**Seasonal Spatial Patterns in Seabird and Marine Mammal Distribution in the Eastern
Chukchi and Western Beaufort Seas: Identifying Biologically Important Pelagic Areas**

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Abstract

The Chukchi and Beaufort seas are undergoing rapid climate change and increased human activity. Conservation efforts for upper trophic level predators such as seabirds and marine mammals require information on species' distributions and identification of important marine areas. Here we describe broad-scale distributions of seabirds and marine mammals. We examined spatial patterns of relative abundance of seabirds and marine mammals in the eastern Chukchi and western Beaufort seas during summer (15 June–31 August) and fall (1 September–20 November) from 2007–2012. We summarized 49 206 km of shipboard surveys for seabirds and 183 157 km of aerial surveys for marine mammals into a grid of 40-km X 40-km cells. We used Getis-Ord Gi* hotspot analysis to test for cells with higher relative abundance than expected when compared to all cells within the study area. We identified cells representing

single-species and taxonomic group hotspots, cells representing hotspots for multiple species, and cells representing hotspots for both seabirds and marine mammals. The locations of hotspots varied among species but often were located near underwater canyons or over continental shelf features and slopes. Hotspots for seabirds, walrus, and gray whales occurred primarily in the Chukchi Sea. Hotspots for bowhead whales and other pinnipeds (i.e., seals) occurred near Barrow Canyon and along the Beaufort Sea shelf and slope. Hotspots for belugas occurred in both the Chukchi and Beaufort seas. There were three hotspots shared by both seabirds and marine mammals in summer: off Wainwright in the eastern Chukchi Sea, south of Hanna Shoal, and at the mouth of Barrow Canyon. In fall, the only identified shared hotspot occurred at the mouth of Barrow Canyon. Shared hotspots are characterized by strong fronts caused by upwelling and currents, and these areas can have high densities of euphausiids in summer and fall. Due to the high relative abundance of animals and diversity of taxa, these sites are clearly important areas of congregation for seabirds and marine mammals that should be prioritized in the development of management and conservation plans.

Keywords: Chukchi Sea, Beaufort Sea, seabirds, marine mammals, distribution, Getis-Ord G_i^* hotspot analysis

1. Introduction

The Pacific Arctic Ocean, encompassing the Chukchi Sea, western Beaufort Sea and the Arctic Ocean adjoining those seas, is exhibiting changes in its physical and biological characteristics faster than subarctic or temperate regions (Grebmeier et al., 2010; Serreze and Francis, 2006; Wassmann et al., 2011). The consensus of global circulation models indicate that

continued warming will lead to ice free summers in the Arctic within the next 30 years (e.g., Wang and Overland, 2009). The reduced extent and persistence of sea ice will facilitate shipping opportunities (Reeves et al., 2012), oil and gas exploration, and coastal development through arctic regions of northern Alaska, Canada, and Russia. As a result, seabirds and marine mammals will experience new influences from increased human presence associated with development (Humphries and Huettman, 2014; Reeves et al., 2013), while facing changes to their natural world at a rapid and accelerating pace (Gradinger, 1995; Fischbach et al., 2007; Grebmeier et al., 2010; Jay et al., 2011; Wassmann et al. 2011). To address these changes, conservation efforts for large upper trophic level predators such as marine birds (hereafter, seabirds) and marine mammals will require basic information on the distribution and abundance of species, and the identification of important marine areas. Seabirds and marine mammals depend on the marine environment for their food and spend most (seabirds and pinnipeds) or all (cetaceans) of their lives at sea. Their distribution patterns can serve as indicators of changes in marine ecosystems over seasonal, interannual, or even longer time scales (Moore and Huntington, 2008; Piatt et al., 2007). Species-specific diets and foraging behaviors of these predators provide tractable links to physical and biological oceanography (Bluhm and Gradinger, 2008; Gonzles-Sols and Shaffer, 2009). Numerous studies have linked physical oceanography with the distribution and abundance of cetaceans (e.g., Staben et al., 2012; Stafford et al., 2013) and seabirds (e.g., Piatt and Springer, 2003; Gall et al., 2013b; Hunt et al., 2013). Both seabirds and marine mammals rely on physical properties that concentrate prey or, for many seabird species, make prey more accessible near the surface (Bost et al., 2009; Moore et al., 2000; Russell et al., 1999). Therefore, we expect that species of both taxa would overlap spatially and perhaps temporally, especially when they share a common prey such as euphausiids (Euphausiidae spp). Seabirds and marine

mammals have been observed foraging symbiotically (Au and Pittman, 1986; Obst and Hunt, 1990; Anderson and Lovvorn, 2008). However, few studies have integrated data on the distribution and abundance of both seabirds and marine mammals into an analysis of mesoscale patterns over a large region (but see Santora and Veit, 2013), and none have done so in the eastern Chukchi and western Beaufort seas. Our study combines several sources of survey data to identify at sea aggregations of seabirds and marine mammals in the eastern Chukchi and western Beaufort seas.

The distribution and abundance of seabirds and marine mammals is heavily influenced by the presence or absence of sea ice. Because ice coverage and oceanography change between summer and fall, and because animals have seasonal patterns in foraging and migratory behavior, we compare summer and fall distributions for selected species and foraging guilds.

Our objective was to identify areas of aggregation (hereafter, hotspots) of seabirds and marine mammals using densities (seabirds) and encounter rates (marine mammals) derived from vessel and aerial survey data, respectively. From the results of the hotspot analysis, we suggest what factors might influence the location of aggregations and how the factors might vary based on foraging strategy or prey species. We also identified “shared” hotspots used by both seabirds and marine mammals, to focus on areas that are associated with these taxonomically diverse upper trophic level predators in the eastern Chukchi and western Beaufort seas. These hotspots are ecologically important, as evident from the relatively high densities of animals; therefore, they should be considered important marine areas in a management context.

2. Methods

2.1 Study Area

Our study area (Fig. 1) encompassed Pacific Arctic marine waters from Bering Strait (65.8° N), north across the eastern Chukchi Sea shelf and slope (73° N), west to Wrangel Island (169° W) and east across the Beaufort Sea shelf and slope to the Mackenzie River Delta (135° W), with the majority of survey effort occurring in US waters. Our study area is composed primarily of continental shelf habitat, including the wide, shallow (primarily 20–50 m deep) shelf of the eastern Chukchi Sea and the narrow (~ 20 km–100 km wide), deeper (0 to 200 m deep) shelf of the western Beaufort Sea, which parallels the coastlines of Alaska and Canada (Fig. 1). There are several important features that incise the shelves, influencing water flow and prey aggregation. Hope Basin (50–100 m deep) is a major submarine feature located north of Bering Strait. Barrow Canyon is a submarine feature that parallels shore in the northeastern Chukchi, extending from near Wainwright to the mouth that empties into the Arctic Ocean north of Point Barrow. The study area also includes Mackenzie Canyon, a large submarine feature extending northwest from the Mackenzie River Delta into the Arctic Ocean.

2.1.1 Oceanography

The eastern Chukchi Sea is strongly influenced by two water masses flowing north from the Bering Strait: 1) the cold (3–6 °C), high salinity oceanic Bering Sea Water; and 2) the warmer, low salinity Alaskan Coastal Water (Coachman et al., 1975; Woodgate et al. 2005). Bering Sea Water bifurcates in the Hope Basin (Fig. 1), flowing northward around two shallow areas, Herald Shoal and Hanna Shoal (defined by the 40 m isobath), which are separated by the Central Channel (Coachman et al., 1975; Day et al., 2013b). Hanna Shoal is almost entirely in our study area (Fig. 2). Although the main Hanna Shoal plateau is much smaller than that of Herald Shoal, a large area of shallows extend southwest of the Hanna Shoal plateau, between the Central

Channel and Icy Cape (Fig. 1); we refer to this large shallow (< 40 m deep) area as the “greater Hanna Shoal” area.

Currents flowing clockwise around Herald and Hanna shoals supply nutrients to support areas of high primary productivity of variable spatial extent in the northeastern Chukchi Sea (Hill et al., 2005). The currents themselves are formed by water funneling through Herald Canyon in the northwestern Chukchi Sea, the Central Channel in the central Chukchi Sea, and Barrow Canyon in the northeastern Chukchi Sea (Weingartner et al., 2005; Pickart et al., 2008, 2010). Most of the Alaskan Coastal Water continues northeast along bathymetric contours near the Alaska coast, forming a boundary current of varying strength, depending on wind strength (Weingartner et al., 2005). These northward-flowing water masses encounter cold, hyper-saline bottom water and fresh meltwater from arctic pack ice, which can strongly influence water column stratification (Weingartner et al., 2013) and the formation of thermohaline fronts that facilitate prey aggregation (Hunt et al. 1990; Piatt and Springer, 2003; Ainley et al. 2005). Other regional currents include the Siberian Coastal Current, which carries water from the northern coast of Siberia southeast along the Russian coast; subsurface Atlantic Water, which runs eastward along the Chukchi and Beaufort slopes; and the Beaufort Gyre, which runs westward in the Arctic Basin (Fig. 1).

