Haul-out behavior and aerial survey detectability of seals in the Bering and Chukchi seas

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## Abstract

Ice-associated seals rely on sea ice for a variety of activities, including breeding, molting, pupping, and resting. In the Arctic, many of these activities occur in spring and early summer (April-June) as sea ice begins to melt and retreat northward. Rapid acceleration of climate change in Arctic ecosystems is thus of concern as the quantity and quality of suitable habitat is forecast to decrease. In this paper, we use data collected from satellite-linked telemetry tags deployed between 2005 and 2020 to investigate the seasonal timing and environmental factors affecting sea ice use by seals (specifically, bearded, ribbon, and spotted seals) in the Bering, and Chukchi seas. In addition to providing baseline data on phenology, these data also allow us to refine availability estimates needed to accurately estimate abundance from aerial survey counts of seals basking on ice (i.e., to correct for the proportion of animals that are in the water while surveys are conducted). Using generalized linear mixed pseudo-models to properly account for temporal autocorrelation, we fit models with a variety of covariates (e.g., day-of-year, solar hour, age-sex class, wind speed, barometric pressure, temperature, precipitation) to examine their ability to explain variation in hourly haul-out records. We found evidence for strong diurnal and within season patterns in haul-out behavior, as well as strong weather effects (particularly wind and temperature). In general, seals were more likely to rest on ice in the middle of the day and when wind speed was low and temperatures were higher. Haul-out propensity increased through March and April, peaking in May and early June before declining again. The timing and frequency of haul-out events also varied based on species and age-sex class. For ribbon and spotted seals, models with year effects were highly supported, indicating that the timing and magnitude of haul-out behavior varied among years. There was no support linking the variability in haul-out timing to annual sea ice extent. Our analysis also emphasizes the importance of accounting for weather factors affecting haul-out behavior when interpreting the number of seals counted in aerial surveys.

keywords: availability; generalized linear mixed pseudo-model; haul-out behavior; phenology; Phocidae; sea ice

# Introduction

The global climate crisis is causing considerable reduction in Arctic sea ice extent, volume, and seasonal presence [[1](#ref-kwok2018erl)–[3](#ref-wang2017dsrpitsio)]. These changes have ripple effects on Arctic ecosystems, taxa, and the human communities who live in the region [[4](#ref-huntington2020ncc)]. Such disruptions are a particular cause of concern for ice-associated seals (ringed, bearded, spotted, and ribbon seals) which depend on spring and early summer sea ice (March-June) in the Bering and Chukchi seas as a platform for important functions such as pupping, nursing, breeding, and molting [[5](#ref-boveng2009a)–[8](#ref-kelly2010)]. Limited data and large knowledge gaps prevent our ability to make definitive predictions about the ultimate effects of changes in sea ice on the behavior, abundance, and distribution of these seals. Knowledge about biological constraints on the phenology of reproductive and molting behavior is generally lacking, so it is difficult to predict the readiness with which ice-associated seal species will be able to adapt to future changes (e.g., by adjusting pupping or molting schedules to earlier dates or different locales). Additionally, trends in abundance of these species are largely unknown, so it is difficult to say what effect, if any, declines in sea ice habitat have had, or will have, on seal densities.

For ice-associated seals, haul out is tightly linked with sea ice. Ribbon seals rest out of the water almost exclusively on sea ice and are mostly pelagic outside the spring pupping, breeding, and molting season [[9](#ref-burns1981)]. While spotted and bearded seals do rest on beaches during ice-free months, they strongly prefer sea ice as a resting platform during the spring and early summer [[10](#ref-burns2009)]. The very remote nature of the Bering and Chukchi seas mean direct observation of seal behavior is limited. Bio-logging devices are, thus, especially useful tools for collecting key information on movement and haul-out behavior for these species. Records of time spent out of the water provide valuable data for identifying covariates that explain variation in haul-out behavior. For instance, in the Antarctic, Bengtson and Cameron [[11](#ref-bengtson2004pb)] relied on bio-logging data to demonstrate greater haul-out propensity in juvenile crabeater seals (*Lobodon carcinophaga*) than adults, with highest probabilities in February and at times close to solar noon. In the Arctic, Von Duyke et al. [[12](#ref-vonduyke2020ee)] demonstrated seasonal changes between diurnal and nocturnal haul-out behavior of ringed seals. Bengtson et al. [[13](#ref-bengtson2005pb)] documented a higher propensity for ringed seal basking near solar noon, as did Ver Hoef et al. [[14](#ref-verhoef2014sm)] in an analysis of bearded (*Erignathus barbatus*), ribbon (*Histriophoca fasciata*), and spotted (*Phoca largha*) seals using much larger sample sizes. Olnes et al. [[15](#ref-olnes2020pb)] showed that the proportion of time bearded seals spent hauled out progressively increased through spring and summer. And, Ver Hoef et al. [[14](#ref-verhoef2014sm)] found haul-out probabilities increased gradually starting in March and peaking in May and June for bearded, ribbon, and spotted seals. However, their primary focus was estimating seal abundance, and like a subsequent analysis by Conn et al. [[16](#ref-conn2014mee)], they did not attempt to separately analyze haul-out schedules for different age and sex classes (although initial models with sex and age as fixed effects were insignificant at p = 0.05; [[14](#ref-verhoef2014sm)]).

Several authors have used logistic regression-style analyses to estimate the probability of sea ice use from data garnered from bio-loggers. In these models, haul-out probabilities are expressed as a function of predictive covariates, such as time of day, day-of-year, sex, age class, and environmental conditions (e.g., [[17](#ref-reder2003pb)], [[11](#ref-bengtson2004pb)], [[13](#ref-bengtson2005pb)], [[18](#ref-udevitz2009cjz)], and [[14](#ref-verhoef2014sm)]). However, sample sizes have often been low and insufficient to permit strong inference about life history and/or seasonal variation in haul-out probabilities. For instance, Bengtson and Cameron’s [[11](#ref-bengtson2004pb)] study included 5 adult and 2 juvenile crabeater seals, while Bengtson et al.’s [[13](#ref-bengtson2005pb)] study was based on 6 telemetered ringed seals (*Phoca hispida*) in the Chukchi Sea. These studies are often further limited by logistical constraints on tagging fieldwork and the attachment duration or operational life of satellite tags.

Ultimately, knowledge of trends in phenology and abundance (or life history surrogates such as survival and recruitment) will be necessary to make credible quantitative predictions about the effects of the climate crisis on the abundance and distribution of Arctic seal populations. Before we can construct a trend, however, we first need credible data points. Several studies have contributed estimates of the distribution and abundance of ice-associated seal species in the Arctic using aerial surveys (e.g., [[13](#ref-bengtson2005pb)], [[16](#ref-conn2014mee)], and [[14](#ref-verhoef2014sm)]). Such studies are conducted over very large areas and estimation of absolute abundance requires making inference about numerous nuisance processes affecting the observation of seals on ice. This includes availability (only seals basking on ice are available to be counted), detection probability (observers or automated detection systems may miss some seals on ice), species misclassification, and possible disturbance of seals by aircraft [[14](#ref-verhoef2014sm),[16](#ref-conn2014mee)].

In this study, we use data from fifteen years of bio-logger records in a comprehensive investigation of haul-out behavior by three ice-associated seals in the Bering and Chukchi Seas. We focused our effort on bearded, spotted, and ribbon seals and do not include ringed seals the analysis. Ringed seals are unique in their use of snow lairs in the spring months and they warrant a separate study that includes additional environmental covariates such as the onset of snow melt and snow depth. Our goals are threefold. First, we wish to establish baseline estimates for the chronology of haul-out behavior in the critical spring season for each species across different age and sex classes. Second, we wish to refine estimates of haul-out availability corrections for aerial surveys in order to improve estimates of seal abundance. Previously estimated availability correction factors (e.g., [[13](#ref-bengtson2005pb)], [[16](#ref-conn2014mee)], and [[14](#ref-verhoef2014sm)]) accounted for variables such as the time-of-day and day-of-year, but did not investigate meteorological variables that have been shown to influence haul-out behavior of walruses [[17](#ref-reder2003pb),[18](#ref-udevitz2009cjz)]. Further, previous correction factor analyses assumed that tagged seals were representative of the population as a whole, even though the age and sex distribution of telemetered individuals might differ from the population. Third, we explore the annual variability in haul-out timing and possible linkage to dramatic changes in the availability and extent of seasonal sea ice between 2005 and 2020. Our work extends the scope of previous haul-out analyses, includes the influence of meteorological variability and possible ramifications of non-representative age-sex samples, and investigates the potential impact of a changing icescape on the behavior of these species.

# Methods

## Data collection

Haul-out behavior data from 203 bio-loggers deployed on bearded, spotted, and ribbon seals was subset to include only records from 1 March to 15 July between 2005 and 2020. Bio-loggers were of the ‘SPLASH’ or ‘SPOT’ family of tags developed by Wildlife Computers (Redmond, Washington, USA) and either adhered to the hair on the seal or attached to the rear flipper inter-digital webbing. The use of bio-loggers adhered to the back or head provide some benefits over flipper mounted devices (e.g. increased satellite transmittal rates, locations at sea) but these are lost during the annual molt and limits the effective length of haul-out timelines. Additionally, sensors attached to the head or dorsal region are often dry while the seal is at the surface and can slightly bias the percent-dry values recorded by the device. For this study, in cases where both tag types were deployed, percent dry observations from the flipper tag were usually preferred. Sex and age class were determined at the time of deployment by experts in the field. Seals determined to be less than one year were classified as young of the year. subadults are those seals likely greater than one year of age but not yet sexually mature. Adults are likely sexually mature and older than approximately four years. For those tags deployed on young of the year and transmitting into the next year, the age class was advanced to subadult on March 1 of the following year. Table provides a summary of these deployments and data received from them.

