



Ringed seal (*Pusa hispida*) seasonal movements, diving, and haul-out behavior in the Beaufort, Chukchi, and Bering Seas (2011–2017)

Andrew L. Von Duyke¹ | David C. Douglas² | Jason K. Herreman¹ | Justin A. Crawford³

¹Department of Wildlife Management, North Slope Borough, Barrow, AK, USA

²U.S. Geological Survey, Alaska Science Center, Juneau, AK, USA

³Alaska Department of Fish and Game, Arctic Marine Mammal Program, Fairbanks, AK, USA

Correspondence

Andrew L. Von Duyke, North Slope Borough, Department of Wildlife Management, P.O. Box 69, Barrow, AK 99723, USA.
Email: andrew.vonduyke@north-slope.org

Present address

Jason K. Herreman, Alaska Department of Fish and Game, Homer, AK, USA

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Abstract

Continued Arctic warming and sea-ice loss will have important implications for the conservation of ringed seals, a highly ice-dependent species. A better understanding of their spatial ecology will help characterize emerging ecological trends and inform management decisions. We deployed satellite transmitters on ringed seals in the summers of 2011, 2014, and 2016 near Utqiagvik (formerly Barrow), Alaska, to monitor their movements, diving, and haul-out behavior. We present analyses of tracking and dive data provided by 17 seals that were tracked until at least January of the following year. Seals mostly ranged north of Utqiagvik in the Beaufort and Chukchi Seas during summer before moving into the southern Chukchi and Bering Seas during winter. In all seasons, ringed seals occupied a diversity of habitats and spatial distributions, from near shore and localized, to far offshore and wide-ranging in drifting sea ice. Continental shelf waters were occupied for >96% of tracking days, during which repetitive diving (suggestive of foraging) primarily to the seafloor was the most frequent activity. From mid-summer to early fall, 12 seals made ~1-week forays off-shelf to the deep Arctic Basin, most reaching the retreating pack-ice, where they spent most of their time hauled out. Diel activity patterns¹ suggested greater allocation of foraging efforts to midday hours. Haul-out patterns were complementary, occurring mostly at night until April–May when midday hours were preferred. Ringed seals captured in 2011—concurrent with an unusual mortality event that affected all ice-seal species—differed morphologically and behaviorally from seals captured in other years. Speculations about the physiology of molting and its role in energetics, habitat use, and behavior are discussed; along with possible evidence of purported ringed seal ecotypes.

KEYWORDS

Alaska, Arctic, ecotype, marine mammals, phocid, satellite telemetry, spatial ecology, unusual mortality event

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1 | INTRODUCTION

Arctic species face significant ecological challenges owing to rapid climate change. Arctic warming is occurring at twice the global rate (Arctic Monitoring & Assessment Programme, 2017; Overland et al., 2016), and sea-ice loss is outpacing model predictions (Kwok, 2018; Maslanik, Stroeve, Fowler, & Emery, 2011; Stroeve, Holland, Meier, Scambos, & Serrez, 2007; Stroeve & Notz, 2018; Timmermans, Toole, & Krishfield, 2018). Changing sea-ice dynamics are expected to have substantial ecological implications (Arrigo, van Dijken, & Pabi, 2008; Grebmeier et al., 2006; Hoegh-Guldberg & Bruno, 2010) exacerbated by increased disturbances associated with expanding industrial development and commercial shipping (Harsem, Heen, Rodrigues, & Vassdal, 2015; Huntington, 2009; Smith & Stephenson, 2013). Spatiotemporal variability in the rate and magnitude of change in the Arctic adds additional complexity (Kovacs, Lydersen, Overland, & Moore, 2011). Although Arctic species can

serve as sentinels of change (Moore, 2008), knowledge gaps persist in the understanding of many species' basic biology, and addressing those gaps will improve efforts to identify, understand, manage, and adapt to the effects of rapidly changing environmental conditions.

Ringed seals (*Pusa hispida*; Figure 1a) are a small, highly abundant phocid with a circumpolar distribution (Burns, 1970; McLaren, 1958). They are an important component of the Arctic food web as a generalist predator (Crawford, Quakenbush, & Citta, 2015; Dehn et al., 2007; Lowry, Frost, & Burns, 1980), the primary prey of polar bears (*Ursus maritimus*; Stirling & Archibald, 1977), and a valuable subsistence resource for coastal Inuit people. Ringed seals are considered the most ice dependent of the four "ice associated" seal species in the western Arctic (Smith, Stirling, & Taugbøl 1991), which also include: bearded seals (*Erignathus barbatus*), spotted seals (*Phoca largha*), and ribbon seals (*Histiophoca fasciata*). They are well adapted to wintering within shore fast and pack-ice habitats—using their front claws to maintain breathing holes and to excavate lairs

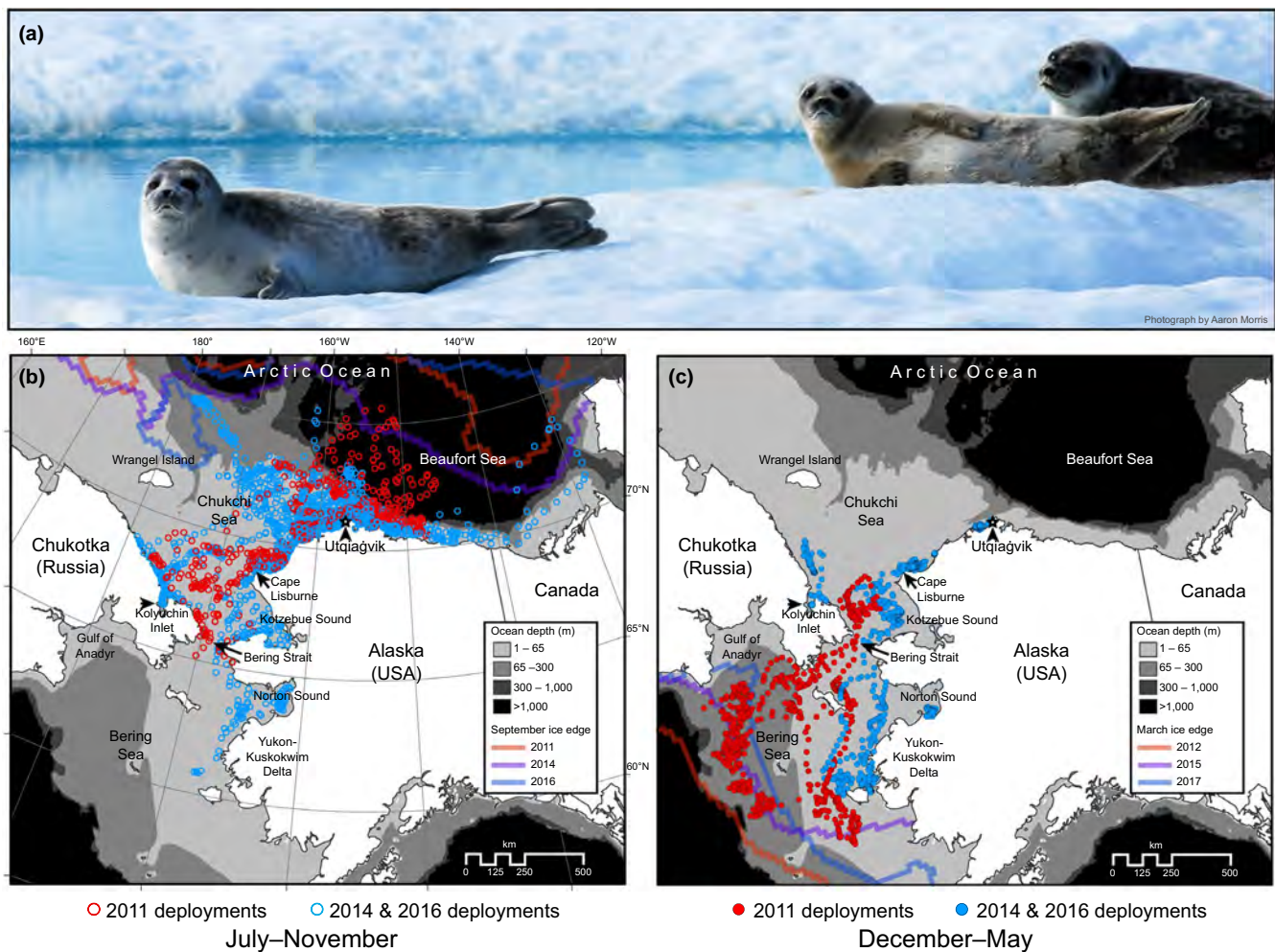


FIGURE 1 (a) Three ringed seals (*Pusa hispida*) hauled out on multi-year ice in the southern Beaufort Sea near Utqiagvik, AK. Note the molting fur on the center seal and the black face of a "rutting" male on the right. Daily CRAWL location estimates ($n = 4,083$) of the 17 ringed seals instrumented with satellite tracking tags are shown for July–September (b) and December–May (c). Colors distinguish seals tagged in 2011 (red, $n = 5$) from those tagged in 2014 and 2016 (blue, $n = 2$ and 10 respectively). The light gray contour at the 65 m isobath corresponds to the vertical line in Figure 7. The colored lines in (b) and (c) indicate the minimum and maximum extent of the sea ice in September and March, respectively, for each of the three tagging periods

in snow that has drifted above these holes (Stirling, 1977). Female ringed seals give birth to and nurse their pups within snow lairs, which are important to pup survival because they provide shelter from the elements and concealment from predators (Smith, 1976; Stirling & Archibald, 1977; Smith, 1980; Smith, Stirling, & Taugbøl 1991; Stirling & Smith, 2004). Sea ice also serves as a platform on which ringed seals haul out during their annual pelage molt in spring (Fay, 1974; Smith & Stirling, 1975)—a time when their epidermis and fur are shed and replaced. This close relationship with sea ice suggests that ringed seals may be sensitive to changes in their habitat (Laidre et al., 2008). Given the ecological importance of ringed seals and the ongoing rapid changes to their sea-ice habitats, a characterization of ringed seal movements, diving, and haul-out behavior has practical applications for their management and can contribute to a better understanding of emerging ecological trends in the Arctic.

Previous studies of ringed seal movements in the Beaufort-Chukchi-Bering (BCB) Sea region reported seasonal and demographic movement patterns (Crawford, Frost, Quakenbush, & Whiting, 2012, 2018; Harwood, Smith, & Auld, 2012; Harwood, Smith, Auld, Melling, & Yurkowski, 2015; Kelly et al., 2010), though broad-scale variability in these patterns appeared to be associated with capture location. For example, ringed seals tagged during September 2001 and 2002 just east of the Beaufort Sea in the southwestern Canadian Archipelago (Harwood et al., 2012) made extensive autumn movements westward that terminated primarily in the western Chukchi Sea north of Chukotka (Russia), whereas seals tagged nearby (~250 km to the east) in June and July of 1999, 2000 and 2010 (Harwood et al., 2015) exhibited more localized movements and remained in the southwestern Archipelago throughout autumn and winter. Though similar in phenology, ringed seals captured in Kotzebue Sound, Alaska (Crawford, Frost, et al., 2012; Crawford et al., 2018) moved into the southern Chukchi and Bering seas during winter. Given the enormity of the BCB, the limited number of tracking studies to date, and the apparent differences in spatial distribution and movements associated with tagging locations, there remains a need to document and characterize the movements and behaviors of ringed seals from other locales within the BCB to more fully document this species' spatial ecology.

Here, we present seasonal movements, habitat use, diving, and haul-out behavior of ringed seals instrumented with satellite transmitters in the vicinity of Utqiagvik (formerly Barrow), Alaska—a capture region not represented in prior tracking studies. We illustrate and quantify their movements and behaviors with respect to several geographic and demographic covariates. This work contributes to a growing body of literature about ringed seal spatial use, while also informing broader scale Arctic ecosystem monitoring efforts (Moore et al., 2014).

2 | METHODS

Ringed seals were captured near Utqiagvik, AK (71.3° N, 156.8° W) during June–July of 2011, 2014, and 2016. All captures were made

with nets that were set and continuously monitored near ice floes where seals had been observed. All nets had a lightweight lead-line and a highly visible float-line to ensure that entangled ringed seals could surface to breathe and that observers could readily determine when a capture occurred.

Upon capture, the seals were physically restrained during sampling and instrumentation. Biometric and demographic data were recorded (Table 1; Appendix A), including body mass, standard length, axillary girth, sex, and age class (Geraci & Lownsbury, 2005). Age was determined by counting the alternating light and dark bands on the front claws. Seals with ≥ 5 claw bands were classified as adults (McLaren, 1958); otherwise, they were classified as subadults. One seal with no record of claw bands was designated as a subadult based on its small size and weight (Crawford, Frost, et al., 2012).

Satellite transmitters (hereafter “tags”) provided location and dive data for each seal using the Argos System (Harris et al., 1990). Most seals were instrumented with one primary and one secondary tag, and the data from each were combined into a single tracking time series. While secondary tags were expected to reveal haul-out locations for up to 2 years, only two of the secondary (SPOT) tags ($n = 28$) provided >1 year of data (Appendix A), so we limited this study to the first year of data collection. Because seasonal patterns were of primary interest, we also limited our analyses to seals with tags that provided data beyond December 31 of the deployment year ($n_{2011} = 5$, $n_{2014} = 2$, and $n_{2016} = 10$).

Of the 17 seals in this study, all but two were instrumented with SPLASH tags (Wildlife Computers; $7.6 \times 5.6 \times 3.2$ cm; 125 g in air) as their primary tag, while the remaining two seals were instrumented with CTD tags (Sea Mammal Research Unit; $10.5 \times 7 \times 4$ cm; 545 g in air). All primary tags were attached using 5-min epoxy and/or cyanoacrylate adhesive to either the fur between the shoulder blades or on the head depending on the size of the seal. We anticipated that the primary tags would remain attached to the seals until shed during their annual molt the following spring—a duration of about ten months depending on tagging date. The primary tags provided data on movements, diving, and haul-out behavior. The 2011 primary tags (SPLASH) provided summary statistics for dive duration and maximum dive depth (for dives ≥ 3.5 m deep) as histograms, summarizing 6-hr time blocks. All primary tags deployed in 2016 recorded the start time, end time, and maximum depth (resolution = 0.5 m, $\pm 1\%$) of each individual dive, where start and end times were detected by crossing a 1.0 m depth threshold, and they did not collect 6-hr histogram summaries. The primary tags deployed in 2014 were mixed; all collected 6-hr histograms and some recorded individual dives, but the dive end times relied on a saltwater sensor that was prone to incorrectly pool sequential dives when intervening surface events were not detected. Hence, we only analyzed dive-behavior data collected from tags deployed in 2016. All seals were also instrumented with a secondary tag (Wildlife Computers SPOT; $2.0 \times 2.0 \times 8.3$ cm; 50 g in air). All secondary tags were permanently affixed to the rear flipper by screwing into a backing-plate through two holes punched in the interdigital webbing.

TABLE 1 Attributes and tracking duration for 17 ringed seals marked with satellite transmitters during the summer near Utqiagvik, AK

Seal ID	Sex	Age class	Weight (kg)	Length (cm)	Ax. Girth (cm)	Claw bands	First loc	Last loc	Elapsed days	CRAWL days
PH2011BW03 ^a	M	Subadult	24.8	95	84	4+	16-July-2011	09-June-2012	330	330
PH2011BW10 ^a	F	Adult	26.6	92	72	8+	21-July-2011	01-May-2012	286	276
PH2011BW11 ^a	F	Adult	23.2	93	76	7+	22-July-2011	04-June-2012	319	307
PH2011BW12 ^a	M	Adult	27.2	92	81	8+	22-July-2011	04-May-2012	288	288
PH2011BW13 ^a	M	Adult	34.8	91	84	8+	22-July-2011	11-January-2012	174	174
PH2014BW01 ^{b,c}	M	Adult	53.6	100	95	6	23-July-2014	19-May-2015	301	301
PH2014BW02 ^a	M	Subadult	18.3	74	70	–	23-July-2014	02-February-2015	195	195
PH2016BW01 ^b	M	Adult	50.9	110	101	6+	03-July-2016	04-April-2017	276	276
PH2016BW03 ^b	F	Subadult	24.8	86	81	1+	03-July-2016	26-January-2017	208	195
PH2016BW04 ^b	M	Adult	49.1	114	101	6+	03-July-2016	22-March-2017	263	263
PH2016BW06 ^b	F	Subadult	25.9	86	84	1	03-July-2016	21-January-2017	203	203
PH2016BW09 ^b	F	Adult	46.7	113	101	5+	04-July-2016	23-February-2017	235	205
PH2016BW10 ^b	F	Subadult	40.0	100	92	4	04-July-2016	09-February-2017	221	217
PH2016BW11 ^b	M	Adult	36.6	98	92	5+	04-July-2016	25-February-2017	237	237
PH2016BW12 ^b	M	Adult	36.8	103	93	6+	04-July-2016	06-January-2017	187	180
PH16BRW-120350 ^{c,d}	M	Adult	51.6	112	124	8+	03-July-2016	06-April-2017	278	258
PH16BRW-120353 ^{c,d}	M	Adult	51.6	112	105	7+	03-July-2016	31-January-2017	213	178

Note: These seals reported location data beyond December 31 of the tagging year. Duration between the first and last location is presented as *elapsed days*, while *CRAWL days* denote the total number of days for which the CRAWL movement model estimated the seal's location with a standard error of <25 km. The complete list of captured seals is recorded in Appendix A.

^aSPLASH tag without dive-behavior time series.

^bSPLASH tag with dive-behavior time series.

^c24 × 1 hr % dry (haul-out) data were unavailable.

^dCTD tag with dive-behavior time series.

Using R statistical software v3.4.2 (R Core Team, 2017), we applied a continuous-time correlated random walk model (R-package CRAWL v2.0.1; Johnson, London, Lea, & Durban, 2008) to estimate locations every 6 hr based on the tracking time series. Before applying the CRAWL model, we excluded implausible Argos locations, such as those that were on land or that failed to meet criteria for movement rates and turning angles (Appendix B). For the CRAWL analysis, we converted the locations to a Lambert's equal area map projection centered on the study area. Prior to further analysis, we excluded CRAWL location estimates that had standard errors >25 km (3.5% of all location estimates), which was commensurate with the spatial scale of the lowest-resolution environmental data we used in our modeling. CRAWL locations were augmented with habitat metrics describing the distance to mainland (Wessel & Smith, 1996), bathymetry (National Geophysical Data Center, 2006), sea-ice concentration (Cavalieri, Parkinson, Gloersen, & Zwally, 1996; Maslanik & Stroeve, 1999), and distance to the sea-ice edge. The minimum distance to the ice edge was measured from the midday UTC (03:00 local time) location estimate to the nearest periphery of sea ice ($\geq 15\%$ concentration) composed of ≥ 10 contiguous 25 km pixels. Because there was a 294-day gap between the higher spatial resolution AMSR-E and AMSR-2 sea-ice data sets, we used the 25 km resolution SSM/I sea-ice data in our analyses. Sea-ice concentration was based on the average value within a 50 km radius circle (excluding land) centered on the midday location.

Diurnal and seasonal haul-out behaviors were quantified using data from the primary tags, which binned daily summaries into 24 one-hour increments. The tag reported the fraction (%) of each hour that its saltwater sensor was wet or dry (sampled at 10 s intervals). We defined hours that were $\geq 80\%$ dry as "haul-out" hours. The 80% threshold was robust because the distribution of hourly percent-dry values was strongly bimodal; with 95% of all sampled haul-out hours ($n = 62,279$) being either $\geq 80\%$ dry (11.5%) or $\leq 25\%$ dry (83.5%). We excluded the first week of post-deployment behavior data prior to analysis to reduce potential biases associated with capturing seals close to shore.

Dive-behavior analyses were based on data retrieved from the primary tags deployed in 2016 ($n = 10$) and included parameters for dive duration, dive depth (maximum), and surface duration. We temporally paired the dive metrics with the nearest 6-hr CRAWL location and associated environmental attributes (e.g., ocean depth and sea ice). Dives were classified as bottom dives when the maximum dive depth was $\geq 75\%$ of the mapped ocean depth. We did not attempt to classify bottom-dives in shallow water (<10 m) where relationships between dive depths and water depths become increasingly uncertain due to inaccuracies in both the location and bathymetry data.

By comparing successive dive depths and intervening surface intervals (Appendix C), we classified behavior as: (a) *resting*, when the surface interval between successive dives exceeded 10 min; (b) *repetitive diving*, when ≥ 5 sequential dives attain maximum depths within $\pm 15\%$ of either of the two preceding dives—single dives $> 15\%$ different were allowable within a repetitive-diving episode; and (c) *mixed diving*, for all remaining dives not classified as repetitive.

We partitioned movement, dive, and haul-out data into two habitat types: the shallow continental shelf (<300 m, $n = 3,933$ tracking days) and the deeper Arctic Basin (>1,000 m, $n = 127$ days). Seal locations over the steep shelf-break (300–1,000 m, $n = 23$ days) were excluded from our dive-behavior analyses to avoid highly misrepresentative relationships between dive depth and bottom depth that could arise from modest spatiotemporal mismatches between dive and location data.

Monthly dive summaries included the daily average time spent diving and the proportions of repetitive versus mixed diving. For each month, July–April, we estimated the average daily hours spent diving using the dive-behavior time series of individual dives and surface times, and the 1×24 hr haul-out classifications, both from the 2016 SPLASH-tag deployments ($n = 8$). For each month and seal, we tallied the number of observed hours hauled out as well as the total number of observed hours that were sampled, and we used the resulting ratio to extrapolate an estimate of the total number of hours hauled out during a respective month. The remaining hours (not hauled out) were then allocated to three behavior classes based on proportions derived from the dive-behavior time series. We considered the dive-behavior data to be a representative sample of the time seals spent diving or resting at the surface during the hours they were not hauled out (Appendix D). Surface times >10 min in duration were assigned to "resting" only if the respective period did not overlap with a haul-out hour. If it did overlap, then that surface interval was discarded since it had already been tallied into the haul-out hours above. Dive sequences (including intervening surface times) were classified as "repetitive" or "mixed" as described earlier. For each month and seal, we tallied the total amount of time spent diving (repetitive and mixed) versus resting and used that ratio to allocate the remaining monthly hours "not hauled out" as either engaged in diving or resting. Average daily estimates of time spent diving were calculated by dividing the extrapolated monthly total of hours diving by the number of days in the respective month. We excluded seal months if the average distance to mainland was <5 km, because ocean depths near shore were often less than the tag's designated 3 m threshold for dive detection.

To inform our interpretation of ringed seal movements, habitat use, and haul-out behavior, we built five model sets targeting these response variables (Appendix E): I. Movement Rate, II. Distance to Mainland, III. Distance to Ice-Edge, IV. Ice Concentration, and V. Haul-Out Time. Each response variable was modeled with respect to four independent factors: Sex (MALE vs. FEMALE), AgeClass (ADULT vs. SUBADULT), Season (OPEN-WATER vs. ICE-COVERED), and CapYear (2011/2014.16). Season refers to the general timing of the open-water and ice-covered periods. The ICE-COVERED season, which occurs from December through June was characterized by the advance of sea-ice south into the Bering Sea where it would remain until spring when it would begin to retreat to the north. The OPEN-WATER season occurs from July through November, and is characterized by generally ice-free waters over the continental shelf of the entire Bering

Sea and much of the Chukchi Sea. The factor *CapYear* was included to assess whether a disease outbreak that began in 2011 may have influenced ringed seal movements and/or behavior. Ultimately designated as an “Unusual Mortality Event” (UME) (NOAA, 2011a, 2011b, 2012, 2014; Stimmelmayer et al., 2013), none of the 2011 seals included in our analyses showed obvious symptoms (e.g., alopecia, lethargy, skin inflammation, or unusual molting patterns). However, several other seals captured in 2011 were symptomatic. In contrast, during both the 2014 and 2016 field seasons, no seals were observed to be symptomatic.

All models were constructed using R Statistical Software. Prior to modeling, we removed the first week of data from each seal's time series to reduce any influence of capture and handling. Three response variables: *Movement Rate*, *Distance to Mainland*, and *Distance to Ice Edge* (model sets I–III), were square root transformed prior to analysis and were modeled using linear mixed effects models (R-package *nlme* v. 3.1-140, Pinheiro, Bates, DebRoy, & Sarkar, 2019) assuming a normal distribution and identity link function. To account for spatial autocorrelation, we employed a first-order autoregressive (AR1) structure. Because the data for *Ice Concentration* in model set IV was proportional (i.e., range = 0–1), we used generalized linear mixed models (R-package *glmmTMB*; Brooks et al., 2017) with a beta distribution and logit link. We transformed the data following Smithson and Verkuilen (2006) to address zeros and ones. To understand the use of sea ice when it was generally available, we partitioned the data for model set IV by *Season*, and developed models for the ice-covered period only. *Haul-out Time* (model set V) was also analyzed with R-package *glmmTMB*, but using a Poisson distribution and log link. In this model set, we were interested in understanding the factors associated with time spent when haul-out occurred (not whether haul-out occurred), and so we filtered our data to include only those days with ≥ 1 hr spent hauled out. As such, our models did not require adjustments that would otherwise be needed for zero-inflation. Finally, all models included random effects to account for individual variability among seals.

For each model set, we followed a systematic model selection procedure. First, we generated all possible single- and multivariate mixed models. We assessed model performance based on parsimony (using Akaike's information criterion; AIC_C) and then modified the highest performing models ($\Delta AIC_C < 2$) by adding two-way interaction terms. The full model set was then re-assessed and ranked. Models within each set having the lowest AIC_C were considered “best,” though other models with ΔAIC_C within 2.0 of the highest-ranking model were also deemed comparable (Burnham & Anderson, 2002). Visual inspections of residual plots from all significant models revealed no obvious deviations from homoscedasticity (Zuur, Ieno, Walker, Saveliev, & Smith, 2009). Finally, we used R-package *emmeans* (Lenth, 2019) to estimate marginal mean values from the best models (Appendix F) and to make multiple comparisons because this method is useful for summarizing the effects of factors when subjects are repeatedly measured and have unequal sample sizes (Lenth, 2016).

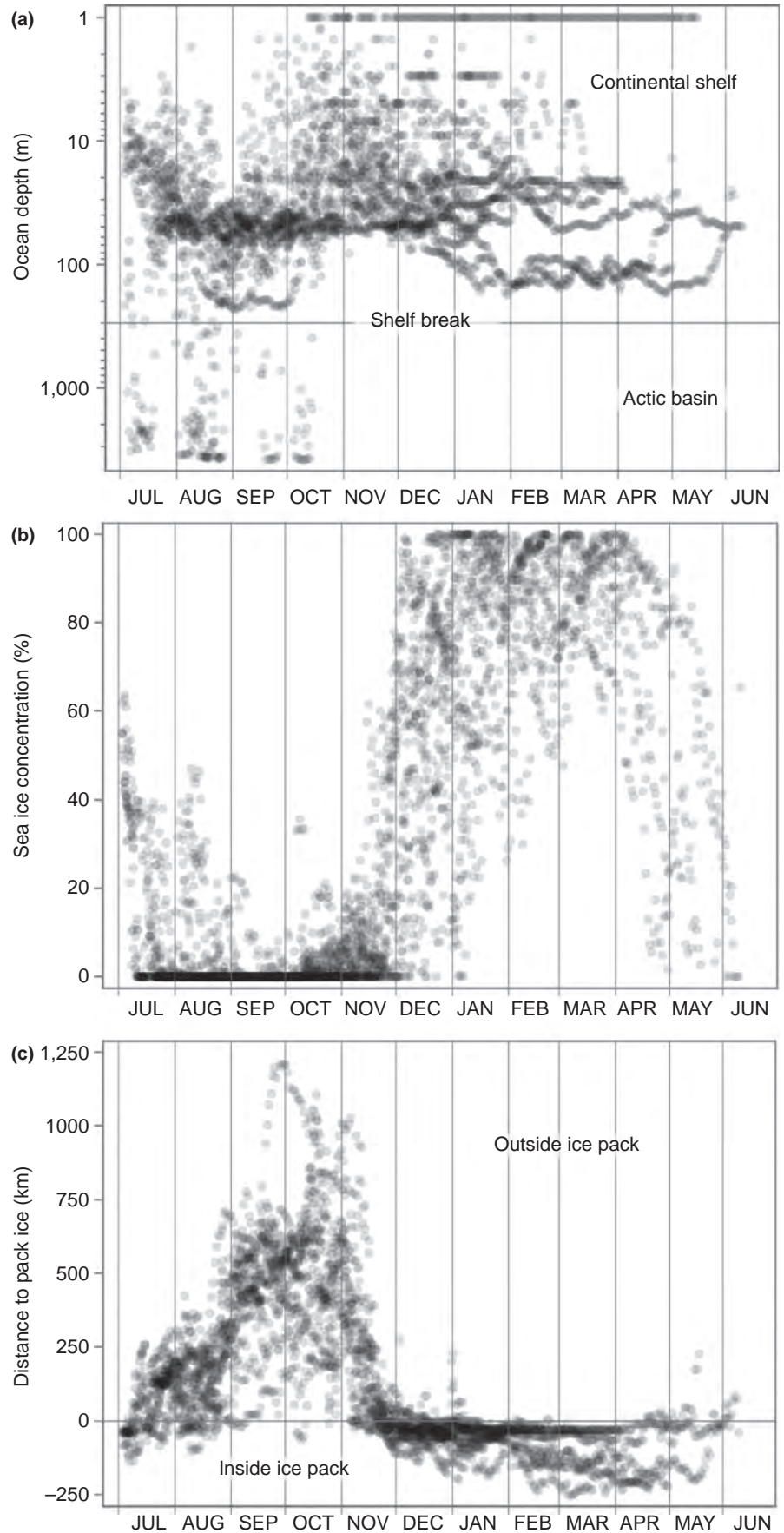
3 | RESULTS

Of the 39 ringed seals captured and tagged (Appendix A), a total of 17 (Table 1) met the criteria for tag longevity in order to be included in our analyses. These 17 ringed seals included 12 adults (9 ♂, 3 ♀) and 5 subadults (2 ♂, 3 ♀). Mean body length was 102.5 cm ($SD = 9.3$) for adults and 88.2 cm ($SD = 10.0$) for subadults. The mean weight of adults was 40.7 kg ($SD = 11.2$) and subadults was 26.8 kg ($SD = 8.0$). The mean length ($\bar{x} = 92$ cm, $SD = 0.8$) and weight ($\bar{x} = 28.0$ kg, $SD = 4.8$) of adult seals tagged in 2011 ($n = 4$) were both significantly less than the mean length ($\bar{x} = 107.8$ cm, $SD = 6.4$) and weight ($\bar{x} = 47.1$ kg, $SD = 6.7$) of adults tagged in 2014 and 2016 ($n = 8$).

