

¹ **Spring haul-out behavior of seals in the Bering
2 and Chukchi Seas: implications for abundance
3 estimation**

⁴ **Josh M. London¹, Paul B. Conn¹, Stacie M. Koslovsky¹, Erin L.
5 Richmond¹, Jay M. Ver Hoef¹, Michael F. Cameron¹, Justin A. Crawford²,
6 Andrew L. Von Duyke³, Lori Quakenbush², and Peter L. Boveng¹**

⁷ **¹Marine Mammal Laboratory, Alaska Fisheries Science Center, National Marine
8 Fisheries Service, NOAA, Seattle, Washington, USA**

⁹ **²Arctic Marine Mammals Program, Alaska Department of Fish and Game, Fairbanks,
10 Alaska, USA**

¹¹ **³Department of Wildlife Management, North Slope Borough, Utqiagvik, Alaska, USA**

¹² Corresponding author:

¹³ Josh M. London¹

¹⁴ Email address: josh.london@noaa.gov

¹⁵ **ABSTRACT**

16 Ice-associated seals rely on sea ice for a variety of activities, including pupping, breeding, molting, and resting.
17 In the Arctic, many of these activities occur in spring (April through June) as sea ice begins to melt and retreat
18 northward. Rapid acceleration of climate change in Arctic ecosystems is therefore of concern as the quantity
19 and quality of suitable habitat is forecast to decrease. Robust estimates of seal population abundance are
20 needed to properly monitor the impacts of these changes over time. Aerial surveys of seals on ice are an efficient
21 method for counting seals but must be paired with estimates of the proportion of seals out of the water to
22 derive population abundance. In this paper, we use hourly percent-dry data from satellite-linked bio-loggers
23 deployed between 2005 and 2021 to quantify the proportion of seals hauled out on ice. This information is
24 needed to accurately estimate abundance from aerial survey counts of ice-associated seals (i.e., to correct for the
25 proportion of animals that are in the water, and so are not counted, while surveys are conducted). In addition to
26 providing essential data for survey ‘availability’ calculations, our analysis also provides insights into the seasonal
27 timing and environmental factors affecting haul-out behavior by ice-associated seals. We specifically focused on
28 bearded (*Ergnathus barbatus*), ribbon (*Histrionophoca fasciata*), and spotted seals (*Phoca largha*) in the Bering and
29 Chukchi seas. Because ringed seals (*Phoca (pusa) hispida*) can be out of the water but hidden from view in snow
30 lairs analysis of their ‘availability’ to surveys requires special consideration; therefore, they were not included in
31 this analysis. Using generalized linear mixed pseudo-models to properly account for temporal autocorrelation,
32 we fit models with covariates of interest (e.g., day-of-year, solar hour, age-sex class, wind speed, barometric
33 pressure, temperature, precipitation) to examine their ability to explain variation in haul-out probability. We
34 found evidence for strong diel and within-season patterns in haul-out behavior, as well as strong weather effects
35 (particularly wind and temperature). In general, seals were more likely to haul out on ice in the middle of the day
36 and when wind speed was low and temperatures were higher. Haul-out probability increased through March
37 and April, peaking in May and early June before declining again. The timing and frequency of haul-out events
38 also varied based on species and age and sex class. For ribbon and spotted seals, models with year effects were
39 highly supported, indicating that the timing and magnitude of haul-out behavior varied among years. However,
40 we did not find broad evidence that haul-out timing was linked to annual sea-ice extent. Our analysis emphasizes
41 the importance of accounting for seasonal and temporal variation in haul-out behavior, as well as associated
42 environmental covariates, when interpreting the number of seals counted in aerial surveys.

43 INTRODUCTION

44 Global climate disruption is causing considerable reduction in Arctic sea ice extent, volume, and
45 seasonal presence (Meier et al., 2014; Wang et al., 2018; Kwok, 2018; Overland, 2021). These
46 changes have tangible effects on Arctic organisms, ecosystems, and the people who live in the region
47 (Huntington et al., 2020). Such disruptions are a particular cause of concern for the ice-associated
48 seals that depend on spring and early summer sea ice (March-June) in the Bering and Chukchi
49 seas as a platform for important life history functions, such as pupping, nursing, breeding behavior,
50 and molting (Boveng et al., 2009, 2013; Cameron et al., 2010; Kelly et al., 2010). Limited data and
51 large knowledge gaps complicate predictions about the ultimate effects of changes in sea ice on the
52 behavior, health, abundance, and distribution of these seals. To date, indices of seal health sampled
53 during periods of declining sea ice differ regionally (Crawford, Quakenbush & Citta, 2015; Harwood
54 et al., 2020). Knowledge about evolutionary constraints on the timing of reproductive and molting
55 behavior is generally lacking, so it is difficult to predict how or if ice-associated seal species will
56 adjust to future changes (e.g., by adjusting pupping or molting schedules to earlier dates or different
57 locales). This is further complicated by the spatio-temporal variation in the phenology of these life
58 history events within regions and throughout their full ranges. Additionally, trends in abundance of
59 these species are unknown, so it is difficult to assess the effect, if any, declines in sea-ice habitat have

60 had, or will have, on seal demography.

61 Statutory requirements (e.g., United States Marine Mammal Protection Act (MMPA), United
62 States Endangered Species Act (ESA)) for timely estimates of population abundance and trends mean
63 improved aerial survey effort is needed for these species. Those survey efforts must also be paired
64 with improved knowledge of haul-out behavior to ensure appropriate survey design, robust methods,
65 and accurate estimates. Several studies have contributed estimates of the distribution and abundance
66 of ice-associated seal species in the Arctic using aerial surveys (e.g., Bengtson et al. (2005), Conn et al.
67 (2014), and Ver Hoef et al. (2014)) and more recent efforts have significantly expanded on previous
68 survey effort. Such abundance studies are conducted over very large areas and estimation of absolute
69 abundance requires making inference about numerous issues affecting the observation of seals on
70 ice. These include availability (only seals on ice are available to be counted), detection probability
71 (observers or automated detection systems may miss some seals on ice), species misclassification,
72 and possible disturbance of seals by aircraft (Ver Hoef et al., 2014; Conn et al., 2014). Refining
73 these inferences will improve the accuracy of abundance estimates and, hopefully, allow credible
74 predictions about the effects of climate disruptions on the abundance and distribution of Arctic seal
75 populations.

76 How ice-associated seals use sea ice as a haul-out platform varies among species. Ribbon seals
77 (*Histriophoca fasciata*) haul out of the water almost exclusively on sea ice and are mostly pelagic
78 outside the spring pupping, breeding, and molting season (Boveng & Lowry, 2018). Although
79 spotted (*Phoca largha*) and bearded (*Erignathus barbatus*) seals occasionally rest on coastal land,
80 they primarily use sea ice as a haul-out platform during the spring and early summer (Frost & Burns,
81 2018). Ringed seals (*Phoca (pusa) hispida*) — not included in this study — haul out on sea ice but
82 primarily use snow lairs on sea ice during winter and spring.

83 The remoteness of the Bering and Chukchi seas means direct scientific observation of seal behavior
84 is impractical. Thus, bio-logging devices are especially useful tools for collecting key information
85 on movement and haul-out behavior for these species. Bio-logging records of time spent out of the
86 water provide valuable data for identifying covariates that explain variation in haul-out behavior. For
87 instance, Von Duyke et al. (2020) used satellite-linked bio-loggers to corroborate seasonal changes
88 between diurnal and nocturnal haul-out behavior of ringed seals previously described by Kelly and
89 Quakenbush (1990) using VHF radio tags and direct observation. Bengtson et al. (2005) documented
90 a higher propensity for ringed seal basking near solar noon, as did Ver Hoef et al. (2014) in an analysis
91 of bearded, ribbon, and spotted seals using much larger sample sizes. Olnes et al. (2020) showed
92 that the proportion of time bearded seals spent hauled out progressively increased through spring
93 and summer, and Ver Hoef et al. (2014) found haul-out probabilities increased gradually starting in
94 March and peaked in May and June for bearded, ribbon, and spotted seals. Such analyses have not
95 been limited to the Arctic. In the Antarctic, Bengtson and Cameron (2004) relied on bio-logging data
96 to demonstrate greater haul-out propensity in juvenile crabeater seals (*Lobodon carcinophaga*) than
97 adults, with highest probabilities in February and at times close to solar noon.

98 Knowledge of haul-out patterns is not only important for understanding natural history and ecol-
99 ogy, but also for developing ‘availability’ correction factors for aerial surveys. Specifically, researchers
100 need to know the fraction of seals hauled out (versus in the water) when aerial surveys are conducted.
101 Studies estimating availability correction factors for seals typically use logistic regression-style anal-
102 yses to estimate the time-specific probability of being hauled out based on ‘wet/dry’ data relayed
103 by bio-loggers. In these models, haul-out probabilities were expressed as a function of predictive

104 covariates, such as time-of-day, day-of-year, sex, age class, and environmental conditions (e.g., Reder
105 et al. (2003), Bengtson & Cameron (2004), Bengtson et al. (2005), Udevitz et al. (2009), Lonergan et
106 al. (2013), Ver Hoef et al. (2014), Southwell et al. (2008), and Niemi et al. (2023)). However, sample
107 sizes have often been insufficient to permit strong inference about demographic and/or seasonal
108 variation in haul-out probabilities. For instance, Bengtson and Cameron's (2004) study included 5
109 adult and 2 juvenile crabeater seals, while Bengtson et al.'s (2005) study was based on 6 ringed seals in
110 the Chukchi and Beaufort seas. These studies were often further limited by logistical constraints on
111 fieldwork and the attachment duration or operational life of bio-loggers. In this study, we addressed
112 some of these limitations by deploying small bio-loggers designed for longer-term attachment on
113 rear flippers of a subset of the study individuals. These devices are designed to collect data through
114 the molt period (when those adhered to the hair – a more conventional method – would fall off) and,
115 in some situations, provide multiple years of data.

116 In this study, we used data collected from multiple bio-logging deployments spanning a 16-year
117 period to investigate the haul-out behavior of bearded, ribbon, and spotted seals in the Bering and
118 Chukchi seas. Our goals were threefold. First, we wished to establish baseline estimates for the
119 chronology of haul-out behavior in the critical spring season for each species across different age
120 and sex classes. Second, we sought to refine estimates of haul-out availability corrections for aerial
121 surveys in order to improve estimates of seal abundance. Previously estimated availability correction
122 factors (e.g., Bengtson et al. (2005), Conn et al. (2014), and Ver Hoef et al. (2014)) accounted for
123 variables such as the time-of-day and day-of-year, but did not investigate the impact of weather
124 variables. Such variables have been shown to influence walrus haul-out behavior (Udevitz et al.,
125 2009) and we expected weather conditions to also influence seal haul-out behavior and including
126 them within the model framework will benefit our estimates of seal availability during aerial surveys.
127 Third, we aimed to assess the annual variability in haul-out timing and possible linkage to changes
128 in the extent of seasonal sea ice between 2005 and 2021. Our work extends the scope of previous
129 haul-out analyses, includes the influence of weather variability, and investigates the potential impact
130 of changing sea-ice extent on the behavior of these species.

131 METHODS

132 Data collection

133 For this study we used haul-out behavior data and location estimates from bio-loggers deployed on
134 bearded, ribbon, and spotted seals in the Bering, Chukchi, and western Beaufort seas by multiple
135 organizations as part of collaborative investigations from 2005 through 2021. Seals were captured
136 using nets and bio-loggers were attached during studies based in coastal communities or on research
137 ships (Figure 1). Ship-based capture events occurred during spring near the southern ice edge in the
138 Bering Sea between 2005 and 2018. Land-based capture events occurred between 2005 and 2020 from
139 May to October, generally between the Alaska coastal communities of Scammon Bay in the Bering Sea,
140 Utqiagvik in the Chukchi Sea, and Nuiqsut in the Beaufort Sea. Data from additional deployments
141 along the Kamchatka peninsula in the western Bering Sea are also included. We refer readers to the
142 primary literature for detailed capture and bio-logger attachment methods (see publications listed
143 in Supplemental Information Table S1). NOAA-led research was conducted under the authority of
144 Marine Mammal Protection Act Research Permits Nos. 782-1676, 782-1765, 15126, and 19309 issued
145 by the National Marine Fisheries Service, and Letters of Assurance of Compliance with Animal
146 Welfare Act regulations, Nos. A/NW 2010-3 and A/NW 2016-1 from the Alaska Fisheries Science

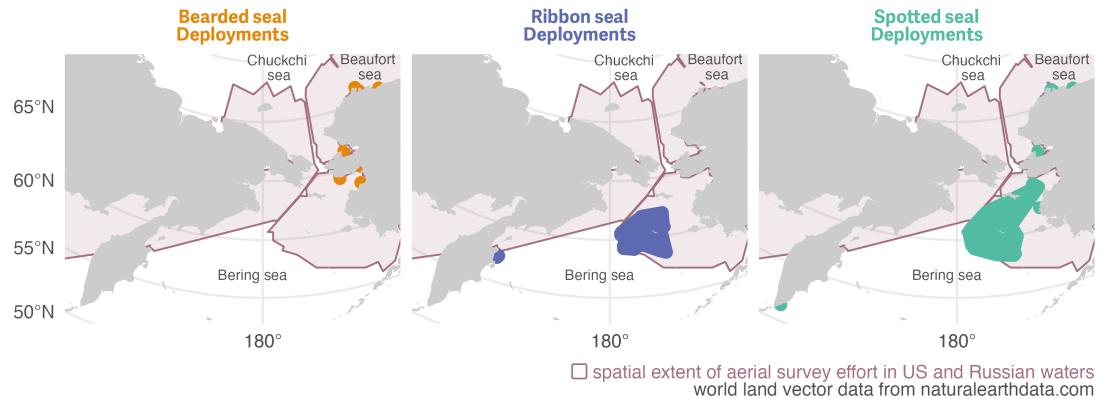


Figure 1. Initial bio getLogger deployment areas for bearded, ribbon, and spotted seals in the study between 2005 and 2020 across multiple regions within the Bering, Chukchi, and western Beaufort seas.

Solid regions shown for each species are minimum concave polygons buffered by 60 km for enhanced visibility. The larger, shaded region indicates the spatial extent of aerial survey effort to date in the Bering, Chukchi, and Beaufort seas. Deployments were initiated across a range of months but only haul-out data from 1 March to 15 July were included in the analysis. See Figure 3 for the spatial distribution of observed data used in the study and Supplemental Materials S1 for additional deployment details. World land vector data from <https://naturalearthdata.com>.

147 Center/Northwest Fisheries Science Center Institutional Animal Care and Use Committee (IACUC).
 148 ADF&G and NSB field work was covered by Research Permits Nos. 358-1585, 358-1787, 15324, and
 149 20466 and by ADF&G IACUC permits Nos. 06-16, 09-21, 2014-03, 2015-25, 2016-23, 0027-2017-27,
 150 0027-2018-29, 0027-2019-041.

151 We created a subset of haul-out behavior data from 250 bio-loggers deployed on 35 bearded, 110
 152 ribbon, and 105 spotted seals to include only records from 1 March to 15 July between 2005 and
 153 2022. Bio-loggers were of the 'SPLASH' or 'SPOT' family of tags developed by Wildlife Computers
 154 (Redmond, Washington, USA). Deployments consisted of either a single 'SPLASH' device, a single
 155 'SPOT' device, or both types. Devices were either adhered to the hair on the seal or attached through
 156 the rear flipper inter-digital webbing. The use of bio-loggers adhered to the back or head provides
 157 some benefits over flipper mounted devices (e.g. increased satellite transmittal rates, locations at
 158 sea) but these fall off during the following annual molt, which, depending on deployment date,
 159 limits the duration of haul-out data they provide especially during the focus months of our study.
 160 Additionally, bio-loggers attached to the head or dorsal region are often dry while the seal is floating at
 161 the surface, inducing a slight positive bias in the hourly percent-dry values reported by the bio logger.
 162 For this study, in cases where both bio logger types were deployed, we preferred hourly percent-dry
 163 observations from the flipper tag. All data were transmitted by the deployed instruments via the
 164 Argos satellite network and location data were either derived from Argos transmissions or transmitted
 165 FastLoc GPS data.

166 Sex and age class (non-dependent *young-of-the-year*, sexually immature *subadults*, and mature
 167 *adults*) were estimated at the time of deployment by various combinations of length, claw growth
 168 ridges (McLaren, 1958), and pelage characteristics. Seals determined to be less than one year were

169 classified as young-of-the-year. For those bio-loggers deployed on young-of-the-year and transmitting
170 into the next year (6 ribbon seals; 3 spotted seals), the age class was advanced to subadult on 1 March
171 of the following year – the assumed anniversary of their birth. Subadults are those seals likely greater
172 than one year of age but less than four years. Adults are individuals that are likely older than four
173 years. Table 1 provides a summary of these deployments and data received from them.

Table 1. Summary of bio-logger data by seal species and age classification from 1 March to 15 July 2005-2021.

Seal hours represents the sum of hourly observations across all seals used in the analysis. Because young-of-the-year are advanced to subadult on 1 March of the following year, some individual seals are represented in both columns in this table

Species	Sex	Age Class		
		Adult	Subadult	Young-of-the-Year
Bearded seal	F	1 (1,776 seal hours)	16 (21,648 seal hours)	
Bearded seal	M	2 (2,108 seal hours)	16 (17,232 seal hours)	
Ribbon seal	F	33 (35,128 seal hours)	18 (15,984 seal hours)	13 (3,734 seal hours)
Ribbon seal	M	24 (27,465 seal hours)	19 (13,046 seal hours)	9 (4,228 seal hours)
Spotted seal	F	23 (21,970 seal hours)	21 (19,559 seal hours)	11 (13,417 seal hours)
Spotted seal	M	20 (31,793 seal hours)	21 (17,210 seal hours)	12 (11,285 seal hours)

174 Haul-out behavior data were recorded in a manner standard across Wildlife Computers bio-
175 loggers and transmitted via the Argos satellite network as hourly percent-dry timelines. For each
176 hour of a day, the wet/dry sensor was polled by the tag firmware every few seconds and the percent
177 of the hour in the dry state was calculated (Figure 2). On board the bio-logger, hourly percent-dry
178 calculations were rounded to the nearest 10% inclusive of 0% and 100% along with additional values
179 at 3% and 98%. This compression resulted in additional data transmission as each message consisted
180 of two complete 24-hour records. Memory capacity allowed caching of percent-dry records for several
181 weeks or months and each message was transmitted several times to ensure reception at the satellite.
182 Bio-loggers were deployed and programmed in a manner to maximize data transmission during the
183 spring pupping and molting period, though hourly percent-dry data were not always successfully
184 transmitted. This is due to a variety of factors including satellite coverage, tag availability (e.g., tags
185 mounted to the rear flipper often do not transmit while at sea), tag performance, duty cycling, and
186 atmospheric interference. Fortunately, missing records do not substantially bias inference about
187 haul-out probabilities (Conn et al., 2012).

