



Modeling ringed seal *Pusa hispida* habitat and lair emergence timing in the eastern Bering and Chukchi Seas

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ABSTRACT: Ringed seals *Pusa hispida* are reliant on snow and sea ice for denning, and a better understanding of ringed seal habitat selection and timing of emergence from snow dens (also called lairs) is needed to quantify and predict effects of climate change in the Arctic. We used generalized additive models to assess relationships between ringed seal counts, from spring aerial surveys in the Bering Sea (2012 and 2013) and Chukchi Sea (2016), and spatiotemporal covariates including survey date, remotely sensed snow and sea-ice values, and short-term weather data. We produced separate models for total ringed seal counts and for pup counts within each region. Our models showed that in both areas, total ringed seal counts increased over the course of the spring, especially after 15 May, indicating emergence from lairs and/or the onset of basking behavior. For the more northerly Chukchi Sea, we found a substantial unimodal effect of snow melt progression and a positive effect of snow depth on total ringed seal counts. In contrast, Bering Sea total ringed seal counts and pup counts in both regions were affected much more strongly by date than by habitat variables. Overall, our findings demonstrate that snow depth and melt play an important role in the timing of ringed seal den emergence, particularly in the Chukchi Sea, and suggest that ringed seal denning may be affected by continued shifts in melt and snow depth associated with climate change.

KEY WORDS: Ringed seal · *Pusa hispida* · Habitat models · Emergence · Chukchi Sea · Bering Sea · Snow · Sea ice

1. INTRODUCTION

Ringed seals *Pusa hispida* depend on snow and ice for critical life history functions such as pupping, molting, and resting (Smith 1976, Hammill & Smith 1991, Kelly et al. 2010b, Piffold et al. 2012). These ice-associated marine mammals are an important nutritional and cultural resource for coastal Arctic Indigenous communities (Hovelsrud et al. 2008, Huntington et al. 2016) and are also ecologically important as a

keystone species and the primary prey for polar bears *Ursus maritimus* (Ferguson et al. 2005, Stirling et al. 2008). Ringed seals are at risk due to loss of sea ice and changes in snow cover and were listed as 'threatened' under the US Endangered Species Act in 2012 due to predicted climate impacts (Kelly et al. 2010b, Hezel et al. 2012, National Marine Fisheries Service 2012); globally, however, ringed seals are listed as 'Least Concern' on the IUCN Red List (Lowry 2016). Environmental change in the Arctic is ongoing and

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rapid (Hezel et al. 2012, Onarheim et al. 2018, Post et al. 2019, Webster et al. 2019), and it is critical to investigate ringed seal habitat selection before further change occurs.

Ringed seals are unique among pinnipeds in that they depend not only on sea ice, but also, in most of their range, on the snow on top of the sea ice. In the spring, these seals give birth to their pups in sub-nivean (snow-covered) dens ('lairs') excavated from the accumulated snow above their breathing holes, providing protection from hypothermia and predation while pups are young and vulnerable (Kumlien 1879, Furgal et al. 1996, Stirling & Smith 2004, Kelly et al. 2010b). Later in the season, ringed seals and their pups emerge from their lairs onto the surface of the sea ice to bask and molt (Kelly et al. 2006). Insufficient snow depth to construct lairs, or premature collapse of lairs due to early warming events followed by freeze-thaw cycles, could expose young pups to dangerous temperatures (Kelly 2001, Stirling & Smith 2004). Higher predation rates have been observed in years when rain events have caused lairs to collapse particularly early, exposing pups on the sea ice to polar bears, foxes, and avian predators (Stirling & Smith 2004). Without lairs for protection, at some sites as many as 100% of ringed seal pups have been observed to have been killed by predators (Smith & Lydersen 1991). The integrity of the lair is also important: greater snow depth over lairs has been correlated with less successful predation by polar bears as well as fewer predation attempts (Hammill & Smith 1991, Furgal et al. 1996). Thus, both depth of snow and sufficient duration of snow cover are necessary for adequate pup survival.

While the role of lairs is clear, the relationship between snow conditions and ringed seal density or pup survival has not been well quantified in the Bering and Chukchi Seas. Forecasts of ringed seal habitat have been based on a minimum snow depth of 20 cm of spring snow cover on top of flat sea ice so that drifts of 50 cm can accumulate along ice ridges for denning (Hezel et al. 2012, Ferguson et al. 2017, Reimer et al. 2019). This 20 cm minimum is derived from *in situ* observations of snow depths during ringed seal lair studies in Svalbard (Lydersen & Gjertz 1986, Smith & Lydersen 1991) and the Canadian Arctic (Smith & Stirling 1975). Under this criterion, the Bering Sea would already be predicted as unsuitable habitat for ringed seals (Kelly et al. 2010b), despite the fact that ringed seals still occupy this region (Crawford et al. 2012, Moreland et al. 2013, Conn et al. 2014). This discrepancy could indicate that ringed seals in the Bering Sea have been

successfully reproducing in shallower snow depths (Fedoseev 1965), are mostly non-breeding subadults (Crawford et al. 2012, but see Kelly in press), or are occupying low-quality habitat in which they may not persist indefinitely.

Ringed seal habitat with sufficient snow depth for denning is expected to decline in the future due to more precipitation falling as rain rather than snow, a shorter sea-ice season during which snow can accumulate, and snow melting earlier in the spring, perhaps before vulnerable pups are ready to be exposed on the ice (Markus et al. 2009, Kelly et al. 2010b, Hezel et al. 2012, Webster et al. 2014, 2021, Dou et al. 2021). Assessing the role of snow depth and melt in broad-scale ringed seal habitat selection and emergence timing, particularly in the Bering and Chukchi Seas, is important for understanding how seals may be impacted by ongoing changes. On-ice surveys of lair habitat in the Chukchi and northern Bering Seas in the 1980s provided valuable data on local-scale habitat characteristics and emergence (Frost et al. 1989, Kelly & Quakenbush 1990), but such studies have been limited to nearshore habitats for logistic and safety considerations. Other work in the region has been conducted using radio or satellite telemetry tags (Kelly & Quakenbush 1990, Crawford et al. 2012, Von Duyke et al. 2020), which provide information on habitat selection for a limited number of individuals. Visual aerial surveys to assess habitat selection for a larger portion of the ringed seal population have been conducted in parts of the Bering Sea (Braham et al. 1984) and Chukchi Sea (Burns & Harbo 1972, Frost et al. 1988, Bengtson et al. 2005), but in each case, temporal coverage during the spring was narrow or surveys began at southern latitudes and progressed northward, thereby limiting the ability of investigators to determine whether patterns in ringed seal detections were due to survey timing, habitat suitability, or both. Interpreting aerial survey data is further complicated by the need to account for short-term, weather-related changes in seal haul-out probability (Moulton et al. 2002, Frost et al. 2004, Hamilton et al. 2018). Additionally, most data on historical, current, and predicted environmental conditions are available at a coarse spatial resolution, and investigating patterns in ringed seal distribution at a comparable resolution is necessary to maximize the conservation and management value of these data sources. Evaluating lair habitat characteristics and the timing of emergence from snow lairs in the region therefore requires aerial surveys of large spatial and temporal coverage in order to match the resolution of predictive covariates.

