

# Modeling haul-out behavior of walrus in Bering Sea ice

Mark S. Udevitz, Chadwick V. Jay, Anthony S. Fischbach, and Joel L. Garlich-Miller

**Abstract:** Understanding haul-out behavior of ice-associated pinnipeds is essential for designing and interpreting population surveys and for assessing effects of potential changes in their ice environments. We used satellite-linked transmitters to obtain sequential information about location and haul-out state for Pacific walrus, *Odobenus rosmarus divergens* (Illiger, 1815), in the Bering Sea during April of 2004, 2005, and 2006. We used these data in a generalized mixed model of haul-out bout durations and a hierarchical Bayesian model of haul-out probabilities to assess factors related to walrus haul-out behavior, and provide the first predictive model of walrus haul-out behavior in sea ice habitat. Average haul-out bout duration was 9 h, but durations of haul-out bouts tended to increase with durations of preceding in-water bouts. On average, tagged walrus spent only about 17% of their time hauled out on sea ice. Probability of being hauled out decreased with wind speed, increased with temperature, and followed a diurnal cycle with the highest values in the evening. Our haul-out probability model can be used to estimate the proportion of the population that is unavailable for detection in spring surveys of Pacific walrus on sea ice.

**Résumé :** Il est essentiel de comprendre le comportement d'échouerie chez les pinnipèdes associés aux glaces pour planifier et interpréter les inventaires démographiques et pour évaluer les effets des changements potentiels dans leurs environnements glaciaux. Nous avons utilisé des émetteurs reliés aux satellites pour obtenir des informations séquentielles sur la position et l'état d'échouerie de morses du Pacifique (*Odobenus rosmarus divergens* (Illiger, 1815)) dans la mer de Béring en avril 2004, 2005 et 2006. Ces données utilisées dans un modèle de mélange généralisé de durée des épisodes d'échouerie et un modèle hiérarchique bayésien des probabilités d'échouerie nous servent à évaluer les facteurs reliés au comportement d'échouerie chez les morses et à mettre au point le premier modèle prédictif sur le comportement d'échouerie chez les morses dans un habitat de glace de mer. Les morses marqués passent en moyenne 9 h par épisode d'échouerie, mais les durées des périodes d'échouerie ont tendance à s'allonger en fonction de la durée des périodes précédentes passées en mer. Globalement, les morses marqués passent en moyenne seulement 17 % de leur temps en échouerie sur la glace de mer. La probabilité d'échouerie diminue en fonction de la vitesse du vent, augmente avec la température et suit un cycle journalier avec un maximum en soirée. Notre modèle de probabilité des échoueries peut servir à estimer la proportion de la population qui est à l'abri de la détection lors des inventaires printaniers des morses du Pacifique sur la glace de mer.

[Traduit par la Rédaction]

## Introduction

The Pacific walrus (*Odobenus rosmarus divergens* (Illiger, 1815)) is one of two subspecies of walrus (*Odobenus rosmarus* (L., 1758)) worldwide, and one of five ice-associated pinnipeds in the Bering Sea (Burns et al. 1981). Walrus use sea ice for birthing, nursing, resting, molting, access to offshore foraging areas, and refuge from predation and disturbance (Fay 1982). Projected changes in the distribution of seasonal ice in the Bering Sea (Overland and Wang 2007) will likely affect walrus distribution and behavior and could affect the status of this population (Ray et al. 2006; Rausch et al. 2007).

The amount of time that ice-associated pinnipeds spend on ice depends on physiological requirements such as those

associated with reproduction, foraging, nursing, and molting, and is constrained by environmental conditions affecting thermoregulation (Wells et al. 1999). Knowledge of how temporal and environmental factors affect haul-out behavior is essential for understanding the biology of these species as well as for practical applications such as determining the best times to conduct surveys (Southwell 2005) and establishing baselines for evaluating industrial effects (Moulton et al. 2002). Environmentally induced changes in haul-out behavior could affect populations by altering energy requirements of individual walrus (Fay and Ray 1968) or disease transmission rates (Burek et al. 2008).

Factors such as time of day, weather, and other environmental conditions have been related to haul-out behavior of various pinnipeds (Simpkins et al. 2003b; Bengtson and

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Cameron 2004; Frost et al. 2004; Reder et al. 2004; Hayward et al. 2005). Walrus using terrestrial haul-out sites spend about 65%–85% of their time in the water (Born and Knutsen 1997; Gjertz et al. 2001; Jay et al. 2001; Born et al. 2005; Acquarone et al. 2006; Lydersen et al. 2008). Haul-out behavior of walrus at these sites has been related to factors such as time of day, wind, temperature, and precipitation (Fay and Ray 1968; Salter 1979; Born and Knutsen 1997). Very little is known about haul-out behavior of walrus in sea ice habitats; the only previously published quantitative information was based on proportions of walrus observed in the water during aerial surveys and walrus hunts in the Bering Sea (Fay and Ray 1968) and telemetry data from a single male in the Greenland Sea (Born et al. 2005).

The US Fish and Wildlife Service, the US Geological Survey, and the Russian agencies GiproRybFlot (Research and Engineering Institute for the Development and Operation of Fisheries) and ChukotTINRO (Pacific Research Institute of Fisheries and Oceanography, Chukotka Branch) collaborated to conduct a range-wide survey of the Pacific walrus population in April 2006. This time period was selected for the survey because the entire Pacific walrus population is within the ice pack of the Bering Sea at that time (Gilbert 1999). The survey used high-altitude infrared imagery to detect and enumerate walrus on sea ice (Burn et al. 2006; Udevitz et al. 2008). Satellite-linked radio tags were deployed on walrus in the Bering Sea during March and April 2004–2006, to provide data that could be used to estimate the portion of the population that was in the water and therefore not available to be detected with the infrared imagery. Previous surveys of the Pacific walrus population only enumerated walrus hauled out on ice or land and did not account for the portion of the population in the water (Gilbert 1999).

Here, we report results from this 3-year tagging study. Our objectives were to (i) use the radio-tag data to quantify the portion of time walrus spend hauled out on Bering Sea ice during April, (ii) quantify factors that might be related to that haul-out behavior, and (iii) develop a model of haul-out behavior that could be used to estimate the portion of the population that was in the water during an April survey. Our analyses considered both the probability of a walrus being hauled out on the ice and the durations of individual bouts of haul-out or in-water activity. We use a generalized mixed effects model (McCullagh and Nelder 1999; Littell et al. 2006) and information theoretic methods (Burnham and Anderson 2002) to make inferences about durations of individual bouts of activity relative to characteristics of the bouts and walrus. We use a Bayesian analogue of this model (Gelman et al. 1997) to consider effects of these factors as well as weather and time of day on haul-out probabilities. The Bayesian model allowed imputation of missing values for weather data and simultaneous model selection in one general framework. Inclusion of the additional covariates provided a model that could be used to estimate the portion of the population that was in the water during a survey. Both models used random effects, as necessary, to account for synchronicity and individual heterogeneity in walrus behavior.

## Materials and methods

### Field methods

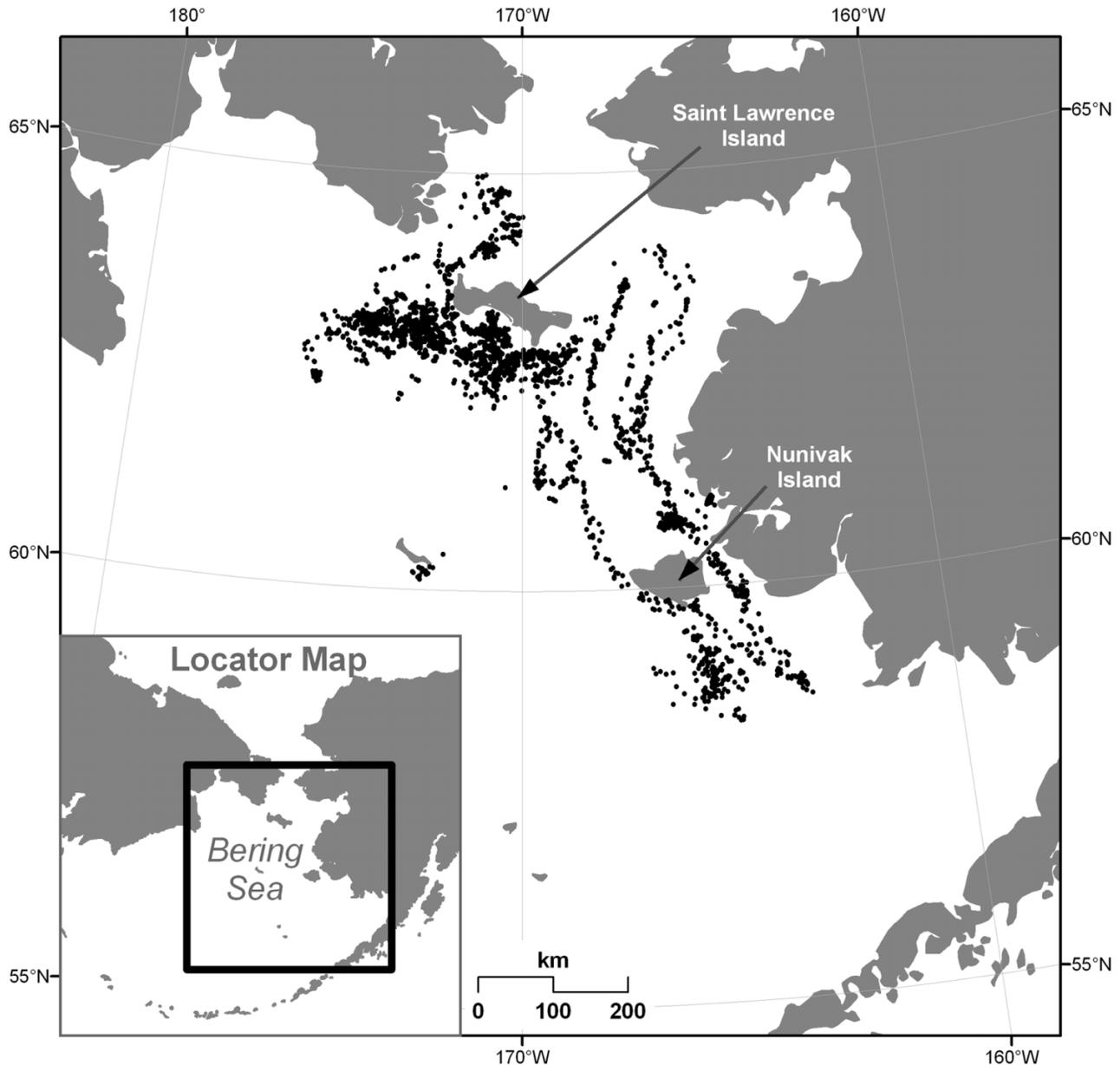
Satellite radio tags were deployed on walrus hauled out on Bering Sea ice during 8–20 April 2004, 17–19 March 2005, and 24–30 March 2006. In 2004 and 2005, deployments were in the southeastern Bering Sea near Nunivak Island (Fig. 1). In 2006, deployments were in the northern Bering Sea south of St. Lawrence Island (Fig. 1). In all years, we used aircraft reconnaissance to locate areas with aggregations of hauled-out walrus. We used ice-hardened vessels or icebreakers to access these areas and made final approaches to walrus in small boats or on foot. Radio tags were deployed with air guns or crossbows from a distance of about 10 m (Jay et al. 2006). The tags were fitted with barbed heads that embedded in the animal's blubber layer on impact. We attempted to place tags in the dorsal region midway between the shoulders on each targeted walrus.

