23
PBEA	June 3–4	May 27–29	May 16–June 1	May 28–June 2	May 19–25
PBMC	June 4	May 27–28	May 16–June 4	June 2	May 19–25
PBMW	June 3–4	May 27	May 16–June 1	May 27	May 19–23
PBUP	June 4	May 27–29	May 16–June 1	NS	May 23
PBVL	June 3–4	May 27–29	May 16–June 1	May 28–June 1	May 19–25
PBVLW	June 4	May 27	May 16–June 1	May 28–June 1	May 19–25
PNDB	May 31	June 3	May 18–30	NS	May 24
WB	May 31	June 2–3	May 18–30	NS	May 24

Note: NS indicates that the bay unit was not surveyed.

where $y_{i,t}$ is the observed number of seals in bay unit *i* at time *t* and $\lambda_{i,t}$ is the expected number of seals in bay unit *i* at time *t*. We model the expected number of seals as a linear function of environmental variables and random effects:

$$\lambda_{i,t} = \exp\left(\theta_i + Z_{i,t} + \sum\nolimits_{k=1}^{K} \beta_k x_{k,i,t}\right), \tag{1}$$

where is the k_{th} covariate value observed in bay unit *i* in year *t*, β is the k_{th} coefficient, θ_i is an intercept term, and $Z_{i,t}$ is a random effect term. We model the random effects as an autocorrelated process such that

$$\mathbf{Z} \sim \mathrm{MVN}(0, \Sigma),$$

where **Z** is a vector of the random effects and Σ is a covariance matrix where the covariance is defined as

$$\mathrm{cov}(Z_{i.u}, Z_{i,v}) = \sigma^2 \exp\left(\frac{|u - v|}{\phi}\right), \tag{2}$$

where $\phi > 0$ is the parameter that controls the rate of decay in autocorrelation, $\sigma^2 > 0$ is the variance and $u - v$ represents the difference in years between two observations of bay unit i. This covariance function acts as a nonparametric smoother that allows for flexible shapes in the trend similar to a GAM (Johnson & Fritz, 2014; Munch et al., 2005). Because of the limited number of observed years, we assumed a relatively simple covariance function where ϕ is the same for all sites and there is no covariance among sites such that $\mathrm{cov}(Z_{i,u}, Z_{j,v}) = 0$ in all cases where $i \neq j$. Thus, we assumed the same covariance function is shared by all bay units. Biologically this assumes that all unmeasured demographic forces that cause temporal autocorrelation are equal across all bay units. Given the relatively small geographical area of the study, we consider these assumptions to be reasonable.

2.3 | Covariates

For each ledge surveyed, we collected information on survey time relative to low tide, and survey time relative to solar mid-day. These factors have been shown to significantly affect the number of harbor seals hauled out (Boveng et al., 2003; Frost et al., 1999; Ver Hoef & Frost, 2003). Tidal information was from https://tidesandcurrents.noaa.gov/ relative to Rockland Maine. As the time of low tide differs only by approximately 30 min over the length of the coast, we did not adjust survey time at each ledge relative to low tide in Rockland.

Because our analysis was at the bay unit level, we calculated the mean value and variance for time from low tide and time from solar midday across all observed ledges within a bay unit. To model the effect of time from low tide on seal counts, we used the absolute value under the assumption that time from low tide was most important and not whether the tide is rising or dropping. So, for example, a value of -2 (i.e., 2 hr before low tide) and 2 (2 hr after low tide) would both be given a value of 2. We modeled all environmental covariate effects as linear functions. We included all covariates in the analysis of both the nonpup data and the pup data. For the pup data we also included Julian date as a covariate. For this variable we included a quadratic effect to allow some flexibility in estimating the timing of peak pupping.

We only had covariates for years 2001, 2012, and 2018, because the time that each individual ledge was surveyed was not available in the historic data. For years without covariates, we assumed that sampling occurred over a similar range of conditions as the years with covariates. We treated the true value of the covariates as an unobserved state with a prior distribution. Therefore, we used the years with covariate values to develop informed priors on sampling conditions without covariate values such that

$$x_{k,i,t} \sim \mathrm{Normal}(\mu_k, \sigma_k),$$

where μ_k is the mean value of the k_{th} observed covariate of interest across all years and bay units and σ_k is the variance. Because sampling protocols were similar in the earlier surveys, we assumed no systematic change in the distribution of these covariates over time. To test the sensitivity of our assumed priors, we increased the variance threefold and assessed and calculated the percentage change in the posterior standard deviation of the abundance estimates.

