Seasonal sea ice dynamics drive movement and migration of juvenile bearded seals *Erignathus barbatus*

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ABSTRACT: We analyzed how juvenile bearded seals *Erignathus barbatus* use and move through sea ice and consider how future ice conditions might affect bearded seal distribution and behavior. In October 2004, 2005, 2006, and 2009, we tagged 29 (16 female and 13 male) juvenile (0–2 yr old) bearded seals with Argos satellite transmitters in Kotzebue Sound, Alaska, USA, who then freely moved through the Chukchi and Bering Seas. Movement data were initially analyzed using behavior discriminating state-space models. These results were subsequently analyzed with mixed-effects models to relate inferred behavioral state to environmental variables (sea ice, water depth, season, distance to ice edge) and then with a modified resource selection function using the same environmental variables. Sea ice concentration was highly predictive of use, but had a non-linear effect, with seals preferring intermediate concentrations and areas closer to the ice edge (defined here as 15% sea ice concentration). Behavior was also affected by sea ice and other environmental conditions. When seals were in dense sea ice, they were likely to express an encamped movement pattern; when in open water or sparse ice, they tended to express transiting behavior. The seasonal migratory behavior of bearded seals, at least in juveniles, appears to result from tracking the sea ice edge as it seasonally expands and recedes over the Bering and Chukchi continental shelves. The association with the ice edge suggests that bearded seal habitat will shift as the climate warms.

KEY WORDS: Bearded seals · *Erignathus barbatus* · Movement behavior · Foraging ecology · Benthic predator · Biologging

INTRODUCTION

Bearded seals *Erignathus barbatus* are important Arctic and sub-Arctic benthic-foraging marine predators (Stirling & Archibald 1977, Burns 1981, Cameron et al. 2010). They are of major cultural significance and an important natural resource to many Arctic indigenous peoples who have relied on this species for construction materials, clothing, and food for millennia (Kishigami 2000, Cameron et al. 2010). Despite their importance to Arctic ecosystems and peoples, details of bearded seal life history, ecology, and behavior are relatively poorly documented. Indigenous hunters living in communities along the coast of the Bering, Chukchi, and Beaufort Seas have accumulated a significant body of traditional knowledge on bearded seal ecology and distribution (Whiting et al. 2011). Although this knowledge is quite detailed around traditional hunting periods and places, it does not extend beyond that scope and remains an incomplete picture. Scientifically observed natural history data have supplemented this traditional knowledge

(Burns 1981, Fedoseev 1984, Kingsley et al. 1985), but inference from these studies is constrained by logistical difficulty and limited spatial scope.

Understanding behavior of juvenile bearded seals may be particularly important. In long-lived mammals, the first year of life is typically the most critical to long-term survival (McMahon et al. 2000, Breed et al. 2013, Bowen et al. 2015). Juvenile mortality is usually higher than all other age classes, and this is certainly true in bearded seals: about 60% of bearded seal pups die before age 1, and an additional 12% die before age 3 (Frost et al. 1983). In most long-lived mammals, however, individuals that survive the juvenile period usually experience years of low mortality through their prime reproductive years and thus juvenile survival is a key demographic parameter (Gaillard et al. 2000).

Juvenile survival is low for a number of reasons. Juveniles are immature, physically less capable foragers, poor competitors against adult conspecifics, more vulnerable to predators, and more likely to engage in risky behavior (Sullivan 1989, Gaillard et al. 2000, Shier & Owings 2007). Juveniles are also novice foragers, less adept at prey capture and less able to locate resource patches (Weathers & Sullivan 1989). In social species with long dependent stages, resource patches and least-cost travel paths are often transmitted culturally from older conspecifics or parents (Clark & Mangel 1986, Valone 1989). By contrast, most pinnipeds, including all Arctic phocids, are solitary with short dependent stages; the 3 wk lactation period of bearded seals offers limited opportunity for vertical (parent to offspring) information transmission. Movement and habitat associations would develop through learning and could consequently differ considerably from adults.

Bearded seals inhabit shallow, seasonally ice-covered circumpolar Arctic and sub-Arctic waters. They typically avoid shore-fast and heavy multi-year ice, preferring pack ice with natural openings and areas of open water (leads, fractures, and polynyas), through which they breathe, haul out, and forage (Burns 1981, Kingsley et al. 1985). The Bering and Chukchi Seas are covered by sea ice in late winter and spring, but mostly — and more recently — are entirely ice free in late summer and fall. These seasonal ice dynamics are believed to be the major driver of seasonal movement patterns of adult bearded seals (Burns 1981, Cameron et al. 2010, 2018).

Bearded seals are primarily benthic foragers, often preferring areas shallow enough that light can reach the sea floor (Burns 1981). Bearded seal diet is diverse, consisting mostly of epifaunal invertebrates such as crabs, shrimps, and snails; infaunal bivalves; and demersal fishes (Lowry et al. 1980, Hjelset et al. 1999, Dehn et al. 2007). As such, their effective range is thought to be restricted to areas where seasonal sea ice occurs over relatively shallow waters (Burns 1981, Fedoseev 1984). The Bering and Chukchi Seas overlay large areas of continental shelf, providing extensive areas of potential habitat. This shallow intercontinental shelf is approximately 1.5 million square kilometers in area, encompassing about half of the Bering Sea and nearly all of the Chukchi (Burns 1981).

Previous treatments of bearded seal movement were descriptive and mostly based on sightings near shore, from cruises near the spring ice front, and a few aerial surveys of limited temporal and spatial scope (Burns 1981, Kelly 1988, Cameron et al. 2010, Conn et al. 2014, Ver Hoef et al. 2014, Melnikov 2017). Few analyses of bearded seal tracking data have been published. In the Bering–Chukchi, some important data have been published (Cameron et al. 2010, 2018), and a few small bearded seal tracking datasets have also been used as demonstration data for movement model development (McClintock et al. 2017). Bearded seal tracking data from the North Atlantic are also extremely limited (Gjertz et al. 2000, Watanabe et al. 2009).

All previous work has indicated that sea ice is a key habitat resource for bearded seals throughout the year. Aside from pupping, ice serves as a platform for resting and perhaps thermoregulation (Lydersen & Kovacs 1999). In late winter and early spring, the Bering–Chukchi population of bearded seals is widely but not uniformly distributed in the broken, drifting pack ice ranging from the Chukchi and Beaufort Seas south to the ice front in the Bering Sea. As the ice retreats in the spring, most adults in the Bering Sea are thought to move north through the Bering Strait. There they spend the summer and early fall at the southern edge of the Chukchi and Beaufort Sea pack ice at the wide, fragmented margin of multi-year ice (Burns 1981, Cameron et al. 2010). A smaller number of bearded seals, mostly juveniles, remain near the coasts in bays and brackish estuaries of the Bering and Chukchi Seas during summer and early fall instead of moving with the ice edge (Burns 1981). As sea ice forms in the fall and winter, both juveniles and adults are believed to move south with the advancing ice edge through the Bering Strait and into the Bering Sea where they winter.

Here, using a biologging approach, we investigated these seasonal movements and habitat use in juvenile (young of year and 1 and 2 yr olds) bearded seals that remain near coasts in the summer. We took

this approach to corroborate earlier observations and observations from aerial surveys, more precisely estimate and analyze habitat preference and sea ice use, and understand how sea ice affects the movement and behavior of juveniles so that we might better predict how sea ice degradation will impact this important species in the coming years.