2.1.2 Ice cover

Sea ice cover in the Arctic advances and retreats seasonally, which has implications for seabird and marine mammal distributions. During the winter, the offshore regions of the Chukchi and Beaufort seas are completely covered by ice except for occasional open water polynyas; maximal annual sea ice extent reaches southward into the Bering Sea in March. This ice cover generally retreats north of Bering Strait by June and continues to retreat northward in the

Chukchi Sea while, concurrently, sea ice retreats westward from the Mackenzie River Delta as a result of warm freshwater runoff (Carmack and MacDonald, 2002; Nghiem et al., 2014, Wood et al., *this issue*). The Chukchi and Beaufort ice-free areas thus expand towards each other in July-August, with the last remaining ice cover often lingering over Hanna Shoal. During the years of this study, sea ice retreated entirely from the continental shelf by early September (Wood et al., *this issue*). Sea ice cover and the timing of its retreat in the spring influences primary productivity in the region (e.g., Gradinger, 1995; Arrigo et al., 2008; Arrigo and van Dijken, *this issue*) and, along with wind direction and strength, contribute to the strength of water column stratification during the summer and fall (Weingartner et al., 2013).

2.1.3 Seabird and marine mammal community

The cliffs and talus slopes located on mainland coasts and islands of the southern Chukchi and northern Bering seas support millions of breeding seabirds in large mixed-species colonies (Stephensen and Irons, 2003). The foraging ranges of some of these seabirds include the Chukchi Sea. An estimated 12 million seabirds use the Bering Strait region in summer, primarily auklets (*Aethia* spp.), murre (*Uria* spp.), puffins (*Fratercula* spp.), black-legged kittiwakes, (*Rissa tridactyla*) and other gulls (e.g., *Larus* spp.) as well as migrant shearwaters (*Puffinus* spp) (USFWS, 2014). In the middle of Bering Strait, approximately 4.7 million seabirds nest on Big Diomede and Little Diomede islands (USFWS, 2014). A colony with ~ 51 000 seabirds is located on an island at the head of Kotzebue Sound (Fig. 1), but otherwise a lack of large islands or rocky cliffs on the mainland in the Chukchi and Beaufort seas limits seabird nesting habitat. The northernmost significant seabird colonies are located on the Chukchi coastline of Alaska between Cape Thompson and Cape Lisburne (Fig. 1), and together total approximately one million nesting seabirds (USFWS 2014; Appendix A).

At least fifteen cetacean and pinniped species are found in the study area, which includes feeding areas and migratory pathways that are used during different seasons (Moore et al., 2000; Quakenbush et al., 2010a, b; Allen and Angliss, 2013; Clarke et al., 2014). The most abundant cetacean species in the region are the bowhead whale (*Balaena mysticetus*) (Braham, 1984; Givens et al., 2013), gray whale (*Eschrichtius robustus*) (Rice et al., 1984; Laake et al., 2012), and beluga (*Delphinapterus leucas*) (Stewart and Stewart, 1989). There are no onshore pinniped breeding rookeries in the study area, although walrus (*Odobenus rosmarus*) will haul out on shorelines in large numbers in the absence of sea ice (Jay et al., 2011, 2012). Four species of ice seals (bearded seal [*Erignathus barbatus*], ringed seal [*Pusa hispida*], ribbon seal [*Histiophoca fasciata*], and spotted seal [*Phoca largha*]) occur in the area. These species use the pack ice and ice floes as platforms to give birth and raise pups (Burns, 1981a, b; Frost and Lowry, 1981; Boveng et al., 2009). Spotted seals haul out along the study area coastline to molt in summer (Frost et al., 1993). Polar bears (*Ursus maritimus*) search the pack ice and floes for prey or carcasses, and females den inland where there is appropriate habitat along the coast (Amstrup et al., 2000; Fischbach et al., 2007). Six additional marine mammal species are sighted in the study area infrequently or rarely: fin whales (*Balaenoptera physalus*), humpback whales (*Megaptera novaeangliae*), minke whales (*Balaenoptera acutorostrata*), narwhals (*Monodon Monoceros*), killer whales (*Orcinus orca*), and harbor porpoises (*Phocoena phocoena*) (e.g., Clarke et al., 2013b; COSEWIC, 2004; Gaskin, 1984).

2.2 Data Collection

2.2.1 Seabirds

To identify seabird hotspots, we analyzed data from ship-based surveys conducted by the US Fish and Wildlife Service (FWS) and by ABR, Inc.—Environmental Research & Services

(ABR) from June through November 2007—2012. Total seabird survey effort included 49 206 km of survey lines (Fig. 2). The FWS surveys were conducted in conjunction with a variety of research programs (Kuletz et al., 2008). As a result, FWS transect layouts were opportunistic, although they often followed the host project's systematic station sampling grid; they also collected data along transits between stations or ports. The ABR seabird surveys were primarily conducted within oil and gas lease sale areas in the northeastern Chukchi Sea (see Gall et al., 2013a) along a series of parallel survey lines spaced ~4 km apart that ran through 3 study-area boxes that were each ~3,000 km². The boxes were located 100–230 km offshore of Wainwright, Alaska. The ABR surveys also collected data along opportunistic transits between Nome, Wainwright, and the offshore study-area boxes. The research vessels used as survey platforms for the FWS and ABR surveys ranged from 128 m (420 ft) icebreakers to 35 m (115 ft) converted trawlers. Sampling methods were consistent across platforms.

Seabird surveys used a single observer stationed inside on the vessel's bridge who recorded all birds seen within a radius of 300 m in a 90° arc from bow to beam on one side of the ship, using 10x binoculars, as needed, for species identification. Birds were recorded continuously if they were on the water or actively foraging, whereas flying birds were counted during instantaneous scans of the survey window, with intervals depending on ship's speed (typically ~1 scan/min) to avoid overestimating the density of flying birds (Tasker et al., 1984; Gould and Forsell, 1989). For each observation, we recorded species and number of birds. We attempted to avoid recounting birds following the ship. Surveys were conducted when conditions were favorable, with seas ranging from Beaufort Sea State 0 to 5 (corresponding to winds < 22 kts), and observations were truncated to 200 m or 100 m in a given transect if observation conditions restricted visibility.

Observations were entered directly into a laptop computer integrated with a global positioning system (GPS) and the software Dlog (R.G. Ford Consulting, Portland, OR; FWS 2007—2012, ABR 2008) or the software TigerObserver (TigerSoft, Las Vegas, NV; ABR 2009—2012). These programs georeferenced every observation and recorded vessel time and location (latitude and longitude) at 20-sec intervals to track survey effort.

2.2.2 *Marine mammals*

To identify marine mammal hotspots, we used data from line-transect aerial surveys conducted by the National Marine Mammal Laboratory and funded by the Bureau of Ocean Energy Management (e.g., Clarke et al., 2013a) from mid-June through late October of 2007—2012. These surveys were designed to study the distribution, relative abundance, and behavior of marine mammals in the northeastern Chukchi and western Beaufort seas. They were broad-scale and systematic, with transects spaced approximately 19 km apart, encompassing 230 000 km² from 140° W to 169° W and 68° N to 72° N. Transect lines in the western Beaufort Sea were oriented generally north—south. Transect lines in the northeastern Chukchi Sea also were oriented north—south in 2007—2008, but in 2009 were reoriented to be perpendicular to the coastline (i.e., roughly southeast—northwest). A total of 183 157 km of aerial transects were completed that covered coastal, continental shelf and slope, and basin habitats.

We conducted the surveys at 300–460 m (1000–1500 ft) altitude, approximately 200 km/hr (110 kts), in fixed-wing de Havilland Twin Otter and twin turbine Aero Commander 690 aircraft with left and right bubble windows to allow uninterrupted view from the horizon to the trackline. The survey team consisted of two pilots, two primary observers, and a data recorder who recorded all marine mammals sighted. The aircraft broke away from straight and level flight to circle sightings, as necessary, to confirm species identification, estimate group size, and

determine whether calves were present. For each marine mammal sighting, we recorded species (identified to highest possible taxonomic resolution), habitat, behavior, group size, and number of calves sighted. We took photographs opportunistically of some sightings to confirm species identification, group size, or presence of calves. Surveys were not conducted when the wind force was consistently at or above a Beaufort Sea State 6 (≥ 22 kts).

We recorded data on a laptop computer integrated with a portable GPS unit and customized software. The program recorded automatic updates on latitude, longitude, altitude, aircraft heading, and time every 5 min (2007—2008) or 30 sec (2009—2012). Environmental data, including sea ice type and concentration and Beaufort Sea State were recorded every 5 min or whenever conditions changed.

2.3 Data Analysis

We prepared data and conducted analyses in a geographic information system (ArcGIS 10.1, Redlands, CA) framework. The selected projection was a North Pole stereographic 180 degree re-positioned to approximately -175 degrees in order to minimize high latitude distortions. The final maps were re-projected for familiarity of readers.

2.3.1 Temporal boundaries

To identify seasonal hotspots, we analyzed seabird and marine mammal data for a period spanning six years (2007—2012) that represented overlapping seabird and marine mammal survey effort. Spatio-temporal variability in animal distribution is affected by reproductive, feeding, and migratory behavior (among other factors), which vary seasonally. To capture the general seasonal changes in seabird and marine mammal distribution and density in the study area, we conducted separate analyses on data from two seasons, summer (15 June–31 August; Figs. 2A, 2C) and fall (1 September–20 November; Figs. 2B, 2D), by pooling data across years.