Table : Summary of bio-logger deployments across seal species and age classification from 1 March to 15 July. Total seal hours represents the sum of available data across all seals.

|  | | Age Class | | |
| --- | --- | --- | --- | --- |
| Species | Sex | Adult | subadult | Young of Year |
| Bearded seal | F | 1 (1776 seal hours) | 6 (8760 seal hours) |  |
| Bearded seal | M | 2 (1676 seal hours) | 7 (9048 seal hours) |  |
| Ribbon seal | F | 32 (35104 seal hours) | 18 (15984 seal hours) | 13 (3734 seal hours) |
| Ribbon seal | M | 24 (27465 seal hours) | 19 (13046 seal hours) | 9 (4275 seal hours) |
| Spotted seal | F | 20 (18446 seal hours) | 11 (11643 seal hours) | 11 (13417 seal hours) |
| Spotted seal | M | 16 (25966 seal hours) | 11 (11816 seal hours) | 12 (11285 seal hours) |

Tags that fall off due to molt or mortality and remain on ice or land can still send data to satellites and we did not want to include data from these tags in our analyses. As such, start and end times of each deployment were made by experts who examined several simultaneous data streams (e.g., tag locations and dive behavior) to determine when tags ceased providing data consistent with seal behavior. Sensor readings outside of these start and end times were discarded prior to analysis. After approximately 9 months, a few (7) devices deployed on the rear flipper of bearded seals reported implausible sensor data. All data after the first instance of unrealistic values were censored from this analysis. Figure shows a calendar distribution of these data across the study season for each species. Observations are concentrated in the months of May and June due to the timing of deployment (April and May) and the timing of molt (May and June). During molt, seals (and their attached bio-loggers) spend more time out of the water and more data is transmitted. Molt timing also impacts when many deployments end as any tags adhered to the hair will fall off.

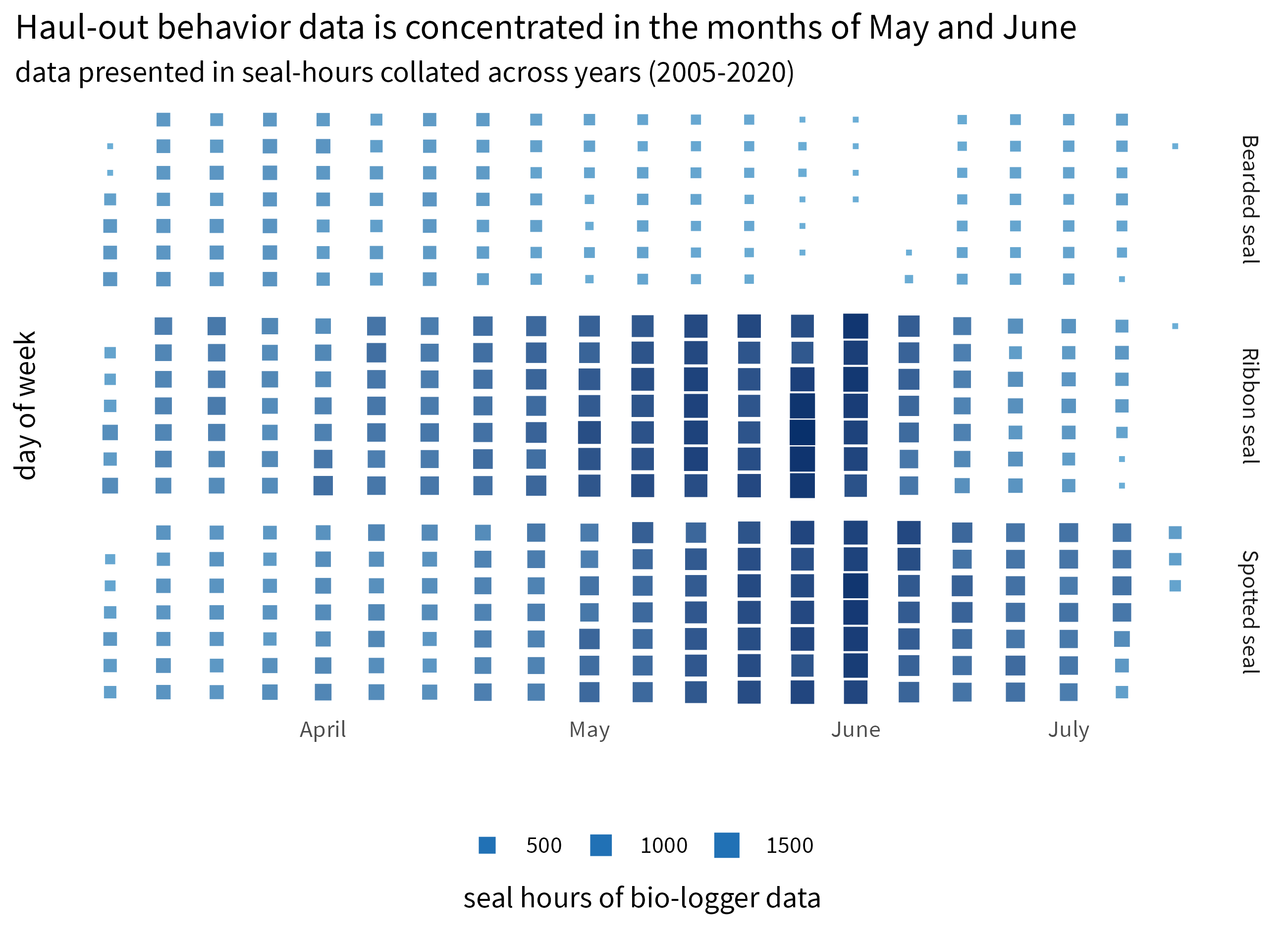


Figure : Distribution of of haul-out behavior data from 1 March to 15 July for each species. The higher density of data from May and June coincides with peak molting when seals (and their attached bio-loggers) are more likely hauled out. Additionally, a majority of deployments started in April and May. Data were collated across all years between 2005 and 2020.

Haul-out behavior data was recorded and transmitted via the Argos satellite network as hourly percent-dry timelines. For each hour of a day, the wet/dry sensor was polled by the tag firmware every few seconds and a percent of the hour in a dry state was calculated (). Each data transmission message consisted of a complete 24-hour record. Tags were deployed and programmed in a manner to maximize data transmission during the spring pupping and molting period. However, not all days during the deployment were successfully transmitted. This is due to a variety of factors including satellite coverage, tag availability (i.e. tags mounted to the rear flipper are not available to the surface while the seal is at sea), tag performance, duty cycling, and extra-terrestrial interference.

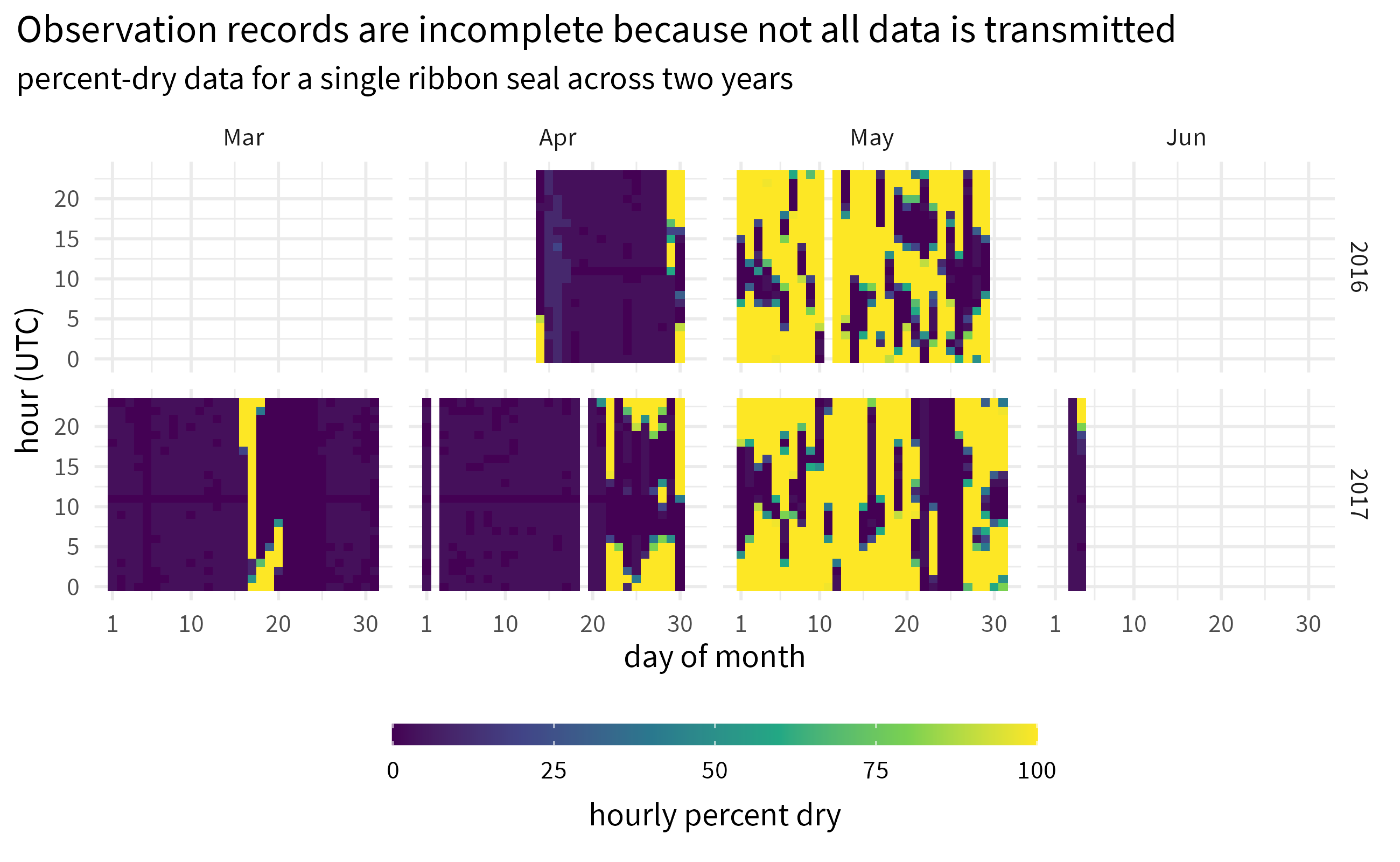


Figure : Haul-out behavior observations recorded by a bio-logger deployment on a ribbon seal over two years during the months of March, April, May, and June. Empty areas of the plot represent missing data that was not successfully transmitted from the tag

Of key interest in this study is the relationship between haul-out behavior and a variety of environmental covariates that vary with space and time. We explored use of a movement model to predict locations at specific times. However, the sparse nature of data from some tags, 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 location error was used for the weight. Any days where haul-out observations were present without any location data were filled from the last calculated daily location and any days where the location intersected with land were removed from the dataset. Figure shows the spatial distribution of available haul-out behavior data for each species across the study area.