We deployed tags opportunistically, as walrus groups were encountered, while attempting to distribute tags as widely as possible among walrus in each tagging region (i.e., the regions near Nunivak Island or St. Lawrence Island). Our deployment technique required us to target individuals lying with their backs exposed, and that could be approached downwind without obstruction from neighboring walrus. The barbed heads were too large for the thin skin and blubber layers of young animals (Jay et al. 2006), so we deployed tags only on adult walrus. Within these constraints, we also attempted to distribute tags approximately equally between males and females. When possible, we used a crossbow sampling system to obtain tissue biopsies from tagged walrus, and final sex determination was based on molecular analysis of these samples (Fischbach et al. 2008). Sex was classified as undetermined for walrus without biopsy samples. Protocols for walrus tagging and associated activities were reviewed and approved by the US Geological Survey, Alaska Science Center Animal Care and Use Committee and conducted under US Fish and Wildlife Service Permit No. MA801652-3.

Three different types of radio tags were used (Jay et al. 2006), differing primarily in the structure of their barbed heads, their radio housing, and the configuration of their on-board software (Table 1). Each radio tag had a conductivity sensor with external contacts that detected whether it was in or out of water. Depending on the tag, conductivity was measured every 1–10 s with the results accumulated over periods of 20–60 min (Table 1). We refer to these 20–60 min periods as “behavioral intervals” (or just “interval” if the context is clear). If  $\geq 85\%$  or  $\geq 90\%$  (Table 1) of the measurements for a given behavioral interval indicated the tag was out of water, the animal was considered to be hauled out during that interval. We defined a “haul-out bout” as the period of time a walrus spent on the ice between in-water intervals. Likewise, we defined an “in-water bout” as the period of time a walrus spent in the water between hauled-out intervals.

Data on haul-out state were continuously recorded and stored, but transmissions were restricted according to duty cycles that varied among tags (Table 1). Transmissions were also suspended whenever the radio tag was submerged to conserve battery life. Tags had battery capacities that al-

**Fig. 1.** Geographic locations associated with data on haul-out status for 43 walrus (*Odobenus rosmarus divergens*) monitored with satellite-linked radio tags in the Bering Sea, April 2004–2006. These are the locations of the 2 341 observations of haul-out behavior with associated location data (Table 5) used for modeling haul-out probabilities.



lowed transmissions for at least 3 to 4 weeks. Information from 1–5 days of consecutive behavioral intervals was encoded in each transmission. Thus, the information from any given behavioral interval was received if there was at least one successful transmission during the 1–5 day period while this information was stored on the tag. This provided considerable redundancy and resulted in a nearly continuous record of haul-out behavior. We retained data only from transmissions that passed a checksum test designed to identify transmission errors (Peterson and Brown 1961). We excluded all data from the first 24 h after deployment of each tag because the tagging process may have altered behavior during this period. We also excluded all data from the last recorded behavior period (i.e., last series of intervals with the same recorded behavior) because the transmitter must

have either stopped functioning or been shed during this period.

#### Data preparation

Records of haul-out data were received and geographic locations of tagged walrus were estimated by the Argos location and data collection system (Collecte Localisation Satellites 2007). Location estimates were filtered, using the Douglas Argos-Filter Algorithm (Douglas 2006), to retain only those locations with spatial errors expected to average less than about 5 km. This filter assesses the plausibility of locations based on spatial redundancy, Argos location quality, maximum rate of movement, and turning angles of successive movements. We set the algorithm to retain (i) all standard class locations, (ii) nonstandard class locations

**Table 1.** Characteristics of satellite-linked radio tags used to collect data on haul-out behavior of walrus (*Odobenus rosmarus divergens*) in the Bering Sea, 2004–2006.

Attachment type <sup>a</sup>	Year	No. of tagged walrus <sup>b</sup>	Duty cycle <sup>c</sup>	Dry rule <sup>d</sup>	Interval length (min) <sup>e</sup>
Tether	2004	1	On 18 h starting 0600 UTC, maximum 400 tx per d	≥85%	60
Tether	2005	1	On 18 h starting 1600 UTC, maximum 250 tx per d	≥85%	60
Implant	2004	4	On 24 h	≥85%	60
Implant	2005	4	On 18 h starting 1600 UTC, maximum 100 tx per d	≥85%	60
Post	2004	7	On 24 h	≥90%	20
Post	2006	26	On 14 h starting 1700 UTC	≥90%	30

<sup>a</sup>Attachment types are described by Jay et al. (2006).

<sup>b</sup>Includes only walrus with haul-out data used for modeling.

<sup>c</sup>Daily time period during which transmissions are made and, in cases where the number of transmissions per day is limited, the maximum number of transmissions (tx) allowed per day.

<sup>d</sup>Percentage of the conductivity measurements for a given interval that must indicate the tag was out of water if the walrus is to be considered hauled out during that interval.

<sup>e</sup>Length of the time interval during which conductivity measurements are accumulated to determine haul-out status for the interval.

within 2 km of the previous or subsequent location, and (iii) remaining locations based on a distance-angle-rate filter that accepted a maximum walrus speed of 10 km/h and rejected locations at the apex of highly acute angles (RATECOEF = 25, Douglas 2006).

We obtained estimates of air temperature (at 2 m above sea level), barometric pressure (at sea level), and wind speed (at 10 m above sea level) from the North American Regional Reanalysis (NARR) data set produced by the National Centers for Environmental Prediction (Mesinger et al. 2006). This data set contained estimates at 3 h intervals (0300, 0600, ..., 2400 Alaska Standard Time (AST)) for each point in an approximately 20 km × 20 km grid covering the Bering Sea.

We considered data only from April of each year, to correspond with the time period when a range-wide survey of the Pacific walrus population was conducted in 2006. The month of April extends from what is typically the end of the breeding season to when the population begins migrating to summer ranges (Fay 1982). We used location data (and associated NARR data) from all tagged walrus during this period to estimate parameters for imputation distributions of weather variables (see below). For analyses of walrus behavior (i.e., haul-out probabilities or bout durations), we further restricted consideration to walrus with tags that provided continuous sequences of at least 10 days of haul-out data. This restriction eliminated data from tags that functioned only briefly or intermittently. All tags provided substantially more locations for intervals when walrus were hauled out than for intervals when they were in water because the tags could not transmit when they were submerged. However, a properly functioning tag, placed dorsally between the shoulders, could transmit much of the time while a walrus was on the water surface. Therefore, for behavior analyses, we also restricted consideration to walrus with tags that provided location information for at least 2% of the in-water behavioral intervals.

Analyses of bout durations were based on all of the complete bouts within this telemetry data set. A bout was considered complete if there were no missing data on haul-out state for any interval between the initiating and terminating changes in haul-out state. Duration of each bout was esti-

mated by summing the durations of the included behavioral intervals.

Analyses of haul-out probabilities required linkage of walrus behavior to NARR weather data. Therefore, for these analyses, we restricted our consideration of walrus telemetry data to only those behavioral intervals that included a NARR time point. Though behavioral intervals varied in length (depending on tag type, Table 1), we assumed that the estimated behavior for the interval containing a NARR time point provided the best estimate of the behavior at that time point. If there was more than one Argos location associated with a behavioral interval, we used the location that was closest in time to the NARR time point. In cases of ties, we used the earliest location. Not all behavioral intervals had associated Argos locations. This is because, whereas we obtained a nearly continuous record of haul-out behavior from each tagged walrus, Argos locations could be obtained only at the actual times of transmissions and then only if the quality and number of transmissions were sufficient. For behavioral intervals with Argos locations, we estimated the corresponding weather conditions to be those of the NARR time point at the NARR grid point closest to the Argos location. For behavioral intervals without Argos locations, we used imputation to estimate associated weather conditions as described below.

### Analysis of bout durations

We used a generalized linear mixed effects model (McCullagh and Nelder 1999; Littell et al. 2006) with an identity link and lognormal errors to model bout durations. The form of this model was

$$Z_{ij} \sim \text{Lognormal}(\eta_{ij})$$

where

$$\eta_{ij} = \beta_0 + \beta_1 X_{1ij} + \dots + \beta_K X_{Kij} + \omega_i$$

and  $Z_{ij}$  is duration of the  $j$ th bout (hours) for walrus  $i$ ;  $X_{kij}$ ,  $k = 1, \dots, K$ , are values of the associated covariates; and  $\omega_i$  is a random effect for walrus  $i$ , with

$$\omega_i \sim \text{Normal}(0, \sigma_\omega^2)$$

As potential covariates, we considered a three-level cate-

**Table 2.** Akaike’s information criterion (AIC) values for models of walrus (*Odobenus rosmarus divergens*) haul-out and in-water bout durations in the Bering Sea, April 2004–2006.

Model	Variables <sup>a</sup>	No. of parameters	AIC	ΔAIC <sup>b</sup>
1	DRY, LBOUT, DRY × LBOUT	6	2754	0
2	YEAR, DRY, LBOUT, DRY × LBOUT	8	2756	3
3	SEX, DRY, LBOUT, DRY × LBOUT	8	2757	4
4	YEAR, SEX, DRY, LBOUT, DRY × LBOUT	10	2759	5
5	DRY, LBOUT	5	2767	13
6	LBOUT	4	2890	137
7	DRY	4	2991	237
8	Null	3	3074	320

<sup>a</sup>Null model includes only an intercept and the random effect of walrus. Other models also include the variables indicated. Variables are as follows: YEAR, year (2004, 2005, or 2006); SEX, sex (female, male, or undetermined); DRY, haul-out state (0 = in water, 1 = hauled out on ice); LBOUT, length of previous bout (log hours); and DRY × LBOUT, interaction of DRY and LBOUT.

<sup>b</sup>ΔAIC is the difference between the AIC value for the specified model and the model with the lowest AIC value, calculated before rounding.

gorical variable for the year of tagging (2004 or 2005 versus 2006), a three-level categorical variable for sex of the walrus (female or male versus undetermined), a binary variable that identified current haul-out state (in water versus hauled out on ice), duration of the previous bout (log hours), and the interaction between current haul-out state and duration of previous bout (Table 2). Inclusion of a random effect for walrus, along with an effect for duration of previous bout, accounted for potential correlations among repeated observations on the same walrus. Specifying duration of previous bout as a separate fixed effect allowed explicit estimation of the magnitude of this effect.

We initially fit a series of models containing different plausible subsets of the covariates (Table 2). These models were fit with maximum likelihood, and Akaike’s information criterion (AIC, Burnham and Anderson 2002) was used to select the final model. The final model was then refit with restricted maximum likelihood (Littell et al. 2006) to reduce bias in estimates of the variance components (Littell et al. 2006). Deviance and deviance residuals were used to assess the fit of the final model to the data (McCullagh and Nelder 1999).

**Analysis of haul-out probabilities**

We used data on haul-out state and weather conditions associated with the individual behavioral intervals for each walrus to model the probability of a walrus being hauled out on the ice at any given time. The sample of behavioral intervals with associated Argos locations taken by itself, however, would provide substantially biased estimates of haul-out probabilities because, as noted above, the probability of obtaining a location was higher during intervals when a walrus was hauled out than when it was in the water. To eliminate this telemetry-induced bias, and to fully utilize all of the information in the data, we used imputation (Ibrahim et al. 2005) to estimate values of weather variables for behavioral intervals that did not have associated Argos locations and therefore could not be directly linked to NARR grid points. We used a Bayesian approach (Ibrahim et al. 2005) to incorporate imputation of missing weather values with simultaneous model selection (Yang et al. 2005). This

approach required specification of models for the observed data (likelihood) and the parameters (prior distributions), along with models for the missing data values, which were treated as additional parameters to be estimated. For model selection, this framework was embedded in an additional level of hierarchy that required specification of a prior distribution for the models themselves (Dellaportas et al. 2002). We used Markov Chain Monte Carlo (MCMC) methods, implemented with WinBUGS software (Spiegelhalter et al. 2003), for estimation. All inference was based on estimated posterior distributions.