Dates for the seasons were based on annual cycles in oceanography, sea ice (Stabeno et al., 2012), and animal ecology. During these years, ice break-up in the Bering Strait region occurred by mid-June, defining the start of the summer period. Because waters in the study area typically are warmest and most ice-free in late August or early September, we designated September as the start of the fall period. The end of the fall period (mid-November) was determined by advancing sea ice and deteriorating survey conditions that precluded further survey efforts.

2.3.2 *Seabird data*

The seabird data were collected along transects of various lengths and divided into ~ 3-km segments to calculate bird density (birds/km²), thereby correcting for effort but not for detectability. The centroid of each 3-km segment was used to georeference estimated densities for each segment and assign the segments to cells in a 40-km x 40-km grid overlaid on the study area. For each cell, we calculated the density of seabirds for each season as the mean of all segments within a cell, pooled across years.

We conducted analyses on “Total Seabirds”, four “foraging strategy” groups, and 16 individual seabird species (Appendix A, B). For each season we mapped distribution and hotspots for all species and groups with sufficient data for analysis (see below); we present the foraging strategy groups and a few representative species in Results, with maps for other species in Appendix C. The Total Seabirds group included combined density for all species and unidentified birds, allowing us to incorporate less abundant species and examine the distribution of total avifauna. For this analysis, we included members of the families Gaviidae (loons), Procellariidae (fulmars, shearwaters), Phalacrocoracidae (cormorants), Alcidae (auks), Laridae (gulls and terns), and Stercorariidae (jaegers), plus the taxa phalaropes (genus *Phalaropus*) and marine species of Anatidae (eiders and other seaducks).

We classified seabird taxa into four foraging strategy groups: surface-feeding birds, subsurface-feeding birds, benthic-feeding birds, and shearwaters. These groups included seabirds identified at least to family (Appendix B). Seabirds can be divided by dietary guild (i.e., planktivores or piscivores), but many of the seabirds in our study area feed on diverse prey groups (Dragoo et al., 2012a). In particular, euphausiids are a common prey for most of the surface and subsurface feeders. We considered shearwaters a separate foraging strategy group because they feed on small fishes, euphausiids, and zooplankton, and can feed on the surface or dive to 70 m (Skira, 1979; Weimerskirch and Sagar, 1996; Burger, 2001). Additionally, shearwaters become very abundant in the study area in late summer and early fall (Gall et al., 2013b) and would dominate distribution patterns of the surface-feeding or subsurface-feeding groups, if included.

We recorded 30–40 species of seabirds/yr in the study area; however, for species-specific analyses, we examined 16 species (plus shearwaters as a group) that accounted for the majority of birds during at least one of the seasons or were identified as a species of management interest in the Circumpolar Seabird Monitoring Plan (Petersen et al., 2008). Three species did not have sufficient sightings ($n = 30$ cells; see Section 2.4, Hotspot analysis) to conduct the analysis for both seasons (Table 1). For species-specific analyses, we included only those birds identified to species. Exceptions to the species-identification rule were shearwaters (a foraging strategy group) and phalaropes; these included unidentified birds of their genera. Sooty shearwater (*Puffinus griseus*) and short-tailed shearwater (*P. tenuirostris*) are difficult to distinguish in the field and sooty shearwaters are rare north of the Aleutian Islands (Howell, 2012); all shearwaters that we identified to species were short-tailed shearwaters, therefore, we consider the group “shearwaters” to be short-tailed shearwaters. The group “phalaropes” includes red (*Phalaropus*

fulicarius) and red-necked phalaropes (*P. lobatus*), with the former the more numerically dominant in the study area. The two phalarope species are ecologically similar and often occur in large mixed-species flocks when at sea. Preliminary examination of the raw data by month found no obvious bias in the proportion of unidentified birds for either of these genera.

While nesting and raising chicks during the breeding season, seabirds become central place foragers and often are aggregated near their colonies (Ashmole, 1971; Coulson, 2002). Colony locations are selected by birds because they provide available nesting habitat in close proximity to good foraging habitat (Ashmole, 1971; Coulson, 2002), but the aggregation of birds near colonies could potentially overshadow the relative importance of foraging areas farther from colonies. Therefore, for colonial species that breed in or near the study area, we analyzed hotspots two ways: first, all cells in the study area were included; second, cells that fell within a 40-km buffer around identified colonies were removed. We removed these cells near colonies for the 15 largest colonies in the study area (Fig 1, Appendix B), based on population estimates in the North Pacific Seabird Colony Database (USFWS, 2014). These colonies accounted for ~ 99% of all birds in the 35 colonies that occur within 40 km of the study area boundaries. We did not, however, remove colony cells for gulls and terns because those species breed in low numbers at the main colonies but also nest in widely distributed small coastal colonies or as individual pairs.

2.3.3 *Marine mammal data*

For the marine mammal analyses, we used all marine mammal sightings made during transect and circling-on-transect effort, with the exception of sightings of dead animals or animals on land. To georeference marine mammal sightings, the geographic position of the sighting was used, if available; otherwise, the position of the aircraft when the sighting was

abeam was used. The observations and survey effort were assigned to cells in the same 40-km x 40-km grid used for the seabird data. The marine mammal data were converted to estimates of encounter rate (animals/km). The encounter rate in each cell was calculated by pooling (within each season, across all years) the sightings and survey effort in that cell.

The species and taxonomic groups with sightings in a sufficient number of cells ($n = 30$ cells) to conduct the hotspot analysis (Table 1) were bowhead whale, beluga, gray whale, walrus, and a multi-species group of all pinnipeds except those confirmed to be walrus (hereafter, other pinnipeds). The latter group included ringed seals, spotted seals, ribbon seals, and bearded seals and two categories of pinnipeds that could not be positively identified to species, “small unidentified pinnipeds,” and “unidentified pinnipeds.” The two “unidentified pinniped” categories may have included some walrus sightings that could not be positively identified to species. The species or taxonomic groups that could be identified and were recorded during our study but that were not included in hotspot analyses due to insufficient sample size were bearded seals, fin whales, minke whales, killer whales, humpback whales, and polar bears.

The summer encounter rate for belugas in a single cell over Barrow Canyon (located at 71.905° N, 154.947° W) was nearly eight times higher than the next highest beluga encounter rate; therefore, this cell swamped the hotspot analysis, making all other cells where belugas were encountered disappear from the analysis. To control for the influence of this area of high encounter rates, the Barrow Canyon cell was initially omitted from the summer hotspot analysis for belugas and then added onto the map *post hoc*, after other hotspots outside of the canyon had been identified.

2.4 Hotspot analysis

We identified “hotspots” as areas where cells with high relative abundance values were spatially clustered. The effort-corrected estimates of densities (seabirds) or encounter rates (marine mammals) do not account for detection bias and are therefore both measures of ‘relative abundance’; for simplicity, we hereafter use “relative abundance” to refer to either seabird density or marine mammal encounter rates. We chose a 40-km x 40-km resolution for the hotspot analysis because this scale ensured an adequate sample size of both seabird and marine mammal sightings in each cell. Observations were summarized over the full area of the cell using the centerpoint of the cell for georeferencing.

For the hotspot analysis, we set minimal sampling effort criteria for each cell, which varied between seabird and marine mammal taxa because of differences in survey effort and type, and the generally higher encounter rates for birds. For the seabird analyses, cells were required to have a minimum of 20 km of survey coverage within a given season, pooled across all years. Preliminary analysis with Bering Sea seabird data found that the variance of the mean density estimate does not appreciably change with > 20 km of transects, even for fairly rare species (M. Renner, Tern Again Consulting, Homer, AK, *pers comm.*). For the marine mammal analyses, the minimal survey effort for pooled years was 56.6 km, corresponding to the length of the hypotenuse of a cell.

We chose the Getis-Ord G_i^* analysis (hereafter G_i^* ; Getis and Ord, 1992) to define hotspots because it can identify spatially explicit areas of high use based upon specific test criteria, independent of the magnitude of abundance. Hotspots are defined at the resolution of a single cell, but local and global (corresponding to the full extent of the study area) information is used to determine statistical significance. Thus, a cell with high relative abundance will not always be a statistically significant hotspot defined by the G_i^* if the distribution of cells with high relative

abundance is uniform throughout the study area. Likewise, a cell can be a statistically significant hotspot with respect to other cells for a given species even if the relative abundance within that cell is not extremely high for that animal and season in the study area. Consequently, the *Gi** analysis can be used to identify hotspots for species with low relative abundance, provided that they occur in a sufficient number of cells within the study area to produce reliable results. Because this analysis evaluates the pattern of distribution over a study area, it requires a minimal sample size of at least 30 cells with positive relative abundance values. If an entire population of 10 000 animals were found within a single cell, there would be insufficient data to run the hotspot analysis because this would represent an effective sample size of one cell. If animals were sparsely distributed, such that a single sighting of a single animal is found in at least 30 cells, there would be a sufficient sample size to conduct the analysis. Alternatively, if animals are distributed in clusters, such that sightings of tens or hundreds of animals are found in at least 30 cells, the sample size would be sufficient to conduct the analysis. In the latter scenario, if the population were distributed in hotspots, there would be aggregations of neighboring cells with clusters of sightings.

