Version of Record: https://www.sciencedirect.com/science/article/pii/S0278434323002133
Manuscript_e01cc6556c2bc659c817d08247ea1d72

Journal: Continental Shelf Research

Title: Oceanographic influences on spotted seal foraging in the Pacific Arctic

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Abstract

Satellite Relay Data Loggers that are equipped with Conductivity, Temperature, and Depth sensors (CTD-SRDLs) are an important tool for identifying how oceanography influences an animal's foraging behavior and how foraging may be affected by environmental change. Spotted seals (*Phoca largha*) are one of four species of sea ice-associated seals that occur in the Bering, Chukchi, and Beaufort seas of the Pacific Arctic. Between 2016 and 2020, 23 spotted seals were equipped with CTD-SRDLs, which collected temperature and salinity profiles as the seals dove through the water column. We first examined the oceanographic characteristics along seal tracks using data from the CTD-SRDLs, and then modeled seal behavioral state (resident or transiting) as a function of sea ice and oceanographic conditions extracted from the inferred oceanographic space. We then related these findings to habitat associated with the predominant fish prey species identified from seal stomach contents, which included Arctic cod, saffron cod, Pacific herring, rainbow smelt, and capelin. Spotted seals mostly dove to near-bottom depths, including frequent dives to the sea floor. During the ice-free season in the Chukchi Sea, pups were mostly likely to be in the resident state (i.e., possible foraging) when near-bottom conditions were colder and less saline. Seals were also more likely to be in the resident state when far offshore and in areas with colder bottom temperatures. Behavior related to possible offshore foraging was more associated with non-pup seals and possible nearshore foraging was more associated with pups. During the ice-covered season, seals were more likely to be in the resident state when bottom temperatures were colder, and this relationship was stronger for non-pups than for pups and for females than for males. Our use of satellite telemetry, oceanographic modeling, and biological sampling support the understanding that spotted seals are generalists in both prey species and foraging habitat.

Key words: Ice seals; biologging; Alaska; Bering Sea; Beaufort Sea; Chukchi Sea

1. Introduction

Satellite Relay Data Loggers (SRDLs), or transmitters, are an extremely important tool for better understanding the movements and dive behavior of marine mammals in large, challenging environments such as the Pacific Arctic (Lowry et al. 1998, Crawford et al. 2011, Jay et al. 2014, Von Duyke et al. 2020, Olnes et al. 2020a,b). Information collected from SRDLs equipped with Conductivity, Temperature, and Depth (CTD) sensors (hereafter referred to as CTD-SRDLs) provide temperature and salinity profiles as an animal moves through the water column and are particularly useful in describing the marine environment at a spatial scale relevant to the animal (Gryba et al. 2019, Citta et al. 2020, 2021). Thus, movements that may be associated with foraging, such as periods of resident behavior (also known as area-restricted search) or targeted dive depths can be associated with oceanographic conditions.

Spotted seals (*Phoca largha*) are one of four species of sea ice-associated seals that occur in the Bering, Chukchi, and Beaufort (BCB) seas of the Pacific Arctic. Ice-associated seals depend upon sea ice for part of their life cycle. In winter, BCB spotted seals associate with the ice edge in the Bering Sea (Burns 1970, Lowry et al. 1998, Rugh et al. 1997), using it as a platform for resting between feeding bouts, as well as a platform for pupping and molting in the spring. In summer, spotted seals disassociate from sea ice, forage in open water, and haul out on land (Burns 1970, Frost et al. 1993, Lowry et al. 1998). As such, spotted seals occur in the Bering Sea year-round, but expand their range into the Chukchi and Beaufort seas in summer as the sea ice retreats northward (Burns 1970, Citta et al. 2018). Within these waters, spotted seals remain on the continental shelf, where depths are less than 200 m (Burns 1970, Citta et al. 2018).

Shelf waters make up the entire northern Bering and Chukchi seas, whereas the shelf in the Beaufort Sea is relatively narrow (~100 km) along Alaska's northern coast.

Spotted seals primarily eat fish (Bukhtiyarov et al. 1984, Dehn et al. 2007), but also consume amphipods and shrimp (Quakenbush et al. 2009). Such prey have various habitat associations and the conditions that aggregate them may vary by species or over space and time. On the continental shelf, habitats for spotted seal prey are partly defined by water masses with temperature and salinity characteristics that reflect their spatial origins and seasonal evolution (e.g., Eisner et al. 2013). These water masses trend from warmer and fresher over the eastern shelf to cooler and saltier over the western shelf. The main shelf currents flow south to north, carrying nutrients, heat, fresh water, and biota from the Bering Sea through the Bering Strait and across the Chukchi Sea to the Arctic Basin (Coachman et al. 1975, Walsh et al. 1989, Stabeno et al. 1999, Weingartner et al. 2005, Berline et al. 2008, Clement Kinney et al. 2009, Maslowski et al. 2014). Boundaries between water masses (i.e., fronts and stratifications) may have strong salinity or temperature gradients that can aggregate zooplankton and attract higher trophic level predators such as fish (e.g., Woodson and Litvin 2015) or whales (Moore et al. 1995, Citta et al. 2015, Citta et al. 2020, Citta et al. 2021). Spotted seals may forage along fronts, stratified regimes, or target water masses with specific temperatures or salinities that contain their primary prey.

In addition to hydrography, sea ice may also influence spotted seal foraging patterns. This is because sea ice alters the marine environment below it and spotted seals may be more likely to forage in productive areas near ice upon which they can rest, as is known for walruses (*Odobenus rosmarus divergens*, Jay et al. 2014) and likely the case for ice seals (Burns 1970). Both sea ice and oceanographic conditions are changing in the Pacific Arctic (Huntington et al.

2020). Sea ice extent, concentration, and thickness have declined during the 21st century; the autumn advance of sea ice southward now occurs later in the year, while the spring retreat of sea ice to the north occurs earlier in the year (Wang et al. 2018). Reductions in sea ice contribute to warming surface waters in many parts of the region (Baker et al. 2020). In years with low ice extent, the area of the Bering Sea Cold Pool, cold water (<2° C) that persists along the bottom throughout the year, is diminished (Clement Kinney et al. 2022). These changes may alter invertebrate, fish, and marine mammal distributions, and associated trophic dynamics (Mueter et al. 2021). For example, less sea ice resulting in less sympagic (ice-associated) primary production and more pelagic primary production could reduce benthic productivity because less phytoplankton gets deposited on the sea floor, with potential consequences for species at higher trophic levels that feed on benthic organisms (Bluhm and Gradinger 2008, Wang et al. 2016, Mueter et al. 2021). However, recent measurements of significant carbon deposition to the sea floor during the warm summer of 2018 suggest a potential for benthic productivity to remain high in the region despite sea ice loss and warmer waters (O'Daly et al. 2020). Less ice, warmer water temperatures, and a shrinking of the Bering Sea Cold Pool may also allow subarctic fish species to expand their range into Arctic waters (Grebmeier et al. 2006a), altering the assemblage of available prey species. Such changes are likely to affect spotted seal distribution, foraging, and movement behavior.

Changes to the Pacific Arctic may also lead to changes in how spotted seals interact with human populations in Alaska. Spotted seals are an important subsistence species for Alaska Natives in most coastal villages from Bristol Bay to the Canadian border in the Beaufort Sea, with an estimated 5,200–8,200 harvested annually in Alaska (Nelson et al. 2019). Environmental change that would alter spotted seal distribution or movement patterns could affect their availability for harvest by Alaska Natives. Further, environmental changes and shifts in species' distributions may increase spotted seal predation of species targeted by commercial fisheries in Alaskan waters (e.g., walleye pollock; *Gadus chalcogrammus*). Hence, improving our understanding of spotted seal foraging and how they may be affected by environmental change is important and timely.

Our primary goal was to better understand how the oceanography of the BCB area may influence spotted seal foraging behavior using data collected by animal-borne instrumentation. Between 2016 and 2020, 23 spotted seals were equipped with CTD-SRDLs that provided animal movement and oceanographic data. We used these data to examine relationships among physical oceanography and movements indicative of foraging for spotted seals during the ice-free period (July–November) in the Chukchi Sea and the ice-covered period (December–April) in the Bering Sea. We define 'foraging' as searching for and obtaining food and assume that examining spotted seal dive and movement behavior provides insights into foraging behavior. We assumed the depths targeted by spotted seal dives are indicative of where in the water column seals are foraging. We hypothesized that spotted seal movement behavior, and more specifically, when spotted seals exhibit resident behavior, would be influenced by water temperature and salinity, and hydrographic fronts and stratified features in both seasons, and by sea ice presence during the ice-covered period. We then summarized spotted seal prey from seal stomach contents, and their habitat preferences, as potential explanations for relationships found between movement behavior and oceanography. We discuss the advantages and limitations of oceanographic data collected by animal-borne instrumentation based on the results of this study.

2. Materials and Methods

We first summarized the information provided by the CTD-SRDLs, spotted seal movements and habitat use, and the dive depths that seals targeted. We then used a state-space model to define seal movement behavioral states and explored how they relate to oceanographic fields inferred from data provided by the CTD-SRDLs. Lastly, patterns of movement behavior were related to the habitat associations of prey found in seal stomachs. All statistical analyses were performed in R statistical software version 4.3.1 (R Core Team 2023).

2.1. Spotted seal movements, habitat use, and dive behavior

Information on seal movement, haul-out, and dive behavior was provided by CTD-SRDLs that were attached to captured spotted seals (n = 23, Table 1). Seals were captured and instrumented in the months of July through October (2016–2019) at three locations in Alaska: the Colville River (near Nuiqsut) and Dease Inlet (near Utqiaġvik), which are on the northern coast in the Beaufort Sea, and at Scammon Bay on the western coast of Alaska in the Bering Sea. Seal sex and age were determined in the field and seals were classified as adults (>5 years old), subadults (1–5 years old), or pups (<1 year old) based on age estimates using claw annuli (McLaren 1958). For our analyses, we grouped adults and subadults into a single 'non-pup' age class.

The CTD-SRDLs were manufactured by the Sea Mammal Research Unit in St. Andrews, Scotland (http://www.smru.st-andrews.ac.uk/Instrumentation/CTD/) and were programmed to provide location data via the Argos satellite system (http://www.argos-system.org/), dive behavior, haul-out durations, and temperature and salinity profiles for a subset of dives. Dive and oceanographic data were continuously collected but subsampled and simplified to facilitate transmission.