A total of 52,431 satellite locations were received; the median number of locations per seal was 2,778 (range = 2,146–6,020) and the median tracking duration was 239 days (range = 178–331). The median time interval between sequential locations was 0.52 hr (range = 0.01–1,157), with few long temporal gaps (99th percentile = 20.3 hr). Higher-quality locations (Argos classes = 1, 2, and 3) comprised 7,471 (7.2%) of the seal locations. Filtering excluded 3,757 lower-quality locations (Argos classes = 0, A, B, or Z). After applying the CRAWL model and excluding 596 estimated locations with SEs > 25 km, the final data set contained 16,260 location estimates, representing 4,083 individual seal tracking days (median = 237 tracking days/seal; range = 174–330). During the period when all 17 seals were tracked (August to December) the median cumulative distance traveled was 4,790 km/seal (range = 2,719–5,988) (Figure 3d).

Ringed seals occupied continental shelf waters on $> 96\%$ of the tracking days, with some seals making off-shelf forays into the Arctic Basin in July to October (Figure 1b). All ringed seals occupied waters with sea ice during winter, but most occupied open-water south of the pack-ice during September–October (Figure 2). With one notably early southward movement into the Bering Sea in mid-September, all seals had moved south of Utqiagvik by early November. Some seals continued to move during winter while others occupied specific locales for extended periods. Eight seals (6 adults, 2 subadults) moved south through the Bering Strait from November to mid-December, while nine others (7 adults, 2 subadults) remained in the Chukchi Sea into January (Figure 3a). Of the four 2011 seals that wintered in the Bering Sea, three moved to deeper waters south of the Gulf of Anadyr (Figures 1b and 3b), while the fourth 2011 seal and all four of the 2016 seals that wintered in the Bering Sea moved south to waters near the Yukon-Kuskokwim Delta (Figures 1b and 3b). There was high seasonal variability in distance to mainland during both the ice-covered (Jan to Jun) and open-water (Jul to Dec) seasons (Figure 3c). From November to January, distance to mainland was generally less and not as variable because many seals were near the Bering Strait (Figure 3c). Six of 10 seals tagged in 2016 remained in the Chukchi Sea for the duration of winter tracking—four along the Alaskan coast between Utqiagvik and Cape Lisburne, one at the mouth of Kotzebue Sound, and one at Kolyuchin Inlet in northern Chukotka. One 2014 seal moved into the western Chukchi Sea during winter,

FIGURE 2 Seasonal time series of daily ringed seal habitat attributes: (a) ocean depth; (b) mean sea-ice concentration (within a 50 km radius); and (c) distance to the edge of the pack-ice—where negative values represent distances from inside the ice pack. Ocean depth (a) is shown on a log scale with a horizontal line at the shelf-break (300 m depth)



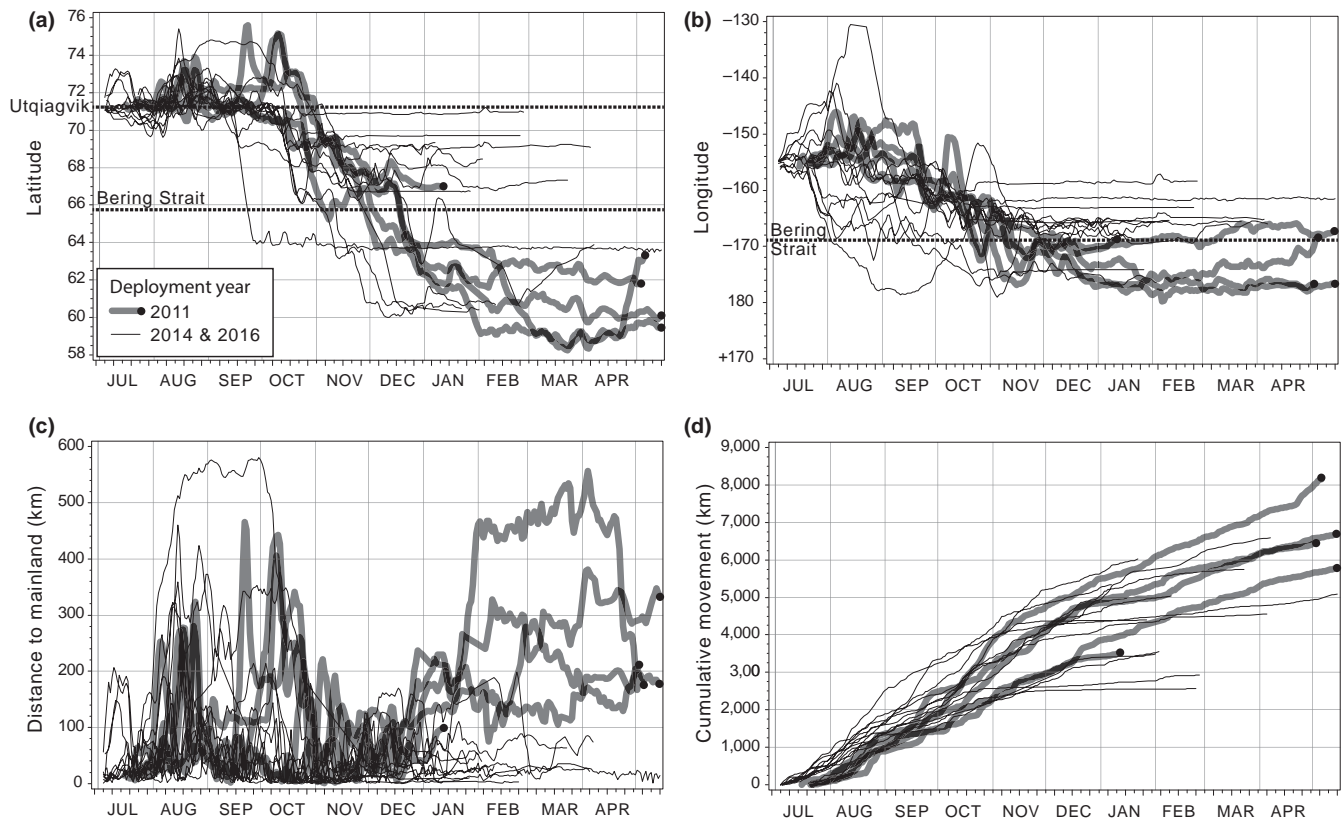


FIGURE 3 Seasonal movements of 17 ringed seals with respect to (a) latitude, (b) longitude, (c) distance to mainland (islands excluded), and (d) cumulative daily tracking distance. Thin black lines are seals tagged in 2014 and 2016. Thick gray lines with black terminal dots are seals tagged in 2011. Distances calculated based on daily CRAWL location estimates. Seventeen seals provided data through January, and then, sample size declined to 12, 8, 7, 5, and 2 seals during February through June, respectively

just north of the coast of Chukotka; and one 2011 seal was near the Bering Strait when its tag stopped transmitting in February 2012.

Ringed seal movements, spatial use, and habitat attributes varied over yearly and seasonal scales, and with respect to demographic variables (Figure 4; Appendix F). Movement rate was best described by a model with an interaction between *Season* and *CapYear* (i.e., year of tag deployment), with the greatest rates occurring during the open-water season and also the 2011 ice-covered season. A univariate model that included *CapYear* best described distance to mainland, with seals in 2011 occupying areas significantly farther offshore (120.6 km vs. 46.5 km; Appendix F). The distance to the ice edge was best explained by a bivariate model that included *Season* and *CapYear*, both of which were significant. As expected, the presence of ice negatively influenced the distance from the sea-ice edge, with seals remaining closer to and deeper within the pack-ice during the ice-covered season. Meanwhile, the seals tagged in 2011 tended to stay closer to and deeper within the pack-ice than seals tagged in 2014 or 2016. The concentration of sea ice occupied was best explained by a bivariate model that included *AgeClass* and *CapYear*, but both factors fell short of statistical significance ($p = .060$ and $.067$ respectively). Finally, the time spent hauled out on the ice was best explained by a model in which *Sex* and *Season* interacted. During the ice-covered season, males spent less time hauled out (on days with ≥ 1 haul-out hour) than during the open-water season ($p = .026$).

Though not statistically significant ($p = .087$), the largest difference in marginal mean haul-out hours was between males and females during the ice-covered season.

From July to mid-October, 12 of 17 tagged seals (71%) undertook forays into the deep Arctic Basin (Figure 5; Appendix G): including 7 males (2 subadult) and 5 females (1 subadult). All 2011 seals ($n = 5$) ventured into the Arctic Basin, contributing 9 of the 16 observed forays. The median duration of the forays was 7 days (range = 2–21) (Figure 5). While in the presence of sea ice in the Arctic Basin, seals tended to haul out for extended periods of time (median duration = 11 hr, maximum duration = 34 hr, $n = 42$; Appendix G)—usually returning directly thereafter to the continental shelf. Three seals made a second foray off-shelf to the ice edge (Figure 5). During three other forays, seals failed to encounter substantive ice cover and haul-outs were not recorded (Appendix G). Diving behavior in the Arctic Basin consisted of both mixed- and repetitive dives, with the latter comprising 40% of the recorded dives ($n = 2,119$). Repetitive dives were occasionally punctuated by intermittent deeper dives of 200–300 m (Figure 6); on occasion these deeper dives immediately preceded repetitive diving to deeper strata.

By December, all seals tended to occupy regions with high sea-ice concentration on the continental shelf (Figure 2). By March and April, among seals that wintered in the Bering Sea (two adult females, one juvenile male, and three adult males), the juvenile and

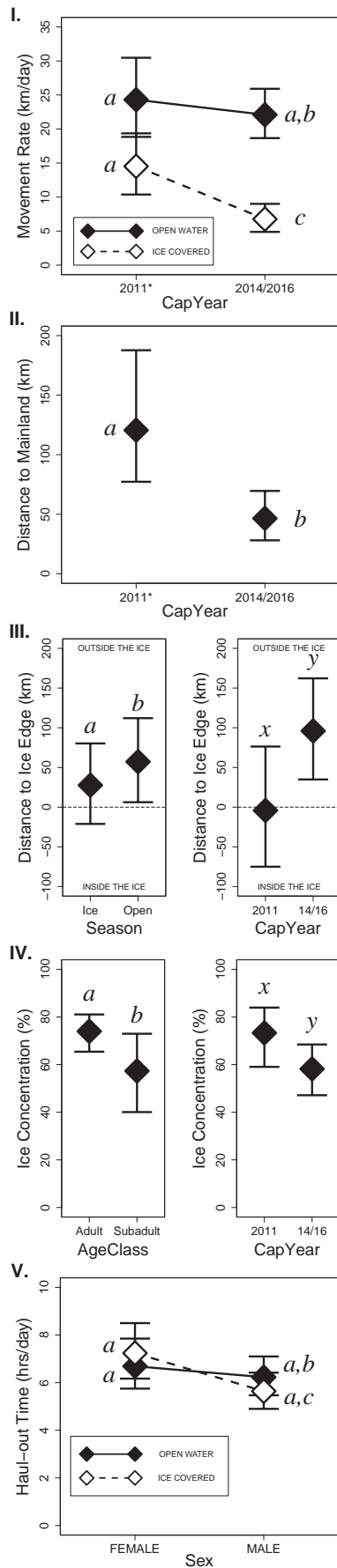


FIGURE 4 Marginal means [diamonds] with 95% CI for models of (I) movement rate, (II) distance to mainland, (III) distance to ice edge, (IV) concentration of ice occupied, and (V) haul-out time. Figures show the estimated marginal means generated from the best model from each of the five model sets (Table 3; Appendix E). The factor *Season* is designated as OPEN-WATER (Jul–Nov) and ICE-COVERED (Dec–Jun). The factor *CapYear* is designated according to year of tag deployment (2011 vs. 2014/16). The factor *AgeClass* is designated as ADULT and SUBADULT, and *Sex* is as FEMALE and MALE. Negative values in panel III—*Distance to Ice Edge (km)* refer to distances from inside the pack ice to the ice edge, and positive values from outside the pack ice to the ice edge. Note that panels I and V depict interactions, panel II depicts a univariate model, and panels III and IV depict bivariate models. *Year of Unusual Mortality Event

two adult males began making modest northward movements, but all remained south of the Bering Strait (Figure 3a). In April, the average sea-ice concentration occupied by seals began to decrease (Figure 2b), suggesting that they were not aggressively pursuing the retreating ice edge northward. While we observed no statistically significant differences in the distance to ice edge based on sex or age class (Figure 4; Appendix F), we do note that, over the entirety of the year, adults tended to occupy higher concentrations of ice than subadults (79.98% vs. 57.32% respectively; $p = .060$). Those seals tagged in 2011 also appeared to occupy regions deeper within the pack-ice than the seals tagged in 2014 or 2016 (Figure 4; Appendix F), though this was not significant ($p = .067$). No other differences in sea-ice location or concentration based on sex or age class were observed.

The daily activity budget was dominated by diving ($\bar{X} = 16.5$ hr/day); with most of that time ($\bar{X} = 13.2$ hr/day) spent repetitive diving (Table 2). Other than in July, which showed the lowest monthly mean, the proportion of daily hours spent diving remained relatively constant. The proportion of repetitive dives was consistent from July to January (~80%) but decreased in February to 55%, though by this time the sample size had declined to two adult males. Bottom-dives comprised 65% of all dives recorded on the continental shelf ($n = 96,414$). During 7,369 episodes of repetitive diving (consisting of 67,355 dives), 78% met the criteria for bottom-dives (Figure 7). Dive histogram data from seals tagged in 2011 also indicated that most dives over the continental shelf were bottom-dives (Figure 8). The median dive duration was 3.9 min (99th percentile = 10.7 min, $n = 81,916$). Approximately 67% of all dives recorded ranged from 2.5 to 5.5 min (Figure 9a). The median surface duration between dives was 0.7 min (~42 s) (99th percentile = 4.1 min, $n = 76,964$). With increasing dive depth (up to 270 m), dive duration increased asymptotically while the intervening surface time increased exponentially (Figure 9b). The regressions of dive and surface times in Figure 9b used the medians of 10-m dive-depth bins; however, it should be noted that the maximum dive durations in each of those bins were consistently 10–12 min—which may represent the physiological dive-duration limit for ringed seals (Lydersen, Ryg, Hammill, & O'Brien, 1992).

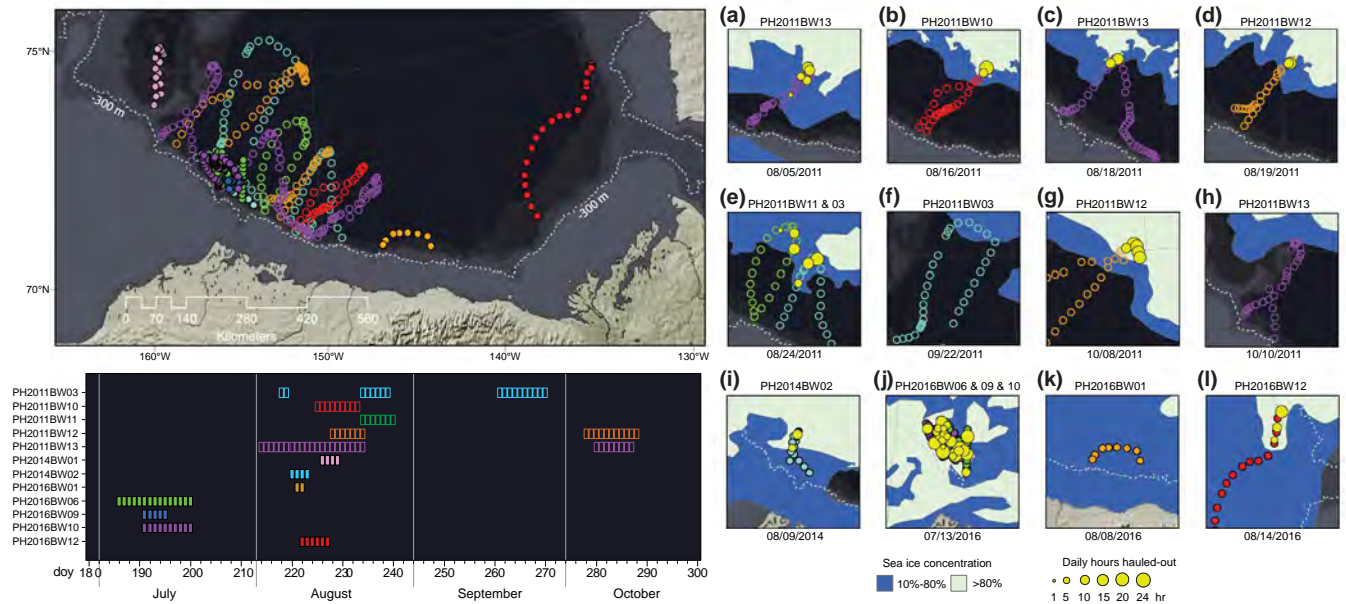


FIGURE 5 Off-shelf forays into deeper water. In all panels, seals instrumented in 2011 are distinguished by open symbols, and those in 2014 and 2016 by solid symbols. *Upper left*—Locations (4 per day) of 12 ringed seals when occupying waters >1,000 m deep, colored by individual seal. *Lower left*—Rectangles indicate dates spent off-shelf, with the same colors as the locations shown above. *Right*—Distribution of sea-ice and haul-out behavior during forays into waters >1,000 m deep ($n = 11$ seals). Days when one or more haul-out hours were recorded are overlaid as yellow dots scaled in size by the total hours hauled out that day. Sea-ice conditions (U.S. National Ice Center, 2019) on the date (shown below each panel) correspond temporally with the more northerly locations and show two classes of ice concentration: marginal (blue, 10%–80%) and contiguous (light blue, >80%)

Monthly diurnal frequency distributions of dive-behavior observations that were classified into each of four behavior classes revealed daily patterns that changed seasonally (Figure 10). For example, there was a higher frequency of repetitive dives during mid-day for depths >25 m only (Figure 10a,b)—becoming increasingly prevalent as day-length diminished from late summer into autumn and winter. The shape and magnitude of the mixed-dive histograms (Figure 10c) somewhat resembled the resting histograms, but with less-well defined diel and monthly patterns. Resting behavior exhibited diel and monthly patterns that were somewhat complementary to those observed for repetitive dives >25 m deep (Figure 10d).

Hourly percent-dry time series data were obtained for an average of 72% ($SD = 8.9\%$) of the tracking period. After excluding data from the first week of satellite tag deployment and data that were collected off-shelf, the median duration of uninterrupted haul-out bouts was 3 hr (range 1–28, $n = 1,025$ haul-outs). Time spent hauled out per day was significantly longer during the open-water than during the ice-covered season for males (6.23 vs. 5.64 hr/day) (Figure 4; Appendix F). There was no significant difference in the daily time spent hauled out between seals tagged in 2011 and those tagged in 2014 and 2016. Terrestrial haul-out behavior was frequently observed among untagged ringed seals near Utqiagvik in the summer of 2011—a number of which were captured and tagged (Appendix A). Observations of terrestrial haul-outs are extremely rare for ringed seals in Alaska (North Slope Borough, *unpublished data*) and no such behavior was documented in 2014 or 2016. Also,

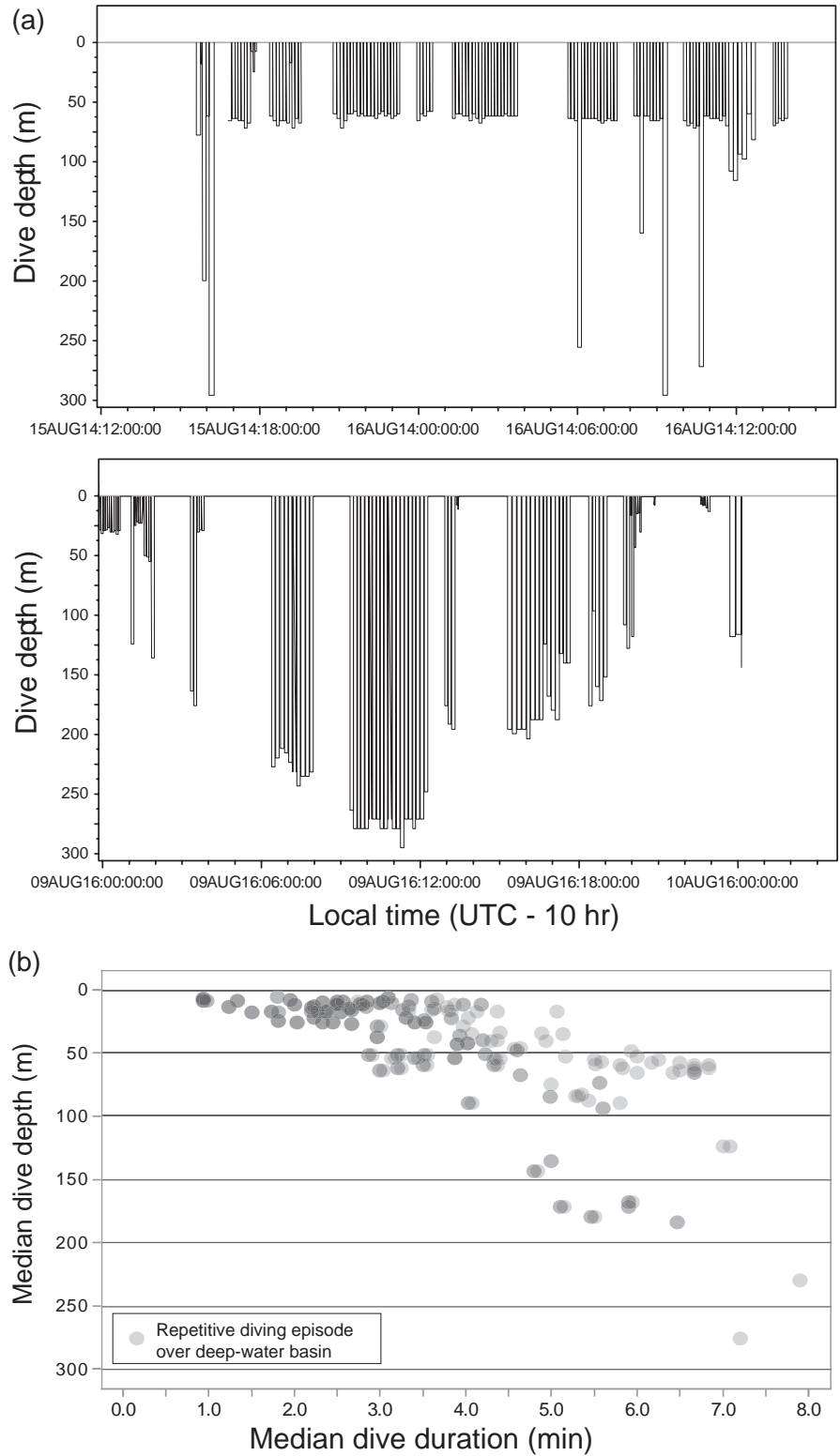
during 2014 and 2016 on days with a CRAWL location estimate, 86% of the haul-out hours occurred >10 km from the coast.

The proportion of tagged seals hauled out exhibited patterns that varied both diurnally and monthly (Figure 11). In July, 15%–20% of the seals were hauled out during any given hour of the day with little indication of a diel pattern. The proportion of seals hauled out declined from August through October, with a subtle indication of nocturnal preference. From November through March, the proportion of seals that hauled out nocturnally increased. Haul-out behavior switched from nocturnal to diurnal in April and May as seals showed a strong midday preference; however, by April to late May the sample size had declined to two adult males.

4 | DISCUSSION

Ringed seals instrumented with satellite transmitters near Utqiagvik, Alaska provided movement and dive-behavior data that both corroborated and expanded prior knowledge. The ringed seals in our study migrated to the southern Chukchi and Bering seas for winter, like those tagged by Crawford, Frost, et al. (2012) near Kotzebue, Alaska, and those tagged by Harwood et al. (2012) near the entrance of Amundsen Gulf, Canada. Data from tens of thousands of individual dives provided new insights into ringed seal foraging behavior, notably a propensity to repeatedly dive to depths at or near the ocean floor. Unique to this study were several brief mid- and late-summer movements into the deep-water

FIGURE 6 *Top*—Example of repeated diving to ~60 m depth by one seal during one day while occupying the deep-water Arctic Basin. Note the occasional exploratory dives to 200–300 m depths. *Center*—Example of relatively deep repetitive dives in the Arctic Basin (by one seal during one day) suggesting that prey may be present in deeper strata, and supporting the notion that exploratory dives can have payoffs. *Bottom*—Records of repetitive-diving episodes in the Arctic Basin. Relatively few repetitive dive episodes occurred at depths >100 m (max ~275 m; shown in *Center* panel)



Arctic Basin, where seals spent most of their time hauled out on the available pack-ice. Though not statistically significant, we provide some evidence of demographic segregation in sea-ice concentration between adult and subadult seals as observed by Crawford, Frost, et al. (2012). However, other factors may also have been involved. For example, in the winter of 2011–2012, the sea-ice maximum extent (in March) in the Bering Sea was the largest ever

recorded in the satellite record (since 1979), as was the average sea-ice concentration (77%) (Fetterer, Knowles, Meier, Savoie, & Windnagel, 2017). By comparison, average sea-ice concentration in March in the Bering Sea was 64% in 2015 and 68% in 2017. Further, the seals tagged in 2011 displayed physical traits and spatial distributions that were consistent with the purported existence of a pelagic ringed seal ecotype. In the sections that follow,

Month	n	Diving (h)		Repetitive (%)		Sample (%)	
		Mean	SD	Mean	SD	Mean	SD
July	8	14.7	2.0	80.0	15.5	19.2	7.2
August	7	17.1	2.0	80.2	4.0	34.1	10.8
September	7	17.3	3.3	81.1	10.0	24.8	10.8
October	7	17.4	5.1	81.8	9.3	32.2	14.6
November	6	16.4	2.3	81.3	12.9	29.0	11.5
December	6	16.5	3.0	82.5	8.8	30.7	12.3
January	5	16.2	3.9	80.1	9.3	18.4	3.5
February	2	16.3	0.5	54.6	16.4	15.8	3.1
Pooled	48	16.5	3.1	79.9	11.4	26.5	11.6

Note: Sample (%) is the fraction of the month for which we obtained dive-behavior time series data for any given seal month. For each month, at least a 10% sample of the dive-behavior time series data was required for a seal to be included in the respective monthly estimate ("n" is a seal month). Analysis used the 8 SPLASH tags deployed in 2016. Seal months with an average distance from the coast of <5 km were excluded (n = 4 seal months).

