



Foraging habitats of lactating northern fur seals are structured by thermocline depths and submesoscale fronts in the eastern Bering Sea

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ARTICLE INFO

Available online 28 July 2012

Keywords:

Habitat selection
First-passage time
Submesoscale features
Finite-size Lyapunov exponent
Cox proportional hazard model
USA
Alaska
Eastern Bering Sea

ABSTRACT

The relationships between fine-scale oceanographic features, prey aggregations, and the foraging behavior of top predators are poorly understood. We investigated whether foraging patterns of lactating northern fur seals (*Callorhinus ursinus*) from two breeding colonies located in different oceanographic domains of the eastern Bering Sea (St. Paul Island—shelf; Bogoslof Island—oceanic) were a function of submesoscale oceanographic features. We tested this by tracking 87 lactating fur seals instrumented with bio-logging tags (44 St. Paul Island, 43 Bogoslof Island) during July–September, 2009. We identified probable foraging hotspots using first-passage time analysis and statistically linked individual areas of high-use to fine-scale oceanographic features using mixed-effects Cox-proportional hazard models. We found no overlap in foraging areas used by fur seals from the two islands, but a difference in the duration of their foraging trips—trips from St. Paul Island were twice as long (7.9 d average) and covered 3-times the distance (600 km average) compared to trips from Bogoslof Island. St. Paul fur seals also foraged at twice the scale (mean radius = 12 km) of Bogoslof fur seals (6 km), which suggests that prey were more diffuse near St. Paul Island than prey near Bogoslof Island. Comparing first passage times with oceanographic covariates revealed that foraging hotspots were linked to thermocline depth and occurred near submesoscale surface fronts (eddies and filaments). St. Paul fur seals that mixed epipelagic (night) and benthic (day) dives primarily foraged on-shelf in areas with deeper thermoclines that may have concentrated prey closer to the ocean floor, while strictly epipelagic (night) foragers tended to use waters with shallower thermoclines that may have aggregated prey closer to the surface. Fur seals from Bogoslof Island foraged almost exclusively over the Bering Sea basin and appeared to hunt intensively along submesoscale fronts that may have converged prey within narrow bands near the surface. Bogoslof fur seals also foraged closer to their island which was surrounded by strong surface fronts, while fur seals from St. Paul Island traveled > 100 km and extended some trips off-shelf to the basin to forage at similar oceanographic features. The relative distribution and accessibility of prey-concentrating oceanographic features can account for the observed inter-island foraging patterns, which may in turn have population level consequences for the two fur seal colonies.

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1. Introduction

The distribution and abundance of prey resources varies spatially and temporally in dynamic marine environments. Physical processes can play an important role in ocean mixing and aggregating prey in many pelagic systems (Mann and Lazier, 2006). In theory, localized areas where prey are retained and enhanced can create dense

resource patches that can be efficiently exploited by marine predators. Studies of spatial aggregations in tropical marine systems have revealed strong trophic links from primary and secondary production through to micronecton and top predators (Benoit-Bird and Au, 2003; Benoit-Bird and McManus, 2012). However, the relationships between fine-scale oceanographic features, prey aggregations, and the foraging of upper predators remain poorly understood in many sub-polar systems.

The eastern Bering Sea is a model system in which to explore relationships between the physical environment and foraging patterns of top marine predators. It supports large breeding aggregations of marine birds and marine mammals across a wide range of habitats. This highly productive ecosystem is characterized by strong and variable currents, eddies, and shifting fronts that regulate the

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distribution of nutrients from the deep basin to the shallow continental shelf regions (Brodeur et al., 2002; Hunt et al., 2002; Okkonen et al., 2004; Stabeno et al., 2001, 2008). The positions and widths of the fronts in the Bering Sea are not static, but vary significantly depending upon the strength of the winds and tides which are the dominant physical forcing mechanisms (Kachel et al., 2002; Overland et al., 1999). Such variability has a pronounced effect on the role of fronts as sites for prolonged production, and occasionally as barriers to the exchange of nutrients between hydrographic regions.

Temperature regimes are well defined in the eastern Bering Sea at the mesoscale by the major isobaths, but are highly dynamic at the submesoscale (< 10 km) (Stabeno et al., 2001, 2008; Sullivan et al., 2008). This is exemplified by a transition zone that divides the well-structured, two temperature layer domain that typically sits over the middle continental shelf (< 100 m) from the three diffuse layers over the outer shelf (< 200 m) (Coachman, 1986). There is also a remnant subsurface layer of water < 2 °C (cold-pool) from the spring ice melt that occupies the middle-shelf and both features shift position inter-annually. Nutrient rich slope water is brought onto the shelf via eddies, meanders of the major northward currents, and disturbances created by bottom topography (Schumacher and Stabeno, 1994; Stabeno and van Meurs, 1999). Such features influence the annual positions of fronts over the shelf and basin in this dynamic system, and likely aggregate and retain the production (e.g., Brodeur et al., 2002; Flint et al., 2002) that in turn attracts top predators.

Northern fur seals (*Callorhinus ursinus*) are important top predators that inhabit two oceanographic regions in the eastern Bering Sea (Fig. 1). The population breeding over the continental shelf on the Pribilof Islands Archipelago (on St. Paul Island and St. George Island) constitutes roughly half of the world population and has declined since the 1950s (Trites, 1992; Towell et al., 2006; Testa, 2011; York and Hartley, 1981). The second population breeds over the Bering Sea basin on the minute pinnacle that is Bogoslof Island. This relatively small population was discovered in 1980 (Lloyd et al., 1981) and has rapidly increased in numbers since 1995 (Allen and Angliss, 2011; Loughlin and Miller, 1989; Ream et al.,

1999). Tracking lactating female fur seals on both islands has revealed notable differences in foraging patterns (durations and distance; Springer et al., 2008) that might be explained by regional differences in oceanography and may provide insight into the diverging population trends of the two islands.

Physical oceanography likely influences regional differences in the abundance (quantity), composition (quality), and distribution (accessibility) of prey—and may underlie the contrasting foraging patterns of fur seals on Bogoslof Island and the Pribilof Islands. Lactating fur seals have high energy requirements (Arnould, 1997; Gittleman and Thompson, 1988; Trillmich, 1996) and may reveal disparities in environmental conditions more readily than other groups of foraging fur seals (Costa et al., 1989; Trillmich, 1990). Females give birth on land in July and behave as central place foragers as they alternate foraging trips with periods of nursing through November (Gentry, 1998). This income provisioning strategy relies on there being predictable and profitable foraging areas for lactating fur seals to maintain energy reserves and support pups throughout the nursing period. Shifts in the distribution or concentration of preferred prey could detrimentally affect foraging success and extend the foraging trips of females seeking to meet their energy needs. Changes in the availability, aggregation, and retention of prey are likely a function of oceanographic processes occurring at different scales (Mann and Lazier, 2006).

A number of pinniped species have been documented interacting with mesoscale (~50–300 km) oceanographic features (e.g., Arnould and Kirkwood, 2008; Bradshaw et al., 2004; Baylis et al., 2008; Bailleul et al., 2010; Dragon et al., 2010; Guinet et al., 2001; Lea and Dubroca, 2003; Simmons et al., 2010), including northern fur seals (Ream et al., 2005; Sterling, 2009). However, linking foraging in marine predators to finer scale oceanographic features (submesoscale) has been more challenging because of the difficulty of precisely knowing the positions and activities of animals at sea relative to oceanographic parameters (but see Kuhn, 2011; Trathan et al., 2008; Tew Kai et al., 2009). Fortunately, advances in animal-borne telemetry, remotely sensed environmental data, and statistical frameworks now allows for

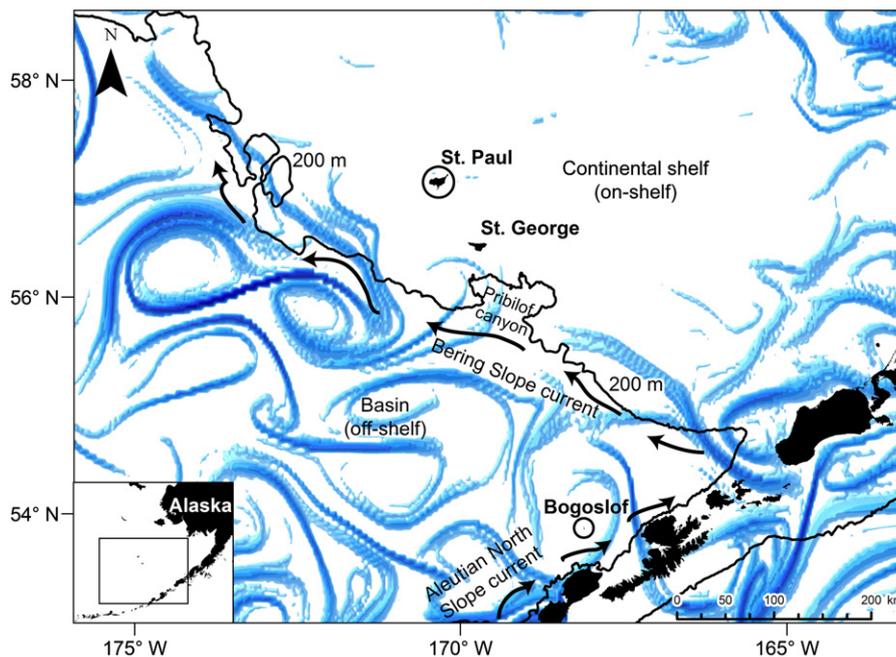


Fig. 1. Map of the eastern Bering Sea showing the locations of St. Paul Island and Bogoslof Island in relation to the positions of submesoscale surface fronts (Lagrangian coherent structures) on Aug. 1, 2009. The Lagrangian coherent structures had a resolution of 4 km over 4 days, and fronts were defined as > 0.2 finite-size Lyapunov exponents per day. The 200 m isobath marks the approximate location of the shelf-break dividing the Bering Sea basin (west) from the continental shelf (east). Note the lack of strong surface fronts around St. Paul Island as detected by the finite-size Lyapunov exponent method.

the collection and analysis of finer-scale data to better address submesoscale questions from tagged individuals.

The goal of our study was to investigate whether foraging patterns of northern fur seals from two breeding colonies located in different oceanographic domains could be associated with submesoscale oceanographic features. We tested this by tracking a large number of lactating, foraging northern fur seals at high-resolution and linking individual areas of high-use to fine-scale oceanographic features within a rigorous statistical habitat selection framework. Specifically, we tracked lactating females during summer to (1) compare foraging behaviors; (2) determine areas of high use along foraging trips; (3) quantify the influence of submesoscale oceanography on foraging intensity; and (4) relate habitat selection to the dominant oceanographic features near islands situated in different geographic domains.

2. Material and methods

2.1. Animal handling and instrumentation

Lactating northern fur seals were instrumented at St. Paul Island (57.1°N–170.3°W, Reef rookery, $n=44$ females) and Bogoslof Island (53.9°N–168.0°W, $n=43$ females), Alaska, with Mk10-F GPS enabled time-depth recorders (Wildlife Computers, WA, USA) from July 11 to September 19, 2009 (Table S1). Each GPS tag was paired with a VHF transmitter to assist with instrument recovery (Advanced Telemetry Systems, MN, USA). The archival Mk10-F tags recorded depth (0.5 m resolution), external temperature (0.52 s response, 0.05 °C resolution, 0.1 °C accuracy, Hill *pers. comm.*), and light level once per second. Fastloc™ GPS fixes were attempted every 15 min while the animal was at the surface. Instruments did not relay data through the Argos satellite network but rather needed to be physically recovered to access the data.

Females on St. Paul Island were tagged at Reef rookery with the expectation that they would forage in all hydrographic domains around St. Paul Island (Robson et al., 2004). Instruments were deployed on fur seals from 3 rookeries on Bogoslof Island to ensure tracks were representative for the island. Seals were captured using a mobile blind (July) or with a hoop-net (August and September) and transferred to a custom-made restraint board (Gentry and Holt, 1982). Animals were physically restrained and devices were glued to the dorsal pelage along the seal's midline using 5-min epoxy (Devcon®, MA, USA). Hoop-netted females were weighed (± 0.1 kg) using an MSI-7200 Dyna-Link digital scale (Measure Systems International, Seattle, WA). Standard lengths (± 1 cm) and girths (± 1 cm) were also measured whenever possible for all animals, but were challenging to obtain from the mobile blind. Animals were recaptured, physically restrained, re-measured, and devices were removed following foraging trips (deployment interval=5–39 days, Table S1). Capture teams based on each island redeployed instruments on successive animals after the data were recovered to increase the sample size of tagged individuals.

