

Inferring foraging locations and water masses preferred by spotted seals *Phoca largha* and bearded seals *Erignathus barbatus*

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ABSTRACT: Spotted seals *Phoca largha* and bearded seals *Erignathus barbatus* are ice-associated seals that have overlapping range in the Beaufort, Chukchi, and Bering Seas, but have different foraging ecologies. The link between foraging behaviour and specific oceanographic variables is not well understood for these species, nor is the influence of different dive metrics when modelling their foraging behaviour. To explore the value of different dive metrics to estimate foraging behaviour, and the relationships between foraging and water bodies/oceanographic variables, we tagged 3 spotted seals and 2 bearded seals with satellite telemetry tags that recorded movement and oceanographic data. To infer foraging behaviour, we included dive metrics in Bayesian state-space switching models, and found that models that included depth-corrected dive duration were more parsimonious than models that included dive shape. The addition of vertical movements to the model enabled better determination of foraging areas (inferred from area-restricted searches) and provided insights into the probabilities of switching between foraging and transiting behaviours. The collection of oceanographic data *in situ* at a scale relevant to seals helped identify water masses, and how they were used, and potential oceanographic cues used by seals to identify foraging locations. Fine-scale spatiotemporal clustering analysis revealed spotted and bearded seal foraging 'hotspots' in the Chukchi and Bering Seas that overlap with hotspots identified for other marine mammals and marine birds.

KEY WORDS: Ice-associated seals · Foraging · Bayesian state-space models · Satellite telemetry · Oceanographic variables · Spotted seals · Bearded seals · MARES

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1. INTRODUCTION

The distribution of marine forage resources (e.g. nutrients, prey) is often driven by spatiotemporally variable oceanographic processes that can last from

hours to weeks and sometimes months (Gende & Sigler 2006, Suryan et al. 2006, Sigler et al. 2012). Intermit- tent peaks in these marine resources underpin notice- able increases in foraging rates by mobile predators, creating foraging 'hotspots' in areas of increased pro-

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ductivity for a wide range of species (e.g. Grebmeier et al. 2015). Given the potential for a changing climate to shift the distributions of wide-ranging marine predators (e.g. Kovacs et al. 2011, Hamilton et al. 2019), there is a need to better understand the spatial ecology of Arctic marine species, particularly the relationships between a range of oceanographic variables and individual behaviours. These efforts offer stakeholders information on the potential impacts of human activities such as commercial fisheries or shipping activities (e.g. Santora et al. 2017), how species may be or may not be adapting to ecosystem changes, and how conservation management of species may have to change (Moore & Reeves 2018). This information also has implications for Indigenous communities that rely upon marine mammals for subsistence. For example, reduced access to culturally important subsistence species can result in declining community health (e.g. Butler 2016) and food security (e.g. Brinkman et al. 2016).

Given their wide range, high mobility, and remote locations, current approaches to characterizing the spatial ecology of marine mammals have typically relied upon the analysis of movement data with respect to remotely sensed environmental covariates (e.g. satellite imagery of surface temperature, surface chlorophyll, and sea surface height; e.g. Block et al. 2011). However, for species feeding in the water column or on the benthos, such approaches may be unsatisfactory as they assume a strong relationship between environmental conditions at the surface and those occurring at depth where the animals forage — data that are often collected at much different scales than animal movement data. While the relationship between pelagic and benthic productivity in the Pacific sector of the Arctic has been tightly coupled (Grebmeier et al. 2006), changing ocean conditions may be shifting some of these relationships, thereby highlighting the importance of linking marine mammal movements to environmental data throughout the water column (Grebmeier et al. 2006). Of particular value to this approach is the documentation of oceanographic variables throughout the water column at scales that are biologically relevant to individual animals (Fedak 2004, Cox et al. 2018). Extensive oceanographic data have been collected *in situ* via satellite telemetry tags on marine mammals in the Antarctic, North Atlantic and North Pacific (Biuw et al. 2007, Fedak 2013, Guinet et al. 2013, Treasure et al. 2017) and have resulted in increased understanding of the links between marine mammal habitat use and their environment (e.g. Bestley et al. 2013, Hindell et al. 2016), although gaps are apparent in the

Arctic. The present investigation begins to fill this data gap by deploying satellite telemetry tags that document *in situ* oceanographic variables, spatial movements, and behaviours of 2 upper trophic Arctic marine predators.

Given their different foraging ecologies and overlapping range, the analysis of spotted seal *Phoca largha* and bearded seal *Erignathus barbatus* movement and behaviour lends itself to understanding the relationship between oceanographic variables and habitat use. While both pinnipeds are ice-associated, spotted seals and bearded seals have different foraging ecologies, and are typically classified as pelagic and benthic foragers, respectively (Burns 1981, Stirling et al. 1982, Bukhtiyarov et al. 1984, Kingsley et al. 1985, Dehn et al. 2007). Thus, it is plausible that, while they are sympatric, each species' niche necessitates different approaches to their use of habitat. Conversely, significant environmental and/or ecological 'events' (e.g. sea ice dynamics, seasonally variable productivity) may result in similarities in habitat use (e.g. Yurkowski et al. 2019). A few key studies highlight these characteristics. In the Alaskan Arctic, Lowry et al. (1998) used satellite-linked transmitters to identify sequential haul-out locations of spotted seals separated by long foraging trips. Boveng & Cameron (2013) used state-space modelling to describe regional trends in resting, foraging, and transiting by bearded seals tagged in Kotzebue Sound, Alaska. Specifically, the frequencies of those behaviours differed between bearded seals that migrated through the Chukchi/Beaufort Sea and those that remained in the northeast Chukchi Sea. McClintock et al. (2017) linked multiple environmental and behavioural variables to bearded seal movement to infer multiple types of behaviour. Juvenile bearded seal habitat selection, modelled using satellite tracks, indicated that they select habitat near the ice edge (Cameron et al. 2018), but show behavioural variability based on sea ice density (Breed et al. 2018).

Two-dimensional movement data (i.e. surface movements alone) have been used to distinguish directed, persistent movement (referred to as transiting) and foraging behaviours, assuming that area-restricted search (ARS) suggests foraging behaviour (e.g. Jonsen et al. 2005, Breed et al. 2012, Cotté et al. 2015). The disadvantage to inferring foraging from ARS is that it does not indicate if prey were captured and/or the degree of foraging effort exerted by individuals. Nevertheless, based on surface locations collected daily or every second day, state-space models effectively inferred areas of foraging and transiting for grey seals *Halichoerus grypus* and hooded seals

Cystophora cristata via differences in the distributions of step length and turning angle to define foraging behaviour (Jonsen et al. 2005). Breed et al. (2012) were able to differentiate between searching and transiting in the surface plane to define foraging behaviour in California sea lions *Zalophus californianus*, using location data collected approximately every 1–2 h. Note that we use the term ‘foraging’ as a proxy for ARS throughout the paper.