In this study, we used aerial survey data in the Bering and Chukchi Seas to investigate spatiotemporal patterns in ringed seal counts and habitat selection. The surveys used here were the largest ever conducted for ringed seals in the Arctic, enabling comparison of 2 understudied regions and evaluation of remotely sensed covariates as a tool for monitoring ringed seal lair habitat. We considered a suite of temporal and environmental covariates expected to be important for ringed seals, including survey date, remotely sensed snow and sea-ice variables, and short-term weather variables; we assessed relationships between these covariates and seal detections using generalized additive models (GAMs). Improved understanding of the timing of emergence from lairs, and the environmental variables influencing that timing, is needed for planning future survey campaigns and will in turn facilitate better accuracy in ringed seal abundance estimates and long-term monitoring for a species listed as ‘threatened’ under the US Endangered Species Act. Information on the relationship between ringed seals and snow conditions at broad spatial scales will also help inform predictions of climate impacts on ringed seals and their conservation and management in a rapidly changing ecosystem.

2. MATERIALS AND METHODS

2.1. Ringed seal survey data

We used photographic observations of ringed seals collected during large-scale aerial surveys conducted in the eastern Bering (2012–2013) and Chukchi (2016) Seas (Fig. 1). Surveys were conducted in April and May of each year, coinciding with the transition period from snow-covered sea ice to snow melt and ice break-up during which emergence from lairs is expected (Kelly et al. 2010b). In total, these surveys covered 116 000 km of survey track. Surveys collected data on all 4 species of ice-associated seals found in the Pacific Arctic (ringed seals, bearded seals *Erignathus barbatus*, ribbon seals *Histiophoca fasciata*, and spotted seals *Phoca largha*). Preliminary analyses from the 2012 Bering Sea surveys were reported by Conn et al. (2014).

Moreland et al. (2013) report on detailed methods for the Bering Sea survey design and imaging systems, and Chukchi Sea surveys used a similar imaging system with updated Prosilica GT6600c color cameras and cooled long-wave infrared cameras (FLIR A6750sc SLS); therefore, we do not report full

technical details here. Briefly, thermal and color images were taken simultaneously throughout each survey from automated systems and a mount installed in the bellyport of fixed-wing aircraft. Computer automation was used to detect seals from thermal signatures, and human observers then used associated digital photographs to classify detections by species and species identification confidence (positive: 100% confident, likely: 51–99%, or guess: $\leq 50\%$) (see McClintock et al. 2015). Seal detections where species could not be identified (0% confident) were classified as ‘Unknown.’ Detections were also classified by age (pup or non-pup); further breakdown of age class (e.g. breeding and non-breeding) or by sex was not possible from the imagery, and thus our analysis did not distinguish between these categories.

All values of species identification confidence (positive, likely, guess) (McClintock et al. 2015) were used for analysis. In the overall dataset of ringed seal detections from both regions, the breakdown of species identification confidence was 52% positive, 41% likely, and 7% guess. Species identifications were

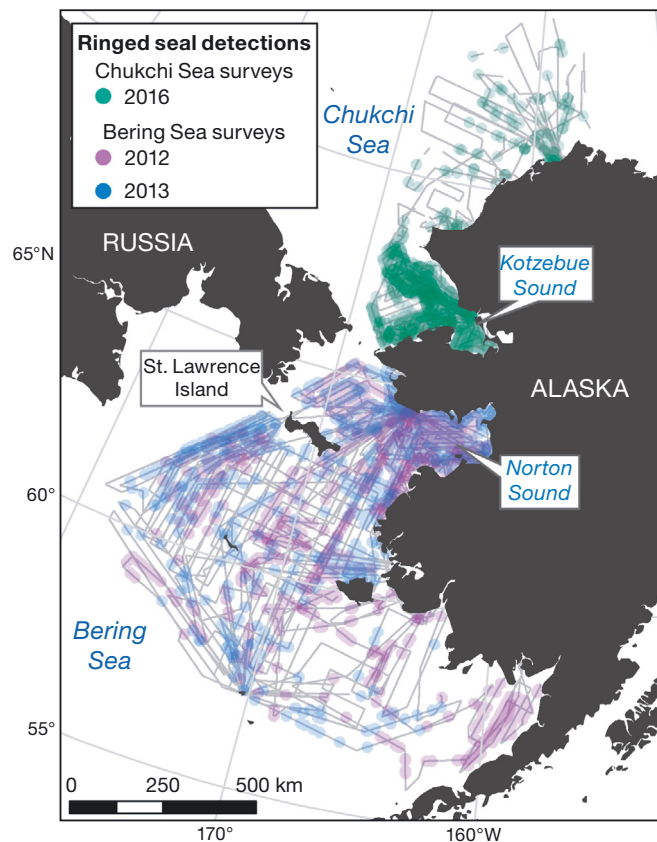


Fig. 1. Ringed seal detections from the Bering Sea (2012 and 2013) and Chukchi Sea (2016) aerial surveys. Gray lines indicate survey tracks

made with similar confidence in the Bering Sea surveys (53% positive, 35% likely, 11% guess) and the Chukchi Sea surveys (51% positive, 41% likely, 5% guess). There was a latitudinal trend in species identification confidence in the Bering Sea, with means of 60.9, 62.2, and 62.9° N for 'guess,' 'likely,' and 'positive' confidence values, respectively, whereas there was no latitudinal trend in species identification confidence apparent in the Chukchi Sea. No temporal trend in species identification confidence was apparent in either region. Previous analyses of a subset of the 2012 Bering Sea survey imagery estimated that 2% of true spotted seals *Phoca largha* and 1% of true bearded seals *Erignathus barbatus* were misidentified as ringed seals, and nearly all true ringed seals (94%) were correctly identified as ringed seals (McClintock et al. 2015). In that analysis, accounting for species misidentification did not change the estimated proportion of ringed seals in the imagery sample (McClintock et al. 2015).

2.2. Modeling approach and predictor variables

We binned ringed seal detections by geographic location and date using a variant of the 25 × 25 km Equal-Area Scalable Earth (EASE) 2.0 grid to match the scale at which satellite remote sensing products are commonly available. Survey effort per grid cell per date was calculated from the combined area of the color camera footprints given the altitude of the aircraft at the time each image was taken. At the target altitude of 1000 ft (~305 m), the color cameras had a total cross-track swath of 392 m for the Chukchi surveys and the larger Bering survey platform, and a swath of 229 m for the smaller Bering survey platform, and any perturbations from the target altitude produced proportional changes in swath (Moreland et al. 2013). Cases of <1 km² of effort per cell–date combination were discarded for analysis. This produced n = 688 unique cell–date combinations for the Chukchi Sea, containing 5001 ringed seals of all ages (i.e. total ringed seals) including 181 pups, and n = 2544 cell–date combinations for the Bering Sea, containing 3358 ringed seals of all ages including 65 pups. Ringed seals cannot be reliably detected in thermal or color imagery when underneath the insulated roof of a snow lair (Kingsley et al. 1990, Amstrup et al. 2004), and therefore all seal detections were from seals exposed on the sea ice.

We selected a suite of covariates that we hypothesized would influence ringed seal counts via spatial differences in habitat suitability and/or tem-

poral differences in haul-out probability and emergence from snow lairs. We expected habitat suitability to be related to snow depth, sea-ice concentration, presence of landfast ice, and other spatial covariates including latitude, longitude, and distance to the coastline. Emergence and short-term haul-out probability were expected to be influenced by the day of the year for each survey, year (applicable for the Bering Sea only), an index of snow melt progression, and weather variables including air temperature, wind speed, and barometric pressure. The snow, sea-ice, and weather variables are each described in greater detail as follows.

