

¹ Spring haul-out behavior of seals in the Bering and Chukchi seas

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¹⁴ ABSTRACT

¹⁵ Ice-associated seals rely on sea ice for a variety of activities, including pupping, breeding, molting, and resting. In
¹⁶ the Arctic, many of these activities occur in spring (April – June) as sea ice begins to melt and retreat northward.
¹⁷ Rapid acceleration of climate change in Arctic ecosystems is therefore of concern as the quantity and quality
¹⁸ of suitable habitat is forecast to decrease. Improved estimates of seal population abundance are needed to
¹⁹ properly monitor the impacts of these changes over time. In this paper, we use hourly percent-dry data from
²⁰ satellite-linked bio-loggers deployed between 2005 and 2021 to quantify the proportion of seals hauled out on
²¹ ice. This information is needed to accurately estimate abundance from aerial survey counts of ice-associated
²² seals (i.e., to correct for the proportion of animals that are in the water while surveys are conducted). In addition
²³ to providing essential data for survey ‘availability’ calculations, our analysis also provides insights into the
²⁴ seasonal timing and environmental factors affecting haul-out behavior by ice-associated seals. We specifically
²⁵ focused on bearded (*Erignathus barbatus*), ribbon (*Histriophoca fasciata*), and spotted seals (*Phoca largha*) in the
²⁶ Bering and Chukchi seas. Because ringed seals (*Phoca (pusa) hispida*) can be out of the water but hidden from
²⁷ view in snow lairs analysis of their ‘availability’ to surveys requires special consideration; therefore, they were
²⁸ not included in this analysis. Using generalized linear mixed pseudo-models to properly account for temporal
²⁹ autocorrelation, we fit models with covariates of interest (e.g., day-of-year, solar hour, age-sex class, wind
³⁰ speed, barometric pressure, temperature, precipitation) to examine their ability to explain variation in haul-out
³¹ probability. We found evidence for strong diel and within-season patterns in haul-out behavior, as well as strong
³² weather effects (particularly wind and temperature). In general, seals were more likely to haul out on ice in the
³³ middle of the day and when wind speed was low and temperatures were higher. Haul-out probability increased
³⁴ through March and April, peaking in May and early June before declining again. The timing and frequency of
³⁵ haul-out events also varied based on species and age-sex class. For ribbon and spotted seals, models with year
³⁶ effects were highly supported, indicating that the timing and magnitude of haul-out behavior varied among
³⁷ years. However, we did not find broad evidence that haul-out timing was linked to annual sea ice extent. Our
³⁸ analysis emphasizes the importance of accounting for seasonal and temporal variation in haul-out behavior, as
³⁹ well as associated environmental covariates, when interpreting the number of seals counted in aerial surveys.

40 **INTRODUCTION**

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

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

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

80 The remoteness of the Bering and Chukchi seas means direct scientific observation of seal behavior
81 is impractical. Thus, bio-logging devices are especially useful tools for collecting key information
82 on movement and haul-out behavior for these species. Bio-logging records of time spent out of the
83 water provide valuable data for identifying covariates that explain variation in haul-out behavior. For

84 instance, Von Duyke et al. (2020) used satellite-linked bio-loggers to corroborate seasonal changes
85 between diurnal and nocturnal haul-out behavior of ringed seals previously described by Kelly and
86 Quakenbush (1990) using VHF radio tags and direct observation. Bengtson et al. (2005) documented
87 a higher propensity for ringed seal basking near solar noon, as did Ver Hoef et al. (2014) in an analysis
88 of bearded, ribbon, and spotted seals using much larger sample sizes. Olnes et al. (2020) showed
89 that the proportion of time bearded seals spent hauled out progressively increased through spring
90 and summer, and Ver Hoef et al. (2014) found haul-out probabilities increased gradually starting in
91 March and peaked in May and June for bearded, ribbon, and spotted seals. Such analyses have not
92 been limited to the Arctic. In the Antarctic, Bengtson and Cameron (2004) relied on bio-logging data
93 to demonstrate greater haul-out propensity in juvenile crabeater seals (*Lobodon carcinophaga*) than
94 adults, with highest probabilities in February and at times close to solar noon.

95 Knowledge of haul-out patterns is not only important for understanding natural history and
96 ecology, but also for developing “availability” correction factors for aerial surveys. Specifically,
97 researchers need to know the fraction of seals hauled out (versus in the water) when aerial surveys are
98 conducted. Studies estimating availability correction factors for seals typically use logistic regression-
99 style analyses to estimate the time-specific probability of being hauled out based on ‘wet/dry’ data
100 relayed by bio-loggers. In these models, haul-out probabilities were expressed as a function of
101 predictive covariates, such as time-of-day, day-of-year, sex, age class, and environmental conditions
102 (e.g., Reder et al. (2003), Bengtson & Cameron (2004), Bengtson et al. (2005), Udevitz et al. (2009),
103 Lonergan et al. (2013), Ver Hoef et al. (2014), Southwell et al. (2008), and Niemi et al. (2023)).
104 However, sample sizes have often been insufficient to permit strong inference about demographic
105 and/or seasonal variation in haul-out probabilities. For instance, Bengtson and Cameron’s (2004)
106 study included 5 adult and 2 juvenile crabeater seals, while Bengtson et al.’s (2005) study was based on
107 6 ringed seals in the Chukchi and Beaufort seas. These studies were often further limited by logistical
108 constraints on fieldwork and the attachment duration or operational life of bio-loggers. In this study,
109 we addressed some of these limitations by deploying small bio-loggers designed for longer-term
110 attachment on rear flippers of a subset of the study individuals. These devices are designed to collect
111 data through the molt period (when those adhered to the hair would fall off) and, in some situations,
112 provide multiple years of data.

113 In this study, we used 16 years of bio-logging data to investigate the haul-out behavior of bearded,
114 ribbon, and spotted seals in the Bering and Chukchi seas. Our goals were threefold. First, we wished
115 to establish baseline estimates for the chronology of haul-out behavior in the critical spring season
116 for each species across different age and sex classes. Second, we sought to refine estimates of haul-out
117 availability corrections for aerial surveys in order to improve estimates of seal abundance. Previously
118 estimated availability correction factors (e.g., Bengtson et al. (2005), Conn et al. (2014), and Ver
119 Hoef et al. (2014)) accounted for variables such as the time-of-day and day-of-year, but did not
120 investigate the impact of weather variables. Such variables have been shown to influence walrus
121 haul-out behavior (Udevitz et al., 2009) and we expect weather conditions to also influence seal
122 haul-out behavior and including them within the model framework will benefit our estimates of seal
123 availability during aerial surveys. Third, we aimed to assess the annual variability in haul-out timing
124 and possible linkage to changes in the extent of seasonal sea ice between 2005 and 2020. Our work
125 extends the scope of previous haul-out analyses, includes the influence of weather variability, and
126 investigates the potential impact of changing sea-ice extent on the behavior of these species.

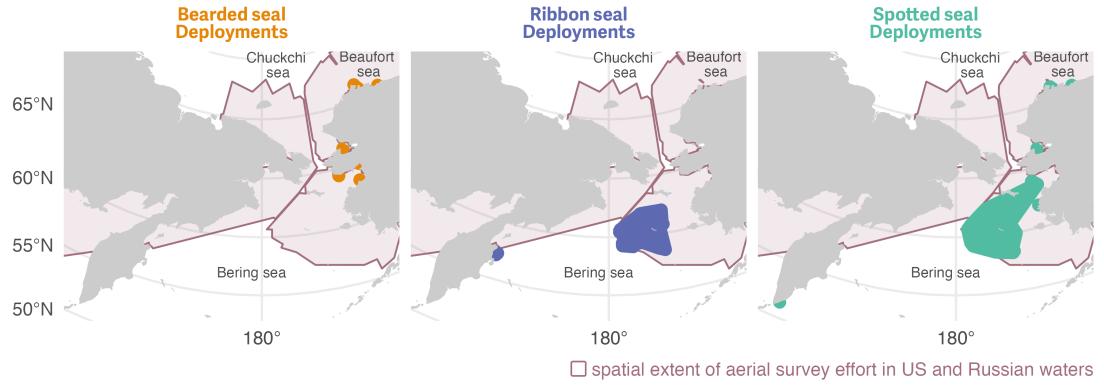


Figure 1. Initial bio-logger deployment areas for bearded, ribbon, and spotted seals in the study between 2005 and 2020 across multiple regions within the Bering, Chukchi, and western Beaufort seas.

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.

127 METHODS

128 Data collection

129 For this study we used haul-out behavior data and location estimates from bio-loggers deployed on
 130 bearded, ribbon, and spotted seals in the Bering, Chukchi, and western Beaufort seas by multiple
 131 organizations as part of collaborative investigations from 2005 through 2021. Seals were captured
 132 using nets and bio-loggers were attached during studies based in coastal communities or on research
 133 ships. Ship-based capture events occurred during spring near the southern ice edge in the Bering
 134 Sea between 2005 and 2018. Land-based capture events occurred between 2005 and 2020 from May
 135 to October, generally between the Alaska coastal communities of Scammon Bay in the Bering Sea,
 136 Utqiagvik in the Chukchi Sea, and Nuiqsut in the Beaufort Sea (Supplemental Material, S1). Data
 137 from additional deployments along the Kamchatka peninsula in the western Bering Sea are also
 138 included. We refer readers to Figure 1 and the primary literature for detailed capture and bio-logger
 139 attachment methods (see also Supplemental Material, S1).

140 We created a subset of haul-out behavior data from 250 bio-loggers deployed on 35 bearded, 110
 141 ribbon, and 105 spotted seals to include only records from 1 March to 15 July between 2005 and
 142 2021. Bio-loggers were of the ‘SPLASH’ or ‘SPOT’ family of tags developed by Wildlife Computers
 143 (Redmond, Washington, USA). Deployments consisted of either a single ‘SPLASH’ device, a single
 144 ‘SPOT’ device, or both types. Devices were either adhered to the hair on the seal or attached through
 145 the rear flipper inter-digital webbing. The use of bio-loggers adhered to the back or head provides
 146 some benefits over flipper mounted devices (e.g. increased satellite transmittal rates, locations at
 147 sea) but these fall off during the following annual molt, which, depending on deployment date,
 148 limits the duration of haul-out data they provide especially during the focus months of our study.