Characterizations of dive data (i.e. the third dimension), including dive shape (e.g. U-shaped or V-shaped dives), dive duration, and related parameters (e.g. duration at the bottom of a dive), have also been used to infer foraging by marine mammals (e.g. Kelly & Wartzok 1996, Fedak et al. 2001, Simpkins et al. 2001, Sparling et al. 2007, Heerah et al. 2015, Ramasco et al. 2015). For example, U-shaped dives, which have longer bottom durations than V-shaped dives, have been assumed to indicate foraging—or, at least, time in a prey patch—since the availability of food is assumed to extend time spent at depth (e.g. Hindell et al. 1991, Thompson et al. 1991, Le Boeuf et al. 1992, Kelly & Wartzok 1996, Fedak et al. 2001). Conversely, V-shaped dives have been thought to be less informative about foraging activity. Sparling et al. (2007) found that longer dives and longer bottom durations, or dives most likely to be U-shaped dives, were associated with prey capture for grey seals. Prey density as it relates to search time is also likely to be a factor, as demonstrated by the benthic-foraging Australian fur seal *Arctocephalus pusillus doriferus* which had dives with longer bottom duration when there were fewer prey-encounter events (Foo et al. 2016). Ramasco et al. (2015), however, concluded that dive shapes reflect benthic versus pelagic foraging rather than foraging versus non-foraging dives. Simpkins et al. (2001) and Heerah et al. (2014) have expanded on the use of dive shapes, distinguishing transiting and searching based on movement patterns including ARS. Bestley et al. (2015) found behavioural differences among species by including dive shape as a covariate on the transition between states in state-space models to explore whether vertical movement patterns can be used to infer shifts between transiting and foraging.

Overall, the utility of spatial movements at the surface and dive patterns to define foraging activity has varied among species. Horizontal surface movements likely reflect responses to large-scale environmental conditions (e.g. presence of sea ice), while vertical movements may reflect localized prey availability (Bailleul et al. 2007). Therefore, combining movements in both dimensions may provide a more com-

plete understanding of foraging patterns—in particular, whether seals use surface water characteristics to determine favourable foraging conditions at depth.

Our study aimed to use oceanographic data (i.e. temperature, salinity, and fluorescence) collected *in situ* to characterize water conditions in which spotted and bearded seals may preferentially forage, thereby improving our understanding of their foraging locations and behaviour. We also explored the impact of adding 2 different dive parameters (i.e. dive shape identified by time allocated at depth [TAD] and depth-corrected dive duration [DCDD]) into correlated random-walk state-space switching models for these species and the resulting ability to infer foraging. Hotspot analysis was also applied to the movement data to determine significant spatiotemporal clusters of foraging activity, with the goal of identifying persistent foraging hotspots. Finally, our results could guide future larger-scale investigations that employ satellite telemetry and oceanographic data to help understand habitat use and characteristics at scales relevant to marine mammals.

2. MATERIALS AND METHODS

2.1. Tagging and data collection

Spotted and bearded seals were captured and tagged in cooperation with Native Alaskan subsistence hunters between mid-August and mid-September 2015 in Dease Inlet and Kugrua Bay (Fig. 1). Seals were captured using tangle nets deployed from a vessel or from the shore. The nets (50 m long by 5 m deep) were made from braided nylon monofilament, 25 cm mesh size, with a light lead line so that entangled seals could easily surface to breathe. All nets were monitored continuously during deployment. All seals were physically restrained (i.e. no chemical sedation) during handling. Upon capture, seals were moved to shore where they were measured (i.e. girth, length), aged using claw bands (McLaren 1958), and weighed using a tripod scale. Satellite telemetry tags were attached to the fur between the shoulder blades using 5 min epoxy. This attachment method allows the tags to be shed during the subsequent spring pelage moult (a maximum duration of about 10 mo depending on tagging date). Tagged seals were released at or near their capture location typically within 1 h of capture. Five juvenile seals—3 spotted seals (2 males, 1 female) and 2 male bearded seals—were tagged. The spotted seals were tagged in August, 2 in Dease Inlet and 1 in Kugrua Bay. Both

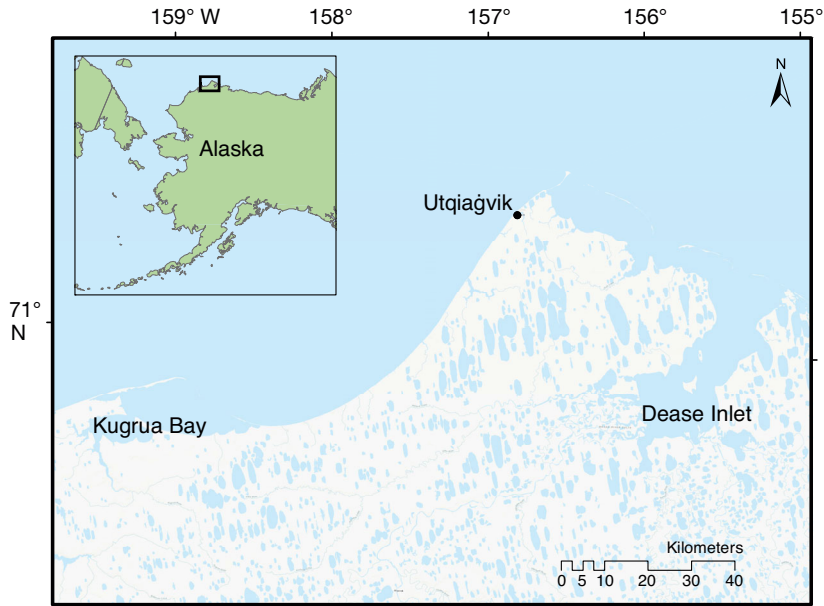


Fig. 1. Study area, with spotted seal *Phoca largha* and bearded seal *Erignathus barbatus* tagging locations (Dease Inlet and Kugrua Bay). Inset: Alaska

bearded seals were tagged in Dease Inlet in September (Fig. 1, Table 1). The duration of tag data transmission ranged from 117 to 168 d.

Each seal was fitted with a Sea Mammal Research Unit (SMRU) conductivity, temperature, depth (CTD)–fluorometer tag. In addition to location (including location uncertainty as classified by Argos; CLS 2016), the SMRU tags transmitted dive profiles (e.g. dive depth at 4 different times during a dive), and oceanographic data consisting of temperature, salinity, and fluorescence (a proxy for chlorophyll *a*) (SMRU 2016). Dive recording started when sensors were wet for 8 s and deeper than 1.5 m. Dive profile data were transmitted using the broken stick algorithm (Fedak et al. 2001), resulting in 4 inflection points describing the shape of the dives. Oceanographic data were collected during the dive ascent with a 10 m delay, i.e. collection only started once

seals were 10 m above their deepest depth to prevent data collection during what could be time at the bottom of the dive. Once activated, CTD and fluorometer sensors sampled the entire water column from the greatest dive depth to the surface every second. Oceanographic data were transmitted only for the deepest dive within every 12 h period (Photopoulou et al. 2015) to increase tag longevity and address bandwidth limitations when transmitting data. All data were transmitted via the Argos satellite system (www.argos-system.org) when the seal was at the surface. Based on satellite coverage at this latitude (71.5° N), the SMRU tags connected to the Argos system up to 10 times d⁻¹.