MATERIALS AND METHODS

Tag deployment

Juvenile bearded seals (ranging from 0–2 yr) were caught in Kotzebue Sound during September– October of 2004–2006 and 2009. Seals were caught at the end of the open-water season using specially designed large-mesh nets measuring 3.7 m deep × 15–30 m long.

Nets were constructed of 30.5 cm stretched nylon mesh netting with foam-core float line and 5 kg/100 m lead line. They were dyed in various shades of blue and green with blotches of black made to appear as holes in the net. Nets were set and anchored in shallow water (2–3 m) near shore. Anchors were attached to the float line instead of the lead line to ensure that seals entangled near the ends of nets could reach the surface to breathe.

Once caught, seals were disentangled from the net, taken ashore, and placed on stretchers where they were measured and sex was determined. Satellite-linked dive recorders (SLDRs; SPLASH tags manufactured by Wildlife Computers) were glued to the hair on the upper back using quick-setting marine epoxy. Each tag measured 10.7 × 3.8 × 3.5 cm and weighed 145 g in air. SLDRs communicated to the Argos satellite network which collected between 6 and 15 locations d^{-1} of various quality for each seal. Tags were not duty cycled and locations were collected through the day; on average, locations were collected 114 min apart (SD 32–376 min). About 0.6% of relocations were collected with a temporal delay from the previous relocation of greater than 1 d, and about 9% were collected with temporal delays greater than 4 h. Temporal delays between the remaining 91% of relocations were less than 4 h. Where gaps longer than 2 d occurred, tracks were broken into segments and these periods of missing data were excluded from analysis; longer temporal gaps tended to occur toward the end of tracks as tag battery voltage dropped. In total, 29 seals were captured and tagged in approximately equal sex ratio (13 males, 16 females), with deployments concentrated mostly in 2005 (14) and 2009 (9) and an additional 2 deployments in 2004 and 4 in 2006.

State-space model fitting

Argos tracking data were fit with a 2-state switching state-space model (sSSM) to better estimate locations from noisy Argos data and infer behavioral state from movement patterns (Breed et al. 2009, Jonsen et al. 2013). Models were fit hierarchically using a 4 h time step following the methods described by Breed et al. (2009); the selected time step generally fit the recommendations of Breed et al. (2011) given the quality of the data. The model inferred 2 behavioral states based on fitted movement parameters (correlation: γ, and turning angle: θ). 'Resident' behavior (alternatively referred to as 'foraging' or 'encamped' states in other publications) produces correlated random walk (CRW) parameters with θ near 180° and γ near 0, while 'transit' behavior produces movement with θ near 0° and γ near 1 between consecutive displacements. See Breed et al. (2009) for more details.

Effect of covariates on behavior and habitat use

After sSSM fitting, we used the sSSM location estimates to fit a series of mixed-effects models using the statistical computing software R (R Core Team 2016) in a second layer of analysis to understand the effects of season, sex, and habitat covariates on seal movement behavior and habitat use. Habitat covariates included sea-ice concentration, water depth, distance to nearest shoreline, and distance to ice edge (considered the nearest area of 15% sea-ice concentration). Time of year was split into 3 categories (September– November; December–January; February–April) and we included sex as an explanatory covariate. Year and individual were included as random effects (see Table 1). Bathymetry data (ETOPO2) were taken from the National Geophysical Data Center (2006) at 2 km resolution. Sea ice data of 12.5 km resolution are publicly available, and described by Cavalieri et al. (2014). Sea ice density, which ranged from 0 to 100%, was logit transformed after rescaling to (0.025, 0.975), while water depth, distance to shore, and distance to ice edge were log transformed before model fitting. To accommodate the probability that intermediate sea ice densities might be preferred and thus preference is non-linear, we included the square of the sea-ice concentration as well. Finally, in order to create more interpretable interactions with sea ice, we made

a 2-category sea ice variable, is_{ice} (see Table 1), which was 0 where sea ice concentration was <15% and 1 where it was >15% — the concentration we defined to be the sea ice edge. Including interactions between is_{ice} and other factors allowed us to effectively estimate how other environmental conditions affected behavior or probability of use in front of (<15%) or behind (>15%) the ice edge.

Factors affecting habitat use

To understand how various environmental and demographic covariates affected the probability that a bearded seal used a particular habitat, we implemented a modified resource selection function (RSF) analysis. In a typical RSF that uses logistic regression (which we describe in more detail later), the set of real cases (i.e. the relocation data from the tracked or otherwise relocated animals) is matched and compared to control locations that are randomly selected from an individual animal's or a group's potentially useable habitat (Manly et al. 2007). In this analysis, there was no clear way to delineate the potential habitat region from which control locations might reasonably be selected.

To resolve this, we generated control locations by simulating the movement patterns of each bearded seal from CRW parameters estimated from the tracking data (see below and Supplement 1 at www.int-res.com/articles/suppl/m600p223_supp.pdf, and see Cameron et al. 2018 for full methodological details). We used this approach because both the real and control locations are autocorrleated and will bias the estimated parameter variances of the logistic regression downward such that they are unrealistically small (Fieberg et al. 2010). The actual parameter estimates themselves, however, should be unbiased (Schabenberger & Gotway 2005). Thus, we simulated 20 CRW trackways for each real track, which were then used as the control cases for 20 separately fit logistic regressions (described in more detail below). We discarded the estimated variances from each of 20 logistic regression model fits, but retained the parameter estimates. Variances were instead calculated from the population of parameter estimates of 20 separate model fits, which should then yield a reasonably unbiased estimate of parameter uncertainty from which 95% confidence intervals could be calculated. This assumes the parameter estimates are normally distributed, which appeared to be the case upon inspection of the estimates, and that each of the 20 Monte Carlo simulated trackways were independ-

ent of each other. From this point we proceeded with normal parametric inference. For each parameter, we tested the null hypothesis that regression coefficients equaled 0; standard errors and p-values were obtained by assuming that mean regression coefficients were distributed normally with standard deviation as obtained from the 20 Monte Carlo fits of the logistic regression. This allowed us to assess the probability that the uncertainty region around each parameter estimate contained 0 (i.e. the p-value).

The models themselves were generalized linear mixed models fit using the glmer function from the R package lme4 (Bates et al. 2016), using the binomial family with logit link (a logistic regression, as per a typical RSF). The response variable was 'use,' which indicated whether the location was associated with the control track (0) or the real track (1). These were related to the series of environmental covariates (x) via estimated parameters (β). The basic structure of the model is:

$$\text{logit}(\eta_{i,j}) = \beta_0 + \beta_1 x_{1,i,j} + \beta_2 x_{2,i,j} \ldots \beta_p x_{p,i,j} + \nu_j \quad (1)$$

$$use_{i,j} \sim \text{Binomial}(\eta_{i,j}, 1) \quad (2)$$

where i indexes the individual relocations and control points of the jth seal, and ν_j is the random effect of the jth seal. Thus $\eta_{i,j}$ is the linear predictor, which is logit linked to observations ($use_{i,j}$) via a binomial error function. The overall interpretation is of a modified RSF (Manly et al. 2007).

Simulating animal movements

To produce the Monte Carlo control locations described above, we first consider that animal tracks can be represented as sequential movement vectors, each characterized by elapsed time, bearing and length, from which secondary components can be calculated (e.g. dividing length by elapsed time yields average speed). Locations from animal movements are autocorrelated in space and time for many reasons, including physical limitations on travel speeds, the influences of habitat, behavior (resting), etc. There has been increasing interest in studying and modeling animal movements with a new surge of papers and ideas (see Hooten et al. 2017).

