

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

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¹⁵ **ABSTRACT**

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

43 INTRODUCTION

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

60 had, or will have, on seal demography.

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

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

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

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

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

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

¹³¹ METHODS

¹³² Data collection

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

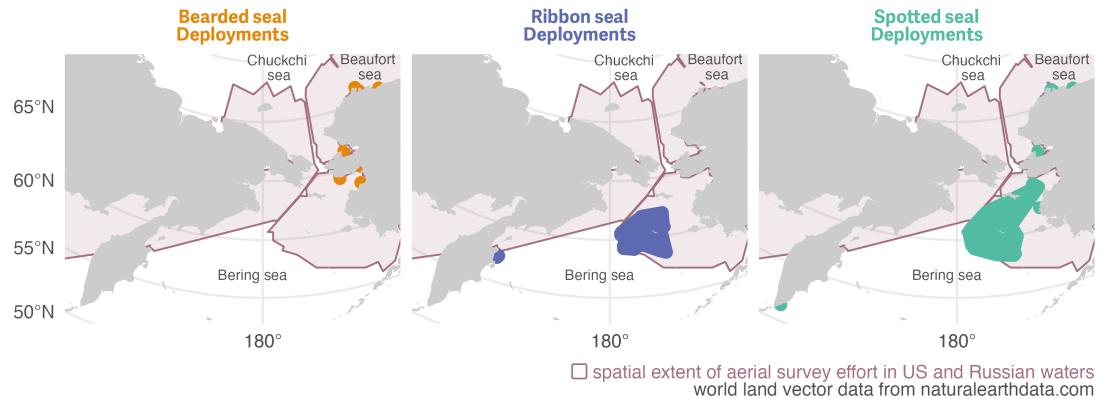


Figure 1. Initial bio getLogger deployment areas for bearded, ribbon, and spotted seals in the study between 2005 and 2020 across multiple regions within the Bering, Chukchi, and western Beaufort seas.