We used 2 snow variables derived from satellite passive microwave data to understand lair habitat and emergence timing. First, passive microwave-derived dates of snow melt onset (Belchansky et al. 2004) were computed on the same grid as used for analysis. We subtracted the melt date for each cell from the survey date and used this as an index of melt progression (hereafter 'melt index') across time and space. Negative melt index values indicate surveys that occurred before melt onset, and positive values indicate surveys that occurred after melt onset. Second, we used the NASA Cryosphere database of 25 km gridded snow depths on sea ice (Markus & Cavalieri 1998, Comiso et al. 2003). Because the algorithm to determine snow depth only functions for dry snow (Markus & Cavalieri 1998), depths are not available during the spring survey period after melt has begun. To accommodate this, we used the average snow depth during the month of March as a proxy for yearly spring snow depth in each cell. Missing values near coastlines or the southern margin of the study area were imputed using the 'autoKriging' function (Hiemstra et al. 2009) in the R 3.6.1 programming environment (R Core Team 2017) for both snow datasets.

For sea-ice concentration, we used 25 km gridded daily data from the National Snow & Ice Data Center (<https://nsidc.org/data/nsidc-0051>). We also included a binary classification of whether each portion of seal survey effort covered landfast ice. We plotted the segments of survey track passing through each cell on each survey date over concurrent NASA Worldview satellite imagery (<https://worldview.earthdata.nasa.gov>) in ArcGIS (Environmental Systems Research Institute 2016) and visually delineated what portion of the survey track crossed over landfast ice. Segments containing at least one-third landfast ice along their length were classified as covering landfast ice.

The North American Regional Reanalysis (Mesinger et al. 2006) database was used for weather co-

variates to account for short-term differences in haul-out probability (Kelly et al. 2006, Hamilton et al. 2018). Specifically, we included air temperature ($^{\circ}\text{C}$) at 2 m above sea level, wind speed $^{1/3}$ (m s^{-1}), and barometric pressure (Pa) reduced to mean sea level at the time of each survey. Each of these weather covariates was available at a 32 km resolution and in 3 h intervals, and we matched them with the centroid of each surveyed grid cell by nearest time and location.

We used GAMs in the ‘mgcv’ package (Wood 2017) in Program R (R Core Team 2017) to relate these covariates to ringed seal counts. We produced separate models for ringed seals in the Bering and Chukchi Seas due to the lack of spatial and temporal overlap between the survey campaigns, changes to survey equipment, and possible demographic habitat partitioning (Crawford et al. 2012, but see Kelly in press). Within these 2 regions, we produced separate models for total ringed seal counts and for pup counts only, for a total of 4 models.

We used seal counts per cell–date combination as the response variable in all models, with an offset for area surveyed per grid cell (see Eq. 1 below). We used a Tweedie distribution and log link to account for zero-inflation and overdispersion in the seal counts (Miller et al. 2013). All continuous covariates were encoded as $s()$ smooths with a thin-plate regression spline basis. We encoded all interaction terms as tensor products to accommodate covariates with fundamentally different units (Wood 2017). In each case, we used a $ti()$ formulation, which estimated interaction effects separately from any main effects while preserving identifiability, because we expected covariates within these interaction terms (e.g. snow depth and latitude) to also have their own main effects on seal counts.

We screened for multicollinearity among covariates using variance inflation factors (VIFs), and removed 1 variable at a time until all VIFs were <5 (Zuur et al. 2009). As a result, distance to coast was removed from the Chukchi Sea models and air temperature was allowed to remain in the models as an interaction with date (main effect removed). We also included an interaction term between melt index and latitude, and between snow depth and latitude, because ringed seals in the northernmost part of the study area might be especially reliant on deep, persistent snow cover for thermal insulation and protection from polar bears, which are more common in the Chukchi and northern Bering Seas than in the southern Bering Sea (Amstrup et al. 2005, Wilson et al. 2016). We included an interaction

term between snow depth and melt index because lairs in the deepest snow likely become exposed at a more advanced stage of melt than lairs in shallow snow. Lastly, we included an interaction term between latitude and longitude to permit greater flexibility when modeling spatial variation in basking behavior. Thus, the general formula for each global GAM was:

$$\begin{aligned} \text{Ringed seal count} \sim & s(\text{survey date}) + s(\text{snow depth}) \\ & + s(\text{melt index}) + s(\text{ice concentration}) + s(\text{pressure}) \\ & + s(\text{windspeed}) + s(\text{latitude}) + s(\text{longitude}) \\ & + ti(\text{latitude}, \text{longitude}) + ti(\text{melt index}, \text{latitude}) \\ & + ti(\text{snow depth}, \text{latitude}) + ti(\text{snow depth}, \text{melt index}) \\ & + ti(\text{temperature}, \text{survey date}) + \text{as.factor}(\text{landfast ice}) \\ & + \text{offset}(\log(\text{effort})) \end{aligned} \quad (1)$$

with the addition of $s(\text{distance to coast})$ and $\text{as.factor}(\text{year})$ for the Bering Sea models.

We used the ‘double penalty’ automated selection approach provided by the ‘mgcv’ package, in which an additional shrinkage penalty is applied to the null space of each smoothed covariate (Marra & Wood 2011, Wood 2017). Under this approach, predictors with weak contributions to the response can be effectively shrunken out of the model, with estimated effective degrees of freedom (edf) of nearly zero. We considered any smoothed covariates with $\text{edf} < 0.1$ to have a negligible effect in the model. Because the double penalty approach does not operate on categorical variables, we then tested whether year (applicable for the Bering Sea only) and landfast ice classification should be retained. We removed these categorical terms from the full model in Eq. (1), re-applied the double penalty approach to all continuous variables, and used Akaike’s information criterion (AIC) to evaluate whether the model had been improved. We selected the model with the lowest AIC as the best model for total counts and pup counts within each region. If models were within 2 AIC units ($\Delta\text{AIC} \leq 2$), we selected the most parsimonious model as the best model (Arnold 2010).

Prediction plots were generated for each smoothed covariate on the response scale and visually examined to assess their effect on ringed seal counts. Model validation was performed using the ‘gam.check()’ function in ‘mgcv’ (Wood 2017), by plotting model residuals with respect to each covariate, and by performing chi-squared goodness-of-fit tests on randomized quantile residuals (Dunn & Smyth 1996, Algorithm 3 from Conn et al. 2018). We also produced comparative maps of observed and model-fitted seal densities to evaluate the success of each model in capturing spatial patterns.

3. RESULTS

3.1. Models for total ringed seal counts

The model that best explained total ringed seal counts in the Bering Sea retained all smoothed covariates after applying the 'double penalty' automated model selection approach (Table 1), and landfast ice classification was removed based on AIC (see Table A1 in the Appendix). The model explained a moderate proportion of variation in the data (R^2 -adj = 54.9%). The model that best explained total ringed seal counts in the Chukchi Sea also retained all smoothed covariates and dropped the landfast ice classification, but explained a larger proportion of variation in total seal counts, with R^2 -adj = 78.5%. For models of both seas, date had a strong effect on seal counts, with very few seals before 20 April, followed by increasing counts over the course of the spring. Increases in seal counts were particularly sharp after 15 May, as illustrated in Fig. 2. Models of both seas also estimated a positive unimodal effect of melt on ringed seal counts, with a weak peak at approximately 10 d before melt onset for the Bering Sea and a strong peak at ap-

proximately 15 d after melt onset for the Chukchi Sea. The effect of snow depth in the Bering model was weakly unimodal, with a peak in seal counts at a March snow depth of ~20 cm, whereas in the Chukchi model, the effect of snow depth was positive and approximately linear.

Latitude had a weakly negative effect on seal counts below 61°N in the Bering Sea, and a moderately negative effect on seal counts above 70°N in the Chukchi Sea. Both the Bering and Chukchi total count models performed well overall at capturing observed spatial patterns in ringed seal densities (Fig. 3), with highest seal densities in Norton Sound followed by the area southwest of St. Lawrence Island for the Bering Sea model, and outside the mouth of Kotzebue Sound for the Chukchi model.