149 Additionally, bio-loggers attached to the head or dorsal region are often dry while the seal is floating at
150 the surface, inducing a slight positive bias in the hourly percent-dry values reported by the bio-logger.
151 For this study, in cases where both bio-logger types were deployed, we preferred hourly percent-dry
152 observations from the flipper tag. All data were transmitted by the deployed instruments via the
153 Argos satellite network and location data were either derived from Argos transmissions or transmitted
154 FastLoc GPS data.

155 Sex and age class (non-dependent *young-of-the-year*, sexually immature *subadults*, and mature
156 *adults*) were estimated at the time of deployment by various combinations of length, claw growth
157 ridges (McLaren, 1958), and pelage characteristics. Seals determined to be less than one year were
158 classified as young-of-the-year. For those bio-loggers deployed on young-of-the-year and transmitting
159 into the next year, the age class was advanced to subadult on 1 March of the following year – the
160 assumed anniversary of their birth. Subadults are those seals likely greater than one year of age but
161 less than four years. Adults are individuals that are likely older than four years. Table 1 provides a
162 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 (21,588 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)

163 Haul-out behavior data were recorded in a manner standard across Wildlife Computers bio-
164 loggers and transmitted via the Argos satellite network as hourly percent-dry timelines. For each
165 hour of a day, the wet/dry sensor was polled by the tag firmware every few seconds and the percent
166 of the hour in the dry state was calculated (Figure 2). On board the bio-logger, hourly percent-dry
167 calculations were rounded to the nearest 10% inclusive of 0% and 100% along with additional values
168 at 3% and 98%. This compression resulted in additional data transmission as each message consisted
169 of two complete 24-hour records. Memory capacity allowed caching of percent-dry records for several
170 weeks or months and each message was transmitted several times to ensure reception at the satellite.
171 Bio-loggers were deployed and programmed in a manner to maximize data transmission during the
172 spring pupping and molting period, though hourly percent-dry data were not always successfully
173 transmitted. This is due to a variety of factors including satellite coverage, tag availability (e.g., tags

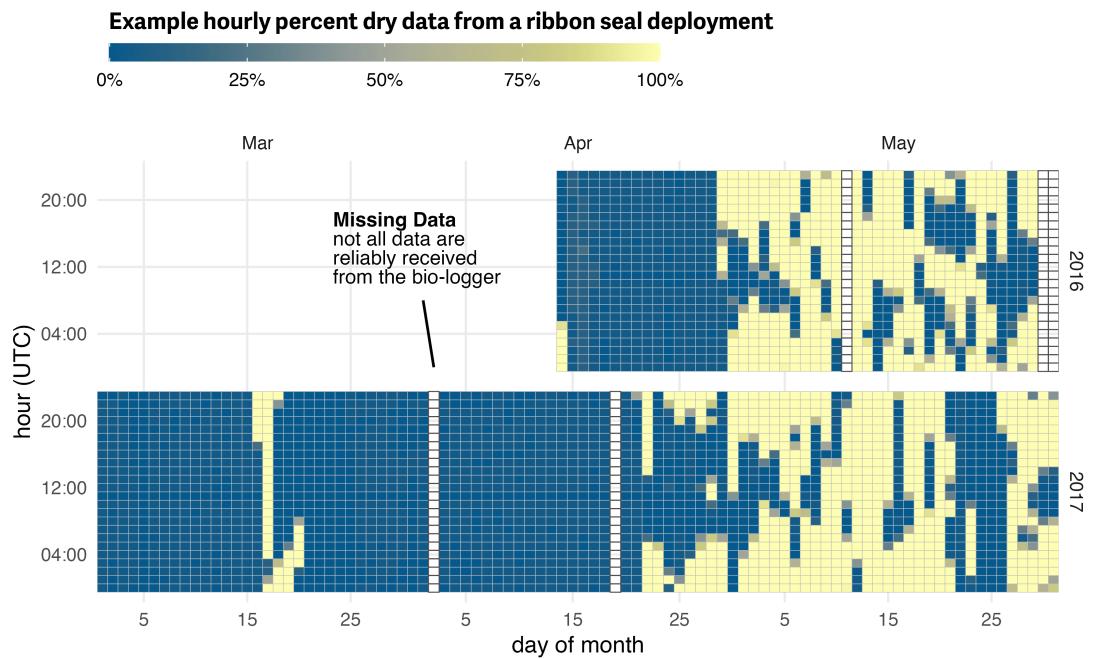


Figure 2. Example percent-dry actogram from bio-logger data

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.

174 mounted to the rear flipper often do not transmit while at sea), tag performance, duty cycling, and
 175 atmospheric interference. Fortunately, missing records do not substantially bias inference about
 176 haul-out probabilities (Conn et al., 2012).

177 Tags that fell off due to molt, attachment failure, or seal mortality and remained on ice or land
 178 may have continued to send data to satellites; i.e., a detached bio-logger that is dry (either on ice
 179 or land) will record and transmit data suggesting the seal is hauled out. Therefore, end times of
 180 each deployment were identified by examining bio-logger locations, percent-dry records, and dive
 181 behavior (if available) to determine when bio-loggers ceased providing data consistent with seal
 182 behavior. For example, a data record that ended with several consecutive days (~10+ days) of 100%
 183 dry observations and with locations indicating the tag was on land were truncated to the final stretch
 184 of 100% dry observations. The vast majority of deployments ended with the device detaching in
 185 the water and the deployment end date was obvious. There is no perfect algorithm for identifying
 186 deployment end dates and each deployment in question was considered separately. While not perfect,
 187 we are confident our reliance on expert opinion and examination of multiple data streams provided
 188 the best option. Data outside of the deployment start and end times were discarded prior to analysis.

189 Of key interest in this study was the relationship between haul-out behavior and weather covariates
 190 that vary with time and seal location. The use of modern bio-loggers that record and transmit
 191 behavioral data while simultaneously providing location estimates was key to this objective. We

192 explored the use of a continuous-time correlated random walk (Johnson et al., 2008) movement
193 model to predict locations at specific times. However, the sparse nature of data from some bio-loggers,
194 especially those mounted to the rear flipper, resulted in poor modeling performance or convergence
195 issues. For this study, we calculated a weighted average daily location where the inverse of the
196 estimated Argos or FastLoc GPS location error was used for the weight. Each Argos location estimate
197 was assigned an error radius based on either the categorical location quality ($3 = 250$ m, $2 = 500$ m,
198 $1 = 1500$ m, $0 = 2500$ m (Lopez et al., 2013); we chose 2500 m for location classes *A* and *B*) or, when
199 available, the estimated error radius from the Argos Kalman filter algorithm. Location estimates
200 from FastLoc GPS were all assigned an error radius of 50 m. On days when haul-out observations
201 were present but location data were missing we used the seal's last calculated weighted average
202 daily location; days when the location intersected with land were removed from the seal's record.
203 We recognize that bearded and spotted seals haul out on land. However, assessing the relationship
204 between haul-out behavior and weather covariates and seals' availability for aerial surveys on land
205 was outside the scope of this study. Additionally, any daily locations on land were likely more
206 reflective of coordinate averaging and measurement error, rather than actual use of coastal features.

207 Explanatory variables

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

224 For all seal species, we considered the following variables when modeling the hourly haul-out
225 behavior: day-of-year, solar hour, temperature, wind speed, barometric pressure, precipitation, and
226 wind chill (represented by a *wind:temperature* interaction (Udevitz et al., 2009)). Ribbon and spotted
227 seal models included age-sex class and interactions between day-of-year and age-sex class, but we
228 omitted these from bearded seal models due to poor representation of age-sex classes (Table 1).
229 Bearded seal models included a latitudinal effect (and an interaction with day-of-year), because
230 bearded seals occupy a substantial range during the spring and we were interested in possible
231 differences in the timing of haul-out behavior along a latitudinal gradient. We omitted the latitudinal
232 effect from ribbon and spotted seal models because, during the spring, these species are most prevalent
233 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
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	northly 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.

234 Haul-out modeling

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

240 To properly account for temporal dependence and to take advantage of computational efficiency,
 241 we used generalized linear mixed pseudo-models (GLMPMs; (Ver Hoef, London & Boveng, 2010))
 242 to model variation in haul-out behavior as a function of (1) covariate predictors, (2) temporally
 243 autocorrelated random effects, and (3) individual random effects representing heterogeneity in
 244 individual behavior. We used the glmmLDT package (Ver Hoef, London & Boveng, 2010) to
 245 implement GLMPMs. We explored two different model formulations for our data and we fit separate
 246 models to bearded, ribbon, and spotted seal data sets as we expected differing behavior by species.
 247 Separate models for each species were also needed because a single, very large data set proved
 248 computationally intractable. In our first model formulation and for each species, we fitted a year-

249 independent model that predicted average haul-out behavior as a function of demographic, weather,
250 seasonal, and diurnal effects. Second, for ribbon and spotted seals (which had considerably more
251 data than bearded seals), we fitted models that included all the effects from the first model, but
252 also permitted annual variation in haul-out timing. This second set of models was used to examine
253 whether haul-out patterns varied by year and to determine the annual timing of apparent peaks in
254 haul-out behavior. For both models, we assumed an hourly Bernoulli response (a binary 0-1 response
255 dependent upon whether the tag was greater than 50% dry for a given hour) where the linear predictor
256 was modeled on the logit scale. This is consistent with previous approaches (London et al., 2012; Ver
257 Hoef et al., 2014) and only 6.995% of our observations fell between 10% and 90% hourly percent-dry.