The *Gi** analysis starts by determining the distance over which the values of relative abundance are correlated among cells. This distance can vary among taxa. For each species or taxonomic group, an average nearest neighbor value (i.e., distance between cells where the taxon is present) was used to seed an incremental spatial autocorrelation (Global Moran's *I*) process, which in turn determined the neighborhood *d*, based on the location of "peaks" of autocorrelation, identifying where spatial autocorrelation was highest. When there were multiple peaks in spatial autocorrelation, we used the first peak (see Table 1) to inform the spatial weights matrix. Once the neighborhood was defined, the minimum number of neighboring cells was set

using a spatial weights matrix. The matrix informed every cell's relationship to all others in the neighborhood (*i.e.*, it *was* or *was not* a neighbor within d). Within the spatial weights matrix, relative abundance values for each cell were normalized by the multiplicative factor $1/n$ (where n = number of neighbors). The parameterized spatial weights matrix for each species was used as input for the G_i^* analysis. Each cell's normalized relative abundance values were compared to the values of all other cells falling within that neighborhood (the local sum), and then compared to the sum of values for all the cells in the study area (the global sum). If the calculated local sum was significantly ($P < 0.05$) different from the expected local sum (assuming a random distribution of relative abundance values throughout the study area), that cell was considered a 'hotspot'. All G_i^* analyses were conducted using the hotspot analysis tool in Arc GIS 10.1.

We mapped distributions of relative abundance in the summer and fall for each species or taxonomic group for which we could conduct a hotspot analysis. We standardized the relative abundance cut-offs for each species and taxonomic group across all maps to allow comparison of distributions between summer and fall seasons. To describe areas with the greatest number of hotspot cells and identify hotspots shared by both seabirds and marine mammals, we overlaid all hotspot (significant at $\alpha = P < 0.05$) maps for the four seabird foraging strategy groups (surface, subsurface, benthic, and shearwaters) and five marine mammal groups (bowhead whale, gray whale, beluga, walrus, and other pinnipeds).

Although the persistence of hotspots within or among years is important to understanding the dynamics of distribution patterns, we do not examine persistence here due to sample size limitations for both seabirds and marine mammals and to inconsistent spatial coverage across years. When possible, we discuss patterns in relative abundance and hotspot persistence.

3. Results

3.1 Seabirds

3.1.1 Total Seabirds

In summer, hotspots for Total Seabirds occurred north of Bering Strait, in Hope Basin, west of Cape Lisburne, near Icy Cape, off Wainwright, over the west end of Hanna Shoal, and in Barrow Canyon (Fig. 3A). In summer the removal of cells near large colonies (to minimize their influence on other foraging areas) did not alter the location of hotspots, with two exceptions: hotspots in Bering Strait near the Diomedede islands were removed, and the hotspot over Hanna Shoal was added (Table 2). In fall, hotspots were clustered north of Bering Strait and off Cape Lisburne, and one hotspot occurred northeast of Mackenzie River Delta (Fig. 3B).

3.1.2 Foraging strategy groups and species

The surface-feeding group was widely distributed in the eastern Chukchi Sea and in the western Beaufort Sea over the shelf and slope, as far east as Demarcation Point in summer and Banks Island in fall. In summer, the hotspots were just north of Bering Strait, near Cape Lisburne, near Wainwright, over Hanna Shoal, and at the mouth of Barrow Canyon (Fig. 4A). The removal of colony cells did not affect the results other than eliminating the hotspot just north of Bering Strait. In fall, hotspots were clustered between Bering Strait and Hope Basin, west of Cape Lisburne, and south of Hanna Shoal; no hotspots were identified in the western Beaufort Sea (Fig. 4B).

Species-specific hotspots of surface-feeding birds occurred primarily in areas identified as hotspots for the group as a whole. Black-legged kittiwakes are one of the most common and widespread species of surface-feeding seabirds in the region. Removing colony cells did not affect locations of hotspots beyond the colonies for this species (Table 2). In summer, their

hotspots occurred just north of Bering Strait and over Barrow Canyon (Fig. 4C); in fall, their hotspots occurred between Bering Strait and Hope Basin and west of Cape Lisburne (Fig. 4D). Kittiwakes did not, however, have any hotspots offshore near Hanna Shoal in either season, despite that being a hotspot for surface-feeding birds as a group. In summer, phalaropes had hotspots north of Bering Strait, off Cape Lisburne, between Wainwright and Hanna Shoal, and off Harrison Bay in the Beaufort Sea (Fig. 4E). In fall phalarope hotspots were more southerly and occurred between Bering Strait, Hope Basin and Point Hope, with one hotspot near Icy Cape (Fig. 4F). Other surface-feeding species with relatively low abundance but for which hotspots could be identified were arctic tern (*Sterna paradisaea*), glaucous gull (*Larus hyperboreus*), Ross's gull (*Rhodostethia rosea*), and Sabine's gull (*Xema sabini*), all of which primarily had hotspots in the northern Chukchi and western Beaufort seas (see Appendix C for distribution maps).

The subsurface-feeding group was widely distributed and had high relative abundance in the eastern Chukchi Sea but was nearly absent in the western Beaufort Sea. Their hotspots generally occurred farther south than those of the surface-feeding group. In summer, this group had hotspots just north of Bering Strait, over Hope Basin, near Cape Lisburne, near Wainwright, and over Barrow Canyon (Fig. 5A). Removing colony cells added one hotspot each near Wainwright and over Barrow Canyon (Table 2). In fall, hotspots occurred in a north–south line between Bering Strait and the head of Hope Basin. No hotspots were identified near Wainwright or Hanna Shoal despite high relative abundance (Fig. 5B), indicating that the birds were randomly distributed throughout the northeastern Chukchi Sea in fall.

In addition to the group hotspots identified just north of Bering Strait and over Barrow Canyon, species-specific hotspots indicated that important aggregations of some subsurface-

feeding birds occur offshore in the northeastern Chukchi Sea in summer and fall. In summer, thick-billed murres (*Uria lomvia*; Fig. 5C), least auklet (*Aethia pusilla*; Fig. 5E), and crested auklet (*A. cristatella*; Fig. 5G) all had hotspots just north of Bering Strait and at least one hotspot over or near Hanna Shoal. The removal of colony cells resulted in identification of four additional hotspots for least auklet and six additional hotspots for crested auklet, in Hope Basin and between Hanna Shoal and Wainwright (Table 2). In fall, thick-billed murres (Fig. 5D) and crested auklet (Fig. 5H) had hotspots in the northeastern Chukchi Sea, whereas least auklets (5F) had hotspots from Bering Strait to Hope Basin.

Other subsurface-feeding species included common murre (*Uria aalge*), tufted puffin (*Fratercula cirrhata*), and horned puffin (*F. corniculata*), all of which generally had hotspots in the southern Chukchi Sea. Subsurface-feeders with identified hotspots in the northeastern Chukchi Sea (see Appendix C for maps) were parakeet auklets (*Aethia psittacula*), and in fall only, ancient murrelets (*Synthliboramphus antiquus*), and Kittlitz's murrelets (*Brachyramphus brevirostris*); the latter also had one hotspot near Hope Basin. Black guillemots (*Cepphus grille*) occurred in offshore waters in fall, with hotspots over the slope north of the mouth of Barrow Canyon and on the continental shelf near Camden Bay (Appendix C).

The benthic-feeding group was distributed over the eastern Chukchi and western Beaufort shelves in low relative abundance. In summer, hotspots occurred close to the coast near Cape Lisburne, off of Wainwright, and in the western Beaufort Sea in Harrison Bay (Fig. 6A). In fall, hotspots occurred in the eastern Chukchi Sea near Icy Cape, over southern Hanna Shoal, over the mouth of Barrow Canyon, and in the western Beaufort Sea in Camden Bay and offshore of the Mackenzie River Delta (Fig. 6B).

The shearwater group had higher maximal relative abundance than any other foraging strategy group. They occurred in high relative abundance in the eastern Chukchi Sea in summer and fall, with lower relative abundance in the western Beaufort, and very low relative abundance east of Prudhoe Bay. (Fig. 7A, B). In summer, hotspots occurred in Hope Basin, near Icy Cape, and over the mouth of Barrow Canyon (Fig. 7A). In fall, hotspots occurred just north of Bering Strait, near Cape Lisburne, and at the mouth of Barrow Canyon (Fig. 7B).

3.2 Marine mammals

3.2.1 Cetaceans

Bowhead whales were distributed throughout the northeastern Chukchi and western Beaufort seas in both summer and fall. Relative abundance for bowhead whales was lower and hotspots were distributed farther from shore in summer (Fig. 8A) than in fall (Fig. 8B). In both seasons, all hotspots were located in the western Beaufort Sea. In summer, hotspots occurred near the mouth of Barrow Canyon, over the outer shelf between Oliktok Point and Prudhoe Bay, and between the 50-m and 200-m isobaths near Demarcation Point (Fig. 8A). There was one cell identified as a hotspot near shore in Camden Bay, resulting from two sightings of one animal each, located near the offshore boundary of the cell. In fall, hotspots were grouped over the continental shelf from the mouth of Barrow Canyon to Cape Halkett, north of Oliktok Point, off Point Thomson, and near Demarcation Point (Fig. 8B).

