INFLUENCE OF PHYSICAL AND BIOLOGICAL OCEANOGRAPHY ON THE STRUCTURE OF THE SEABIRD COMMUNITY IN THE NORTHEASTERN CHUKCHI SEA

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INFLUENCE OF PHYSICAL AND BIOLOGICAL OCEANOGRAPHY ON THE STRUCTURE OF THE SEABIRD COMMUNITY IN THE NORTHEASTERN CHUKCHI SEA

A

DISSERTATION

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By

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ABSTRACT

The Chukchi Sea is losing seasonal ice cover as global temperatures rise, facilitating human access to the region for activities such as oil and gas exploration, shipping, and tourism. Processes and responses to environmental change by marine ecosystems are often challenging to quantify because they are hidden under water. Seabirds, however, offer visible evidence of the health and status of marine ecosystems. I studied the community structure, variability in abundance and distribution, and habitat associations of seabirds in the eastern Chukchi Sea. My results provide insights into the influence of climate change on seabirds and a benchmark against which to evaluate possible impacts of anthropogenic activity. Repeated sampling of systematic transects in the northeastern Chukchi Sea during the ice-free seasons of 2008–2012 showed that the community consisted of ~40 species and was dominated numerically by planktivorous seabirds, particularly Crested Auklets (*Aethia cristatella*) and Short-tailed Shearwaters (*Puffinus tenuirostris*). In contrast, benthic-feeding birds were rare. The abundance of seabirds in the offshore northeastern Chukchi Sea varied by up to two orders of magnitude among years and birds generally were more abundant in September than August. Despite these seasonal and interannual variations in abundance, the species composition was similar among years, with anomalies occurring only in years of persistent ice cover. I compared data from this recent period (2008–2012) with data from historical surveys (1975–1981) to evaluate decadal trends in seabird abundance and composition and related those changes to reductions in seasonal ice cover. The seabird community shifted from one consisting primarily of piscivorous seabirds to one consisting primarily of planktivorous seabirds. This shift suggests that zooplankton prey are more accessible now to avian predators as seasonal ice cover has declined. I explored the relationships between seabirds, hydrography, and zooplankton abundance with spatially explicit generalized additive models. The associations of seabirds with habitat characteristics varied with foraging method and preferred prey. Species that fed primarily by pursuit diving were more abundant in warm, weakly stratified water, whereas surface-feeding species were more abundant in cold, strongly stratified water. Planktivorous seabirds (auklets, shearwaters, and phalaropes) were more abundant within 20 km of thermal surface fronts and in contrast, omnivores (gulls and murres) were more abundant far from thermal fronts. For 5 of the 8 seabird species, information about prey biomass improved predictions of seabird abundance, although the relationships were not as clear as they were for the physical habitat characteristics indicative of processes that aggregate prey. Advective processes that transport oceanic species of zooplankton from the Bering Sea to the Chukchi Sea, together with the local influence of sea ice on physical and biological processes, strongly influence the distribution of seabirds, particularly the planktivorous species. Scientists and decision-makers can use the results of this multi-species and multi-disciplinary study as a benchmark to assess the ecological consequences of anthropogenic activity against the backdrop of climate change that is affecting the Chukchi Sea.

DEDICATION

To María Lucia Rueda Terán de Pradilla
To whom I owe my curiosity and love of reading, dogs, and chocolate
Tu risa me acompañará siempre, Abuelita

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GENERAL INTRODUCTION

The seasonally ice-covered Chukchi Sea shelf is among the largest continental shelves in the world. It also is highly productive, although much of the primary production and zooplankton biomass can be attributed to the northward flow of nutrient-rich oceanic water, which originates far to the south, in the basin of the Bering Sea (Coachman et al., 1975; Springer and McRoy, 1993; Grebmeier et al., 2006). This influx of oceanic nutrients and plankton sustains a seabird community that would otherwise have little prey available (Springer et al., 1989). Despite an understanding of the importance of advection to the food web of the Chukchi Sea, questions remain about the processes that link the Bering and Chukchi ecosystems (Springer et al., 1996). Seasonal and interannual changes in advection may have profound effects on the distribution and abundance of non-breeding, staging, and migratory seabirds that rely on these resources during the open-water season (June to mid-October).

In addition to its rich marine resources, the Chukchi Sea is of great interest for offshore oil development. Exploration for offshore oil began in arctic Alaska in the 1970s and led to exploratory drilling of 5 wells in 1989 and 1990. Two of these wells, known as Klondike and Burger, are located ~80–100 km west of the village of Wainwright. These areas were not pursued beyond exploration at that time, and there was no further activity until February 2008, when nearly 3 million acres in the Chukchi Sea surrounding Klondike and Burger were leased for oil exploration (73 FR 209, 2008). Studies of marine ecology were conducted sporadically in 1975–1982 as part of the National Oceanic and Atmospheric Administration's Outer Continental Shelf Environmental Assessment Program (OCSEAP; e.g., Feder et al., 1994; Barber et al., 1997; Gillispie et al., 1997), but there was no systematic approach to studies, like was seen the Bering Sea (e.g., Inner Shelf Transfer and Recycling [ISHTAR]; Walsh and McRoy, 1986; Walsh et al., 1989). Research on seabirds continued, albeit on a reduced scale, through the 1980s and focused primarily on the southern Chukchi Sea (e.g., Springer et al., 1984; Divoky and Springer, 1988; Piatt and Springer, 2003). Over the past decade, there has been resurgence in oceanographic research motivated by the need to inform managers and industry about natural resources, ecological function, and environmental changes in the northeastern Chukchi Sea.

Much of the interest in seabirds in this area has concentrated on mainland seabird colonies (e.g., Springer et al., 1984; Hatch et al., 2000; Dragoo et al., 2013) and on seabirds at sea in the vicinity of the Hope Basin (e.g., Piatt and Springer, 2003), which lies immediately north of Bering Strait, in the southeastern Chukchi Sea. Another area of research has focused on use of the coastal-lagoon systems of the northeastern Chukchi Sea by birds. Early work by Johnson et al. (1993) described baseline use of the Chukchi lagoon systems near Point Lay, whereas recent work has focused on monitoring population trends of birds in all lagoon systems in northern and northwestern Alaska (e.g., Dau and Larned, 2004 and related annual reports). Aerial surveys for and satellite telemetry of migrating and staging Spectacled (*Somateria fischeri*) and Steller's eiders (*Polysticta stelleri*), both of which are protected under the Endangered Species Act (ESA) of 1973, as amended (PL 93-205; 16 USC §1531), in the Chukchi Sea have indicated that shallow, nearshore waters of Ledyard Bay and Peard Bay form important stopover areas for migrating Spectacled and King (*S. spectabilis*) eiders in both the summer and fall (Larned and Balogh, 1997; Oppel et al., 2009). In fact, the USFWS designated the nearshore waters of Ledyard Bay as critical habitat for Spectacled Eiders in 2001 (50 CFR Part 17).

In comparison with the well-known coastal seabird community, few historical data on the at-sea distribution and abundance of seabirds are available for the offshore region of the northeastern Chukchi Sea. Offshore studies were limited primarily because of heavy sea-ice cover. As an example of how inaccessible this area was 4 decades ago, a map of sea-ice cover of the northeastern Chukchi in late September–early October (Fig. 3 in Watson and Divoky, 1970) shows that nearly the entire region was inaccessible to sampling from an icebreaker. Despite these limitations, dedicated naturalists have been recording seabird observations from ships in the Chukchi Sea for decades.

One of the earliest historical accounts of seabird species in the Chukchi Sea was based on surveys in the western Chukchi Sea in July–August 1928 that suggested that Pomarine Jaegers (*Stercoriarus pomarinus*) and Black-legged Kittiwakes (*Rissa tridactyla*) were among the most abundant seabirds in the Chukchi (Jaques, 1930). Later, Swartz (1967) examined the at-sea distribution of seabirds in the central and southern Chukchi during the environmental studies at Cape Thompson. Surveys were conducted opportunistically in the 1970s and 1980s that covered the Chukchi Sea from the Bering Strait to the northern edge of the continental shelf (Divoky, 1987; Watson and Divoky, 1970). These historical studies provided snapshots of the community composition and density of seabirds in the northeastern Chukchi Sea (Divoky, 1987) but did not address the variability of this community or link species explicitly to their marine habitat.

Subsequent studies have indicated that piscivorous seabirds (including Black-legged Kittiwakes) were the primary seabirds north of Bering Strait (Piatt and Springer, 2003; Hunt et al., 2013; Whitehouse et al., 2014) and concluded that the Chukchi Sea was a system that relied on Arctic cod (*Boreogadus saida*) to feed the bulk of higher trophic level predators foraging in the pelagic environment (Piatt and Springer, 2003; Hopcroft et al., 2008). The challenge is that these studies were relying in large part on seabird data collected in the 1970s and 1980s. Preliminary data from surveys conducted in 2007 hinted that, although the pelagic system did appear to depend on Arctic cod during the OCSEAP studies, decades of reductions in ice cover may have ushered in a new Arctic system powered by plankton (Eisner et al., 2013; Gall et al., in review—this dissertation).

I employed a multi-scale approach to gain a better understanding the geographic and temporal structure of the seabird community and its contribution to ecosystem function in the northeastern Chukchi Sea. The first chapter focuses on three study areas where ConocoPhillips Alaska, Inc. (Klondike study area), Shell Exploration & Production Company (Burger study area), and Statoil (Statoil study area) have several lease blocks for offshore oil exploration and development. I used statistical models to explore the relationship between the seabird community and physical oceanography within these study areas by using data collected during the open-water seasons of 2008–2010. Information from this chapter also was included in a multidisciplinary analysis and preliminary description of the ecology of the northeastern Chukchi Sea (Day et al., 2013a)

The second chapter considers broader spatial and temporal scales than the first chapter by exploring changes in the seabird community of the eastern Chukchi Sea from the coast to areas located up to 185 km offshore over the past 4 decades. I considered all of the species occurring within the study area. Some of the species that were recorded over the past 7 years were new to the Chukchi Sea, and these patterns in species occurrence were summarized in the context of ongoing range expansion and community change (Day et al., 2013b).

The third chapter used physical and biological oceanographic data to develop spatially explicit models that predict the distribution and abundance of 8 species of seabirds common to the Hanna Shoal region of the northeastern Chukchi Sea. Together, these three chapters provide a complete contemporary picture of the seabird community, quantify the variability within and among seasons and over decades, and establish a benchmark against which to measure the effects of ecological and anthropogenic change to the ecosystem of the northeastern Chukchi Sea.

CHAPTER 1: STRUCTURE AND VARIABILITY OF THE MARINE-BIRD COMMUNITY IN THE NORTHEASTERN CHUKCHI SEA [1]

1.1 Abstract

We examined the seasonal and interannual variation in the marine-bird community and its relationship to physical oceanography in the northeastern Chukchi Sea in 2008–2010 as part of a multi-year, interdisciplinary study. We sampled 3 study areas, each ~3,000 km^2, located in the offshore northeastern Chukchi Sea: Klondike, Burger, and Statoil. We quantified the marine habitat by measuring strength of stratification, depth of the mixed layer, and temperature and salinity in the upper mixed layer. The total density of seabirds was highest in 2009, when warm (5–6 °C), moderately saline (31–31.5) Bering Sea Water (BSW) extended across Burger and Klondike at all depths. Bird density was generally higher in Klondike than in Burger in 2008 and 2009; densities did not differ significantly among study areas in 2010, when BSW covered all 3 study areas. The relative abundance of alcids in all study areas combined increased from 2008 to 2010. Klondike was numerically dominated by alcids and tubenoses in all years, whereas Burger was numerically dominated by larids and tubenoses in 2008 and by alcids in 2009 and 2010; Statoil also was numerically dominated by alcids in 2010. Least auklets, crested auklets, and northern fulmars were positively associated with strong stratification and high salinity (>31) in the upper mixed layer, characteristics that indicated the presence of BSW. Phalaropes were positively associated with salinity but negatively associated with stratification, suggesting that well-mixed water provides better foraging opportunities for these surface-feeding planktivores. The distribution and abundance of marine birds, particularly the planktivorous species, is influenced by advective processes that transport oceanic species of zooplankton from the Bering Sea to the Chukchi Sea. This transport apparently differed among years and resulted in a broader northeastward intrusion of Bering Sea Water and greater total abundance of planktivorous seabirds in the region in 2009 than in 2008 or 2010.

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1.2 Introduction

The seasonally ice-covered Chukchi Sea shelf is among the largest continental shelves in the world. It also is highly productive, although much of the primary production and zooplankton biomass can be attributed to the northward flow of nutrient-rich oceanic water that originates far to the south, in the basin of the Bering Sea (Springer and McRoy, 1993; Grebmeier et al., 2006). This influx of nutrients and oceanic plankton sustains a marine-bird community that would otherwise have little prey available (Springer et al., 1989). Despite an understanding of the importance of advection to the food web of the Chukchi Sea, questions remain about the spatial and temporal scales of processes that link the Bering and Chukchi ecosystems (Springer et al., 1996). Seasonal and interannual changes in advection may have profound effects on the distribution and abundance of non-breeding, staging, and migratory birds that rely on marine resources during the open-water season (June to mid-October). These relationships between community structure and oceanography must be explored if marine birds are to serve as informative indicators of ecosystem change (Piatt et al., 2007).

Descriptions of the avifaunal communities of the northeastern Chukchi Sea are rare and tend to focus on a few species of interest (e.g., Divoky, 1976), rather than considering all of the bird species that feed in the marine environment during the open-water season (e.g., waterfowl, loons, phalaropes, larids [gulls and terns], procellariids, and alcids). Attention to the marine-bird community elsewhere in the Chukchi Sea has been focused primarily on the breeding colonies at Cape Lisburne and Cape Thompson (Springer et al., 1984; Springer et al., 1989) and on summarizing data collected at sea south of 69° 30’ N (Divoky and Springer, 1988; Piatt and Springer, 2003). Recent efforts to describe the circumpolar species diversity and distribution of marine birds do not include regionally important taxa such as auklets and phalaropes (Bluhm et al., 2011; Huettmann et al., 2011), that are critical to understanding energy flow in this ecosystem (Piatt and Springer, 2003).

Marine-birds can display habitat preferences for water masses and water-column structure that enhance the abundance and the accessibility of prey (Haney, 1991; Elphick and Hunt, 1993; Piatt and Springer, 2003). For example, in the northern Bering Sea and Bering Strait, bird species that rely primarily on zooplankton such as euphausiids and copepods (hereafter referred to as planktivorous species) include least (*Aethia pusilla*), and crested auklets (*A. cristatella*) and typically are associated with oceanic Anadyr Water (Springer et al., 1987;

Elphick and Hunt, 1993; Piatt and Springer, 2003). In contrast, species that primarily rely on fish such as black-legged kittiwakes (*Rissa tridactyla*) and thick-billed murres (*Uria lomvia*) typically are associated with Bering Shelf Water and Alaskan Coastal Water (Springer et al., 1987; Elphick and Hunt, 1993; Piatt and Springer, 2003). Bird species that are more flexible in their foraging requirements, however, may also be more flexible in their habitat relationships. Short-tailed shearwaters (*Puffinus tenuirostris*) can consume euphausiids, shrimp, and fish (Hunt et al., 2002) and are found in all water masses of the northern Bering and southern Chukchi seas (Piatt and Springer, 2003). Within water masses, species often are segregated spatially to exploit those hydrographic features that best meet their specific foraging ecology (Haney, 1991; Russell et al., 1999; Piatt and Springer, 2003). Hence, understanding the mechanisms that link the seabird community to the marine habitat in the northeastern Chukchi Sea requires quantifying both water-mass characteristics (e.g., temperature, salinity) and water-column structure.

Historical studies conducted in the late 1970s and early 1980s provided a snapshot of the community composition and density of seabirds in the northeastern Chukchi Sea (Divoky, 1987) but did not address the variability of this community or link species to their habitat. In this study, we employed a systematic survey design to quantify the temporal variability in the marine-bird community and relate it to the physical oceanography of the northeastern Chukchi Sea. The objectives of this study were to: (1) describe seasonal, spatial, and interannual variation in the distribution, abundance, and community composition of marine birds; (2) describe seasonal, spatial, and interannual variation in physical oceanography; and (3) explore relationships between the abundance of 8 marine-bird species and the hydrographic structure of their habitat.

1.3 Study area

In the Chukchi Sea, the net flow of water is northward through Bering Strait and toward the Arctic Ocean (Coachman et al., 1975). The broad northward flow through Bering Strait is steered by bathymetry into three main branches—one east of Hanna Shoal that feeds into Barrow Canyon, one west of Herald Shoal that feeds into Herald Valley, and one between the two shoals, referred to as the Central Channel flow (Fig. 1.1; Weingartner et al., 1998, 2005). This separation also is evident in water-mass properties (Woodgate et al., 2005). Within the Chukchi Sea, the Alaska Coastal Current (ACC) lies east near the Alaska coastline and flows northward, carrying Alaskan Coastal Water (ACW), a warm (>2 °C), low-salinity (<32.2) water mass that originates south of Bering Strait. The currents farther offshore move Bering Sea Water (BSW; Coachman et al., 1975), a warm (>2 °C), high-salinity (>32.4) water mass, northward through the Central Channel and Herald Valley (Weingartner et al., 2005). This BSW is a mixture of Anadyr Water and Bering Shelf Water from south of Bering Strait, so it has a higher nutrient content and transports greater numbers of oceanic zooplankton than does ACW (Walsh et al., 1989; Springer and McRoy, 1993).

In addition to these water masses that are advected northward, water in the Chukchi Sea is modified during the fall and winter by ice formation and during the spring by ice melt. As is the case with ACW, cold (–1 to + 2 °C), low-salinity (<30) Meltwater (MW) is depleted of nutrients and large oceanic zooplankton. In the summer, the bottom half of the water column usually still contains cold (–2 to +1 °C), salty (>32) Winter Water (WW) left over from the previous winter, whereas the surface layer consists of either MW or BSW. This stratification increases from spring to summer and typically erodes in the fall as strong winds, cooling, and freezing enhance vertical mixing (Weingartner et al., 2005).

This study was conducted in the northeastern Chukchi Sea, in a region extending ~110–180 km west of the village of Wainwright, off of the northwestern coast of Alaska and included 3 study areas that are of interest for oil and gas exploration: Klondike, Burger, and Statoil (Fig. 1.1). The Klondike study area was located on the eastern side of the Central Channel and nearest the inflow of BSW, whereas the Burger study area was located to the northeast of Klondike and on the southern slope of Hanna Shoal. The Statoil study area was located to the north of both Klondike and Burger; its western edge was near to the Central Channel and its eastern half lay on the southern slope of Hanna Shoal. The ACC flows east of all 3 study areas, exiting the area via Barrow Canyon, whereas the Central Channel flow passes over or just west of Klondike and Statoil.

1.4 Methods

1.4.1 Data collection

We conducted research cruises during 3 seasons in 2008–2010 that covered the entire open-water period of the northeastern Chukchi Sea (Fig. 1.2): late summer (hereafter "Jul/Aug"), early fall (hereafter "Aug/Sep"), and late fall (hereafter "Sep/Oct"). The Klondike and Burger study areas consisted of boxes that were ~56 km on a side (Fig. 1.1). The Statoil box was configured to encompass several Statoil oil-lease blocks and had the same total area as Klondike and Burger. These ~3,000-km² study-area boxes were the primary focus of all sampling. We conducted line-transect surveys for birds along a series of parallel survey lines that ran north–south through the study areas. The sampling grid included lines on the eastern and western boundaries of each study area and lines spaced ~1.8 km apart within each study area, creating a set of 31 parallel survey lines in Klondike and Burger that were ~56 km long each. Because the Statoil box was not square, its survey lines were of variable length, ranging from 42 to 56 km. We surveyed continuously when the ship was moving along a straight-line course at a minimal velocity of 9.3 km h^{-1} (5 kt; Tasker et al., 1984; Gould and Forsell, 1989) and recorded environmental conditions every 10 minutes. We collected data 9–12 h day^{-1} during daylight hours, weather and ice conditions permitting. We generally stopped surveys when sea height was Beaufort 6 (seas ~2–3 m) or higher, although we occasionally continued to sample if observation conditions were still acceptable (e.g., if seas were at the lower end of Beaufort 6 and we were traveling with the wind and seas). One observer stationed on the bridge of the vessel recorded all birds seen within a radius of 300 m in a 90° arc from the bow to the beam on one side of the ship (the count zone), locating and identifying seabirds with 10X binoculars as needed. For each bird or group of birds, we recorded species, total number of individuals; distance from the observer when sighted (in 50-m bins), and radial angle of the observation from the bow of the ship.

In the count zone, we counted all birds on the water, taking care to avoid recounting the same individuals. For flying birds, however, we conducted scans for them ~1 time min^{-1} (the exact frequency varied with ship's speed) and recorded an instantaneous count (or "snapshot") of all birds flying within the count zone. The snapshot method reduces the bias of overestimating the density of flying birds (Tasker et al., 1984; Gould and Forsell, 1989). We counted only those flying birds that entered the count zone from the sides or front and excluded flying birds that entered from behind the ship (i.e., an area that already had been surveyed) to avoid the possibility of counting ship-following birds.

We entered all data directly into a computer connected to a global positioning system (GPS) with DLog software (R. G. Ford Consulting, Portland, OR) in 2008 and TigerObserver software (TigerSoft, Las Vegas, NV) in 2009 and 2010. These programs time-stamped and geo-referenced every observation.

Within each study-area box, we surveyed the hydrography at a series of 25 stations that were fixed in a grid with ~13.8-km (7.5-NM) spacing. We collected data with a Seabird SBE-19+V2 CTD sampling at 4 Hz that was lowered through the water-column at a rate of ~0.5 m sec^{-1}. Measured variables included pressure, temperature, and conductivity, which then were converted to depth, temperature (±0.005 °C), and salinity (±0.02).

1.4.2 Data analyses

Marine-bird distribution and abundance

We analyzed trends in the seasonal distribution and abundance of a suite of 8 ecologically diverse species that represented a variety of prey preferences and foraging methods, thereby providing a comprehensive view of the seabird community as a whole. We estimated corrected densities (birds km^{-2}) within each study area by using line-transect sampling analyses available in the program DISTANCE 6.0 Release 2 (Thomas et al., 2010) and followed analytical methods described by Buckland et al. (2001, 2004). This approach accounts for the decrease in probability of detecting a bird with increased distance from the survey line. These corrected density estimates were calculated with the formula:

$$\hat{D} = \frac{n \cdot \hat{E}(s)}{L \cdot \hat{P}_c}$$

where $\widehat{D}$ is the corrected density estimate, n is the total number of observations seen on transects, $\hat{E}(s)$ is the mean flock size, L is the total length of survey lines sampled, and $\hat{P}_c$ is the probability of detection estimated by the model (Buckland et al., 2001).

Each focal species had >350 observations total, which provided enough data to model the probability of detection with confidence. We pooled species of similar size, conformation, and detection probability into detection groups as follows: small alcids (crested auklets, least auklets), light-colored large birds (black-legged kittiwakes, glaucous gulls [*Larus hyperboreus*], northern fulmars [*Fulmarus glacialis*]), and phalaropes (red-necked [*Phalaropus lobatus*] and red [*P. fulicarius*] phalaropes, which are difficult to distinguish during this period and are treated hereafter collectively). We modeled detection functions for short-tailed shearwaters and thick-billed murres individually because preliminary examination of the perpendicular-distance histograms suggested that their respective detection probabilities were different from those of other focal species. All shearwaters we identified were short-tailed shearwaters; in addition, no other *Puffinus* spp. are known to occur north of Bering Strait (Kessel and Gibson, 1978).

We calculated perpendicular sighting distances from the radial angle of observation and the maximal value of the corresponding detection-distance bin after truncating all data at 250 m, following procedures recommended by Buckland et al (2001). For each detection group, we fitted models that used 1 of 2 possible key functions (half-normal or hazard-rate) to the distribution of perpendicular distances to find the model that best estimated the probability of detection. We included covariates in the model sets to account for possible differences in detection among observation platforms (i.e., vessel), observers, and sea-surface conditions (measured on the Beaufort scale). The fit of each model was assessed with Akaike's Information Criterion (AIC), diagnostic plots, and a Kolmogorov–Smirnov goodness-of-fit test (following Buckland et al., 2004). For each detection group, we regressed log (observed flock size) against estimated detection probability to test for "size bias" (i.e. the tendency to observe more large flocks at large distances). In all cases, the regression slope was not significantly different from zero ($P > 0.10$), so we used mean observed flock size as an estimate of $\hat{E}(s)$.

Once a detection model was selected for a detection group (Table 1.1), we calculated species-specific corrected density estimates by running separate analyses that filtered for each species and then applied the group detection probability to the uncorrected estimates. We calculated corrected densities of each species by study area, season, and year. We calculated variances with the delta method and calculated log-normal, z-based, two-sided 95% confidence intervals for the estimates of density with equations 3.71–3.74 in Buckland et al. (2001). This method assumed that encounter-rate estimates were independent of detection probabilities among years, seasons, and study areas and pooled estimates of $\hat{P}_c$ and $\hat{E}(s)$ by covariates.

We used ANOVAs to examine differences in bird densities between the Klondike and Burger study areas, among seasons, and among years for each species. We examined the seasonal trend in bird densities at Statoil in 2010 but did not include Statoil in the ANOVA analysis because it was surveyed only twice and only in 2010. We report mean values as ± 95% confidence interval (CI) unless otherwise stated. In all statistical tests, the level of significance (α) was 0.05. All distance sampling and ANOVA analyses were conducted with the statistical software R 2.13.0 (http://www.r-project.org).

We also used the geo-located observations to generate maps of distribution and abundance for individual species of interest. First, we assigned the density value of each transect to its respective transect centroid coordinate. We then used the inverse-distance-weighted (IDW) interpolation technique of the Spatial Analyst extension of ArcMap GIS software (Environmental Systems Research Institute, Inc., Redlands, CA) to generate contours of similar density, based on the mean density for each grid-cell centroid. To conduct the IDW analysis, we first overlaid a 1,000 × 1,000-m grid over the study area. The IDW interpolation technique calculated the distance-weighted mean density of up to 9 centroids within 7,000 m of each 1,000-m pixel in the study area. This analysis produced contoured portrayals of bird densities on maps within each of the 3 study areas.

Seabird community analysis

For the analysis of community composition, we included all bird observations that were identified at least to family. We summarized seabird species-composition by study area, season, and year (Magurran, 2004). We aggregated individual species into 6 taxonomic species-groups prior to analysis to simplify the interpretation and presentation of results: waterfowl (family Anatidae, including geese, swans, and ducks), loons (family Gaviidae), tubenoses (family Procellariidae, including fulmars and shearwaters), phalaropes (shorebirds of the family Scolopacidae that spend most of their lives on the ocean), larids (families Laridae and Stercorariidae, including gulls, terns, and jaegers), and alcids (family Alcidae, including murres, dovekies [*Alle alle*], guillemots, murrelets, auklets, and puffins).

We used multivariate analyses and descriptive statistics to explore seasonal and interannual changes in the structure of the seabird community. We grouped the data into sample units by study area, season, and year, then used ordination for analysis of the 2008–2010 seabird data from all study areas. We used the taxonomic species-groups to calculate a Bray–Curtis similarity matrix (Bray and Curtis, 1957) to which we applied non-metric multidimensional scaling (MDS; Clarke and Green, 1988). This ordination technique visualizes the similarity in community composition among samples as distances mapped in 2-dimensional space (Clarke and Green, 1988). Finally, we determined the dominant species assemblages composing each sample. The MDS analysis was conducted with the package ‘vegan’ (Oksanen et al., 2011) in R.

Physical oceanography

We processed data from CTD downcasts according to the manufacturer's recommended procedures (SBE Data Processing manual) and further screened for anomalous spikes, dropouts, and density inversions. We averaged data from the vertical profiles to 1 dbar (~ 1 m) to examine seasonal and interannual variations in the characteristics and distribution of water masses over our study areas. For each survey, we plotted CTD data as vertical sections along transects that extend from southwest to northeast and across the Klondike and Burger study areas. These transects were selected because they compose the broadest possible coverage from the survey cruises in all 3 years. For data collected in 2010, we also examined plots of salinity and temperature averaged over the mixed layer and contoured by latitude and longitude to compare Klondike, Burger, and Statoil.

Habitat associations

We used generalized linear models (GLMs) to examine the relationship between hydrography and seabird abundance for each of the 8 focal species. We quantified the structure of the water column with 4 explanatory variables: depth of the mixed layer (meters), strength of stratification (calculated as the maximal value of change in density m^{-1} [$\delta\rho/\delta z$]), average temperature of the mixed layer, and average salinity of the mixed layer (Fig. 1.3). These values were averaged from 25 fixed stations within each study area in each season and year.

Models were specified as negative binomial with a log-link to meet the assumptions of normality and account for overdispersion in the data (Zuur et al., 2009). We examined the correlation coefficients and variance inflation factors (VIF) of the explanatory variables for collinearity (Zuur et al., 2009). All correlation coefficients were <0.50, and all VIF were <3, indicating no collinearity. We assessed model adequacy with plots of residuals, normal probability, and Cook's distance.

We constructed a model set for each species that included all possible additive combinations of the 4 oceanographic variables that describe the characteristics of water-masses in this region (Table 1.2). We also included a model specifying constant abundance to confirm that significant variation in abundance was explained by the other models in the candidate set. All models included an offset term of log (effective area surveyed [i.e., transect length*transect width*$\hat{P}_c$]) to account for survey effort and the species-specific probability of detection (Hedley et al., 2004). Models were weighted based on the difference between each model's AIC_c value and that of the top-ranked model, and the weights were normalized to sum to 1 over all models considered (Burnham and Anderson, 2002). The model with the lowest AIC_c value was selected as the best approximating model given the data, and models within 2 AIC_c units of the top-ranked model were considered well supported by the data for drawing inferences (Burnham and Anderson, 2002). We used model-averaged estimates from the candidate model set ($\Delta\ AIC_c \leq 2$) to draw inference about variation in seabird abundance. Model-averaged estimates and unconditional standard errors account for model selection uncertainty (Burnham and Anderson, 2002). All GLM analyses were conducted with the package MASS (Venables and Ripley, 2002) in R.

1.5 Results

1.5.1 Marine-bird distribution and abundance

Seabirds were more abundant overall in 2009 than they were in 2008 or 2010 (Table 1.3). In 2008, we estimated a total of 80,200 birds (95% CI: 68 300–94,300 birds) of 31 species during all surveys combined. In 2009, we estimated a total of 537,800 birds (95% CI: 474,300–609,900 birds) of 24 species during all surveys combined. In 2010, we added the Statoil study area and estimated a total of 217,300 birds (95% CI: 196,200–240,600 birds) of 29 species during all surveys combined.

Planktivorous birds

Crested auklets were the most abundant species recorded in all 3 years of the study (Fig.1.4). Densities differed significantly among seasons and between study areas in all 3 years ($P < 0.001$ for STUDY AREA*SEASON*YEAR). Crested auklets were more abundant in Klondike than in Burger in 2008, more abundant in Burger than in Klondike in 2009, and not significantly different among study areas in 2010 (Fig. 1.4). Least auklet densities also differed significantly between study areas and among seasons in all 3 years ($P < 0.001$ for STUDY AREA*SEASON*YEAR). Densities of least auklets were higher in Klondike than in Burger in all 3 seasons of 2008, but there was no consistent trend in other years (Fig. 1.4). Phalarope densities differed significantly between study areas and among seasons in all 3 years ($P < 0.001$ for STUDY AREA*SEASON*YEAR). Phalaropes were seen in patchy, dispersed feeding flocks, primarily in Aug/Sep and Sep/Oct in 2008, in Jul/Aug and Aug/Sep in 2009, and in Aug/Sep in 2010 (Fig. 1.4).

Piscivorous birds

Black-legged kittiwake densities differed significantly between study areas and among seasons (*P* < 0.001 for STUDY AREA*SEASON). They were distributed widely, occurring in both study areas and in all 3 seasons during 2008 and 2009 (Fig. 1.5). In 2010, Black-legged kittiwakes occurred in all 3 study areas in Jul/Aug and Aug/ Sep but were absent from Burger in Sep/Oct (Fig. 1.5). Thick-billed murre densities were consistently higher in Klondike than in Burger and were lowest in Sep/Oct in all years (*P* < 0.001 for STUDY AREA and SEASON; Fig. 1.5). In 2010, densities of thick-billed murres in Burger and Statoil were lower than densities in Klondike and followed a similar seasonal pattern of decline from Jul/Aug onward; densities in Burger approached zero in Sept/Oct.

Omnivorous birds

Short-tailed shearwaters were the second-most-abundant species in all 3 years of the study. Their densities differed significantly between study areas and among seasons in all 3 years (*P* < 0.001 for STUDY AREA*SEASON*YEAR). They generally were more abundant in Klondike than in Burger in 2008 and 2009 but were not significantly different among study areas in 2010 (Fig. 1.6). In all years, short-tailed shearwaters were most abundant in Aug/Sep (Fig. 1.6). Northern fulmar densities varied among seasons and years (*P* < 0.001 for SEASON*YEAR). They were significantly more abundant in Klondike than in Burger in 2008 (Fig. 1.6), but densities did not differ significantly among study areas in 2009 or 2010. Glaucous gull densities differed significantly among study areas, seasons, and years ($P \leq 0.01$ for STUDY AREA*SEASON*YEAR). Like short-tailed shearwaters, they also were widespread, occurring in all study areas and in all seasons surveyed except for Klondike in Jul/Aug 2009 (Fig. 1.6).

1.5.2 Community analysis

We recorded a total of 34 species in these study areas during 2008–2010 (Appendix A). Multivariate analyses of the seabird community indicated that species composition varied primarily among years and showed a consistent pattern of seasonal change. The MDS ordination separated into 3 groups, with some overlap (misclassification) of study areas by season and year (Fig. 1.7). The stress coefficient of the ordination was 0.09, indicating a good fit to the data (Clarke and Ainsworth, 1993).Samples from 2008 and 2010 represented distinct groups with little overlap (Fig. 1.7A). In contrast, 2009 overlapped both of the other years in Jul/Aug and

Sep/Oct but showed a distinct community structure in Aug/Sep. When the points in the MDS ordination were grouped by season, there was a shift in community composition from Jul/Aug to Aug/Sep; then, the community structure shifted back toward the Jul/Aug structure in Sep/Oct (Fig. 1.7B). Much of this pattern was driven by the extreme seasonal changes in species composition in Burger during 2008 (Fig. 1.8).

The patterns in species composition identified in the multivariate analyses were reflected in changes in the relative abundance of each of the 6 species-groups among study areas, seasons, and years (Fig. 1.8). Most notably, the relative abundance of alcids in all study areas combined increased from 2008 to 2010. Klondike was dominated numerically by alcids (primarily crested auklets) and tubenoses (primarily short-tailed shearwaters) in all years. Burger was dominated numerically by larids (primarily black-legged kittiwakes) and tubenoses in 2008, but alcids were most abundant in 2009. In 2010, alcids were the most abundant species-group in all 3 study areas and in all seasons, composing 65–88% of all birds. Waterfowl and loons were the least common species-groups and consisted primarily of flocks of long-tailed ducks (*Clangula hyemalis*) and pacific loons (*Gavia pacifica*), respectively.

1.5.3 Physical oceanography

In all years, warm, moderately saline Bering Sea Water (BSW) flowed northward into the vicinity of the study areas, gradually replacing the cold, saline Winter Water (WW) formed during the previous winter and sharing the surface layer with cold, fresh Meltwater (MW; Fig. 1.9 and 1.10). This WW was representative of the entire water column during the winter and was modified in the upper layer during the spring and summer by ice melt and advection. The timing and extent of the advection, as indicated by increases in the temperature (Fig. 1.9) and salinity (Fig. 1.10) of the upper mixed layer, varied among study areas and years. In all years, the salinity and temperature were higher over Klondike than over Burger, indicating that BSW always was present. In contrast, MW was present over Burger in all years, although its spatial extent varied widely among years (extensive in 2008, restricted to the northeastern corner in 2009, and restricted to the northeastern half in 2010).

The interannual variation in marine habitat characteristics was most apparent during Aug/Sep. In 2008, temperatures in the upper mixed layer ranged from 3.5 °C on the western edge of Klondike to 0–2 °C over Burger, with a front clearly visible between the two study areas (Fig.

1.9; top row, middle panel). In 2009, the mixed layer was nearly homogenous across both study areas, with a slight decrease in temperature from 5.5 °C to 4.5 °C (Fig. 1.9, middle row, middle panel) and a gradual decrease in salinity from 31.5 to 30 from the southwestern corner of Klondike to the northeastern corner of Burger (Fig. 1.10, middle row, middle panel). In 2010, temperatures over Klondike (6–8 °C) were twice those over Burger (3–4 °C), with values in Statoil spanning the range between the other 2 study areas (3–6 °C; Fig. 1.9, bottom row, middle panel).

Vertical sections of density indicate that the strength and depth of stratification varied considerably among years and study areas (Fig. 1.11). Stratification was strong throughout 2008 and moderate in 2010, with the pycnocline at ~20–25 m. In 2009, the pycnocline was weaker and deeper (~30 m) than in the other years. Klondike was consistently less stratified than Burger (Fig. 1.11), because Burger contained more low-salinity MW in the upper half of the water column and more high-salinity WW in the lower water column than Klondike did.

1.5.4 Habitat associations

Alcids (3 species), phalaropes, and northern fulmars were associated with distinct oceanographic habitats (Fig. 1.12). The best-fitting models for these 5 taxa included strength of stratification, and models for 4 of these taxa also included average salinity of the upper mixed layer (Table 1.4). The best-fitting models for crested auklets and thick-billed murres also included average temperature of the mixed layer. In all cases, the parameter values in the best-fitting models were significantly different from zero. The best-fitting models for these 5 taxa also included mixed-layer depth, but the parameter estimates were not significantly different from zero, indicating that this variable was not a strong predictor of seabird abundance. The best-fitting models for short-tailed shearwaters, black-legged kittiwakes, and glaucous gulls, indicated that none of the environmental variables significantly explained variation in abundance of these species.

Due to the uncertainty in model selection, we relied on model-averaged parameter estimates and confidence intervals to draw inferences about the relationship between each environmental variable and seabird abundance (Burnham and Anderson, 2002). Strength of stratification was the best predictor of abundance for 5 of the taxa (Fig. 1.12). Least auklets, crested auklets, thick-billed murres, and northern fulmars were positively associated with strength of stratification, whereas phalaropes were negatively associated with it (Fig. 1.12). Salinity was positively associated with the abundance of 4 taxa: least auklets, crested auklets, phalaropes, and northern fulmars. Temperature was positively associated with the abundance of thick-billed murres. The depth of the mixed layer was not associated with the abundance of any species.

1.6 Discussion

1.6.1 Bering Sea Water boundary region

We propose here that the oceanography differs among the 3 study areas seasonally and interannually (see also Weingartner et al., 2013) and that these differences create spatial and temporal differences in the structure of the seabird community in the northeastern Chukchi Sea. The movement of oceanic water northward through Bering Strait influences the patterns of productivity throughout the Chukchi Sea (Grebmeier et al., 2006). *In-situ* primary production in the Bering Sea Water (BSW) near Bering Strait is on the order of ~470 g C m^{-2} yr^{-1}, whereas production in the northern Chukchi Sea generally is on the order of ~80 g C m^{-2} yr^{-1} (Sambrotto et al., 1984; Hansell et al., 1989; Hill et al., 2005). The BSW also advects large oceanic zooplankton into the area from the Bering Sea Basin (Grebmeier et al., 2006), and these large zooplankton can graze much of the phytoplankton when they are present. In contrast, shelf zooplankton associated with resident waters typically do not significantly graze much of the primary production, which falls to the bottom and nourishes a high-biomass, diverse benthic community (Feder et al., 1994; Grebmeier et al., 2006; Blanchard et al., this volume a, this volume b).

In the southern Chukchi Sea, an oceanographic front between BSW and Alaskan Coastal Water (ACW) is the defining feature that separates distinct benthic communities (Grebmeier et al, 2006; Bluhm et al., 2009), with higher biomass and bivalve abundance under BSW and lower biomass under ACW. In our study areas, communities also are structured by processes associated with a front at times, but the water masses involved are different from those found farther south. Despite the shallow bathymetry, our study areas straddle a region that resembles the interface found at a shelf break in that there is a transition from a stream of oceanic water entrained in the Central Channel to a 2-layer water column with little transport trapped over Hanna Shoal.

In terms of the fate of primary production, Klondike appears to be a more pelagic-dominated system than Burger, with a transition between these two states falling between the study areas (Day et al., this volume). This transition zone is seen clearly in Statoil, which was added to the study in 2010 and spans the longitudes between Klondike and Burger. The gradient in seabird community structure is oriented east–west at the mesoscale of these study areas (10s–100s km), rather than north–south and is consistent with observations from the southern Chukchi Sea (Piatt and Springer, 2003; Grebmeier et al. 2006). As evident in the plots of temperature and salinity, the Central Channel flow was visible along the western edge of the Klondike study area throughout the open-water season of 2008, and much of that study area was dominated by its associated water mass—BSW. In contrast, the surface of Burger had no strong current flow and was dominated by Meltwater at the surface and Winter Water on the bottom (i.e., it functioned more as shelf or coastal water than as oceanic water). This oceanographic boundary between the 2 study areas shifted to the northeast in 2010, a warmer year when the pack ice retreated almost entirely before the start of our sampling. In that year, the water-column structure indicated that BSW dominated the upper mixed layer in Klondike in Jul/Aug and expanded toward the northeast, into Burger and Statoil, in Aug/Sep. These oceanographic distinctions between the Klondike and Burger study areas were least apparent in 2009, the warmest year of the study, when the water-column was essentially BSW down to 30 m and across most of both study areas (Weingartner et al., 2013). In that year, the boundary between water advected that summer and water modified during the preceding winter was located in the northeastern corner of the Burger study area when we began sampling in early August.