Chi-squared goodness-of-fit tests on randomized quantile residuals produced p-values of <0.001 for the Bering Sea total count model and 0.1 for the Chukchi Sea total count model. For both datasets, lack of fit was primarily a result of underpredicting very large ringed seal counts (Fig. 4). As such, covariate confidence intervals (Fig. 2) for these models should be interpreted conservatively.

Table 1. Results of generalized additive models (GAMs) produced for ringed seal total counts and pup counts within the Bering and Chukchi Seas. Grayed values indicate variables that were not included in the best model (NA) or smoothed terms with effective degrees of freedom (edf) <0.1 which we considered to have been effectively shrunken out of the model. Note that p-values for GAMs do not account for uncertainty in the estimation of the smoothing parameters and should be considered approximate (Wood 2017)

Parametric term	Bering total counts		Chukchi total counts		Bering pups		Chukchi pups	
	Estimate	p	Estimate	p	Estimate	p	Estimate	p
Intercept	-2.40	<0.0001	-2.77	<0.0001	-6.47	<0.0001	-10.74	0.004
Landfast ice = Yes	NA	NA	NA	NA	NA	NA	NA	NA
Year = 2013	0.81	<0.0001	NA	NA	NA	NA	NA	NA
Smoothed term	edf	p	edf	p	edf	p	edf	p
Date	7.07	<0.0001	4.12	<0.0001	2.76	<0.0001	1.75	<0.0001
Melt index	5.57	<0.0001	2.69	<0.0001	<0.0001	0.470	<0.0001	0.711
Snow depth	2.28	<0.005	2.25	<0.0001	<0.001	0.254	<0.0001	0.585
Latitude	2.64	<0.0001	0.99	<0.0001	2.23	<0.0001	3.10	<0.005
Longitude	4.50	<0.0001	5.43	<0.0001	<0.0001	0.393	2.91	<0.001
Sea-ice concentration	0.99	<0.0001	2.79	<0.0001	<0.001	0.311	<0.0001	0.470
Barometric pressure	4.16	<0.0001	1.15	0.068	<0.0001	0.502	1.14	0.028
Wind speed ^{1/3}	2.95	<0.0001	0.89	0.002	0.54	0.139	<0.0001	0.799
Distance to coast	1.67	0.047	NA	NA	4.88	<0.0001	NA	NA
Latitude:Longitude	7.12	<0.0001	2.63	<0.0001	2.99	<0.005	<0.0001	0.595
Melt index:Latitude	2.71	0.032	0.71	0.144	<0.001	0.320	0.51	0.227
Snow depth:Melt index	6.91	<0.0001	3.46	<0.0001	0.61	0.098	1.12	0.031
Snow depth:Latitude	3.49	0.009	0.65	0.108	<0.0001	0.398	0.81	0.077
Air temperature:Date	11.15	<0.0001	0.60	0.162	<0.0001	0.691	0.76	0.109

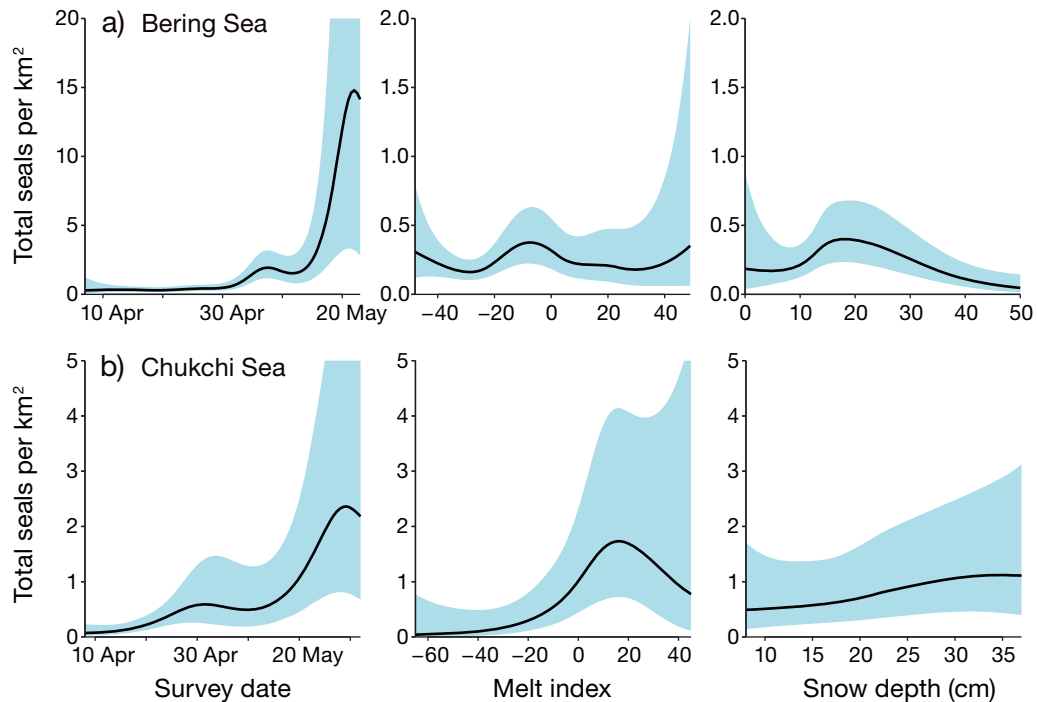


Fig. 2. Effect of survey date, melt index (difference between survey date and melt onset date, where positive values indicate surveys that occurred after melt onset), and snow depth on predicted total ringed seal counts in the best model for the (a) Bering Sea and (b) Chukchi Sea when only the respective covariate is allowed to vary. When generating the plots, latitude and longitude were set to the approximate center of Norton Sound for the Bering Sea model and Kotzebue Sound for the Chukchi Sea model. The year for the Bering Sea was set to 2012 and all other covariates included in the models were held constant at their means. Shading indicates 95% confidence intervals for predicted seal densities. Note that the scales of the y-axes for the Bering Sea vary

3.2. Models for pups only

The Bering Sea pup model retained the smoothed terms for survey date, latitude, wind speed, and distance to coast as well as the interaction terms between latitude and longitude and between snow depth and melt index (Table 1). The categorical variables of survey year and landfast ice classification were removed based on AIC (Table A1). For the Chukchi Sea pup model, the smoothed terms for survey date, latitude, longitude, and barometric pressure as well as the interaction terms between melt index and latitude, snow depth and melt index, snow depth and latitude, and air temperature and date were retained. Landfast ice classification was removed via AIC. In both the Bering and Chukchi best models of pup counts, date had a strong effect on pup counts, with near-zero pup counts before 20 April, followed by increases in pup counts that continued until 10 May in the Bering model and throughout the spring in the Chukchi model (Fig. 5). The best model of Bering Sea pup counts showed no effect of melt index or snow depth, whereas the Chukchi pup model showed a near-zero but slightly unimodal

effect of melt peaking at ~ 10 d before melt onset, and a positive effect of snow depth with maximum pup densities predicted at ~ 27 cm. The Bering Sea model explained a low proportion of the variation in pup counts with R^2 -adj = 11.8%, whereas the Chukchi Sea model explained a moderate proportion of the variation in pup counts (R^2 -adj = 68.2%).