2.4 | Trends and abundance

To estimate trends and calculate final estimates of abundance, we first standardized counts across bay units to a common set of ideal environmental conditions when the maximum number of seals are hauled out. We assumed ideal conditions occur when both time from solar midday and time from low tide are at zero and there is no variance in the conditions across the bay unit (i.e., when the value of all covariates is set to zero). Therefore, we treated true count under ideal conditions as a latent state such that

$$N_{i,t} = \exp\ (\theta_i + Z_{i,t}), \tag{3}$$

where $N_{i,t}$ represents the true number of seals hauled out under ideal conditions. For each year, we calculated the abundance of seals at ideal conditions by summing across bay units as

$$N_t = \sum N_{i,t}. \tag{4}$$

Next, we fitted linear regressions to these standardized estimates following the method of Johnson and Fritz (2014), however, to do so it is first necessary to augment missing observations. To estimate during the unsampled years we sampled the random effects from their multivariate conditional distribution and some across to calculate as above. We next calculated linear estimates of change in standardized abundance using simple linear regression by regressing abundance on time. We chose an 8-year period because this window of time is considered a reliable threshold for conducting MMPA stock assessments (Wade & Angliss, 1997). For every Markov chain Monte Carlo (MCMC) draw from the posterior of abundance we calculated the slope of abundance over time with a simple linear regression. To calculate the percent change in abundance we performed the analysis on the log of abundance. We estimated trends for nonpups and pups separately.

To attain final estimates of abundance we needed to adjust for the fraction of seals not hauled out under ideal conditions as there is some proportion of seals not hauled out even when conditions are ideal (Boveng et al., 2003). Therefore, our final abundance estimates for each year with survey data are calculated as

$$A_t = \frac{N_t}{p}, \tag{5}$$

where p is the fraction hauled out under ideal conditions. Simpkins et al. (2003) estimated p to be 0.835 ($SE = 0.026$) for a population of harbor seals in Alaska. We do not have an estimate of for this population but Waring et al. (2015) estimated the average fraction hauled out over a range of survey conditions. Their estimate of 0.43 ($SE = 0.06$) is much lower than the estimate of Simpkins et al. (2003) because it is not adjusted to ideal conditions. To use all the available information, we developed two separate methods to incorporate these different estimates of haul-out probability and their uncertainty into our analysis.

2.4.1 | Method 1

For the first approach, to calculate a final estimate of abundance we used the estimate of 0.835 and standard error of 0.026 for the proportion of seals hauled out under ideal conditions reported by Simpkins et al. (2003) to develop a Beta prior distribution such that

$$p_1 \sim \mathrm{Beta}(\mathrm{a}_1, \mathrm{b}_1),$$

where p_1 is the proportion of seals hauled out under ideal conditions and a_1 and b_1 are parameters of a Beta distribution chosen so that its mean and standard deviation equal the estimate and standard error reported in Simpkins et al. (2003), respectively. We then calculate the final adjusted abundance estimate as

$$A_{1,t} = \frac{N_t}{p_1} \tag{6}$$

where $A_{1,t}$ represents the final estimate of seal abundance from *Method 1* for survey year t.