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

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

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

267 For the second set of models examining inter-annual variation in sea ice use, we fitted models
268 with year by day-of-year interactions. However, in this case we only included *year:day* and *year:day*²,
269 omitting the main effects of year as well as *year:day*³ interactions because models with the latter
270 effects were numerically unstable. However, the modeled interactions were sufficient to allow shifts
271 in haul-out distribution, as one can show mathematically that a simple horizontal shift in timing
272 of haul-out distributions does not affect the main effects or cubic terms in a polynomial regression
273 model. Bearded seals were not included in this examination of inter-annual variation because of
274 limited data across many years in the study.

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

288 Visualizing the marginal or conditional effect of an individual weather covariate (where all other
289 weather covariates are being held at mean values) on haul-out probability was difficult in this analysis

290 because of the collinearity between covariates as well as the spatial and temporal variation across
291 such a large region. The relationship of each weather covariate with haul-out probability, averaged
292 over the other weather conditions, was more variable than model coefficients would imply. That said,
293 important insights can be gained from plots of marginal effects. To create these plots, we predicted
294 haul-out probability across the full range of each weather covariate while fixing hour of the day at
295 local solar noon and day-of-year at 15 May. For the other weather covariate values, we chose not
296 to use a fixed mean value because we expect weather to vary within day over the season (e.g. the
297 temperature at solar noon will gradually increase from March through June). To account for this, we
298 fit a simple generalized additive model for each weather covariate with smooth terms for day-of-year
299 and solar hour. We used predicted values from the generalized additive model in lieu of holding
300 other weather covariates at a fixed mean value which would not capture seasonal change. The
301 visualizations also include vertical lines representing 95% confidence intervals around the predicted
302 haul-out probability to better communicate the variation in model uncertainty.

303 We also assessed whether the annual variation in maximum spring sea ice extent in the Bering Sea
304 influenced the seasonal peak of seal haul-out probability. In particular, we used sea ice concentration
305 data from the Nimbus-7 SMMR and DMSP SSM/I-SSMIS Passive Microwave Dataset, Version 1
306 (Cavalieri et al., 1996) to calculate maximum sea ice extent. All sea ice concentration grid cells (25 km^2)
307 in the study area with greater than 15% concentration were counted daily to get the total sea ice
308 extent for each day between 15 February and 15 July across all years. Maximum spring sea ice extent
309 was simply the largest daily count of grid cells with greater than 15% concentration for each year.
310 A separate regression model, built on the results of the haul-out model, was used to evaluate the
311 relationship between the annual computed peak haul-out day (as the response) with the maximum
312 sea ice extent (as the predictor).

313 RESULTS

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

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

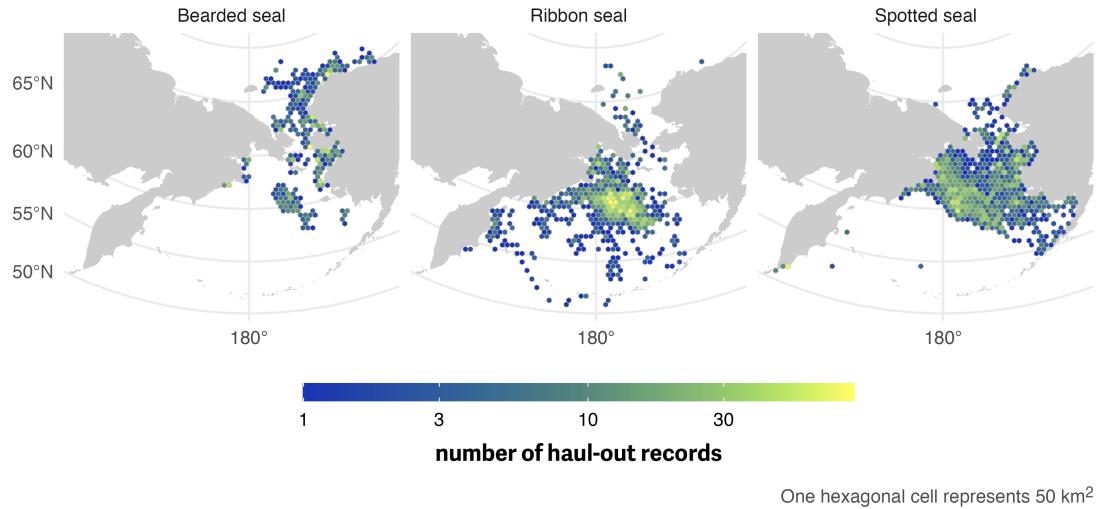


Figure 3. Spatial distribution of haul-out records from 1 March through July 15 for bearded, ribbon, and spotted seal.

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

332 **Bearded Seals**

333 Age and sex class were not included in the model for bearded seals due to our lower sample size for
 334 adult and young-of-year age classes. As such, results are shown for all ages (Figure 5; see also S1).
 335 Additionally, after approximately 9 months, 7 devices deployed on the rear flipper of bearded seals
 336 reported implausible hourly percent-dry data (100% dry for several weeks but indicative of movement
 337 and increasing transmission rates (see Boveng & Cameron (2013))). All data after the first instance of
 338 unrealistic values were censored from this analysis. In addition to a peak around local solar noon, the
 339 bearded seal model predicted additional haul-out activity around local midnight. In concert with the
 340 lower magnitude of haul-out probability, bearded seal haul-out behavior was also more protracted
 341 throughout the spring season compared to ribbon (Figure 7) and spotted seals (Figure 9). Overall,
 342 bearded seals were less likely to haul out and had a bi-modal distribution of haul-out probability
 343 across the day.

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

350 **Ribbon Seals**

351 Ribbon seals exhibited a pattern of gradually increasing haul-out probability in April that peaks in late
 352 May for subadults and in early June for adults (Figure 7; see also S2). There is an apparent seasonal
 353 progression with subadults hauling out earlier in the season followed by adult males and, then, adult
 354 females. Haul-out behavior was clearly centered around local solar noon and expanded to other

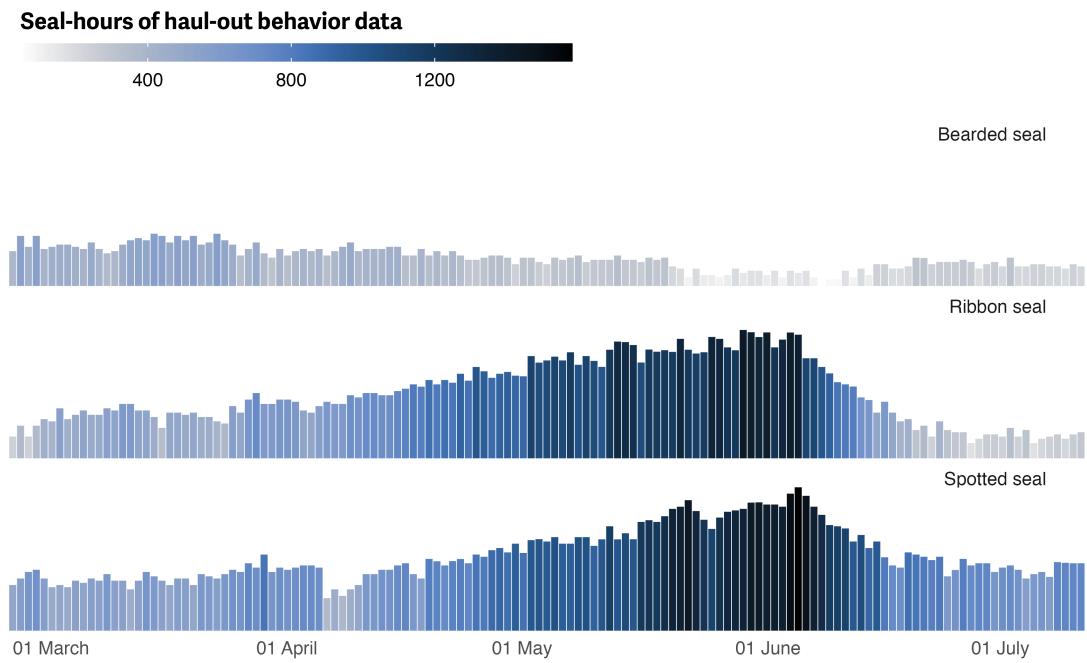


Figure 4. Seasonal distribution of haul-out behavior observations by species

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.

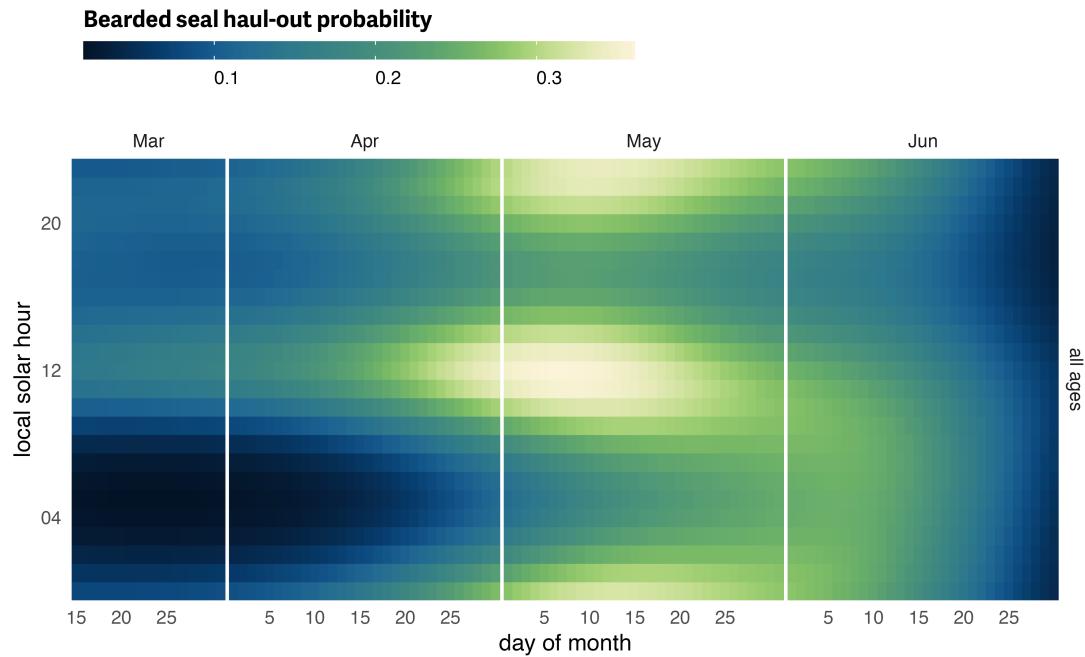


Figure 5. Bearded seal predicted haul-out probability

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.