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

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

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

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

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

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

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

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

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

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

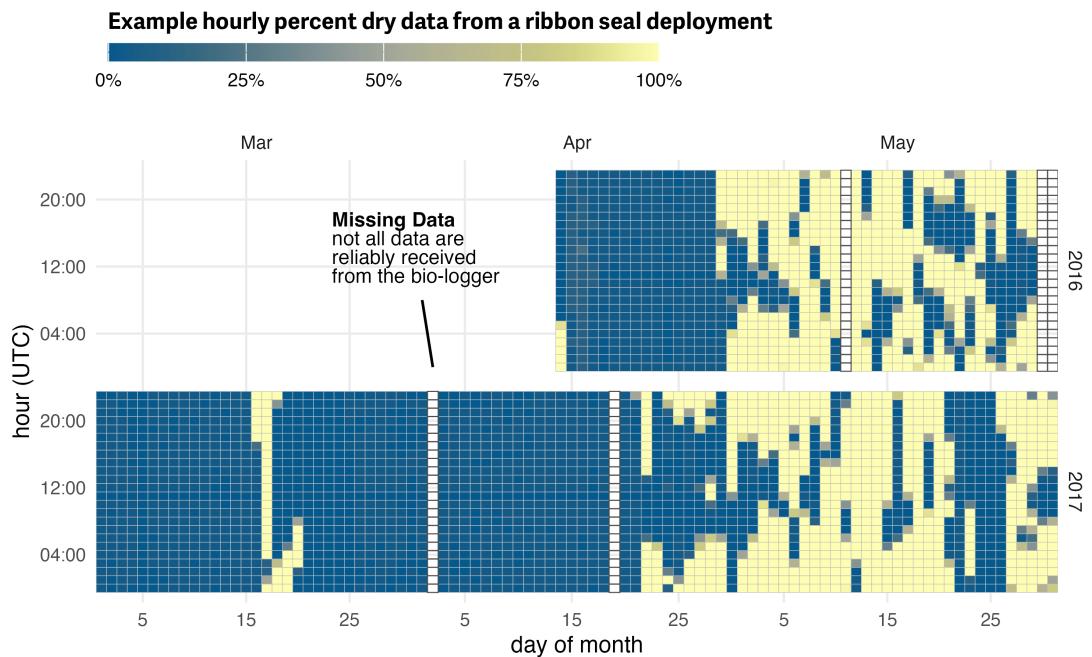


Figure 2. Example percent-dry actogram from bio-logger data

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

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 ($3 = 250 \text{ m}$, $2 = 500 \text{ m}$, $1 = 1500 \text{ m}$, $0 = 2500 \text{ m}$ (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 effects). We calculated local solar hour using the {solaR} package (Perpiñán, 2012) within the R statistical environment (R Core Team, 2021) based on the weighted daily average locations. We also linked the weighted average daily locations to weather values from the North American Regional Reanalysis (NARR) model produced by the National Centers for Environmental Prediction (Mesinger et al., 2006). The NARR model assimilates observational data to produce a long-term picture of weather over North America and portions of the surrounding seas. Weather variables are made available across the region 8 times daily. For this study, NARR weather values were limited to the extent of our study area over the Bering, Chukchi, and Beaufort seas at 3-hr intervals based on the original grid resolution of 32 km (1024 km²). The following weather variables are known to affect haul-out behavior in other Arctic pinnipeds (Reder et al., 2003; Udevitz et al., 2009; Perry, Stenson & Buren, 2017) and were interpolated and assigned to daily seal locations using a bilinear method: 1) air temperature at 2 m above the Earth's surface, 2) wind consisting of northerly and easterly vector components converted to wind speed using the Euclidean norm, 3) barometric pressure at sea level, and 4) precipitation (Table 2).

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

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

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

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

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

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

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

245 Haul-out modeling

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

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

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

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

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

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

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

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

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

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

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

324 RESULTS

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

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

343 Bearded Seals

344 Age and sex class were not included in the model for bearded seals due to our lower sample size for
345 adult and young-of-year age classes. As such, results are shown for all ages (Figure 5; see also S1).

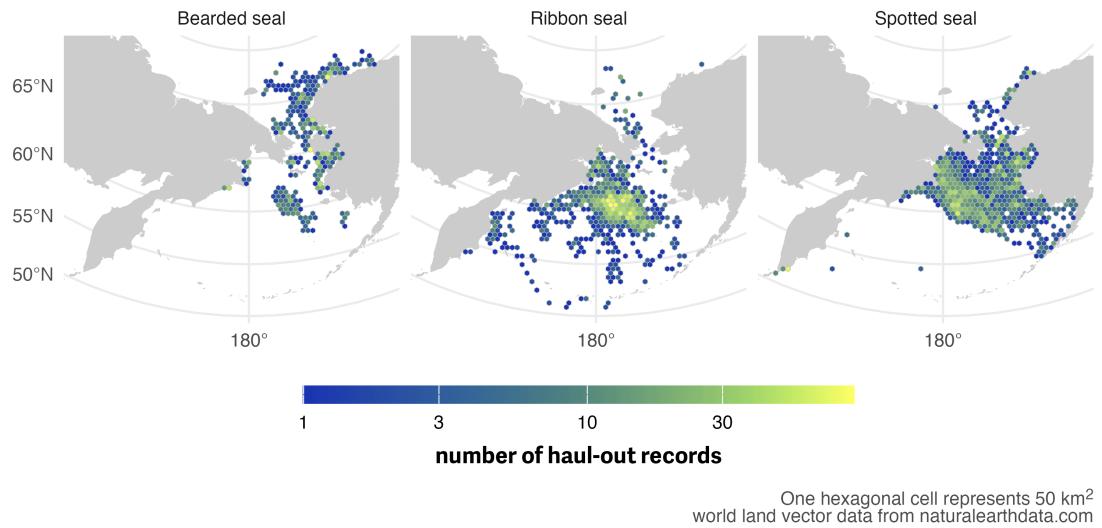


Figure 3. Spatial distribution of haul-out records from 1 March through July 15 for bearded, ribbon, and spotted seal.

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

346 Additionally, after approximately 9 months, 7 devices deployed on the rear flipper of bearded seals
 347 reported implausible hourly percent-dry data (100% dry for several weeks but indicative of movement
 348 and increasing transmission rates (see Boveng & Cameron (2013))). All data after the first instance of
 349 unrealistic values were censored from this analysis. In addition to a peak around local solar noon, the
 350 bearded seal model predicted additional haul-out activity around local midnight. In concert with the
 351 lower magnitude of haul-out probability, bearded seal haul-out behavior was also more protracted
 352 throughout the spring season compared to ribbon and spotted seals (see below). Overall, bearded
 353 seals were less likely to haul out and had a bi-modal distribution of haul-out probability across the
 354 day.
 355