2.2. Horizontal movement analysis

Foraging and transiting behaviours of tagged seals were first inferred using Bayesian correlated random-walk state-space switching models (hereafter referred to as state-space models) which were based on surface movements only: move persistence (i.e. step length), and turning angle (Jonsen et al. 2005, Jonsen 2016). A hierarchical approach was taken for each species (Jonsen 2016) to ‘borrow strength’ between animals by assuming that movement parameters are the same between animals, while still inferring behaviours separately for multiple animals. The Bayesian analysis predicted a posterior distribution based on the combined distributions of the model parameters and states based on the data. The posterior distributions were estimated using Markov chain Monte Carlo simulations involving up to 10 000 com-

Table 1. Spotted seal *Phoca largha* and bearded seal *Erignathus barbatus* capture dates, approximate morphometric measurements, tag duration, and number of dive profiles

Species Capture date	Location	Seal ID	Sex	Estimated age (yr)	Weight (kg)	Last trans- mission date	Tag transmission duration (d)	No. of dive profiles
Spotted seal								
Aug 11, 2015	Dease Inlet	SS1	Female	3	66	Dec 5, 2015	117	7789
Aug 13, 2015	Dease Inlet	SS2	Male	5	84	Jan 11, 2016	152	9486
Aug 20, 2015	Kugrua Bay	SS3	Male	3	57	Jan 3, 2016	137	8802
Bearded seal								
Sep 8, 2015	Dease Inlet	BS1	Male	1	113–125	Feb 22, 2016	168	6728
Sep 17, 2015	Dease Inlet	BS2	Male	0	93	Feb 26, 2016	144 ^a	11 530

^aBreak in transmission Oct 6–24, 2015

binations of parameter estimates that are sampled from specified distributions. The state-space model was completed by running 2 simulations (chains), with a burn-in of 20 000 samples (number of samples during the adaptation phase of the modelling) and 30 000 iterations (number of posterior samples after burn-in) for bearded seals, and 10 000 samples and 40 000 iterations for spotted seals. The initial burn-in and iterations values were selected based on published values (e.g. Bestley et al. 2013) and were modified for each species for model convergence. To improve model performance during posterior sampling, the chains were thinned so that every 10th sample was retained. The time step selected for each species, which was dependent upon the number of locations and model convergence, was 4.8 h for bearded seals and 2.4 h for spotted seals. Analyses were conducted using R 3.3.1 (R Core Team 2016) and WinBUGS (Lunn et al. 2000).

2.3. Dive parameters and inclusion into movement analysis

We characterized all dives deeper than 4 m using 3 dive parameters: (1) dive zone, which was dependent on whether the dive was benthic or pelagic; (2) dive shape based on TAD (Fedak et al. 2001); and (3) a DCDD parameter.

All dives were classified as either benthic or pelagic depending on the relationship between maximal dive depth and location-specific bathymetry. The location-specific bathymetry were based on dive locations that were derived from the estimated tracks generated by the state-space models (accounting for Argos location error) and were matched to the Alaska Region Digital Elevation Model (ARDEM 2.0; Danielson et al. 2015) with 1×1 km resolution bathymetry to determine the distance between the maximal depth of the dive and the ocean bottom. Dives were classified as pelagic if the proportion of the water column used was <0.95 , otherwise they were classified as benthic (Jessopp et al. 2013). Although the dive information provided by the tags was limited to when transmissions were received (i.e. not every location had dive information), this type of dive classification provided a coarse estimate of dive zone. Given the resolution of the bathymetry data (1×1 km), the error associated with estimated dive locations, the limitations of dive transmissions, and the error associated with the reported dive depths, dive zone was not included in further modelling, but was used to aid in the interpretation of seal habitat use and behaviour.

TAD (Fedak et al. 2001) was calculated for each dive, to distinguish between V-shaped and U-shaped dives. We followed Fedak et al. (2001) to determine the 'true' mean swim speed for each species by plotting TAD against a range of minimal speeds ($0\text{--}1.5 \text{ m s}^{-1}$, calculated as $2 \times \text{maximal depth} \div \text{dive duration}$) separately for a suite of potential mean swim speeds (ranging from 1 to 3 m s^{-1}). Once the 'true' mean swim speed was identified (1.75 m s^{-1} for spotted seals and 1.5 m s^{-1} for bearded seals), a subset of dive profiles was randomly selected, visually inspected, and categorized as either U- or V-shaped. Based on this subset, a threshold TAD between U- and V-shaped dives was estimated at 0.8.

DCDD was used to determine if a dive was longer or shorter than expected, given the dive depth. This parameter was estimated for each dive by calculating the standardized residuals between dive duration and depth. The residuals were calculated for each seal separately by fitting a linear model with the individual seal as an interaction term (maximal dive depth \times individual seal). Prior to analysis, the maximal dive depths for spotted seals were log-transformed to meet normality assumptions. Residuals from these models represent the variation in dive duration after accounting for the effects of depth on dive duration, specific to each individual. Values >0 are longer-than-expected dives given the observed maximal dive depth, and values <0 are shorter-than-expected dives.

To determine if the 2 dive parameters provided additional information to the movement models, we added TAD and DCDD as a covariate into the state-space models separately, so that the transition between behavioural states varies with the covariate (Bestley et al. 2015). TAD and DCDD were included as continuous variables in the state-space models. The modelling approach averaged the covariate over the selected time steps. We compared the results of state-space models incorporating the dive covariates with those based only on surface movements, using the deviance information criterion (DIC; Spiegelhalter et al. 2002). DIC is similar to the Akaike information criterion (AIC) in that models are penalized for having greater complexity and rewarded for having greater fit (Spiegelhalter et al. 2002). Lower values therefore constitute a better tradeoff of model fit for a given complexity and the model with the lowest DIC is considered best.

2.4. Foraging hotspot analysis

To determine areas that may be important foraging habitat, the state-space model outputs, using the

model with the lowest DIC, of both species were combined and a temporal weighted Anselin Moran's *I* analysis (Anselin 1995) was performed using ArcGIS 10.1 (ESRI 2012). Anselin Moran's *I* was used to indicate if a given point is significantly clustered in time and space with other points of the same value. In our case, this involved identifying clusters of inferred foraging locations. Anselin Moran's *I* was selected over other methods, such as kernel density, because it provides a local approach that considers the point's relationship with its 'neighbours' only (rather than all of the points), and also provides a statistic to determine whether significant relationships were positive or negative. The distance to define spatial autocorrelation was set to 24 km so that all points had at least 1 neighbour (i.e. the maximal distance between 2 points in the data was 24 km). To define temporal clustering, the temporal weighting was set to 2 wk (i.e. foraging that occurred within 2 wk of each other was defined as temporally clustered). These spatial and temporal scales were selected to capture meso-scale processes (e.g. fronts, eddies) that are likely to be associated with areas of higher productivity (Dickey 2003).

2.5. Environmental parameters and relationships to behaviour

To compare seal behaviour with the environmental data collected by the satellite telemetry tags, we first examined the CTD and fluorometry data, and any outliers were removed. We derived and defined the following environmental metrics:

- Surface temperature (°C), where the surface was defined as the measurement taken closest to 4 m from the surface
- Surface salinity (PSU), where the surface was defined as the measurement taken closest to 4 m from the surface
- Maximal fluorescence (mV) recorded during the entire depth profile
- The water mass (e.g. Bering summer water) at maximal dive depth based on the salinity and temperature collected by the SMRU tags. Six different water masses in the study area were identified, using density and temperature, in line with previous literature (e.g. Pickart et al. 2019).

We explored the relationships between oceanographic parameters and behavioural state (i.e. transiting and foraging), estimated from the state-space models, using generalized linear mixed models (GLMMs) and Wilcoxon rank sum. The environmen-

tal metrics were linked to the nearest inferred behaviour in time. We used logit-linked binomial GLMMs with a response of '1' for foraging (i.e. ARS) and '0' for transiting, to relate environmental metrics to inferred behaviours for each species and examined the residuals for normality. Environmental metrics, time (day of the year or month), and dive characteristics (TAD, DCDD, and dive zone [benthic vs. pelagic]) were included as fixed effects. We also included individual random effects on the intercept and slopes to account for variation among seals in their responses to environmental conditions. We tested for collinearity among fixed effects by calculating pairwise correlations (Zuur et al. 2009). Models were fit using the R package 'lme4' (Bates et al. 2015), and model fit and parsimony were compared using small-sample Akaike information criterion (AICc) calculated using the R package 'AICcmodavg' (Mazerolle 2016). Typically, models with values of delta AICc >10 are considered to have no support (Burnham & Anderson 2002). The p-values were based on asymptotic Wald tests as calculated in 'lme4' (Bates et al. 2015).