188 Tags that fell off due to molt, attachment failure, or seal mortality and remained on ice or land
189 may have continued to send data to satellites; i.e., a detached bio-logger that is dry (either on ice
190 or land) will record and transmit data suggesting the seal is hauled out. Therefore, end times of
191 each deployment were identified by examining bio-logger locations, percent-dry records, and dive
192 behavior (if available) to determine when bio-loggers ceased providing data consistent with seal
193 behavior. For example, a data record that ended with several consecutive days (~10+ days) of 100%

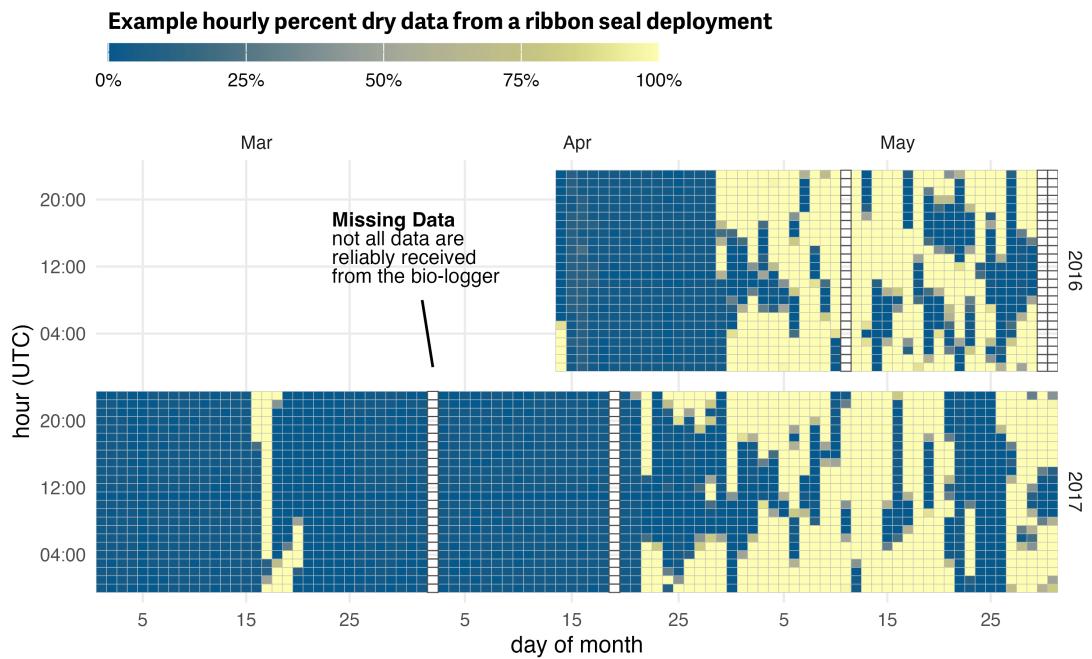


Figure 2. Example percent-dry actogram from bio-logger data

Haul-out behavior observations recorded by a bio-logger deployed on a ribbon seal over two years during the months of March, April, and May. This actogram plot represents the transmitted hourly percent-dry values. Not all data during a deployment are reliably transmitted from the bio-logger and because data are transmitted in 24-hour chunks occasional missing days are present in the record. Here, missing data that were not successfully received from the device are represented as empty rectangles.

194 dry observations and with locations indicating the tag was on land were truncated to the final stretch
 195 of 100% dry observations. The vast majority of deployments ended with the device detaching in
 196 the water and the deployment end date was obvious. There is no perfect algorithm for identifying
 197 deployment end dates and each deployment in question was considered separately. While not perfect,
 198 we are confident our reliance on expert opinion and examination of multiple data streams provided
 199 the best option. Data outside of the deployment start and end times were discarded prior to analysis.

200 Of key interest in this study was the relationship between haul-out behavior and weather covariates
 201 that vary with time and seal location. The use of modern bio-loggers that record and transmit
 202 behavioral data while simultaneously providing location estimates was key to this objective. We
 203 explored the use of a continuous-time correlated random walk (Johnson et al., 2008) movement
 204 model to predict locations at specific times. However, the sparse nature of data from some bio-loggers,
 205 especially those mounted to the rear flipper, resulted in poor modeling performance or convergence
 206 issues. For this study, we calculated a weighted average daily location where the inverse of the
 207 estimated Argos or FastLoc GPS location error was used for the weight. Each Argos location estimate
 208 was assigned an error radius based on either the categorical location quality ($3 = 250 \text{ m}$, $2 = 500 \text{ m}$,
 209 $1 = 1500 \text{ m}$, $0 = 2500 \text{ m}$ (Lopez et al., 2013); we chose 2500 m for location classes *A* and *B*) or, when
 210 available, the estimated error radius from the Argos Kalman filter algorithm. Location estimates
 211 from FastLoc GPS were all assigned an error radius of 50 m. On days when haul-out observations

were present but location data were missing we used the seal's last calculated weighted average daily location; days when the location intersected with land were removed from the seal's record. We recognize that bearded and spotted seals haul out on land. However, assessing the relationship between haul-out behavior and weather covariates and seals' availability for aerial surveys on land was outside the scope of this study. Additionally, any daily locations on land were likely more reflective of coordinate averaging and measurement error, rather than actual use of coastal features.

Explanatory variables

In addition to sex and age class, we analyzed variables that might help explain variation in haul-out probabilities. These included day-of-year (for seasonal effects) and local solar hour (for diurnal effects). We calculated local solar hour using the {solaR} package (Perpiñán, 2012) within the R statistical environment (R Core Team, 2021) based on the weighted daily average locations. We also linked the weighted average daily locations to weather values from the North American Regional Reanalysis (NARR) model produced by the National Centers for Environmental Prediction (Mesinger et al., 2006). The NARR model assimilates observational data to produce a long-term picture of weather over North America and portions of the surrounding seas. Weather variables are made available across the region 8 times daily. For this study, NARR weather values were limited to the extent of our study area over the Bering, Chukchi, and Beaufort seas at 3-hr intervals based on the original grid resolution of 32 km (1024 km²). The following weather variables are known to affect haul-out behavior in other Arctic pinnipeds (Reder et al., 2003; Udevitz et al., 2009; Perry, Stenson & Buren, 2017) and were interpolated and assigned to daily seal locations using a bilinear method: 1) air temperature at 2 m above the Earth's surface, 2) wind consisting of northerly and easterly vector components converted to wind speed using the Euclidean norm, 3) barometric pressure at sea level, and 4) precipitation (Table 2).

For all seal species, we considered the following variables when modeling the hourly haul-out behavior: day-of-year, solar hour, temperature, wind speed, barometric pressure, precipitation, and wind chill (represented by a *wind:temperature* interaction (Udevitz et al., 2009)). Ribbon and spotted seal models included age-sex class and interactions between day-of-year and age-sex class, but we omitted these from bearded seal models due to poor representation of age-sex classes (Table 1). Bearded seal models included a latitudinal effect (and an interaction with day-of-year), because bearded seals occupy a substantial range during the spring and we were interested in possible differences in the timing of haul-out behavior along a latitudinal gradient. We omitted the latitudinal effect from ribbon and spotted seal models because, during the spring, these species are most prevalent near the southern ice edge in the Bering Sea (Conn et al., 2014).

Table 2. Explanatory covariates used in analyses of binary haul-out records for bearded, spotted, and ribbon seals.

Note that we also considered select interactions (see article text) between these primary covariates. For instance, wind chill was represented by the interaction temperature:wind.

Covariate	Type	Description
Age-sex class	Categorical	young-of-the-year, subadult, adult male and adult female

Table 2. Explanatory covariates used in analyses of binary haul-out records for bearded, spotted, and ribbon seals.

Note that we also considered select interactions (see article text) between these primary covariates. For instance, wind chill was represented by the interaction temperature:wind.

Covariate	Type	Description
Hour	Continuous; Fourier basis	local solar hour using 6 variables of a Fourier-series basis
Day	Continuous	linear, quadratic, and cubic effects of day-of-year
Precip	Continuous	convective precipitation kg/m ² (NARR)
Pressure	Continuous	atmospheric pressure at sea level (kPa) (NARR)
Temp	Continuous	air temperature (C) at 2m above the earth's surface (NARR)
Wind	Continuous	northerly and easterly vector components for wind (NARR) converted into a single wind speed via the Euclidean norm
Northing	Continuous	latitude divided by the mean latitude across all locations (for bearded seals only)
Year	Continuous	For the set of models examining inter-annual variation in sea-ice use, we fitted models with the addition of year by day-of-year interactions.

245 Haul-out modeling

246 Haul-out records for seals are often characterized by sequential hours spent hauled out on ice
 247 alternating with long periods in the water (Figure 2). Commonly used statistical models for binary
 248 data (e.g. logistic regression) assume independence among responses, an assumption that is clearly
 249 violated if hourly responses are modeled. Any analysis that ignores temporal autocorrelation in
 250 responses will thus have overstated precision (Betts et al., 2006).

251 To properly account for temporal dependence and to take advantage of computational efficiency,
 252 we used generalized linear mixed pseudo-models (GLMPMs; Ver Hoef, London & Boveng (2010))
 253 to model variation in haul-out behavior as a function of (1) covariate predictors, (2) temporally
 254 autocorrelated random effects, and (3) individual random effects representing heterogeneity in
 255 individual behavior. We used the glmmLDTs package (Ver Hoef, London & Boveng, 2010) to
 256 implement GLMPMs. We explored two different model formulations for our data and we fit separate
 257 models to bearded, ribbon, and spotted seal data sets as we expected differing behavior by species.
 258 Separate models for each species were also needed because a single, very large data set proved
 259 computationally intractable. In our first model formulation and for each species, we fitted a year-
 260 independent model that predicted average haul-out behavior as a function of demographic, weather,
 261 seasonal, and diurnal effects. Second, for ribbon and spotted seals (which had considerably more
 262 data than bearded seals), we fitted models that included all the effects from the first model, but

263 also permitted annual variation in haul-out timing. This second set of models was used to examine
264 whether haul-out patterns varied by year and to determine the annual timing of apparent peaks in
265 haul-out behavior. For both models, we assumed an hourly Bernoulli response (a binary 0-1 response
266 dependent upon whether the tag was greater than 50% dry for a given hour) where the linear predictor
267 was modeled on the logit scale. This is consistent with previous approaches (London et al., 2012; Ver
268 Hoef et al., 2014) and only 7.005% of our observations fell between 10% and 90% hourly percent-dry.

269 We followed Ver Hoef et al. (2014) in using linear, quadratic, and cubic effects of day-of-year
270 to represent temporal changes in behavior during the season. However, unlike previous models
271 for harbor seals (London et al., 2012) and ice-associated seals (Ver Hoef et al., 2014), which treated
272 hour-of-day as a 24-level categorical variable to capture diurnal cycles, we adopted a continuous
273 formulation based on Fourier series that provides a flexible model while preserving the inherent
274 circularity needed for time-of-day effects (i.e., hour 0 should be equal to hour 24). It also represents
275 hour-of-day with 6 parameters, which is a considerable reduction when compared to a 24-parameter
276 variable. According to this approach, we used the following specification for hour-of-day effects:

$$H_t = \alpha_1 \cos\left(\frac{\pi t}{4}\right) + \alpha_2 \sin\left(\frac{\pi t}{4}\right) + \alpha_3 \cos\left(\frac{\pi t}{6}\right) + \alpha_4 \sin\left(\frac{\pi t}{6}\right) + \alpha_5 \cos\left(\frac{\pi t}{12}\right) + \alpha_6 \sin\left(\frac{\pi t}{12}\right)$$

277 where H_t gives the effect for solar hour t and α_i are estimated parameters (regression coefficients).

278 For the second set of models examining inter-annual variation in sea-ice use, we fitted models
279 with year by day-of-year interactions. However, in this case we only included *year:day* and *year:day²*,
280 omitting the main effects of year as well as *year:day³* interactions because models with the latter
281 effects were numerically unstable. However, the modeled interactions were sufficient to allow shifts
282 in haul-out distribution, as one can show mathematically that a simple horizontal shift in timing
283 of haul-out distributions does not affect the main effects or cubic terms in a polynomial regression
284 model. Bearded seals were not included in this examination of inter-annual variation because of
285 limited data across many years in the study.

286 A typical model fitting exercise would also include a model selection process. However, AIC
287 (and similar criteria) is not suitable when using pseudo-likelihoods, because pseudo-data generated
288 in the model fitting process (Ver Hoef, London & Boveng, 2010) differ between models (Ten Eyck
289 & Cavanaugh, 2018). After fitting GLMPM models, we instead used ‘type III’ *F*-tests to calculate
290 *p*-values (Ver Hoef, London & Boveng, 2010) to evaluate model performance and important terms.
291 We also produced predictions of haul-out behavior as a function of three influential predictors
292 (e.g. solar hour, day-of-year, age-sex). Weather covariates for these predictions were based on daily
293 or hourly smoothed weather covariate values across the study region. Such predictions were then
294 used to develop haul-out probability surfaces, explore conditional effects of weather covariates, and
295 determine annual peaks in haul-out activity. The timing of peak haul-out behavior was further used
296 to regress against the annual maximum sea-ice extent in the study region. Predictions before 15
297 March and after 30 June were not included in visualizations or other evaluations to avoid spurious
298 model predictions at the edge of the data range.

299 Visualizing the marginal or conditional effect of an individual weather covariate (where all other
300 weather covariates are being held at mean values) on haul-out probability was difficult in this analysis
301 because of the collinearity between covariates as well as the spatial and temporal variation across
302 such a large region. The relationship of each weather covariate with haul-out probability, averaged
303 over the other weather conditions, was more variable than model coefficients would imply. That said,

304 important insights can be gained from plots of marginal effects. To create these plots, we predicted
305 haul-out probability across the full range of each weather covariate while fixing hour of the day at
306 local solar noon and day-of-year at 15 May. For the other weather covariate values, we chose not
307 to use a fixed mean value because we expect weather to vary within day over the season (e.g. the
308 temperature at solar noon will gradually increase from March through June). To account for this, we
309 fit a simple generalized additive model for each weather covariate with smooth terms for day-of-year
310 and solar hour. We used predicted values from the generalized additive model in lieu of holding
311 other weather covariates at a fixed mean value which would not capture seasonal change. The
312 visualizations also include vertical lines representing 95% confidence intervals around the predicted
313 haul-out probability to better communicate the variation in model uncertainty.

314 We also assessed whether the annual variation in maximum spring sea-ice extent in the Bering Sea
315 influenced the seasonal peak of seal haul-out probability. In particular, we used sea-ice concentration
316 data from the Nimbus-7 SMMR and DMSP SSM/I-SSMIS Passive Microwave Dataset, Version 1
317 (Cavalieri et al., 1996) to calculate maximum sea-ice extent. All sea-ice concentration grid cells (25
318 km²) in the study area with greater than 15% concentration were counted daily to get the total sea ice
319 extent for each day between 15 February and 15 July across all years. Maximum spring sea-ice extent
320 was simply the largest daily count of grid cells with greater than 15% concentration for each year.
321 A separate regression model, built on the results of the haul-out model, was used to evaluate the
322 relationship between the annual computed peak haul-out day (as the response) with the maximum
323 sea-ice extent (as the predictor).

324 RESULTS

325 Figure 3 shows the spatial distribution of weighted locations with available haul-out behavior data
326 used for analysis of each species across the study area. Figure 4 shows the temporal distribution of
327 all haul-out data across the study season for each species. Observations of ribbon and spotted seals
328 were concentrated in the months of May and June due to the timing of deployment (April and May)
329 and the timing of molt (May and June). During molt, seals (and their attached bio-loggers) spend
330 more time out of the water and more data are transmitted. Molt timing also impacts when many
331 deployments end as any bio-loggers adhered to the hair will fall off. Relative to the other species in
332 the study, there were fewer deployments of bio-loggers on bearded seals. This resulted in fewer data
333 observations overall and noticeably lower in numbers May and June. The majority of deployments
334 on bearded seals occurred in August and September and, by May, bio-loggers had either fallen off or
335 their batteries were depleted. Therefore, observations for bearded seals were concentrated in March
336 (Figure 4).

337 Across all three seal species, generally, models omitting year effects suggested that day-of-year,
338 solar hour, age-sex class, temperature, and wind substantially influenced haul-out behavior of all
339 three species, with F tests producing p -values less than 0.05 for variables embodying these effects
340 and/or their interactions. Haul-out probabilities typically increased throughout March and April,
341 reaching a peak in May and early June before declining again. Diurnal patterns were present, with
342 maximum haul-out behavior centered around local solar noon.

343 Bearded Seals

344 Age and sex class were not included in the model for bearded seals due to our lower sample size
345 for adult and young-of-year age classes. As such, results are shown for all ages (Figure 5; see also

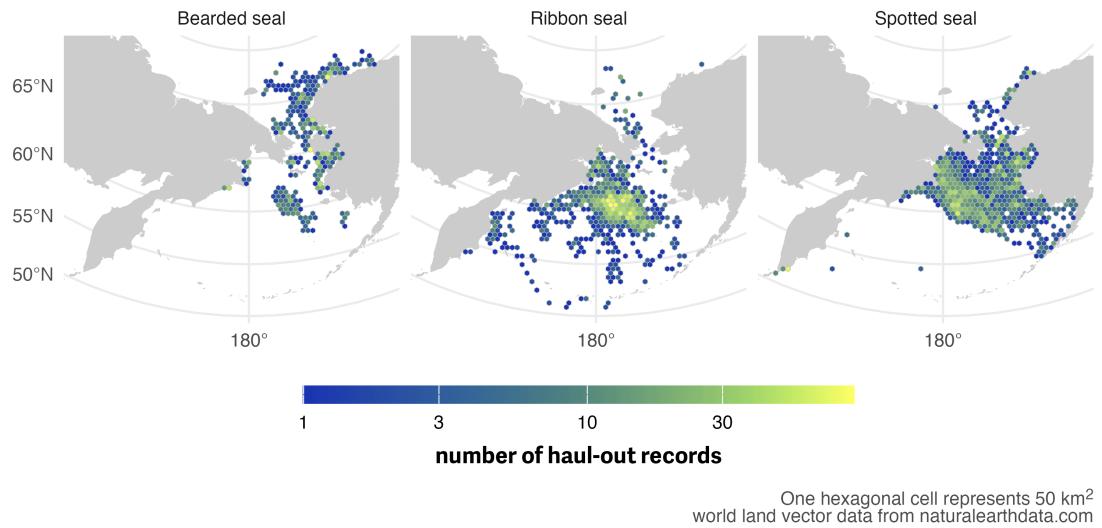


Figure 3. Spatial distribution of haul-out records from 1 March through July 15 for bearded, ribbon, and spotted seal.