Latitude was influential in both pup models, with a strongly negative effect on counts at latitudes below 61°N in the Bering Sea or above 69°N in the Chukchi Sea. In our mapped density plots, the Bering Sea pup model captured higher densities of pups in Norton Sound and southwest of St. Lawrence Island, but otherwise did not perform as well as the other 3 models in capturing spatial patterns in densities (Fig. 6). The Chukchi pup model, in contrast, captured spatial patterns in pup densities very well (Fig. 6), and only predicted pups in the southern Chukchi Sea in accordance with the distribution observed in the surveys. Both models predicted a low average density of pups, although observed and predicted pup densities were lower in the Bering Sea than the Chukchi Sea.

Chi-squared goodness-of-fit tests on randomized quantile residuals produced a p-value of 0.1 for the

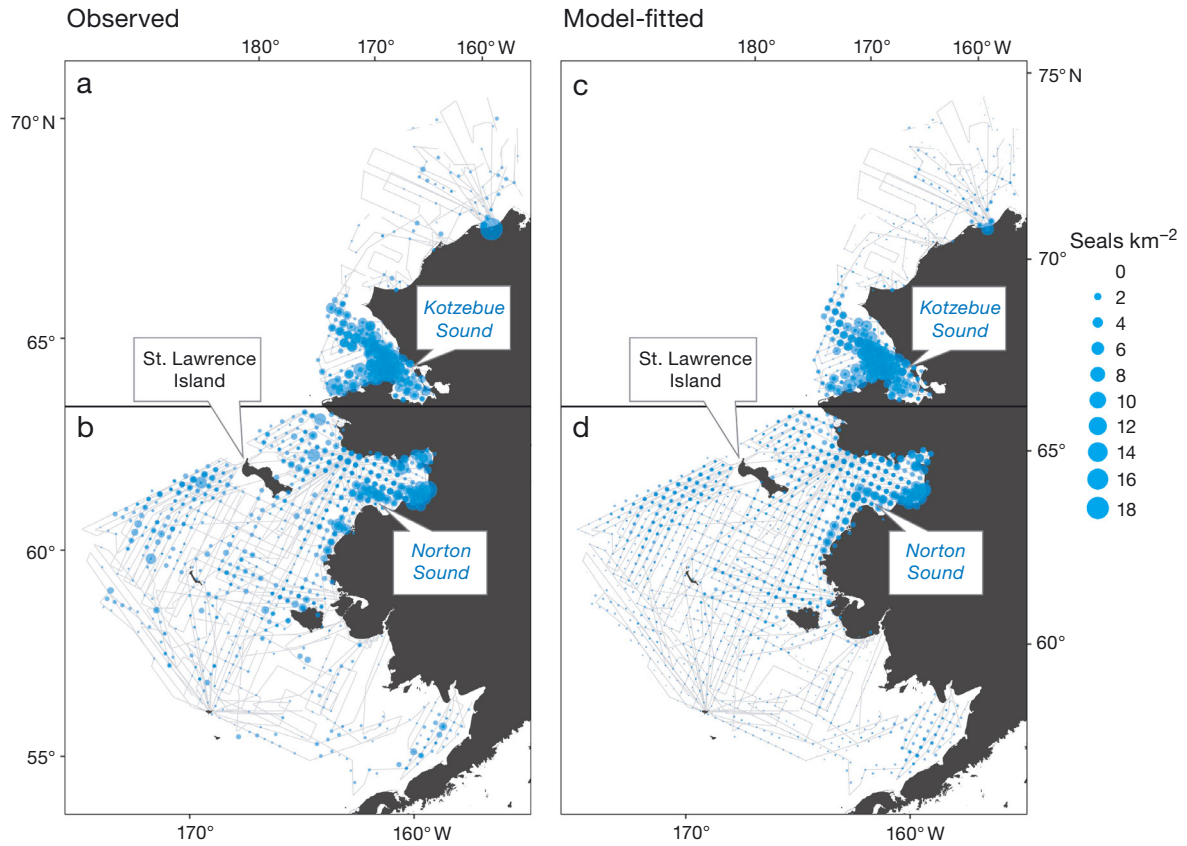


Fig. 3. Comparison of observed ringed seal densities in the (a) Chukchi Sea and (b) Bering Sea to densities fitted by (c,d) their respective best models. Tracklines from the aerial surveys are shown in gray

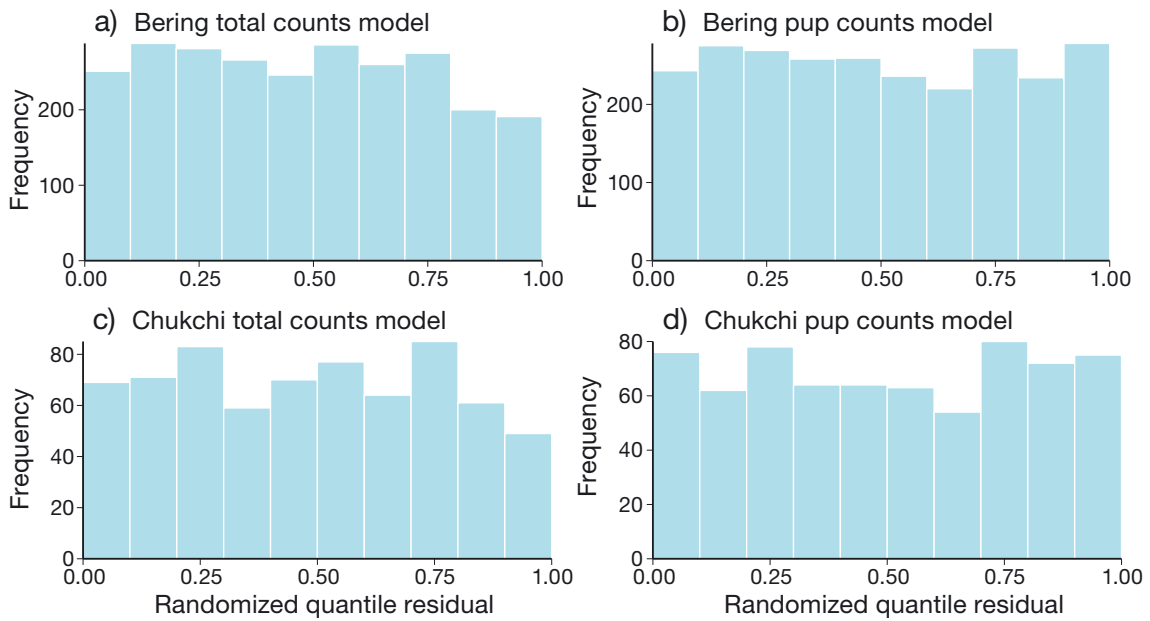


Fig. 4. Binned randomized quantile residuals examining the fit of the best models for Bering and Chukchi Sea (a,c) total ringed seal counts and (b,d) pup counts, assuming counts were Tweedie distributed. For a well-fitting model, randomized quantile residuals should be approximately uniformly distributed on (0,1)

