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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 2021. 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.

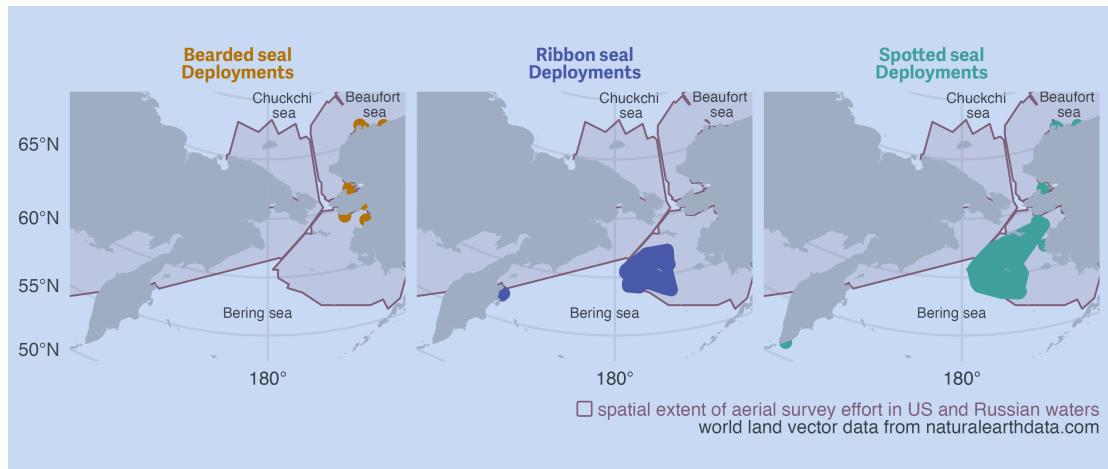


Figure 1. Initial bio-logger deployment areas for bearded, ribbon, and spotted seals in the study between 2005 and 2020 across multiple regions within the Bering, Chukchi, and western Beaufort seas.

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). NOAA-led research was conducted under
 140 the authority of Marine Mammal Protection Act Research Permits Nos. 782-1676, 782-1765, 15126,
 141 and 19309 issued by the National Marine Fisheries Service, and Letters of Assurance of Compliance
 142 with Animal Welfare Act regulations, Nos. A/NW 2010-3 and A/NW 2016-1 from the Alaska Fisheries
 143 Science Center/Northwest Fisheries Science Center Institutional Animal Care and Use Committee
 144 (IACUC). ADF&G and NSB field work was covered by Research Permits Nos. 358-1585, 358-1787,
 145 15324, and 20466 and by ADF&G IACUC permits Nos. 06-16, 09-21, 2014-03, 2015-25, 2016-23,
 146 0027-2017-27, 0027-2018-29, 0027-2019-041.

147 We created a subset of haul-out behavior data from 250 bio-loggers deployed on 35 bearded, 110

148 ribbon, and 105 spotted seals to include only records from 1 March to 15 July between 2005 and
 149 2022. Bio-loggers were of the ‘SPLASH’ or ‘SPOT’ family of tags developed by Wildlife Computers
 150 (Redmond, Washington, USA). Deployments consisted of either a single ‘SPLASH’ device, a single
 151 ‘SPOT’ device, or both types. Devices were either adhered to the hair on the seal or attached through
 152 the rear flipper inter-digital webbing. The use of bio-loggers adhered to the back or head provides
 153 some benefits over flipper mounted devices (e.g. increased satellite transmittal rates, locations at
 154 sea) but these fall off during the following annual molt, which, depending on deployment date,
 155 limits the duration of haul-out data they provide especially during the focus months of our study.
 156 Additionally, bio-loggers attached to the head or dorsal region are often dry while the seal is floating at
 157 the surface, inducing a slight positive bias in the hourly percent-dry values reported by the bio-logger.
 158 For this study, in cases where both bio-logger types were deployed, we preferred hourly percent-dry
 159 observations from the flipper tag. All data were transmitted by the deployed instruments via the
 160 Argos satellite network and location data were either derived from Argos transmissions or transmitted
 161 FastLoc GPS data.

162 Sex and age class (non-dependent *young-of-the-year*, sexually immature *subadults*, and mature
 163 *adults*) were estimated at the time of deployment by various combinations of length, claw growth
 164 ridges (McLaren, 1958), and pelage characteristics. Seals determined to be less than one year were
 165 classified as young-of-the-year. For those bio-loggers deployed on young-of-the-year and transmitting
 166 into the next year (6 ribbon seals; 3 spotted seals), the age class was advanced to subadult on 1 March
 167 of the following year – the assumed anniversary of their birth. Subadults are those seals likely greater
 168 than one year of age but less than four years. Adults are individuals that are likely older than four
 169 years. Table 1 provides a summary of these deployments and data received from them.

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

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

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

170 Haul-out behavior data were recorded in a manner standard across Wildlife Computers bio-
 171 loggers and transmitted via the Argos satellite network as hourly percent-dry timelines. For each
 172 hour of a day, the wet/dry sensor was polled by the tag firmware every few seconds and the percent

of the hour in the dry state was calculated (Figure 2). On board the bio-logger, hourly percent-dry calculations were rounded to the nearest 10% inclusive of 0% and 100% along with additional values at 3% and 98%. This compression resulted in additional data transmission as each message consisted of two complete 24-hour records. Memory capacity allowed caching of percent-dry records for several weeks or months and each message was transmitted several times to ensure reception at the satellite. Bio-loggers were deployed and programmed in a manner to maximize data transmission during the spring pupping and molting period, though hourly percent-dry data were not always successfully transmitted. This is due to a variety of factors including satellite coverage, tag availability (e.g., tags mounted to the rear flipper often do not transmit while at sea), tag performance, duty cycling, and atmospheric interference. Fortunately, missing records do not substantially bias inference about haul-out probabilities (Conn et al., 2012).

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

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

Explanatory variables

In addition to sex and age class, we analyzed variables that might help explain variation in haul-out probabilities. These included day-of-year (for seasonal effects) and local solar hour (for diurnal

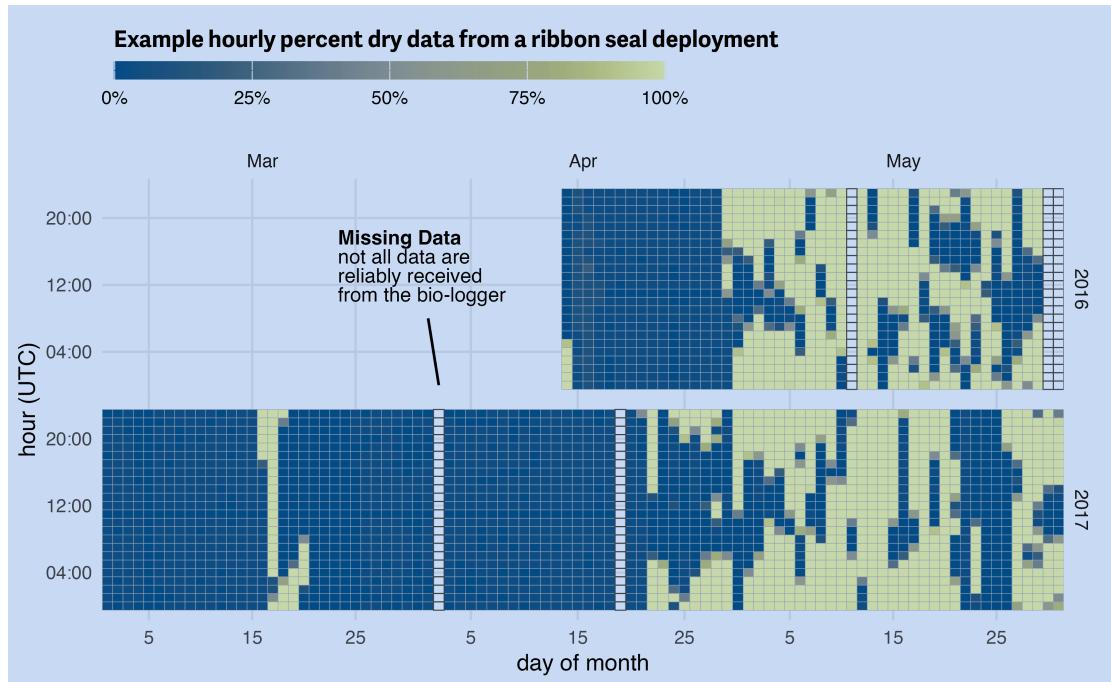


Figure 2. Example percent-dry actogram from bio-logger data

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.