Linking location estimates with haul-out records in space and time allows for inclusion of weather covariates in the final model. For this visualization, data were collated across all years between 2005 and 2020 and each hexagonal cell represents an area of 50 km². World land vector data from <https://naturalearthdata.com>.

346 Supplemental Information Fig. S1). Additionally, after approximately 9 months, 7 devices deployed
 347 on the rear flipper of bearded seals reported implausible hourly percent-dry data (100% dry for several
 348 weeks but indicative of movement and increasing transmission rates (see Boveng & Cameron (2013))).
 349 All data after the first instance of unrealistic values were censored from this analysis. In addition to a
 350 peak around local solar noon, the bearded seal model predicted additional haul-out activity around
 351 local midnight. In concert with the lower magnitude of haul-out probability, bearded seal haul-out
 352 behavior was also more protracted throughout the spring season compared to ribbon and spotted
 353 seals (see below). Overall, bearded seals were less likely to haul out and had a bi-modal distribution
 354 of haul-out probability across the day.

355 When exploring the influence of weather, bearded seal haul-out probability was strongly affected
 356 by wind ($F_{1,42728} = 130.468$; $p = <0.001$) and temperature ($F_{1,42728} = 19.5$; $p = <0.001$) with much
 357 higher haul-out probability during periods of higher temperatures and low wind speeds (Figure 6).
 358 Not surprisingly, wind chill ($F_{1,42728} = 14.54$; $p = <0.001$) was also important. Barometric pressure
 359 ($F_{1,42728} = 7.779$; $p = 0.005$) was also significant factor although less apparent (Figure 6). Any effect
 360 of precipitation was not a significant influence on haul-out probability ($F_{1,42728} = 0.519$; $p = 0.471$).

361 **Ribbon Seals**

362 Ribbon seals exhibited a pattern of gradually increasing haul-out probability in April that peaks in late
 363 May for subadults and in early June for adults (Figure 7; see also Supplemental Information Fig. S2).
 364 There is an apparent seasonal progression with subadults hauling out earlier in the season followed
 365 by adult males and, then, adult females. Haul-out behavior was clearly centered around local solar
 366 noon and expanded to other hours later in the spring as seals entered their molting period. Subadults
 367 showed an earlier start and more intense haul-out activity in April and May. The young-of-the-year

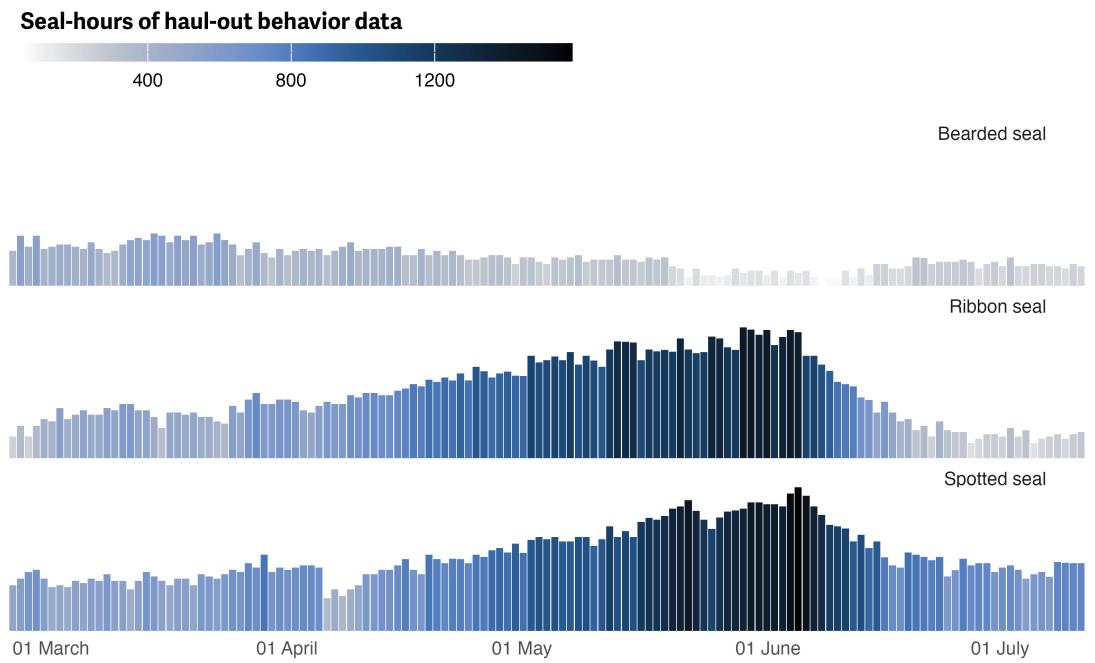


Figure 4. Seasonal distribution of haul-out behavior observations by species

Distribution of hourly percent-dry bio-logger data from 1 March to 15 July for each species. Data are grouped by day-of-year and presented in seal-hours collated across all years between 2005 and 2020. Seal-hours of data are represented as a color gradient and bar height. The higher amount of data from May and June in ribbon and spotted seals coincides with peak molting when seals (and their attached bio-loggers) are more likely hauled out. Additionally, many bio-logger deployments started in April and May. The overall reduced quantity of observations from bearded seals is reflective of the lower number of bio-logger deployments in the study and the fact that the majority of deployments on bearded seals occurred in August and September; therefore most bio-loggers deployed had exhausted their batteries.

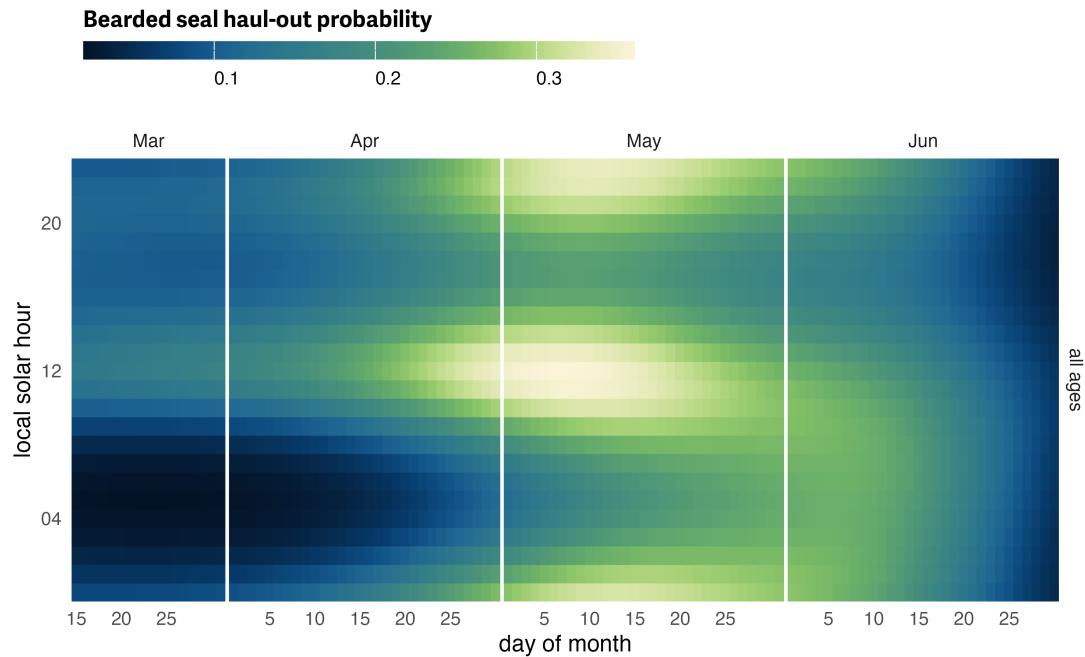


Figure 5. Bearded seal predicted haul-out probability

Predicted hourly haul-out probability of bearded seals (all ages and sex classes) from 15 March to 30 June for all age and sex classes combined. Predictions in July and before 15 March were not included to avoid spurious model predictions at the edge of the data range. Weather covariate values in the prediction were based on a simple generalized additive model for each weather covariate with smooth terms for day-of-year and solar hour to account for anticipated variability within a day over the season. Note, our model predicts lower haul-out probability for bearded seals overall compared to ribbon and spotted seals and the color scales are not directly comparable.

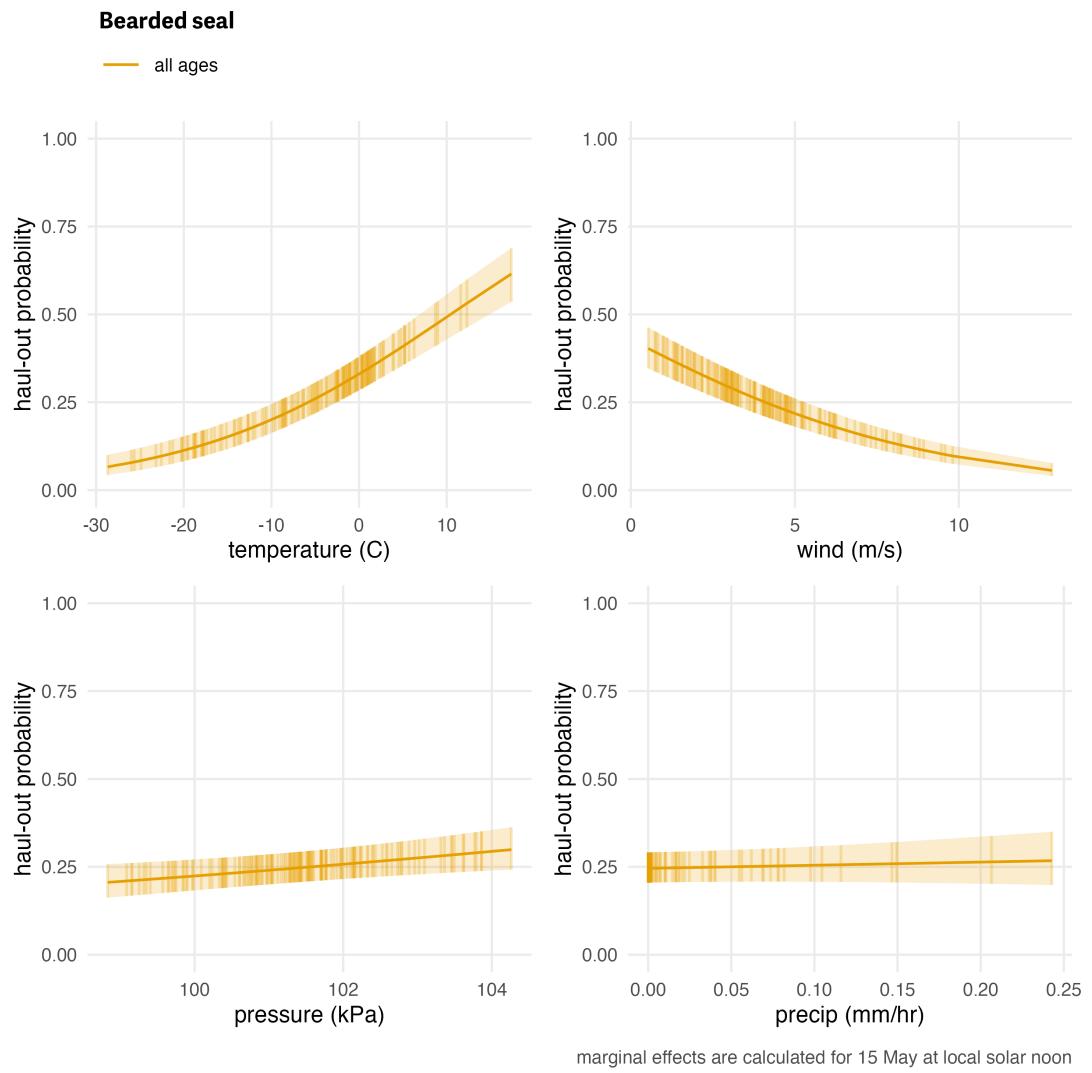


Figure 6. Influence of weather covariates on bearded seal haul-out probability

Marginal effects of temperature, wind, barometric pressure, and precipitation on the predicted haul-out probability of bearded seals combined across all age and sex classifications. Hour of the day was fixed at local solar noon and day-of-year fixed at 15 May. The other weather covariate values were predicted from a simple generalized additive model for each weather covariate with smooth terms for day-of-year and solar hour to account for anticipated variability within a day over the season. While the marginal effect of the covariate is continuous, points and vertical lines representing the 95% confidence interval around the predicted haul-out probability are shown only at observed weather values to give an indication of how the observations are distributed across the range of weather values.

records began after weaning and the model predictions seemed to indicate development of in-water activities (e.g. swimming, foraging) in May and, like adults, haul-out behavior was centered around solar noon. Adult females had a more protracted haul-out season compared to males, and more time was spent hauled out in June compared to adult males and subadults.

The haul-out probability for ribbon seals was mostly influenced by temperature ($F_{1,99540} = 6.87$; $p = 0.009$) and wind ($F_{1,99540} = 49.314$; $p = <0.001$) with barometric pressure ($F_{1,99540} = 3.446$; $p = 0.063$) having a milder impact. Ribbon seals were more likely to haul out when temperatures were relatively warm and less likely to haul out at higher winds and lower pressure values (Figure 8). Neither wind chill ($F_{1,99540} = 1.83$; $p = 0.176$) nor precipitation ($F_{1,99540} = 0$; $p = 0.989$) were a significant influence on haul-out probability. Compared with bearded seals, the effect of weather covariates on the predicted haul-out probability for ribbon seals was less striking. Because our ribbon seal model included age and sex class, we can visualize the different influences of weather covariates on those classes and see that subadults differ from adult males and females (Figure 8).

Spotted Seals

Compared to ribbon seals, spotted seals showed a longer spring haul-out season that was less intensely centered on solar noon (Figure 9; see also Supplemental Information Fig.S3). Adults of both sexes spent considerable time in April, May and June hauled out. Adult spotted seal males had a more protracted haul-out season compared to females, and more time out of the water in June (Figure 9). This likely reflects the triad behavior in spotted seals when suitor males haul out with nursing females. As with ribbon seals, the young-of-the-year records began after weaning and the model predictions reflected development of in-water activities (e.g. swimming, foraging) in May and haul-out behavior centered around solar noon.

Spotted seal haul-out behavior was less affected by the weather covariates compared to ribbon and bearded seals but their influence on the model was still significant in some cases. Temperature ($F_{1,115189} = 5.384$; $p = 0.020$), wind ($F_{1,115189} = 45.718$; $p = <0.001$), and barometric pressure ($F_{1,115189} = 9.445$; $p = 0.002$) were all significant. Spotted seals were more likely to be on the ice when temperatures were relatively warm and less likely to haul out at higher wind speeds. Wind chill ($F_{1,115189} = 0.72$; $p = 0.396$) and precipitation ($F_{1,115189} = 0.773$; $p = 0.379$) were not as influential as the other covariates. Differences in the magnitude of response between the age-sex classes were present and consistent across each of the weather covariates (Figure 10). There was a consistent ranking of adult males being the most likely to haul out, followed by adult females, and, then, subadults. This differs from ribbon seals which showed more overlap between adult males and adult females and that subadults were most likely to haul out across the presented range of weather covariates.

