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FEATURE ARTICLE

Characteristics of ringed seal *Pusa hispida* ('natchiq') denning habitat in Kotzebue Sound, Alaska, during a year of limited sea ice and snow

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ABSTRACT: Sea ice and snow are essential to Arctic ecosystems, playing key roles in the lives of Arctic marine mammals and the Indigenous Peoples who rely on them. Ringed seals *Pusa hispida* ('natchiq' in Iñupiaq) use snow-covered dens on sea ice for pupping, but quantitative information on denning habitat requirements is limited, and it is unknown how changes in snow depth and sea-ice extent will impact ringed seals. Here, an Indigenous Elder Advisory Council and a multidisciplinary group of scientists used knowledge co-production to quantify fine-scale ringed seal habitat selection patterns in Kotzebue Sound, Alaska (USA), during a year of unprecedentedly limited snow and sea-ice availability. Together, we conducted unoccupied aerial vehicle-based surveys during spring 2019 and related seal counts to survey date, bathymetry, and novel proxies for snow depth and surface roughness that we derived from Landsat 8 surface reflectance and validated with on-ice measurements. Generalized additive models showed that counts of seal groups (all age classes) and pups were associated with later survey dates, deeper water, and habitat with bright Landsat 8 pixel values and intermediate pixel variability, which in turn were correlated with deep snow and surface roughness. We observed shallow snow depths, early sea-ice breakup, and high seal densities consistent with the extreme lack of ice available in 2019. Indigenous Knowledge, intentionally woven with scientific data, provided novel and more nuanced understandings of snow and sea-ice conditions for seals. Our results may give a glimpse at future ringed seal habitat and selection in a warming Arctic.

A ringed seal *Pusa hispida* (natchiq) mother and pup outside a partially melted lair in Kotzebue Sound.
Photo: Jessica Lindsay. NMFS MMPA Research Permit No. 19309

KEY WORDS: Ringed seals · Snow · Sea ice · Knowledge co-production · Marine mammals · Arctic ecosystems · Interdisciplinary science

1. INTRODUCTION

Climate change is expected to continue having profound global impacts over the next century (Post et al. 2019). In the Arctic, temperatures are rising at nearly 4 times the global average rate, sea-ice extent

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is diminishing rapidly, and snow depth on sea ice is declining as a result of warmer and shorter ice seasons (Onarheim et al. 2018, Webster et al. 2019, Lam et al. 2022, Rantanen et al. 2022). These changes present challenges for Arctic marine mammals and for the Arctic Indigenous Peoples who rely on them.

Ringed seals *Pusa hispida* ('natchiq' in Iñupiaq) are circumpolar ice-associated seals that have evolved a close dependence on snow and sea ice. In the Alaska Arctic, ringed seals are found in the seasonal sea-ice zones of the Bering, Chukchi, and Beaufort Seas. In contrast to other seal species that follow the ice edge south in winter, ringed seals are uniquely adapted to occupy areas of landfast ice (up to 100% sea-ice concentration) by maintaining breathing holes ('alluaq') in the ice. As snow accumulates, seals will convert one or more of these breathing holes into snow-covered dens or 'lairs' ('sisi') in which they give birth to their pups in the spring (Smith & Stirling 1975, Kelly et al. 2010b). Lairs provide ringed seal pups with essential protection from cold temperatures (Taugbøl 1982, Kelly et al. 1986) and predation by polar bears *Ursus maritimus* ('nanuq'), foxes, and avian predators (Stirling & Archibald 1977, Stirling & Smith 2004). Climate change is expected to decrease the depth of spring snow cover available for ringed seal lairs, and earlier onset of snow melt and sea-ice breakup may further affect pup survival (Smith & Harwood 2001, Stirling & Smith 2004, Kelly et al. 2010b, Hezel et al. 2012, Reimer et al. 2019).

As a result, each of the 5 subspecies of ringed seal has been listed under the US Endangered Species Act as 'threatened' (Arctic, Okhotsk, and Baltic subspecies; NMFS 2012) or 'endangered' (Saimaa and Ladoga subspecies; NMFS 1993, 2012). The Arctic subspecies *P. h. hispida* is the most widely distributed, including in the Alaska Arctic where the seals are found in the seasonal sea-ice zones of the Bering, Chukchi, and Beaufort Seas. This seasonal ice provides essential habitat in spring, with solitary females giving birth to their pups in March–April followed by a ~39 d nursing period, then mating in May near the lair while pups are still nursing. The ice continues to be important for basking and molting on the surface in May–June, either at the site of former lairs that have melted open or at nearby breathing holes (Hammill et al. 1991, Kelly et al. 2010b, Kelly 2022). Compared to other parts of the Arctic, ringed seals in Alaska tend to have smaller body sizes (Kovacs et al. 2021) and, perhaps relatedly, smaller lair dimensions (Hauser et al. 2021a), but little quantitative information on lair habitat requirements is available for the region.

Snow depth is thought to be a critical dimension of Arctic ringed seal habitat. There is no simple relationship between snow depth on level ice and snow depth in drifts behind deformed ice features, but drifts can be many times deeper and may be the only place snow is found early in the season (e.g. Liston et al. 2018). *In situ* studies from the European and Canadian Arctic found that within areas with a minimum snow depth of 20 cm on flat ice, ringed seal lairs were located in deeper snow drifts (>50 cm) that accumulated in areas of rougher ice along pressure ridges (Smith & Stirling 1975, Lydersen & Gjertz 1986, Smith & Lydersen 1991). Some studies consider 20 cm as the minimum snow depth required for ringed seals, below which survival may be affected (Hezel et al. 2012, Reimer et al. 2019). Regional mean spring snow depths in recent decades have already been below the purported 20 cm minimum in the Bering Sea (Kelly et al. 2010b) and near or below 20 cm in the Chukchi and Beaufort Seas (Stroeve et al. 2020). However, ringed seals are still widespread in these regions (Conn et al. 2014, Lindsay et al. 2021, P. L. Boveng et al. unpubl.), suggesting that further investigation into ringed seal snow depth requirements is needed.

Ringed seal persistence is of direct importance to coastal Indigenous communities throughout the Arctic for whom seals are a valued nutritional, spiritual, and cultural resource (Hovelsrud et al. 2008, Huntington et al. 2016, Gryba et al. 2021). In Alaska, ringed seals are legally and sustainably harvested by communities such as Kotzebue (Qikiqtaġruk), which is home to the Indigenous Qikiqtaġruŋmiut Iñupiaq people (Nelson et al. 2019). Traditionally, residents have hunted ringed seals on the sea ice in the spring and in the water in the fall for seal meat, skins, and blubber (Georgette & Loon 1993, Huntington et al. 2016, Nelson et al. 2019). Kotzebue is located in the southeastern Chukchi Sea on the shore of Kotzebue Sound, with landfast and pack ice forming each winter that provides habitat for ringed seals and other ice-associated seal species.

Climate-related impacts on seal habitat have already been noted in Kotzebue Sound, including earlier sea-ice breakup (Hauser et al. 2021b), and Iñupiaq hunters report that increasingly flat sea-ice conditions are limiting the availability of snow drifts suitable for ringed seal lairs (Huntington et al. 2016, 2017, this study). Meanwhile, shorter sea-ice seasons have produced declines in snow depth on sea ice in the Chukchi Sea (Webster et al. 2014, 2018, Stroeve et al. 2020). Historically, the entirety of Kotzebue Sound has tended to freeze over during the winter, with the landfast ice edge extending out past the mouth of the Sound into the Chukchi Sea (Mahoney et al. 2014, Witte et al. 2021). However, the winters of 2017–2018 and 2018–2019 were a stark departure from this pattern. During these 2 winters, ice formed over only a small fraction of Kotzebue Sound, surface flooding limited the depth of dry snow available for lairs, and snowmelt and sea-ice breakup took place abnormally early (Hauser et al. 2021b, Mahoney et al. 2021, Witte et al. 2021). As climate change continues, these 'anomalous' conditions may become commonplace, with these winters serving as a possible preview of conditions to come (Webster et al. 2021).

To better anticipate the effects of climate change on ringed seals in Kotzebue Sound and on the people who harvest them, it is necessary to improve our understanding of ringed seal lair habitat selection during years of limited sea-ice and snow availability. Through a co-production of knowledge approach, local Qikiqtaġruŋmiut Elders identified the question 'What snow and ice properties promote ringed seal denning and pupping (i.e. birthing and nursing pups)?' as a research topic of key importance to the Kotzebue community. Ringed seal lair habitat characteristics in parts of Kotzebue Sound were studied *in situ* in the 1980s (Frost et al. 1989, Kelly & Quakenbush 1990, Hauser et al. 2021a) and via broad-scale, crewed aerial surveys in 1985–1987 (Frost et al. 1988), 1999–2000 (Bengtson et al. 2005), and 2016 (Lindsay et al. 2021, P. L. Boveng et al. unpubl.). Each of these studies has made valuable contributions to our understanding of ringed seal habitat, but none to date has simultaneously incorporated both (1) extensive coverage of areas of spring sea-ice habitat that are unsafe to travel on foot, such as in the warm years that are increasingly common, and (2) evaluation of habitat availability and selection at a fine, sub-kilometer spatial scale.