2.2. GPS and dive data analysis

GPS fixes were filtered to remove locations resulting from unlikely travel speeds (*i.e.*, > 3 m/s), and the salt-water switches on the tags were used to determine the start and end of each foraging trip. The GPS locations had a high temporal resolution (mean=17.4 post filtered locations per day) and were linearly interpolated to reconstruct the tracks (Tremblay et al., 2006). Metrics for each foraging excursion included time away from the rookery (± 0.1 d), total distance traveled, and maximum distance from the rookery (± 0.1 km). Distance traveled was calculated by summing distances between GPS points while maximum distance

was defined as the straight-line distance from the rookery to the furthest point on the track. All length calculations used the great-circle distance (WGS84-geoid) option in the *sp* package (Bivand et al., 2008) for R software (R Development Core Team, 2009).

Dive data were zero-offset corrected using Wildlife Computer's DAP program (v.2.063) with dives defined as those reaching a minimum of 5 m. Dives were further classified as foraging dives for behavioral analyses if they exceeded 20 s (Baylis et al., 2008; Kuhn et al., 2010; Kuhn, 2011). Each dive was enumerated and broken into descent, bottom, or ascent portions using 80% of the maximum dive depth as the transition points. Maximum depth (m), duration (s), bottom duration (s), as well as ascent and descent rates (m/s) were calculated for each dive. Bottom deviations (*i.e.*, vertical deviations > 1.0 m during the bottom segment of each dive) were counted as they may be indicative of feeding behavior. The position of each dive was determined by interpolating their start and end times (as recorded by the tag's clock) along the reconstructed swimming track. The total number of dives, total number of bottom deviations, as well as the mean dive duration, bottom duration, ascent rate and descent rate were calculated for 12 km (St. Paul fur seals) and 6 km (Bogoslof fur seals) intervals along each foraging track to compare dive-based feeding proxies with first-passage time (see Section 2.3).

The Mk10 external temperature data were processed according to Simmons et al. (2009). External temperature readings were aligned with the depth sensor by applying a 1-s time lag and corrected by subtracting 0.05 °C. Dives were binned at 1-m intervals and temperature values were interpolated using a hermite spline. As most seal dives occurred at < 1 m/s, temperature measures were averaged more often than interpolated for a given depth. Each dive was classified as occurring during daylight hours or at night using the civil twilight tables (where the sun is 6° below the horizon) for the community of St. Paul (for fur seals originating from St. Paul Island) and Dutch Harbor (for fur seals originating from Bogoslof Island) (<http://www.usno.navy.mil/USNO/astronomical-applications/data-services>). All dive classifications and statistics were accomplished using custom scripts in R.

The timing of diving within a day/night cycle appears to reflect alternative foraging strategies in northern fur seals (Goebel et al., 1991). Fur seals from Bogoslof Island made 98% ($\pm 0.5\%$) of their foraging dives during the night. However, two foraging strategies were evident for St. Paul fur seals based on the proportion of time they spent diving at night. The first group resembled animals from Bogoslof Island as they made 95% (group mean $\pm 0.8\%$) of their foraging dives at night and were termed the Nocturnal group. The second group was termed the Cathemeral group since they made substantial use of both the dark and the light portions of the day cycle by foraging throughout the night and into the next morning. This Cathemeral group only made 69% (group mean $\pm 2.7\%$) of their foraging dives at night with all individuals making a minimum of 18% of their dives during the day which were typically to the ocean bottom.

2.3. First-passage time

First-passage time (FPT) is the time required for a tracked seal to cross a circle of a given radius (Fauchald and Tveraa, 2003). We used this scale dependent measure of search effort to identify areas along each track that were intensively used by the fur seals. We assumed that increased habitat use was indicative of increased foraging effort and verified this assumption by comparing dive behaviors with FPT (see Section 2.2). Direct and faster movements across a defined area resulted in low FPT values (*i.e.*, low residency times), while tortuous or slower movements produced relatively high FPTs (*i.e.*, high residency times). Using FPT in statistical habitat models violates the assumptions underlying traditional parametric models such as

Gaussian generalized linear models (Freitas et al., 2008b). However, FPTs are continuous event-time measurements that can take advantage of the temporal autocorrelation inherent in telemetry studies, and therefore can be used as a response variable in survival models such as Cox proportional hazards models (Section 2.5).

We interpolated a position every 2 km along the GPS derived track to spatially standardize the foraging tracks and remove potential biases associated with oversampling some areas or with animals that provided a greater number of locations. A 2 km interval was chosen because it was the mean and median distance between successive filtered GPS locations at sea for both St. Paul Island and Bogoslof Island groupings. FPT was thus calculated for each of the generated positions for radii ranging from 2 to 40 km at 2 km intervals using the *adehabitat* software package in R (Calenge, 2006).

FPT values will increase with increasing radius size, as more of the path is included in the FPT calculation (Fig. 2A). However, the variance of the mean FPT calculated for each radius should reflect the consistency with which the fur seals spent time in each circle. Thus the radius with the maximum FPT variance should be the one that best differentiates between low and high FPT, and reflects the spatial scale within which animals concentrated their time (Fauchald and Tveraa, 2003, 2006; Freitas et al., 2008b).

The mean, log-transformed FPT variances were plotted for each fur seal grouping (*i.e.*, St. Paul Nocturnal, St. Paul Cathemeral, and Bogoslof) to determine the maximum variance. The radius of the circle that generated the highest mean variance was 12 km for both foraging strategies from St. Paul fur seals and was 6 km for Bogoslof fur seals (Fig. 2B). The radii with the maximum variance was chosen as the common length-scale (interval between retained points) for all fur seals in each foraging group as this facilitated comparing individuals within groups, removed some of the stochasticity from individual differences, and defined the minimum allowable resolution for the environmental covariates (see Section 2.4). Given the majority of fur seal dives took place after civil twilight, we also explored the impact of restricting data (to night periods only) had on relationships between FPT and environmental covariates prior to statistical modeling. All FPT points (including likely daytime resting behavior) or a subset of solely night time FPT points were correlated with environmental covariates for the strictly nocturnal diving groups (St. Paul Nocturnal, Bogoslof). In all the cases, FPTs taken from interpolated fur seal tracks (at 12 km intervals for St. Paul trips and 6 km for Bogoslof trips) were used to compare the time spent in different areas as a response to changes in the environment (see Section 2.5).

2.4. Environmental covariates

A number of environmental parameters may explain the time that fur seals spent foraging along their tracks. We therefore tested (Section 2.5) whether the relative foraging intensity could be explained by six environmental parameters: water temperature at 1 m ($^{\circ}\text{C}$), thermocline depth (m), mean temperature above the thermocline ($^{\circ}\text{C}$), total chlorophyll in the upper 100 m (mg/m^3), ocean depth (m), and distance to the nearest front (km). Temperature measured by the Mk10 at 1 m was considered to be a proxy for sea surface temperature, and was interpolated to the nearest FPT location. Constraining the temperatures to those obtained at 1 m ensured that they were from the water column and were not biased by air temperatures when the tag was exposed while the animals surfaced to breathe.

Thermocline depth, mean temperature above the thermocline, and total chlorophyll in the upper 100 m of the water column were derived from 247 CTD profiles obtained via ship sampling in the study area from July 18 to August 14, 2009. Sampling was designed primarily to sample the distributions and habitat conditions of forage fish and krill and consisted of a series of paired stations separated by 10 km long transects (Fig. 3). Stations were stratified among three,

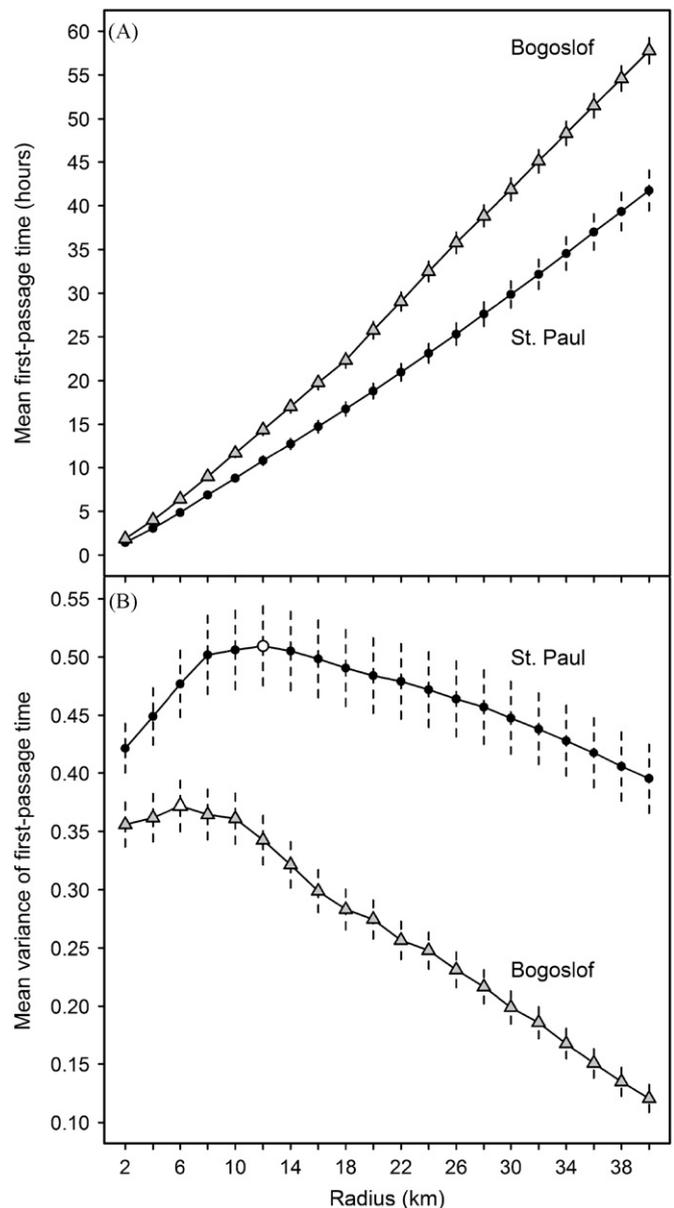


Fig. 2. Mean first passage time (A) and the mean variance of logged first passage time (B) (\pm SE) in relation to area radius for lactating northern fur seals foraging from St. Paul Island ($n = 44$) and Bogoslof Island ($n = 43$). First-passage time is the time required for a tracked seal to cross a circle of a given radius. Peak variance occurred at radii of 12 km for St. Paul trips and 6 km for Bogoslof trips.

hydrographically distinct zones (Coachman, 1986): middle shelf with bottom depths less than 100 m (45 stations); outer shelf with bottom depths between 100 and 200 m (81 stations); and slope/basin with depths greater than 200 m (121 stations) (Benoit-Bird et al., 2011). A Sea-Bird SBE19plus CTD with a WetLabs ECO-flntu fluorometer was lowered to a depth of 100 m or 1 m from the bottom if the sea floor was < 100 m from the surface. Data were low pass filtered and edited to account for heaving of the ship before the raw data were converted to variables of interest using factory calibrations. Thermoclines were defined as the greatest slope in temperature data from each cast and gradients were confirmed visually. Pre-determined fluorometer calibration equations were confirmed via periodic field samples of water filtered for chlorophyll in the area of the experiment. CTD variables were converted into predicted surface rasters using inverse distance weights in ArcGIS geospatial analyst (v. 9.3.1) and values were extracted to FPT points. Inverse distance

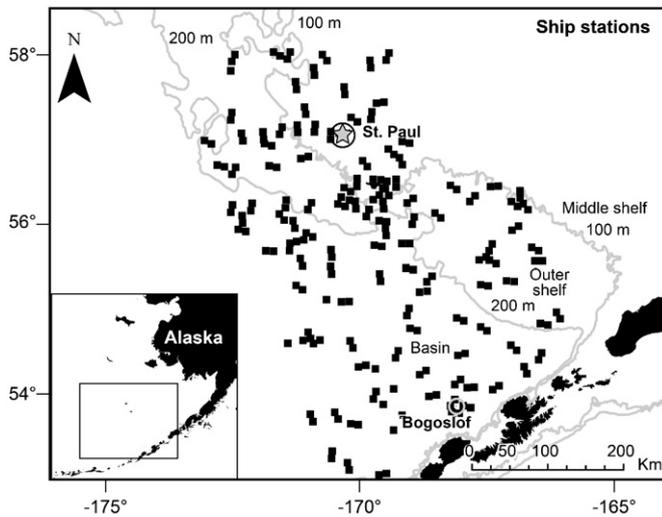


Fig. 3. Sampling stations in the eastern Bering Sea ($n = 247$) where CTD profiles were obtained from July 18–Aug 14, 2009 to measure thermocline depth, mean water temperature above the thermocline, and total chlorophyll in the upper 100 m of the water column.

interpolation was used as it is a conservative method well suited to smoothly varying variables such as temperature, and it retains the original sampled values. Ocean depth was extracted for each FPT location from a 30 arc-s gridded global bathymetry model (GEBCO_08 Grid, <http://www.gebco.net>).