1.6.2 Variations in marine-bird abundance and community structure

The distribution of seabirds, particularly the planktivorous species, is influenced in the northeastern Chukchi Sea by advective processes that transport oceanic species of zooplankton from the Bering Sea. Planktivorous seabirds are most abundant in areas where their prey is concentrated within 20 m of the surface (Hunt et al., 1990; Haney, 1991; Piatt and Springer, 2003), so they are responsive to conditions that make their prey both abundant and accessible. Total seabird abundance was highest in 2009, lowest in 2008, and intermediate in 2010 (Table 1.3); and this variation reflected changes in the location and strength of the boundary between BSW and MW (Figures 1.9 and 1.10), although the connections to zooplankton populations appeared less clear (Questel et al., 2013). The year of lowest total seabird abundance (2008) was associated with the coldest overall water temperatures, weak stratification, late inflow of BSW that did not develop until Sep/Oct, and the lowest biomass of large zooplankton. The year of highest total seabird abundance (2009) was associated with the strongest and earliest intrusion of warm BSW into the study region, but it was accompanied by only intermediate biomass of large zooplankton. The warm BSW established vertical stratification of the water-column in Jul/Aug that persisted until Sep/Oct. Both planktivorous and piscivorous seabird species prefer to forage in areas where the water-column is stratified, concentrating prey (Piatt and Springer, 2003); foraging conditions in 2009 were ideal for these marine predators. The year of intermediate seabird abundance (2010) was associated with later intrusion of BSW, later establishment of stratification during Aug/Sep, and the highest biomass of large zooplankton (e.g., large calanoid copepods and euphausiids). Based on the limited sampling conducted in Burger in Sep/Oct, it appears that the stratification weakened, but persisted; this persistent stratification was reflected in the persistence of substantial numbers of seabirds in the study area. We unfortunately lack information on the vertical distribution of zooplankton to explore these interactions further; consequently, we can only speculate on the mechanisms.

In addition to changes in total abundance, the community composition changed among seasons and years. This seasonal shift is partially dictated by the development of open water. As the ice retreats and foraging habitat becomes available, species move in from foraging areas to the south and from terrestrial breeding areas. Of the colonial seabirds, thick-billed murres, common murres (*U. aalge*), and black-legged kittiwakes nest in large numbers on cliffs along the Chukchi coast as far north as Cape Lisburne and are common offshore during Jul/Aug and Aug/Sep (Divoky, 1987; Kuletz et al., 2008). Species that nest on the tundra, such as phalaropes and jaegers, move out to sea in Aug/Sep and join millions of short-tailed shearwaters that migrate from their breeding grounds in Australia to forage in the Northern Hemisphere during the austral winter (Baduini et al., 2001). Finally, ice-associated gulls such as Ross's gulls (*Rhodostethia rosea*) and ivory gulls (*Pagophila eburnea*) migrate from high-arctic breeding areas in Russia and Canada into the Chukchi Sea as the ice advances southward in the late fall.

The seasonal pattern in species-composition was similar from year to year, with the numerical dominance shifting from primarily alcids in Jul/Aug (except for Burger in 2008) to a mix of auklets, shearwaters, and phalaropes (all of which are primarily zooplankton-feeders) in

Aug/Sep, then shifting back toward the initial composition in Sep/Oct. The same differences in community composition occurred among years, with 2008 (and especially the Burger study area) distinct from the other 2 years, primarily because of the low densities of alcids in that year. Densities of diving species such as alcids and short-tailed shearwaters fluctuated by four orders of magnitude among years, whereas the variation in the density of surface-feeding gulls among years was only one order of magnitude. This fairly consistent contribution from larids among years indicates that most of the variation in the seabird community can be attributed to birds that are primarily planktivorous.

Planktivorous seabirds

The distribution and abundance of individual species of planktivorous seabirds demonstrates the relationship between foraging ecology and foraging habitat as defined by physical oceanography. Crested auklets consume primarily euphausiids (e.g., *Thysanoessa* spp.) and large copepods (e.g., *Neocalanus cristatus*, *Eucalanus bungii*) characteristic of oceanic water (Bédard, 1969; Kitaysky and Golubova, 2000; Gall et al., 2006). Least auklets consume both oceanic and neritic copepods (e.g., *Calanus marshallae*; Hunt et al., 1998; Gall et al., 2006). Crested auklets typically forage at depths up to 25 m (Hunt et al., 1998), whereas, least auklets' small size (~90 g) and physiology restrict their diving to the upper 10–15 m of the water-column (Hunt 1997). Both of these species rely on internal waves to push pycnoclines towards the surface, concentrating prey within their foraging depth (Haney et al., 1991; Hunt et al., 1998). South of Bering Strait, these species occur near fronts between oceanic Anadyr Water and Bering Shelf Water and in stratified water if the upper mixed layer is Bering Shelf Water (Elphick and Hunt, 1993; Hunt, 1997). Our habitat models indicate that the abundance of crested and least auklets was positively associated with stratification, a hydrographic feature that concentrates prey within the water-column (Elphick and Hunt, 1993; Hunt, 1997), and salinity, an indicator of the presence of BSW. The spatial patterns of crested auklet distribution varied among seasons and years, suggesting that the birds were responding to interannual variations in their habitat (Fig. 1.13). In 2008, their distribution was similar to the distribution of BSW and highest in Klondike, whereas, in 2009 and 2010, years when BSW extended over more of the study areas, crested auklets were found in high abundance throughout all of the study areas (Fig.1.13). Oceanographic characteristics associated with crested and least auklets in the northeastern Chukchi Sea are consistent with habitat that maximizes the abundance and accessibility of oceanic copepods.

The distribution and abundance of planktivorous species that feed at or near the surface also reflected their respective foraging strategies. Phalaropes have the most restricted foraging habitat of the planktivorous species we studied; they forage only on the surface and typically are associated with microscale divergence and convergence fronts that concentrate prey within ~0.2 m of the surface (Brown and Gaskin, 1988). Unlike least and crested auklets, the abundance of phalaropes was negatively associated with stratification. Additionally, their distribution was highly clumped, and they were particularly abundant when and where there were filaments of cold water at or near the surface (e.g., Klondike in Aug/Sep 2008, Burger in Jul/Aug 2009).

Piscivorous seabirds

The variation in distribution and abundance of piscivorous species, as indicated by black-legged kittiwakes and thick-billed murres, is probably related to the difference in foraging strategies between these two species. Despite being classified as piscivorous (Piatt and Springer, 2003), black-legged kittiwakes are surface-feeding gulls that will consume both fishes and large zooplankton (Hobson, 1993; Jodice et al., 2006; Iverson et al., 2007), and thick-billed murres are diving alcids that also will consume both fishes and larger zooplankton (Woo et al., 2008). Thick-billed murres occurred almost exclusively in Klondike in all years and disappeared by Sep/Oct of each year. Their abundance was positively associated with stratification, suggesting that they had very restricted foraging habitat that was located primarily in BSW. Black-legged kittiwakes were not associated with any of the oceanographic variables that we examined. They had a consistent seasonal pattern of abundance in Burger in all years, but densities in Klondike tended to be highest when BSW occupied more of Klondike than it did of Burger (Fig. 1.14), suggesting that black-legged kittiwakes were foraging on prey species associated with BSW but may be less restricted in their foraging requirements than are thick-billed murres. These results are consistent with patterns observed in the southeastern Bering Sea, where black-legged kittiwakes were found to be widespread foragers, whereas thick-billed murres foraged close to their breeding colonies (Sigler et al. 2012).

Omnivorous seabirds

The distribution of short-tailed shearwaters did not appear tightly coupled with particular features of the water-column. Short-tailed shearwaters are fairly large seabirds that consume a variety of large zooplankton, in addition to fish and squid (Hunt et al. 2002; Jahncke et al., 2005) and can dive as deep as 70 m to forage (Weimerskirch and Cherel, 1998). The magnitude of interannual variation in the abundance of short-tailed shearwaters during this study was similar to that of primarily planktivorous seabirds, but their seasonal pattern of abundance was consistent among years (i.e., always highest in Aug/Sep; Fig. 1.15), suggesting that they are responding to oceanographic structure at a broader spatial scale than what was sampled in this study.

The distribution and abundance of the other omnivorous species, as characterized by northern fulmars and glaucous gulls, reflected their flexibility in foraging behavior. Both species were present in low densities in all 3 years—densities considerably lower than the high, but variable, densities of planktivorous species—and both were most abundant in 2009, least abundant in 2010, and intermediate in abundance in 2008. Like the planktivorous seabirds, northern fulmars were positively associated with salinity and stratification, perhaps indicating a greater reliance on zooplankton than the generalist short-tailed shearwaters and glaucous gulls; however, they were less abundant in 2010 than in 2008, which was the year of lowest alcid and phalarope abundance. Glaucous gulls were the least abundant of the 8 focal species in our study and showed a consistent seasonal pattern of increasing abundance from Jul/Aug to Sep/Oct in all years. They had no apparent association with oceanographic variables at the scale of the study areas.

Rare species

The presence and absence of species among years also demonstrates the influence of physical oceanography on seabird community structure. In 2008, when water temperatures remained cold until late in the open-water season, we observed ice-associated species such as ivory gulls (*Pagophila eburnea*) and black guillemots (*Cepphus grille*). In 2009, when water temperatures were warm for most of the open-water season, we did not see the ice-associated species, migrating waterfowl (e.g., king eiders [*Somateria spectabilis*], common eiders [*S. mollissima*]), migrating waterbirds (e.g., red-throated loons [*Gavia stellata*]), or species that would be considered at the edge of their range (e.g., dovekies, pigeon guillemots [*Cepphus columba*]); these species were recorded only in 2008 and/or 2010.

Perhaps the most curious presence of a rare species outside of its range was the appearance of Ancient Murrelets (*Synthliboramphus antiquus*) in all 3 study areas in Aug/Sep 2010 and lingering in Klondike and Burger into Sep/Oct 2010. The closest known breeding populations of this small, nocturnal alcid are in the Aleutian Islands, ~1600 km south of the Chukchi Sea, and its winter range is largely unknown (Gaston and Shoji, 2010). There are no records of Ancient Murrelets in the northern Chukchi Sea in the North Pacific Pelagic Seabird Database (USGS, 2010) in the ~35 years of data prior to 2007, and there are few records of these birds north of Bering Strait in the fall (Kessel, 1989). Surveys conducted by the USFWS, however, recorded 68 Ancient Murrelets in the Chukchi Sea in Sep/Oct 2007 (Kuletz et al., 2008), suggesting that this species is an occasional visitor to the region and is common in years when it is present.

1.6.3 Conclusions

The 3 study areas in the northeastern Chukchi Sea collectively have a diverse marine-bird community of more than 30 species and, at times, maximal densities of >60 birds km^{-2} within a study area. There is extensive seasonal and interannual variation in the abundance of the seabirds in this area that is attributable primarily to planktivorous species. The greatest number of birds generally occurs in Aug/Sep (approximately 20 August to approximately 20 September), presumably reflecting a variety of factors that may include the timing of melt of sea ice, seasonal changes in the oceanography of the area, bird migration, nesting phenology and breeding success of birds in the Arctic. Despite this general seasonal trend, there is interannual variation in the timing of species-specific maximal abundance and this variation appears related to the strength and timing of inflow of Bering Sea Water from south of Bering Strait.

The scientific community is moving beyond describing this system to quantifying the spatial and temporal scales of processes in this region. We demonstrated that differences in the seabird community reflect oceanographic differences between Klondike and Burger, with Statoil representing elements of the other 2 study areas (Day et al., 2013). We propose that the Klondike study area is more of a pelagic-dominated ecosystem and the Burger study area is more of a benthic-dominated ecosystem, with Statoil tending to be more pelagic in its western half (that part nearest the Central Channel; similar to Klondike) and more benthic in its eastern half (similar to Burger). Several other components of this multidisciplinary study also suggest a similar structuring of the ecosystem (Blanchard et al., this volume a, this volume b; Questel et al., this volume).

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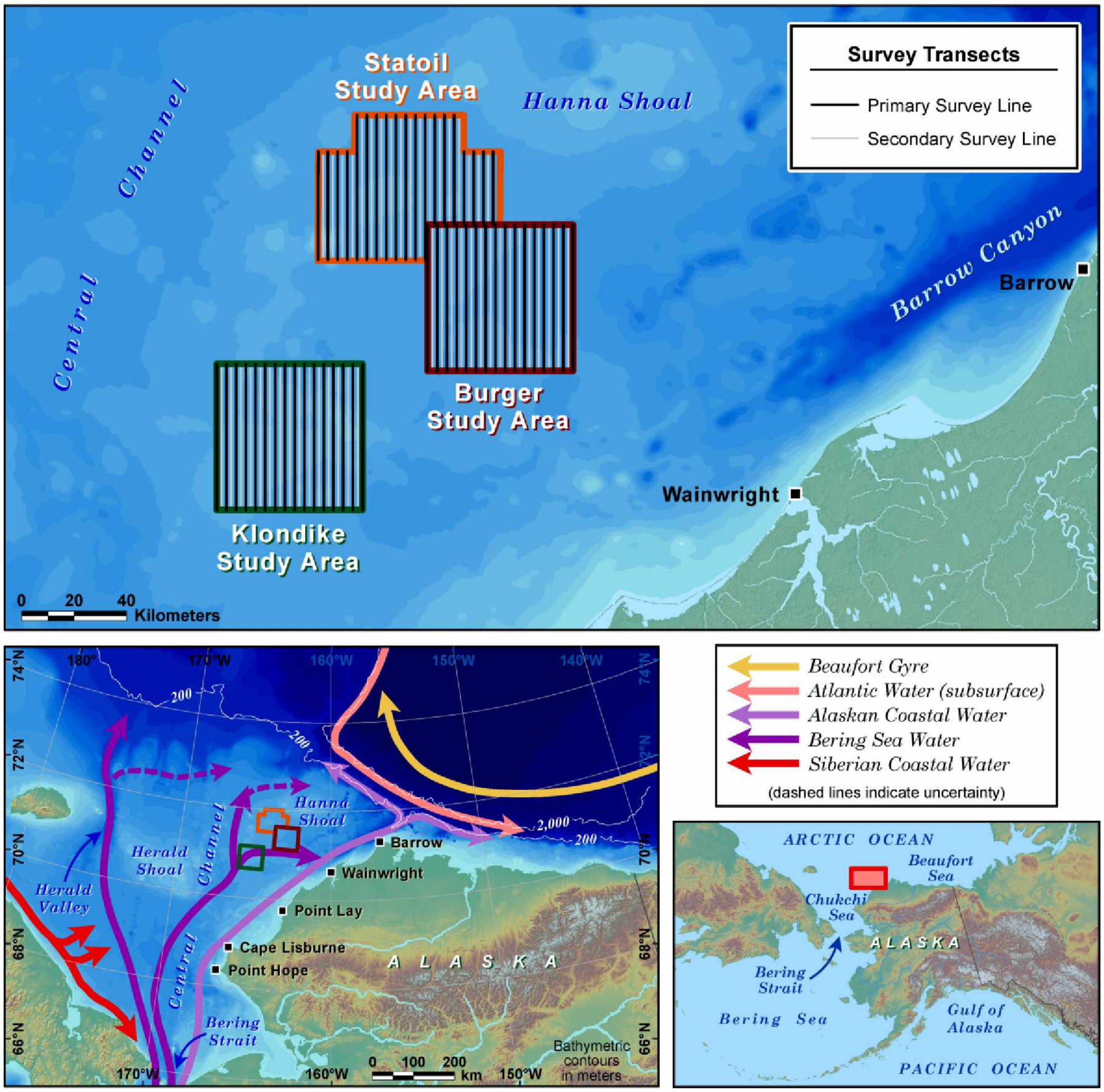

Figure 1.1 Northeastern Chukchi Sea, Alaska, showing main oceanographic features and study-area boxes.

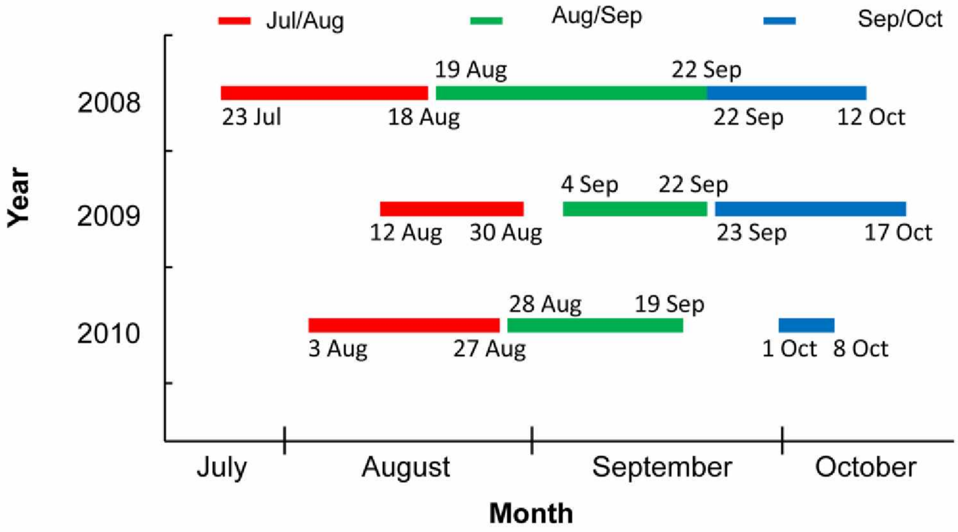

Figure 1.2 Timing of boat-based surveys for marine birds in the northeastern Chukchi Sea, 2008–2010.

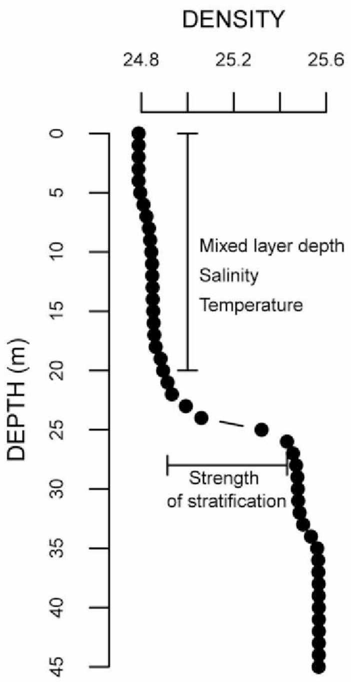

Figure 1.3 Depth profile illustrating the oceanographic variables used to quantify habitat characteristics.

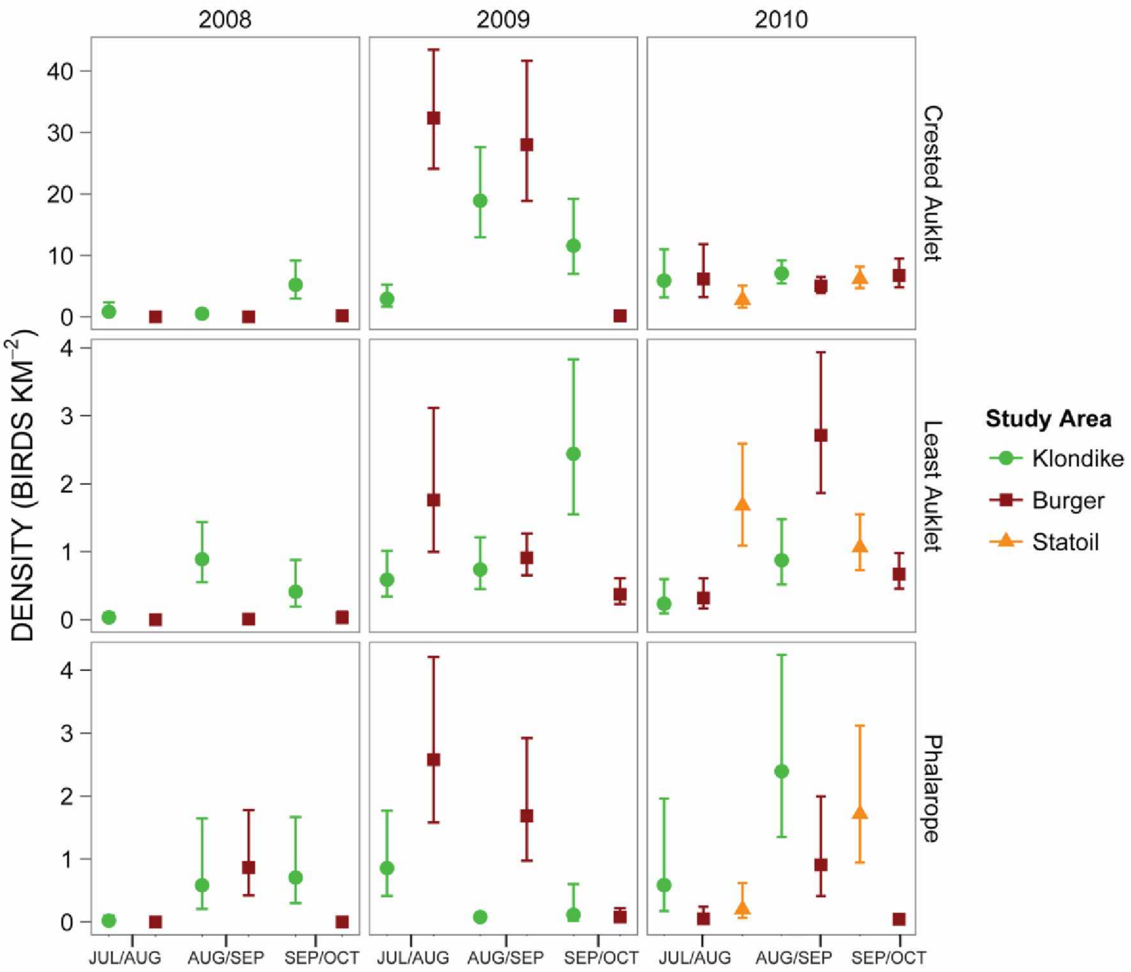

Figure 1.4 Mean density (birds km^{-2}) of crested auklets, least auklets, and phalaropes on transect in the Klondike, Burger, and Statoil study areas in 2008–2010. Error bars represent 95% confidence intervals. Range of values on the y-axis differs among species.

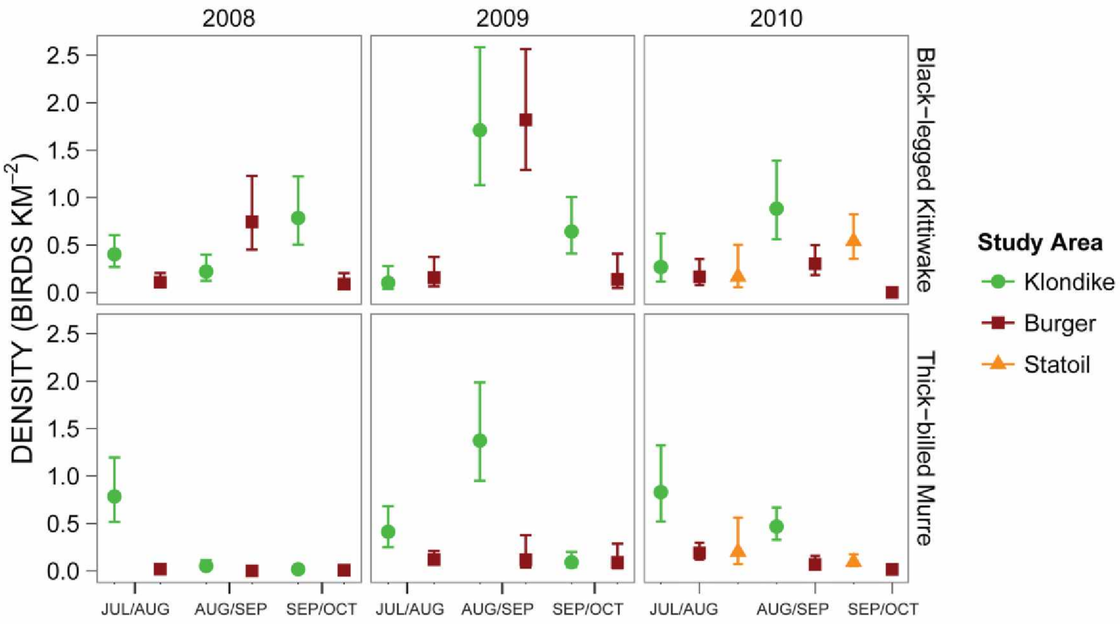

Figure 1.5 Mean density (birds km^{-2}) of black-legged kittiwakes and thick-billed murres on transect in the Klondike, Burger, and Statoil study areas in 2008–2010. Error bars represent 95% confidence intervals.

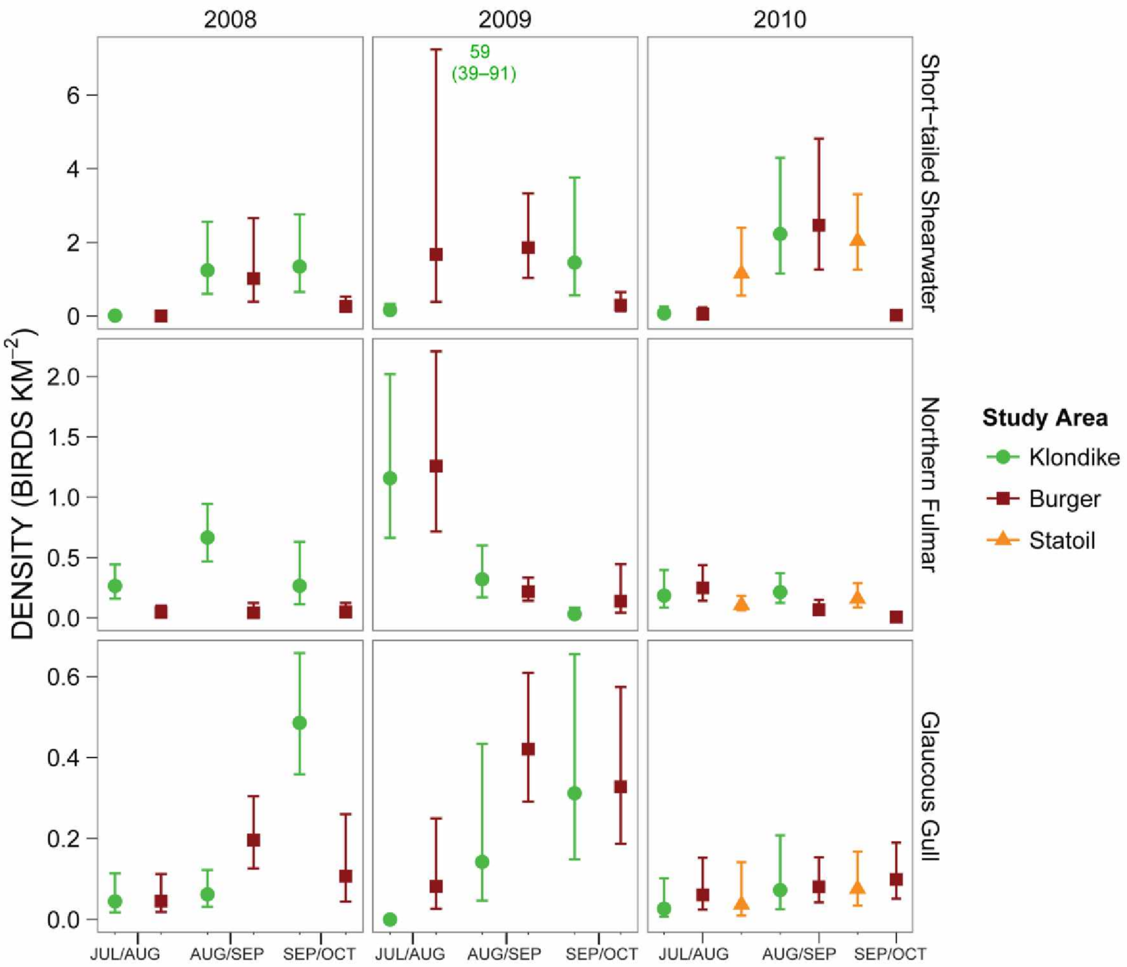

Figure 1.6 Mean density (birds km^{-2}) of short-tailed shearwaters, northern fulmars, and glaucous gulls on transect in the Klondike, Burger, and Statoil study areas in 2008–2010. Error bars represent 95% confidence intervals. Range of values on the y-axis differs among species.

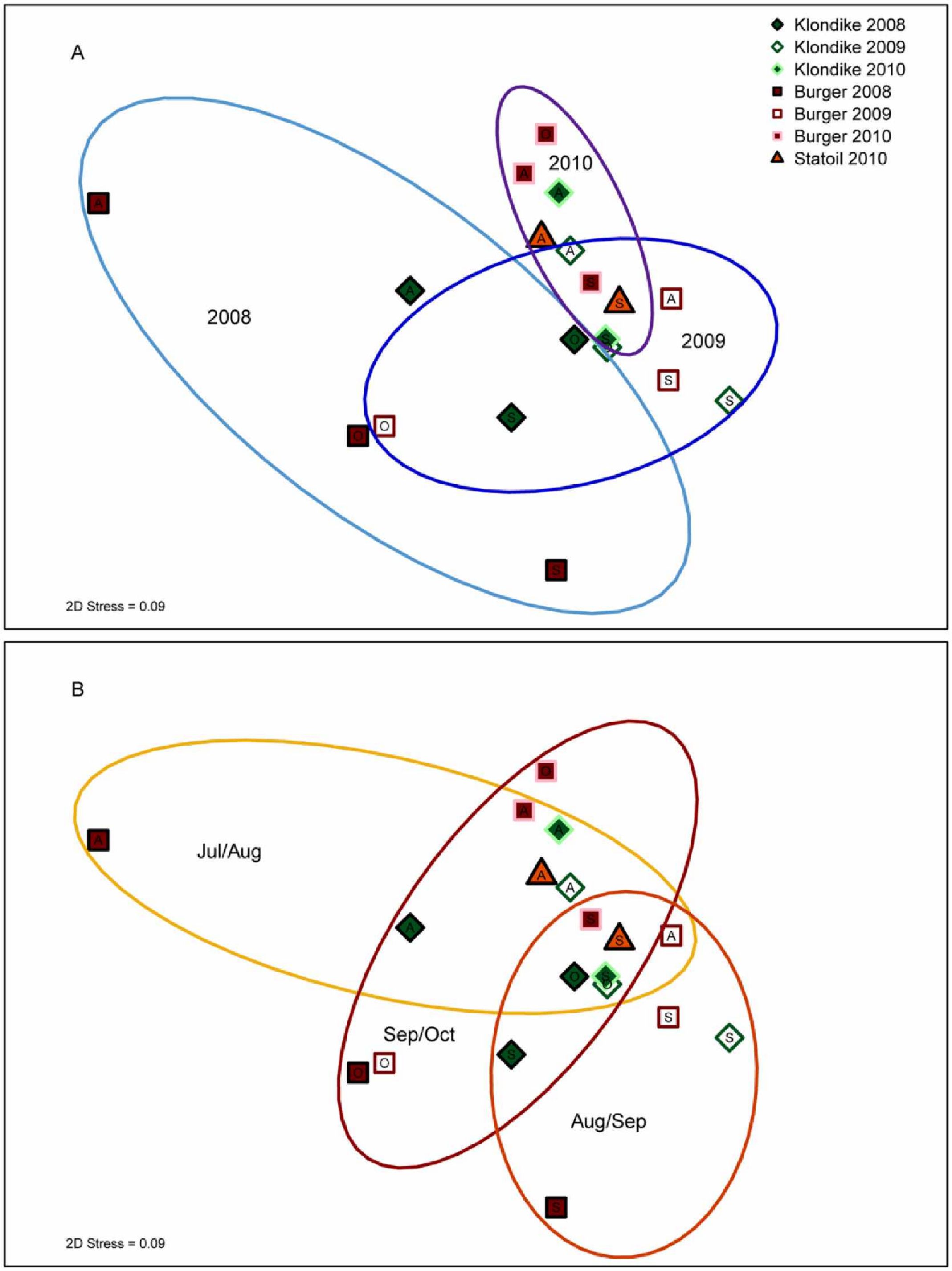

Figure 1.7 Non-metric multidimensional scaling ordination plot of seabird abundance recorded in the northeastern Chukchi Sea during 2008–2010. Distance between samples represents similarity in composition. Samples are grouped by year (A) and by season (B). Letters within the symbols indicate the month of sampling

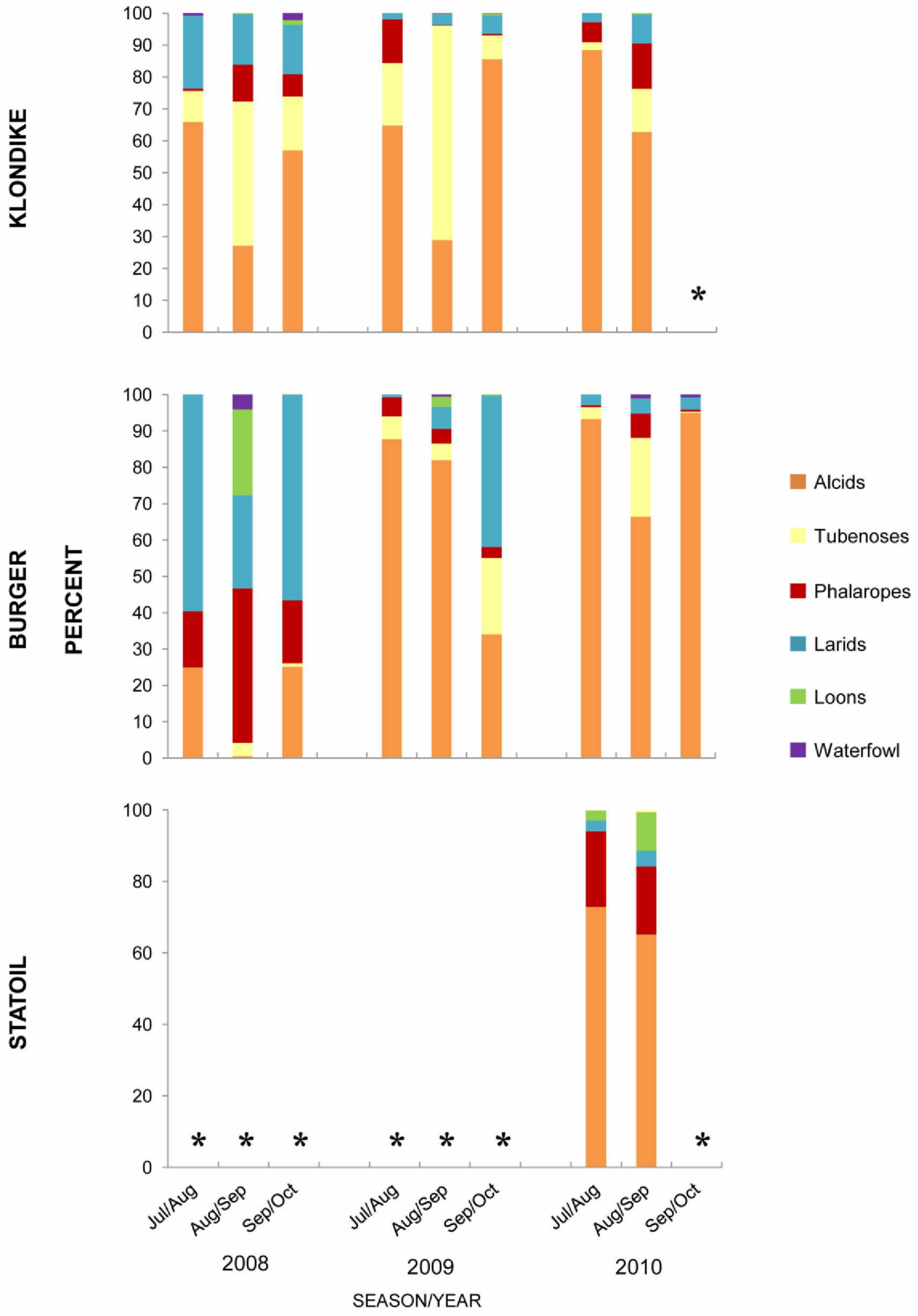

Figure 1.8 Species-composition of the seabird community in the Klondike, Burger, and Statoil study areas, 2008–2010. Asterisks indicate no data.

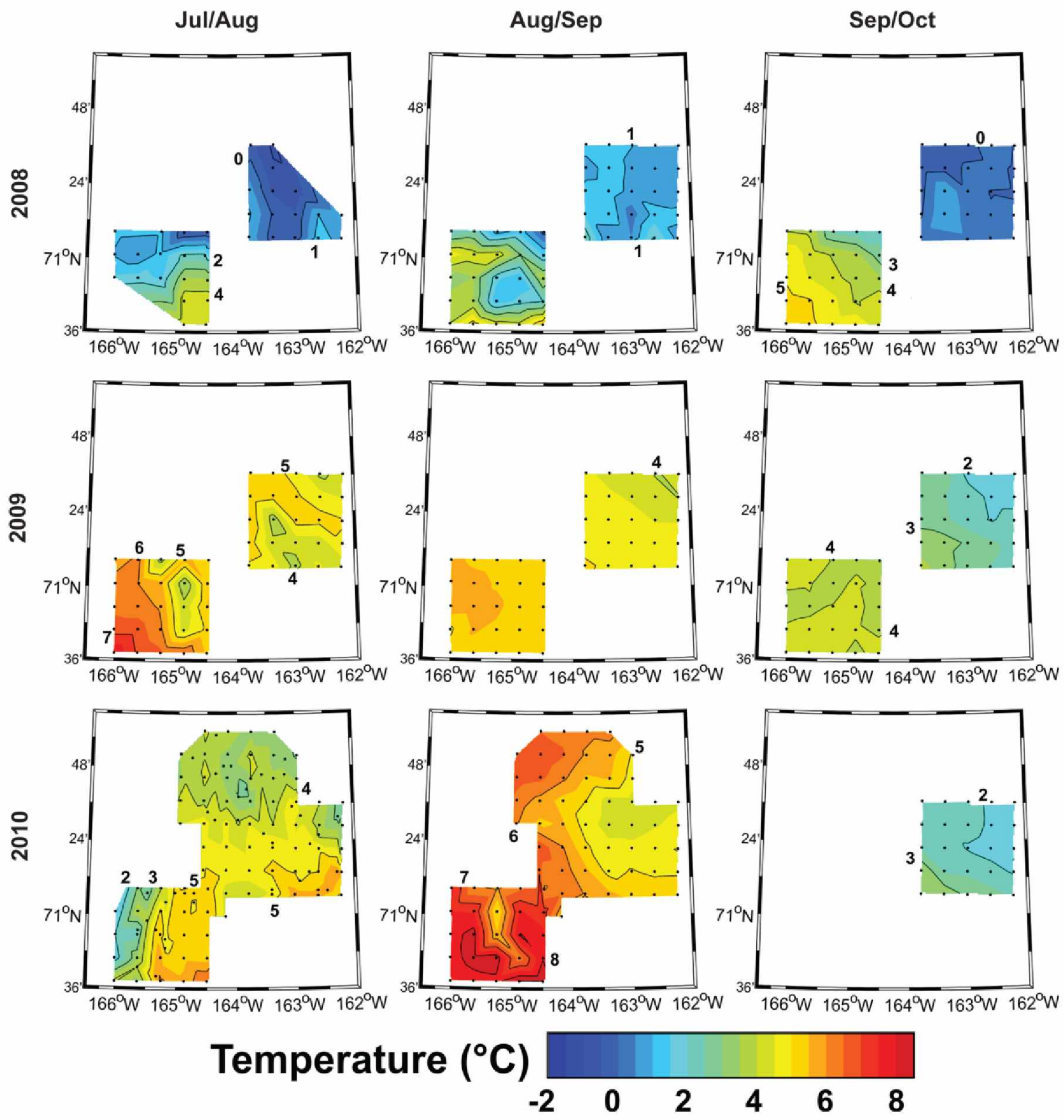

Figure 1.9 Plan view of temperatures averaged over the upper 10 m of the water column for surveys conducted in the northeastern Chukchi Sea during Jul/Aug, Aug/Sep, and Sep/Oct, 2008–2010. Klondike is in the lower left, Burger is on the right, and Statoil (2010 only) is above and left of Burger.