Here, multidisciplinary scientists collaborated with an Elder Advisory Council to address this knowledge gap, using a combination of on-ice measurements and remote sensing data from satellites and drone-based aerial surveys, set within a knowledge co-production framework, to quantify the snow and ice surface properties associated with ringed seal denning and pupping in Kotzebue Sound. Our goals were to (1) explore the utility of satellite-derived proxies for snow depth and surface roughness, which we hypothesized would be important for ringed seals, and (2) make inferences about ringed seal habitat selection for these variables during a year of unusually limited snow and sea-ice availability.

2. MATERIALS AND METHODS

2.1. Knowledge co-production approach

This study is part of a larger, interdisciplinary project called Ikaaġvik Sikukun (Iñupiaq for 'ice bridges') exploring research questions related to sea-ice change in the community of Kotzebue, Alaska. Knowledge co-production between scientists and Iñupiaq Qikiqtaġruŋmiut Elders is central to this project. Broadly, knowledge co-production bridges scientific and Indigenous Knowledge systems to attain novel insights that are only possible when working together (Ellam Yua et al. 2022). This approach also recognizes the need for equitable partnerships between Arctic researchers and Indigenous communities, in contrast with extractive research that uses Indigenous Knowledge without involving the knowledge holders in the study design, interpretation, and dissemination of results (Ellam Yua et al. 2022). In this project, a set of 6 research questions was co-developed in collaboration with an Elder Advisory Council of 4 Iñupiaq Elders (co-authors J.G., C.H., R.J.S., and R.S.) with a long personal history of subsistence hunting and experience on the sea ice. The Elders were involved in all subsequent research stages as well, including fieldwork, model development, and interpretation of results as detailed below. For more information on Ikaaġvik Sikukun's knowledge co-production approach, see Hauser et al. (2021b), Mahoney et al. (2021), and Witte et al. (2021).

2.2. Aerial surveys with unoccupied aerial vehicles (UAVs)

We conducted aerial surveys of ringed seal habitat on the landfast ice near Kotzebue in spring 2019. A pilot year of surveys was also conducted in 2018 for logistics and identifying image resolution requirements. Surveys were performed with a UAV, specifically an HQ-90B fixed-wing aircraft with vertical takeoff and landing, manufactured by Latitude Engineering (Zappa et al. 2020). Surveys were focused on 3 areas identified in collaboration with the Elder Advisors: (1) Sisualik, where Elder C.H. commonly hunts for ringed seals, (2) Sadie Creek, where Elders J.G., R.J.S., and R.S. have extensive hunting experience, and (3) the outflow of the Noatak River channel from the landfast ice edge, a site that plays a key role in the breakup of the landfast ice each spring (Witte et al. 2021) (Fig. 1a). Surveys were conducted from 30 April to 15 May, coinciding with the timing of pre-

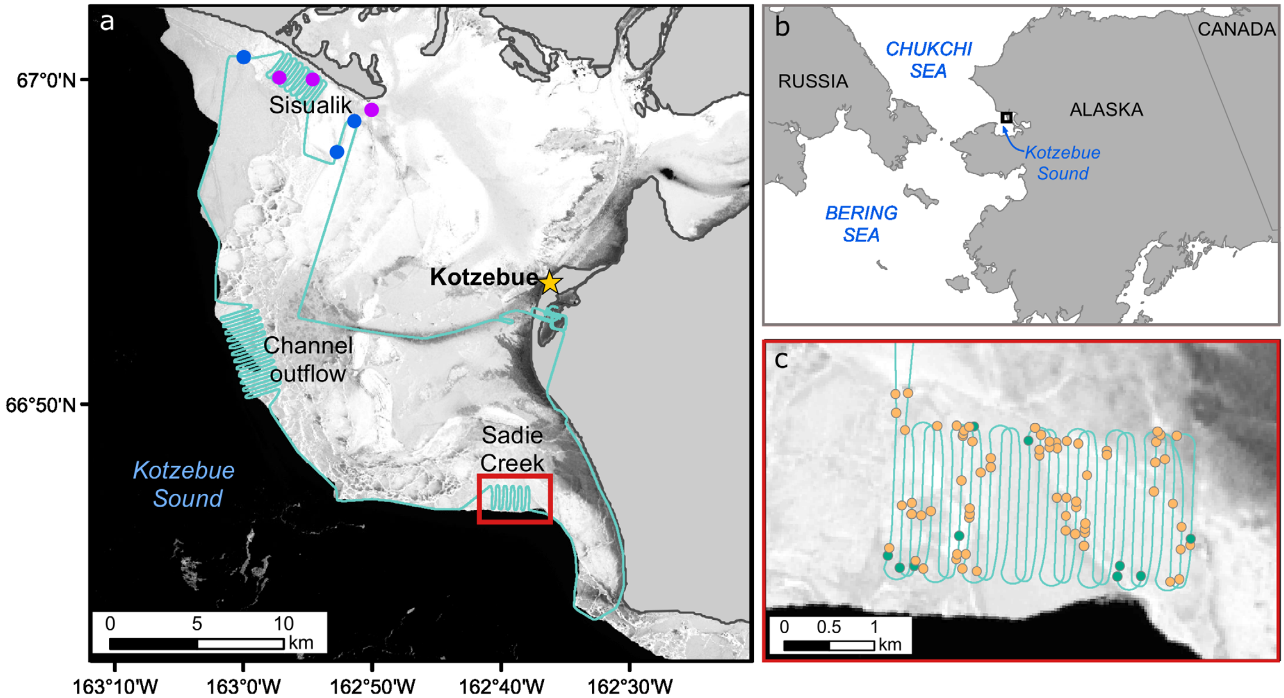

Fig. 1. (a) Representative flight path, with targeted survey areas at Sisualik, the Noatak channel outflow, and Sadie Creek, Alaska. Points indicate on-ice survey locations (blue = snow depth and surface roughness, purple = snow depth only). Land is overlaid in solid gray, water in the background satellite image appears black, and sea ice is white to gray. (b) Location of Kotzebue Sound, Alaska. The small black box corresponds with the mapped area in panel (a). (c) Ringed seal detections from 15 May 2019 at Sadie Creek (red box in panel [a]); green = pups, orange = non-pups. The background satellite image (panels a and c) is from Landsat 8 on 6 May 2019

vious aerial surveys for ringed seals (Conn et al. 2014, Lindsay et al. 2021) and the transition period from snow-covered sea ice to snow melt and ice breakup during which lairs are expected to melt and collapse (Kelly et al. 2010b). UAV surveys were conducted approximately every 2–6 d, dependent on weather conditions suitable for flying and other Ikaaġvik Sikukun science missions beyond the scope of this paper. Sadie Creek and the channel outflow site were each surveyed 3 times within this period (Sadie Creek on 30 April, 9 May, and 15 May; channel outflow on 30 April, 7 May, and 9 May), whereas Sisualik was surveyed twice (6 and 9 May) due to early breakup of the landfast ice north of Kotzebue.

Thermal and color images were taken simultaneously throughout each survey for seal detection and identification using adjacent thermal (Atom 1024) and color (Cheetah 9MP) cameras, with one of each type facing directly downward beneath the UAV (Zappa et al. 2020). Surveys were conducted at a target altitude of 152 m (500 ft) to 229 m (750 ft), with higher altitude transits (up to 305 m or 1000 ft) between survey sites dependent on other Ikaaġvik Sikukun research objectives. At the 152 m target altitude, the color camera produced an imaged swath width of 135.9 m across the track line with an image resolution of 3.3 cm pixel^{-1}, while the thermal infrared camera produced an imaged swath width of 106.2 m with an image resolution of 10.37 cm pixel^{-1}; variations in altitude produced proportional changes in swath. Imagery was manually reviewed in Streams software (version 7, IO Industries) to identify which images contained thermal hotspots. Corresponding color images were then examined in detail to detect seals and count the number of individuals at each breathing hole or lair site visible in the image. As the snow and sea ice degrades during melt, it becomes increasingly difficult to distinguish between breathing holes and lair sites in aerial imagery, so all structure types were pooled together for analysis. Seals were identified to species and classified by age (pup or non-pup). Confidence in species identifications and age classifications was recorded as 'certain', 'likely', or 'guess' according to McClintock et al. (2015). Images and survey effort from altitudes >229 m (750 ft) were discarded due to a high proportion of 'guess' confidence values.

2.3. Modeling habitat selection

2.3.1. Landsat 8 satellite pixel metrics as proxies for snow depth and surface roughness

In collaboration with the Elder Advisory Council, we hypothesized that snow depth and surface roughness would be important for ringed seal habitat. Because we were unable to measure these quantities directly, we instead used pixel neighborhood metrics from Landsat 8 imagery as novel proxies for snow depth and surface roughness. Specifically, visual assessment of an exploratory map of ringed seal detections over concurrent satellite imagery suggested that seal locations were spatially correlated with areas of high brightness and/or the boundaries between areas of high and low brightness (i.e. bright next to dark) (Fig. 1c). In late spring, as snow melt progresses, the surface of the sea ice becomes exposed, revealing areas of bare ice and melt ponds. In imagery from Landsat 8 at this time of year, the brightest areas correspond with patches of lingering snow, which in turn correspond to areas where the snow was deeper earlier in the winter (Petrich et al. 2012). In contrast, bare ice and melt ponds appear darker and indicate regions where the snow was shallower. The darkest regions of the imagery correspond to open water. The areas with deepest snow are associated with sea-ice ridges, which are the primary topographic features of the ice. These areas are also likely to be the first to accumulate snow (Liston et al. 2018) and therefore the distribution of snow cover in late spring may also be reflective of early-season snow cover at the time when lairs are constructed. Individual ridges and the snow drifts that form next to them typically have widths of between 10 and 50 m. However, since sea-ice ridges tend to form linear features separating areas of smooth ice, we expect to find the deepest snow drifts adjacent to areas of bare ice or melt ponds in late spring. Accordingly, we expect areas with snow deep enough to accommodate lairs to be characterized at this key melt stage by both high mean brightness and high brightness variability within a neighborhood of Landsat 8 pixels.