Annual variation in haul-out timing

The second set of models, which included annual variation in haul-out patterns, uncovered significant contributions for linear and quadratic interactions between day and year for only spotted seals ($day:year$, $F_{15,115144} = 4.445$; $p = <0.001$; $day^2:year$, $F_{15,115144} = 5.854$; $p = <0.001$). Ribbon seals showed no significant contribution for interactions between day and year ($day:year$, $F_{10,99510} = 0.516$; $p = 0.880$; $day^2:year$, $F_{10,99510} = 0.549$; $p = 0.856$). Predicted distributions of haul-out activity were largely unimodal, but varied some among and within years with respect to the timing and magnitude of haul-out peaks (Figure 11). It is important to note that predicted variation in annual haul-out patterns likely reflected both process error and sampling variability. While we did remove any years

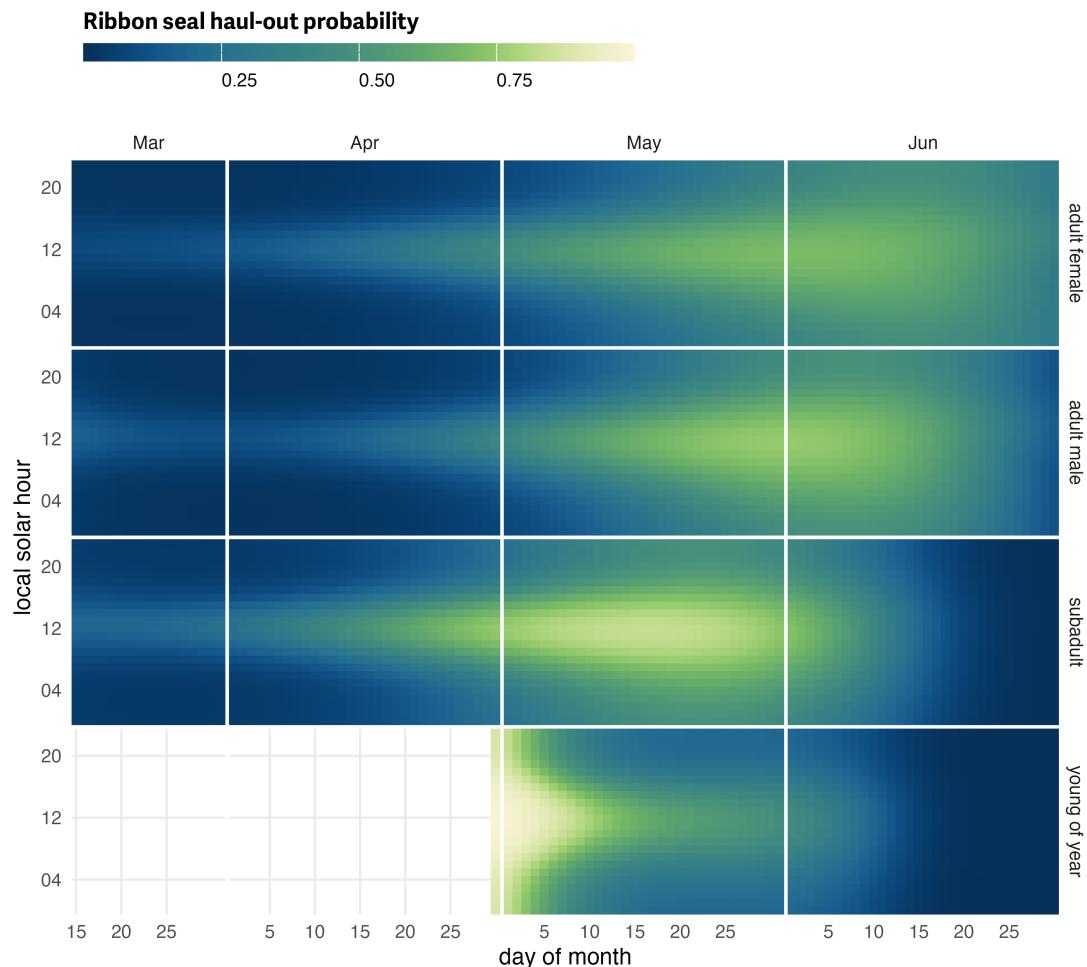


Figure 7. Ribbon seal predicted haul-out probability

Predicted hourly haul-out probability of ribbon seals from 15 March to 30 June for each age and sex class used in the model. Weather covariate values in the prediction were based on a simple generalized additive model for each weather covariate with smooth terms for day-of-year and solar hour to account for anticipated variability within a day over the season. Predictions for young of the year show their transition from newly weaned pups resting on the ice to more in-water activities. Predictions in July and before 15 March were not included to avoid spurious model predictions at the edge of the data range.

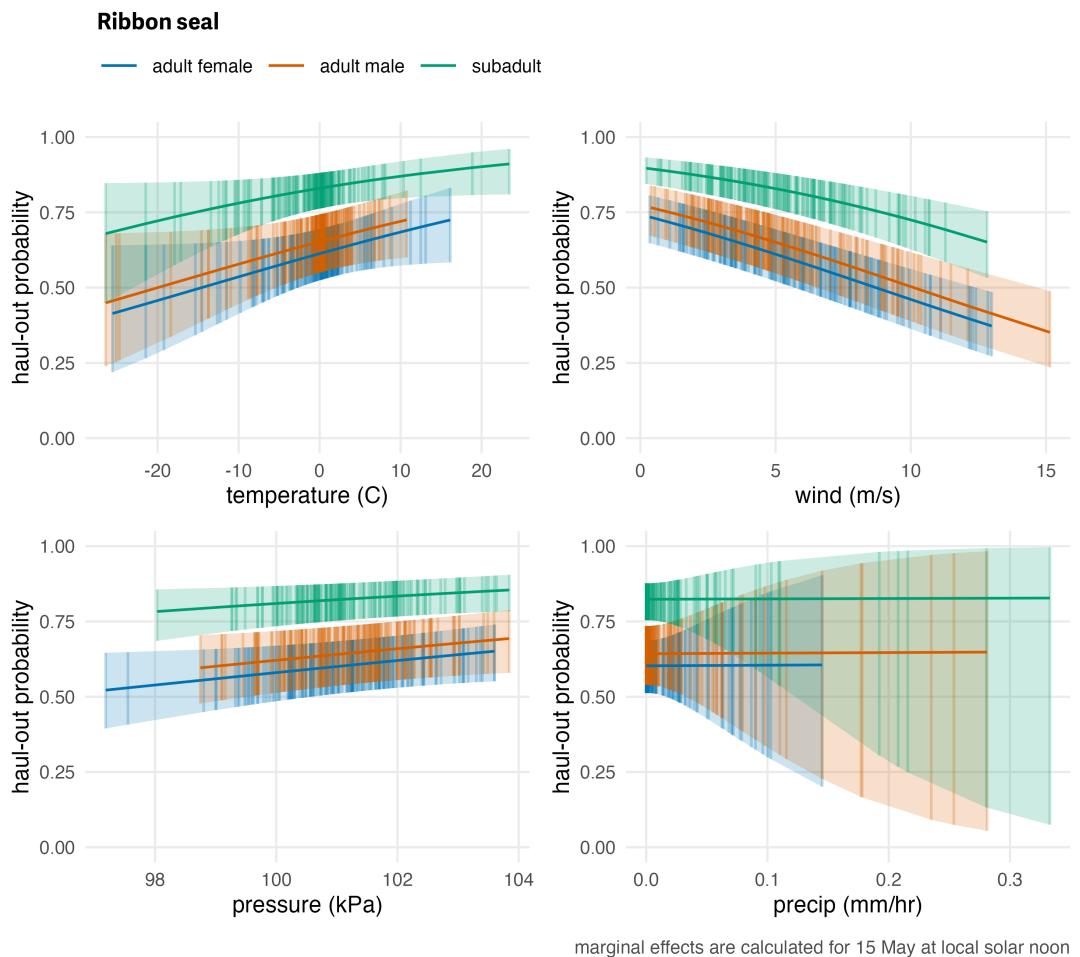


Figure 8. Influence of weather covariates on ribbon seal haul-out probability

Marginal effects of temperature, wind, barometric pressure, and precipitation on the predicted haul-out probability of ribbon seals within each age and sex classifications. Hour of the day was fixed at local solar noon and day-of-year fixed at 15 May. The other weather covariate values were predicted from a simple generalized additive model for each weather covariate with smooth terms for day-of-year and solar hour to account for anticipated variability within a day over the season. While the marginal effect of the covariate is continuous, points and vertical lines representing the 95% confidence interval around the predicted haul-out probability are shown only at observed weather values to give an indication of how the observations are distributed across the range of weather values.

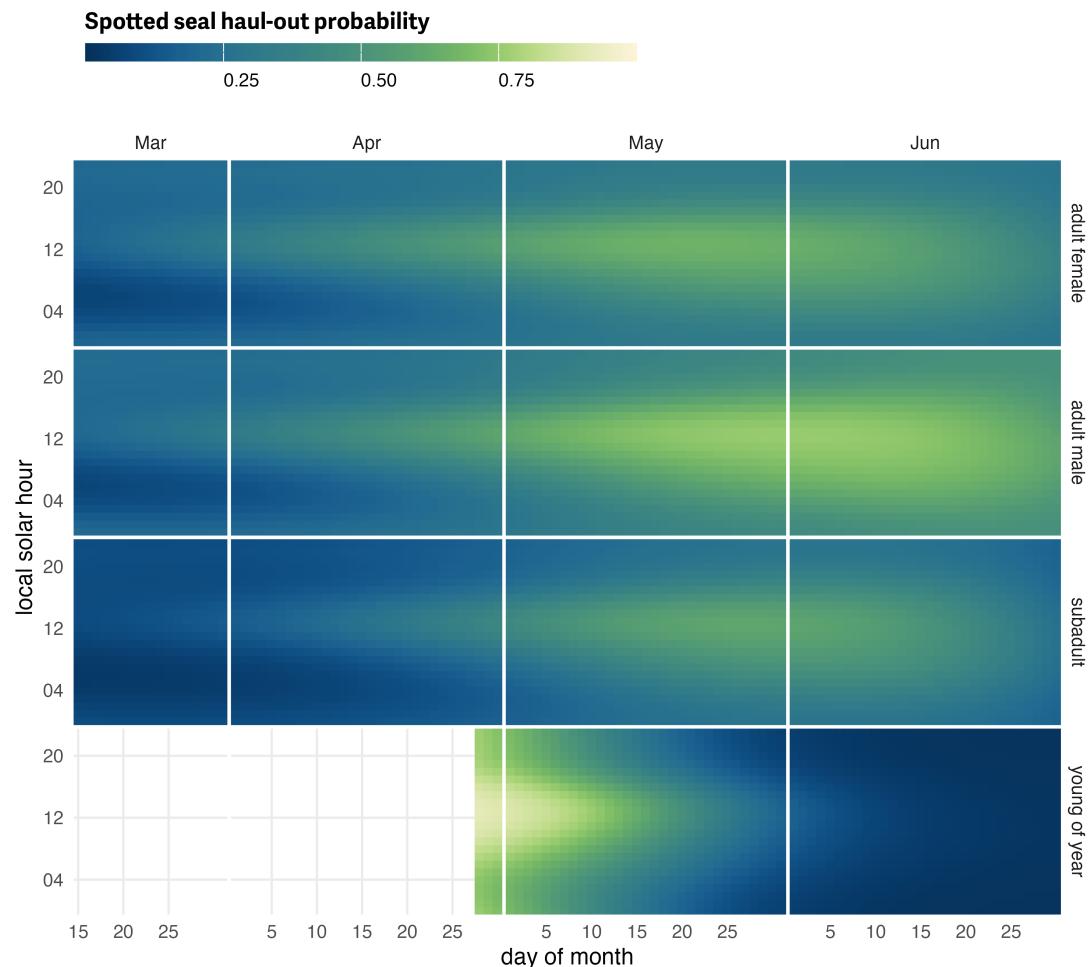


Figure 9. Spotted seal predicted haul-out probability

Predicted hourly haul-out probability of spotted seals from 1 March to 30 June for each age and sex class used in the model. Weather covariate values in the prediction were based on a simple generalized additive model for each weather covariate with smooth terms for day-of-year and solar hour to account for anticipated variability within a day over the season. As with ribbon seals, predictions for young of the year show their transition from newly weaned pups resting on the ice to more in-water activities. Predictions in July and before 15 March were not included to avoid spurious model predictions at the edge of the data range.

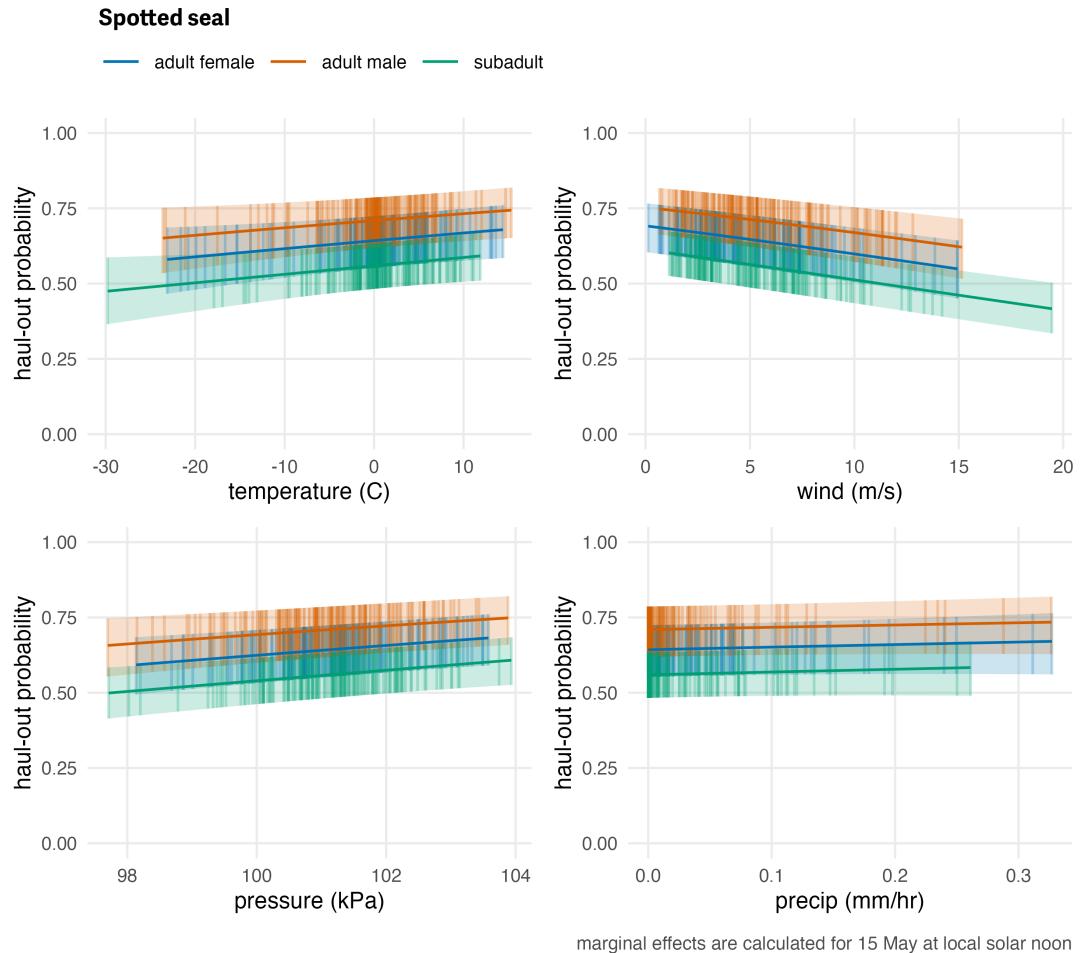


Figure 10. Influence of weather covariates on spotted seal haul-out probability

Marginal effects of temperature, wind, barometric pressure, and precipitation on the predicted haul-out probability of spotted seals within each age and sex classification. Hour of the day was fixed at local solar noon and day-of-year fixed at 15 May. The other weather covariate values were predicted from a simple generalized additive model for each weather covariate with smooth terms for day-of-year and solar hour to account for anticipated variability within a day over the season. While the marginal effect of the covariate is continuous, points and vertical lines representing the 95% confidence interval around the predicted haul-out probability are shown only at observed weather values to give an indication of how the observations are distributed across the range of weather values.

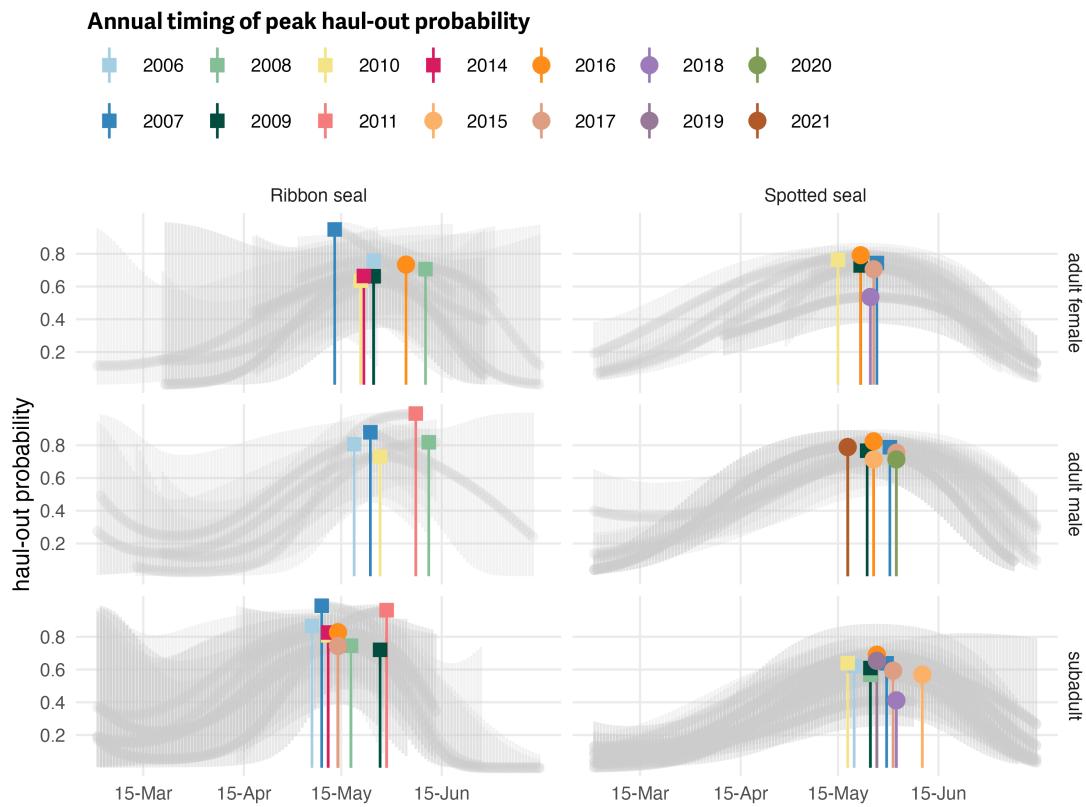


Figure 11. Annual variability in the timing of peak haul-out probability for ribbon and spotted seals.

Spring haul-out probability (colored markers) for ribbon and spotted seals across 14 years are shown. The full seasonal range of annual predictions along with uncertainty are presented as grey lines. Covariates were fixed at local solar noon and weather covariate values were predicted from a simple generalized additive model for each weather covariate with smooth terms for day-of-year and solar hour to account for anticipated variability within a day over the season. Only those groups (age:sex + year) that included observations from more than one seal are shown. Additionally, any groups where data were only available after 1 June or before 1 May are not included.

411 where only one deployment in a species + age:sex group was present, there were still some years
 412 where the pattern shown was informed by a small number of individuals that may not represent
 413 population-level patterns.

414 The annual timing of peak haul-out probability for ribbon seals and adult male spotted seals
 415 appeared to have no relationship with the amount of yearly maximum sea-ice extent in the study area.
 416 For ribbon seals and adult male spotted seals, p -values were substantially larger than 0.05 (ribbon
 417 seal adult females: $R^2 = 0.004$, $p = 0.896$; ribbon seal adult males: $R^2 = 0.059$, $p = 0.693$; ribbon seal
 418 subadults: $R^2 = 0.007$, $p = 0.828$; spotted seals adult males: $R^2 = 0.004$, $p = 0.889$). Adult female and
 419 subadult spotted seals both showed a negative trend (peak haul-out occurs later in years with less sea
 420 ice) but neither with a significant relationship
 421 (spotted seal adult female: $R^2 = 0.456$, $p = 0.141$; spotted seal subadults: $R^2 = 0.369$, $p = 0.062$).