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

361 **Ribbon Seals**

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

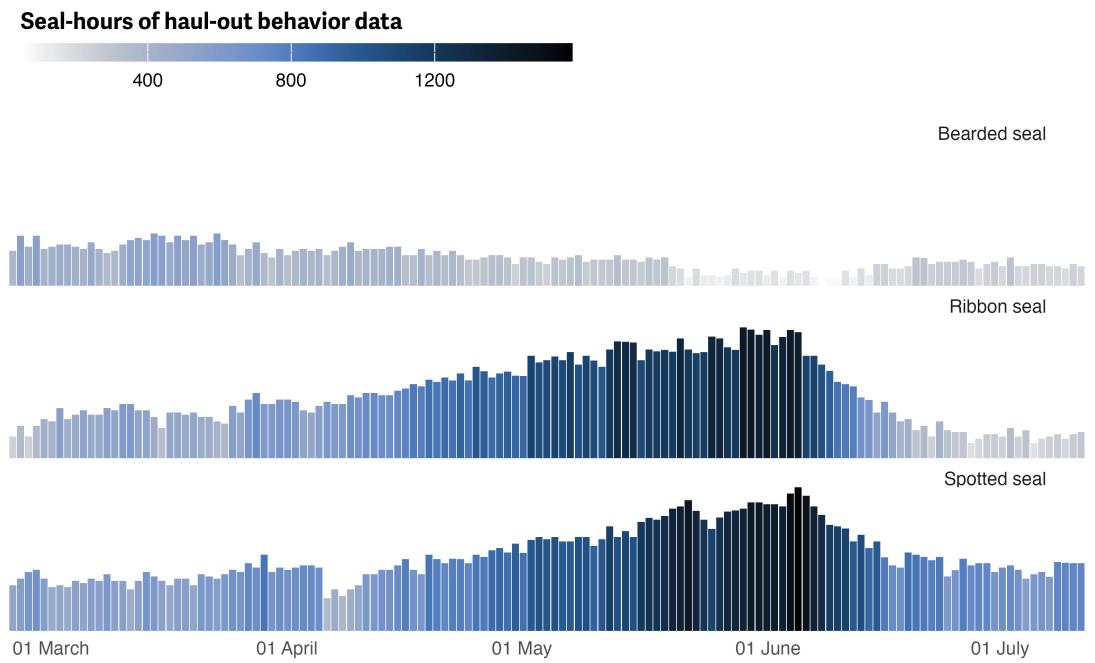


Figure 4. Seasonal distribution of haul-out behavior observations by species

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.

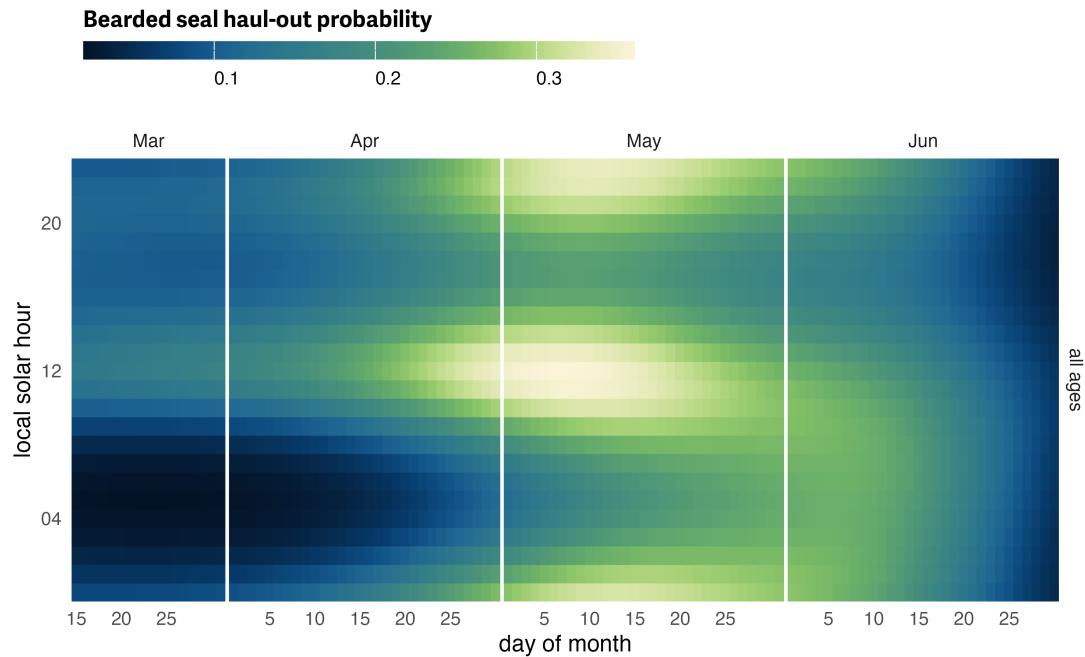


Figure 5. Bearded seal predicted haul-out probability

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.