TABLE 2 Monthly estimates of the mean hours per day spent diving, and the proportion (%) of those hours spent engaged in episodes of repetitive diving to similar depths

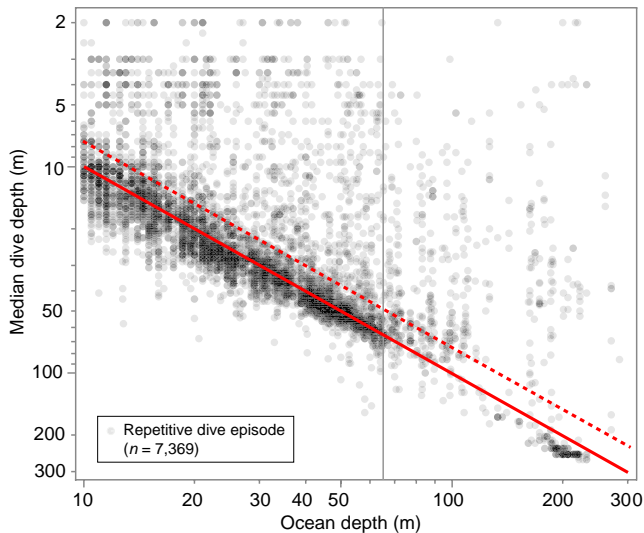


FIGURE 7 Median dive depth recorded during episodes of repetitive diving to similar depths in relation to the average ocean depth at locations on the day of the diving. Analysis was restricted to days when seals were located in water 10–300 m deep. The solid red line denotes a 1:1 dive depth to ocean depth relationship, and the dotted red line denotes the dive-depth threshold for classification as *bottom diving*. The gray vertical line denotes the 65 m isobath which is demarcated in Figure 1 with the light gray shading. Note log scales on both axes. See Figure 8 for a summary of dive behavior based on the dive histogram data received from tags deployed in 2011. Dives that implausibly exceeded ocean depth were likely due to errors in the estimated seal locations, errors, or generalizations in the coarse-resolution bathymetry data, or imprecision in assigning locations to dives

we expand upon these topics and offer speculations about how ringed seal movements, energy requirements, and physiological states may have interacted to shape the behaviors we observed.

Ringed seals tagged near Utqiagvik almost exclusively utilized continental shelf habitat in the Chukchi and Bering seas (Figure 1). All

seals traveled extensively during autumn, covering vast cumulative distances (see Harwood et al., 2012) on migrations that lasted until early winter (Figure 3d). During winter, movements were restricted for some seals, extensive for others, and habitats occupied were varied and widely distributed (from 57°N to 70° N latitude). Some seals stayed close to the coast in relatively shallow water, even stopping and maintaining a localized winter residency (Figures 1 and 3), while others went far offshore into the Bering Sea and moved continuously all winter in the dynamic pack-ice. Diversity in behavior and of habitats occupied suggests that, as a species, ringed seals can exploit a breadth of niches. We found some evidence of demographic habitat partitioning (Figure 4; Appendix F). Adults appeared to occupy winter habitats with higher sea-ice concentration, suggesting that different reproductive and life-history states (e.g., mating adults vs. growing subadults) may lead to different habitat requirements Crawford, Frost, et al. (2012). Adult and subadult ringed seals tagged by Crawford, Frost, et al. (2012) near Kotzebue, Alaska, wintered in distinctly different regions, with subadults moving farther south into the Bering Sea, while adults stayed primarily in the southern Chukchi Sea. Though we also noted evidence suggesting demographic differences in habitat use (Figure 4; Appendix F), our results were not statistically significant. Our results indicate, however, that year of tag deployment was important to understanding the movements of ringed seals (Figures 3 and 4), which may be important in light of the UME that began in 2011.

Most of the seals in our study (71%) made brief (~week long) off-shelf forays during summer that appeared to be deliberate and sometimes far-ranging efforts to reach the retreating sea ice (Figure 5, Appendix G). Broad-scale movements by ringed seals during the open-water season are not unprecedented, such as populations in Svalbard that make long distance movements to seasonally access productive habitats (Freitas, Kovacs, Ims, Fedak, & Lydersen, 2008; Hamilton, Lydersen, Ims, & Kovacs, 2015). Off-shelf movements by Utqiagvik seals were notable because they

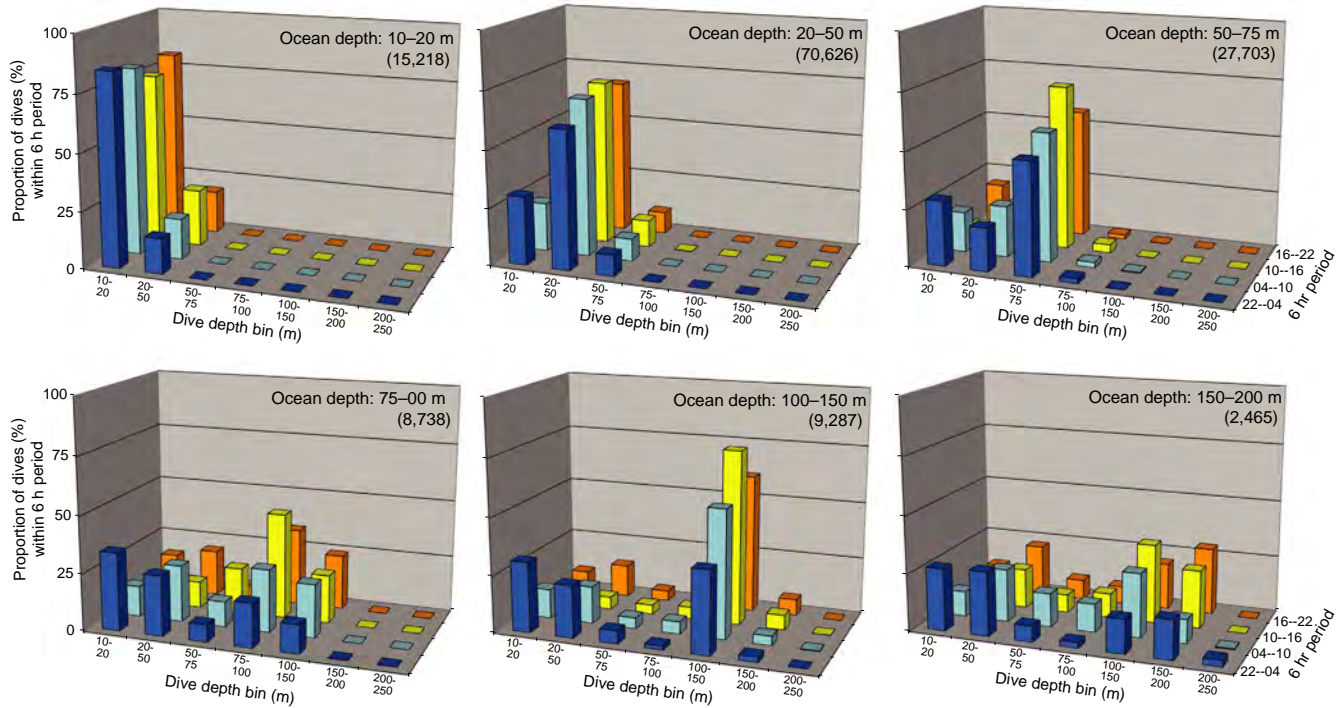


FIGURE 8 Dive histogram data corroborating daytime bottom-diving behavior among the ringed seals tagged in 2011. SPLASH tags deployed on ringed seals in 2011 ($n = 5$) provided summarized “histogram” data containing the number of dives to ocean-depth intervals during four 6-hr periods (charted here in local time, UTC-10 hr). We partitioned dive data into days when seals were located where the ocean depths were congruent with the six most commonly visited dive-depth bins and charted the relative proportion of dives in each depth bin, for each 6-hr period. Numbers in parentheses are the number of dives summarized in the respective chart. Results corroborate that most dives attained depths near the ocean bottom (as in Figure 7) and that deeper diving was more common during the midday (10:00–16:00) hours (as in Figure 10)

apparently abandoned more productive continental shelf habitat (Born, Teilmann, Acquarone, & Riget, 2004; Kingsley, Stirling, & Calvert, 1985; Teilmann, Born, & Acquarone, 1999) in favor of deep-water Arctic Basin habitat of generally lower quality (Frey et al., 2016). Given their dive-depth constraints (Lydersen et al., 1992), ringed seals that forage in deep water may have limited access to prey or incur higher foraging costs (Hamilton et al., 2015). Upon reaching the sea ice in the Arctic Basin, ringed seals spent more time hauled out than foraging. That 25% of these seals returned for a second time suggests potential benefits that may result from this behavior. This apparent motivation to haul out may reveal physiological constraints, such as those relating to the energetics of their molt (Crawford, Vagle, & Carmack, 2012; Majewski et al., 2016).

Distinct patterns in the dive data suggest that the ringed seals in our study frequently engaged in focused bouts of repetitive diving, the attributes of which are suggestive of active foraging behavior. Specifically, tagged seals repeatedly dove to near-constant depths, showed near-constant dive durations and intervening surface times (Appendix C), and exhibited this behavior during substantial portions of the day (Table 2). Focused foraging behaviors can maximize energetic profitability when they result in repeated capture and consumption of aggregated prey—a strategy that makes energetic sense in patchy environments (Schoener, 1971). Repetitive diving also occurred more frequently during midday, when ambient light is

brightest (Figure 10), and was spatially allocated in favor of habitats where prey species are known to aggregate—that is, the continental shelf seafloor (Benoit, Simard, Gagné, Geoffroy, & Fortier, 2010). If repetitive-diving bouts are indeed indicative of active foraging efforts, then their prevalence in the data show that ringed seals forage on average >12 hr/day from August through January (Table 2).

The tendency for most repetitive-diving bouts to occur at or near the seafloor (Figure 7) may be related to the ecology of their prey. Ringed seals prey upon zooplankton (Lowry et al., 1980) and planktivorous fish (Crawford et al., 2018), both of which make synchronous diel vertical migrations (DVM) into deeper waters during the brightest hours of the day (Hays, 2003; Rabindranath et al., 2011; Stich & Lampert, 1981)—but, as potential prey themselves, face trade-offs between their own metabolic needs and predation risk (Pearre, 2003). Among Arctic cod (*Boreogadus saida*), which are an important forage species for ringed seals (Holst, Stirling, & Hobson, 2001), the larger and more energy-rich adults have greater metabolic stores and lower food limitation that enables them to remain longer at depth—decoupling them from closely following the DVM of zooplankton into shallower water where predation risk is higher (Benoit et al., 2010). Dense aggregations of adult cod that form in the demersal zone can physically displace smaller conspecifics into shallower water (Benoit et al., 2010; David et al., 2016; Farley et al., 2017). Thus, Arctic cod physiology and behavior may set

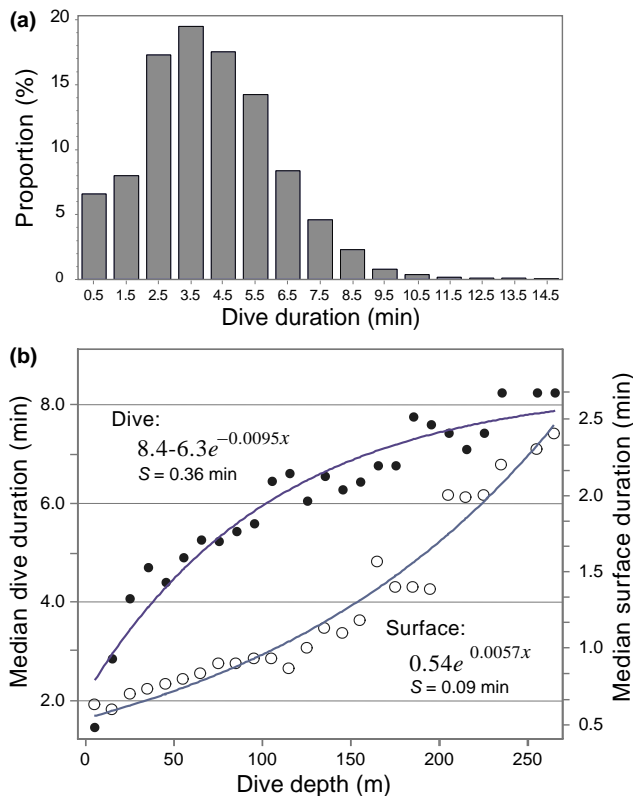


FIGURE 9 (a) Dive duration frequency distribution across 1-min duration bins. (b) Logarithmic regressions fitted to median dive duration (solid circles) and median surface duration (open circles) as a function of median dive depth in 10-m depth intervals (using only intervals with $n \geq 10$ dives). Standard error of the regression (S) represents the average distance (minutes) that the medians fall from the regression line. Analysis used the dive-behavior time series collected by SPLASH and CTD tags deployed in 2016 ($n = 10$), for dives ≤ 15 min in duration ($n = 81,916$)

up an energetic trade-off in which ringed seal forage resources are partitioned by prey body-size (i.e., benefits to seals) and prey depth (i.e., cost to seals). Repetitive diving to the bottom may thus reflect optimal foraging (Waddington & Holden, 1979) in which larger and more energy-rich cod are targeted (Bowen, Tully, Boness, Bulheier, & Marshall, 2002). This behavior would be consistent with an energy maximization strategy (Bergman, Fryxell, Gates, & Fortin, 2001; Santini & Chelazzi, 1996) that invests more energy into deeper or longer dives to achieve a higher net energetic intake rate than would be possible by foraging on more accessible but less energetically profitable prey. It may also partially explain the tendency for larger bodied seals to dive less frequently, but for longer durations (Crawford et al., 2018).

Repetitive diving occasionally occurred in the very deep waters of the Arctic Basin (Figure 6b). This behavior has been reported previously (Gjertz, Kovacs, Lydersen, & Wiig, 2000) and may be related to concentrations of primary productivity occurring in the upper water column during the late summer/early fall (Ardyna et al., 2013). Subsurface primary productivity is attractive to zooplankton and planktivorous fish (Crawford, Vagle, et al., 2012; Farley et al., 2017;

Greenstreet et al., 2006; Majewski et al., 2016), potentially creating foraging patches that also attract ringed seals (Scott et al., 2010). Relatively shallow repetitive-diving bouts over the deep-water Arctic Basin were occasionally punctuated by single dives to substantially greater depths (Figure 6a). Perhaps exploratory in nature (Simpkins, Kelly, & Wartzok, 2001), these intermittent deep dives are consistent with a strategy of searching alternative foraging patches to minimize lost foraging opportunities (Kohlmann & Risenhoover, 1998; Lima, 1985), which may be more profitable in habitats with lower prey densities, heterogeneously distributed prey, or when a foraging patch is nearing depletion (McNair, 1983). Our observation of ringed seals shifting their repetitive-diving behavior into deeper strata in the water column (Figure 6b) suggests that exploratory dives may have been profitable on occasion.

Temporal patterns of diving, resting at the surface, and hauling out (Figures 10 and 11) suggest that ringed seals modify their daily activities in response to ambient conditions and as an adjustment to the potentially high sensitivity of their prey to light (Berge et al., 2020). Repetitive diving to depths >25 m was more common during midday and became increasingly frequent at midday as day-length diminished in winter. Repetitive dives <25 m deep did not show a diel or seasonal pattern. Although ambient light rapidly attenuates with water depth (Naik, D'Sa, Gomes, Goés, & Mouw, 2013), pinniped vision is well adapted to low-light levels (Levenson & Schusterman, 1999). That ringed seals engaged in deeper foraging dives more often during midday, especially during the dark winter, suggests that visual hunting tactics may be important to foraging success (Hanke, Wieskotten, Marshall, & Dehnhardt, 2013).

Resting and haul-out were more prevalent behaviors at night (Figures 10 and 11). We found that during onset of the ice-covered season, seals hauled out more often during the darkest hours of the day (Figure 11), consistent with previously observed patterns of nocturnal haul-out behavior in ringed seals (Crawford et al., 2018; Härkönen et al., 2008; Kelly et al., 2010). Furthermore, diurnal patterns from the binned dive data reported by tags deployed in 2011 were consistent with the aforementioned patterns that ringed seals dove most often to depths near the seafloor and during midday (Figure 8).

The relative value of habitat and the profitability of behavioral strategies may vary over annual cycles of ringed seal life history. For example, beginning in late spring, ringed seals undergo their annual pelage molt; an important physiological event in which several epidermal layers and the fur are shed and regenerated. This process is facilitated by infusing the epidermis with blood—providing the nutrients, oxygen, and warmth needed for tissue regeneration—but unsustainable levels of heat conduction from molting seals occurs when they are immersed in frigid Arctic waters (Boily, 1995). The high metabolic demands of the molt (Feltz & Fay, 1966; Ryg, Smith, & Ørtriland, 1990) potentially set up a scenario in which ringed seals face energetic trade-offs between foraging and hauling out. While molting, ringed seals appear to modify their behavior to compensate for their heat loss by hauling out more—particularly during the warmer midday hours in May and June (Figure 11) (Kelly

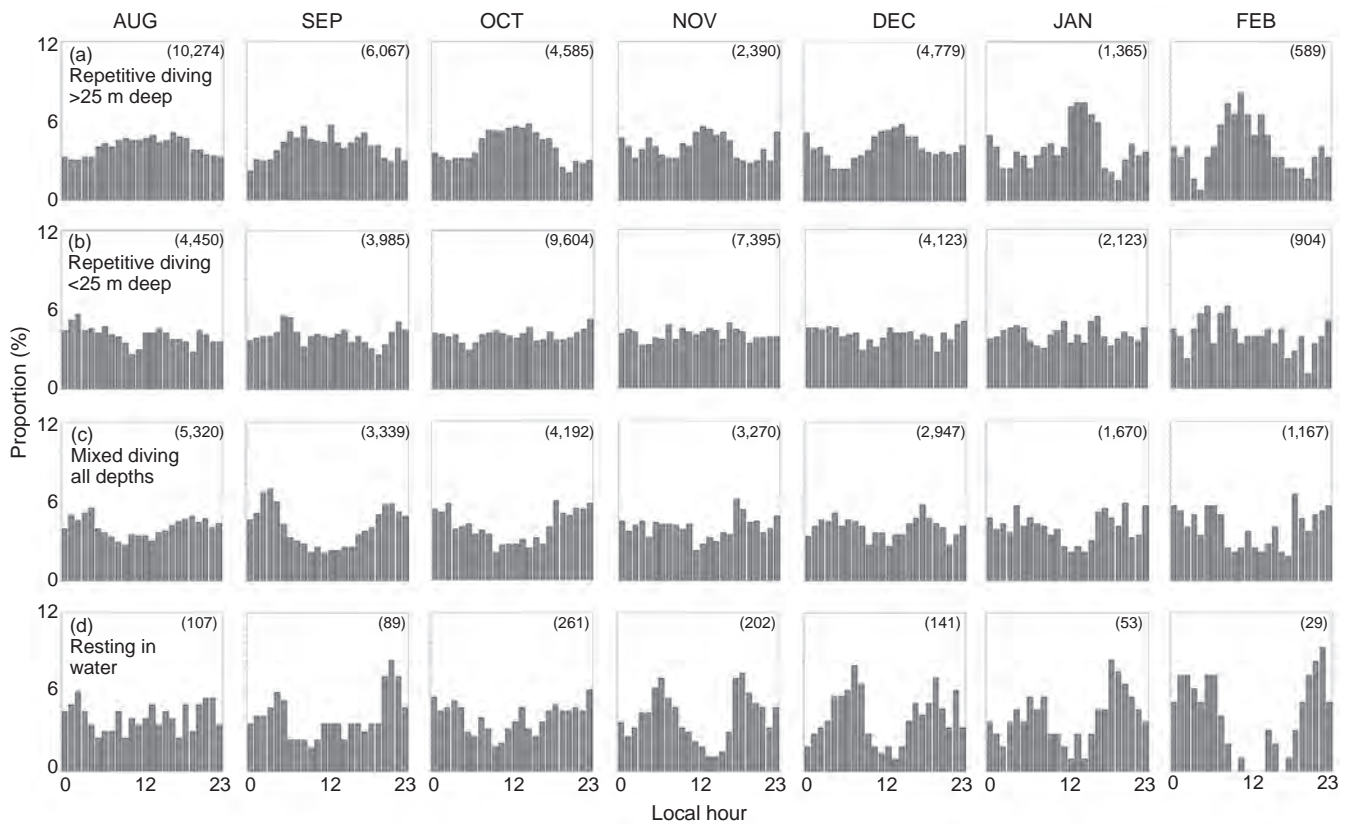


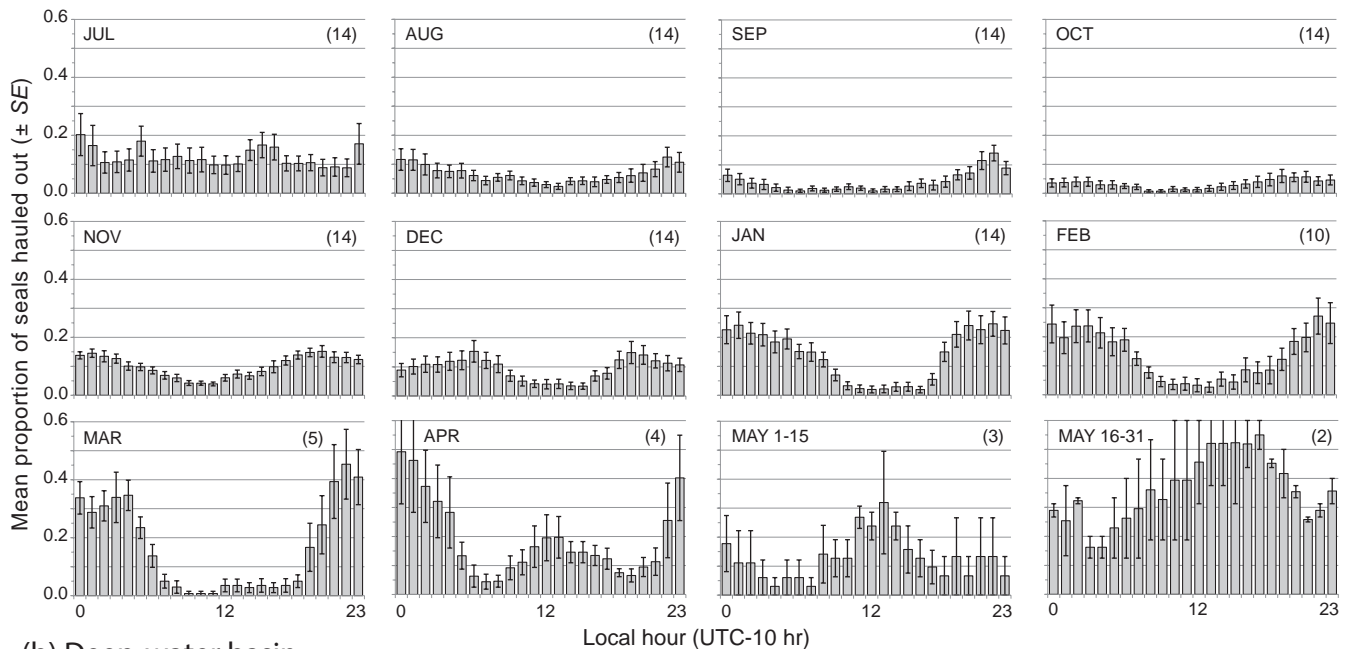
FIGURE 10 Proportion of dive-behavior classifications that occurred in each hour of the day (local, UTC-10 hr) in each of 7 months. Episodes of repetitive diving during which median dive depth was (a) >25 m or (b) ≤ 25 m deep; (c) episodes of diving to mixed depths, and (d) periods of resting at the surface for >10 min while also unassociated with haul out. Sample sizes (number of dives or resting periods) are shown in the upper right of each panel. Data are summarized from the dive-behavior time series collected from SPLASH tags deployed in 2016 ($n = 8$ ringed seals)

et al., 2010; Kelly & Quakenbush, 1990)—and foraging less (Young & Ferguson, 2013). Behavioral strategies that lower energetic losses while simultaneously accelerating completion of the molt should be favored (Berta, Sumich, & Kovacs, 2015; McLaren, 1958), as possibly evidenced in our data by long movements to distant sea ice followed by extended haul-out time in lieu of feeding. When considering the long-range movements that ringed seals made to the Arctic Basin in the mid-late summer, it seems plausible that the pursuit of available sea ice for the purpose of hauling out represents a behavioral strategy that weighs the relative quality of habitat against its value toward meeting a seal's physiological requirements.

The inclusion of the factor *CapYear*, which appeared in four of the five “best” models from our model sets (Table 3; Appendices E and F), was in response to two noteworthy events that occurred in 2011–2012. The first event was the emergence of a disease among ice seals that caused an abnormal molt, skin lesions, lethargy, mortality, and/or the unusual tendency to haul out on land (Herreman, *pers. obs.*). This disease was ultimately designated as an UME by NOAA. The second noteworthy event was the unusually early breakup of the sea ice in July of 2011, which was followed in March 2012 by the greatest sea-ice maximum and mean sea-ice concentrations recorded in the Bering Sea since start of the satellite record in 1979 (Fetterer et al., 2017). It is conceivable that annual variations in

sea-ice dynamics can drive physiologically mediated seal behavior. For example, given the energetic importance of hauling out during the molt, it is plausible that early sea-ice breakup can motivate energetically depleted seals to use terrestrial haul-outs out of necessity. Whether and to what extent the UME affected the decision for when/where to haul out cannot be ascertained given the data available. However, despite earlier sea-ice breakup dates in both 2015 and 2017, no terrestrial haul-out behavior was observed (A. Von Duyke, *pers. obs.*), suggesting that the UME may have affected ringed seal behavior. Though none of the seals tagged in 2011 displayed obvious symptoms of the UME at the time of capture, they were later determined to be both morphologically and behaviorally different from seals tagged in 2014 and 2016. Specifically, the 2011 seals were smaller (Table 1) and, after release, moved at higher rates, over longer durations, and ventured farther offshore (Figures 3c,d and 4; Appendix F). Ultimately, all five of the 2011 seals in this investigation made forays beyond the shelf-break into the deep-water Arctic Basin where they hauled out more than they foraged. The distinctive morphology, behavior, and spatial distribution of the seals tagged in 2011 do call attention to reports of two purported ringed seal ecotypes: (a) a smaller pelagic “pack-ice seal” and (b) a larger coastal “fast-ice seal” (Fedoseev, 1975; Finley, Miller, Davis, & Koski, 1983; Freuchen, 1935; Gorlova, Krylovich, Savinetsky, & Khasanov, 2012;

(a) Continental shelf



(b) Deep-water basin

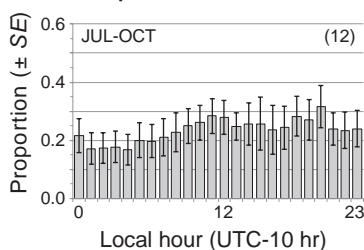


FIGURE 11 Monthly diurnal haul-out behavior shown as the mean proportion (\pm SE) of ringed seals hauled out during each local hour (UTC-10 hr) when seals were (a) over the continental shelf, and (b) during forays into the deep-water Arctic Basin. Monthly sample sizes (n seals) are shown in parentheses. May is split into two periods. Data obtained during deep-water forays (July–October) were pooled to bolster sample size

Model set	Response variable	Model
I	MOVEMENT RATE	<u>Season</u> + <u>CapYear</u> + <u>Season:CapYear</u>
II	DISTANCE TO MAINLAND	<u>CapYear</u>
III	DISTANCE TO ICE-EDGE	<u>Season</u> + <u>CapYear</u>
IV	ICE CONCENTRATION	AgeClass + CapYear
V	HAUL-OUT TIME	<u>Sex</u> + Season + <u>Sex:Season</u>

Note: Underlined variables are statistically significant ($\alpha = 0.05$). Full model sets generated by this procedure are presented in Appendix E.

TABLE 3 Top models explaining variance in movement rate, distance from the mainland, concentration of sea ice occupied, distance from sea-ice edge, and haul-out duration as a function of sex, age class, season, and capture year

McLaren, 1958). The different morphometric and behavioral characteristics of the seals tagged in 2011 were consistent with the notion of a smaller, more offshore pack-ice ecotype. Could annual sea-ice variability, natural life-cycles, and energetic perturbations brought on by disease have worked together to bring a population of seals into an area they do not normally occupy, thereby making them more available for capture? If these two purported ringed seal ecotypes exist, and occupy different niches, it is plausible that one ecotype may experience and/or respond differently to ecological change. It

is beyond the ability of our data to disentangle environmental variability from the possible existence and influence of ringed seal ecotypes. Nevertheless, our results are intriguing and highlight the need to better understand the population structure of ringed seals from regions that are difficult to access, as this may be important to ringed seal conservation and management, and to Arctic marine ecology.