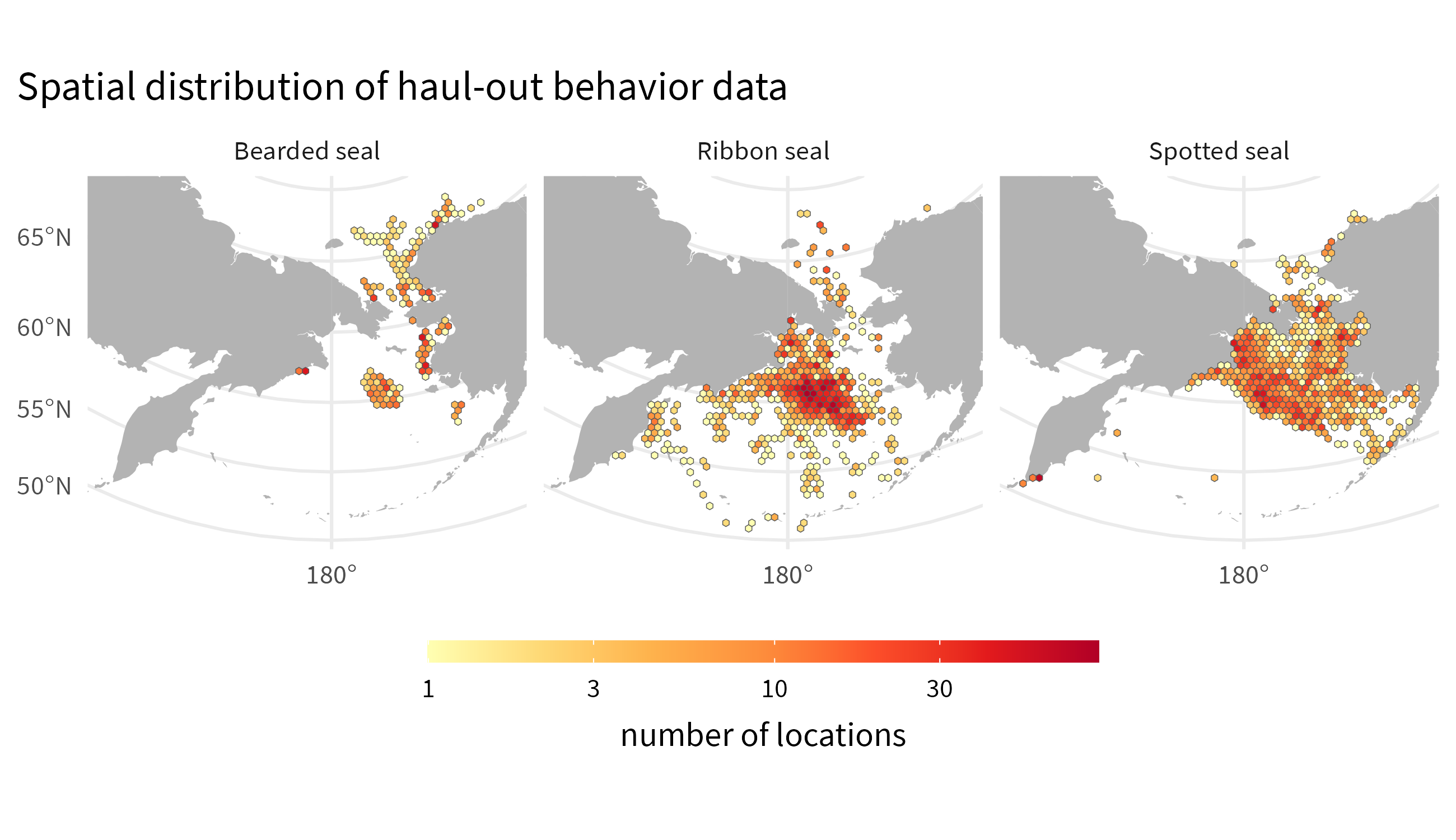


Figure : Spatial distribution of haul-out data during the months of March through July for each of the three species. Data were collated across all years between 2005 and 2020.

## Explanatory variables

In addition to sex and age class (non-dependent *young of the year*, sexually immature *subadults*, and mature *adults*), we gathered additional variables that might help explain variation in haul-out probabilities. These included day-of-year (for seasonal effects) and solar hour (for diurnal effects). Solar hour was calculated using the {solaR} package [[19](#ref-perpinan2012jss)] within the R statistical environment [[20](#ref-rcoreteam2019)] using the daily locations. We also compiled several meteorological variables shown to affect haul-out behavior in other Arctic pinnipeds [[17](#ref-reder2003pb),[18](#ref-udevitz2009cjz),[21](#ref-perry2017)]. In particular, we linked locations from satellite tags to key weather values from the North American Regional Reanalysis (NARR) model produced by the National Centers for Environmental Prediction [[22](#ref-mesinger2006bams)]. The NARR model assimilates observational data to produce a long-term picture of weather over North America. Numerous weather variables are made available across the region 8 times daily. For this study, NARR weather values were subset to the extent of our study area over the Bering and Chukchi Seas at 3-hr intervals based on a grid resolution of 32 km (1024 sq. km) The following meteorological variables were interpolated and assigned to seal locations using a bilinear method: 1) air temperature at 2m 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 ).

Models for all species include the following effects: day-of-year, solar hour, temperature, wind speed, barometric pressure, precipitation, and wind chill (represented by a wind temperature interaction; [[18](#ref-udevitz2009cjz)]), together with day-of-year and time of day interactions to permit diurnal patterns to change throughout the year). Spotted and ribbon 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 ). Bearded seal models did include a latitudinal effect (and an interaction with day-of-year) since bearded seals occupy a substantial range 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 since, during the spring, these species are most prevalent near the southern ice edge in the Bering Sea [[16](#ref-conn2014mee)].

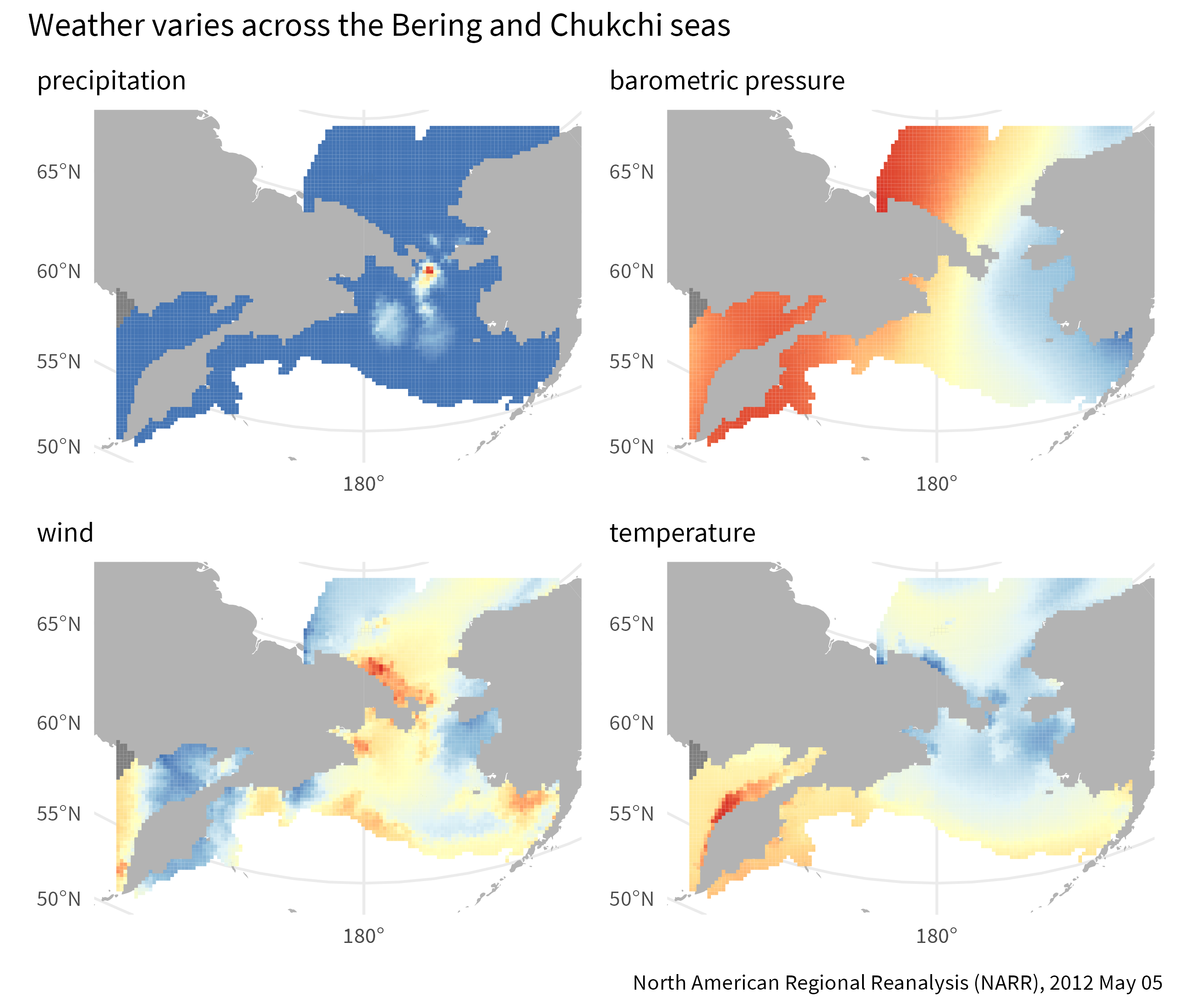


Figure : Example spatial distribution of weather covariates across the study region for 2012 May 05. The NARR was used to predict weather covariates for each hour in a percent dry timeline record.

Notably missing from this list of explanatory variables is any spatial-temporal representation of sea ice concentration, area, or extent. This may seem counter-intuitive when modeling the haul-out behavior of seal species with such a close association to sea ice. Seals haul out in the presence of sea ice and we could assess the local concentration of sea ice during these events. However, seals also spend time in the water away from sea ice. Thus, the challenge is how best to associate that seal’s at-sea behavior with a sea ice concentration. Would it be the concentration at the last known haul-out event? The next known haul-out event? Or, the closest sea ice concentration available? Without a meaningful means to associate a sea ice covariate with the seal throughout the duration of the observation record, such parameters are not viable for inclusion in this model.

We did explore whether the annual variation in spring sea ice extent in the Bering Sea influences the peak timing of seal haul-out behavior. For this, all sea ice concentration grid cells (25 km2) in the study area with greater than 15% concentration were summed to get total sea ice extent for each day between 15 February and 15 July across all years (2005-2020). The maximum sea ice extent for each year was determined from this calculation. We obtained sea ice concentration data from the Nimbus-7 SMMR and DMSP SSM/I-SSMIS Passive Microwave Dataset, Version 1 [[23](#ref-cavalieri1996)].