2.4.2 | Method 2

The Simpkins et al. (2003) estimate may not be appropriate for our study as it was estimated during a different season and for a different population of harbor seals than the current study. We therefore implemented a second approach where we derived an estimate for the fraction of seals hauled out under ideal conditions directly from our model estimates and the correction factor estimate of Waring et al. (2015). Similar to *Method 1* we use the estimate of 0.43 and standard error of 0.06 for the overall proportion of seals hauled out in Waring et al. (2015) to develop an informative Beta prior distribution such that

$$p_W \sim \mathrm{Beta}(\mathrm{a_W}, \mathrm{b_W}),$$

where p_W is the proportion of seals hauled out over a range of conditions and $\mathrm{a_W}$ and $\mathrm{b_W}$ are parameters of the Beta distribution chosen so that its mean and standard deviation equal the estimate and standard error reported in Waring et al. (2015), respectively. Next, we assume that the ratio of the observed count to the final abundance estimate should equal such that

$$p_W = \frac{Count_t}{A_{2,t}}, \tag{7}$$

where $Count_t$ is the combined sum of raw counts across all bay units in year t and $A_{2,t}$ is our final abundance estimate from *Method 2* for year t. Similar to *Method 1*, we assume N_t needs to be adjusted by the proportion of seals hauled out under ideal conditions such that

$$A_{2,t} = \frac{N_t}{p_2}, \tag{8}$$

where p_2 is our estimated proportion of seals hauled out at ideal conditions. Both p_2 and $A_{2,t}$ are unknown; however, we can rearrange equations and calculate p_2 as

$$p_2 = \frac{p_W N_t}{Count_t}, \tag{9}$$

where p_2 represents our study-specific estimate of the proportion of seals hauled out under ideal conditions analogous to p_1. We calculated p_2 for each year that included a full survey (i.e., we excluded 2012). We then averaged p_2 across years as our final estimate.

For *Method 2*, we estimated p_2 separately for pups and nonpups. For both methods, we calculated abundance estimates separately for pups and nonpups. For total abundance we summed the two quantities to derive a posterior distribution for total abundance. Final estimates were calculated by averaging estimates of abundance from *Method 1* and *Method 2* giving equal weight to both methods. We calculated N_{MIN} from the lower bound of the 80% credible interval obtained from the posterior distribution of the averaged abundance estimates.

We fitted all models using MCMC sampling implemented with the JAGS software (Plummer, 2003). We included a burn-in of 200,000 samples and two chains of 800,000 with a thinning rate of 800. We assessed convergence by examining trace-plots and calculating Gelman-Rubin diagnostics. For model selection, we applied the Watanabe-Akaike information criterion (WAIC) as this metric performs well with hierarchical models (Hooten & Hobbs, 2015). To assess goodness of fit, we calculated Bayesian *p*-values for nonpup and pup models separately.

3 | RESULTS

3.1 | Environmental covariates

Model selection based on WAIC values indicated that the model that included time from low tide and time from solar midday was the best model for the nonpup count data, although minor differences in WAIC values indicated support for alternative models (Table 2). Bayesian *p*-values of .46 indicated a good fit of the model to the data. There was a significant negative effect of both average time from low tide and average time from solar midday on seal count as evidenced by 95% credible intervals that did not include zero (Table 3). This negative effect indicates that nonpup counts decreased the farther away from low tide and solar midday that a survey is conducted. Sensitivity analysis showed that a threefold increase in the variance of the informed priors resulted in a <4% increase in the variance of the abundance estimates.

For the pup count data, WAIC values indicated that the model with average time from low tide as the only covariate was the best model (Table 4). However, similar to the nonpup analysis, minor differences in WAIC values indicated support for alternative models. Bayesian *p*-values of .42 indicated a good fit of the model to the data. There was a significant negative effect of time from low tide on pup count as evidenced by 95% credible intervals

TABLE 2 Model selection using Watanabe-Akaike information criterion (WAIC) for different models fit to the nonpup harbor seal data. Models included average observed time from low tide (T), variance in observed time from low tide (V_T), average observed time from solar midday (S) and variance in average observed time from solar midday (V_S). For each model, the difference in WAIC from the top model (ΔWAIC) are provided.

Model	WAIC	ΔWAIC
$T + S$	1,576	0
$T + S + V_T$	1,579	3
$T + S + V_S$	1,579	3
T	1,582	6

TABLE 3 Posterior estimates and 95% credible intervals for nonpups.