Further implications of sea-ice dynamics—particularly reductions in sea-ice availability—may include energetic consequences due to the disruption of the relationships among access to sea ice

for haul-out, prey access, and seal physiology. Under ideal conditions, hauling out on sea ice in high-quality foraging habitat (i.e., continental shelf) could enable molting ringed seals to partially offset energetic costs accrued from reproduction, lactation, and molting (Ryg & Øritsland, 1991), particularly if they can profitably capture prey. However, earlier northward retreat of pack-ice (Comiso, Meier, & Gersten, 2017) may lead to overall reductions in habitat quality by shifting available sea-ice haul-outs to less productive off-shelf waters (i.e., Arctic Basin). Under such conditions, ringed seals in Alaska may have to choose to: (a) forage in more productive habitat while hauling out less (Hamilton, Kovacs, Ims, & Lydersen, 2018)—potentially incurring energetic costs associated with heat loss and/or an extended molt; (b) haul out on remnants of sea ice, even if located in lower-quality habitat—which may facilitate a faster molt, but come at the cost of fewer (i.e., lost) and/or less productive foraging opportunities; or (c) haul out on land (Lydersen, Vaquie-Garcia, Lydersen, Christensen, & Kovacs, 2017) near higher-quality foraging habitat—again facilitating the molt, but likely increasing predation risk. Several seals tagged in 2011 behaved in a manner consistent with the second option, though they did not venture off-shelf until mid-summer/early fall (Figure 5), which is well after the normal molt period. Though they exhibited some repetitive-diving behavior (i.e., foraging), most of their time was spent hauled out on the ice. Off-shelf forays in 2014 and 2016 were less frequent and occurred earlier in the summer (Figure 5). Currently, it is unknown whether a protracted or otherwise complicated molt (e.g., UME) could motivate seals to make late-summer forays to the retreating pack-ice in order to haul out. A more complete understanding of phocid molting physiology with respect to energetics may help clarify the drivers of this behavior, including the relative value of habitat over the course of a seal's annual life-cycle. The quality of a habitat (i.e., its value to an animal's fitness) is a function of local environmental conditions and eco-physiological constraints (Charnov, 1976; Lima, 1983), the interactions of which can shape habitat selection via the profitability of different behaviors. How this occurs may not be straightforward and, given their dynamic environment and the many possible scenarios encountered by ringed seals, is likely the net sum of numerous behavioral adjustments that optimize energy intake given the relative ratios of costs and benefits (Born et al., 2004; Ferguson & Higdon, 2006; Stephens & Krebs, 1986).

Based on their high abundance and wide distribution (Reeves, 1998), ringed seals are a very successful species, likely due to behavioral plasticity that has allowed them to exploit a variety of habitats throughout the circumpolar north. To date, ringed seals in the Bering and Chukchi seas have not exhibited declines in body condition, growth, or reproduction observed in other populations (Crawford et al., 2015). In the face of an accelerating trend toward earlier, more rapid, and/or more extensive summer sea-ice melt (Comiso et al., 2017), as well as recent dramatic losses of winter sea ice in the Bering Sea (Siddon & Zador, 2018), a more comprehensive understanding of the energetic consequences and behavioral trade-offs (Laidre et al., 2008) faced by ringed seals throughout their life-cycle is needed to help guide their conservation and management.

5 | CONCLUSIONS

This study adds to a growing body of knowledge about ringed seal movements and behaviors. Seals were captured in a region that had received little prior investigation and were instrumented with satellite transmitters capable of providing location, information about individual dives, and hourly haul-out status. Like other ringed seal tracking studies in the Beaufort and Chukchi seas, most of the seals we tagged near Utqiagvik moved into the southern Chukchi and Bering seas during winter. They occupied a diversity of habitats and spatial distributions, from close to shore and very localized, to far offshore and wide-ranging in the drifting sea ice. The ringed seals we captured in 2011, concurrent with a UME that affected all ice-seal species, were physically smaller than seals captured in other years and maintained a more pelagic distribution, raising speculation that the UME could have facilitated the tagging of a “pelagic” ringed seal ecotype that would not have otherwise been available for capture nearshore. Many ringed seals, especially those tagged in 2011, made forays into the deep Arctic Basin with an apparent intent to reach the pack-ice to haul out. Focused bouts of repetitive diving occurred over the continental shelf for >12 hr/day, usually to depths at or near the ocean floor. Hauling out tended to be progressively more nocturnal from winter to early spring; but abruptly switched in May to a pronounced daytime haul-out pattern with onset of the molt.

As a “threatened” species (Endangered Species Act [ESA]) (National Marine Fisheries Service, 2012), recovery criteria for ringed seals is drawn from the best available science about their habitat use and behavior; as well as knowledge about the dynamics of pinniped populations overall (Conn et al., 2014). Given the potential for increases in human/wildlife conflicts in the Arctic (Harsem et al., 2015; Smith & Stephenson, 2013), mitigation and recovery strategies for ringed seals will benefit from better information about their movements and behavior. Ongoing conservation efforts for polar bears—another ESA threatened species—will also benefit from an improved ecological understanding of ringed seals (Durner et al., 2009; Wilson, Horne, Rode, Regehr, & Durner, 2014). And, because the Arctic is a stochastic environment (Walsh, 2008) where rapid climate mediated change is already occurring (Post et al., 2013), continued research that fills gaps in poorly sampled regions will contribute to a more comprehensive understanding of the Arctic as an ecosystem, and therein the eco-physiological processes that are important to the conservation and management of ringed seals—a vulnerable species with high ecological and cultural value (Condon, Collings, & Wenzel, 1995; Huntington, Quakenbush, & Nelson, 2016).

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CONFLICT OF INTEREST

The authors declare no conflict of interest.

AUTHOR CONTRIBUTION

Andrew L. Von Duyke: Conceptualization (lead); Data curation (equal); Formal analysis (equal); Funding acquisition (lead); Investigation (lead); Methodology (equal); Project administration (lead); Resources (lead); Software (equal); Supervision (lead); Validation (equal); Visualization (equal); Writing-original draft (lead); Writing-review & editing (lead). **David C. Douglas:** Conceptualization (equal); Data curation (equal); Formal analysis (equal); Funding acquisition (supporting); Investigation (supporting); Methodology (equal); Project administration (supporting); Resources (supporting); Software (equal); Supervision (supporting); Validation (equal); Visualization (equal); Writing-original draft (supporting); Writing-review & editing (supporting). **Jason K. Herreman:** Conceptualization (supporting); Data curation (supporting); Formal analysis (supporting); Funding acquisition (equal); Investigation (equal); Methodology (supporting); Project administration (equal); Resources (supporting); Software (supporting); Supervision (equal); Validation (supporting); Visualization (supporting); Writing-original draft (supporting); Writing-review & editing (supporting). **Justin A. Crawford:** Conceptualization (equal); Data curation (equal); Formal analysis (supporting); Funding acquisition (supporting); Investigation (equal); Methodology (equal); Project administration (supporting); Resources (equal); Software (equal); Supervision (supporting); Validation (supporting); Visualization (supporting); Writing-original draft (supporting); Writing-review & editing (supporting).

DATA AVAILABILITY STATEMENT

The data set analyzed for this study is available from the Dryad Digital Repository <https://doi.org/10.5061/dryad.zpc866t65> (Von Duyke, Douglas, Herreman, & Crawford, 2020).

ORCID

Andrew L. Von Duyke  <https://orcid.org/0000-0002-7831-7388>

David C. Douglas  <https://orcid.org/0000-0003-0186-1104>

Justin A. Crawford  <https://orcid.org/0000-0002-6854-8756>

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SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section.

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**J. Olnes, J. Crawford, J. J. Citta,
M. L. Druckenmiller, A. L. Von Duyke &
L. Quakenbush**

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Movement, diving, and haul-out behaviors of juvenile bearded seals in the Bering, Chukchi and Beaufort seas, 2014–2018

J. Olnes¹ · J. Crawford¹ · J. J. Citta¹ · M. L. Druckenmiller² · A. L. Von Duyke³ · L. Quakenbush¹Received: 25 June 2019 / Revised: 5 March 2020 / Accepted: 25 June 2020
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Abstract

Bearded seals (*Erignathus barbatus*) are abundant in the Pacific Arctic and are an important subsistence resource for many Alaska Native communities. The Pacific Arctic is warming rapidly with substantial consequences predicted for ice-associated marine mammals, such as the bearded seal, which led to its 2012 listing as Threatened under the U.S. Endangered Species Act. We provide the most comprehensive description of juvenile bearded seal movement, diving, and haul-out behaviors for the Pacific Arctic, obtained from 24 seals tagged with satellite-linked data recorders along Alaska's coast from 2014 to 2018. Most seals (19 of 24) made north–south movements with the seasonal extent of sea ice, however, all three seals tagged north of Bering Strait made minimal north–south movements and two seals tagged in the Bering Sea moved north as sea ice advanced south. All seals primarily occupied shallow coastal waters and areas with intermediate-concentration pack ice or that were near the ice edge. Seals spent half their time near the sea floor. Hauling out occurred less in the winter and increased during spring and summer, coinciding with the annual molting period. When ice was at its minimum extent, seven seals frequently hauled out on land. Juvenile bearded seals made use of much of the continental shelf in the Bering, Chukchi and Beaufort Seas, and their use of a broad range of ice concentrations and willingness to haul out on land suggests some resilience to changing sea ice conditions. However, whether the behaviors we documented in juveniles are similar for adult bearded seals remains unclear.

Keywords Alaska · *Erignathus barbatus* · Pacific arctic · Sea ice · Satellite telemetry

Introduction

The Pacific Arctic is rapidly warming with significant consequences predicted for ice-associated marine mammals (Laidre et al. 2015). Bearded seals (*Erignathus barbatus*) are an ice-associated species with a circumpolar distribution. In the Pacific Arctic, they occupy the Bering, Chukchi, and

Beaufort (BCB) Seas, are ecologically important as benthic foragers, and are an important food source for both polar bears (*Ursus maritimus*, Stirling and Archibald 1977) and Alaska Native peoples. Alaska Natives, who harvest an estimated 6700 bearded seals annually (Nelson et al. 2019), are concerned about how changing ice conditions are affecting the annual movements of marine mammals and their availability for harvest (Huntington et al. 2016). Similar concerns linked to decreases in ice extent over the next century (Wang et al. 2018) have led to listing bearded seals as a threatened species (Cameron et al. 2010; NOAA 2012). To best anticipate how bearded seals may respond to less ice, and to make informed decisions regarding their management as a threatened species, it is important to understand their present movements and diving behavior in the BCB.

The distribution of bearded seals in the BCB is largely determined by bathymetry and sea ice. Because they are primarily benthic feeders, their distribution is constrained to shelf waters < 200 m deep (Burns 1981) and they are known to use most, if not all, of the continental shelf between

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✉ J. Olnes
justin.olnes@alaska.gov

¹ Alaska Department of Fish and Game Arctic Marine Mammal Program, 1300 College Rd., Fairbanks, AK 99701, USA

² National Snow and Ice Data Center, University of Colorado Boulder, Boulder, CO 80309, USA

³ Department of Wildlife Management, North Slope Borough, Utqiagvik, AK 99723, USA

Alaska and Russia (Muto et al. 2018; see Fig. 3 in Citta et al. 2018). Bearded seals use sea ice for important life history events; whelping, nursing, and molting all take place on sea ice, as well as resting between foraging bouts (Burns 1981; Kelly 1988). Consequently, bearded seals make north–south movements associated with the advance and retreat of sea ice over shelf waters throughout the year. Most bearded seals are thought to winter in seasonal pack ice in the Bering Sea, and in summer their distribution shifts northwards as sea ice retreats, into the northern Bering Sea and the Chukchi and Beaufort Seas (Kelly 1988; Melnikov 2017; Cameron et al. 2018; Breed et al. 2018; Citta et al. 2018). However, some bearded seals are present in the Chukchi and Beaufort Seas year-round, as confirmed by acoustic monitoring of their underwater vocalizations (MacIntyre et al. 2013).

Data on the distribution and behavior of bearded seals can be obtained using satellite telemetry (e.g., Boveng and Cameron 2013; Breed et al. 2018; Hamilton et al. 2018). Although researchers have developed methods for capturing juveniles (<2 years old), they have yet to develop methods to reliably capture adults in the BCB. Methods used to capture adults in Svalbard (Hamilton et al. 2018) typically do not work, possibly because bearded seals are hunted for subsistence within the BCB (unlike Svalbard) and are more wary of boats. Only three adult bearded seals have been captured and instrumented with satellite tags in the BCB region (Boveng and Cameron 2013, Alaska Department of Fish and Game *unpublished data*). Studies that focus on juveniles, however, are warranted because juvenile bearded seals may occupy different habitats than adults, as has been observed for ringed seals (*Phoca hispida*) (Crawford et al. 2012), they may establish fidelity to wintering locations that they continue to use as adults (Boveng and Cameron 2013), and because decreases in seasonal sea ice due to climate change may alter the distribution and behavior of bearded seals of all age classes.

Two recent studies reported the movement patterns of juvenile bearded seals in the Bering Sea (Breed et al. 2018; Cameron et al. 2018). Using data from seals tagged near Kotzebue, Alaska, in 2004–2006 (Cameron et al. 2018), along with additional seals tagged in 2009 (Breed et al. 2018), these studies found that juveniles exhibited a strong preference for the ice edge (10–15% ice concentration), which delineates the pack ice (> 15% concentration) from open water (<15%). This preference drives their north–south movements as the sea ice advances and retreats annually. Both studies concluded that this preference for the ice edge would cause juvenile bearded seal movements to shift northward over time as sea ice extent and duration decrease.

In addition to providing movement data, satellite tags can also provide seal diving and haul-out data. Although a number of studies examine dive behavior of bearded seals in Svalbard, Norway (e.g., Gjertz et al. 2000; Hamilton et al.

2018), little information on juvenile bearded seal dive and haul-out behaviors has been published for the BCB region. In a report, Boveng and Cameron (2013) provided haul-out information for two adult and five sub-adult bearded seals tagged near Kotzebue, Alaska, in the southern Chukchi Sea, 2009–2012. This report provided a summary of dive depths and durations and how haul-out behavior varied over season and time-of-day; however, it did not relate dive data to environmental covariates, such as ice concentration, distance from land, or bathymetry (Boveng and Cameron 2013).

In this study, we summarize the movement, diving, and haul-out behavior of 24 juvenile bearded seals tagged during 2014–2018. Our first objective was to describe patterns of movement and habitat use. We predicted that bearded seals would exhibit similar patterns of movement as described by Cameron et al. (2018) and Breed et al. (2018); making north–south movements in response to seasonal changes in sea ice extent. Our data, however, were collected from seals tagged at multiple locations in the BCB, rather than a single location (Kotzebue Sound, Chukchi Sea). We therefore expected that seals tagged from different regions would exhibit different movements and use different parts of the BCB. Our second objective was to describe diving and haul-out behaviors relative to habitat variables: water depth, distance from land, sea ice concentration and distance from the ice edge. We predicted that most dives would be to the sea floor, and that the proportion of time seals haul out would increase with increasing ice concentration and during the annual molt. By describing habitats associated with increased benthic diving and hauling out, we planned to identify habitats important for bearded seals. Given the scarcity of data on bearded seal movements and diving behaviors in the BCB, this analysis greatly improves our understanding of juvenile bearded seal biology.

Methods

Study region

We studied juvenile bearded seal movements and activity in the Bering, Chukchi and Beaufort Seas (BCB). Because bearded seals are benthic foragers, bearded seal habitat is thought to be limited to relatively shallow continental shelf waters, which are found in the northern Bering Sea, across the entire Chukchi Sea, and in a relatively narrow (< 200 km wide) strip along the Alaskan and Canadian coasts in the Beaufort Sea. Sea ice advances annually throughout the winter and spring months (December–April), covering the Chukchi and Beaufort Seas and, at its maximum extent, may extend to the shelf break in the Bering Sea. Through summer and fall (May–November), the sea ice retreats northward to

its minimum extent when shelf waters in the BCB are now typically ice-free.

Seal capture and tagging

Juvenile bearded seals were captured and tagged at six different locations along Alaska's northern and western coasts (Fig. 1, Table 1) in summer and fall (June–November), 2014–2018. Teams consisting of Alaska Department of Fish and Game (ADFG) biologists, North Slope Borough biologists, and Alaska Native subsistence hunters located seals along coastlines or rivers and captured them using monofilament entanglement nets, measuring 27.4 m by 3.7 m. Upon capture, seals were quickly brought to shore and removed from the nets. Curvilinear length, straight length, and axillary girth were all measured while seals were belly-down. We also determined seal sex visually and estimated age via claw annuli (McLaren 1958). Blood, a whisker, and skin samples were collected from most individuals to aid with biomonitoring efforts. Neither the capture nor the processing of seals required sedation. After tagging, seals were released on land and observed until they entered the water on their own.

Captured seals were fitted with one of two primary tags. SPLASH tags (Wildlife Computers, Redmond, WA, USA, $n=14$, Table 1) weighed 125 g and had user-programmable data products. CTD tags (Sea Mammal Research Unit, St. Andrews, Scotland, $n=8$) weighed 545 g and were pre-programmed by the Sea Mammal Research Unit. In addition, seals were also fitted with flipper-mounted SPOT tags (Wildlife Computers, $n=24$) that weighed 39 g.

SPLASH tags provided location data via the Argos satellite system, and diving and dry-time (surfacing or hauled out) information was transmitted in three formats. Dive data were transmitted as individual dive profiles as well as in the form of histograms that summarized dive information based on user-defined bins. Dive profiles provided information on individual dives that included the duration and maximum dive depth. To isolate dive behavior from wave action, tags were programmed such that dives were only recorded if a seal dove deeper than 2 m, then the duration of the dive was recorded as the time between surfacing events as indicated by the wet/dry switch on the tags. Dive histograms summarize dive duration, maximum dive depth, and time-at-depth. We programmed all SPLASH tags to summarize dive information in 6-h intervals (05:00–10:59, 11:00–16:59, 17:00–22:59, 23:00–04:59 AKST). For dive duration, each dive within a 6-h interval was tallied into one of 14 intervals that were defined by dive length: < 1 min, 1–2 min, 2–3 min, 3–4 min, 4–5 min, 5–6 min, 6–7 min, 7–8 min, 8–9 min, 9–10 min, 10–12 min, 12–14 min, 14–16 min, and > 16 min. For maximum dive depth, intervals were defined as < 2 m, 2–4 m, 4–10 m, 10–20 m, 20–36 m, 36–50 m, 50–76 m,

76–100 m, 100–126 m, 126–150 m, 150–176 m, 176–200 m, 200–250 m, and > 250 m. For time-at-depth, intervals were defined in the same way as maximum dive depth, but rather than tally dives, the proportion of the 6-h interval that a seal spent within a given depth range was provided. Dry-times were summarized in a different manner. Rather than summarizing data within 6-h intervals, the percent dry-time was recorded for each hour of the day. Each minute was defined as dry if the tag registered as dry for more than 30 s.

CTD tags also provided location (via Argos satellites), dive profile, and dry-time information. Dive duration and maximum depth were provided in each dive profile. Individual dives were determined by a 1.5 m depth threshold (dive starts and ends when seal goes below and above 1.5 m). Similarly, haul-out data with the duration of each individual haul-out were provided. CTD tags did not summarize dive or haul-out information over summary periods as did the SPLASH tags. As a result, data from CTD tags were only used for location estimates and summaries of individual dive durations and depths.

Flipper-mounted SPOT tags provided location data via the Argos satellite system and dry-time summaries in the form of percent dry-timelines. Dry-time data were summarized in the same way as for SPLASH tags. Because SPOT tags are mounted on the hind flipper, dry-time summaries isolate time spent hauled out from time spent at the surface, whereas dry-times from head-mounted SPLASH tags includes both time at the surface and time hauled out. We therefore relied on data from SPOT tags for all analyses related to haul-out behavior. Two of the twenty-four seals only received SPOT tags because they were molting (Table 1).

Diving and haul-out data

We summarized diving and haul-out data for juvenile bearded seals in the BCB by calculating mean and longest dive durations (min) and the mean and deepest dive depths (m) from seals with either SPLASH or CTD tags using individual dive profiles. Individual dive durations were considered up to 30 min in length. Only 12 of 39,252 (0.03%) raw dive records from the CTD tags and 677 of 97,415 (0.7%) raw dive records from SPLASH tags recorded dives longer than 30 min. Although it is possible seals may make longer dives, we consider this an appropriate limit to separate true dive durations from unrealistic dive records until more information regarding bearded seal diving capabilities become available.

For individuals with SPLASH tags, we summarized the proportion of time spent diving below 4 m, the dive rate (h^{-1}), the benthic dive rate, the proportion of dives that were benthic, and the proportion of time spent near the sea floor. SPLASH tags were programmed to summarize

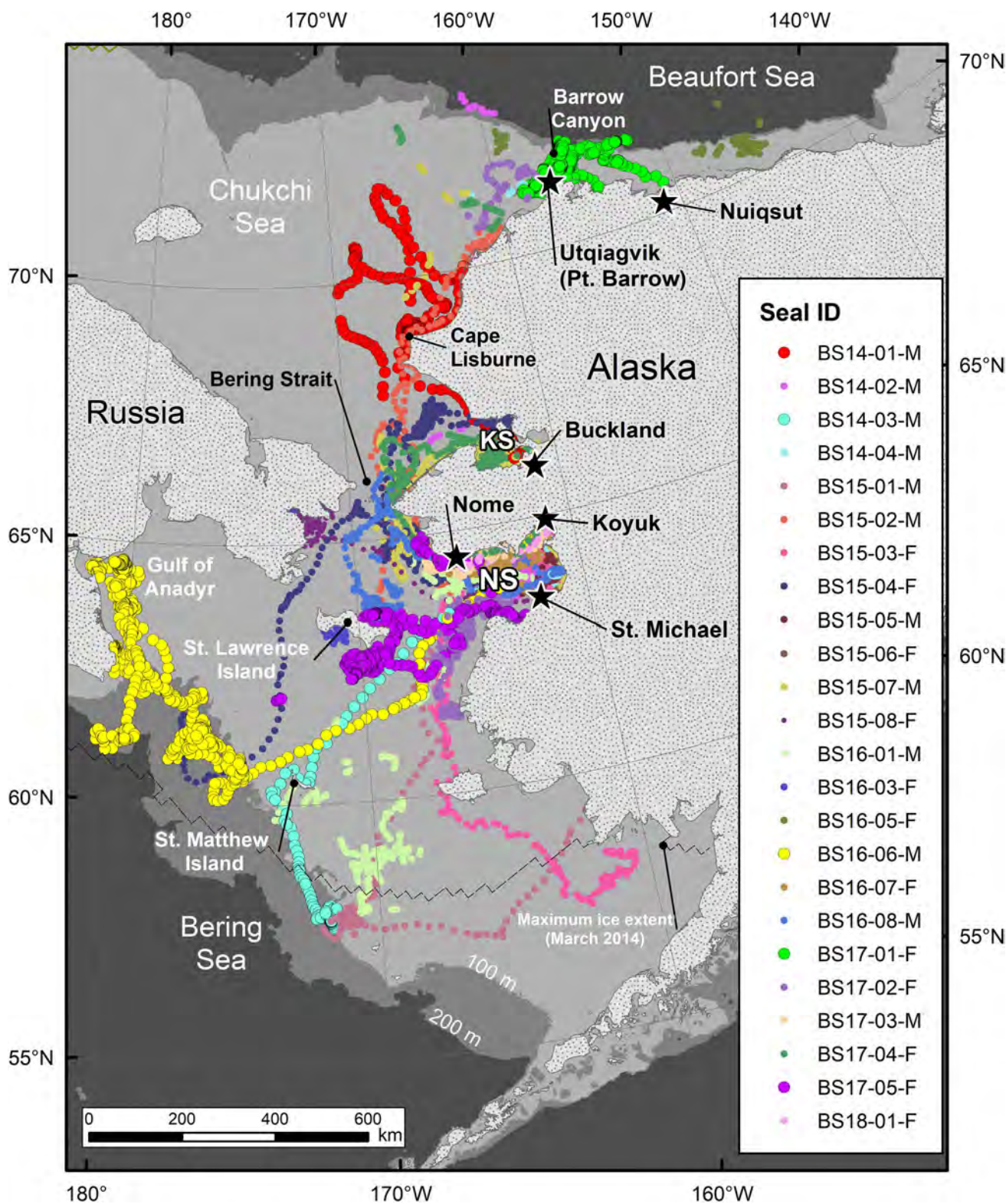


Fig. 1 Estimated locations for 24 juvenile bearded seals (*Erignathus barbatus*) tagged during 2014–2018. Larger circles denote seals discussed in the text. Black stars denote tagging locations and grey shading represents the continental shelf (waters <200 m deep). ‘KS’ and

‘NS’ are Kotzebue Sound and Norton Sound, respectively. Dashed line is the maximum sea ice extent that occurred during the study period (March 2014)

Table 1 Information on 24 bearded seals (*Erignathus barbatus*) tagged during 2014–2018 in the Beaufort, Chukchi, and Bering Seas

Year	Tagging location	Seal	Sex	Age	Length (cm)	Axillary girth (cm)	Tags	Start date	End date	Days with locations
2014	BKC*	BS14-01-M	Male	Pup	154/141	116	SPLASH/SPOT	6/18/2014	5/22/2015	206
2014	KKA	BS14-02-M	Male	Pup	161/158	121	SPLASH/SPOT	9/27/2014	12/29/2015	165
2014	KKA	BS14-03-M	Male	Pup	164/147	125	SPLASH/SPOT	9/28/2014	11/13/2014	45
2014	KKA	BS14-04-M	Male	Pup	142/137	104	SPLASH/SPOT	10/2/2014	7/18/2015	130
2015	KKA	BS15-01-M	Male	Pup	149/135	112	SPLASH/SPOT	8/19/2015	10/9/2015	52
2015	KKA	BS15-02-M	Male	Pup	148/141	114	SPLASH/SPOT	8/21/2015	10/20/2015	61
2015	KKA	BS15-03-F	Female	Pup	148/134	112.5	SPLASH/SPOT	8/23/2015	1/19/2016	145
2015	KKA	BS15-04-F	Female	Pup	145/139	110	SPLASH/SPOT	8/20/2015	1/2/2016	136
2015	SMK	BS15-05-M	Male	Pup	144/130	110	SPLASH/SPOT	8/22/2015	8/31/2015	10
2015	SMK	BS15-06-F	Female	Yearling	161/142	114	SPLASH/SPOT	8/23/2015	8/28/2015	6
2015	SMK	BS15-07-M	Male	Yearling	151/137	109	SPLASH/SPOT	8/23/2015	9/10/2016	205
2015	SMK	BS15-08-F	Female	Yearling	159/147	108	SPLASH/SPOT	8/27/2015	12/11/2015	89
2016	SMK	BS16-01-M	Male	Pup	147/143	106	SPLASH/SPOT	7/4/2016	6/16/2017	94
2016	SMK	BS16-03-F	Female	Pup	139/130	120	SPOT	10/6/2016	3/20/2017	19
2016	BRW	BS16-05-F	Female	Yearling	162/145	127	SPOT	8/19/2016	7/16/2017	41
2016	KKA	BS16-06-M	Male	Pup	150/138	119	CTD/SPOT	9/22/2016	6/6/2017	192
2016	KKA	BS16-07-F	Female	Pup	138/132	114	SPLASH/SPOT	9/25/2016	6/7/2017	225
2016	NOM	BS16-08-M	Male	Yearling	155/146	126	CTD/SPOT	11/11/2016	3/11/2017	92
2017	NUI	BS17-01-F	Female	Yearling	170/155	121	CTD/SPOT	8/11/2017	9/9/2018	253
2017	KKA	BS17-02-F	Female	Pup	152/135	107	CTD/SPOT	10/4/2017	7/11/2018	162
2017	KKA	BS17-03-M	Male	Pup	161.5/153	113.5	CTD/SPOT	9/22/2017	6/29/2018	64
2017	KKA	BS17-04-F	Female	Yearling	158/144.5	120	CTD/SPOT	9/24/2017	7/25/2018	180
2017	NOM	BS17-05-F	Female	Pup	/		CTD/SPOT	10/20/2017	5/22/2018	140
2018	KKA	BS18-01-F	Female	Yearling	152/142	105	CTD/SPOT	10/3/2018	10/15/2018	13

'Pups' are thought to have been born the year of capture and 'yearlings' are thought to have been born the year prior, based on visible claw annuli. Lengths are belly-down curvilinear length and belly-down straight length (separated by "/"). 'Start Date' and 'End Date' refer to the beginning and end of satellite tag transmission

*BKC Buckland, KKA Koyuk, SMK St. Michael, BRW Utqiagvik (Barrow), NOM Nome, NUI Nuiqsut

this information over every 6-h period represented by an associated location estimate. We explored methods for summarizing this data over 6-h periods using data from CTD tags, however, we found results were dependent on the total duration of time captured by the CTD tags (surface time + dive time) within a 6-h period. Because few records existed where an entire 6-h interval was captured by the CTD tags, we limited our dive summary analysis to SPLASH tag data only. We defined diving as going below 4 m as a conservative threshold to differentiate foraging dives from shallower subsurface movements associated with travel or time at the surface. The proportion of time diving below 4 m was derived from time-at-depth histograms. Histograms that recorded seals were below 4 m for more than 90% of the time ($n=37$) were removed as this was considered unlikely. Dive rates were derived from maximum dive depth histograms, where all dives below 4 m for each 6-h interval were summed and then divided by six to obtain an hourly rate. We defined the benthic dive rate as the number of dives per hour where the seal dove

to the sea floor. We calculated the number of benthic dives from the maximum-dive-depth histograms. Because each 6-h histogram summary has an associated location estimate (see below), we associated maximum dive depths to the depth of the bottom at that location. Water depth was derived using a 1-km digital elevation model produced by the Alaska Ocean Observing System (AOOS; Danielson et al. 2008). We considered dives within the depth bin that included the depth of the bottom at that location as benthic (McClintock et al. 2017). For example, if the water depth at the bottom for a given location was 19 m, then dives in the dive depth bin 10–20 m were considered benthic, but dives in the depth bin 4–10 m were not. The number of benthic dives were summed and then divided by six to obtain an hourly rate. We calculated the proportion of dives that were benthic by dividing the benthic dive rate by the dive rate. The proportion of time spent near the sea floor was calculated using time-at-depth histograms. We used the proportion of time each seal spent within depth bins that corresponded to the water depth at the bottom,

or deeper, for each location as estimates of the proportion of time spent near the sea floor.