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

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

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

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

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

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
Wind	Continuous	northerly and easterly vector components for wind (NARR) converted into a single wind speed via the Euclidean norm
Northing	Continuous	latitude divided by the mean latitude across all locations (for bearded seals only)
Year	Continuous*	For the set of models examining inter-annual variation in sea-ice use, we fitted models with the addition of year by day-of-year interactions*

241  **Haul-out modeling**

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

247 To properly account for temporal dependence and to take advantage of computational efficiency,
 248 we used generalized linear mixed pseudo-models (GLMPMs; Ver Hoef, London & Boveng (2010))
 249 to model variation in haul-out behavior as a function of (1) covariate predictors, (2) temporally
 250 autocorrelated random effects, and (3) individual random effects representing heterogeneity in
 251 individual behavior. We used the glmmLDT package (Ver Hoef, London & Boveng, 2010) to
 252 implement GLMPMs. We explored two different model formulations for our data and we fit separate
 253 models to bearded, ribbon, and spotted seal data sets as we expected differing behavior by species.
 254 Separate models for each species were also needed because a single, very large data set proved
 255 computationally intractable. In our first model formulation and for each species, we fitted a year-
 256 independent model that predicted average haul-out behavior as a function of demographic, weather,
 257 seasonal, and diurnal effects. Second, for ribbon and spotted seals (which had considerably more
 258 data than bearded seals), we fitted models that included all the effects from the first model, but
 259 also permitted annual variation in haul-out timing. This second set of models was used to examine
 260 whether haul-out patterns varied by year and to determine the annual timing of apparent peaks in
 261 haul-out behavior. For both models, we assumed an hourly Bernoulli response (a binary 0-1 response
 262 dependent upon whether the tag was greater than 50% dry for a given hour) where the linear predictor
 263 was modeled on the logit scale. This is consistent with previous approaches (London et al., 2012; Ver
 264 Hoef et al., 2014) and only 7.005% of our observations fell between 10% and 90% hourly percent-dry.

265 We followed Ver Hoef et al. (2014) in using linear, quadratic, and cubic effects of day-of-year
 266 to represent temporal changes in behavior during the season. However, unlike previous models
 267 for harbor seals (London et al., 2012) and ice-associated seals (Ver Hoef et al., 2014), which treated

268 hour-of-day as a 24-level categorical variable to capture diurnal cycles, we adopted a continuous
 269 formulation based on Fourier series that provides a flexible model while preserving the inherent
 270 circularity needed for time-of-day effects (i.e., hour 0 should be equal to hour 24). It also represents
 271 hour-of-day with 6 parameters, which is a considerable reduction when compared to a 24-parameter
 272 variable. According to this approach, we used the following specification for hour-of-day effects:

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

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

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

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

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

309 haul-out probability to better communicate the variation in model uncertainty.

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

320 RESULTS

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

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

339 Bearded Seals

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

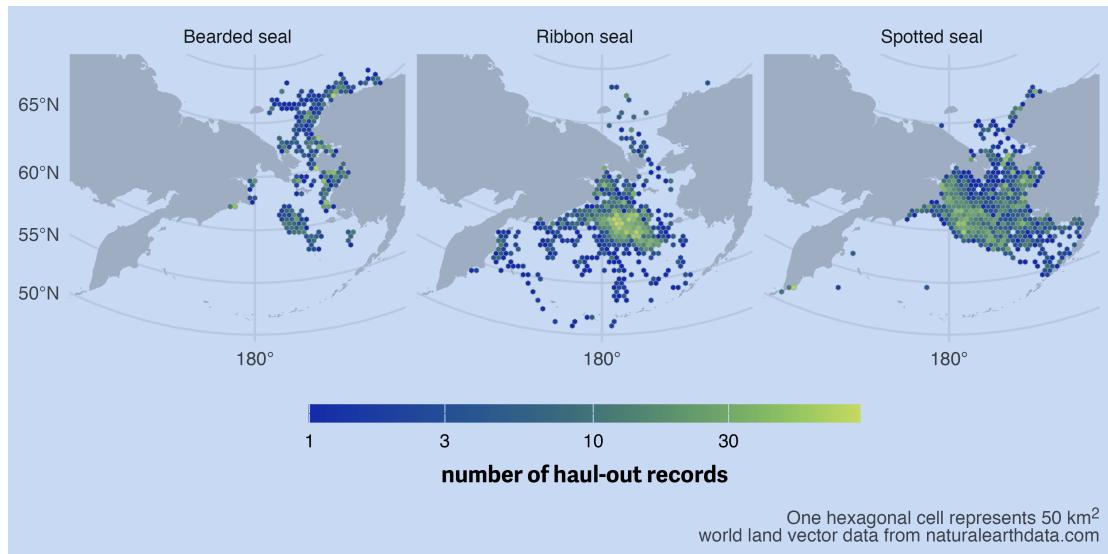


Figure 3. Spatial distribution of haul-out records from 1 March through July 15 for bearded, ribbon, and spotted seal.

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 km^2

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

Ribbon Seals

Ribbon seals exhibited a pattern of gradually increasing haul-out probability in April that peaks in late May for subadults and in early June for adults (Figure 7; see also S2). There is an apparent seasonal progression with subadults hauling out earlier in the season followed by adult males and, then, adult females. Haul-out behavior was clearly centered around local solar noon and expanded to other hours later in the spring as seals entered their molting period. Subadults showed an earlier start and more intense haul-out activity in April and May. The young-of-the-year records began after weaning and the model predictions seemed to indicate development of in-water activities (e.g. swimming, foraging) in May. Adult females had a more protracted haul-out season compared to males, and more time was spent hauled out in June compared to adult males and subadults.

The haul-out probability for ribbon seals was mostly influenced by temperature ($F_{1,99540} = 6.87; p = 0.009$) and wind ($F_{1,99540} = 49.314; p < 0.001$) with barometric pressure ($F_{1,99540} = 3.446; p = 0.063$) having a milder impact. Ribbon seals were more likely to haul out when temperatures were relatively warm and less likely to haul out at higher winds and lower pressure values (Figure 8). Neither wind chill ($F_{1,99540} = 1.83; p = 0.176$) nor precipitation ($F_{1,99540} = 0; p = 0.989$) were a significant influence on haul-out probability. Compared with bearded seals, the effect of weather covariates on the predicted haul-out probability for ribbon seals was less striking. Because our ribbon

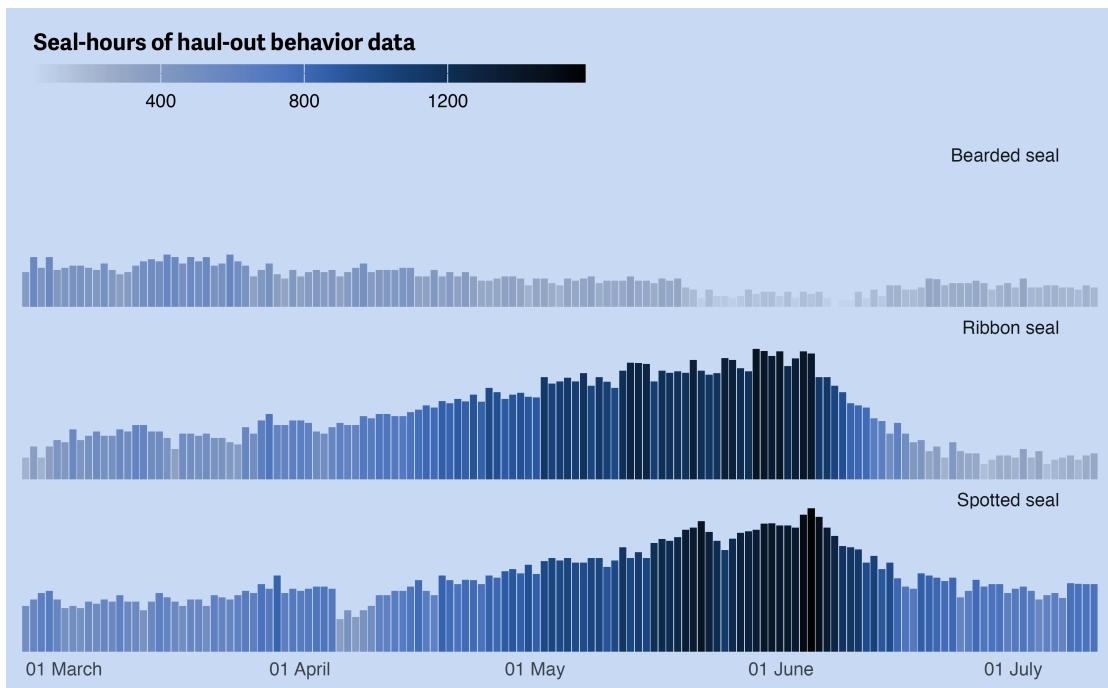


Figure 4. Seasonal distribution of haul-out behavior observations by species

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.