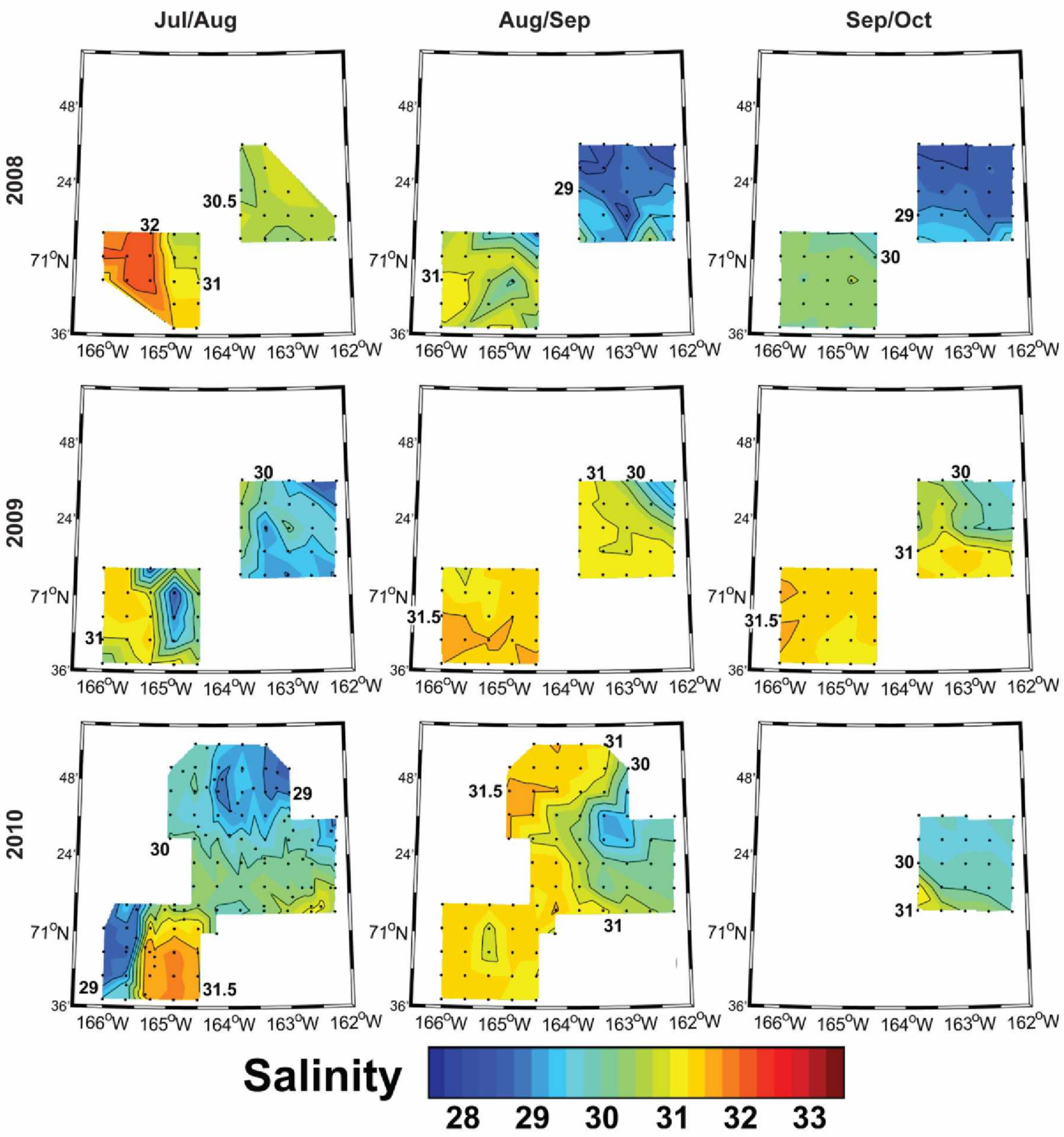

Figure 1.10 Plan view of salinities averaged over the upper 10 m of the water column for surveys conducted in the northeastern Chukchi Sea during Jul/Aug, Aug/Sep, and Sep/Oct, 2008–2010. Klondike is in the lower left, Burger is on the right, and Statoil (2010 only) is above and left of Burger.

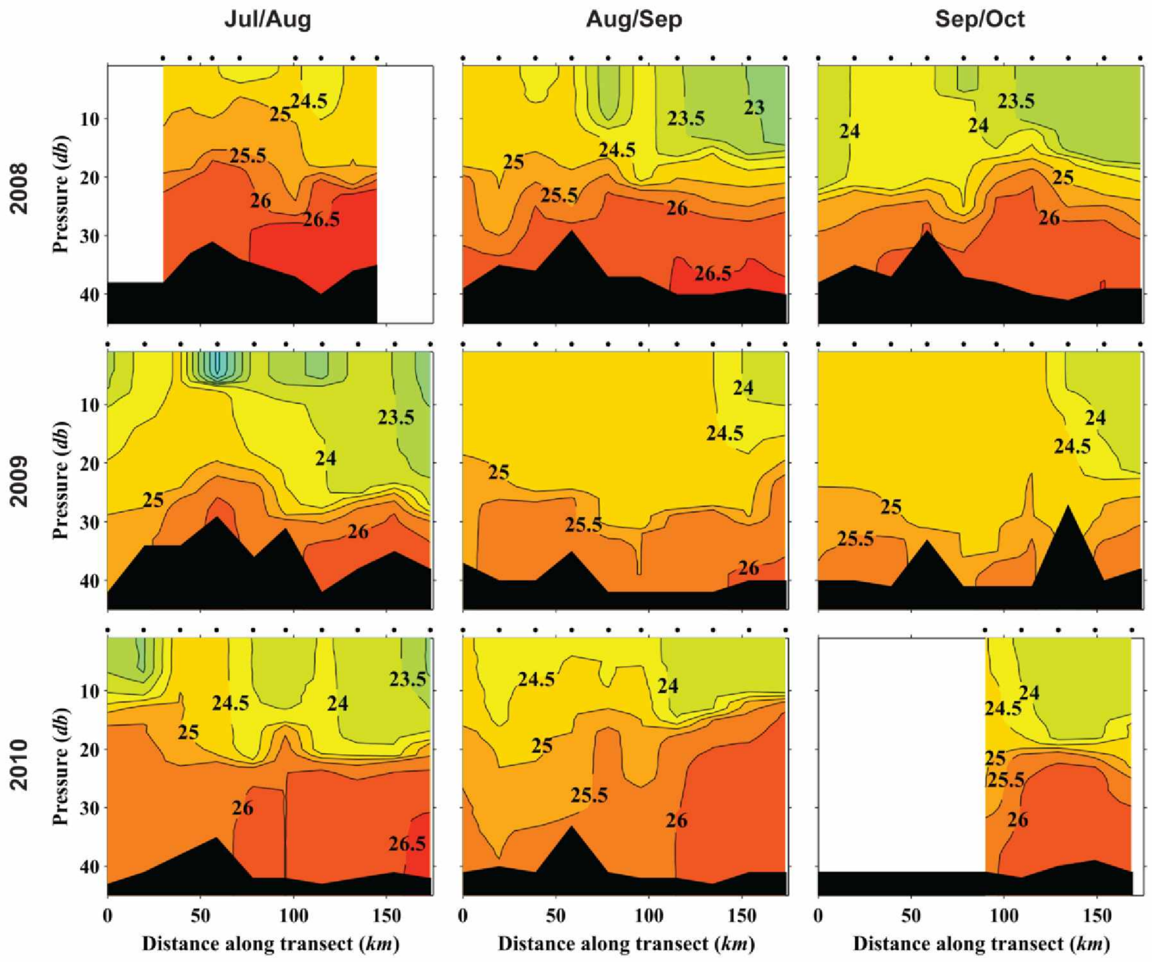

Figure 1.11 Vertical sections of density from the southwest corner of Klondike to the northeast corner of Burger in the northeastern Chukchi Sea during Jul/Aug, Aug/Sep, and Sep/Oct, 2008 – 2010.

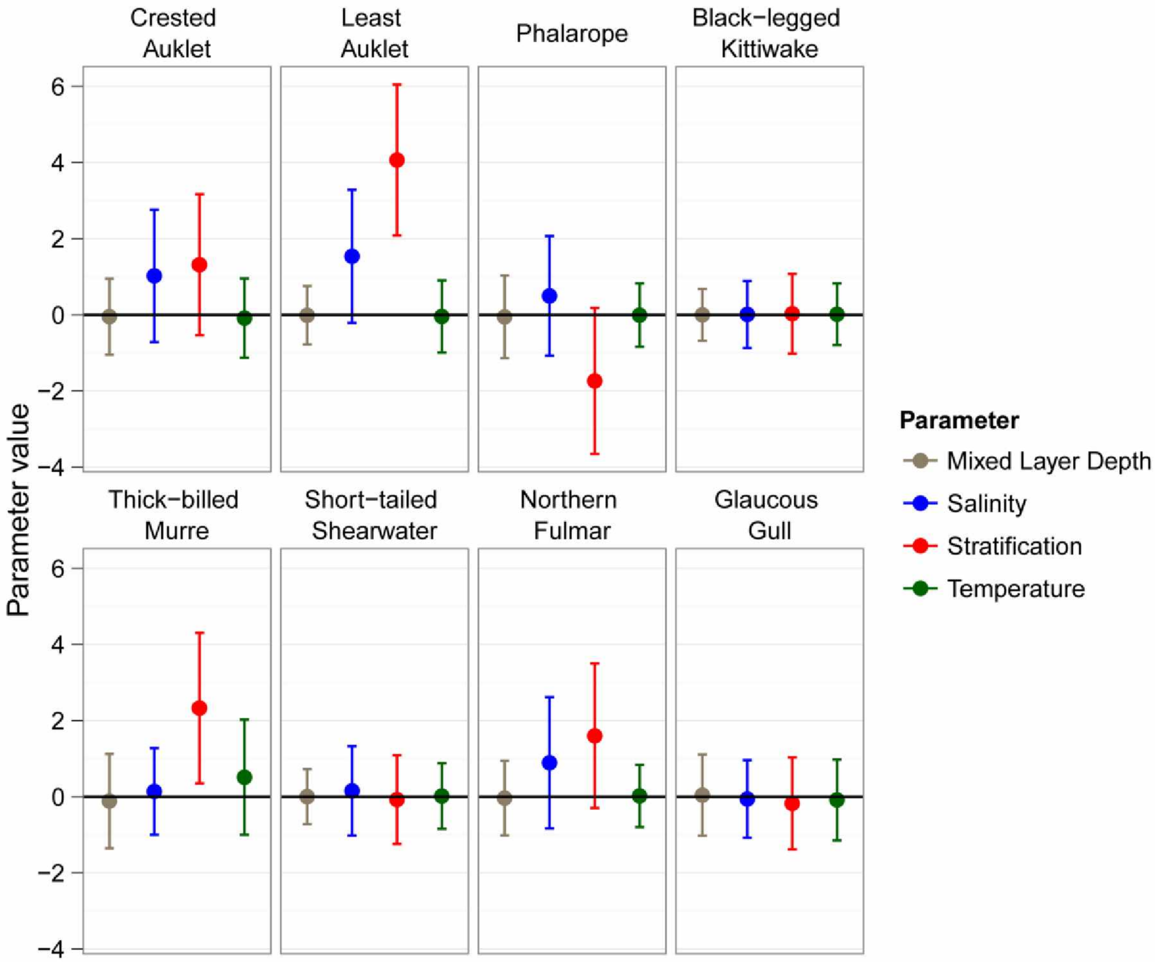

Figure 1.12 Model-averaged parameter estimates and unconditional confidence intervals that indicate the relationship between oceanographic characteristics and seabird abundance for 8 taxa in the northeastern Chukchi Sea. Parameter values are on log-scale because a log-link was used in the models to satisfy the assumptions of linear models.

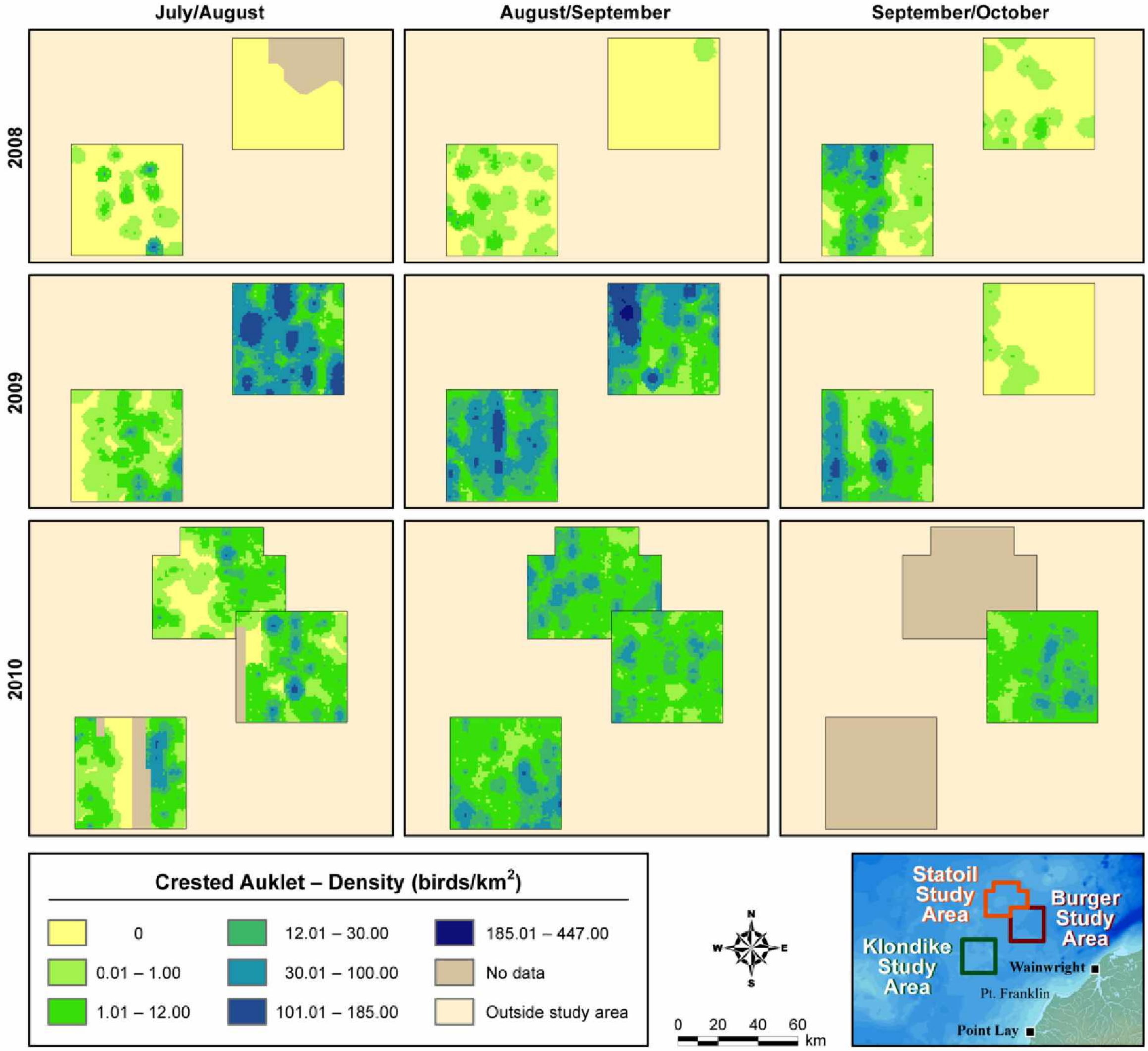

Figure 1.13 Distribution of estimated densities (birds km^{-2}) of crested auklets recorded on transect in the Klondike, Burger, and Statoil study areas of the northeastern Chukchi Sea in 2008–2010, by season and year.

Figure 1.14 Distribution of estimated densities (birds km^{-2}) of black-legged kittiwakes recorded on transect in the Klondike, Burger, and Statoil study areas of the northeastern Chukchi Sea in 2008–2010, by season and year.

Figure 1.15 Distribution of estimated densities (birds km^{-2}) of short-tailed shearwaters recorded on transect in the Klondike, Burger, and Statoil study areas of the northeastern Chukchi Sea in 2008–2010, by season and year.

Table 1.1 Detection function models used to calculate corrected densities by taxon.

Species	Key	Covariates	Probability of detection (flock)	CV (%)	Mean flock size
Crested Auklet	Half-normal	observer + vessel	0.66	1.3	4.3
Least Auklet					1.8
Black-legged Kittiwake	Half-normal	observer	0.58	2.1	1.7
Glaucous Gull					1.2
Northern Fulmar					1.4
Red Phalarope	Half-normal	none	0.52	4.2	4.2
Red-necked Phalarope					
Short-tailed Shearwater	Half-normal	observer + vessel	0.71	1.9	4.9
Thick-billed Murre	Hazard-rate	none	0.82	1.9	1.7

Table 1.2 Candidate models to relate seabird abundance to oceanographic variables during the open-water seasons 2008–2010 in the northeastern Chukchi Sea. In this table, n represents counts, MLD is the mixed-layer depth, and eff.area is an offset included in all models that accounts for survey effort and detection probability.

Habitat factors	Potential Models
null	n~1 + eff.area
depth of stratification	n~MLD + eff.area
temperature of foraging habitat	n~temperature + eff.area
salinity of foraging habitat	n~salinity + eff.area
strength of stratification	n~stratification + eff.area
salinity and thickness of the mixed layer	n~MLD + temperature + eff.area
temperature and thickness of the mixed layer	n~MLD + salinity + eff.area
water-column structure	n~MLD + stratification + eff.area
temperature and water-column structure	n~MLD + temperature + stratification + eff.area
salinity and water-column structure	n~MLD + salinity + stratification + eff.area
water-mass characteristics only	n~temperature + salinity + eff.area
all mixed-layer characteristics	n~MLD + temperature + salinity + stratification + eff.area

Table 1.3 Estimated abundance of seabirds counted during boat-based marine surveys in the northeastern Chukchi Sea, by study area, year, and season. Values in parentheses are 95% confidence intervals.

	Study area			
Year/season	Klondike	Burger	Statoil	Total
2008				
Jul/Aug	8400	1000	--	9400
	(5900–11 900)	(700–1400)	--	(6800–12 900)
Aug/Sep	18 800	127 300	--	30 400
	(14 300–24 900)	(100 900–160 600)	--	(24 400–37 700)
Sep/Oct	26 500	22 500	--	40 500
	(17 100–40 800)	(14 200–35 700)	--	(31 100–52 800)
2009				
Jul/Aug	17 200	13 200	--	146 100
	(13 200–22 300)	(9200–18 900)	--	(119 000–179 600)
Aug/Sep	214 800	109 300	--	324 100
	(171 700–268 700)	(83 300–143 400)	--	(272 100–386 000)
Sep/Oct	44 500	37 400	--	67 600
	(37 300–53 200)	(31 100–45 100)	--	(49 500–92 400)
2010				
Jul/Aug	33 300	7200	20 400	69 400
	(24 400–45 500)	(5000–10 300)	(15 000–27 700)	(54 400–88 400)
Aug/Sep	60 400	7300	42 100	124 100
	(42 600–85 500)	(5500–9500)	(35 200–50 400)	(111 800–137 800)
Sep/Oct	--	23 800	--	23 800
	--	(18 400–30 800)	--	(18 400–30 800)

Table 1.4 Model selection results from the effects of oceanographic variables on abundance of 8 taxa of seabirds. We present the variables included in each model, the difference in adjusted Akaike's information criterion between the top-ranked model and other candidate models (ΔAICc), and the AICc weight for each model.

Species/Taxon	Formula	AICc	ΔAICc	Weight
Least Auklet	n~stratification + salinity + eff.area	199.59	0.00	0.45
	n~temperature + salinity + stratification + eff.area	200.98	1.39	0.22
	n~MLD + salinity + stratification + eff.area	201.31	1.72	0.19
	n~MLD + temperature + salinity + stratification + eff.area	202.28	2.69	0.12
Crested Auklet	n~MLD + temperature + salinity + stratification + eff.area	286.57	0.00	0.15
	n~stratification + salinity + eff.area	287.03	0.46	0.12
	n~salinity + eff.area	287.26	0.69	0.11
	n~1 + eff.area	287.73	1.16	0.09
	n~MLD + salinity + eff.area	287.81	1.24	0.08
	n~temperature + salinity + stratification + eff.area	288.01	1.44	0.07
	n~temperature + salinity + eff.area	288.66	2.09	0.05
Thick-billed Murre	n~MLD + temperature + stratification + eff.area	164.22	0.00	0.46
	n~MLD + temperature + salinity + stratification + eff.area	165.23	1.01	0.28
Northern Fulmar	n~MLD + salinity + stratification + eff.area	173.07	0.00	0.26
	n~stratification + salinity + eff.area	173.11	0.03	0.26
	n~MLD + salinity + eff.area	174.79	1.72	0.11
	n~MLD + temperature + salinity + stratification + eff.area	174.86	1.79	0.11
	n~temperature + salinity + stratification + eff.area	174.95	1.87	0.10
Phalaropes	n~MLD + salinity + stratification + eff.area	187.96	0.00	0.26
	n~MLD + temperature + salinity + stratification + eff.area	189.61	1.64	0.11
	n~stratification + eff.area	189.76	1.80	0.11
	n~MLD + salinity + eff.area	189.83	1.87	0.10
	n~stratification + salinity + eff.area	189.96	2.00	0.09

Table 1.4 continued…

Species/Taxon	Formula	AICc	ΔAICc	Weight
Glaucous Gull	n~MLD + temperature + eff.area	145.85	0.00	0.18
	n~MLD + eff.area	146.57	0.73	0.13
	n~1 + eff.area	146.77	0.93	0.11
	n~MLD + salinity + eff.area	147.14	1.29	0.10
	n~temperature + eff.area	147.63	1.78	0.07
	n~MLD + temperature + stratification + eff.area	147.69	1.84	0.07
Black-legged Kittiwake	n~1 + eff.area	192.26	0.00	0.28
	n~temperature + eff.area	194.06	1.79	0.11
	n~salinity + eff.area	194.23	1.97	0.10
	n~stratification + eff.area	194.25	1.98	0.10
	n~MLD + eff.area	194.26	2.00	0.10
Short-tailed Shearwater	n~1 + eff.area	208.12	0.00	0.21
	n~salinity + eff.area	208.72	0.60	0.16
	n~temperature + eff.area	209.60	1.48	0.10
	n~MLD + eff.area	209.90	1.78	0.09
	n~stratification + eff.area	209.93	1.81	0.09

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Appendix 1.1. List of all marine-bird species recorded during boat-based marine surveys in the northeastern Chukchi Sea, 2008–2010. Iñupiaq names are provided when known. Primary prey categories were determined from a review of 94 peer-reviewed journal articles, coded as B = benthic invertebrates; F = fish; O = omnivorous; and P = zooplankton.

Species-group/species	Scientific name	Iñupiaq name	Primary prey
WATERFOWL			
Spectacled Eider	*Somateria fischeri*	qavaasuk	B
King Eider	*S. spectabilis*	qiŋalik	B
Common Eider	*S. mollissima*	amauligruaq	B
White-winged Scoter	*Melanitta fusca*	killalik	B
Long-tailed Duck	*Clangula hyemalis*	aahaaliq	B
LOONS			
Red-throated Loon	*Gavia stellata*	qaksrauq	F
Pacific Loon	*G. pacifica*	malġi	F
Yellow-billed Loon	*G. adamsii*	tuutlik	F
TUBENOSES			
Northern Fulmar	*Fulmarus glacialis*		O
Short-tailed Shearwater	*Puffinus tenuirostris*		O
SHOREBIRDS			
Red-necked Phalarope	*Phalaropus lobatus*	qayiuġun	P
Red Phalarope	*P. fulicarius*	auksruaq	P
LARIDS			
Black-legged Kittiwake	*Rissa tridactyla*		F
Ivory Gull	*Pagophila eburnea*		F
Sabine's Gull	*Xema sabini*	aqargigiaq	O
Ross's Gull	*Rhodostethia rosea*		P
Herring Gull	*Larus argentatus*	nauyatchiaq	O
Glaucous Gull	*L. hyperboreus*	nauyavasrugruk	O
Arctic Tern	*Sterna paradisaea*	mitqutailḷaq	F
Pomarine Jaeger	*Stercorarius pomarinus*	isuŋŋaġluk	F
Parasitic Jaeger	*S. parasiticus*	miġiaqsaayuk	F
Long-tailed Jaeger	*S. longicaudus*	isuŋŋaq	F

Appendix 1.1 continued…

Species-	Scientific name	Iñupiaq name	Primary prey
ALCIDS			
Dovekie	*Alle alle*		P
Common Murre	*Uria aalge*	aqpaq	F
Thick-billed Murre	*U. lomvia*		F
Black Guillemot	*Cepphus grylle*	iŋaġiq	F
Pigeon Guillemot	*C. columba*		F
Kittlitz's Murrelet	*Brachyramphus brevirostris*		P
Ancient Murrelet	*Synthliboramphus antiquus*		P
Parakeet Auklet	*Aethia psittacula*		P
Least Auklet	*A. pusilla*		P
Crested Auklet	*A. cristatella*		P
Horned Puffin	*Fratercula corniculata*		F
Tufted Puffin	*F. cirrhata*	qilaŋq	F

Appendix 1.2. Estimated abundance (birds km^{-1}) of marine birds recorded during boat-based surveys in the northeastern Chukchi Sea, by study area and season, 2008.

	Klondike			Burger		
Species-group/Species	Jul/ Augt	Aug/ Sep	Sept/ Oct	Jul/ Augt	Aug/ Sep	Sep/ Oct
WATERFOWL						
Spectacled Eider	0 (0-0)	0 (0-0)	0 (0-0)	0 (0-0)	0 (0-0)	0 (0-0)
King Eider	0 (0-0.02)	0 (0-0)	0.01 (0-0.08)	0 (0-0)	0.01 (0-0.03)	0 (0-0)
Common Eider	0 (0-0)	0 (0-0)	0 (0-0)	0 (0-0)	0.03 (0.01-0.18)	0 (0-0)
Unidentified eider	0 (0-0)	0.04 (0.01-0.24)	0.04 (0.01-0.19)	0 (0-0)	0.06 (0.01-0.28)	0 (0-0)
Long-tailed Duck	0.14 (0.03-0.66)	0 (0-0)	0.19 (0.08-0.45)	0 (0-0)	0.3 (0.1-0.96)	0 (0-0)
LOONS						
Red-throated Loon	0 (0-0)	0 (0-0)	0 (0-0)	0 (0-0)	0.01 (0-0.04)	0 (0-0)
Pacific Loon	0 (0-0)	0 (0-0.02)	0.13 (0.08-0.2)	0 (0-0)	0.18 (0.07-0.46)	0.02 (0.01-0.05)
Yellow-billed Loon	0 (0-0)	0.02 (0-0.09)	0.01 (0-0.03)	0 (0-0)	0.01 (0-0.07)	0 (0-0)
Unidentified loon - large	0 (0-0)	0 (0-0)	0 (0-0)	0 (0-0)	0 (0-0)	0 (0-0)
Unidentified loon	0 (0-0)	0 (0-0)	0 (0-0.03)	0 (0-0)	0.1 (0.04-0.29)	0 (0-0)
TUBENOSES						
Northern Fulmar	0.27 (0.16-0.44)	0.67 (0.47-0.95)	0.27 (0.11-0.63)	0.05 (0.02-0.1)	0.04 (0.01-0.12)	0.05 (0.02-0.12)
Short-tailed Shearwater	0.01 (0-0.05)	1.24 (0.6-2.56)	1.34 (0.65-2.76)	0 (0-0)	1.02 (0.39-2.66)	0.26 (0.13-0.53)
Unidentified procellarid	0 (0-0)	0 (0-0)	0.11 (0.02-0.79)	0 (0-0)	0 (0-0)	0 (0-0.03)
PHALAROPES						
Red-necked Phalarope	0 (0-0)	0.12 (0.03-0.48)	0.61 (0.21-1.77)	0 (0-0)	0.41 (0.18-0.95)	0 (0-0)
Red Phalarope	0.02 (0-0.1)	0.03 (0.01-0.17)	0.01 (0-0.05)	0 (0-0)	0 (0-0)	0 (0-0)
Unidentified phalarope	0 (0-0)	0.44 (0.13-1.51)	0.09 (0.03-0.22)	0 (0-0)	0.46 (0.18-1.17)	0 (0-0)

Appendix 1.2 continued…

	Klondike			Burger		
Species-group/Species	Jul/ Aug	Aug/ Sep	Sep/ Oct	Jul/ Aug	Aug/ Sep	Sep/ Oct
LARIDS						
Black-legged Kittiwake	0.4 (0.27-0.6)	0.22 (0.12-0.4)	0.79 (0.5-1.22)	0.11 (0.06-0.21)	0.74 (0.45-1.23)	0.09 (0.04-0.2)
Ivory Gull	0 (0-0)	0 (0-0)	0 (0-0)	0 (0-0)	0 (0-0)	0.02 (0-0.06)
Sabine's Gull	0.04 (0.01-0.12)	0.44 (0.15-1.3)	0.04 (0.01-0.1)	0.02 (0-0.05)	0 (0-0)	0 (0-0)
Ross's Gull	0 (0-0)	0 (0-0)	0 (0-0)	0 (0-0)	0 (0-0)	0.76 (0.31-1.86)
Herring Gull	0 (0-0.02)	0 (0-0)	0.12 (0.04-0.33)	0 (0-0)	0 (0-0)	0.01 (0-0.04)
Glaucous Gull	0.04 (0.02-0.11)	0.06 (0.03-0.12)	0.49 (0.36-0.66)	0.05 (0.02-0.11)	0.2 (0.13-0.3)	0.11 (0.04-0.26)
Unidentified gull - small	0 (0-0)	0 (0-0)	0 (0-0)	0 (0-0)	0 (0-0)	0 (0-0)
Unidentified gull - large	0 (0-0)	0 (0-0)	0 (0-0)	0 (0-0)	0.01 (0-0.04)	0 (0-0)
Arctic Tern	0 (0-0)	0.12 (0.02-0.61)	0 (0-0)	0 (0-0)	0 (0-0)	0 (0-0)
Pomarine Jaeger	0.1 (0.06-0.17)	0.05 (0.02-0.12)	0 (0-0.03)	0.02 (0-0.06)	0.02 (0-0.07)	0 (0-0)
Parasitic Jaeger	0.01 (0-0.04)	0.01 (0-0.03)	0 (0-0)	0.01 (0-0.03)	0 (0-0)	0 (0-0)
Long-tailed Jaeger	0 (0-0)	0 (0-0)	0 (0-0)	0 (0-0)	0 (0-0)	0 (0-0)
Unidentified jaeger	0 (0-0)	0 (0-0)	0 (0-0)	0 (0-0)	0 (0-0)	0 (0-0)
ALCIDS						
Dovekie	0 (0-0.03)	0 (0-0)	0.01 (0-0.04)	0 (0-0)	0 (0-0)	0.01 (0-0.06)
Common Murre	0.05 (0.02-0.09)	0 (0-0)	0.06 (0.02-0.16)	0 (0-0)	0 (0-0)	0 (0-0)
Thick-billed Murre	0.78 (0.52-1.19)	0.05 (0.02-0.11)	0.02 (0.01-0.05)	0.02 (0.01-0.05)	0 (0-0)	0.01 (0-0.04)
Unidentified murre	0	0.03	0.02	0	0.01	0.07

Appendix 1.2 continued…

	Klondike			Burger		
Species-group/Species	Jul/ Aug	Aug/ Sep	Sep/ Oct	Jul/ Aug	Aug/ Sep	Sep/ Oct
	(0-0.02)	(0.01-0.09)	(0.01-0.07)	(0-0)	(0-0.04)	(0.01-0.39)
Black Guillemot	0.04 (0.02-0.1)	0 (0-0)	0 (0-0)	0.02 (0-0.06)	0 (0-0)	0.04 (0.01-0.17)
Pigeon Guillemot	0.02 (0.01-0.06)	0 (0-0)	0 (0-0)	0.01 (0-0.05)	0 (0-0)	0 (0-0)
ALCIDS (continued)						
Kittlitz's Murrelet	0 (0-0)	0 (0-0)	0 (0-0)	0 (0-0)	0 (0-0)	0 (0-0)
Ancient Murrelet	0 (0-0)	0 (0-0)	0 (0-0)	0 (0-0)	0 (0-0)	0 (0-0)
Unidentified murrelet	0 (0-0)	0 (0-0)	0.04 (0.01-0.2)	0 (0-0)	0 (0-0)	0 (0-0)
Parakeet Auklet	0 (0-0)	0.02 (0-0.17)	0 (0-0)	0 (0-0)	0 (0-0)	0.26 (0.06-1.14)
Least Auklet	0.03 (0.01-0.1)	0.89 (0.55-1.44)	0.41 (0.19-0.88)	0 (0-0)	0.01 (0-0.04)	0.03 (0.01-0.11)
Crested Auklet	0.83 (0.29-2.36)	0.52 (0.29-0.93)	5.22 (2.98-9.15)	0 (0-0)	0.01 (0-0.04)	0.16 (0.06-0.44)
Unidentified auklet	0 (0-0.02)	0.08 (0.03-0.19)	0.38 (0.14-1.07)	0 (0-0)	0 (0-0)	0.01 (0-0.04)
Horned Puffin	0.01 (0-0.03)	0 (0-0)	0 (0-0)	0.02 (0-0.08)	0 (0-0)	0 (0-0)
Tufted Puffin	0.03 (0.01-0.06)	0 (0-0)	0 (0-0.02)	0 (0-0)	0 (0-0)	0 (0-0)
Unidentified puffin	0 (0-0)	0 (0-0)	0 (0-0)	0 (0-0)	0 (0-0)	0 (0-0)
Unidentified alcid - small	0 (0-0)	0 (0-0)	0.01 (0-0.04)	0 (0-0)	0 (0-0)	0.05 (0.02-0.14)
Unidentified alcid	0 (0-0)	0.01 (0-0.02)	0.04 (0.02-0.11)	0 (0-0)	0.03 (0.01-0.13)	0.01 (0-0.04)

Appendix 1.3 Estimated abundance (birds km^{-1}) of marine birds recorded during boat-based surveys in the northeastern Chukchi Sea, by study area and season, 2009.

	Klondike			Burger		
Species-group/Species	July/ Aug	Aug/ Sep	Sep/ Oct	Jul/ Aug	Aug/ Sep	Sep/ Oct
WATERFOWL						
Spectacled Eider	0 (0-0)	0.01 (0-0.04)	0 (0-0)	0 (0-0)	0 (0-0)	0 (0-0)
King Eider	0 (0-0)	0 (0-0)	0 (0-0)	0 (0-0)	0 (0-0)	0 (0-0)
Common Eider	0 (0-0)	0 (0-0)	0 (0-0)	0 (0-0)	0 (0-0)	0 (0-0)
Unidentified eider	0 (0-0)	0.1 (0.02-0.58)	0.01 (0-0.04)	0 (0-0)	0.01 (0-0.07)	0.03 (0.01-0.19)
Long-tailed Duck	0 (0-0)	0.09 (0.02-0.41)	0.01 (0-0.06)	0 (0-0)	0.22 (0.08-0.62)	0 (0-0)
LOONS						
Red-throated Loon	0 (0-0)	0 (0-0)	0 (0-0)	0 (0-0)	0 (0-0)	0 (0-0)
Pacific Loon	0 (0-0)	0.12 (0.06-0.27)	0.1 (0.05-0.21)	0 (0-0)	1.02 (0.61-1.7)	0 (0-0.03)
Yellow-billed Loon	0 (0-0)	0.04 (0.01-0.23)	0 (0-0.03)	0 (0-0)	0.13 (0.05-0.34)	0 (0-0)
Unidentified loon - large	0 (0-0)	0 (0-0)	0 (0-0)	0 (0-0)	0 (0-0)	0 (0-0)
Unidentified loon	0 (0-0)	0.03 (0.01-0.16)	0.02 (0.01-0.07)	0 (0-0)	0.17 (0.08-0.35)	0 (0-0)
TUBENOSES						
Northern Fulmar	1.16 (0.66-2.02)	0.32 (0.17-0.6)	0.03 (0.01-0.09)	1.26 (0.72-2.21)	0.22 (0.14-0.33)	0.14 (0.04-0.45)
Short-tailed Shearwater	0.16 (0.08-0.33)	59.76 (39.06-91.43)	1.45 (0.56-3.76)	1.67 (0.39-7.23)	1.86 (1.03-3.33)	0.29 (0.13-0.65)
Unidentified procellarid	0 (0-0)	0 (0-0)	0 (0-0)	0 (0-0)	0 (0-0)	0 (0-0)

Appendix 1.3 continued…

Species-group/Species	Klondike Jul/ Aug	 Aug/ Sep	 Sep/ Oct	Burger Jul/ Aug	 Aug/ Sep	 Sep/ Oct
PHALAROPES						
Red-necked Phalarope	0.33 (0.16-0.68)	0.08 (0.05-0.14)	0.02 (0-0.11)	1.8 (0.97-3.32)	0.95 (0.52-1.73)	0.04 (0.01-0.21)
Red Phalarope	0.03 (0-0.16)	0 (0-0)	0.02 (0-0.11)	0.13 (0.03-0.59)	0.29 (0.12-0.69)	0.01 (0-0.05)
Unidentified phalarope	0.5 (0.16-1.51)	0 (0-0)	0.08 (0.01-0.47)	0.64 (0.32-1.29)	0.45 (0.15-1.34)	0.04 (0.01-0.11)
LARIDS						
Black-legged Kittiwake	0.1 (0.04-0.28)	1.71 (1.13-2.58)	0.64 (0.41-1.01)	0.16 (0.07-0.37)	1.82 (1.29-2.56)	0.14 (0.05-0.41)
Ivory Gull	0 (0-0)	0 (0-0)	0 (0-0)	0 (0-0)	0 (0-0)	0 (0-0)
Sabine's Gull	0 (0-0)	0.01 (0-0.04)	0.01 (0-0.05)	0 (0-0)	0 (0-0)	0.01 (0-0.07)
Ross's Gull	0 (0-0)	0 (0-0)	0 (0-0)	0 (0-0)	0 (0-0)	0.3 (0.17-0.51)
Herring Gull	0 (0-0)	0.06 (0.03-0.16)	0 (0-0)	0.05 (0.02-0.12)	0.01 (0-0.09)	0 (0-0)
Glaucous Gull	0 (0-0)	0.14 (0.05-0.43)	0.31 (0.15-0.66)	0.08 (0.03-0.25)	0.42 (0.29-0.61)	0.33 (0.19-0.57)
Unidentified gull - small	0 (0-0)	0 (0-0)	0.02 (0-0.08)	0 (0-0)	0 (0-0)	0 (0-0)
Unidentified gull - large	0 (0-0)	0 (0-0)	0 (0-0)	0 (0-0)	0 (0-0)	0 (0-0)
Arctic Tern	0 (0-0)	0 (0-0)	0 (0-0)	0.01 (0-0.08)	0.01 (0-0.07)	0 (0-0)
Pomarine Jaeger	0.05 (0.01-0.14)	0.12 (0.05-0.28)	0 (0-0)	0.07 (0.04-0.13)	0.01 (0-0.03)	0 (0-0)
Parasitic Jaeger	0 (0-0)	0 (0-0)	0 (0-0)	0 (0-0)	0 (0-0)	0 (0-0)
Long-tailed Jaeger	0.01 (0-0.04)	0 (0-0)	0 (0-0)	0.01 (0-0.05)	0 (0-0)	0 (0-0)
Unidentified jaeger	0 (0-0)	0.01 (0-0.03)	0 (0-0)	0 (0-0)	0.01 (0-0.03)	0 (0-0)

Appendix 1.3 continued…

	Klondike			Burger		
Species-group/Species	Jul/ Aug	Aug/ Sep	Sep/ Oct	Jul/ Aug	Aug/ Sep	Sep/ Oct
ALCIDS						
Dovekie	0 (0-0)	0 (0-0)	0 (0-0)	0 (0-0)	0 (0-0)	0 (0-0)
Common Murre	0 (0-0)	0.04 (0.01-0.09)	0.02 (0-0.08)	0 (0-0)	0.01 (0-0.08)	0.08 (0.01-0.55)
Thick-billed Murre	0.41 (0.25-0.68)	1.37 (0.95-1.99)	0.09 (0.04-0.2)	0.12 (0.07-0.21)	0.12 (0.04-0.38)	0.09 (0.03-0.29)
Unidentified murre	0 (0-0)	0.15 (0.07-0.31)	0.03 (0.01-0.15)	0 (0-0)	0.04 (0.01-0.22)	0.01 (0-0.04)
Black Guillemot	0 (0-0)	0 (0-0)	0 (0-0)	0 (0-0)	0 (0-0)	0 (0-0)
Pigeon Guillemot	0 (0-0)	0 (0-0)	0 (0-0)	0 (0-0)	0 (0-0)	0 (0-0)
Kittlitz's Murrelet	0 (0-0)	0.01 (0-0.05)	0 (0-0)	0 (0-0)	0 (0-0)	0.08 (0.01-0.45)
Ancient Murrelet	0 (0-0)	0 (0-0)	0 (0-0)	0 (0-0)	0 (0-0)	0 (0-0)
Unidentified murrelet	0 (0-0)	0 (0-0)	0 (0-0)	0 (0-0)	0 (0-0)	0 (0-0)
Parakeet Auklet	0 (0-0)	0.12 (0.06-0.24)	0 (0-0)	0 (0-0)	0 (0-0)	0 (0-0)
Least Auklet	0.59 (0.34-1.01)	0.74 (0.45-1.21)	2.44 (1.55-3.83)	1.76 (1-3.11)	0.91 (0.65-1.27)	0.37 (0.23-0.61)
Crested Auklet	2.93 (1.64-5.23)	18.91 (12.94-27.62)	11.57 (6.98-19.19)	32.36 (24.09-43.48)	28.03 (18.85-41.67)	0.15 (0.06-0.4)
Unidentified auklet	0.07 (0.02-0.19)	0.3 (0.18-0.51)	0.09 (0.03-0.26)	0.08 (0.02-0.29)	0.15 (0.06-0.37)	0 (0-0)
Horned Puffin	0.03 (0.01-0.11)	0.01 (0-0.05)	0 (0-0)	0 (0-0)	0 (0-0)	0 (0-0)
Tufted Puffin	0.01 (0-0.04)	0 (0-0)	0 (0-0)	0 (0-0)	0 (0-0)	0 (0-0)
Unidentified puffin	0 (0-0)	0 (0-0)	0 (0-0)	0 (0-0)	0 (0-0)	0 (0-0)
Unidentified alcid - small	0 (0-0)	0 (0-0)	0.09 (0.02-0.31)	0 (0-0)	0 (0-0)	0.15 (0.06-0.35)
Unidentified alcid	0 (0-0)	0.1 (0.05-0.22)	0 (0-0)	0 (0-0)	0.06 (0.02-0.19)	0 (0-0)

Appendix 1.4 Estimated abundance (birds km^{-1}) of marine birds recorded during boat-based surveys in the northeastern Chukchi Sea, by study area and season, 2010.