Distance to the nearest surface front was calculated from 4-day maps of surface Lagrangian coherent structures (e.g. transport barriers, filament edges, or eddy boundaries realized from tracing fluid flows). These maps (e.g. Fig. 1) were derived from absolute geostrophic current velocities using the finite-size Lyapunov exponent (FSLE) method. The method is well suited to study the properties of transport in fluid flow (Boffetta et al., 2001; d'Ovidio et al., 2004) and enables the study of processes below the scales typically provided by altimetry (Hernández-Carrasco et al., 2011). Low FSLE values coincide with areas of low dispersion rates (e.g. eddy cores) and where regions of high FSLE values are associated with areas of high dispersion such as the outer part of eddies or strong surface fronts (d'Ovidio et al., 2004; Resplandy et al., 2009). As such, frontal boundaries can be detected retrospectively when the calculation is performed over a time-series of geostrophic currents. Geostrophic velocities used to produce frontal maps were in turn produced by gridded, sea-surface height data merged from multi-mission, delayed-time (corrected) satellite altimetry using optimal interpolation (Aviso, France, <http://www.aviso.oceanobs.com>).

FSLEs measure the exponential speed at which fluid particles separate from an initial set distance to a final prescribed distance, and were computed at position x and time t as

$$\lambda = \frac{1}{\tau} \log \frac{\delta_f}{\delta_0} \quad (1)$$

where δ_0 is the initial separation distance of two tracers, δ_f is the final separation distance, and τ is the first time the δ_f distance is reached. When computing submesoscale structures in the ocean, typical FSLE values along boundaries fall in the range of 0.1–1.0 FSLE/d, indicating that a large scale tracer anomaly can be structured into a submesoscale eddy or filament (distinct, thread-like water mass) within a few days (Cotté et al., 2011). Separation values were set as $\delta_0 = 0.04^\circ$ latitude (which is equivalent to approximately 4 km in the southeastern Bering Sea) and as $\delta_f = 0.6^\circ$ latitude (~ 67 km). FSLEs ≥ 0.2 were retained to be conservative when defining filaments or frontal edges capable of

influencing fur seal foraging. The position of the nearest frontal edge was extracted for each FPT point using ArcGIS from temporally aligned FSLE rasters and fur seal tracks. Distance (km) to the feature was calculated in *R* to quantify the association between FPT locations and fronts. Serial autocorrelation was avoided and independence of the environmental data was maintained by sampling covariates at 6 km (Bogoslof Island) or 12 km (St. Paul Island) intervals along fur seal tracks (equal to the maximum FPT variance for each island) as the intervals were larger than the 4 km minimum resolution of the data (Freitas et al., 2008b).

2.5. Habitat selection modeling

The six environmental covariates (water temperature at 1 m, thermocline depth, mean temperature above the thermocline, total chlorophyll in upper 100 m, ocean depth, and distance to the nearest front) were first plotted against FPTs to explore potential correlations in the data *sensu* Freitas et al. (2009). The associated 95% confidence intervals were calculated via the adjusted percentile method with 5000 bootstrapping samples. We then evaluated the effect of the six candidate variables on fur seal movements (as quantified via raw FPT) using mixed-effects Cox proportional hazards (CPH) models (Pankratz et al., 2005; Freitas et al., 2008b). The CPH model was defined as

$$h(t) = \exp(\beta_1 X_1 + \beta_2 X_2 + \beta_3 X_3 + \dots + \beta_p X_p + b) h_0(t) \quad (2)$$

where $h(t)$ is the risk or likelihood an animal will leave an area (defined as a circle of 6 or 12 km radius in this case) at time t , X_x are the explanatory oceanographic covariates in the model, β_x are the regression coefficients fit to each variable by the modeling process, b is the per-subject random effect, and $h_0(t)$ is the baseline hazard function (i.e. the hazard when all covariates equal zero or a pre-defined baseline). Including the b random-effect term allowed the model to account for some of the individual level variability exhibited by the fur seals. Spatial autocorrelation was incorporated within the analysis by using foraging trips as the statistical unit (b) and inherently by comparing used locations within a path (structured by the same autocorrelation process) as opposed to comparing used areas to a null model of positions derived without autocorrelation (Fieberg et al., 2010).

CPH models assume that hazards are proportional throughout the study period (i.e., covariates have the same influence on FPT throughout the course of the foraging trip). We tested this assumption visually by plotting Schoenfeld residuals for each covariate against $\log(\text{time})$ and by testing if slopes were zero (Kleinbaum and Klein, 2005). Most of the continuous covariates were deemed non-proportional and were therefore categorized based on their quantile distributions and re-tested to satisfy model assumptions. All possible combinations of the six covariates were fit during model selection. An interaction term between distance to fronts and total chlorophyll in the upper 100 m was also included to investigate whether FPTs at different distances to fronts were affected by the level of chlorophyll. Fur seal groups (St. Paul Nocturnal, St. Paul Cathemeral, and Bogoslof) were modeled separately to compare habitat selection differences between them.

CPH models were evaluated and fit in *R* using the *survival* and *coxme* packages (Therneau, 2009; Therneau and Lumley, 2009). Model selection was performed using AIC corrected for effective sample size:

$$AICc = -2\log(L) = 2k + \frac{2k(k+1)}{n-k-1} \quad (3)$$

where $\log(L)$ is the penalized log likelihood and k is the penalized degrees of freedom from the CPH model, while n is the sample size (number of FPT points). After appropriate models were chosen, hazard ratios (\exp^β) were calculated from the coefficients

of all retained covariates. In this context, they provided quantitative assessment of the relative influence that specific habitat features had on FPT (Freitas et al., 2008b). Values less than one implied that the environmental covariate was advantageous for foraging while values greater than one implied that the feature or category had a negative influence. Coefficients with values close to zero or with confidence intervals that span zero were considered to have little to no impact on foraging time as they produced neutral hazard ratios ($\exp^\beta = 1$). Models were run using all seal trips and with a subset of trips to mid-August when ship CTD data collection was terminated. Hazard ratios were essentially unchanged for the 3 fur seal groups when all trips were modeled compared to trips limited to the ship collection period therefore the entire fur seal data set was used. Summary statistics are presented as means \pm standard error.

3. Results

3.1. Animal movements and dive analysis

A total of 182 foraging trips were recorded from 87 lactating northern fur seals (54 St. Paul Island, 128 Bogoslof Island; Table S2). Trips (number of days and distance) from St. Paul Island were significantly different from those from Bogoslof Island (two sample t-tests, $p < 0.001$). Trips from St. Paul Island took longer (mean = 7.9 vs. 3.3 d; range = 4.2–16.9 vs. 0.2–13.16 d), covered a greater distance (mean = 604.5 vs. 197.1 km; range = 243.5–1267.0 vs. 0.46–519.7 km), and went further from the rookery (mean = 227.8 vs. 73.5 km; range = 78.7–462.4 vs. 0.2–189.7 km) compared to trips from Bogoslof Island. As a result, many more repeat trips were recorded from Bogoslof fur seals (85 repeat trips from 39 seals, range = 2–9 trips per seal) than from St. Paul fur seals (10 repeat trips from 5 seals, range = 2–4 trips per seal) during the study period. St. Paul fur seals foraged widely as expected (Fig. 4), radiating in all directions from the island with a notable concentration of southward trips. Trips from the Nocturnal group were often directed beyond the shelf-break while Cathemeral fur seals

generally foraged over the continental shelf. Bogoslof fur seals did not pass through the Aleutian chain but constrained their foraging trips to the southeastern Bering Sea basin (Fig. 4).

Given the large disparity in trip duration between islands, trip length was standardized (km per d) to compare distances covered by animals that made multiple short trips from Bogoslof Island with those that made single trips from St. Paul Island over an equivalent time period. On average, St. Paul fur seals traveled 26% further per day (mean = 76.0 vs. 60.4 km) after accounting for variable times at-sea. St. Paul fur seals also made fewer foraging dives (dives > 20 s) per km when foraging trips were standardized (mean = 2.1 vs. 2.8 dives/km).

We recorded 139,032 foraging dives (72,202 St. Paul Island; 66,830 Bogoslof Island.). They showed that St. Paul Nocturnal fur seals ($n = 29$ trips) were primarily shallow, epipelagic divers (Q_1 – Q_3 depth range = 10–22 m) that foraged widely over the shelf, slope and basin. In contrast, St. Paul Cathemeral fur seals ($n = 25$ trips) dove primarily on-shelf and over a wider depth range (Q_1 – Q_3 = 8–49 m) by clustering many short dives in the upper water column throughout the night followed by longer, deeper dives to the sea floor during the early daylight hours. Foraging dives by Bogoslof fur seals were consistently shallow (Q_1 – Q_3 depth range = 10–21 m) and took place primarily over the basin with rare exceptions along the margins of the continental shelf or the Aleutian slope.

3.2. First-passage time

The scale of area-restricted searches for foraging trips from St. Paul Island (12 km) was double the size of trips from Bogoslof Island (6 km). A total of 2618 FPTs were used to model St. Paul trips (Nocturnal group = 1466; Cathemeral group = 1152) and ranged from 2.2–70.3 h at a 12 km radius, which translated to average transiting speeds of 10.9–0.34 km/h (3.0–0.1 m/s). Average FPTs were similar between the St. Paul fur seal groups (Nocturnal group mean = 9.9 ± 0.3 h; Cathemeral group mean = 10.2 ± 0.3 h).

Of the 128 total foraging trips from Bogoslof Island, 111 trips (3929 FPTs) were deemed to provide sufficient track resolution

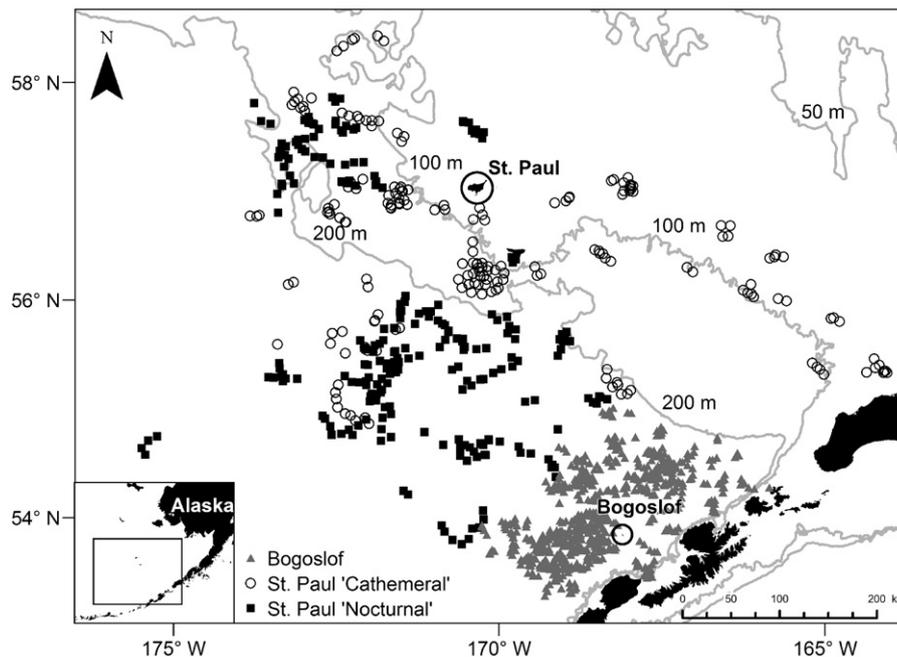


Fig. 4. Areas used intensively by lactating northern fur seals tagged on St. Paul Island ($n = 44$ females) and Bogoslof Island ($n = 43$, filled triangles) from Jul–Sep, 2009. St. Paul trips were subdivided into those consisting of $> 90\%$ night dives (Nocturnal, filled squares); and those that made $< 90\%$ nighttime dives (Cathemeral, open circles). Areas of intense use were defined as areas with the top 16.7% (sextile) of first-passage times calculated for foraging trips from each island (St. Paul > 15.9 h; Bogoslof > 9.5 h). First passage times were calculated within a radius of 6 km for Bogoslof fur seals ($n = 660$ intense-use FPTs) and 12 km for St. Paul fur seals ($n = 437$ intense-use FPTs).

(> 4 FPTs per trip) for modeling habitat selection. FPTs ranged from 1.29 to 44.0 h at a radius of 6 km which is equivalent to average transit speeds of 9.3–0.27 km/h (2.6–0.08 m/s). Average FPT for Bogoslof trips was 6.0 ± 0.2 h, but must be doubled (~ 12 h) for a relative comparison of residence times with St. Paul based trips due to the differences in FPT spatial scale. However, the average swim speed between island groupings could be directly compared side by side and was notably slower for fur seals from Bogoslof Island (1.7 vs. 2.8 m/s).