3. RESULTS

3.1. Movement and dive parameters

The state-space models without dive covariates fit unique distributions for move persistence and turning angle for each behavioural state (i.e. foraging vs. transiting) for both species; the models converged (Gelman-Rubin values ≤ 1.1 for each parameter) with minimal overlap between distributions of the inferred parameters. The addition of dive covariates (i.e. TAD and DCDD) into the state-space models only improved model parsimony (i.e. lower DIC values) in 1 case when compared to state-space models without the covariates (Table 2). The model that included DCDD as a covariate was more parsimonious than the model with TAD for both species, except during the first time period (September–October) for bearded seals (Table 2). As a result, the models that included DCDD (Fig. 2) were used to infer foraging activity for spotted and bearded seals in the subsequent analysis.

When comparing the amount of predicted foraging and transiting behaviour between the 3 models, we found that areas of inferred foraging activity differed in some instances for both species. For spotted seals, the inclusion of dive covariates increased the number of foraging locations around Hanna Shoal and in the central Chukchi Sea for seal SS1; just north of the

Table 2. Deviance information criterion (DIC) values of the spotted seal *Phoca largha* and bearded seal *Erignathus barbatus* state-space models (SSMs). The DIC values shown are for each model subset for models based on surface locations without dive covariates, and those including the dive parameters time allocated at depth (TAD) and depth-corrected dive duration (DCDD) as covariates. The lowest DIC values are in **bold**

Model scenario	Spotted seals			Bearded seals		
	Aug 11– Oct 1, 2015	Oct 2– Nov 30, 2015	Dec 1, 2015– Jan 11, 2016	Sep 8– Oct 5, 2015	Oct 6– Nov 30, 2015	Dec 1, 2015– Feb 26, 2016
SSM Surface	−42680	−51506	−13002	−14958	−24780	−50211
SSM TAD	−42334	−51325	−13210	−14797	−24770	−50199
SSM DCDD	−42654	−51334	−13228	−14789	−24777	−50209

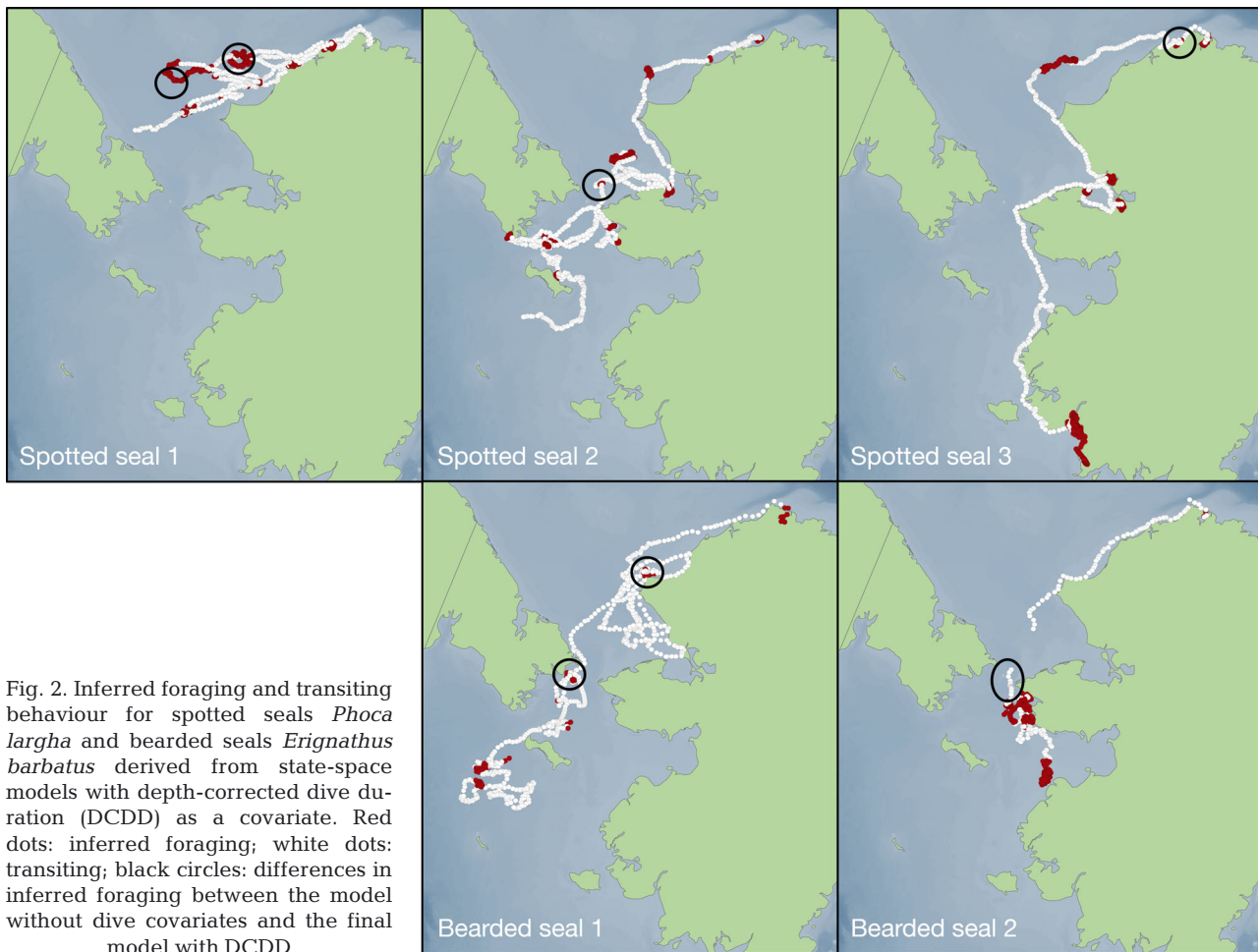


Fig. 2. Inferred foraging and transiting behaviour for spotted seals *Phoca largha* and bearded seals *Erignathus barbatus* derived from state-space models with depth-corrected dive duration (DCDD) as a covariate. Red dots: inferred foraging; white dots: transiting; black circles: differences in inferred foraging between the model without dive covariates and the final model with DCDD

Bering Strait for seal SS2; and just east of Peard Bay for seal SS3 (Fig. 2; see Table 1 for seal ID numbers). Adding the dive covariates to the bearded seal model reduced the number of inferred foraging areas just south of the Bering Strait for seal BS2 but indicated additional foraging areas west of Wevok, and south of the Bering Strait for seal BS1 (Fig. 2).

The inclusion of dive covariates in the state-space models allowed us to explore switching behaviours

(i.e. from foraging to transiting and remaining in transiting) and their relationship with the dive covariates. We considered dive zone (pelagic vs. benthic dives) and the range of the covariate data, examining both TAD and DCDD. For spotted seals, the probability of remaining in transiting behaviour was unrelated to TAD (i.e. the probability of remaining in transiting was close to 1 for both pelagic and benthic dives), and was only weakly influenced by DCDD

(Fig. 3). In contrast, there was an increased probability of spotted seals switching from foraging to transiting during both pelagic and benthic dives once seals started performing U-shaped dives (i.e. the probability increased from 0 to 0.5 when TAD exceeded 0.8), but was again minimally influenced by DCDD (Fig. 3). For bearded seals, the probability of staying in transiting behaviour varied when conducting V-shaped dives for both pelagic and benthic dives (TAD < 0.8), but was unrelated to U-shaped dives (i.e. probability approached 1 when TAD > 0.8; Fig. 4). Similarly, the

probability of bearded seals remaining in transiting behaviour was not influenced by DCDD. The probability of bearded seals switching from foraging to transiting during benthic dives increased sharply when they switched to U-shaped dives (i.e. probability increased from 0 to 0.5 when TAD exceeded 0.9), while the switching probabilities during pelagic dives remained low. The probability of switching from foraging to transiting increased for both benthic and pelagic dives once DCDD became longer than the average duration for a given depth (DCDD > 0; Fig. 4).