We selected a clear-sky Landsat 8 image from 6 May 2019 (LC08_L1TP_081013_20190506_20190507_01_RT; Fig. 1a,c), which captured the key melt stage described above for the landfast ice in Kotzebue Sound, with snow patches only remaining in areas that had had especially deep snow. Specifically, we used Band 4 (wavelength range 640–670 nm, 30 m resolution) downloaded from the US Geological Survey and processed with Acolite atmospheric correction software (Vanhellemont 2019). Each pixel in the processed image represented calibrated surface reflectance of light at a wavelength of 655 nm such that pixel values ranged from 0 (low brightness, i.e. light completely absorbed) to 1 (high brightness, i.e. light completely reflected).

2.3.2. Model construction

We binned UAV survey effort and ringed seal counts from each survey date into 210 × 210 m grid cells, corresponding with 7 × 7 satellite pixels. Only cell-date combinations for which at least half of the grid cell was surveyed were retained for analysis. Within each grid cell, we calculated the mean surface reflectance (hereafter 'pixel brightness') and the standard deviation of surface reflectance ('pixel variability') from the Landsat 8 image in ArcGIS Desktop 10.5 (Environmental Systems Research Institute). In addition to the proxies for snow depth and surface roughness, we also included other variables hypothesized to be important to ringed seal habitat and/or the probability of seals hauling out on the sea ice. We calculated bathymetry (m depth) (IBCAO; Jakobsson et al. 2012) and distance to the coastline (km) from the centroid of each grid cell. We also included variables for survey date and for temperature (°C) and wind speed (m s^{-1}) at the start of each survey to account for temporal changes in the proportion of seals hauled out or concealed inside of snow lairs, measured at the Ralph Wien Memorial Airport in Kotzebue (weather data available at NOAA National Centers for Environmental Information [NCEI] Climate Data Online [CDO] Tool: https://www.ncdc.noaa.gov/cdo-web/, Station WBAN:26616).

We modeled the relationship between these environmental covariates and ringed seal counts using generalized additive models (GAMs) in the 'mgcv' package (Wood 2017) in Program R version 3.6.1 (R Core Team 2017). We produced separate models for (1) the number of groups of ringed seals (i.e. multiple seals around 1 breathing hole were considered 1 group) of combined age classes, and (2) the number of pups. The Elders indicated that groups would be a more meaningful indicator of denning habitat selection than raw counts of individual seals because ringed seals exhibit mating competition during the breeding season, with many males sometimes hauling out at the same breathing hole competing for access to a nearby female (Krafft et al. 2007, Kelly et al. 2010a, Elders R. J. Schaeffer & R. Schaeffer Sr.

pers. comm.). Thus, a higher number of seals hauled out at the same structure could indicate mating behavior rather than lair habitat quality, and counts of indi-vidual seals would be spatially autocorrelated with each other.

A negative binomial distribution was used due to over-dispersion in the seal counts (Ver Hoef & Boveng 2007, Zuur et al. 2009). All single-covariate terms were encoded as s() smooths. We also included a ti() tensor interaction term between pixel brightness and variability (Wood 2017), because areas with both high pixel brightness and variability might be especially likely to contain deep snow. We used variance inflation factors (VIFs) with a cutoff of VIF ≤ 4 and pairwise Pearson correlation tests (cutoff of $p \leq 0.5$) to screen for multicollinearity between covariates, and found correlations between bathymetry and distance to coast, survey date and wind, and survey date and temperature; thus none of these pairs was allowed to be in candidate models at the same time (Zuur et al. 2009). An offset for survey effort was included in all candidate models. Each candidate model therefore consisted of pixel brightness, pixel variability, an interaction term between pixel brightness and variability, either bathymetry or distance to coast, and either survey date or air temperature and wind speed.

We fitted each of the permissible combinations within the global model above (i.e. with bathymetry instead of distance to coast, and vice versa), and applied the 'double penalty' approach within the 'mgcv' package which automatically identifies covariates with weak contributions to the response and shrinks them out of the model (Marra & Wood 2011). We considered any covariates with effective degrees of freedom (edf) of <0.1 to have effectively been dropped by the double penalty approach. We then used Akaike's information criterion (AIC) to identify the best model for combined age classes and for pups. The gam.check() function (Wood 2017), rootograms (Kleiber & Zeileis 2016), and quantile–quantile plots with simulated data from the fitted model were used to check for violations of model assumptions (Augustin et al. 2012, Feng et al. 2020).

We generated prediction plots for each covariate on the response scale and visually assessed them to determine the influence of each covariate on counts of ringed seal groups or pups. Predicted counts were expressed as densities, or counts per square kilometer (i.e. survey effort in the GAM formula was set to 1 km^2). Maps of predicted seal counts per square km were also produced for the full area of landfast ice west of the Noatak River channel, including areas that were not surveyed by the UAV. Sandbars were excluded from the prediction area using supervised classification performed on a low-tide Sentinel 2 image from 14 August 2018 (US Geological Survey 2019), as these areas are inaccessible to ringed seals.

The Elder Advisory Council then examined these prediction maps for model validation using their Indigenous Knowledge and decades of hunting experience. Specifically, Elders identified areas on the map where high vs. low predicted seal counts were supported by their Knowledge of the true distribution of ringed seals around Kotzebue, as well as areas where predicted seal counts were not supported. In areas where Elders identified the model as performing poorly, they then relied on their knowledge of the area to hypothesize why this would be the case, such as a missing habitat variable that could be explored in future research.

2.4. On-ice surveys

The relationship between the satellite pixel metrics, snow depth, and surface roughness was validated using *in situ* data collected on the sea ice in April 2019. We also opportunistically collected measurements of ringed seal breathing holes and lairs. All on-ice data were collected offshore of Sisualik, an area that was deemed safe to travel by Elders where an established trail and shallow bathymetry made on-ice work safer than in other areas of the landfast ice near Kotzebue during the unprecedented ice conditions in spring 2019 (Mahoney et al. 2021). All on-ice measurements were collected after the onset of melt and thus do not reflect the maximum snow depths reached during the 2018–2019 melt season. However, while the absolute snow depths may have changed, the position of snow drifts is strongly associated with rough ice (Liston et al. 2018) and can be expected to be consistent throughout the sea-ice season. Accordingly, we consider the distribution of snow drifts collected during our April on-ice surveys to be consistent with that of earlier in the sea-ice season when lairs were constructed, as well as the late stage of melt visible in the Landsat 8 satellite image from 6 May 2019, when only patches of particularly deep snow remained.

Snow depth was measured using a Magnaprobe, which provides measurements accurate to within 1 cm. Snow depth surveys were performed at 4 sites in early April 2019 and another 4 in late April 2019, including re-surveys of 2 sites from earlier in the month to assess how continued melt and subsidence of the snowpack had affected snow depth during the intervening weeks. In total, we collected 7118 snow depth measurements spanning 238 satellite pixels (30 m resolution). We calculated the mean *in situ* snow depth within each of the satellite pixels and performed a linear regression between snow depth and pixel brightness, using measurements from all on-ice survey dates (i.e. both early and late April) to maximize our sample size.

We measured *in situ* surface roughness using a terrestrial LiDAR scanner, which produces a fine-scale 3D digital elevation model of the height of the snow surface for the entire area within the range of the scanner. We performed 3 LiDAR surveys in early and late April 2019 at sites encompassing a range of ice roughness, from flat sea ice to low ridges. Within each area of 3 × 3 satellite pixels (90 × 90 m, n = 42), we computed the standard deviations of both pixel brightness and LiDAR surface height, and again performed a linear regression using all on-ice survey dates. These linear regressions were then combined with the results of the habitat selection models. Specifically, we identified the values of pixel brightness and variability that corresponded with the highest ringed seal counts in the prediction plots above, and then used the linear regression results to convert these values into estimates of snow depth and surface roughness, respectively. Although we validated the relationship between pixel variability and surface roughness at a smaller scale (90 × 90 m) than what we used in the model implementation (210 × 210 m), we do not expect this to have any significant effect on the results. A linear regression between pixel values calculated at 90 and 210 m scales generated an R^2 value of 74 %, a slope of 1.17, and an intercept of 0.006.

3. RESULTS

3.1. Aerial surveys and habitat selection models

In total, UAV survey effort used for analysis covered 27.7 km^2 (~5 %) of the landfast ice adjacent to Kotzebue. We binned our ≤750 ft aerial survey effort by date and grid cell, and produced 906 cell–date combinations containing 297 ringed seal detections ('groups' of seals hauled out at a single breathing hole or lair site), consisting of 621 adults and 63 pups. Dividing these detections by our total area surveyed, we observed mean ringed seal densities of 24.4 individual seals km^{-2} (all ages), 10.5 groups km^{-2} (all ages), and 2.4 pups km^{-2}. Median group size was 2 ringed seals per group, with a maximum group size of 12 seals. All detections were of ringed seals, other than 3 images containing spotted seals *Phoca largha* ('qasigiaq', 29 total individuals) and 2 images containing bearded seals *Erignathus barbatus* ('ugruk' , 7 individuals). Each detection of spotted or bearded seals occurred at the ice edge, whereas ringed seals were detected both at the ice edge and in the interior of the landfast ice.