The basic likelihood for the observed data was a generalized linear mixed effects model with

$$[1] \quad Y_{it} \sim \text{Bernoulli}(p_{it})$$

where

$$\text{logit}(p_{it}) = \beta_0 + \beta_1 X_{1it} + \dots + \beta_K X_{Kit} + \omega_i + \tau_t$$

$Y_{it}$ , in this likelihood, is a binary variable indicating whether or not walrus  $i$  was hauled out on the ice during interval  $t$ , and  $X_{kit}$ ,  $k = 1, \dots, K$ , are values of the associated covariates.  $\omega_i$  and  $\tau_t$  are random effects for walrus and time point, respectively, with

$$\omega_i \sim \text{Normal}(0, \sigma_\omega^2)$$

$$\tau_t \sim \text{Normal}(0, \sigma_\tau^2)$$

The random effects account for variation among walruses and among time points that is not accounted for by the fixed effects. These random effects also provide an effective mechanism to account for important aspects of the overall correlations that may result from using data from different walruses at the same time point and different time points for the same walrus. The random time effect, for example, accounts for synchrony in walrus behavior. We used a lag variable, discussed below, to account for potential serial correlation among repeated observations on the same walrus. The intercept and random effects were included in all mod-

els we considered, with non-informative prior distributions given by

$$\beta_0 \sim \text{Normal}(0, 1.0 \times 10^6)$$

$$1/\sigma_\omega^2 \sim \text{Gamma}(0.001, 0.001)$$

$$1/\sigma_\tau^2 \sim \text{Gamma}(0.001, 0.001)$$

As noted above, all of the weather covariates had missing values for some behavioral intervals. However, there was considerable information about the missing values contained in observations for other walrus with non-missing data for behavioral intervals near the same time. This is because all tagged walrus tended to be in the same general subregion of the Bering Sea during any given behavioral interval, and weather conditions tended to be similar within localized regions. Therefore, we modeled the missing values for weather covariates as

$$X_{kit} \sim \text{Normal}(\mu_{kt}, \sigma_{kt}^2)$$

where  $\mu_{kt}$  is the mean and  $\sigma_{kt}^2$  is the variance estimated from all of the non-missing data within 6 h of interval  $t$  (i.e., from the series of five successive intervals beginning at interval  $t - 2$ ). This resulted in a separate imputation distribution for each variable at each time point, with an average imputed value for any given time point that was the mean for the corresponding 12 h window, and a variance that reflected the variation in observed values for that window. Using random draws from these distributions in each MCMC iteration allowed the imputation uncertainty to be accounted for as a part of the variability in the estimated posterior distributions for model parameters and haul-out probabilities. We used this approach for estimating missing values, rather than simple interpolation of missing locations and subsequent linkage to NARR grid points, because plots of walrus movements indicated that interpolation would likely result in many large errors relative to the scale of the grid points, and it was not clear how the uncertainty associated with the interpolation could be adequately accounted for during the subsequent model selection and estimation processes.

We considered a series of models that differed in the covariates that were included as fixed effects. Potential covariates represented effects for time of day, weather, year, sex, and previous haul-out state (Table 3). We considered five different representations for the time-of-day effect. To provide a representation that did not impose any functional form on the relation, we used an eight-level categorical variable (TOD1) that allowed estimation of a different effect for each of the eight NARR time points per day. Plots of the data suggested that there might be more structure to this effect, however, with haul-out proportions generally increasing to their highest values in the evening (1800 AST) and then decreasing to their lowest values by late morning (0900–1200 AST). Therefore, we also considered a potentially more parsimonious representation as a smooth, sym-

metric, diurnal cycle (TOD2) specified by the two-parameter sine function

$$\beta_1 \cos(2\pi X_{1it}/24) + \beta_2 \sin(2\pi X_{1it}/24)$$

where  $X_{1it}$  is hours past midnight. We also considered three other potentially more parsimonious categorical representations of the time-of-day effect. These included a binary covariate (TOD3) that distinguished only between the morning period (0900–1200 AST) and a base level, a binary covariate (TOD4) that distinguished only between the evening period (1800 AST) and a base level, and a three-level covariate (TOD5) that distinguished between both the morning and evening periods and a base level. We allowed no more than one of these representations of the time-of-day effect to be included in any single model.

As weather covariates, we considered barometric pressure, air temperature, wind speed, and the interaction of air temperature and wind speed, which allowed for a windchill effect on walrus behavior. We also considered the absolute change in barometric pressure over the past 3 h, over the past 12 h, and over the past 24 h, and the interactions of these changes with the current barometric pressure. These interactions allowed for the possibility that walrus might respond differently to changes in pressure depending on the current barometric pressure. We allowed no more than one time scale for change in barometric pressure to be included in any single model. Also, we did not allow interactions to be included without the associated main effects. All weather variables were normalized for use in analyses.

Finally, we also considered three-level categorical covariates for the year of tagging (2004 or 2005 versus 2006) and sex of the walrus (female or male versus undetermined), and a binary covariate that distinguished between whether or not the walrus was hauled out on the ice at the previous time point. This last variable provided a mechanism to account for serial correlation among repeated observations on the same walrus (with a correlation structure that decays exponentially relative to the 3 h time steps of the model), as well as providing a direct estimate of the magnitude of this effect. Thus, including the possibility of no effect for each of the covariates, there were 6 possible representations for time-of-day effects, 5 possible representations for the combined effects of temperature and wind, 11 possible representations for the combined effects of barometric pressure and its change over time, and the possibility of including (or excluding) effects for year, sex, and previous haul-out state. Taking all combinations of these possibilities resulted in a total of 2 640 models that we considered.

We followed the approach of Ntzoufras (2002) to implement a MCMC technique (Dellaportas et al. 2002) for model selection. This approach involved the introduction of an indicator vector  $\boldsymbol{\gamma}$  with elements  $\gamma_k$ ,  $k = 1, \dots, K$ , inserted as coefficients of the  $\beta_k$  in likelihood [1]. We let  $\gamma_k = 1$  if the variable corresponding to  $\beta_k$  was included in the model and  $\gamma_k = 0$  otherwise. Thus, every possible model was uniquely represented by its value for  $\boldsymbol{\gamma}$ , which consisted of a sequence of ones and zeros indicating which variables were or were not included in the model. The objective of this approach was to provide an estimate of the posterior probability of each considered model that could be used as a basis for model selection.

**Table 3.** Variables considered for inclusion in a model of walrus (*Odobenus rosmarus divergens*) haul-out probabilities in the Bering Sea, April 2004–2006.

Variable	Description	Marginal posterior probability <sup>a</sup>
<b>Time-of-day variables</b>		
TOD1	Time of day (0300, 0600, 0900, 1200, 1500, 1800, 2100, 2400)	0.00
TOD2	Time of day (sine function)	0.07
TOD3	Time of day (2 categories: 0900–1200, other)	0.28
TOD4	Time of day (2 categories: 1800, other)	0.32
TOD5	Time of day (3 categories: 0900–1200, 1800, other)	0.30
<b>Weather variables</b>		
PRS	Barometric pressure	0.01
PD03	Absolute value of change in barometric pressure over last 3 h	0.01
PD12	Absolute value of change in barometric pressure over last 12 h	0.01
PD24	Absolute value of change in barometric pressure over last 24 h	0.01
PX03	Interaction of PRS and PD03	0.00
PX12	Interaction of PRS and PD12	0.00
PX24	Interaction of PRS and PD24	0.00
TMP	Air temperature	0.36
WND	Wind speed	1.00
TXW	Interaction of TMP and WND	0.02
<b>Other variables</b>		
YEAR	Year (2004, 2005, or 2006)	0.00
SEX	Sex (female, male, or undetermined)	0.00
LDRY	Previous haul-out state	1.00

<sup>a</sup>Proportion of MCMC model selection iterations that included the specified variable in the model, based on the final 100 000 iterations from three separate chains of 200 000 iterations each.

Prior distributions for the  $\gamma_k$  were specified as

$$\gamma_k^* \sim \text{Bernoulli}(p_k)$$

where  $\gamma_k^* = \gamma_k$  except in the cases of  $\gamma_k$  corresponding to multivariate variables (i.e., categorical variables with more than two levels). In those cases,  $\gamma_k^*$  represented the full set of  $\gamma_k$  associated with the effect. The  $p_k$  were specified so that all 2 640 models being considered had equal prior probabilities (Ntzoufras 2002). Given the  $p_k$ , these prior distributions were conditionally independent, but the  $p_k$  themselves could depend on which other variables were in the model.

Prior distributions for the  $\beta_k$  associated with univariate variables were specified as

$$\beta_k \sim \text{Normal}(\mu_k, \sigma_k^2)$$

with

$$\mu_k = \gamma_k m_k + (1 - \gamma_k) M_k$$

$$\sigma_k^2 = \gamma_k s_k + (1 - \gamma_k) S_k$$

where  $m_k = 0$  and  $s_k = 100$  to provide relatively non-informative priors when the associated variables were included in the model.  $M_k$  was the mean and  $S_k$  was the variance for  $\beta_k$ , estimated from a preliminary run of a full model (i.e., containing that variable and a full set of additional variables permitted in the same model), as suggested by Ntzoufras (2002). Priors for  $\beta_k$  associated with multivariate variables were multivariate Normal with parameters that were the multivariate analogues of  $\mu_k$  and  $\sigma_k^2$ .

For MCMC estimation of the posterior distribution, we

used three separate chains of 200 000 iterations each. The first chain was initialized with all elements of  $\gamma$  set to 0 as starting values (i.e., the chain was initialized with a model that did not include any of the variables). Subsequent chains were initialized with values for  $\gamma$  that had low estimated posterior probability from the previous chains. We discarded the first 100 000 iterations from each chain and used the last 100 000 for estimation. To ensure that each of the separate chains converged, we examined the posterior probabilities estimated after adding each successive block of 10 000 iterations. We checked that addition of these subsequent blocks did not change the relative ranking of the top models and did not change the estimated posterior probabilities of these models by more than 0.01. We also checked that the three separate chains all converged to the same set of top-ranked models and that the estimated posterior probabilities for these models did not vary by more than 0.01 among chains. The final 100 000 iterations from each chain were combined to give 300 000 iterations used for estimating the posterior distribution of the models.

We used the posterior distribution of the models to select variables for inclusion in a final model. We then used MCMC to estimate posterior distributions of the parameters of this model based on likelihood [1] with only the selected variables and without the additional structure required for model selection. Prior distributions for the parameters in this model were as described above except that we also specified non-informative priors for the  $\beta_k$  associated with the selected univariate variables as

$$\beta_k \sim \text{Normal}(0, 1.0 \times 10^6)$$

We used analogous multivariate Normal distributions as

priors for  $\beta_k$  associated with the selected multivariate variables.

We also estimated posterior distributions of predicted haul-out state based on this final model. We estimated these posteriors for two different types of predictions (Gelman et al. 1997). First, we estimated the predicted haul-out state for each of the observations in the data. These were obtained by estimating  $Y_{it}$  in likelihood [1], using the estimated values of the parameters at each iteration of a chain. Because these predictions were based on the observed values associated with the random effects (and possibly previous haul-out state), they were applicable to specific walrus at specific points in time and were primarily useful for assessing how well the model fit the data. We used posterior means of these predictions for comparison with observed haul-out proportions.