Raw location data returned by Argos includes estimates of error characterized by “quality classes”. The error radius for higher-quality locations in classes 3, 2, or 1 is determined by Argos, whereas lower-quality locations classified as 0, A, or B must have their error radius estimated. Locations in class Z are unreliable and were removed. Raw location data and associated error quality classes were used to estimate locations at specific time intervals and to infer behavioral state (transiting or resident) using the R package ‘bsam’ (version 1.1.3, Jonsen et al. 2005, Jonsen 2016). This 2-state switching state-space model (sSSM) is structured around a correlated random walk process that accounts for location error, estimates movement parameters for two inferred behavioral states across all seals, and then applies these parameters to estimate individual seal locations and behavioral state for discrete time intervals. Seals that are ‘transiting’ make directed movements (i.e., low turn angles) and have longer step-lengths between successive locations, whereas seals in a ‘resident’ state change direction frequently and have shorter step-lengths. Behavioral state ranges from 0 to 1, with values near 0 indicating transiting behavior and values near 1 indicating resident behavior.

To determine which time interval produced the most defined behavioral states (i.e., bimodal distribution), we compared model results using 3-hour, 6-hour, and 12-hour time intervals. For each time interval, the model was run with 40,000 iterations and a burn-in period of 10,000 iterations, which were then thinned by 10 to eliminate autocorrelation. Diagnostic plots provided by the ‘bsam’ package affirmed that using a 6-hour interval resulted in the highest quality model with the most well-defined behavioral states.

For each estimated 6-hour location, we determined the water depth, distance from land, and sea ice concentration. Bathymetry came from a 1-km digital bathymetric model produced by the Alaska Ocean Observing System (AOOS, Danielson et al. 2008). The shoreline was determined using the global, self-consistent, hierarchical, high-resolution shoreline database (Wessel and Smith 1996). Daily sea ice concentration was obtained from the National Snow and Ice Data Center and consisted of remotely sensed, passive microwave data that assigned ice concentration to a spatial grid with a cell resolution of 25 x 25 km (DiGirolamo et al. 2022).

All data types provided by the CTD-SRDLs include a time stamp that can be used to locate each datum along an individual seal's track through linear interpolation. We first used the R function 'as.ltraj' (package: 'adehabitatLT', Calenge 2006) to calculate the distance (in meters) between each estimated location, and then generated a 'track distance' variable, which was the cumulative distance traveled along each seal's track. We then interpolated the distance along each track at which either a dive or CTD profile was recorded based on each datum's time stamp relative to the time stamp of each estimated 6-hr location (package: 'zoo', function: 'na.approx', Zeileis and Grothendieck 2005). Aligning each data type along a seal's track via their time stamps allowed us to relate information across datasets.

The CTD-SRDLs transmit dive behavior data for the calculation of the Time-At-Depth (TAD) index (Fedak et al. 2001). The TAD index is a metric quantifying dive behavior, where values approaching 1 indicate the animal spent most of its dive near the maximum depth of the dive (i.e., 'square-shaped' dives). Conversely, values approaching 0 indicate the animal spent most of its dive near the surface or at mid-depths and minimal time at the maximum dive depth (i.e., 'V-shaped' dives). The maximum depth achieved during each dive and its duration were also recorded by the CTD-SRDLs.

Haul-out behavior is determined by a wet-dry sensor on the CTD-SRDL that identifies the start and end time for each haul-out bout. A seal haul-out bout begins when the CTD-SRDL registers as dry for 10 minutes and ends when wet for 40 seconds. Using these haul-out bouts, we formatted a haul-out variable as the proportion of time a seal was registered as hauled out during a 6-hour period centered on each location estimate.

We summarized the distance from land, water depth, and sea ice concentration used by seals, the proportion of the water column used during each seal dive, and the TAD index for when seals were in the Chukchi Sea during the ice-free season and in the Bering Sea during the ice-covered season. We examined differences in habitat use and dive behavior among seal sex and age classes, and behavioral state. The proportion of time hauled out was only used in models of seal movement behavior.

2.2. Seal movement behavior and oceanography inferred from CTD-SRDLs

For a subset of dives, the CTD-SRDLs collected oceanographic information in the form of temperature and salinity profiles. Up to 18 temperature and salinity (derived from conductivity) measurements were collected at depths throughout the dive, based on the dive depth, including measurements at the maximum depth achieved.

We used data from the temperature and salinity profiles to fill in the oceanographic grid space in which seals were moving and diving (e.g., Citta et al. 2021). The 2-dimensional grid space was defined by track distance (km) along the horizontal axis and water depth (m) along the vertical axis. The number of cells and cell size was determined by the ratio of maximum water depth encountered and track distance and was specific to each seal track such that the grid was square for the interpolation and then back-transformed to the original dimensions. Temperature and salinity values for each cell within the grid space were calculated by inverse distance weighting the 10 closest temperature or salinity measurements from the CTD profiles. The grid was then smoothed using a moving average of the 10 closest grid cells; the outcome being a track with estimated behavioral states (transiting or resident) aligned with dives of known depth, both of which were overlaid on the 2-D temperature and salinity fields. Near-surface (2 m depth) and near-bottom (5 m above sea floor) temperature and salinity data were extracted at each 6-hour location associated with a behavioral state. The near-surface and near-bottom sea water densities were then calculated from the corresponding temperature and salinity values after which the vertical density differences were calculated (bottom density minus surface density). Similarly, we calculated the horizontal difference for near-surface and near-bottom temperature and salinity as the difference over 10 km or 25 km of track distance, where values were extracted from the interpolated oceanographic space 5 km (or 12.5 km) in front of and 5 km (or 12. 5 km) behind each 6-hour location estimate.

We modeled seal behavioral state as a function of oceanography extracted from the interpolated oceanographic space and sea ice conditions using linear mixed effects models (package: ‘nlme’, Pinheiro et al. 2022). We conducted separate modeling exercises based on region and season, for the Chukchi Sea during the open water season and for the Bering Sea during the ice-covered season. Locations above 65.6° N were considered in the Chukchi Sea and locations below were considered in the Bering Sea. Our response variable was the logit-transformed behavioral state. For both regions and seasons, surface temperature and salinity, bottom temperature and salinity, and the vertical density difference, all extracted from the interpolated oceanographic space, were explanatory variables associated with oceanography.

Horizontal differences were not used because most estimated values were zero. Additionally, we considered other explanatory variables associated with season specific variables, including sea ice and distance traveled from shore (see below). We also included a categorical haul-out variable, where a seal was considered hauled out ("yes") if the haul-out variable was > 0.33, indicating a seal hauled out for at least 2 hours during a 6-hour period, and not hauled out ("no") if the value was < 0.33. All explanatory variables included two-way interaction terms with seal sex and age class (pup or non-pup). All numerical variables were standardized to facilitate model convergence and interpretation of effect size. Temporal autocorrelation was addressed in all models using a spherical autocorrelation function. Models were initially fitted using maximum likelihood. We first determined the random effect structure using likelihood ratio tests (Zuur et al. 2009). After determining the random effect structure, we then fit several candidate models that were compared using Akaike's Information Criterion (AIC) using a two-tiered approach. We first compared several candidate models to test the broad hypotheses of whether seal movement behavior was influenced by temperature or salinity, or by surface or bottom conditions. The top performing model from this set was then fed into the 'dredge' function in R, which can fit and provide AIC values for all possible combinations of explanatory variables (package: 'MuMIn', Bartoń 2022). We selected the top performing model as the most parsimonious model within 2 AIC units of the lowest AIC score. The top performing model was fit again using restricted maximum likelihood (REML) to achieve better parameter estimates (Zuur et al. 2009).

In addition to the modeling framework described above, we included unique variables that were specific to each season and region, based on either seal behavior or the presence of sea ice. For the Chukchi Sea during the ice-free season (July–November), we created a categorical trip distance variable based on the observed behavior of spotted seals and their use of land-based haul-outs during this time. We first separated individual 'trips' by periods when seals traveled towards land and then turned back away from land within 20 km of shore. Trips where the maximum distance traveled away from land was <20 km were labeled as 'near' distance, trips where the maximum distance was >20 km but <75 km were labeled as 'mid' distance, and trips where the maximum distance traveled from land was >75 km were labeled as 'far' distance. All locations within 5 km of land were labeled as 'coastal' locations. Our categorical trip distance variable was used as an interaction term with our oceanographic variables as we hypothesized that the effect of each variable on seal movement behavior would differ based on trip distance.

For models of seal movement behavior in the Bering Sea during the ice-covered season (December–April), we included sea ice variables. Specifically, we include sea ice concentration and a 'distance from the ice edge' variable, where the ice edge was defined as the 15% ice concentration contour. Spotted seals are known to strongly prefer the marginal ice zone near the ice edge (Burns 1970, Lowry et al. 2000). We additionally created a categorical sea ice variable where the 'no ice' category was defined as <15% ice concentration and the 'ice' category was defined as >15% ice concentration. We included the categorical ice variable as an interaction term with all oceanographic variables.

2.3. Fish prey identified from seal stomach contents

We summarized stomach contents data collected from spotted seals harvested for subsistence during 2000–2020 (Quakenbush et al., 2009; ADF&G unpublished data), focusing specifically on fish prey. Spotted seal stomachs were collected from the Alaska Native subsistence harvest as part of a biomonitoring program for assessing the health and status of seals. Fish prey are primarily identified to species by their otoliths, ear bones that are more resistant to digestion and thus often found in stomachs. Left- and right-side otoliths are distinguishable, and therefore a count of either side found within a seal stomach can provide a minimum number of individuals of a given species that were recently consumed by the seal. Otoliths from sculpins (Family Cottidae), flatfish (Family Pleuronectidae), snailfish (Family Liparidae), and pricklebacks (Family Stichaeidae) are small and may have degraded faster than otoliths of other species, making them more difficult to identify to genus or species; therefore, these fish taxa were only considered at the family level for our analyses.

Digestion times in pinnipeds are relatively short; soft parts are typically identifiable within 6 h of ingestion (Sheffield et al. 2001) and hard parts within 24 h (Murie and Lavigne 1986). Our sample of instrumented seals moved an average (± SE) of 44 ± 13 km in 24 h, and as such, stomach contents represent the prey consumed near the sampling location. Samples collected from Shishmaref were used to represent the coastal and nearshore environment of the Chukchi Sea during the ice-free season. Samples collected from St. Lawrence Island (Gambell and Savoonga) and Hooper Bay, were used to represent the central Bering Sea and eastern Bering Sea, respectively, during the ice-covered season.

We first assigned whether each fish species was present (1) or absent (0) based on the occurrence of species-specific otoliths in the stomach. We also determined the relative abundance (RA) of each fish species to compare fish quantities consumed by each seal. RA_{ij} was calculated as the number of fish species *i* consumed by an individual seal *j* divided by the total number of fish consumed by seal *j*:

$$RA_{ij} = \frac{n\ of\ fish\ i\ found\ in\ seal\ j}{total\ n\ of\ fish\ found\ in\ seal\ j}$$

Thus, for each sampled seal, we determined the presence or absence of each fish species and the proportion of otoliths that were from each fish species.

