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

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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.

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

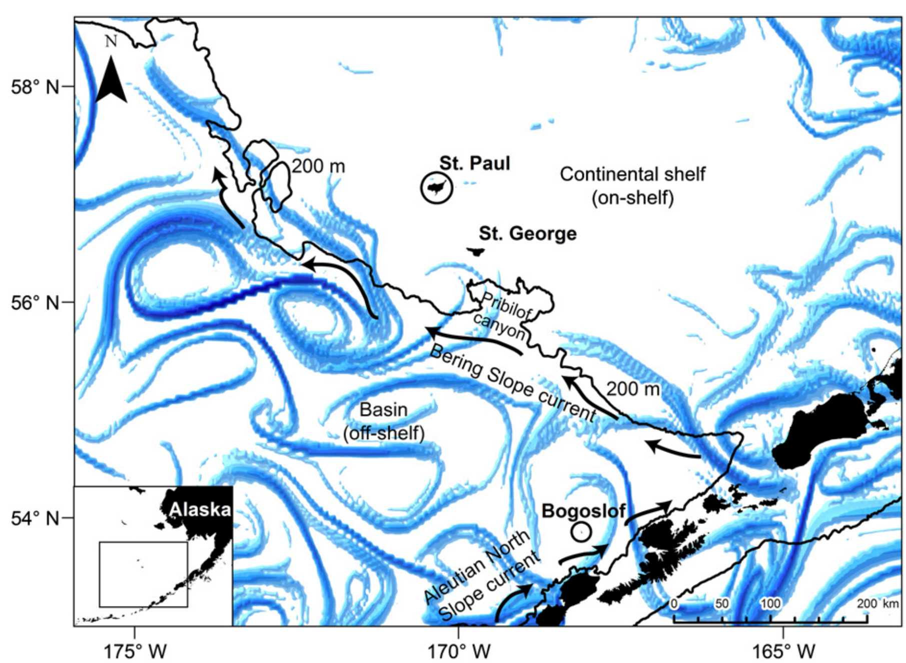

Fig. 1. Map of the eastern Bering Sea showing the locations of St. Paul Island and Bogoslof Island in relation to the positions of submesoscale surface fronts (Lagrangian coherent structures) on Aug. 1, 2009. The Lagrangian coherent structures had a resolution of 4 km over 4 days, and fronts were defined 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.