Model selection via AIC indicated that survey date and bathymetry were preferred over weather variables and distance to coast for both group and pup counts (Table A1 in Appendix 2). We then applied the double penalty approach, and the models for group counts and pup counts retained all covariates (edf > 0.1). Accordingly, the final models for group counts and for pup counts each consisted of survey date, bathymetry, pixel brightness, pixel variability, and an interaction term between pixel brightness and variability (Table 1). The models explained 36.8 and 31.8 % of the variation in group counts and pup counts, respectively.

Table 1. Results of generalized additive models (GAMs) produced for ringed seal group counts (all age classes) and pup counts. 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). Each model was formulated as: Ringed seal count~ s(pixel brightness) + s(pixel variability) + s(survey date) + s(bathymetry) + ti(pixel brightness, pixel variability) + offset(effort)

	Group counts (all age classes)		Pup counts	
Parametric term	Estimate	p	Estimate	p
Intercept	1.391	<0.0001	0.063	0.8140
Smoothed term	edf	p	edf	p
Date	2.129	<0.0001	0.982	0.0234
Pixel brightness	2.499	<0.0001	1.657	0.1823
Pixel variability	4.165	<0.0001	1.653	0.0124
Pixel brightness: Pixel variability	0.621	0.1800	1.718	0.0062
Bathymetry	3.720	<0.0001	0.959	<0.0001

The effects of covariates on ringed seal group counts and pup counts were similar (Figs. 2 & 3). Confidence intervals were wide when sampling of the environmental covariate was sparse; e.g. few observed values were available over sea ice with low pixel brightness values or high pixel variability, resulting in greater uncertainty in the relationship between seal counts and the respective covariate in these ranges. Bathymetry had a positive effect, with very few groups or pups predicted at water depths below 2 m. Counts of groups or pups increased approximately linearly with survey date, with higher counts observed later in the survey period. Pixel brightness had a unimodal effect on counts, with highest counts predicted at a brightness of approximately 0.75 for groups and 0.7 for pups. For both group counts and pup counts, pixel variability had a strong and unimodal effect with peak counts at a pixel variability of ~0.06 (Figs. 2 & 3). Example UAV images taken within grid cells meeting these pixel conditions are shown in Fig. 4.

Prediction maps (Fig. 5) of the full area of landfast ice west of the Noatak River channel showed highest predicted seal counts near the channel outflow and southeast of Sadie Creek, and this pattern was supported by the Elders' Indigenous Knowledge upon reviewing the maps. The models performed well at capturing the habitat selection patterns observed in the data, with low vs. high seal counts near Sadie Creek (location i in Fig. 5) matching well with those shown in Fig. 1c based on visual assessment by the Elders and authors. The area southeast of Sadie Creek (Fig. 5, location ii) was specifically identified by the Elders as being a place with ice piles that provide good habitat for denning, birthing, and nursing. However, the Elders indicated that the high counts predicted by the model immediately north of town (Fig. 5, location iii) were unrealistic; ringed seals do occasionally occupy this area, but not in high numbers.

Few seals were predicted southeast of Sisualik or near the coastline south of Kotzebue, consistent with the Elders' experience. Elders agreed that there would typically be fewer seals near Sisualik than near Cape Blossom or at the ice edge, noting that local hunters would typically travel farther west beyond the mapped area rather than hunting at Sisualik. In typical years with more extensive sea ice, seal

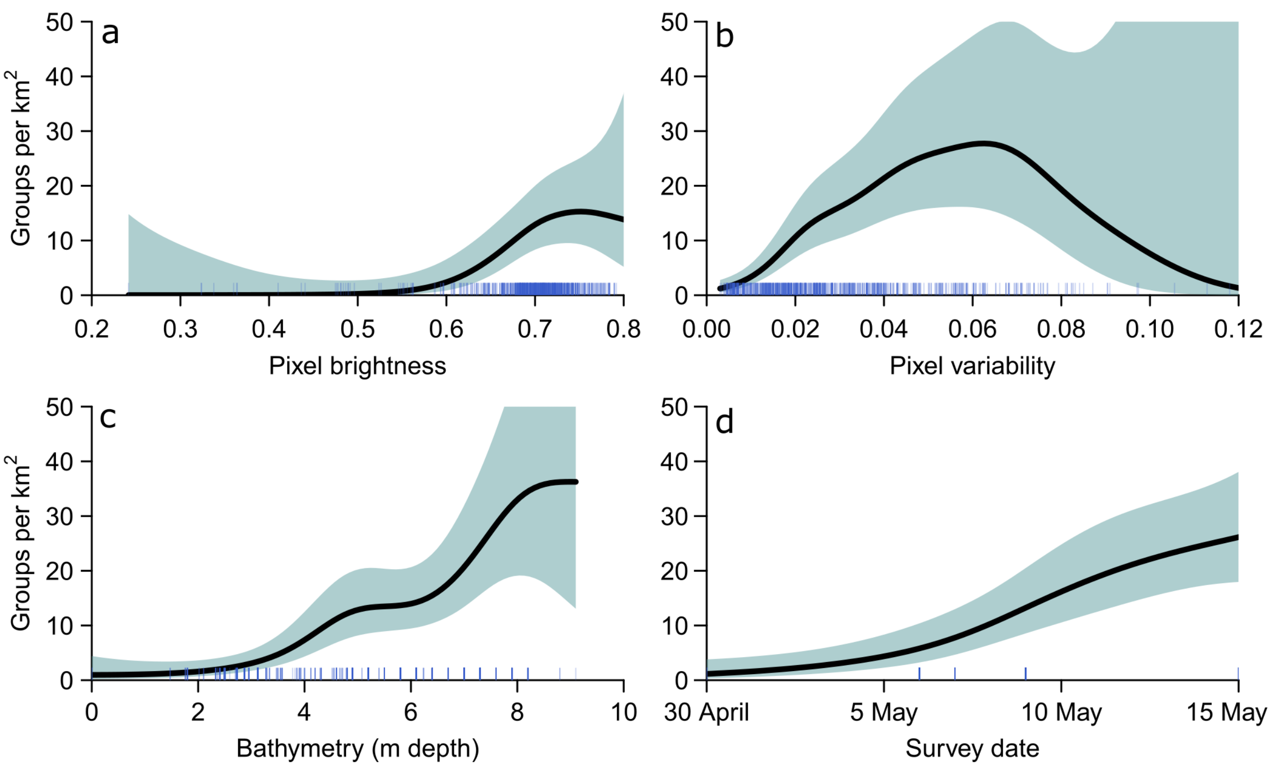

Fig. 2. Effects of covariates on the predicted counts of ringed seal groups per km^2 when only (a) pixel brightness, (b) pixel variability, (c) bathymetry, and (d) survey date are allowed to vary, with all other covariates held constant at their means. Shading represents the 95% confidence intervals. Blue tick marks along the *x*-axis illustrate the distribution of observed values used in the model