In some of these new models, authors attempt to incorporate habitat in directing movement (Christ et al. 2008, Forester et al. 2009, Potts & Lewis 2014), or relate movement to habitat (Bestley et al. 2013). However, to create the Monte Carlo pseudotracks, our goal was not a model of animal movement per se,

but rather to project movement in the absence of environmental influences for the purpose of comparison to real tracks. Building covariates into the sSSM (e.g. Bestley et al. 2013) would have certainly been more elegant. However, it remains difficult to incorporate many covariates into such models, and many proposed implementations remain at the demonstration phase of development. Instead we take an approach that is more pragmatic and simpler to analyze, and though less elegant still yields reasonable inference.

Pseudotracks were simulated so that they were structurally similar (i.e. in terms of vector components) to their paired real tracks, but without the influence of habitat. To do this, we used time values for each simulated track that were identical to those of their paired observed track, which was simplified by the fact that the sSSM already produced temporally regular location estimates for the real tracks. The distance components of each simulated track were modeled using the step-length distributions of the real data. Similarly, sequential bearings were expected to be both autocorrelated and related to speed, so we also modeled the bearing components of each simulated vector. Using these models for speed and bearing, we simulated 20 tracks for each of the 29 animals (see Fig. 1 for an example of one of the 20 simulated pseudotrack sets). Full details of the simulation are available in Cameron et al. (2018) and Supplement 1.

We assessed a range of biologically reasonable models and interactions using the covariates listed in Table 1. A likelihood-based model-selection procedure (such as Akaike's information criterion, AIC) was not valid because the mean and standard error obtained for each logistic regression parameter were based on Monte Carlo methods. Instead, model selection followed a backward stepwise procedure based on p-values. We started with a model that had all single effect covariates, an interaction between is_{ice} and D_{edge}, plus the interaction of sex with all other covariates and the $is_{ice} \times D_{edge}$ interaction. We then removed interaction terms that were least significant one at a time. After obtaining only those interactions still significant at $\alpha = 0.05$, we then started to remove single effects that were least significant until a parsimonious model was obtained with all terms significant at $\alpha = 0.05$. The final model was interpreted as an RSF, where the intercept

was not meaningful, but the regression coefficients indicated preference or avoidance in the direction of the coefficient.

Factors affecting movement behavior

Conditions affecting the expressed movement behavior (as inferred by the sSSM) were analyzed using a logistically transformed response variable, sSSM inferred behavioral state B, fit in a mixed-effects linear regression using the R package nlme (Pinheiro et al. 2017) with the following structure:

$$\text{logit}(B_{i,j}) \sim \beta_0 + \beta_1 x_{1,i,j} + \beta_2 x_{2,i,j} \ldots \beta_p x_{p,i,j} + \phi \, \text{logit}(B_{i-1,j}) + \nu_j + \varepsilon_{i,j} \qquad (3)$$

where $B_{i,j}$ is the sSSM inferred behavioral state expressed along a continuum between 0 and 1 (see Breed et al. 2009 for discussion of using these contin-
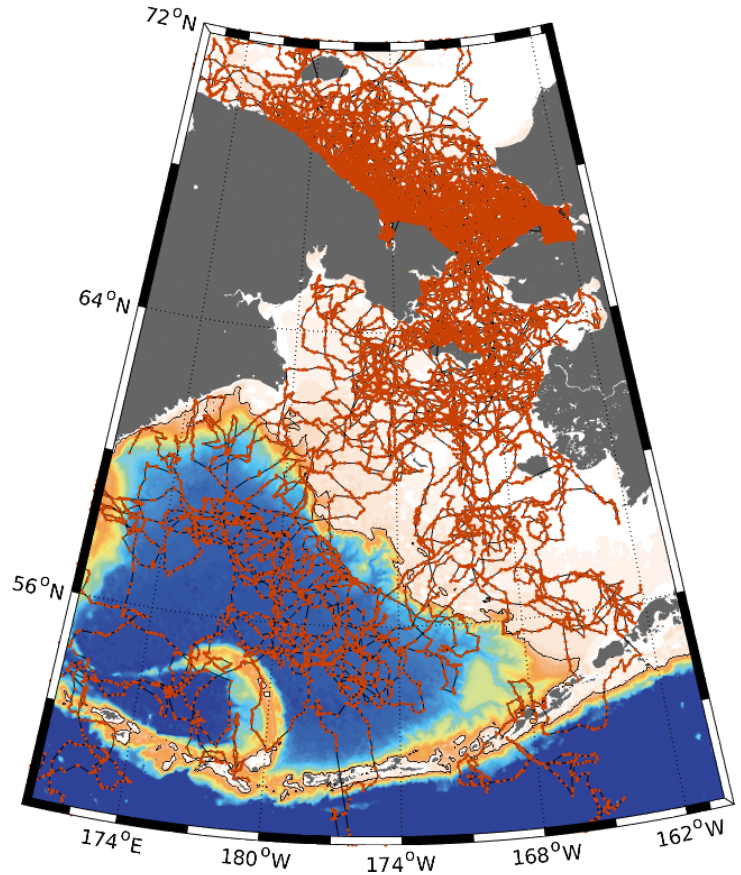

Fig. 1. One set of pseudotracks used in the resource selection function (RSF) analysis of bearded seals. Twenty similar sets were probabilistically generated using parameters estimated from real tracks. Pseudotrack locations were subsequently used as case controls to estimate RSF parameters against the real relocation data (see 'Materials and methods' and Supplement 1)

Table 1. Definitions of variables used in mixed-effects and generalized linear mixed models. The first 7 variables were used as main fixed effects, while B was used as a response variable in bearded seal behavior models. Year and individual were included as random effects and are not listed

Variable	Definition
D_{sh}	Distance to shore, i.e. nearest coastline (continuous, log transformed)
D_{edge}	Distance to sea ice edge (15% concentration) (continuous, log transformed)
SI_{conc}	Sea ice concentration (expressed continuously between 0 and 1, logit transformed)
SI_{conc}^2	SI_{conc} squared, added to capture preference for intermediate sea ice density
Sex	Male or female (categorical)
$Dpth$	Water depth (continuous, log transformed)
ssn	Season; split into 3 categories (September–November; December–January; February–April)
is_{ice}	Simple categorical on sea ice density to make for more interpretable interactions
	Sea ice concentration >15%, $is_{ice} = 1$, otherwise $is_{ice} = 0$
B	Switching state-space model (sSSM) inferred behavioral state, expressed continuously between 0 and 1

uous estimates), x values represent covariates and β values are the respective estimated parameters, ϕ is the autocorrelation parameter, ν_j is the individual random effect, and $\varepsilon_{i,j}$ is the uncorrelated residual variation. This approach allowed us to incorporate random effects and a first-order autocorrelation parameter so that bias in variance and parameter estimates attributable to autocorrelation is controlled. A variety of models were tested using the explanatory variables listed in Table 1 and biologically reasonable interactions to explain inferred behavioral state (B). As these models were fit using ordinary maximum likelihood, they were compared using AIC.