High FPTs were associated with high numbers of dives > 20 s (Fig. 5) for trips from both islands. In addition, high FPTs were correlated with increased numbers of bottom deviations, relative

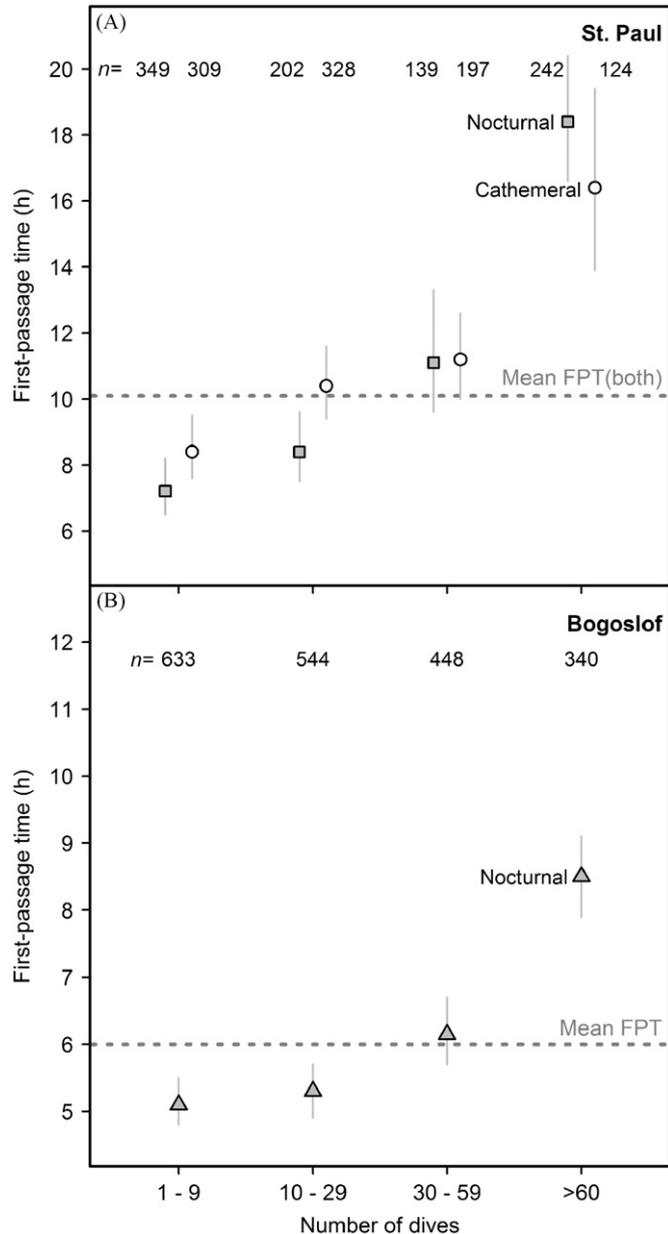


Fig. 5. Increasing first-passage time (FPT) with increasing numbers of dives lasting > 20 s along foraging tracks of lactating northern fur seals tagged on St. Paul Island (A) and Bogoslof Island (B). St. Paul trips were subdivided into those consisting of > 90% nighttime dives (Nocturnal, filled squares); and those that made < 90% nighttime dives (Cathemeral, open circles). Mean FPTs, bootstrapped 95% confidence intervals, and number of FPT points (n) are shown for each island and dive category. Overall mean FPTs are displayed as dashed lines. Note that the FPT scale for the Bogoslof panel is half that of the St. Paul panel as the Bogoslof FPT area radius (6 km) was half that of St. Paul (12 km).

bottom time and dive ascent rates (data not shown). Sextiles (6-quantiles) were calculated for each island separately, and the top 16.7% of FPT values (St. Paul trips > 15.9 h; Bogoslof trips > 9.5 h) were defined as areas of high use for visualization purposes (e.g., Fig. 4). Locations with percentile values > 83.3% were plotted in select figures for clarity (as noted in the captions) as they represented only the areas used most intensively by foraging northern fur seals. Variances of log FPT over 2–40 km radii ranged from 0.41 to 0.51 for northern fur seals from St. Paul Island while those from Bogoslof Island ranged from 0.13 to 0.37 (Fig. 2B).

Comparing mean FPTs against categorized covariates using either all FPT values or just a subset of those values obtained at night revealed similar trends for both the St. Paul Nocturnal group and the Bogoslof population (see Section 3.3). All FPT points were therefore included in their respective habitat selection analysis. Raw, not mean or categorized, FPT values were used as the response variable for all habitat selection modeling.

3.3. Habitat selection modeling

The relative importance of covariates varied between fur seals foraging in different regions despite groups having similar top CPH models (Fig. 6). Two models were given similar weighting for the St. Paul Nocturnal fur seals (Table S3), but only hazards for the first model are reported in Table 1. The influence of chlorophyll as an additional covariate in the second model was extremely limited (hazard ratio = 1.08, $CI(\beta) = -0.08$ to 0.23) and had no effect on other covariates.

Areas of intense use (visualized as top 16.7% of FPTs) occurred closest to fronts when trips took place near the shelf-break or over the basin (e.g., Fig. 7A and B, Animation S1) and a corresponding higher risk (likelihood) of leaving was noted for areas > 10 km from frontal edges. For example, the risk of a fur seal moving to the next 12 km portion of its path was 55% greater in areas > 20 km from a front than in areas < 4 km from a front. Intense use of areas near the shelf break and over the basin where frontal activity was greatest resulted in a coincidental lowering of risk (increasing habitat selection) in increasingly deeper waters. Fur seals in this group tended to transit quickly through areas with thermoclines > 35 m deep and trends were similar whether daytime FPT points were included or excluded (Fig. 8A).

Pockets of shallow thermoclines were encountered off-shelf but were primarily exploited when foraging on-shelf (e.g., Fig. 9B). Fittingly, higher risks of moving to the next 12 km portion of the track (reduced habitat selection) were progressively greater when thermoclines deepened. Mean temperature above the thermocline was retained in the model but had no discernible influence on animal movements (see confidence intervals in Table 1). Increasing risk was noted for increasing surface temperatures over the observed range (4.0–10.0 °C).

All covariates were included in the top-ranked model for the St. Paul Cathemeral fur seal group (Table S4). Total chlorophyll in the upper 100 m again had no clear effect on animal movements. Neither did the interaction between high relative chlorophyll and increasing distances to the nearest front (see respective CI in Table 2). Their exclusion from the two next best models had negligible impacts on remaining model coefficients or hazard ratios (Table 2). Distances > 4 km away from fronts had a limited effect on area use (< 28% increase over baseline risk) but there was no trend with increasing distance. Cathemeral trips rarely encountered strong surface fronts (hence their limited effect) but a few intersected them at the shelf-break or just beyond resulting in some increased selection for deeper ocean depths but only > 200 m (Table 2).

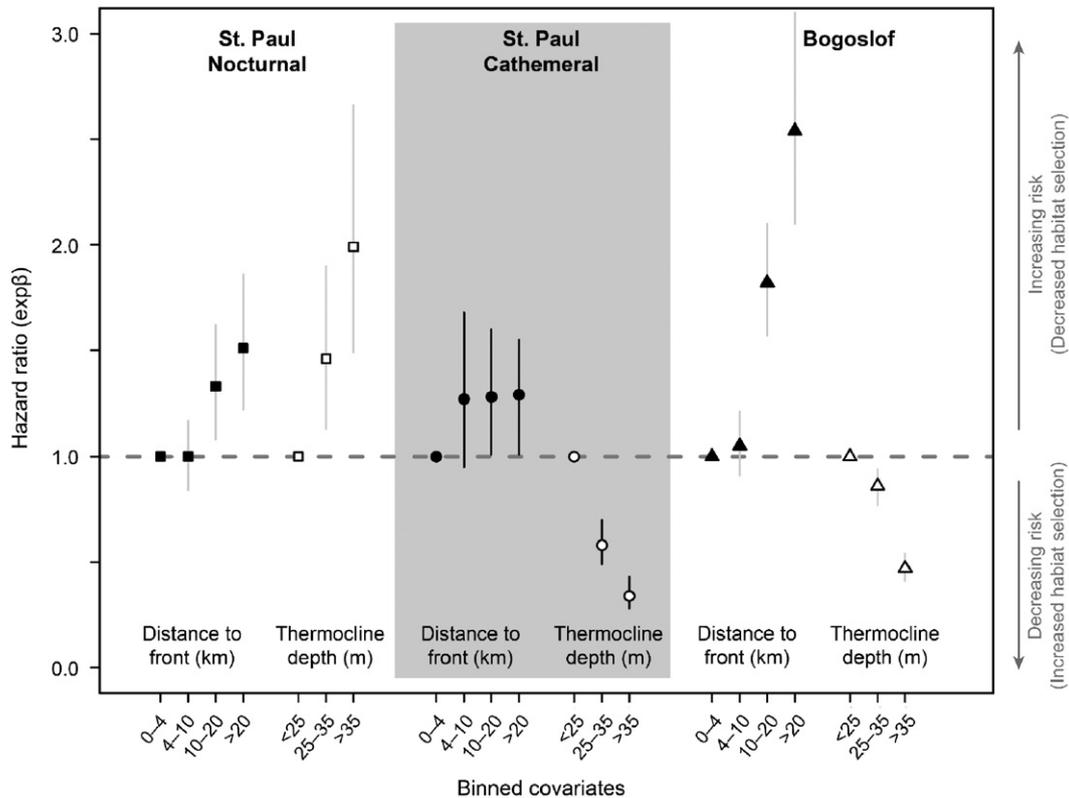


Fig. 6. Summary of key hazard ratio estimates ($\exp\beta$) and 95% confidence intervals ($\exp\beta(CI)$) from top-ranked Cox proportional hazards models describing habitat use (time spent within a specified radius) by 3 groups of foraging, lactating northern fur seals (see Tables 1–3). Estimates are relative to the first binned category of each covariate (distance to nearest front and thermocline depth) which is the baseline hazard (dashed line, $HR = 1.0$). Hazard ratios > 1.0 indicate increasing risk (likelihood) of fur seals leaving an area (reduced habitat selection) while ratios < 1.0 infer decreasing risk (increased habitat selection).

Table 1

Estimates from the top-ranked Cox proportional hazards model predicting habitat use (time spent within a 12 km radius) by foraging, lactating northern fur seals from the St. Paul Nocturnal group as determined by AICc (see Table S3). Number of first passage time points (n), coefficients (β), hazard ratios ($\exp\beta$), and 95% confidence intervals ($CI(\beta)$) are shown for each covariate/category affecting the risk of fur seals moving to the next 12 km portion of their track. Categorical values are relative to their first class. Front: distance to nearest front; depth: ocean depth; TC: thermocline depth; TempTC: mean temperature above thermocline; Temp1 m: temperature at 1 m; Chl: total chlorophyll in upper 100 m. Note: β -values > 0 ($\exp\beta > 1.00$) indicate increased risk (likelihood) of leaving, while β -values < 0 ($\exp\beta < 1.00$) infer decreased risk (i.e. increasing habitat selection).

Model covariate	N	β	$\exp\beta$	$CI(\beta)$
<i>Front+Depth+TC+TempTC+Temp1 m; (AICc wi=0.54)</i>				
Front (0–4 km)	752	–	–	–
Front (> 4–10 km)	209	0.00	1.00	–0.17 to 0.16
Front (> 10–20 km)	153	0.28	1.33	0.08 to 0.48
Front (> 20 km)	352	0.41	1.51	0.20 to 0.62
Depth (0–100 m)	325	–	–	–
Depth (> 100–200 km)	377	–0.52	0.59	–0.72 to –0.32
Depth (> 200–350 km)	44	–0.78	0.46	–1.15 to –0.41
Depth (> 350 km)	720	–1.46	0.23	–1.74 to –1.18
TC (< 25 m)	144	–	–	–
TC (25–35 m)	969	0.38	1.46	0.12 to 0.64
TC (> 35 m)	353	0.69	1.99	0.40 to 0.98
TempTC	1466	–0.07	0.93	–0.17 to 0.03
Temp1 m	1466	0.13	1.14	0.03 to 0.22

In contrast to the St. Paul Nocturnal group, high FPT areas were associated with the deepest thermoclines (Figs. 8B and 9A) for Cathemeral fur seals. Progressively decreasing risk corresponded with deepening thermoclines (e.g. 66% less risk in areas where thermoclines > 35 m deep compared to < 25 m deep). Surface temperature was consistently retained yet had no effect on where

fur seals concentrated their foraging time (see CI, Table 2). Reduced risk was noted for increasing mean temperatures above the thermocline (observed range = 2.4–9.7 °C).