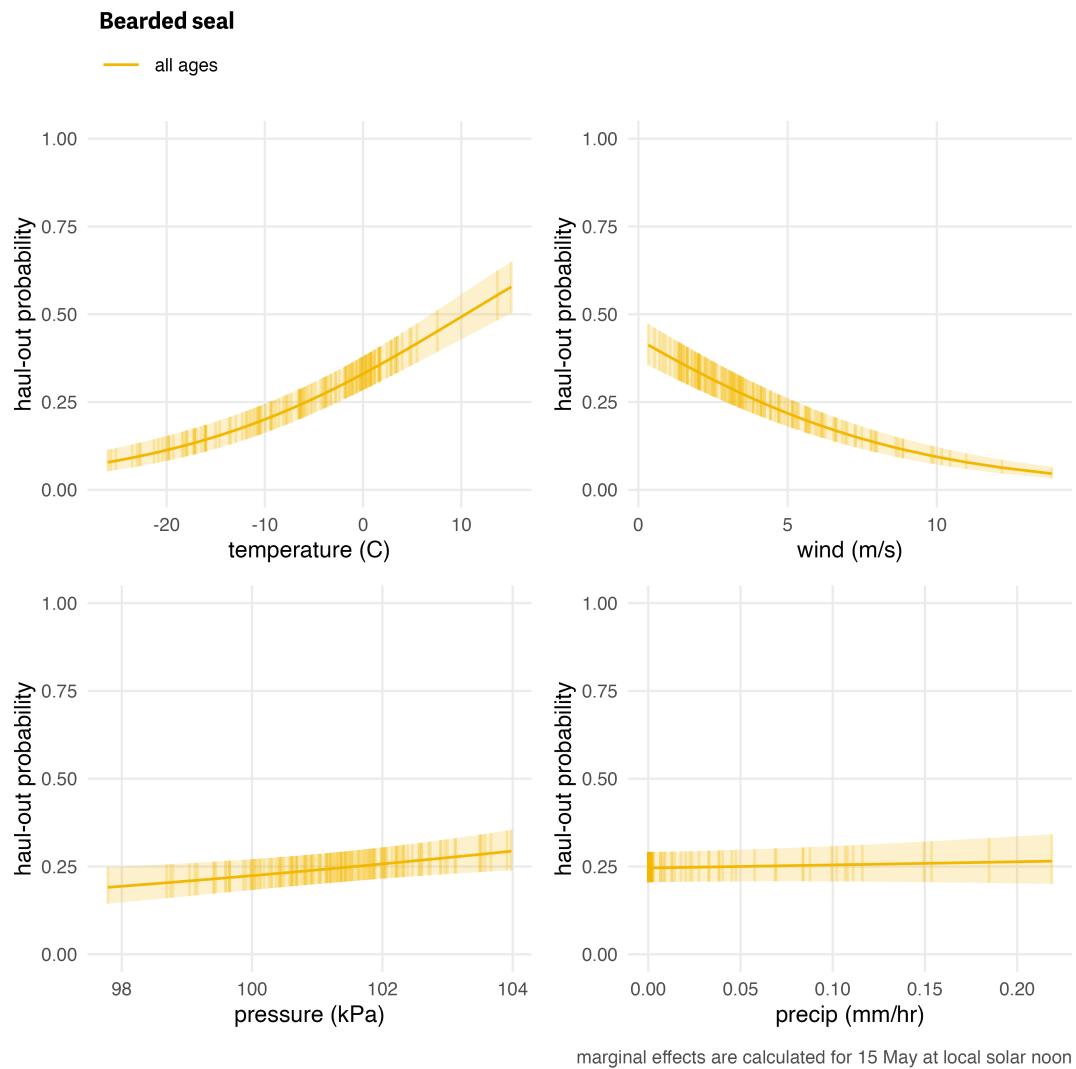


Figure 6. Influence of weather covariates on bearded seal haul-out probability

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.

355 hours later in the spring as seals entered their molting period. Subadults showed an earlier start and
356 more intense haul-out activity in April and May. The young-of-the-year records began after weaning
357 and the model predictions seemed to indicate development of in-water activities (e.g. swimming,
358 foraging) in May. Adult females had a more protracted haul-out season compared to males, and more
359 time was spent hauled out in June compared to adult males and subadults.

360 The haul-out probability for ribbon seals was mostly influenced by temperature ($F_{1,99540} = 6.87$;
361 $p = 0.009$) and wind ($F_{1,99540} = 49.314$; $p = <0.001$) with barometric pressure ($F_{1,99540} = 3.446$; p
362 = 0.063) having a milder impact. Ribbon seals were more likely to haul out when temperatures
363 were relatively warm and less likely to haul out at higher winds and lower pressure values (Figure
364 8). Neither wind chill ($F_{1,99540} = 1.83$; $p = 0.176$) nor precipitation ($F_{1,99540} = 0$; $p = 0.989$) were a
365 significant influence on haul-out probability. Compared with bearded seals, the effect of weather
366 covariates on the predicted haul-out probability for ribbon seals was less striking. Because our ribbon
367 seal model included age and sex class, we can visualize the different influences of weather covariates
368 on those classes and see that subadults differ from adult males and females (Figure 8).

369 **Spotted Seals**

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

377 Spotted seal haul-out behavior was less affected by the weather covariates compared to ribbon
378 and bearded seals but their influence on the model was still significant in some cases. Temperature
379 ($F_{1,114807} = 5.462$; $p = 0.019$), wind ($F_{1,114807} = 46.954$; $p = <0.001$), and barometric pressure ($F_{1,114807}$
380 = 10.214; $p = 0.001$) were all significant. Spotted seals were more likely to be on the ice when
381 temperatures were relatively warm and less likely to haul out at higher wind speeds. Wind chill
382 ($F_{1,114807} = 0.559$; $p = 0.455$) and precipitation ($F_{1,114807} = 0.763$; $p = 0.382$) were not as influential
383 as the other covariates. Differences in the magnitude of response between the age-sex classes were
384 present and consistent across each of the weather covariates (Figure 10). There was a consistent
385 ranking of adult males being the most likely to haul out, followed by adult females, and, then,
386 subadults. This differs from ribbon seals which showed more overlap between adult males and
387 adult females and that subadults were most likely to haul out across the presented range of weather
388 covariates.

389 **Annual variation in haul-out timing**

390 The second set of models, which included annual variation in haul-out patterns, uncovered significant
391 contributions for linear and quadratic interactions between day and year for only spotted seals
392 (day:year, $F_{15,114762} = 4.345$; $p = <0.001$; day²:year, $F_{15,114762} = 5.827$; $p = <0.001$). Ribbon seals
393 showed no significant contribution for interactions between day and year (day:year, $F_{10,99510} = 0.516$;
394 $p = 0.880$; day²:year, $F_{10,99510} = 0.549$; $p = 0.856$). Predicted distributions of haul-out activity were
395 largely unimodal, but varied some among and within years with respect to the timing and magnitude
396 of haul-out peaks (Figure 11). It is important to note that predicted variation in annual haul-out
397 patterns likely reflected both process error and sampling variability. While we did remove any years

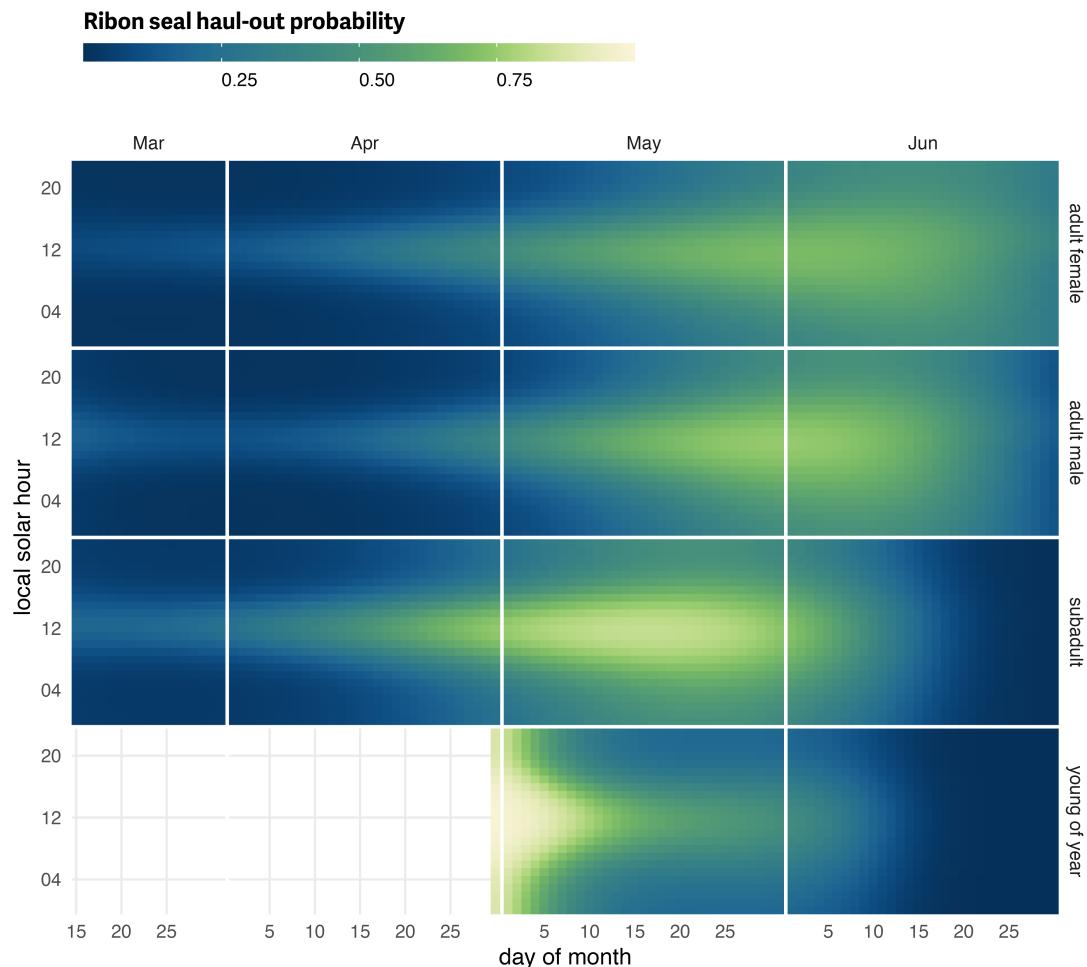


Figure 7. Ribbon seal predicted haul-out probability

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.