RESULTS

sSSM fits

The model identified and inferred 2 clear behavioral/movement states. The overall seasonal movement pattern followed the expected migratory pattern, with many animals initially moving north from the capture area before freeze-up while open water was still extensive. As sea ice formed, seals gradually moved south, passing through the Bering Strait and wintering mostly in the Bering Sea (a few individuals wintered just north of the Bering Strait in the Chukchi Sea). In the fall (October–November), seal movement tended to be more directed and rapid (transiting behavior), while later in the season after freeze-up, resident-type movement behavior was much more likely (Fig. 2). sSSMs also handled Argos error to produce better location estimates and those better estimates were used in all subsequent analyses.
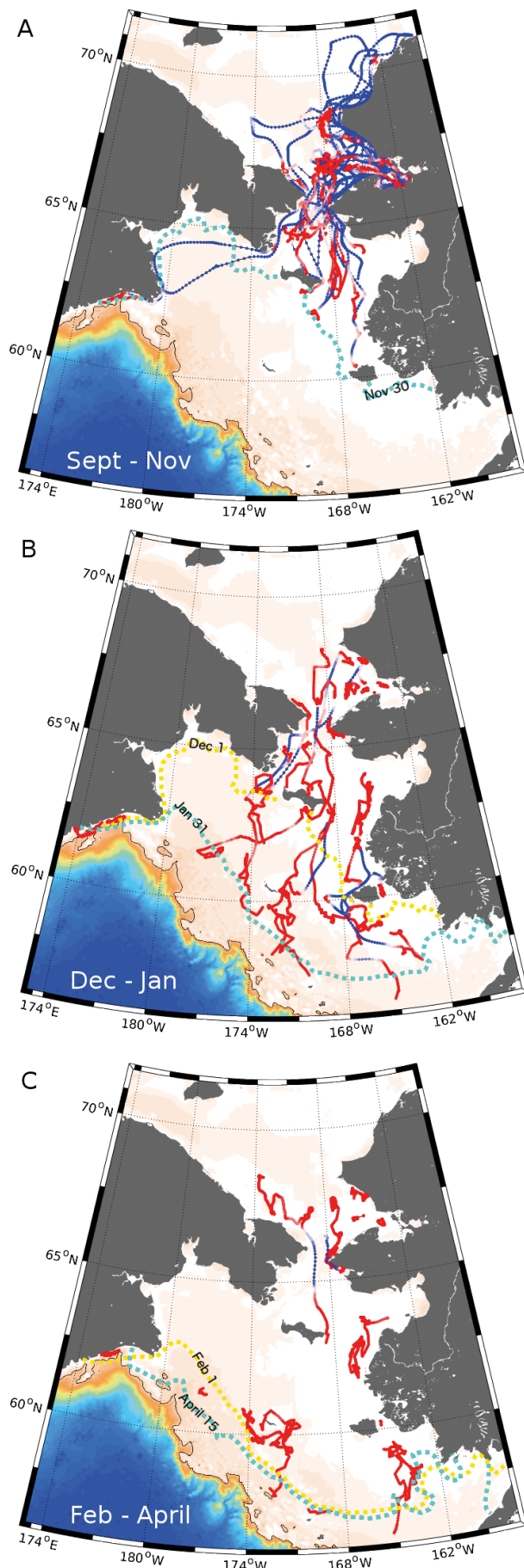
After freeze-up, some segments of movement pathways were inferred as 'resident' during long durations of straight movements but with very short move steps (as compared to movements inferred as 'transit'). These almost certainly represent seals drifting passively on ice floes. In some sense, one could think of this as a third behavior, but as seals are moving passively, the sSSM inference of 'resident' is not unreasonable as the observed movement pattern during periods drifting on pack ice is more similar to 'resident' than 'transit' behavior. See Auger-Méthé et al. (2016) for further discussion of state-space model inference of behavior in tracked animals moving in drifting sea ice.

Habitat selection

The backward stepwise selection began by including all main effects and all pairwise interactions of the variables listed in Table 1 and also 3-way interaction between D_{edge}, is_{ice}, and season. The least informative effects were sex and all but 1 interaction including sex, which were not significant at $\alpha = 0.05$ and were dropped in the first few rounds. Subsequently, the main effect of season was dropped; it was only important in the context of its effect on other covariates (i.e. as interactions). Season altered relationships between use and sea ice concentration, distance to the ice edge, and distance from shore. The final model and parameter estimates are shown in Table 2.

The relationship between use and sea ice concentration was extremely important. However, the results differed from recent analyses by Cameron et al. (2018), which found that probability of use more or less steadily increased with sea ice concentration and plateaued at 80% and did not appreciably dip from this peak as density increased from 80 to 100%. Our analysis found that use was more strongly explained by the SI_{conc}^2 term. This predicted an inverse parabolic relationship, with probability of use clearly peaking in sea ice concentrations of around 50–60% (Fig. 3), and substantially decreasing as concentra-

tions increased beyond 60%. In fact, the linear term SI_{conc} did not differ from 0 in winter and spring.

The relationship with sea ice differed in the fall. The fall season featured a general lack of access to sea ice in the first month, which was prior to the seasonal expansion of sea ice cover over the Chukchi and Bering Shelves. This may explain the relatively flat selection surface for sea ice concentration compared to other seasons (Fig. 3). In general, probability of use increased farther from shore as indicated by the positive parameter shown in Table 2, but this relationship was weaker in the fall. Seals seem to move farther offshore when sea ice is available to rest on and/or they are forced away from shore by shore-fast ice.

A few other results are notable. We found evidence that females used somewhat shallower areas than males for this juvenile age class, but other habitat covariates did not differ between the sexes. Probability of use generally increased with water depth. There was a significant interaction between distance to ice edge and whether the seal was in front of or behind the ice edge. The probability of use was generally lower in front of the ice edge and dropped more rapidly as compared to behind the edge (Fig. 4). An overall predictive figure using sea ice data observed on 23 November 2009 visualizes the strong relationship between sea ice edge and predicted use; young bearded seals preferred to be near the ice edge and in intermediate sea ice concentrations (Fig. 5).

Movement behavior

Initial explorations of candidate models and covariates affecting inferred behavioral state (B) suggested that sea ice and season would be key variables. However, these were not the only effects explaining movement behavior. In addition to these main effects, we selected several key interactions that address specific hypotheses about how covariate interactions might alter expressed behavior. In par-

Fig. 2. Switching state-space model (sSSM) fits of all bearded seal tracks, broken down by season: (A) September–November, (B) December–January, (C) February–April. Blue indicates inferred directed movement; red indicates inferred encamped/resident behavior. Tracks are plotted against bathymetry (100 m contour is drawn for reference). Additionally, the position of the 15% ice edge is shown at the beginning (yellow) and end (cyan) of the season plotted. Ice data are from the 2009–2010 season, but are generally representative of the freeze-up phenology. In panel (A), the ice edge on 1 October is north of the projected area and is therefore not plotted