Table : Explanatory covariates used in analyses of binary haul-out records for ice-associated seals.

| Covariate | Type | Source | Description |
| --- | --- | --- | --- |
| Age-sex class | Categorical | Field Assessment | Classes included young-of-year, subadult, adult male and adult female. Young-of-year tags surviving past ~Feb 1 of the next year were treated as subadult in subsequent years. |
| Hour | Continuous; Fourier basis | Bio-logger | We modeled solar hour using 6 variables of a Fourier-series basis to allow circularity, flexibility, and dimension reduction |
| Day | Continuous | Bio-logger | Linear, quadratic, and cubic effects of day-of-year were modeled |
| Precip | Continuous | NARR | Convective precipitation (kg/m2) |
| Pressure | Continuos | NARR | Atmospheric pressure at sea level (kPa) |
| Temp | Continuous | NARR | Air temperatures predicted at 2m above the earth’s surface |
| Wind | Continuous | NARR | Northerly and easterly vector components for wind were downloaded and converted into a single wind speed via the Euclidean norm. |
| Northing | Continuous | Bio-logger | For bearded seals a measurement of northing was caclulated as latitude divided by the mean latitude across all locations |

## Haul-out modeling

Haul-out records for seals are often characterized by multiple hours spent basking on ice alternating with long periods of foraging (Figure ). Commonly used statistical models for binary data (e.g. logistic regression) assume independence among responses, an assumption that is clearly violated if hourly responses are modeled. Any analysis that ignores temporal dependence in responses will thus have overstated precision.

To properly account for temporal dependence within a computationally tractable framework, we used generalized linear mixed pseudo-models (GLMPMs; [[24](#ref-verhoef2010cs)]) to model variation in haul-out behavior as a function of (1) covariate predictors, (2) temporally autocorrelated random effects, and (3) individual random effects representing heterogeneity in individual behavior. We used the {glmmLDTS} package [[24](#ref-verhoef2010cs)] to implement GLMPMs in the R programming environment . Owing to the large number of records, we fit separate models to bearded, ribbon, and spotted seal data sets. We fit two different models to our datasets. First, for each species, we fitted a year-independent model that predicted average haul-out behavior as a function of demographic, environmental, seasonal, and diurnal effects. Second, for ribbon and spotted seals (which had considerably more data than bearded seals), we fitted models that included all the effects from the first model, but also permitted annual variation in haul-out timing. This second class of models was used to examine whether haul-out patterns varied by year, and to determine the annual timing of apparent peaks in haul-out behavior.

We followed Ver Hoef et al. [[14](#ref-verhoef2014sm)] in using linear, quadratic, and cubic effects of day-of-year to represent seasonal changes in behavior. However, unlike previous models for harbor seals [[25](#ref-london2012)] and ice-associated seals [[14](#ref-verhoef2014sm)], which treated hour-of-day as a 24-level categorical variable to capture diurnal cycles, we adopted a continuous formulation based on Fourier series that provides a flexible model while preserving the inherit circularity needed for time-of-day effects (i.e., hour 0 should be equal to hour 24). It also represents hour-of-day with 6 variables, which is a considerable reduction when compared to a 24 variable model, especially when fitting models with interactions between hour-of-day and other variables (e.g., age-sex class, day-of-year). According to this approach, we used the following specification for hour-of-day effects:

where gives the effect for solar hour and for = 1, 2, or 3 and = 1 or 2 are estimated parameters (regression coefficients).

For the second set of models examining inter-annual variation in sea ice use, we fitted models with year by day-of-year interactions. However, in this case we only included yearday and yearday2, omitting the main effects of year as well as yearday3 interactions as models with the latter effects were numerically unstable. However, the modeled interactions were sufficient to allow shifts in haul-out distribution, as one can show mathematically that a simple horizontal shift in timing of haul-out distributions does not affect the main effects or cubic terms in a polynomial regression model.

A typical model fitting exercise would also include a model selection process. However, AIC (and similar criteria) is not suitable when using pseudo-likelihoods. After fitting GLMPM models, we used “type III” F-tests to calculate p-values [[24](#ref-verhoef2010cs)] and rely on those insights to evaluate model performance and important terms. We also produced predictions of haul-out behavior as a function of influential predictors (e.g. solar hour, day-of-year, age-sex). Weather covariates for these predictions were based on daily or hourly (GAM) smoothed weather covariate values across the study region. Such predictions were then used to develop haul-out probability surfaces, explore marginal effects of weather covariates, and determine annual peaks in haul-out activity. The timing of peak haul-out behavior was further used to regress against the annual maximum sea ice extent in the study region.

## Stable stage distributions

I didn’t update this at all from Paul’s previous text other than to revise some of the latex equations and add references. Would be good to confirm all of this is still appropriate and makes sense.

Previous availability correction factors used in aerial surveys for ice-associated Arctic seals (e.g. [[13](#ref-bengtson2005pb)], [[16](#ref-conn2014mee)], and [[14](#ref-verhoef2014sm)]) ignored any age- and sex-based variation in haul-out probabilities. The implicit assumption is that the behavior of telemetered animals represents the population as a whole. However, if haul-out probabilities are related to sex- and age-class, and if there are tangible differences between the age- and sex-structure of the telemetered sample and that of the population, correction factors computed in this way may lead to biased abundance estimates.

To determine how much of a potential problem this is for our data, we compared estimates of haul-out probabilities that (1) ignored sex- and age-structure, and (2) accounted for sex- and age-structure, adjusting for the relative proportion of seals in each sex- and age-class. To simplify comparisons, we fitted two additional GLMPMs to ribbon and spotted seal haul-out datasets. In the first model, we expressed haul-out probabilities as a function of solar hour and day-of-year. In the second, we also included effects of sex-age class and sex-age interactions with solar hour and day-of-year. To adjust for the proportion of seals in each age class, we calculated a predicted population-averaged haul-out probability at solar noon as a function of day-of-year () as

where is the proportion of the population of seals in age class and sex . Typically, we do not know exactly, but can use information about likely mortality and reproductive schedules of seals to approximate using stable stage distributions calculated from matrix population models ().

To calculate plausible values for we obtained natural mortality predictions from a hierarchical meta-analysis of phocid natural mortality [[26](#ref-trukhanova2018ee)]. We then assumed a 50/50 sex ratio at birth, 1 pup per litter, and reproductive schedules as reported by Fedoseev [[27](#ref-fedoseev2000)] for seals in the western Bering Sea to formulate Leslie matrices Ai for each species i. Stable age distributions were then determined by normalizing the dominant eigenvector of so that they summed to one . Given a stable age distribution, we calculated the proportion of the population by sex and stage (young of the year: 0-1 year; subadult: at least one year but sexually immature; adult: sexually mature) using data on sexual maturity from Fedoseev [[27](#ref-fedoseev2000)]. In particular, the expected proportion of the population that are sex and young-of-year was set as , while the expected proportion that are subadults and adults were set to

and

Here, gives the anticipated proportion of animals of species and sex that are sexually mature. Further details on mortality, reproductive and maturity schedules, and matrix modeling methods are presented in Appendix A.

# Results

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

## Ribbon Seals

Ribbon seals show a pattern of gradually increasing haul-out probability in April that peaks in May for subadults and in June for adults. The behavior is clearly centered around local solar noon and expands to other hours later in the season as seals enter their molting period. Subadults showed an earlier start and more intense haul-out activity in April and May. The young of the year records begin after weaning and the model predictions demonstrate the ontogeny of in-water activities (e.g. diving, foraging) in May. Adult females have a more protracted season compared to males and more time spent resting in June and July. The model suggests adult male ribbon seals complete their molt by the end of June. Lastly, for adults of both sexes there is some indication for a shift to a nocturnal haul-out pattern in late June and July.

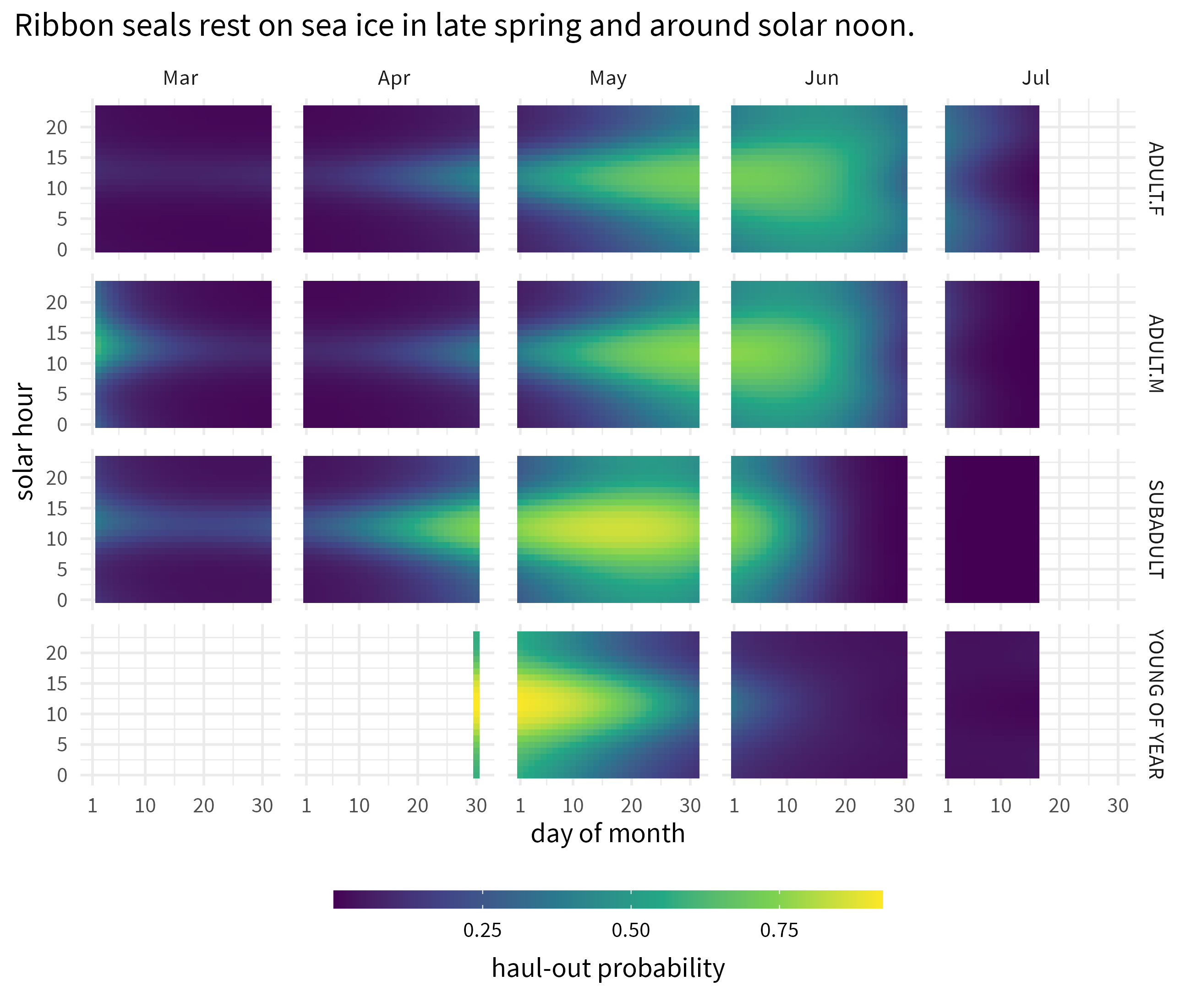


Figure : Predicted haul-out probability of ribbon seals from 1 March to 15 July for each age and sex class used in the model.