Belugas were distributed more widely and had higher relative abundance in summer (Fig. 8C) than in fall (Fig. 8D). In summer, hotspots occurred in Ledyard Bay, near Icy Cape, at the mouth of Barrow Canyon, and over the slope farther east in the Beaufort Sea (Fig. 8C). In fall, there were fewer hotspots and they occurred in Hope Basin, at the mouth of Barrow Canyon, and in deep waters of the Arctic Basin (Fig. 8D).

Gray whales were distributed throughout the northeastern Chukchi Sea and into the western Beaufort Sea only as far east as Dease Inlet. In both summer and fall, high relative abundance and hotspots occurred in the nearshore zone from near Wainwright to the mouth of Barrow Canyon (Figs. 9E, F). In fall, additional hotspots occurred in Hope Basin.

3.2.1 Pinnipeds

Walrus were distributed primarily in the eastern Chukchi Sea, and were observed no farther east than offshore of Harrison Bay. In summer, relative abundance was generally high from Point Lay to Hanna Shoal and near the mouth of Barrow Canyon (Fig. 9A), whereas relative abundance was lower throughout the same region in fall (Fig. 9B). In summer a cluster of hotspots (and adjoining cells with high relative abundance) occurred over Hanna Shoal. In fall, hotspots occurred near Point Lay and on and just south of Hanna Shoal (Fig. 9B).

In summer and fall, other pinnipeds were distributed throughout the study area (Fig. 9C), with higher relative abundance near the easternmost portion of the study area in fall than in summer (Fig. 9D). In summer, only one hotspot occurred in the eastern Chukchi Sea (in the Central Channel), with the remaining hotspots occurring in the Beaufort Sea east of Barrow Canyon, near Dease Inlet and offshore of Harrison Bay, and from Demarcation Point to the slope (Fig. 9C). In fall, hotspots occurred over the slope north of Dease Inlet and over the shelf north of Point Thomson. A single hotspot was identified near the coast east of Demarcation Point, but only a small portion of this cell included water, suggesting it could be a statistical artifact.

3.3 Shared hotspots

3.3.1 Seabird foraging strategy groups

In summer, most of the hotspots for the four seabird foraging strategy groups occurred in the eastern Chukchi Sea, with a few hotspots over Barrow Canyon, and as far east as Harrison Bay

in the western Beaufort Sea (Fig. 10A). Only two hotspots were shared by two of the seabird groups, at Bering Strait and west of Cape Lisburne; in both cases these were shared by the surface feeding and subsurface feeding groups.

In fall, seabird hotspots were similar in distribution to those in summer, although there were more hotspots shared by multiple foraging groups near Bering Strait and in Hope Basin (Fig. 10B). In fall, hotspots between Bering Strait and southern Hope Basin were shared by multiple foraging groups, including surface-feeding seabirds, subsurface-feeding seabirds, and shearwaters. One hotspot west of Cape Lisburne was shared by the surface-feeding and shearwaters groups. There were only three seabird foraging group hotspots in the Beaufort Sea, in Camden Bay and on the shelf northeast of the Mackenzie River Delta (Fig. 10B)

3.3.2 *Marine mammals*

The hotspots for five marine mammal species and taxonomic groups generally were located more northerly and easterly than were those for seabirds (Figs. 10A, B); however, to some extent, this result reflects the lack of aerial survey coverage in the southern Chukchi Sea (Fig. 2B). In summer, most of the hotspots for marine mammals in the eastern Chukchi Sea occurred nearshore between Ledyard Bay and Point Barrow, and in the Hanna Shoal area. In the western Beaufort Sea, there were hotspots in the Barrow Canyon area and scattered eastward over the continental shelf and slope to approximately Demarcation Point (Fig. 10A). A hotspot near Point Barrow was shared by bowhead whales and gray whales. North of Demarcation Point, one hotspot was shared by bowhead whales and other pinnipeds, and one hotspot was shared by belugas and other pinnipeds.

In fall, marine mammal hotspots in the eastern Chukchi Sea occurred from Hope Basin northward, with a cluster of hotspots from Icy Cape to Hanna Shoal, and the largest cluster of

hotspots in the Barrow Canyon area. Another cluster of hotspots occurred in the western Beaufort Sea, over the shelf and slope, from north of Prudhoe Bay to east of Demarcation Point (Fig. 10B). In fall, only a single hotspot was shared by two mammal species: belugas and gray whales in the Hope Basin (Fig. 10B).

3.3.3 *Seabird foraging strategy groups and marine mammals*

Hotspots for the four seabird foraging strategy groups and five marine mammal species/taxonomic groups totaled 51 cells in summer and 44 cells in fall (Figs. 10A, B), but only five cells in summer (in three areas) and one cell in fall were shared by seabirds and marine mammals. In summer, two shared hotspots occurred nearshore and west of Wainwright (surface-feeding birds, benthic-feeding birds, and gray whales), one occurred south of Hanna Shoal (surface-feeding birds and walrus), and two near the mouth of Barrow Canyon (surface-feeding birds, shearwaters, bowhead whales, and belugas; Fig. 10A). In fall, the only shared hotspot occurred at the mouth of Barrow Canyon (shearwaters and gray whales; Fig. 10B).

4. Discussion

4.1 Distribution of seabirds

Our results provide new information on seabird hotspots in the eastern Chukchi and western Beaufort seas, and describe distribution patterns within the the study area for select taxonomic groups. The northern Bering and southern Chukchi seas are recognized as having high densities of birds at sea (Drew and Piatt, 2005; Humphries and Huettmann, 2014; Wong et al., 2014) and some of the largest seabird colonies in the world. Colonies with millions of seabirds occur at several sites on St. Lawrence Island in the northern Bering Sea, the Diomedede islands in the middle of Bering Strait, and on both the Russian and U.S. coastlines in the southern Chukchi Sea (Appendix A; Piatt and Springer, 2003; Stephensen and Irons, 2003). We identified specific

577 areas of aggregation, using broad-scale coverage, during summer and fall open water seasons.
578 Wong et al. (2014) highlighted the importance of the southern Chukchi Sea relative to the
579 northeastern Pacific and Alaskan and Canadian Arctic, but relied on limited spatial coverage (a
580 single continuous transect line) over multiple years that crossed our study area only in July. Gall
581 et al. (2013) identified seasonal and interannual variation in seabird abundance and community
582 structure in the Chukchi Sea during 2007—2010, based on intensive surveys of three study areas
583 within the oil and gas lease sale area (incorporated into this study). There have been considerably
584 fewer seabird surveys of the western Beaufort Sea, but those surveys have found very low
585 densities of seabirds in pelagic waters in that region (Divoky, 1984; USGS 2014; Wong et al.,
586 2014).

587 For seabirds, removing colony cells did not alter the location of hotspots; rather, doing so
588 added new cells that reaffirmed the importance of the greater Hanna Shoal area and Barrow
589 Canyon, particularly for auklets, and to a lesser degree for thick-billed murre. In the majority of
590 cases, the location of hotspots was robust to colony effects, suggesting that these areas were
591 important to seabirds beyond proximity to breeding sites, or alternatively, that seabirds regularly
592 forage > 40 km from their colonies. However, there are few large seabird colonies bordering the
593 eastern Chukchi Sea, likely due to the low quantity of suitable nesting habitat. Two abundant
594 species in the area, least and crested auklet, nest on the Diomed islands in the Bering Strait or
595 south of our study area, in the northern Bering Sea; only small numbers of parakeet auklets nest
596 anywhere in the Chukchi Sea (Dragoo et al., 2012b).

597 For total seabirds, there appears to be a general shift in relative abundance and hotspot
598 locations from the northeastern Chukchi Sea in the summer to the southeastern Chukchi Sea in
599 fall. One exception is the continued use of the greater Hanna Shoal area by crested auklets. Many

auklets observed in this area in the fall appeared to be flightless (AEG, KJK, unpublished data), suggesting that birds were undergoing extensive wing molt. The change in total seabird distribution from summer to fall might reflect southward movement prior to the return of sea ice in November; however, there were differences among seabird groups and individual species. For example, the subsurface-feeding group showed a distinct shift southward in fall, whereas the surface-feeding group still had a hotspot west of Icy Cape during that season. Shearwaters show evidence of a distributional split in fall, with birds still using waters between Bering Strait and outer Ledyard Bay, and high relative abundance over Barrow Canyon, but lower relative abundance in waters between these areas, compared to summer. Thick-billed murres, which may forage at fronts where prey availability is predictable (Decker and Hunt, 1996), also used the same hotspot at the mouth of Barrow Canyon in both summer and fall, suggesting that this site provides consistently good foraging conditions throughout the open water season.

During summer the surface-feeding group had a high number of hotspots along the Arctic Basin shelf break. Surface feeders require that prey be at or near the surface; accordingly, they frequent sites with strong upwelling associated with fronts, which concentrate and carry zooplankton to the surface and attract small fish (Russell et al., 1999; Yen et al., 2006). In summer, both Barrow Canyon and the waters between Hanna Shoal and Wainwright also have physical characteristics that provide these conditions [Sec. 4. 4 below].