To understand the implications of the model with respect to walrus behavior in general, however, it is more useful to have predictions that would be applicable to any walrus, selected from the population at any given point in time. Thus, we also estimated predicted haul-out state for specific combinations of variable values, while integrating over effects that were walrus- or time-specific (i.e., the random effects of walrus and time point, and possibly the fixed effect of previous haul-out state). This was accomplished by including additional observations with the specified combinations of variable values, but with missing values for haul-out state and the walrus- and time-specific variables. Current haul-out state was estimated at each iteration using the estimated values of the parameters and random values for the walrus- and time-specific variables. The random values for the walrus- and time-specific variables were selected independently, with equal probability from their distributions in the data.

For MCMC estimation with the selected model, we again used three separate chains, but with only 7 000 iterations each. One chain was initialized with starting values of zero for each of the  $\beta_k$ . The other chains were initialized with starting values of  $\beta_k = \mu_k \pm z|u_k|$ , where  $u_k$  was the median value for  $\beta_k$  estimated from a preliminary run of a single chain, and  $z$  was selected to be as large as possible without causing numerical overflows. We discarded the first 3 000 iterations from each chain and used the last 4 000 for estimation. We assessed convergence by examining the trace for each parameter over the iterations within chains (Spiegelhalter et al. 2003), Gelman–Rubin statistics for comparisons among chains (Brooks and Gelman 1998), and the ratio of MCMC error to the posterior standard error for each parameter (Spiegelhalter et al. 2003). The final 4 000 iterations from each chain were combined to give 12 000 iterations for estimating posterior distributions of parameters and haul-out probabilities. We summarized posterior distributions in terms of means and 95% credibility intervals (with limits defined as the 2.5% and 97.5% quantiles of the posterior distribution).

## Results

Analyses were based on behavior data from 43 walrus (Tables 4 and 5). Periods with behavior data spanned 10–30 April in 2004 and the entire month of April in 2005 and 2006 (Fig. 2).

**Table 4.** Numbers of observations of haul-out and in-water bouts for tagged walrus (*Odobenus rosmarus divergens*) in the Bering Sea, April 2004–2006.

Year	No. of walrus	No. of haul-out bouts	No. of in-water bouts
2004	12	71	70
2005	5	40	41
2006	26	255	264
Total	43	366	375

## Bout durations

The behavior data included observations of 741 complete bouts of walrus in-water or on-ice activity (Table 4). Observed durations of the periods walrus spent in water ranged up to 303 h, but only 2% of these (8 bouts) lasted longer than 180 h, and the average duration was 46 h (Fig. 3). Observed durations of periods walrus spent hauled out on ice tended to be much shorter, ranging only up to 42 h, with an average of 9 h per bout (Fig. 3).

There was no evidence of differences in bout durations being related to sex of the walrus or year of tagging (Table 2). The lowest-AIC model of bout duration contained effects for current haul-out state, duration of previous bout, and the interaction of these two effects (Table 2). We selected this model for obtaining final estimates of the parameters (Table 6). The estimated random effect of walrus was about the same magnitude as its standard error (Table 6), suggesting that there was little additional correlation among observations of the same walrus that was not accounted for by other variables in the model. Removing this random effect increased the AIC value of the model by only 0.74, and had little effect on other parameter estimates, so we retained this effect in the final model. Examination of deviance and deviance residuals did not indicate any lack of fit for this final model.

Model predictions were consistent with observed differences in durations of on-ice and in-water bouts, but the model underestimated the longest durations (Figs. 3 and 4). This discrepancy was most evident for in-water bouts because these included several extreme values for observed durations (Fig. 3). There was reasonably good correspondence between distributions of predicted and observed durations for all values less than the mean observed durations (Fig. 3). Mean predictions were also reasonably close to observed values for all except the longest in-water bouts (Fig. 4).

Estimated mean durations tended to be shorter for haul-out bouts than for in-water bouts overall, but in both cases, duration increased with duration of the preceding bout (Fig. 5). Differences in rates of increase corresponded to the interaction term in the model (Table 6). Estimated mean haul-out bout durations increased from about 2 to 11 h as preceding in-water bouts increased from 1 to 303 h (Fig. 5). Mean in-water bout durations increased from about 4 to 46 h as preceding on-ice bouts increased from 1 to 42 h (Fig. 5). For both on-ice and in-water bouts, the effect of preceding bout duration diminished as bouts got longer (Fig. 5).

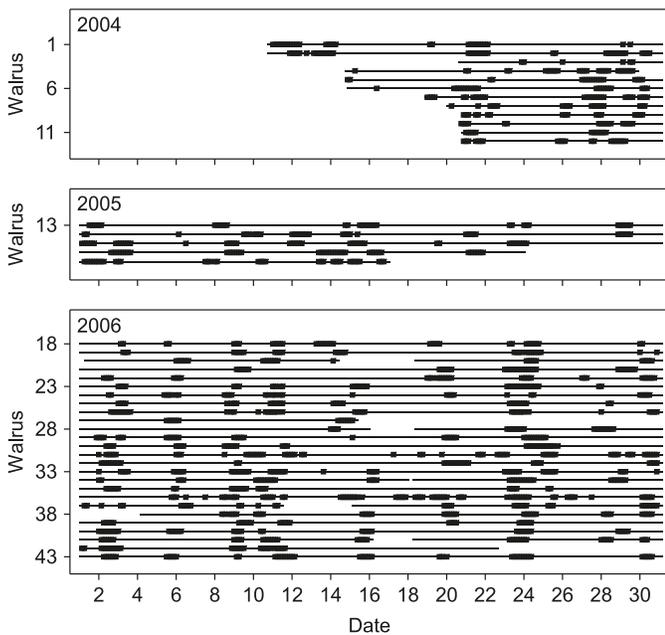
**Table 5.** Numbers of observations of haul-out behavior and geographic location for tagged walrus (*Odobenus rosmarus divergens*) in the Bering Sea, April 2004–2006.

Year	No. of walrus	No. of behavioral intervals <sup>a</sup>	Total no. of observations <sup>b</sup>	No. of observations with locations
2004	12	162	1299	570
2005	5	239	1027	175
2006	26	240	5915	1596
Total	43	641	8241	2341

<sup>a</sup>Includes a maximum of eight behavioral intervals per walrus per day that coincided with NARR time points and could be used for modeling haul-out probabilities (see text).

<sup>b</sup>An observation is a record of haul-out state for one walrus during one behavioral interval. Totals include all observations of haul-out behavior used in the model, but not the additional observations of weather conditions used only for imputation.

**Fig. 2.** Chronologies of haul-out behavior for 43 radio-tagged walrus (*Odobenus rosmarus divergens*) in the Bering Sea, April 2004–2006. Horizontal lines indicate the time periods with data from the specified walrus. Bold segments indicate periods when the walrus were hauled out on sea ice.

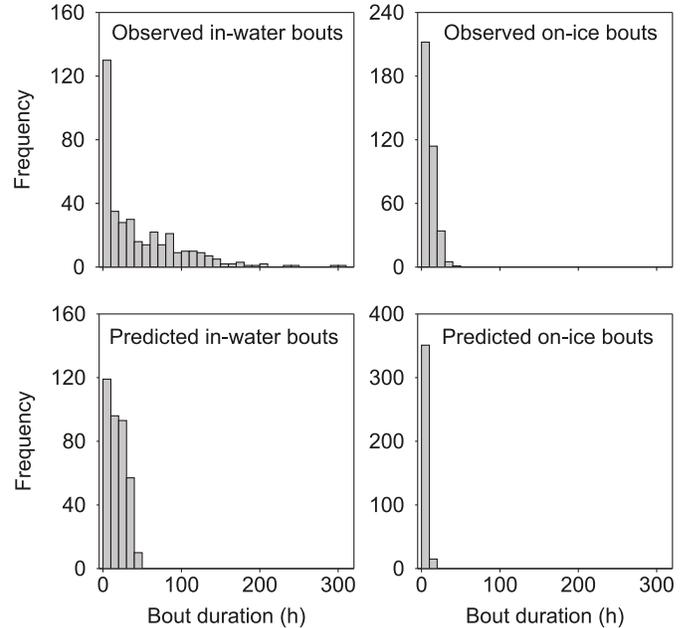


**Haul-out probabilities**

There were 8241 observations of walrus haul-out behavior associated with NARR time points (Table 5). Argos locations were obtained for 28% of these observations (Table 5). Individual walrus spent 7% to 30% (mean = 17%) of their time hauled out on sea ice (Fig. 6). Considering only behavioral intervals with data for at least 10 tagged walrus ( $n = 322$  intervals), the percentage of walrus hauled out during a given interval ranged from 0 to 71 (mean = 17%, Fig. 7). None of the tagged walrus were hauled out during 25% (79) of those intervals.

There were an additional 47 walrus with transmitters that did not function well enough to be included in the be-

**Fig. 3.** Frequency histograms of observed and predicted durations of bouts of in-water and on-ice activity by walrus (*Odobenus rosmarus divergens*) in the Bering Sea, April 2004–2006.



havior data set, but provided 1514 additional locations for time points within 6 h of at least one time point in the behavior data set. These were used to supplement the 2341 behavior observations that had locations (Table 5) to estimate means and variances for the weather imputation distributions. Means and variances for individual imputation distributions were estimated based on 2–107 observations (mean number of observations per estimate = 29) from the corresponding 12 h windows. Plots of weather variables for the 2341 behavior observations with locations (and therefore non-missing weather values, Table 5) indicated that the imputation models were reasonable (Fig. S1).<sup>2</sup>

Each of the 18 variables we considered (Table 3) was included in at least one model visited in the early iterations of at least one of the Markov chains used for model selection.

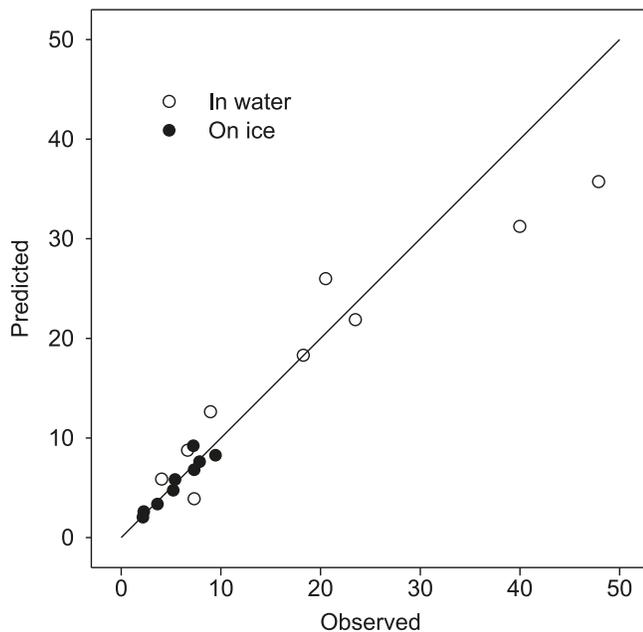
<sup>2</sup>Supplementary data for this article are available on the journal Web site (<http://cjz.nrc.ca>) or may be purchased from the Depository of Unpublished Data, Document Delivery, CISTI, National Research Council Canada, Building M-55, 1200 Montreal Road, Ottawa, ON K1A 0R6, Canada. DUD 5306. For more information on obtaining material refer to <http://cisti-icist.nrc-cnrc.gc.ca/eng/ibp/cisti/collection/unpublished-data.html>.

**Table 6.** Parameter estimates for a model of durations of periods walrus (*Odobenus rosmarus divergens*) spent in water and hauled out on ice in the Bering Sea, April 2004–2006.