All covariates were retained for CPH modeling for trips from Bogoslof Island (Table S5) but as with the other groups, total chlorophyll in the upper 100 m had no effect on fur seal foraging (Table 3). Areas near fronts were sites of intense use (e.g., Fig. 7C and D, Animation S2) with lower FPT observed > 10 km from the features regardless of the inclusion or exclusion of daytime FPT (Fig. 10). Corresponding higher risks were noted for locations > 10 km from fronts. For example, the probability of a fur seal moving to the next 6 km section of the track was 154% greater in areas > 20 km from a front compared to areas < 4 km from the feature. Depth was retained, yet had no influence on fur seal movements ($\exp\beta = 1.0$) which was not surprising for animals diving < 30 m on average in areas typically > 400 m deep. Areas with deeper thermoclines coincided with regions of concentrated fronts and, accordingly, with decreased risk of leaving these areas. Area use intensified with increasing mean temperature above the thermocline (observed range = 0.4–8.6 °C) and with increasing surface temperature (observed range = 5.4–9.5 °C). Areas with relatively high levels of total chlorophyll in the upper 100 m at increasing distances from fronts showed increasing habitat selection contrary to expectations that higher chlorophyll values nearer to fronts would engender increased use.

4. Discussion

The data collected by lactating fur seals, ships, and satellites revealed significant differences in the foraging behaviors of two northern fur seal colonies that can be explained by fine-scale

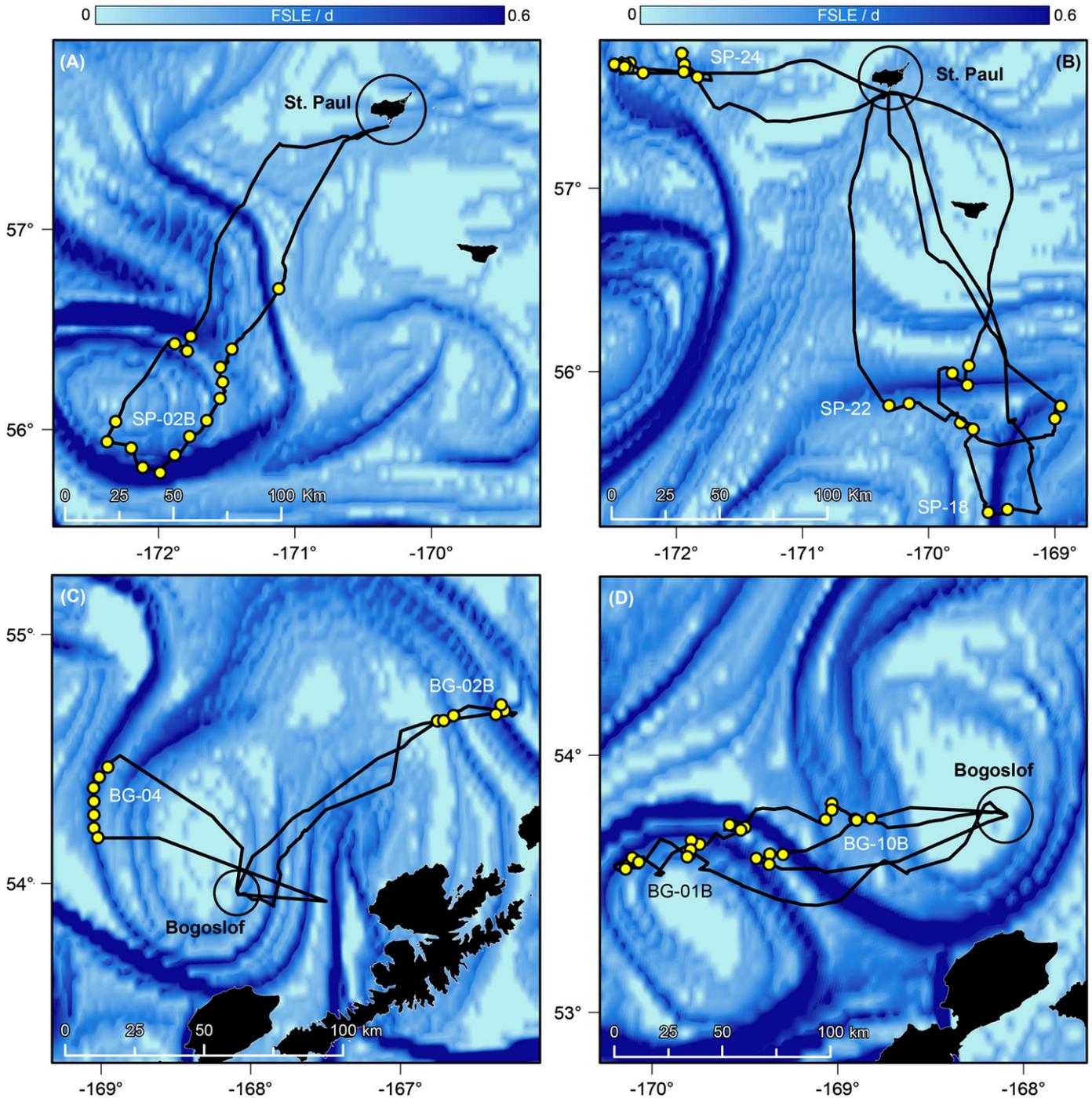


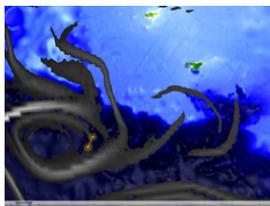
Fig. 7. Examples of northern fur seals foraging locations in relation to submesoscale fronts (Lagrangian coherent structures defined as >0.2 finite-size Lyapunov exponents per day). Complete foraging tracks are shown with continuous lines for each numbered individual, and areas of intense use are shown by yellow points during A) Jul 23–31, B) Aug 13–27, C) Jul 17–26, and D) Jul 22–28, 2009. Intense use was defined as the top 16.7% (sextile) of first-passage times, and time spent by fur seals was calculated within areas having radiuses of 6 km for trips from Bogoslof Island and 12 km for trips from St. Paul Island. Lagrangian coherent structure maps have a resolution of 4 km over 4-days. The plotted tracks are among the clearest examples showing the interaction between high-use areas and fronts.

oceanographic features. Foraging trips were longer and the size of area-restricted searches was larger for fur seals from St. Paul Island compared to seals from Bogoslof Island. Hotspots for lactating females occurred near dynamic submesoscale surface fronts and with thermocline depth classes that generally matched individual dive patterns. The relative use of these features by fur seals may coincide with regional accessibility. In 2009, submesoscale surface fronts were not equally available to the lactating females from the two breeding populations. Such differences in the regional accessibility of strong surface fronts and

thermoclines may account for the differing foraging patterns of St. Paul and Bogoslof fur seals.

4.1. Animal movements and dive analysis

The 87 lactating females instrumented during the study period represent the largest single season tag deployment to date on adult female northern fur seals. There were no handling mortalities during the study, however an additional female tagged on St. Paul Island was not re-sighted following her departure from



Animation 1. Example of northern fur seals originating from St. Paul Island foraging along a submesoscale surface front over the central shelf-break and basin of the eastern Bering Sea. Individual fur seals are represented by coloured lines. First passage times are calculated at equal intervals along the fur seal track and are shown as yellow points (animated with halos where larger halos equal greater residence time). Fronts are depicted as black/grey bands and are 4-day snapshots of a dynamic system. Time at bottom is in (GMT).

the rookery (2 d post-tagging) resulting in the loss of the instrument. The large number of tagged individuals revealed significant foraging trip differences between islands, but no overlap in their respective foraging areas (Fig. 4). St. Paul based trips were twice as long (7.9 d average), 3-times as far (228 km average max distance from rookery), and covered 3-times greater distance (600 km average) compared to trips from Bogoslof Island. Ranges of these metrics barely overlapped, indicating substantial biological differences between colonies.

Fur seals from Bogoslof Island traveled 26% less per day while at sea and returned more frequently to shore to nurse their pups compared with those from St. Paul Island. This difference in time spent at-sea between nursing bouts could significantly affect milk delivery rates to pups and thereby impact pup size at weaning or the timing of weaning between populations. This is consistent with the finding of others that pups on Bogoslof Island gained more mass per day during the lactation period and were heavier than pups on St. Paul Island in mid-October (Springer et al., 2008). Foraging longer and further from rookeries to obtain prey may reflect reduced prey availability (Costa, 2008), quality, or accessibility and suggests that fur seals from St. Paul Island had more difficulty obtaining sufficient prey compared to conspecifics from Bogoslof Island (see Section 4.3).

Our large sample size re-affirms the understanding that northern fur seals in the eastern Bering Sea are generally nocturnal divers. Nocturnal diving has been well documented for female fur seals from the Pribilofs (Goebel et al., 1991; Gentry, 1998; Kuhn et al., 2010) which are presumed to primarily target juvenile (age 0 and 1) walleye pollock (*Theragra chalcogramma*) that migrate vertically to the upper portion of the water column (Antonelis et al., 1997; Gudmundson et al., 2006; Sinclair et al., 2008; Zeppelin and Orr, 2010). Similarly, we found that fur seals foraging almost exclusively at night (the Nocturnal group) exhibited a shallow diving pattern (< 30 m) and did so primarily off-shelf or over the shelf-break as shown by Goebel et al. (1991). In contrast, fur seals that foraged at night and also during the day (the Cathemeral group) did so primarily over the continental shelf. They exhibited the typical shallow dive pattern at night followed by deeper dives that typically reached the ocean-bottom during early morning. Such benthic dives would allow fur seals to target and trap prey against the sea-floor, and is a strategy that could be more successful during daylight hours, particularly if prey migrated below the scattering layer during the day (Schabetsberger et al., 2000). Adult pollock are also typically found nearer the ocean bottom and such larger prey may be targeted during bottom dives. Other semi-demersal prey such as Pacific sandlance (*Ammodytes hexapterus*) and Atka mackerel (*Pleurogrammus monoptyerygius*) begin their diurnal vertical migration in the early daylight hours (Hobson, 1986; Nichol and Somerton, 2002) when they would be available and vulnerable to

deeper diving fur seals as they move off the bottom. Females from Bogoslof Island foraged primarily in the deep basin waters surrounding Bogoslof Island and were predominantly shallow, night-time divers. Their dive behavior matches the strongly diel pattern of their nearly exclusive prey: northern smoothtongue (*Leurolglossus schmidtii*) and gonatid squids (Sinclair et al., 2008; Zeppelin and Orr, 2010).

4.2. First-passage time

FPT peaks were detected for foraging northern fur seals and areas of intense use were identified for each trip at the spatial scales that best differentiated low and high FPTs. St. Paul animals foraged at twice the scale (mean radius=12 km) of Bogoslof animals (6 km). This indicates that St. Paul fur seals employed a wider area-restricted search pattern, and suggests that prey fields were more diffuse near St. Paul Island than Bogoslof Island.

Mean variances in FPTs were low while the standard errors were high for northern seals in general as calculated for radii of 2–40 km (Fig. 2B). We attribute this to the lack of distinct northern fur seal foraging grounds and the constrained nature of foraging trips during the pup rearing season. As income breeders and central place foragers, female fur seals must balance the competing demands of foraging and pup provisioning over a brief period. This may explain their tendency to swim at high-speed and forage throughout their trips—rarely slowing on their circuit away from the rookery. This type of travel, coupled with high inter-animal variability led to low overall variance between areas of increasing radii along the tracks. This was particularly notable for foraging trips from St. Paul Island where fur seals employed nocturnal and cathemeral strategies. Our FPT variance structure was narrower than similar FPT analyses of long-term deployments on arctic marine mammals (Freitas et al., 2008a, 2009) and short-term deployments on seabirds (Pinaud, 2008; Suryan et al., 2006; Weimerskirch et al., 2007). The FPT variances for seabirds and arctic marine mammals were wider and likely indicative of extended foraging in well-defined areas between long stretches of direct travel.

Concern has been raised that track-based measures of area use intensity such as FPT fail to coincide with areas defined by other feeding proxies for diving predators at fine scales (Robinson et al., 2007), but this was not the case in our study. The number of dives (Fig. 5), the number of bottom deviations, and the relative dive bottom time all increased in areas with increasing FPT for trips from both islands. Ascent rates were also positively associated with FPTs for trips from St. Paul Island but not for trips from Bogoslof Island. These dive metrics have been previously used to infer foraging behavior in marine predators (Dragon et al., 2010; Scheffer et al., 2010; Trathan et al., 2008) including northern fur seals (Kuhn, 2011) and provides confirmation that increasing FPTs in our study are indicative of increased foraging activity at least at scales of 6 and 12 km.