Table 2. Selected final resource selection function model, parameter estimates, 95% confidence intervals (CI), and p-values indicating if uncertainty regions around parameter estimates include 0. Variables are defined in Table 1

| Effect	Linear estimate	±95% CI	Pr > t
Intercept	−0.170	−1.593, 1.253	0.8173
$\log(D_{sh})$	1.620	1.524, 1.717	<0.0001
$\log(Dpth)$	1.227	0.828, 1.626	<0.0001
$\mathrm{logit}(SI_{conc}):ssn = fall$	−0.206	−0.242, −0.170	<0.0001
$\mathrm{logit}(SI_{conc}):ssn = winter$	0.042	−0.028, 0.112	0.2665
$\mathrm{logit}(SI_{conc}):ssn = spring$	−0.006	−0.038, 0.025	0.7021
$\mathrm{logit}(SI_{conc})^2:ssn = fall$	−0.062	−0.069, −0.056	<0.0001
$\mathrm{logit}(SI_{conc})^2:ssn = winter$	−0.110	−0.135, −0.086	<0.0001
$\mathrm{logit}(SI_{conc})^2:ssn = spring$	−0.115	−0.125, −0.105	<0.0001
$\log(D_{sh}):is_{ice} = 1$	−0.644	−0.731, −0.556	<0.0001
$\log(Dpth):is_{ice} = 1$	0.922	0.788, 1.055	<0.0001
$\log(Dpth):sex = female$	−0.348	−0.475, −0.221	<0.0001
$\log(D_{sh}):\log(Dpth)$	−0.526	−0.553, −0.499	<0.0001
$\log(D_{sh}):ssn = spring$	0.467	0.371, 0.561	<0.0001
$\log(D_{sh}):ssn = winter$	0.485	0.429, 0.542	<0.0001
$\log(D_{edge}):is_{ice} = 0:ssn = all$	−0.334	−0.555, −0.112	0.0082
$\log(D_{edge}):is_{ice} = 0:ssn = spring$	−0.687	−0.869, −0.505	<0.0001
$\log(D_{edge}):is_{ice} = 0ssn = winter$	−0.641	−0.878, −0.404	<0.0001
$\log(D_{edge}):is_{ice} = 1:ssn = fall$	−0.486	−0.708, −0.263	0.0004
$\log(D_{edge}):is_{ice} = 1:ssn = spring$	−0.490	−0.719, −0.260	0.0005
$\log(D_{edge}):is_{ice} = 1:ssn = winter$	−0.565	−0.798, −0.333	0.0001
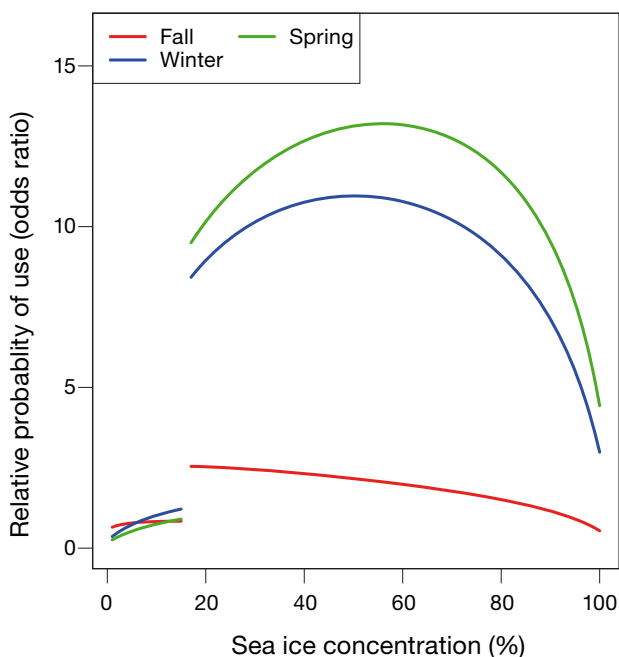
Fig. 3. Relative probability of use by bearded seals as function of sea ice concentration predicted from the selected model. Variables other than sea ice concentration were held constant: depth = 90 m, distance from ice edge = 30 km. The discontinuity at 15% sea ice concentration results from is_{ice} (see Table 1) switching from 0 to 1

ticular we asked the following questions: Does sex alter the effect of sea ice on movement behavior? Does sex affect how distance from shore or distance from ice edge affects movement behavior? Does season affect how distance from shore or distance from ice edge affects movement behavior? And finally, how does depth interact with sex, sea ice, or season to affect expressed movement behavior?

To address these questions, we constructed a full model containing 6 main effects (SI, SI^2, ssn, $Dpth$, D_{sh}, D_{edge}; see Table 1) and 9 pairwise interaction terms (sex was included only in interactions to test how it influenced the effects of other covariates). The full model had 21 degrees of freedom (shown in Table 3). In our multi-model comparison, we tested all possible models but limited models to have at least 5 covariates to lower the total number of models needed to be fit. The top 14 models are shown in Table 3 and include the full model which ranked 14th; the remainder of the fitted models are shown in Supplement 2 at www.int-res.com/articles/suppl/m600p223_supp.xlsx.

AICs indicate that the top models (shown in Table 3) are all nearly equivalent. However, a large number of models have no support (full selection table in Supplement 2), so the covariates included in the selected models are clearly predictive. We could take a multi-model averaging approach to resolve the equivalence; however, our goal is not prediction per se. Instead, we interpret the consistent pattern of inclusion of covariates across the top models. Main effects of distance to shore (D_{sh}), sea ice concentration (SI_{conc}), and season were always included. Interactions with distance to shore and distance to ice edge were likewise always included. Parameter estimates of a model including only these key variables are shown in Table 4.

Parameter estimates indicate that young bearded seals are sensitive to distance to shore, and the closer the seals are to shore, the more likely they are to exhibit a transiting movement pattern (Table 4). Transiting movement is also considerably more likely during the fall than in winter or spring, consistent with Fig. 2. When other variables are held constant, increasing sea ice concentration decreases the probability of transit behavior. Increasing distance from the ice edge also decreased the probability of transiting behavior (and thus increased the probability of resident behavior), but only behind the ice edge. At extremely high sea ice densities,
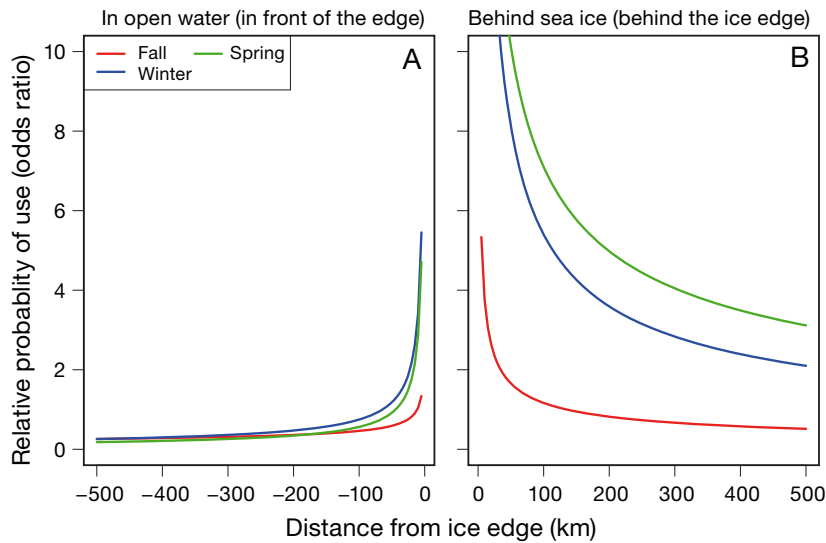
Fig. 4. Predicted relative probability of use by bearded seals as a function of distance (A) in front of (in open water) and (B) behind (in dense ice) the sea ice edge (defined as 15 % sea ice concentration). Other covariates were held fixed

bearded seals appear to be unable to switch into the transit state (Fig. 6). Distance to shore was also important and seasonally variable. In winter and spring, animals that were more distant from shore were more likely to express a resident state. Finally, female behavior seemed more affected by distance from shore than male behavior, but this effect is weak compared to other effects (Table 4).