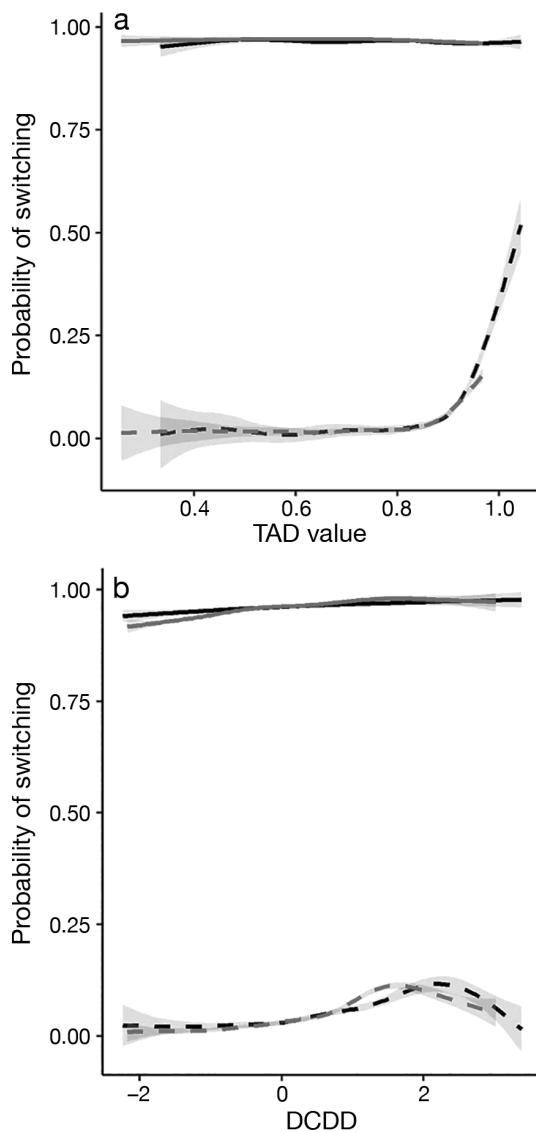


Fig. 3. Estimated relationships between (a) time allocated at depth (TAD) or (b) depth-corrected dive duration (DCDD) and probabilities of switching between foraging and transiting for spotted seals *Phoca largha*. Solid lines: remain transiting; dashed lines: switch from foraging to transiting; grey: pelagic dives; black: benthic dives; shading: 95 % confidence interval

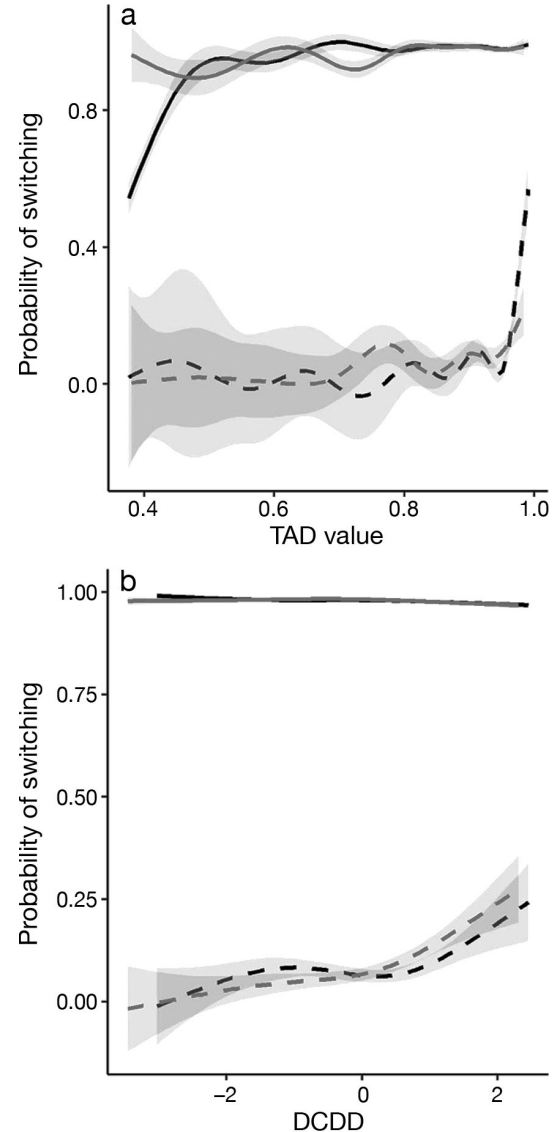


Fig. 4. Estimated relationships between (a) time allocated at depth (TAD) or (b) depth-corrected dive duration (DCDD) and probabilities of switching between foraging and transiting for bearded seals *Erignathus barbatus*. Solid lines: remain transiting; dashed lines: switch from foraging to transiting; grey: pelagic dives; black: benthic dives; shading: 95 % confidence interval

3.2. Foraging hotspots

Inferred foraging for both species clustered significantly in space and time in Dease Inlet and south of the Bering Strait near Port Clarence Bay (Fig. 5), as highlighted by the temporally weighted Anselin Moran's I analysis of the state-space model that included DCDD. Foraging for 1 bearded seal was also significantly clustered west of St. Lawrence Island and west of Norton Sound. Similarly, foraging for 2 spotted seals was significantly clustered to the west of Point Lay, west of Point Hope, and in Kotzebue Sound (Fig. 5).

3.3. Environmental relationships

The majority of the oceanographic data collected by sensors on all 5 seals' tags throughout the Chukchi and Northern Bering seas were within anticipated temperature–salinity and fluorescence ranges for these regions based on *in situ* data from many previous studies (e.g. Gong & Pickart 2015, Pisareva et al. 2015). Data that were not within the anticipated ranges were then excluded from further analysis. The environmental data collected by the seals' tags were used to identify the water masses through which the seals moved (Fig. 6). Assuming foraging is associated with water characteristics at maximal dive depth, our data revealed different use of water masses for foraging activity among and within species. Spotted seals primarily foraged in warm Pacific-origin summer waters—predominantly Bering summer water (BSW), and, to a lesser extent, Alaskan coastal water (ACW; Table 3). The 2 bearded seals