From these data, we estimated the frequency of occurrence (FO) and the mean RA for each fish species within each of our region and season groupings using generalized linear models (function: 'glm'). We assessed differences between age classes for FO_i with the binary presence/absence data, using a generalized linear model with a binomial distribution and a logit-link function (i.e., logistic regression). Using this methodology, we are technically estimating the *probability* of occurrence, however, we use the term *frequency* of occurrence to maintain consistency with prior studies of seal diet (Pierce and Boyle 1991, Tollit et al. 2010, Crawford et al. 2015). We also assessed differences between age classes for the mean RA_i using a generalized linear model with a binomial distribution and a logit-link function, however, because the RA_{ij} is a proportion, we also needed to weight each RA value by the total number of fish found within each stomach, which effectively converts our proportional data into a binary format. Fish species with a FO >0.2 (i.e., 20%) for at least one region/season/age class category were considered major prey species. Fish prey species with a FO <0.2 and all unidentified fish were pooled into one group ('other fish'), for which the mean RA was also calculated. Results for both the FO and RA analyses are presented as percentages.

3. Results

All seals combined, we received data for 80,452 locations, 112,011 individual dives, and 7,109 CTD profiles. The CTD-SRDLs transmitted for 190 ± 47 days (mean ± SD; range 117–288 days) (Table 1). During the period each tag was operating, seals spent an average of 28 ± 29 cumulative days hauled out. Despite a large record of dives, total dive time covered by dive and surface records only accounted for an average of 7 ± 3% of total operation time after accounting for periods when seals were hauled out, meaning that most dive records were not transmitted, likely due to the prioritization of CTD profile data. The median distance between CTD profiles was 11 km (mean ± SD: 20 ± 33 km).

3.1. Spotted seal movements, habitat use, and dive behavior

Diagnostic plots affirmed that a 6-hour interval was most appropriate for estimating locations and behavioral states using the sSSM, resulting in 14,981 estimated locations ('#sSSM locs', Table 1). The median distance between estimated locations was 8 km (mean ± SD: 11 ± 12 km). Seals exhibited periods of resident and transiting behavior throughout their movements (Fig. 1). During the ice-free season, seals were primarily in the Chukchi Sea, Bering Strait, and the northeastern Bering Sea, whereas during the ice-covered season seals were primarily in the Bering Sea or moving south towards the Bering Sea (Fig. 1). Seals that were tagged in the Bering Sea remained in the Bering Sea, whereas seals that were tagged in the Beaufort Sea moved into the Chukchi Sea during the ice-free season and most continued south into the Bering Sea in advance of the ice-covered season.

Seals tended to remain closer to land during the ice-free season (median: 24 km, mean ± SD: 52 ± 60 km) than during the ice-covered season (70 km, 75 ± 55 km) when seals were more often at distances >100 km from land (Fig. 2 a). Seals tended to use shallower depths when in the Chukchi Sea during the ice-free season (median: 31 m, (mean ± SD: 28 ± 24 m) than in the Bering Sea during the ice-covered season (40 m, 47 ± 30 m) when seals more often used waters >75 m deep (Fig. 2 a). During the ice-free season, seals rarely encountered sea ice (4% of locations in >15% sea ice concentration). Seals used sea ice during the ice-covered season (56%

of locations in sea ice) but were also in open water (44% of locations in open water). Both pup (median: 0%, mean ± SD: 18 ± 25%) and non-pup (34%, 35 ± 26%) seals were most often in areas with low sea ice concentrations during the ice-covered season, however, non-pups also frequently used areas with higher ice concentrations whereas pups primarily remained in areas with <25% sea ice concentration (Fig. 2 a). Pups tended to occur outside the pack ice south of the ice edge (median: -25 km, mean ± SD: -32 ± 148 km) whereas non-pups were more often within the pack ice (35 km, 27 ± 89 km), although seals of all age classes were distributed around the marginal ice zone and the ice edge. There was no association between the habitat seals used and behavioral state.

Dive behavior was nearly identical during both seasons and in both seas and did not differ among sexes, age classes, or behavioral state (Fig. 2 b). While the maximum dive depths reached by seals included depths throughout the water column, more were closer to the bottom than near the surface (median dive depth: 85% of water column). Most dives (59%) were >75% of water depth, while only 10% of dives were <25% of water depth. In addition, 15% of all dives in water >10 m deep were within 1 m of the sea floor. Most (73%) of all dives had a TAD index >0.75, and the median TAD index (0.87) indicated that seals primarily made square-shaped dives, where most time was spent at the maximum depth of the dive.

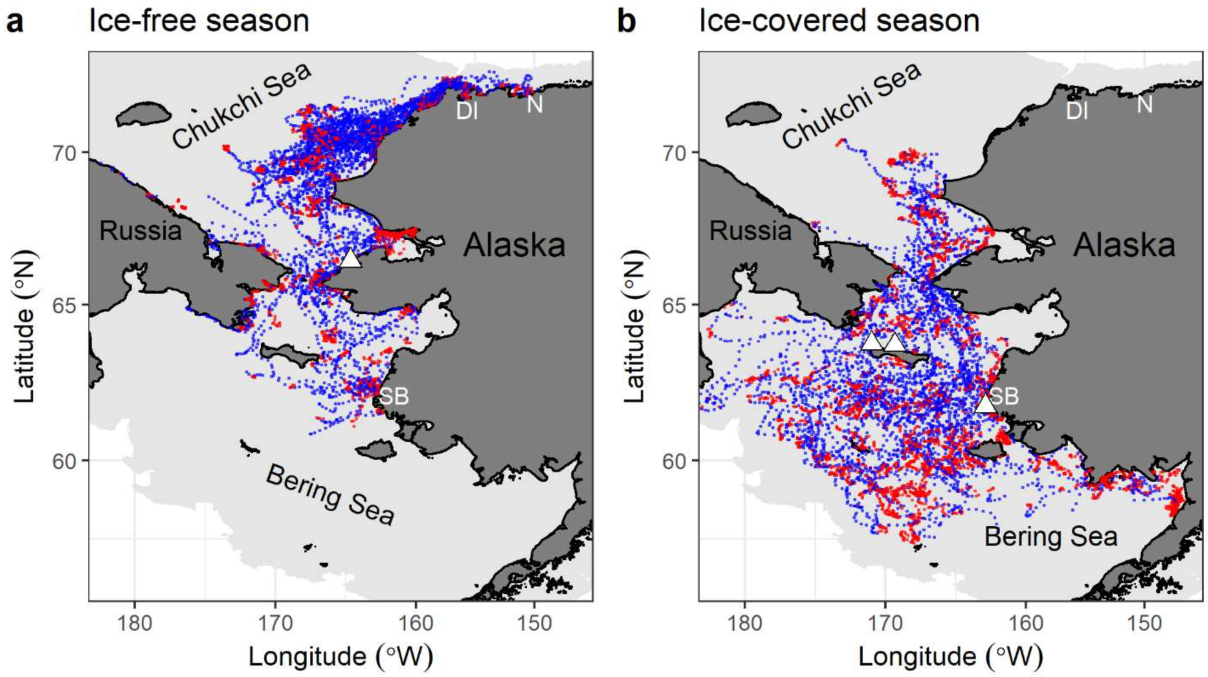

Fig. 1. Estimated locations and behavioral states for spotted seals (n = 23) tagged in the Bering (Scammon Bay (SB)) and Beaufort (Nuiqsut (N), Dease inlet (DI)) seas of Alaska during the ice-free season (a, July–November) and the ice-covered season (b, December–April), 2016–2020. Red indicates resident behavior and blue indicates transiting behavior. Light gray shading is the continental shelf, defined by the 200 m depth contour. White triangles represent locations where spotted seal stomachs were collected from the Alaska Native subsistence harvest (Ice-free season: Shishmaref, Ice-covered season, north to south: Gambell, Savoonga, and Hooper Bay).