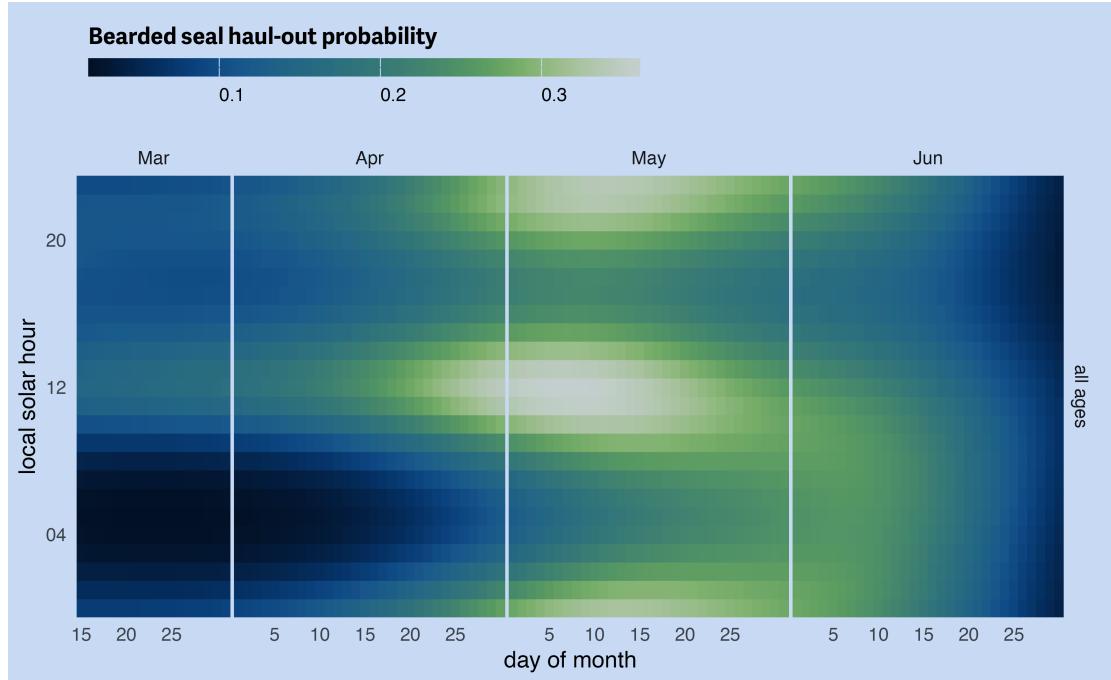


Figure 5. Bearded seal predicted haul-out probability

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.

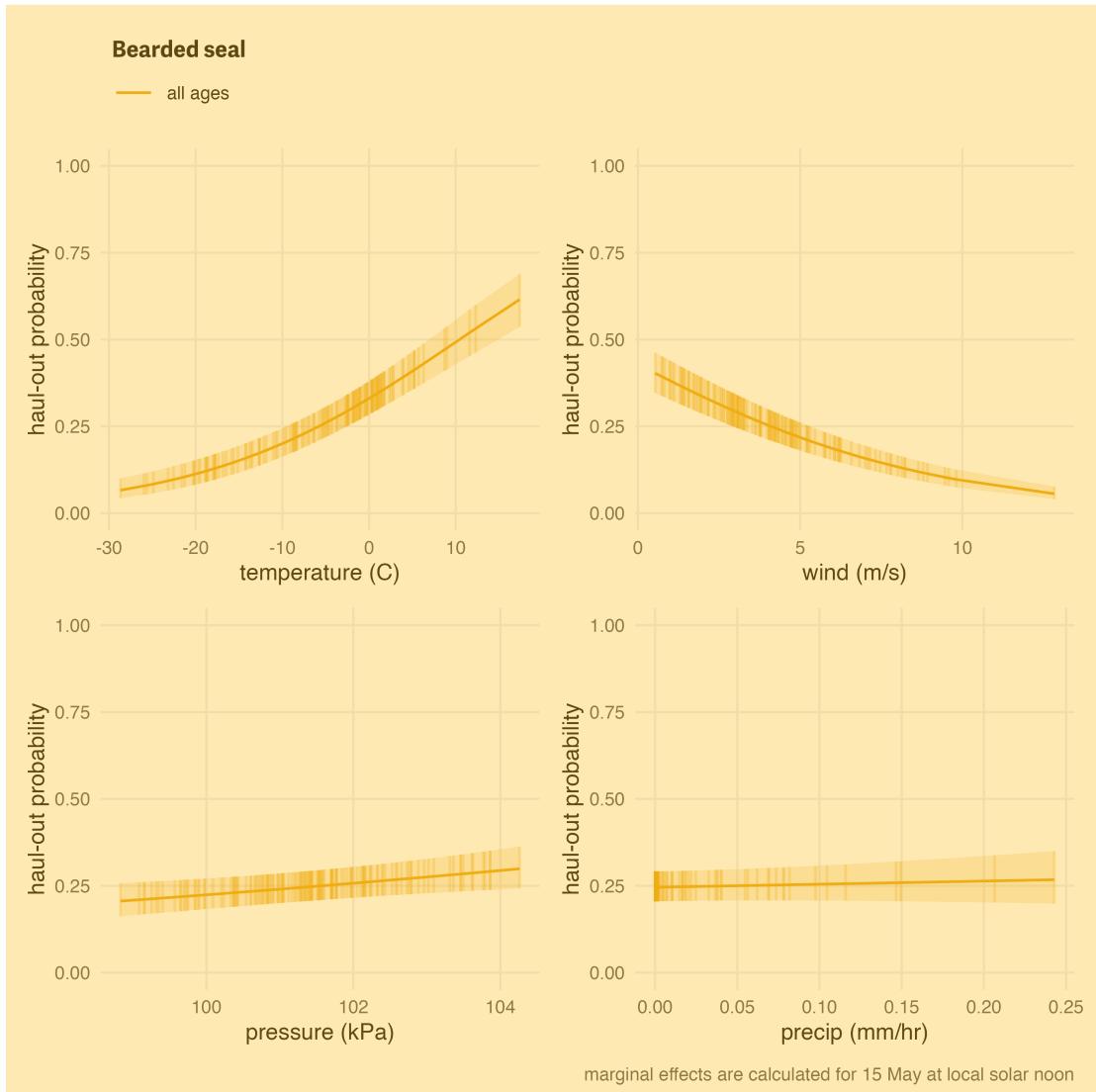


Figure 6. Influence of weather covariates on bearded seal haul-out probability

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.