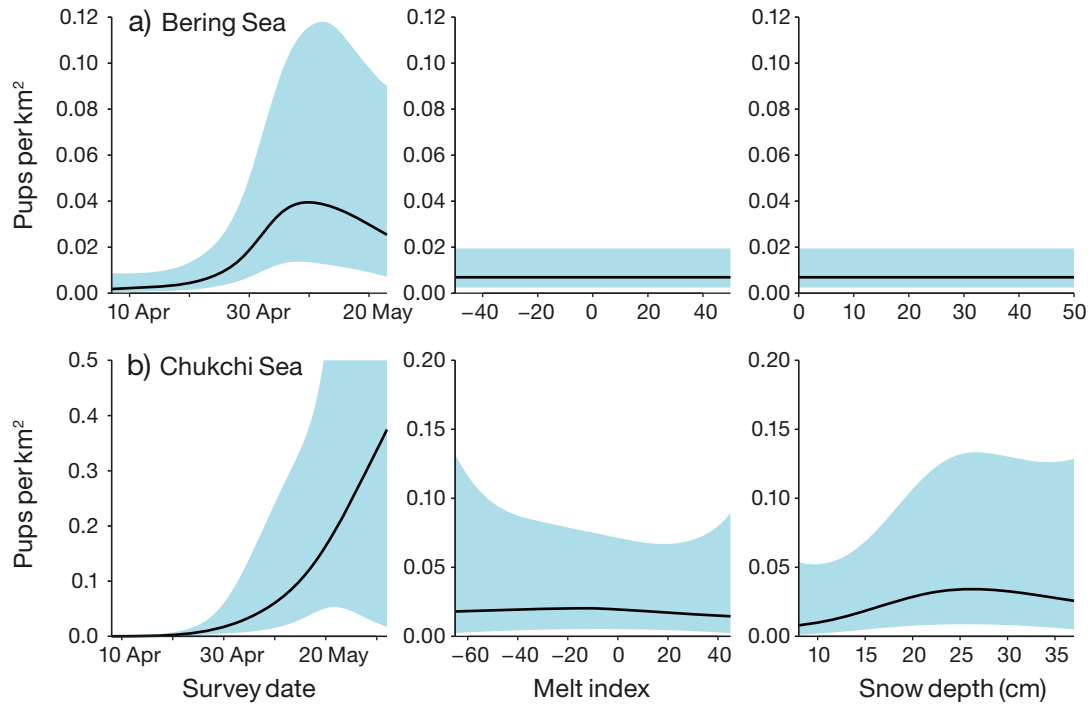


Fig. 5. Effect of survey date, melt index, and snow depth on predicted pup counts in the best model for the (a) Bering Sea and (b) Chukchi Sea when only the respective covariate is allowed to vary. y-axes for the Chukchi Sea vary; other details as in Fig. 2

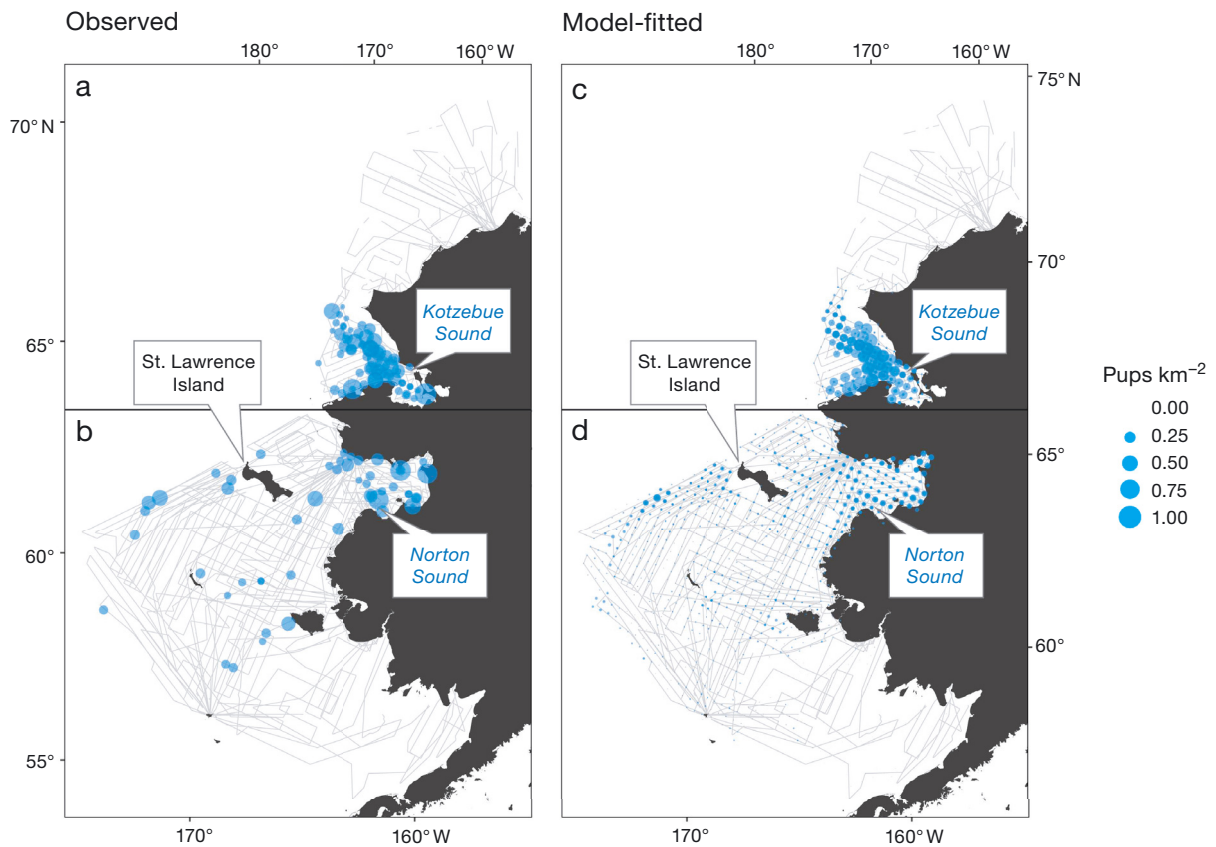


Fig. 6. Comparison of observed ringed seal pup densities in the (a) Chukchi Sea and (b) Bering Sea to densities fitted by (c,d) their respective best models. Tracklines from the aerial surveys are shown in gray

Bering Sea pup model and $p = 0.4$ for the Chukchi Sea pup model (Fig. 4), indicating that the Tweedie models fitted count data from both regions reasonably well.

4. DISCUSSION

Our models showed that in both the Bering and the Chukchi Seas, total ringed seal counts and pup counts increased over the course of the spring, especially after 15 May for total counts and after 30 April for pups. Date had a much stronger effect than habitat variables for pup models in both regions and for Bering Sea total counts; these total counts were also weakly associated with melt and snow depth. For Chukchi total counts, we found a substantial unimodal effect of melt onset and a positive effect of snow depth. These findings demonstrate that snow depth and melt play an important role for ringed seals even at the coarse 25 km scale used in our analysis.

During aerial surveys for ringed seals, seals in the water or inside of snow lairs are unavailable for detection by visual observers or by thermal cameras; therefore, only seals exposed on the sea ice can reliably be detected. Ringed seals also spend less time out of the water prior to emergence and basking (Kelly et al. 2006, 2010a, Martinez-Bakker et al. 2013). These factors hinder the interpretation of ringed seal survey data when emergence dates are unknown, as areas of high-quality habitat may appear to be unoccupied if surveyed prior to emergence from lairs. Our models indicate that total ringed seal counts increase sharply around 15 May in both the Bering and the Chukchi Seas, indicating emergence from lairs and the onset of basking behavior. Ringed seals in the Beaufort Sea monitored via satellite telemetry also showed abrupt changes in haul-out behavior in mid-May (Von Duyke et al. 2020). The timing of these events varies interannually (Kelly et al. 2006), but our results nonetheless provide important information that can be used to monitor for future shifts in emergence as conditions in the Arctic continue to change. In the nearer term, aerial survey campaigns should interpret low apparent densities from before 15 May with caution, as seals may be concealed within snow lairs.