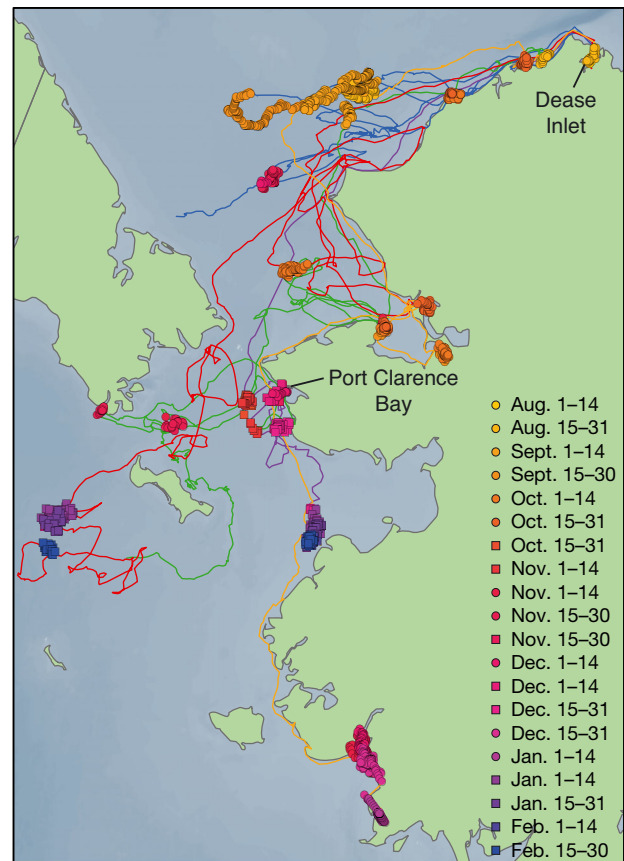


Fig. 5. Anselin Moran's I analysis results of spatially and temporally correlated foraging activity between species and individuals. Significantly correlated foraging for spotted seal *Phoca largha* is shown in circles and for bearded seal *Erignathus barbatus* is shown in squares. Colour of circles and squares indicates time, and lines are the individual tracks for each tagged seal (SS1: blue; SS2: green; SS3: orange; BS1: red; BS2: purple)

Table 3. Proportion (%) and number of dives to each water body by individual spotted seals *Phoca largha* and bearded seals *Erignathus barbatus* and by inferred behaviour from state-space models with depth-corrected dive duration (DCDD) as a covariate. ACW: Alaskan coastal water; AW: Atlantic water; BSW: Bering summer water; MW: melt water; NVWW: newly ventilated winter water; RWW: remnant winter water. **Bold** values: highest proportion of inferred foraging; –: no data

Individual	Behaviour	Primary water body	Proportion (and number) of dives to each water body at depth					
			ACW	AW	BSW	MW	NVWW	RWW
Spotted seals								
SS1	Foraging	BSW	22 (8)	–	67 (25)	8 (3)	–	3 (1)
	Transiting	BSW/ACW	40 (16)	–	40 (16)	10 (4)	–	10 (4)
SS2	Foraging	BSW	43 (12)	–	57 (16)	–	–	–
	Transiting	ACW	35 (25)	–	27 (19)	15 (11)	13 (9)	10 (7)
SS3	Foraging	BSW	27 (3)	–	73 (8)	–	–	–
	Transiting	ACW	53 (8)	–	47 (7)	–	–	–
Bearded seals								
BS1	Foraging	NVWW	–	–	7 (3)	37 (16)	42 (18)	14 (6)
	Transiting	BSW	15 (26)	–	32 (57)	12 (22)	15 (26)	26 (46)
BS2	Foraging	BSW	–	–	100 (1)	–	–	–
	Transiting	MW	14 (2)	–	28 (4)	43 (6)	–	14 (2)

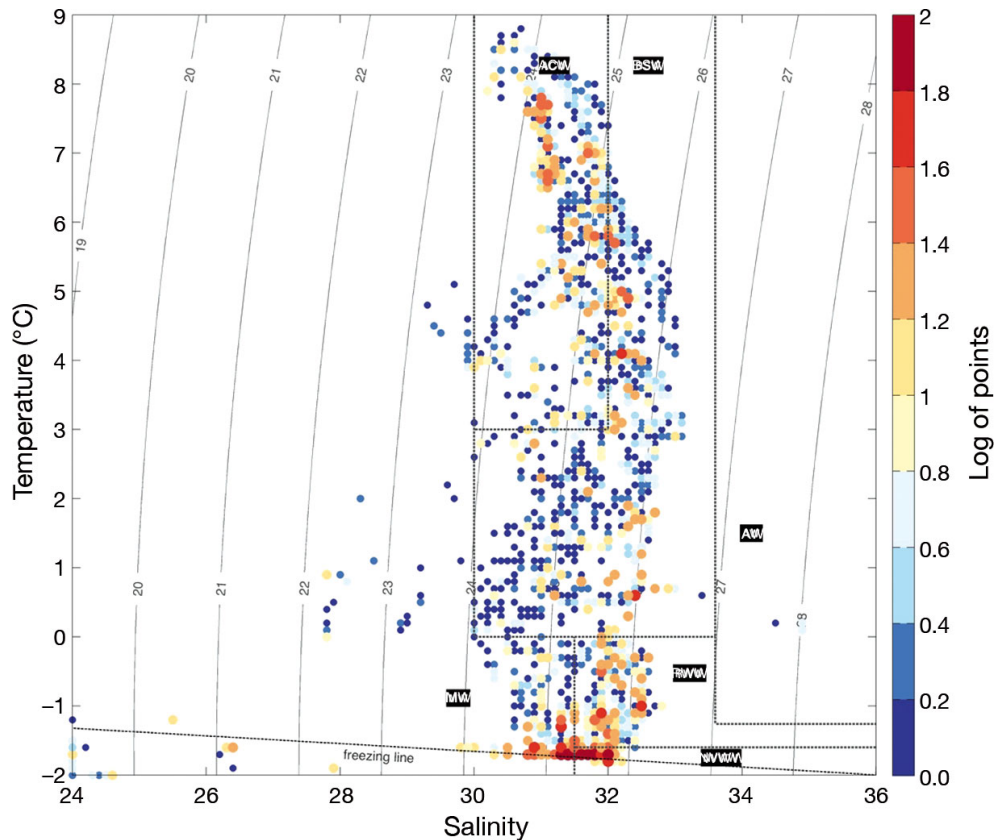


Fig. 6. Volumetric temperature–salinity (TS) plot from data collected by the CTD satellite tags deployed on spotted seals *Phoca largha* and bearded seals *Erignathus barbatus*. The colour denotes the log of the number of points within bins of 0.1°C in temperature and 0.1 PSU in salinity. The water masses, identified by the temperature and salinity data, correspond to: Alaskan coastal water (ACW), Atlantic water (AW), Bering summer water (BSW), melt water (MW), newly ventilated winter water (NVWW), and remnant winter water (RWW); contour lines: potential density in kg m^{-3} ; freezing line: freeze point of sea water as a function of salinity

differed in their preferred use of water masses. Seal BS2 foraged predominantly in BSW, while seal BS1 foraged primarily in cold Pacific-origin water — both newly ventilated winter water (NVWW) and, slightly less often, remnant winter water (RWW).

Modelling the relationship between surface movements, dive parameters, and environmental metrics using GLMMs did not converge due to little difference among the limited number of oceanographic profiles collected by each individual. We attempted to overcome this problem by assuming that a water mass is the actual target of the foraging dive (and therefore most relevant to the choice of foraging habitat), and we limited environmental metrics to the water mass only. For spotted seals, we found significant relationships between foraging and BSW and ACW (Table 4). We subsequently attempted to reintroduce at least 1 of the other dive characteristics parameters; however, due to data limitations, none of those models converged. For bearded seals, no models converged.