Parameter	Definition	Estimate	*SD*	Upper	Lower
β_1	Average time from low tide	−0.23	0.08	−0.06	−0.39
β_2	Average time from solar midday	−0.08	0.04	−0.01	−0.16
	Variance in random effects	0.28	0.03	0.34	0.24
	Temporal range parameter	1.30	0.96	3.72	0.38

TABLE 4 Model selection results using Watanabe-Akaike Information Criterion (WAIC) for different models fit to the pup harbor seal data. Models included average observed time from low tide (T), variance in observed time from low tide (V_T), average observed time from solar midday (S), variance in average observed time from solar midday (V_S) and Julian Date (JD). For each model, the difference in WAIC from the top model (ΔWAIC) are provided.

Model	WAIC	ΔWAIC
T	960	0
$T + JD + JD^2$	962	2
$T + VT + S + JD$	965	5
$T + V_T + S + VS + JD$	965	5

that did not include zero (Table 5). Sensitivity analysis showed that a threefold increase in the variance of the informed priors resulted in a < 7% increase in the variance of the abundance estimates.

3.2 | Trends

The overall trend in nonpup harbor seal abundance predicted from the model showed evidence of a slight increase in abundance until approximately 2001, where abundance appears to peak and then showed a slight decreasing trend over time (Figure 2a). Posterior estimates of the 8-year moving average of percent increase ranged from a high of 2.1% with a posterior probability of positive growth of .97 early in the time series to a low of −1.9% with a posterior probability of negative growth of .95 towards the middle of the time series (Figure 2b).

The trend for pup abundance was similar to the trend for nonpups with a slight increase in abundance until 2001 and then declining thereafter (Figure 3a). Posterior estimates of the 8-year moving average of percent increase ranged from a high of 9.1% with a posterior probability of positive growth that was >.99 early in the time series to a low of −2.5% with a posterior probability of negative growth of .94 towards the end of the time series (Figure 3b).

TABLE 5 Posterior estimates and 95% credible intervals for pups.

Parameter	Definition	Estimate	*SD*	Upper	Lower
β_1	Average time from low tide	−0.34	0.15	−0.01	−0.69
	Variance in random effects	0.61	0.09	0.87	0.49
	Temporal range parameter	4.23	3.95	15.09	0.43

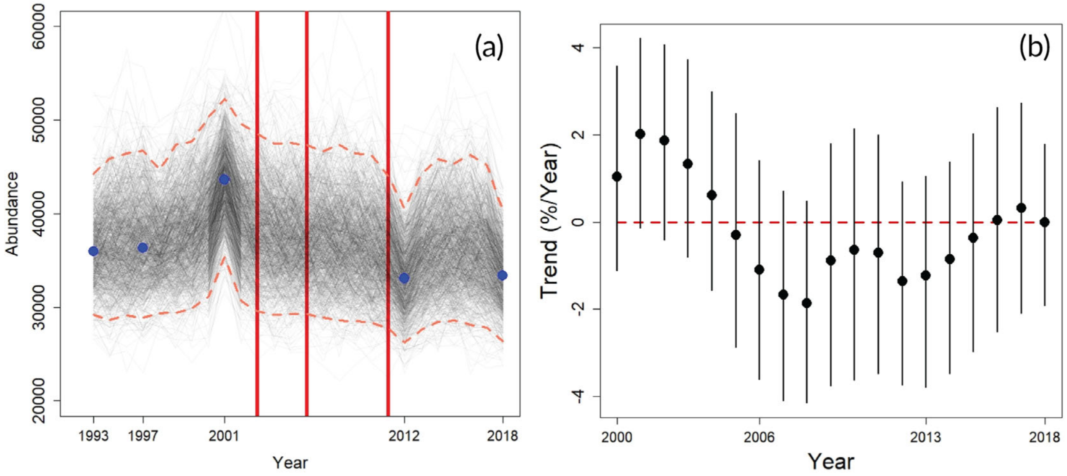

FIGURE 2 Estimates of standardized abundance (i.e., counts adjusted to ideal conditions) from 1,000 MCMC draws from the posterior distribution (gray line) and 95% Bayesian credible intervals (dotted lines) for nonpup harbor seals from the top model(a) and average percent change in nonpup abundance with 95% Bayesian credible intervals (vertical lines) around the posterior mean over a trailing 8-year moving window starting from 1993 (b). Blue dots indicating mean abundance estimates for years with survey data and vertical red bars showing years with Unusual Mortality Events are shown in panel (a).