Despite verifying the FPT technique with correlates of foraging behavior, short resting bouts along the paths could inflate FPT values. We strongly suspect some limited travel devoid of dive activity observed immediately following intense diving bouts may indicate resting or sleep, which would positively bias residence time and weaken the link between FPT and foraging time. Regardless of the confounding effect of daytime sleeping and resting on FPT (our measure of active foraging) and its association with either thermoclines or oceanographic fronts, we still found a strong relationship between the two. Interestingly, neither mean dive duration nor mean bottom duration increased with increasing numbers of hours spent in a defined area (6 or 12 km). This supports the idea that individual lactating northern fur seals have well-defined search and foraging strategies within the water column. Increased frequency of habitual

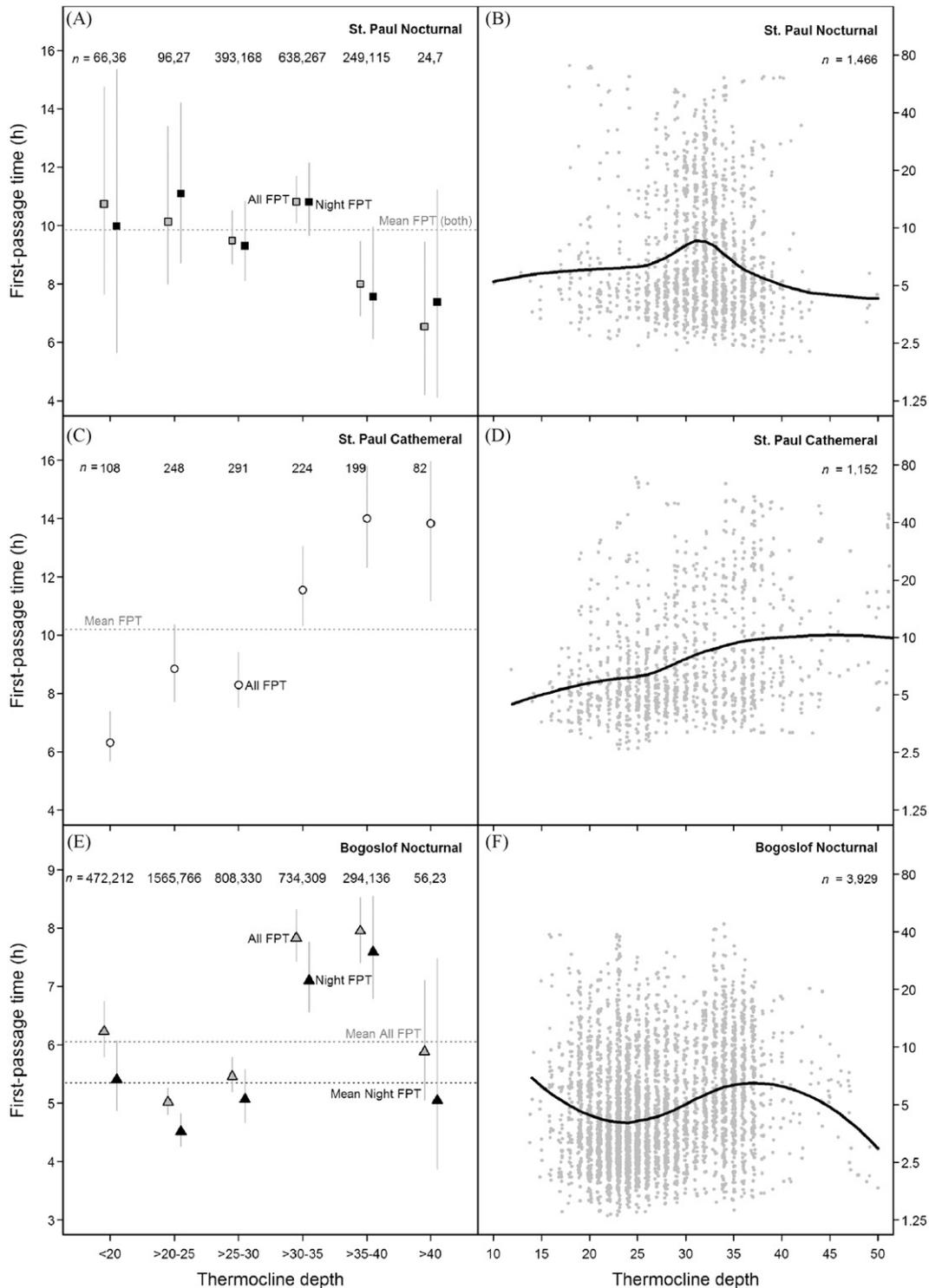


Fig. 8. Contrasting relationships between first-passage time (FPT) and thermocline depth for lactating northern fur seals foraging from St. Paul Island and Bogoslof Island. St. Paul trips were subdivided into those consisting of > 90% nighttime dives (Nocturnal, squares); and those that made < 90% nighttime dives (Cathemeral, circles). Mean FPTs are shown with bootstrapped 95% confidence intervals, and the number of FPT estimates (n) per depth category (panels A, C, E) both including (All FPT) and excluding (Night FPT) daytime FPT estimates. Cathemeral trips shown as All FPT estimates only as > 18% of dives on these trips occurred in the daytime. Overall mean FPTs are displayed as horizontal dashed lines. Additional depth bins are shown than were included in the Cox models to better highlight FPT trends. Note that the untransformed scale for Bogoslof panels are half those for St. Paul animals as the Bogoslof FPT area radius (6 km) was half that of St. Paul (12 km). Also shown are panels of jittered FPT values on a log₁₀ scale plotted against jittered depth values with fitted loess curves for each trip grouping (panels B, D, F). The log scale was used to depict the full range of FPT data and did not affect the loess statistic.

dive behavior within an area is seemingly indicative of intense foraging as opposed to increasing dive-time or bottom-time at the scale of our study.

Using all FPT values or just values obtained at night showed similar patterns in how fur seals concentrated their time relative

to oceanographic variables (e.g., Figs. 8 and 10). Nightfall may have triggered the epipelagic foraging strategy employed by nocturnal foragers, but changes in key oceanographic parameters appear to have driven the overall intensity of area use independent of whether dives occurred exclusively at night.

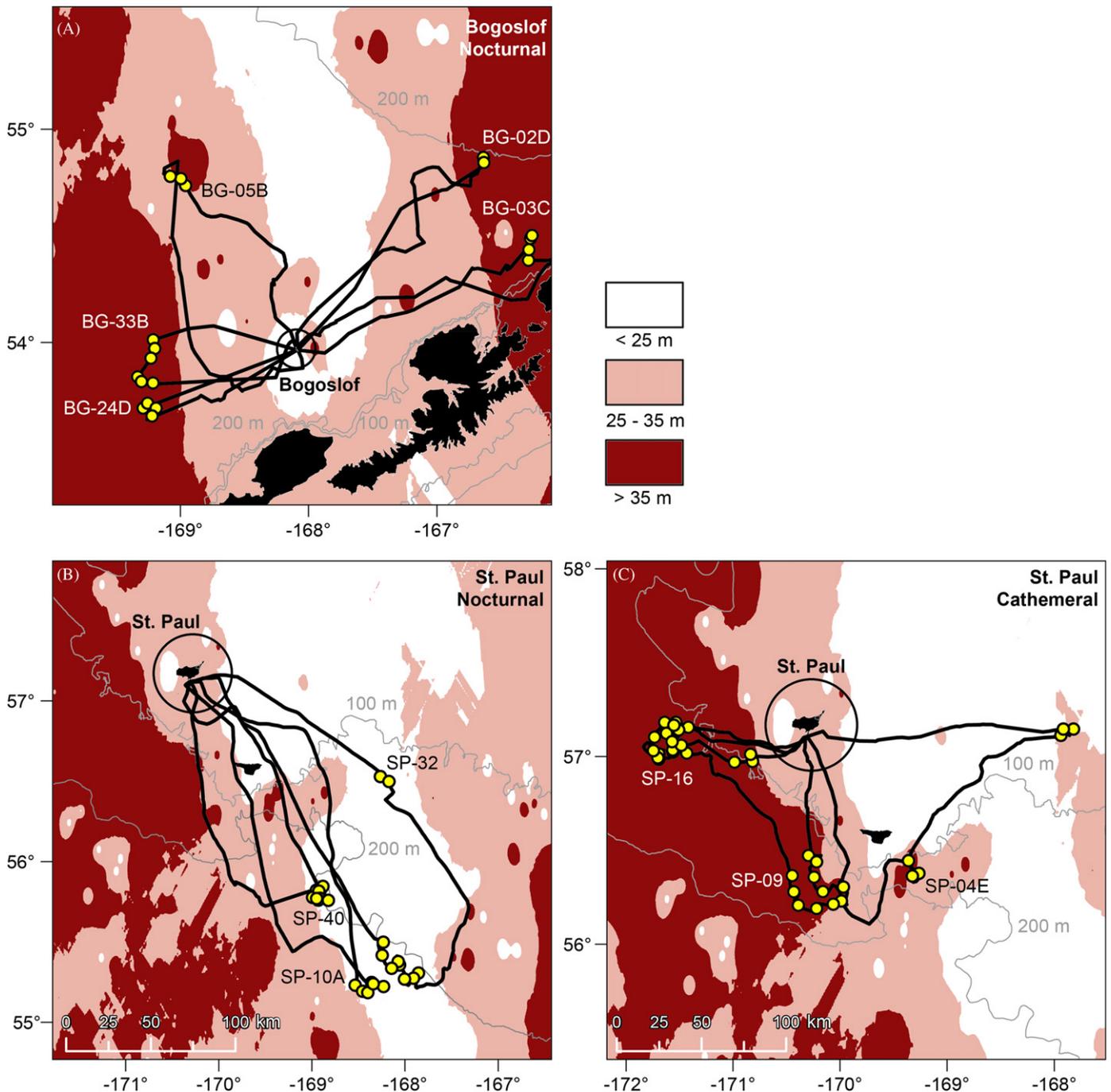


Fig. 9. Examples of foraging locations of northern fur seals in relation to three thermocline depths classes (< 25 m in white, 25–35 m medium, and > 35 m in dark). Complete trips are shown for the numbered lactating females by the continuous lines, and areas of intense use are shown with the yellow points. St. Paul trips were subdivided into those consisting of > 90% nighttime dives (Nocturnal, panel B); and those that made < 90% nighttime dives (Cathemeral, panel C). Intense use was defined as the top 16.6% (sextile) of first-passage time (FPT) with FPT calculated within a radius of 6 km for Bogoslof fur seals and 12 km for St. Paul fur seals. The plotted tracks are among the clearest examples showing the interaction with different thermocline depths.

4.3. Habitat selection modeling

A similar set of environmental parameters explained the foraging behaviors of fur seals from both islands. This suggests that a common set of mechanisms structured northern fur seal foraging in the eastern Bering Sea during our study (Tables 1–3). However, the relative importance of these oceanographic parameters on residency times (primarily foraging time) along foraging tracks was notably different between trips originating from St. Paul Island and Bogoslof Island and also between Nocturnal and Cathemeral strategies of St. Paul fur seals (Fig. 6). Areas of

intense use (high FPTs) were associated with short distances to submesoscale fronts, with thermocline depths that tended to coincide with group specific dive strategies, and occasionally with somewhat elevated temperatures in the upper portion of the water column. The importance of these variables changed in relation to their relative presence within the oceanographic domains exploited by different groups of fur seals. For example, strong fronts were concentrated over the Bering Sea basin (Fig. 1) while stratified waters that produced sharp thermoclines (at shallow and mid-water depths) were primarily located over the shelf.

Table 2

Estimates from the top three ranked Cox proportional hazards models predicting habitat use (time spent within a 12 km radius) for foraging, lactating northern fur seals from the St. Paul Cathemeral group as determined by AICc (see Table S4). Number of first passage time points (n), coefficients (β), hazard ratios (\exp^β), and 95% confidence intervals ($CI(\beta)$) are shown for each covariate/category affecting the risk of fur seals moving to the next 12 km portion of their track. Categorical values are relative to their first class. Front: distance to nearest front; Depth: ocean depth; TC: thermocline depth; TempTC: mean temperature above thermocline; Temp1 m: temperature at 1 m; Chl: total chlorophyll in upper 100 m. Note: β -values > 0 ($\exp^\beta > 1.00$) indicate increased risk (likelihood) of leaving, while β -values < 0 ($\exp^\beta < 1.00$) infer decreased risk (i.e. increasing habitat selection).