	Study Area/Season						
	Klondike		Statoil		Burger		
Species-group/species	Jul/ Aug	Aug/ Sep	Jul/ Aug	Aug/ Sep	July/ Aug	Aug/ Sep	Sep/ Oct
WATERFOWL							
Spectacled Eider	0 (0-0)	0 (0-0)	0 (0-0)	0 (0-0)	0 (0-0)	0 (0-0)	0 (0-0)
King Eider	0 (0-0)	0 (0-0)	0 (0-0)	0 (0-0)	0 (0-0)	0 (0-0)	0.01 (0-0.09)
Common Eider	0 (0-0)	0 (0-0)	0 (0-0)	0 (0-0)	0 (0-0)	0 (0-0)	0.02 (0-0.12)
Unidentified eider	0 (0-0)	0 (0-0)	0 (0-0)	0 (0-0)	0.11 (0.02-0.65)	0 (0-0)	0.05 (0.01-0.18)
Long-tailed Duck	0 (0-0)	0 (0-0)	0.01 (0-0.05)	0.07 (0.01-0.33)	0 (0-0)	0.1 (0.02-0.49)	0.04 (0.01-0.19)
LOONS							
Red-throated Loon	0 (0-0)	0 (0-0)	0 (0-0)	0 (0-0)	0 (0-0)	0 (0-0)	0 (0-0)
Pacific Loon	0 (0-0)	0.06 (0.02-0.24)	0 (0-0)	0.01 (0-0.04)	0 (0-0)	0.04 (0.01-0.11)	0 (0-0)
Yellow-billed Loon	0 (0-0)	0 (0-0)	0 (0-0)	0 (0-0)	0 (0-0)	0 (0-0)	0 (0-0)
Unidentified loon - large	0 (0-0)	0 (0-0)	0 (0-0)	0 (0-0)	0 (0-0)	0 (0-0)	0 (0-0)
Unidentified loon	0 (0-0)	0 (0-0)	0 (0-0)	0.02 (0.01-0.12)	0 (0-0)	0 (0-0)	0 (0-0)
TUBENOSES							
Northern Fulmar	0.19 (0.09-0.4)	0.21 (0.12-0.37)	0.11 (0.06-0.18)	0.16 (0.09-0.29)	0.25 (0.14-0.44)	0.07 (0.03-0.15)	0.01 (0-0.04)
Short-tailed Shearwater	0.07 (0.02-0.26)	2.23 (1.15-4.3)	1.15 (0.55-2.4)	2.04 (1.26-3.31)	0.05 (0.01-0.23)	2.47 (1.26-4.82)	0.02 (0.01-0.07)
Unidentified procellarid	0 (0-0)	0 (0-0)	0 (0-0)	0 (0-0)	0 (0-0)	0 (0-0)	0 (0-0)

Appendix 1.4 continued…

	Study Area/Season						
	Klondike		Statoil		Burger		
Species-group/species	Jul/ Aug	Aug/ Sep	Jul/ Aug	Aug/ Sep	July/ Aug	Aug/ Sep	Sep/ Oct
PHALAROPES							
Red-necked Phalarope	0.01 (0-0.07)	0.82 (0.39-1.69)	0.12 (0.03-0.51)	0.89 (0.32-2.46)	0.04 (0.01-0.2)	0.31 (0.13-0.78)	0 (0-0)
Red Phalarope	0.24 (0.04-1.46)	0.05 (0.01-0.14)	0 (0-0)	0.41 (0.17-1)	0 (0-0)	0.3 (0.08-1.12)	0.05 (0.02-0.1)
Unidentified phalarope	0.33 (0.1-1.11)	1.53 (0.78-2.99)	0.09 (0.03-0.26)	0.41 (0.17-0.99)	0.01 (0-0.06)	0.29 (0.08-1.04)	0 (0-0)
LARIDS							
Black-legged Kittiwake	0.27 (0.12-0.62)	0.88 (0.56-1.39)	0.17 (0.05-0.5)	0.54 (0.36-0.82)	0.17 (0.08-0.35)	0.3 (0.18-0.5)	0 (0-0)
Ivory Gull	0 (0-0)	0 (0-0)	0 (0-0)	0 (0-0)	0 (0-0)	0 (0-0)	0 (0-0)
Sabine's Gull	0.02 (0-0.1)	0.14 (0.04-0.48)	0.07 (0.03-0.19)	0 (0-0)	0.02 (0-0.09)	0 (0-0)	0 (0-0)
Ross's Gull	0 (0-0)	0 (0-0)	0 (0-0)	0 (0-0)	0 (0-0)	0 (0-0)	0.19 (0.09-0.41)
Herring Gull	0 (0-0)	0 (0-0)	0 (0-0)	0.01 (0-0.05)	0 (0-0)	0.01 (0-0.05)	0 (0-0)
Glaucous Gull	0.03 (0.01-0.1)	0.07 (0.03-0.21)	0.04 (0.01-0.14)	0.08 (0.03-0.17)	0.06 (0.02-0.15)	0.08 (0.04-0.15)	0.1 (0.05-0.19)
Unidentified gull - small	0 (0-0)	0 (0-0)	0 (0-0)	0 (0-0)	0 (0-0)	0 (0-0)	0 (0-0)
Unidentified gull - large	0 (0-0)	0 (0-0)	0 (0-0)	0 (0-0)	0 (0-0)	0 (0-0)	0 (0-0)
Arctic Tern	0 (0-0)	0.2 (0.04-0.9)	0 (0-0)	0 (0-0)	0.02 (0-0.09)	0 (0-0)	0 (0-0)
Pomarine Jaeger	0 (0-0)	0.08 (0.04-0.17)	0.02 (0-0.06)	0.02 (0.01-0.05)	0.04 (0.02-0.11)	0.01 (0-0.03)	0 (0-0)
Parasitic Jaeger	0 (0-0)	0 (0-0)	0 (0-0)	0 (0-0)	0 (0-0)	0.01 (0-0.03)	0 (0-0)
Long-tailed Jaeger	0.02 (0.01-0.07)	0 (0-0)	0 (0-0)	0 (0-0)	0 (0-0)	0.01 (0-0.04)	0 (0-0)
Unidentified jaeger	0 (0-0)	0 (0-0)	0 (0-0)	0 (0-0)	0 (0-0)	0 (0-0)	0 (0-0)

Appendix 1.4 continued…

	Study Area/Season						
	Klondike		Statoil		Burger		
Species-group/species	Jul/ Aug	Aug/ Sep	Jul/ Aug	Aug/ Sep	July/ Aug	Aug/ Sep	Sep/ Oct
ALCIDS							
Dovekie	0	0	0	0.01	0	0	0.01
	(0-0)	(0-0)	(0-0)	(0-0.04)	(0-0)	(0-0)	(0-0.03)
Common Murre	0	0.03	0	0	0	0.01	0
	(0-0)	(0.01-0.07)	(0-0)	(0-0.03)	(0-0)	(0-0.03)	(0-0)
Thick-billed Murre	0.83	0.47	0.2	0.09	0.19	0.07	0.02
	(0.52-1.32)	(0.33-0.67)	(0.07-0.56)	(0.05-0.17)	(0.12-0.3)	(0.03-0.16)	(0.01-0.05)
Unidentified murre	0.03	0.01	0.01	0.01	0	0.01	0
	(0.01-0.12)	(0-0.04)	(0-0.05)	(0-0.03)	(0-0)	(0-0.04)	(0-0)
Black Guillemot	0.01	0	0.01	0	0.01	0	0
	(0-0.06)	(0-0)	(0-0.04)	(0-0)	(0-0.05)	(0-0)	(0-0)
Pigeon Guillemot	0	0	0	0	0	0	0
	(0-0)	(0-0)	(0-0)	(0-0)	(0-0)	(0-0)	(0-0)
Kittlitz's Murrelet	0.02	0.01	0.01	0	0	0.01	0
	(0-0.14)	(0-0.04)	(0-0.07)	(0-0)	(0-0)	(0-0.04)	(0-0)
Ancient Murrelet	0	0.1	0	0.24	0	0.06	0.18
	(0-0)	(0.03-0.31)	(0-0)	(0.12-0.5)	(0-0)	(0.02-0.17)	(0.07-0.44)
Unidentified murrelet	0	0	0	0	0	0	0
	(0-0)	(0-0)	(0-0)	(0-0)	(0-0)	(0-0)	(0-0)
Parakeet Auklet	0	0.04	0.07	0.01	0	0.08	0.08
	(0-0)	(0.02-0.08)	(0.02-0.24)	(0-0.05)	(0-0)	(0.03-0.22)	(0.03-0.22)
Least Auklet	0.23	0.88	1.68	1.06	0.32	2.71	0.67
	(0.09-0.6)	(0.52-1.48)	(1.09-2.59)	(0.73-1.55)	(0.17-0.61)	(1.87-3.94)	(0.46-0.98)
Crested Auklet	5.89	7.06	2.76	6.17	6.16	5.03	6.74
	(3.16-10.99)	(5.43-9.18)	(1.51-5.08)	(4.66-8.17)	(3.2-11.83)	(3.88-6.51)	(4.8-9.48)
Unidentified auklet	0.07	0.1	0.02	0.01	0.01	0.15	0
	(0.02-0.27)	(0.05-0.19)	(0-0.07)	(0-0.04)	(0-0.05)	(0.08-0.31)	(0-0.03)
Horned Puffin	0.03	0	0.01	0	0.03	0	0
	(0.01-0.11)	(0-0)	(0-0.04)	(0-0.03)	(0.01-0.13)	(0-0.03)	(0-0)
Tufted Puffin	0.01	0	0.01	0	0	0	0
	(0-0.06)	(0-0)	(0-0.04)	(0-0)	(0-0)	(0-0.03)	(0-0)
Unidentified puffin	0	0	0	0	0.01	0	0
	(0-0)	(0-0)	(0-0)	(0-0)	(0-0.06)	(0-0)	(0-0)
Unidentified alcid - small	0	0	0	0	0	0	0.05
	(0-0)	(0-0)	(0-0)	(0-0)	(0-0)	(0-0)	(0.02-0.13)
Unidentified alcid	0.16	0.03	0.01	0.01	0	0.02	0
	(0.02-1.14)	(0.01-0.08)	(0-0.04)	(0-0.08)	(0-0)	(0.01-0.06)	(0-0)

CHAPTER 2: ECOLOGICAL SHIFT FROM PISCIVOROUS TO PLANKTIVOROUS SEABIRDS IN THE CHUKCHI SEA, 1975–2012[1]

2.1 Abstract

Summer ice cover in the Arctic Ocean reached the lowest minimal extent on record in 2012. Sea ice now forms later and melts earlier than it did 30 years ago, and it now melts completely in all parts of the Chukchi Sea. This decline in sea ice is expected to have repercussions on the trophic structure in this environment, and there are indications that changes already have taken place in the seabird community. We compared boat-based survey data on seabirds that were collected in the Chukchi Sea between July and October during 1975–1981 (historical data) with surveys conducted during 2007–2012 (recent data).We related the composition of the seabird community to sea-ice cover to explore how it may be responding to changes in the oceanography of the Chukchi Sea. The seabird community historically was composed predominantly of piscivorous Black-legged Kittiwakes (*Rissa tridactyla*) and murres (*Uria* spp.). In contrast, the seabird community now is composed predominantly of planktivorous seabirds such as Crested Auklets (*Aethia cristatella*) and Short-tailed Shearwaters (*Puffinus tenuirostris*), both species that prey primarily on euphausiids. Total abundance of seabirds declined in three of four strata in the eastern Chukchi Sea, primarily due to declines in piscivorous and omnivorous species. These changes in the abundance and community composition of seabirds were associated with changes in ice cover. Earlier ice retreat appears to contribute to an environment that is more favorable to the sustained production of large oceanic copepods and euphausiids. We propose that long term changes (4 decades) in the abundance and composition of the seabird community reflect an increase in the availability of large zooplankton prey in the region.

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2.2 Introduction

Summer ice cover in the Arctic Ocean reached the lowest minimal extent on record in 2012 (Laxon et al., 2013). Because sea-ice cover strongly influences habitat in the Arctic (Mueter & Litzow, 2008; Hunt et al., 2013), this decline is anticipated to have repercussions on the trophic structure of this environment. Pelagic ecosystems in polar regions are particularly sensitive to changes in ice cover; these changes already have been documented at multiple trophic levels (Kitaysky & Golubova, 2000; Ainley et al., 2005; Beaugrand, 2009; Kwasniewski et al., 2012). The effects of climate change on seabirds are indirect, operating through changes in local and regional food webs and within pelagic habitats (Sydeman et al., 2012).

The timing and patterns of ice melt can alter the productivity of polar shelf seas by influencing water-column structure and the availability of light for supporting photosynthesis (Hunt et al., 2011; Palmer et al., 2013). For example, in the northern Bering Sea, there has been a shift over the past 3 decades from a benthic-dominated system to one dominated numerically by pelagic organisms (Grebmeier et al., 2006a). The Chukchi Sea relies on water masses advected from the Bering Sea for much of its primary and secondary productivity (Grebmeier et al., 2006b), suggesting that changes observed in the northern Bering Sea also will affect the ecology of the Chukchi Sea. A second factor influencing productivity in the Chukchi Sea is environmental conditions during the open-water season that promote further growth of Pacific zooplankton once they reach the Chukchi Sea. We anticipate that as the open-water season begins earlier, the increase in light and water column heating in regions formerly covered with ice can promote further development of zooplankton biomass (Questel et al., 2013) that then is available as prey for higher trophic levels such as seabirds.

Historical studies of the avifaunal communities of the northeastern Chukchi Sea conducted in the late 1970s and early 1980s provided a snapshot of the community composition and density of seabirds (Divoky, 1987) but did not address the variability of this community or link species to their habitat. Recent efforts to describe the circumpolar species diversity and distribution of marine birds (Bluhm et al., 2011; Huettmann et al., 2011) do not include regionally important taxa such as auklets and phalaropes that are critical to understanding energy flow in this ecosystem (Piatt & Springer, 2003). Fortunately, many of the historical seabird surveys were conducted as part of the Outer Continental Shelf Environmental Assessment

Program (OCSEAP) following protocols that are similar to those currently used to survey seabirds. The data from those historical surveys were archived by the U.S. Geological Survey (USGS) in the North Pacific Pelagic Seabird Database (NPPSD) and now offer a rare opportunity to combine historical data with surveys that have been conducted recently to assess the effects of climate change in Alaskan arctic waters on a multi-decadal scale.

We compared boat-based survey data collected in the Chukchi Sea during 1975–1981 (historical period) with surveys conducted during 2007–2012 (recent period) to determine how the seabird community has responded to changes in the physical and biological oceanography of the Chukchi Sea. Specifically, our objectives were to (1) compare species composition of historical seabird communities with recent ones; (2) assess changes in the relative abundance of focal species between the two time periods; and (3) examine relationships between seabird community and changes in the timing and extent of sea ice in the region over the past 4 decades that have driven changes in the open-water pelagic habitat.

2.3 Methods

2.3.1 Study area

In the Chukchi Sea, the net flow of water is northward through Bering Strait and toward the Arctic Ocean (Coachman et al., 1975). The broad northward flow through Bering Strait is steered by bathymetry into three main branches—one east of Hanna Shoal that feeds into Barrow Canyon, one west of Herald Shoal that feeds into Herald Valley, and one between the two shoals, referred to as the Central Channel flow (Figure 2.1; Weingartner et al., 1998, 2005). This separation also is evident in water-mass properties (Weingartner et al., 2005, 2013) that define the oceanic habitat used by seabirds. Within the Chukchi Sea, the Alaska Coastal Current (ACC) lies east near the Alaska coastline and flows northward, carrying Alaskan Coastal Water (ACW), a warm (>2 °C), low-salinity (<32.2) water-mass that originates south of Bering Strait. The currents farther offshore move Bering Sea Water (BSW; Coachman et al., 1975), a warm (>2 °C), high-salinity (>32.4) water-mass, northward through the Central Channel and Herald Valley (Weingartner et al., 2005). This BSW is a mixture of Anadyr Water and Bering Shelf Water from south of Bering Strait with a higher nutrient content and transports greater numbers of oceanic zooplankton, especially larger zooplankton, than does ACW (Walsh et al., 1989; Springer & McRoy, 1993).

In addition to the warm, Bering-derived summer water-masses advected northward through Bering Strait, Chukchi shelf waters are modified during the fall and winter by ice formation and during the spring by ice melt. Ice formation rejects brine that sinks to the sea floor and forms cold (–2 to +1 °C), salty (>32) Winter Water (WW) below the ice layer. In the spring, ice melts at the surface and forms cold (–1 to +2 °C), low-salinity (<30) Meltwater (MW) that is depleted of nutrients. This MW eventually becomes mixed with waters below by summer winds. In the summer, the bottom layer of the water-column often still contains WW left over from the previous winter, whereas the surface layer consists of either MW or BSW, depending on location. This stratification increases from spring to summer and typically erodes in the fall as strong winds, cooling, and freezing enhance vertical mixing (Weingartner et al., 2005).

This study was conducted in the eastern Chukchi Sea, in an area bounded by Bering Strait to the south, the U.S.–Russia maritime boundary (168° 58’ 37” W) to the west, and 73 °N to the north and included a total area of 231,868 km^2 (Figure 2.1). We divided the study area into 4 strata to account for the effects that latitude, water-masses, and currents can have on determining oceanic habitat (Piatt & Springer 2003). The Southern Chukchi stratum has an area of 53,631 km^2 and is influenced by strong flows through Bering Strait of Bering Shelf Water and Anadyr Water to the west and ACW to the east. The Nearshore stratum has an area of 35,673 km^2 and is influenced by coastal flows that carry predominantly ACW, although there are episodic flow reversals in the northern half of this stratum that transports slope waters up Barrow Canyon (Aagaard & Roach, 1990; Weingartner et al., 1999). This stratum also receives waters that flow eastward from the Central Channel that eventually enter Barrow Canyon (Weingartner et al., 2005). The Offshore stratum has an area of 81,159 km^2 and is influenced by both the Central Channel flow that entrains Bering Sea Water along the western edge and resident waters over Hanna Shoal that are characterized by a two-layer water column with MW on top and WW on the bottom. The Northern stratum has an area of 61,405 km^2 and includes the continental slope into the Arctic Basin. This stratum is influenced by waters flowing north from the Chukchi and upwelling along the continental shelf-break from the Arctic Ocean.

2.3.2 Data collection

Historical data were collected by researchers during 1975–1981 (Figure 2.2) from ships of opportunity following protocols developed by the U.S. Fish and Wildlife Service (USFWS; Tasker et al., 1984, Gould and Forsell, 1989). These data were archived in the NPPSD, which is maintained by the USGS. We included historical data that were collected on the Russian side of the maritime boundary because the agreement establishing this boundary was not signed until 1990 (U.S. Department of State 1990). We conducted research cruises during 2007–2012 that covered much of the open-water period (roughly, July – October) of the northeastern Chukchi Sea (Figure 2.2) and followed a sampling protocol that was comparable to methods used to collect the historical data. We combined data sets from 4 recent studies that we conducted in the region to obtain coverage in all strata (Table 2.1): the Chukchi Sea Environmental Studies Program (CSESP; 2008–2012; Gall et al., 2013a), the Alaska Monitoring and Assessment Program (AKMAP; 2010–2011; Morgan et al., 2012), surveys conducted for the U.S. Fish and Wildlife Service (USFWS) near Barrow (2009–2010, Morgan et al., 2010); and surveys conducted by the USFWS on ships of opportunity associated with a variety of research programs (2007–2012; Kuletz et al., 2008; Kuletz & Labunski, 2015).

We surveyed continuously when the ship was moving along a straight-line course at a minimal velocity of 9 km/h, recording environmental conditions every 10 min. We collected data 9–12 h/day during daylight hours, weather and sea-ice conditions permitting. We generally stopped surveys when sea height was Beaufort 6 (seas ~2–3 m) or higher, although we occasionally continued to sample if observation conditions were still acceptable (e.g., if seas were at the lower end of Beaufort 6 and we were traveling with the wind and seas). One observer stationed on the bridge of the vessel recorded all birds seen within a radius of 300 m in a 90° arc from the bow to the beam on one side of the ship (the count zone), locating and identifying seabirds with 10X binoculars as needed. For each bird or group of birds, we recorded species, total number of individuals, and behavior.

In the count zone, we counted all birds seen on the water, taking care to avoid recounting the same individuals. For flying birds, we conducted scans ~once/min (the exact frequency varied with ship's speed) and recorded an instantaneous count (or "snapshot") of all birds flying within the count zone. This snapshot method reduces the bias of overestimating the density of flying birds (Tasker et al., 1984, Gould and Forsell, 1989). We counted only those flying birds that entered the count zone from the sides or front and excluded flying birds that entered from behind the ship (i.e., an area that already had been surveyed) to avoid the possibility of counting ship-following birds.

We entered all data directly into a computer connected to a global positioning system (GPS) with DLog software (R. G. Ford Consulting, Portland, OR) or TigerObserver software (TigerSoft, Las Vegas, NV). These computer programs time-stamped and georeferenced every observation and recorded the survey track line in ~ 20 sec intervals.

2.3.3 Data analysis

Community analysis

We used multivariate analyses and descriptive statistics to explore seasonal and interannual changes in the structure of the seabird community. For the multivariate analysis, we included all bird observations that were identified to species. We grouped the data into sample units by stratum and year and used ordination for analysis. We used the species information to calculate a Bray–Curtis similarity matrix (Bray & Curtis, 1957) to which we applied non-metric multidimensional scaling (nMDS; Clarke & Green, 1988). This ordination technique then visualizes the similarity in overall community composition among samples as distances mapped in 2-dimensional space (Clarke & Green, 1988). The stress coefficient of the 2D ordinations was 0.177, indicating adequate fit to the data (Clarke & Ainsworth, 1993). We examined the variation in species composition among strata and time periods with permutational multivariate analysis of variance (PERMANOVA), which partitions variation and requires no assumptions about the distribution or correlations among the variables (Anderson, 2001). We used the package vegan (Oksanen et al., 2011) for the MDS analysis; all statistical analyses were conducted in R 3.0.1 (R Core Team 2013).

We included all bird observations that were identified at least to family in summaries of changes in species assemblages by stratum and year (Magurran, 2004). We aggregated species into 4 ecological groups that represented foraging guilds (Table 2.2): planktivores, omnivores, piscivores, and benthivores. We examined differences between historical and recent periods to examine the hypothesis of a shift in community structure between periods.

Density analysis

We compared the density of birds during the historical period with density during the recent period in each of 4 strata of the eastern Chukchi Sea to determine whether there have been long-term changes in the seabird community. For this comparison, we used total birds and 8 focal species from among the 10 most abundant species that represented the 4 foraging guilds, thereby providing an overview of functional ecological groups within the seabird community.

We pooled years within the 2 time periods and evaluated changes in abundance on each transect by using generalized linear models with period, region, and the interaction between these factors as explanatory variables (package MASS; Venables and Ripley, 2002). We modeled the error terms with a negative binomial distribution to account for overdispersion in count data and used the area (km^2) of each transect as an offset to account for survey effort. We excluded the Northern region in comparisons for species that were not recorded there during the historical time period. Because distance data were not available for the historical observations, we could not correct the density estimates for detection probability.

We summarized sea-ice conditions during the years included in our study to evaluate the direction and magnitude of change in ice cover. For the years 1979–2012, we used Special Sensor Microwave Imagery (SSM/I) passive microwave satellite sensor data from the National Snow and Ice Data Center (NSIDC; www.nsidc.org) to quantify the timing of ice advance, ice retreat, and changes in percent sea-ice cover in each stratum. These data are available from the fall and winter of 1978–1979 to the present. We use the daily data product from the standard 25-km grid derived using the NASA Team algorithm (Cavalieri et al., 2008) for consistent data resolution throughout the analysis period. Prior to 1979, data from satellites were less reliable, so, for the years 1975–1978, we used data from aerial surveys of ice cover in the Chukchi Sea. These original ice charts were scanned and summarized 4 times/month (1st, 8th, 15th, and 23rd days of each month) to provide ice cover in tenths on a grid 0.25 °N × 0.25 °W. Data are available from the Alaska Center for Climate Assessment and Policy (http://seaiceatlas.snap.uaf.edu/).

The date of sea-ice retreat was defined as the date when the sea-ice cover was <10% within a stratum. Similarly, the date of sea-ice advance was defined as the date when sea-ice cover was ≥10% within a stratum. The number of ice-free days was defined as the number of days elapsed between the date of sea-ice retreat and the date of sea-ice advance.

We also assessed the influence of changing sea-ice conditions on the density of seabirds directly by modeling the influence of days of ice-free water on the density of 6 species of seabirds that had sufficient sample size in both historical and recent periods. Because the 3 metrics of ice are highly correlated ($r > 0.8$), we selected only the number of days of ice-free water as the proxy for oceanographic change to avoid issues of collinearity. For this analysis, the number of days ice-free was calculated individually for each 25-km grid cell.

We built logistic regression models where presence of seabirds within a grid cell was the dependent variable, and the duration of ice-free water and stratum (Southern, Nearshore, Offshore, and Northern) were independent variables. We started with full models, including the interaction of terms DAYS ICE-FREE and STRATUM and used backwards-stepwise removal of terms with $P > 0.05$ from Wald tests (Hosmer et al., 2013). Because the area sampled varied among grid cells, we included sampling area as an offset. We evaluated strength of the models with Akaike's Information Criterion (AIC) and likelihood ratio tests comparing them to the null model. We drew inference from the model best supported by the data (Burnham & Anderson, 2002).

2.4 Results

2.4.1 Community composition

We compiled seabird data collected in the eastern Chukchi Sea on 1,675 km^2 of surveys during 1975–1981 and on 15,157 km^2 of surveys during 2007–2012 (Table 2.1). These surveys recorded 58,905 birds during the historical period and 225,948 birds during the recent period. Mean densities ranged 0–19.9 birds/km^2 in the historical period and 0–9.3 birds/km^2 in the recent period (Table 2.2).

Over the past 37 years, the seabird community has included a total of 50 species, of which 39 were recorded in both historical and recent time periods; 4 species (Iceland Gull, Red-legged Kittiwake, Harlequin Duck, Black Scoter) were recorded only during 1975–1981, and 7 species (Ancient Murrelet, Pelagic Cormorant, Mew Gull, Aleutian Tern, Pigeon Guillemot, Marbled Murrelet, Fork-tailed Storm-Petrel) were recorded only during 2007–2012 (Table 2.2).

Multivariate analyses of the seabird community indicated that species-composition varied primarily between the two periods (Figure 2.3a), shifting from a community dominated by piscivorous birds to one dominated by planktivorous birds (Figure 2.4); this shift was evident in all strata (Figure 2.3b). The MDS ordination separated into 2 groups, with overlap caused primarily by differences among strata (Table 2.3). The Northern stratum showed the biggest shift in community structure over time (Figure 2.3b), converging in composition with the other regions in the recent years in which it was sampled.

The patterns in species-composition identified in the multivariate analyses were reflected in changes in the relative abundance of each of the 4 feeding guilds among strata and years (Figures 2.4 and 2.5). Most notably, the relative abundance of piscivores in all regions decreased from the historical period to the recent period (Figure 2.4). The Northern stratum was dominated numerically by planktivores in 1976 and 2009–2012, but planktivores were absent from there in 1977 and rare in 2007, suggesting high variability in species-composition (Figure 2.5). The relative abundance of planktivores in the Offshore stratum increased from the 1970s to the 1980s, with planktivores dominating numerically in 2007–2012. In the historical period, the Nearshore and Southern strata were dominated numerically by planktivores in some years and by piscivores and benthic-feeding birds in other years; however, in the recent period, species-composition was less variable, with planktivores dominating numerically in both strata in most years from 2007–2012. Benthic-feeding birds (primarily eiders) composed 2–85% of all birds, depending on the stratum and year (Figure 2.5), because they sometimes occurred in large groups (up to 1,500 birds). Similarly, planktivores composed 67–90% of all birds in some strata and historical years because Short-tailed Shearwaters also occurred in large groups.

2.4.2 Changes in seabird density

The total density of seabirds has declined significantly in 3 of the 4 strata in the eastern Chukchi Sea over the past 37 years ($P < 0.01$ for PERIOD*STRATUM), with the largest declines occurring in the Nearshore stratum (Figure 2.6). Only the Northern stratum showed no significant difference in density between the two time periods. These declines are driven primarily by declines in the density of piscivorous and omnivorous species. Piscivorous Black-legged Kittiwakes and omnivorous Glaucous Gulls were less abundant in all strata during the recent period than during the historical period (Figure 2.7). Declines of both species were greatest in the Nearshore stratum, with mean decreases of 16.5 birds/km^2 for Black-legged Kittiwakes and 20.2 birds/km^2 for Glaucous Gulls. Northern Fulmars were present in low abundance (<0.6 birds/km^2) both historically and recently. Their density increased in the Northern, Nearshore, and Southern strata but showed no significant change in the Offshore stratum. Thick-billed Murres now are less abundant in the Offshore and Southern strata than they were in the historical period and showed no significant change in abundance in the Nearshore stratum during the recent period.

Planktivorous Crested and Least auklets and Short-tailed Shearwaters were more abundant in recent years than they were in historical years (Figure 2.8), with the largest increases for Crested Auklets in the Offshore stratum (estimated mean increase: 6.1 birds/km^2), for Least Auklets in the Southern stratum (estimated mean increase: 3.6 birds/km^2), and for Short-tailed Shearwaters in the Nearshore stratum (estimated mean increase: 7.1 birds/km^2). Further, Least Auklets and Short-tailed Shearwaters were not recorded in the Northern Stratum in the historical period. In contrast, phalaropes were less abundant in the Southern stratum recent years than they were in historical years (Figure 2.6) and showed no significant change in abundance in the other strata.

2.4.3 Changes in sea-ice cover

The duration of open water (defined as 25-km^2 grid cells with <10 % ice cover) in the Northern, Offshore, and Nearshore strata of the eastern Chukchi Sea has increased by ≥50 days over the past 3 decades (Figure 2.9). Sea ice now forms later and melts earlier than it did 30 years ago, and it now melts completely in all strata of the eastern Chukchi Sea. Prior to 1990, there were years in which only the Southern stratum would be considered ice-free. During the 1990s, the ice retreated from all but the Northern stratum in every year; since 2002, the entire eastern Chukchi Sea has been ice-free for at least 50 days each year.

These changes in ice cover are associated with changes in the presence of seabirds, although the relationships between ice cover and seabird abundance varied among taxa and strata (Figure 2.10). Black-legged Kittiwakes, Glaucous Gulls, and phalaropes were more likely to occur in years with few ice-free days. The negative association with ice-free days was strongest for these three species in the Southern and Nearshore strata. In the Northern stratum, Black-legged kittiwakes and glaucous gulls also were less likely to occur in years of many ice-free days whereas phalaropes had a low probability of occurrence regardless of ice conditions. In the Offshore stratum, however, there was little evidence of a negative relationship for any of these species.

Crested auklets, northern fulmars, and short-tailed shearwaters were more likely to occur in years with many ice-free days and this relationship was consistent in all strata (Figure 2.10). The probability of occurrence for these three species generally was highest in the Offshore stratum. In the Northern stratum, the probability of occurrence for crested auklets was similar to that in the Offshore stratum in years with >50 days ice-free whereas short-tailed shearwaters had a lower probability of occurrence than in the Offshore and northern fulmars were least likely to occur there. In the Nearshore stratum, probabilities of occurrence paralleled and were lower than probabilities in the Offshore stratum. In the Southern stratum, northern fulmars and short-tailed shearwaters had similar probabilities of occurrence whereas crested auklets were least likely to occur.

2.5 Discussion

Over the past 40 years, there has been an increase in the proportion of subarctic seabirds, and particularly planktivorous species, in the eastern Chukchi Sea during the open-water period of late July to early October. Many species that breed or summer in the Bering Sea have historically moved northward into the Chukchi Sea during periods of maximal ice retreat (Watson & Divoky 1970, Divoky 1987). Our recent data indicate that, as summer ice cover has declined, a suite of planktivorous species, including Short-tailed Shearwaters, Least and Crested auklets, and Northern Fulmars, now is present farther north and in higher abundance than it was historically. Although they penetrated beyond Cape Lisburne only in late August and early September in the 1970s and 1980s, we now see these species regularly as far as 72 °N and remaining into late October. Other species such as Kittlitz’s and Ancient murrelets are more episodic in their use, showing up in large numbers in some years but not at all in others. Nonetheless, all of these Bering Sea species have become common throughout the eastern

Chukchi Sea, indicating that seabird distributions have changed in response to a warming and increasingly ice-free Arctic.

2.5.1 Changes in community composition

The seabird community of the Chukchi Sea contains a list of species that has changed little over the past 40 years, but the relative abundance of species has shifted in favor of planktivorous seabirds that are coming north from the Bering Sea. Based on only the historical data, phalaropes were thought to replace auklets as the dominant planktivorous birds north of Bering Strait (Piatt & Springer, 2003); in fact, planktivorous seabirds in general were assumed to be insignificant consumers in the Chukchi Sea as a whole (Piatt & Springer, 2003; Hunt et al., 2013). The data presented here and in other recent studies indicate that, although planktivorous seabirds did not dominate the seabird community in the 1970s and early 1980s, they have become the numerically dominant feeding guild of the 2000s and 2010s, particularly those species common in the Bering Sea such as Crested Auklets and Short-tailed Shearwaters (Sigler et al., 2011; Gall et al., 2013b; Wong et al., 2014; Kuletz et al., 2015).

Species typically associated with the high Arctic and sea ice include Ivory and Ross's gulls and Black Guillemots. Historically, they occurred consistently in the Chukchi Sea, but in low numbers (Watson & Divoky, 1970; Divoky, 1987). They rarely have been recorded in recent years, despite a large increase in effort from historical surveys. Ice has retreated entirely from the Chukchi Shelf in every summer since 1996 and is delayed in re-forming in the fall, restricting the habitat available for these birds.

Species only recently recorded in the eastern Chukchi Sea are species that either nest in the Bering Sea and/or North Pacific or have made the transit from the Atlantic Ocean. The Short-tailed Albatross, Rhinoceros Auklet, Ancient Murrelet, Mew Gull, and Fork-tailed Storm Petrel all are Pacific species that have been able to extend their ranges northward, presumably in response to reductions in ice and warming climatic conditions in the Chukchi Sea (Day et al. 2013). Incidental observations recently recorded off-transect included the Northern Gannet, an Atlantic species that was recorded in the Pacific for the first time in 2010 (Day et al., 2013). It presumably traversed the Northwest Passage during a period of open water. If so, it is one of three seabird species from the North Atlantic recorded in the Pacific in recent years (Atlantic

Puffin—Kharitonov 2009; Great Black-backed Gull—Day et al. 2013). Of the species recorded only during the historical period, Red-legged Kittiwakes are considered endemic to the Bering Sea and Iceland Gulls are an Atlantic species. These species may have been vagrant individuals, or may have been misidentified; Red-legged Kittiwakes are very similar to the more common Black-legged Kittiwake and Iceland Gulls are very similar to Thayer's Gulls which migrate through the Chukchi Sea (Snell, 2002). We anticipate that as summer ice cover continues to decline and ship traffic increases, incidental observations of Bering Sea and Atlantic species will become more common in the Chukchi Sea.

2.5.2 Changes in density

As species that breed in the Bering Sea (e.g., Crested and Least auklets, Northern Fulmars) or even farther south in Australia (Short-tailed Shearwaters) have become more abundant in the eastern Chukchi Sea over the past 40 years, species that breed along the Chukchi coast (e.g., Black-legged Kittiwakes, Thick-billed Murres) and inland on the Arctic Coastal Plain (e.g., Glaucous Gulls, phalaropes) appear to be less abundant. These latitudinal shifts in abundance are consistent with the retreat of sea ice opening up habitat and creating conditions in the Chukchi Sea that more closely resemble the productive areas of the northern Bering Sea (Sigler et al., 2011). Species that rely primarily on prey of Pacific origin (Crested Auklets, Northern Fulmars, and Short-tailed Shearwaters) are more likely to occur as sea-ice cover declines whereas those that forage in arctic waters (Black-legged Kittiwakes, Glaucous Gulls, and phalaropes) are less likely to occur, suggesting that ice cover is an ecological driver that affects variations in seabird abundance interannually and over longer timescales.

Birds that are surveyed at sea include both breeding and non-breeding individuals, providing an ecosystem perspective that includes free-ranging animals not necessarily restricted by central-place foraging (Ainley et al., 2012). The distribution and abundance of seabirds within 40 km of large breeding colonies such as the Diomede Islands, Cape Lisburne, and Cape Thompson may be influenced by the availability of nesting habitat (Swartz, 1967; Piatt & Springer, 2003; Wong et al., 2014). Our data, however, spanned the entire open-water season, including September, which is after most birds have fledged from colonies. The birds that we surveyed include non-breeding birds, birds that may have attempted to breed but failed, and birds that bred successfully. Regardless of their breeding status in a given year, most birds are free of their land-bound constraints by September, so their presence and abundance in the study area implies that food resources are available and energetically profitable to acquire.

Decline of piscivorous species

The decline in the density of seabirds in the eastern Chukchi Sea was driven primarily by declines in density of black-legged kittiwakes and glaucous gulls in the Nearshore stratum (i.e., within 40 km of the coast). The Southern stratum also has experienced a decline in density of total birds, primarily due to declines of Black-legged Kittiwakes, Thick-billed Murres, and phalaropes. Black-legged Kittiwakes and Thick-billed Murres are more cosmopolitan in their distribution than are Glaucous Gulls and phalaropes, with their summer ranges including the Pacific Arctic and subarctic. Like Glaucous Gulls, however, Black-legged Kittiwakes and murres are flexible foragers that rely on prey other than oceanic zooplankton and are often associated with Alaskan Coastal Water (ACW; Swartz 1967; Piatt & Springer 2003). Phalaropes are planktivorous, but they are restricted to foraging at or near the surface and on *Calanus* spp., zooplankton that are characteristic of ACW (Brown & Gaskin 1988; Haney & Stone 1988). The declines in abundance of these 4 species that rely on prey resources associated with ACW suggest a possible reduction in the abundance of fish species in this water mass as annual sea-ice cover has declined. Alternatively, declines in the density of these birds may be related to the expansion of available habitat as sea ice retreats earlier. With an increase in available habitat, the birds can disperse over a larger area, decreasing the density (birds km^{-2}) while the total abundance in the region remains similar. Although a decline in density would account for the apparent decline in abundance of piscivorous birds in the Nearshore stratum, it does not account for the increase in the density of planktivorous birds, particularly short-tailed shearwaters.

Population trends measured at one of the two biggest seabird colonies in the eastern Chukchi Sea provide some additional insight into the long-term change in foraging conditions in ACW. The productivity of Black-legged Kittiwakes shows a long-term decline (chicks/nest start) during the 40 years that nests have been monitored at the Cape Lisburne breeding colony, with productivity below the long-term (1976–2012) mean in all but 2 years since 2000 (Dragoo et al., 2013). Despite this decline in productivity, counts of adult kittiwakes and Thick-billed Murres present at the colony have increased during the same period. The decline in productivity, coupled with the increase in number of birds loafing at the colony rather than engaging in chick-rearing, suggests that food availability may be limiting breeding activity (Golet et al., 2004). Because they are long-lived species, these birds may be foregoing breeding to maximize their own survival (Golet et al., 1998). Rather than traveling north to forage after the breeding season, they may be heading south to foraging locations in the northern Bering Sea where fish and other preferred prey may be more readily available (Sigler et al., 2011; Stabeno et al., 2012).