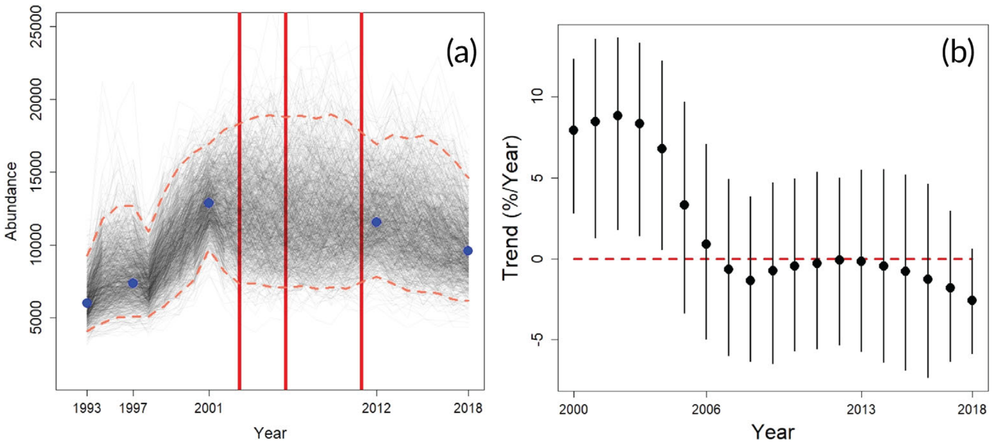

FIGURE 3 Estimates of standardized abundance (i.e., counts adjusted to ideal conditions) from 1,000 MCMC draws from the posterior distribution (gray line) and 95% Bayesian credible intervals (dotted lines) for pup harbor seals from the top model (a) and average percent change in pup standardized abundance with 95% Bayesian credible intervals (vertical lines) around the posterior mean over a trailing 8-year moving window (b). Blue dots indicating mean abundance estimates for years with survey data and vertical red bars showing years with Unusual Mortality Events are shown in panel (a).

TABLE 6 Harbor seal abundance estimates using the proportion of seals hauled out under ideal conditions from Simpkins et al. (2003) (*Method 1* described in text).

Stage	Year	Estimate	*SD*	*CV*	Upper	Lower
Pups	1993	7,204	1,607	0.22	11,135	4,844
Nonpups	1993	43,165	4,700	0.11	53,234	34,813
Total	1993	50,661	4,918	0.10	60,921	41,828
Pups	1997	8,780	1,820	0.21	13,108	5,967
Nonpups	1997	43,594	4,685	0.11	54,064	35,079
Total	1997	52,781	4,939	0.09	63,074	43,822
Pups	2001	15,416	2,313	0.15	20,522	11,416
Nonpups	2001	52,173	5,258	0.10	62,041	42,207
Total	2001	67,923	5,661	0.08	78,685	57,230
Pups	2012	13,840	2,897	0.21	20,437	9,381
Nonpups	2012	39,730	4,733	0.12	49,201	31,262
Total	2012	53,799	5,421	0.10	64,534	43,868
Pups	2018	11,466	2,576	0.22	17,484	7,321
Nonpups	2018	40,040	4,364	0.11	48,350	31,515
Total	2018	51,878	4,951	0.10	61,693	42,404

3.3 | Abundance

Final abundance estimates varied depending on the method used to estimate abundance. Estimates of the proportion of seals hauled out at ideal conditions was 0.61 for nonpups and 0.60 for pups with posterior standard deviations of 0.10 and 0.13, respectively. These estimates are lower than the estimate of 0.84 from Simpkins et al. (2003) and higher than the estimate of 0.43 from Waring et al. (2015). As a result, abundance estimates using only *Method 1* (Table 6) are substantially lower than abundance estimates using only *Method 2* (Table 7). For 2018, the most

TABLE 7 Harbor seal abundance using the proportion of seals hauled out over a range of conditions from Waring et al. (2015) (*Method 2* described in text).