For auklets and fall migrants such as shearwaters, phalaropes, and murrelets, the hotspots identified in the Chukchi Sea are indicative of non-breeding or post-breeding seabirds traveling from the Bering Sea or Beaufort Sea to the Chukchi Sea specifically to forage, presumably because prey is abundant. Phalaropes migrating south used the greater Hanna Shoal area during summer, but their hotspots shifted towards Bering Strait in fall. In contrast, crested auklets had

hotspots near or over Hanna Shoal in both seasons. The median foraging range for breeding least auklets is estimated to be ~ 50 km (Obst et al., 1995), and even the larger-bodied crested auklet is not likely to make daily transits of ~ 600 km, the distance between the closest colonies (Diomedede islands) and the greater Hanna Shoal area. Least and crested auklets nesting in the northern Bering Sea are still feeding chicks in late July and August (Gall et al., 2006; Sheffield Guy et al., 2009), thus individuals of these species in the Hanna Shoal area in summer would be failed breeders or non-breeding birds. However, least and crested auklets nesting in the Aleutian Islands complete chick rearing by late July or early August (Dragoo et al., 2012a), and these post-breeding birds could be present in the Chukchi Sea at this time. Occupation of the greater Hanna Shoal area by crested auklets appears to be a recent phenomenon (i.e., over the last decade; Gall et al., 2013b). Possibly, reduced sea ice cover and longer ice free periods in fall in recent years has opened new forage areas for auklets and other seabirds. Post-breeding seabirds that are replenishing energy reserves while molting and flightless would require abundant, high quality prey that is concentrated and consistently available (King, 1974). Our results indicate that the greater Hanna Shoal area is an important foraging, and for auklets, possibly also a molting area in fall.

Benthic-feeding seabirds (i.e., seaducks) were much less common than the other foraging strategy groups in offshore waters, where most of our surveys were conducted, as reflected in the predominantly nearshore locations of their hotspots, with the exception of a hotspot south of Hanna Shoal in the fall. Notwithstanding the low occurrence of seaducks in the deep areas we primarily surveyed, the shallow (10 – 40 m) shelves of the western Beaufort and eastern Chukchi seas are important foraging areas for eiders. Within the nearshore corridor, Lovvorn et al. (*this issue*) found that the eider's benthic prey show high inter-annual variability in biomass and

accessibility due to ice scouring, which subsequently could affect eider distribution among years. Overall this nearshore corridor, particularly Ledyard Bay, provide post-breeding migration and staging areas for seaducks moving to the western Chukchi Sea and south to the Bering Sea (Fischer and Larned, 2004; Oppel et al., 2009; Phillips et al., 2007; Sexson et al., 2014; Lovvorn et al., this issue). Although some king eiders (*Somateria spectabilis*) undergo wing molt in the Alaska sector of the Beaufort Sea (Phillips et al., 2007), most of this species, as well as common eider (*S. mollissima*) (Petersen and Flint, 2002) and spectacled eider (*S. fischeri*) (Petersen et al., 1999) appear to molt and winter in coastal areas of the western Chukchi and Bering seas. This is consistent with the generally higher densities of benthic foragers we found in the western and southern portion of our study area in fall.

4.2 Distribution of marine mammals

Our results provide insight into the current broad-scale distribution of bowhead whales in Alaskan waters and highlight the importance of the western Beaufort Sea shelf in summer and fall. Despite good survey coverage of the northeastern Chukchi Sea in summer, all of the hotspots for bowhead whales occurred near the mouth of Barrow Canyon and across the shelf and slope in the western Beaufort Sea. The location of the bowhead whale hotspot near Point Barrow in both seasons was consistent with high proportional use of that area by 54 bowhead whales tagged in 2006 – 2012 (Citta et al., *this issue*). The aerial surveys also recorded high relative abundance and additional hotspots farther east on the Beaufort Sea shelf, especially in fall. One bowhead whale hotspot was identified nearshore in Camden Bay, although bowhead whales are not consistently found in that area (Clarke et al., 2013a; NMML data); therefore, their distribution in nearshore Camden Bay may be associated with ephemeral foraging opportunities. The population of western Arctic bowhead whales is increasing (Givens et al., 2013) and the

longer ice-free season in the western Beaufort Sea may facilitate use of the shelf by bowhead whales (Ashjian et al., 2010; Moore et al., 2010).

Belugas occur throughout the eastern Chukchi and western Beaufort seas in summer and fall, and our identification of hotspots over the slope bordering the Arctic Basin are consistent with previous studies (Moore et al., 2000; Richard et al., 2001; Suydam et al., 2005, Hauser et al., 2014). The importance of Barrow Canyon to foraging belugas has been documented by both aerial and acoustic surveys (Moore et al., 2000; Stafford et al., 2013), and our removal of the cell with extremely high relative abundance of belugas over Barrow Canyon was key to identifying other hotspots. In summer, additional beluga hotspots were found in the nearshore area from Ledyard Bay to Wainwright in the northeastern Chukchi Sea. These hotspots were likely due to the congregation of belugas from the Eastern Chukchi Sea stock near Kasegaluk and Omalik lagoons in June and July for feeding, mating, and calving (Frost et al., 1993; Suydam et al., 2001). In addition, the area west/southwest of Wainwright recently was found to have high biomass indices of arctic cod (*Boreogadus saida*; Arctic Eis, 2013; Logerwell et al., *this issue*), which is a significant component of beluga diets (Frost and Lowry, 1984). A second hotspot during both summer and fall included the slope waters of the western Beaufort Sea. In fall, both the Eastern Chukchi Sea and the Beaufort Sea stocks of belugas may occur in this area (Richard et al., 2001; Suydam et al., 2001, 2005; North Slope Borough, unpublished data, Hauser et al., 2014). A third hotspot for belugas was Hope Basin, but only during fall. Hope Basin has low fish abundance (Arctic EIS, 2013; Eisner et al., 2013); however, this area is also characterized by a recurrent long-term frontal system (Coachman et al., 1975; Belkin et al., 2003), which is thought to enhance both pelagic and benthic biomass (Bluhm et al., 2007). Belugas from the Eastern Chukchi Sea and Beaufort Sea stocks eat a diversity of prey, including Arctic and saffron cod,

shrimp, octopus, and echiurids (Frost and Lowry, 1984; Moore et al., 2000; Quakenbush et al., *in press*). Our study includes areas frequented by migrating and foraging animals; the Hope Basin could have high relative abundance of belugas due to animals engaging in either activity.

The distributional patterns we found for bowhead whales and belugas in the fall generally agree with results from aerial surveys conducted in 1982–1991 (Moore et al., 2000), with two exceptions that can be explained by differences in the areas surveyed in the older and more recent time periods. In the summer, we found hotspots for bowhead whales and belugas in the Beaufort Sea, whereas Moore et al. (2000) found no bowhead whales and few belugas west of Prudhoe Bay. The summer surveys described by Moore et al. (2000) were generally limited to the waters farther east (east of 150°W). In the Chukchi Sea, Moore et al. (2000) did not include waters south of 70°N in their analysis; we identified a hotspot for belugas in that area.

In contrast to the bowhead whale and beluga, gray whale hotspots were concentrated in the eastern Chukchi Sea between Wainwright and Barrow Canyon. We identified hotspots for gray whales in Hope Basin in fall and near Barrow Canyon in both seasons. The influx of nutrient-rich waters from the Pacific and high sedimentation rates associated with seasonal sea ice coverage result in high biomass of benthic infauna in Hope Basin (Grebmeier et al., 2006), which attracts foraging gray whales (Bluhm et al., 2007). The 1982–1991 surveys also found gray whales over Hope Basin (Moore et al., 2000), suggesting long-term use of that area. Our study did not identify Hanna Shoal as an area of high relative abundance for gray whales or as a gray whale hotspot, whereas this area was heavily occupied by gray whales in the 1980s and 1990s (Moore et al., 2000). Fresh mud plumes indicative of foraging behavior by gray whales are regularly sighted by aerial marine mammal observers near Barrow Canyon during both summer and the fall (Clarke et al., 2013a), indicating that gray whales forage there consistently. Gray

whales occur more frequently in the eastern Chukchi Sea than they did in past decades, perhaps in response to declines in the biomass of benthic infauna at historical foraging grounds in the northern Bering Sea (Moore et al., 2003) or to the increased gray whale abundance (Laake et al., 2012). These changes in distribution have occurred coincident with spatial and temporal reductions in sea ice (Moore and Huntington, 2008).

Similar to gray whales, walrus, another benthic feeder, were sighted only in the western half of the study area (no farther east than Harrison Bay). When comparing relative abundance of walrus between seasons, it is important to remember that walrus sighted on shore in the mass coastal haulouts were not included in the analysis. In summer, all walrus hotspots were clustered over Hanna Shoal, where sea ice remains over the shoal late into summer, providing sea ice platforms where walrus rest while diving to forage on the bottom (Jay et al., 2011). The lower number of hotspots for walrus in fall is consistent with the tendency for walrus to be sighted in smaller groups in the water at that time (e.g., Clarke et al., 2013a); however, the probability of detecting swimming walrus is likely much lower than for walrus on sea ice (Speckman et al., 2011), particularly in high sea states, and this bias could affect the number and distribution of hotspots identified in fall. In fall, high relative abundance from outer Ledyard Bay north to Wainwright and the hotspot at Point Lay coincide with the mass coastal haulouts of walrus observed during fall 2009–2011. In those years, sea ice in preferred offshore foraging areas had disappeared by mid- to late summer; walrus foraged in nearshore areas despite relatively low prey availability there, and they made extensive foraging trips to offshore foraging grounds on the southern margins of Hanna Shoal (Jay et al., 2012).