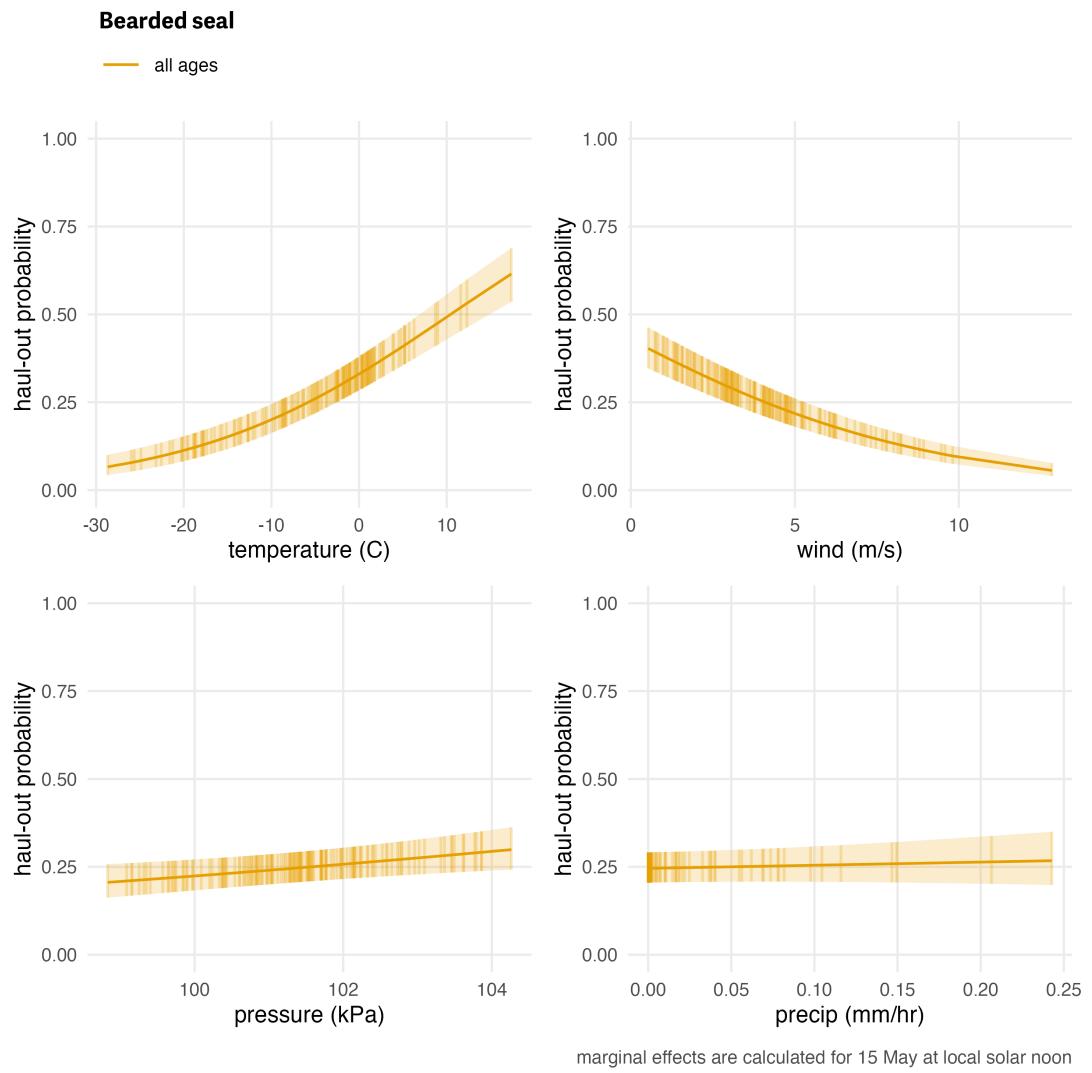


Figure 6. Influence of weather covariates on bearded seal haul-out probability

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.

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

372 The haul-out probability for ribbon seals was mostly influenced by temperature ($F_{1,99540} = 6.87$;
373 $p = 0.009$) and wind ($F_{1,99540} = 49.314$; $p = <0.001$) with barometric pressure ($F_{1,99540} = 3.446$; p
374 = 0.063) having a milder impact. Ribbon seals were more likely to haul out when temperatures
375 were relatively warm and less likely to haul out at higher winds and lower pressure values (Figure
376 8). Neither wind chill ($F_{1,99540} = 1.83$; $p = 0.176$) nor precipitation ($F_{1,99540} = 0$; $p = 0.989$) were a
377 significant influence on haul-out probability. Compared with bearded seals, the effect of weather
378 covariates on the predicted haul-out probability for ribbon seals was less striking. Because our ribbon
379 seal model included age and sex class, we can visualize the different influences of weather covariates
380 on those classes and see that subadults differ from adult males and females (Figure 8).

381 **Spotted Seals**

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

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

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

402 The second set of models, which included annual variation in haul-out patterns, uncovered significant
403 contributions for linear and quadratic interactions between day and year for only spotted seals
404 (day:year, $F_{15,115144} = 4.445$; $p = <0.001$; day²:year, $F_{15,115144} = 5.854$; $p = <0.001$). Ribbon seals
405 showed no significant contribution for interactions between day and year (day:year, $F_{10,99510} = 0.516$;
406 $p = 0.880$; day²:year, $F_{10,99510} = 0.549$; $p = 0.856$). Predicted distributions of haul-out activity were
407 largely unimodal, but varied some among and within years with respect to the timing and magnitude
408 of haul-out peaks (Figure 11). It is important to note that predicted variation in annual haul-out
409 patterns likely reflected both process error and sampling variability. While we did remove any years
410 where only one deployment in a species + age:sex group was present, there were still some years