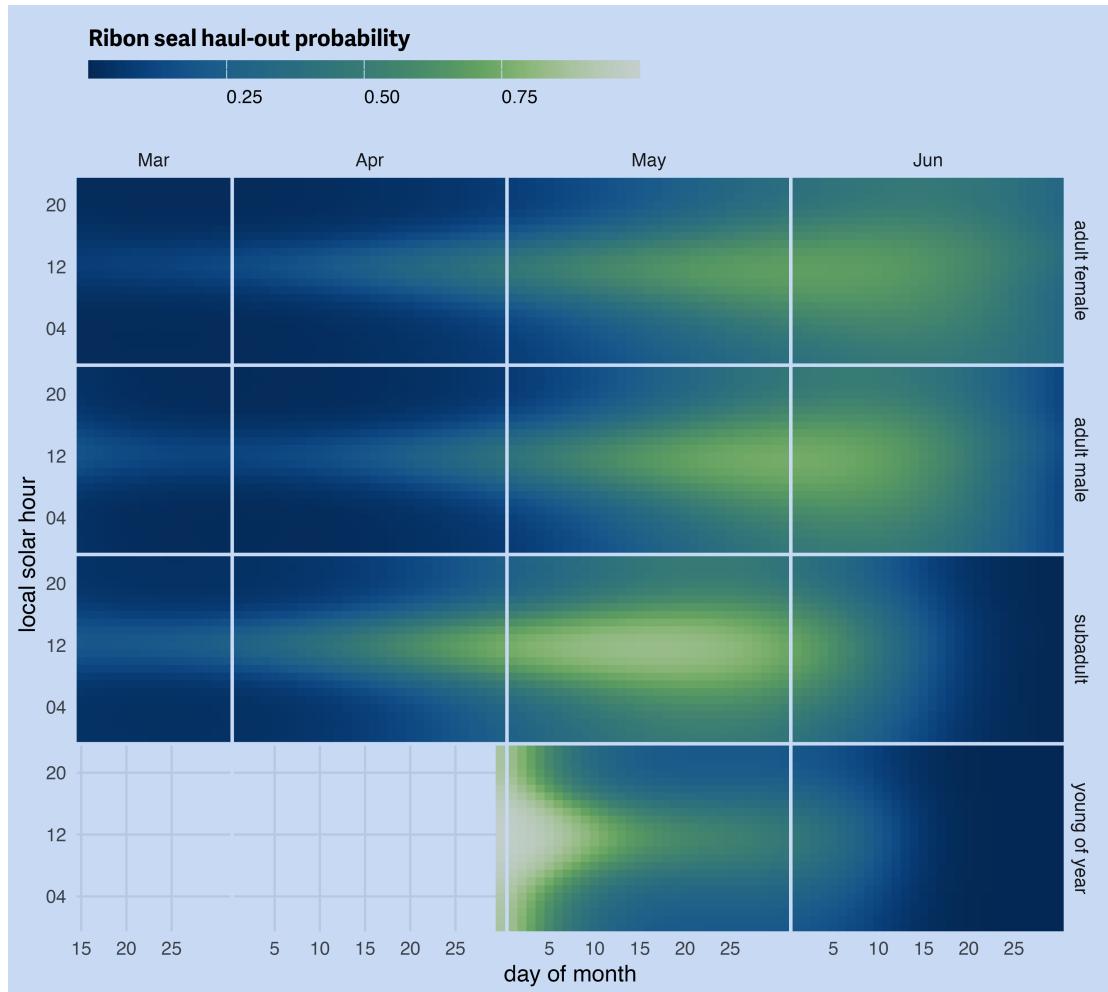


Figure 7. Ribbon seal predicted haul-out probability

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.

374 seal model included age and sex class, we can visualize the different influences of weather covariates
375 on those classes and see that subadults differ from adult males and females (Figure 8).

376 Spotted Seals

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

384 Spotted seal haul-out behavior was less affected by the weather covariates compared to ribbon
385 and bearded seals but their influence on the model was still significant in some cases. Temperature
386 ($F_{1,115189} = 5.384; p = 0.020$), wind ($F_{1,115189} = 45.718; p = <0.001$), and barometric pressure ($F_{1,115189}$
387 = 9.445; $p = 0.002$) were all significant. Spotted seals were more likely to be on the ice when
388 temperatures were relatively warm and less likely to haul out at higher wind speeds. Wind chill
389 ($F_{1,115189} = 0.72; p = 0.396$) and precipitation ($F_{1,115189} = 0.773; p = 0.379$) were not as influential
390 as the other covariates. Differences in the magnitude of response between the age-sex classes were
391 present and consistent across each of the weather covariates (Figure 10). There was a consistent
392 ranking of adult males being the most likely to haul out, followed by adult females, and, then,
393 subadults. This differs from ribbon seals which showed more overlap between adult males and
394 adult females and that subadults were most likely to haul out across the presented range of weather
395 covariates.

396 Annual variation in haul-out timing

397 The second set of models, which included annual variation in haul-out patterns, uncovered significant
398 contributions for linear and quadratic interactions between day and year for only spotted seals
399 (day:year, $F_{15,115144} = 4.445; p = <0.001$; day²:year, $F_{15,115144} = 5.854; p = <0.001$). Ribbon seals
400 showed no significant contribution for interactions between day and year (day:year, $F_{10,99510} = 0.516;$
401 $p = 0.880$; day²:year, $F_{10,99510} = 0.549; p = 0.856$). Predicted distributions of haul-out activity were
402 largely unimodal, but varied some among and within years with respect to the timing and magnitude
403 of haul-out peaks (Figure 11). It is important to note that predicted variation in annual haul-out
404 patterns likely reflected both process error and sampling variability. While we did remove any years
405 where only one deployment in a species + age:sex group was present, there were still some years
406 where the pattern shown was informed by a small number of individuals that may not represent
407 population-level patterns.

408 The annual timing of peak haul-out probability for ribbon seals and adult male spotted seals
409 appeared to have no relationship with the amount of yearly maximum sea-ice extent in the study area.
410 For ribbon seals and adult male spotted seals, p -values were substantially larger than 0.05 (ribbon
411 seal adult females: $R^2 = 0.004, p = 0.896$; ribbon seal adult males: $R^2 = 0.059, p = 0.693$; ribbon seal
412 subadults: $R^2 = 0.007, p = 0.828$; spotted seals adult males: $R^2 = 0.004, p = 0.889$). Adult female and
413 subadult spotted seals both showed a negative trend (peak haul-out occurs later in years with less
414 sea ice) with a significant relationship for adult female spotted seals (spotted seal adult female: $R^2 =$
415 0.456, $p = 0.141$; spotted seal subadults: $R^2 = 0.369, p = 0.062$).

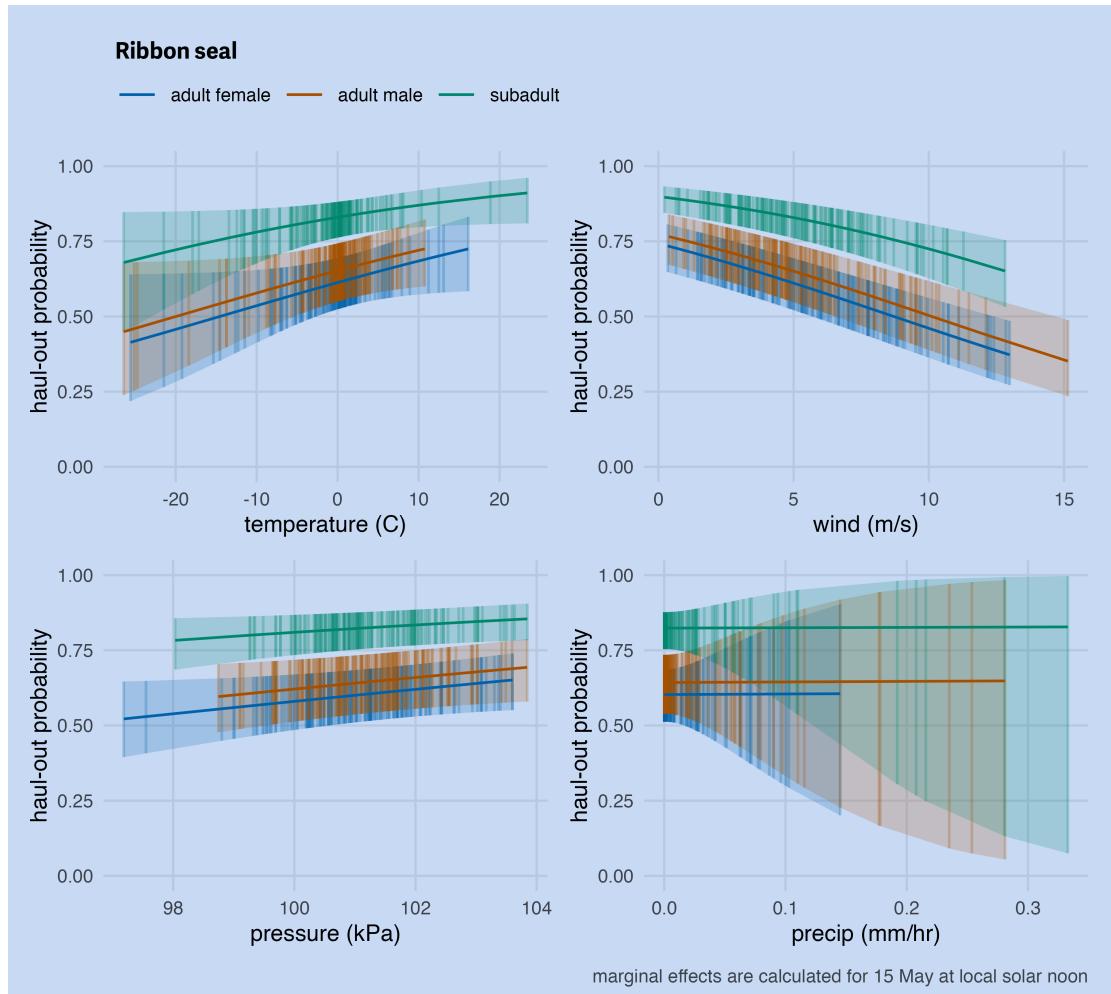


Figure 8. Influence of weather covariates on ribbon seal haul-out probability

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.