Parameter	Description <sup>a</sup>	Estimate	SE
$\beta_0$	Intercept	1.04	0.14
$\beta_1$	Coefficient for DRY = 0	0.86	0.18
$\beta_2$	Coefficient for LBOUT	0.23	0.04
$\beta_3$	Coefficient for (DRY = 0) $\times$ LBOUT	0.28	0.07
$\sigma_\omega^2$	Variance for random walrus effect	0.06	0.04
$\sigma^2$	Residual variance	2.34	0.12

<sup>a</sup>See text and Table 2 for descriptions of variables.

**Fig. 4.** Comparison of observed and predicted durations of bouts of in-water and on-ice activity by walrus (*Odobenus rosmarus divergens*) in the Bering Sea, April 2004–2006. Each point represents a mean value for approximately 40 bouts, grouped in sets of increasing duration of previous bout. Predictions that exactly match observations would lie on the indicated 45° line.



However, all three chains converged to a relatively small set of models that accounted for most of the posterior probability (Table 7) within the first 10 000–20 000 iterations. Further iterations served to more precisely estimate the posterior probabilities and rankings within this small set. Final estimates of posterior probabilities were nonzero for only 122 of the 2640 models originally considered. Only 7 models had posterior probabilities  $> 0.02$  (Table 7). All models with positive posterior probabilities contained variables for wind speed and previous haul-out state (Table 3). Models that also contained a time-of-day effect accounted for a combined 97% of the posterior probability (Table 3). Models that contained a temperature effect accounted for 36% of the posterior probability (Table 3). No other variable had a marginal posterior probability of more than 0.02 (Table 3).

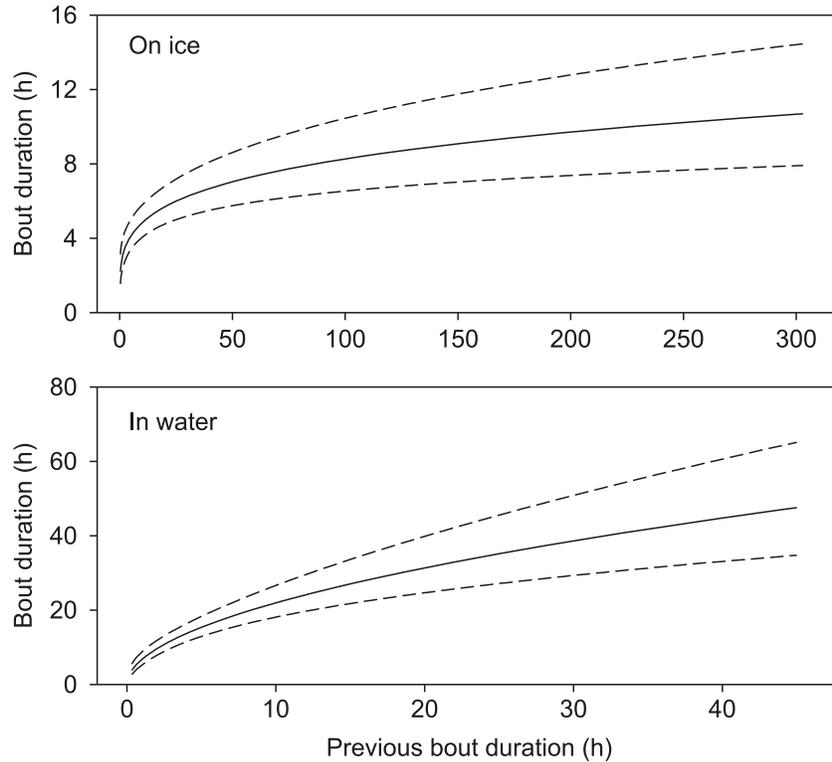
Taken together, the top seven models accounted for 91%

of the total posterior probability (Table 7). The top three models (models 1–3, Table 7), accounting for a combined 54% of the posterior probability, all contained variables for time of day, wind, and previous haul-out state, differing only slightly in the form of the time-of-day effect. Time-of-day effects were represented in these models as contrasts between haul-out probabilities for the evening period, the morning period, or both of these periods versus all other times. The next three models (models 4–6, Table 7) accounted for an additional 31% of the posterior probability. These models were the same as the top three except they also each included the temperature variable. Taken together, the top six models suggest that walrus haul-out behavior may have differed among all three time periods and may have been related to both wind speed and temperature, though the temperature relation may have been relatively weak. The only other model with an individual posterior probability greater than 0.02 (model 7, Table 7) was the same as the top three models except it represented the time-of-day effect as a sine function. The sine function is consistent with a time-of-day effect that cycles among three levels, but with a posterior probability of only 0.06 for this model, it is apparently not as effective as the categorical representations of this effect in the top six models. Therefore, we focused further analyses on the model (model 5, Table 7) that distinguished among three time-of-day levels and included both wind speed and temperature effects.

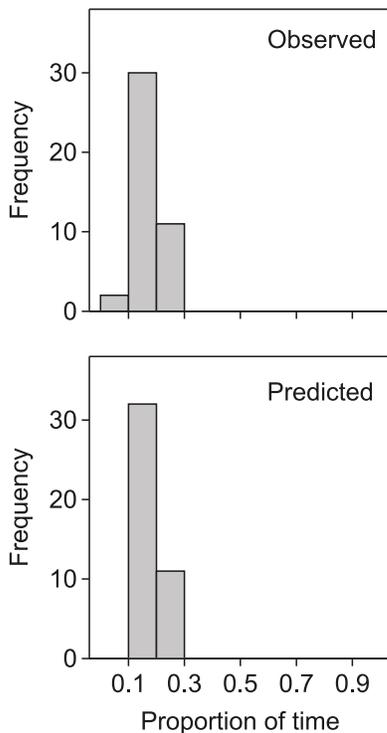
Examination of parameter traces, Gelman–Rubin statistics, and ratios of MCMC to posterior errors indicated that MCMC chains for the selected model converged within 3000 iterations. Parameters for the selected model all had 95% credibility intervals that did not include zero (Table 8). After accounting for fixed effects in the model, the additional variation in haul-out behavior among different time points was substantially larger than the variation among different walrus (Table 8).

For comparison with observed haul-out proportions (Figs. 6 and 7), we calculated averages of posterior mean predicted haul-out probabilities for each walrus and each behavioral interval. Distributions of these predictions were very similar to observed distributions of haul-out probabilities, with predicted proportions of time spent hauled out ranging from 0.11 to 0.29 (mean = 0.17) for individual walrus (Fig. 6), and predicted proportions of walrus hauled out during a given interval ranging from 0.01 to 0.65 (mean = 0.17, Fig. 7). There was also a reasonably good correspondence between the predicted probabilities and ob-

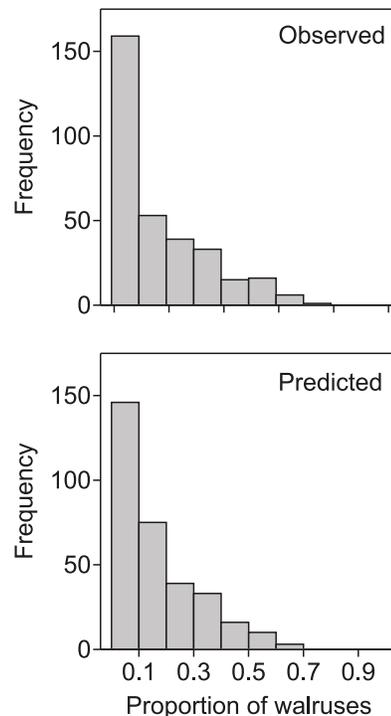
**Fig. 5.** Estimated durations of bouts of in-water and on-ice activity by walrus (*Odobenus rosmarus divergens*) as functions of previous bout duration, in the Bering Sea, April 2004–2006. Plotted values are means with 95% confidence intervals.



**Fig. 6.** Frequency histogram of observed and predicted proportions of time individual walrus (*Odobenus rosmarus divergens*,  $n = 43$  walrus) were hauled out on Bering Sea ice during April of the year in which they were tagged, 2004–2006. Predicted proportions are averages of posterior mean predicted haul-out probabilities.



**Fig. 7.** Frequency histogram of observed and predicted proportions of tagged walrus (*Odobenus rosmarus divergens*) hauled out on Bering Sea ice at selected points in time, April 2004–2006. The histogram includes only time points with data for at least 10 walrus ( $n = 322$  behavioral intervals). Predicted proportions are averages of posterior mean predicted haul-out probabilities.



**Table 7.** Posterior probabilities for models of walrus (*Odobenus rosmarus divergens*) haul-out probabilities in the Bering Sea, April 2004–2006.

Model	Variables <sup>a</sup>	Posterior probability <sup>b</sup>
1	TOD4, WND, LDRY	0.22
2	TOD5, WND, LDRY	0.18
3	TOD3, WND, LDRY	0.14
4	TOD3, WND, TMP, LDRY	0.12
5	TOD5, WND, TMP, LDRY	0.10
6	TOD4, WND, TMP, LDRY	0.09
7	TOD2, WND, LDRY	0.06

**Note:** Table includes all considered models with posterior probabilities > 0.02.

<sup>a</sup>Variables included in addition to the intercept and random effects, as described in the text. See text and Table 3 for description of variables.

<sup>b</sup>Proportion of MCMC model selection iterations that included the specified set of variables, based on the final 100 000 iterations from three separate chains of 200 000 iterations each.

served proportions for individual behavioral intervals (Fig. 8).

After integrating over the random effects of time and walrus in this model, previous haul-out state was the effect most strongly related to current haul-out state (Figs. 9, 10, 11). At mean values for temperature and wind speed, posterior mean haul-out probabilities were from 0.63 to 0.75 higher for walruses that were hauled out during the previous interval than for walruses that were in the water during the previous interval (Fig. 9). Likewise, when other factors were held constant, haul-out probabilities ranged from 0.64 to 0.81 higher over the range of temperatures (Fig. 10) and from 0.31 to 0.77 higher over the range of wind speeds (Fig. 11) for walruses that were hauled out during the previous interval. Credibility intervals for haul-out probabilities did not overlap in any of the cases that differed only with respect to previous haul-out state (Figs. 9, 10, 11).

Haul-out probabilities increased with temperature (Fig. 10) and decreased with wind speed (Fig. 11). Holding other variables constant, differences in posterior mean haul-out probabilities were larger over the range of observed wind speeds (difference = 0.58 for walruses previously on ice, 0.12 for walruses previously in water, Fig. 11) than over the range of observed temperatures (difference = 0.18 for walruses previously on ice, 0.01 for walruses previously in water, Fig. 10). Credibility intervals for all of these predicted haul-out probabilities broadly overlapped, however (Figs. 10 and 11). For given values of temperature and wind, haul-out probabilities increased from morning to evening, and differences in posterior means (evening – morning = 0.16 for walruses previously on ice, 0.04 for walruses previously in water, Fig. 9) were about the same as the corresponding differences attributable to temperature effects. Credibility intervals for these probabilities also broadly overlapped (Fig. 9).