The other pinniped group was distributed throughout the study area in both seasons, although our results suggest a more intensive use of the western Beaufort Sea shelf than the

eastern Chukchi Sea. Analyses of the 1989–1991 aerial surveys (Frost et al., 1993) identified hotspots for other pinnipeds in or near Kasegaluk Lagoon; we did not include that area in our analysis because our aerial surveys did not cover that area. We did find high relative abundance of pinnipeds at Icy Cape in the fall, although this area was not identified as a statistically significant hotspot. Because our analysis did not include pinnipeds hauled out on land, we underrepresented this taxonomic group, as some species molt on land. Seals, particularly subadults, can be highly mobile during the summer and fall. For example, satellite-tagged ringed seals moved westward from the Canadian Beaufort Sea to the Chukchi Sea from September to October and moved south through Bering Strait by December (Harwood et al., 2012). The combination of highly mobile individuals with a variety of species-specific foraging behaviors may account for the distribution of this group throughout the Chukchi Sea.

4.3 Hotspots shared by seabirds and marine mammals

Hotspots for seabird foraging strategy groups tended to occur primarily in the eastern Chukchi Sea, especially in the fall, whereas marine mammal hotspots tended to occur farther north and east, in the western Beaufort Sea. These overall patterns are partly due to spatial differences in sampling, with few seabird surveys in the western Beaufort Sea and no marine mammal surveys south of 68° N in the eastern Chukchi Sea. However, despite limitations of sampling effort, there is supporting evidence to suggest that these general patterns reflect true differences between seabird and marine mammal distributions throughout the eastern Chukchi and western Beaufort seas. For seabirds, our survey coverage was fairly consistent across most of the study area, even if individual cells were not surveyed at the same intensity. A separate set of surveys of the Beaufort Sea in 2008–2011 also recorded low numbers of seabirds there (Wong et al., 2014), and it is unlikely that we consistently missed aggregations of seabirds in the

western Beaufort Sea. Similarly, although there were low whale encounter rates where aerial survey coverage was minimal between Hope Basin and Point Lay, there were also few whale sightings and acoustic detections in this area during shipboard surveys in 2011 (NOAA, 2011), and few whale calls were detected by autonomous passive acoustic recorders deployed in this area during the summers of 2009 and 2010 and the winters of 2008-2009, 2009-10, 2010-11 (Hannay et al., 2013).

We identified hotspots for: 1) seabird species/taxonomic groups; 2) marine mammal species/taxonomic groups; and 3) seabird and marine mammal species/taxonomic groups combined. Areas of aggregation for multiple taxonomic groups included Bering Strait, Hope Basin, the waters between Wainwright and Hanna Shoal, and Barrow Canyon. Hotspots that were shared by seabird and marine mammal taxa occurred only in the northeastern Chukchi Sea and near Barrow Canyon. A series of hotspots extending from Point Barrow to the slope was shared in summer by bowhead whales, gray whales, belugas, thick-billed murre (a subsurface feeder), Sabine's gulls and arctic terns (two surface feeders), and the surface-feeding group. In fall, the shared hotspot was located ~20–60 km offshore at the mouth of Barrow Canyon; shearwaters and gray whales were numerically dominant there, but other species that shared that hotspot in fall included the surface-feeding Ross's gull and glaucous gull, and the subsurface-feeding thick-billed murre and Kittlitz's murrelet. Notably, soft bottom benthic community predators such as walrus and seaducks did not share these hotspots. The variety of species and total abundance of seabirds and marine mammals in the Barrow Canyon area during both seasons is indicative of abundant prey and the influence of physical properties that concentrate prey in the water column, thereby providing optimal foraging conditions at the surface and in the water column.

784 4.4 *Physical and biological attributes of the hotspots*

785 Hotspots tended to be near or over channels (e.g., between Hanna Shoal and Wainwright),
786 steep canyon walls (e.g., the eastern edge of Hope Basin and Barrow Canyon), and continental
787 shelves and slopes (e.g., in the western Beaufort Sea). Bering Strait is a narrow conduit for
788 nutrient-rich waters and zooplankton (Walsh et al., 1989; Springer et al. 1989, Schell et al.,
789 1998) and a passageway for seabirds and marine mammals. Given its biological richness and the
790 fact that it also is the only corridor for migrating seabirds and marine mammals between the
791 Pacific Arctic and the Bering Sea, Bering Strait is a *de facto* hotspot for seabirds and marine
792 mammals (Humphries and Huettmann, 2014; Smith et al., 2014). Without removal of the colony
793 cells around the Diomedede islands, Bering Strait was identified as a hotspot for most seabirds, and
794 was likely so for marine mammals, although there has been no recent aerial survey coverage
795 there during summer and fall (but see Speckman et al., 2011 for spring surveys).

796 The enhanced productivity from currents advecting nutrients northward through the Bering
797 Strait extends into Hope Basin (Grebmeier et al., 1989, 2006, Walsh et al. 1989), where we
798 found hotspots primarily along the slope of the basin, particularly near the 50 m contour, for
799 surface-feeding and subsurface-feeding seabirds, beluga, and gray whale. The eastern slopes of
800 Hope Basin are where Bering Sea Water meets the eddies and gyres emerging from outer
801 Kotzebue Sound, which can form a pool of high primary productivity along with strong currents
802 (Coachman et al., 1975; Grebmeier and McRoy, 1989).

803 Farther north, the greater Hanna Shoal area was occupied by seabirds with a variety of diets
804 and foraging behaviors, particularly subsurface-feeders; this group includes planktivores
805 (auklets), omnivores (shearwaters, thick-billed murre, murrelets), and more strictly piscivorous
806 species (common murre, puffins). The diving birds tend to favor shallow areas where

zooplankton and associated fish occur < 60 m deep and where strong fronts or pycnoclines concentrate prey (Davoren et al., 2003; Decker and Hunt, 1996; Hunt, 1997; Hunt et al., 1990, 1998). In summer, the greater Hanna Shoal area was a hotspot for benthic-feeding walrus and, to lesser degree, surface-feeding seabirds (including phalaropes and Sabine's gull). The greater Hanna Shoal area has high benthic biomass (Grebmeier et al., 2006), and, when sea ice is present, it provides ideal walrus habitat in summer (Jay et al., 2012). For surface-feeding seabirds, an additional attraction to the greater Hanna Shoal area may have been the aggregation of walrus on the sea ice; kittiwakes and gulls are found in association with walrus hauled out on sea ice (KJK, *pers. obs.*) and may be scavenging on walrus scat or carcasses or taking advantage of walrus activity that could displace prey out from under the protection of ice floes. Conversely, walrus will prey on seabirds, particularly murre (Mallory et al., 2004) and possibly spectacled eiders (Lovvorn et al., 2010), and thus present a risk to nearby seabirds in the water.

Barrow Canyon exhibits episodes of high primary productivity and associated high benthic biomass (Grebmeier et al., 2006). Recent studies have proposed that the enhanced productivity near Barrow Canyon extends through all trophic levels (Pickart et al., 2013). This productivity is sustained by a combination of: (1) a longer open-water season that promotes primary productivity; (2) physical mechanisms that transport the high-nutrient winter water into the euphotic zone; and (3) concentrations of zooplankton and fish that attract seabirds and marine mammals (Pickart et al., 2013). The fronts created in the confluence of currents near Point Barrow concentrate and trap prey, such as copepods and euphausiids, in predictable areas, depending on wind strength and direction. The northeastward-flowing Alaskan Coastal Current moves along the southern edge of Barrow Canyon, while strong easterly winds drive euphausiids on-shelf from the Beaufort Sea slope, blocking off-shelf movement of these and other prey

(Ashjian et al., 2010; Okkonen et al., 2011). This dense aggregation of copepods and euphausiids on the western Beaufort shelf near Point Barrow attracts foraging bowhead whales (Ashjian et al., 2010; Okkonen et al., 2011). Pelagic and demersal fishes also aggregate there in response to the zooplankton, and these aggregations facilitate the foraging of piscivores such as belugas (Stafford et al., 2013). The shearwaters and other seabirds that aggregate near Barrow Canyon appear to take advantage of the same conditions.

There is growing evidence that seabirds and marine mammals from the Bering Sea are using the central and northeastern Chukchi Sea more than they did in past decades. A shift in distribution northwards into the Chukchi Sea, or longer periods of occupation in the Chukchi or Beaufort seas, have been documented for humpback whales, fin whales, minke whales, and killer whales (Clarke et al., 2013b; Clarke et al., 2014). Additionally, radio-tagged walrus have been found to arrive in the Chukchi Sea earlier and remain later in fall in recent years, as sea ice retreats earlier in summer and freeze-up is delayed to October or November (Jay et al., 2012). Seabird communities have also changed in the eastern Chukchi Sea (Gall et al., 2013b), and once-rare species (e.g., ancient murrelet) occur regularly (Gall et al., 2013b) and new species (e.g., short-tailed albatross [*Phoebastria albatrus*]) have been recorded there (Day et al., 2013a). Key features of the ‘new Arctic’ (Wood et al., *this issue*) include earlier ice melt, high primary productivity (Brown and Arrigo, 2012), and a large biomass of zooplankton (Eisner et al., 2013). Pelagic fishes in the region exploit the available zooplankton, including abundant arctic cod and forage fishes such as capelin (*Mallotus villosus*) and sand lance (*Ammodytes hexapterous*) (Arctic Eis, 2013; Eisner et al., 2013). An added benefit to upper trophic level predators is that the forage fishes that occur in the eastern Chukchi Sea in late summer have higher energetic content than do conspecifics at lower latitudes, including those in the northern Bering Sea

(Arctic Eis, 2013). Finally, the energetic content of zooplankton, euphausiids, and forage fishes reach their peak during fall (Montevecchi and Piatt, 1984; Hop and Gjøsæter, 2013; Arctic Eis, 2013), which could make the extra time and energy required to access these northern forage sites worthwhile for upper trophic level predators preparing for winter.