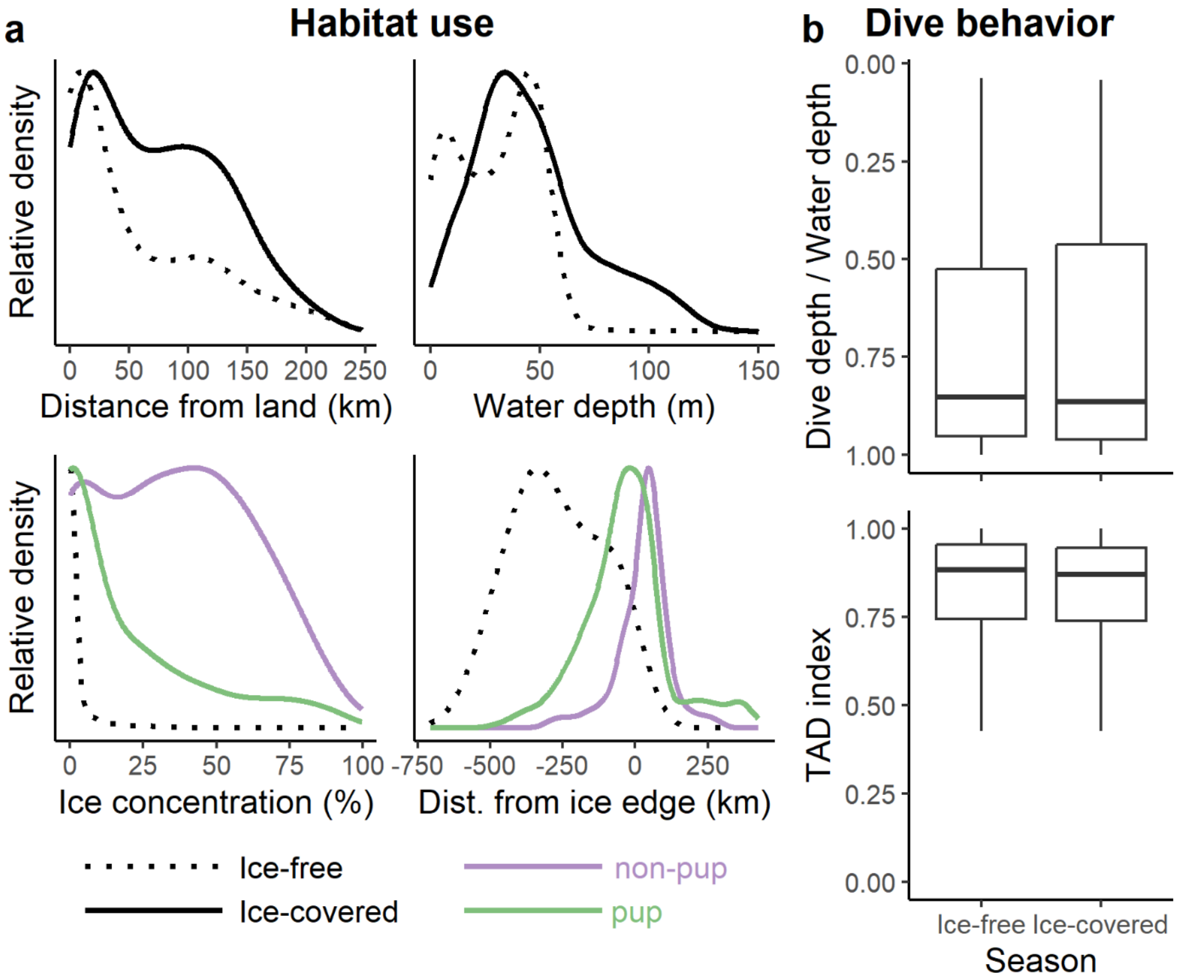

Fig. 2. Habitat use (a) and dive behavior (b) for spotted seals during the ice-free (July–November) and ice-covered (December–April) seasons. For habitat use, distances from land, water depths, ice concentrations, and distances from the ice edge are shown with relative density plots. Plots for ice concentration and distance from the ice edge depict relative densities for all seals during the ice-free season and separately for non-pup and pup seals during the ice-covered season. Negative distances from the ice edge represent densities in ice concentrations <15% or open-water and positive distances represent densities in ice concentrations ≥15%. Dive behavior includes the proportion of the water column used by each dive, and the Time-At-Depth (TAD) index (where values approaching 1 indicate the seal spent most of its dive near the maximum depth of the dive and values approaching 0 indicate the seal spent most of its dive near the

surface or at mid-depths), both of which are displayed as box plots, where the thick horizontal line is the median, and the box is the interquartile range.

3.2. Seal movement behavior and oceanography inferred from CTD-SRDLs

Merging location, dive, and CTD data by interpolating the location of each datum along a seal's track allowed us to visualize how seal behavior relates to the oceanographic space seals move through (Fig. 3, Supplement 1, Figs. S1–S44). In the Chukchi Sea during the ice-free season, seals encountered areas with warmer and fresher water when closer to shore, and cooler, more saline waters at the bottom and when farther from shore. During much of the ice-free season, seals were in areas where warmer water (>3° C) extended to the sea floor (60 ± 20% of each seal track during the ice-free season (mean ± SD)). In the Bering Sea during the ice-covered season, ice-covered waters used by seals tended to be less stratified and cooler. In most cases water temperatures were -1 °C or colder throughout the water column when under sea ice. When seals moved out of the sea ice and closer to the shelf break in the central Bering Sea, water temperatures were warmer (see Fig. S18 or Fig. S26 in Supplement 1).

Our top-performing movement behavior model for the ice-free period in the Chukchi Sea included bottom temperature ($X^2 = 19.43$, d.f. = 1, p = <0.001), bottom salinity ($X^2 = 13.11$, d.f. = 1, $p < 0.001$), trip distance ($X^2 = 63.10$, d.f. = 1, $p < 0.001$), age class ($X^2 = 0.63$, d.f. = 1, p = 0.42), and interactions between these terms (Table 2, Supplement 2). The model included interactions between bottom temperature and trip distance ($X^2 = 11.29$, d.f. = 1, p = 0.01), bottom temperature and age class ($X^2 = 5.27$, d.f. = 1, p = 0.02), and bottom salinity and age class ($X^2 = 4.99$, d.f. = 1, p = 0.02). The resident state was more likely when bottom temperatures were colder for pups, and also for non-pups, but only during far-distance trips (Table 2, Fig. 4). Among trip distances, seals were more likely to be in a resident state when near the coast (<5 km from land), and during near-distance (<20 km) trips from land, however, the interaction term between trip distance and bottom temperature resulted in the resident state also being more likely during far distance trips when bottom temperatures were colder (Table 2, Fig. 4). Seals were least likely to enter the resident state during mid-distance trips from land (20 – 75 km). For bottom salinity, the relationship with seal movement was significant for pups only, where pups were more likely to be in the resident state when bottom salinities were fresher (Fig. 4).

For the ice-covered season in the Bering Sea, our top performing model included bottom temperature ($X^2 = 7.60$, d.f. = 1, $p = 0.005$), age class ($X^2 = 15.97$, d.f. = 1, $p < 0.001$), sex ($X^2 = 1.30$, d.f. = 1, $p = 0.25$), and interactions between bottom temperature and age class ($X^2 = 7.02$, d.f. =1, $p = 0.008$) and bottom temperature and sex ($X^2 = 6.59$, d.f. = 1, $p = 0.01$) (Table 2, Supplement 2). The resident state was significantly associated with colder bottom temperatures, and this relationship was stronger for females than males and for non-pups than for pups (Fig. 4).

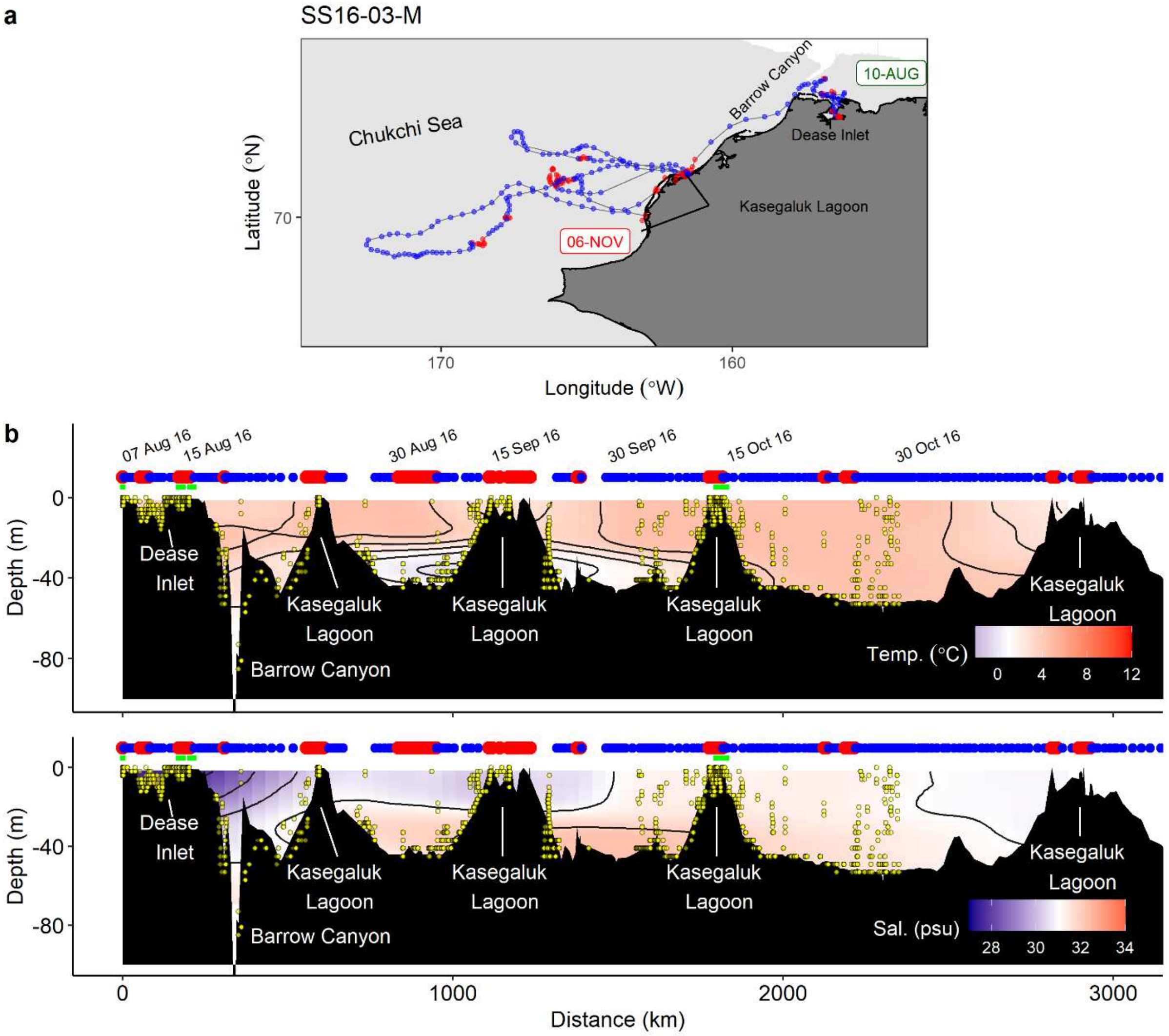

Fig. 3. (a) Track of estimated locations for spotted seal *SS16-03-M* that overlap with oceanographic data presented in (b), from 10 August to 6 November 2016. Red locations indicate resident behavior and blue locations indicate transiting behavior (start date in green, end date in red). Light gray shading is the continental shelf, defined by the 200 m depth contour. (b) Oceanographic and dive profile along the track of seal *SS16-03-M*, shown in (a). The location of each CTD profile along a seal's track was determined by interpolating the location based on time stamps. Then, inverse distance weighting was used to create a 2-dimensional representation of the oceanographic conditions the seal moved through. Temperature (top panel) and salinity (bottom

panel) contour intervals are 1°C and 1 psu, respectively. Bathymetry is shown in black. Yellow dots are maximum dive depth for dives transmitted as dive data (not CTD data). Circles above each plot are location estimates along the track, colored by behavioral state as in (a). Green squares below location estimates indicate periods when the seal was hauled out. This seal did not encounter sea ice while the CTD-SRDL was transmitting.