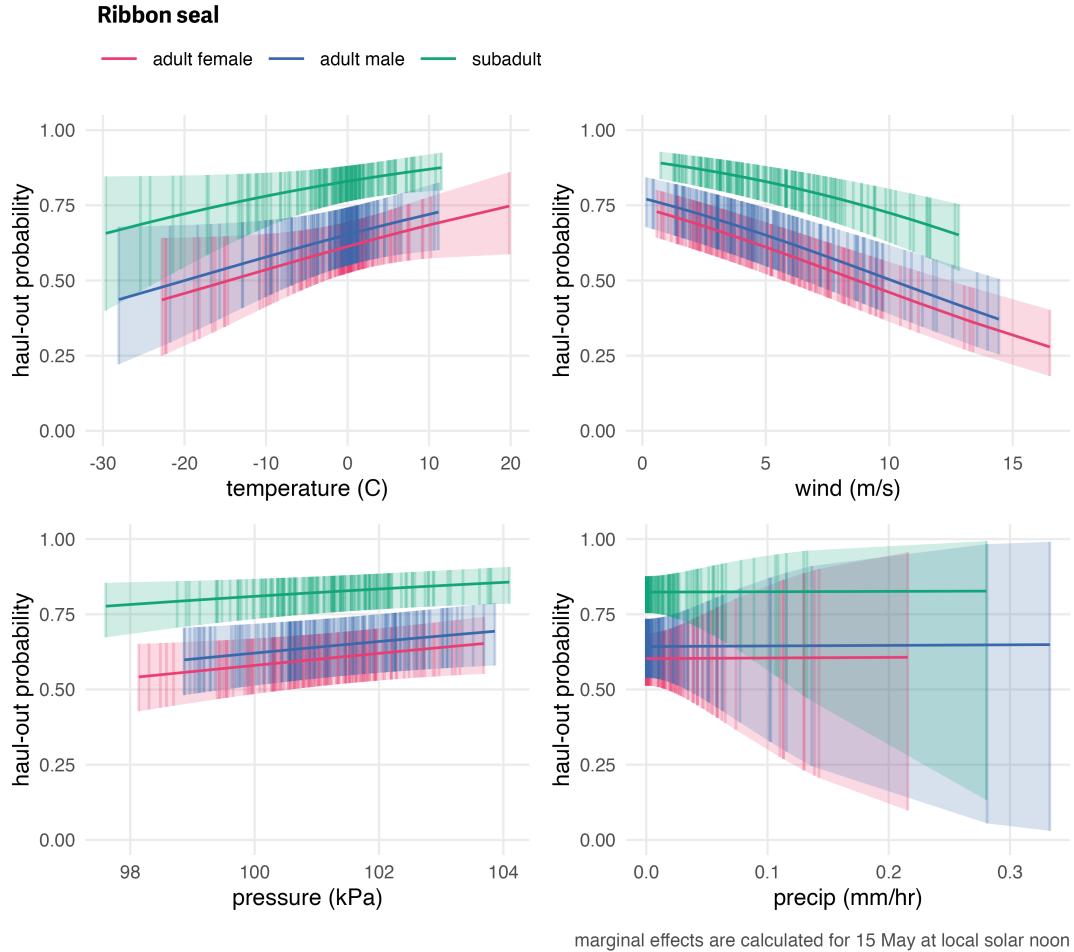


Figure 8. Influence of weather covariates on ribbon seal haul-out probability

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.

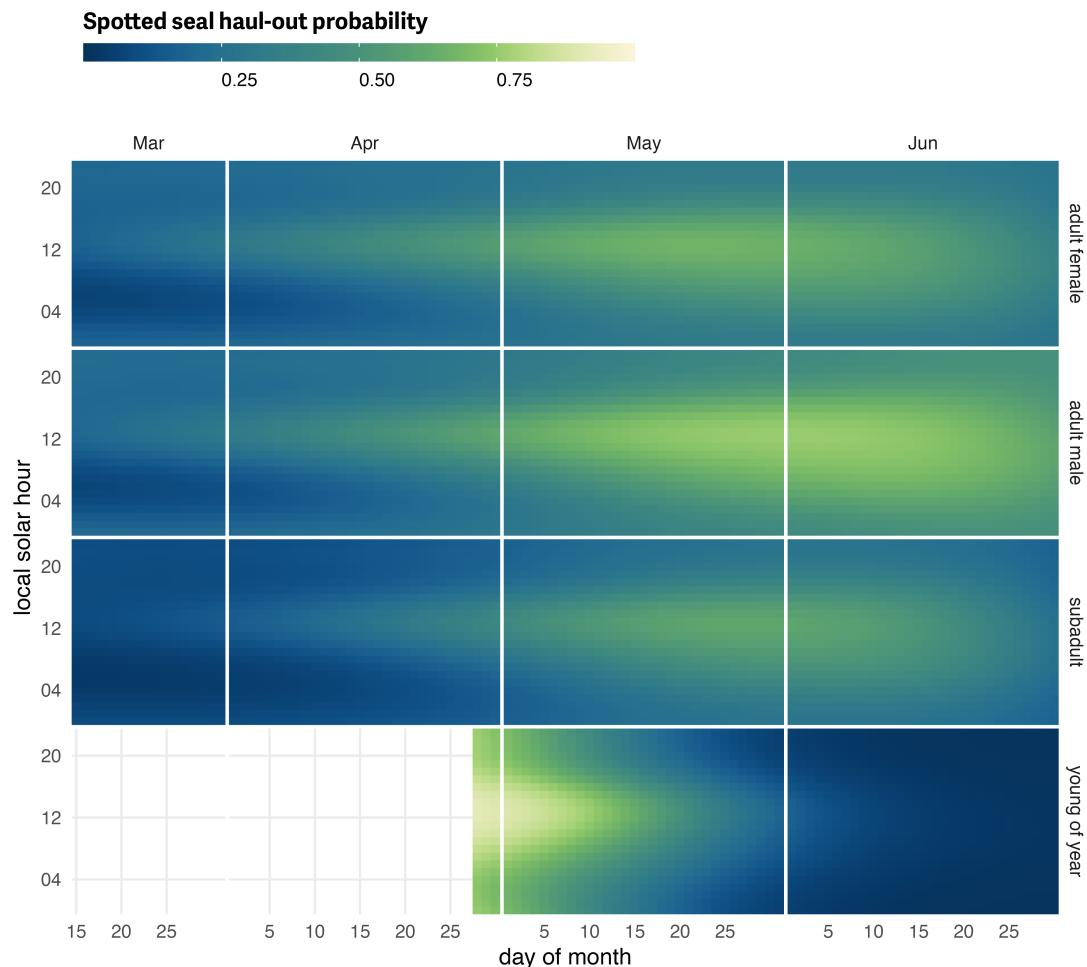


Figure 9. Spotted seal predicted haul-out probability

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.

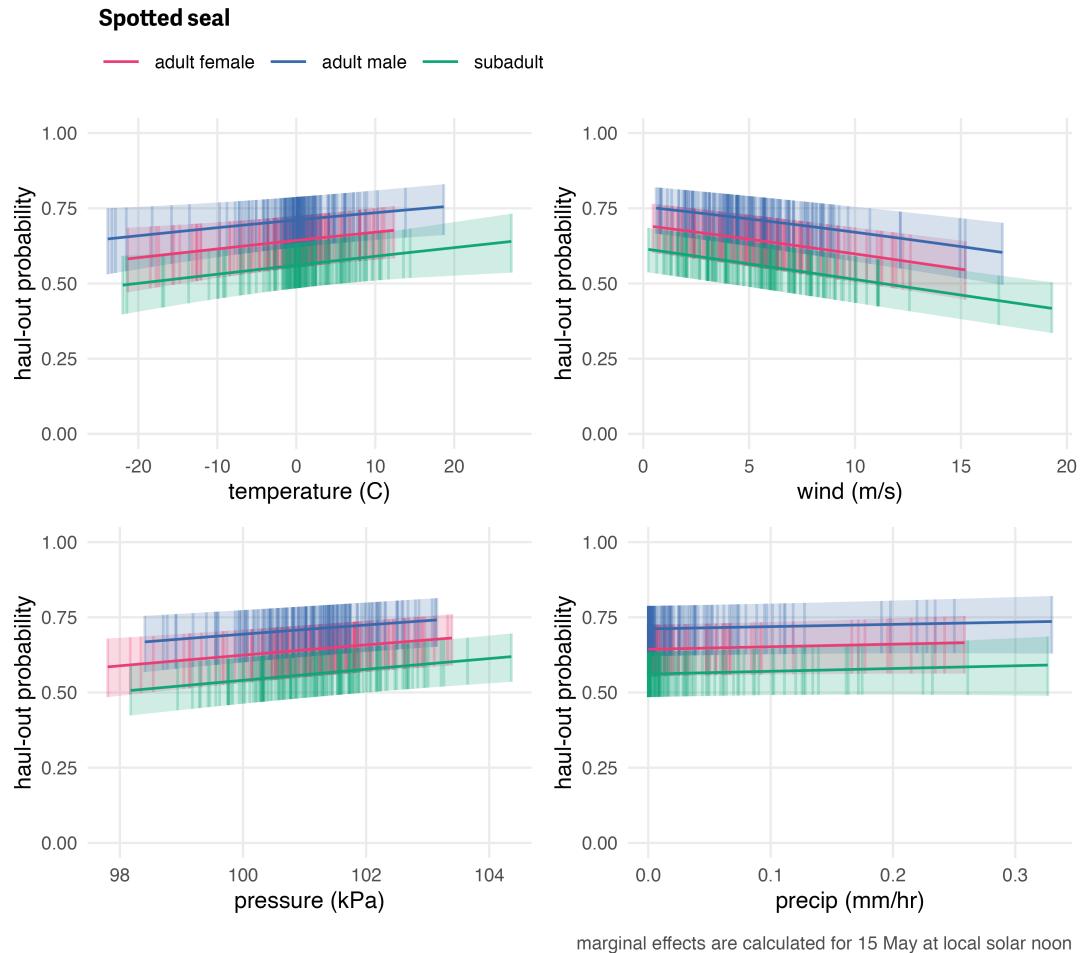


Figure 10. Influence of weather covariates on spotted seal haul-out probability

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.