422 **DISCUSSION**

423 We modeled data from bio-loggers deployed on bearded, ribbon, and spotted seals to examine factors
424 affecting their haul-out behavior on sea ice in the Bering and Chukchi seas. Our analysis shows all
425 three species of seal haul out progressively more through the spring and peak near mid-May to early
426 June before declining again. This pattern aligns well with what has been previously documented
427 qualitatively (Boveng et al., 2009; Cameron et al., 2010; Boveng & Cameron, 2013) and confirms our
428 haul-out data are likely quantifying population-level behavioral patterns. Beginning in spring, seals
429 preferentially haul out on ice shortly after solar noon, which allows seals to maximize absorption of
430 solar radiation thought to facilitate the molting process (Feltz & Fay, 1966). Interestingly, bearded
431 seals appear to have two peaks in haul-out activity within a day, one shortly after solar noon, and
432 one centered near solar midnight. This, of course, could be an artifact of our limited sample size for
433 bearded seal deployments across all age classes. However, a similar bi-modal pattern has been seen
434 in ringed seals (Von Duyke et al., 2020) and suggests that bearded and ringed seals may be operating
435 under different constraints than ribbon and spotted seals. Bearded and ringed seals are distributed
436 across higher latitudes that experience extended daylight hours during spring which may allow more
437 flexibility in alternating resting and foraging events. Other factors such as predation by polar bears
438 (which is rare for ribbon and spotted seals in the Bering Sea) may also explain differing haul-out
439 patterns. The change in haul-out behavior during the season was less pronounced in bearded seals
440 compared to ribbon and spotted seals. This aligns with findings from Thometz et al. (Thometz et al.,
441 2021) who observed a mean molting period of 119 ± 2 days and a relatively stable resting metabolic
442 rate for bearded seals during that time. While ribbon seals were not considered in that study, spotted
443 and ringed seals underwent molt periods of just 33 ± 4 and 28 ± 6 days and had increased resting
444 metabolic rates.

445 Unlike previous analyses of seal haul-out behavior in spotted and ribbon seals (e.g. (Ver Hoef,
446 London & Boveng, 2010), (Conn et al., 2014)), we also investigated the influence of sex-age class on
447 haul-out probabilities of both species (but not for bearded seals because of low sample size). Field
448 identification of age class can be inexact, particularly when differentiating subadults from adults. In
449 the case of ribbon seals, subadults often have less distinct ribbons than adults. Spotted seal pelage
450 cannot be used to reliably discern adults from subadults. Despite these challenges, we feel the age
451 classifications used in this analysis are useful in testing for age-related effects on haul-out behavior.

452 Although ribbon and spotted seals exhibited a unimodal diel haul-out pattern generally centered
453 around local solar noon, there were key differences across species, age, and sex that match our
454 understanding from natural history descriptions of their ecological behavior. Spotted seals are known
455 to form triads during the breeding season where a female and dependent pup are accompanied on
456 the ice by a suitor male (Frost & Burns, 2018). The male waits for the female to wean the pup and
457 enter estrus, and fends off any other potential suitor males. Triad formation results in both males
458 and females spending a large portion of the day hauled out on ice and a protracted spring haul-out
459 season for both sexes. While females are still nursing the pup and not yet in estrus they may be less
460 inclined to interrupt their haul out and enter the water where the suitor male would attempt mating.
461 We see this reflected in the predicted haul-out patterns, with both males and females exhibiting a
462 broad distribution of time out of the water throughout the solar day and the season. Ribbon seals are
463 not known to form triads and our model predicts a progression of increased haul-out behavior with
464 females starting earlier in the season than males. Notably, female ribbon seals spend a large portion of
465 the day in the water during the pupping period, aligning with the hypothesis that ribbon seal females

466 continue foraging while nursing. Subadult ribbon and spotted seals begin elevated haul-out behavior
467 earlier in the spring and follow a pattern seen in other phocids where yearlings and subadults molt
468 first followed by adult females and males (Thompson & Rothery, 1987; Kirkman et al., 2003; Reder et
469 al., 2003). Also of note is the early development in newly weaned pups of haul-out behavior centered
470 around solar noon observed in this study.

471 We also investigated the influence of weather on haul-out probabilities, including wind speed,
472 temperature, barometric pressure, precipitation, and wind chill. These have been investigated for
473 walruses (e.g. Udevitz et al. (2009)) and a few select studies of ice-associated seals (Perry, Stenson
474 & Buren, 2017; Hamilton & Evans, 2018). In our study, ribbon seal haul-out behavior was notably
475 influenced by weather, with wind, temperature, and barometric pressure all being important compo-
476 nents of the model. Spotted seals were most affected by wind and barometric pressure. For bearded
477 seals, the model indicated wind and temperature had the greatest impact. In general, and as might
478 be expected, seals were more likely to haul-out when daily temperatures were warmer, winds speeds
479 were lower, barometric pressure was higher, and precipitation was lower. Those weather conditions
480 are general indicators of increased solar radiation and lower convective heat loss, both of which
481 provide energetic benefits (see additional discussion in Supplemental Material **Exploring Insolation**
482 (**Solar Radiation**) as a Model Covariate regarding the potential use of solar radiation directly). Low
483 winds and precipitation could also enhance predator detection. Our results highlight the importance
484 of incorporating weather covariates when analyzing haul-out behavior and calculating availability
485 corrections for aerial surveys.

486 Notably missing from our list of haul-out model explanatory variables is any spatial-temporal
487 representation of sea-ice concentration, area, or extent. This may seem counterintuitive when
488 modeling the haul-out behavior of seal species with such a close association to sea ice; seals haul out
489 in the presence of sea ice, and we could assess the local concentration of sea ice during these events
490 (see (Olnes et al., 2020)). This, however, expands the scope of our analysis into the realm of habitat
491 selection and many of our deployments consisted of a single device attached to the rear flipper of the
492 seal which meant we only received locations when seals were hauled out on sea ice, limiting our
493 ability to fully evaluate fine-scale habitat preferences related to sea ice. Insight into how seals use
494 and interact with sea ice during an extended period when the availability and characteristics of sea
495 ice is rapidly changing is important (Breed et al., 2018; Cameron et al., 2018) but ancillary to the
496 focus of this analysis – and, in the end, not possible given key limitations of our data. Additionally,
497 our study was limited to the spring season when seal haul-out behaviors are strongly influenced by
498 pupping, nursing, breeding behavior, and molt. These drivers are likely more influential on haul-out
499 behavior than sea-ice concentration. Crawford et al. (2019) compared haul-out probability models
500 for ringed seals and found those that only included season (and not sea-ice concentration) were the
501 most parsimonious. For all of these reasons, we have elected not to use sea-ice concentration *as a*
502 *predictor for haul-out probability* in the present study.

503 Our models detected small deviations in the timing and magnitude of annual peaks in haul-out
504 behavior for ribbon and spotted seals. The timing of peak haul-out activity appears to fall within
505 a relatively narrow time window of 3-4 weeks in late May and early June. This consistency across
506 15 years is likely a reflection of the relationship between a critical photoperiod and the timing of
507 important life history stages (Temte, 1994; Bronson, 2009). However, along with a critical photoperiod,
508 ribbon and spotted seals are dependent upon the presence of sea ice for pupping and molt. We did not
509 find large support in our models for a relationship between the timing of peaks in haul-out behavior

510 and the amount of yearly maximum sea ice. This could indicate that, while the extent of spring sea ice
511 in the Bering Sea varied widely during our study period, seals were still able to locate sea ice and haul
512 out. Only a small portion of our data was from 2018 – 2019, years of extreme low spring ice extent in
513 the Bering Sea that appeared to impact body condition of ribbon and spotted seals (Boveng et al.,
514 2020), so we may currently lack sufficient contrast in ice extent to characterize an effect on the timing
515 of peak haul-out probability. We should expect, however, that some minimal threshold in the spatial
516 extent or density of sea ice will have a meaningful impact on the timing of peak haul-out behavior —
517 if there is no sea-ice, seals will not haul out or they will be forced to use terrestrial haul-out sites which
518 were not part of the evolution of their normal behaviors. Additionally, while from an ecological
519 perspective the haul-out behavior appears consistent, the interannual differences in timing and
520 magnitude are large enough to have important ramifications on calculations of abundance and trend.
521 Those ramifications will only be exacerbated if climate variability amplifies interannual differences.

522 Previous attempts to estimate the abundance of phocid seals from aerial survey data in the Bering
523 and Chukchi seas (e.g. Bengtson et al. (2005), Conn et al. (2014), Ver Hoef et al. (2014)) have used
524 estimated haul-out probabilities to correct for the proportion of animals that are in the water and
525 thus unavailable to be counted. Although several of these studies allowed haul-out probabilities to
526 vary by day-of-year and time-of-day, they have not accounted for variability among years, weather
527 conditions, or in the age-sex class of the sample. In this paper, we have shown that there can
528 be considerable differences in the haul-out probability of seals on ice based on these factors and
529 subsequent analyses have shown the potential for considerable bias in abundance estimates if such
530 covariates are unaccounted for (see Conn & Trukhanova (2023) for discussion about the importance
531 of including stable age- and stage-proportions). We recommend that future abundance analyses
532 employ availability models that account for them. For instance, it is relatively straightforward to
533 obtain weather reanalysis products (e.g. NARR, ERA5) for times and locations that are surveyed and
534 to construct a relevant correction factor based on predictions of GLMPMs. The most challenging
535 element in developing availability correction factors is with annual variability. It can be difficult to
536 get a sufficient sample size to estimate year-specific correction factors, particularly because research
537 teams would likely need to deploy bio-loggers on seals and conduct aerial surveys concurrently,
538 requiring considerably more personnel and money. One possible suggestion is to include year as a
539 random effect within models for aerial survey counts such that, without specific knowledge of any
540 particular year, the among-year variance is included in the modeled standard errors. Regardless of
541 the specific approach, future estimates of Arctic seal abundance will require specific consideration
542 of annual variability and changes in the timing of peak haul-out behavior when estimating trends,
543 as one will not know if moderate differences in abundance estimates are attributable to changes in
544 abundance or changes in haul-out behavior.

545 Predictions of absolute haul-out probability in this paper were somewhat different than those
546 previously reported for these species, especially for bearded seals. For instance, Ver Hoef et al. (2014)
547 and Conn et al. (2014) used haul-out correction factors with maximums of 0.66 for bearded seals,
548 0.62 for ribbon seals, and 0.54 for spotted seals, where these maximums corresponded to times near
549 local solar noon in mid-late May. Results here suggest a haul-out probability on May 20 at local solar
550 noon of 0.304 (95% CI: 0.258 – 0.354) for bearded seals across all age and sex classes, 0.715 (95% CI:
551 0.62 – 0.794) for adult male ribbon seals, 0.661 (95% CI: 0.576 – 0.738) for adult female ribbon seals,
552 0.74 (95% CI: 0.654 – 0.811) for adult male spotted seals, and 0.66 (95% CI: 0.571 – 0.739) for adult
553 female spotted seals. Our estimates of haul-out probability reflect increased sample sizes in terms

554 of number of individuals, inclusion of weather covariates, and improvements to the way data were
555 prepared prior to analysis and should be the basis for any future estimates of seal abundance from
556 aerial surveys in the Bering and Chukchi seas.

557 We focused this paper on haul-out behavior of bearded, ribbon, and spotted seals. Ringed seals
558 are also present in the Bering and Chukchi seas but exhibit a unique complicating factor. Adult
559 ringed seals build subnivean lairs under the snow on top of the sea ice, where they haul out and
560 where females rear pups until conditions are good for basking (Frost et al., 2004). Thus, the wet-dry
561 sensor on a bio-logger could indicate that an animal is hauled out, but if it is within a lair, it is not
562 available to be detected during an aerial survey. We hope to address availability of ringed seals using
563 data from satellite tags, replicate survey tracks, and auxiliary information about snow depth and
564 timing of melt in a future study (see, e.g., Lindsay et al. (2021)).

565 Our analysis emphasizes the importance of accounting for seasonal and temporal variation in
566 haul-out behavior, as well as associated weather covariates, when interpreting the number of seals
567 counted in aerial surveys. The rapid acceleration of climate change in Arctic ecosystems is already
568 occurring and is forecast to decrease the quantity and quality of suitable habitat for ice-associated seals
569 that rely on sea-ice for a variety of activities. Improved estimates of seal population abundance from
570 aerial surveys are needed to properly monitor the impacts of these changes on seal populations over
571 time. Those monitoring surveys will need to be paired with continued investigation and assessment
572 of seal haul-out behavior to allow credible predictions about the effects of climate disruptions on the
573 abundance and distribution of Arctic seal populations.

574 AUTHOR CONTRIBUTIONS

- 575 • **Josh M. London:** investigation, conceptualization, methodology, formal analysis, validation,
576 software, writing: original draft, writing: review and editing, visualization, and data curation
- 577 • **Paul B. Conn:** conceptualization, methodology, formal analysis, software, validation, writing:
578 original draft, writing: review and editing
- 579 • **Stacie K. Hardy:** investigation, data curation, methodology, validation, writing: review and
580 editing
- 581 • **Erin L. Richmond:** data curation, investigation, methodology, validation, writing: review and
582 editing
- 583 • **Jay M. Ver Hoef:** conceptualization, methodology, software, writing: review and editing
- 584 • **Michael F. Cameron:** investigation, project administration, writing: review and editing
- 585 • **Justin A. Crawford:** investigation, methodology, validation, data curation, writing: review
586 and editing
- 587 • **Lori T. Quakenbush:** investigation, methodology, supervision, project administration, writing:
588 review and editing
- 589 • **Andrew L. Von Duyke:** investigation, methodology, validation, data curation, writing: review
590 and editing
- 591 • **Peter L. Boveng:** investigation, conceptualization, supervision, project administration, writing:
592 review and editing

593 DATA AVAILABILITY

594 This manuscript was developed as a reproducible research compendium and was originally
595 published as a pre-print at bioRxiv (London et al. (2022); <https://doi.org/10.1101/>

596 2022.04.07.487572). All data used in the study and code are available on GitHub
597 (<https://github.com/noaa-afsc/berchukseals-haulout>) and major versions
598 archived at Zenodo (<https://doi.org/10.5281/zenodo.4638221>). Original data sources
599 for telemetry are archived as part of datasets at the United States Animal Telemetry Network
600 (<https://portal.atn.ioos.us/>; <https://doi.org/10.24431/rw1k8er>), archived
601 at Movebank (see Movebank ID 732321226), or associated with other published manuscripts
602 (see supplemental material S1). Collated and cleaned data products needed to replicate the
603 analysis along with the results of all model fits are also available and versioned as an R package on
604 GitHub (<https://github.com/noaa-afsc/berchuksealsHauloutFits>) and archived
605 at Zenodo (<https://doi.org/10.5281/zenodo.10056308>).

606 ACKNOWLEDGMENTS

607 We recognize that the species and ecosystems we studied are within the ancestral and present-day
608 environs of the Inupiat and Yup'ik people who, through many uncredited contributions of traditional
609 knowledge, provided early western naturalists and scientists with much of what gets described as the
610 'basic biology' of Arctic seals. The deployment of bio-logging devices used in this study were often
611 done in collaboration with Alaska Native seal hunters and with the approval of their communities. We
612 would like to especially acknowledge the Alaska communities of Kotzebue, Koyuk, Nome, Nuiqsut,
613 Scammon Bay, St. Michael, Utqiagvik, and Ulguniq (Wainwright) and the following individuals:
614 James Adams, Jeff Barger, David Barr, Wendell Booth, Cyrus Harris, Nereus 'Doc' Harris, Grover
615 Harris, Lee Harris, Tom Jones, Frank Garfield, Brenda Goodwin, Henry Goodwin, John Goodwin,
616 Pearl Goodwin, Willie Goodwin, Brett Kirk, Noah Naylor, Virgil Naylor Jr., Virgil Naylor Sr., Dan
617 Savetilik, Chuck Schaeffer, Ross Schaeffer, Allen Stone, and Randy Toshavik from Kotzebue; Merlin
618 Henry from Koyuk; Tom Gray from Nome; Vernon Long and Richard Tukle from Nuiqsut; Morgan
619 Simon, River Simon, and Al Smith from Scammon Bay; Alex Niksik Jr. from St. Michael; Billy Adams,
620 James Aiken, Tim Aiken, Howard Kittick, Gilbert Leavitt, Isaac Leavitt, J.R. Leavitt, Bobby Sarren,
621 and Joe Skin from Utqiagvik; Mary Ellen Ahmaogak, Enoch Oktollik, Shawn Oktollik, Stacey Osborn,
622 and Fred Rexford from Ulguniq. We would also like to acknowledge the support of the Ice Seal
623 Committee.

624 We are grateful for the assistance in catching and sampling seals by Ryan Adam, James Bailey,
625 Michelle Barbieri, John Bengtson, Gavin Brady, Anna Bryan, Vladimir Burkanov, Cynthia Christman,
626 Sarah Coburn, Shawn Dahle, Rob Delong, Stacy DiRocco, Deb Fauquier, Shannon Fitzgerald, Kathy
627 Frost, Scott Gende, Craig George, Tracey Goldstein, Jeff Harris, Jason Herreman, Markus Horning,
628 John Jansen, Shawn Johnson, Charles Littnan, Lloyd Lowry, Brett McClintock, Erin Moreland, Aaron
629 Morris, Mark Nelson, Justin Olnes, Lorrie Rea, Bob Shears, Gay Sheffield, Kayla Scheimreif, Brent
630 Stewart, Alexy Trukhin, Dave Withrow, and Heather Ziel. We also appreciate the commitment to
631 science and safety by all officers and crew of the NOAA ship *Oscar Dyson*, the NOAA ship *MacArthur*
632 *II*, the *MV Tayfun*, and the *RV Thomas G. Thompson*.

633 Telemetry data from the Alaska Department of Fish and Game (ADF&G) and the North Slope
634 Borough Department of Wildlife Management (NSB) were important contributions to the findings
635 presented here. Deployments in the western Bering Sea were done in collaboration with Russian
636 colleagues and North Pacific Wildlife Consulting, LLC.

637 The findings and conclusions in the paper are those of the author(s) and do not necessarily
638 represent the views of the National Marine Fisheries Service, NOAA. Any use of trade, product, or

639 firm names does not imply an endorsement by the U.S. Government.