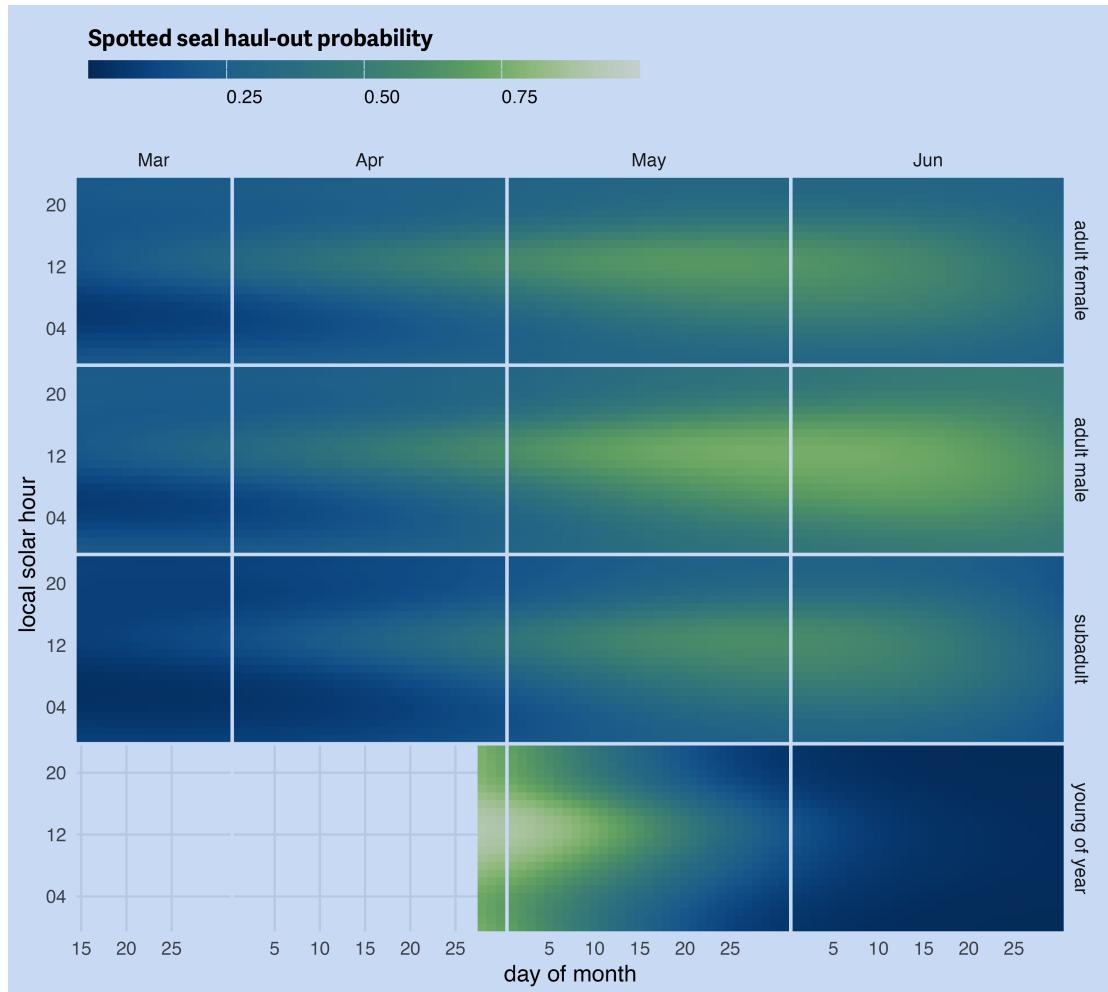


Figure 9. Spotted seal predicted haul-out probability

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.

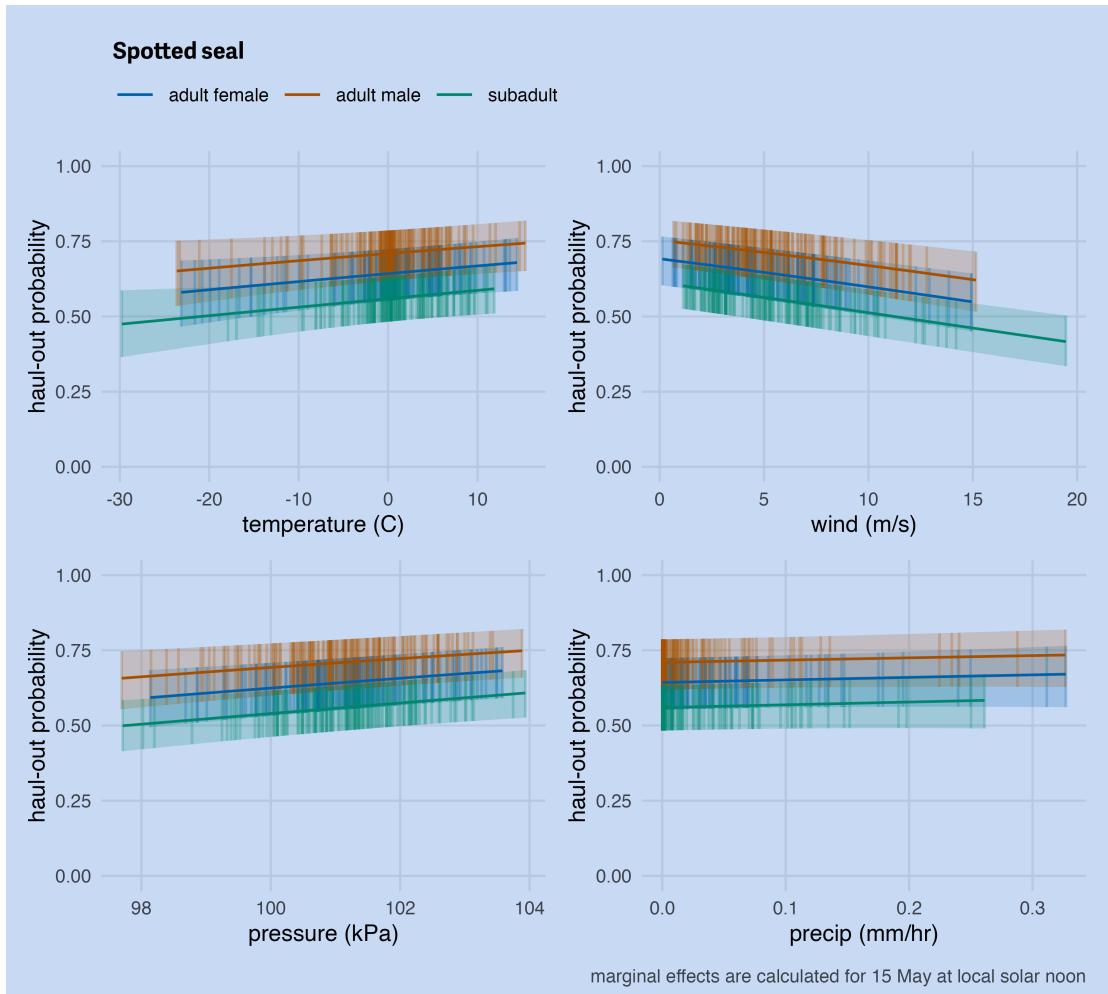


Figure 10. Influence of weather covariates on spotted seal haul-out probability

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.