The haul-out probability for ribbon seals was strongly influenced by each of the weather covariates included within the model except precipitation. The impact of temperature ( = 15.782; = <0.01), wind ( = 72.674; = <0.01), and barometric pressure ( = 9.581; = 0.00197) was especially noticeable as ribbon seals were less likely to haul out at higher winds and lower pressure values and more likely to be on the ice when temperatures were relatively warm. Wind chill ( = 2.792; = 0.09476) showed a moderately negative influence on haul-out probability.

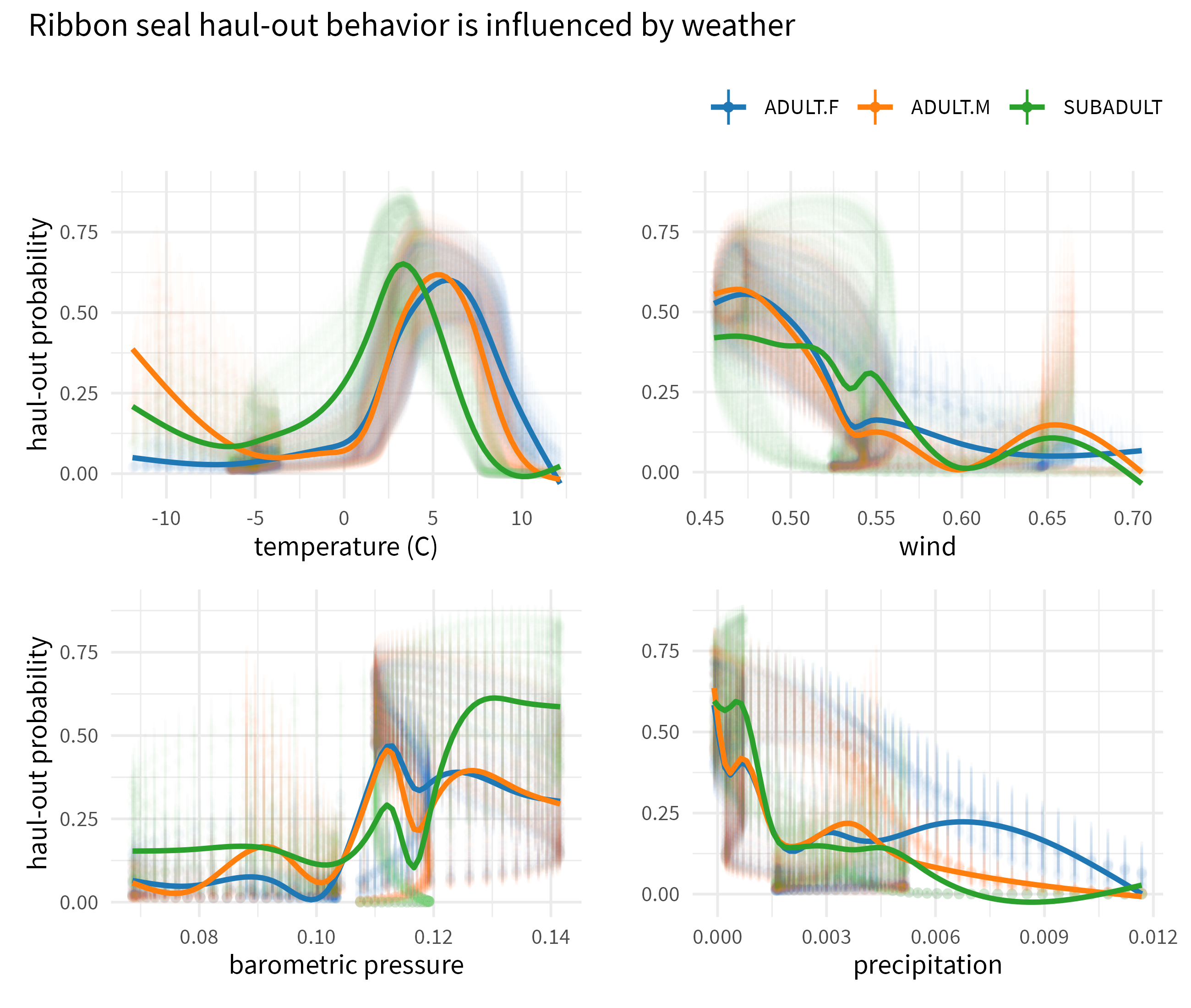


Figure : Predicted haul-out probability of ribbon seals across a range of weather conditions.

## Spotted Seals

Compared to ribbon seals, spotted seals showed a longer spring haul-out season that is less intensely centered on solar noon. Adults of both sexes spend considerable time in April and May resting on the ice. As with ribbon seals, the young of the year records begin after weaning and the model predictions demonstrate the ontogeny of in-water activities (e.g. diving, foraging) in May.

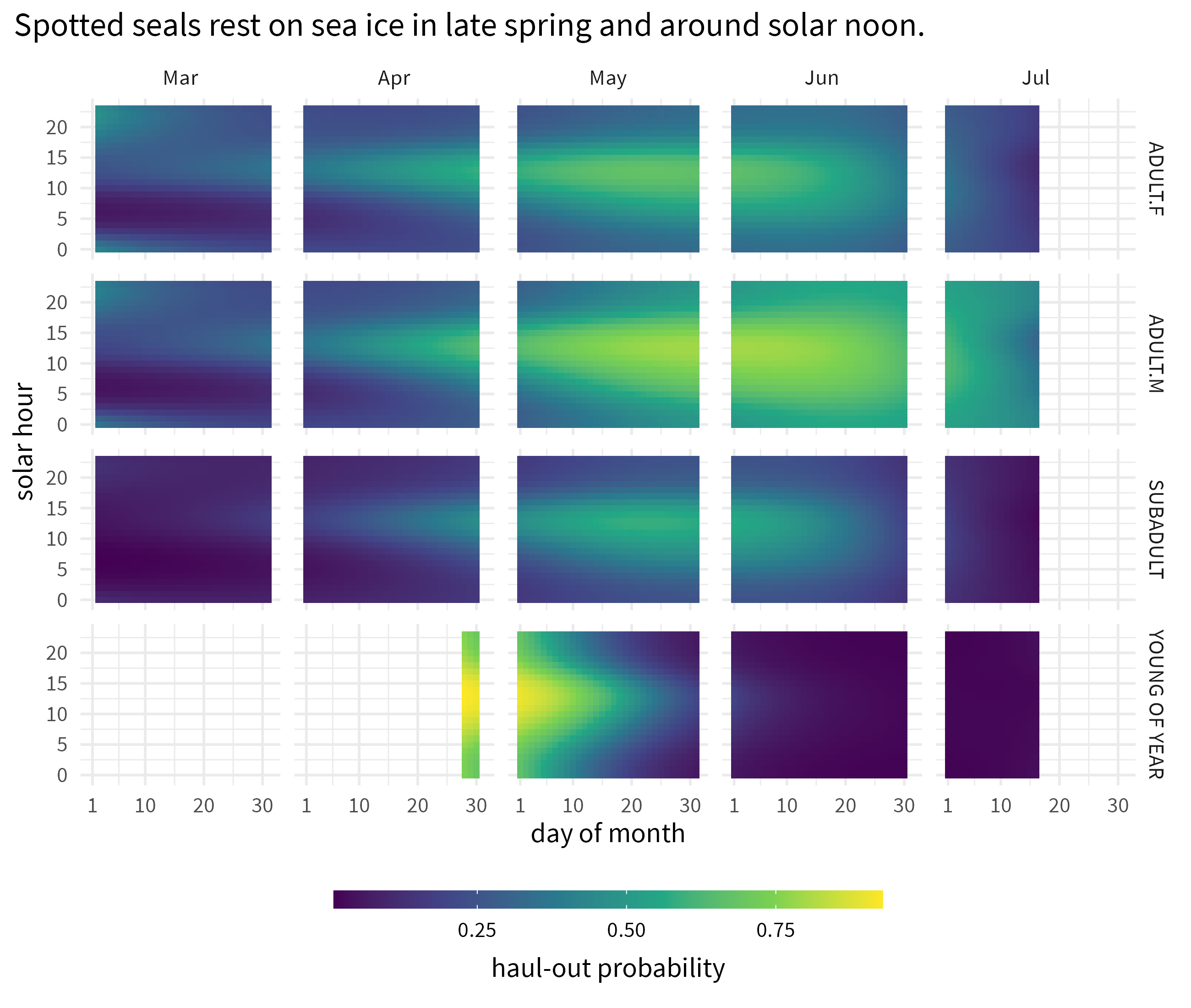


Figure : Predicted haul-out probability of spotted seals from 1 March to 15 July for each age and sex class used in the model.

Spotted seal haul-out behavior appears most strongly influenced by barometric pressure ( = 5.088; = 0.0241) and wind ( = 15.028; = <0.01) with temperature having a moderate influence ( = 2.765; = 0.09633). Spotted seals were less likely to haul out at higher winds and more likely to be on the ice when temperatures were relatively warm. Wind chill (temperature wind) and precipitation were not as influential. Differences in the magnitude of response between the age-sex classes is present and consistent across each of the weather covariates.