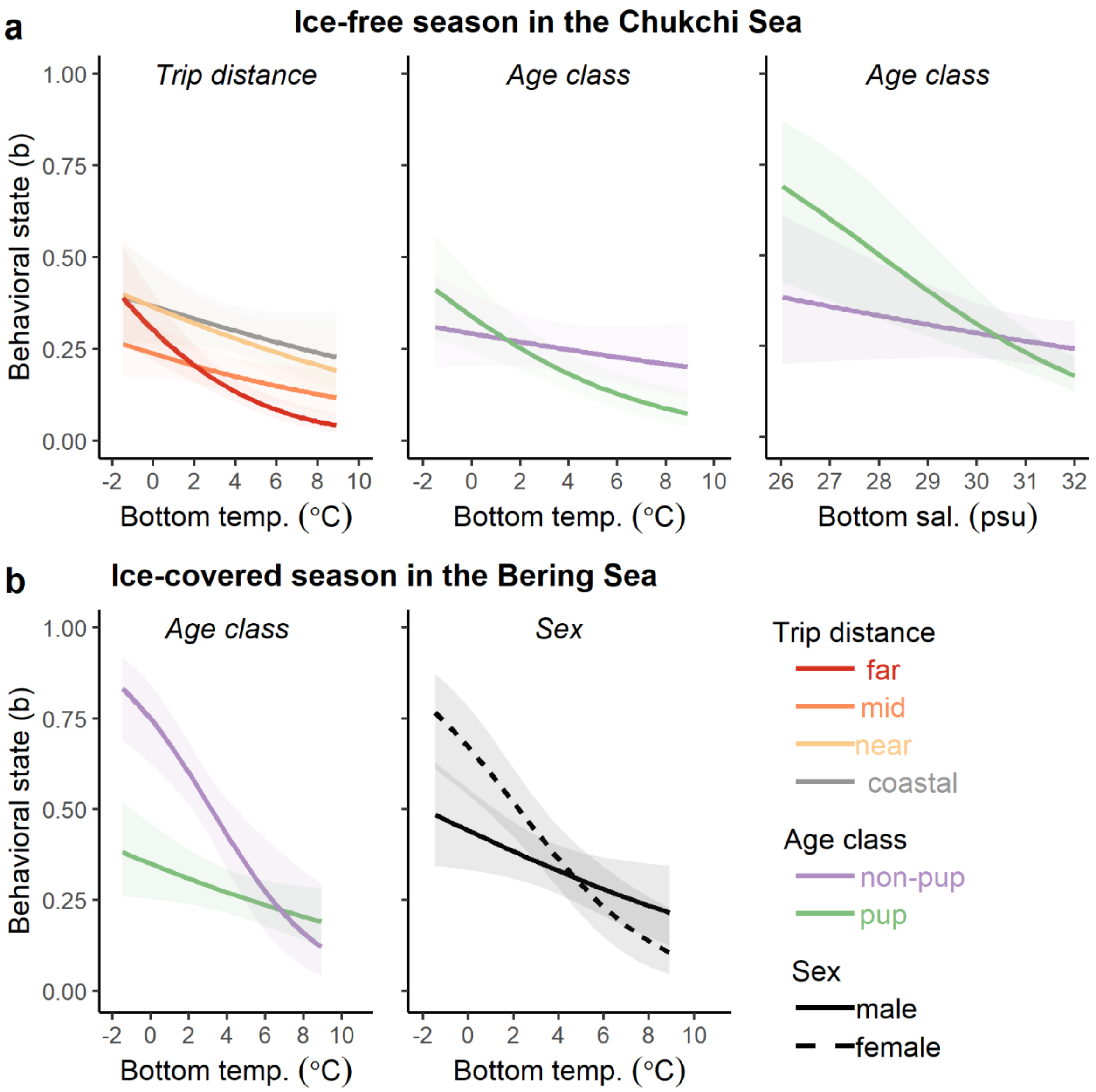

Fig. 4. Seal behavioral state (i.e., resident or transiting) relative to statistically significant oceanographic variables for the (a) ice-free and (b) ice-covered seasons. Values approaching 1 represent increasing resident behavior and values approaching 0 represent transiting behavior. Lighter bands are the 95% confidence bands around each line.

3.3. Fish prey identified from seal stomach contents

Stomach contents from 521 non-pup spotted seals harvested near Shishmaref were used to represent the nearshore diet of seals in the Chukchi Sea during the ice-free season. Individual seals consumed an average (± SE) of 2.1 ± 0.06 fish species (maximum = 9). Pacific herring (*Clupea pallasii*, FO ± 95% CI = 57% ± 3%), saffron cod (*Eleginus gracilis,* 36% ± 4%), and rainbow smelt (*Osmerus mordax,* 29% ± 4%) had the highest frequencies of occurrence (Fig. 5a). Of these, saffron cod was the most abundant prey species in seal stomachs (mean RA ± 95% CI = 38% ± 3%); followed by Pacific herring (23% ± 3%), rainbow smelt (12% ± 2%), and Arctic cod (*Boreogadus saida,* 12% ± 2%) (Fig. 5b). Pup (n = 276) and non-pup fish diets were generally similar (Figs. 5 and 6); however, pups had a significantly lower FO (36% ± 5%) and mean RA (8% ± 4%) for Pacific herring, lower mean RA for Arctic cod (7% ± 3%) and a higher mean RA for saffron cod (54.3% ± 5.2%) (Supplement 3).

Stomach contents from 18 non-pup seals harvested at St. Lawrence Island were used to represent seal diet during the ice-covered season in the central Bering Sea. Seals consumed an average (± SE) of 3.4 ± 0.5 fish prey species (maximum = 10). Major fish prey species included Arctic cod (FO ± 95% CI = 44% ± 22%), saffron cod (39% ± 23%), walleye pollock (*Gadus chalcogrammus* 33% ± 24%), capelin (*Mallotus villosus,* 28% ± 24%), and sculpins (22% ± 24%). Capelin (mean RA ± 95% CI = 30% ± 16%), saffron cod (23% ± 16%) and Arctic cod (20% ± 17%) were the most abundant fish prey consumed by non-pup seals (Fig. 5). Most fish species had a lower FO among pups than for non-pups (Figs. 5a and 6a), but this difference was only significant for walleye pollock (FO for pups: 5% ± 22%) (Supplement 3). For pups, Arctic cod had the highest FO (24% ± 22%) and the mean RA for Arctic cod was significantly higher than for non-pups (53% ± 25%) (Fig. 6b, Supplement 3).

Stomach contents from 14 non-pup seals harvested at Hooper Bay were used to represent the nearshore diet during the ice-covered season in the Bering Sea. The average number of fish prey species (± SE) found in seal stomachs for this group was 3.6 ± 0.5 (maximum = 7). Prey species with the highest frequencies of occurrence were saffron cod (FO ± 95% CI = 86% ± 14%), rainbow smelt (64% ± 29%), and Arctic cod (36% ± 29%). Saffron cod (mean RA ± 95% CI = 74% ± 10%), rainbow smelt (14% ± 7%), and Arctic cod (9% ± 16%) were the most abundant prey consumed by this group (Fig. 5). Too few pup seals were harvested at Hooper Bay to make statistical comparisons.

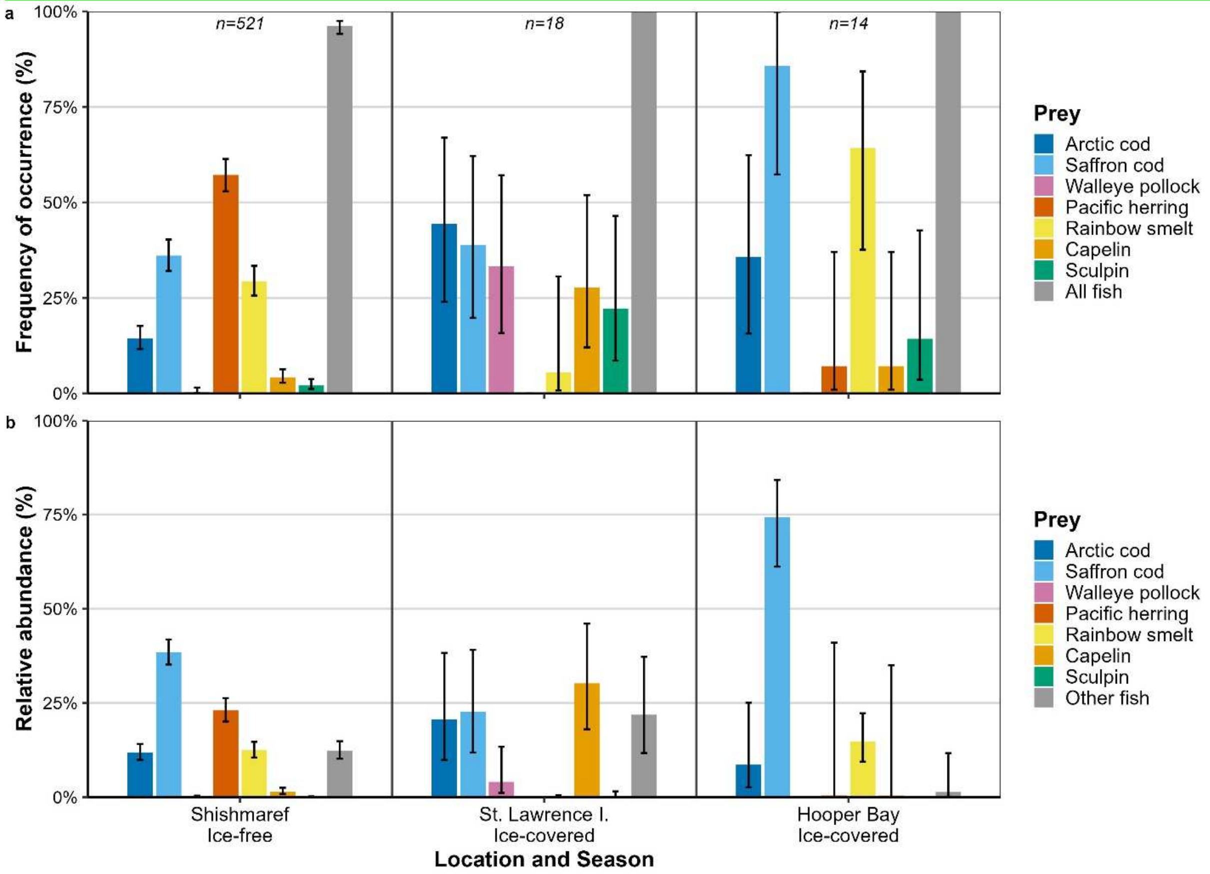

Figure 5. Frequency of occurrence (a, FO_i ± 95% Confidence Interval (CI)) and mean relative abundance (b, RA_i ± 95% CI) of fish prey identified in stomach contents of non-pup spotted seals (≥ 1 year of age). Spotted seals were sampled near Shishmaref during the ice-free season and near St. Lawrence Island and Hooper Bay during the ice-covered season during 2000–2020. Prey items presented were those with a FO ≥ 20% for at least one location/season group of spotted seals.