Model covariate	n	β	\exp^β	$CI(\beta)$
<i>Front + Depth + TC + TempTC + Temp1 m + Chl + (Front × Chl); AICc wi=0.62</i>				
Front (0–4 km)	296	–	–	–
Front (> 4–10 km)	166	0.24	1.27	–0.05 to 0.52
Front (> 10–20 km)	196	0.24	1.28	0.01 to 0.47
Front (> 20 km)	494	0.23	1.25	0.01 to 0.44
Depth (0–100 m)	628	–	–	–
Depth (> 100–200 km)	362	–0.09	0.92	–0.25 to 0.08
Depth (> 200–350 km)	37	–0.58	0.56	–0.98 to –0.19
Depth (> 350 km)	125	–1.03	0.36	–1.37 to –0.69
TC (< 25 m)	293	–	–	–
TC (25–35 m)	537	–0.54	0.58	–0.72 to –0.36
TC (> 35 m)	322	–1.07	0.34	–1.29 to –0.85
TempTC	1152	–0.14	0.87	–0.21 to –0.07
Temp1 m	1152	0.01	1.01	–0.07 to 0.10
Chl (< 350 mg/m ³)	817	–	–	–
Chl (> 350 mg/m ³)	335	0.14	1.15	–0.16 to 0.44
Front (0–4 km) × Chl (> 350 mg/m ³)	137	–	–	–
Front (> 4–10 km) × Chl (> 350 mg/m ³)	74	–0.55	0.57	–0.96 to –0.15
Front (> 10–20 km) × Chl (> 350 mg/m ³)	70	0.00	1.00	–0.40 to 0.40
Front (> 20 km) × Chl (> 350 mg/m ³)	54	0.14	1.15	–0.28 to 0.57
<i>Front + Depth + TC + TempTC + Temp1 m; AICc wi=0.13</i>				
Front (0–4 km)	296	–	–	–
Front (> 4–10 km)	166	0.20	1.22	–0.01 to 0.41
Front (> 10–20 km)	196	0.22	1.25	0.01 to 0.44
Front (> 20 km)	494	0.19	1.22	0.00 to 0.39
Depth (0–100 m)	628	–	–	–
Depth (> 100–200 km)	362	–0.05	0.95	–0.22 to 0.12
Depth (> 200–350 km)	37	–0.52	0.59	–0.91 to –0.13
Depth (> 350 km)	125	–0.96	0.38	–1.28 to –0.64
TC (< 25 m)	293	–	–	–
TC (25–35 m)	537	–0.58	0.56	–0.76 to –0.40
TC (> 35 m)	322	–1.09	0.33	–1.31 to –0.87
TempTC	1152	–0.15	0.86	–0.22 to –0.08
Temp1 m	1152	0.00	1.00	–0.08 to 0.08
<i>Depth + TC + TempTC + Temp1 m; AICc wi=0.12</i>				
Depth (0–100 m)	628	–	–	–
Depth (> 100–200 km)	362	–0.05	0.95	–0.22 to 0.11
Depth (> 200–350 km)	37	–0.55	0.58	–0.93 to –0.16
Depth (> 350 km)	125	–1.07	0.34	–1.37 to –0.77
TC (< 25 m)	293	–	–	–
TC (25–35 m)	537	–0.59	0.56	–0.77 to –0.41
TC (> 35 m)	322	–1.17	0.31	–1.38 to –0.96
TempTC	1152	–0.15	0.86	–0.22 to –0.08
Temp1 m	1152	0.00	1.00	–0.08 to 0.09

The Nocturnal group from St. Paul Island (>95% night dives) adhered strictly to foraging at night and employed shallow pelagic dives over the shelf, off-shelf, or near the shelf-break (Fig. 4). These wide ranging fur seals regularly encountered submesoscale surface fronts as they left shelf waters (Fig. 1A and B). CPH analysis showed risks of leaving an area that had submesoscale surface fronts similar for areas less than 4 km and 10 km, after which risks increased with increasing distance from these features. This suggests that fur seals hunted intensively along submesoscale fronts when foraging off-shelf, ostensibly targeting highly constrained prey in these narrow ribbons. Areas over deeper water were increasingly used (Table 1) but there was no concurrent increase in dive depth in the TDR records. This suggests that ocean depth was not a driving feature *per se* for this group but rather was a static indicator for dynamic features, such as eddy-derived fronts, that develop inter-annually along the shelf-break due to topographic interactions with

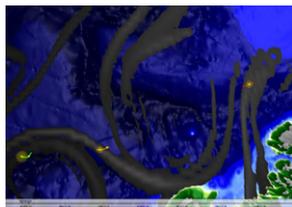
portions of the northward flowing Bering Slope Current (Ladd, pers. comm.; Stabeno et al., 1999, 2001).

Fur seals in the St. Paul Nocturnal group were influenced most strongly by thermocline depth (Table 1) and may be related to the extended time spent over shelf waters, even when transiting to the basin. The fur seals concentrated their foraging efforts in areas where thermoclines were shallowest, presumably where diel migrating juvenile pollock were most abundant and easily accessible from the surface at night. Fur seals in this group appeared to adjust their maximum dive depth as thermoclines deepened (mean max depth: 21 m at thermoclines < 25 m; 27 m at thermoclines > 25–35 m; 37 m at thermoclines > 35 m) which could explain the wide confidence intervals observed for this covariate (Fig. 8A). Nonetheless, these fur seals clearly spent the least time in areas where thermoclines were deepest and where prey would be less likely to be encountered by fur seals that

Table 3

Estimates from the top-ranked Cox proportional hazards model predicting habitat use (time spent within a 6 km radius) by foraging, lactating northern fur seals from Bogoslof Island as determined by AICc (see Table S5). Number of first passage time points (n), coefficients (β), hazard ratios (\exp^{β}), and 95% confidence intervals ($CI(\beta)$) are shown for each covariate/category affecting the risk of fur seals moving to the next 6 km portion of their track. Categorical values are relative to their first class. Front: distance to nearest front; Depth: ocean depth; TC: thermocline depth; TempTC: mean temperature above thermocline; Temp1 m: temperature at 1 m; Chl: total chlorophyll in upper 100 m. Note: β -values > 0 ($\exp^{\beta} > 1.00$) indicate increased risk (likelihood) of leaving, while β -values < 0 ($\exp^{\beta} < 1.00$) infer decreased risk (i.e. increasing habitat selection).

Model covariate	n	β	\exp^{β}	$CI(\beta)$
<i>Front+Depth+TC+TempTC+Temp1 m+Chl+(Front × Chl); AICc wi=1.00</i>				
Front (0–4 km)	2124	–	–	–
Front (> 4–10 km)	799	0.05	1.05	–0.09 to 0.19
Front (> 10–20 km)	697	0.60	1.82	0.45 to 0.74
Front (> 20 km)	309	0.93	2.54	0.74 to 1.13
Depth	3929	0.00	1.00	0.00 to 0.00
TC (< 25 m)	1739	–	–	–
TC (25–35 m)	1644	–0.16	0.86	–0.26 to –0.06
TC (> 35 m)	546	–0.75	0.47	–0.88 to –0.62
TempTC	3929	–0.18	0.83	–0.23 to –0.14
Temp1 m	3929	–0.23	0.80	–0.29 to –0.16
Chl (< 450 mg/m ³)	1782	–	–	–
Chl (> 450 mg/m ³)	2147	–0.01	0.99	–0.12 to 0.11
Front (0–4 km) × Chl (> 450 mg/m ³)	1236	–	–	–
Front (> 4–10 km) × Chl (> 450 mg/m ³)	472	0.01	1.01	–0.18 to 0.20
Front (> 10–20 km) × Chl (> 450 mg/m ³)	341	–0.53	0.59	–0.73 to –0.33
Front (> 20 km) × Chl (> 450 mg/m ³)	120	–0.65	0.52	–0.94 to –0.37



Animation 2. Example of northern fur seals originating from Bogoslof Island foraging along submesoscale surface fronts over the southern basin of the eastern Bering Sea. Individual fur seals are represented by coloured lines. First passage times are calculated at equal intervals along the fur seal track and are shown as yellow points (animated with halos where larger halos equal greater residence time). Fronts are depicted as black/grey bands and are 4-day snapshots of a dynamic system. Time at bottom is in (GMT).

constrained the vast majority of their dives to the upper 30 m of the water column.

The Cathemeral group from St. Paul Island (> 18% day dives) regularly mixed shallow night dives with deeper benthic day dives during foraging trips that primarily remained over the continental shelf (Fig. 4). Trips constrained to the shelf rarely intersected filaments with the exception of some animals that ventured over the shelf-break to the southwest of St. Paul Island where they interacted with surface fronts. As a result, there was no trend in the risks of leaving areas beyond 4 km (one map pixel) from fronts for the group as a whole (Table 2). There was also no difference in the risks between areas less than 100 or 200 m deep as foraging hotspots were generally evenly distributed between the isobaths on-shelf. Increased habitat selection for waters beyond the shelf-break (> 200 m) were driven by the few animals that foraged pelagically along fronts over the basin and did not represent an affinity for deeper water.

Fur seals in the St. Paul Cathemeral group were impacted most strongly by thermocline depth (Table 2), but they increasingly selected habitats with deeper thermoclines in contrast to the Nocturnal group. This presumably allowed the fur seals to forage effectively by trapping prey between the thermocline and the benthos during deeper daytime dives on the shelf. Interestingly, Cathemeral fur seals did not appear to adjust their mean maximum dive depths as thermocline depth changed (mean max depth: 49 m at thermoclines < 25 m; 45 m at thermoclines > 25–

35 m; 52 m at thermoclines > 35 m) which would typify daytime dives targeting the ocean bottom as opposed to the thermocline itself.

Northern fur seals from Bogoslof Island showed little variation in foraging behavior as trips consisted primarily of shallow night diving restricted to the basin (Fig. 4). Submesoscale fronts resulting from interactions of topographic features with the eastward flowing Aleutian North Slope Current (Stabeno et al., 1999) dominated the waters around the island (e.g., Fig. 1). Consequently, foraging fur seals in this population were influenced most strongly by distance to fronts (Table 3). Risk of moving to the next 6 km of their foraging track was similar for areas < 4 km and < 10 km from fronts, but increased rapidly at distances beyond 10 km. The increasing use of areas with deeper thermoclines contrasted with the shallow diving recorded for the group. However, the relationship between thermoclines and foraging behavior may be confounded with fronts based on the co-occurrence of deeper thermoclines with frontal edges. Overlaying frontal maps (e.g. Fig. 1) on the thermocline surface (e.g. Fig. 9C) reveals a ring of deeper thermoclines coinciding with persistent frontal edges.

We suspect that strong winds maintained well-mixed surface waters in the vicinity of the surface fronts in the southeastern Bering Sea and restricted thermoclines to depths > 35 m. Fur seals foraging intensively along fronts in these areas would coincidentally be using waters with deeper (and possibly weaker) thermoclines. Fur seal prey can transit through density gradients and it would be more likely to occur if a weaker thermocline resulted in a less aggregated zooplankton layer. This likely explains why the fur seals seemingly failed to adjust their maximum dive depth under different thermocline conditions (maintained a max dive depth of 18–20 m for thermocline depths < 25 m, > 25–35 m, and > 35 m).

Chlorophyll and temperature parameters were often included in our top CPH models, yet their impacts on fur seal foraging were difficult to interpret. Increased levels of total chlorophyll in the upper 100 m showed some minor trends with increasing FPT when plotted as a single covariate (hence its inclusion as a parameter in the CPH models), but it failed to influence fur seal foraging movements when other parameters were set to base levels of risk. The interaction term between fronts and chlorophyll was also surprisingly inconsequential when quantifying relative