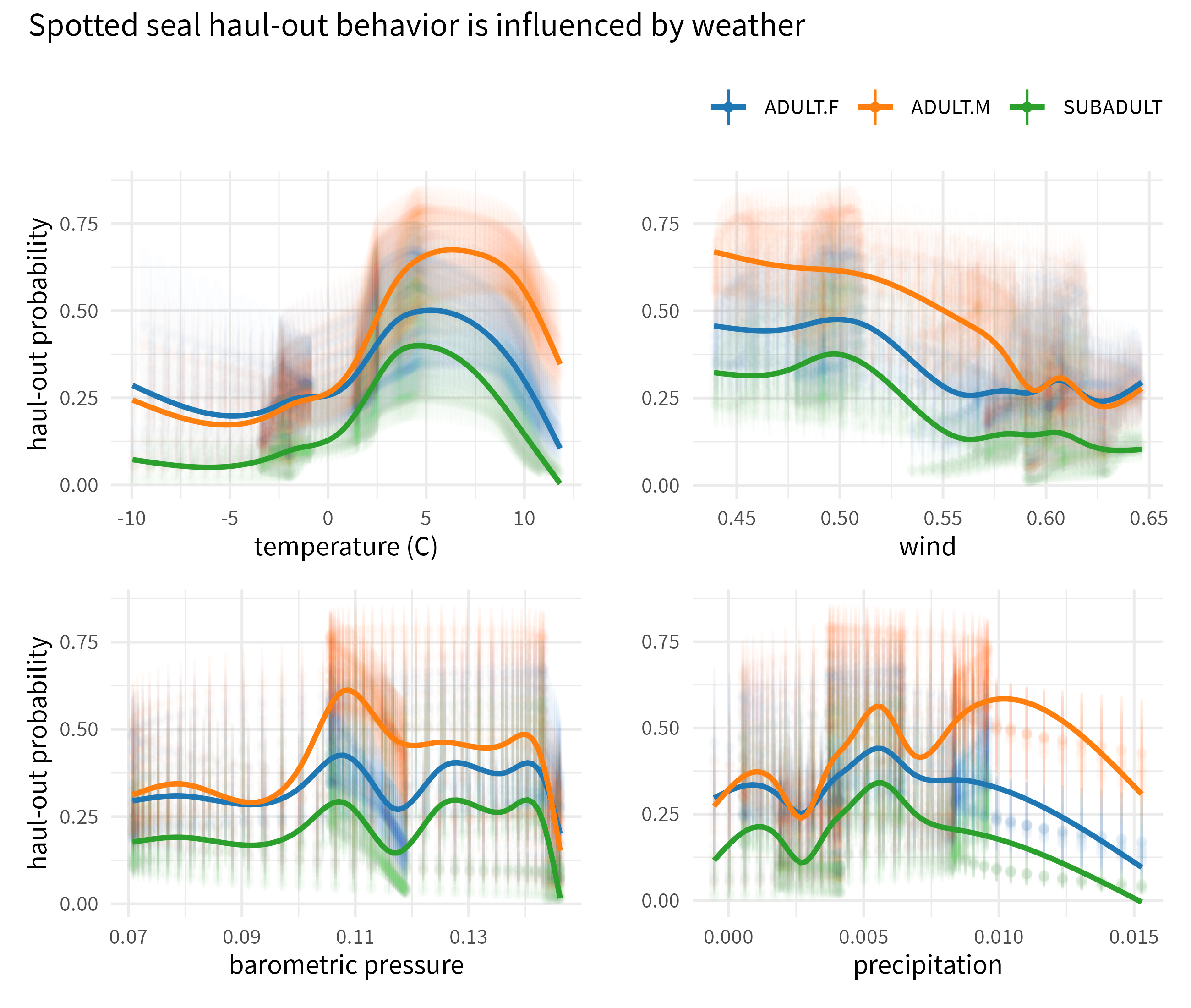


Figure : Predicted haul-out probability of spotted seals across a range of weather conditions.

## Bearded Seals

Age and sex class were not included in the model for bearded seals and, as such, results are shown for all ages. Unlike ribbon and spotted seals, bearded seals were predicted to have a bi-modal distribution of haul-out probability across the day. In addition to a peak around local solar noon, the bearded seal model predicts additional haul-out activity around local midnight. The haul-out behavior is also more protracted throughout the spring season compared to ribbon and spotted seals.

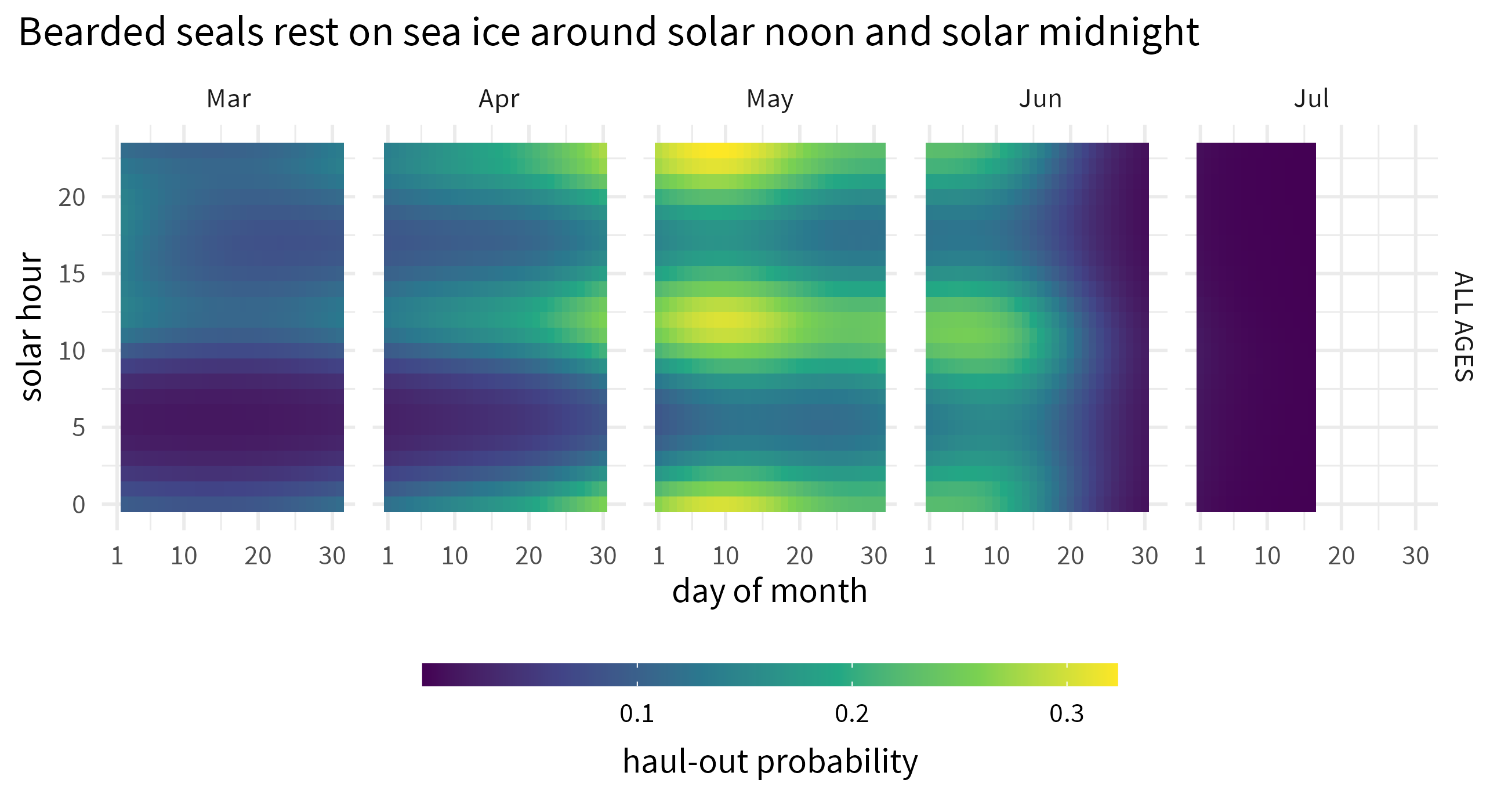


Figure : Predicted haul-out probability of bearded seals from 1 March to 15 July for each age and sex class used in the model.

Like ribbon and spotted seals, bearded seal haul-out probability appears most influenced by wind ( = 115.729; = <0.01) and temperature ( = 15.633; = <0.01). Additionally, wind chill was also a significant influence ( = 4.188; = 0.04073). Any influence of barometric pressure or precipitation is less apparent.