The overall interpretation in the context of the RSF findings suggests simply that the deeper animals were in the ice pack (as ice density approached 100 %), the more likely they were to be in a resident state. Conversely, open water was associated with a transiting behavioral state.
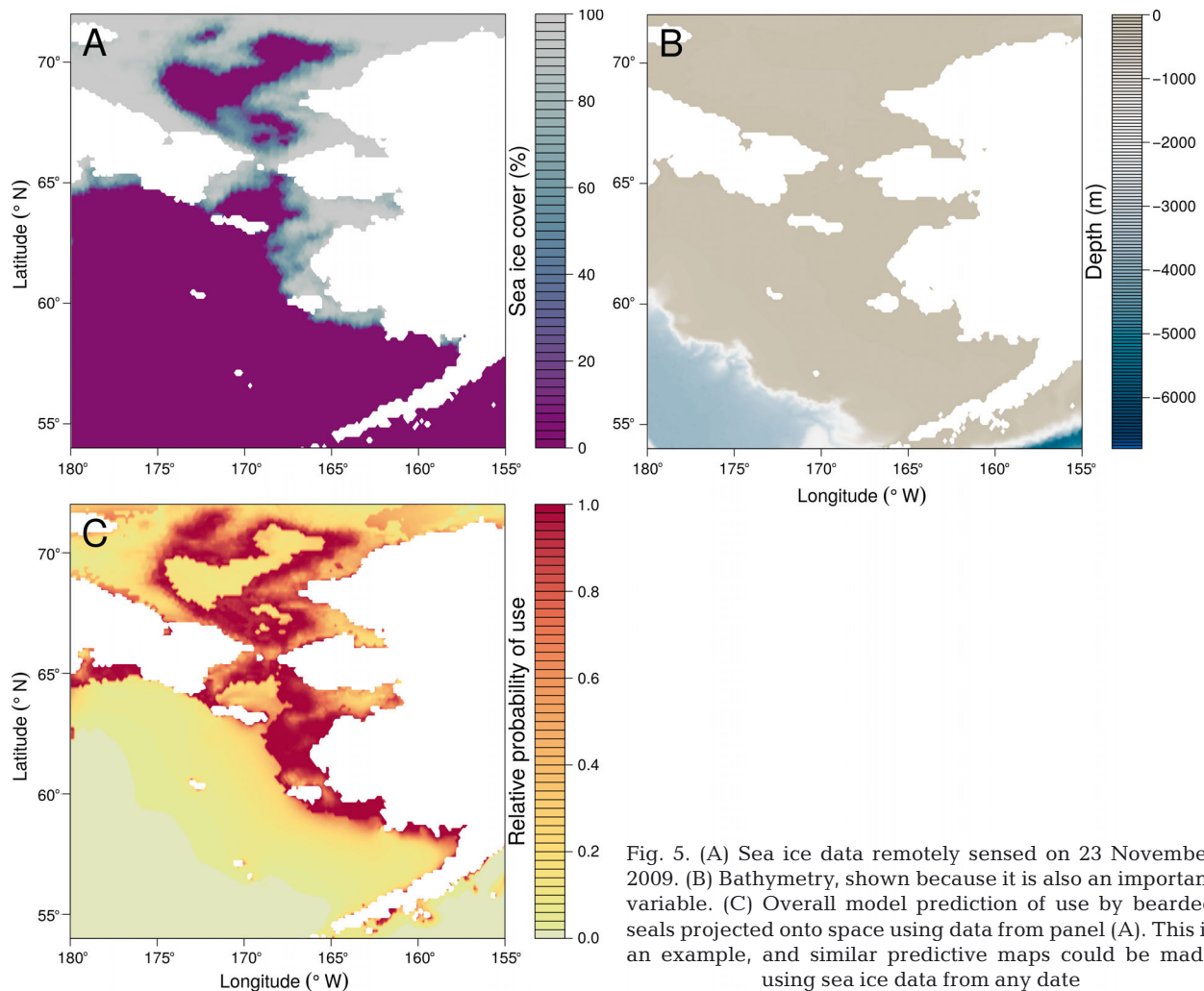

Fig. 5. (A) Sea ice data remotely sensed on 23 November 2009. (B) Bathymetry, shown because it is also an important variable. (C) Overall model prediction of use by bearded seals projected onto space using data from panel (A). This is an example, and similar predictive maps could be made using sea ice data from any date

Table 3. Multi-model selection table for covariates and interactions predicting switching state-space model (sSSM) inferred behavioral state of bearded seals. Pluses (+) indicate the inclusion of a covariate or interaction. The top 14 models are listed, with the last row showing the full model. The full selection table is provided in Supplement 2. See Table 1 for variable definitions. AIC: Akaike's information criterion

D_{sh}	SI	SI^2	ssn	$Dpth{:}SI$	$Dpth{:}ssn$	$Dpth{:}sex$	$D_{sh}{:}SI$	$D_{sh}{:}ssn$	$D_{sh}{:}sex$	$D_{edge}{:}SI$	$D_{edge}{:}ssn$	$SI{:}sex$	AIC
+	+	+	+	+			+	+	+	+	+		−8556.1
+	+	+	+	+		+	+	+	+	+	+		−8555.9
+	+		+		+	+	+	+	+	+	+		−8555.5
+	+	+	+	+	+	+	+	+	+	+	+		−8555.5
+	+		+	+			+	+	+	+	+		−8555.4
+	+		+			+	+	+	+	+	+		−8555.4
+	+	+	+		+	+	+	+	+	+	+		−8555.4
+	+		+		+		+	+	+	+	+		−8555.3
+	+		+	+	+	+	+	+	+	+	+		−8555.2
+	+	+	+		+		+	+	+	+	+		−8555.2
+	+	+	+	+			+	+	+	+	+	+	−8555.2
+	+	+	+	+		+	+	+	+	+	+	+	−8555.1
+	+		+		+	+	+	+	+	+	+	+	−8554.7
+	+	+	+	+	+	+	+	+	+	+	+	+	−8554.7

Table 4. Parameter estimates for key variables affecting switching state-space model (sSSM) inferred behavioral state of bearded seals. Positive parameters indicate that the effect increases the probability of directed/more correlated movement patterns, negative parameters indicate that the effect increases the probability of more resident/less correlated movement patterns. Variables are defined in Table 1

Effect	Linear estimate	95% CI	Pr > t
Intercept	−1.935	0.570	<0.0001
$logit(SI_{conc})$	−0.066	0.023	<0.0001
$log(D_{sh})$	0.041	0.025	0.0026
$ssn = spring$	2.173	0.325	<0.0001
$ssn = winter$	0.434	0.172	<0.0001
$logit(SI){:}log(D_{edge})$	0.002	0.006	0.0852
$logit(SI){:}log(D_{sh})$	0.013	0.006	<0.0001
$log(D_{edge}){:}ssn = spring$	−0.025	0.022	0.0294
$log(D_{edge}){:}ssn = winter$	−0.018	0.018	0.0027
$log(D_{sh}){:}ssn = spring$	−0.490	0.073	<0.0001
$log(D_{sh}){:}ssn = winter$	−0.108	0.043	<0.0001
$log(D_{sh}){:}sex2$	0.056	0.029	0.0002

DISCUSSION

The effects that sea ice loss will have on bearded and other ice seals is a serious potential impact of climate change (Cameron et al. 2010). Sea ice loss is understood to affect lower trophic levels of Arctic marine food webs through increased primary productivity, changes in plankton community structure, and altered benthic–pelagic coupling (Arrigo & van Dijken 2015, Barber et al. 2015).