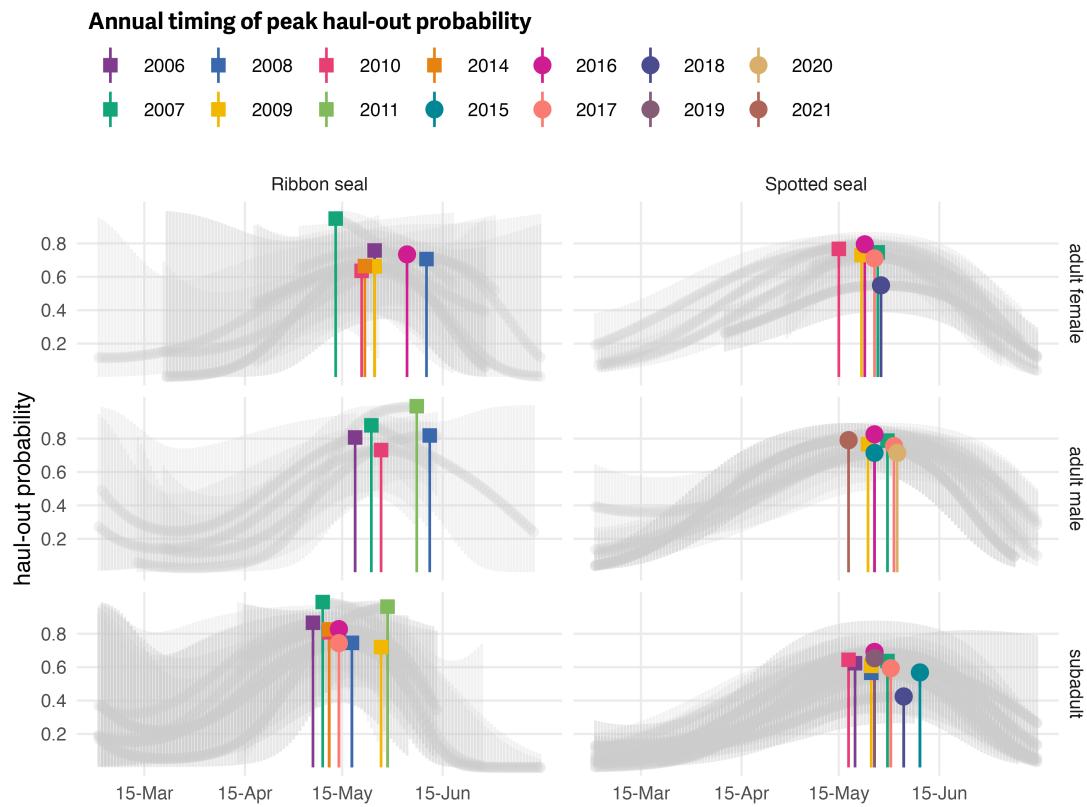


Figure 11. Annual variability in the timing of peak haul-out probability for ribbon and spotted seals.

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.

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

401 The annual timing of peak haul-out probability for ribbon seals and adult male spotted seals
 402 appeared to have no relationship with the amount of yearly maximum sea ice extent in the study area.
 403 For ribbon seals and adult male spotted seals, p -values were substantially larger than 0.05 (ribbon
 404 seal adult females: $R^2 = 0.004$, $p = 0.896$; ribbon seal adult males: $R^2 = 0.059$, $p = 0.693$; ribbon seal
 405 subadults: $R^2 = 0.007$, $p = 0.828$; spotted seals adult males: $R^2 = 0.003$, $p = 0.903$). Adult female and
 406 subadult spotted seals both showed a negative trend (peak haul-out occurs later in years with less
 407 sea ice) with a significant relationship for adult female spotted seals (spotted seal adult female: $R^2 =$
 408 0.663, $p = 0.049$; spotted seal subadults: $R^2 = 0.384$, $p = 0.056$).

409 **DISCUSSION**

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

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

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

453 seal females continue foraging while nursing. Subadult ribbon and spotted seals begin elevated
454 haul-out behavior earlier in the spring and follow a pattern seen in other phocids where yearlings
455 and subadults molt first followed by adult females and males (Thompson & Rothery, 1987; Kirkman
456 et al., 2003; Reder et al., 2003).

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

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

489 Our models detected small deviations in the timing and magnitude of annual peaks in haul-out
490 behavior for ribbon and spotted seals. The timing of peak haul-out activity appears to fall within
491 a relatively narrow time window of 3-4 weeks in late May and early June. This consistency across
492 15 years is likely a reflection of the relationship between a critical photoperiod and the timing of
493 important life history stages (Temte, 1994; Bronson, 2009). However, along with a critical photoperiod,
494 ribbon and spotted seals are dependent upon the presence of sea ice for pupping and molt. We did not
495 find large support in our models for a relationship between the timing of peaks in haul-out behavior
496 and the amount of yearly maximum sea ice. This could indicate that, while the extent of spring sea ice

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

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

Predictions of absolute haul-out probability in this paper were somewhat different than those previously reported for these species, especially for bearded seals. For instance, Ver Hoef et al. (2014) and Conn et al. (2014) used haul-out correction factors with maximums of 0.66 for bearded seals, 0.62 for ribbon seals, and 0.54 for spotted seals, where these maximums corresponded to times near local solar noon in mid-late May. Results here suggest a haul-out probability on May 20 at local solar noon of 0.304 (95% CI: 0.258 – 0.354) for bearded seals across all age and sex classes, 0.715 (95% CI: 0.62 – 0.794) for adult male ribbon seals, 0.661 (95% CI: 0.576 – 0.738) for adult female ribbon seals, 0.742 (95% CI: 0.655 – 0.813) for adult male spotted seals, and 0.663 (95% CI: 0.574 – 0.742) for adult female spotted seals. Our estimates of haul-out probability reflect increased sample sizes in terms of number of individuals, inclusion of weather covariates, and improvements to the way data were prepared prior to analysis and should be the basis for any future estimates of seal abundance from

541 aerial surveys in the Bering and Chukchi seas.

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

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

559 AUTHOR CONTRIBUTIONS

- 560 • **Josh M. London:** investigation, conceptualization, methodology, formal analysis, validation,
561 software, writing: original draft, writing: review and editing, visualization, and data curation
- 562 • **Paul B. Conn:** conceptualization, methodology, formal analysis, software, validation, writing:
563 original draft, writing: review and editing
- 564 • **Stacie K. Hardy:** investigation, data curation, methodology, validation, writing: review and
565 editing
- 566 • **Erin L. Richmond:** data curation, investigation, methodology, validation, writing: review and
567 editing
- 568 • **Jay M. Ver Hoef:** conceptualization, methodology, software, writing: review and editing
- 569 • **Michael F. Cameron:** investigation, project administration, writing: review and editing
- 570 • **Justin A. Crawford:** investigation, methodology, validation, data curation, writing: review
571 and editing
- 572 • **Lori T. Quakenbush:** investigation, methodology, supervision, project administration, writing:
573 review and editing
- 574 • **Andrew L. Von Duyke:** investigation, methodology, validation, data curation, writing: review
575 and editing
- 576 • **Peter L. Boveng:** investigation, conceptualization, supervision, project administration, writing:
577 review and editing

578 DATA AVAILABILITY

579 This manuscript was developed as a reproducible research compendium. All data and code are avail-
580 able on GitHub (<https://github.com/noaa-afsc/berchukseals-haulout>) and major
581 versions archived at Zenodo (<https://doi.org/10.5281/zenodo.4638221>). Original data
582 sources for telemetry are archived at the United States Animal Telemetry Network, archived at

583 Movebank, or associated with other published manuscripts (see supplemental material S1). Collated
584 and cleaned data products needed to replicate the analysis along with the results of all model fits are
585 also available and versioned as an R package on GitHub (<https://github.com/noaa-afsc/berchuksealsHauloutFits>) and archived at Zenodo.
586

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⁷⁷⁹ **SUPPLEMENTAL MATERIAL**

⁷⁸⁰ **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=Alaska Department of Fish and Game; NSB=North Slope Borough; NMFS=NOAA National Marine Fisheries Service; NPWC=North Pacific Wildlife Consortium

Institution	Year Deployed	Location	Publication(s)	Permits	No. Seals	Sex	Age Class
ADFG	2017	Colville River, Nuiqsut	Olnes et al 2020	15324	1	F	subadult
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

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

Institution	Year Deployed	Location	Publication(s)	Permits	No. Seals	Sex	Age Class
NMFS	2008	Bering Sea		782-1765	1	M	subadult
NMFS	2009	Bering Sea		782-1765	28	F, M	adult, subadult, young of year
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

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

Institution	Year Deployed	Location	Publication(s)	Permits	No. Seals	Sex	Age Class
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
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

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

⁷⁸² The following series of figures (**S1**, **S2**, and **S3**) show the seasonal variability in predicted haul-out
⁷⁸³ probability and the associated 95% confidence intervals for bearded, ribbon, and spotted seals. The
⁷⁸⁴ predictions shown are based on the same data used in **5**, **7**, and **9** but selected for three local solar
⁷⁸⁵ hours (07:00, 12:00, and 17:00) so the confidence intervals can also be shown and comparisons can
⁷⁸⁶ be made.