Stage	Year	Estimate	*SD*	*CV*	Upper	Lower
Pups	1993	10,039	1,586	0.16	13,902	7,980
Nonpups	1993	58,935	8,164	0.14	79,751	46,795
Total	1993	69,294	8,341	0.12	90,453	56,921
Pups	1997	12,239	1,868	0.15	16,583	9,687
Nonpups	1997	59,699	8,225	0.14	79,614	47,720
Total	1997	71,956	8,393	0.12	91,679	59,986
Pups	2001	21,398	3,128	0.15	29,366	16,953
Nonpups	2001	70,875	9,775	0.14	94,222	56,774
Total	2001	92,588	10,300	0.11	117,732	78,284
Pups	2012	19,292	3,038	0.16	26,641	15,204
Nonpups	2012	53,626	7,897	0.15	73,626	42,224
Total	2012	73,741	8,463	0.11	94,410	61,219
Pups	2018	15,973	2,454	0.15	21,823	12,695
Nonpups	2018	54,270	7,445	0.14	72,285	43,397
Total	2018	70,663	7,805	0.11	89,842	58,774

TABLE 8 Model averaged abundance estimates for harbor seals by life history stage (nonpups vs. pups) and their totals. Abundance estimates were averaged among two separate methods for estimating the fraction of seals hauled out under ideal conditions.

Stage	Year	Estimate	*SD*	*CV*	Upper	Lower
Pups	1993	8,688	1,307	0.15	12,047	6,913
Nonpups	1993	51,110	4,875	0.10	62,947	43,745
Total	1993	60,092	5,030	0.08	71,791	52,469
Pups	1997	10,553	1,462	0.14	14,201	8,342
Nonpups	1997	51,892	4,859	0.09	63,125	44,225
Total	1997	62,500	4,986	0.08	74,100	54,387
Pups	2001	18,470	1,803	0.10	22,921	15,719
Nonpups	2001	61,851	5,598	0.09	75,167	52,937
Total	2001	80,484	5,851	0.07	93,894	71,292
Pups	2012	16,600	2,374	0.14	22,652	13,171
Nonpups	2012	46,949	4,997	0.11	58,203	39,070
Total	2012	64,148	5,444	0.08	75,804	54,907
Pups	2018	13,836	2,071	0.15	18,930	10,696
Nonpups	2018	47,371	4,461	0.09	57,674	39,977
Total	2018	61,336	4,816	0.08	72,132	53,577

recent estimate of abundance for this population, the abundance estimate was 51,858 with a N_{MIN} of 47,641 from *Method 1* versus an abundance estimate of 70,663 with an N_{MIN} of 64,798 from *Method 2*. The model averaged total abundance estimate for 2018 is 61,336 ($CV = 0.08$), with a N_{MIN} of 57,637 (Table 8). Regardless of method, estimates of abundance indicated that abundance was highest in 2001 and lowest in 1993 for nonpups, pups and the combined total (Tables 6–8).

4 | DISCUSSION

Using a Bayesian hierarchical method to model sparse survey data for harbor seals in Maine allowed us to augment missing data and combine information across all surveys to estimate trends and abundance. Prior to this study, updated information on trends and abundance was lacking for this population. Our analysis provides evidence that both nonpup and pup abundance continued to grow in the 1990s until the early 2000s followed by a decrease in nonpup abundance between 2001 and 2012 and a decrease in pup abundance between 2012 and 2018. Overall, changes in abundance between 2012 and 2018 were minor suggesting that this population currently is stable.

Previous to our analysis, Johnston et al. (2015) provided some evidence that this harbor seal population might have declined between 2000 and 2012. However, their study used bycatch and strandings data as indices of abundance so they could not provide estimates of the rate of decline. Our results broadly corroborate the speculation of Johnston et al. (2015) but provide new information by extending the analysis to 2018 and providing stage-specific rates of decline for both pups and nonpups. Waring et al. (2015) used the 2012 survey data used in this study to update abundance estimates and showed that the estimate was 23% lower than the 2001 estimate reported in Gilbert et al. (2005). However, because of the uncertainty in the estimate, they could not conclude if this decline was statistically significant and did not formerly test for a decline in abundance. Our posterior probability shows a high probability of negative growth for nonpups between 2001 and 2012 but little evidence for change in pup abundance. By extending the analysis out to 2018, we found little evidence that nonpups are continuing to decline although there is some evidence of a decline in pup abundance.