We also summarized the proportion of time hauled out from the SPOT flipper tags. These data summarize the proportion of each hour of the day a seal spent hauled out. To obtain a single value, we summed the proportion of each hour hauled out for each hour within a given 6-h interval and divided by six.

Location data processing

SPLASH tags provide summary histograms of dive data at 6-h intervals. To associate dive summaries with habitat covariates at the location where dive data were summarized, we estimated seal locations at the midpoints in time represented by the dive histograms (2:00, 8:00, 14:00, 20:00 AKST) using a correlated random walk process (CRW, package: *crawl*, Johnson et al. 2008) in R statistical software 3.5.1 (R Core Team 2018). Location data generated by the Argos system have an associated error that is used to assign each location to a quality class. Locations in classes 3, 2, or 1 have associated error calculated by the Argos system; error for locations in quality classes 0, A, or B were estimated by the CRW model. Prior to running the CRW model, it was necessary to filter the raw location data ($n = 56,767$) to improve model fitting (Johnson et al. 2008). Locations assigned to class Z are least reliable and were removed. We further removed unlikely locations determined by a Speed-Distance-Angle (SDA) filter (package: *argosfilter*, Frietas et al. 2008) in R. We used default angular settings as described in Frietas et al. (2008) and a velocity threshold of 2.5 m s^{-1} , based on prior analyses of ringed seal movements in the BCB (Crawford et al. 2018). The SDA filter removed 3988 locations. We then manually removed 1712 locations that fell on land prior to running the CRW model. We used the global, self-consistent, hierarchical, high-resolution shoreline database to determine whether points fell on land or not (Wessel and Smith 1996). The CRW output ($n = 21,618$) was further filtered to retain only 6-h location estimates that were within 24-h of a raw location estimate, and ultimately generated a total of 11,329 location estimates to be used for analyses.

Statistical analysis

All statistical analyses were performed in R statistical software version 3.5.1 (R Core Team 2018). In all models, individual seal and tag year were nested random effects.

We explored patterns of movement and habitat use by comparing changes in latitude, water depth (log-transformed), distance from land (log-transformed), ice concentration and the distance from the ice edge used by seals across months. Daily ice data were obtained from the

National Snow and Ice Data Center (NSIDC) and consisted of remotely sensed, passive microwave data that assigned ice concentration to a spatial grid with a cell resolution of $25 \times 25 \text{ km}$ (years 2014–2017 data source ID: NSIDC-0051, year 2018 data source ID: NSIDC-0081, <https://nsidc.org/>). We defined the pack ice as having $> 15\%$ ice concentration, the ice edge as having 15% ice concentration, and open water as having $< 15\%$ ice concentration. We used linear mixed effects models for each response variable with month as the explanatory variable and accounted for temporal autocorrelation via a first-order autoregressive correlation structure (package: 'nlme', Pinheiro et al. 2019). For modeling monthly changes in latitude, we included an interaction term that grouped seals by the sea in which they were tagged (i.e., Bering, Chukchi or Beaufort). Seals tended to occupy either sparse ice near the ice edge or more concentrated pack ice away from the ice edge in a bimodal pattern of ice concentration use across months (Online Resource 1). We therefore also calculated the monthly mean ice concentration used by seals south of the ice edge in open water and north of the ice edge in pack ice. By doing so, we observed how seals occupied two ranges of ice concentration (low and high) and how our sample of seals shifted from primarily occupying one range or another across months. Statistical significance was determined using type III Wald Chi-square tests (X^2) for mixed effects models with an alpha value of 0.05 (package: 'car', Fox and Weisberg 2019). Significant models were used to estimate population-level means and 95% confidence intervals. We then calculated the marginal R-Squared (R_m^2), which estimates the amount of variation explained by the fixed effects for mixed effects models (package: 'MuMIn', Nakagawa and Schielzeth 2013). These analyses were performed using our final dataset of location estimates.

We also explored how dive and haul-out data varied with habitat variables. This analysis also used mixed effects models and only included data derived from SPLASH and SPOT tags because these tags provided summary information for the entire 6-h durations represented by each location estimate. We specifically modeled how the proportion of time diving ($n = 1831$ 6-h location estimates), the dive rate ($n = 1843$), the proportion of time spent at the sea floor ($n = 1831$), and proportion of time hauled out ($n = 1963$) varied with distance from land, water depth, ice concentration, a squared ice concentration term and distance from the ice edge. To accomplish this, we built 17 candidate models for each response variable that included combinations of our four main habitat variables, as well as categorical season and ice variables and their interactions with our habitat variables. Our seasonal categories were fall (September–November), winter (December–January), spring (February–May) and summer (June–August). For dive variables, we omitted the 'spring' category because of insufficient data. Our categorical ice variable was a binary 'ice'/'no ice' variable

where the cut-off value was 15% ice concentration (the ice edge). For these models, we used an autoregressive-moving average (ARMA) correlation structure to account for temporal autocorrelation. All explanatory variables were scaled to have a mean of zero and standard deviation of 1 to allow for direct comparison of effect sizes and improve model fitting. Final model selection was determined using Akaike's Information Criterion (AIC); we chose the single most parsimonious model for inference, even when top models differed by less than 2. We additionally modeled the proportion of time hauled out by season, time of day and their interaction because haul-out behavior is partly driven by the annual molt, which occurs in the spring and summer months. As a result, haul-out behavior may be driven more by time of year than by habitat variables, and by time of day because warmer skin temperatures (warmed by solar radiation) may facilitate molting (Feltz and Fay 1966).

Results

Capture, tagging, and body measurements

During 2014–2018, 24 (11 female and 13 male) juvenile bearded seals were captured and instrumented with tags that transmitted for 6–459 days (mean \pm S.D.: 209 ± 136 days, Table 1). These tags provided location data for an average of 114 ± 75 days ($68 \pm 29\%$ of days) (Table 1). All seals were captured during the ice-free periods of summer and fall. Curvilinear length (152 ± 8 cm), standard length (141 ± 7 cm), and axillary girth (115 ± 7 cm) varied minimally across individuals (Table 1).

Patterns of movement

Movements of juvenile bearded seals were highly variable (Fig. 1). For example, one male (BS14-01-M) tagged in June 2014 near Buckland in Kotzebue Sound, traveled north in the Chukchi Sea and spent all of August near Cape Lisburne, Alaska. This male then returned to Kotzebue Sound and spent the entire 2014/2015 winter there. Another male (BS14-03-M), tagged in late September 2014 near Koyuk, traveled south soon after capture, directly to St. Matthew Island in the Bering Sea. This male continued southeast to the 100 m isobath where it remained until transmissions ended in mid-November. These movements occurred entirely in open water, well-ahead of the advancing sea ice. A male (BS16-06-M), tagged in September 2016 near Koyuk, traversed the Bering Sea soon after being tagged and spent all winter and spring along the western edge of the Gulf of Anadyr, Russia. A female (BS17-01-F), tagged in August 2017 near Nuiqsut, traveled west to Barrow Canyon, north of Utqiagvik, and spent 11 months in this vicinity. Another

female (BS17-05-F), tagged in late October 2017 near Nome, spent all winter just south of St. Lawrence Island. These five examples highlight the diversity of movements of juvenile bearded seals; some seals remained near shore or close to where they were tagged, whereas others traversed the BCB region spending time far from land.

Despite significant variation in movement among individuals, there was a strong latitudinal pattern in juvenile seal movements across months (Fig. 2, $X^2_{11} = 74.15$, $p < 0.001$) that varied by tagging region (Fig. 2, $X^2_{24} = 863.49$, $p < 0.001$), with these two factors explaining 55% of the pattern in latitudinal movements ($R^2_m = 0.55$). Seals tagged in the Bering Sea ($n = 21$) made broad latitudinal movements across months. During January through May, these seals used areas well south of Bering Strait (65.75° N). By June, most seals started moving north into or near the Chukchi Sea and then gradually moved south back to the Bering Sea during September and October. The one seal tagged in the Chukchi Sea (BS14-01-M, described above) exhibited an intermediate pattern in latitudinal movements; after spending some of the open water period in the northern Chukchi Sea ($70\text{--}71^\circ$ N) in September, it primarily occupied latitudes around $66\text{--}67^\circ$ N from late September 2014 to May 2015. Seals tagged in the Beaufort Sea ($n = 2$) stayed above 70° N throughout the year, moving south only slightly ($< 1^\circ$ N) during November and December.

With respect to habitat variables, mean distances from land and mean water depths at seal locations varied minimally across months (Fig. 3a, b). Although statistically significant differences were found across months ($X^2_{11} = 75.73$, $p < 0.001$), these differences explained only 3% of the

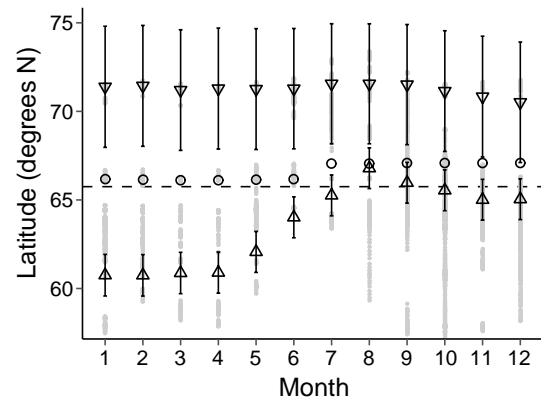


Fig. 2 Mean latitudinal distribution of juvenile bearded seals (*Erigonathus barbatus*) by month ($\pm 95\%$ CI), 2014–2018. Mean latitudes are shown by sea in which seals were tagged (Beaufort: triangles pointed down ($n = 2$), Chukchi: open circles ($n = 1$), and Bering: triangles pointed up ($n = 21$)). Dashed line at 65.75° N represents the Bering Strait boundary between the Bering and Chukchi Seas. Grey dots are raw data. Confidence intervals (95%) for the one seal tagged in the Chukchi Sea are omitted for visual clarity

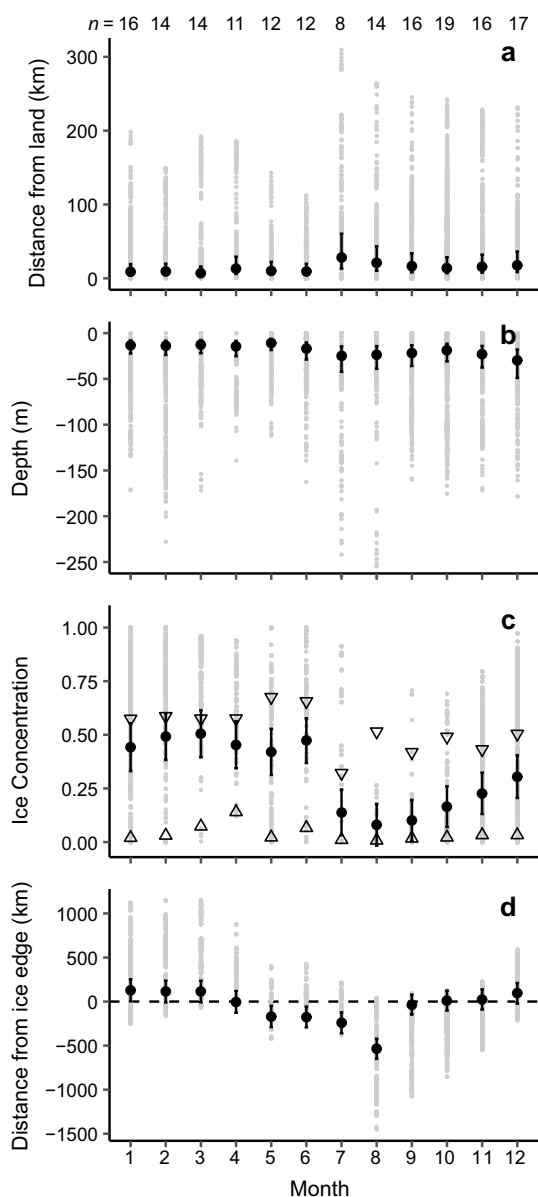


Fig. 3 Patterns in habitat variables (mean \pm 95% CI) by month for juvenile bearded seals (*Erignathus barbatus*): **a** distance from land, **b** water depth, **c** ice concentration and **d** distance from the ice edge. For (c), mean monthly ice concentration occupied by seals north of the ice edge (defined as 15% ice concentration) are represented by triangles pointed down, seals south of the ice edge are represented by triangles pointed up. Black circles are the mean for all seals. In the distance from ice edge plot (d), values < 0 represent locations south of the ice edge in open water, and values > 0 represent locations north of the ice edge in the pack ice. For all plots, grey dots are raw data, and the number of seals represented in each month (n) is provided at the top of the figure

variation in distance from land ($R^2_m = 0.03$). Seals primarily stayed within 30 km of land, rarely moved more than 100 km from land, and moved farther from land in the summer and fall (July–December) than in the winter and spring (Fig. 3a). Similarly, seals were primarily located in waters 10–35 m

deep, but within this small range statistically significant differences were found among months (Fig. 3b, $X^2_{11} = 77.75$, $p < 0.001$), explaining 5% of the variation in water depths used ($R^2_m = 0.05$). Seals occupied slightly deeper waters in the summer and fall (~16 to 30 m) than in late winter and spring (~10 to 14 m).

As expected, ice concentrations used by seals differed across months (Fig. 3c, $X^2_{11} = 346.31$, $p < 0.001$, $R^2_m = 0.22$). Although the mean ice concentrations occupied by all seals from January to June were between 42 and 50% ice coverage, the actual distribution of seals was bimodal across these months, as seals occupied either pack ice or low ice concentrations at the ice edge (Online resource 1), except in March and April when most seals were in pack ice. In pack ice north of the ice edge, seals primarily used areas with 57–67% ice concentration and, when south of the ice edge, used areas with 2–14% ice concentration. During July, one seal remained in the Bering Sea in open water, three seals moved north with the ice and remained in areas of 0–23% ice concentration, while two other seals remained in pack ice in the Beaufort Sea, in ice concentrations > 80%. During August, seals mainly occupied areas with < 25% ice concentration, though one seal remained in ~50% ice. As sea ice advanced south during September–December, more seals occupied areas with higher ice concentrations. The distance and location of seals relative to the ice edge differed across months (Fig. 3d, $X^2_{11} = 1444.41$, $p < 0.001$, $R^2_m = 0.21$). During the winter and early spring (December–April), seals were mainly at the ice edge or north of it in the pack ice. During the summer (June–August), seals were mainly found south of the ice edge in open water as the ice retreated, and their distance from the ice edge increased despite the seals traveling north. During September–November, as the ice began to advance south, seals were primarily south of, but within 200 km, of the ice edge.

Diving and haul-out behavior

Seals spent most of their time diving below 4 m (mean proportion of time diving (\pm S.D.): 0.62 ± 0.29 , Table 2). Most dives were < 10 min (mean dive duration: 4.39 ± 2.63 min), however, many seals dove for periods up to 30 min. Mean dive rate was 7.22 ± 4.58 dives h^{-1} and, of these, $85 \pm 3\%$ were benthic dives. Bearded seals spent half of their time near the sea floor (mean proportion of time near sea floor: 0.50 ± 0.30). Seals dove to the bottom at depths greater than 100 m, and two seals that traveled beyond the continental shelf dove deeper than 200 m; seal BS17-01-F dove to 471 m in Barrow Canyon, north of Utqiagvik. When not diving, seals were primarily hauled out (mean proportion of time hauled out: 0.33 ± 0.39).

Some patterns in dive behavior were influenced by ice concentration. For dive rate (dives below 4 m h^{-1}), the

Table 2 Summary of diving and haul-out behavior (mean \pm S.D.) for each juvenile bearded seal (*Erignathus barbatus*) in this study

Seal	Tag	Dives	Dive duration (min)	Dive depth (m) (Water depth (m))	Proportion time diving > 4 m	Dive rate (h ⁻¹)
BS14-01-M	SPLASH	5994	5.76 \pm 4.57	14 \pm 9 (16 \pm 10)	0.69 \pm 0.23	4.44 \pm 10.26
BS14-02-M	SPLASH	8543	4.93 \pm 2.95	16 \pm 5 (24 \pm 50)	0.59 \pm 0.28	8.10 \pm 13.97
BS14-03-M	SPLASH	–	–	– (74 \pm 39)	0.67 \pm 0.22	7.42 \pm 2.50
BS14-04-M	SPLASH	2668	6.01 \pm 3.88	4 \pm 4 (7 \pm 13)	0.12 \pm 0.26	1.87 \pm 14.74
BS15-01-M	SPLASH	2766	5.01 \pm 1.86	60 \pm 37 (65 \pm 29)	0.62 \pm 0.24	10.24 \pm 20.53
BS15-02-M	SPLASH	7720	3.48 \pm 1.48	20 \pm 14 (22 \pm 14)	0.61 \pm 0.26	12.23 \pm 19.58
BS15-03-F	SPLASH	6782	4.84 \pm 2.56	19 \pm 15 (21 \pm 10)	0.62 \pm 0.28	7.97 \pm 10.19
BS15-04-F	SPLASH	16,176	4.61 \pm 2.03	27 \pm 17 (34 \pm 24)	0.65 \pm 0.26	9.45 \pm 11.56
BS15-05-M	SPLASH	1135	2.51 \pm 2.21	7 \pm 5 (11 \pm 5)	0.60 \pm 0.20	30.74 \pm 63.17
BS15-06-F	SPLASH	1040	2.84 \pm 2.12	5 \pm 3 (8 \pm 6)	0.30 \pm 0.34	20.40 \pm 51.64
BS15-07-M	SPLASH	18,740	3.56 \pm 2.28	16 \pm 12 (18 \pm 13)	0.69 \pm 0.23	11.92 \pm 13.30
BS15-08-F	SPLASH	11,195	3.65 \pm 2.41	19 \pm 16 (24 \pm 18)	0.72 \pm 0.23	10.62 \pm 15.75
BS16-01-M	SPLASH	1151	5.25 \pm 4.72	13 \pm 9 (43 \pm 24)	0.68 \pm 0.29	10.36 \pm 30.77
BS16-03-F	SPOT	–	–	–	–	–
BS16-05-F	SPOT	–	–	–	–	–
BS16-06-M	CTD	4492	5.56 \pm 2.24	59 \pm 43 (76 \pm 45)	–	–
BS16-07-F	SPLASH	12,823	4.18 \pm 2.14	19 \pm 8 (16 \pm 4)	0.71 \pm 0.25	9.52 \pm 12.38
BS16-08-M	CTD	3146	4.30 \pm 2.40	22 \pm 17 (33 \pm 11)	–	–
BS17-01-F	CTD	12,845	5.51 \pm 2.63	49 \pm 39 (74 \pm 64)	–	–
BS17-02-F	CTD	3148	3.98 \pm 1.47	15 \pm 6 (22 \pm 14)	–	–
BS17-03-M	CTD	1606	3.31 \pm 1.79	16 \pm 10 (12 \pm 10)	–	–
BS17-04-F	CTD	10,133	4.19 \pm 2.10	11 \pm 5 (14 \pm 10)	–	–
BS17-05-F	CTD	2026	4.29 \pm 1.83	27 \pm 14 (32 \pm 12)	–	–
BS18-01-F	CTD	1091	3.49 \pm 1.75	11 \pm 7 (16 \pm 4)	–	–
All Seals		135,220	4.39 \pm 2.63	23 \pm 24 (33 \pm 0)	0.62 \pm 0.29	7.22 \pm 4.58

Seal	Deepest dive (m) (Deepest depth (m))	Longest dive (min)	Benthic dive rate	Proportion dives benthic	Proportion time at bottom	Proportion time hauled out
BS14-01-M	58 (62)	29.35	3.30 \pm 3.26	0.79 \pm 0.34	0.51 \pm 0.30	0.20 \pm 0.26
BS14-02-M	28 (545)	29.85	7.34 \pm 4.27	0.92 \pm 0.20	0.53 \pm 0.29	0.31 \pm 0.36
BS14-03-M	100–126 (112)	–	6.18 \pm 2.79	0.78 \pm 0.30	0.41 \pm 0.22	–
BS14-04-M	19 (87)	29.68	1.53 \pm 2.98	0.83 \pm 0.37	0.09 \pm 0.23	0.29 \pm 0.35
BS15-01-M	114 (111)	17.68	7.48 \pm 2.77	0.89 \pm 0.22	0.42 \pm 0.21	–
BS15-02-M	62 (61)	14.18	8.29 \pm 4.49	0.79 \pm 0.31	0.45 \pm 0.27	–
BS15-03-F	58 (50)	27.85	7.39 \pm 2.86	0.91 \pm 0.21	0.59 \pm 0.27	0.38 \pm 0.40
BS15-04-F	149 (145)	25.68	7.71 \pm 3.35	0.86 \pm 0.26	0.52 \pm 0.27	0.15 \pm 0.28
BS15-05-M	21 (18)	13.35	5.64 \pm 3.55	0.68 \pm 0.41	0.47 \pm 0.26	–
BS15-06-F	16 (19)	17.85	7.03 \pm 3.29	0.82 \pm 0.40	0.39 \pm 0.32	0.84 \pm 0.25
BS15-07-M	70 (58)	29.01	8.91 \pm 4.06	0.83 \pm 0.25	0.57 \pm 0.26	0.14 \pm 0.29
BS15-08-F	70 (63)	19.51	6.36 \pm 4.54	0.66 \pm 0.42	0.55 \pm 0.32	0.08 \pm 0.16
BS16-01-M	31 (105)	29.85	5.57 \pm 3.45	0.93 \pm 0.24	0.60 \pm 0.31	0.24 \pm 0.34
BS16-03-F	–	–	–	–	–	0.22 \pm 0.34
BS16-05-F	–	–	–	–	–	0.32 \pm 0.35
BS16-06-M	219 (290)	12.91	–	–	–	0.39 \pm 0.38
BS16-07-F	34 (27)	29.98	8.04 \pm 3.85	0.89 \pm 0.18	0.58 \pm 0.27	0.36 \pm 0.40
BS16-08-M	61 (59)	14.25	–	–	–	0.20 \pm 0.28
BS17-01-F	471 (1122)	25.91	–	–	–	0.19 \pm 0.33
BS17-02-F	77 (112)	7.75	–	–	–	0.31 \pm 0.38
BS17-03-M	33 (32)	8.92	–	–	–	0.18 \pm 0.28

Table 2 (continued)

Seal	Deepest dive (m) (Deepest depth (m))	Longest dive (min)	Benthic dive rate	Proportion dives benthic	Proportion time at bottom	Proportion time hauled out
BS17-04-F	37 (61)	24.58	–	–	–	0.24 ± 0.33
BS17-05-F	45 (60)	8.92	–	–	–	0.35 ± 0.40
BS18-01-F	45 (27)	9.58	–	–	–	0.46 ± 0.44
All Seals	–	–	6.61 ± 4.04	0.85 ± 0.28	0.50 ± 0.30	0.33 ± 0.39

intercept-only (null) model performed best (Online Resource 2). The proportion of time diving was best explained by our model that only included ice concentration ($X^2_1 = 31.21$, $p < 0.001$). Seals dove at a relatively constant rate throughout the year and across ice concentrations, but the proportion of time diving declined slightly as ice concentration increased ($\beta = -0.06$). For every 10% increase in ice concentration the proportion of time spent diving decreased by ~2.4%, however, this relationship only explained 6% of the variation in the proportion of time spent diving ($R^2_m = 0.06$). The proportion of time spent near the sea floor was also negatively associated with ice concentration (Fig. 4a, $\beta = -0.08$, $X^2_1 = 9.36$, $p = 0.002$), water depth (Fig. 4b, $\beta = -0.10$, $X^2_1 = 29.52$, $p < 0.001$), and its interaction with our categorical ice variable (Fig. 4b, $\beta = -0.11$, $X^2_1 = 4.21$, $p = 0.04$). Time spent near the sea floor was positively associated with distance from land (Fig. 4c, $\beta = 0.06$, $X^2_1 = 15.68$, $p < 0.001$), except during summer when distance from land had a negligible effect on time spent near the bottom (Fig. 4c, $\beta = -0.06$, $X^2_1 = 7.13$, $p = 0.03$). Combined, however, these variables explained only 10% of the variation in time spent near the sea floor ($R^2_m = 0.10$).

The proportion of time hauled out was best explained by our full model, however, only season ($X^2_3 = 178.90$,

$p < 0.001$) and distance from the ice edge, when in pack ice ($X^2_1 = 5.11$, $p = 0.02$), were significant. In pack ice, seals spent a lower proportion of time hauled out the farther out they were from the ice edge and were not likely to haul-out at all when more than 500 km from the ice edge ($\beta = -0.19$). We also modeled the proportion of time hauled out by time of day ($X^2_3 = 44.61$, $p < 0.001$) and its interaction with season ($X^2_{12} = 206.70$, $p < 0.001$), which explained 17% of the variation in time hauled out ($R^2_m = 0.17$). Seals hauled out more during the spring (mean proportion of time: 0.38) and summer (0.57) than during fall (0.26) and winter (0.17) (Fig. 5). In spring, seals were more likely to haul out during the day (11:00–23:00 AKST), than at night. In summer and fall, seals were equally likely to haul out during all times of day. During the summer and early fall (July–October) when ice was at its minimum extent, seals that remained near the ice edge hauled out on ice ($n = 6$) whereas seals that were south of the ice in the Bering Strait region hauled out on land ($n = 7$, Fig. 6). Two seals used both strategies in separate years. Seal BS14-02-M hauled out on land near Koyuk in October of 2014 but hauled out on ice along the shelf break in the Chukchi Sea in August of 2015. Similarly, seal BS15-07-M hauled out on land near

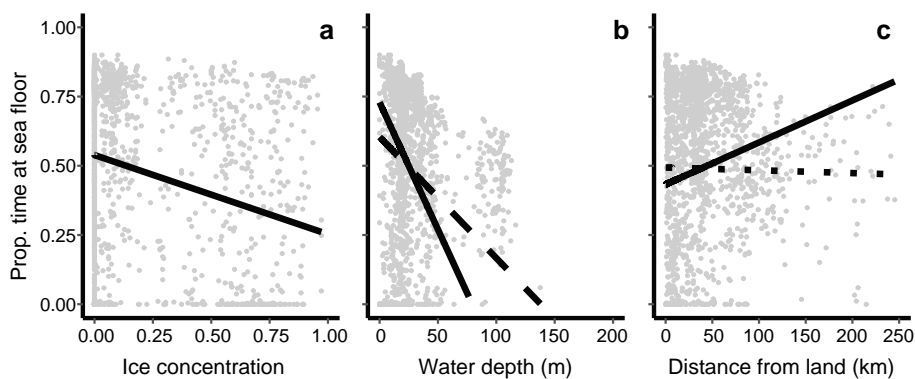


Fig. 4 The proportion of time juvenile bearded seals (*Erignathus barbatus*) spent near the sea floor relative to the habitat variables **a** ice concentration, **b** water depth, and **c** distance from land. For ice concentration (**a**), solid line is the relationship during summer, fall and winter. For water depth (**b**), solid line depicts the proportion of time at the sea floor when seals are north of the ice edge in the pack ice

(defined as 15% ice concentration), and dashed line depicts this relationship when seals are south of the ice edge in open water. For distance from land (**c**), the dotted line is the relationship during summer months (June–August) and the solid line is the relationship for fall and winter (September–January). For all plots, grey dots are raw data

Fig. 5 The proportion of time (mean \pm 95% CI) juvenile bearded seals (*Erignathus barbatus*) spent hauled out by season and hour of day

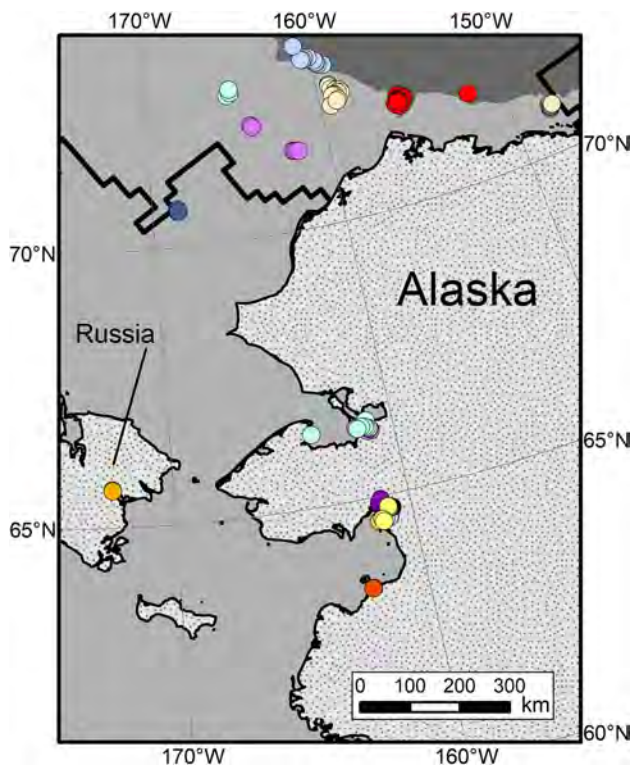
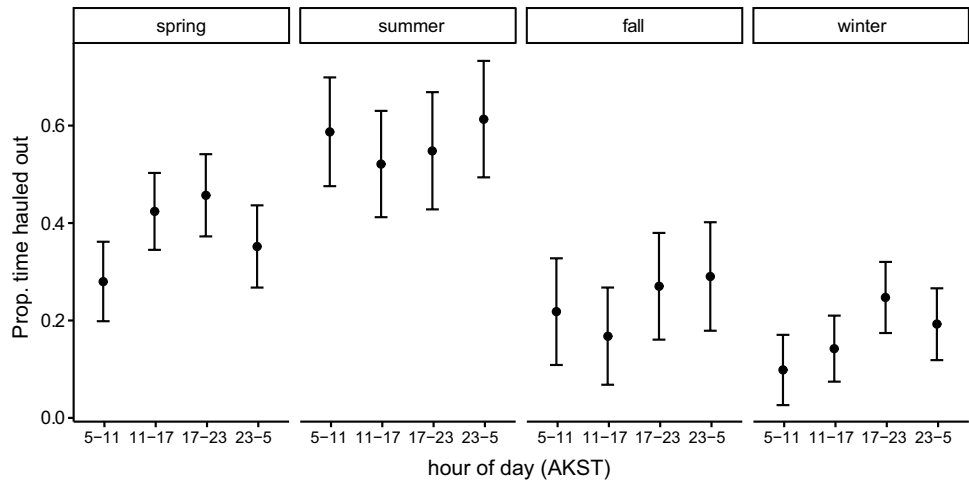


Fig. 6 Haul-out locations on sea ice or land for juvenile bearded seals (*Erignathus barbatus*) that hauled out more than 20% of the time for a given 6-h interval during the period of minimum sea ice extent (July–October, colored circles represent individual seals). Grey shading represents shelf break (waters < 200 m deep) and line is maximum monthly ice extent for July–October over the shelf during the study period (2014–2018) which occurred in July 2014

Buckland in October of 2015 but hauled out on ice in the Chukchi Sea in July–September of 2016.