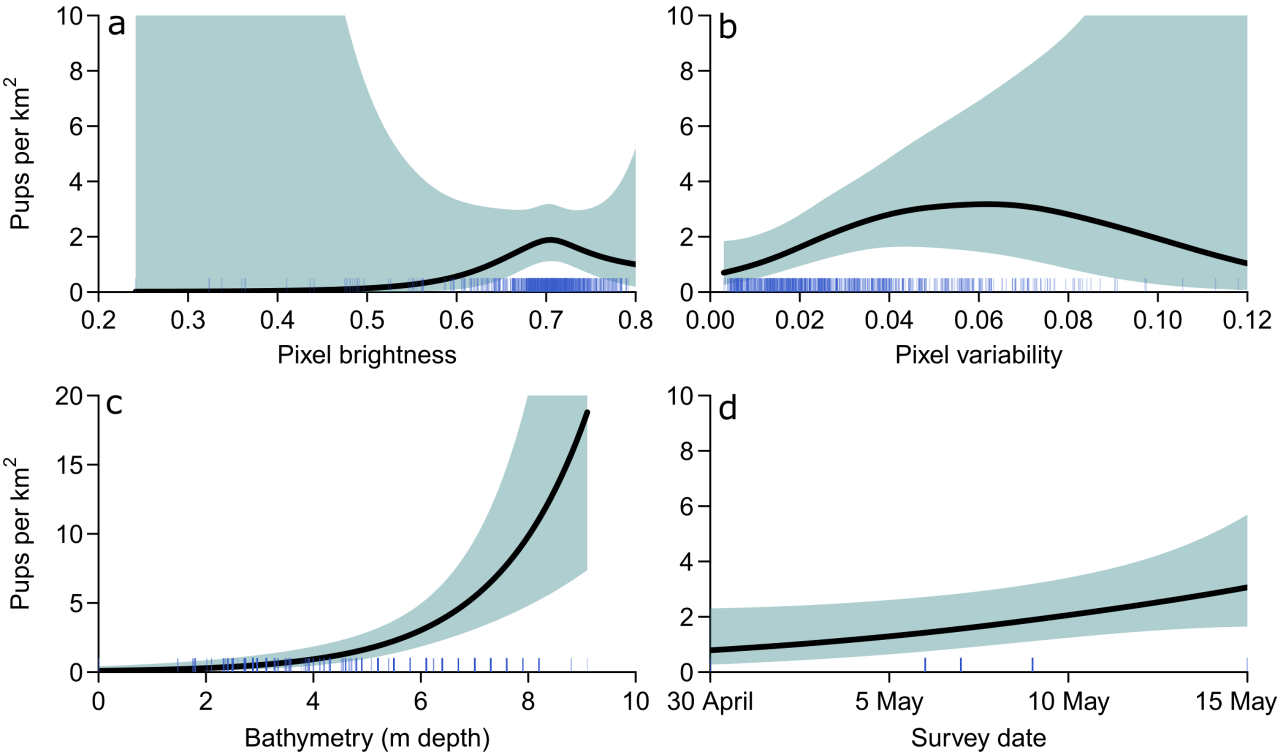

Fig. 3. As in Fig. 2, but for predicted counts of ringed seal pups

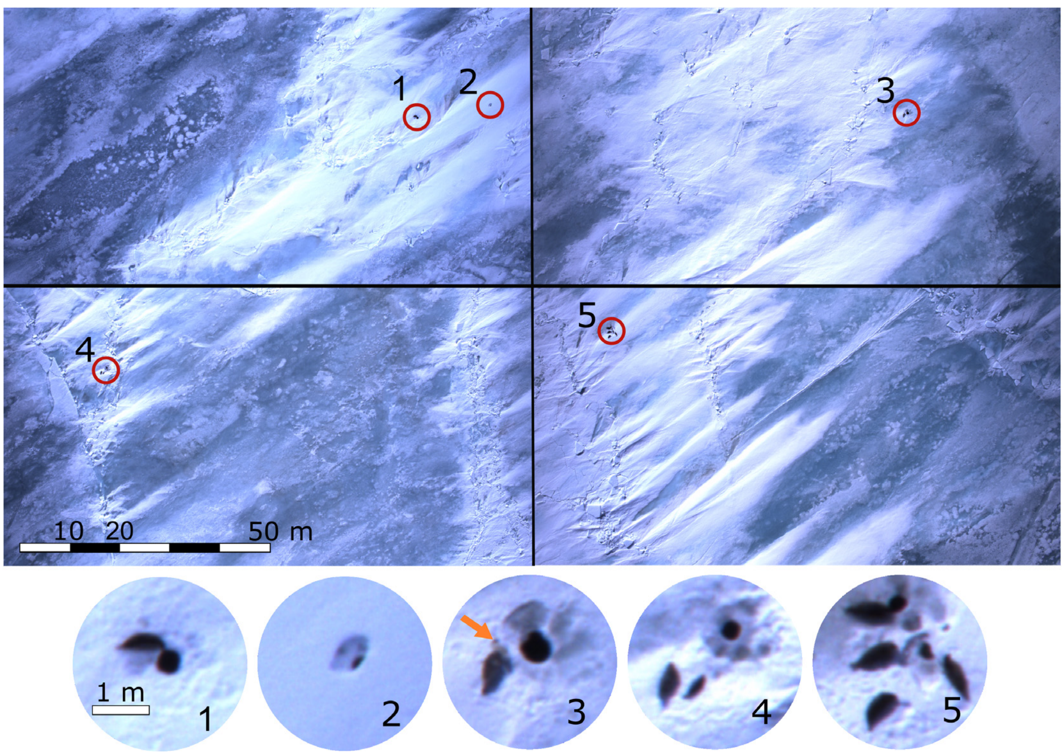

Fig. 4. Four examples of unmanned aerial vehicle images from grid cells meeting the pixel conditions identified from the model as corresponding with the highest predicted ringed seal counts (pixel brightness of ~0.7 and variability of ~0.06). Scale bars are approximate due to slight variations in altitude. Ringed seals and ringed seal structures are highlighted with red circles, each of which is magnified at the bottom of the figure. 1: Adult seal at breathing hole. 2: Possible lair (partially melted open) in snow drift. 3: Mother and pup in white lanugo pelage (small off-white shape touching the head of the mother seal, marked with an orange arrow pointing toward the pup's head) at breathing hole. 4: Mother and pup at breathing hole. 5: Group of 4 adult seals at 2 neighboring structures

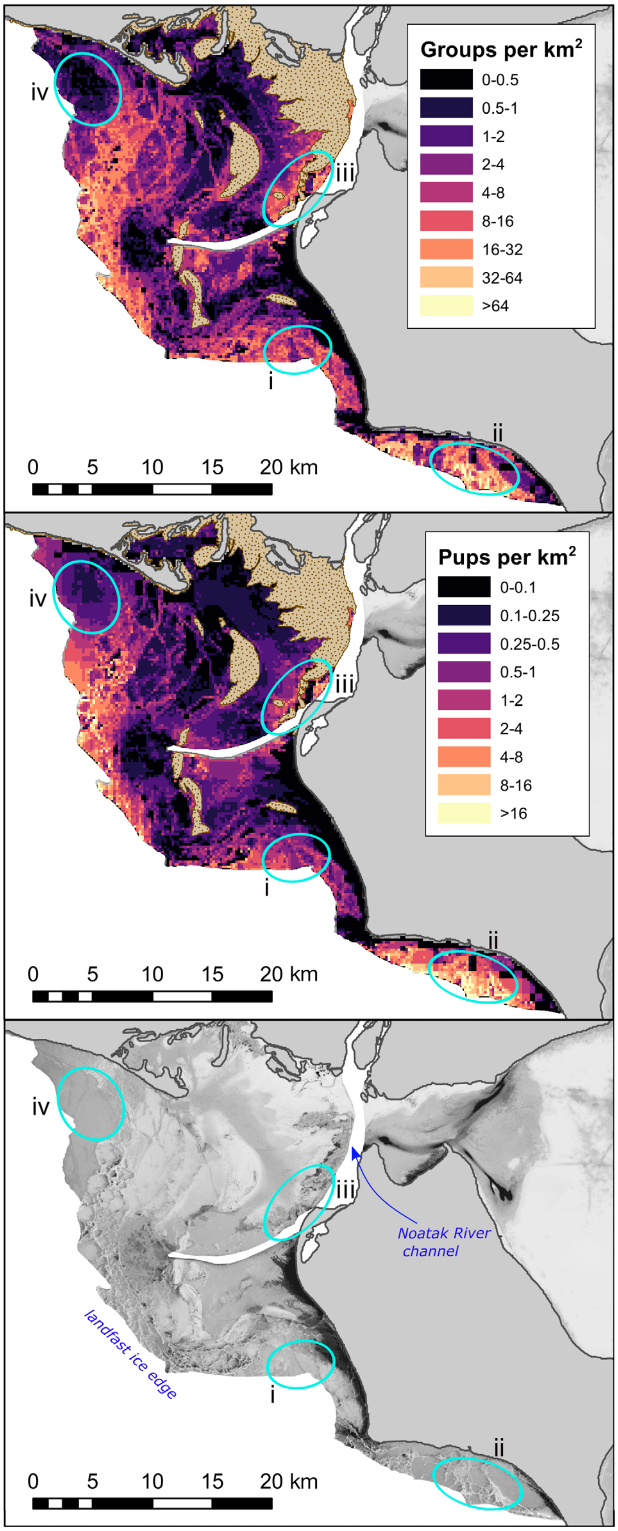

Fig. 5. Predicted counts per km^2 of (a) groups of ringed seals and (b) ringed seal pups produced by their respective best models. When generating predictions, date was set to our mean survey date of 9 May. The brown stippled regions indicate sandbars inaccessible to ringed seals. (c) Original Landsat 8 image for reference. Circled locations i–iv correspond with areas highlighted by the Elder Advisory Council (see Sections 3.1 and 4)

densities would be higher just west of Sisualik (location iv in Fig. 5; Elder C. Harris pers. comm.) where a lead in the ice often forms after an east wind. However, in 2019 the sea ice in this area was smooth and relatively snow-free, causing the model to predict low counts of seal groups and pups there. The lead edge spanning from the channel outflow northward to the coast was historically used as a place to hunt seals that haul out there between bouts of foraging, but in recent times, increasingly thin ice has made hunting in this area too dangerous (Elder R. Schaeffer Sr. pers. comm.). Each Elder commented that in typical years, ringed seal densities would not be so high within our study area and so near to town; rather, the densities we observed would be seen ~30 km to the northwest at the lead edge of the landfast ice at the mouth of Kotzebue Sound.

3.2. On-ice surveys

Snow depths measured over larger areas during our on-ice surveys in early and late April ranged from 0 to 90 cm with a mean of 26 cm (n = 7118). For the 2 sites that we were able to visit twice for repeat coverage in early and late April, mean snow depths were 10 cm lower in late April than they had been earlier in the month due to melt and/or subsidence of the snowpack. When averaged within each Landsat 8 pixel (n = 238), mean snow depths for the full survey period ranged from 13 to 41 cm, with a grand mean of 25 cm. We additionally measured snow depths at 8 ringed seal breathing holes and 3 lairs that were opportunistically encountered, with means of 19 cm and 28 cm, respectively. The standard deviation of surface height ('surface roughness') within 3 × 3 Landsat 8 pixels (n = 42) ranged from 0.8 to 14.9 cm, with a mean roughness of 3.9 cm.

Within our on-ice survey areas, we found positive relationships between *in situ* snow measurements made in April and quantities derived from Landsat 8 imagery acquired on 6 May. Specifically, *in situ* snow depth was correlated with pixel brightness, and *in situ* surface roughness was correlated with pixel variability (Fig. 6; Table A2), with R^2 values of 31 and 25%, respectively. Our habitat selection models thus predicted highest seal counts in grid cells with a pixel brightness corresponding to a mean snow depth of 25.3 cm (95% prediction interval 16.2–34.5 cm), and a pixel variability corresponding to 8.3 cm surface roughness (95% prediction interval 3.1–13.5 cm).