Increase of planktivorous species

Shearwaters have been among the most abundant seabirds in the Chukchi Sea since the earliest shipboard surveys (Swartz, 1967; Watson & Divoky, 1970; Divoky, 1987). At that time, they were not recorded in the Northern stratum of the Chukchi Sea and occurred irregularly in the Beaufort Sea (Divoky, 1987), indicating that the Chukchi represented the northernmost limit of annual migration from breeding colonies in Australia for most of these birds. In the past 40 years, their abundance in the Chukchi Sea has increased, and they are now being recorded nearly annually in the Beaufort Sea (USGS, 2014). Recent surveys determined that they continue to be among the most abundant birds in the Chukchi Sea and they are most abundant within 40 km of the coast , where they are foraging in ACW (Gall et al., 2013b; Wong et al., 2014; Kuletz et al., 2015). This increase is a contrast to the decline in abundance of piscivorous birds within the same stratum.

The Offshore stratum that historically was dominated numerically by Black-legged Kittiwakes and Thick-billed Murres has been taken over by Crested Auklets, which are now the most abundant seabirds in August and September (Gall et al., 2013b; Kuletz et al., 2015). The increase in abundance of Crested Auklets is consistent with the hypothesis that euphausiids are transported through the Central Valley of the Chukchi Sea (Berline et al., 2008; Ashjian et al., 2010) and the reduction in ice cover is enhancing the accessibility of prey. Not only are Crested Auklets feeding in the Offshore stratum during and after the breeding season, it appears that they may be flightless for a few weeks in the area as they complete their molt (AEG, KJK, pers. obs). The limited mobility and the energetic demands associated with molt suggest that the food supply is reliable enough to support these physiological demands.

There are, of course, challenges in making comparisons with historical data, particularly when those data were collected opportunistically and by different researchers. The historical data were collected from ships of opportunity where the tracks were nonrandom and the survey coverage differed among years and strata. The only stratum that was surveyed in all 6 years of the historical period was the Nearshore stratum, whereas survey coverage in the Northern stratum was limited due to heavy ice cover. The reduction in ice cover of the past 40 years means that there has been an increase in the availability of open water and therefore, greater opportunity for ship-based surveys in the northern parts of the Chukchi Sea. Survey coverage also was greatly increased in the Offshore stratum in recent years because of interest in areas that are currently leased for oil and gas exploration. Despite the uneven sampling coverage, the trends in all areas of the eastern Chukchi Sea consistently indicate a northward expansion of subarctic seabirds, especially planktivorous ones, into the Chukchi Sea.

2.5.3 System-wide changes and implications

Earlier ice retreat and a longer ice-free season (Wang & Overland, 2009, 2012) may contribute to an environment that is more favorable to primary and secondary production. The increase of light availability through thinner winter ice and the earlier ice retreat can lead to higher production by ice algae along the coast and at ice edges (Brown & Arrigo, 2012; Palmer et al., 2013). So far, models base on satellite observations suggest there has been a 65% increase in primary productivity in the Chukchi Sea associated with the increase in open water and the longer growing season in 2007 than there was in 1998–2002 (Arrigo et al., 2008). In a shallow Chukchi Sea with less ice cover, increased easterly winds could intensify shelf-break upwelling (Carmack & Chapman, 2003; Mathis et al., 2012) that will enhance the nutrient supply, and support larger phytoplankton and zooplankton throughout the open-water season (Lane et al., 2008).

In addition to an increase of in situ production in the Chukchi Sea, there also is evidence that northward flow through Bering Strait is increasing (Woodgate et al., 2012), which should increase the advection of phytoplankton and zooplankton into the Chukchi Sea (Springer et al., 1989). These Pacific zooplankters are being advected into a region where warming summer waters can sustain higher growth rates and develop greater zooplankton biomass (Questel et al., 2013). Although the historical zooplankton community is not as well-documented as the seabird community, there are suggestions of higher zooplankton abundance and biomass along the

Chukchi shelf-break in the 2000s than historically (Lane et al., 2008) and of increased abundance of meroplankton over the northeastern Chukchi shelf between 1991–1992 and 2007–2008 (Matsuno et al., 2011). Concurrently there has been an increase in the bowhead whale population of 3.7% year^{-1} during 1978–2011 (Givens et al., 2013). These large planktivores prey on zooplankton, especially euphausiids, which are the primary prey of Crested Auklets and Short-tailed Shearwaters and transit the Chukchi Sea to reach Barrow Canyon, where many bowhead whales feed (Berline et al., 2008). The steady annual increase in the bowhead population indicates that their preferred prey is readily available.

The Chukchi Sea is the transition zone from the highly productive waters of the northern Bering Sea to the low productivity of the Arctic Ocean. As recently as 2003, the boundary between these two systems was identified in the southern Chukchi Sea (Piatt & Springer, 2003). As sea ice retreats earlier in the summer and the Chukchi remains ice-free for longer each year, the boundary between these two systems appears to be shifting northward. These connections have stretched the biogeographic province characterized by zooplankton, surface fish, and seabirds associated with Bering Sea Water so that it now extends from the Chirikov Basin north of St. Lawrence Island to include the eastern Chukchi Sea as far north as Barrow Canyon (Sigler et al., 2011).

We propose that the changes in the abundance and composition of the seabird community in the eastern Chukchi Sea reflect an increase in the availability of zooplankton prey in the region. The increase in abundance of planktivorous species of seabirds in the Chukchi Sea suggests that large zooplankton persist in the water column of the Chukchi Sea for longer now than they did 40 years ago. This longer persistence allows for the seabird community, especially planktivorous alcids, to remain in the Chukchi Sea throughout the summer and fall to exploit this food resource that is available over the wide and shallow Chukchi shelf. As long as the Chukchi Sea continues to freeze in winter, however, the process of ice formation will maintain a pool of cold Winter Water that acts a thermal barrier to many Bering Sea species of fishes, particularly in the offshore area (Sigler et al., 2011; Day et al., 2013; Hunt et al., 2013). Without an established community of plankton-feeding fishes, seabirds and marine mammals may remain the primary predators on zooplankton in the Chukchi Sea.

The reduction in ice cover of the Chukchi Sea is not only opening up habitat for birds, whales, and zooplankton, it is providing humans the opportunity to explore for oil and gas, develop commercial shipping routes, and consider the viability of a commercial fishery. This study provides a long-term perspective on the environment of the Chukchi Sea to help inform policy-makers and managers responsible for spatial planning, permitting, and ecosystem-based management of marine resources (Schwemmer et al., 2011; Ainley et al., 2012). The possible effects of anthropogenic stressors must be considered in light of the shifting baseline of a seabird community and an entire marine ecosystem that is actively responding to a warming and increasingly ice-free Arctic.

2.6 Acknowledgments

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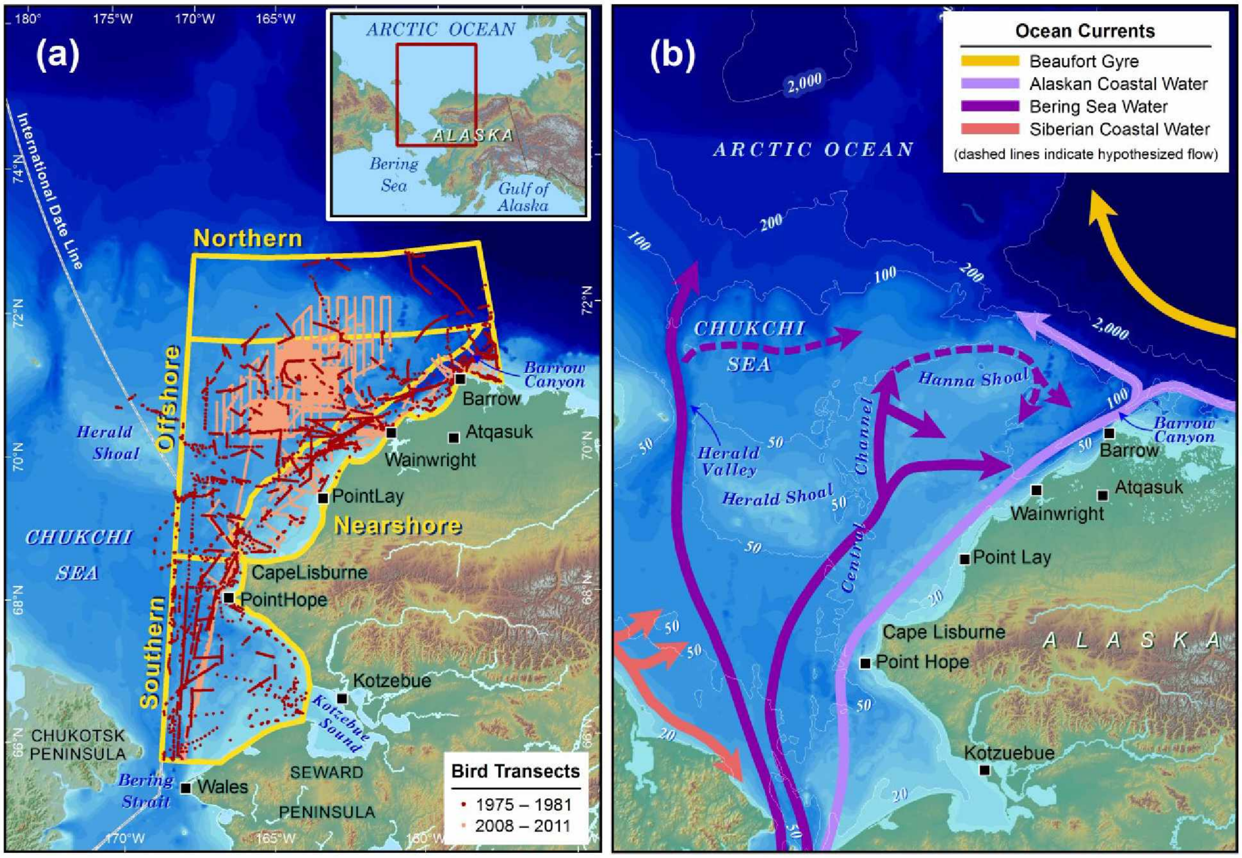

Figure 2.1 The eastern Chukchi Sea, showing (a) oceanographic strata, survey locations; and (b) currents.

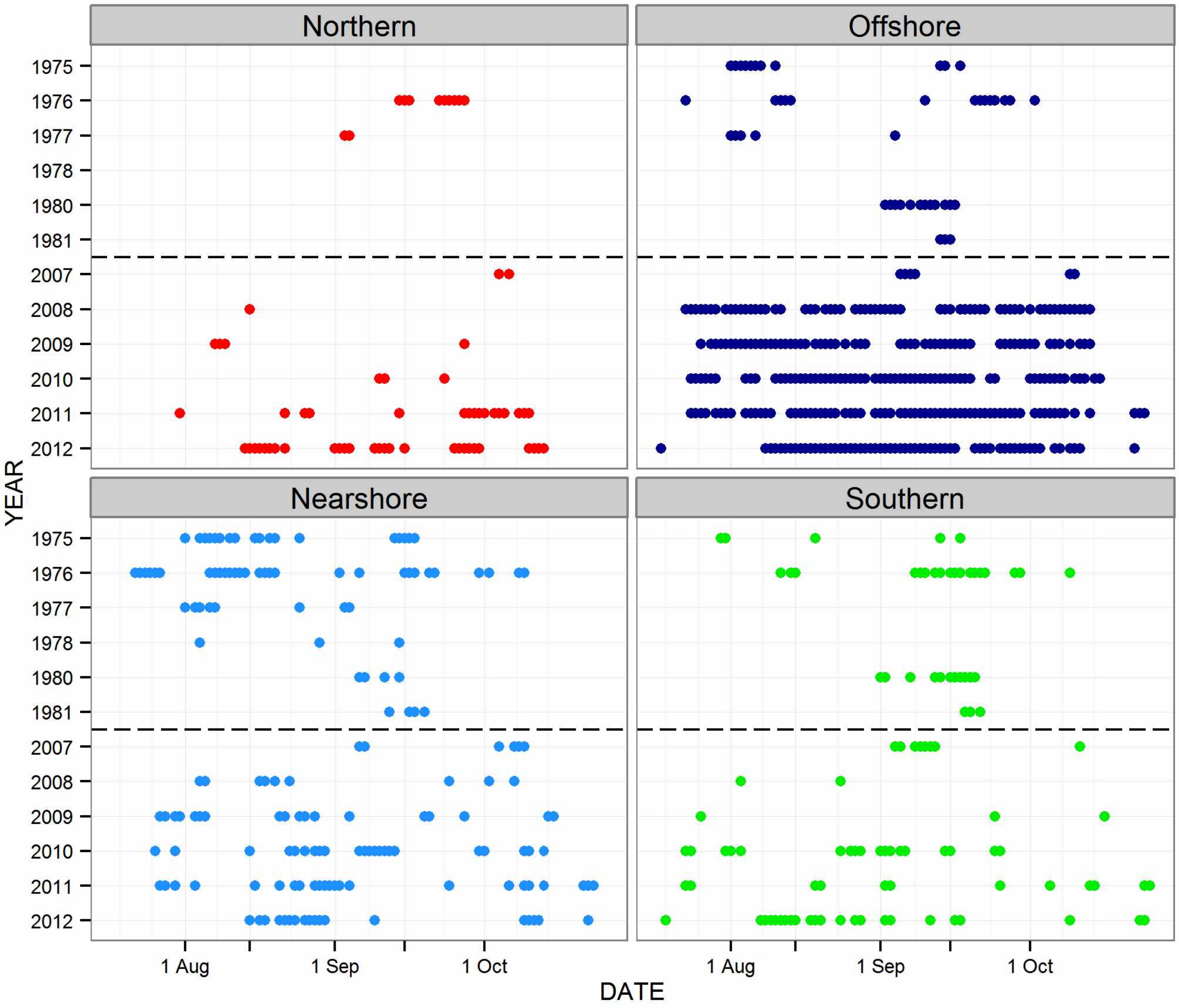

Figure 2.2 Timing of ship-based surveys for marine birds in the Chukchi Sea, 1975–2012. Horizontal dashed line separates historical data from recent data.

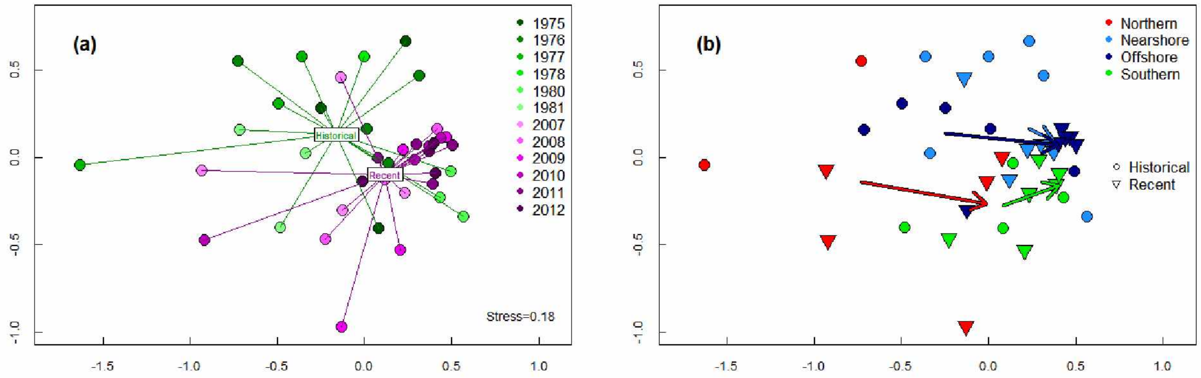

Figure 2.3 Non-metric multidimensional scaling (nMDS) ordination plot of Bray–Curtis similarities for seabirds recorded in the Chukchi Sea during 1975–2012. Each point represents one stratum-year and distance between points represents similarity in composition. Points are identified (a) by year, with period centroids labeled; and (b) by stratum with arrows indicating the vector of change in composition by year.

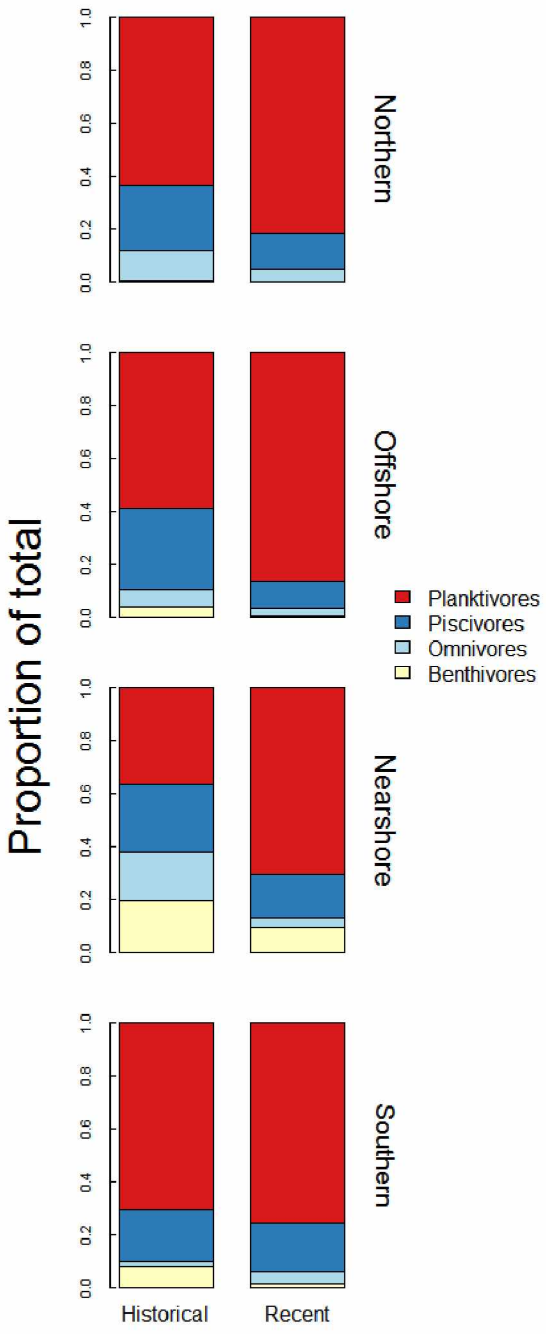

Figure 2.4 Foraging guilds that compose the seabird community in the Chukchi Sea. Rows correspond to the Northern, Offshore, Nearshore, and Southern strata and columns correspond to the historical (1975–1981) and recent (2007–2012) periods.

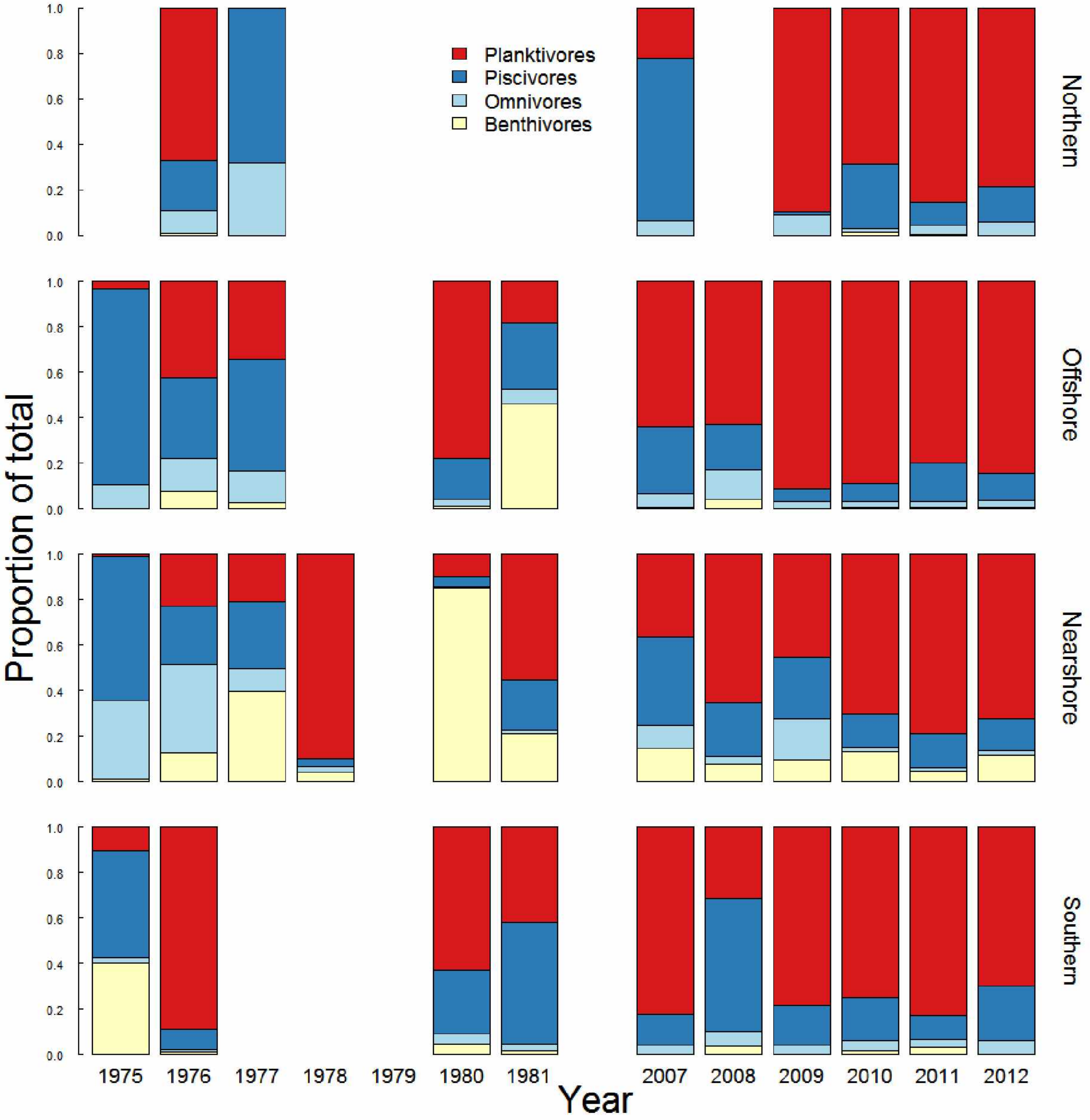

Figure 2.5 Foraging guilds that compose the seabird community in the Chukchi Sea by year, 1975–2012. Rows correspond to the Northern, Offshore, Nearshore, and Southern strata.

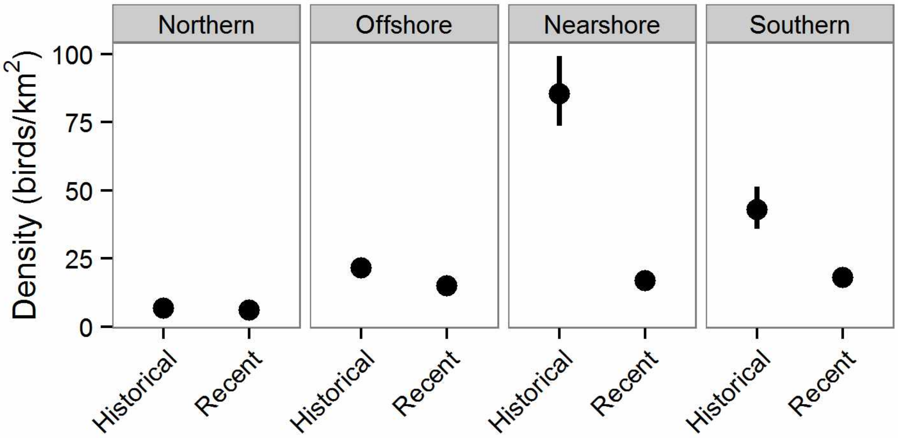

Figure 2.6 Density of all seabirds in the eastern Chukchi Sea during historical (1975–1981) and recent (2007–2012) periods. These values are predicted from generalized linear models that account for geographic stratum, period, and the negative-binomial distribution of the data. Error bars represent 95% confidence intervals.

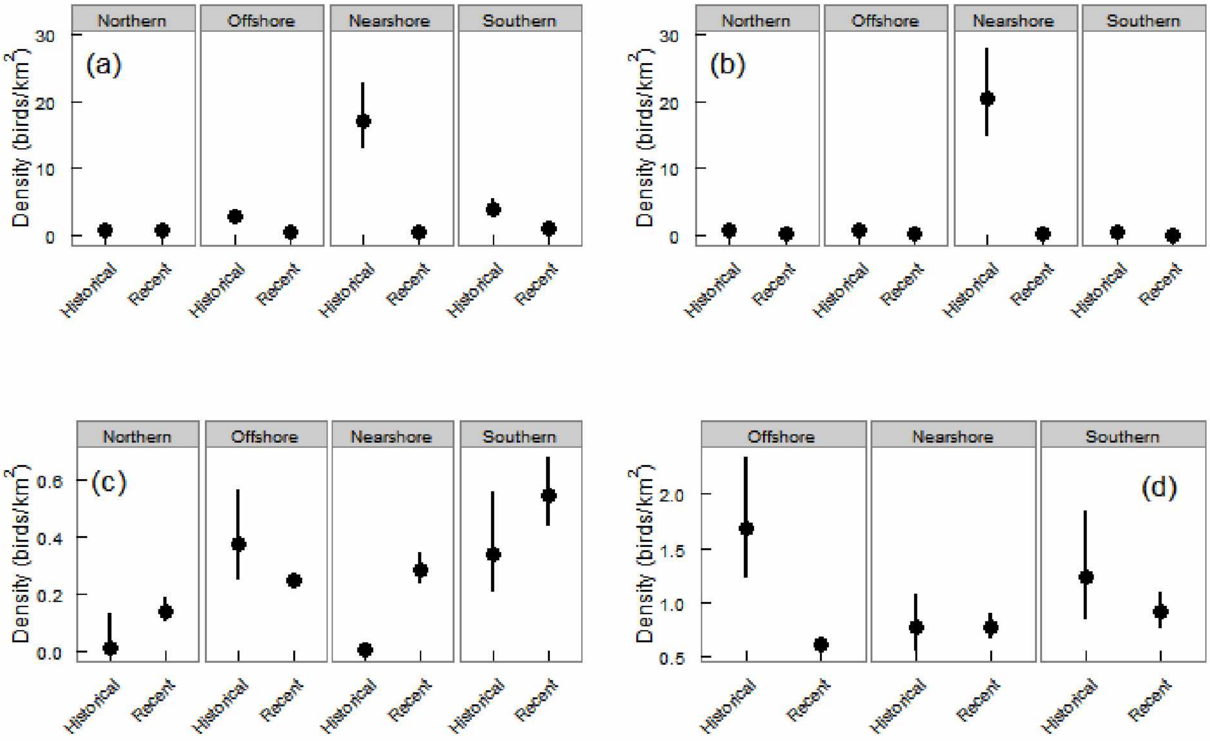

Figure 2.7 Density of omnivorous and piscivorous seabirds in the eastern Chukchi Sea. Panels correspond to (a) Black-legged Kittiwakes, (b) Glaucous Gulls, (c) Northern Fulmars, and (d) Thick-billed Murres in the eastern Chukchi Sea during historical (1975–1981) and recent (2007–2012) periods. These values are predicted from generalized linear models that account for geographic stratum, period, and the negative-binomial distribution of the data. Error bars represent 95% confidence intervals. Thick-billed Murres in Northern stratum could not be modeled because they were not recorded in the historical period.

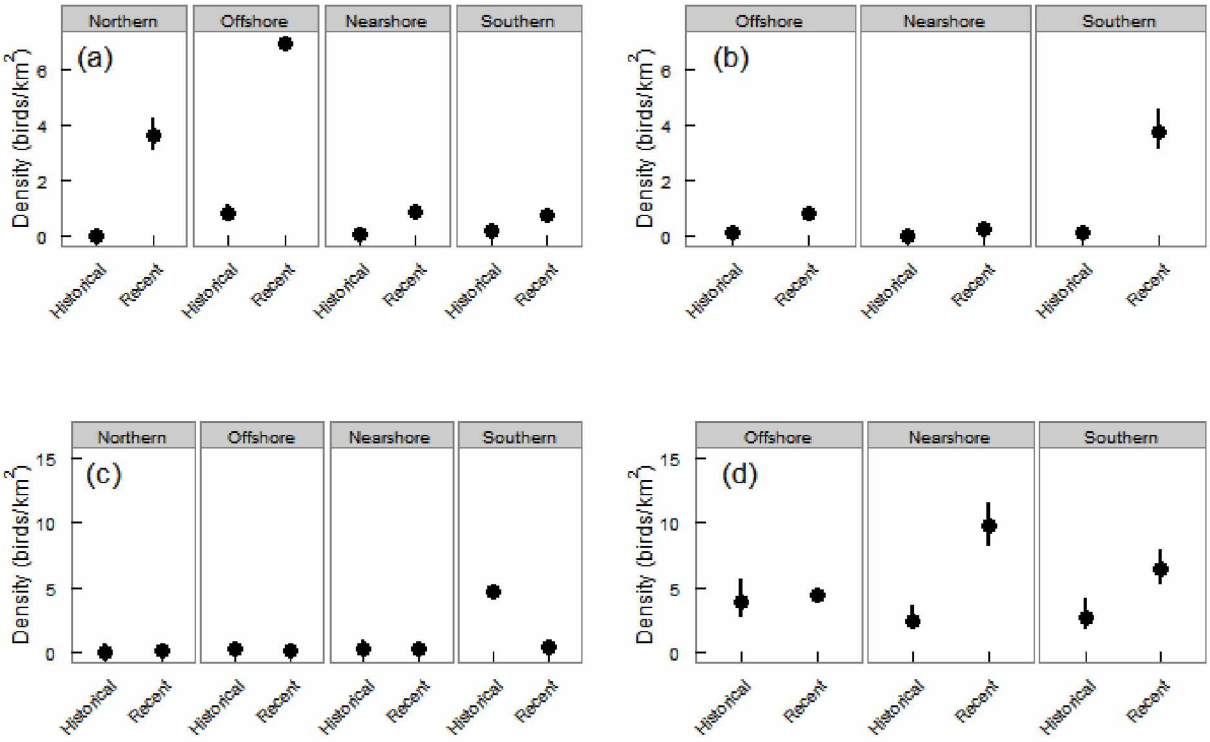

Figure 2.8 Density of planktivorous seabirds in the eastern Chukchi Sea. Panels correspond to (a) Crested Auklets, (b) Least Auklets, (c) phalaropes, and (d) Short-tailed Shearwaters in the eastern Chukchi Sea during historical (1975–1981) and recent (2007–2012) surveys. These values are predicted from generalized linear models that account for geographic stratum, period, and the negative-binomial distribution of the data. Error bars represent 95% confidence intervals. Least Auklets and Short-tailed Shearwaters in Northern stratum could not be modeled because they were not recorded in the historical period.

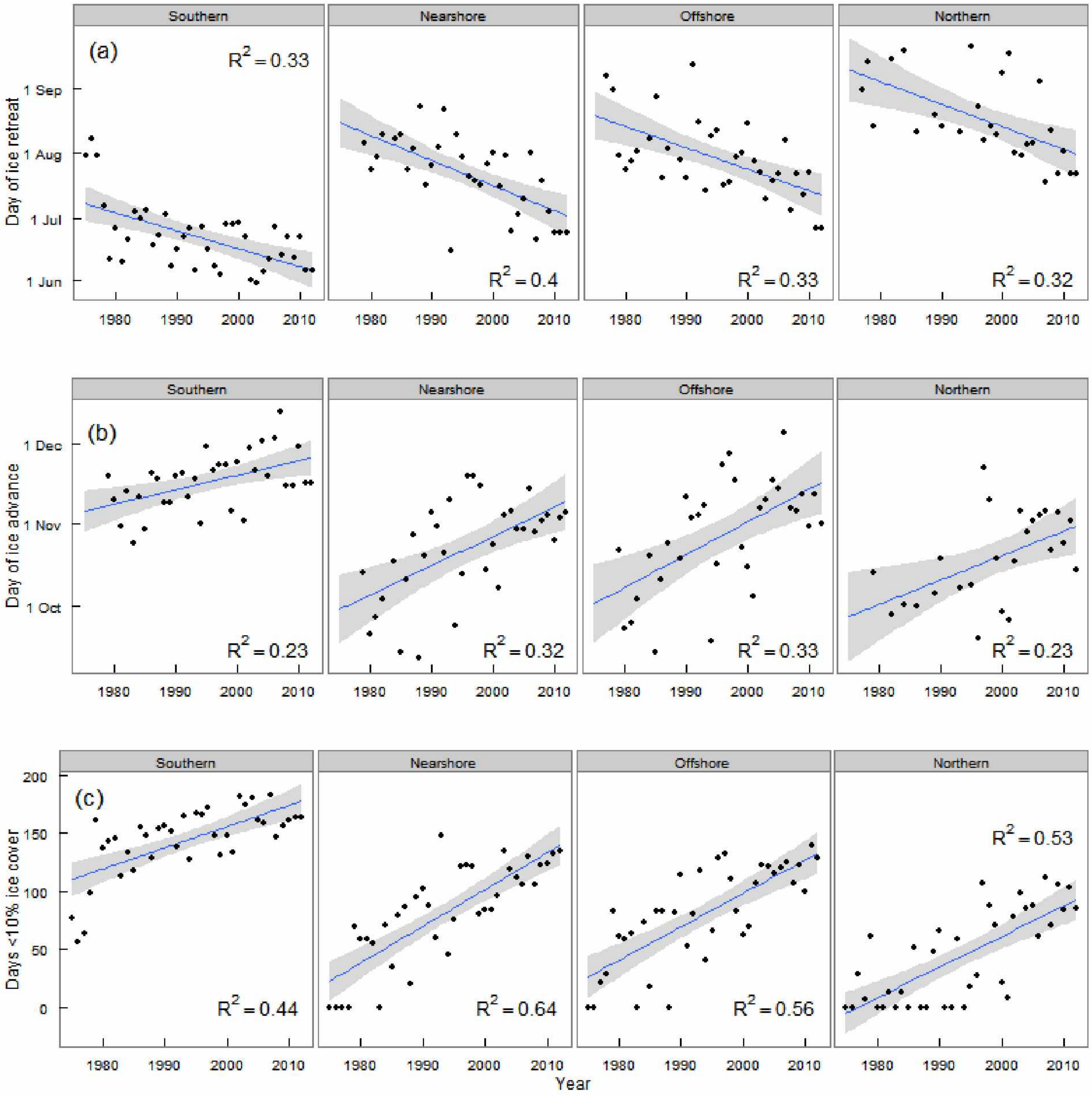

Figure 2.9 Linear trends in sea-ice cover in the Chukchi Sea. Panels correspond to (a) date of ice retreat, (b) date of ice advance, and (c) number of days with <10% ice cover in the Chukchi Sea, by geographic stratum, 1975–2012. Lines are the least-squares linear fit, and the gray shading is the 95% confidence interval around the fit of the line.

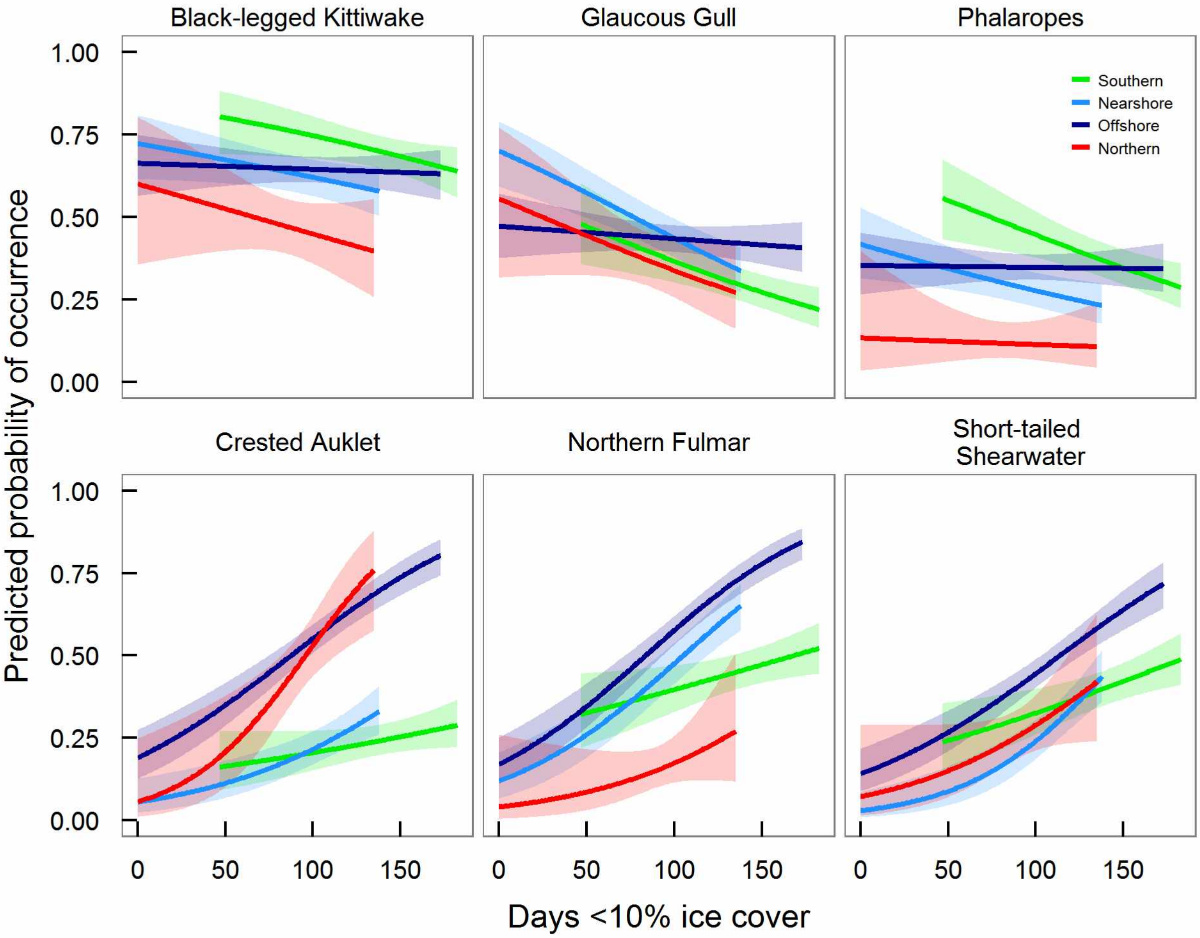

Figure 2.10 Relationship between ice cover and predicted probability of occurrence for 6 species of seabirds in the eastern Chukchi Sea, 1975–2012. Values and 95% confidence intervals are predicted from logistic regression models of the effects of the number of days with <10% ice cover and geographic stratum on the probability of seabird occurrence.

Table 2.1 Area (km²) surveyed for seabirds in the Chukchi Sea, 1975–1981 and 2007–2012.

	Region			
Year	Southern	Nearshore	Offshore	Northern
1975	78	166	215	--
1976	245	210	187	55
1977	--	64	53	18
1978	--	31	--	--
1980	82	20	84	--
1981	28	91	48	--
2007	294	168	116	107
2008	78	139	1,907	29
2009	64	252	1,890	54
2010	303	465	2,316	40
2011	238	487	1,916	373
2012	447	537	2,461	475

Table 2.2. Summary of species identified during seabird surveys in the Chukchi Sea, 1975–2012.