It is difficult to isolate mechanisms influencing trends in this population due to limited information on demographic parameters. Increases in competition from gray seals and predation from white sharks may be exerting some influence. Gray seal populations have increased by as much as 26.3% in some regions within the Gulf of Maine (den Heyer et al., 2021; Wood et al., 2020). In some of these areas where gray and harbor seals overlap, such as southeastern Massachusetts, counts of harbor seals in spring have progressively declined since 2009, and haul-outs historically occupied by harbor seals are now occupied by gray seals (Pace et al., 2019). Similarly, harbor seal declines at Sable Island, Canada were attributed to increased competition from the increasing gray seal population on the island (Bowen et al., 2003). In addition to gray seals, white sharks have also increased dramatically in the Gulf of Maine in recent decades (Curtis et al., 2014). Lucas and Stobo (2000) showed that predation from white sharks may have also contributed to the rapid decline of harbor seals on Sable Island. Although it is difficult to directly quantify the effect of these factors on abundance in this population, our analysis suggests that they are not currently causing the same rapid declines as was observed on Sable Island.

Mortality caused from disease may also be influencing abundance trends in this population. A number of UMEs have been documented in this population during the time series of survey effort including in 2003, 2006 and, 2011 (Hayes et al., 2019). In particular, increased mortality observed in 2006 and 2011 was attributed to PDV (Hayes et al., 2019). In European populations, mortality from PDV events totaled more than 23,000 in 1988 and 30,000 in 2002 (Härkönen et al., 2006). Some local population suffered mortality as high as 60%. Although we do not have direct estimates of mortality for this population, strandings data of observed mortalities from the UMEs in 2006 and 2011 where under 1,000 animals which is less than 2% of the 2001 estimate (D. Fauquier, personal communication) Therefore, mortality caused from these events does not appear as severe as European populations. One possibility is that this population is at or near its carrying capacity. Abundance may have exceeded carrying capacity in 2001 and PDV may be acting as a density-dependent mechanism keeping the population at equilibrium.

The long-term impact of PDV on trends can vary among populations. In the Wadden Sea, mortality was severe but followed by rapid growth resulting in relatively quick rebounds in abundance (Brasseur et al., 2018). Conversely, populations of British harbor seals showed no evidence of an increase in abundance 5 years following a PDV event in 2002 (Lonnergan et al., 2007). The strandings data from the UMEs in 2006 and 2011 shows that mortalities appeared to be predominantly pups. This increased pup mortality may partly explain the difference in trends we observed in our analysis. A large mortality of pups between the 2001 survey and the 2012 survey may have resulted in a reduced number of immature juveniles in 2012 but not necessarily a decrease in breeding females resulting in a decrease in overall nonpup abundance but not pup abundance. However, by 2018 these depressed year classes may have resulted in fewer breeding females, and therefore, a decrease in pups but no change in nonpups between 2012 and 2018. Interestingly, mortality from the most recent PDV event in 2018 was predominantly made up of subadults and adults. It is also important to note this event occurred after the 2018 survey and appears to be the most severe (>1,600 mortalities), therefore, continued monitoring will be necessary to estimate the current trajectory of this population.

In addition to demographics, there are several factors that may have influenced counts and ultimately estimates of abundance that were difficult to control for in this study. In our study we assumed haul-out probabilities are constant among years. Other studies have shown little interannual variation in haul-out probabilities for harbor seals (Simpkins et al., 2003; Thompson et al., 2005); however, these studies were conducted during the molting season, and we cannot necessarily conclude that changes in haul-out behavior are minimal during the pupping season. Another factor that could vary among surveys is the timing of pupping. Brasseur et al. (2015) observed a consistent change in the timing of pupping to an earlier date in a Dutch population of gray seals. Changes in the timing of pupping would not only impact our counts of pups but could also impact the immigration of nonpups into the study site. Finally, changes in movement patterns and out of the study area particularly among juveniles could affect estimates of nonpups (Waring et al., 2015).