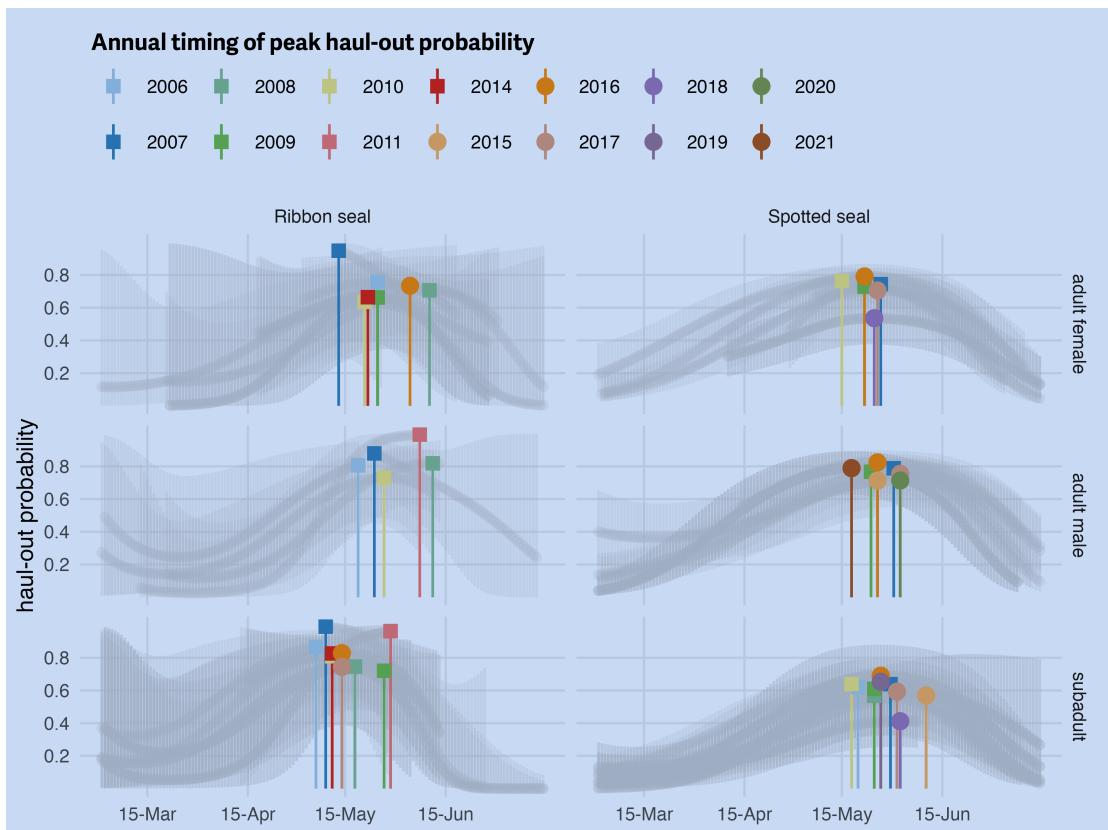


Figure 11. Annual variability in the timing of peak haul-out probability for ribbon and spotted seals.

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.

416 **DISCUSSION**

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

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

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

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

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

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

496 Our models detected small deviations in the timing and magnitude of annual peaks in haul-out
497 behavior for ribbon and spotted seals. The timing of peak haul-out activity appears to fall within
498 a relatively narrow time window of 3-4 weeks in late May and early June. This consistency across
499 15 years is likely a reflection of the relationship between a critical photoperiod and the timing of
500 important life history stages (Temte, 1994; Bronson, 2009). However, along with a critical photoperiod,
501 ribbon and spotted seals are dependent upon the presence of sea ice for pupping and molt. We did not
502 find large support in our models for a relationship between the timing of peaks in haul-out behavior
503 and the amount of yearly maximum sea ice. This could indicate that, while the extent of spring sea ice

504 in the Bering Sea varied widely during our study period, seals were still able to locate sea ice and haul
505 out. Only a small portion of our data was from 2018 – 2019, years of extreme low spring ice extent in
506 the Bering Sea that appeared to impact body condition of ribbon and spotted seals (Boveng et al.,
507 2020), so we may currently lack sufficient contrast in ice extent to characterize an effect on the timing
508 of peak haul-out probability. We should expect, however, that some minimal threshold in the spatial
509 extent or density of sea ice will have a meaningful impact on the timing of peak haul-out behavior —
510 if there is no sea-ice, seals will not haul out or they will be forced to use terrestrial haul-out sites which
511 were not part of the evolution of their normal behaviors. Additionally, while from an ecological
512 perspective the haul-out behavior appears consistent, the interannual differences in timing and
513 magnitude are large enough to have important ramifications on calculations of abundance and trend.
514 Those ramifications will only be exacerbated if climate variability amplifies interannual differences.

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

537 Predictions of absolute haul-out probability in this paper were somewhat different than those
538 previously reported for these species, especially for bearded seals. For instance, Ver Hoef et al. (2014)
539 and Conn et al. (2014) used haul-out correction factors with maximums of 0.66 for bearded seals,
540 0.62 for ribbon seals, and 0.54 for spotted seals, where these maximums corresponded to times near
541 local solar noon in mid-late May. Results here suggest a haul-out probability on May 20 at local solar
542 noon of 0.304 (95% CI: 0.258 – 0.354) for bearded seals across all age and sex classes, 0.715 (95% CI:
543 0.62 – 0.794) for adult male ribbon seals, 0.661 (95% CI: 0.576 – 0.738) for adult female ribbon seals,
544 0.74 (95% CI: 0.654 – 0.811) for adult male spotted seals, and 0.66 (95% CI: 0.571 – 0.739) for adult
545 female spotted seals. Our estimates of haul-out probability reflect increased sample sizes in terms
546 of number of individuals, inclusion of weather covariates, and improvements to the way data were
547 prepared prior to analysis and should be the basis for any future estimates of seal abundance from

548 aerial surveys in the Bering and Chukchi seas.

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

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

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584 review and editing

585 DATA AVAILABILITY

586 This manuscript was developed as a reproducible research compendium and was originally published
587 as a pre-print at bioRxiv (London et al. (2022); [https://doi.org/10.1101/2022.04.07.
588 487572](https://doi.org/10.1101/2022.04.07.487572)). All data used in the study and code are available on GitHub ([https://github.com/
589 noaa-afsc/berchukseals-haulout](https://github.com/noaa-afsc/berchukseals-haulout)) and major versions archived at Zenodo (<https://zenodo.org/record/6200333>)

doi.org/10.5281/zenodo.4638221). Original data sources for telemetry are archived as part of datasets at the United States Animal Telemetry Network (<https://portal.atn.ioos.us/>), archived at Movebank (see Movebank ID 732321226), or associated with other published manuscripts (see supplemental material S1). Collated and cleaned data products needed to replicate the analysis along with the results of all model fits are also available and versioned as an R package on GitHub (<https://github.com/noaa-afsc/berchuksealsHauloutFits>) and archived at Zenodo (<https://doi.org/10.5281/zenodo.10056308>).

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782 **SUPPLEMENTAL MATERIAL**

783 **0.1 Additional Bio-logger Deployment Details**

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

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

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

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

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

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

784 **0.2 Supplemental Figures Showing Confidence Intervals Associated with Predictions**

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

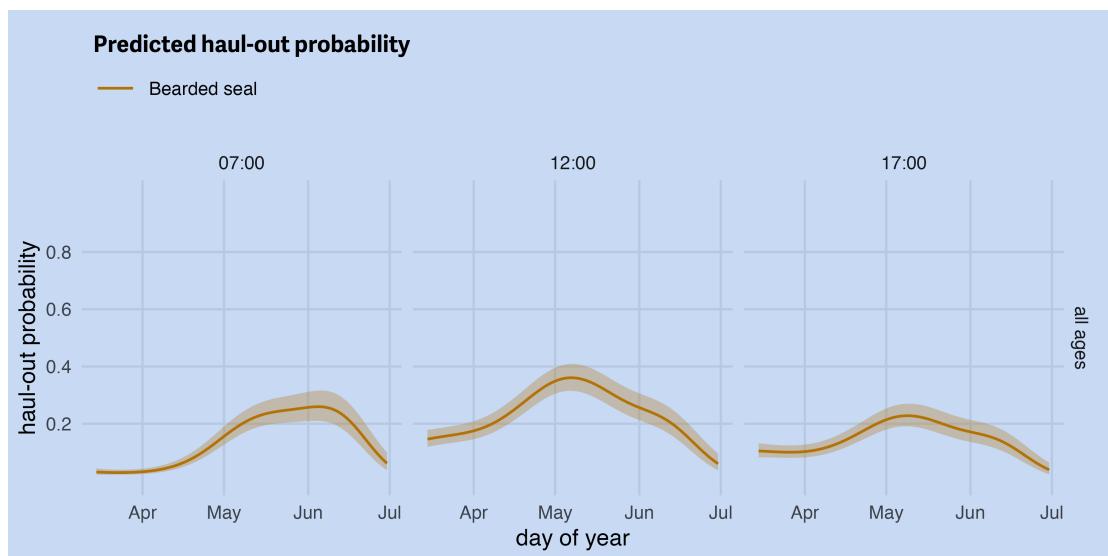


Figure S1. Seasonal variability in haul-out probability and the associated 95% confidence intervals (shaded area) for bearded seals.

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.