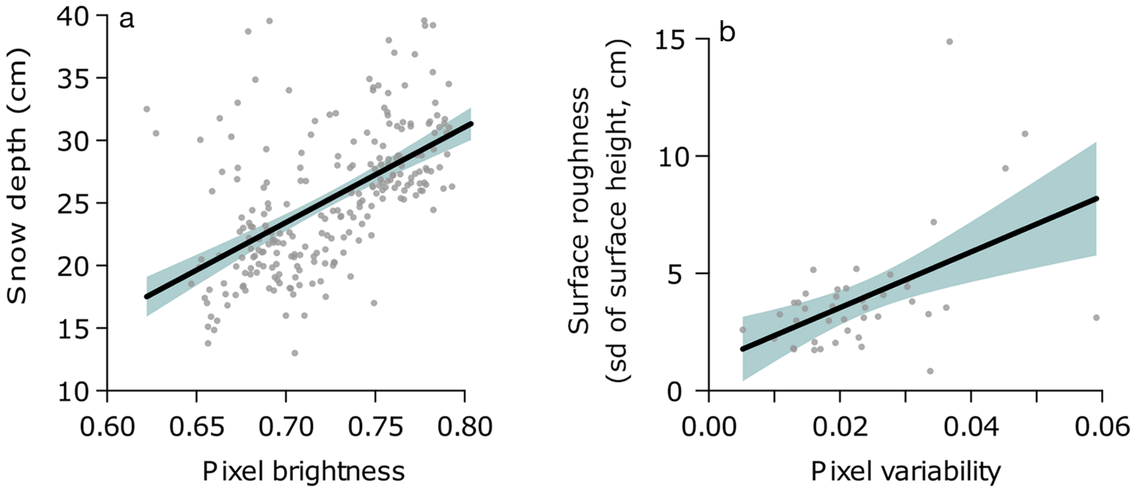

Fig. 6. Linear regressions of (a) *in situ* snow depth and Landsat 8 pixel brightness, and (b) *in situ* surface roughness (standard deviation of surface height) and Landsat 8 pixel variability (standard deviation of pixel brightness). Shaded regions represent 95% confidence intervals

4. DISCUSSION

We used a knowledge co-production approach together with novel satellite imagery-based proxies of snow depth and surface roughness to quantify fine-scale ringed seal habitat selection in Kotzebue Sound in April–May 2019 during a year of limited snow and sea-ice availability. Our models showed that ringed seal group counts (all ages) and pup counts were both associated with Landsat pixel brightness, which our on-ice versus satellite regressions show is positively correlated with snow depth in April. Recent analyses of broader-scale aerial surveys in the Chukchi Sea similarly showed a positive association between ringed seal counts and snow depths from 25 km satellite passive microwave data (Lindsay et al. 2021), and our results now extend this to 1/100 the spatial resolution.

Group counts and pup counts also both showed a positive, unimodal association with Landsat pixel variability, which our on-ice versus satellite regressions indicate is correlated with surface roughness. We suggest that the snow cover on areas of flat ice was not deep enough for constructing lairs, particularly earlier in the winter when lairs are established (Kelly & Quakenbush 1990) and most snow is held in drifts associated with rough ice (Liston et al. 2018). The reason for lower seal counts in the roughest ice areas is less clear, but these areas may have been associated with sandbars and shallow bathymetry inaccessible to seals, been more difficult to establish breathing holes compared to areas of thinner ice (Stirling et al. 1982), and/or particularly jumbled ice may not be beneficial for the basking and molting that were taking place during our aerial survey period. Broader-scale aerial surveys in Kotzebue Sound in the 1980s found lower densities of ringed seals in areas of highly deformed ice (Frost et al. 1988), while on-ice studies in the same decade found that ringed seal pup lairs were located in rougher ice than simple haul-out lairs or breathing holes (Frost et al. 1989, Hauser et al. 2021a). During the basking period when seals are no longer protected by lairs, hauling out at breathing holes on flatter ice may enable exposed seals to more easily surveil their surroundings for approaching predators (Frost et al. 1989, Kelly 2022, Elder R. J. Schaeffer pers. comm.). If this occurred during our aerial surveys and some seals were hauled out away from the lairs in which they overwintered, our results may underestimate the importance of snow depth and ice roughness to ringed seal lairs.

Our findings on the importance of deep snow and rough ice are also supported by the Indigenous Knowledge of our Elder Advisory Council, who describe ice piles and snow drifts as important components of ringed seal habitat in Kotzebue Sound. When hunting ringed seals in the spring, the Elders know that areas of rough ice are more likely to contain denning adult females, which are more desirable for consumption than the pungent meat of rutting males. The Elders also agreed that ringed seals in Kotzebue Sound are associated with deeper bathymetry, and indicated that prey such as saffron cod (tomcod) *Eleginus gracilis* ('uugaq') and Pacific herring *Clupea pallasii* ('uqsruqtuuq') may be more abundant in those areas.

The Elders provided valuable insights on the distribution of ringed seals in areas of the landfast ice that we were not able to cover during our aerial surveys. For example, our models predicted high counts of ringed seal groups and pups in the area southeast of Cape Blossom near Riley Wreck (location ii in Fig. 5). Elder R.S., who has hunting experience near Riley Wreck, agreed that it is good habitat for ringed seals and a reliable place for hunting due to ice piles that consistently form there each year, allowing snow drifts to accumulate for dens (Elder R. Schaeffer Sr. pers. comm.). The Elders highlighted the area immediately north of Kotzebue (location iii in Fig. 5) as a region where the counts predicted by our model are unrealistically high. One potential explanation they offered for the model's poor performance in this region is that some of the ice adjacent to the sandbars may freeze to the seafloor, rendering a larger area inaccessible to seals than we accounted for. The Elders also suggested that ringed seals may avoid this area due to strong currents from the Noatak River channel or the proximity to town (e.g. hunters and snowmobile activity), which were not considered in our model and could be explored in future research.

4.1. Limits to inference

4.1.1. Proxies for snow depth and surface roughness

Snow depth and surface roughness were of primary interest from the outset of our project, and we originally intended to estimate these characteristics from an airborne LiDAR instrument carried by the UAV. However, UAV motion during the aerial surveys resulted in airborne LiDAR measurements that could not be readily corrected for quantifying habitat, and remotely sensed snow depth products from satellite passive microwave data are only available at a coarse 25 km resolution that would not be suitable for the fine-scale habitat selection objectives of this study. The use of Landsat pixel metrics as proxies for snow depth and surface roughness at 210 m resolution was thus chosen post hoc based on preliminary mapping of our seal detections (Fig. 1c), a practice which may result in findings that are unique to the dataset at hand and not generalizable to other datasets (Burnham & Anderson 2002). However, in our case, snow depth and surface roughness were hypothesized to be important predictors of ringed seal group and pup counts from the beginning; it is only the method of quantifying these values that was developed later, and the results of our habitat selection models are supported by evidence from previous ringed seal studies and the Elder Advisory Council.

The original intent of our on-ice snow depth and surface roughness surveys was to ground-truth the airborne LiDAR, and not to validate Landsat pixel metrics as ultimately done for our analyses. As a result, our on-ice dataset overlapped with only a small number of satellite pixels. Additionally, despite our efforts to survey a range of habitat types, the places we were able to safely sample on the ice do not capture the full range of satellite pixel brightness and variability (and thus probably snow depth and surface roughness) present elsewhere on the landfast ice near Kotzebue. For example, the roughest place we sampled on the ice corresponded with a satellite pixel variability of ~0.06, but some of the more jumbled sea ice covered in our aerial surveys at the channel outflow site had a pixel variability of up to 0.12. Estimating habitat conditions in these areas would thus require extrapolating beyond what we were able to ground-truth. Furthermore, our habitat selection models suggested that optimal surface roughness for ringed seals occurred at the very upper limit of the conditions we were able to sample *in situ*, so we advise interpreting our surface roughness results in relative terms (i.e. that ringed seals selected for 'intermediate' surface roughness) and interpreting the quantitative 8.3 cm surface roughness estimate with caution. Future studies could build upon ours by systematically collecting on-ice data on snow depth and surface roughness over a larger number of satellite pixels and a wider range of habitat conditions.

The on-ice measurements of snow depth and surface roughness used to correlate Landsat pixel values with on-ice conditions were collected after the onset of melt. Therefore, although we expect the spatial distribution of snow drifts to be consistent, and our models estimated that counts of ringed seal groups and pups peaked at a snow depth of ~25.3 cm, this likely underestimates the snow depth from earlier in the spring before the snow pack had degraded. We also caution that this estimate is for mean snow depth across an entire 210 m grid cell, with deeper snow drifts likely accumulating in areas of rough ice.

4.1.2. Aerial surveys

Aerial surveys for ringed seals can only detect seals hauled out on top of the snow or ice surface, and not seals that are concealed underwater or inside a snow lair (Kingsley et al. 1990). In some areas of deep snow, seals in lairs would therefore have not been detected prior to melt, potentially influencing our habitat selection results. We attempted to account for this by including a term for survey date in our models, as the proportion of seals available for detection tends to increase over the course of the spring as lairs melt and seals begin to bask (Kelly et al. 2006, Lindsay et al. 2021). Our choice to focus aerial surveys on 3 specific areas rather than random stratified sampling of the entire landfast ice area around Kotzebue means that our model predictions outside the 3 areas should be interpreted with caution, although validation by the Elder Advisors bolsters our confidence in the spatial distribution of ringed seals. In a small number of cases where the UAV flight path was near the margin of a grid cell, it is possible that seals were actually located in the adjacent cell rather than the cell to which they were assigned. A longer time series of aerial surveys, including aerial surveys conducted in multiple years, would strengthen our habitat selection results.