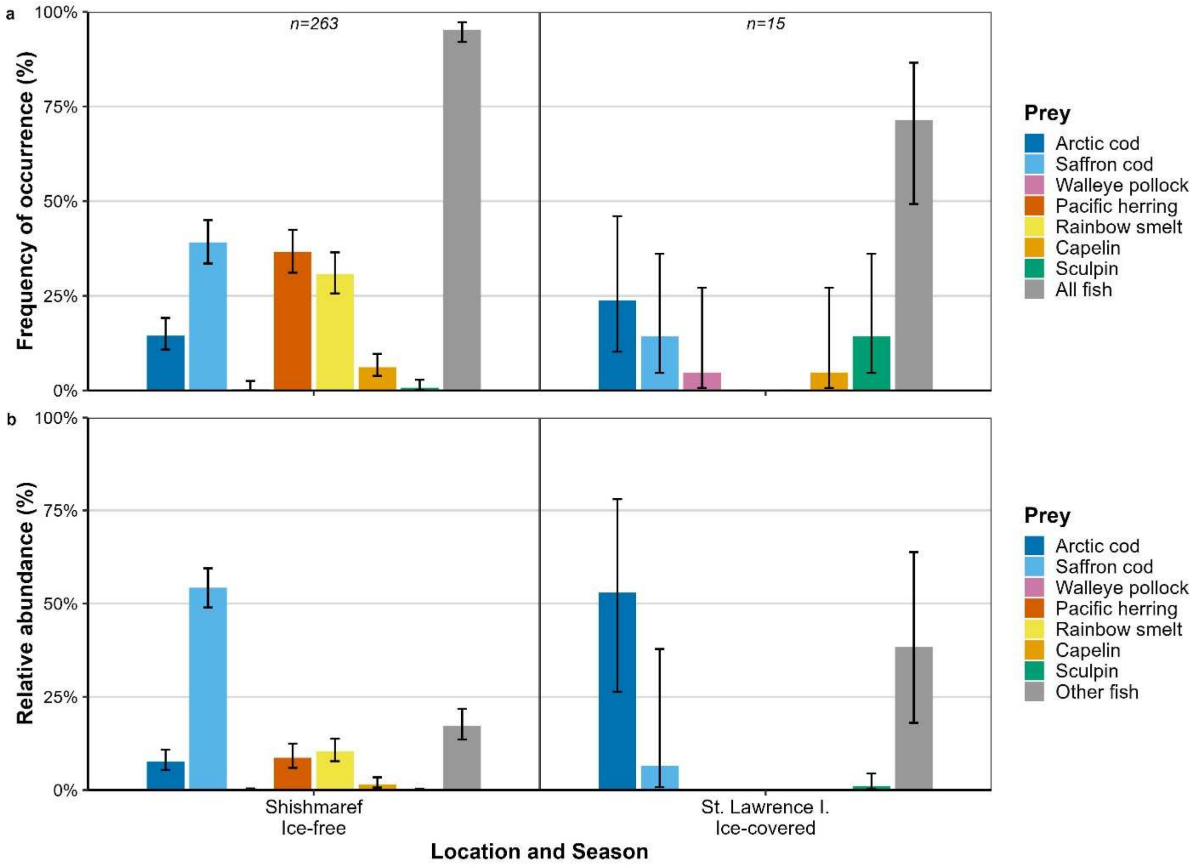

Figure 6. Frequency of occurrence (a, FO_i ± 95% Confidence Interval (CI)) and mean relative abundance (b, RA_i ± 95% CI) of fish prey identified in stomach contents of spotted seal pups (<1 year of age). Spotted seals were sampled near Shishmaref during the ice-free season and near St. Lawrence Island and Hooper Bay during the ice-covered season during 2000–2020. Prey items presented were those with a FO ≥ 20% for at least one location/season group of spotted seals.

4. Discussion

Spotted seals exhibited varying degrees of resident behavior, which we consider indicative of foraging, in nearly all conditions they encountered. This is somewhat expected for generalists, as spotted seals are considered (Boveng et al. 2009), given their broad movements and piscivorous diet that includes many species. Nonetheless, we found patterns and relationships that improve our understanding of spotted seal foraging, most notably that resident behavior was consistently associated with near-bottom conditions and that spotted seal dives were mainly to near-bottom depths. Differences in habitats used and movement behavior among spotted seal sexes and age classes further suggest different foraging behavior among demographic groups may be occurring.

4.1. Assumptions

We assumed that in most cases, the resident behavioral state was associated with foraging. Alternatively, the resident state may also be associated with hauling out, resting at sea, or possibly unknown behaviors. Using the haul-out data transmitted by the CTD-SRDLs, we attempted to account for resident periods that were due to hauling out. For the ice-free period, only 17% of all six-hour intervals contained haul-out bouts of any duration and only 28% of all resident intervals contained a haul-out bout of any duration. Similarly for the ice-covered period, 19% of all six-hour intervals contained haul-out bouts of any duration and only 28% all resident intervals contained a haul-out bout of any duration. As such, the behavior responsible for most resident locations was not seals hauling out. Spotted seals may rest at sea, but this behavior is not well documented for this species. We evaluated the potential for resting at sea when our limited surface and dive records were available and found no differences between behavioral state and time at the surface. It is likely, however, that some periods of resident behavior included in the model dataset were not related to foraging, and that some foraging occurred while in the transiting state, and that the occurrence of both reduced our ability to describe true relationships between foraging and oceanography based on movement behavior.

Seal stomach content data represent a short period prior to the seal being harvested. Thus, some prey found in areas away from harvest locations may not be present in the stomach, or prey in the stomach may only be representative of the localized area around the harvest location. However, the primary prey that we found in our samples of seal stomachs are broadly distributed on the shelf (i.e., saffron cod throughout the nearshore environment or Arctic cod abundant in northern Bering and Chukchi seas, Eisner et al. 2013, De Robertis et al, 2017). Comparisons of prey found in our sample of seal stomachs with samples collected from other locations in prior studies helps to affirm the broader importance of the species we identified from our limited sample (see below).

4.2. Spotted seal foraging ecology and prey

4.2.1. Ice-free season

During the ice-free season, spotted seals were mostly nearshore, in part because they haul out on land during this time (Frost et al. 1993, Lowry et al. 1998). This is one reason why the ‘coastal’ trip distance category was most strongly associated with the resident state as it encompassed land-based haul-outs and associated resting behavior as well as possible nearshore foraging. In the Chukchi Sea, commonly used coastal areas included those around Kasegaluk Lagoon, within Kotzebue Sound, and along the northern coast of Chukotka, Russia. In the Bering Sea, commonly used areas included Scammon Bay and the nearby waters north of Nunivak Island, Golovin Bay in Norton Sound, and bays along the eastern coast of Chukotka. Many of these areas were also used by spotted seals tagged in the early 1990s (Lowry et al. 1998). Commonly used coastal haulouts may appeal to seals for their relative safety as well as their proximity to both nearshore and offshore foraging (Quakenbush 1988, Frost et al. 1993, Lowry et al. 1998). For example, the use of Kasegaluk Lagoon by spotted seals is well documented (Frost et al. 1993); the name, 'Kasegaluk' is a variation of the Iñupiaq word for spotted seal, qasiġiaq. The barrier islands offer a safe area to haul out that is less accessible to land-based predators. Hunters have remarked that when seals arrive in the spring, they sink when killed, but later in fall they float, indicating seals foraged intensely and built-up fat during this time (Frost et al. 1992). This pattern is corroborated by changes in observed blubber thickness of subsistence harvested seals, which tend to have thinner blubber in the spring and increasingly thicker blubber in the summer and autumn (ADFG, unpublished data).

Warmer, fresher, and less stratified waters are prevalent along Alaska's coast in both the Bering and Chukchi seas during the ice-free season (Stabeno et al. 1999, Eisner et al. 2013, Baker and Hollowed 2014), and spotted seals appear to spend substantial time in this environment. Fresher coastal waters are known to contain both Arctic and saffron cod (De Robertis et al. 2017), as well as rainbow smelt (Eisner et al. 2013, Logerwell et al. 2015). These species were among the most prevalent in subsistence harvested seal stomachs during the ice-free season from Shishmaref, as was Pacific herring (Fig. 5). Although we only have prey samples from Shishmaref, spotted seals are likely targeting these species in the nearshore environment more broadly. For example, Arctic cod, rainbow smelt, and Pacific herring have all been documented in the vicinity of Kasegaluk lagoon during the ice-free season when spotted seals are present (Frost et al. 1993). Pacific herring may be more prevalent in the nearshore environment of the Bering Sea than in the Chukchi Sea during the ice-free season (De Robertis et al. 2017) and have been documented as an important prey species for spotted seals in the eastern Bering Sea (Lowry et al. 1979). Although not prevalent in our sample from Shishmaref, pink (*Oncorhynchus gorbuscha*) and chum salmon (*O. keta*) are also present in less stratified coastal water during the ice-free season (Eisner et al. 2013), as well as lagoons (Logerwell et al. 2015), and are likely important fish prey for spotted seals later in the summer (Fedoseev 2000).

Commonly used coastal haulouts may also be selected due to their proximity to offshore foraging locations (Lowry et al. 1998). For example, spotted seals often moved offshore to forage and then returned to the barrier islands at Kasegaluk lagoon (Figs. S1, S3, S5, S19, S21, S29, S31, S35, S37, S39, S43 in Supplement 1). When far offshore in the Chukchi Sea (>75 km from land), a resident state was more likely to occur in colder near-bottom waters indicative of a western Bering Sea origin. Waters of western Bering Sea origin are known to be more productive and carry nutrients that support a rich benthic community in the central Chukchi Sea (Feder et al. 1994), and to contain higher concentrations of zooplankton, such as copepods (Brodsky 1950, Hopcroft et al. 2010) and euphausiids (Berline et al. 2008), that in turn may attract Arctic cod (Gray et al. 2016) and Pacific herring (Volkov and Murphy 2007, Andrews et al. 2016), respectively. Indeed, nearly half of all spotted seal resident locations in the Chukchi Sea during the ice-free season occurred in the vicinity of the Central Channel, which is a primary pathway by which nutrient-rich Bering Sea waters are moved across the Chukchi shelf (Weingartner et al. 2005).