Discussion

This description of 24 juvenile bearded seal movements, diving, and haul-out behaviors derived from satellite tag data for the BCB region is the most comprehensive to date. Juvenile bearded seals in this study spent most of their time diving to the sea floor in shallow water (< 35 m deep) within 30 km of land. Seals tagged in the Bering Sea made north–south movements that allowed them to stay within the seasonally advancing and retreating sea ice for at least half the year (December–June), primarily occupying areas near the ice edge. Seals tagged in the Chukchi and Beaufort seas did not make extensive north–south movements, but by remaining at higher latitudes, also occupied areas with sea ice for much of the year, though deeper in the pack ice and away from the ice edge.

The patterns of sea ice use by bearded seals that we found were broadly consistent with prior studies. Cameron et al. (2018) found juvenile bearded seals preferred intermediate to high ice concentrations (peaking around 80%), and the ice edge (0–25% ice concentration), with a stronger preference for the ice edge. We also found that seals tended to occupy low concentration ice near the ice edge or areas with intermediate to high ice concentrations in the pack ice (Fig. 3c). Breed et al. (2018) found that juvenile bearded seals north of the ice edge select mean ice concentrations of 50–60% and we found that juveniles north of the ice edge used ice with 57–67% concentration.

However, not every seal in our study made north–south movements in response to seasonally changing ice extent, as emphasized in other studies (Burns 1981; Cameron et al. 2018; Breed et al. 2018). Five of the 24 (21%) seals in our study did not move north and south with advancing and retreating ice. These differences were most pronounced for seals tagged in the Beaufort and Chukchi Seas, although less so for the seal tagged in the Chukchi Sea. The two seals tagged in the Beaufort Sea stayed in that region for the entire

duration of tag transmission and seal BS17-01-F spent two winters (2017/2018 and 2018/2019) near Barrow Canyon. Although the seal tagged in the Chukchi Sea near Buckland in Kotzebue Sound (BS14-01-M) made some north–south movements, it did not move south in the Bering Sea with the advancing ice edge, but rather, wintered in Kotzebue Sound, far north of the ice edge. In Cameron et al. (2018), 17 of 26 seals (65%) tagged in Kotzebue Sound moved south to winter in the Bering Sea, suggesting that seals found in Kotzebue Sound in the summer may winter in the Bering or Chukchi Seas. Two of 21 seals that we tagged in the Bering Sea did not move southwards with advancing sea ice. Despite being tagged in the Bering Sea (Norton Sound) in September 2017, seal BS17-04-F spent the 2017/2018 winter just north of Bering Strait in the southern Chukchi Sea. The other, seal BS18-01-F tagged near Koyuk in Norton Sound moved north as the ice advanced south during fall to winter in the central Chukchi Sea. In late summer, six seals did not travel farther north than the Bering Strait region, even as the ice retreated north to the shelf break. During this time, juveniles that did follow the retreating ice north hauled out on the ice, while seals farther south hauled out on land (Fig. 6).

The proportion of time seals spent hauled out increased steadily from March to August (even though the number of seals monitored in each month declined). This trend almost certainly represents increased haul-out durations due to molting, which is thought to peak in May and June (Burns 1981). Nearly all primary tags stopped transmitting by May, either because seals had begun shedding their hair, causing the tags to fall off, or the tag depleted its battery and was no longer able to communicate with satellites. That seals continued to haul out frequently in the summer months may indicate an extended molting process (Cameron et al. 2010), or that seals haul out more during summer for other reasons.

Although bearded seals primarily occupied coastal areas, many individuals moved far from shore into the central Bering and Chukchi Seas. These seals may have been traveling to productive offshore foraging locations, as indicated by the positive relationship between time spent at the sea floor and distance from land during fall and winter (Fig. 4c). Areas around St. Matthew Island, the 100 m isobath in the Bering Sea (used by five seals in this study, and three seals in Cameron et al. (2018)), and the eastern-central Chukchi Sea (used by five seals in this study) may be areas far from shore that provide good foraging (Antonelis et al. 1994; Springer et al. 1996; Schonberg et al. 2014; Citta et al. 2018).

We found that foraging was primarily benthic year-round. Dives generally lasted less than 10 min and averaged ~4.5 min (Table 2). Bearded seals near Svalbard, Norway, dove to similar depths for similar durations even though they occupied narrower shelf and glacially fed fjord habitats. Seals in both regions primarily dove to depths of

40 m or less, with maximum dive depths reached by juveniles from both regions being notably similar (471 m in the BCB versus 480 m in Svalbard) (Gjertz et al. 2000). Near Svalbard, recently weaned seals tended to dive for durations less than 10 min, with most dives 5–10 min long (Gjertz et al. 2000), and adults dove for similar durations (Hamilton et al. 2018). Interestingly, many seals in our study dove for periods greater than 25 min (records from both SPLASH and CTD tags), whereas recently weaned seals in Svalbard did not dive more than 15 min (Gjertz et al. 2000), and the maximum dive duration among adults was 24 min (Hamilton et al. 2018). Our data suggests that bearded seals can dive for up to 30 min or more, however, some dive duration records were unrealistically long (hours–days) for SPLASH tags and we had no way to distinguish false records from accurate ones. We suspect that using a wet/dry threshold to determine the end of a dive was the cause of the problem for SPLASH tags and that tags breaking the surface would sometimes not detect ‘dry’ conditions, thereby aggregating multiple dives into a single dive. However, CTD tags, which end individual dive records once the seal goes above 1.5 m, produced maximum dive durations of 39 min, suggesting that use of a depth threshold (rather than a wet/dry sensor) reduces the risk of dives being aggregated and should be standard practice in the future. A study of dive physiology for Weddell seals (*Leptonychotes weddellii*) found a similar distribution of dive durations (mode of 4.5 min, most dives less than 20 min), however, several seals made longer dives up to 82 min (Castellini et al. 1992). Future studies may find bearded seals, especially adult bearded seals, to be capable of longer duration dives.

Because few adults have been instrumented with satellite tags in the BCB, it is difficult to know how these results for juveniles relate to the behavior of older bearded seals. In a study of five sub-adult (including one juvenile) and two adult bearded seals tagged in the BCB region, all individuals primarily stayed within 50 km of the coast (Boveng and Cameron 2013), similar to the juveniles in our study. In the same study, seals rarely hauled out in winter; instead, the probability of hauling out increased until late March or April when tags fell off, coinciding with the molt (Boveng and Cameron 2013). Our results support a similar start to the molting period for juveniles that may extend later into the summer. As seals reach sexual maturity, males occupy breeding territories during winter and spring (Van Parijs and Clark 2006). This age-related behavior, along with increased knowledge of suitable foraging areas, may influence differences in adult versus juvenile behavior, such as increased site fidelity and reduced long-distance movements (Gjertz et al. 2000; Van Parijs and Clark 2006). Additionally, we documented that juveniles haul out on land ($n=7$). This behavior has also recently been documented for one adult in the BCB (ADFG unpublished data), although it has been

observed for adults in Russia (Kelly 1988) and Svalbard, Norway (see discussions in Merkel et al. (2013) and Kovacs et al. (2019)) and is well known to Alaska Native hunters (Gryba et al. *in prep*).

Our results suggest that juvenile bearded seals appear to be generalists in terms of the habitat that they use, traversing great distances over a wide range of latitudes, occupying a variety of ice concentrations throughout the year, and hauling out on both land and sea ice. Documenting their broad use of the region is attributable to capturing and tagging seals in multiple locations throughout their range in Alaska. As has been suggested for bearded seals in Svalbard (Hamilton et al. 2018), the ability to exploit a variety of habitats should benefit seals by increasing their resilience to climate related changes in the BCB region. Whether adult bearded seals exhibit similar behaviors, however, is unknown. For now, live-capturing adults continues to be a challenge that limits the inferences that can be made about bearded seal biology in the BCB region. Beyond the need to instrument adults with satellite tags, efforts to tag and monitor juvenile bearded seals should continue as a means of detecting and characterizing long-term changes in behavior that may occur in a rapidly changing Arctic.

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Movements and Habitat Use of Pacific Arctic Seals and Whales via Satellite Telemetry and Ocean Sensing

**Lori Quakenbush
John Citta
Stephen Okkonen**

**ONR Code 322 Marine Mammals and Biology
6.1 Peer Review**

23 April 2019



OBJECTIVES

To relate oceanographic variables to habitat use of Arctic seals and whales

- deploy satellite tags capable of collecting CTD information
- work with subsistence hunters and local governments
- provide location and CTD data to ONR in real-time
- build predictive models that can assess the role of changing ocean conditions on marine mammal distribution



Timeline

- Grant then awarded to ADFG in September 2016; abbreviated field season in 2016
- Full field seasons in 2017 and 2018
- We are beginning data analysis during a one-year, no-cost extension ending May 2020



TECHNICAL APPROACH



TECHNICAL APPROACH



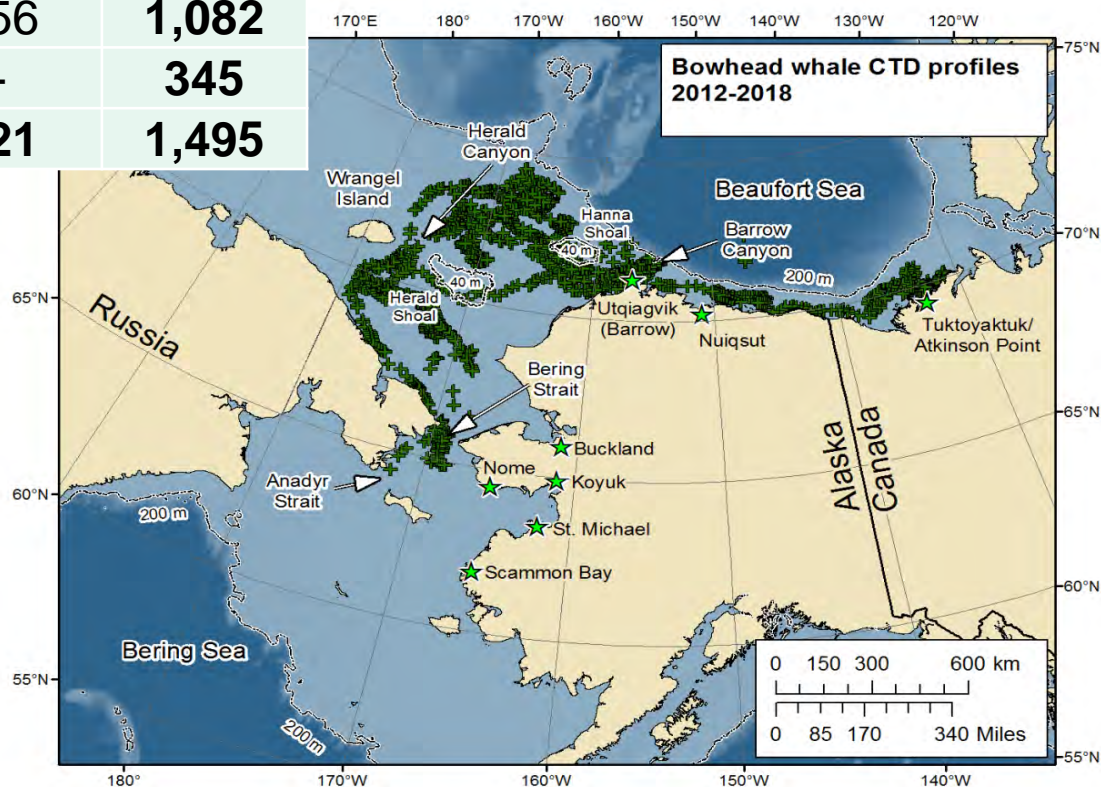
ACCOMPLISHMENTS

Bowhead whale CTD profiles

Sea	Summer	Winter	Total
Bering Sea	3	65	68
Chukchi Sea	826	256	1,082
Beaufort Sea	345	-	345
Total	1,174	321	1,495

Summer: June-November

Winter: December-May



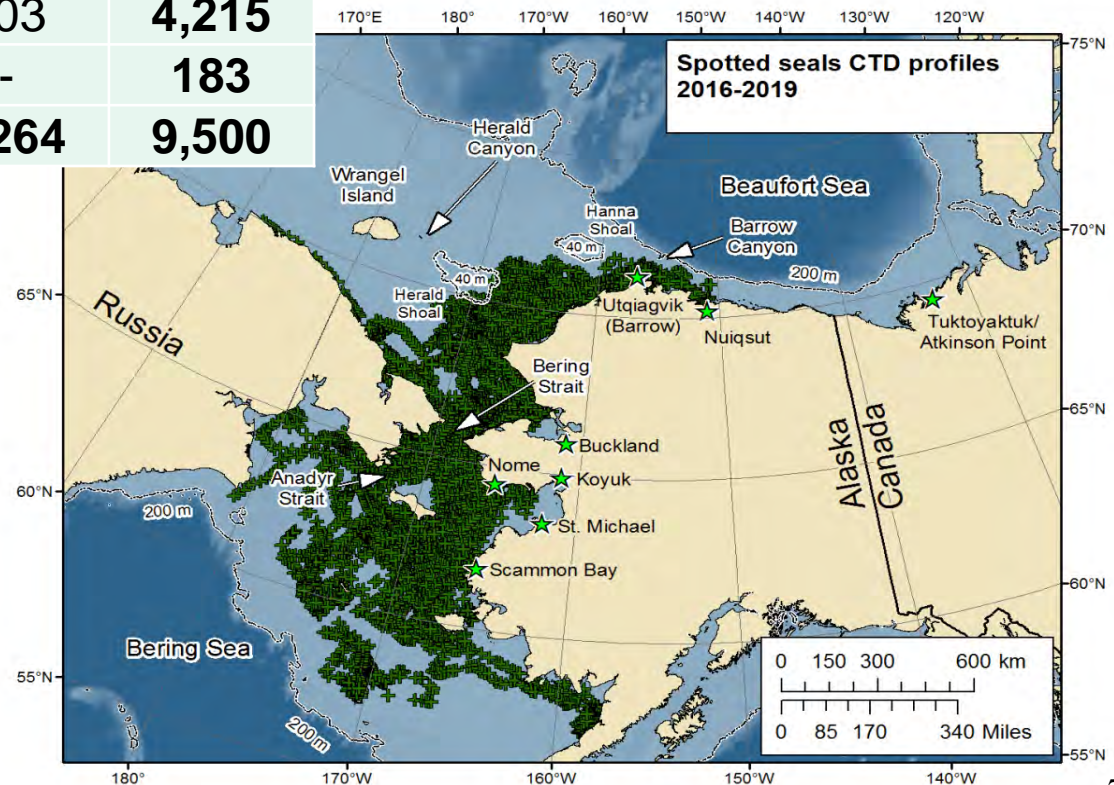
ACCOMPLISHMENTS

Spotted seal CTD profiles

Sea	Summer	Winter	Total
Bering Sea	1,241	3,861	5,102
Chukchi Sea	3,812	403	4,215
Beaufort Sea	183	-	183
Total	5,236	4,264	9,500

Summer: June-November

Winter: December-May



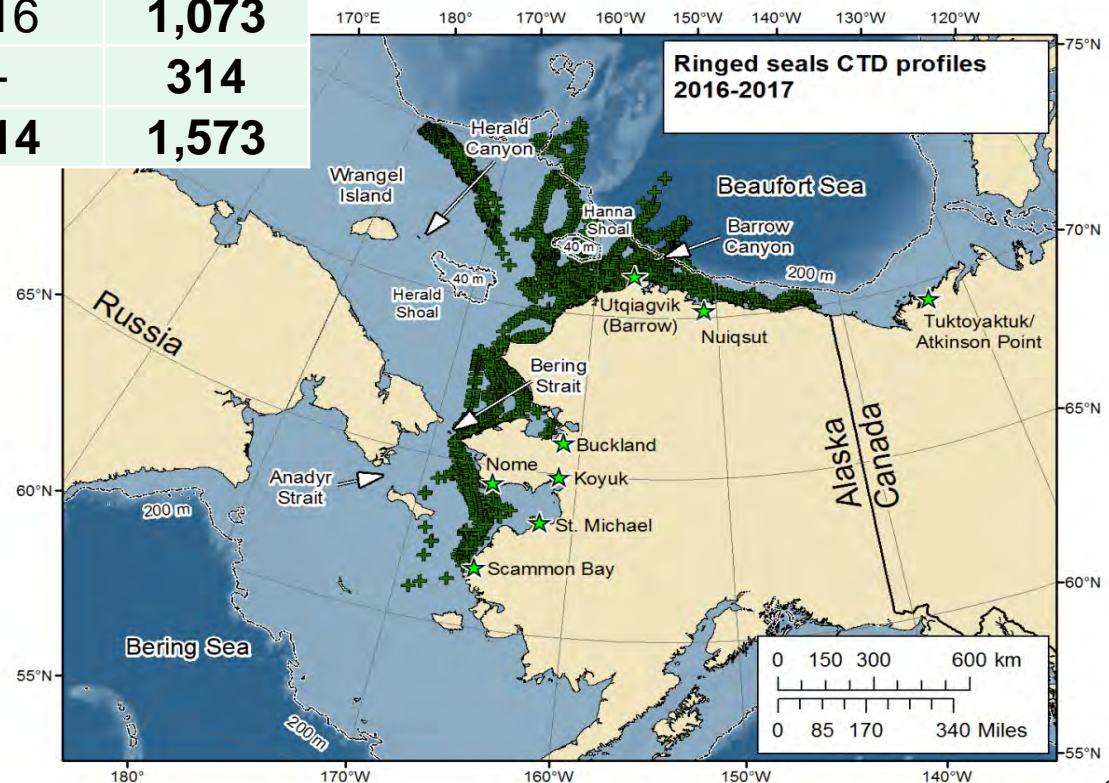
ACCOMPLISHMENTS

Ringed seal CTD profiles

Sea	Summer	Winter	Total
Bering Sea	76	110	186
Chukchi Sea	957	116	1,073
Beaufort Sea	314	-	314
Total	1,347	314	1,573

Summer: June-November

Winter: December-May



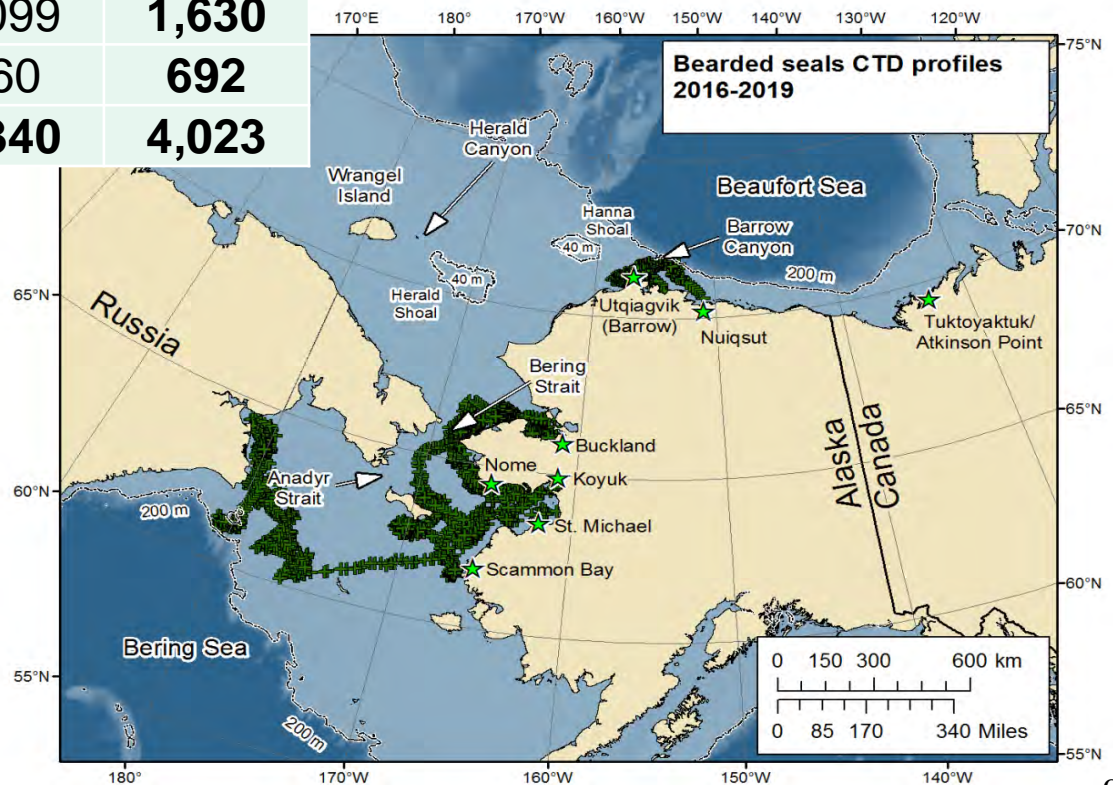
ACCOMPLISHMENTS

Bearded seal CTD profiles

Sea	Summer	Winter	Total
Bering Sea	620	1,081	1,701
Chukchi Sea	531	1,099	1,630
Beaufort Sea	532	160	692
Total	1,683	2,340	4,023

Summer: June-November

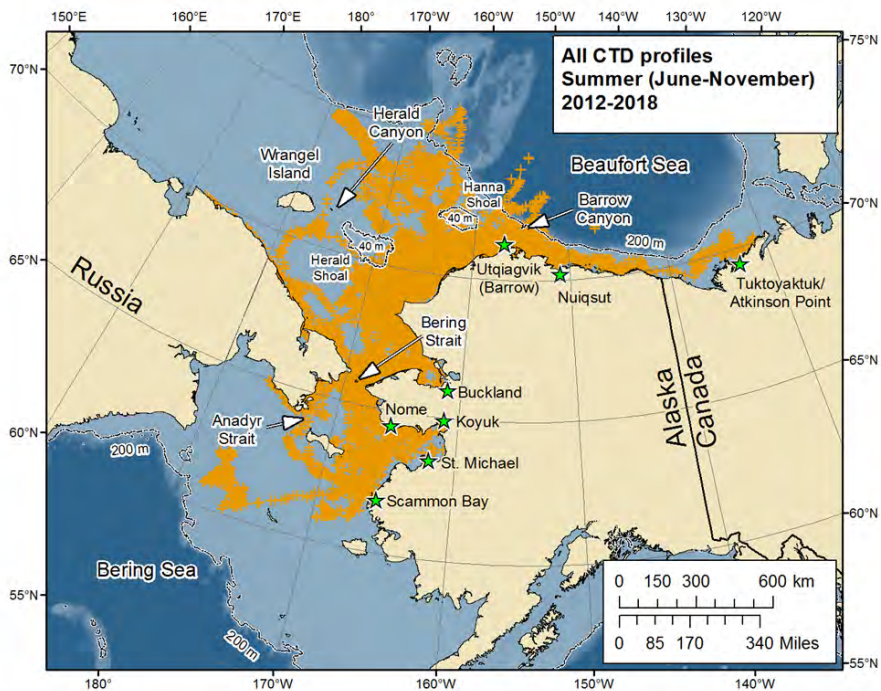
Winter: December-May



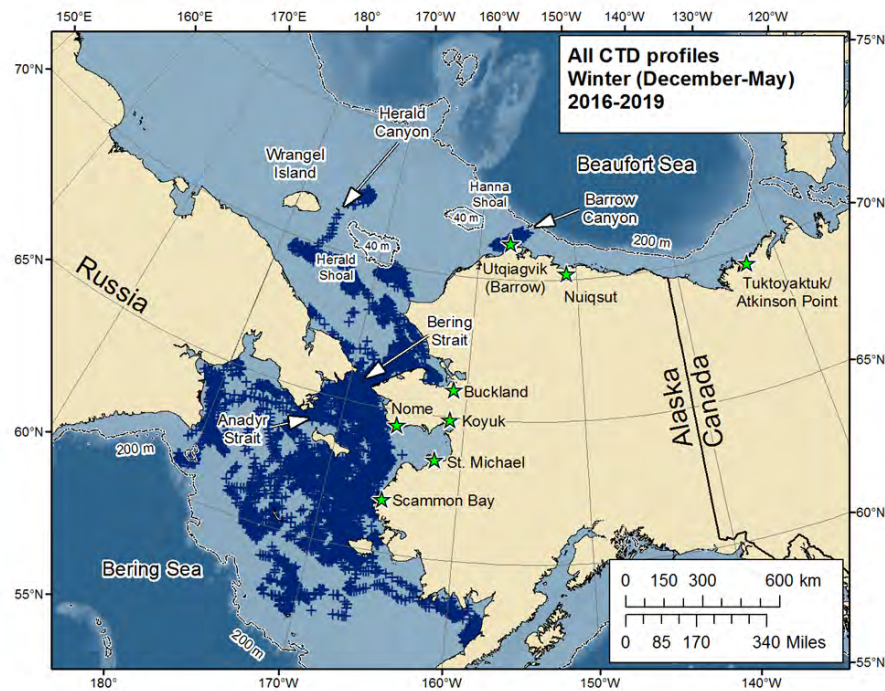
ACCOMPLISHMENTS

All CTD profiles

Summer: June-November; n=9,440



Winter: December-May; n=7,239





TECHNICAL APPROACHES

Note: We just finished up the second season of tagging, so analyses are just beginning.

For understanding animal movements, we use CTD data two ways:

1. Use CTD data as ancillary information to inform results of other analyses.
2. Use CTD data directly as predictors of habitat use in resource selection models. This is more powerful when combined with oceanographic model data.