4.2. Influence of anomalous conditions on model results

4.2.1. Snow depth in lair habitat

Our study period in April–May 2019 coincided with unusually limited availability of sea ice and dry snow depth, and these conditions provide important context for interpreting our model results. The snow depths observed during our on-ice and aerial surveys may have been at the margin of suitability for ringed seal lair habitat, and the snow depth estimates from our habitat selection models and on-ice/satellite regressions should be interpreted conservatively as a result. Previous on-ice studies have suggested that ringed seals would need 20 cm of snow on flat ice for lairs so that areas of rough ice can accumulate deeper snow drifts of >50 cm (Lydersen & Gjertz 1986). A 'typical' snow drift depth of 54 cm was recently used in the critical habitat designation for ringed seals in Alaska under the Endangered Species Act (NMFS 2021). However, the 3 lairs we opportunistically measured *in situ* in April 2019 were located in drifts with an average depth of only 28 cm, which barely exceeds the diameter of an adult ringed seal (Lydersen & Gjertz 1986) and was described by the Elder Advisory Council as being unusually shallow for lairs (Fig. 7).

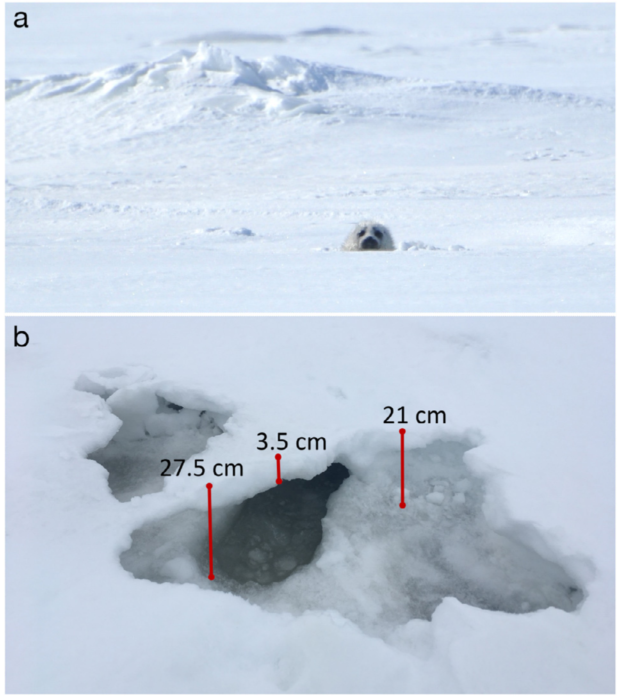

Fig. 7. (a) White-coated ringed seal pup at a melted-open lair on 23 April 2019. (b) Close-up view of the same lair the next day, overlain with measurements of floor to ceiling height and roof thickness

Our lair sample size is small (n = 3) and limited to structures that had already melted open, and there may have been more robust lairs in the area that were still concealed under the snow. We were also only able to measure ringed seal lairs in a small portion of the landfast ice near Sisualik due to concerns about travel safety on the ice, so areas elsewhere on the landfast ice may have had more suitable habitat conditions; indeed, our models predicted higher counts of groups and pups at areas we were not able to visit on foot (are just east of circled location iv in Fig. 5). Nonetheless, our mean lair snow depth of 28 cm is a stark departure from previous studies. Lairs located in southern Kotzebue Sound in 1983 were found in drifts with a mean snow depth of 66.2 cm, and the minimum snow depths observed were 58 cm for a pup lair and 35 cm for a haul-out lair, which still exceeds the conditions we found in 2019 (Hauser et al. 2021a). When snow depths were shallow in northern Kotzebue Sound in 1984 (16.9 cm on flat ice), proportions of lairs were substantially lower than in more southerly areas with deeper snow (Kelly & Quakenbush 1990). This suggests that optimal snow depths for lair habitat may be deeper than the estimates given by our models.

4.2.2. Sea-ice availability

When reviewing the maps of predicted ringed seal counts near Kotzebue (Fig. 5), each member of the Elder Advisory Council placed heavy emphasis on the unusually limited availability of landfast ice in Kotzebue Sound in winter 2018–2019. We speculate that these sea-ice conditions caused the concentration of ringed seals into extreme densities of groups, individuals, and pups observed in our aerial surveys (Fig. 8a) and predicted by our models. In contrast to the sea-ice conditions during previous aerial surveys for ringed seals (Frost et al. 1988, Bengtson et al. 2005, Lindsay et al. 2021), ringed seals during our survey year had very little habitat available to them for denning, basking, and molting (Fig. 8b,c). It is therefore possible that ringed seals that would otherwise have overwintered elsewhere in the Sound (or even elsewhere in the Bering or Chukchi Seas) were instead concentrated onto the small area of landfast ice adjacent to Kotzebue.

The densities of ringed seals observed in our UAV surveys (mean of 24.4 ind. km^{-2}) were higher than in previous studies in Kotzebue Sound (Frost et al. 1988, Bengtson et al. 2005, Lindsay et al. 2021). When broader-scale surveys were conducted for ringed seals in Kotzebue Sound in 2016 under more extensive sea-ice conditions (Fig. 8c), seal densities were much lower close to Kotzebue, and the distribution of seals was instead more diffuse across the Sound, with high densities near the mouth of the Sound as the Elders described (Fig. 3a in Lindsay et al. 2021). A reduction in harvest pressure in recent years (see Table 9 in Ice Seal Committee 2019, Elder J. Goodwin pers. comm.) was suggested as an additional potential cause of higher ringed seal densities closer to town than in the past. Repeating our study in years with greater ice coverage and exploring the importance of access to open water in such winters were highlighted by the Elders as areas for future research.

4.3. Implications of changing habitat conditions

In addition to the potential for the anomalous snow and ice conditions we observed in 2018–2019 to influence our habitat model results, they may serve as a preview of future habitat conditions, with implications for ringed seal populations as their denning habitat continues to change. Data on seals harvested by Alaska Native communities in the Bering and Chukchi Seas suggest that ringed seals in Alaska have yet to experience population-level effects on pup survival (Crawford et al. 2015). It is possible, however, that pup survival, denning, and molting in Kotzebue Sound were affected by the conditions in 2019 based on insights from the Elder Advisory Council and observations of pups still in lanugo at the time of sea-ice breakup. Ringed seals are expected to be increasingly affected by habitat change as the conditions in 2019 become more common and severe, with increasingly limited sea-ice area, declining dry snow depth, and advancing sea-ice breakup timing.

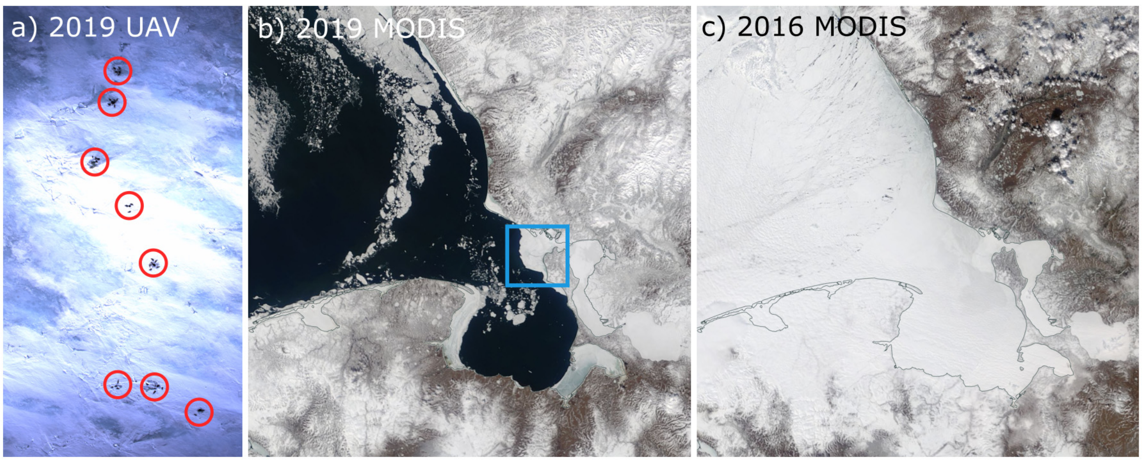

Fig. 8. (a) Example unmanned aerial vehicle image showing high densities of ringed seals in 2019, with 8 ringed seal groups (circled in red) containing 29 individual seals. The image covers roughly 56 × 106 m of sea ice. These high densities were likely related to (b) the low availability of sea ice habitat in our study area (blue square) and the southeastern Chukchi Sea in 2019 compared to more typical years, with (c) 2016 as an example where the imaged area is nearly 100% covered with landfast and pack ice. MODIS satellite images in panels (b) and (c) are from NASA Worldview from 6 May 2019 and 6 May 2016, as 2016 was the most recent year of ringed seal surveys in the Chukchi Sea prior to our study

4.3.1. Snow depth and pup survival

We were unable to assess pup survival during our study, but shallow snow depths are thought to have negative impacts on ringed seal pup survival. In the past, shallow snow conditions such as those of 2018–2019 provided easy opportunities for exposed pups to be found by avian predators and Iñupiaq hunters looking to catch pups for their valuable fur (Elder J. Goodwin pers. comm.). Historically, however, this was a rare occurrence, and previous snow depths tended to be deeper than observed during our 2019 study period. Each Elder commented that predation by red fox *Vulpes vulpes* (‘kayuqtuq’) or Arctic fox *V. lagopus* (‘tiġiganniaq’) on ringed seal pups may have been higher in Kotzebue Sound under the shallow snow conditions of 2019, with thinner lairs being easier to detect and break into, as well as melting earlier in the spring. Any effects of snow availability on pup survival may have been compounded by the limited sea-ice extent, with Elders suggesting that having pups condensed into a small, nearshore area likely required less search effort from foxes venturing out onto the sea ice.