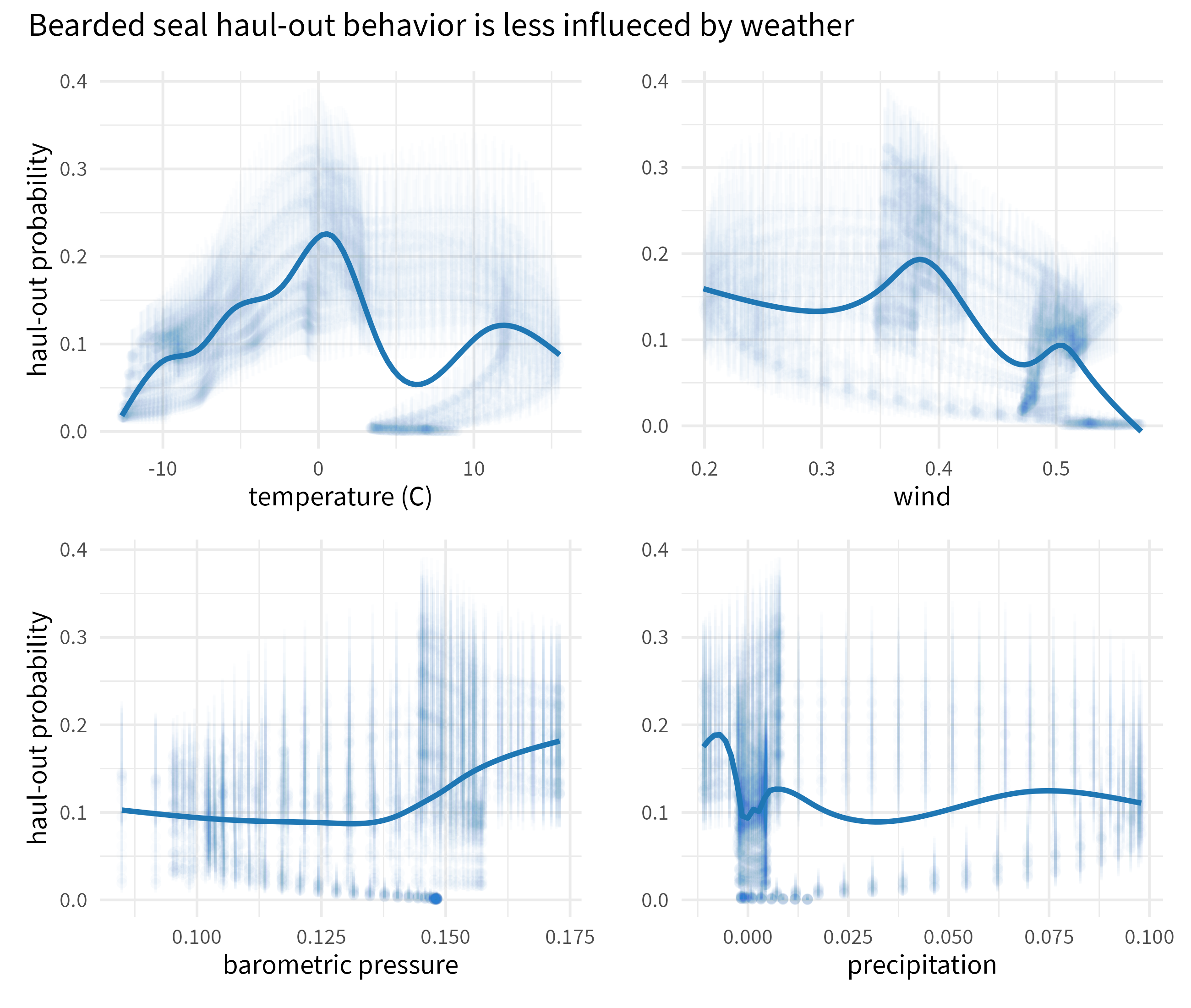


Figure : Predicted haul-out probability of bearded seals across a range of weather conditions.

## Annual variation in haul-out

The second set of models that included annual variation in haul-out patterns uncovered significant contributions for linear and quadratic interactions between day and year in both ribbon seals (day:year, = 4.116; = <0.01; day2:year, = 4.652; = <0.01) and spotted seals (day:year, = 6.889; = <0.01; day2:year, = 6.683; = <0.01). Predicted distributions of haul-out activity were largely unimodal, but varied some among and within years with respect to the timing and magnitude of haul-out peaks (Figure ). It is important to note that predicted variation in annual haul-out patterns likely reflects both process error and sampling variability. While we did remove any years where only one deployment in a species + age-sex group was present, there are still some years where the pattern shown is informed by a small number of tags that may not represent population level processes.

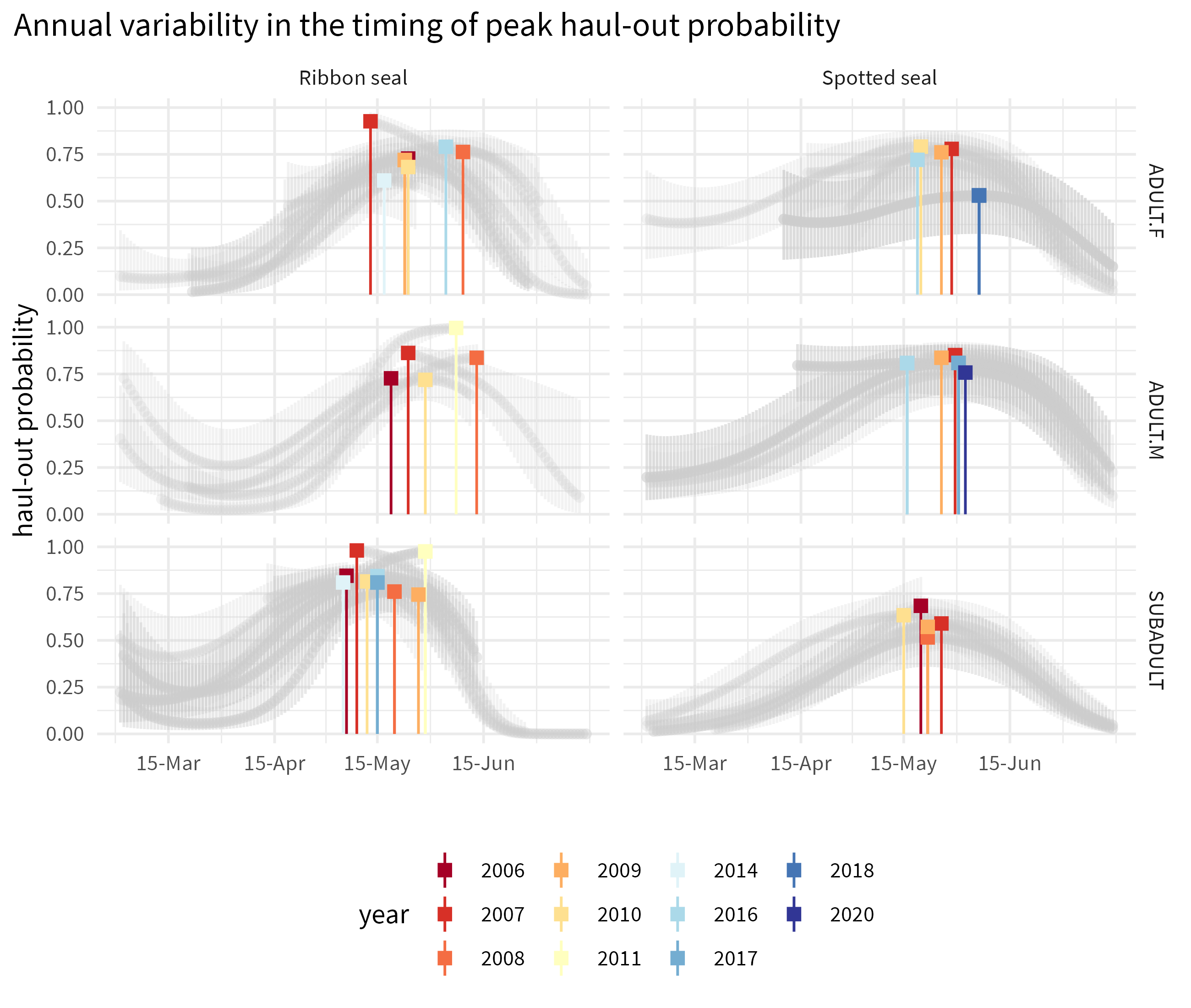


Figure : Annual variability in the timing of peak haul-out probability for ribbon and spotted seals across 10 years. Predictions are shown for local solar noon and under smoothed weather conditions. Only those groups (age-sex + year) that included observations from more than one seal are shown. Additionally, any groups where the underlying data started after 01-June or ended before 01-May are not included.

The timing of peak haul-out probability for ribbon and spotted seals appeared to have only a limited to no relationship with the amount of yearly maximum sea ice extent. Adult female and subadult spotted seals show a negative trend line but no indication that the observed trend is meaningful (spotted seal adult female: = 0.542, = 0.156; spotted seal subadults: = 0.322, = 0.318). For ribbon seals and adult male spotted seals, -values were substantially larger than 0.05 (ribbon seal adult females; = 0.035, = 0.689; ribbon seal adult males: = 0.116, = 0.575; ribbon seal subadults: = 0.015, = 0.754; spotted seals adult males: = 0.001, = 0.975).

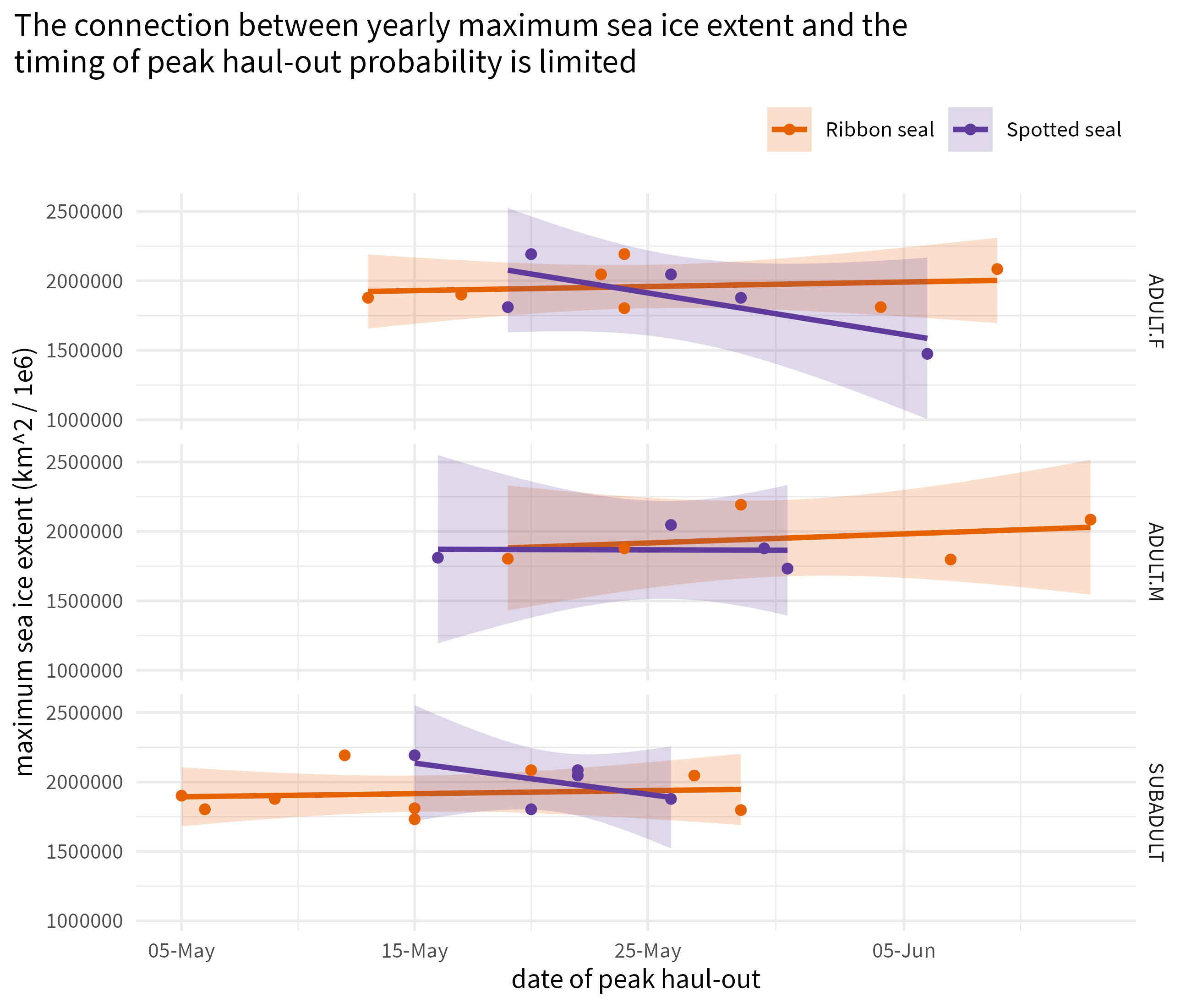


Figure : Annual timing of peak haul-out behavior analyzed against the yearly maximum area of sea ice extent in the study area. While spotted seal adult females and subadults show a negative trend line, none of the relationships were determined to be significant.