Spotted seals of both age classes and sexes used both nearshore and offshore environments while in the Chukchi Sea during the ice-free period. However, our movement model results, along with where each demographic group was more likely to be in a resident state, suggest that pups may behave differently than non-pups. Pups were most likely to enter the resident state when encountering fresher and/or colder bottom water (Fig. 4). Fresher conditions near the bottom would mostly occur in the coastal or nearshore environment where river discharge would influence water salinity. As such, 42% of all resident locations for pups occurred during coastal or near-distance trips, whereas 35% occurred during far-distance trips (>75 km from land). For non-pups, however, most resident locations (60%) were associated with far-distance trips whereas only 24% of resident locations occurred when seals were closer to land (near-distance or coastal trips). Although the percentage of locations associated with far-distance trips was nearly equal between age classes (53% non-pups, 47% pups), 65% of all far-distance resident locations come from non-pup seals, therefore the significant relationship between bottom temperature and behavioral state for far-distance trips is mainly representing the behavior of non-pup seals. These results indicate a nearshore relationship between resident behavior and near bottom water conditions that is more associated with pups, and an offshore relationship that is more associated with non-pup seals, albeit with substantial overlap in behavior among age classes. The prey identified from seal stomach contents fits this pattern, as the relative abundance of saffron cod, prey found in the nearshore environment, was higher for pups than for non-pups (Figs. 5 and 6). The higher occurrence of Pacific herring in the stomachs of non-pups may reflect that this species is targeted by non-pups in the nearshore environment, but also may reflect some offshore foraging, as adult Pacific herring occur in colder, offshore waters (Eisner et al. 2013). Otolith lengths, which can be used to estimate fish length (Munk 2012), and therefore estimate fish age (Niggol 1982), indicated that most Pacific herring in stomach samples from non-pup seals harvested at Shishmaref were of adult size classes. Further, seals of both age classes were least likely to enter the resident state during mid-distance trips (between 20 and 75 km from land, Fig. 4, Table 2), resulting in a bimodal pattern of the resident state and trip distance. In terms of foraging behavior, this pattern may reflect spotted seals foraging in both nearshore and offshore environments, but that offshore foraging as a behavior is more likely for older seals. Such a pattern is reasonable given the increased energetic demands and likelihood that the skills needed to successfully travel to and forage in the deeper waters of the central Chukchi Sea are learned over time.

Given the frequency of dives to the sea floor, spotted seals may also move offshore to forage on benthic prey, as the Bering and Chukchi shelves are known to have high benthic productivity (Grebmeier et al. 2006b). Although we focused on fish in this study, spotted seals also consume crustaceans (e.g., amphipods, and shrimp, especially Crangonidae; Quakenbush et al. 2009). In addition to stomach contents, stable isotope analysis has confirmed that a portion of spotted seal diet is obtained from benthic communities sustained by sympagic production (Wang et al. 2016). Spotted seals are not physiologically limited from foraging at the bottom of the continental shelf, where depths are shallow (<200 m). As such, seals may dive throughout the water column in search of food, as indicated by our dive data, and opportunistically feed on prey that may occur at any depth.

4.2.2. Ice-covered season

Spotted seals are typically found in the Bering Sea during the ice-covered season where they are known to be abundant in the marginal ice zone (Burns 1970, Lowry et al. 1998, Citta et al. 2018), as was the case for seals in our study (Figs. 1 and 2). We expected that the resident state would relate to sea ice conditions. Despite 84% of haul-outs occurring on sea ice during the ice-covered season, and 76% of resident locations occurring in sea ice, none of the top performing models of movement behavior included a sea ice variable (Supplement 2). This outcome is partly explained by spotted seals using areas with low sea ice concentrations that would not restrict their movements. Further, only 23% of resident locations were associated with a haul-out during the ice-covered season, meaning that most resident locations were not associated with seals hauling out on sea ice. Sea ice, and the ice edge specifically, are clearly important habitats for spotted seals, but the lack of association between sea ice conditions and behavioral state suggests that other factors are influencing spotted seal movements within the marginal ice zone.

Relative to the ice-free season, waters were less stratified and more uniform under sea ice and tended to be cooler and more saline. Although waters appeared more uniform, our movement model still identified a relationship with bottom temperature, where the resident state was most likely when bottom temperatures were colder. Saffron cod, Arctic cod, and rainbow smelt were the most prevalent prey consumed by seals in the nearshore environment at Hooper Bay whereas walleye pollock and capelin were identified in seal diets near St. Lawrence Island, our sample representing the central Bering Sea (Fig. 5). Capelin are known to occur in cooler, more saline waters of the central Bering Sea (Eisner et al. 2013) and to be consumed by seals in the western Bering Sea (Bukhtiyarov et al. 1984, Fedoseev 2000). In addition to capelin, other primary prey consumed by spotted seals in the western Bering Sea include walleye pollock, Arctic cod, saffron cod, and sand lance (*Ammodytes hexapterus*) (Fedoseev 2000). Broad use of the marginal ice zone, the resident state being associated with bottom temperature, and dives primarily to near-bottom depths all suggest that seals may target the near-bottom zone throughout the Bering Sea for foraging, where they may encounter many different prey species.

The relationship between bottom temperature and movement behavior was stronger for non-pups than pups, and for females than for males. Non-pup females were in the resident state 77% of the time during the ice-covered season, versus 59% of the time for non-pup males and ~40% of the time for pups. Adult females have greater energetic demands during this time of pregnancy, pupping, and lactating. The strong relationship between the resident state and bottom temperature for non-pups and for females suggests that these patterns may reflect non-pup females spending more time foraging, and/or targeting specific, energy-rich prey with more narrowly defined habitat associations, such as capelin (Perez 1994, Brodeur et al. 1999), which were the most abundant prey for non-pups but among the least abundant prey for pups (Figs. 5 and 6).

Our study period aligned with two years of record-low sea ice in the Bering Sea that dramatically altered many ecosystem processes in the region (Baker et al. 2020, Huntington et al. 2020). During the winters of 2017/2018 and 2018/2019, sea ice extent was minimal and much of the central Bering Sea remained ice-free throughout the winter. During these years, seals continued to use the central Bering Sea, but hauled out at St. Lawrence, St. Matthew, and Nunivak islands between foraging bouts instead of using sea ice (Supplement 1, Figs. S17, S25, S33, and S35). Interestingly, seals in the central Bering during these low ice years encountered warmer waters that extended to the sea floor (Supplement 1, Fig. S18 and S26). Conditions during the winter of 2019/2020 were more typical of previous years and seals in the central Bering Sea encountered colder water, likely in part due to greater sea ice extent (Supplement 1, Figs. S38, S42 and S44). The significant association between the resident state and colder bottom temperatures for all seals, and for female non-pups in particular, could mean that reduced sea ice extent and warmer waters occurring in the central Bering Sea would affect spotted seal movements that are likely associated with foraging (i.e., seals would remain in more northern waters with colder bottom temperatures). Years with less ice and warmer water may also allow currently important or novel prey species (e.g., Pacific cod, *Gadus macrocephalus*; Spies et al. 2019) to occur farther north than usual (Stabeno et al. 2012, Mueter et al. 2021), or become more abundant (e.g., pink and chum salmon, Logerwell et al. 2015). Such changes could allow spotted seals to continue foraging in similar areas despite waters becoming warmer, in which case we would expect the relationship between the resident state and colder bottom temperatures to weaken over time. However, studies of other marine mammals in the BCB area have suggested that altered diets or foraging behavior due to environmental change has contributed to declines in body condition (Boveng et al. 2020, Choy et al. 2020), either due to a decoupling of sea ice and good foraging habitat or lower nutritional quality of altered diets. It is not clear whether such changes will result in cumulative fitness costs, or benefits, to spotted seals.

4.3 Opportunities and limitations of oceanographic data from CTD-SRDLs

Oceanographic data collected by CTD-SRDLs are useful for understanding the environment animals encounter and how it may influence behavior. Our visualizations of the environment seals encountered along their tracks (Fig. 3 and Supplement 1) highlight the utility of these data for learning about marine mammal biology. We expect our approach of using the CTD profile data to generate an interpolated oceanographic space that can then be related to animal movements or dive behavior will be applicable to other studies using animal-borne instrumentation. We programmed our tags to prioritize the transmission of CTD profiles over dive behavior data, resulting in substantial gaps in dive records. Moving forward, we recommend reconfiguring the CTD-SRDL settings to achieve a more balanced transmission of both data types. This would allow for the incorporation of dive data into the movement model as described in Gryba et al. (2019), while also providing sufficient information to generate the interpolated oceanographic space. However, balancing these data products, which both require relatively large amounts of data to transmit, may reduce the duration of tag operation. Alternatively, researchers may find such data useful for more integrated approaches that could include environmental data, such as oceanography, into the movement modeling and assignment of multiple behavioral states using R packages such as ‘momentuHMM’ (McClintock et al. 2017, McClintock and Michelot 2018). Further, data from CTD-SRDLs can be useful to oceanographers seeking to better understand shelf environments in places and at times where ship-based surveys are rare, such as in the winter under sea ice, for documenting changes in oceanography over time, and to validate powerful oceanographic models.

One important limitation is that the CTD-SRDLs only provide information about the oceanographic conditions seals encountered along their tracks, which may not include all conditions available to them or that might influence their behavior. For example, we hypothesized that the resident behavioral state would be associated with hydrographic fronts or stratified waters. Hydrographic fronts are known to be oceanographic hotspots that can aggregate prey at multiple trophic levels (Woodson and Litvin 2015), however, this is not well documented in the BCB region. We attempted to capture fronts by calculating the horizontal differences in temperature and salinity for various track distances, but most differences turned out to be zero. This outcome could occur if spotted seals move along these fronts more so than crossing through them. To explore this possibility, we selected periods where seals were in the resident state for at least three days and overlaid these locations onto modeled temperature and salinity fields obtained from the Regional Arctic System Model (RASM; Maslowski et al. 2012, Clement Kinney et al. 2022; https://nps.edu/web/rasm), a pan-Arctic coupled ice-ocean simulation forced with realistic reanalyzed atmospheric data from the 1958–2021 Japanese 55-year Reanalysis (JRA-55, Kobayashi and Iwasaki 2016). Plotting locations onto RASM temperature and salinity fields suggested that many of these longer periods of resident behavior occurred in the vicinity of hydrographic fronts (Fig. 7, Supplement 4). More work is needed to establish the importance of such fronts for foraging and doing so will require a combination of CTD-SRDL and modeled oceanographic data.