Foraging guild/Species	Scientific name	Historical density (birds/km^2)				Recent density (birds/km^2)			
		Southern	Nearshore	Offshore	Northern	Southern	Nearshore	Offshore	Northern
PLANKTIVORES									
Sooty Shearwater	*Puffinus griseus*	0.002	–	–	–	–	0.020	0.000	–
Short-tailed Shearwater	*Puffinus tenuirostris*	1.854	2.276	1.750	–	6.763	9.255	4.384	0.336
Red-necked Phalarope	*Phalaropus lobatus*	0.009	–	0.003	–	0.173	0.151	0.210	0.066
Red Phalarope	*Phalaropus fulicarius*	4.400	3.097	5.713	0.805	0.630	0.127	0.105	0.019
Ross's Gull	*Rhodostethia rosea*	0.113	0.036	0.269	3.056	0.007	0.058	0.056	0.341
Dovekie	*Alle alle*	–	0.007	0.005	–	0.001	0.001	0.002	0.002
Kittlitz's Murrelet	*Brachyramphus brevirostris*	0.025	0.036	0.003	–	0.001	0.115	0.012	0.019
Ancient Murrelet	*Synthliboramphus*	–	–	–	–	0.060	0.028	0.054	0.048
Parakeet Auklet	*Aethia psittacula*	0.510	0.360	0.412	–	0.204	0.031	0.044	–
Least Auklet	*Aethia pusilla*	0.171	0.012	0.131	–	3.830	0.274	0.804	0.266
Crested Auklet	*Aethia cristatella*	0.182	0.036	0.531	0.014	0.702	0.961	7.031	3.653
PISCIVORES									
Red-throated Loon	*Gavia stellata*	0.009	0.024	–	–	0.004	0.003	0.002	0.001
Pacific Loon	*Gavia pacifica*	0.251	0.613	0.155	0.014	0.021	0.216	0.084	0.006
Common Loon	*Gavia immer*	0.104	0.010	0.036	–	–	0.001	0.002	–
Yellow-billed Loon	*Gavia adamsii*	0.002	0.040	–	–	–	0.008	0.010	–
Pelagic Cormorant	*Phalacrocorax pelagicus*	–	–	–	–	–	0.001	–	–
Black-legged Kittiwake	*Rissa tridactyla*	2.622	7.937	1.880	0.682	1.005	0.554	0.503	0.635
Ivory Gull	*Pagophila eburnea*	–	0.002	0.235	0.587	0.005	–	0.001	0.006
Mew Gull	*Larus canus*	–	–	–	–	0.001	–	–	–
Iceland Gull	*Larus glaucoides*	–	0.002	–	–	–	–	–	–
Aleutian Tern	*Sterna aleutica*	–	–	–	–	0.001	–	–	–
Arctic Tern	*Sterna paradisaea*	0.055	1.161	0.012	0.027	0.005	0.034	0.015	0.001
Common Murre	*Uria aalge*	0.150	0.028	0.080	–	0.562	0.219	0.085	0.006
Thick-billed Murre	*Uria lomvia*	0.717	0.721	0.965	–	0.951	0.760	0.613	0.096
Black Guillemot	*Cepphus grylle*	0.005	0.105	0.117	0.177	0.009	0.011	0.006	0.024
Pigeon Guillemot	*Cepphus columba*	–	–	–	–	0.004	0.001	0.001	–
Marbled Murrelet	*Brachyramphus marmoratus*	–	–	–	–	0.001	–	–	–
Horned Puffin	*Fratercula corniculata*	0.424	0.014	0.037	–	0.155	0.021	0.012	0.001

Table 2.2 continued…

Foraging guild/Species	Scientific name	Historical density (birds/km²)				Recent density (birds/km²)			
		Southern	Nearshore	Offshore	Northern	Southern	Nearshore	Offshore	Northern
OMNIVORES									
Northern Fulmar	*Fulmarus glacialis*	0.311	0.007	0.175	0.014	0.546	0.261	0.248	0.141
Fork-tailed Storm-	*Oceanodroma furcata*	–	–	–	–	0.003	0.004	–	–
Red-legged Kittiwake	*Rissa brevirostris*	0.007	–	0.005	–	–	–	–	–
Sabine's Gull	*Xema sabini*	0.012	1.003	0.019	0.027	0.011	0.020	0.036	0.007
Herring Gull	*Larus argentatus*	–	0.007	0.009	–	0.004	0.006	0.008	–
Thayer's Gull	*Larus thayeri*	–	0.019	–	–	–	0.001	–	–
Slaty-backed Gull	*Larus schistisagus*	–	0.019	–	–	0.001	–	–	–
Glaucous-winged Gull	*Larus glaucescens*	0.037	0.005	0.007	–	0.001	–	–	–
Glaucous Gull	*Larus hyperboreus*	0.408	7.218	0.531	0.600	0.079	0.201	0.129	0.123
Pomarine Jaeger	*Stercorarius*	0.048	0.814	0.121	0.027	0.065	0.022	0.029	0.010
Parasitic Jaeger	*Stercorarius*	0.021	0.188	0.063	0.027	0.027	0.009	0.004	0.006
Long-tailed Jaeger	*Stercorarius*	0.014	0.088	0.046	–	0.004	0.002	0.002	0.000
Tufted Puffin	*Fratercula cirrhata*	0.062	0.010	0.003	–	0.107	0.008	0.007	–
BENTHIVORES									
Steller's Eider	*Polysticta stelleri*	0.007	–	–	–	–	0.003	–	–
Spectacled Eider	*Somateria fischeri*	0.012	2.583	–	–	0.027	0.023	0.001	–
King Eider	*Somateria spectabilis*	1.391	0.466	0.005	–	0.057	0.144	0.017	0.007
Common Eider	*Somateria mollissima*	0.233	2.626	0.009	–	0.072	0.236	0.011	0.002
Harlequin Duck	*Histrionicus*	0.002	–	–	–	–	–	–	–
Surf Scoter	*Melanitta perspicillata*	0.023	–	0.005	–	–	0.001	–	–
White-winged Scoter	*Melanitta fusca*	–	0.040	–	–	0.023	0.011	0.004	–
Black Scoter	*Melanitta nigra*	0.021	1.139	–	–	–	–	–	–
Long-tailed Duck	*Clangula hyemalis*	0.267	1.838	0.507	–	0.030	1.008	0.055	0.002

Table 2.3 Results of PERMANOVA testing for differences in species composition of seabirds among strata and time periods in the Chukchi Sea, 1975–1981 and 2007–2012. Analysis was based on Bray-Curtis dissimilarities from log-transformed data. Each term was tested using 1000 random permutations of the stratum-year samples.

Source	df	Mean Squares	F	R^2	P
Time period	1	1.18	3.80	0.09	<0.001
Stratum	3	0.63	2.01	0.13	0.002
Residuals	35	0.31		0.78	
Total	39			1.00	

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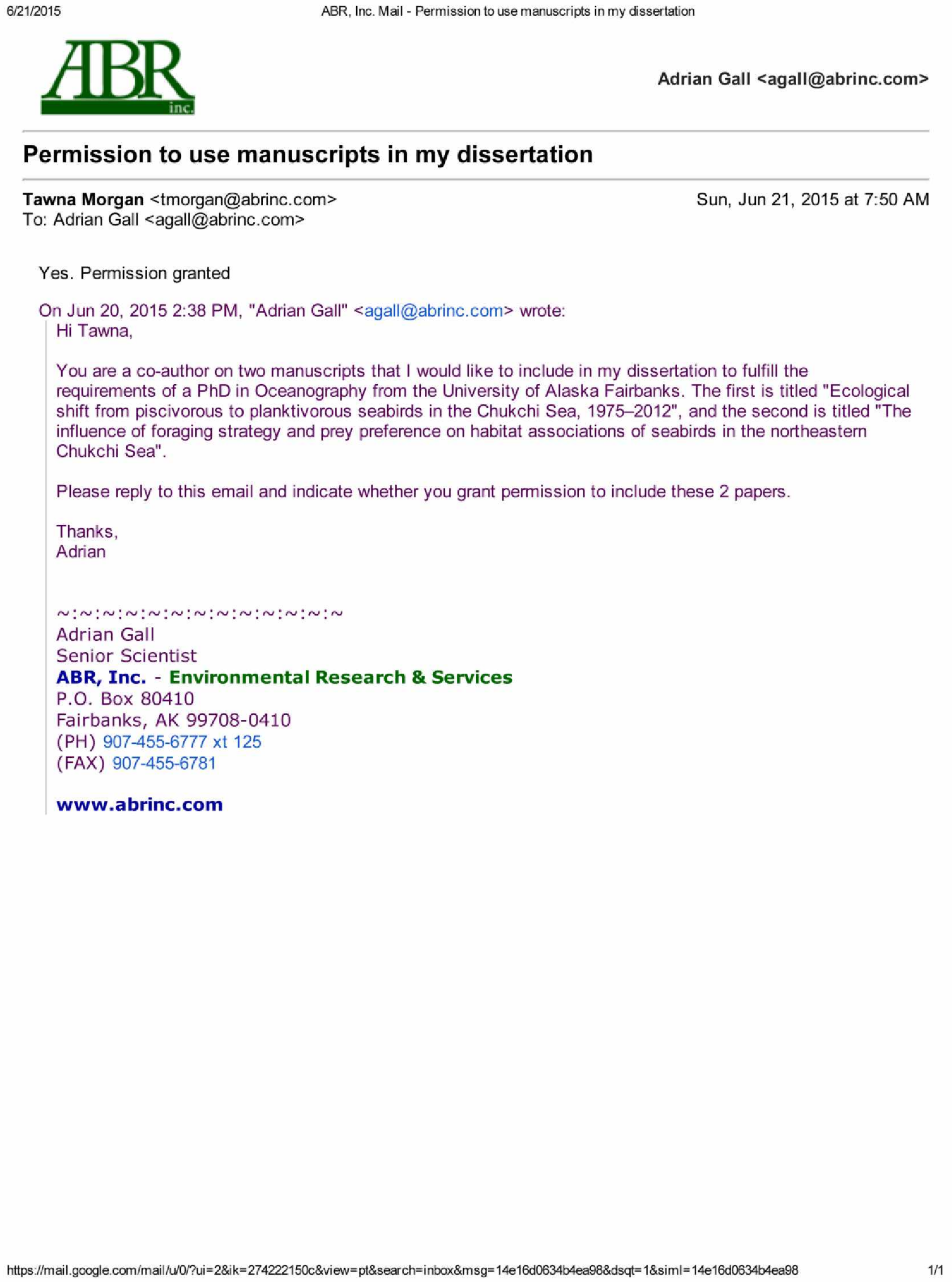
Appendix 2.1 Parameter estimates ± standard error from logistic regression models of the effects of date of sea-ice retreat and number of ice-free days (days with ≤ 10% ice cover) on the probability of seabird occurrence in the eastern Chukchi Sea.

Species	Parameter	Estimate	SE	Z	*P*
Black-legged Kittiwake	(Intercept)	1.304075	0.216472	6.024	<0.001
	ndays	-0.00338	0.001292	-2.619	0.019
	RegionNE	-0.46652	0.17851	-2.613	0.009
	RegionOF	-0.3688	0.155118	-2.378	0.017
	RegionNC	-1.1313	0.219709	-5.149	<0.001
Glaucous Gull	(Intercept)	0.468	0.469		0.319
	ndays	-0.009	0.003		0.003
	RegionNE	0.545	0.607		0.370
	RegionOF	-0.275	0.545		0.614
	RegionNC	-0.674	0.708		0.342
	ndays:RegionNE	-0.001	0.004		0.821
	ndays:RegionOF	0.005	0.004		0.151
	ndays:RegionNC	0.005	0.006		0.382
Phalaropes	(Intercept)	-0.480	0.466		0.304
	ndays	0.000	0.003		0.979
	RegionNE	0.743	0.598		0.214
	RegionOF	-0.698	0.557		0.210
	RegionNC	-1.643	0.951		0.084
	ndays:RegionNE	-0.009	0.004		0.030
	ndays:RegionOF	0.004	0.004		0.245
	ndays:RegionNC	0.001	0.009		0.905
Crested Auklets	(Intercept)	-3.156	0.696		0.000
	ndays	0.013	0.004		0.002
	RegionNE	0.132	0.915		0.885
	RegionOF	1.953	0.757		0.010
	RegionNC	0.313	1.019		0.759
	ndays:RegionNE	0.002	0.006		0.742
	ndays:RegionOF	-0.002	0.005		0.689
	ndays:RegionNC	0.014	0.008		0.084
Short-tailed Shearwaters	(Intercept)	-0.836	0.467		0.073
	ndays	0.004	0.003		0.134
	RegionNE	-0.959	0.637		0.132
	RegionOF	-0.031	0.548		0.956
	RegionNC	-1.934	1.007		0.055
	ndays:RegionNE	0.008	0.004		0.055
	ndays:RegionOF	0.005	0.004		0.186
	ndays:RegionNC	0.006	0.009		0.478



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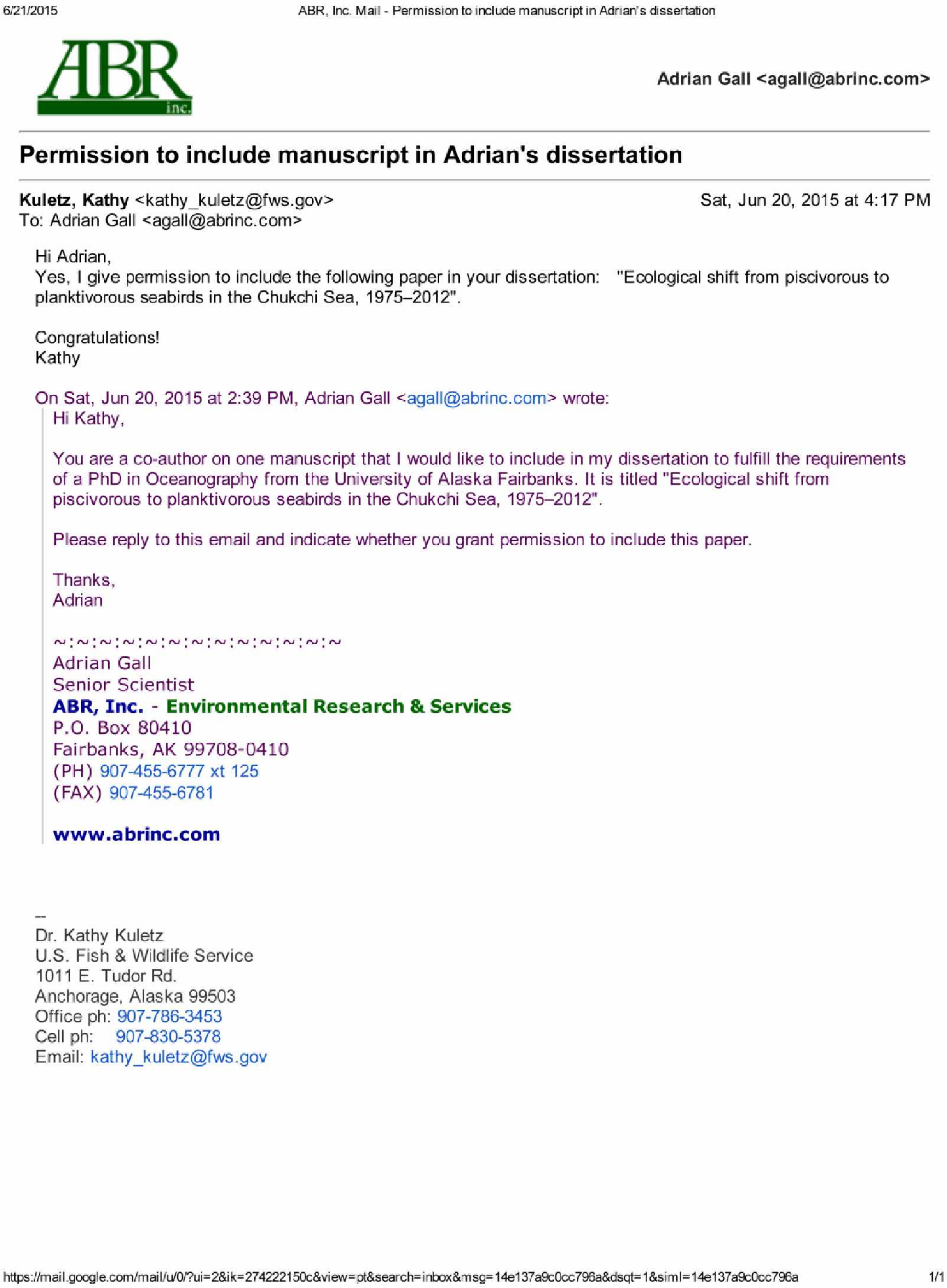

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Appendix 2.3 Permission from co-author Kathy Kuletz to include manuscript in the dissertation

CHAPTER 3: THE INFLUENCE OF FORAGING STRATEGY AND PREY PREFERENCE ON HABITAT ASSOCIATIONS OF SEABIRDS IN THE NORTHEASTERN CHUKCHI SEA[1]

3.1 Abstract

We examined relationships between oceanography and the distribution and abundance of eight focal taxa of seabirds in the northeastern Chukchi Sea during 2011–2012. We used ship-based surveys to sample seabird abundance in the ~39,000-km² Greater Hanna Shoal study area. Concurrently with the seabird surveys, we measured temperature, salinity, and zooplankton biomass at stations located on a systematic grid throughout the study area. The associations of seabirds with habitat characteristics varied with preferred prey and foraging method. The relationship with temperature in the upper 10 m of the water column varied with foraging strategy, in that pursuit-diving birds were more abundant in warm, weakly stratified water, whereas surface-feeding birds were more abundant in cold, strongly stratified water. Planktivorous seabirds (auklets, shearwaters, and phalaropes) were more abundant within 20 km of thermal surface fronts, whereas omnivores (gulls and murres) were more abundant far from fronts. The distribution of seabirds, particularly the planktivorous species, is strongly influenced by advective processes that transport oceanic species of zooplankton from the Bering Sea to the Chukchi Sea. For five of the eight seabird species studied, information about prey biomass improved predictions of seabird abundance, although the relationships were not as clear as they were for the physical habitat characteristics indicative of processes that aggregate prey. These models are an important step in understanding species-habitat relationships and providing reliable estimates of seabird distribution and abundance in an area of interest for transportation and for oil and gas development.

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3.2 Introduction

Populations of seabirds that breed on the Arctic Coastal Plain of Alaska, in the southern Chukchi and Bering seas, and even in the Southern Hemisphere migrate to the Chukchi Sea during the open-water season to capitalize on 2–3 months of productivity before retreating with the onset of ice formation in November (Swartz 1967, Divoky & Springer 1988, Piatt & Springer 2003, Oppel et al. 2009). Reductions in the extent and duration of seasonal ice cover in the Chukchi Sea (Stroeve et al. 2012, Plotnikov & Pustoshnova 2012) are contributing to an increase in vessel traffic and oil and gas exploration in an area that previously was considered too risky to access (Carmack & Wassmann 2006, Reeves et al. 2014). The seasonal window of operations for these anthropogenic activities still is limited by ice cover and coincides with the period of maximal marine productivity that is exploited by marine predators such as seabirds. We need to understand the spatial dynamics of seabirds to help plan for, and mitigate the effects of, anthropogenic activity on marine ecosystems that already are adjusting to the stress of a rapidly changing climate (González-Solís & Shaffer 2009, Louzao et al. 2009).

One of the biggest challenges for understanding the physical and biological processes that contribute to patterns of seabird distribution is coupling measurements of marine habitat with the distribution of seabirds in space and time. Remote sensing has greatly advanced our ability to sample the environment over large spatial extent and with high resolution. This approach, however, is limited by cloud cover, which is dense and frequent over the northeastern Chukchi Sea, and is limited in that it samples only the top few millimeters of the water column. These surface measurements provide little insight into the vertical structure of the water column that can indicate processes that aggregate prey and offer no measures of zooplankton or fish that are the primary prey for seabirds. These aspects of habitat are best quantified by *in situ* sampling that preferably is concurrent with surveys of seabirds to capture a complete snapshot of the dynamic pelagic environment where both the habitat and the animals are highly mobile.

Seabirds are highly mobile, although that mobility varies by species. Some seabirds are adapted to maximize flying efficiency at the expense of foraging within the water column whereas others are adapted to dive up to 70 m for their prey, sacrificing energy-efficient flight. Comparisons among species that vary in their mobility, differential abilities to exploit the water column, prey preferences, and modes of foraging strengthen inference about habitat characteristics and help to identify features of particular importance for conservation or management.

Here, we build on a previous effort to understand the relationship between 8 taxa of seabirds and their marine environment in the northeastern Chukchi Sea (Gall et al. 2013). That study examined relationships between seabirds and physical oceanography summarized at a course spatial resolution (~50 km grid-cell) and limited spatial extent (~9,300 km^2). In this study, we increased the resolution of the analysis (~3 km grid-cell), expanded the spatial extent of the study area, and included information on zooplankton abundance and distribution to explore the physical and biological processes that influence seabird distribution. Specifically, we used generalized additive models to elucidate the physical and biological factors that affect the distribution and abundance of eight taxa of seabirds in the northeastern Chukchi Sea. We selected this suite of species to understand how differences in prey preference and foraging strategy influence habitat selection.

3.3 Methods

3.3.1 Study area

This study was conducted in the northeastern Chukchi Sea, with data collection focused in an area extending ~100–200 km northwest of the village of Wainwright (Figure 3.1). The Greater Hanna Shoal (GHS) study area is ~39,000 km^2 and is bounded by 2 currents that flow from the Chukchi Sea to the Arctic Ocean: the Central Channel flow over the central portion of the shelf and the Alaskan Coastal Current along the coast of Alaska (Weingartner et al. 2005, 2013a,b).

Observers surveyed seabirds along a series of parallel survey lines spaced 2, 3, or 4 NM (3.7, 5.6, or 7.4 km) apart in 3 boxes of particular interest for oil and gas exploration, plus broad-scale survey lines in the GHS study area outside of the boxes that were spaced 7.5 NM (13.8 km) apart (Figure 3.2). In addition to standardized survey lines, we also sampled opportunistically when transiting to, from, and within the GHS study area. We sampled physical and biological oceanography at stations on a grid with 7.5–15 NM (~14–28 km) spacing (Figure 3.2).

3.3.2 Data collection

We conducted seabird surveys during September and early October 2011 and 2012, when the entire study area was ice-free. We conducted the surveys as consecutive 10-min counting periods (hereafter, transect segments) when the ship was moving along a straight-line course at a minimal velocity of 9.3 km/h (5 kt; Tasker et al. 1984, Gould and Forsell 1989). We collected data 9–12 h/day during daylight hours, weather and ice conditions permitting. Surveys generally were stopped when sea height was Beaufort 6 (seas ~2–3 m [~6–10 ft]) or higher, although we occasionally continued to sample if the visibility still was good (e.g., if seas were at the lower end of Beaufort 6 and we were traveling downwind). One observer stationed on the bridge of the ship recorded all birds seen within a radius of 300 m in a 90° arc from the bow to the beam on one side of the ship (the count zone) and located and identified seabirds with 10X binoculars. For each bird or group of birds, we recorded: species (or identity to lowest possible taxon); total number of individuals; distance from the observer when sighted; radial angle of the observation from the bow of the ship; and behavior.

We counted all birds on the water within the count zone, taking care to avoid recounting the same individuals. For flying birds, however, we conducted scans for them ~1 time/min (the exact frequency varied with ship's speed) and recorded an instantaneous count ("snapshot") of all birds flying within the count zone. This "snapshot" method reduces the bias of overestimating the abundance of flying birds (Tasker et al. 1984, Gould & Forsell 1989). We counted only those flying birds that entered the count zone from the sides or front and did not count flying birds that entered from behind the ship (i.e., an area that already had been surveyed), to avoid counting possible ship-following birds.

We entered observations of all birds directly into a computer connected to a global positioning system (GPS) with TigerObserver software (TigerSoft, Las Vegas, NV); this program time-stamped and geo-referenced every observation entered in real time. The primary GPS connected to the data-collection computer occasionally lost communication with satellites, resulting in missing locations for observations and transect cutoff points. We interpolated the ship's location between known waypoints by using its speed and the time of the observation to fill these GPS data gaps.

3.3.3 Data analysis

We selected 8 focal taxa for statistical analyses from among the 10 most-abundant species in both years: Crested Auklet (*Aethia cristatella*), Least Auklet (*A. pusilla*), phalaropes (*Phalaropus* spp.), Short-tailed Shearwater (*Puffinus tenuirostris*), Black-legged Kittiwake (*Rissa tridactyla*), murres (*Uria aalge* and *U. lomvia*), Glaucous Gull (*Larus hyperboreus*), and Northern Fulmar (*Fulmarus glacialis*; Table 3.1). Because Red-necked and Red phalaropes often occur in mixed-species flocks and are difficult to distinguish at a distance, especially during the molt, we combined observations of these 2 species with those of unidentified phalaropes and treated them collectively as phalaropes. We also combined observations of Thick-billed and Common murres with those of unidentified murres to obtain a large enough sample size to test habitat relationships of these large diving alcids; these 2 species use similar foraging areas in the Chukchi Sea (Hatch et al. 2000). These 8 focal taxa represented a variety of foraging methods and prey preferences, thereby providing an overview of the main functional ecological groups of the seabird community.

Estimating density

We estimated detection-corrected densities (birds/km^2) of birds within the study area by using line-transect sampling analyses and followed analytical methods described by Buckland et al. (2001, 2004). This approach accounts for the decrease in probability of detecting a bird with increased distance from the survey line. These methods account for the decrease in probability of detecting an animal with increased distance from the survey line and for possible differences in detection among observation platforms, observers, sea-surface conditions, and solar glare. We assigned all species to one of 6 detection groups based on their similarity in size, color, behavior, and/or perpendicular-distance histograms and fitted models that used 1 of 2 possible key functions (half-normal or hazard-rate) to the distribution of observation distances to find the model that best estimated the probability of detection (Table 3.1). The corrected density estimates were calculated with the formula:

$$\hat{A} = \frac{n \cdot \hat{E}(s)}{L \cdot \hat{P}_a}$$

where $\hat{A}$ is the corrected abundance estimate, n is the total number of observations on transects, $\hat{E}(s)$ is the mean flock size, L is the total length of transects sampled, and $\hat{P}_a$ is the probability of detection estimated by the model (Buckland et al. 2001). Full details of data analysis are provided in Gall et al. (2013). The distance analysis was conducted with the statistical package mrds (Laake et al. 2013) for R. We used R v. 3.0.1 (http://www.r-project.org) for all analyses.

Habitat models

We used detection-corrected abundance estimates to investigate the influence of physical and biological oceanography on the distribution and abundance of 8 focal taxa over the GHS study area in 2011 and 2012. We standardized the length of transect segments to 3 km and estimated the corrected abundance on each segment by following the process for modeling detection probabilities described above. We considered 10 environmental variables to model the occurrence and abundance of 8 taxa of seabirds (6 physical oceanographic variables, 2 biological oceanographic variables, and latitude and longitude to account for spatial structure in the data). All spatial data were projected into Universal Transverse Mercator Zone 3 to facilitate interpretation of distance as measurements in km.

Physical oceanographic factors

Physical oceanographic variables included temperature and salinity in the upper 10 m of the water-column, temperature and salinity in the lower 10 m of the water-column, mixed-layer depth, strength of stratification, and distance to the nearest temperature front. Salinity and temperature are characteristics that define water-masses in this region. The 2 resident water-masses in the Chukchi Sea are cold (≤0 °C), saline (32–33) Winter Water (WW) found below the mixed layer and cold (–1.5 to +1 °C), fresh (28–30) Meltwater (MW) found in surface waters. The third water-mass of interest is warm (3–8 °C), moderately saline (30–32) Bering Sea Water (BSW) that originates in the Bering Sea and flows northward, transporting large zooplankton of Pacific origin to the Chukchi Sea and gradually replaces MW in the surface layer. The mixed-layer depth is a characteristic of the water-column that we considered to be a proxy for foraging conditions. A shallow mixed-layer depth can indicate stratification that enhances prey availability by concentrating prey at the pycnocline, whereas a deep mixed-layer depth can indicate a well-mixed water column that enhances prey availability at the surface (Mackas et al.

1985, Hunt et al. 1998, Russell et al. 1999). These 5 variables were derived from measurements at fixed oceanographic stations throughout the GHS study area (Figure 3.2) with a conductivity-temperature-depth (CTD) meter (SBE-19+V2 CTD; Sea-Bird Electronics, Inc., Bellevue, WA). The instrument sampled at 4 Hz and was lowered through the water-column at a rate of ~0.5 m/sec. Data were processed according to the manufacturer's recommendations and screened for anomalous spikes, dropouts, and density inversions (Weingartner et al. 2013a). We averaged the station data to 1 decibar (~1 m) vertical profiles.

We used Inverse Distance Weighted (IDW) interpolation to assign physical-oceanographic values derived from CTD measurements to each cell within a 3.0×3.0-km grid. We selected the best inverse distance power (IDP) value by using model cross-validation. First, we split the oceanographic data-set into a model-building set and a test set. The model-building set included a random subset of 75% of the original data-set. We then ran IDW models, permitting IDP values to vary between 1 and 10, and identified the IDP value that produced the lowest root-mean-square error when comparing the model-building and test sets for a given year. This value then was applied to all data for that year to produce year-specific grids of oceanographic covariates to include in the spatial models.

The final physical-oceanographic variable considered was distance to a surface thermal front. Oceanographic fronts mark the boundaries between water-masses that have different properties (e.g., temperatures and/or salinities). Seabirds often are associated with fronts, presumably because differences in density between water masses allow horizontal flow convergence across the front and vertical advection of plankton that enhances food availability (Decker and Hunt 1996, Hoefer 2000, Ainley et al. 2009, Ribic et al. 2011). These fronts can be identified on maps of sea-surface temperatures (SST) as strong gradients in SST over short horizontal distances (Etnoyer et al. 2004, O'Hara et al. 2006). Fronts over the shallow shelf of the Chukchi Sea can be dynamic, so using data from CTD sampling, which was offset from the seabird sampling by 1–10 days, may not have the temporal resolution to capture the features that are influencing seabird distributions. To detect thermal surface fronts, we used temperature collected by a hull-mounted thermosalinograph (SBE-21, Sea-Bird Electronics, Inc, Bellevue, WA). Data points were collected at the start of every seabird transect (i.e., every 10 min). We interpolated these data to the same 3.0×3.0-km grid with the IDW modeling procedures described for CTD data. We calculated the maximal absolute difference in temperature for each cell by using a 3 pixel×3 pixel moving window to identify the rate of change in temperature values among cells (Etnoyer et al. 2004). We used grid cells that had a horizontal change in temperature that was ≥2 SD of the differences observed across the entire grid to indicate areas of oceanographic fronts between water-masses. Finally, we calculated the distance of each observation from the centroid of the nearest front cell.

Biological oceanographic factors

We used 2 biological oceanographic variables (biomass of Pacific zooplankton and of arctic zooplankton) as direct indicators of prey availability for planktivorous seabirds (Hovinen et al. 2014) and as proxies of prey availability for piscivorous seabirds. Zooplankton were sampled at oceanographic stations with a pair of 505-μm-mesh Bongo nets 60 cm in diameter that were towed obliquely at an average speed of ~1 m/sec (2 kt) for 10 min. Samples were preserved in 10% formalin buffered with sodium hexametaphosphate (hexamine) and later were identified to the lowest taxonomic category possible, enumerated, and measured (Questel et al. 2013). For our analysis, we included only those individuals identified to genus. The Pacific-zooplankton category included *Neocalanus* spp., *Eucalanus* spp., and *Thysanoessa* spp., and the arctic-zooplankton category included only *Calanus* spp. We summarized the zooplankton data by station and cruise and interpolated the values to the same 3.0×3.0-km grid with the IDW procedures described above for the other oceanographic variables.

We conducted a preliminary assessment of the 10 variables proposed to explain the variation in the distribution and abundance of seabirds in the GHS study area. We explored the statistical distribution of the data with histograms and Cleveland dot-plots, both of which indicated few outliers. We assessed collinearity among the independent variables with pair-plots, correlations, and variance-inflation factors (VIFs; Zuur et al. 2009). VIFs detect multi-dimensional collinearity among variables, with VIF values <3 indicating that collinearity is negligible (Zuur et al. 2009, Hovinen et al. 2014). In our data-set, temperature in the bottom 10 m of the water-column and salinity in the upper layer and bottom showed strong collinearity (VIFs >4) and were not included with other environmental variables when developing the model set. We used only temperature in the top 10 m of the water column (hereafter, upper temperature) to include in the model set in combination with other environmental variables (Figure 3.3).

Model fitting

We assembled the variables in 18 generalized additive models (GAMs) to explore specific hypotheses about oceanographic conditions that influence spatial patterns of seabird abundance (Table 3.2). An advantage of GAMs over generalized linear models is that GAMs can fit smooth, flexible functions to the explanatory variables, rather than being constrained to linearity (Clarke et al. 2003, Vilchis et al. 2006). We assigned oceanographic covariates to each 3-km segment based on values from the 3.0×3.0-km grid cell in which the midpoint of the segment fell. The abundance of seabirds on each segment, $\hat{n}_j$, was modeled as a function of the spatially referenced covariates using a GAM of the form:

$$E[\hat{d}_j] = \beta_0 + \sum_{k=1}^{K} f_k$$

where β_0 is an intercept and f_k are the smooth functions of the K spatially referenced explanatory variables.

Smooth functions in the model were fit by using thin-plate regression splines with a maximal basis of 5 and a penalty to reduce the complexity of the term while maintaining good fit (Wood 2006). We selected the model best supported by the data (hereafter, best model) based on the lowest AIC value (Burnham & Anderson 2002) and validated the best model for each taxon by examining plots of residual distributions, comparison with covariates, and comparison with fitted values (Wood 2006, Zuur et al. 2009). In the 2 cases in which there were competing models (i.e., models within 2 ΔAIC units of each other), we selected as the best model the one with the fewest parameters, which in both cases also was the model with the lowest AIC value. *P*-values are approximate because they are based on degrees of freedom estimated by cross-validation, rather than from known values (Wood 2006, Zuur et al. 2009).

We used the best model for each species to predict its density over the entire GHS study area. We estimated the coefficient of variation of the density estimates in each grid-cell as the standard error of the estimate divided by the predicted value (Miller et al. 2013). The coefficient of variation for each cell was plotted to evaluate the uncertainty in the predictive model. We used the R package pscl (Zeileis et al. 2008) to fit the models, the raster package (Hijmans 2014) to convert predicted values into a geotiff file, and ArcGIS 10.2 to present the results.

3.4 Results

We surveyed a total of 804 km^2 in 2011 and 801 km^2 in 2012. Of the 8 focal taxa, Crested Auklets were the most commonly observed and the most abundant species, phalaropes were the least commonly observed species, and phalaropes and Glaucous Gulls were the least abundant species (Table 3.3).

3.4.1 Oceanographic structure

In both years, warm (3–8 °C), moderately saline (30–32) BSW flowed northward into the study-area (Figure 3.3), sharing the bottom layer with cold (–1.5 to +1 °C), saline (31–33) WW formed during the previous winter and sharing the surface layer with cold, fresh (28–30) MW (Figure 3.4). WW was representative of the entire water-column during the winter and was modified in the upper layer during the spring and summer by advection and ice-melt. Although the intrusion of BSW into the study area as a whole occurred in both years, the extent of the intrusion, the temperature of that water-mass, and the persistence of WW below the pycnocline varied between years. In 2011, BSW extended over most of the region in Aug, with temperatures as high as 9 °C in the southernmost part of the study area. The mixed layer cooled in Sep, and remnants of WW were present in the bottom 5–10 m of the water column. In Aug 2012, BSW occurred over the southern half of the study area; this water cooled substantially in Sep. In addition, a strong front developed in Sep that in 2012 extended from the center of the southeastern boundary of the study area to the center of the northwestern side; BSW appeared to go no farther north.

3.4.2 Habitat associations

The model that best fit the data for 6 of the 8 focal species included smooth terms of latitude, longitude, upper temperature, mixed-layer depth, distance to a front, biomass of Pacific zooplankton, and biomass of arctic zooplankton (Table 3.4). The effect of each covariate on seabird abundance is conditional on the other covariates included in the model; despite being included in the top-ranked models, several of the variables failed to account for significant variation in the abundance of seabirds. Mixed-layer depth showed weak relationships with abundance for 7 focal species and was not included in the model for Glaucous Gulls (Figures 3.5 and 3.6). Distance to front also was not included in the best model for Glaucous Gulls. The biomass of Pacific zooplankton was not statistically significant as an explanatory variable for every seabird species (Table 3.4); it failed to account for significant variation in the abundance of Crested Auklets (approximate $P = 0.51$), phalaropes (approximate $P = 0.35$) and Black-legged Kittiwakes (approximate $P = 0.02$). Details of model selection results are provided in Appendix A.

The 4 planktivorous species differed in habitat preferences, after taking prey availability into account (Figure 3.5). For auklets, temperature in the upper 10 m was the strongest predictor of abundance. Crested Auklets were most abundant in areas with warm (>4 °C) upper temperatures, whereas Least Auklets were more abundant in areas in areas of cool (<4 °C) upper temperatures. Both species decreased in abundance with increasing distance to a thermal surface front. For Short-tailed Shearwaters and phalaropes, the distance to a front was the strongest predictor of abundance, in that both were more abundant within 60 km of a front. Both species declined in abundance as upper temperature increased from 0 °C to 4 °C. Shearwaters, however, increased in abundance as upper temperatures continued to warm from 4 °C to 8 °C, whereas phalaropes remained at low abundance as upper temperatures warmed. Mixed-layer depth was a poor predictor of abundance for planktivores, with no influence on auklets or phalaropes and an inconsistent relationship with abundance in Short-tailed Shearwaters. Differences in habitat preferences also were apparent in the geographical separation among the 4 planktivorous species. Crested and Least auklets were distributed throughout the range of latitude in the eastern GHS (Figure 3.7), whereas Short-tailed Shearwaters and phalaropes were most abundant in the southern GHS study area (Figure 3.8).

The response to prey abundance also differed among planktivorous seabirds, after accounting for physical-habitat preferences (Figure 3.5). The abundance of Least Auklets and Short-tailed Shearwaters was positively associated with the biomass of Pacific zooplankton but increased only above a threshold of 20 mg/m^3. The abundance of Crested Auklets and phalaropes was not influenced by the biomass of Pacific zooplankton. Least Auklets were positively associated with the biomass of arctic zooplankton, but only above a threshold of 50 mg/m^3.

Crested Auklets, Short-tailed Shearwaters, and phalaropes were negatively associated with the biomass of arctic zooplankton, but only above a threshold of 100 mg/m³.

Omnivorous Northern Fulmars and Glaucous Gulls were more abundant in areas of cooler upper temperatures (<~4 °C; Figure 3.6). Northern Fulmars were not influenced by distance to a front or mixed-layer depth, and neither of these habitat variables was included in the best-fitting model for Glaucous Gulls. Despite similarities in habitat associations, these two species of omnivorous seabirds differed in their spatial distribution throughout the northeastern Chukchi Sea (Figure 3.9), with Northern Fulmars more abundant in the western half of the GHS (i.e., BSW) and Glaucous Gulls more abundant in the eastern half of the GHS (i.e., two-layered MW and WW). These two species of seabirds also differed in their association with arctic zooplankton, which may be considered another proxy for identifying a water-mass, regardless of its physical properties. Northern Fulmars were negatively associated with the biomass of arctic zooplankton, whereas Glaucous Gulls were positively associated with the biomass, but only above 70 mg/m³. The abundance of both bird species was negatively associated with the biomass of Pacific zooplankton when it was <15 mg/m³, but there was no significant influence on abundance above that threshold.

Piscivorous Black-legged Kittiwakes and murres had distributions that differed in extent, areas of peak abundance (Figure 3.10), and habitat characteristics (Figure 3.6). Black-legged Kittiwakes were distributed throughout the GHS study area and were most abundant over Hanna Shoal, in areas of cold (<2 °C) upper temperatures and areas that were >60 km from a front. They were least abundant where the mixed-layer depth was <10 m. Murres were most abundant south of Hanna Shoal, in areas of warm (>6 °C) upper temperatures and areas that were >40 km from a front. Mixed-later depth had no significant influence on the abundance of murres (Figure 3.6). Both species were positively associated with the biomass of Pacific prey above a threshold of 5 mg/m³, although the relationship was not statistically significant for Black-legged Kittiwakes. The biomass of Arctic prey was negatively associated with the abundance of murres and had no consistent influence on the abundance of Black-legged Kittiwakes.

3.5 Discussion

The distribution of seabirds in the northeastern Chukchi Sea, particularly the planktivores, is influenced by advective processes that transport BSW and its associated community of oceanic zooplankton northward from the Bering Sea. The abundance of all 8 focal taxa was related to temperature in the upper 10 m of the water column, which is an indicator of the water mass present near the surface. Planktivores are the most abundant feeding guild of seabirds in the northeastern Chukchi Sea during the open-water period (Gall et al. 2013), indicating that zooplankton are sufficiently abundant to support ≥1 million seabirds for at least a few weeks in August and September. Because these advected zooplankton also are important prey for pelagic and demersal fishes in the Chukchi Sea, the biomass of zooplankton could serve as a proxy for fish abundance (Vlietstra 2005, Ainley et al. 2009), which has been difficult to quantify in this region (Norcross et al. 2010, 2013). Total seabird abundance in our study area was lower in 2012 than in 2011. This interannual variation reflected overall lower water temperatures in 2012, but associations with the abundance of zooplankton were less clear.

We do not yet fully understand all of the mechanisms that concentrate prey and create efficient foraging conditions for seabirds in the northeastern Chukchi Sea. In years that are consistently cold due to the presence of sea ice, low overall seabird abundance can be expected because these conditions limit the rate of advection of Pacific zooplankton into the region, limit zooplankton growth and development and, therefore, limit the biomass of prey of Pacific origin available to seabirds (Day et al. 2013). In warmer years, however, the expected magnitudes of seabird abundance or even seasonal trends in abundance still are challenging to predict. Clearly, the interactions among BSW, MW, and WW affect the strength, location, depth, and persistence of fronts and pycnoclines, all of which are features that can affect how accessible prey is to seabirds (Decker & Hunt 1996; Hunt et al. 1996, 1998) and probably are cues that seabirds use to find aggregations of prey. In addition, the thermal conditions and nutrients advected from the Bering Sea affect the biomass of zooplankton available (Questel et al. 2013). The challenge lies in identifying the functional shape and spatial scale of the relationship between the abundance of seabirds and their prey, after accounting for variations in habitat. We addressed this challenge here by developing statistical models to quantify these relationships.