640 REFERENCES

- 641 Bengtson JL, Cameron MF. 2004. Seasonal haulout patterns of crabeater seals (*Lobodon carcinophaga*).
642 *Polar Biology* 27:344–349. DOI: [DOI 10.1007/s00300-004-0597-1](https://doi.org/10.1007/s00300-004-0597-1).
- 643 Bengtson JL, Hiruki-Raring LM, Simpkins MA, Boveng PL. 2005. Ringed and bearded seal densities
644 in the eastern Chukchi Sea, 1999–2000. *Polar Biology* 28:833–845.
- 645 Betts MG, Diamond A, Forbes G, Villard M-A, Gunn J. 2006. The importance of spatial autocorrelation,
646 extent and resolution in predicting forest bird occurrence. *Ecological Modelling* 191:197–224.
- 647 Boveng PL, Bengtson JL, Buckley TW, Cameron MF, Dahle SP, Kelly BP, Megrey BA, Overland JE,
648 Williamson NJ. 2009. [Status review of the spotted seal \(*Phoca largha*\)](#). U.S. Dep. Commer., NOAA
649 Tech. Memo. NMFS-AFSC-200:153.
- 650 Boveng PL, Bengtson JL, Cameron MF, Dahle SP, Logerwell EA(ElizabethA), London JM, Overland
651 JE, Sterling JT, Stevenson DE 1970-, Taylor BL 1954-, Ziel HL 1974-. 2013. [Status review of the](#)
652 [ribbon seal \(*Histriophoca fasciata*\)](#). U.S. Dep. Commer., NOAA Tech. Memo. NMFS-AFSC-255:174.
- 653 Boveng PL, Cameron MF. 2013. *Pinniped movements and foraging: seasonal movements, habitat*
654 *selection, foraging and haul-out behavior of adult bearded seals in the Chukchi Sea. Final Report,*
655 *BOEM Report 2013-01150*. Anchorage, Alaska: Bureau of Ocean Energy Management, Alaska
656 Outer Continental Shelf Region.
- 657 Boveng P, Lowry L. 2018. Ribbon seal (*Histriophoca fasciata*). In: Bernd Würsig, J. G. M. Thewissen,
658 Kit Kovacs eds. *Encyclopedia of Marine Mammals: Third Edition*. London: Academic Press,
659 811–813.
- 660 Boveng PL, Ziel HL, McClintock BT, Cameron MF. 2020. Body condition of phocid seals during a
661 period of rapid environmental change in the Bering Sea and Aleutian Islands, Alaska. *Deep Sea Re-*
662 *search Part II: Topical Studies in Oceanography* 181–182:104904. DOI: [10.1016/j.dsr2.2020.104904](https://doi.org/10.1016/j.dsr2.2020.104904).
- 663 Breed GA, Cameron MF, Ver Hoef JM, Boveng PL, Whiting A, Frost KJ. 2018. Seasonal sea ice
664 dynamics drive movement and migration of juvenile bearded seals *Erignathus barbatus*. *Marine*
665 *Ecology Progress Series* 600:223–237.
- 666 Bronson FH. 2009. Climate change and seasonal reproduction in mammals. *Philosophical Transac-*
667 *tions of the Royal Society B* 364:3331–3340. DOI: [10.1098/rstb.2009.0140](https://doi.org/10.1098/rstb.2009.0140).
- 668 Cameron MF, Bengtson JL, Boveng PL, Jansen JK(JohnK, Kelly BP, Dahle SP, Logerwell
669 EA(ElizabethA), Overland JE, Sabine CL, Waring GT, Wilder JM. 2010. [Status review of the](#)
670 [bearded seal \(*Erignathus barbatus*\)](#). U.S. Dep. Commer., NOAA Tech. Memo. NMFS-AFSC-
671 211:246.
- 672 Cameron MF, Frost KJ, Ver Hoef JM, Breed GA, Whiting AV, Goodwin J, Boveng PL. 2018. Habitat
673 selection and seasonal movements of young bearded seals (*Erignathus barbatus*) in the Bering
674 Sea. *PLoS ONE* 13:e0192743. DOI: [10.1371/journal.pone.0192743](https://doi.org/10.1371/journal.pone.0192743).
- 675 Cavalieri DJ, Parkinson CL, Gloersen P, Zwally H. 1996. Sea ice concentrations from Nimbus-7 SMMR
676 and DMSP SSM/I-SSMIS passive microwave data. Boulder, Colorado USA: NASA National Snow
677 and Ice Data Center Distributed Active Archive Center
- 678 Conn PB, Hoef JMV, McClintock BT, Moreland EE, London JM, Cameron MF, Dahle SP, Boveng
679 PL. 2014. [Estimating multispecies abundance using automated detection systems: Ice-associated](#)
680 [seals in the Bering Sea](#). *Methods in Ecology and Evolution* 5:1280–1293.
- 681 Conn PB, Johnson DS, London JM, Boveng PL. 2012. Accounting for missing data when assessing

- 682 availability in animal population surveys: an application to ice-associated seals in the Bering Sea.
683 *Methods in Ecology and Evolution*:1039–1046.
- 684 Conn PB, Trukhanova IS. 2023. Modeling vital rates and age-sex structure of Pacific Arctic pho-
685 cids: influence on aerial survey correction factors. *Marine Mammal Science* 39:648–661. DOI:
686 [10.1111/mms.12992](https://doi.org/10.1111/mms.12992).
- 687 Crawford JA, Frost KJ, Quakenbush LT, Whiting A. 2019. Seasonal and diel differences in dive and
688 haul-out behavior of adult and subadult ringed seals (*Pusa hispida*) in the Bering and Chukchi
689 seas. *Polar Biology* 42:65–80. DOI: [10.1007/s00300-018-2399-x](https://doi.org/10.1007/s00300-018-2399-x).
- 690 Crawford JA, Quakenbush LT, Citta JJ. 2015. A comparison of ringed and bearded seal diet,
691 condition and productivity between historical (1975–1984) and recent (2003–2012) periods
692 in the Alaskan Bering and Chukchi seas. *Progress in Oceanography* 136:133–150. DOI:
693 [10.1016/j.pocean.2015.05.011](https://doi.org/10.1016/j.pocean.2015.05.011).
- 694 Feltz ET, Fay FH. 1966. Thermal requirements in vitro of epidermal cells from seals. *Cryobiology*
695 3:261–264.
- 696 Frost KJ, Burns JJ. 2018. Spotted Seal: *Phoca largha*. In: Würsig B, Thewissen JGM, Kovacs KM eds.
697 *Encyclopedia of Marine Mammals (Third Edition)*. Academic Press, 928–931. DOI: [10.1016/B978-0-12-804327-1.00244-2](https://doi.org/10.1016/B978-0-12-804327-1.00244-2).
- 698 Frost KJ, Lowry LF, Pendleton G, Nute HR. 2004. Factors affecting the observed densities of ringed
699 seals, *Phoca hispida*, in the Alaskan Beaufort Sea, 1996–99. *Arctic* 57:115–128.
- 700 Hamilton V, Evans K. 2018. Establishing growth chronologies from marine mammal teeth: a method
701 applicable across species. *Journal of Experimental Marine Biology and Ecology* 505:24–34. DOI:
702 <https://doi.org/10.1016/j.jembe.2018.04.006>.
- 703 Harwood LA, Smith TG, Alikamik J, Alikamik E, Lea EV, Stirling I, Wright H, Melling H, Zhu X.
704 2020. Long-term, harvest-based monitoring of ringed seal body condition and reproduction in
705 Canada's western arctic: an update through 2019. *Arctic* 73:206–220. DOI: [10.14430/arctic70428](https://doi.org/10.14430/arctic70428).
- 706 Huntington HP, Danielson SL, Wiese FK, Baker M, Boveng P, Citta JJ, De Robertis A, Dickson DMS,
707 Farley E, George JC, Iken K, Kimmel DG, Kuletz K, Ladd C, Levine R, Quakenbush L, Stabeno
708 P, Stafford KM, Stockwell D, Wilson C. 2020. Evidence suggests potential transformation of the
709 Pacific Arctic ecosystem is underway. *Nature Climate Change*:342–348. DOI: [10.1038/s41558-020-0695-2](https://doi.org/10.1038/s41558-020-0695-2).
- 710 Johnson DS, London JM, Lea M-A, Durban JW. 2008. Continuous-time correlated random walk
711 model for animal telemetry data. *Ecology* 89:1208–1215.
- 712 Kelly BP, Bengtson JL, Boveng PL, Cameron MF, Dahle SP, Jansen JK, Logerwell EA, Overland JE,
713 Sabine CL, Waring GT, Wilder JM. 2010. *Status review of the ringed seal (Phoca hispida)*. U.S.
714 Department of Commerce.
- 715 Kelly BP, Quakenbush LT. 1990. Spatiotemporal use of lairs by ringed seals (*Phoca hispida*). *Canadian
716 Journal of Zoology* 68:2503–2512.
- 717 Kirkman SP, Bester MN, Pistorius PA, Hofmeyr GJG, Jonker FC, Owen R, Strydom N. 2003. Variation
718 in the timing of moult in southern elephant seals at Marion Island : research article. *South African
719 Journal of Wildlife Research - 24-month delayed open access* 33:79–84. DOI: [10.10520/EJC117173](https://doi.org/10.10520/EJC117173).
- 720 Kwok R. 2018. Arctic sea ice thickness, volume, and multiyear ice coverage: losses and coupled vari-
721 ability (1958–2018). *Environmental Research Letters* 13:105005. DOI: [10.1088/1748-9326/aae3ec](https://doi.org/10.1088/1748-9326/aae3ec).
- 722 Lindsay JM, Laidre KL, Conn PB, Moreland EE, Boveng PL. 2021. *Modeling ringed seal *Pusa hispida*
723 habitat and lair emergence timing in the eastern Bering and Chukchi Seas*. *Endangered Species
724 Research* 13:1–14. DOI: [10.1080/19382375.2021.638300](https://doi.org/10.1080/19382375.2021.638300).

- 726 *Research* 46:1–17.
- 727 London JM, Conn PB, Hardy SK, Richmond EL, Ver Hoef JM, Cameron MF, Crawford JA, Von Duyke
728 AL, Quakenbush LT, Boveng PL. 2022. Spring haul-out behavior of seals in the Bering and Chukchi
729 seas. *bioRxiv*:2022–04. DOI: <https://doi.org/10.1101/2022.04.07.487572>.
- 730 London JM, Ver Hoef JM, Jeffries SJ, Lance MM, Boveng PL. 2012. Haul-out behavior of harbor
731 seals (*Phoca vitulina*) in Hood Canal, Washington. *PLoS ONE* 7:e38180. DOI: [10.1371/journal.pone.0038180](https://doi.org/10.1371/journal.pone.0038180).
- 732 Lonergan M, Duck C, Moss S, Morris C, Thompson D. 2013. Rescaling of aerial survey data with
733 information from small numbers of telemetry tags to estimate the size of a declining harbour
734 seal population. *Aquatic Conservation-Marine and Freshwater Ecosystems* 23:135–144. DOI: [DOI
735 10.1002/Aqc.2277](https://doi.org/10.1002/Aqc.2277).
- 736 Lopez R, Malardé JP, Royer F, Gaspar P. 2013. Improving Argos Doppler location using multiple-
737 model Kalman filtering. *Geoscience and Remote Sensing, IEEE Transactions on* PP:1–12. DOI:
738 [10.1109/tgrs.2013.2284293](https://doi.org/10.1109/tgrs.2013.2284293).
- 739 McLaren IA. 1958. Some aspects of growth and reproduction of the bearded seal, *Erignathus barbatus*
740 (Erxleben). *Journal of the Fisheries Research Board of Canada* 15:219–227.
- 741 Meier WN, Hovelsrud GK, Oort BEH van, Key JR, Kovacs KM, Michel C, Haas C, Granskog MA,
742 Gerland S, Perovich DK, Makshtas A, Reist JD. 2014. Arctic sea ice in transformation: A review
743 of recent observed changes and impacts on biology and human activity. *Reviews of Geophysics*
744 52:185–217.
- 745 Mesinger F, DiMego G, Kalnay E, Mitchell K, Shafran PC, Ebisuzaki W, Jović D, Woollen J, Rogers
746 E, Berbery EH, Ek MB, Fan Y, Grumbine R, Higgins W, Li H, Lin Y, Manikin G, Parrish D, Shi
747 W. 2006. North American Regional Reanalysis. *Bulletin of the American Meteorological Society*
748 87:343–360. DOI: [10.1175/BAMS-87-3-343](https://doi.org/10.1175/BAMS-87-3-343).
- 749 Niemi M, Nykänen M, Biard V, Kunnasranta M. 2023. Seasonal changes in diel haul-out patterns
750 of a lacustrine ringed seal (*Pusa hispida saimensis*). *Ecology and Evolution* 13:e10264. DOI:
751 [10.1002/ece3.10264](https://doi.org/10.1002/ece3.10264).
- 752 Olnes J, Crawford J, Citta JJ, Druckenmiller ML, Von Duyke AL, Quakenbush L. 2020. Movement,
753 diving, and haul-out behaviors of juvenile bearded seals in the Bering, Chukchi and Beaufort
754 seas, 2014–2018. *Polar Biology*. DOI: [10.1007/s00300-020-02710-6](https://doi.org/10.1007/s00300-020-02710-6).
- 755 Overland JE. 2021. Rare events in the Arctic. *Climatic Change* 168:1–13.
- 756 Perpiñán O. 2012. *solaR: Solar Radiation and Photovoltaic Systems with R*. *Journal of Statistical
757 Software* 50:1–32.
- 758 Perry EA, Stenson GB, Buren AD. 2017. Attendance and nursing patterns of harp seals in the harsh
759 environment of the northwest Atlantic. *Polar Biology* 40:151–160. DOI: [10.1007/s00300-016-1938-6](https://doi.org/10.1007/s00300-016-1938-6).
- 760 R Core Team. 2021. *R: A language and environment for statistical computing*. Vienna, Austria.
- 761 Reder S, Lydersen C, Arnold W, Kovacs KM. 2003. Haulout behaviour of High Arctic harbour seals
762 (*Phoca vitulina vitulina*) in Svalbard, Norway. *Polar Biology* 27:6–16.
- 763 Southwell CJ, Paxton CGM, Borchers DL, Boveng PL, Nordøy ES, Blix AS, De La Mare WK. 2008.
764 Estimating population status under conditions of uncertainty: the Ross seal in East Antarctica.
765 *Antarctic Science* 20:123–133.
- 766 Temte JL. 1994. Photoperiod control of birth timing in the harbour seal (*Phoca vitulina*). *J. Zool.*
767 233:369–384.
- 768
- 769

- 770 Ten Eyck P, Cavanaugh JE. 2018. An Alternate Approach to Pseudo-Likelihood Model Selection in
771 the Generalized Linear Mixed Modeling Framework. *Sankhya B* 80:98–122. DOI: [10.1007/s13571-017-0130-5](https://doi.org/10.1007/s13571-017-0130-5).
- 773 Thometz NM, Hermann-Sorensen H, Russell B, Rosen DAS, Reichmuth C. 2021. Molting strategies
774 of Arctic seals drive annual patterns in metabolism. *Conservation Physiology* 9:coaa112. DOI:
775 [10.1093/conphys/coaa112](https://doi.org/10.1093/conphys/coaa112).
- 776 Thompson P, Rothery P. 1987. Age and sex differences in the timing of moult in the common seal,
777 *Phoca vitulina*. *Journal of Zoology* 212:597–603.
- 778 Udevitz MS, Jay CV, Fischback AS, Garlich-Miller JL. 2009. Modeling haul-out behavior of walruses
779 in Bering Sea ice. *Can. J. Zool* 87:1111–1128. DOI: [10.1139/Z09-098](https://doi.org/10.1139/Z09-098).
- 780 Ver Hoef JM, Cameron MF, Boveng PL, London JM, Moreland EE. 2014. A spatial hierarchical
781 model for abundance of three ice-associated seal species in the eastern Bering Sea. *Statistical
782 Methodology* 17:46–66. DOI: <http://dx.doi.org/10.1016/j.stamet.2013.03.001>.
- 783 Ver Hoef JM, London JM, Boveng PL. 2010. Fast computing of some generalized linear mixed pseudo-
784 models with temporal autocorrelation. *Computational Statistics* 25:39–55. DOI: [10.1007/s00180-009-0160-1](https://doi.org/10.1007/s00180-009-0160-1).
- 786 Von Duyke AL, Douglas DC, Herreman JK, Crawford JA. 2020. Ringed seal (*Pusa hispida*) seasonal
787 movements, diving, and haul-out behavior in the Beaufort, Chukchi, and Bering Seas (2011–2017).
788 *Ecology and Evolution* 10:5595–5616. DOI: [10.1002/ece3.6302](https://doi.org/10.1002/ece3.6302).
- 789 Wang M, Yang Q, Overland JE, Stabeno P. 2018. Sea-ice cover timing in the Pacific Arctic: The present
790 and projections to mid-century by selected CMIP5 models. *Deep Sea Research Part II: Topical
791 Studies in Oceanography* 152:22–34. DOI: <https://doi.org/10.1016/j.dsr2.2017.11.017>.

793 **SUPPLEMENTAL MATERIAL**

794 **0.1 Additional Bio-logger Deployment Details**

Table S1. The timing, location, and institutions responsible for the bio-logger deployments used in this study along with research permits and any associated publications.