Another potential benefit of foraging in the Chukchi Sea, particularly for post-breeding seabirds from lower latitudes (e.g., ancient murrelets and crested auklets from the Aleutian Islands and Kittlitz's murrelets from the Gulf of Alaska) are the longer daylight hours that might enable longer periods of foraging. In August and September, the Barrow region has ~ 6 hr more daylight than the northern Gulf of Alaska (at ~ 60° N). At Point Barrow, acoustic moorings show that euphausiids migrate to the surface during twilight (S. Okkonen, University of Alaska, Fairbanks, unpublished data). Diving thick-billed murres have been shown to track nocturnal vertical movements of prey in the Bering Sea, with a preference for shallow prey patches (Benoit-Bird et al., 2012). The extended twilight period might facilitate foraging on zooplankton and the forage fishes that follow them, for diving seabirds, while also increasing access to prey for surface-feeding birds. The difference in daylight hours between the Chukchi Sea and lower latitudes is greatest from June through August and remains slightly greater throughout most of September. With a combination of longer daylight hours and more energy-rich prey, we would expect concurrent peaks in seabird abundance during August and September, when seabirds replenish energy reserves prior to migration. Indeed, peak densities of seabirds near the greater Hanna Shoal area were typically highest in September during 2008–2010 (Gall et al., 2013b)

4.5 Management implications and future directions

Our broad-scale analyses suggest several hypotheses that could be examined to improve our understanding of upper trophic level predator distribution and ecosystem links in the eastern

Chukchi and western Beaufort seas. First, the few hotspots shared by multiple species or taxonomic groups suggest that taxa may partition habitat. The spatial separation of species might simply reflect different diets, but it also could indicate interference competition among species. The most likely site to explore fine-scale mechanisms of temporal or spatial separation is over Barrow Canyon, where densities of whales, shearwaters, and other species suggest the potential for competition for prey, or competitive exclusion.

Second, if competition does exist, it may be a recent phenomenon and is likely to increase, given recent population increases in whales (Givens et al., 2013; Laake et al., 2012) and the influx of planktivorous seabirds into the northeastern Chukchi Sea (Gall et al., 2013b). In contrast, some seabird species might benefit from increased interactions with marine mammals, such as phalaropes and other surface-feeders that gain access to prey species forced to the surface by foraging gray whales (Obst and Hunt, 1990; Grebmeier and Harrison, 1992).

Third, it is unknown if the occurrence of non-breeding seabirds (i.e., post-breeding auklets and murrelets, or migratory shearwaters) and migrating gray whales in the eastern Chukchi Sea are indicative of better foraging opportunities in the Arctic or poor foraging conditions in the Bering Sea. Moore et al. (2003) suggested that gray whales were expanding their foraging range because benthic biomass in the northern Bering Sea had decreased. Similarly, planktivorous auklets could be seeking better foraging in the Chukchi Sea. Although zooplankton are advected past breeding colonies in the northern Bering Sea (Piatt and Springer, 2003), there is clear indication that seabirds from more southerly breeding areas travel hundreds of kilometers farther north to forage in late summer and fall. There is not currently a monitoring program for auklets on St. Lawrence Island in the northern Bering Sea, but indications from the latest studies of least and crested auklet reproductive success indicate a decline for both species over four years

between 2005 and 2009 (Dragoo et al., 2012a), which might be indicative of low prey availability within foraging range of those colonies (see Gall et al., 2006; Sheffield Guy et al., 2009). However, the predicted continued loss of sea ice (Wang and Overland, 2009; this issue), could eventually reduce availability of key prey species such as arctic cod, which are part of the sea ice ecosystem (Gradinger and Bluhm, 2004; Hop and Gjøsæter, 2013). Tracking individually tagged birds, or monitoring their breeding populations, would improve our understanding of how these abundant planktivorous seabirds might be impacted by observed changes in the Arctic.

Finally, conflicts between human activity and seabirds and marine mammals are likely to increase as shipping and development move into the Arctic (Quakenbush et al., 2010b; Reeves et al., 2013; Humphries and Huettmann et al., 2014; Smith et al., 2014). The hotspots we have identified as important for multiple taxa, Bering Strait, Wainwright to Hanna Shoal, Barrow Canyon, and the western Beaufort Sea shelf and slope, also have high potential for human activity. In an analysis of circumpolar Arctic shipping and seabird abundance, Humphries and Huettmann (2014) identified Bering Strait as having the highest overlap between human activities and seabird diversity and abundance. Furthermore, Reeves et al. (2013) found that over half of the circum-Arctic range of bowhead whales, belugas, and narwhals overlaps known or suspected offshore oil and gas deposits, and the observed and expected increase in ship traffic increases the risk of ship strikes and adds noise to the underwater environment, with unknown consequences to marine mammal populations. The northeastern Chukchi Sea has been and will continue to be a focus of potential oil and gas development (BOEM, 2014). Increased shipping through ice-free waters (Smith and Stephenson, 2013) and the development of infrastructure will increase coastal traffic to the city of Barrow and, hence, over Barrow Canyon. Information about

spatio-temporal patterns in relative abundance and habitat requirements of upper trophic level species, and the human communities that depend on them, can inform planning, mitigation, and response actions. By identifying areas of high seabird and marine mammal use, we hope to assist management considerations and focus future studies on the mechanisms affecting top predators in the Chukchi and Beaufort seas.

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Tables

Table 1. Species and taxonomic groups used for hotspot analysis, for summer and fall, including number of sightings within the study area, number of occupied 40 x 40 km cells, and nearest

neighbor value (km); the latter was used to seed the incremental spatial autocorrelation process. Getis-Ord G_i^* analysis could not be conducted on species or taxonomic groups with fewer than 30 occupied cells in a given season.

Table 2. Areas where additional hotspot cells were identified (“new”) for Total Birds, surface-feeding group, subsurface-feeding group, and selected colonial species, in the G_i^* hotspot analysis after removal of colony buffer cells in summer. Light to dark shades of orange indicate relative abundance; green cells had hotspots within the region.

Figures

Figure 1. Study area, showing marine and terrestrial points of reference and locations of seabird colonies with 40 km buffers applied to analysis to reduce the effect of seabird aggregations near colonies during summer. Note that some locations represent several colonies as listed in the North Pacific Seabird Colony Database.

Figure 2. Survey effort for seabird surveys during summer (A) and fall (B) and for marine mammals during summer (C) and fall (D).

Figure 3. Distribution and hotspots (red-highlighted cells) for all seabirds combined in summer (A) and fall (B). Density scale is unique to each season.

Figure 4. Summer (left column) and fall (right column) distribution and significant hotspots (red-highlighted cells) for surface-feeders (A, B), and two relatively abundant species within

that group: black-legged kittiwakes (C, D) and phalaropes (E, F). See Appendix B for species included in the surface-feeding group.

Figure 5. Summer (left column) and fall (right column) distribution and significant hotspots (red-highlighted cells) for the subsurface-feeding group (A, B) and for three relatively abundant species within that group: thick-billed murre (C, D), least auklets (E, F), and crested auklets (G, H). See Appendix B for species included in the subsurface-feeding group.

Figure 6. Summer (A) and fall (B) distribution and significant hotspots (red-highlighted cells) of benthic-feeding seabirds (see Appendix B for list of species included).

Figure 7. Summer (A) and fall (B) distribution and significant hotspots (red-highlighted cells) of the shearwater foraging strategy group (likely all short-tailed shearwaters).

Figure 8. Summer (A) and fall (B) distribution and significant hotspots (red-highlighted cells) in for bowhead whales (A, B), belugas (C, D), and gray whales (E, F).

Figure 9. Summer (left column) and fall (right column) distribution and significant hotspots (red-highlighted cells) for walrus (A, B) and other pinnipeds (C, D).

Figure 10. Seabird and marine mammal hotspots for summer (A) and fall (B). The species or forage groups included in the shared seabird and marine mammal hotspots are labeled.

Appendix

A. Seabird colonies within our study area (roughly south to north) for which cells within 40 km from the colonies were removed. Several colonies were close together, making their separate locations indistinguishable in Figure 1. Some of these estimates were made prior to 2000, or were based on visual surveys, thus they are meant to provide only a general idea of the relative abundance of species and colony sizes.

B. Seabird species list and their assigned foraging strategy group used for analysis.

C. Distribution and significant hotspots (red-highlighted cells) for marine birds for which the Getis-ord G^* analysis could be conducted (minimum of 30 cells within a season). For some species, analysis could only be conducted for either summer or fall.