The relationship of environmental metrics to inferred behaviours (based on Wilcoxon rank sum) varied between species and among individuals (Table 5). For seal BS1, sea surface temperatures differed significantly during inferred foraging and transiting ($p < 0.01$), as did maximal fluorescence ($p < 0.01$). For spotted seals, surface temperature was significantly higher during foraging for 2 of the seals (SS1, $p = 0.04$; SS2, $p < 0.01$). Surface salinity ($p < 0.01$ for both

Table 4. Association between spotted seal *Phoca largha* foraging behaviour and water body using generalized linear mixed models. *Significant ($\alpha = 0.05$)

Water body	Coefficient	SE	p
Alaskan coastal water	-1.04	0.27	<0.01*
Bering summer water	1.29	0.34	<0.01*
Melt water	-0.90	0.80	0.26
Newly ventilated winter water	1.26	0.72	0.08
Remnant winter water	0.70	0.65	0.28

Table 5. Summary of oceanographic variables and water bodies by individual spotted seals *Phoca largha* and bearded seals *Erignathus barbatus* and behaviour for state-space models with depth-corrected dive duration (DCDD) as a covariate. *Significantly different between behaviours (Wilcoxon rank sum test [$\alpha = 0.05$]). IQR: interquartile range

Individual	Behaviour	Surface temperature (°C)		Surface salinity (PSU)		Maximal fluorescence (mV)	
		Median	IQR	Median	IQR	Median	IQR
Spotted seals							
SS1	Foraging	5.6*	1.0 to 6.8	31.9	31.6 to 32.2	1.1*	0.7 to 1.5
	Transiting	1.5*	−0.2 to 6.2	31.3	31.2 to 31.9	0.7*	0.5 to 0.9
SS2	Foraging	4.2*	3.5 to 7.3	31.8*	31.4 to 32.4	2.4*	1.6 to 2.6
	Transiting	0.9*	−1.6 to 4.2	31.1*	30.8 to 31.8	1.7*	1.2 to 2.2
SS3	Foraging	6.5	6.2 to 7.0	31.8*	31.7 to 32.0	2.2	2.0 to 2.7
	Transiting	6.2	5.7 to 6.8	31.3*	31.0 to 31.6	1.8	1.5 to 2.5
Bearded seals							
BS1	Foraging	−1.6*	−1.7 to −1.4	31.5	31.4 to 31.8	1.0*	0.9 to 1.2
	Transiting	−0.3*	−1.5 to 3.5	31.8	31.3 to 32.1	1.2*	1.0 to 2.2
BS2	Foraging	2.6	1.4 to 2.8	30.1	27.8 to 30.4	0.9	0.7 to 1.0
	Transiting	0.5	−1.1 to 3.0	30.4	29.4 to 30.9	0.9	0.8 to 1.1

seals) and maximal fluorescence were also significantly higher during foraging than during transiting for 2 of the seals ($p < 0.01$ for SS1 and SS2), and SS3 had the same trend, although it was not significant (Table 5).

4. DISCUSSION

The oceanographic data collected by seal-borne sensors, such as those deployed in this study, highlighted the value of adding environmental data to the analysis of habitat selection and the advantage of collecting it *in situ* at the scale relevant to individuals. In our study, relationships between behaviours and environmental conditions were apparent for both spotted and bearded seals. For example, surface temperature and water column fluorescence were significantly higher when spotted seals were foraging than when they were transiting. Thus, the animal-borne oceanographic sensors may have revealed a preference for pelagic feeding in high-productivity waters.

Spotted and bearded seal behaviour in relationship to oceanographic variables, such as temperature and fluorescence, have not been well studied. Spotted seals and their relationships to the ice edge have been noted (e.g. Lowry et al. 2000), but to our knowledge, links between their movement or behaviour and oceanographic variables had not been evaluated. Bearded seals' relationships to their environment in Alaska have been explored (e.g. Breed et al. 2018, Cameron et al. 2018), but similar to spotted seals, do not include relationships to specific oceanographic

variables such as temperature. Hamilton et al. (2018) linked bearded seal behaviour in Svalbard, Norway, to their environment, finding that gradients in water temperature and salinity, collected via animal-borne sensors, helped to explain variation in diving behaviour in adult bearded seals.

The ability to identify water masses from animal-borne sensors provides further insights into habitat use. The scale at which the oceanographic data are collected and the ability to identify water masses at different depths is one of the strengths of such data collection (e.g. Dragon et al. 2010, Vacqu  -Garc  a et al. 2015), although the data can be limited if the tags are not recoverable, as was the case in this study. To our knowledge, our study is the first to provide water mass analysis for spotted and bearded seals in Alaskan waters, and all but one of the seals in our study exhibited inferred foraging more often in BSW during their fall and winter movements in the Chukchi and Northern Bering seas. BSW can be associated with high nutrient concentrations and a high overall phytoplankton standing-crop biomass (Danielson et al. 2017). Thus, the affinity for BSW may reflect conditions necessary for foraging hot-spots and hot-times. Similar to our results, bowhead whales also appeared to be somewhat selective for BSW in the Chukchi Sea (Citta et al. 2018a). More data will be needed to fully identify and characterize the variables driving the timing and location of foraging by spotted and bearded seals. Nevertheless, the use of oceanographic sensors on marine-mammal satellite tags provides an opportunity to explore habitat selection by marine mammals at the scale of identifiable water masses.

Unlike previous studies of spotted and bearded seals, which have looked at dive parameters and movement to infer foraging and habitat selection (e.g. McClintock et al. 2017, Breed et al. 2018, Cameron et al. 2018), our investigation focused on the association of dive parameters with switching between behaviours, and related movements or behaviours to environmental data collected *in situ*. Although our study had limited numbers of tagged animals, and inference to the population level or across all age groups is limited, the use of the CTD–fluorometry tags and associated diving information collected by these tags provides insights into the utility of exploring dive parameters when modelling movement for these species. Additionally, the differences in spatial predictions of inferred foraging between the models with and without the dive covariates highlights the importance of exploring the addition of dive parameters, particularly when using the method to identify important or critical habitat.

Similar to previous studies (e.g. Ramasco et al. 2015), some of our results based on dive parameters to explain foraging activity were mixed. For example, models using surface movement only fit the data better than those also including dive parameters. One consideration is that our study did not differentiate between resting activity and ARS (e.g. McClintock et al. 2017), and as a result, may have overestimated ARS. Another consideration is that movement models that accounted for DCDD provided a better fit than those with only TAD (or dive shape). Although dive shape may provide information on activity while switching between behaviours, it does not appear to adequately reflect foraging activity for juvenile spotted and bearded seals in our study. Nevertheless, the models with both movement and dive parameters suggest a broader context in which to understand the ecological trade-offs associated with habitats that differ in their relative value and how this relates to animal behaviour (Carter et al. 2016, McClintock et al. 2017).

The juvenile spotted seals from this study showed similar general movement patterns to those tagged in previous studies, but showed differences in habitat utilization. For example, Lowry et al. (2000) found that spotted seals tagged in the southern Chukchi Sea exhibited a shift from nearshore to offshore habitat use through the fall, and linked the preferred use of the nearshore in summer and early fall to the likely abundance of prey. The subsequent movement of those seals offshore in late fall was presumed to reflect the movement of prey offshore. The spotted seals in our study also showed foraging in the near-

shore habitat in summer and fall, but foraging activity also occurred in areas farther from shore, and some individuals typically remained in nearshore habitat into the winter. More data will be needed to adequately identify variables driving foraging behaviour and locations, but state-space modelling of additional spotted seal behaviour may reveal nearshore and offshore areas frequently utilized for foraging activities. Additionally, the use of finer-scale dive information may allow for identification of more detailed dive characteristics and foraging in shallow areas (e.g. in rivers).

McClintock et al.'s (2017) models of bearded seal movement identified benthic and mid-water foraging in the Chukchi and Northern Bering seas. In our study, bearded seals conducted minimal inferred foraging in the Chukchi Sea, except for Dease Inlet and near Point Barrow, with increased foraging once they were south of Bering Strait. It is possible that the higher frequency of inferred foraging in the McClintock et al. (2017) study was the result of attributing benthic dives during transiting to foraging behaviour, or that inferred foraging activity in our study is underestimated and too strongly coupled with ARS movements, which does not identify opportunistic feeding that may occur during transiting. Breed et al. (2018) also predicted areas of resident behaviour for bearded seals (or ARS as we have defined it) in the Chukchi Sea when looking at individual specific tracks, but predict low resident behaviour at the species level in the Chukchi Sea.