TECHNICAL APPROACH ISSUES

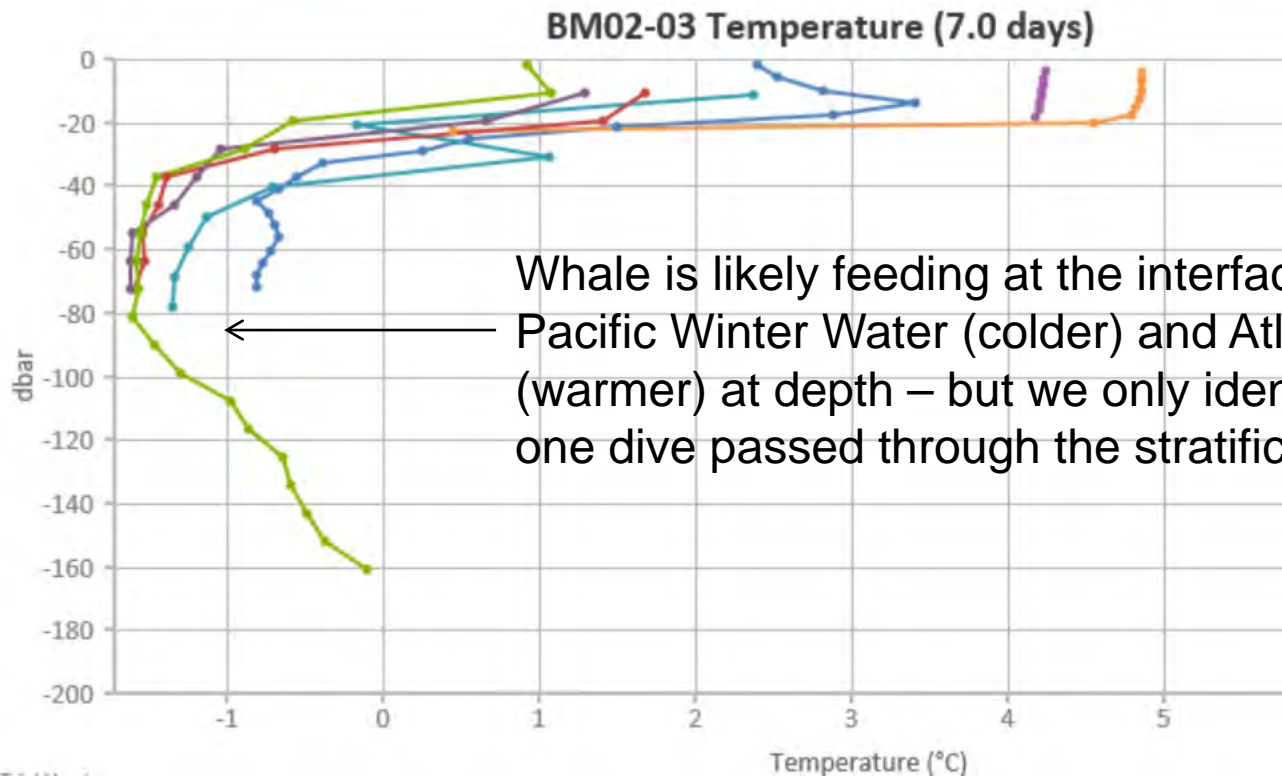
Why pair CTD data with oceanographic model data?

1. Animal-borne tags are limited to sampling temperature and salinity where the animal visited. We can compare different behaviors within animal tracks.
2. With oceanographic model data, we can also examine what the animal may have avoided. Temperature and salinity data must come from a source separate from the tag.

Issues

2018-Sep-28

2018-Oct-05



Whale is likely feeding at the interface between Pacific Winter Water (colder) and Atlantic Water (warmer) at depth – but we only identify this because one dive passed through the stratification.



CURRENT WORK

Bowhead whales

Habitat models using CTD data collected in the Chukchi Sea

Winter range shift with declining sea ice

Effect of wind on bowhead foraging in the north-central Chukchi

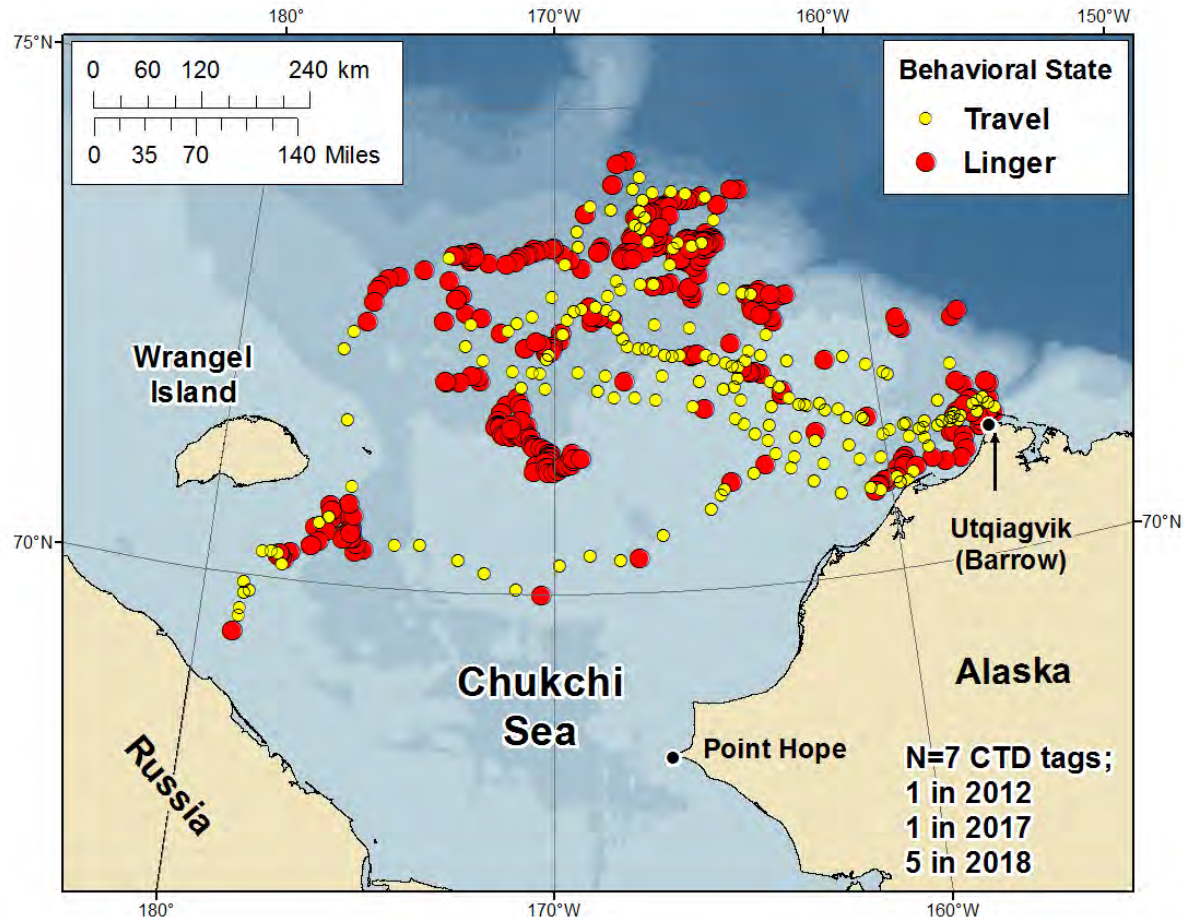
Spotted seals

Habitat models using CTD data collected in the Chukchi Sea

HABITAT MODELS FOR BOWHEADS

Habitat use of bowhead whales

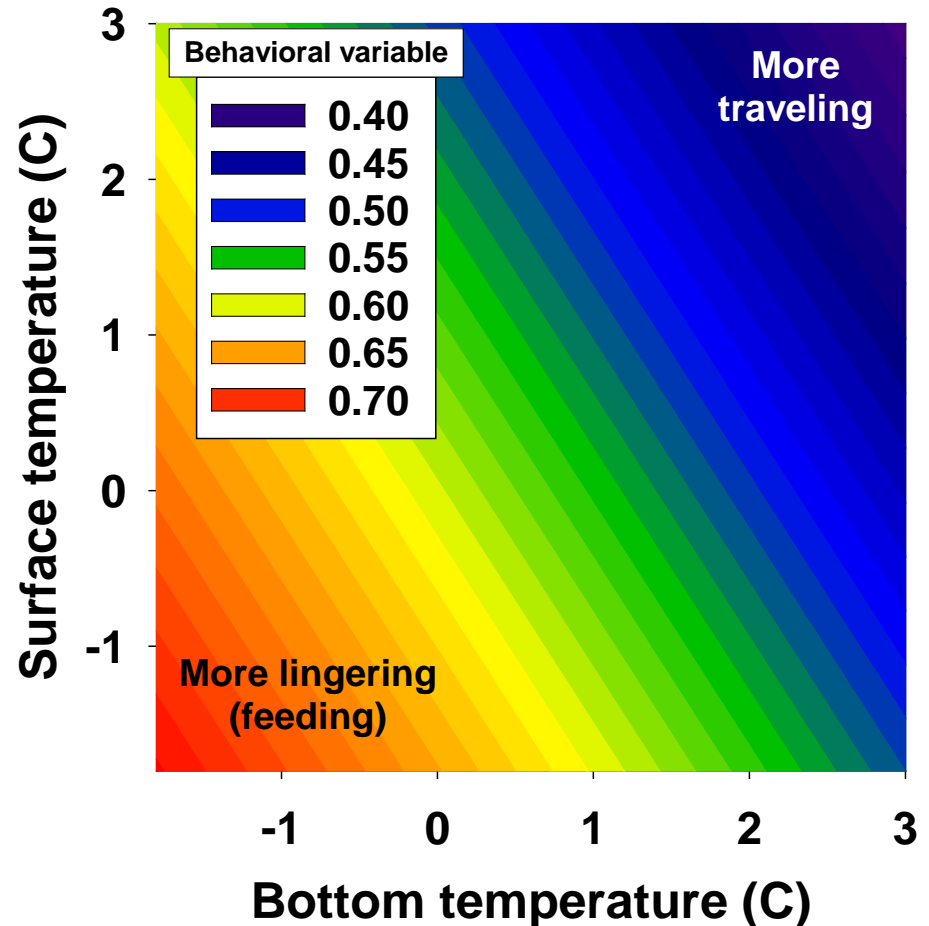
- Estimated behavioral states (traveling vs. lingering) using 'bsam' in R.
- Examined how behavior was related to oceanographic variables.



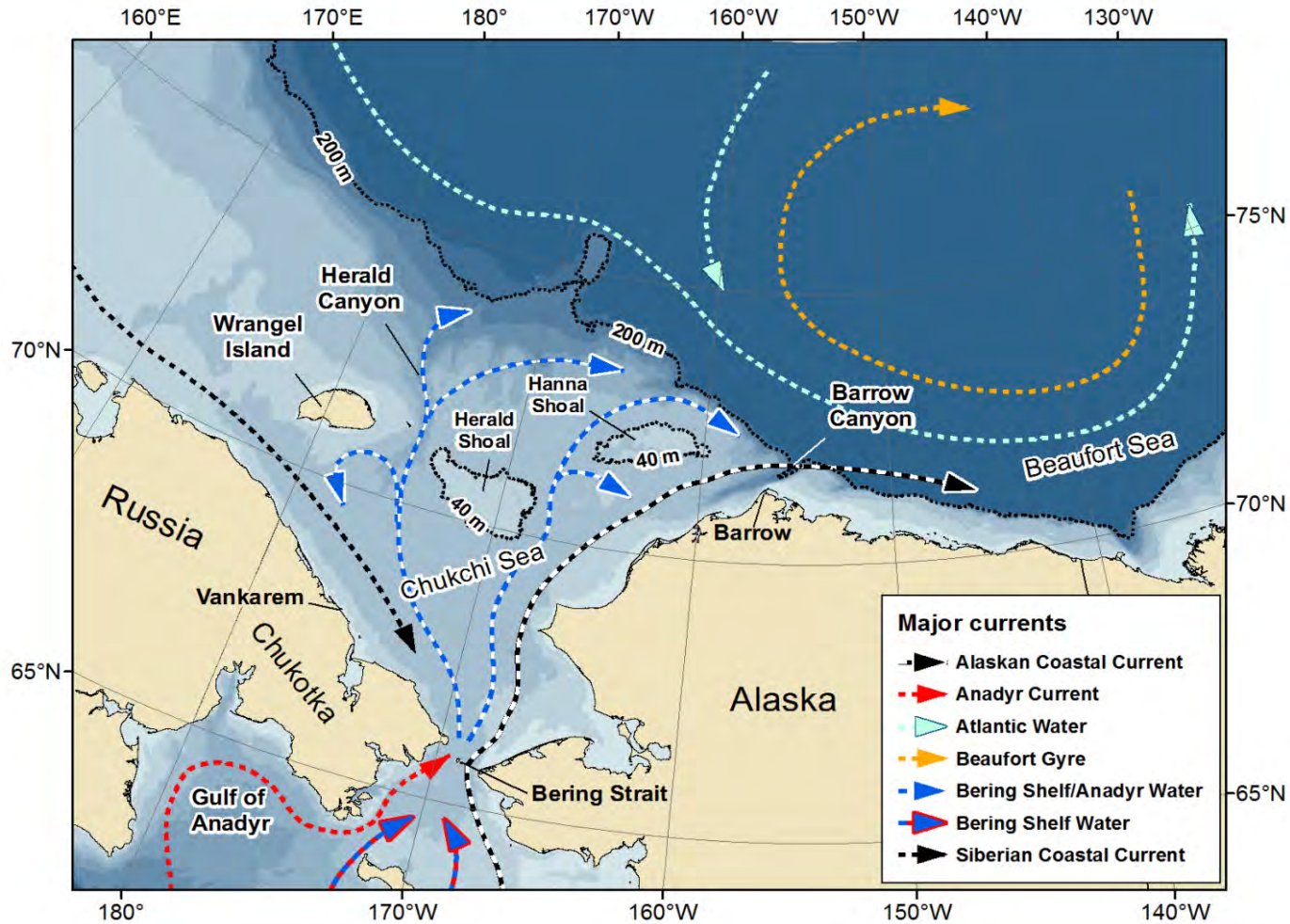
HABITAT MODELS FOR BOWHEADS

Variables:

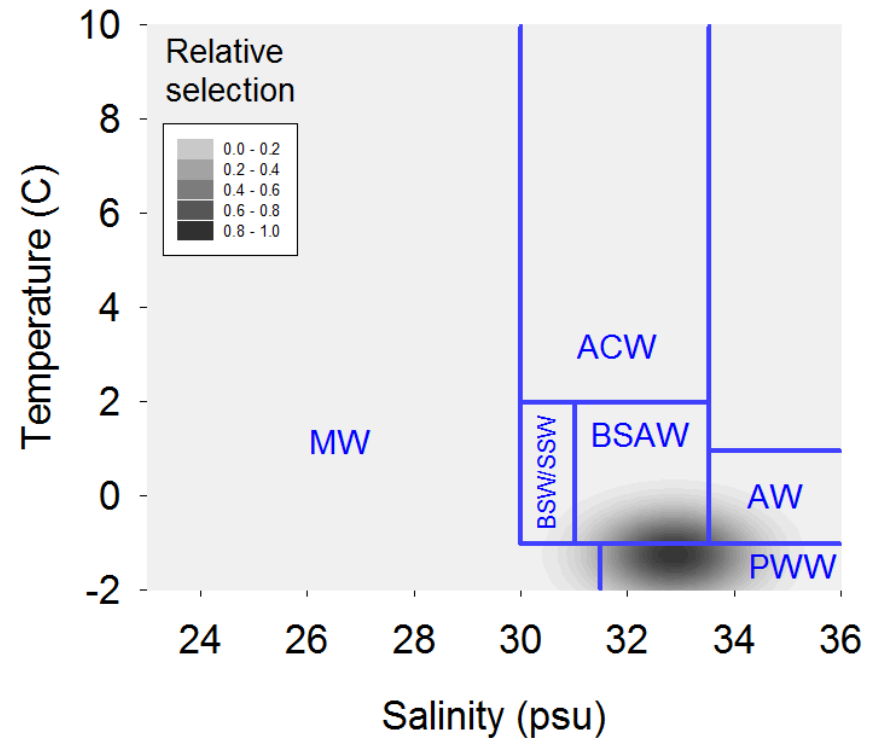
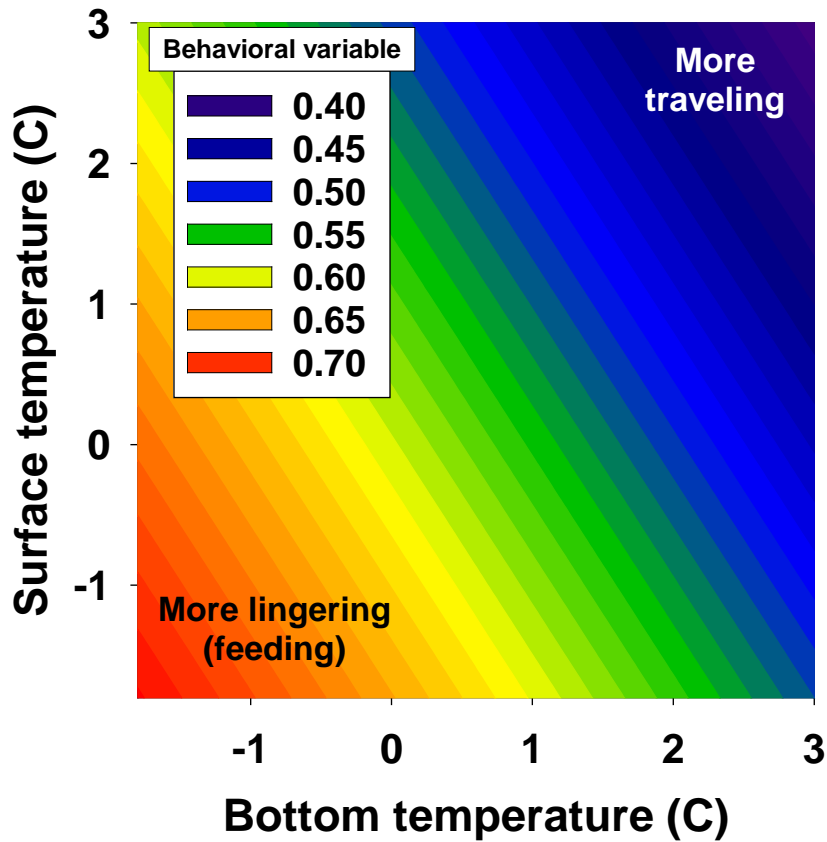
- E-W winds, E-W winds the prior day
- Bottom slope
- Bottom slope/depth
- Vertical gradient in salinity and temp within dives (stratified layers).
- Surface temp and salinity, bottom temp and salinity, and their squared terms



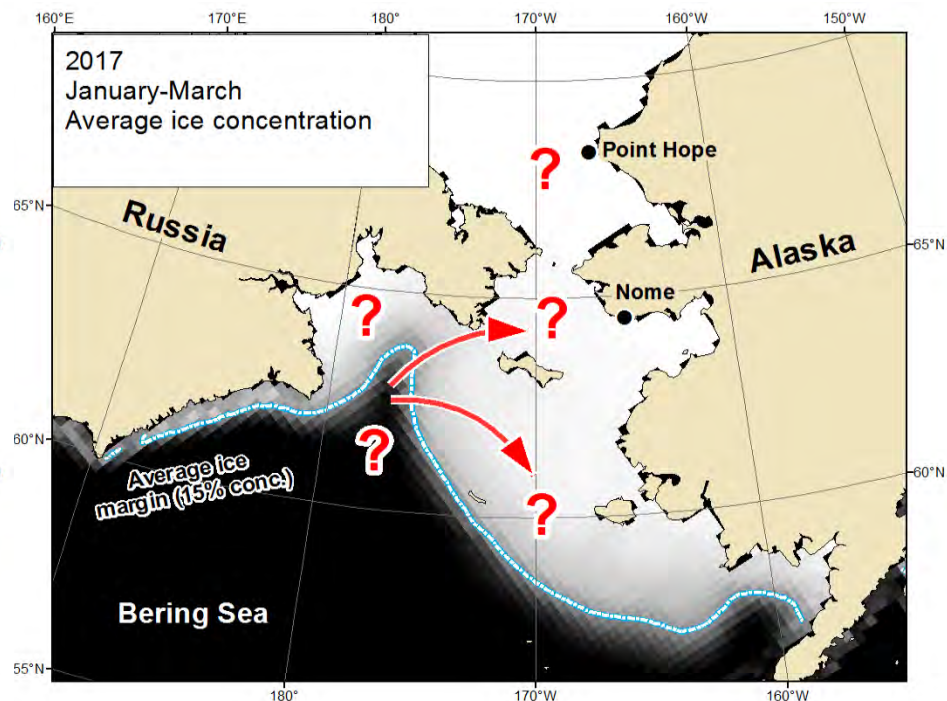
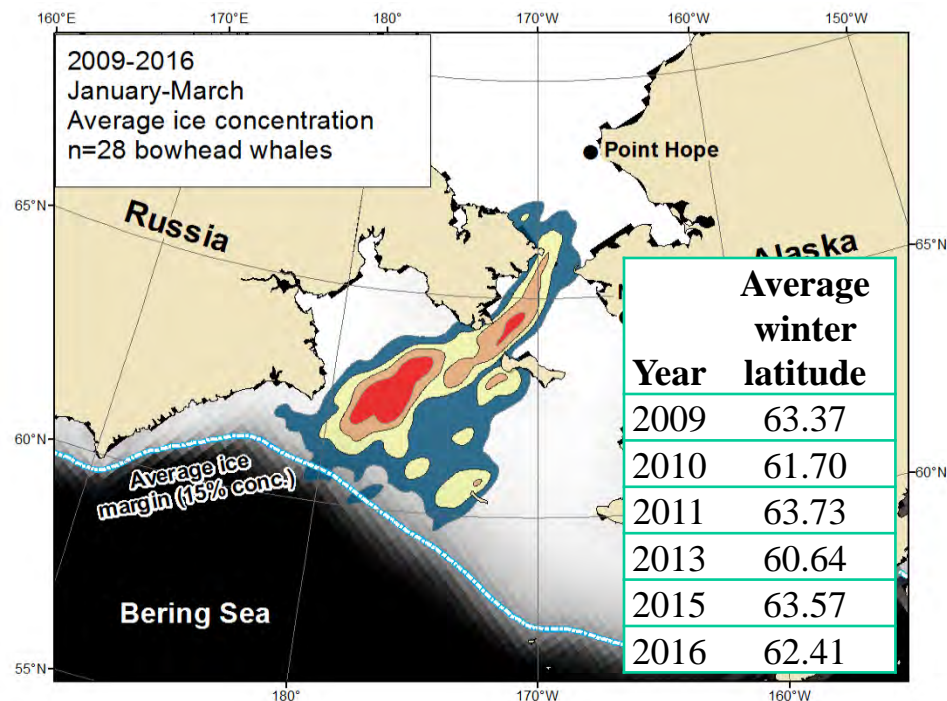
HABITAT MODELS FOR BOWHEADS



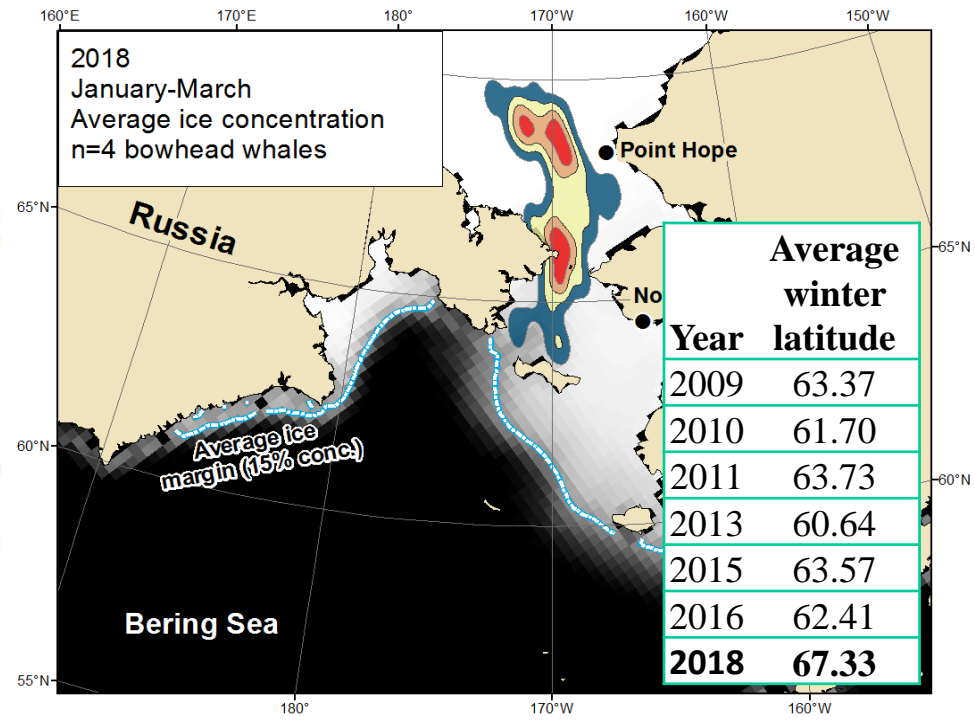
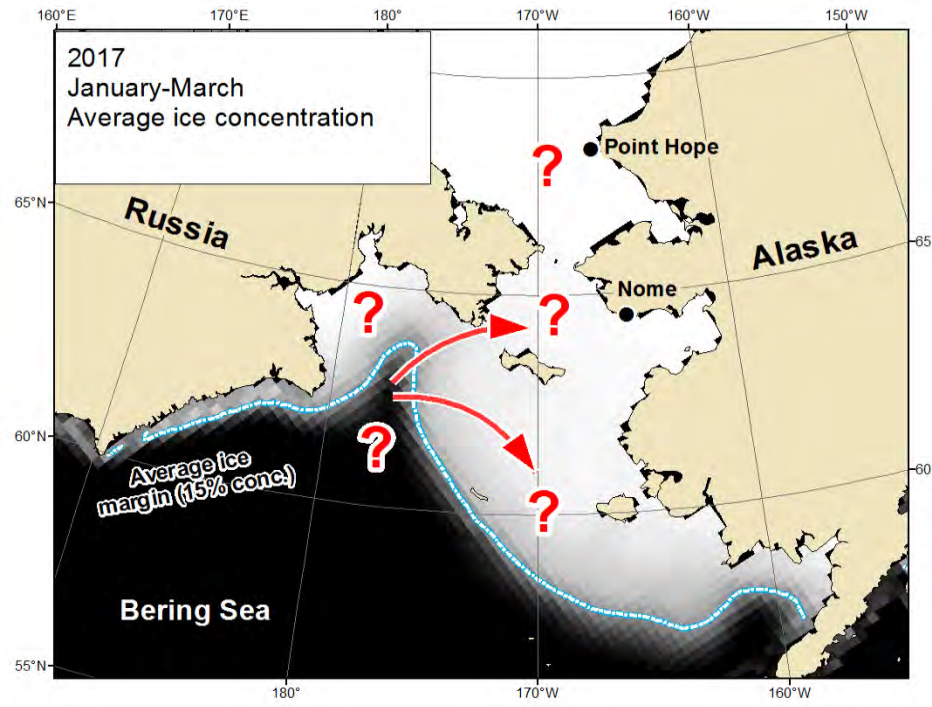
HABITAT MODELS FOR BOWHEADS



WINTER RANGE SHIFT OF BOWHEADS



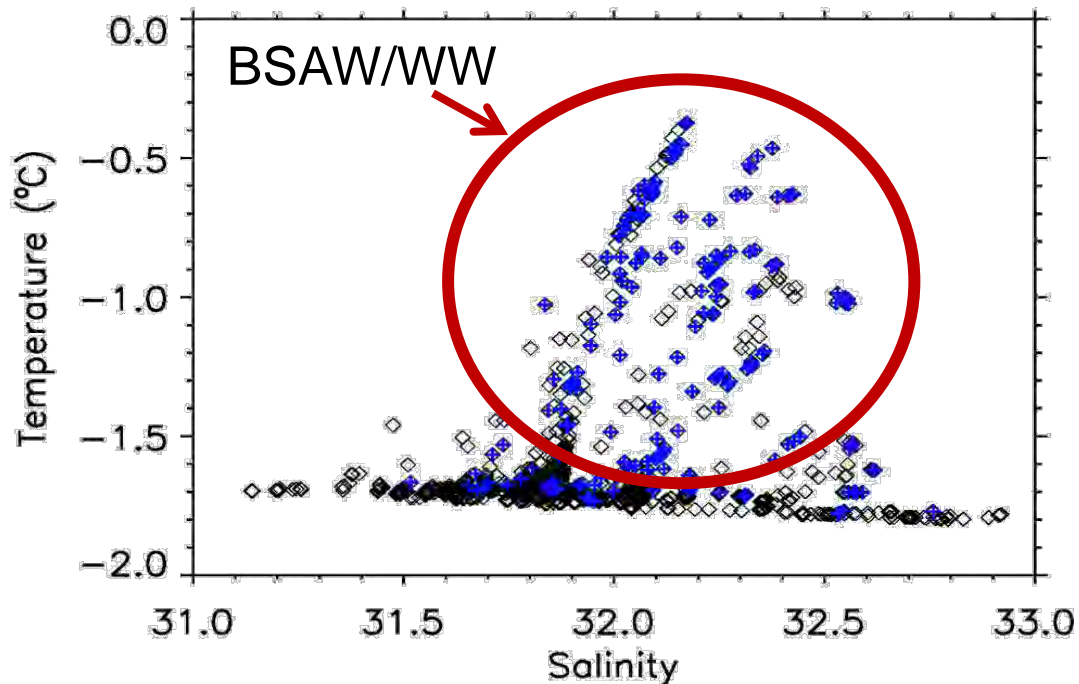
WINTER RANGE SHIFT OF BOWHEADS



WINTER RANGE SHIFT OF BOWHEADS

Data from a CTD tag from January 2018 indicate diving into Bering Shelf Anadyr Water (BSAW) and Winter Water (WW)

BSAW and WW known to have high concentration of krill.



WINDS AND BOWHEAD FORAGING

J.J. Citta et al.

Deep-Sea Research Part II 152 (2018) 121–131

Another question:
 Why do bowhead
 sometimes forage in
 the north-central
 Chukchi Sea and not
 in other years?