3.5.1 Influence of physical oceanography

Observations in the region during 2008–2010 (Gall et al. 2013) focused on 3 study-area boxes that offered a fragmented look at the fronts that develop each summer between BSW that intrudes from the south and MW and WW that are formed on the northeastern Chukchi shelf during winter and spring. Comparisons among the boxes suggested that the structure and variability of the seabird community reflects the flow of BSW northward in the Central Channel. Data collected in 2011–2012 from the GHS study area provide further evidence to support this hypothesis and suggest that far fewer birds use Hanna Shoal during the open-water season than use the areas of deeper (>40 m) water that surround it. Species associated with BSW in the boxes such as Least Auklets, Crested Auklets Thick-billed Murres, and Northern Fulmars were concentrated in the southwestern half of the GHS, with water temperatures in the upper 10 m as the strongest predictors of abundance in the spatial models. In 2012, all of these BSW-associated species appeared to concentrate along a thermohaline front that bisected the GHS from the southeastern boundary near 71 °N to the northwestern boundary near 72 °N.

It is challenging to compare features of hydrography as individual factors because there are correlations among temperature, salinity, and mixed-layer depth. Temperature and salinity near the surface and near the bottom were so highly correlated that they were not included together in models. Instead, they were included singly in the models, and the one parameter with the strongest relationship to seabird abundance (in combination with the other hydrographic and biological factors in the model) essentially served as a proxy for the others. Mixed-layer depth was included in the highly-ranked models but provided little additional explanation for variation in abundance. Strength of stratification was correlated with temperature near the surface, such that colder waters were more strongly stratified than were warmer waters. Thus, temperature in this study can serve as an indicator of both water-column structure and water-mass near the surface.

Temperature

Of the physical oceanographic characteristics that we measured, water temperature had the strongest relationship with the abundance of seabirds. This relationship generally was monotonic and varied with foraging strategy, with the abundance of diving seabirds increasing and the abundance of surface-feeding birds decreasing as surface waters warmed. There also was a tendency for warm water to be more weakly stratified than cold water was. For species that are strong divers (e.g., Crested Auklets, Thick-billed Murres, Short-tailed Shearwaters), the absence of strong vertical structure would not necessarily inhibit their foraging efficiency because they can exploit much of the water column over the shallow (~50 m deep) Chukchi shelf. Crested Auklets can dive to 25 m, and both Thick-billed Murres and Short-tailed shearwaters have been confirmed to dive to at least 70 m (Weimerskirch & Cherel 1998, Elliott et al. 2009). Birds that feed at or near the surface, however, rely on strong, shallow pycnoclines (Hunt 1997, Fauchald 2009) and possibly other subsurface predators (Hoffman et al. 1981, Ballance et al. 1997, Fauchald 2009) to enhance prey availability in the uppermost layers of the water column. The colder waters found over Hanna Shoal were more strongly stratified than waters farther west near the Central Channel, possibly enhancing foraging conditions for surface-feeding gulls. Both phalaropes and Least Auklets were found close to fronts but on the cold side of them, likely benefitting from the strongly-stratified structure.

In addition to affecting hydrography, water temperature influences the species-composition of zooplankton and fish prey that are available to seabirds. The seasonal progression of community structure for zooplankton in the GHS is influenced by water temperature (Questel et al. 2013), with euphausiids and *Neocalanus* spp. more abundant in warm water and *Calanus* spp. more abundant in cold water. Average water-column temperature also contributes to observed differences in fish species composition and distribution throughout the Chukchi Sea (Norcross et al. 2010, Eisner et al. 2013). Piscivorous Black-legged Kittiwakes were more abundant in cold water that was well within the preferred temperature range of Arctic cod (*Boreogadus saida*; De Robertis and Cokelet 2012, Eisner et al. 2013), whereas murres were more abundant in areas of warm BSW with assemblages of Pacific species, including Pacific herring (*Clupea pallasii*) and capelin (*Mallotus villosus*; Norcross et al. 2010, Eisner et al. 2013). The relationship between seabirds and temperature may be the result of both the physical mechanisms that concentrate prey and the prey that are available within the associated water mass.

Water temperature frequently is found to be a reliable predictor of seabird abundance in offshore waters that range from polar to temperate and even tropical habitat (O'Hara et al. 2006, Vilchis et al. 2006, Bost et al. 2009, Péron et al. 2010, Kappes et al. 2010, Renner et al. 2013).

This association is in part because sea-surface temperature is available through remote sensing and therefore is included in many seabird habitat models. Even in studies that include a suite of *in situ* measurements, however, water temperature often is identified as an important factor. The consistency of this relationship suggests that water temperature is a cue that that seabirds can universally detect and use to identify habitat suitable for foraging. For seabirds in the Chukchi Sea, it is interesting to note that the inflection point for the curves (i.e., the value at which the relationship changed from positive to negative or vice versa) was at 4 °C for all 8 species. Ice-melt in summer can provide low-salinity water to the region that may affect the hydrography, making 4 °C a biologically relevant threshold for defining seabird habitat.

Fronts

Fronts are considered areas of enhanced productivity and often are areas of increased seabird abundance (Hunt et al. 1990, Day 1992, Spear et al. 2001, Ainley et al. 2005, Bost et al. 2009). In contrast to the relationship with temperature, which varied by foraging strategy, the relationship between the abundance of seabirds and surface thermal fronts varied by primary prey. Planktivorous seabirds generally were more abundant close to fronts, whereas piscivorous birds were more abundant far from fronts. Phalaropes and Short-tailed Shearwaters were rare more than 60 km from a front. Phalaropes are small (~50 g) shorebirds that forage only on the surface and typically are associated with fine-scale upwelling and convergence fronts that concentrate prey within ~0.2 m of the surface (Brown & Gaskin 1988, DiGiacomo et al. 2002, Thorne & Read 2013). Phalarope distribution was highly clumped, and they were particularly abundant when and where there were filaments of cold water at or near the surface that were embedded within warmer waters, indicating frontal instabilities that can create patchy structure. Short-tailed Shearwaters are fairly large (~500 g) seabirds that consume a variety of large zooplankton, in addition to fish and squid (Hunt et al. 2002, Jahncke et al. 2005b); although they can forage as deeply as 70 m, they usually forage at or near the surface (Weimerskirch & Cherel 1998, Baduini et al. 2001, Vlietstra et al. 2005) and are associated with fronts when foraging in the Southern Ocean (Woehler et al. 2006). Both Short-tailed Shearwaters and phalaropes rely on the vertical movement of water within fronts to aggregate prey and facilitate foraging (Jahncke et al. 2005b, Thorne and Read 2013).

The relationship with fronts was weaker for auklets than for the other planktivores, although both Crested and Least auklets were less abundant >60 km from a front. Despite having overlapping diet preferences (Hunt et al. 1998; Gall et al. 2006), Crested and Least auklets tend to segregate spatially when foraging (Hunt et al. 1998, Russell et al. 1999). Least Auklets often occur on the stratified side of fronts (Elphick and Hunt 1993, Russell et al. 1999) or over stratified water (Hunt et al. 1993, Russell et al. 1999), whereas Crested Auklets have not shown strong affinities for fronts or stratified water (Elphick and Hunt 1993, Hunt et al. 1998, Russell et al. 1999). Temperature was a stronger predictor of abundance for auklets than was distance to front, suggesting that, although these diving birds generally benefit from processes in and near fronts that aggregate prey, they primarily are keying in on water-masses to find patches of available prey.

The distribution of both pelagic and demersal fish is strongly influenced by water temperature (Norcross et al. 2010, Crawford et al. 2012, De Robertis & Cokelet 2012, Eisner et al. 2013), but there is little evidence to indicate that areas near fronts are necessarily areas of increased fish abundance. In fact, there is evidence from the southern Chukchi that fish abundance is negatively correlated with strong lateral temperature gradients (i.e., fronts; Piatt et al 1991). Murres are often associated with fronts identified by horizontal gradients in temperature (Decker & Hunt 1996, Hoefer 2000, Ainley et al. 2005). In the northeastern Chukchi Sea, however, it appears that both murres and Black-legged Kittiwakes are more abundant in areas of homogenous water masses at the surface, rather than near the boundaries between water masses.

Vertical stratification and subsurface fronts may be more important factors in aggregating prey than are fronts measured at the surface. Properly characterizing preferred habitat for seabirds is challenging, however, because we did not measure these vertical features at the same resolution as we did the distribution of seabirds. We calculated mixed-layer depth from CTD casts at stations spaced ~14 km apart and sampled 1–3 days before or after seabirds were surveyed near the station. This temporal and spatial mismatch may explain why depth of the mixed layer was a poor predictor of seabird abundance in the models, despite being included in most of the best models. High-resolution sampling of hydrography with a towed CTD system concurrent with seabird surveys offers opportunities to quantify better the relationships between hydrography and seabird abundance (e.g., Cox et al. 2013).

3.5.2 Influence of biological oceanography

Seabirds are adapted to sample their habitat in such a way as to maximize their probability of finding food. During the breeding season, seabirds are restricted in habitats available within foraging distance of their colony, which for birds that nest in the southern Chukchi and northern Bering seas is a radius of 20–100 km (Hunt 1997, Hatch et al. 2000, Jahncke et al. 2005a). By September, however, the breeding season in the Northern Hemisphere is finished, so birds nesting in the northeastern Chukchi Sea are free to move to wherever they are most likely to find food. This freedom of movement would appear to meet the key assumptions of the Ideal Free Distribution (IFD) theory, which includes maximized foraging efficiency, freedom to move among prey patches, knowledge of the resources available, equal competition, and a reduction in individual consumption with an increase in predator density (Fretwell & Lucas Jr. 1969). This theory predicts that seabirds will be distributed proportional to the resources available. Although seabirds may not meet all of the assumptions of IFD, they certainly meet more of them during this post-breeding period and, therefore, we can expect the greatest probability of detecting a positive relationship between these marine predators and their prey.

Planktivorous seabirds

The abundance of Least Auklets was positively associated with the biomass of both Pacific and *Calanus* spp. zooplankton, although the relationship was strongest with *Calanus* spp. Least Auklets consume both oceanic (e.g., *N. plumchrus*) and neritic (e.g., *C. marshallae*) copepods, but *Calanus* spp. generally compose the majority of their diet (Hunt et al. 1998, Gall et al. 2006, Guy et al. 2009). Large calanoid copepods are well sampled with bongo nets (Skjoldal et al. 2013), providing an accurate assessment of abundance for this prey assemblage. The model for Least Auklet abundance explained the most variation in their distribution and reinforces the importance of obtaining prey indicators that are accurate and species-specific.

Crested Auklets consume primarily euphausiids (e.g., *Thysanoessa* spp.) and large copepods (e.g., *N. cristatus*, *N. plumchrus*) characteristic of oceanic water from the North Pacific and Bering seas (Bédard 1969, Kitaysky & Golubova 2000, Gall et al. 2006). The abundance of Crested Auklets showed no consistent association with the biomass of either Pacific or arctic zooplankton (the former group included *Neocalanus* spp. and euphausiids). Euphausiids in particular are difficult to sample with bongo nets because they can move quickly and actively avoid nets (Skjoldal et al. 2013). The failure to sample their primary prey adequately may help explain why the spatial models for Crested Auklets explained only 10% of the variation in their abundance. Crested Auklets also may have limited mobility during late August and early September due to molting of flight feathers (A. Gall and K. Kuletz, unpublished data), which could interfere with their ability to stay in contact with mobile prey patches.

The distribution of planktivores that feed at or near the surface reflected their respective foraging strategies more strongly than their prey preferences did. The pattern of interannual variation in the abundance of Short-tailed Shearwaters during this study was similar to that of Crested Auklets, with more birds of both species recorded in 2011 than in 2012. The spatial distribution of Short-tailed Shearwaters, however, was focused farther south than that of Crested Auklets in both years. Shearwaters may remain south to avoid areas of MW and WW found near Hanna Shoal. They may also limit their northward distribution because they are migrants from the Southern Hemisphere and must return to Australia to breed. Although they share a common preferred prey, the differences in habitat preference between Short-tailed Shearwaters and Crested Auklets highlight how feeding guild, foraging strategy, and life history can influence species-specific abundance and distribution.

Phalaropes have the most restricted foraging habitat of the planktivores we studied in detail. The abundance of phalaropes had negative associations with the biomass of Pacific and arctic zooplankton. This negative relationship suggests that the zooplankton we measured do not adequately represent phalarope diets. There is little information about phalarope diets in the Pacific during the non-breeding season. The few studies along the California coast indicate that they feed on euphausiids and fish eggs and rarely take small copepods (Briggs et al. 1984, DiGiacomo et al. 2002). Our results are consistent with other studies that emphasize how phalaropes rely on fine-scale oceanographic processes to concentrate prey (Brown and Gaskin 1988, Hunt et al. 1988, Obst and Hunt 1990, Thorne and Read 2013), processes that clearly are stronger predictors of phalarope abundance than are measures of prey availability.

Omnivorous seabirds

The distribution and abundance of omnivorous species, as indicated by Northern Fulmars and Glaucous Gulls, identified differences in prey preferences despite their flexibility in foraging. Both species were present throughout the study area but at considerably lower abundance than the planktivores. Neither species was strongly associated with changes in prey biomass, although the trends suggest that Northern Fulmars were negatively associated with the biomass of *Calanus* spp. whereas Glaucous Gulls were positively associated with the biomass of these arctic copepods. This weak association with the abundance of prey may have occurred because they are so flexible in their prey selection or because of the limitations of our sampling. Habitat models are sensitive to zero-inflated data (Vilchis et al. 2006, Zuur et al. 2009); therefore, the low overall abundance of these species made it difficult to quantify with confidence the effects of the environmental variables. Despite this limitation, the prey preferences identified in the spatial models are consistent with the life-histories of these species. Northern Fulmars breed only as far north in the Bering Sea as the southern side of the Chukotka Peninsula, just south of Bering Strait (Kondratyev et al. 2000). Although they do eat fish, cephalopods, offal, and carrion in areas with active commercial fisheries, Northern Fulmars specialize on oceanic copepods and euphausiids when they are feeding away from fishing grounds (Jahncke et al. 2005a, Mallory et al. 2012, Matley et al. 2012). Consequently, their habitat associations in the Chukchi Sea reflect their dependence on a prey community of Pacific origin. Glaucous Gulls breed in the circumpolar subarctic and Arctic, have a very general diet, and use a variety of strategies to feed, including scavenging and kleptoparasitism (Weiser & Gilchrist 2012, Matley et al. 2012). It therefore is not surprising that they occur throughout the GHS study area and have a positive association with zooplankton typical of arctic water.

Piscivorous birds

Despite being classified primarily as piscivores by some (e.g., Piatt and Springer 2003), Black-legged Kittiwakes are surface-feeding gulls that consume both fishes and large zooplankton (Hobson 1993, Jodice et al. 2006, Iverson et al. 2007). Thick-billed Murres are diving alcids that eat primarily fishes but also will consume large pelagic invertebrates (Woo et al. 2008). The best habitat models for both species indicated a positive association with the biomass of Pacific zooplankton, a category that included euphausiids. Neither species was associated with changes in biomass of arctic zooplankton, possibly because they rely primarily on prey other than zooplankton or because the zooplankton groups that we used are not strong proxies for the availability of their preferred prey.

3.5.3 Conclusions

These spatial models provide insight into factors that seabirds use to select their foraging habitat. These relationships vary with a combination of prey preferences and foraging strategy. Preferences for water-masses over the shallow shelf of the Chukchi Sea depend on foraging strategy; diving seabirds generally are more abundant in warm BSW, whereas seabirds that feed at or near the surface generally are more abundant in cold, two-layered MW/WW. Preferences for horizontal structure as identified by surface thermal fronts depends on prey preferences, with planktivorous birds more abundant near fronts and piscivorous birds more abundant far from them.

We demonstrate that differences in seabird distribution reflect the shifting dynamics of BSW and its associated biological community throughout the northeastern Chukchi Sea. For some species that consume primarily zooplankton, data on regional zooplankton biomass has improved our ability to predict seabird abundance. For other species, it has served to highlight that birds may rely as much or more on habitat cues to determine their distribution as they do on knowledge of prey resources. Our growing understanding of factors that influence interannual variability is improving our ability to monitor the seabird community and predict the effects of changing environmental conditions in this region of increasing commercial interest.

3.6 Acknowledgments

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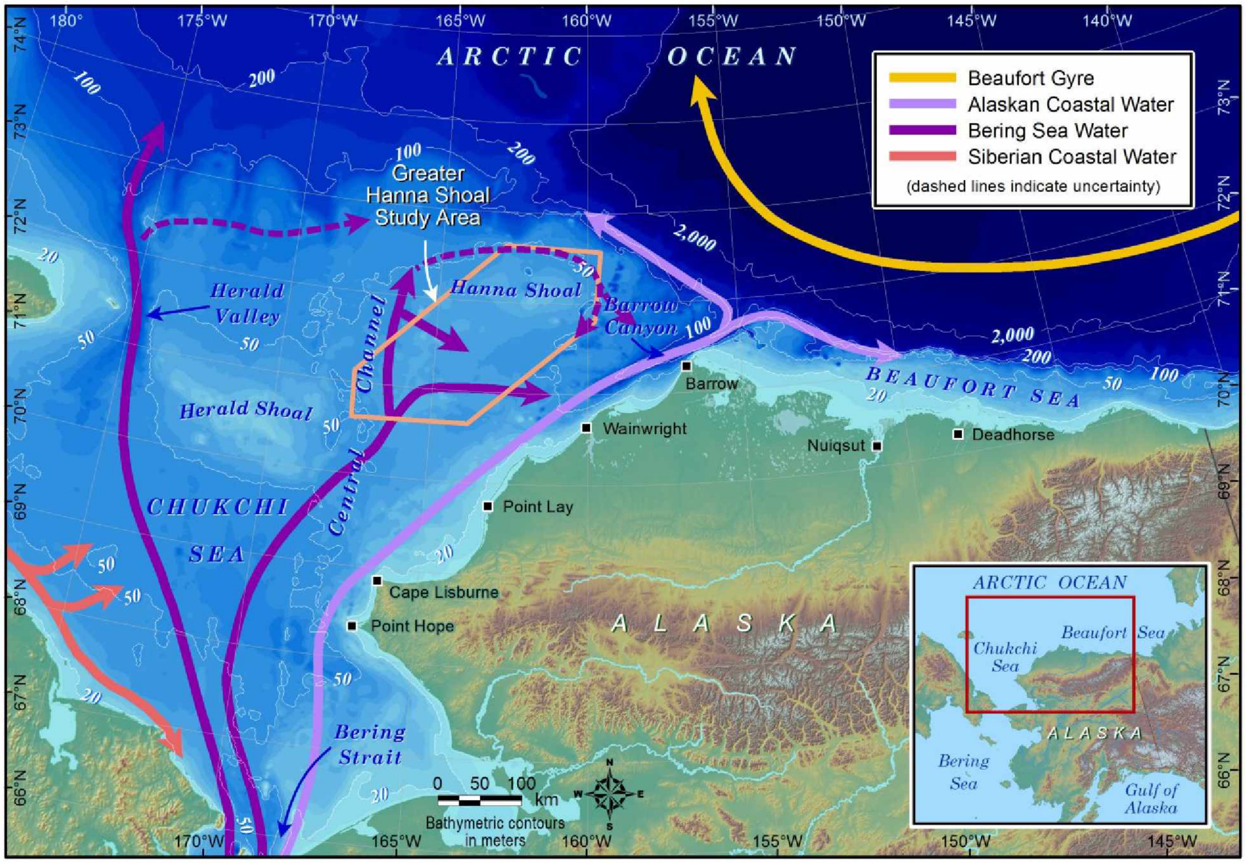

Figure 3.1 Location of the Greater Hanna Shoal study area, northeastern Chukchi Sea, Alaska. Arrows show currents and main water-masses.

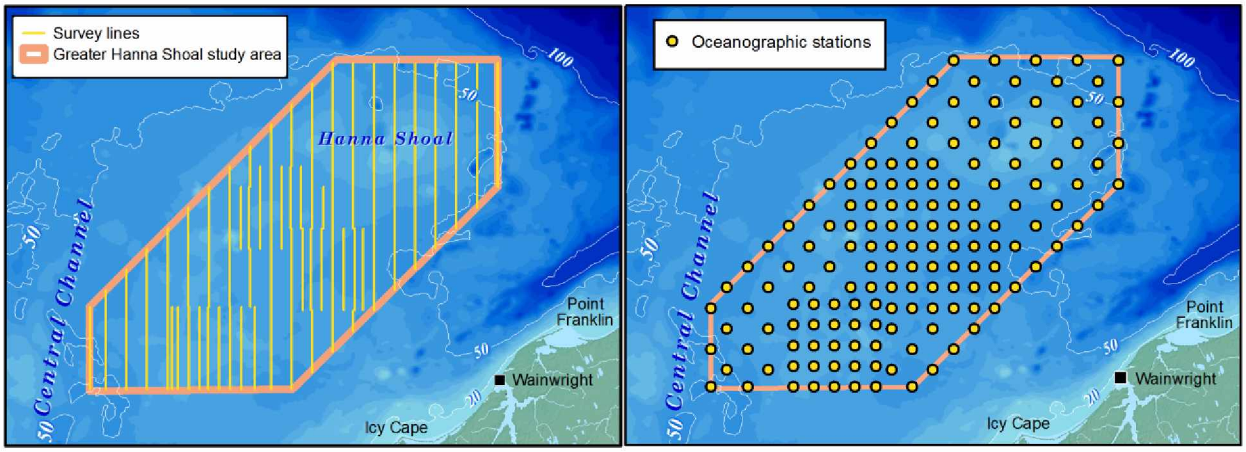

Figure 3.2 Survey lines (left) and oceanographic stations (right) sampled within the Greater Hanna Shoal study area, northeastern Chukchi Sea, Alaska, 2011–2012. There was greater sampling intensity in the vicinity of three oil prospects.

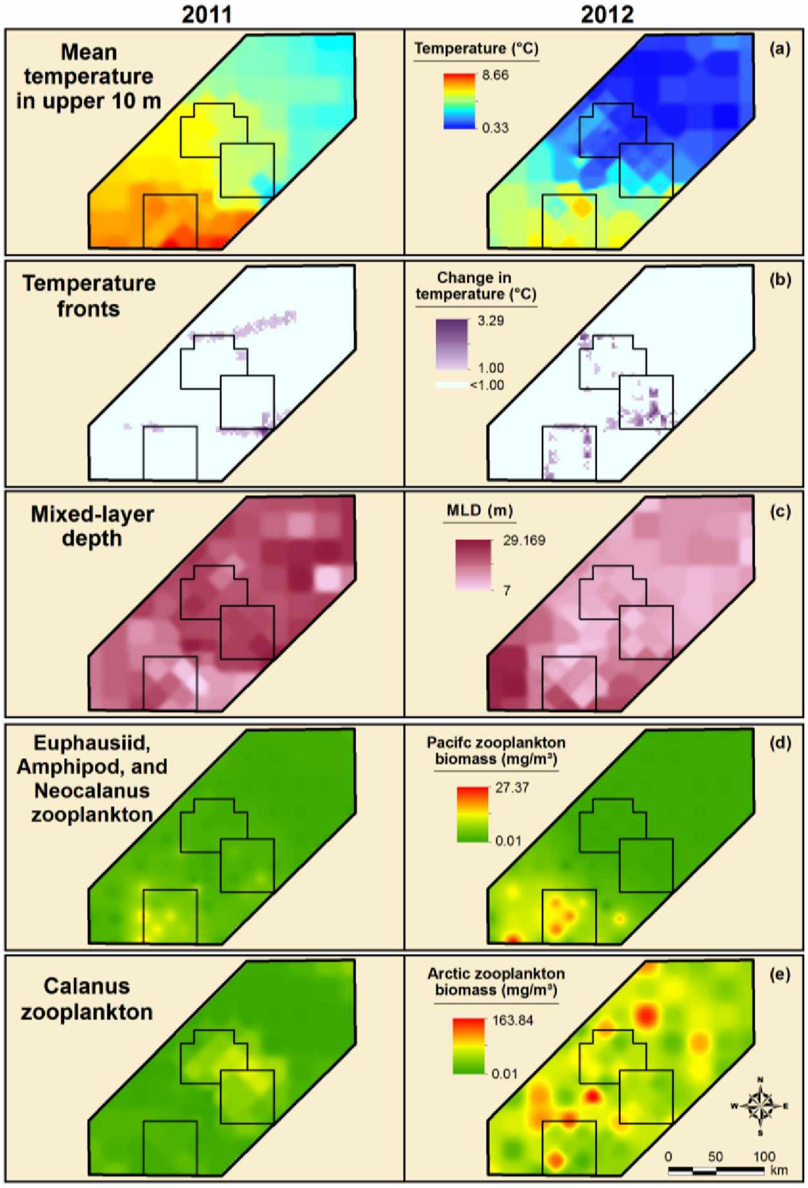

Figure 3.3 Spatial distribution of environmental covariates included in models of seabird abundance in the northeastern Chukchi Sea, 2011 and 2012. Values for (a) mixed-layer depth, (b) mean temperature in the upper 10 m of the water column, (d) biomass of Pacific zooplankton prey, and (e) biomass of arctic zooplankton prey are interpolated over 3.0×3.0-km grids from measurements at stations spaced 14–20 km apart. Values for (c) temperature fronts (i.e., a steep temperature gradient) are interpolated from continuous measurements collected with a hull-mounted thermosalinograph.

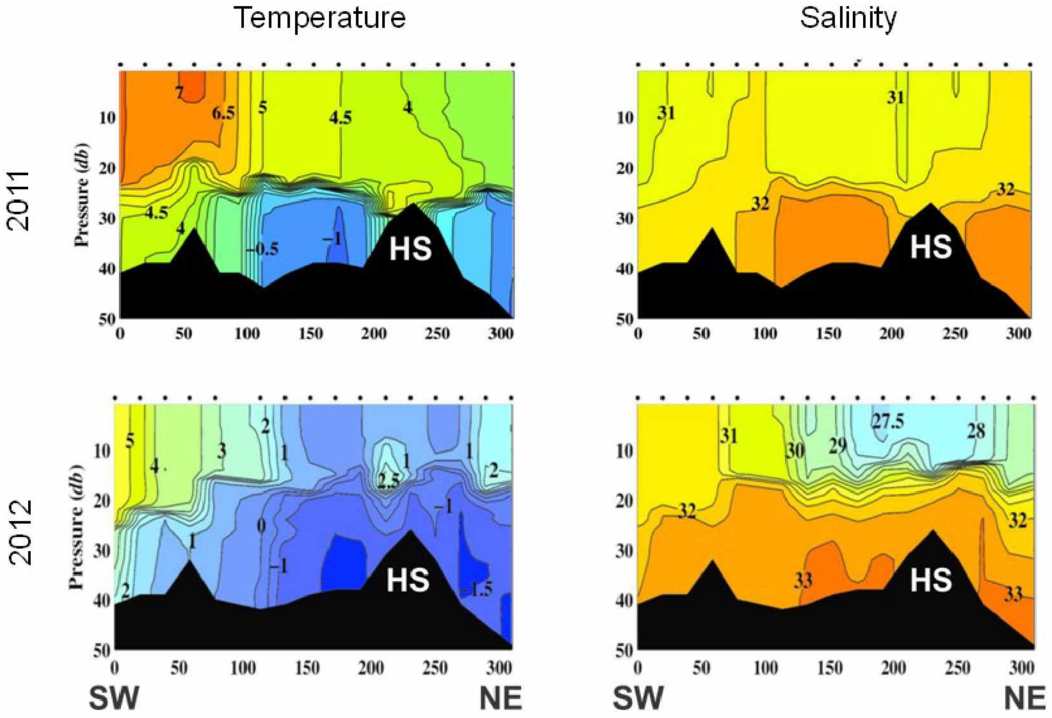

Figure 3.4 Vertical sections of temperature (°C; left) and salinity (right) from the southwestern corner to the northeastern corner of the Greater Hanna Shoal study area, 2011–2012. HS refers to the summit of Hanna Shoal.

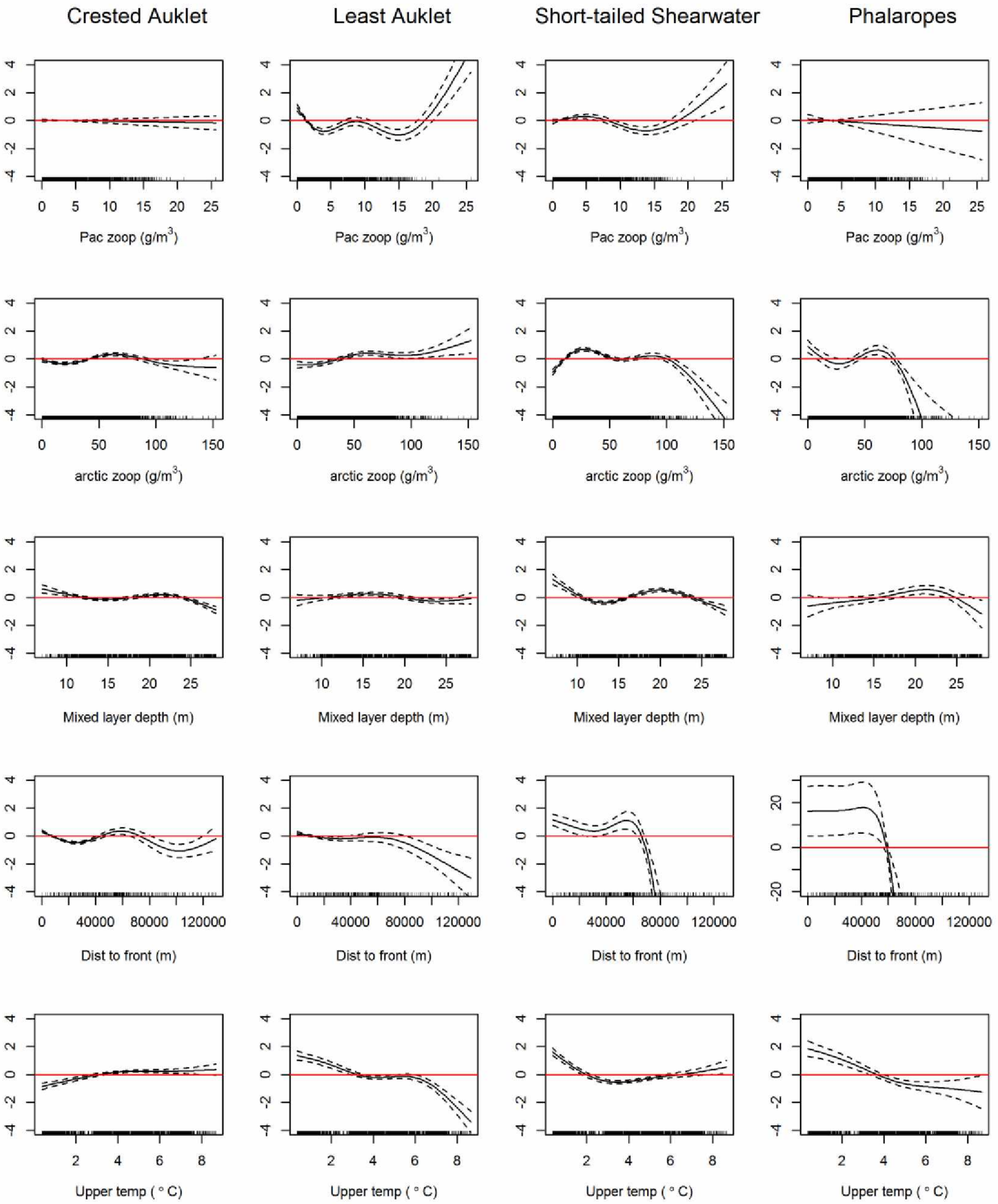

Figure 3.5 Conditional additive effects of oceanographic habitat parameters on the abundance of planktivorous seabirds in the northeastern Chukchi Sea, 2011–2012. Dashed lines represent 95% CI of the effect of the parameter when other covariates are held constant. The distribution of samples is indicated by tickmarks on the X-axis; units of the Y-axis are the additive effect on log(abundance+1).

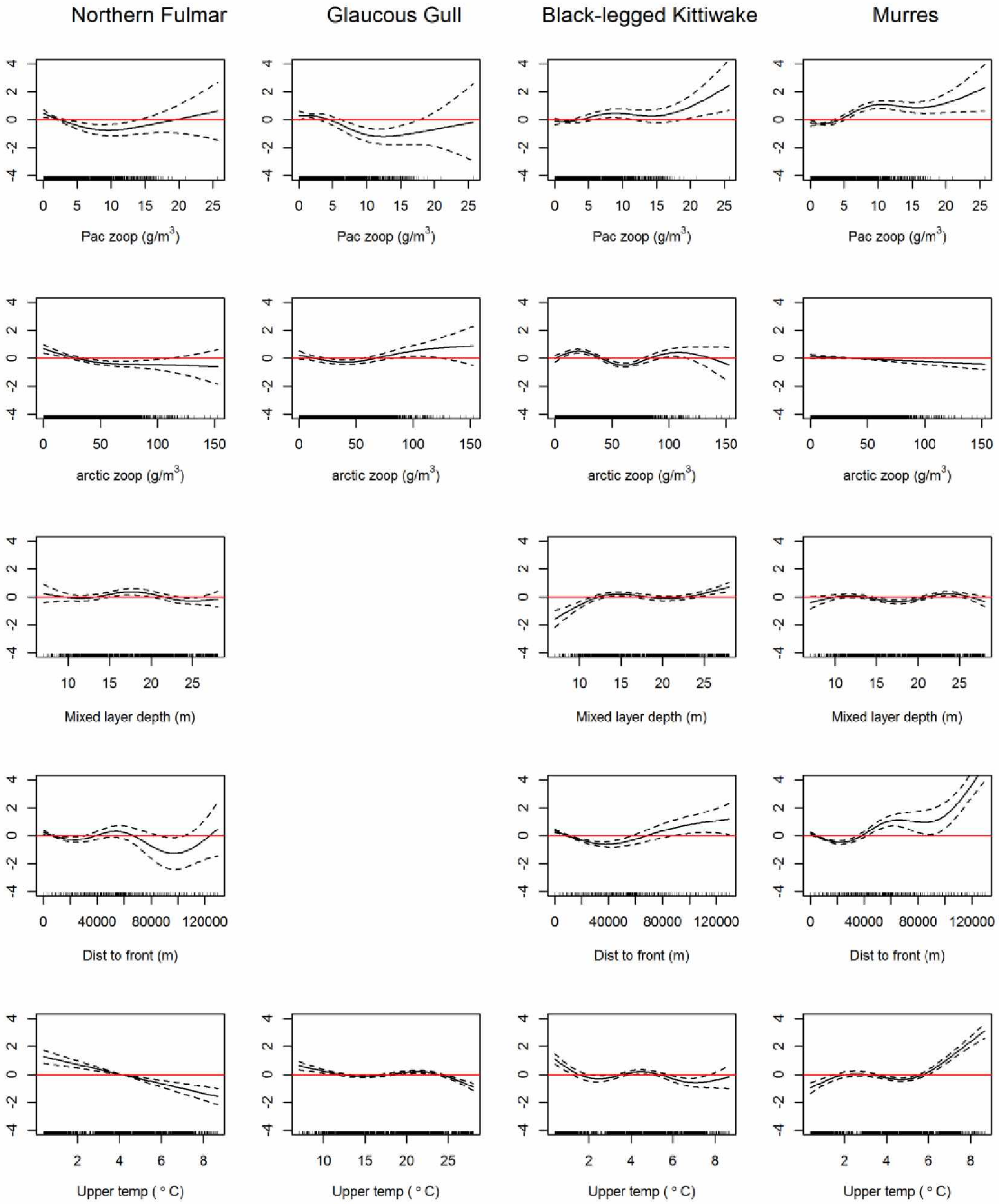

Figure 3.6 Conditional additive effects of oceanographic habitat parameters on the abundance of omnivorous and piscivorous seabirds in the northeastern Chukchi Sea, 2011–2012. Dashed lines represent 95% CI of the effect of the parameter when other covariates are held constant. The distribution of samples is indicated by tickmarks on the X-axis; units of the Y-axis are the additive effect on log(abundance+1).

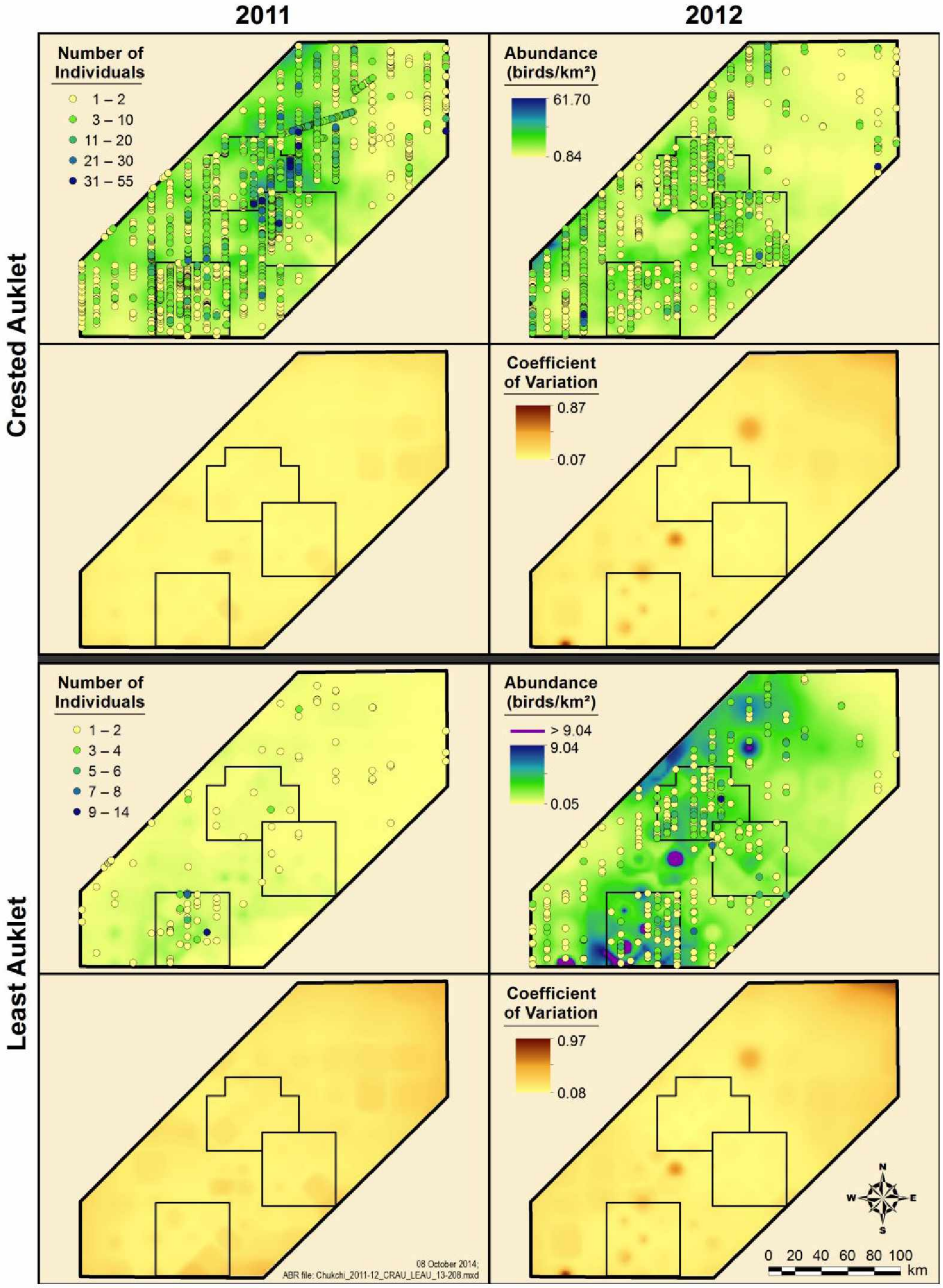

Figure 3.7 Fitted density surface models of Crested and Least auklets (birds/km^2) in the Greater Hanna Shoal study area in Sep 2011 and 2012. Colored circles indicate the original observations. Plots of coefficients of variation (CV) for the predicted surfaces show uncertainty in the predictions of abundance; darker color indicates higher model uncertainty.