Polar bears are uncommon in Kotzebue Sound, but elsewhere in the Arctic, shallower snow depths over ringed seal lairs have been associated with a greater number of predation attempts by polar bears and higher predation success (Hammill & Smith 1991, Furgal et al. 1996). Higher mortality rates of Saimaa ringed seals pups *Pusa hispida saimensis* in Finland have also been observed during years of insufficient snow cover when pups were born exposed on the ice (Ministry of the Environment 2011). Ringed seal pups in Alaska and across the Arctic may be increasingly threatened by predation and hypothermia as snow depth continues to decline.

The Elders indicated that snowfall in winter 2018–2019 was actually above average for the past several decades, with reanalysis data from the National Centers for Environmental Prediction (NCEP) showing that precipitation in 2019 was higher than in any winter since 1979 (Mahoney et al. 2021). However, the sea ice that winter was likely the thinnest ever observed since at least 1945 (Mahoney et al. 2021). Under these conditions, the weight of the snowpack pushed the ice down below sea level, causing flooding of the snowpack. When the snow is saturated with water or when flooded snow subsequently re-freezes into solid ‘snow-ice’, this renders that portion of the snowpack unusable for denning (Kelly et al. 1986, Lukin et al. 2006). Measurements and isostatic calculations of the sea ice and snow in Kotzebue Sound in 2019 indicate that upwards of 50% of the snow depth that year may have been flooded (Figs. 5 & 7 in Mahoney et al. 2021), effectively reducing the amount of dry snow that could be used for ringed seal lairs. Melt also occurred early in 2019, which would have caused the snowpack to thin from thermal compaction earlier than usual (Mahoney et al. 2021). Thus, in addition to projected decreases in snow accumulation on sea ice (Webster et al. 2021), flooding and early melt of the snowpack may also affect ringed seal lair habitat in future years when snow conditions are similar to those of 2018–2019.

4.3.2. Early sea-ice breakup

In addition to the limited sea-ice extent and dry snow depths in Kotzebue Sound in 2019, we also observed abnormally early sea-ice breakup with the potential to impact ringed seal pup survival and molting. In our final surveys of the Sisualik and channel outflow sites on 9 May, we observed many pups still in their natal lanugo, and thus thought to still be nursing (Kelly 2022). Only a few days later on 14 May, a large piece of the landfast ice near Kotzebue containing both of these survey sites broke away and by 20 May completely disintegrated.

Little quantitative information is available on how early sea-ice breakup affects the survival and body condition of ringed seal pups. Pups may begin swimming and learning to feed autonomously within a week of being born (Lydersen 1995, Lydersen & Kovacs 1999). However, pups are born without a blubber layer for insulation and instead rely on their lanugo, which is only an effective insulator when dry (Smith et al. 1991); access to sea ice for hauling out is therefore critical for young pups. Pups also nurse for an average of 39 d, and their mother's nutrient-rich milk is essential for growing blubber during this time (Hammill et al. 1991). When breakup occurs prior to weaning and molting, it is unclear whether pups in lanugo are able to maintain body temperature or obtain sufficient nutrients via continued contact with their mother or autonomous feeding. Smith & Harwood (2001) observed unusually early breakup in the eastern Amundsen Gulf in the Canadian Arctic on 15 May 1998, and pups in lanugo that were harvested that summer tended to have significantly poorer body conditions than pups that had already molted. In a recent demographic model for ringed seals in the Amundsen Gulf, pup survival was set to begin decreasing if breakup occurred earlier than 20 May, with complete mortality if breakup occurred earlier than 15 April (Reimer et al. 2019). The Elders suggested that early breakup may present tradeoffs for pup survival, combining a reduced risk of predation by foxes with an increased risk of drowning during spring storms. They described commonly seeing dead seals of all ages, but particularly pups, washing up on beaches after storms, hypothesizing that the seals drowned in the rough water without ice to haul out upon and rest.

Early sea-ice breakup may also be detrimental to ringed seal molting, as ringed seals of all ages need a resting platform during this process to elevate their skin temperature (Carlens et al. 2006). In Nunavut, Canada, Inuit community members report that seals molt inadequately when sea-ice breakup occurs too early, and that pups may have a difficult time shedding their lanugo (Laidler et al. 2010). Ringed seals in Hudson Bay declined in abundance after an abrupt warming event, and Ferguson et al. (2017) speculated that early sea-ice breakup may have interfered with molting and predisposed seals to disease. We were unable to assess the molting status of adult seals during our aerial surveys or to observe whether seals successfully molted after breakup, so the impact of sea-ice breakup timing on molting in Kotzebue Sound in 2019 is unknown. Breakup in Kotzebue Sound and the Chukchi Sea has trended earlier in recent decades (Mahoney et al. 2014, Rolph et al. 2018, Fig. S3 in Hauser et al. 2021b), and the effect of breakup timing on molting and the survival of young pups is thus an important area for future research.

4.3.3. Other areas for research

Quantitative research on pup survival across a gradient of snow depth, surface roughness, and early breakup is necessary to better understand how changes in habitat will ultimately affect ringed seal population dynamics. We recommend further investigation into the use of satellite imagery for ringed seal habitat monitoring, particularly considering that remote sensing techniques may become increasingly important as both traditional on-ice sampling methods become less safe and higher-resolution satellite data become commonly available. Additionally, research is needed on how the coarse-scale changes in spring snow depth predicted by global climate models (Hezel et al. 2012, Reimer et al. 2019) translate into finer-scale changes in the depth of snow drifts. The Elder Advisory Council further recommends research into ringed seal health, the effect of prevailing wind direction on the formation of rough ice suitable for lairs, the effects of climate change and ocean acidification on all levels of the Arctic food chain, and the resulting implications for Iñupiat food security.

5. CONCLUSION

We used knowledge co-production and a new remote-sensing methodology to relate ringed seal group counts and pup counts in spring with habitat characteristics in Kotzebue Sound during a year of anomalously little sea ice. Our Elder Advisory Council evaluated model results with their Indigenous Knowledge, providing nuance and context to our interpretation of habitat conditions that would not have been possible without their insight. While the habitat conditions observed during our study cannot be considered representative of previous or 'typical' years in Kotzebue Sound, the abnormally limited availability of landfast ice in winter 2018–2019 may be an analogue of what ringed seal habitat conditions and habitat selection will typically be like in a future of dwindling ice. Our habitat selection models showed that ringed seal groups and pups selected for snow depth and surface roughness, which have both been changing in the Alaska Arctic (Webster et al. 2014, 2018, Huntington et al. 2016). We also observed instances of lairs in shallow snow drifts, early sea-ice breakup when pups were still in lanugo, and high ringed seal densities that may have been linked with the limited availability of sea ice for denning and basking.

Climate-related effects on sea-ice habitat and ice-associated seals can, in turn, impact the Arctic Indigenous Peoples who rely on them. Shorter duration and poorer quality of landfast ice reduces opportunities for Alaska Natives to safely harvest marine mammals and travel across the sea ice (Meier et al. 2014). In Kotzebue Sound, members of our Elder Advisory Council described the sea-ice conditions in winters 2017–2018 and 2018–2019 as being unsafe for ringed seal hunting, and noted that some hunting sites have become unusable in recent years. Another study within our overarching Ikaaġvik Sikukun research project showed that earlier sea-ice breakup has shortened the hunting season for bearded seals (Hauser et al. 2021b). We encourage future studies on ice-associated seals and environmental change in the Arctic to adopt a knowledge co-production approach and collaborate with local communities from project conception to completion. Doing so leads to valuable scientific findings, ensures that research benefits communities, and respects the knowledge and rights held by Arctic Indigenous Peoples concerning the conservation and management of marine resources (Hauser et al. 2021b, Ellam Yua et al. 2022).

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Appendix 1.

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Appendix 2.

Table A1. ΔAIC values for models with permissible combinations of covariates. The 'weather' covariate contains both wind speed and air temperature. Each model also includes pixel brightness, pixel variability, and an interaction term between pixel brightness and variability. The best model for group counts and pup counts is indicated with an asterisk (*)

Non-satellite variables in model	Group counts (all age classes)	Pup counts
Survey date & bathymetry	0*	0*
Survey date & distance to coast	12.15	3.31
Weather & bathymetry	1.22	3.12
Weather & distance to coast	10.80	4.77

Table A2. Results of linear regressions between *in situ* snow depth and pixel brightness, and between *in situ* surface roughness and pixel variability

Response variable	Covariate	Estimate	SE	p
Snow depth	Pixel brightness	0.7636	0.0736	<0.0001
Surface roughness	Pixel variability	1.1882	0.3212	0.0007

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