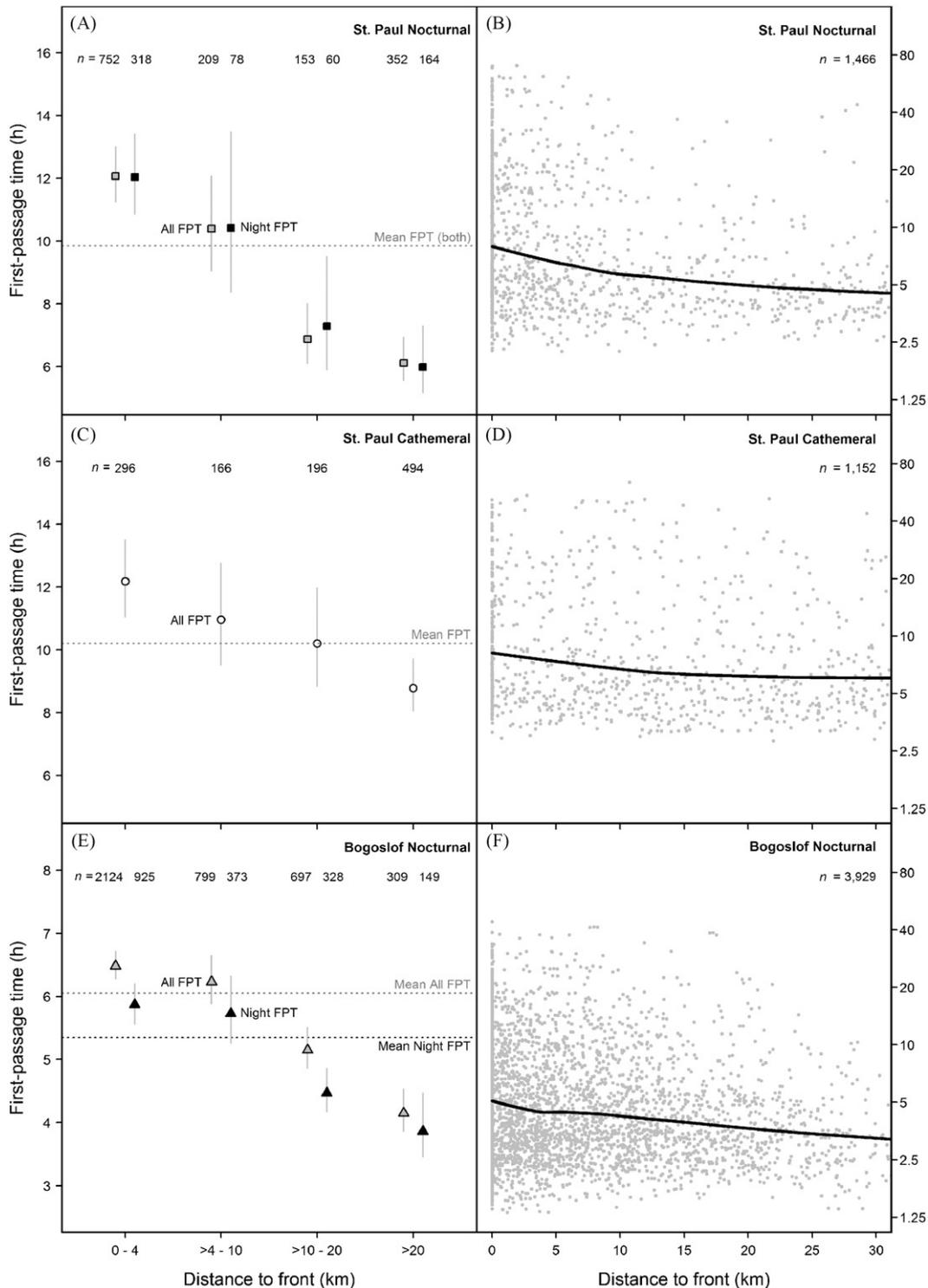


Fig. 10. Decreasing first-passage time (FPT) with increasing distance to the nearest submesoscale front along foraging tracks of northern fur seals tagged on St. Paul Island and Bogoslof Island. St. Paul trips were subdivided into those consisting of > 90% nighttime dives (Nocturnal, filled squares); and those that made < 90% nighttime dives (Cathemeral, open circles). Mean FPTs are shown with bootstrapped 95% confidence intervals, and number of FPT estimates (n) for each distance category (panels A, C, E) both including (All FPT) and excluding (Night FPT) daytime FPT estimates. Cathemeral trips show All FPT estimates only as > 18% of dives on these trips occurred in the daytime. Overall mean FPTs are displayed as dashed lines. Note that the FPT scale for the Bogoslof seals is half that of the St. Paul seals as the Bogoslof FPT area radius (6 km) was half that of St. Paul (12 km). Also shown are panels of jittered FPT values on a log10 scale plotted against jittered distance values with fitted loess curves for each trip grouping (panels B, D, F). The log scale was used to depict the full range of FPT data and did not affect the loess statistic.

habitat use for most northern fur seals. As such, the fronts defined here may better serve to aggregate fur seal prey where they can be efficiently exploited as opposed to stimulating local primary production. Increasing temperature of the water column above the thermocline or at the surface had limited correlation with FPT

in exploratory plots. Temperature may play a role in shaping the distribution of fur seal prey (notably pollock) at the broad scale (Bacheler et al., 2010; Ciannelli et al., 2002; Swartzman et al., 2002), but correlations of near surface temperature or temperature integrated above the thermocline with fur seal foraging were

inconsistent at the finer scale of our study. Unfortunately, similar habitat preference data are lacking for non-commercial species such as gonatid squid and northern smoothtongue.

4.4. Considerations

Dividing foraging trips from St. Paul Island (Nocturnal vs. Cathemeral groups) was appropriate to distinguish which parameters influenced habitat selection for the two groups at a coarse level in our study, but it oversimplified the segregation between nocturnal and cathemeral foraging strategies. Fur seals from St. Paul Island likely adopt a continuum of additional daylight dives to target deeper prey as opposed to the discrete classification we employed with the data. Such vertical partitioning of the water column by foraging females from the same rookery complex could compliment the horizontal segregation of the waters around the Pribilof Islands that exists between rookeries (Robson et al., 2004) and further help alleviate intra-specific competition for a single dominant resource (e.g. diel-migrating walleye pollock).

The methods by which northern fur seals detect fronts and thermoclines remain unclear. Females tracked for multiple trips showed high fidelity to foraging paths and regions as previously reported (Call et al., 2008), yet the lack of direct travel to hotspots encountered earlier suggests that they do not perceive these boundaries from a distance *per se* as speculated for some marine predators (Nevitt, 2008; Tew Kai et al., 2009). Rather, we propose that northern fur seals employ general search tactics (in the horizontal plane) and respond opportunistically to increased prey density in areas where oceanographic features concentrate prey.

In addition to the influence of oceanographic parameters, foraging behavior of fur seals may also be influenced by differences in the quantity or quality of primary prey and by the population sizes of the two colonies. Walleye pollock has a relatively low energy density compared to northern smoothtongue or gonatid squid (Van Pelt et al., 1997; Vollenweider et al., 2011; Whitman, 2010), and fur seals consuming pollock may have to travel further or longer to replenish their energy reserves compared with fur seals that consume prey richer in energy. Nutritional studies involving northern fur seals have been limited, but work with Steller sea lions (*Eumetopias jubatus*) has demonstrated that pinnipeds eating pollock can compensate energetically for low energy fish if sufficient quantities were available (Rosen, 2009). Fur seals from St. Paul Island may need to eat more pollock to acquire a similar energetic return compared to Bogoslof fur seals consuming higher energy prey. However, differences in the duration of foraging trips between populations would be minimized if juvenile pollock were concentrated closer to St. Paul Island (increased density) or were more abundant (increased quantity). Increased intra-specific competition on St. Paul Island may also increase trip duration and trip distance relative to Bogoslof Island where the population is much smaller. Nonetheless, the trip durations we recorded are consistent with other studies covering the current phase of decline from the mid-1980s through 2008 (Goebel et al., 1991; Kuhn et al., 2010; Loughlin et al., 1987; Robson et al., 2004; Springer et al., 2008) when population differences were greater and average trip durations were relatively uniform.

The manner in which our covariates were collected could have influenced the CPH model and our quantitative assessments of the relative effect that 6 specific habitat features had on fur seal foraging. Covariates collected by ship CTD (e.g. thermocline depth and total chlorophyll in the upper 100 m) could be sensitive to the sampling design and/or the limited temporal extent. We evaluated the validity of extending the ship data 6 weeks post collection by comparing covariate hazard ratios from models using all tracked fur seals with those limited to the CTD sampling period but found no

effect. Nevertheless, finer temporal data would have ideally been incorporated in the models. For example, we attempted to include satellite derived maps of chlorophyll to provide more temporally accurate snapshots of surface productivity, but a combination of SeaWiFS imager failures and extensive cloud cover over the study area in the summer of 2009 resulted in large tracts of missing data in even the longest, monthly composited images. Northern fur seals may forage more intensely in areas of increased chlorophyll either at a coarser scale or perhaps at scales similar to this study, however our in-situ measurements did not appear to influence foraging when other covariates were taken into account.

The role of fronts may also be more relevant to all fur seal groups, including the St. Paul Cathemeral foraging strategy, than can be realized via the finite-size Lyapunov exponent (FSLE) methodology. Temperature fronts or other boundaries that concentrate prey without a current component would be overlooked using frontal maps derived from interpolated geostrophic currents. The cold pool is such a feature and has been shown to negatively affect the distribution of demersal (adult ≥ 3 yr) pollock (Ciannelli and Bailey, 2005; Wyllie-Echeverria and Wooster, 1998; Wespestad et al., 2000). The limited number of fur seal tracks north of St. Paul Island could be interpreted as an avoidance of the cold pool; however, this is more likely the result of instrumenting animals on the south side of St. Paul Island given that fur seals from the northeast rookeries (which show a strong fidelity to the shelf region) have been shown to be as likely to forage within the cold pool as outside it (Kuhn, 2011). St. Paul fur seals also typically prey on juvenile pollock (Call and Ream, 2012) which are often missed in bottom trawl surveys and are likely less affected by the extent of the cold pool as they occupy the mid to upper portions of the water column.

Filaments coinciding with fronts separating the outer, middle, and inner domains on the eastern Bering Sea shelf were observed in our dataset (e.g. Fig. 1), although they were neither contiguous nor consistently noted. This was particularly true north and east of the Pribilof Islands, but was related to the variable strength of the current along the 100 m isobath (Reed and Stabeno, 1996; Stabeno et al., 2002) and our conservative cut-off strength of 0.2 FSLE per day when defining a front. The accuracy of the frontal maps also needs to be assessed for the Bering Sea as validations in other regions have shown edge disparities as large as 4 km (d'Ovidio et al., 2004). Most fur seals showed little difference in their response to fronts between distances of 4 and 10 km (1–2.5 pixels) in our analysis. Thus, the interpolated geostrophic data may not track the fronts as accurately as believed and our definition of a surface front may also be overly conservative. As a result, fur seals from St. Paul Island may indeed use shelf fronts that are poorly represented in the 4-d maps we employed. However, they did not result in shorter foraging trips despite being relatively close to St. Paul Island which may indicate that these features aggregate prey to a lesser degree than the fronts detected in this study.

Despite extensive geographic coverage of the eastern Bering Sea, our data represent a single-year snapshot of the linkages between oceanographic parameters and the foraging trips of lactating northern fur seals during the pup rearing period. This limits our ability to predict how fur seals responded to conditions in the past or how they will respond to future oceanographic scenarios. However, some insights can be drawn from the differences in the population-level habitat selection we found. For example, foraging trips from St. Paul Island may become shorter if existing shelf fronts strengthen or additional activity occurs closer to the Pribilof Islands (as seen by the extensive use of strong surface fronts by Bogoslof fur seals). Conversely, Bogoslof seals may have to make longer foraging trips if frontal activity weakens over the basin. The distribution of strong surface fronts relative to the location of breeding beaches differed between colonies (e.g., > 100 km from St. Paul Island), and had noteworthy

effects on the foraging efforts of fur seals that encountered them—particularly during the outbound portion of the foraging trips. We surmise that these horizontal bands extended from the surface through the shallow depths where most females were diving and formed an effective retainer of zooplankton, and hence fur seal prey, along the lengths of the fronts. Thermoclines were ubiquitous around both islands during our study and may be a weaker concentrating feature than submesoscale fronts despite being an important vertical constriction for fur seal prey.

4.5. Conclusions

Lactating northern fur seals from different populations in the eastern Bering Sea fed in different hydrographic domains and selected different at-sea habitats that were consistent with prevalent physical features near their respective colonies. Thermoclines dominated over the highly stratified continental shelf around the Pribilof Islands while strong surface fronts were generally restricted to the shelf-break and over the basin during our study. Cathemeral fur seals from St. Paul Island that fed along the bottom tended to forage in areas with deeper thermoclines that presumably concentrated prey between them and the ocean floor, while epipelagic nocturnal foragers focused on shallower thermoclines which presumably provided easier access to diel migrating prey closer to the surface. Fur seals from Bogoslof Island primarily foraged close to the colony over the Bering Sea basin and hunted intensively along submesoscale fronts that likely aggregated prey via mechanical convergence near the surface. In contrast, fur seals from St. Paul Island generally needed to extend their trips off-shelf to access similar features, but concentrated their foraging near surface fronts whenever they were encountered. Trips from St. Paul Island were longer than from Bogoslof Island, and areas of high use were larger which suggests the prey that St. Paul fur seals encountered were less aggregated compared to prey consumed by Bogoslof fur seals. Most northern fur seals appeared to forage along the physical features that were available to them. We propose that differences in the relative distribution and accessibility of oceanographic features that concentrate prey in an effective manner can account for the observed differences in foraging patterns between colonies, which in turn may have consequences for the colony specific population trends of this piscivorous top-predator.

Acknowledgments

All procedures were conducted under the National Oceanographic and Atmospheric Administration (NOAA) permit no. 14329 and abided by the guidelines of the Committee on Animal Care at the University of British Columbia (permit no. A09-0345). We are indebted to A. Baylis, J. Gibbens, R. Marshall, R. Papish, A. Will, and C. Berger for assistance with animal captures and instrument deployment. We thank K. Benoit-Bird, S. Heppell and the crews of the M/Vs *Frosti* and *Goldrush* for at-sea CTD measurements collected under difficult conditions. We are grateful to C. Freitas for advice on employing first passage time. Altimeter products were produced by *Ssalto/Duacs* and distributed by *Aviso*, with support from *CNES*. R. Joy provided statistical advice while D. Rosen and two anonymous referees provided constructive criticism on earlier versions of the manuscript. This work was conducted as a part of the Bering Sea Integrated Research Program (BSIERP), funded jointly by the US National Science Foundation and the North Pacific Research Board. This is NPRB Publication Number 354 and BEST-BSIERP Bering Sea Project publication number 65.

Appendix A. Supplementary material

Supplementary data associated with this article can be found in the online version at <http://dx.doi.org/10.1016/j.dsr2.2012.07.010>.

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