Institution	Year Deployed	Location	Publication(s)	Permits	No. Seals	Sex	Age Class
Bearded seal							
ADFG	2005	Kotzebue Sound	Cameron et al 2018	358-1585	6	M, F	subadult
ADFG	2006	Kotzebue Sound	Cameron et al 2018	358-1585	2	F, M	subadult
ADFG	2009	Kotzebue Sound	Breed et al 2018	358-1787	4	F, M	subadult
ADFG	2014	Norton Sound, Koyuk River	Olnes et al 2020	15324	2	M	subadult
ADFG	2014	Norton Sound, Nome	Olnes et al 2020	15324	1	M	subadult
ADFG	2015	Norton Sound, St. Michael	Olnes et al 2020	15324	1	M	subadult
ADFG	2016	Elson Lagoon, Utqiagvik	Olnes et al 2020	15324	1	F	subadult
ADFG	2016	Norton Sound, Koyuk River	Olnes et al 2020	15324	2	F, M	subadult
ADFG	2016	Norton Sound, Nome	Olnes et al 2020	15324	1	M	subadult
ADFG	2016	Norton Sound, St. Michael	Olnes et al 2020	15324	2	M, F	subadult
ADFG	2017	Colville River, Nuiqsut	Olnes et al 2020	15324	1	F	subadult

Institution	Year Deployed	Location	Publication(s)	Permits	No. Seals	Sex	Age Class
ADFG	2017	Norton Sound, Koyuk River	Olnes et al 2020	15324	1	F	subadult
ADFG	2017	Norton Sound, Nome	Olnes et al 2020	15324	1	F	subadult
ADFG	2019	Dease Inlet, Utqiagvik	Olnes et al 2021	20466	1	M	adult
NMFS	2005	Kotzebue Sound		358-1585	1	F	subadult
NMFS	2009	Kotzebue Sound	McClintock et al 2017	782-1765	2	M	subadult, adult
NMFS	2011	Kotzebue Sound	McClintock et al 2017	15126	3	F, M	subadult
NMFS	2012	Kotzebue Sound	McClintock et al 2017	15126	1	F	adult
NSB	2012	Elson Lagoon, Utqiagvik		15324	1	M	subadult
NSB	2019	Pittalugruaq Lake		20466	1	F	subadult
Ribbon seal							
NMFS	2005	Ozemoy Gulf, Russia		782-1765	9	F, M	young of year, adult, subadult
NMFS	2006	Bering Sea		782-1765	7	M, F	adult, young of year
NMFS	2007	Bering Sea		782-1765	28	M, F	subadult, adult, young of year
NMFS	2008	Bering Sea		782-1765	1	M	subadult
NMFS	2009	Bering Sea		782-1765	28	F, M	adult, subadult, young of year

Institution	Year Deployed	Location	Publication(s)	Permits	No. Seals	Sex	Age Class
NMFS	2010	Bering Sea		358-1787, 15126	17	M, F	young of year, adult, subadult
NMFS	2014	Bering Sea		15126	13	M, F	subadult, adult, young of year
NMFS	2016	Bering Sea		19309	7	M, F	subadult, adult
Spotted seal							
ADFG	2005	Kotzebue Sound	Von Duyke et al in prep	358-1585	3	F, M	subadult, adult
ADFG	2016	Dease Inlet, Utqiagvik	Von Duyke et al in prep	15324	4	M, F	adult
ADFG	2017	Colville River, Nuiqsut	Von Duyke et al in prep	15324	1	F	subadult
ADFG	2017	Scammon Bay	Von Duyke et al in prep	15324	3	F, M	subadult, adult
ADFG	2018	Dease Inlet, Utqiagvik	Von Duyke et al in prep	20466	1	F	subadult
ADFG	2018	Scammon Bay	Von Duyke et al in prep	20466	1	M	subadult
ADFG	2019	Dease Inlet, Utqiagvik	Von Duyke et al in prep	20466	6	M	adult, subadult
NMFS	2006	Bering Sea		782-1676	5	M, F	young of year, subadult
NMFS	2007	Bering Sea		782-1676	12	F, M	adult, young of year, subadult
NMFS	2009	Bering Sea		358-1787	23	F, M	adult, subadult, young of year

Institution	Year Deployed	Location	Publication(s)	Permits	No. Seals	Sex	Age Class
NMFS	2010	Bering Sea		358-1787, 15126	8	F, M	young of year, adult, subadult
NMFS	2014	Bering Sea		15126	5	M, F	young of year, adult
NMFS	2016	Bering Sea		19309	6	M, F	adult
NMFS	2018	Bering Sea		19309	5	F	adult
NPWC	2009	Kamchatka Peninsula		NA	3	F	adult
NSB	2012	Tiny Island	Von Duyke et al in prep	15324	1	F	adult
NSB	2014	Oarlock Island	Von Duyke et al in prep	15324	6	M, F	subadult, adult
NSB	2014	Seal Island	Von Duyke et al in prep	15324	1	M	subadult
NSB	2015	Oarlock Island	Von Duyke et al in prep	15324	6	M, F	subadult, adult
NSB	2016	Pittalugruaq Lake	Von Duyke et al in prep	15324	3	F	subadult
NSB	2017	Pittalugruaq Lake	Von Duyke et al in prep	15324	1	M	subadult

ADFG=Alaska Department of Fish and Game; **NSB**=North Slope Borough; **NMFS**=NOAA National Marine Fisheries Service; **NPWC**=North Pacific Wildlife Consortium

⁷⁹⁵ **0.2 Supplemental Figures Showing Confidence Intervals Associated with Predictions**

⁷⁹⁶ The following series of figures (**S1**, **S2**, and **S3**) show the seasonal variability in predicted haul-out
⁷⁹⁷ probability and the associated 95% confidence intervals for bearded, ribbon, and spotted seals. The
⁷⁹⁸ predictions shown are based on the same data used in **5**, **7**, and **9** but selected for three local solar
⁷⁹⁹ hours (07:00, 12:00, and 17:00) so the confidence intervals can also be shown and comparisons can
800 be made.

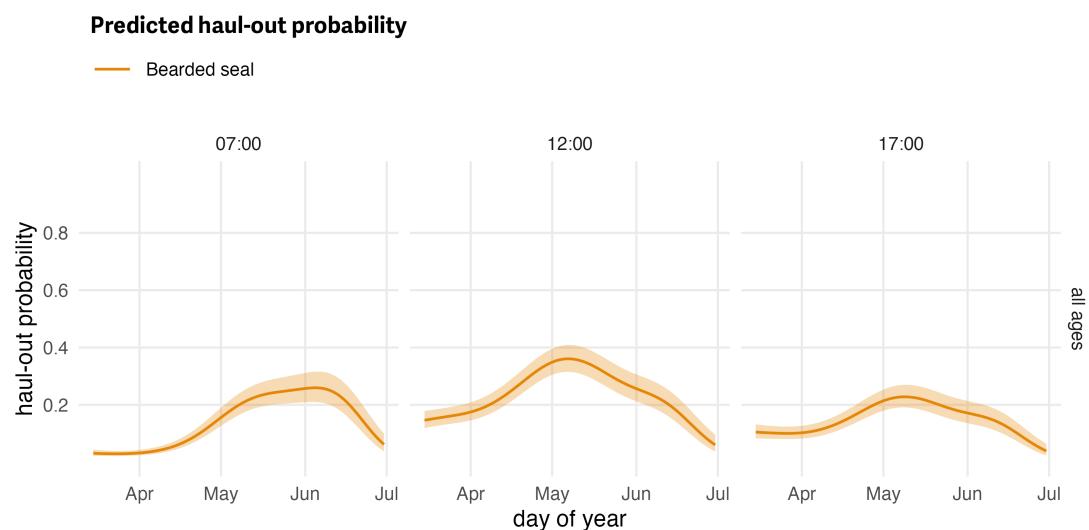


Figure S1. Seasonal variability in haul-out probability and the associated 95% confidence intervals (shaded area) for bearded seals.

Model predictions are shown for three local solar hours (07:00, 12:00, and 17:00). Weather covariate values in the prediction were based on a simple generalized additive model for each weather covariate with smooth terms for day-of-year and solar hour to account for anticipated variability within a day over the season. Age and sex classes are combined into a single 'all ages' category.

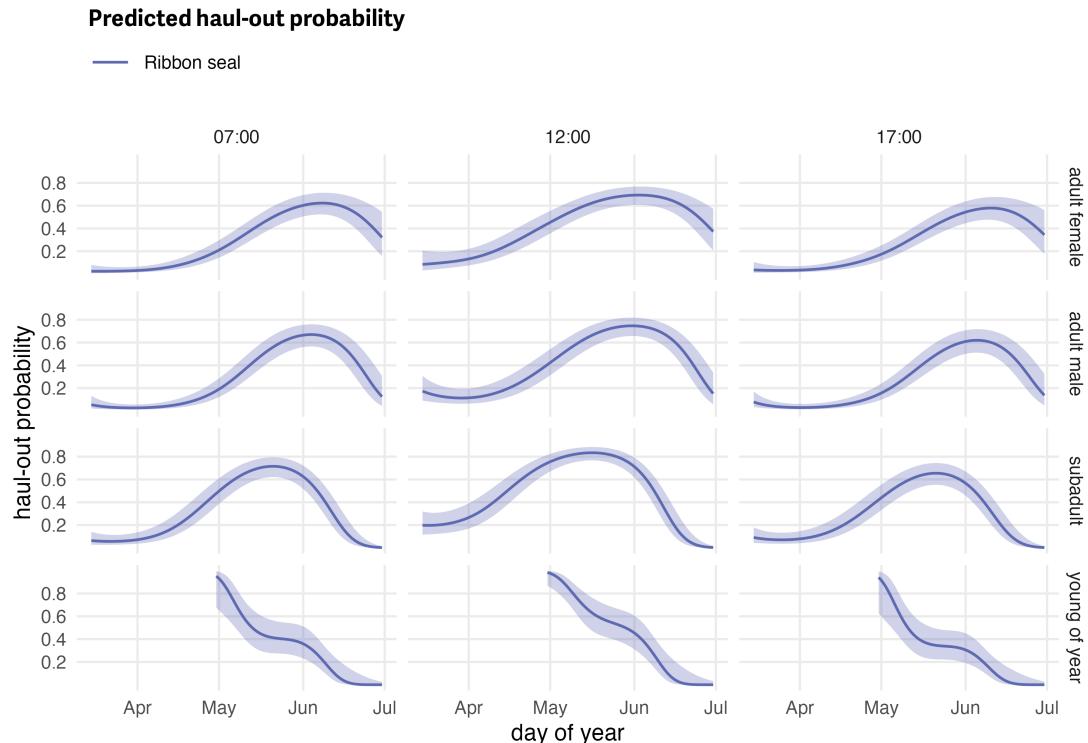


Figure S2. Seasonal variability in haul-out probability and the associated 95% confidence intervals (shaded area) for ribbon seals.

Model predictions are shown for three local solar hours (07:00, 12:00, and 17:00). Weather covariate values in the prediction were based on a simple generalized additive model for each weather covariate with smooth terms for day-of-year and solar hour to account for anticipated variability within a day over the season. Age and sex classes are separated to allow comparisons.

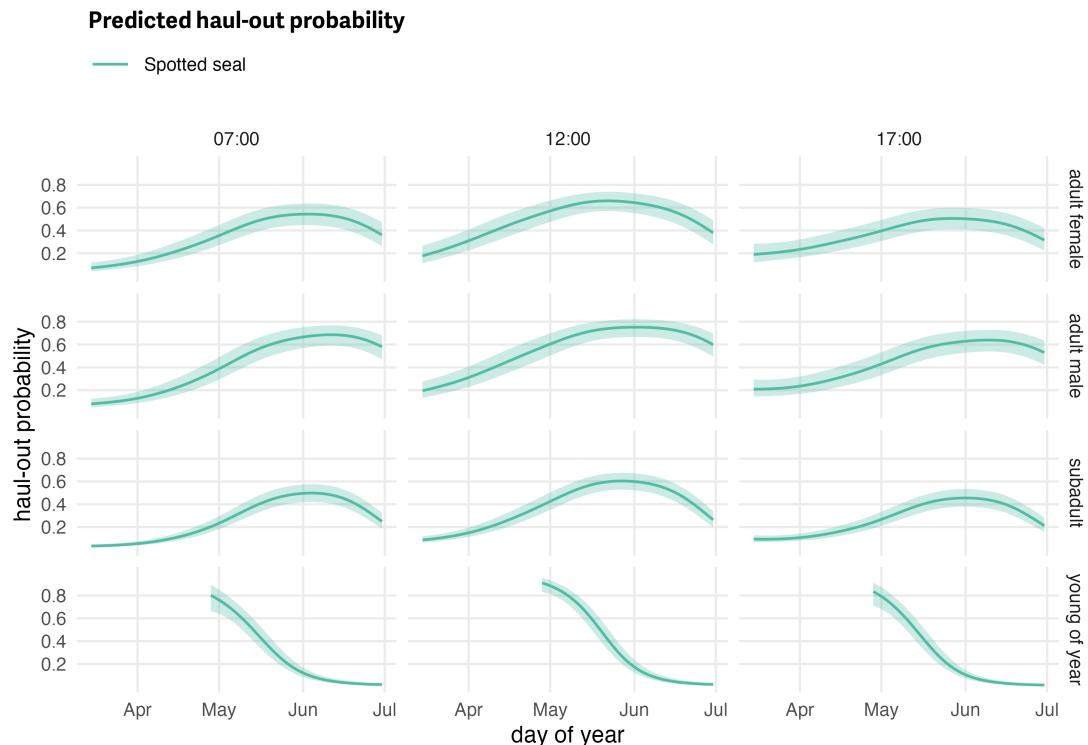


Figure S3. Seasonal variability in haul-out probability and the associated 95% confidence intervals (shaded area) for spotted seals.

Model predictions are shown for three local solar hours (07:00, 12:00, and 17:00). Weather covariate values in the prediction were based on a simple generalized additive model for each weather covariate with smooth terms for day-of-year and solar hour to account for anticipated variability within a day over the season. Age and sex classes are separated to allow comparisons.

801 **0.3 Exploring Insolation (Solar Radiation) as a Model Covariate**

802 **0.3.1 Introduction**

803 During the peer review process for this manuscript, Anthony Fischbach suggested the possibility of
804 using predicted insolation (or solar radiation) values from the reanalysis model as a more direct and,
805 potentially, more informative predictor of the daily haul-out cycle in seals compared to time of day.
806 The notion being that seals are, likely, directly responding to changes in solar radiation throughout
807 the day and not what time of day it is (i.e. seals don't have human watches). Additionally, given the
808 energetic benefits of increased solar radiation it could be more informative as we would expect seals
809 might have a higher haul-out probability on sunnier days and for there to be geographic variability
810 in haul-out behavior associated with geographical differences in insolation. This approach has an
811 additional benefit of being more parsimonious compared to our use of the Fourier series or other
812 approaches to represent hour-of-day in the model (e.g. 24 factors for each hour).

813 Because of these reasons, we considered and explored this possibility for our model and the
814 analysis presented in this manuscript. A key drawback to reliance on solar radiation, in our minds, is
815 that we would lose insight regarding potential diel patterns – solar radiation does not differentiate
816 between dusk or dawn. Bi-modal patterns have been previously observed in ringed seals and our
817 results in this analysis show some indication of increased haul-out probability during dawn compared
818 to dusk periods for bearded seals and some age and sex classes for ribbon and spotted seals. For other
819 phocid species, increased haul-out probability before solar noon or after solar noon has been observed.
820 Importantly, understanding these relationships between haul-out probability and hour-of-day can
821 have important ramifications on aerial survey study design – a key focus of this paper.
822 Another hesitation we had was that solar radiation estimates from reanalysis models have not been
823 previously used as a model covariate within a published study of pinniped haul-out behavior. Thus,
824 for this analysis, we chose to keep our original approach and rely on the Fourier series to capture any
825 hour-of-day effects.

826 That said, we think the idea of solar radiation as a model covariate in pinniped haul-out models
827 is intriguing and worth further exploration. The current availability and increased accessibility to
828 detailed climate reanalysis products that include solar radiation is exciting and we encourage future,
829 more detailed exploration of this as a component in pinniped haul-out analysis. To provide some
830 inspiration, we present some initial efforts and examples for comparison.

831 **0.3.2 Methods**

832 In this manuscript, we rely on the NARR reanalysis model as the source for our weather covariates.
833 However, since our initiation of this analysis, the ERA5 reanalysis model (<https://doi.org/10.24381/cds.adbb2d47>) has become one of the go-to standards for global climate reanalysis and
835 provides an increased temporal resolution to hourly (compared to the 3-hour resolution of NARR).
836 The global coverage of ERA5 provides additional flexibility in that the area of interest is not limited
837 to North America. The ERA5 model provides a number of solar radiation parameters and it was
838 important to evaluate and understand each of these estimates in order to select the one that was
839 likely most relevant to seals. Here, we used the ‘surface short-wave (solar) radiation downwards’
840 parameter. This parameter is described as “*the amount of solar radiation (also known as shortwave
radiation) that reaches a horizontal plane at the surface of the Earth and comprises both direct and
diffuse solar radiation. To a reasonably good approximation, this parameter is the model equivalent of
what would be measured by a pyranometer (an instrument used for measuring solar radiation) at the
surface*” (<https://codes.ecmwf.int/grib/param-db/?id=169>). Thus, this is the value

845 which most closely represents the amount of solar radiation likely felt by a seal hauled out of the
 846 water.

847 ERA5 data is available via the Copernicus climate data store API which can be queried with the
 848 CDS-API Python package (<https://cds.climate.copernicus.eu/api-how-to>). The R
 849 code provided here documents the download of the *surface_solar_radiation_downwards* parameter
 850 for our study area of interest and years of interest. The *reticulate* R package (<https://CRAN.R-project.org/package=reticulate>) allowed interaction with Python. Additionally, note,
 851 extra steps are required to download data on either side of the 180 anti-meridian.

```

library(tidyverse)
library(reticulate)
library(sf)
library(terra)

#import python CDS-API
cdsapiclient <- import('cdsapiclient')
#for this step there must exist the file .cdsapirc
server = cdsapiclient$Client() #start the connection

get_era5 <- function(y) {
  #we create the query
  query <- r_to_py(
    list(
      variable = "surface_solar_radiation_downwards",
      product_type = "reanalysis",
      area = "75/152/47/180", # North, West, South, East
      year = y,
      month = str_pad(2:7, 2, "left", "0"),
      day = str_pad(1:31, 2, "left", "0"),
      time = str_c(0:23, "00", sep = ":") %>% str_pad(5, "left", "0"),
      format = "netcdf"
    )
  )
  #query to get the ncdf
  server$retrieve("reanalysis-era5-single-levels",
                  query,
                  paste0("era5_ssrd_", y, "_left.nc"))

  query <- r_to_py(
    list(
      variable = "surface_solar_radiation_downwards",
      product_type = "reanalysis",
      area = "75/-180/47/-142", # North, West, South, East
      year = y,
      month = str_pad(2:7, 2, "left", "0"),
      day = str_pad(1:31, 2, "left", "0"),
      time = str_c(0:23, "00", sep = ":") %>% str_pad(5, "left", "0"),
      format = "netcdf"
    )
  )
}
```

```

    day = str_pad(1:31, 2, "left", "0"),
    time = str_c(0:23, "00", sep = ":") %>% str_pad(5, "left", "0"),
    format = "netcdf"
)
)
#query to get the ncdf
server$retrieve("reanalysis-era5-single-levels",
                 query,
                 paste0("era5_ssrd_", y, "_right.nc"))

}

years <- as.character(2005:2021)
for(i in 1:length(years)) {
  get_era5(years[i])
}

```

853 To explore performance of our solar radiation parameter within a haul-out model we replaced
 854 the various Fourier series parameters in our model from the manuscript with the ERA5 *surface*
 855 *solar radiation downwards* (era_ssrd_watts) parameter. As with other reanalysis values (from
 856 NARR) in the manuscript, the era-ssrd-watts values are matched in time and space to the seal
 857 haul-out observation data; we use the full hourly temporal resolution from ERA5. The glmmLDS
 858 framework used in the paper does not allow for model comparisons with AIC because of the reliance
 859 on pseudo-likelihood. The bam() function within the mgcv package provides a quick model fitting
 860 option that also allowed us to do some model comparison with AIC. This approach was sufficient
 861 for the general demonstration and exploration purposes here but future research should consider a
 862 range of model fitting frameworks and approaches that might be more appropriate.