Integrating over previous haul-out state as well as the random effects of time and walrus provided estimates of mean haul-out probabilities that ranged from 0.04 to 0.31, following the same general patterns noted above (Figs. 12 and 13). Credibility intervals for these estimates were considerably

larger than for the estimates that depended on previous haul-out state. Lengths of 95% credibility intervals for the haul-out probabilities presented in Figs. 12 and 13 ranged from 0.36 to 0.92, but posterior distributions were bimodal, with most of the probability concentrated around the two modes (Figs. S2 and S3).<sup>2</sup>

## Discussion

Our analysis provides the first fully quantitative characterization of walrus haul-out behavior on Bering Sea ice. Overall, walruses spent a relatively small proportion of their time hauled out on sea ice, averaging about 83% of their time in the water during April. This is within the range of monthly values observed for a single male Atlantic walrus (*Odobenus rosmarus rosmarus* (L., 1758)) in the Greenland Sea that spent 70%–87% of its time in water during October–January (Born et al. 2005). The study of this walrus by Born et al. (2005) provides the only other published telemetry data on time in water for walruses in sea ice habitat. However, the behavioral patterns observed by Born et al. (2005) and in our study are consistent with July–September observations at terrestrial haul-out sites where walruses also spent most of their time (65%–85%) in the water (Born and Knutsen 1997; Gjertz et al. 2001; Jay et al. 2001; Born et al. 2005; Acquarone et al. 2006; Lydersen et al. 2008).

Individual walruses in our study spent an average of 46 h per bout in water and an average of 9 h per bout on ice, but durations of on-ice bouts tended to increase with durations of preceding in-water bouts. Jay et al. (2001) also found that durations of haul-out bouts at terrestrial sites in Bristol Bay, Alaska, increased with durations of preceding in-water bouts. We did not detect any differences in bout durations related to walrus sex or year of tagging.

The average durations we observed for both in-water and on-ice bouts were considerably shorter than those that have been observed for walruses strictly associated with terrestrial haul-out sites, where average in-water durations have ranged from 56 to 143 h and on-land durations have ranged from 20 to 38 h per bout (Born and Knutsen 1997; Gjertz et al. 2001; Jay et al. 2001; Lydersen et al. 2008). Our average value for on-ice bouts is comparable to the average of 11 h per on-ice bout observed by Born and Knutsen (1997) for walruses when they hauled out on sea ice during a year when ice was present near a terrestrial haul-out site that they were also using. Likewise, the average duration we observed for in-water bouts is comparable to the 38 h per in-water interval observed by Born and Knutsen (1997) that same year. There are no previously published data on durations of haul-out bouts for walruses without access to terrestrial haul-out sites.

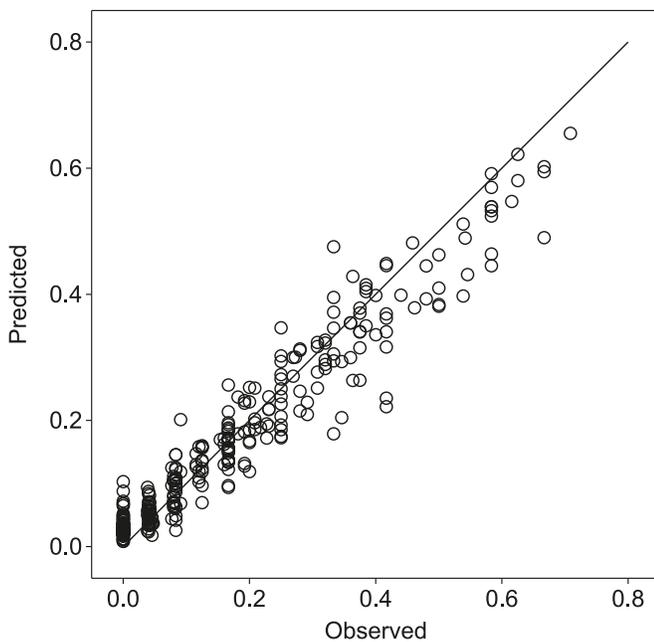
Even though durations of individual bouts of in-water activity tend to be shorter for walruses in sea ice habitat, the overall portion of time spent in water appears to be about the same for walruses using either sea ice or terrestrial haul-out sites. Differences in durations of in-water activity periods associated with use of these sites may be related to differences in distances to foraging areas (Gjertz et al. 2001). Walruses may be able to make shorter and more frequent foraging trips when the trips originate from sea ice rather than terrestrial haul-out sites.

**Table 8.** Parameter estimates for a model of walrus (*Odobenus rosmarus divergens*) haul-out probabilities in the Bering Sea, April 2004–2006.

Parameter	Description <sup>a</sup>	Mean	95% credibility interval	
			Lower limit	Upper limit
$\beta_0$	Intercept	-3.29	-3.47	-3.10
$\beta_1$	Coefficient for TOD5 = evening	0.48	0.15	0.82
$\beta_2$	Coefficient for TOD5 = morning	-0.42	-0.70	-0.15
$\beta_3$	Coefficient for TMP	0.16	0.05	0.27
$\beta_4$	Coefficient for WND	-0.53	-0.65	-0.41
$\beta_5$	Coefficient for LDRY	4.45	4.23	4.67
$\sigma_\tau^2$	Variance for random time effect	0.437	0.235	0.654
$\sigma_\omega^2$	Variance for random walrus effect	0.007	0.001	0.030

<sup>a</sup>See text and Table 3 for descriptions of variables.

**Fig. 8.** Comparison of observed and predicted proportions of tagged walrus (*Odobenus rosmarus divergens*) hauled out on Bering Sea ice at selected points in time, April 2004–2006. Each point represents a behavioral interval with data for at least 10 walrus ( $n = 322$  intervals). Predicted proportions are averages of posterior mean predicted haul-out probabilities. Predictions that exactly match observations would lie on the indicated 45° line.



The probability of walrus being hauled out at any given time was related to wind speed, temperature, and time of day, though the relations were weak relative to relations with other, apparently random, factors. Credibility intervals for parameters related to wind, temperature, and time-of-day effects did not include zero, indicating that these factors were related to haul-out behavior. However, the wide, overlapping credibility intervals for predicted haul-out probabilities indicate there was also a substantial amount of variability in the relations. Variability around the 45° line in Fig. 8 indicates that there was substantial variability even beyond what could be accounted for by random time and walrus effects.

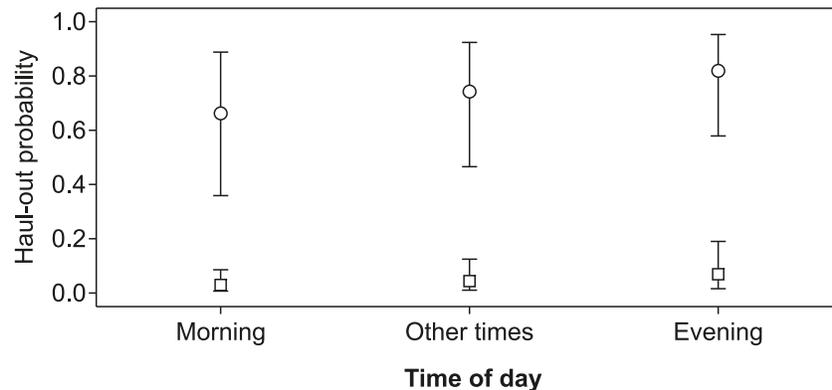
Wind speed was more strongly related than temperature or time of day to haul-out probability. This was evidenced

by its inclusion in 100% of the models with positive posterior probability and the relative magnitudes of differences in haul-out probabilities over the range of wind speed values. Temperature and time-of-day effects were both included in most models with positive posterior probability, but differences in haul-out probabilities associated with these variables were not as large as differences associated with observed variation in wind speed. We found no evidence for any relations of haul-out probabilities to barometric pressure, sex, or year that could not be more parsimoniously characterized in terms of the other weather and time-of-day variables.

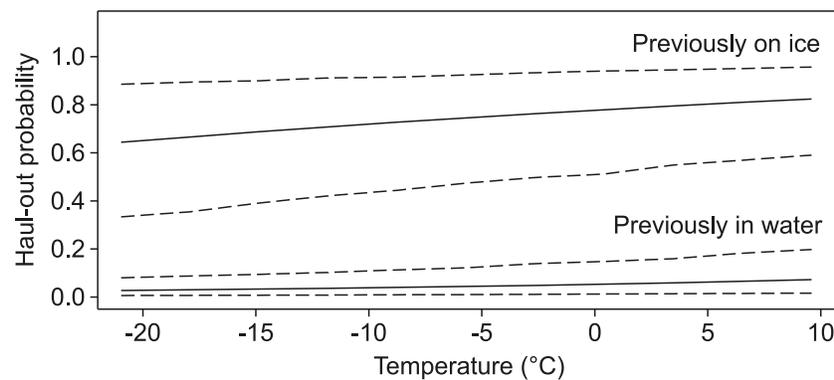
The influence of weather on walrus haul-out behavior is likely to be due, at least partly, to thermoregulatory requirements (Wells et al. 1999). Field biologists and hunters have noted that walrus generally avoid hauling out during periods of intense cold or high wind (Fay and Ray 1968; Mansfield and St. Aubin 1991; Garlich-Miller and Jay 2000). Haul-out behavior of Atlantic walrus at terrestrial haul-out sites has been quantitatively related to wind (Salter 1979; Born and Knutsen 1997), temperature (Salter 1979), and precipitation (Salter 1979; Born and Knutsen 1997). Lydersen et al. (2008) did not detect any relation between wind or temperature changes and haul-out behavior of male walrus using terrestrial haul-out sites in Svalbard, but the range of weather conditions experienced by those animals appears to have been relatively narrow in comparison with the ranges observed during other studies.

Fay and Ray (1968) observed that Pacific walrus in the Bering Sea tended to haul out mostly during the daytime, with peak numbers hauled out during early morning and early afternoon. We also found that walrus tended to haul out mostly during the day, but with haul-out probabilities increasing from their lowest point in late morning to their highest point in the early evening. Some studies of Atlantic walrus have found relations between haul-out behavior and time of day, with haul-out numbers highest during the day (Salter 1979) or in the afternoon and evening (Born and Knutsen 1997), while others have not found any relation (Mansfield and St. Aubin 1991; Lydersen et al. 2008). Detection of diel patterns in walrus haul-out behavior is complicated by correlations with daily temperature patterns (Born and Knutsen 1997) and by the fact that walrus often haul out for periods of up to several days before they return to the water (Gjertz et al. 2001; Jay et al. 2001). Also, diel

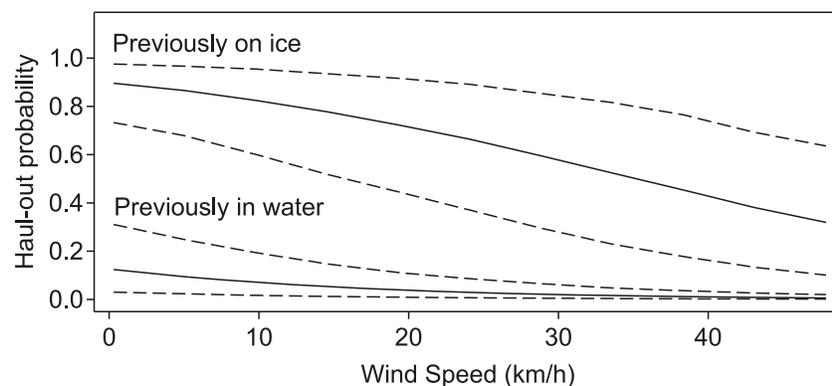
**Fig. 9.** Estimated probabilities of Pacific walrus (*Odobenus rosmarus divergens*) being hauled out on sea ice in April, as functions of time of day and previous haul-out state (squares, previously in water; circles, previously hauled out). Plotted values are posterior means with 95% credibility intervals. Probabilities are estimated at mean values of temperature and wind speed, integrating over random effects due to time and walrus.