In addition to trends, another goal of our analysis was to update the abundance estimate for the most recent year of survey data. Unlike previous abundance estimates that only use one year of survey data and one correction factor (Gilbert et al., 2005; Waring et al., 2015), we produce an abundance estimate using the entire timeseries of survey data and include multiple correction factors. The Simpkins et al. (2003) correction factor by itself may not be appropriate for this study as it was estimated during the molting season and corrected for more environmental conditions than were included in this study. However, because of the limited information on seal haul-out behavior under ideal conditions, we include this value in conjunction with the information from Waring et al. (2015) to reflect the uncertainty in this unknown parameter. A full assessment of uncertainty is critical to facilitating robust decision making in wildlife management (Regan et al., 2005; Taylor et al., 2000). Ignoring components of uncertainty can result in poor management decisions and undesirable outcomes (Artelle et al., 2013; Taylor et al., 2000). In our analysis, we incorporated multiple sources of prior information with the goal of properly characterizing the extent of uncertainty. The results from our analysis allow for the option of pursuing a more or less precautionary approach depending on management objectives and trade-offs among various stakeholders.

Our analysis of this data set highlights the advantages of a Bayesian hierarchical approach for trend and abundance estimation. The dataset used in this analysis was relatively sparse with many unobserved years between surveys and included one partial survey where not all bay units were observed. Also, there was missing information on environmental covariates as well as auxiliary information on correction factors that need to be incorporated to achieve unbiased estimates of abundance. The Bayesian hierarchical framework used here is able to augment missing data by modelling each bay unit as a latent state (Johnson & Fritz, 2014). In addition, the semiparametric structure allows for flexibility in estimating the shape of the trend over time. Finally, we were able to incorporate information from other studies while propagating the uncertainty to the final abundance estimates through the construction of informative priors. Bayesian approaches also offer advantages to the management of marine mammal management as the output can be easily integrated into a decision analysis framework (Wade, 2000). The results from this study should provide critical information to aid in the management of this stock of harbor seals in the future.

There are a number of ways surveys can be implemented that will increase the power to detect trends and achieve more precis estimates of abundance even when resources to conduct frequent, large-scale surveys are limited (Cressie et al. 2009; Taylor et al., 2007). First, we recommend including replicate surveys whenever possible. In our study there was only one year with replicate surveys (2001), but this did not provide enough information to separate observation error from process error. Including replicates within a survey year can decrease the noise from the observation process and result in more precise inferences (Cressie et al., 2009). In addition, if replicates are spread out over the course of a sampling season there will be more opportunity to capture/model shifts in the timing of biological processes such as pupping and molting which may change over time (Brasseur et al., 2015). Second, if the entire population cannot be surveyed on an annual basis, we recommend including index sites. Index sites may not be a viable option for some populations if interannual movement in and out of the site varies substantially or the index sites are not representative of the larger population of interest (Taylor et al., 2007). For harbor seals, however, high fidelity to birth sites suggest that index sites may be a viable option to monitor trends (Taylor et al., 2007). Using the hierarchical structure used here, unobserved sites could be treated as latent states and augmented in years when full surveys are not conducted such as we did for the 2012 partial survey. To summarize, hierarchical methods are powerful statistical tools, but it is important to link them with appropriate sample designs to optimize the ability to make ecological inferences from model output. Designing surveys to complement the strengths of these methods should help mitigate problems associated with sparse data in future surveys for populations where resources to collect data are limited.

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AUTHOR CONTRIBUTIONS

Douglas Sigourney: Data curation; formal analysis; writing – original draft; writing – review and editing. **Kimberly Murray:** Conceptualization; data curation; formal analysis; investigation; methodology; project administration; writing – original draft; writing – review and editing. **James Gilbert:** Conceptualization; data curation; funding acquisition; investigation; methodology; project administration; resources; supervision; writing – review and editing. **Jay Ver Hoef:** Formal analysis; writing – review and editing. **Robert DiGiovanni Jr.:** Data curation; investigation; resources; writing – review and editing. **Beth Josephson:** Data curation; writing – review and editing.

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