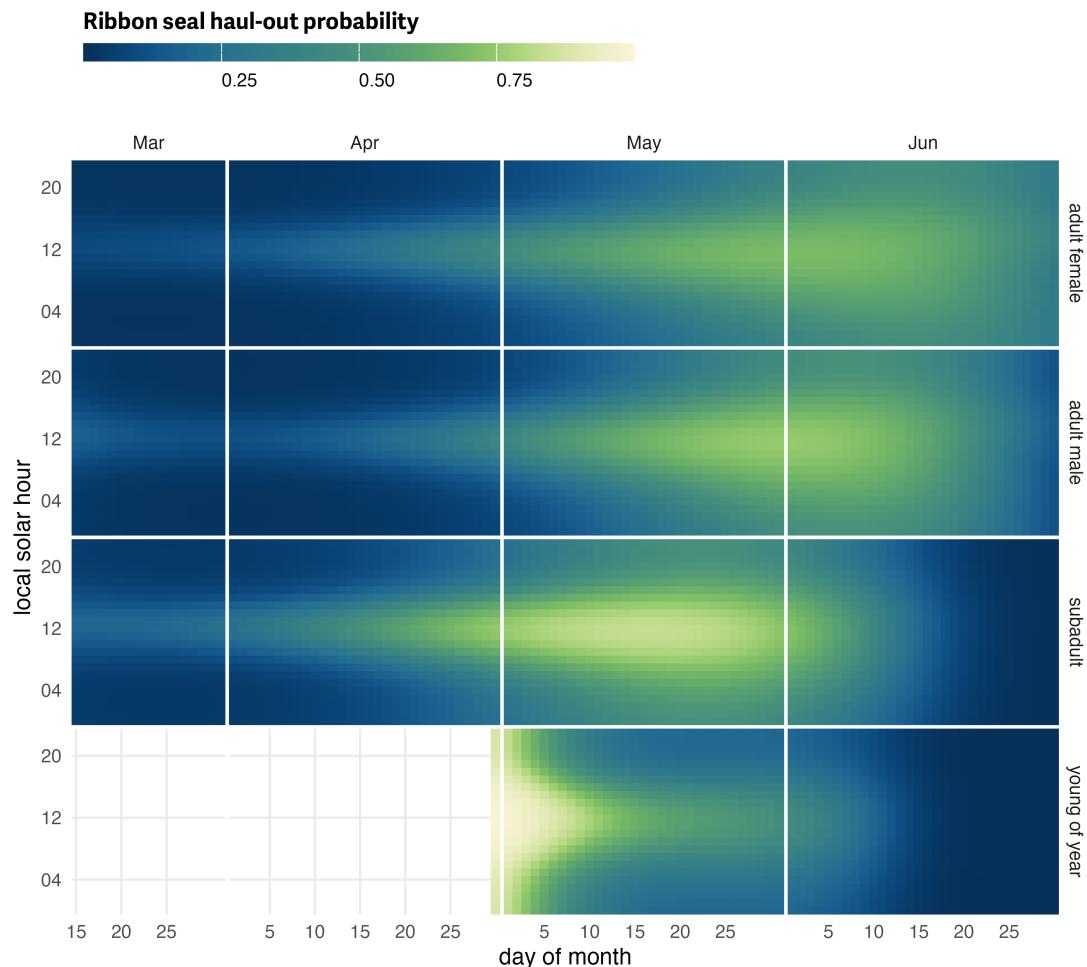


Figure 7. Ribbon seal predicted haul-out probability

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

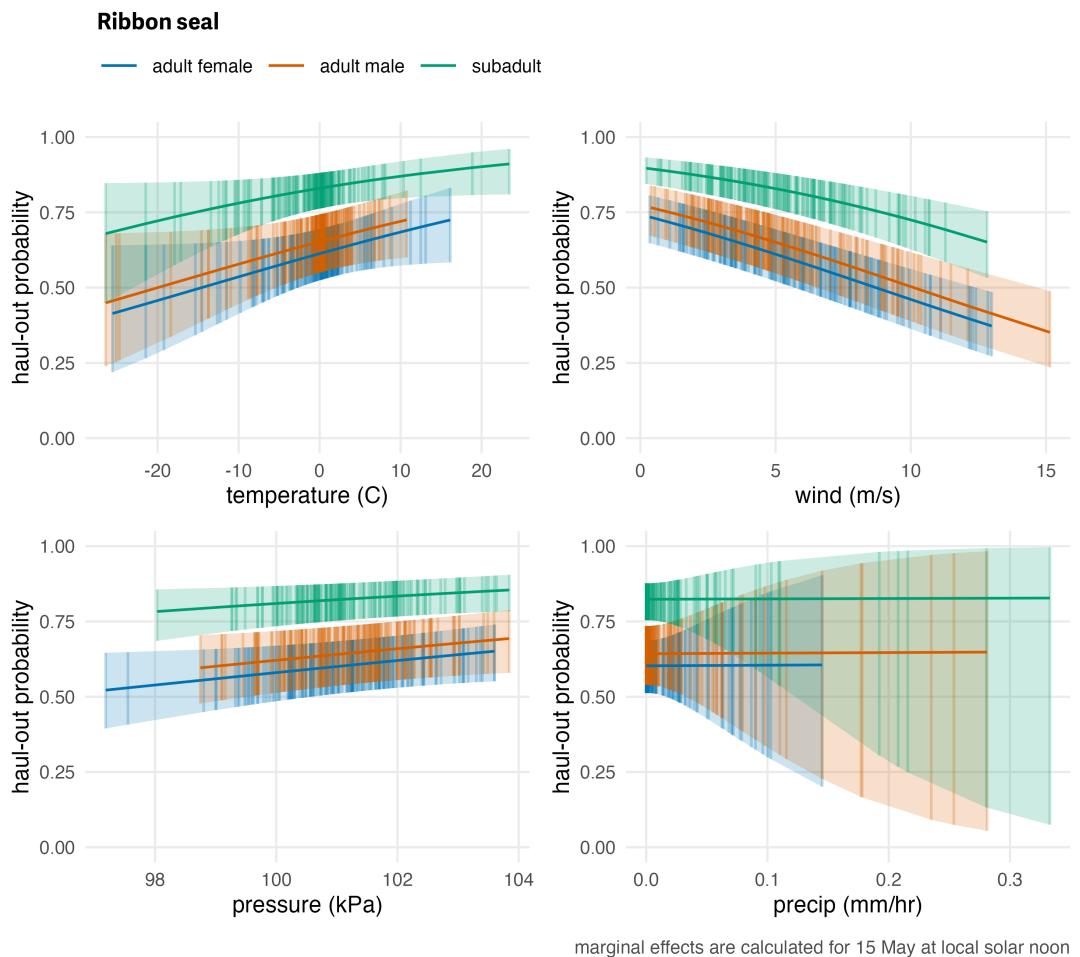


Figure 8. Influence of weather covariates on ribbon seal haul-out probability

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

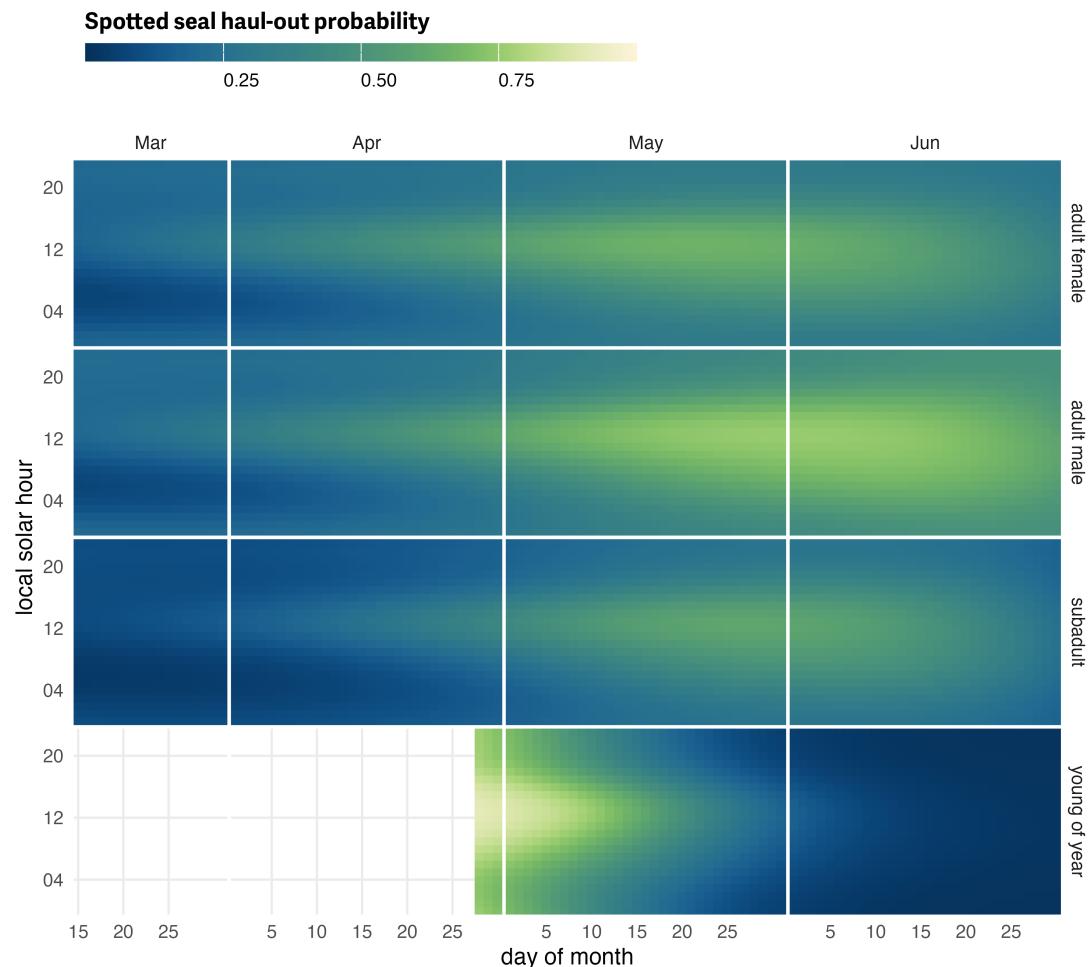


Figure 9. Spotted seal predicted haul-out probability

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

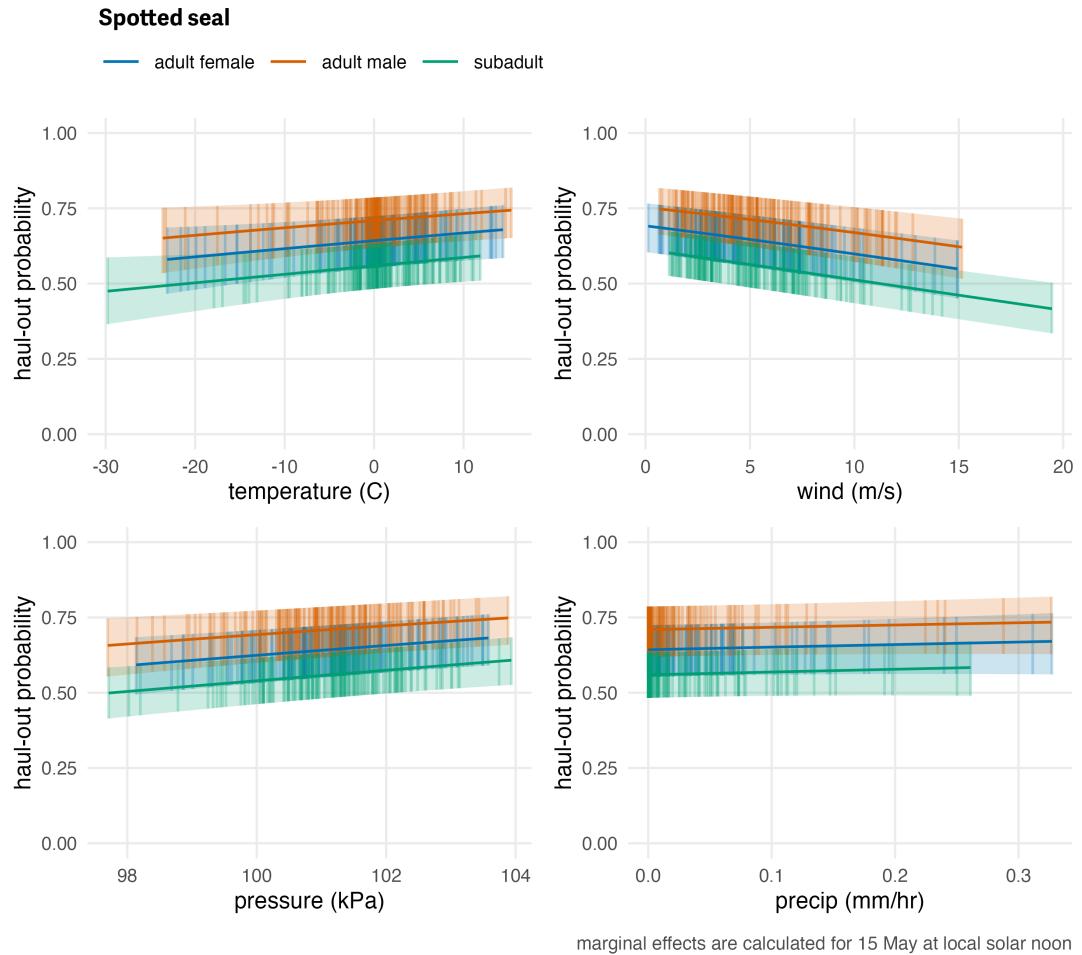


Figure 10. Influence of weather covariates on spotted seal haul-out probability

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

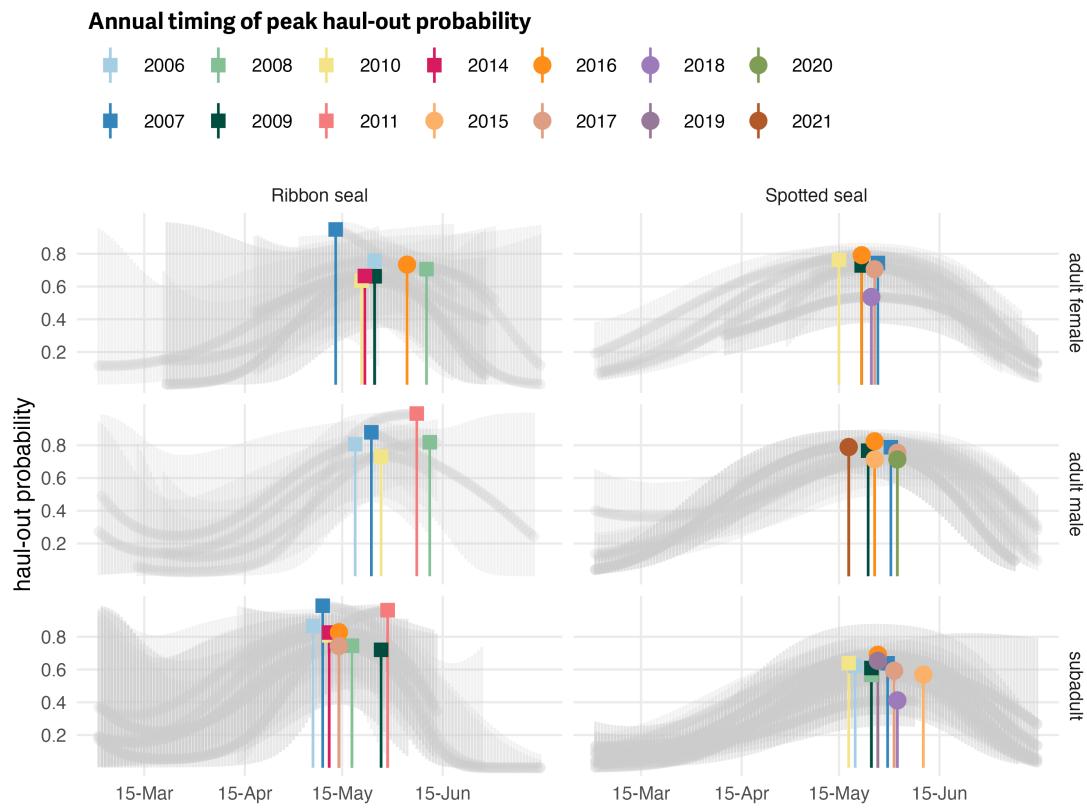


Figure 11. Annual variability in the timing of peak haul-out probability for ribbon and spotted seals.

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

411 where the pattern shown was informed by a small number of individuals that may not represent
412 population-level patterns.