These changes are likely to alter the total primary production in the system, but even if they do not, they will almost certainly affect the temporal and spatial distribution of resources available to mid- and upper-trophic level predators. To the extent that upper trophic level species are adaptable, they will be able to adjust to such temporal and spatial changes in productivity. However, Arctic species at the highest trophic levels often have evolved behavioral dependence on sea ice as a platform. These include species such as ringed seals *Pusa hispida* and polar bears *Ursus maritimus*. In other areas of the Arctic, these species have changed their behavior, are showing poorer body condition, decreased vital demographic rates, and declining population sizes (Kovacs et al. 2011, Molnár et al. 2011, Luque et al. 2014, Hamilton et al. 2015, Pilfold et al. 2017).

Like ringed seals, bearded seals, as well as ribbon *Histriophoca fasciata* and spotted seals *Phoca largha*, which co-occur in the Bering–Chukchi ecosystem, are sea-ice dependent. To date there is no indication that any bearded seal populations have been negatively affected by changes in sea ice extent or phenology (Cameron et al. 2010, Crawford et al. 2015). However, the lack of any negative trends may simply be due to highly uncertain and infrequent population estimates, which is a consequence of the logistical difficulty of surveying this high-Arctic species. Various world population estimates have been made over the past 50 yr, and have ranged from several hundred thousand to over 1 million individuals (Cameron et al. 2010); the variation among estimates shows no temporal trends and likely arises from differing estimation methods and reliance on various strong assumptions.

Still, given the demonstrated effects of sea ice degradation on other Arctic species, bearded seals
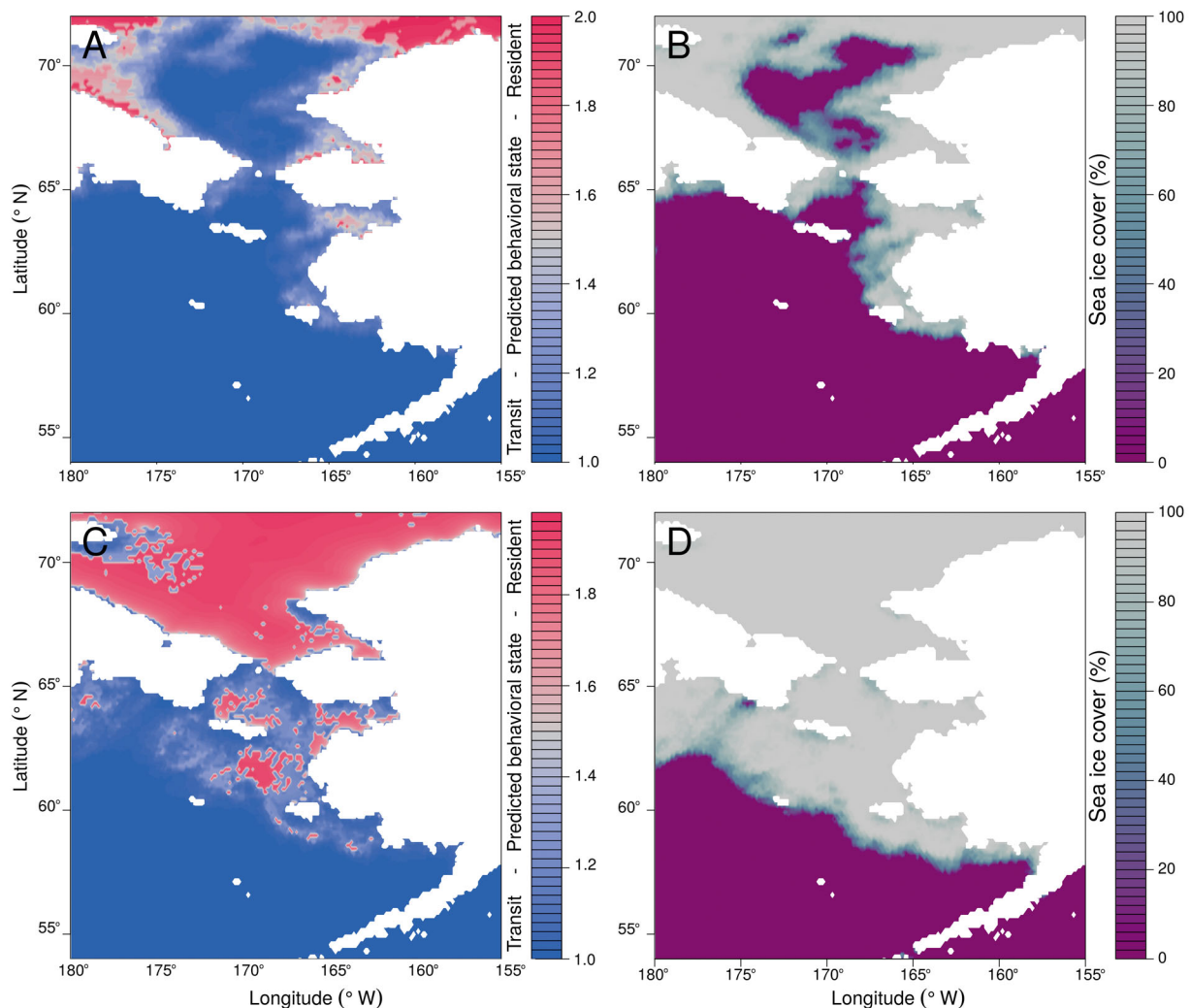
Fig. 6. Predicted bearded seal behavioral state based on environmental covariates projected onto typical sea ice seascapes: (A) late November and (C) early January. Corresponding sea ice densities are shown in (B) and (D). States were predicted from parameters shown in Table 4

are likely now, or will soon be, affected by changes in sea ice even if those effects have not been clearly quantified. Our analysis informs habitat preference and movement behavior of young breaded seals across more or less the entire Chukchi and Bering Sea range and provides continuous longitudinal observations of behavior and habitat preference through the fall, winter, and into the spring as sea ice seasonally expands across the Bering–Chukchi Sea.

Dynamic habitat selection of seasonal sea-ice conditions

Recent analyses from aerial survey data indicate that bearded seals prefer ice concentrations around 60% during April and May (Conn et al. 2014, 2015). During the ice season (winter and spring), our analysis found preferred sea ice concentrations around 50–60%, almost exactly consistent with estimates derived from aerial survey data. However, distance to the sea ice edge, which we defined as 15% concentration, as well as whether an animal was in front of or behind the edge, were important contingent factors modifying the sea ice concentration effect. As a result, during the winter and spring (defined here as December–April), dense sea ice well behind the ice edge was not preferred habitat. In fact, predictions of high probability use areas were relatively small compared to the overall range of bearded seals, and focused on intermediate to dense sea ice immediately proximate to the sea ice edge (Fig. 5). Thus

the location of the ice edge, for the juvenile age classes that our data represent, was an important factor in addition to sea ice concentration. Overall the relationship between bearded seals and sea ice that we report here, using our biologging approach and careful statistical analysis, is remarkably consistent with observations made and reported decades ago based on classic natural history observations and field methods (Burns 1981).

Annual movement patterns in our bearded seal tracking data show an overall migration-like pattern, moving north in the summer to follow the sea ice as it retreats, and then southward in the fall as sea ice advances. This is consistent with a behavioral tracking of preferred habitats as those habitats seasonally shift.