Spotted and bearded seal foraging hotspots overlapped with each other in 2 areas (i.e. Dease Inlet and south of the Bering Strait near Port Clarence Bay) and also overlapped with other species. For example, significantly clustered hotspots where bearded seals foraged coincided with known bowhead-whale core-use areas in Anadyr Strait and the Gulf of Anadyr (Citta et al. 2015). Spotted seal foraging hotspots in fall overlapped spatially with seabird and marine mammal hotspots as identified by Kuletz et al. (2015). Similarly, our identified hotspots overlap with lower trophic levels and potential prey. The bearded seal hotspots south of the Bering Strait and south of St. Lawrence island overlap with areas that can have high benthic biomass (Grebmeier et al. 2015). Citta et al. (2018b) looked at the spatial overlap of 7 cetacean and pinniped species, which included ringed seals *Phoca hispida*, bearded seals, and spotted seals in Alaskan waters. Yurkowski et al. (2019) conducted hotspot analysis for 4 species groups, including cetaceans, pinnipeds, polar bears, and seabirds, providing insights into areas of frequent use. Both of the

approaches applied used spatial correlations which were binned by season, whereas our use of Anselin Moran's I provides additional insights through the application of finer-scale temporal weightings, which indicated that not all foraging areas were significantly correlated in time, even though species presence may have been correlated in space. We believe that our approach, which captures significant temporal overlap of foraging activity, will help better identify persistent foraging habitat, and thus prove valuable for identifying important habitat for these species.

Inference of habitat use is an important output from state-space modelling, but the influence and relationship between behavioural states and dive covariates also provides an effective approach to developing a hypothetical framework for behaviours (Fig. 7).

Although we found that state-space models with DCDD were more parsimonious than those including TAD, we also used the model results from the models including TAD to further explore relationships between switching states and TAD to develop our hypothetical framework. Both the spotted and bearded seals tracked in this study made dives during inferred foraging that were of shorter than expected duration relative to depth. The spotted seals showed a mix of V- and U-shaped dives, and bearded seal dives were predominately U-shaped, a result which may be related to the foraging ecology of each species, with spotted seals typically categorized as pelagic foragers and bearded seals as benthic foragers (Burns 1981, Stirling et al. 1982, Bukhtiyarov et al. 1984, Kingsley et al. 1985, Dehn et al. 2007). More frequent and longer than anticipated U-shaped dives were associated with an increased probability of switching from foraging to transiting for both species. These results suggest that increases in both TAD and DCDD indicate increasing foraging effort, and that this increased effort—perhaps caused by decreased prey density—eventually leads to abandonment of foraging patches as the energetic pay-off decreases (e.g. Boyd 1997). Alternatively, it may just be that such increased foraging efforts can only be sustained for so long before some phys-

iological recovery is needed, forcing the seal to abandon their foraging effort. However, TAD and DCDD had little influence on the probability of bearded and spotted seals switching away from transiting, suggesting that other factors (perhaps environmental) caused the animals to transition into foraging. Studies with more seals and higher-resolution dive data, location data, environmental data, and bathymetry are needed to distinguish between these alternatives.

State-space models illustrated the utility of using oceanographic and dive data from seal-borne satellite CTD–fluorometer tags to infer foraging beyond the analysis of surface movements and remotely sensed environmental data alone. Our results show that different dive metrics should be explored when including them in models to infer foraging activities.

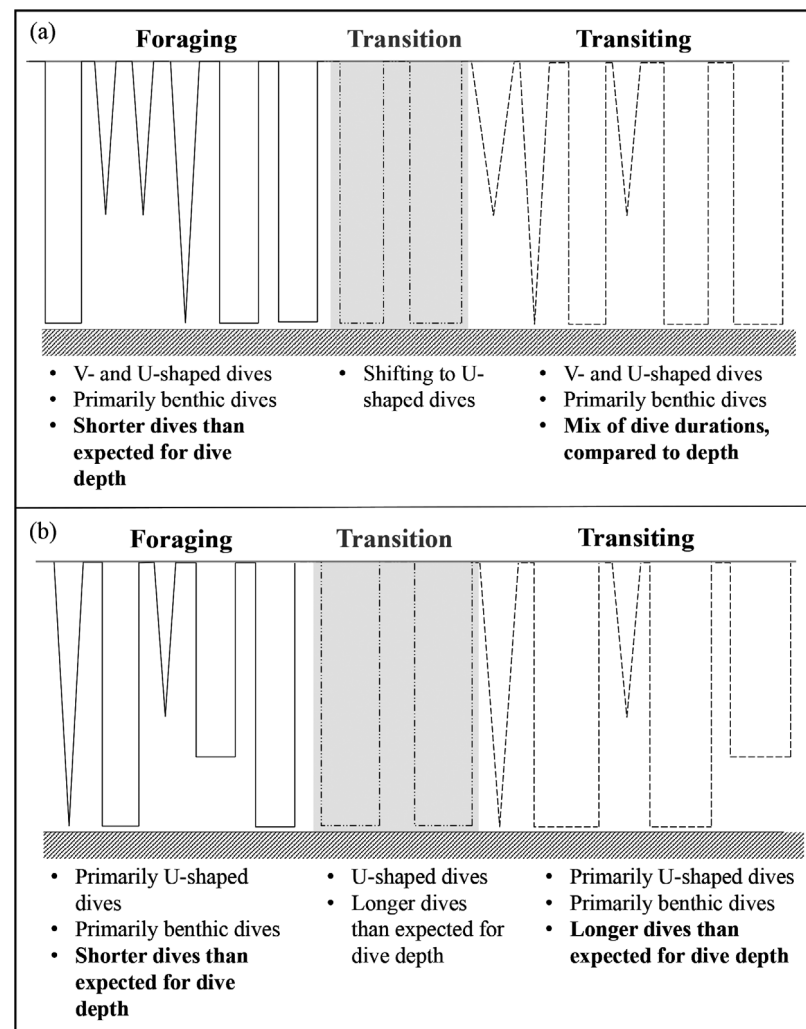


Fig. 7. Hypothesized behavioural framework relating dive metrics (i.e. dive shape and depth-corrected dive duration) to the behaviour of (a) spotted seals *Phoca largha* and (b) bearded seals *Erignathus barbatus*

We identified foraging hotspots based on spatiotemporal overlap of foraging bearded and spotted seals, some of which coincided with high prey density and high-use areas by other species (e.g. Citta et al. 2015, Grebmeier et al. 2015, Kuletz et al. 2015) and provided an approach to identify areas that may have persistently important foraging habitat, thereby providing a basis for understanding important habitat for these species. The environmental data collected *in situ* by oceanographic sensors on marine-mammal satellite tags also provides opportunities to explore habitat selection by marine mammals at the scale of identifiable water masses. Our use of the *in situ* environmental data to better understand finer-scale habitat characteristics for these species shows how this data can be used and that this type of data collection is valuable to identify habitat for both bearded and spotted seals. Finally, the use of animal-borne sensors such as those deployed in this study can provide another approach to environmental monitoring in which upper trophic-level species (i.e. which are likely to exhibit the effects of ecological perturbations first) can serve as sentinels of ecological change (Moore & Kuletz 2018).

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