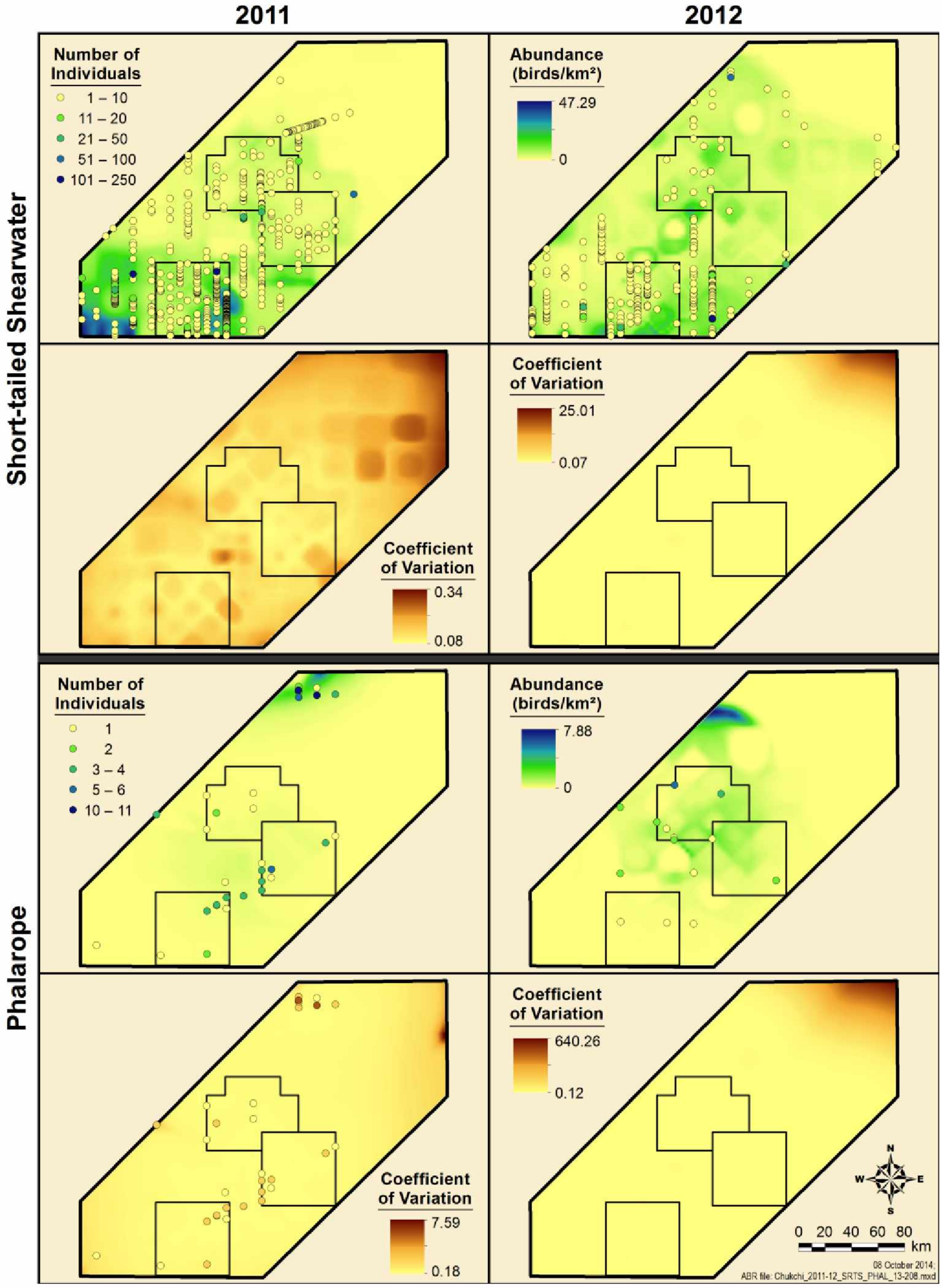

Figure 3.8 Fitted density surface models of Short-tailed Shearwaters and phalaropes (birds/km^2) in the Greater Hanna Shoal study area in Sep 2011 and 2012. Colored circles indicate the original observations. Plots of coefficients of variation (CV) for the predicted surfaces show uncertainty in the predictions of abundance; darker color indicates higher model uncertainty.

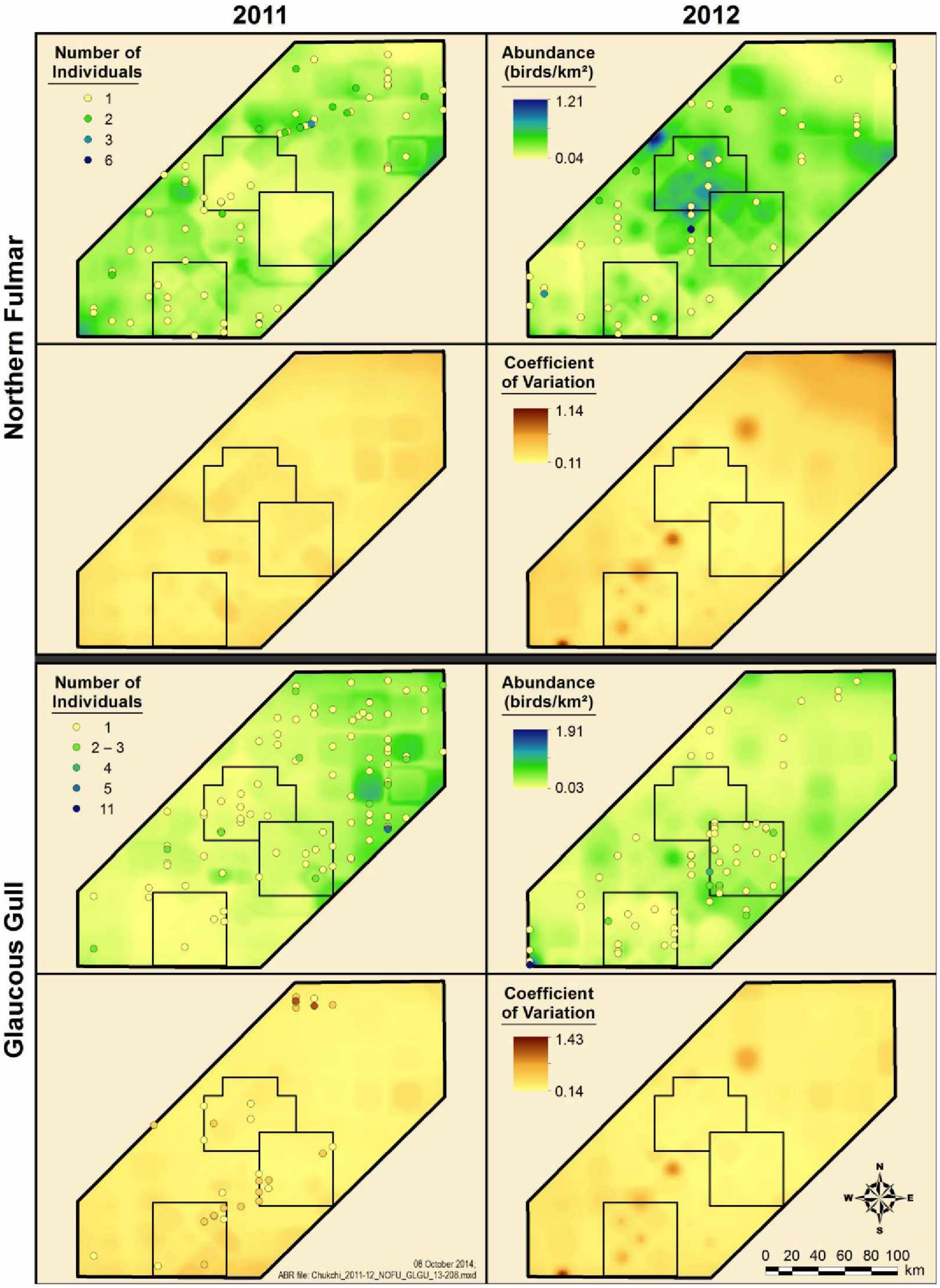

Figure 3.9 Fitted density surface models of Northern Fulmars and Glaucous Gulls (birds/km^2) in the Greater Hanna Shoal study area in Sep 2011 and 2012. Colored circles indicate the original observations. Plots of coefficients of variation (CV) for the predicted surfaces show uncertainty in the predictions of abundance; darker color indicates higher model uncertainty.

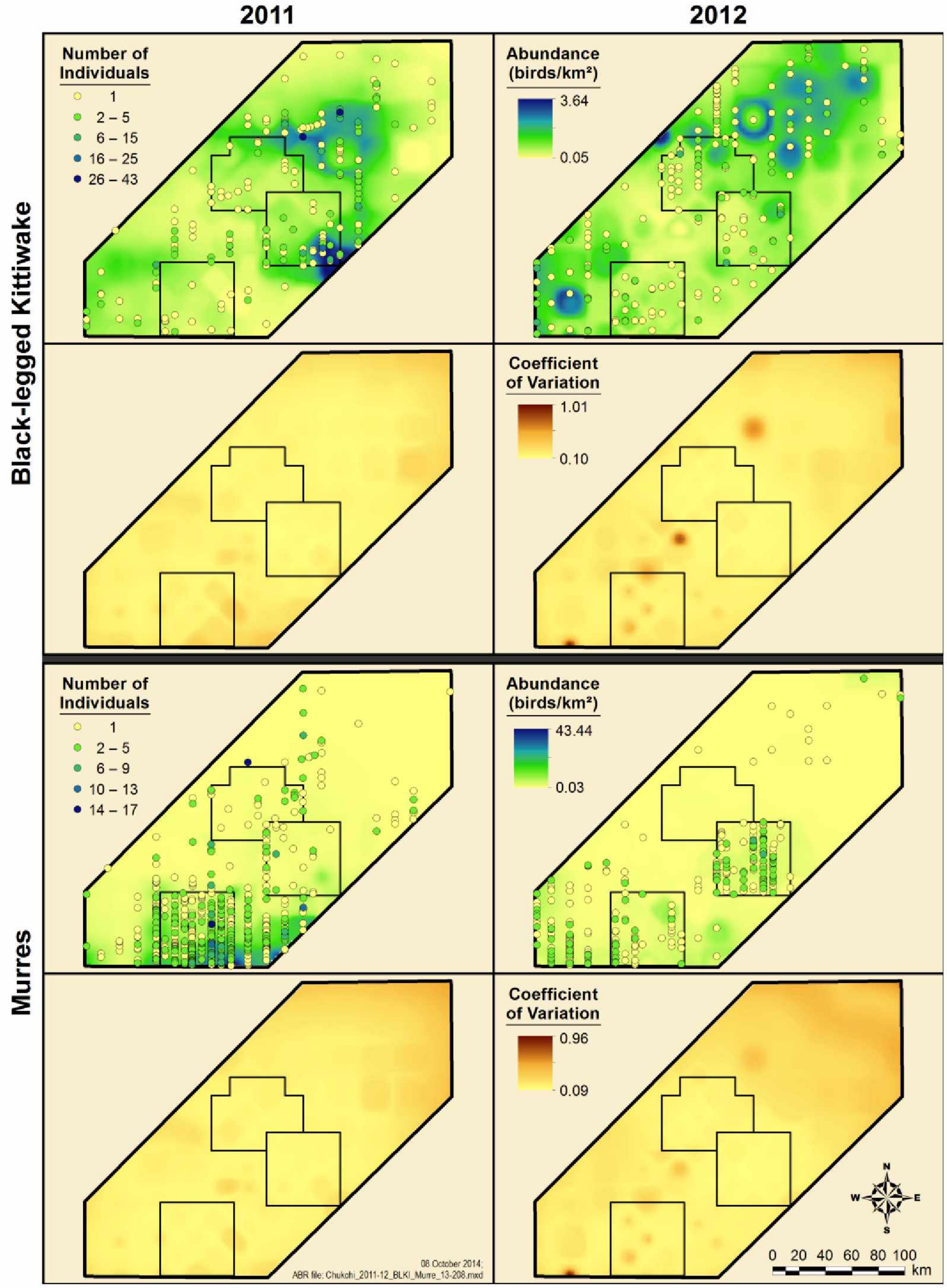

Figure 3.10 Fitted density surface models of Black-legged Kittiwakes and murres (birds/km^2) in the Greater Hanna Shoal study area in Sep 2011 and 2012. Colored circles indicate the original observations. Plots of coefficients of variation (CV) for the predicted surfaces show uncertainty in the predictions of abundance. Darker color indicates higher model uncertainty.

Table 3.1. Detection function models used to calculate corrected densities of 8 focal taxa of seabirds in the northeastern Chukchi Sea.

Species/taxon	Function shape	Covariates	Average probability of detecting a flock	CV[a] (%)	Mean flock size
Crested Auklet	half-normal	observer + vessel + sea state	0.64	1.5	3.6
Least Auklet	hazard-rate	observer + sea state	0.69	2.3	1.9
Black-legged Kittiwake	half-normal	observer	0.58	2.4	2.2
Glaucous Gull[b]	–	–	–	–	1.2
Northern Fulmar[b]	–	–	–	–	1.3
Phalaropes	half-normal	observer + vessel + sea state	0.48	7.5	4.9
Short-tailed Shearwater	hazard-rate	observer	0.73	3.2	3.9
Murres	hazard-rate	observer + sea state	0.77	2.6	1.7

[a] Coefficient of variation of the probability of detection.
[b] Combined with similar species; share one detection-function model.

Table 3.2. Generalized additive models used to explore the relationship between the abundance of 8 taxa of seabirds (N) and oceanography in the northeastern Chukchi Sea, 2011–2012.

Description	Model
Spatial pattern	N~ s(lat) + s(long)
Mean temperature near surface (upper temp)	N~ s(lat) + s(long) + s(TempTop10m)
Mean temperature near bottom	N~ s(lat) + s(long) + s(TempBottom10m)
Mean salinity near surface	N~ s(lat) + s(long) + s(SalTop10m)
Mean salinity near bottom	N~ s(lat) + s(long) + s(SalBottom10m)
Mixed-layer depth	N~ s(lat) + s(long) + s(MLD)
Distance to front	N~ s(lat) + s(long) + s(Dfront)
Biomass of Pacific zooplankton prey	N~ s(lat) + s(long) + s(PacPrey)
Biomass of arctic zooplankton prey	N~ s(lat) + s(long) + s(ArcticPrey)
Biomass of all zooplankton prey	N~ s(lat) + s(long) + s(PacPrey) + s(ArcticPrey)
Mixed-layer depth , upper temperature	N~ s(lat) + s(long) + s(MLD)+ s(TempTop10m)
Prey, mixed-layer depth	N~ s(lat) + s(long) + s(PacPrey) + s(ArcticPrey) + s(MLD)
Prey, upper temperature	N~ s(lat) + s(long) + s(PacPrey) + s(ArcticPrey) + s(TempTop10m)
Prey, distance to front	N~ s(lat) + s(long) + s(PacPrey) + s(ArcticPrey) + s(Dfront)
Prey, mixed-layer depth, upper temperature	N~ s(lat) + s(long) + s(PacPrey) + s(ArcticPrey) + s(MLD) + s(TempTop10m)
Prey, distance to front, upper temperature	N~ s(lat) + s(long) + s(PacPrey) + s(ArcticPrey) + s(Dfront) + s(TempTop10m)
Physical habitat characteristics	N~ s(lat) + s(long) + s(MLD) +s(Dfront) +s(TempTop10m)
Prey, mixed-layer depth, distance to front, upper temperature	N~ s(lat) + s(long) + s(PacPrey) + s(ArcticPrey) + s(MLD) +s(Dfront) +s(TempTop10m)

Table 3.3 Seabird observations and estimated densities with 95% confidence intervals for 8 taxa of seabirds in the Greater Hanna Shoal study area, northeastern Chukchi Sea, 2011 and 2012.

	2011			2012		
Species/taxon	No. flocks	No. individuals	Density (birds km^{-2})	No. flocks	No. individuals	Density (birds km^{-2})
Crested Auklet	1,822	5,794	12.03 (10.75–3.34)	1,939	5,490	11.44 (9.79– 13.43)
Least Auklet	98	157	0.20 (0.25–0.42)	699	1,393	2.90 (2.63– 3.19)
Short-tailed Shearwater	555	1,890	4.70 (3.30– 6.52)	649	1,747	4.36 (3.36– 5.56)
Phalaropes	27	74	0.15 (0.09– 0.23)	44	152	0.37 (0.19– 0.46)
Northern Fulmar	74	85	0.18 (0.14– 0.22)	100	151	0.31 (0.23– 0.42)
Glaucous Gull	81	96	0.20 (0.17– 0.24)	70	94	0.20 (0.14– 0.25)
Black-legged Kittiwake	190	390	0.81 (0.65– 0.98)	228	340	0.71 (0.60– 0.83)
Murres	577	1,023	2.54 (2.16– 2.97)	372	560	1.40 (1.22– 1.58)

Table 3.4. Statistical significance of environmental variables and deviance explained by models for the abundance of 8 taxa of seabirds in the northeastern Chukchi Sea, 2011–2012. *P*-values are approximate, based on degrees of freedom estimated by cross-validation (Zuur et al. 2009); dashes indicate that the variable was not included in the model best supported by the data for that species.

Species/taxon	Percent deviance explained	Variables: Mixed-layer depth	Variables: Temperature (Top 10 m)	Variables: Distance to front	Variables: Biomass Pacific zooplankton	Variables: Biomass arctic zooplankton
Crested Auklet	10	<0.01	<0.01	<0.01	0.51	<0.01
Least Auklet	30	<0.01	<0.01	<0.01	<0.01	<0.01
Short-tailed Shearwater	23	<0.01	<0.01	<0.01	<0.01	<0.01
Phalaropes	29	0.34	<0.01	<0.01	0.35	<0.01
Northern Fulmar	7	0.1	<0.01	<0.01	<0.01	<0.01
Glaucous Gull	9	–	<0.01	–	<0.01	<0.01
Black-legged Kittiwake	12	<0.01	<0.01	<0.01	0.02	<0.01
Murres	36	<0.01	<0.01	<0.01	<0.01	0.05

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Appendix 3.1 Ranking of generalized additive models relating oceanographic variables to the abundance of 8 taxa of seabirds in the northeastern Chukchi Sea. Models were ranked with Akaike's Information Criterion (AIC). The number of terms (*s*), ΔAIC, and AIC weights (AIC wt) are provided for all models. Model formulas are provided in Table 3.2.

Species/taxon	Model	*s*	AIC	ΔAIC	AIC wt
Crested Auklet	Prey, mixed-layer depth, distance to front, upper temperature	7	14318.69	0.00	1.00
	Physical habitat characteristics	5	14382.05	63.36	0.00
	Prey, distance to front, upper temperature	6	14387.74	69.06	0.00
	Prey, mixed-layer depth, upper temperature	6	14432.12	113.43	0.00
	Mean salinity near surface	3	14446.63	127.94	0.00
	Prey, distance to front	5	14458.79	140.10	0.00
	Prey, upper temperature	5	14484.15	165.46	0.00
	Mixed-layer depth, upper temperature	4	14498.64	179.95	0.00
	Prey, mixed-layer depth	5	14508.26	189.57	0.00
	Distance to front	3	14556.41	237.72	0.00
	Mean upper temperature	3	14559.67	240.99	0.00
	Mean salinity near bottom	3	14561.62	242.93	0.00
	Biomass of all zooplankton prey	4	14579.71	261.02	0.00
	Mixed-layer depth	3	14585.10	266.41	0.00
	Mean temperature near bottom	3	14602.90	284.21	0.00
	Biomass of Pacific zooplankton prey	3	14609.34	290.65	0.00
	Biomass of arctic zooplankton prey	3	14644.13	325.44	0.00
	Latitude, longitude	2	14672.37	353.68	0.00
Least Auklet	Prey, mixed-layer depth, distance to front, upper temperature	7	6074.00	0.00	0.95
	Prey, distance to front, upper temperature	6	6079.99	5.99	0.05
	Prey, mixed-layer depth, upper temperature	6	6085.76	11.76	0.00
	Prey, upper temperature	5	6093.66	19.67	0.00
	Physical habitat characteristics	5	6162.52	88.52	0.00
	Mixed-layer depth, upper temperature	4	6188.68	114.68	0.00
	Mean upper temperature	3	6204.38	130.38	0.00
	Prey, mixed-layer depth	5	6215.93	141.93	0.00
	Prey, distance to front	5	6231.88	157.89	0.00
	Biomass of all zooplankton prey	4	6254.71	180.71	0.00
	Mean salinity near bottom	3	6301.84	227.85	0.00
	Mean salinity near surface	3	6407.31	333.32	0.00
	Mean temperature near bottom	3	6412.82	338.82	0.00
	Biomass of arctic zooplankton prey	3	6478.50	404.50	0.00
	Biomass of Pacific zooplankton prey	3	6610.07	536.07	0.00
	Mixed-layer depth	3	6665.85	591.85	0.00
	Distance to front	3	6779.87	705.88	0.00
	Spatial pattern	2	7051.69	977.70	0.00

Appendix 3.1 continued…

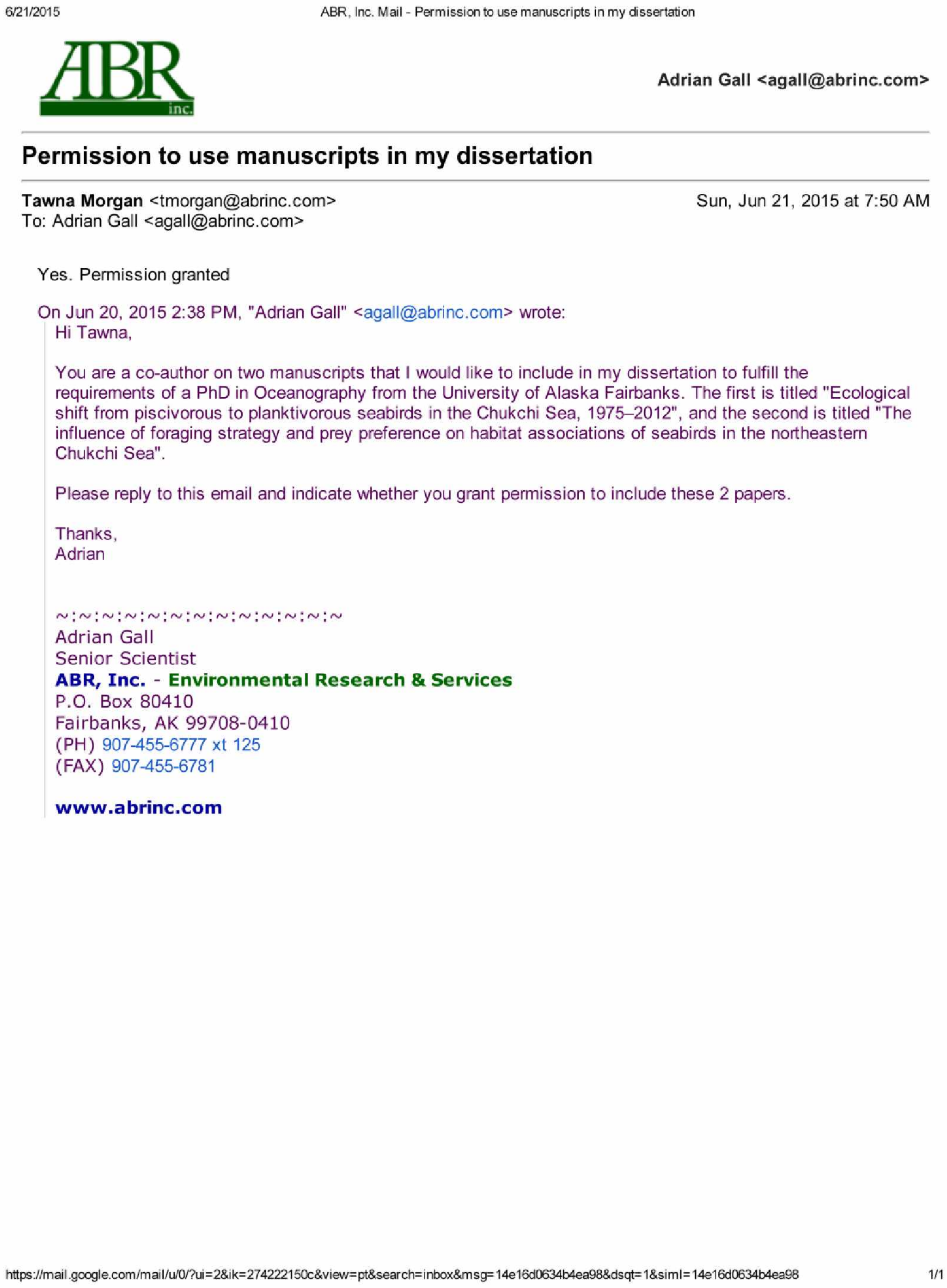
Species/taxon	Model	*s*	AIC	ΔAIC	AIC wt
Short-tailed Shearwater	Prey, mixed-layer depth, distance to front, and upper temperature	7	9446.77	0.00	1.00
	Prey, mixed-layer depth, and upper temperature	6	9544.85	98.09	0.00
	Prey, distance to front, and upper temperature	6	9566.66	119.89	0.00
	Physical habitat characteristics	5	9634.58	187.81	0.00
	Prey and mixed-layer depth	5	9680.56	233.80	0.00
	Prey and upper temperature	5	9684.10	237.33	0.00
	Mixed-layer depth and upper temperature	4	9744.87	298.11	0.00
	Prey and distance to front	5	9814.83	368.06	0.00
	Mean upper temperature	3	9880.40	433.63	0.00
	Mean salinity near bottom	3	9884.94	438.17	0.00
	Biomass of all zooplankton prey	4	9894.62	447.86	0.00
	Mean temperature near bottom	3	9909.00	462.23	0.00
	Mixed-layer depth	3	9935.66	488.89	0.00
	Mean salinity near surface	3	9948.65	501.88	0.00
	Biomass of arctic zooplankton prey	3	9992.01	545.24	0.00
	Biomass of Pacific zooplankton prey	3	10102.95	656.19	0.00
	Distance to front	3	10121.35	674.59	0.00
	Spatial pattern	2	10207.16	760.40	0.00
Phalaropes	Prey, distance to front, and upper temperature	6	1930.05	0.00	0.64
	Prey, mixed-layer depth, distance to front, and upper temperature	7	1931.17	1.13	0.36
	Mean salinity near surface	3	1952.70	22.66	0.00
	Physical habitat characteristics	5	1969.95	39.90	0.00
	Prey and distance to front	5	1986.39	56.35	0.00
	Prey, mixed-layer depth, and upper temperature	6	1987.95	57.90	0.00
	Prey and upper temperature	5	1990.46	60.42	0.00
	Prey and mixed-layer depth	5	2014.04	83.99	0.00
	Biomass of all zooplankton prey	4	2029.93	99.88	0.00
	Biomass of arctic zooplankton prey	3	2044.79	114.74	0.00
	Mixed-layer depth and upper temperature	4	2053.87	123.83	0.00
	Mean upper temperature	3	2060.37	130.32	0.00
	Mean salinity near bottom	3	2061.77	131.73	0.00
	Mean temperature near bottom	3	2066.18	136.14	0.00
	Mixed-layer depth	3	2081.91	151.86	0.00
	Distance to front	3	2089.47	159.43	0.00
	Biomass of Pacific zooplankton prey	3	2105.02	174.97	0.00
	Spatial pattern	2	2129.04	199.00	0.00

Appendix 3.1 continued…

Species/taxon	Model	*s*	AIC	ΔAIC	AIC wt
Northern Fulmar	Prey, mixed-layer depth, distance to front, and upper temperature	7	2533.26	0.00	0.99
	Prey, mixed-layer depth, and upper temperature	6	2543.36	10.10	0.01
	Prey, distance to front, and upper temperature	6	2546.31	13.05	0.00
	Prey and upper temperature	5	2550.38	17.12	0.00
	Mean salinity near surface	3	2562.31	29.05	0.00
	Physical habitat characteristics	5	2568.86	35.60	0.00
	Mixed-layer depth and upper temperature	4	2571.58	38.32	0.00
	Prey and mixed-layer depth	5	2578.61	45.35	0.00
	Mean upper temperature	3	2579.41	46.14	0.00
	Prey and distance to front	5	2582.81	49.55	0.00
	Biomass of Pacific zooplankton prey	3	2594.47	61.21	0.00
	Biomass of all zooplankton prey	4	2596.38	63.11	0.00
	Mixed-layer depth	3	2597.24	63.98	0.00
	Distance to front	3	2602.71	69.45	0.00
	Mean salinity near bottom	3	2617.62	84.36	0.00
	Spatial pattern	2	2625.80	92.54	0.00
	Biomass of arctic zooplankton prey	3	2625.84	92.58	0.00
	Mean temperature near bottom	3	2625.97	92.71	0.00
Glaucous Gull	Prey, mixed-layer depth, and upper temperature	6	2147.44	0.00	0.71
	Prey, mixed-layer depth, distance to front, and upper temperature	7	2149.28	1.84	0.28
	Prey and upper temperature	5	2157.66	10.22	0.00
	Prey, distance to front, and upper temperature	6	2159.61	12.16	0.00
	Prey and mixed-layer depth	5	2167.02	19.57	0.00
	Physical habitat characteristics	5	2178.78	31.33	0.00
	Prey and distance to front	5	2179.96	32.51	0.00
	Biomass of all zooplankton prey	4	2189.44	41.99	0.00
	Mixed-layer depth and upper temperature	4	2193.77	46.32	0.00
	Biomass of arctic zooplankton prey	3	2194.11	46.66	0.00
	Mean upper temperature	3	2199.74	52.29	0.00
	Mean salinity near surface	3	2208.15	60.71	0.00
	Mean temperature near bottom	3	2217.72	70.28	0.00
	Biomass of Pacific zooplankton prey	3	2218.78	71.34	0.00
	Mixed-layer depth	3	2219.33	71.89	0.00
	Mean salinity near bottom	3	2220.57	73.13	0.00
	Spatial pattern	2	2227.90	80.45	0.00
	Distance to front	3	2228.00	80.55	0.00

Appendix 3.1 continued…

Species/taxon	Model	*s*	AIC	ΔAIC	AIC wt
Black-legged Kittiwake	Prey, mixed-layer depth, distance to front, and upper temperature	7	4730.50	0.00	1.00
	Prey, distance to front, and upper temperature	6	4771.47	40.97	0.00
	Prey, mixed-layer depth, and upper temperature	6	4771.54	41.04	0.00
	Prey and mixed-layer depth	5	4775.76	45.26	0.00
	Prey and distance to front	5	4781.80	51.30	0.00
	Physical habitat characteristics	5	4809.15	78.65	0.00
	Prey and upper temperature	5	4815.72	85.22	0.00
	Biomass of all zooplankton prey	4	4821.69	91.19	0.00
	Biomass of arctic zooplankton prey	3	4829.50	99.00	0.00
	Distance to front	3	4864.65	134.15	0.00
	Mixed-layer depth and upper temperature	4	4870.49	139.99	0.00
	Mixed-layer depth	3	4888.21	157.71	0.00
	Mean salinity near surface	3	4900.91	170.41	0.00
	Mean temperature near bottom	3	4904.38	173.88	0.00
	Biomass of Pacific zooplankton prey	3	4906.07	175.57	0.00
	Mean upper temperature	3	4912.19	181.69	0.00
	Mean salinity near bottom	3	4913.94	183.44	0.00
	Spatial pattern	2	4927.49	196.99	0.00
Murres	Prey, mixed-layer depth, distance to front, and upper temperature	7	6224.23	0.00	0.99
	Prey, distance to front, and upper temperature	6	6234.55	10.31	0.01
	Prey, mixed-layer depth, and upper temperature	6	6296.54	72.30	0.00
	Prey and upper temperature	5	6307.01	82.78	0.00
	Physical habitat characteristics	5	6311.48	87.25	0.00
	Mixed-layer depth and upper temperature	4	6399.90	175.67	0.00
	Mean upper temperature	3	6410.31	186.08	0.00
	Prey and distance to front	5	6419.70	195.46	0.00
	Mean salinity near bottom	3	6446.48	222.24	0.00
	Prey and mixed-layer depth	5	6488.36	264.13	0.00
	Mean temperature near bottom	3	6503.03	278.80	0.00
	Biomass of all zooplankton prey	4	6526.70	302.46	0.00
	Biomass of Pacific zooplankton prey	3	6557.42	333.18	0.00
	Biomass of arctic zooplankton prey	3	6585.76	361.52	0.00
	Distance to front	3	6594.24	370.01	0.00
	Mean salinity near surface	3	6595.66	371.43	0.00
	Mixed-layer depth	3	6641.37	417.14	0.00
	Spatial pattern	2	6643.84	419.61	0.00



6/21/2015 ABR, Inc. Mail - Permission to use manuscripts in my dissertation

Adrian Gall <agall@abrinc.com>

Permission to use manuscripts in my dissertation

Tawna Morgan <tmorgan@abrinc.com> Sun, Jun 21, 2015 at 7:50 AM
To: Adrian Gall <agall@abrinc.com>

Yes. Permission granted

On Jun 20, 2015 2:38 PM, "Adrian Gall" <agall@abrinc.com> wrote:

> Hi Tawna,
>
> You are a co-author on two manuscripts that I would like to include in my dissertation to fulfill the requirements of a PhD in Oceanography from the University of Alaska Fairbanks. The first is titled "Ecological shift from piscivorous to planktivorous seabirds in the Chukchi Sea, 1975–2012", and the second is titled "The influence of foraging strategy and prey preference on habitat associations of seabirds in the northeastern Chukchi Sea".
>
> Please reply to this email and indicate whether you grant permission to include these 2 papers.
>
> Thanks,
> Adrian
>
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Appendix 3.2 Permission from co-author Tawna Morgan to include manuscript in the dissertation

GENERAL CONCLUSIONS

The research included in this dissertation explores the relationship between the seabird community and the physical and biological oceanography of the northeastern Chukchi Sea to attain a greater understanding of processes currently influencing the ecological structure of the region. In addition, I compare present and historical distribution and abundance of seabirds to evaluate changes in the seabird community throughout the Chukchi Sea over the past 4 decades and to consider what those changes may imply for the trajectory of arctic ecosystems under the current trend of global warming. This information provides an updated baseline on the distribution and abundance of seabirds that is critical for assessing the potential impacts of climate change, offshore oil and gas development, and shipping traffic in this region.

The first chapter contributes a description of the structure of the seabird community and the species that are currently dominating species-composition. The community-level approach was integrated with analyses of physical, planktonic, benthic, and marine-mammal ecology to provide a multidisciplinary ecological portrait of the northeastern Chukchi Sea (Day et al., 2013a). A unique aspect of this study was the repeated and systematic sampling within and among years that addressed the seasonal variability of the seabird community in the offshore areas of the eastern Chukchi Sea. The extended data set collected over 7 years (2008–2013) is included in a paper that I co-authored identifying areas of aggregation (i.e., ecological hotspots) for marine birds and mammals (Kuletz et al., 2015) and a manuscript exploring the variability of the entire ecosystem and implications for long-term monitoring (Day et al., *in prep*).

The second chapter addresses how the seabird community of the Chukchi Sea has changed over time, shifting from one that was characterized by jaegers and kittiwakes in 1928 (Jaques, 1930) to one dominated by kittiwakes and murres in the 1980s (Divoky, 1987; Piatt and Springer, 2003) and finally to one composed primarily of planktivorous auklets and shearwaters in the 21st century (Gall et al., 2013; Kuletz et al., 2015; Wong et al., 2014). The data collected from this and other studies in the region over the past eight years have increased the number of seabird species recorded in the Chukchi and Beaufort seas. Some of these species may be expanding their ranges northward and some appear to be moving in from the North Atlantic as the Northwest Passage becomes more open (Day et al., 2013b). Additionally, expanded survey effort increased the probability of detecting rare species.

In the third chapter, my explorations of relationships between seabirds and their habitat reveal that both water temperatures and lateral gradients in temperature are good predictors of seabird distribution. For some species, the additional information on the abundance of zooplankton prey improves our ability to predict their distributions. For the most abundant planktivores (Crested Auklets [*Aethia cristatella*] and Short-tailed Shearwaters [*Puffinus tenuirostris*]), however, habitat models do not adequately explain their distribution. This lack of fit of the models points towards the vast array of questions that have yet to be answered with this time-series of data on seabirds and oceanography.

One of the key issues that plague attempts to model animal distributions is that of scale. For seabirds, modeling efforts in the Bering Sea and elsewhere indicate that the correlations between the abundance of seabirds and their prey is stronger at large spatial scales (100s to 1000s of km) than at the small to moderate scales (10s to low 100s of km) that we used (Hunt, 1990; Burger et al., 2004; Fauchald, 2009; Cox et al., 2013). The data sets compiled during this study offer opportunities to explore these relationships at scales broader than the one I selected for the analysis in Chapter 3. Nonetheless, I did detect relationships for some species, particularly those for which their prey was adequately sampled. Hydroacoustics and other methods of sampling zooplankton and fish prey continuously and concurrently with the distribution of seabirds can improve the temporal and spatial resolution of the data in an environment where the locations of prey aggregations and hydrographic structure can change in a matter of hours and days (Weingartner et al., 2013). Towed instruments also offer opportunities to sample the physical environment and prey availability at a scale and resolution that more closely matches the way in which seabirds themselves evaluate their habitat and inform their movement choices (Ainley et al., 2005, Bost et al., 2009).

Combining ship-based observations with studies of instrumented animals can provide information on the timing and scale of movements of the individuals that compose this seabird community. Until the past decade, there had been very few investigations using satellite telemetry or other methods to track individual seabirds in the Chukchi Sea (e.g., Hatch et al., 2000). More recently, the movements of eiders has been documented (Oppel et al., 2009), but, based on my observations, they are a negligible component of the offshore seabird community. The telemetry of loons is giving us a better appreciation for use of the nearshore marine environment during chick-rearing (Rizzolo and Schmutz, 2012). Telemetry and geolocators deployed on Short-tailed Shearwaters are revealing the connectivity not only with the Bering Sea but also with the Southern Ocean, where these Southern Hemisphere breeders go to forage in the austral fall before making the trans-hemispheric trek to spend the austral winter in the Bering and Chukchi seas (Carey et al., 2014). Finally, tracking devices have now shrunk to a scale that is usable on some of the smallest seabirds and are shedding light on the movement of Crested Auklets (Robbins and Jones, 2015) and Kittlitz's Murrelets (*Brachyramphus brevirostris*; M. Kissling, U.S. Fish and Wildlife Service, and J. Piatt, USGS—Alaska Science Center, unpubl. data) from their breeding areas in the Bering Sea and Gulf of Alaska to their post-breeding feeding grounds in the Chukchi Sea. The variety and sheer numbers of planktivorous seabirds that make the trip to the northeastern Chukchi Sea are providing a strong signal of how important and consistent the availability of zooplankton is in the Chukchi Sea, if only for 2–3 months of the year.

These studies of instrumented animals are revealing another element of connectivity between Chukchi Sea and waters south of Bering Strait, but the logistical, technological, and financial constraints of those studies necessarily limit the scope of inference due to small sample sizes. Ship-board surveys also are expensive and logistically complex, but the increase in industrial activity and research effort in the region have provided more opportunities for data collection, both opportunistically by joining other oceanographic expeditions in a "ship of opportunity" program and by design as a systematically sampled component of multidisciplinary studies. The advantage of broad-scale surveys is that they can collect data on the entire community of seabirds and possibly can address questions about the extent and persistence of mixed-species assemblages. These surveys also can obtain community-level data to address trophic transfer to a suite of predators with differing prey preferences and foraging strategies. When these community-level studies are conducted concurrently with species-specific tracking of individuals, we can begin to address the behavioral aspects that influence seabird distribution.

A driver of seabird distributions in the Chukchi Sea that deserves further attention is the effect of oceanographic conditions in the Bering Sea. Productivity in the Chukchi Sea is highly dependent on the advection of heat and nutrients from the Bering Sea (Walsh et al., 1989; Carmack and Wassmann, 2006; Grebmeier et al., 2006). Although local factors such as the persistence of ice cover can affect the hydrology that influences local productivity and prey availability (Day et al., 2013b; Weingartner et al., 2013), the strength and timing of inflow through Bering Strait also are relevant to the availability of prey. The seabirds that compose the majority of the seabird community are primarily residents of the Bering Sea or waters farther south. The variability in their abundance, timing of arrival, and annual days of use from year to year may be influenced by conditions in the Bering Sea as well as by local conditions in the Chukchi Sea. Do birds show up in greater numbers in the Chukchi Sea in a given year because there is little food available in the Bering Sea, forcing them to forage farther to find food? Or are they following a large pulse of zooplankton from the Bering Sea into the Chukchi Sea? Studies that pair concurrent observations of secondary productivity and seabird abundance in both seas would help address these fundamental questions of connectivity between the subarctic and arctic marine ecosystems of the Pacific.

A broader understanding of arctic seabird ecology would be facilitated by encouraging research that crosses international boundaries to paint a more complete picture of the Chukchi Sea that includes the Russian side of the shelf. Projects such as the Russian-American Long-term Census of the Arctic (RUSALCA) have the goal to understand the causes and consequences of the reduction in ice cover throughout the Bering and Chukchi seas and the Arctic Ocean. That project in particular conducts multidisciplinary cruises every two to four years, but the lack of annual and seasonal sampling limits inference about observed variability. Nonetheless, these efforts are shedding light on the physical drivers that shape the zooplankton community throughout the Chukchi shelf (Hopcroft et al., 2010; Ershova et al., 2015). I look forward to a similar synthetic analysis of seabird data that compares seabird communities in the eastern Chukchi Sea where currents flow predominantly north and west with those in the western Chukchi Sea where currents flow north over the central part of the shelf and south along the Siberian coast (Weingartner et al., 1999).

The research I have conducted was part of the Chukchi Sea Environmental Studies Program (CSESP), a cooperative effort between industry (specifically ConocoPhillips, Shell, and Statoil) and university researchers to pool financial and intellectual resources and gain a better understanding of the Chukchi Sea. Outcomes of this effort have included: (1) the development of time-series data collected seasonally and annually with standardized protocols and in repeated locations; (2) quantification of the seasonal, interannual, and spatial variability of physical oceanography and marine ecology; and (3) a transparent and publicly-available repository of data (www.aoos.org/industry-arctic-data) to facilitate the work of policy-makers and managers who will oversee the development, assess environmental impacts, and recommend mitigation. These efforts are a good start, but they must be maintained as oil and gas development proceeds, or the effort and resources committed to date will have limited value in monitoring this ecosystem as it responds to environmental change and increases in anthropogenic activity.

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