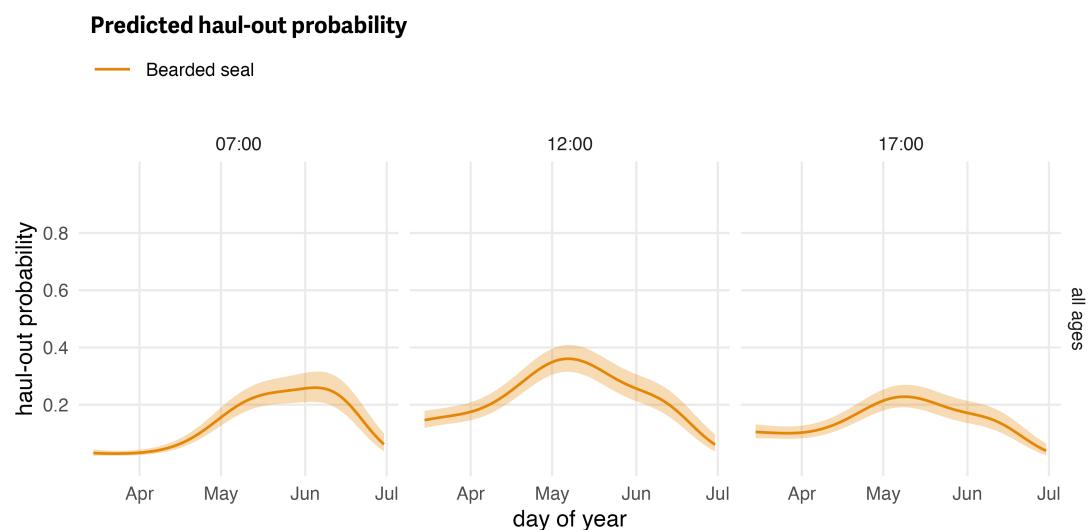


Figure S1. Seasonal variability in haul-out probability and the associated 95% confidence intervals (shaded area) for bearded seals.

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.

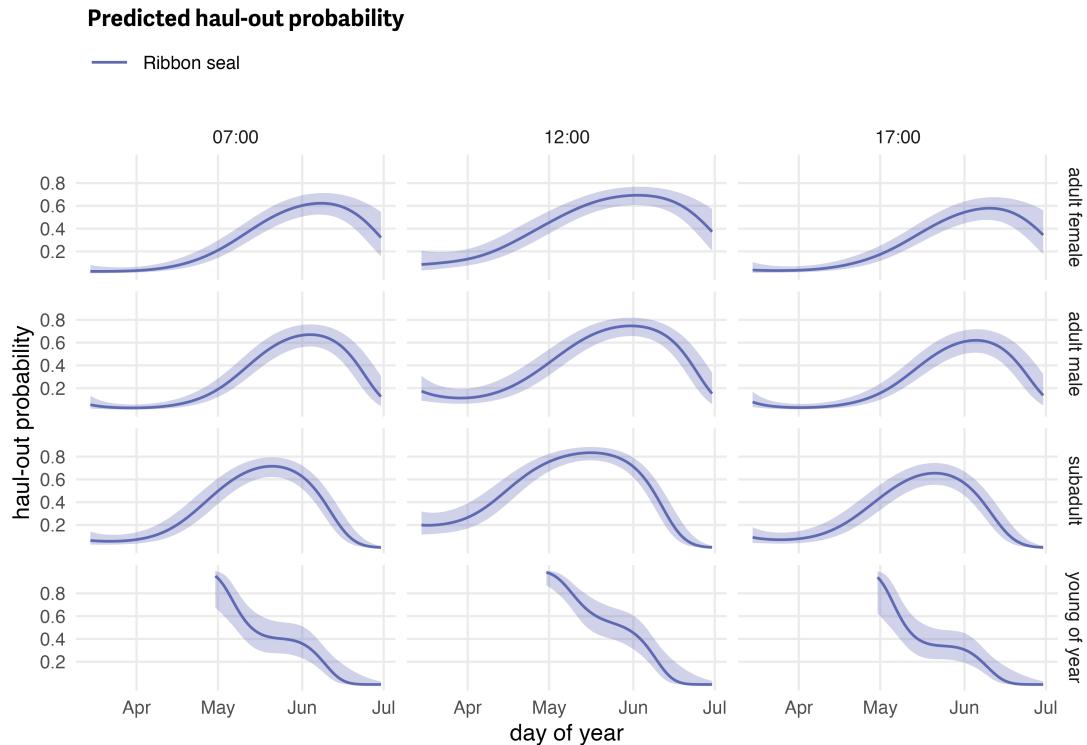


Figure S2. Seasonal variability in haul-out probability and the associated 95% confidence intervals (shaded area) for ribbon seals.

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.

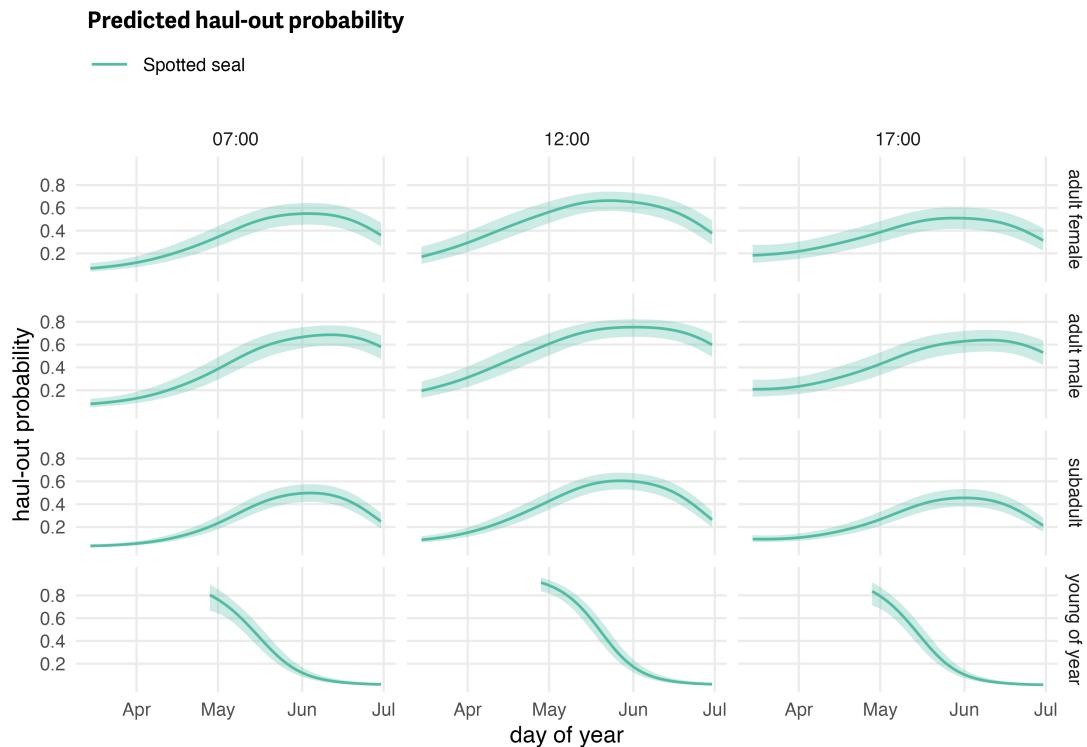


Figure S3. Seasonal variability in haul-out probability and the associated 95% confidence intervals (shaded area) for spotted seals.

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.

787 **0.3 Exploring Insolation (Solar Radiation) as a Model Covariate**

788 **0.3.1 Introduction**

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

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

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

817 **0.3.2 Methods**

818 In this manuscript, we rely on the NARR reanalysis model as the source for our weather covariates.
819 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
820 provides an increased temporal resolution to hourly (compared to the 3-hour resolution of NARR).
821 The global coverage of ERA5 provides additional flexibility in that the area of interest is not limited
822 to North America. The ERA5 model provides a number of solar radiation parameters and it was
823 important to evaluate and understand each of these estimates in order to select the one that was
824 likely most relevant to seals. Here, we used the ‘surface short-wave (solar) radiation downwards’
825 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

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

833 ERA5 data is available via the Copernicus climate data store API which can be queried with the
834 CDS-API Python package (<https://cds.climate.copernicus.eu/api-how-to>). The R
835 code provided here documents the download of the *surface_solar_radiation_downwards* parameter
836 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,
837 extra steps are required to download data on either side of the 180 anti-meridian.
838

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

# import python CDS-API
cdsapi <- import('cdsapi')
#for this step there must exist the file .cdsapirc
server = cdsapi$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 = ":"), # hours
      format = "netcdf"
    )
  )
  #query to get the ncdf
  server$retrieve("reanalysis-era5-single-levels",
                  query,
                  paste0("era5_ssrd_", y, "_right.nc"))
}
```

```

    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])
}

```

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

849 The model specification below was used to specify an mgcv::bam() model that matched the
 850 formula used in the manuscript for ribbon seals. The s(speno, bs = "re") term is the smooth
 851 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)
```

852 Note, the specification for *m1_ribbon* here does not include any AR1 structure for temporal
853 autocorrelation. To include this, we needed to provide a value for ρ (or *rho*). We examined the
854 autocorrelation within the model and used the lag-1 value for ρ . The value for lag-1 autocorrelation
855 was 0.8082 which is rather high but not surprising. We then updated our model specification with a
856 value for ρ as well as the *A1.start* argument which specifies (as either **TRUE** or **FALSE**) the start
857 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)
```

858 The model specification for exploring the use of solar radiation was specified similarly but without
859 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)
```