863 The model specification below was used to specify an mgcv::bam() model that matched the
 864 formula used in the manuscript for ribbon seals. The s(speno, bs = "re") term is the smooth
 865 term for the random effect. All other predictors were the same.

```

m1_ribbon <- mgcv::bam(
  dry ~ age_sex + s(speno, bs = "re") +
  sin1 + cos1 + sin2 + cos2 + sin3 + cos3 +
  poly(day, 3, raw=TRUE) +
  sin1:poly(day, 3, raw=TRUE) +
  cos1:poly(day, 3, raw=TRUE) +
  sin2:poly(day, 3, raw=TRUE) +
  cos2:poly(day, 3, raw=TRUE) +
  sin3:poly(day, 3, raw=TRUE) +
  cos3:poly(day, 3, raw=TRUE) +
  wind*temp2m + pressure + precip +
  age_sex:poly(day, 4, raw=TRUE),
  data = ribbon_model_data,
  family = binomial,

```

```
discrete = TRUE)
```

866 Note, the specification for *m1_ribbon* here does not include any AR1 structure for temporal
867 autocorrelation. To include this, we needed to provide a value for ρ (or *rho*). We examined the
868 autocorrelation within the model and used the lag-1 value for ρ . The value for lag-1 autocorrelation
869 was 0.8082 which is rather high but not surprising. We then updated our model specification with a
870 value for ρ as well as the *A1.start* argument which specifies (as either **TRUE** or **FALSE**) the start
871 point of each block.

```
m2_ribbon <- mgcv::bam(  
  dry ~ age_sex + s(speno, bs = "re") +  
    sin1 + cos1 + sin2 + cos2 + sin3 + cos3 +  
    poly(day, 3, raw=TRUE) +  
    sin1:poly(day, 3, raw=TRUE) +  
    cos1:poly(day, 3, raw=TRUE) +  
    sin2:poly(day, 3, raw=TRUE) +  
    cos2:poly(day, 3, raw=TRUE) +  
    sin3:poly(day, 3, raw=TRUE) +  
    cos3:poly(day, 3, raw=TRUE) +  
    wind*temp2m + pressure + precip +  
    age_sex:poly(day, 3, raw=TRUE),  
  data = ribbon_model_data,  
  family = binomial,  
  AR.start = ar1_start,  
  rho = lag1_ribbon,  
  discrete = TRUE)
```

872 The model specification for exploring the use of solar radiation was specified similarly but without
873 all of the Fourier series parameters and interactions.

```
m2_ssrd_ribbon <- mgcv::bam(  
  dry ~ age_sex + s(speno, bs = "re") +  
    era5_ssrd_watts +  
    poly(day, 3, raw=TRUE) +  
    era5_ssrd_watts:poly(day, 3, raw=TRUE) +  
    wind*temp2m + pressure + precip +  
    age_sex:poly(day, 3, raw=TRUE),  
  data = ribbon_model_data,  
  family = binomial,  
  AR.start = ar1_start,  
  rho = lag1_ribbon,  
  discrete = TRUE)
```

874 The two models were compared with AIC to evaluate whether the reduction in degrees of freedom
875 with fewer terms in the solar radiation model was matched with improved explanatory power in

ERA5 Reanalysis

● downward surface solar radiation

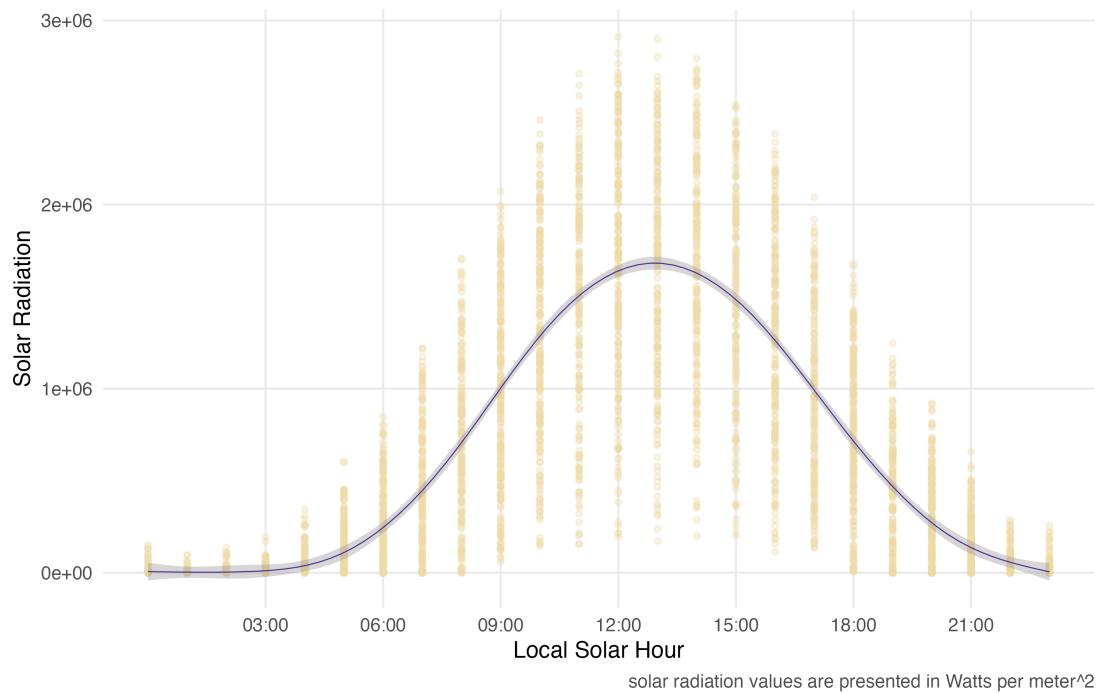


Figure S4. Diel Pattern of Solar Radiation Values from ERA5 Reanalysis.

Downward surface solar radiation estimates from the ERA5 climate reanalysis for 5000 random points within the study area between 2005 and 2021. Solar radiation values are presented in Watts per square-meter and the smoothed line highlights the strong diel pattern.

876 the model fit. While the model and code specified above is for ribbon seals, the same approach was
877 repeated for bearded and spotted seals.

878 A similar approach to that presented in this manuscript for prediction was employed with solar
879 radiation values in lieu of hour of day. For prediction values, quantiles (5% increments) of the
880 observed range of ERA5 solar radiation values were used with 100% representing the maximum
881 observed solar radiation value. This allowed similar data visualizations and easier comparisons to
882 those predictions in the manuscript that include hour of day.

883 **0.3.3 Results**

884 To evaluate whether the solar radiation parameter matched our expectations and compared well
885 with hour of the day, we visualized the variability of the `era5_ssrd` values within our study area as
886 they relate to hour of the day (S4). The unimodal distribution is centered around the middle of the
887 solar day with peak solar radiation coinciding with 13:00 local solar. This suggests solar radiation
888 could be an informative covariate for capturing unimodal diel patterns in haul-out behavior.

889 The bearded seal model matching the specification from the manuscript resulted in 126.13 degrees
890 of freedom and an AIC value of -7428.929. The model with solar radiation resulted in 39.619 degrees
891 of freedom and an AIC value of -6797.378. The ribbon seal model matching the specification from
892 the manuscript resulted in 131.478 degrees of freedom and an AIC value of -16372.29. The model

893 with solar radiation resulted in 115.126 degrees of freedom and an AIC value of -16038.175. The
894 spotted seal model matching the specification from the manuscript resulted in 125.506 degrees of
895 freedom and an AIC value of -23584.373. The model with solar radiation resulted in 109.163 degrees
896 of freedom and an AIC value of -23302.772. Despite the additional terms, the models with the Fourier
897 series representation of hour of day resulted in a lower AIC value and were still preferred models for
898 each of the species.

899 Predictions from the model fits and visualization of those predictions were produced for each
900 species but, here, we only present visualizations from ribbon seals as an example (Figure S5 and
901 Figure S6). Similar seasonal patterns previously observed were still apparent with subadults hauling
902 out earlier in the season followed by adult males and, then, adult females. The observed relationship
903 with hour of day and the centering of peak haul-out probability around solar noon was reflected
904 in these predictions as a one-sided distribution with maximum solar radiation having the highest
905 haul-out probability and minimal solar radiation the least. The seasonal distribution of haul-out
906 probability along with 95% confidence intervals also provided comparable insights (see figures S2
907 and S6). That said, subtle differences in the shape and extent of confidence limits were present.

908 0.3.4 Discussion

909 Solar radiation has potential as an informative covariate in pinniped haul-out models that can be
910 directly linked to seal physiology and expected behavioral changes. The ERA5's *surface solar radiation*
911 *downwards* values aligned with hour of day and maximum values occurred at or just after local solar
912 noon. This highlighted the informative potential for this approach. However, despite an overall
913 reduction in the total number of parameters and degrees of freedom, AIC comparison still favored
914 the models for each species that included hour of day as a Fourier series.

915 This analysis was not intended to be a full comparison – we simply want to demonstrate the
916 potential and inspire further investigation – but, there are three possibilities that might explain the
917 preference for hour of day. First, there are a broad range of solar radiation values represented for
918 each hour of the day. Cloud cover, fog, and precipitation all reduce downward solar radiation at
919 the surface and we might expect this to impact haul-out probability. However, the photoperiod
920 and the timing of sunrise and sunset are not impacted by weather and seals may be responding to
921 these signals more than the amount of solar radiation. Additionally, this study spans a range of
922 physiological cycles and energetic needs and higher solar radiation may not be a consistent driving
923 influence on seals. Increased energy from the sun may be important during molt but less so during
924 pupping and breeding periods. Second, the timing and duration of haul-out behavior may also be
925 influenced by diel patterns in weather (e.g. lower winds in the morning) or ecosystem dynamics
926 (e.g. prey availability) that lead to a skewness in the distribution of haul-out behavior that wouldn't
927 be reliably captured by solar radiation values. Third, this effort is only an initial effort to explore
928 the use of solar radiation in pinniped haul-out models. A more in depth and rigorous exploration
929 of this topic might discover an approach that results in a more parsimonious and preferred model
930 formulation.

931 Again, we want to acknowledge Anthony Fischbach for the suggestion during the peer review
932 process. We think this is an excellent example of the peer review process working to improve the
933 quality of our manuscript and advance the scientific process. We hope others will take our example
934 and expand on it within future analyses.

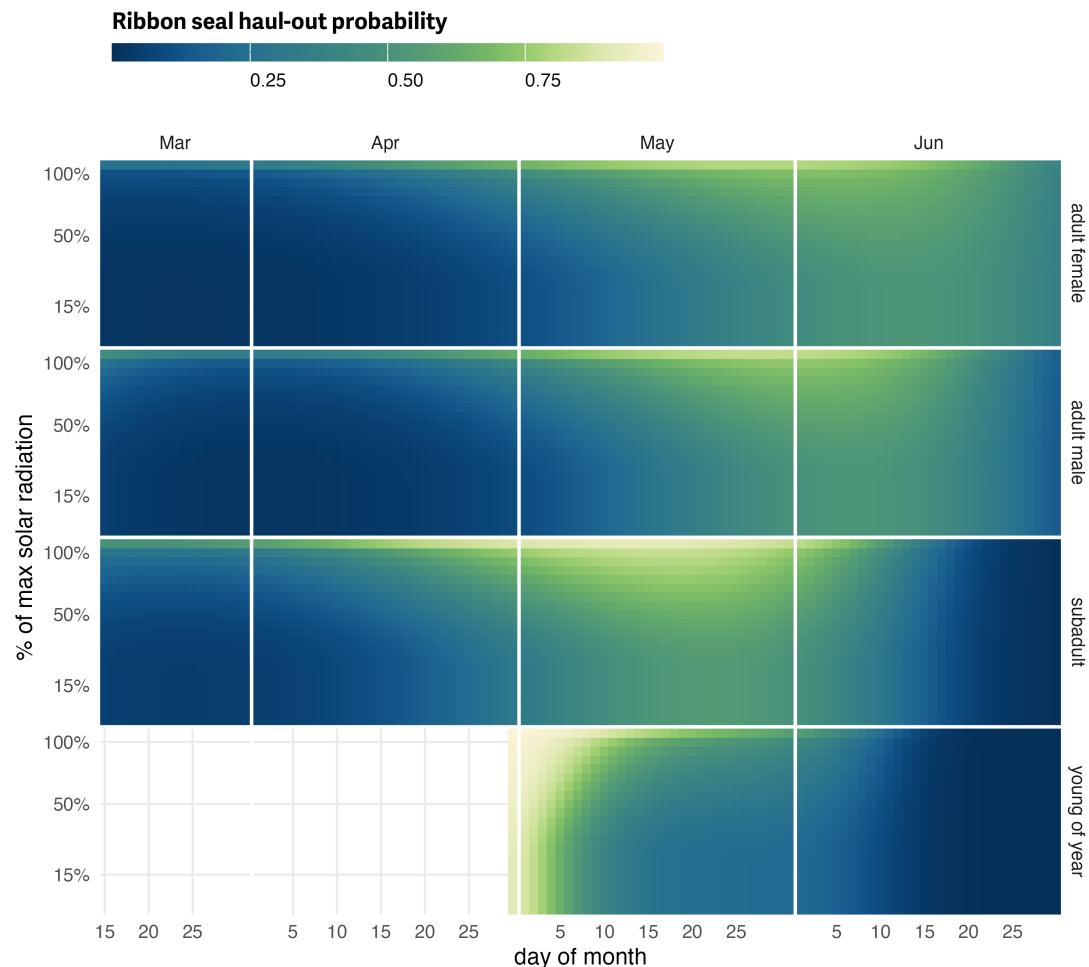


Figure S5. Solar radiation as a predictor of ribbon seal haul-out probability.

Predicted haul-out probability of ribbon seals from 15 March to 30 June for each age and sex class used in the model. In this model, solar radiation was used in lieu of hour of day. The apparent seasonal progression with subadults hauling out earlier in the season followed by adult males and, then, adult females is still notable although maybe not as clear. Predictions for young of the year still show their transition from newly weaned pups resting on the ice to more in-water activities. The overall pattern is in agreement with a one-sided view of Figure 7 where maximum solar radiation is equivalent to local solar noon.

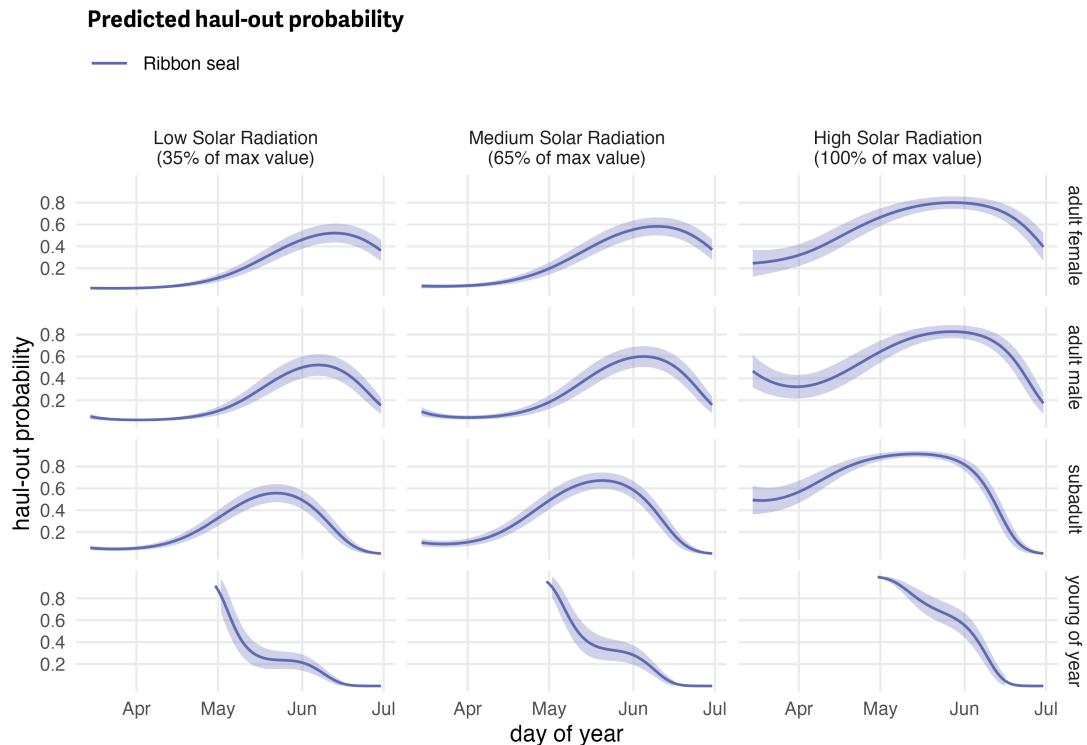


Figure S6. Solar radiation as a predictor of ribbon seal haul-out probability (with uncertainty).

Seasonal variability in haul-out probability and the associated 95% confidence intervals (shaded area) for ribbon seals. In this model predictions are shown for low, medium, and high values of solar radiation (as percentages of the maximum value observed) in lieu of local solar hour. There's general agreement in the overall seasonal patterns between the two approaches but subtle differences in shape and extent of the confidence limits were present (see Figure S2 for comparisons).