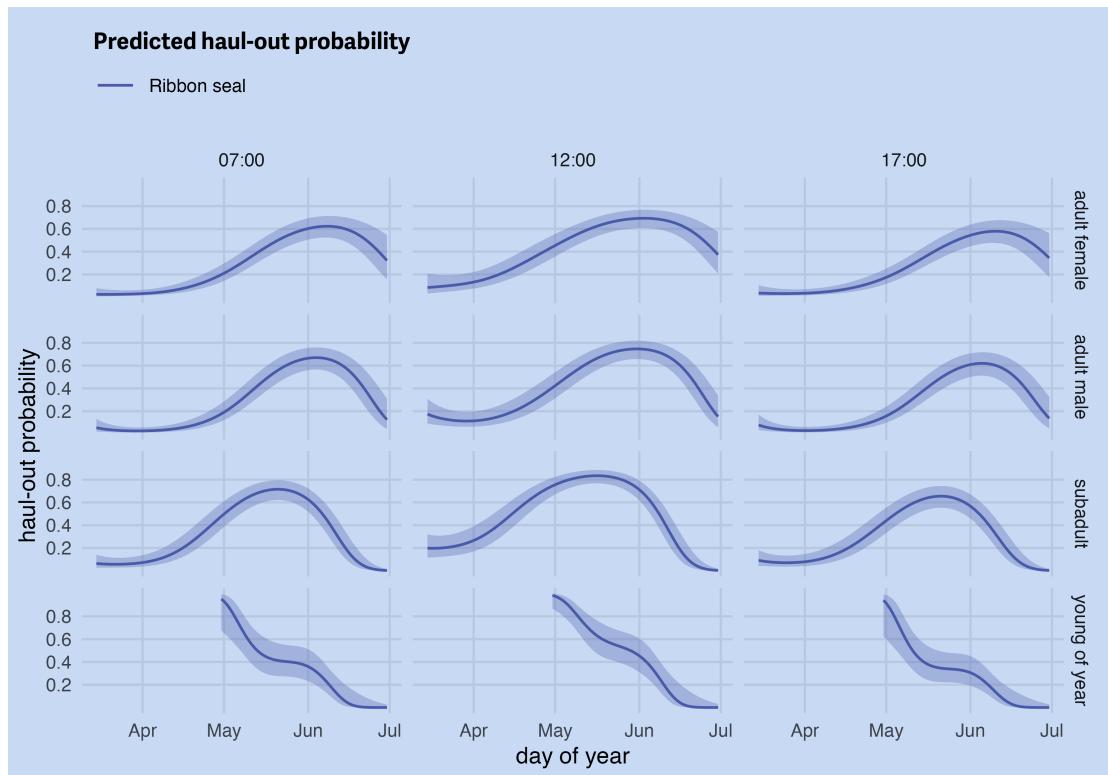


Figure S2. Seasonal variability in haul-out probability and the associated 95% confidence intervals (shaded area) for ribbon seals.

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.

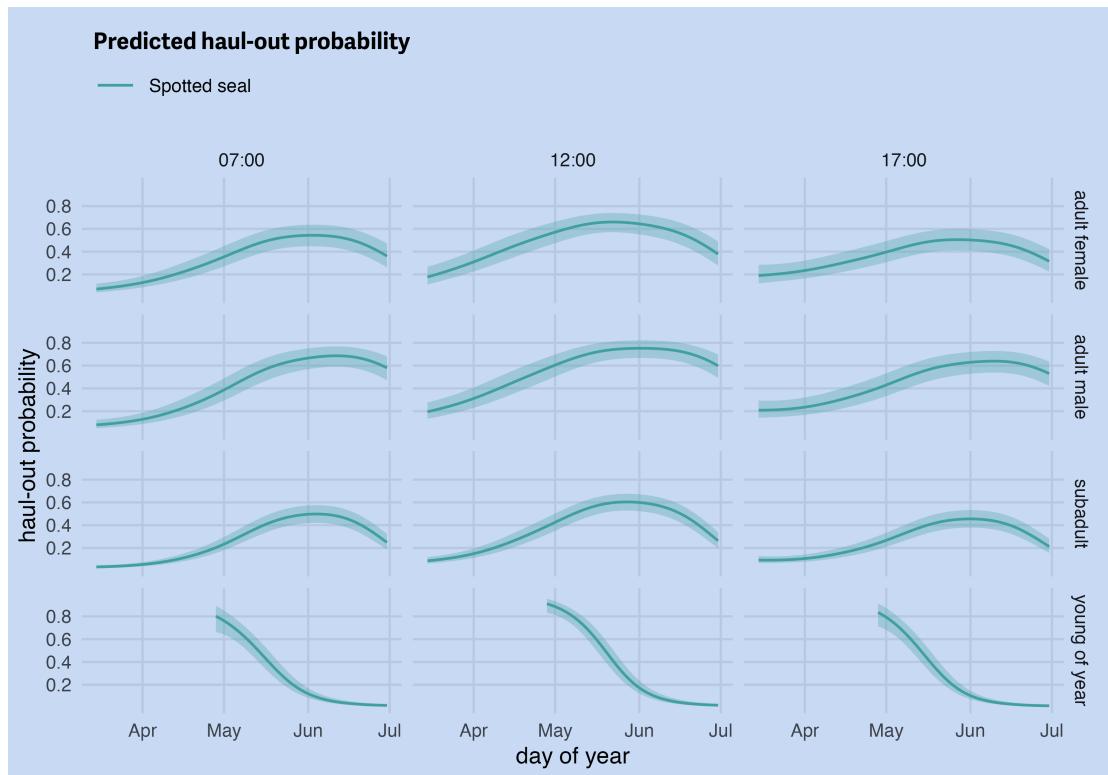


Figure S3. Seasonal variability in haul-out probability and the associated 95% confidence intervals (shaded area) for spotted seals.

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.

790 **0.3 Exploring Insolation (Solar Radiation) as a Model Covariate**

791 **0.3.1 Introduction**

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

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

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

820 **0.3.2 Methods**

821 In this manuscript, we rely on the NARR reanalysis model as the source for our weather covariates.
822 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
823 provides an increased temporal resolution to hourly (compared to the 3-hour resolution of NARR).
824 The global coverage of ERA5 provides additional flexibility in that the area of interest is not limited
825 to North America. The ERA5 model provides a number of solar radiation parameters and it was
826 important to evaluate and understand each of these estimates in order to select the one that was
827 likely most relevant to seals. Here, we used the ‘surface short-wave (solar) radiation downwards’
828 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

834 which most closely represents the amount of solar radiation likely felt by a seal hauled out of the
 835 water.
 836 ERA5 data is available via the Copernicus climate data store API which can be queried with the
 837 CDS-API Python package (<https://cds.climate.copernicus.eu/api-how-to>). The R
 838 code provided here documents the download of the *surface_solar_radiation_downwards* parameter
 839 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,
 840 extra steps are required to download data on either side of the 180 anti-meridian.
 841

```

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 = ":") %>% str_pad(5, "left", "0"),
      format = "netcdf"
    )
  )
}
```

```

    day = str_pad(1:31, 2, "left", "0"),
    time = str_c(0:23, "00", sep = ":") %>% str_pad(5, "left", "0"),
    format = "netcdf"
  )
}

#query to get the ncdf
server$retrieve("reanalysis-era5-single-levels",
                 query,
                 paste0("era5_ssrd_", y, "_right.nc"))

}

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

```

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

852 The model specification below was used to specify an mgcv::bam() model that matched the
 853 formula used in the manuscript for ribbon seals. The s(speno, bs = "re") term is the smooth
 854 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)
```

855 Note, the specification for *m1_ribbon* here does not include any AR1 structure for temporal
856 autocorrelation. To include this, we needed to provide a value for ρ (or *rho*). We examined the
857 autocorrelation within the model and used the lag-1 value for ρ . The value for lag-1 autocorrelation
858 was 0.8082 which is rather high but not surprising. We then updated our model specification with a
859 value for ρ as well as the *A1.start* argument which specifies (as either **TRUE** or **FALSE**) the start
860 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)
```