## Stable stage distributions

This section is unchanged from Paul’s original write up. I have put off revisiting and integrating with my current document/code. Maybe between Paul/Irina/Me we can sort out a quick update. Might just need to walk me through the previous code and make sure I get it properly incorporated with this version

Stable stage distributions calculated using mortality and reproductive schedules produced different patterns for the four species of ice-associated seals residing in Alaskan waters (Fig. X). Ribbon seals mature the fastest, and so can be expected to have the largest proportion of adults and smallest proportion of subadults; conversely, ringed seals mature slowly and are predicted to have roughly equal proportions of adults and subadults (note that we do not attempt to model ringed seal haul-out behavior in this study; see Discussion). Population-level haul-out distributions were somewhat different depending on whether we a) adjusted haul-out probabilities based on stable stage distributions or b) assumed the tagged sample represented the population. In particular, ribbon seal estimates differed somewhat at the beginning of the time series, but the two approaches produced similar estimates (Fig. X) within the window that previous aerial surveys in the region have been conducted (April and May; e.g. Conn et al. 2014). By contrast, during this time period spotted seal haul-out estimates were often ≈10% higher for the approach that adjusted for stable age distributions, presumably because subadults had lower predicted haul-out probabilities than adults but made up a disproportionately high proportion of the tagged sample.

# Discussion

In this paper, we modeled data from bio-logging sensors deployed on bearded, spotted, and ribbon seals to examine factors affecting haul-out behavior on sea ice in the Bering and Chukchi seas. Our analysis shows seals use sea ice progressively more throughout the spring, and with peak use near mid-May to early June before declining again. This pattern aligns well with what has been previously documented and confirms our bio-logging deployments are likely capturing population level behavioral patterns. Seals preferentially haul out on ice shortly after solar noon which coincides with the daily period of maximum solar radiation. The association of daily peak haul-out behavior with mid to later solar hours is commonly noted in pinnipeds and allows seals to maximize absorption of solar radiation. Interestingly, bearded seals appear to have two peaks in haul-out activity across the day, one shortly after solar noon, and one centered near solar midnight. A similar bi-modal pattern has been seen in ringed seals and suggests that bearded and ringed seals may be operating under different constraints than ribbon and spotted seals. Bearded and ringed seals are distributed across higher latitudes and the extended daylight hours may allow more flexibility in optimizing resting periods with foraging. Notably, bearded and ringed seals are subjected to much higher levels of predation from polar bears and human harvest.

are there references for timing of polar bear activity/kills or hunter activity that might lend some additional support for predation as a possible explanation for the bi-modal haul-out pattern? Any data on timing of hunting activity by Alaska communities?

Unlike previous analyses of seal haul-out data (e.g. Ver Hoef et al. 2009, Conn et al. 2014), we also investigated the influence of sex-age class on haul-out probabilities for all species except bearded seals because of low sample size. While both ribbon and spotted seals exhibited a unimodal diel haul-out pattern generally centered around local solar noon, there were key differences across species, age, and sex that match expectations given what we know of their ecological behavior. Spotted seals are known to form triads during the breeding season where a female and dependent pup are accompanied on the ice by a suitor male. The male is waiting for the female to wean the pup and enter estrus and fending off any other males that may be interested. Triad formation results in both males and females spending a large portion of the day hauled out on ice and a protracted spring haul-out season for both sexes. Since breeding occurs in the water, females may also be less inclined to venture out for foraging trips while still nursing the pup. We can see a clear reflection of this in the predicted haul-out behavior with both males and females exhibiting a broad distribution of time out of the water throughout the solar day and the season. Ribbon seals are not known to form triads and our model predicts a progression of increased haul-out behavior with females starting earlier in the season than males. Notably, female ribbon seals spend a large portion of the day in the water during the pupping period and aligns with the hypothesis that ribbon seal females continue foraging while nursing. In the case of both ribbon and spotted seals, subadults are the first to begin meaningful haul-out behavior and reflects a typical phocid pattern where subadults molt first as they do not have any reproductive constraints.

this previous paragraph might benefit from some references e.g. triads in spotted seals, ribbon seal females foraging while nursing, etc paper on dive/foraging behavior of lactating harp seals: <https://doi.org/10.1006/anbe.1993.1312>

We also investigated the influence of environmental covariates on haul-out probabilities, including wind speed, temperature, barometric pressure, precipitation, and wind chill. These have been investigated for walrus (e.g. Udevitz et al. [[18](#ref-udevitz2009cjz)]), but to our knowledge have never been investigated for ice-associated seals. Ribbon seals seem to be the most influenced by weather with wind, temperature, barometric pressure, and precipitation all being important components of the model. Spotted seals were most affected by wind and barometric pressures. And, for bearded seals, the model indicated wind and temperature had the greatest impact. In general, and as might be expected, seals were more likely to haul-out when daily temperatures were warmer, winds speeds were less, barometric pressure was high, and lower rates of precipitation. These weather conditions are likely most beneficial for energetic considerations and may also provide the best situation for predator detection. These results highlight the importance for haul-out behavior models (and subsequent calculations of availability during surveys) to incorporate weather covariates.

Our model uncovered annual deviations in the timing and magnitude of haul-out peaks for ribbon and spotted seals. The timing of peak haul-out activity appears to fall within a relatively narrow time window of 3-4 weeks in late May and early June. This remarkable level of consistency across 15 years is indicative of the adaptations these species have evolved to synchronize their key life history stages with favorable environmental conditions (e.g. availability of sea ice, increased oceanographic productivity, favorable weather conditions). Unfortunately, this may also be indicative of a limited range of plasticity as climatological conditions change. Additionally, while from an ecological perspective the haul-out behavior appears consistent, the interannual differences in timing and magnitude are large enough to have important ramifications on calculations of abundance and trend.

Previous attempts to estimate the abundance of phocid seals from aerial survey data in the Bering and Chukchi Seas (e.g. Bengtson et al. 2005, Conn et al. 2014, Ver Hoef et al. 2014) have used estimated haul-out probabilities to correct for the proportion of animals that are in the water and thus unavailable to be counted during aerial surveys. Although several of these studies allowed haul-out probabilities to vary by day-of-year and time-of-day, previous correction factors have not accounted for variability between years, different weather conditions, and the age-sex class of the sample. In this paper, we have shown that there can be considerable differences in the number of seals hauled out on ice based on these factors. We thus recommend that future abundance analyses employ correction factors that account for these factors. For instance, it is relatively straightforward to obtain weather reanalysis products for times and locations that are surveyed and to construct a relevant correction factor based on predictions of GMPMs. Further, one can apply stable stage distribution estimates from matrix population models to adjust predictions to the “average” prediction of the population. The latter suggestion is particularly appropriate when the age structure of the tagged sample does not reflect the likely age structure of the population. For instance, population weighted estimates can differ substantially from those based on a naïve analysis of the tagged sample, as was the case with analysis of spotted seal data (e.g. Fig X). The most challenging element in developing availability correction factors is with annual variability. It can be difficult to get a sufficient sample size to estimate year-specific correction factors, particularly because research teams would likely need to tag seals and conduct aerial surveys concurrently which requires considerably more personnel and money. One possible suggestion is to estimate a “shift” parameter within models for aerial survey counts that allow the peak of haul-out distributions to be adjusted earlier or later in the year based on the frequency of counts observed over time. Regardless, researchers should anticipate there being some un-modeled heterogeneity in availability probability present in abundance estimates obtained from aerial surveys. This may make trend detection difficult, as one will not know if moderate differences in abundance estimates are attributable to changes in abundance or changes in haul-out frequencies.

Predictions of absolute haul-out probability in this paper were somewhat different than those previously reported for these species, especially for bearded seals. For instance, Ver Hoef et al. (2014) and Conn et al. (2015) used haul-out correction factors with maximums of 0.66 for bearded seals, 0.62 for ribbon seals, and 0.54 for spotted seals, where maximums corresponded to times near solar noon in mid-late May. Applying models that ignore age, sex, and year effects, these probabilities were 0.38, 0.72, and 0.60, respectively, under the current analysis framework. Our current estimates reflect increased sample sizes in terms of number of animals, but also improvements to the way data are prepared prior to analysis.

We focused this paper on haul-out behavior of bearded, ribbon, and spotted seals. Ringed seals are also present in the Bering and Chukchi Seas but exhibit qualitatively different haul-out behavior. For instance, many ringed seals build subnivean layers in the snow on top of the sea ice, which they frequently inhabit before snow melt causes their lairs to collapse (Kelly 1988). Thus, the wet-dry sensor on a satellite tag could indicate that an animal is hauled out, but it could still be unavailable to be detected because it is in a lair. We hope to address availability of ringed seals using data from satellite tags, replicate survey tracks, and auxiliary information about snow depth and timing of melt in a future study.

this could use a better ending with more punch and interest

# Author Contributions

insert broad statement and summary regarding data contribution from AFSC, ADFG, NSB (I still need to lookup details of which org contributed which data). Authors, please add your contribution statement below

*Josh M. London:*

*Paul B. Conn:*

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*Jay M. Ver Hoef:*

*Irina S. Trukhanova:*

*Michael F. Cameron:*

*Peter L. Boveng:*

# Data Availability

Data and code are available as a complete research compendium on GitHub and major versions are archived at Zenodo. Original data sources for telemetry are archived at the United States Animal Telemetry Network.

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We recognize that the species and ecosystems studied in this paper are within the traditional range of the Inpuiaq and Yupik people. And, we would like to acknowledge and thank them as the original stewards of these ecosystems. The deployment of bio-logging devices used in this study were often done in collaboration with Alaska Native communities. We would like to especially acknowledge the communities of Kotzebue, Utqiagvik, and Ulguniq.

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