413 The annual timing of peak haul-out probability for ribbon seals and adult male spotted seals
414 appeared to have no relationship with the amount of yearly maximum sea-ice extent in the study area.
415 For ribbon seals and adult male spotted seals, p -values were substantially larger than 0.05 (ribbon
416 seal adult females: $R^2 = 0.004$, $p = 0.896$; ribbon seal adult males: $R^2 = 0.059$, $p = 0.693$; ribbon seal
417 subadults: $R^2 = 0.007$, $p = 0.828$; spotted seals adult males: $R^2 = 0.004$, $p = 0.889$). Adult female and
418 subadult spotted seals both showed a negative trend (peak haul-out occurs later in years with less
419 sea ice) with a significant relationship for adult female spotted seals (spotted seal adult female: $R^2 =$
420 0.456, $p = 0.141$; spotted seal subadults: $R^2 = 0.369$, $p = 0.062$).

421 **DISCUSSION**

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

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

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

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

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

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

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

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

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

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

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

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

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

573 AUTHOR CONTRIBUTIONS

- 574 • **Josh M. London:** investigation, conceptualization, methodology, formal analysis, validation,
575 software, writing: original draft, writing: review and editing, visualization, and data curation
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589 and editing
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591 review and editing

592 DATA AVAILABILITY

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

595 2022.04.07.487572). All data used in the study and code are available on GitHub
596 (<https://github.com/noaa-afsc/berchukseals-haulout>) and major versions
597 archived at Zenodo (<https://doi.org/10.5281/zenodo.4638221>). Original data sources
598 for telemetry are archived as part of datasets at the United States Animal Telemetry Network
599 (<https://portal.atn.ioos.us/>; <https://doi.org/10.24431/rw1k8er>), archived
600 at Movebank (see Movebank ID 732321226), or associated with other published manuscripts
601 (see supplemental material S1). Collated and cleaned data products needed to replicate the
602 analysis along with the results of all model fits are also available and versioned as an R package on
603 GitHub (<https://github.com/noaa-afsc/berchuksealsHauloutFits>) and archived
604 at Zenodo (<https://doi.org/10.5281/zenodo.10056308>).

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