**Fig. 10.** Estimated probabilities of Pacific walrus (*Odobenus rosmarus divergens*) being hauled out on sea ice in April, as functions of air temperature and previous haul-out state. Temperatures span the range of observed values in the April 2004–2006 data. Plotted values are posterior means with 95% credibility intervals. Probabilities are estimated for the median time of day (i.e., other than morning or evening) and the mean value of wind speed, integrating over random effects due to time and walrus.



**Fig. 11.** Estimated probabilities of Pacific walrus (*Odobenus rosmarus divergens*) being hauled out on sea ice in April, as functions of wind speed and previous haul-out state. Wind speeds span the range of observed values in the April 2004–2006 data. Plotted values are posterior means with 95% credibility intervals. Probabilities are estimated for the median time of day (i.e., other than morning or evening) and the mean value of temperature, integrating over random effects due to time and walrus.

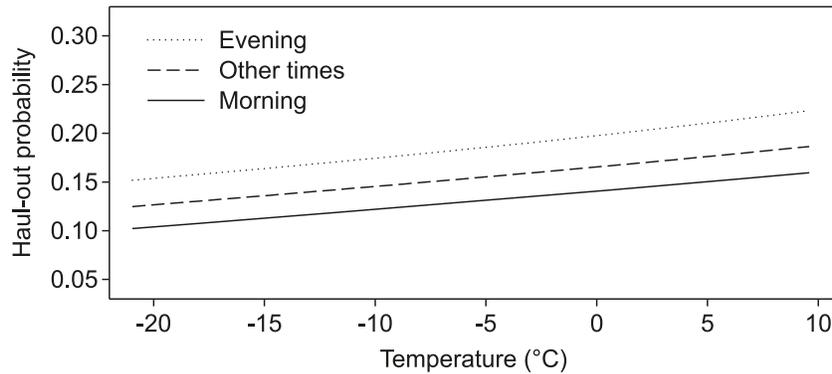


patterns may vary seasonally in response to such factors as day length (Lydersen et al. 2008).

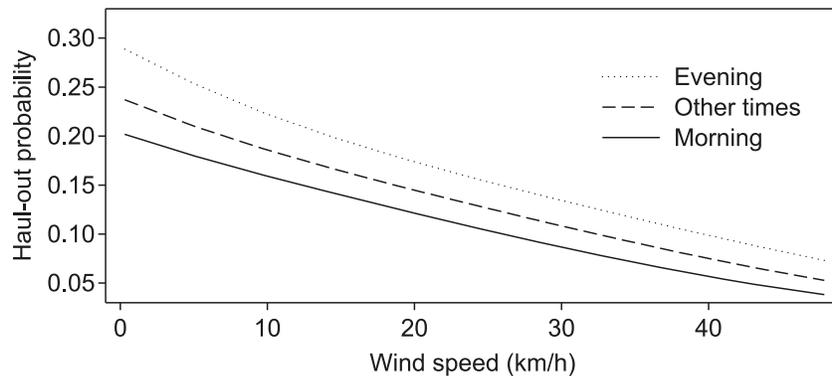
Walrus distribution is related to the seasonal distribution of sea ice (Fay 1982) and to ice characteristics such as coverage, floe size, and thickness (Wartzok and Ray 1980; Simpkins et al. 2003a). Walrus must select floes of suffi-

cient size and thickness to support their weight for hauling out. Topography of sea ice likely influences microclimatic conditions and may affect which floes are selected for hauling out. Given that walrus are in an area with suitable ice, however, it is not known whether characteristics of that ice further influence the probability of hauling out. Our model

**Fig. 12.** Estimated probabilities of Pacific walrus (*Odobenus rosmarus divergens*) being hauled out on sea ice in April, as functions of air temperature and time of day. Plotted values are posterior means. Probabilities are estimated at the mean value of wind speed, integrating over previous haul-out state and random effects due to time and walrus.



**Fig. 13.** Estimated probabilities of Pacific walrus (*Odobenus rosmarus divergens*) being hauled out on sea ice in April, as functions of wind speed and time of day. Plotted values are posterior means. Probabilities are estimated at the mean value of temperature, integrating over previous haul-out state and random effects due to time and walrus.



was based on 3 years of telemetry data covering a range of ice conditions over a large portion of the Bering Sea. Within this range, any effects of ice characteristics on haul-out probabilities are accounted for as a part of the random variation in the model and will result in appropriately increased variability of posterior distributions. Future research should consider the potential for explicitly using remotely sensed data on ice characteristics in models of walrus haul-out behavior.

Previous haul-out state had the strongest relation to haul-out probability of any of the variables we considered. The effect of this variable was clearly evident in the magnitudes of associated differences in haul-out probabilities and the non-overlapping credibility intervals. Part of this effect may be due to physiological, social, or environmental conditions (not captured by other variables we considered) that are related to haul-out behavior and tend to change slowly relative to the 3 h time steps in our model. The result is that individual haul-out or in-water bouts tended to be longer than 3 h (Fig. 2), so the observations for individual walrus were strongly autocorrelated.

Although previous haul-out state is a strong predictor of current haul-out state, it is not useful for estimating haul-out probabilities for walrus with unknown haul-out histories. Estimates that are not conditioned on previous haul-out state (e.g., Figs. 12 and 13) give a more useful characterization of haul-out probabilities because they apply to the

population as a whole. Posterior distributions for these unconditional probabilities tend to be bimodal, with probability concentrated in areas around the modes rather than the mean (Figs. S2 and S3). The modes correspond to the two possible values for previous haul-out state.

Our modeling approach illustrates how a Bayesian framework can be used to combine imputation with simultaneous model selection for a hierarchical model. Our specific approach can be applied directly to studies of other ice-associated pinnipeds by using the same types of telemetry and weather data, but the general approach also has potential for use in any application that develops models as functions of incomplete environmental data. In some applications, it might be desirable to also incorporate model averaging (Burnham and Anderson 2002), rather than basing inferences on a single selected model. With our approach, the estimated posterior probabilities for each model could be used directly as a basis for averaging the estimates from those models.

Pinniped populations are typically monitored based on counts of hauled-out individuals, but these counts must be adjusted or standardized to account for the portion of the population that was in the water when the counts were made (Eberhardt et al. 1979; Green et al. 1995). For estimation of population trends, this issue has usually been addressed by either standardizing survey conditions to minimize differences in haul-out proportions (Jacobs and

Terhune 2000; Simpkins et al. 2003b) or adjusting for differences in conditions by incorporating appropriate covariates in models of the counts (Calkins et al. 1999; Mathews and Pendleton 2006). Estimation of population size generally requires explicit estimates of the proportion of the population hauled out during the survey. Design-based estimates of haul-out proportions can be obtained directly from a sample of individuals during the survey (Thompson et al. 1997; Huber et al. 2001). Model-based estimates can be obtained as functions of covariates that are measured during a survey (Bengtson et al. 2005; Krafft et al. 2006; Sharples et al. 2009). Model-based estimation of haul-out proportions becomes necessary when it is not practical to monitor the haul-out behavior of a representative sample of the target population during the survey.

Our unconditional model can be used along with data from an April survey of walrus on Bering Sea ice to estimate the portion of the population that was in the water during the survey. Posterior distributions of the haul-out probabilities associated with each walrus group detected on the ice in the survey can be estimated using weather conditions from the nearest NARR grid point. Dividing the estimated size of each detected group by the associated haul-out probability and summing over the detected groups on each surveyed transect gives a Horvitz–Thompson expansion (Thompson 2002) that accounts for groups that could not be detected because they were in the water. Variability associated with estimation of the haul-out probabilities can be accounted for by resampling from their estimated posterior distributions as a part of the overall bootstrap variance estimation procedure (Udevitz et al. 2008). Of course, this use of the model assumes haul-out behavior of the tagged walrus sample is representative of walrus behavior throughout the survey area, including areas in which there were no tagged walrus. The extensive area ranged over by the tagged walrus sample (Fig. 1) and the apparent lack of relations between haul-out behavior and sex or year (confounded with region) suggest that this assumption is likely to be reasonable. However, we recommend future validation of the model with additional data from areas of the Bering Sea not sampled in this study, if possible.

Our results indicate that at any given time during April, we can expect a substantial portion, if not the majority, of the Pacific walrus population to be in the water rather than hauled out on the ice. Therefore, it will be essential to account for walrus in the water to obtain a reasonable estimate of the total population size during an April survey. Our model indicates that estimates of the portion of the walrus population in the water will be only weakly dependent on weather conditions and time of day relative to other factors considered as random by the model. However, conditions in the Bering Sea can change dramatically year to year, and even day to day, so accounting for effects of weather and time of day could be important. Because of seasonal changes in walrus behavior (Fay 1982), we would not recommend this model for use outside the April time period for which it was developed. In addition to its survey application though, the model also provides an important step in understanding relations of environmental factors to haul-out behavior of Pacific walrus on sea ice. This understanding will provide the necessary basis for future studies of how

walrus use their sea ice habitats and for assessing potential changes in their behavior relative to projected changes in climate and sea ice (Overland and Wang 2007).

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## References

- Acquarone, M., Born, E.W., and Speakman, J.R. 2006. Field metabolic rates of walrus (*Odobenus rosmarus*) measured by the doubly labeled water method. *Aquat. Mamm.* **32**(3): 363–369. doi:10.1578/AM.32.3.2006.363.
- Bengtson, J.L., and Cameron, M.F. 2004. Seasonal haulout patterns of crabeater seals (*Lobodon carcinophaga*). *Polar Biol.* **27**(6): 344–349. doi:10.1007/s00300-004-0597-1.
- Bengtson, J.L., Hiruki-Raring, L.M., Simpkins, M.A., and Boveng, P.L. 2005. Ringed and bearded seal densities in the eastern Chukchi Sea, 1999–2000. *Polar Biol.* **28**(11): 833–845. doi:10.1007/s00300-005-0009-1.
- Born, E.W., and Knutsen, L.Ø. 1997. Haul-out and diving activity of male Atlantic walrus (*Odobenus rosmarus rosmarus*) in NE Greenland. *J. Zool. (Lond.)*, **243**(2): 381–396. doi:10.1111/j.1469-7998.1997.tb02789.x.
- Born, E.W., Acquarone, M., Knutsen, L.Ø., and Toudal, L. 2005. Homing behaviour in an Atlantic walrus (*Odobenus rosmarus rosmarus*). *Aquat. Mamm.* **31**(1): 23–33. doi:10.1578/AM.31.1.2005.23.
- Brooks, S.P., and Gelman, A. 1998. Alternative methods for monitoring convergence of iterative simulations. *J. Comput. Graph. Statist.* **7**(4): 434–455. doi:10.2307/1390675.
- Burek, K.A., Gulland, F.M.D., and O'Hara, T.M. 2008. Effects of climate change on Arctic marine mammal health. *Ecol. Appl.* **18**(2): S126–S134. doi:10.1890/06-0553.1. PMID:18494366.
- Burn, D.M., Webber, M.A., and Udevitz, M.S. 2006. Application of airborne thermal imagery to surveys of Pacific walrus. *Wildl. Soc. Bull.* **34**(1): 51–58. doi:10.2193/0091-7648(2006)34[51:AOATIT]2.0.CO;2.
- Burnham, K.P., and Anderson, D.R. 2002. Model selection and multimodel inference, second edition. Springer, New York.