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

ERA5 Reanalysis

● downward surface solar radiation

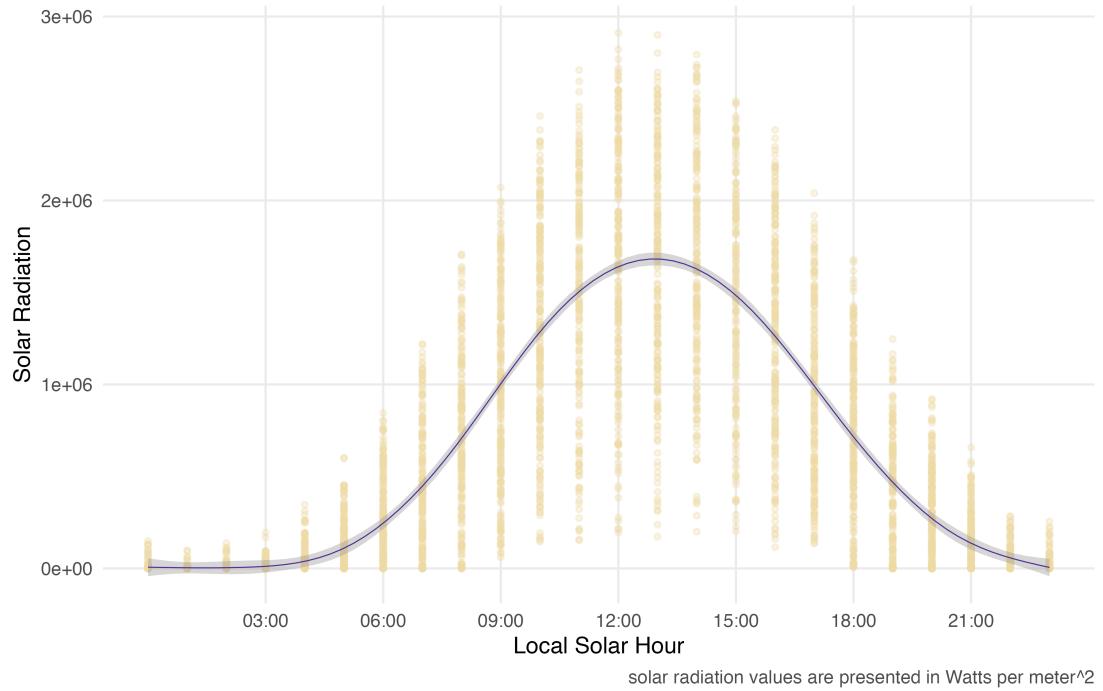


Figure S4. Diel Pattern of Solar Radiation Values from ERA5 Reanalysis.

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.

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

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

0.3.3 Results

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

The bearded seal model matching the specification from the manuscript resulted in 126.13 degrees of freedom and an AIC value of -7428.929. The model with solar radiation resulted in 39.829 degrees of freedom and an AIC value of -6874.298. The ribbon seal model matching the specification from the manuscript resulted in 131.478 degrees of freedom and an AIC value of -16372.29. The model with

879 solar radiation resulted in 114.72 degrees of freedom and an AIC value of -15223.346. The spotted
880 seal model matching the specification from the manuscript resulted in 125.54 degrees of freedom and
881 an AIC value of -23482.051. The model with solar radiation resulted in 108.985 degrees of freedom
882 and an AIC value of -22917.167. Despite the additional terms, the models with the Fourier series
883 representation of hour of day resulted in a lower AIC value and were still preferred models for each
884 of the species.

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

894 **0.3.4 Discussion**

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

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

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

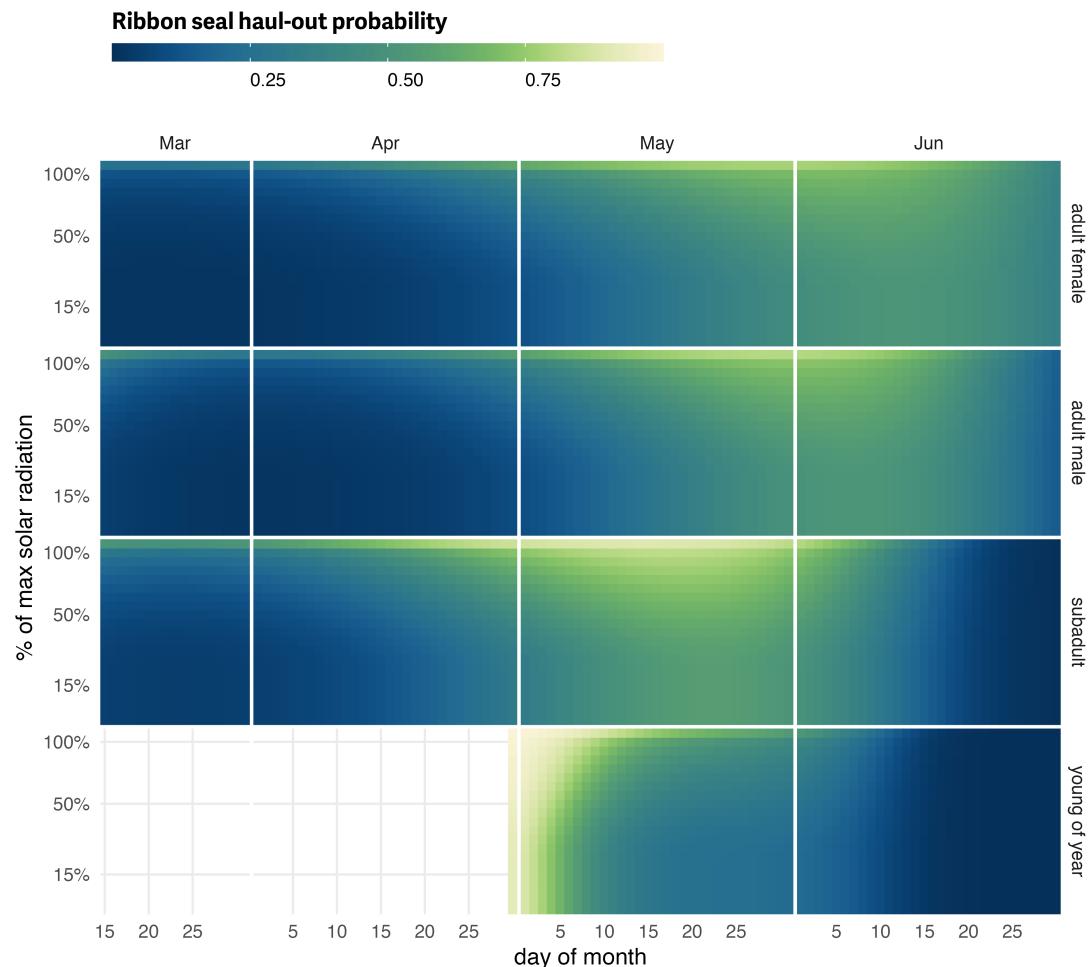


Figure S5. Solar radiation as a predictor of ribbon seal haul-out probability.

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.

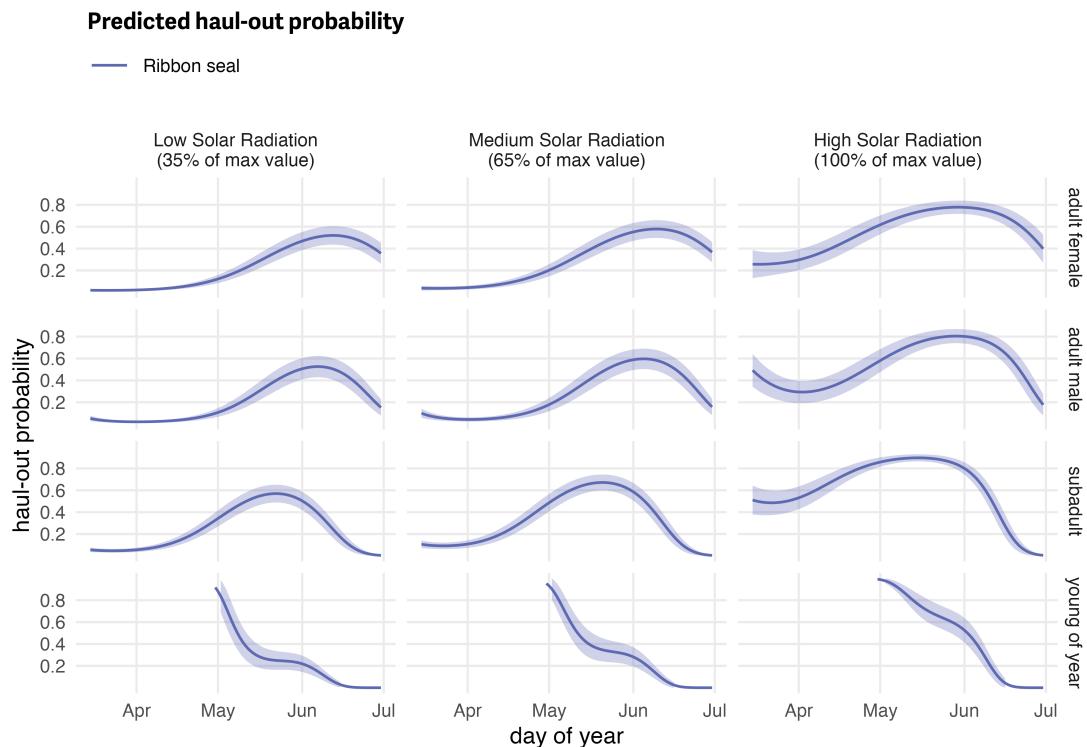


Figure S6. Solar radiation as a predictor of ribbon seal haul-out probability (with uncertainty).

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).