861 The model specification for exploring the use of solar radiation was specified similarly but without
862 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)
```

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

ERA5 Reanalysis

● downward surface solar radiation

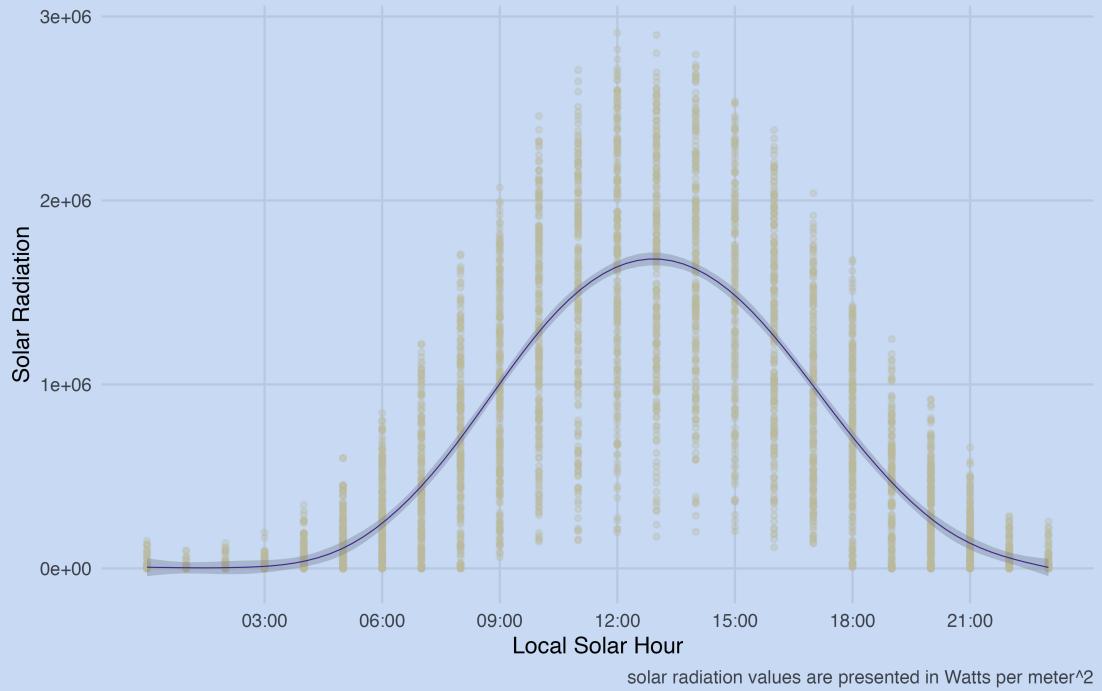


Figure S4. Diel Pattern of Solar Radiation Values from ERA5 Reanalysis.

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 39.619 degrees of freedom and an AIC value of -6797.378. 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 solar radiation resulted in 115.126 degrees of freedom and an AIC value of -16038.175. The spotted seal model matching the specification from the manuscript resulted in 125.506 degrees of freedom and an AIC value of -23584.373. The model with solar radiation resulted in 109.163 degrees of freedom and an AIC value of -23302.772. Despite the additional terms, the models with the Fourier series representation of hour of day resulted in a lower AIC value and were still preferred models for each of the species.

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

0.3.4 Discussion

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

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

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

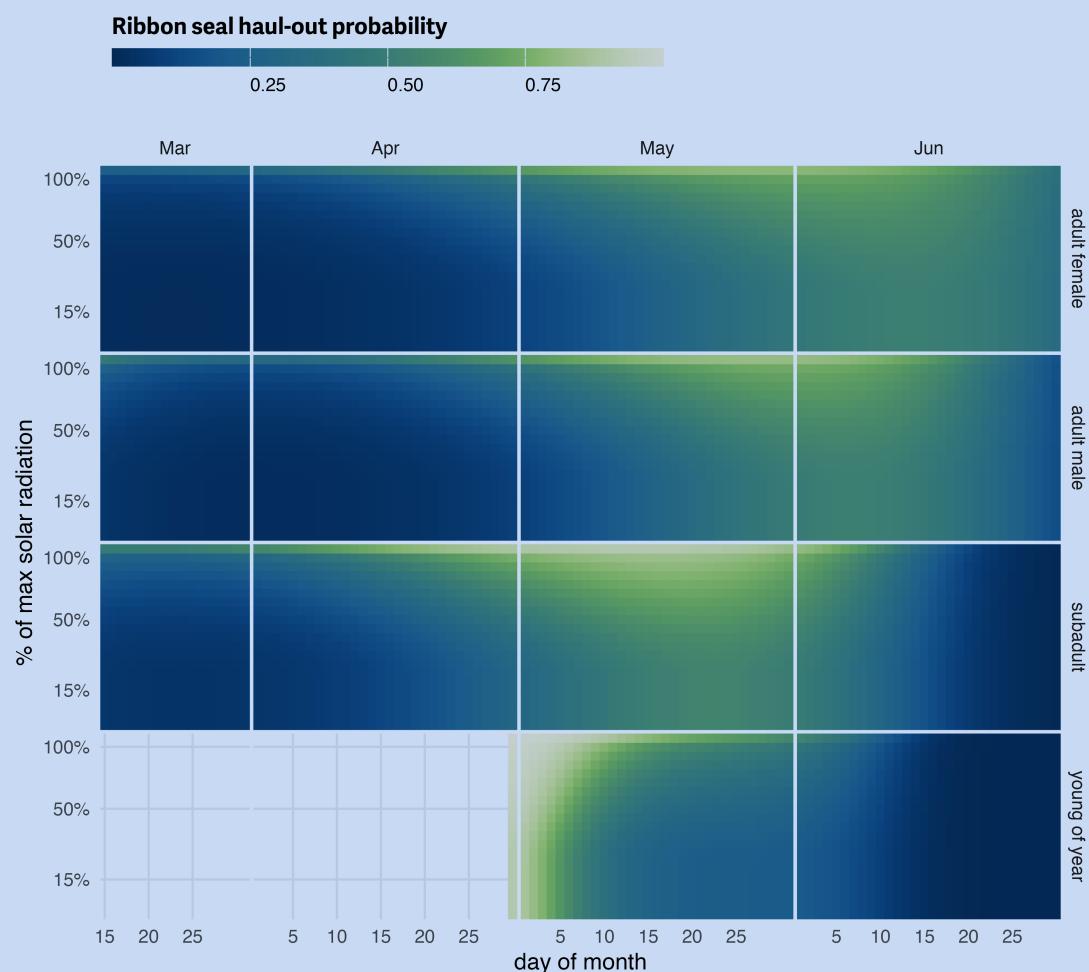


Figure S5. Solar radiation as a predictor of ribbon seal haul-out probability.

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.

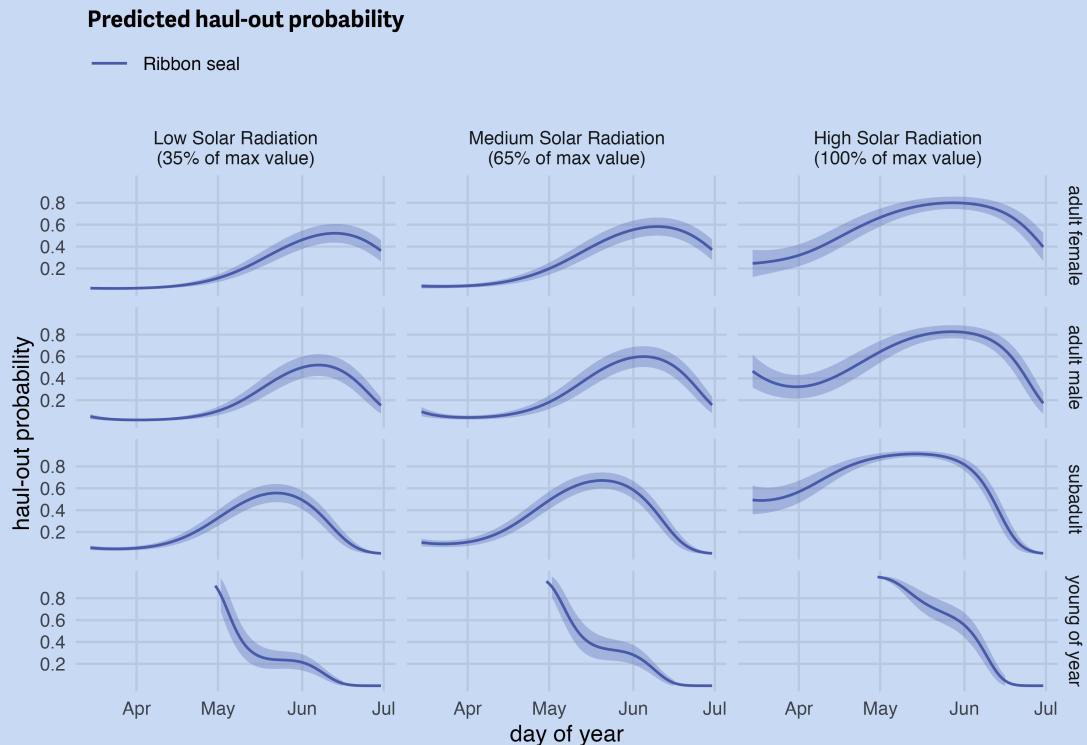


Figure S6. Solar radiation as a predictor of ribbon seal haul-out probability (with uncertainty).

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).