- Burns, J.J., Shapiro, L.H., and Fay, F.H. 1981. Ice as marine mammal habitat in the Bering Sea. *In* The Eastern Bering Sea Shelf: oceanography and resources. Edited by D.W. Hood and J.A. Calder. University of Washington Press, Seattle. pp. 781–797.
- Calkins, D.G., McAllister, D.C., Pitcher, K.W., and Pendleton, G.W. 1999. Steller sea lion status and trend in southeast Alaska: 1979–1997. *Mar. Mamm. Sci.* **15**(2): 462–477. doi:10.1111/j.1748-7692.1999.tb00813.x.
- Collecte Localisation Satellites. 2007. Argos user's manual. Collecte Localisation Satellites, Ramonville-Saint-Agne, France.
- Dellaportas, P., Forster, J.J., and Ntzoufras, I. 2002. On Bayesian model and variable selection using MCMC. *Stat. Comput.* **12**(1): 27–36. doi:10.1023/A:1013164120801.
- Douglas, D.C. 2006. The Douglas Argos-Filter Algorithm [online]. Available from <http://alaska.usgs.gov/science/biology/spatial/douglas.html> [accessed 1 April 2009].
- Eberhardt, L.L., Chapman, D.G., and Gilbert, J.R. 1979. A review of marine mammal census methods. *Wildl. Monogr.* **63**: 1–46.
- Fay, F.H. 1982. Ecology and biology of the Pacific walrus, *Odobenus rosmarus divergens* Illiger. *N. Am. Fauna*, **74**: 1–279.
- Fay, F.H., and Ray, G.C. 1968. Influence of climate on the distribution of walruses, *Odobenus rosmarus* (Linnaeus). I. Evidence from thermoregulatory behavior. *Zoologica*, **53**: 1–14.
- Fischbach, A.S., Jay, C.V., Jackson, J.V., Andersen, L.W., Sage, G.K., and Talbot, S.L. 2008. Molecular method for determining sex of walruses. *J. Wildl. Manag.* **72**(8): 1808–1812. doi:10.2193/2007-413.
- Frost, K.J., Lowry, L.F., Pendleton, G., and Nute, H.R. 2004. Factors affecting the observed densities of ringed seals, *Phoca hispida*, in the Alaskan Beaufort Sea, 1996–99. *Arctic*, **57**: 115–128.
- Garlich-Miller, J., and Jay, C.V. 2000. Proceedings of a Workshop Concerning Walrus Survey Methods. U.S. Fish and Wildlife Service, Region 7, Marine Mammals Management, Technical Report 00-2, Anchorage, Alaska.
- Gelman, A., Carlin, J.B., Stern, H.S., and Rubin, D.B. 1997. Bayesian data analysis. Chapman and Hall, New York.
- Gilbert, J.R. 1999. Review of previous Pacific walrus surveys to develop improved survey designs. *In* Marine mammal survey and assessment methods. Edited by G.W. Garner, S.C. Amstrup, J.L. Laake, B.F.J. Manly, L.L. McDonald, and D.G. Robertson. A.A. Balkema, Brookfield, Vt. pp. 75–84.
- Gjertz, I., Griffiths, D., Krafft, B.A., Lydersen, C., and Wiig, Ø. 2001. Diving and haul-out patterns of walruses *Odobenus rosmarus* on Svalbard. *Polar Biol.* **24**(5): 314–319. doi:10.1007/s003000000211.
- Green, K., Burton, H.R., Wong, V., McFarlane, R.A., Flaherty, A.A., Pahl, B.C., and Haigh, S.A. 1995. Difficulties in assessing population status of ice seals. *Wildl. Res.* **22**(2): 193–199. doi:10.1071/WR9950193.
- Hayward, J.L., Henson, S.M., Logan, C.J., Parris, C.R., Meyer, M.W., and Dennis, B. 2005. Predicting numbers of hauled-out harbour seals: a mathematical model. *J. Appl. Ecol.* **42**(1): 108–117. doi:10.1111/j.1365-2664.2005.00999.x.
- Huber, H.R., Jeffries, S.J., Brown, R.F., DeLong, R.L., and VanBlaricom, G. 2001. Correcting aerial survey counts of harbor seals (*Phoca vitulina richardsi*) in Washington and Oregon. *Mar. Mamm. Sci.* **17**(2): 276–293. doi:10.1111/j.1748-7692.2001.tb01271.x.
- Ibrahim, J.G., Chen, M.-H., Lipsitz, S.R., and Herring, A.H. 2005. Missing-data methods for generalized linear models: a comprehensive review. *J. Am. Stat. Assoc.* **100**(469): 332–346. doi:10.1198/016214504000001844.
- Jacobs, S.R., and Terhune, J.M. 2000. Harbor seal (*Phoca vitulina*) numbers along the New Brunswick coast of the Bay of Fundy in autumn in relation to aquaculture. *Northeast. Nat.* **7**: 289–296.
- Jay, C.V., Farley, S.D., and Garner, G.W. 2001. Summer diving behavior of male walruses in Bristol Bay, Alaska. *Mar. Mamm. Sci.* **17**(3): 617–631. doi:10.1111/j.1748-7692.2001.tb01008.x.
- Jay, C.V., Heide-Jørgensen, M.P., Fischbach, A.S., Jensen, M.V., Tessler, D.F., and Jensen, A.V. 2006. Comparison of remotely deployed satellite radio transmitters on walruses. *Mar. Mamm. Sci.* **22**: 226–236.
- Krafft, B.A., Kovacs, K.M., Andersen, M., Aars, J., Lydersen, C., Ergon, T., and Haug, T. 2006. Abundance of ringed seals (*Pusa hispida*) in the fjords of Spitsbergen, Svalbard, during the peak molting period. *Mar. Mamm. Sci.* **22**(2): 394–412. doi:10.1111/j.1748-7692.2006.00035.x.
- Littell, R.C., Milliken, G.A., Wolfinger, R.D., and Schabenberger, O. 2006. SAS for mixed models. SAS Press, Cary, N.C.
- Lydersen, C., Aars, J., and Kovacs, K.M. 2008. Estimating the number of walruses in Svalbard from aerial surveys and behavioural data from satellite telemetry. *Arctic*, **61**: 119–128.
- Mansfield, A.W., and St. Aubin, D.J. 1991. Distribution and abundance of the Atlantic walrus, *Odobenus rosmarus rosmarus*, in the Southampton Island – Coats Island region of northern Hudson Bay. *Can. Field Nat.* **105**: 95–100.
- Mathews, E.A., and Pendleton, G.W. 2006. Declines in harbor seal (*Phoca vitulina*) numbers in Glacier Bay National Park, Alaska, 1992–2002. *Mar. Mamm. Sci.* **22**: 167–189.
- McCullagh, P., and Nelder, J.A. 1999. Generalized linear models. 2nd ed. Chapman and Hall, Boca Raton, Fla.
- Mesinger, F., DiMego, G., Kalnay, E., Mitchell, K., Shafran, P.C., Ebisuzaki, W., Jovic, D., Woollen, J., Rogers, E., Berbery, E.H., Ek, M.B., Fan, Y., Grumbine, R., Higgins, W., Li, H., Lin, Y., Manikin, G., Parrish, D., and Shi, W. 2006. North American Regional Reanalysis. *Bull. Am. Meteorol. Soc.* **87**(3): 343–360. doi:10.1175/BAMS-87-3-343.
- Moulton, V.D., Richardson, W.J., McDonald, T.L., Elliott, R.E., and Williams, M.T. 2002. Factors influencing local abundance and haulout behavior of ringed seals (*Phoca hispida*) on landfast ice of the Alaskan Beaufort Sea. *Can. J. Zool.* **80**(11): 1900–1917. doi:10.1139/z02-173.
- Ntzoufras, I. 2002. Gibbs variable selection using BUGS. *J. Stat. Softw.* **7**: 1–19.
- Overland, J.E., and Wang, M. 2007. Future regional Arctic sea ice declines. *Geophys. Res. Lett.* **34**(17): L17705. doi:10.1029/2007GL030808.
- Peterson, W.W., and Brown, D.T. 1961. Cyclic codes for error detection. *Proc. Inst. Radio Eng.* **49**: 228–235.
- Rausch, R.L., George, J.C., and Brower, H.K. 2007. Effect of climatic warming on the Pacific walrus, and potential modification of its helminth fauna. *J. Parasitol.* **93**(5): 1247–1251. doi:10.1645/GE-3583CC.1. PMID:18163371.
- Ray, C.G., McCormick-Ray, J., Berg, P., and Epstein, H.E. 2006. Pacific walrus: benthic bioturbator of Beringia. *J. Exp. Mar. Biol. Ecol.* **330**(1): 403–419. doi:10.1016/j.jembe.2005.12.043.
- Reder, S., Lydersen, C., Arnold, W., and Kovacs, K.M. 2004. Haulout behaviour of high Arctic harbour seals (*Phoca vitulina vitulina*) in Svalbard, Norway. *Polar Biol.* **27**(1): 6–16. doi:10.1007/s00300-003-0557-1.
- Salter, R.E. 1979. Site utilization, activity budgets, and disturbance responses of Atlantic walruses during terrestrial haul-out. *Can. J. Zool.* **57**(6): 1169–1180. doi:10.1139/z79-149.
- Sharples, R.J., Mackenzie, M.L., and Hammond, P.S. 2009. Estimating seasonal abundance of a central place forager using

- counts and telemetry data. *Mar. Ecol. Prog. Ser.* **378**: 289–298. doi:10.3354/meps07827.
- Simpkins, M.A., Hiruki-Raring, L.M., Sheffield, G., Grebmeier, J.M., and Bengtson, J.L. 2003a. Habitat selection by ice-associated pinnipeds near St. Lawrence Island, Alaska in March 2001. *Polar Biol.* **26**(9): 577–586. doi:10.1007/s00300-003-0527-7.
- Simpkins, M.A., Withrow, D.E., Cesarone, J.C., and Boveng, P.L. 2003b. Stability in the proportion of harbor seals hauled out under locally ideal conditions. *Mar. Mamm. Sci.* **19**(4): 791–805. doi:10.1111/j.1748-7692.2003.tb01130.x.
- Southwell, C. 2005. Optimising the timing of visual surveys of cre-beater seal abundance: haulout behaviour as a consideration. *Wildl. Res.* **32**(4): 333–338. doi:10.1071/WR04085.
- Spiegelhalter, D.J., Thomas, A., Best, N.G., and Lund, D. 2003. WinBUGS user manual. Version 1.4. MRC Biostatistics Unit, Cambridge, U.K.
- Thompson, S.K. 2002. *Sampling*. 2nd ed. John Wiley and Sons, New York.
- Thompson, P.M., Tollit, D.J., Wood, D., Corpe, H.M., Hammond, P.S., and MacKay, A. 1997. Estimating harbour seal abundance and status in an estuarine habitat in north-east Scotland. *J. Appl. Ecol.* **34**(1): 43–52. doi:10.2307/2404846.
- Udevitz, M.S., Burn, D.M., and Webber, M.A. 2008. Estimation of walrus populations on sea ice with infrared imagery and aerial photography. *Mar. Mamm. Sci.* **24**(1): 57–70. doi:10.1111/j.1748-7692.2007.00169.x.
- Wartzok, D., and Ray, G.C. 1980. The hauling-out behavior of the Pacific walrus. U.S. Department of Commerce, Marine Mammal Commission, Final Report MMC-75/15, Washington, D.C.
- Wells, R.S., Boness, D.J., and Rathbun, G.B. 1999. Behavior. *In* *Biology of marine mammals*. Edited by J.E. Reynolds, III and S.A. Rommel. Smithsonian Institution Press, Washington, D.C. pp. 324–422.
- Yang, X., Belin, T.R., and Boscardin, W.J. 2005. Imputation and variable selection in linear regression models with missing covariates. *Biometrics*, **61**(2): 498–506. doi:10.1111/j.1541-0420.2005.00317.x. PMID:16011697.