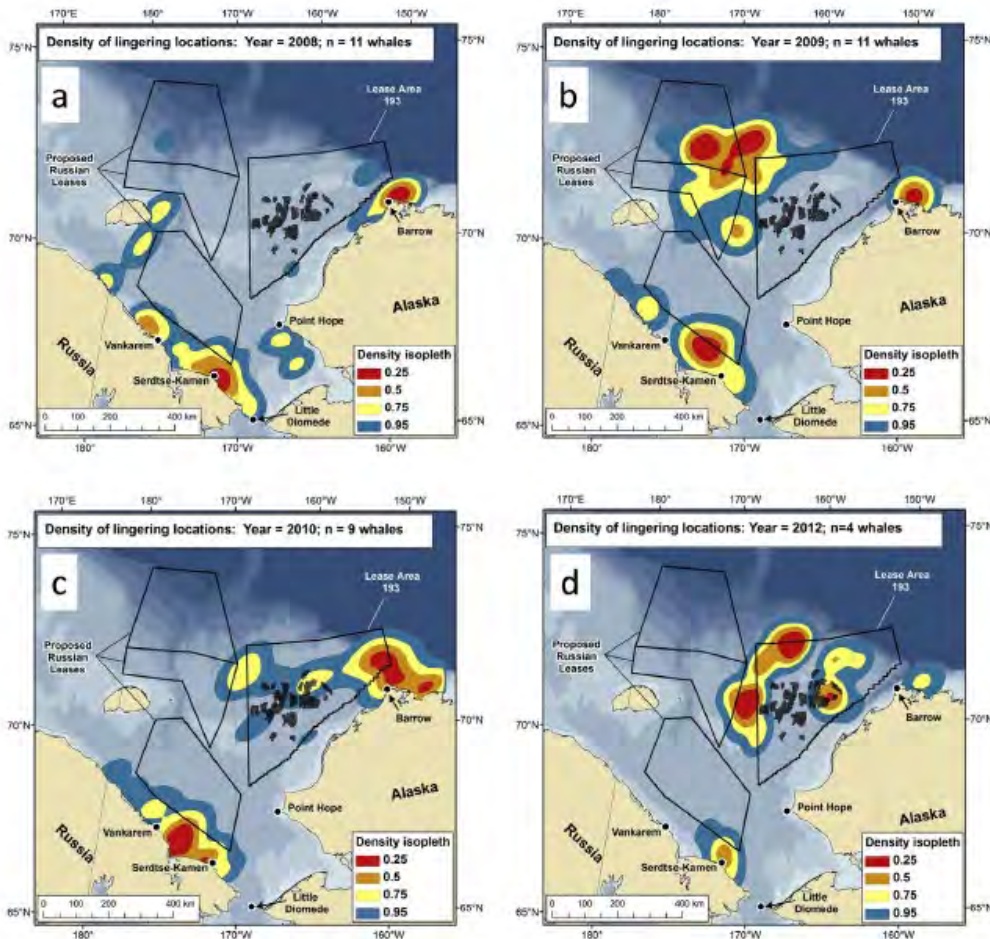
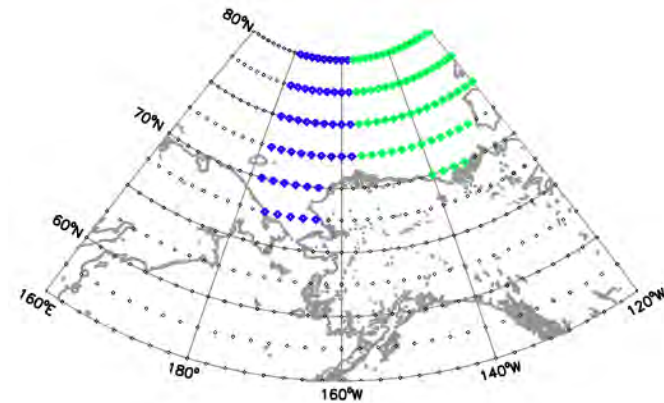


Fig. 4. Kernel densities of bowhead whale locations classified as being associated with lingering in the Chukchi Sea, September–November, 2008, 2009, 2010, and 2012. Tagged bowhead whales did not linger in the central Chukchi in 2006 or 2007

WINDS AND BOWHEAD FORAGING

Examine all correlations between winds and bowhead foraging for average winds during all possible windows (1 to 210 days) for all possible starting days (1 May to 27 Nov). Used steps <10 km as index to foraging.



```

for i = 1 to 210 days
  for j = 1 May to 27 Nov
    for k = 1, 363
      compute  $|r_{\text{bowhead foraging}, U(k)}|$ ,  $|r_{\text{bowhead foraging}, V(k)}|$ 
    endfor
    compute  $\text{Area}_{\text{BCB}}(i,j)$ , where  $|r_{\text{DVMI}, U(k)}|$ ,  $|r_{\text{DVMI}, V(k)}| > 0.707$  ( $p < 0.05$ ; 6 d.f.)
  endfor
endfor

```

Identify average wind conditions i,j for which Area_{BCB} is max

WINDS AND BOWHEAD FORAGING

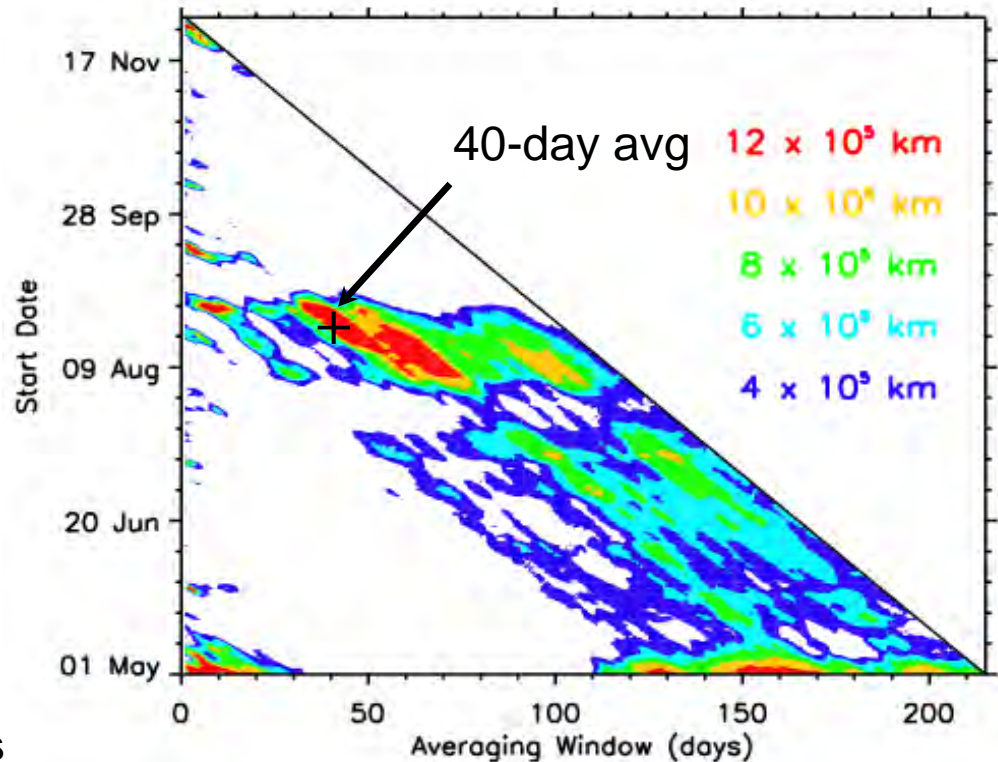
Fraction of 6-hr steps < 10-km
(21 Sep – 27 Nov)

2008	0.343
2009	0.560
2010	0.415
2012	0.684
2014	0.669
2015	0.580
2017	0.544
Mean	0.542

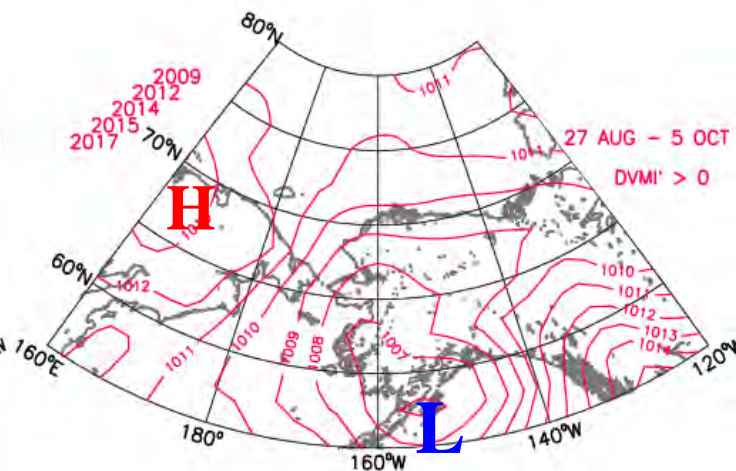
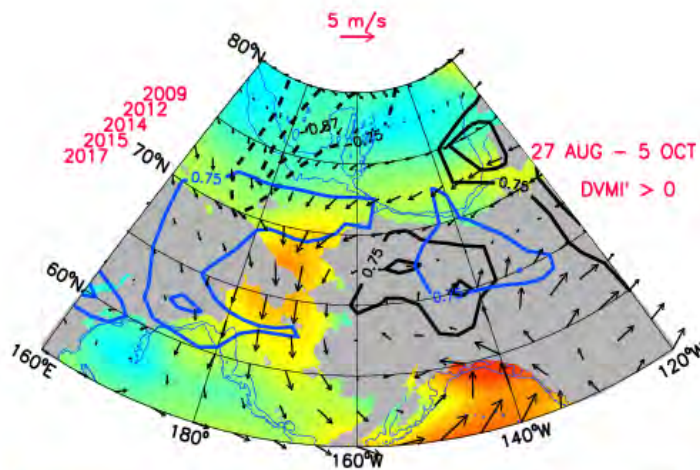
Compute the area where
 $|r_{U, 10km}|, |r_{V, 10km}| > 0.75$
 ($p < 0.05$; 5 d.f.)

Identify average wind conditions
for which area is max

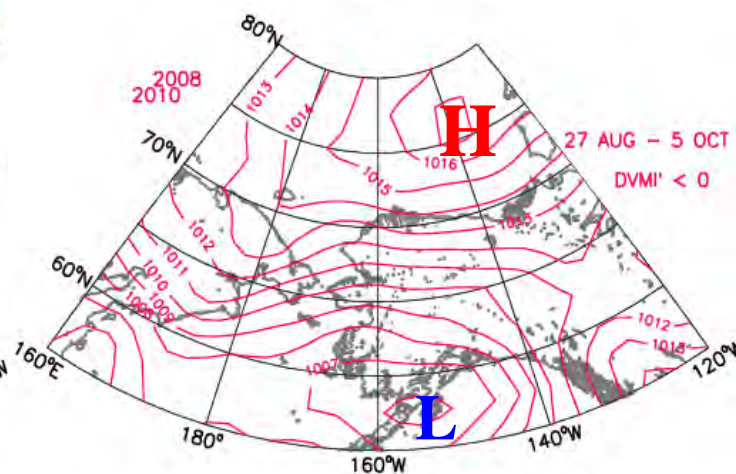
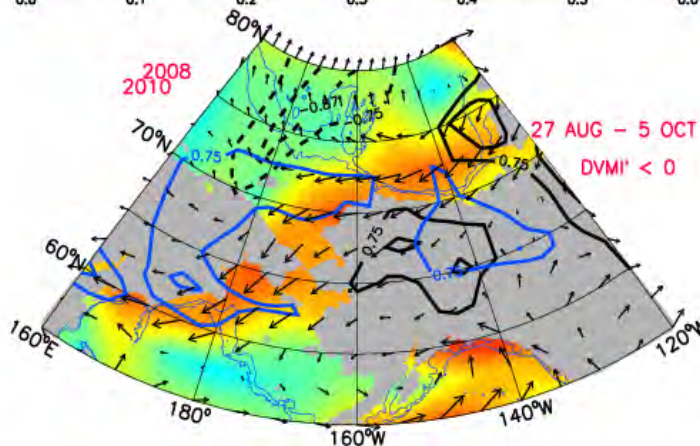
Bering-Chukchi-Beaufort area over which
 $r_{U \times BH}$ and $r_{V \times BH} > 0.75$



WINDS AND BOWHEAD FORAGING



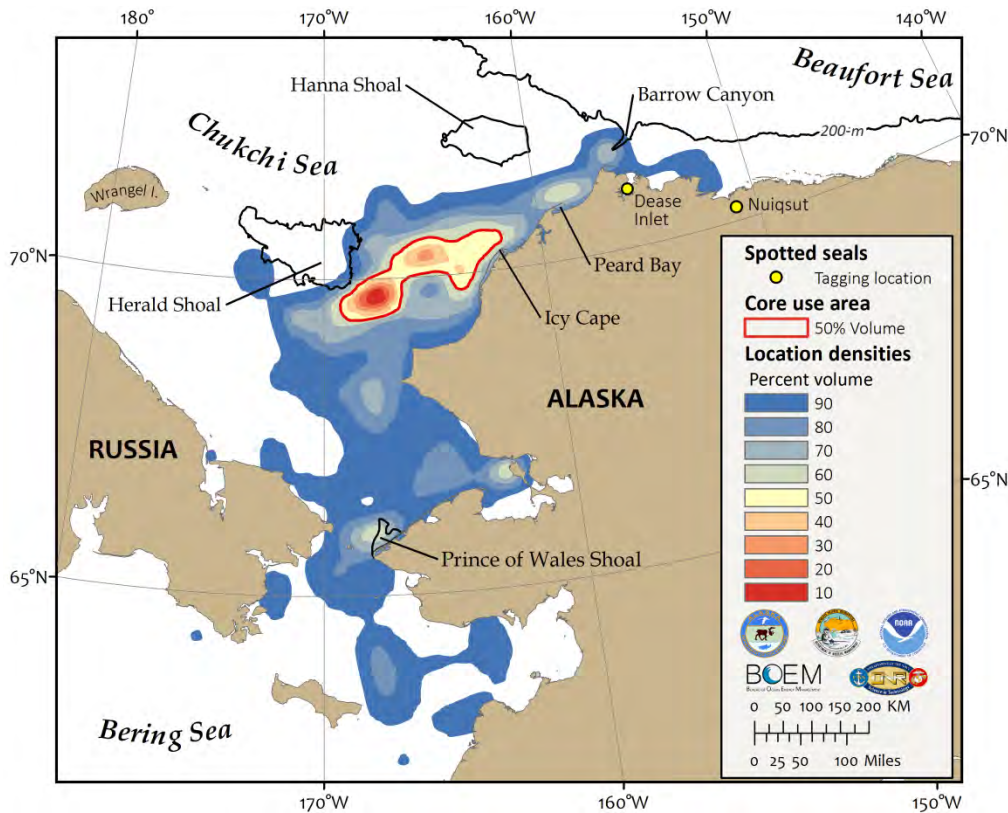
Larger
'foraging'
fraction



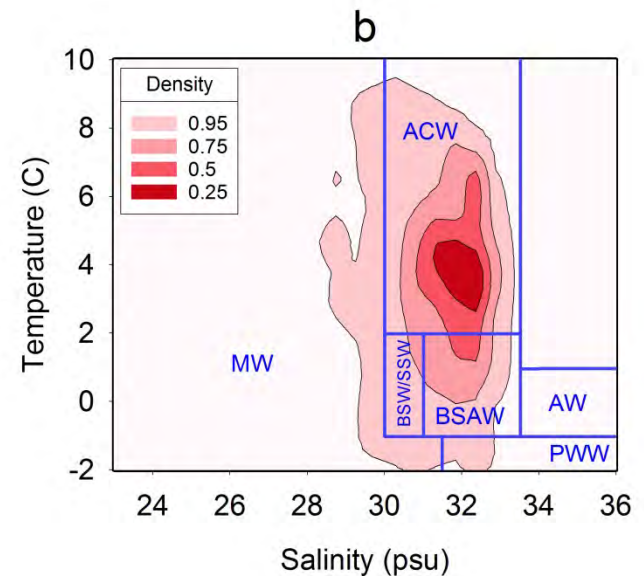
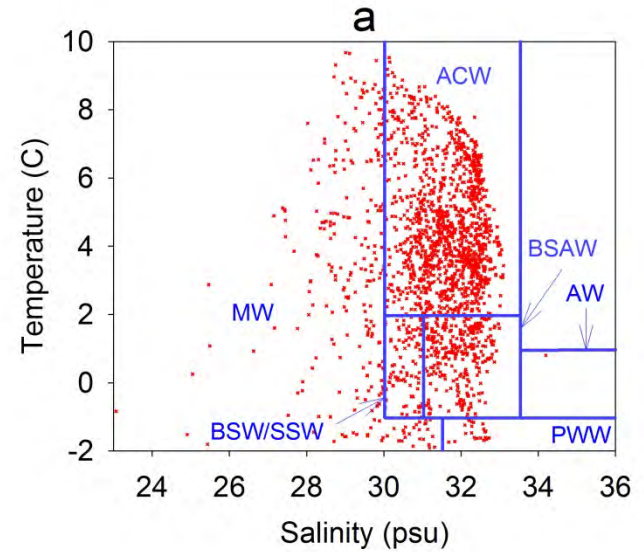
Smaller
'foraging'
fraction

HABITAT MODELS FOR SPOTTED SEALS

Example: spotted seals



Ave forage trip duration: 9.7 d (1-27)
 Ave forage trip distance: 584 km (83-1,160)



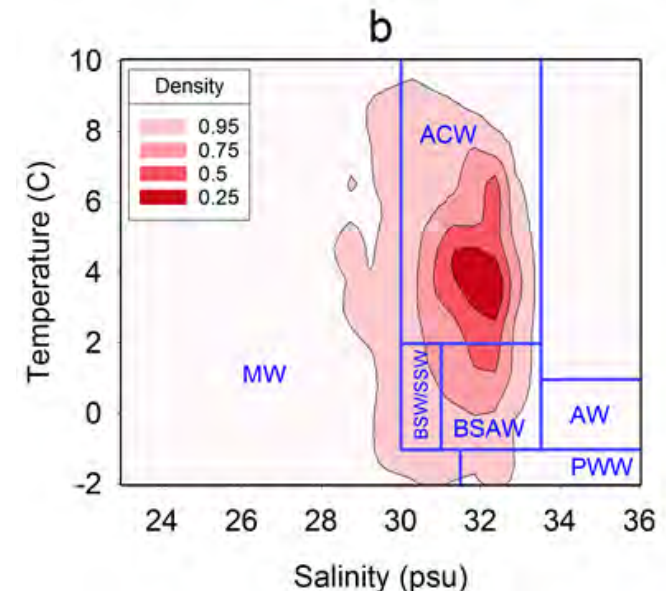
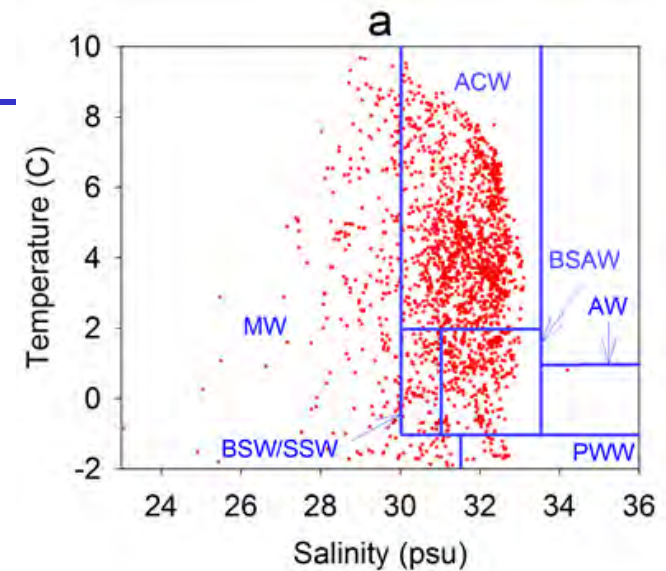


HABITAT MODELS FOR SPOTTED SEALS

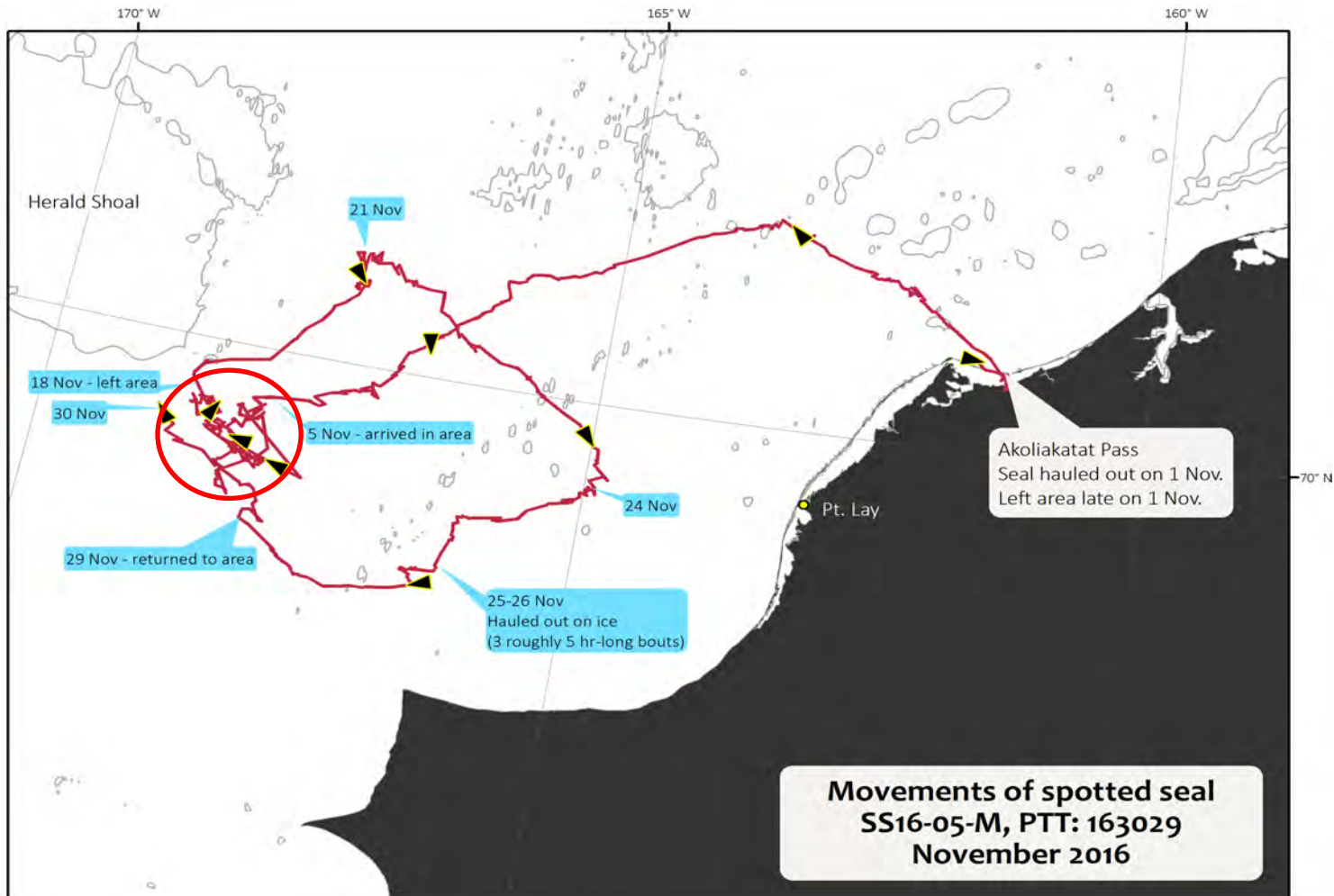
Example: spotted seals

Stomach contents from Shishmaref (1998-2018)
September-November (n=828 stomachs)

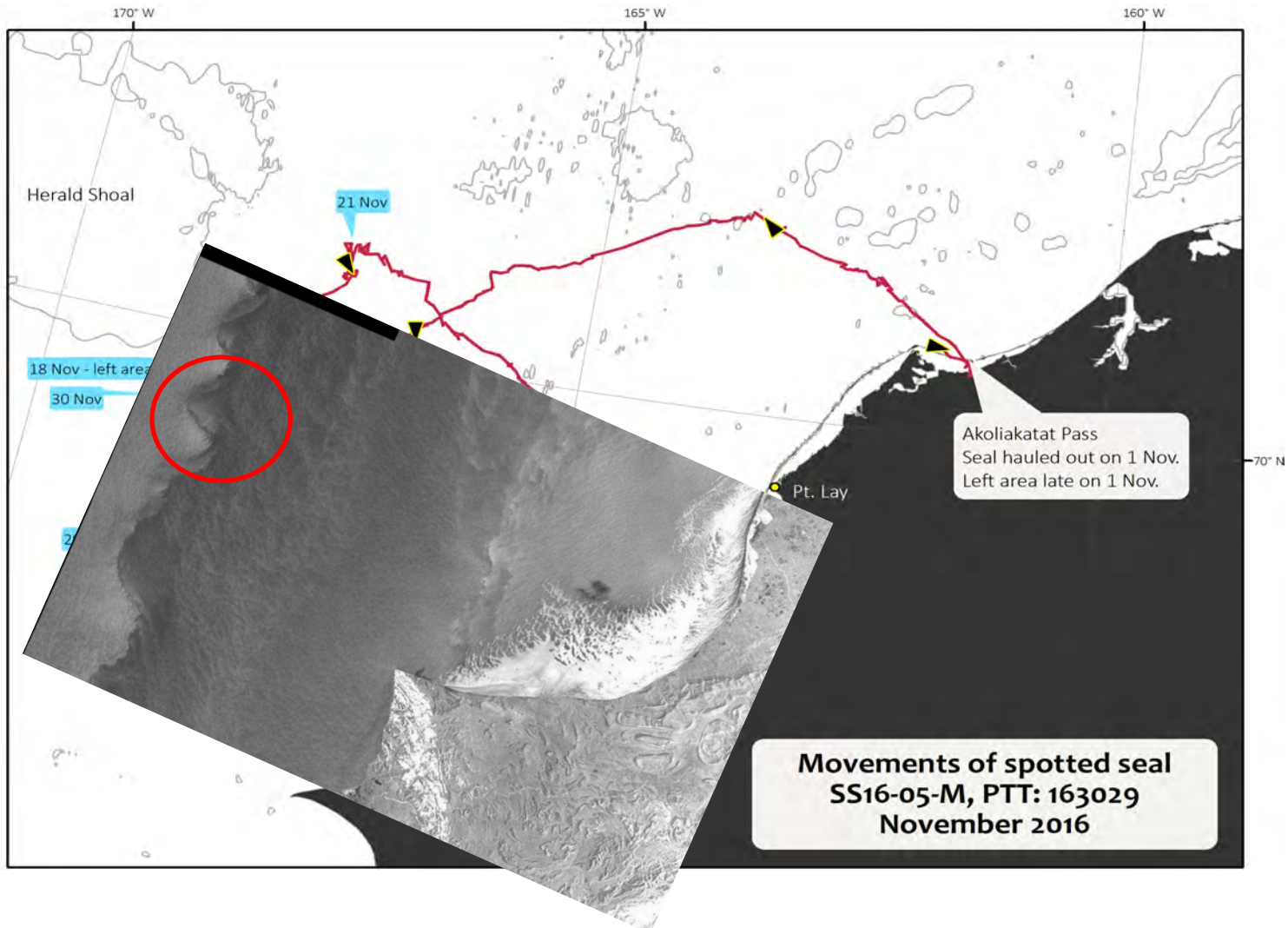
Prey item	%FO	Temp
FISH	96.90%	
<i>Clupea pallasii</i> (Herring)	50.70%	> 4 C
<i>Osmerus mordax</i> (smelt)	29.30%	> 4 C
<i>Boreogadus saida</i> (Arctic Cod)	15.30%	< 4 C
<i>Eleginus glacialis</i> (Saffron Cod)	35.90%	> 2 C



HABITAT MODELS FOR SPOTTED SEALS



HABITAT MODELS FOR SPOTTED SEALS





CURRENT AND FUTURE WORK

- **Over the last two field seasons, we have collected over 15,000 CTD profiles from marine mammals in the Beaufort, Chukchi, and Bering Seas.**
- **We are just beginning to analyze our data, but preliminary investigations look promising.**
 - In the Chukchi Sea, bowhead whales select colder, saltier water masses, foraging in the central Chukchi is correlated with weaker August and September winds.
 - In the Chukchi Sea, spotted seals likely select warmer, fresher water masses



RELEVANCE TO NAVY

- We will be able to predict habitat use of marine mammals with CTD data and other oceanographic variables, such as bathymetry, winds, and/or sea ice. This information will be useful for mitigating Naval activities in the Bering, Chukchi, and Beaufort Seas.
- We are also generating lots of data that will be useful for other projects that the Navy funds or is interested in, such as for testing the ONR-funded RASM oceanographic model.



RECENT PUBLICATIONS, PATENTS, AWARDS

We just finished up the second season of tagging, so analyses and paper writing are just beginning.