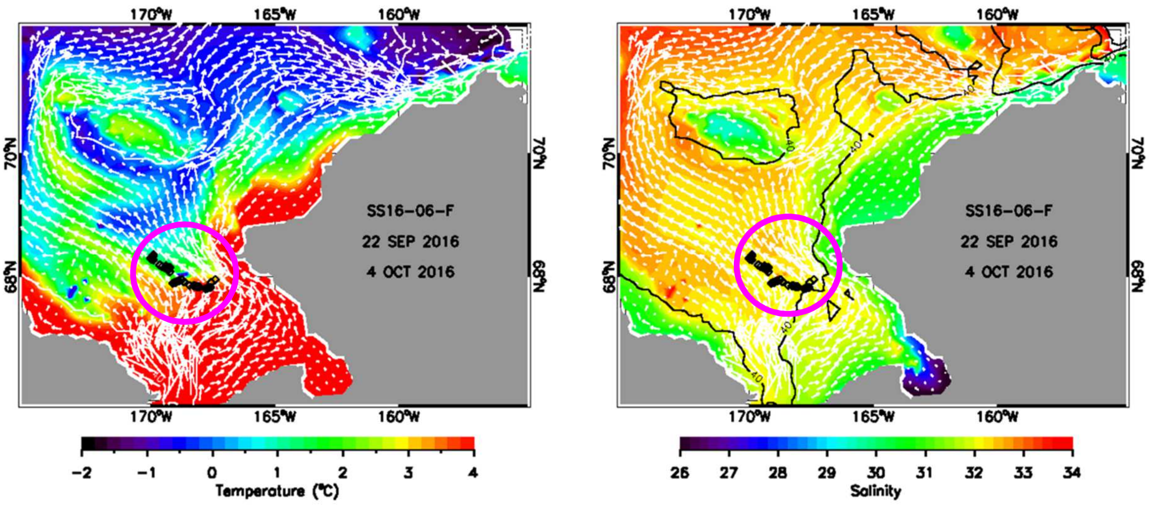

Fig. 7. Oceanographic conditions (bottom temperature (left) and salinity (right)) of Chukchi Sea 22 September – 4 October 2016. Data are from the RASM model. Black dots within magenta circles are resident locations for seal SS16-06-F during this period. White arrows are current velocity. This potentially significant foraging event appears along a hydrographic front, which is most apparent in the temperature field (left).

4.4. Conclusion

Spotted seals are generalists that likely exploit multiple habitats to forage on several fish species. We found that spotted seals used nearshore and offshore habitats throughout the year. During the ice-free season in the Chukchi Sea, spotted seals traveled far offshore and were most likely to be in the resident state when encountering cold bottom temperatures, indicative of waters originating in the Bering Sea. The resident state was also associated with cold bottom temperatures during the ice-covered season in the Bering Sea. Combined with dive behavior that showed seals mostly diving to near-bottom depths, these results suggest that spotted seals mainly forage near the bottom. That the resident state was consistently associated with colder bottom temperatures also suggests that seal behavior may be affected by warming conditions associated with climate change. Annual sampling of stomachs from the subsistence harvest, at multiple locations in both the Bering and Chukchi seas during both the ice-covered and ice-free seasons, will improve our ability to determine the relative importance of spotted seal prey. Such sampling will also document shifts in currently important and novel prey species as conditions change.

Acknowledgements

We dedicate this manuscript to Dr. Stephen Okkonen, in memory of his friendship and contributions to the fields of both physical and biological oceanography. We thank Ryan Adam, Isaac Leavitt, Aaron Morris, Joe Skin, Morgan and River Simon, Yukon and Wybon Rivers, and Al Smith for their assistance with tagging seals. Seal captures were conducted under research permits #15324 and 20466 issued by the National Marine Fisheries Service to the Alaska Department of Fish and Game (ADF&G), and under ADF&G’s Animal Care and Use protocols #27-2017-27, 27-2018-28, 27-2019-41, and 27-2020-35. Information on seal diet would not be available without the willingness of the seal hunters to contribute samples from their harvest, the support of their communities, local governments, and Tribal Councils. We appreciate the support from the North Slope Borough, Department of Wildlife Management, and the Ice Seal Committee. John Burns, Kathy Frost, Lloyd Lowry, and others (ADF&G retired) were instrumental in the development of seal biomonitoring and its great value comes from their early efforts to collect, process, and analyze samples, as well as archive the data. Fish otoliths were identified by William Walker and Louise Biderman. We thank Gay Sheffield, Letty Hughes, Mark Nelson, and Anna Bryan for field collections and sample processing; Juan Leon Guerrero, Heidi Isernhagen, Louise Biderman, Ryan Adam, and many others processed samples in the lab, entered and error-checked data. Data analysis and manuscript preparation were funded by the North Pacific Research Board (project #2118). Seal tagging was funded by the Office of Naval Research (grant #N00014-16-1-3019). Biomonitoring collections were funded by the National Oceanic and Atmospheric Administration (NOAA), National Marine Fisheries Service (NMFS) under awards NA16FX2034, NA05NMF4391187, NA08NMF4390544, and NA11NMF4390200 to the ADFish&G. The RASM project was supported by the Department of Energy (DOE) Regional and Global Model Analysis (RGMA) and the Office of Naval Research (ONR) Arctic and Global Prediction (AGP) programs. The Department of Defense (DOD) High Performance Computer Modernization Program (HPCMP) provided computer resources.

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Tables

Table 1. Summary information for the 23 spotted seals tagged with CTD-SRDL transmitters during 2016–2019 in the Bering and Beaufort seas of Alaska. Summaries include the total number of locations provided by the Argos system (# raw locs) and the number of 6-hour location estimates determined by a 2-state switching state space model (# sSSM locs).

Seal ID	Tagging location	Sex	Age class	Tagging date	First location	Last location	Duration of location data (d)	# CTD profiles	# Dives	# raw locs.	# sSSM locs.
SS16-01-F	DI*	F**	S***	27-Jul-16	28-Jul-16	13-Mar-17	229	0	90	1260	623
SS16-03-M	DI	M	A	03-Aug-16	7-Aug-16	10-Feb-17	187	113	1896	3102	637
SS16-05-M	DI	M	S	14-Aug-16	15-Aug-16	1-Feb-17	170	313	5271	3278	596
SS16-06-F	DI	F	A	17-Aug-16	17-Aug-16	3-Feb-17	169	278	4796	4357	648
SS16-07-M	DI	M	A	17-Aug-16	17-Aug-16	17-Jan-17	153	106	2359	3174	573
SS16-08-M	DI	M	S	25-Aug-16	25-Aug-16	8-Apr-17	226	256	4778	3776	743
SS16-09-F	DI	F	A	25-Aug-16	25-Aug-16	5-Apr-17	223	521	8004	4279	729
SS16-10-F	SB	F	S	18-Oct-16	19-Oct-16	4-Mar-17	137	250	4356	3161	495
SS16-11-F	SB	F	S	18-Oct-16	19-Oct-16	6-May-17	199	352	5573	2942	640
SS17-02-M	SB	M	A	10-Jul-17	11-Jul-17	25-Apr-18	288	305	4354	2777	705
SS17-05-M	DI	M	S	25-Jul-17	27-Jul-17	14-Jan-18	170	429	7502	4895	608
SS17-06-F	N	F	P	09-Aug-17	12-Aug-17	27-Dec-17	137	338	6564	4056	510
SS17-07-M	N	M	S	16-Aug-17	17-Aug-17	11-Jan-18	148	321	5952	4520	516
SS17-08-F	N	F	S	16-Aug-17	17-Aug-17	26-Feb-18	194	428	8190	5476	710
SS18-01-M	SB	M	S	03-Jul-18	4-Jul-18	4-Feb-19	216	269	3768	2250	560
SS18-03-F	DI	F	A	26-Jul-18	26-Jul-18	20-Nov-18	117	185	2754	2006	450
SS18-05-F	N	F	A	09-Sep-18	9-Sep-18	9-Jan-19	122	324	5195	3381	482
SS18-06-M	DI	M	P	20-Sep-18	1-Oct-18	31-May-19	242	578	9109	4952	924
SS18-07-F	DI	F	S	20-Sep-18	21-Sep-18	22-May-19	243	460	5704	4152	914
SS19-01-M	DI	M	A	17-Sep-19	18-Sep-19	15-May-20	241	417	5153	4089	859
SS19-02-M	DI	M	S	17-Sep-19	18-Sep-19	22-Jan-20	127	244	2837	2678	497
SS19-03-M	DI	M	A	17-Sep-19	18-Sep-19	23-Apr-20	219	197	3083	2244	721
SS19-04-M	DI	M	A	18-Sep-19	19-Sep-19	9-May-20	233	425	4719	3647	841
							TOTAL	7109	112011	80452	14981

*DI = Dease Inlet, SB = Scammon Bay, N = Nuiqsut
**F = female, M = male
***A = adult (≥5 yr), S = subadult (1-4 yr), P = pup (<1 yr)

Table 2. Explanatory variables, parameter estimates, significance tests, and interpretation for top candidate models of seal movement behavioral state (resident or transiting) for the ice-free period in the Chukchi Sea and the ice-covered period in the Bering Sea. Parameter estimates are from generalized linear models and the number gives the relative effect size (compared to other parameters) and the sign indicates direction of the relationship with the probability that a seal is in the resident state.

Explanatory variable	Parameter estimate (p-value)	Interpretation
Ice-free in the Chukchi Sea		
Intercept	-0.64 (0.005)	Baseline group is non-pups in coastal areas, which are more likely to be in the transiting state than the resident state
Trip distance (near)	-0.09 (0.36)	No difference in probability of being in resident state for near-distance trips versus using coastal areas for non-pups.
Trip distance (mid)	-0.69 (<0.001)	Less likely to enter resident state during mid-distance trips than when using coastal areas for non-pups.
Trip distance (far)	-0.91 (<0.001)	Less likely to enter resident state during far-distance trips than when using coastal areas, but significant interaction with bottom temperature (below).
Age class (pup)	-0.24 (0.40)	No difference in probability of entering resident state between non-pups and pups.
Bottom temperature	0.009 (0.93)	No trend in bottom temperature and behavioral state for non-pups in coastal areas.
Bottom salinity	-0.11 (0.18)	No trend in bottom salinity and behavioral state for non-pups.
Bottom temp. × near	-0.04 (0.14)	No trend in bottom temperature and behavioral state during near-distance trips for non-pups.
Bottom temp. × mid	-0.03 (0.69)	No trend in bottom temperature and behavioral state during mid-distance trips for non-pups.
Bottom temp. × far	-0.36 (0.001)	The resident state is more likely during far-distance trips when bottom temperatures are colder for non-pups.
Bottom temp. × pup	-0.31 (0.02)	The resident state is more likely when bottom temperatures are colder for pups.
Bottom sal. × pup	-0.27 (0.03)	The resident state is more likely when bottom salinities are fresher for pups.
Ice-covered in the Bering Sea		
Intercept	0.07 (0.76)	Baseline group is non-pup females.
Bottom temperature	-0.87 (<0.001)	The resident state is more likely when bottom temperatures are colder for non-pup females.
Age class (pup)	-0.86 (<0.001)	Pups are less likely to be in the resident state than non-pups.
Sex (male)	-0.27 (0.24)	No significant difference in probability of behavioral state between males and females.
Bottom temp. × pup	0.49 (0.008)	The resident state is more likely when bottom temperatures are colder for pups, but the relationship is weaker than for non-pup females.
Bottom temp. × male	0.39 (0.01)	The resident state is more likely when bottom temperatures are colder for males, but the relationship is flatter than for non-pup females.