We also found notable spatiotemporal effects of snow variables on ringed seal habitat and emergence. Our models showed a unimodal contribution of melt progression to total ringed seal counts, particularly in the Chukchi Sea, suggesting that melt onset and the corresponding weakening structural inte-

grity of lairs may trigger or contribute to emergence. This pattern is in agreement with previous work in the Beaufort Sea which documented a strong correlation between passive microwave-derived melt onset and the timing of ringed seal lair abandonment and basking behavior (Kelly et al. 2006, 2010a); our results now extend this observation to other regions of the Alaskan Arctic and at a larger spatial scale. In addition to the effect of melt, the Chukchi total count model also showed a positive effect of snow depth, highlighting the importance of deeper snow for ringed seal habitat and lair construction. Studies in western Hudson Bay found a positive relationship between ringed seal recruitment and snow depth measured from local weather stations (Ferguson et al. 2005), a negative relationship between pup survival and spatial variability in passive microwave-derived snow depth, and a positive relationship between pup survival and the duration of spring snow cover (Iacozza & Ferguson 2014). Changes in snow depth and melt onset could thus have detrimental effects on ringed seals and their ability to provide pups with lairs of sufficient depth and durability.

4.1. Differences between Bering and Chukchi Sea models

The differences that we observed between our models for the Bering and Chukchi Seas also reveal noteworthy patterns. The relative effect sizes of snow depth and melt onset were stronger in the Chukchi models than in the Bering models where survey date dominated (Figs. 2 & 5). The combination of covariates in the Chukchi models for both total counts and pups explained a larger proportion of the variation than the corresponding Bering Sea models. The Bering Sea total count model also had issues with underfitting in areas of high observed seal densities that we were unable to resolve (Fig. 4). It is possible that a small proportion of the identifications in the Bering Sea were spotted seals that were misidentified as ringed seals (McClintock et al. 2015), potentially obscuring spatiotemporal patterns in ringed seal densities and weakening the ability of the model to assess the influence of covariates on seal density in the Bering Sea. Notably, very few pups were detected during the Bering Sea surveys, with only 25 pups in 2012 and 40 in 2013; in contrast, 185 pups were observed in the Chukchi survey in 2016. As a result, the Bering Sea pup model explained only a small proportion of the observed variation in pup counts, with few pup presences relative to the total

area surveyed (only 53 out of 2544 cell–date combinations). Overall, for both total counts and pups, the snow and sea-ice variables included in our analysis were better able to explain patterns in seal counts in the Chukchi than the Bering Sea.

Together, the regional differences in the proportion of variation explained by the models, combined with the stronger effects of melt and snow depth in both Chukchi models, may suggest lower proportions of pupping and lair usage in the Bering Sea. Pups represented 3.6% of ringed seals detected in the Chukchi Sea compared to only 1.9% in the Bering Sea. This could reflect degraded pupping habitat and/or be due to a larger percentage of young, non-breeding individuals in the Bering Sea (Crawford et al. 2012) who would be less driven to select habitat suitable for lairs. Satellite telemetry studies of ringed seals have observed possible evidence of demographic habitat partitioning, with adults occupying higher sea-ice concentrations compared to subadults (Von Duyke et al. 2020) and of adults overwintering in the Chukchi or northern Bering Sea, while subadults followed the sea-ice edge into the southern Bering Sea (Crawford et al. 2012). Kelly (in press), however, suggested that the patterns observed in these studies may be an artifact of tagging ringed seals during the open-water period; Kelly (in press) did not observe demographic habitat partitioning in a sample of ringed seals tagged during spring in the Chukchi and Beaufort Seas. Frost et al. (1989) commented on sightings of unusually small pups exposed on floes in the Bering Sea, although they did not provide quantitative data to support this, and speculated that younger females may be excluded from higher-quality habitat with sufficient snow depth for constructing lairs (McLaren 1958). If there are fewer breeding individuals in the Bering Sea, or perhaps individuals breeding without the use of lairs, it follows naturally that there would be more variation in the habitat and timing of seal detections, and that modeling this variation would be challenging. The Chukchi Sea could be more optimal habitat for adults, with sea ice persisting for longer into the spring and deeper, longer-lasting snow cover than in the more southerly Bering Sea (Markus et al. 2009, Kelly et al. 2010b). This would thereby provide a platform for pupping and basking over a longer period. Our results, in agreement with previous studies, suggest that the Chukchi Sea may presently be of higher value as breeding habitat for ringed seals.

We caution, however, that surveying the Bering and Chukchi Seas during different years is a potential con-

founding factor that limits our ability to attribute the patterns we observed to persistent regional differences. It is possible that the thermal cameras used in the Bering Sea surveys detected a smaller proportion of pups than the more sensitive thermal cameras used in the Chukchi Sea surveys, but data on pup detection probability are not available. Additionally, following an unusual mortality event in 2010–2011 in which ringed seals exhibited skin lesions and other symptoms (NOAA 2011), the proportion of pups in the ringed seals harvested by Alaska Native communities in 2012 was low (~35%) compared to 2013 (~55%) and 2016 (~75%) (Quakenbush et al. 2020). Thus, the low proportion of variation in pup counts explained by the 2012–2013 Bering Sea pup model compared to the 2016 Chukchi Sea pup model may have been influenced by interannual differences in ringed seal population dynamics.

Ringed seal productivity in the Bering and Chukchi Seas currently appears to be stable or possibly increasing based on biomonitoring data from the region. Compared to 1975–1984, ringed seals harvested by Alaska Native communities in the Bering and Chukchi regions during the open water period in 2003–2012 had better body condition, earlier ages of maturity, and a higher pup-to-adult ratio in the harvest (Crawford et al. 2015). However, some instances of low ringed seal productivity have been observed to coincide with years of unusually thick or persistent sea ice (Stirling et al. 1977, Kingsley & Byers 1998, Harwood et al. 2000, 2012, Stirling 2002), so it is possible that climate change may initially improve denning habitat quality via thinner sea ice before that effect is outweighed by persistent, detrimental losses of sea-ice extent and snow depth. For example, early snow melt and ice breakup were implicated in high rates of ringed seal pup mortality in the White Sea in 1977 (Lukin et al. 2006) and in the Labrador Sea (Stirling & Smith 2004). This threshold may not be reflected yet in harvest data in the Bering and Chukchi Seas. Furthermore, ringed seals may be found hundreds of kilometers away from their breeding home ranges during the open-water harvest period (Gjertz et al. 2000, Freitas et al. 2008, Kelly et al. 2010a, Crawford et al. 2012, Martinez-Bakker et al. 2013), so regional differences in pupping could go undetected. In the Alaskan Arctic, it is possible that improved conditions in some parts of the ringed seal range (e.g. the Chukchi Sea) could be temporarily masking losses of denning habitat in other parts (e.g. the Bering Sea), and the overall trend of stable ringed seal productivity may change as the Arctic continues to warm.

4.2. Considerations in interpretation

We acknowledge that the increases that we observed in ringed seal detections over the course of the spring cannot be attributed solely to emergence from lairs. Increases in ringed seal detections observed during each spring likely reflect several processes which we are unable to conclusively differentiate between in this study: (1) emergence from lairs, (2) changes in haul-out behavior as seals begin to bask and molt, and (3) births of pups. We do not expect pupping to play a large role in our total count models due to the low densities of pups observed in the surveys. However, the contribution of changes in haul-out behavior could be substantial, as previous work has documented that coincident with emergence from lairs, seals begin spending more time hauled out, and also shift their diel patterns to haul out more during the day; both of these changes would make seals more available for detection during mid-day aerial surveys (Kelly & Quakenbush 1990, Kelly et al. 2005, 2006, Von Duyke et al. 2020).