In other ice-associated Arctic animals (Heide-Jørgensen et al. 2002, 2010, Laidre & Heide-Jørgensen 2005), entrapments are frequently reported. However, because bearded seals are capable of creating and maintaining breathing holes, such entrapments likely only restrict movement and probably do not represent a high mortality risk (Burns 1981, Smith 1981, Cleator & Smith 1984). Our behavioral predictions corroborate this conclusion, where, during winter, juvenile bearded seals are predicted to be in the transit behavioral state even when sea ice density is quite high (>80%), whereas at or near 100% sea ice, the behavioral state is highly likely to be resident. This suggests that dense sea ice in winter and spring restricts movement.

Individuals wintering in dense ice might also be expressing a more mature behavioral pattern. Juveniles might not be as capable as mature adults at breaking, maintaining, or defending breathing holes, so thicker ice pack may be more risky for juveniles, and they may avoid it to a greater degree than adults. As they become older and physically mature, these individuals might select areas of denser ice farther behind the ice edge.

The sea ice edge by itself is probably not better foraging habitat than pack ice well behind the sea ice edge. As benthic feeders, bearded seals can use sea ice over any shallow continental shelf area as a haul-out platform from which to forage. As noted, the risk of entrapment, or simply limited access to air due to unbroken sea ice, may increase with increasing distance behind the ice edge. Thus, the sea ice edge affords the same foraging platform as sea ice well behind the edge, but seals tracking the edge may avoid entrapment and have easy access to air while maintaining their ability to move broadly and access a wider range of foraging patches through the winter.

Although annual movements of bearded seals in the Bering and Chukchi Seas have been described as 'migrations' (Dingle & Drake 2007, Cameron et al. 2010), it is unclear if that is an appropriate characterization. Our data suggest that the seasonal movement pattern might be better described as behavioral tracking of preferred habitat, a behavioral paradigm that might be better classified as nomadism (Mueller & Fagan 2008, Singh et al. 2012). The sea ice edge is seasonally dynamic, and bearded seals — in our data juveniles, but likely adults as well — may simply be continuously adjusting their position to be in optimal habitat as the edge moves, a trait typical of nomadic animals. A migration-like movement pattern emerges from the behavioral tracking and the predictable seasonal expansion and retraction of sea ice. The movement pattern observed is probably some intermediate between nomadic and migratory behavior. A truly migratory pattern may arise at maturity, but movement may remain nomadic in adulthood.

Behavioral tracking of dynamic habitat conditions is not unique. Some of the best examples of this phenomenon come from terrestrial species during spring migrations. Elk, for example, abandon montane habitats in the fall as deep winter snows cover forage and are energetically expensive to move through (Bischof et al. 2012, Fryxell & Avgar 2012). In the spring, as these herbivores return to summer ranges, they precisely track green-up to maximize nutrition. This tracking has been coined 'surfing the green wave' as the animals remain at the crest of a moving wave of optimal habitat as green-up moves up elevational or latitudinal gradients (Fryxell & Avgar 2012). The gradual movement of bearded seals in the Bering–Chukchi system, which similarly keeps up with sea ice formation in the fall, is consistent with such behavioral tracking. The fall southward migration might analogously be conceptualized as 'surfing the white wave' of freeze-up.

Juvenile versus adult behavior

This study focused on juvenile bearded seals ranging from approximately 6 mo to 3 yr of age. During the summer and early fall, these young animals are less associated with sea ice than adults, and come into bays and estuaries along the Alaskan coast (Burns 1981, Cameron et al. 2010). This behavior makes them more accessible for capture and tagging than adults, but also reveals that their habitat selection and behavior differs from, and thus may not well represent, adult behavior. Until more adults are

tagged, it remains uncertain how representative these juvenile data are of older age classes, although recent work by Conn et al. (2014) suggests both similarities and differences.

Selection for the ice edge may be a characteristic of juvenile behavior. These young animals may be less able to cope with the fewer breaks and fractures available in dense ice well behind the edge, and may be more susceptible to displacement from the available areas by older animals — a potentially dangerous situation if there are no other breaks in the sea ice nearby (Stirling 1977, Lake et al. 2005). Older individuals who are more experienced and physically mature may be better able to cope with denser ice with fewer breaks, allowing them to winter deeper in the ice pack, and thus adult distributions may be less focused on the sea ice edge — which analyses of spring transect data appear to support (Conn et al. 2014). If this is the case, it is possible that differential habitat selection may explain reported differences in diets across age classes, although it is equally likely that diet differences are due simply to behavioral or physiological ontogeny (Lowry et al. 1980, Weathers & Sullivan 1989, Antonelis et al. 1994). Juveniles in other mammals, including phocids, often segregate from adults to avoid negative intra-specific interactions. The ice edge may be a safer place for juveniles if they do encounter aggressive conspecific adults, which would permit easy escape from harassing adults. However, Stirling & Archibald (1977) reported that seals at the ice edge experience higher levels of polar bear predation, so selection of this habitat may come with the trade-off of increased predation risk (but note that polar bears do not range to the winter ice edge in the southern Bering Sea).

Interpretation in the context of future sea ice loss

The dynamic tracking of the sea ice edge and intermediate sea ice densities by juvenile bearded seals may have some important consequences with respect to their resilience to sea ice degradation. Unlike in many migrating animals which typically move across large tracks of unsuitable habitat before arriving at a summer breeding ground, there is much lower potential for phenological mismatch, as bearded seals do not appear to be migrating per se, and instead simply track the dynamics of optimal habitat. Moreover, bearded seals are benthic foragers and the continental shelf is extensive in the Bering and Chukchi Seas, extending south to the Aleutian Is-

lands in the eastern reaches and north to the 75th parallel. These different regions of the shelf may offer differing food resources to bearded seals, but the broad use observed here and in other tracking studies suggests that most shelf areas are probably relatively interchangeable and their suitability at any given time is determined by presence of enough sea ice that it affords a stable haul-out platform.

There may be an issue whenever the sea ice edge extends (or contracts) such that it is situated over deep ocean water. This can happen in the western Bering Sea during winter, but in eastern regions, where most of our seals wintered, the shelf is contiguous all the way to the Aleutian Islands, and sea ice never extended past the shallow shelf environment. Seals were definitely sensitive to depth, and it may be that, where the ice edge extends well past the edge of the continental shelf, the ice edge may no longer be preferred habitat. In any case, reduced winter sea ice extent is unlikely to seriously impact bearded seals over at least the next few decades, as large areas of winter sea ice will still be positioned over the continental shelf (Cameron et al. 2010).

In other seasons, however, changes in sea ice and the position of the sea ice edge could be more significant. Historically, bearded seals are reported to use multi-year pack ice in the Chukchi and Beaufort Seas during summer and fall (Burns 1970, 1981). Over the period that those observations were made, the summer sea ice minimum still extended far enough south that it extensively overlapped with the Chukchi, Beaufort, and East Siberian continental shelves. More recent minimum summer sea ice extents have retreated far enough north that the sea ice edge only just overlaps the shelf or is just into the deep ocean basin. To date, even where these recent summer minimums have retreated over deep waters, they have remained there only briefly and have still been positioned relatively close to the shelf such that they remained available as a haul-out platform from which relatively short foraging trips can be made. This situation could change relatively quickly in the foreseeable or even near future.

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