We also note that the snow depth and melt onset variables used in our analyses have limitations that require some caution in interpretation. The sea ice present in a given grid cell at the time of the snow depth or melt onset measurements was not necessarily the same sea ice present during the seal surveys, particularly late in the survey period and at southern latitudes where breakup and sea-ice drift are likely to have occurred rapidly. Land 'contamination' is another issue for cells along the coast, causing missing or possibly erroneous values (Bliss et al. 2017). We considered the passive microwave melt onset product by Markus et al. (2009) as an alternative data source, but ultimately used the product from Belchansky et al. (2004), as it had been successfully used in past studies of ringed seal lair abandonment (Kelly et al. 2006).

In addition to these considerations, it is possible that our results may understate the importance of snow depth to ringed seal lair habitat due to scales of selection and detectability. Habitat selection and the relative importance of different predictors such as snow depth may differ on the local scale from the coarse spatial scale of this study. Previous studies with *in situ* sampling have clearly demonstrated the role of lairs constructed in deep snow in preventing predation and hypothermia (Smith & Stirling 1975, Furgal et al. 1996, Stirling & Smith 2004), but this is unlikely to fully be reflected in regional variability in snow depth at the 25 km scale. Deeper snow also likely has a negative effect on detectability, as seals can only be detected at exposed structures. Lairs in

the deepest snowdrifts may become exposed later in the melt process (possibly not even by the end of our survey period in the northern Chukchi Sea) than those in shallower snow. Thus, despite the positive linear effect of snow depth identified in the model of total counts in the Chukchi Sea, the strength of selection for snow depth observed in this study should be considered conservative.

4.3. Directions for future research

Our ability to relate seal distributions to snow variables may improve in the future as technology and/or climatological modeling continue to advance. The recently launched ICESat-2 satellite shows promise for remotely sensed surface roughness (Farrell et al. 2020), and can be used in combination with the CryoSat2 satellite to produce snow depth estimates with high vertical precision (Kacimi & Kwok 2020, Kwok et al. 2020b). Gridded products are so far only available at the same 25 km resolution used in this study. Non-gridded ICESat-2 sea-ice data have a high along-track resolution of ~27–200 m (Kwok et al. 2019) but are only available >25 km from land (Kwok et al. 2020a), limiting their utility over landfast ringed seal habitats. Despite these continued challenges, future ringed seal aerial surveys can maximize the value of this satellite to ringed seal ecological research by aligning survey tracks with ICESat-2 ground tracks.

The upcoming Copernicus Polar Ice and Snow Topography Altimeter (CRISTAL) satellite mission is expected to launch in 2027 and will provide snow depth estimates at a high along-track resolution of 20 m (Kern et al. 2020). A new snow depth product derived using a combination of remotely sensed sea-ice data and weather models (Liston et al. 2020, Stroeve et al. 2020) will soon be publicly available and has the potential to improve on the temporal misalignment between snow depths and ringed seal detections in our study. To determine the value of existing and future snow depth and melt products for habitat monitoring, continued intercomparison and groundtruthing via on-ice or airborne measurements (Bliss et al. 2017, Kwok et al. 2017, 2019, Farrell et al. 2020, Song et al. 2020, Zhou et al. 2021) will be important, including along coastlines to assess the severity of land contamination. Research is also needed to assess how broad-scale snow-depth patterns (e.g. at the 25 km scale used here) correspond to fine-scale habitat features such as snow drifts where lairs are constructed.

Ringed seal habitat in the Bering and Chukchi Seas is expected to change rapidly, and the way that seals interact with these snow and sea-ice characteristics may change as well, making monitoring and conservation for this species especially challenging. It will be important to track environmental change, particularly in areas shown in this study to have higher densities of pups, and to periodically reassess how the spatiotemporal distribution of ringed seals relates to habitat characteristics.

Conducting aerial surveys later in the spring is one way to avoid the complications with den emergence when interpreting density estimates. However, surveying too late can also potentially cause problems, with ringed seals migrating north while surveys are being conducted. Therefore, the development of methods for estimating ringed seal abundance that explicitly address changing availability is a topic of current research. Availability, or the proportion of seals visible to aircraft when flying overhead (Marsh & Sinclair 1989, Bengtson et al. 2005), is ultimately a function of both emergence from lairs and behavioral changes in haul-out probability related to basking. One possible strategy is to account for changes in haul-out behavior using data from tagged seals, and then model overall changes in availability using temporal trends in aerial survey counts. In this manner, one may be able to isolate the magnitude of contributions from haul-out and emergence to increases in spring seal counts, improving the accuracy of ringed seal abundance estimates. Another strategy would be to make use of changes in haul-out diel behavior (Kelly et al. 2006, Von Duyke et al. 2020) from tagged seals to help model emergence using, for example, hidden Markov models (Zucchini et al. 2017).

4.4. Conclusions

Our analysis of ringed seal survey data from the Bering and Chukchi Seas revealed strong temporal patterns in spring seal counts as well as effects of melt onset and snow depth, particularly in the Chukchi Sea. If snow melt is already limiting the time that seals are able to spend in lairs, then as melt dates continue to advance (Bliss et al. 2017), dates of emergence may be forced to advance also. This raises questions about the minimum amount of time that pups need access to lairs, whether these needs will be met in the future, and whether ringed seals will be able to respond to changing conditions via behavioral changes, phenotypic plasticity, and/or natural selection. Some possible responses include shift-

ing breeding areas northward, advancing pupping dates, or sheltering in the lee of ice hummocks. However, the start of pupping is constrained by the timing of sea-ice freeze-up and sufficient snow accumulation, and thus the breeding season would become increasingly narrow; northward range shifts similarly could not continue indefinitely. Warmer temperatures may somewhat reduce the risk of hypothermia in pups in areas with inadequate snow conditions for lairs, but because pups must elevate their metabolic rate even at 0°C if their fur becomes wet (Smith et al. 1991), lairs are likely to remain important for thermal insulation. In the subarctic Sea of Okhotsk, where polar bears are absent, an unknown percentage of pups of the Okhotsk ringed seal subspecies *Pusa hispida ochotensis* shelter in the lee of ice hummocks rather than inside lairs (Fedoseev 1965), although the survival rates of these exposed pups are unknown. It is also possible that earlier melt onset and sea-ice breakup (Johnson & Eicken 2016) could physically reduce polar bear access to ringed seal pups (Hamilton et al. 2017a,b), but if so, it is unclear to what extent this would offset increases in predation risk (Stirling & Smith 2004) due to thinner snow cover over lairs or pups being completely exposed on the sea ice.

The relationships between ringed seal counts and remotely sensed snow variables in our analysis underscore the need to monitor ringed seal habitat and productivity under climate change, particularly in the Chukchi Sea, which our models and other studies (e.g. Crawford et al. 2012) support as being an important area for ringed seal lairs and pupping in the Alaskan Arctic. As capacities for remote sensing improve, continued studies on broad-scale patterns in ringed seal distribution with respect to environmental covariates will be valuable for improving on the limitations of our analysis and for tracking changes in ringed seal habitat selection and suitability.

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Appendix. Model Δ AIC values

Table A1. Δ AIC values for models with and without categorical terms for year and landfast ice. Year was only applicable for the Bering Sea, where surveys were conducted during 2 years. The best model for total counts and pup counts within each region is indicated with an asterisk (*). For the 2 cases in which there was a model with Δ AIC ≤ 2 (Bering total counts and Chukchi pup counts), we selected the model which was most parsimonious and had the lowest AIC value as the best model. NA: not applicable due to having a single year of survey data in the Chukchi Sea

Categorical variables	Bering total counts	Chukchi total counts	Bering pup counts	Chukchi pup counts
None	9.40	0*	0*	0*
Year	0*	NA	23.74	NA
Landfast ice	10.92	2.76	3.00	1.36
Year and landfast ice	1.70	NA	21.43	NA

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