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Seasonal variation in the cross-shelf distribution of seabirds in the southeastern Bering Sea

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ABSTRACT

We tested the hypothesis that the distribution of seabird species' associations across the southeastern Bering Sea shelf reflects the underlying ecology of four bathymetrically-defined hydrographic domains: the Inner or Coastal Shelf Domain (depth (Z) < 50 m), the Middle Shelf Domain (50 m < Z < 100 m), the Outer Shelf Domain (100 m < Z < 200 m), and the Shelf-Slope Domain (200 m < Z < 3000 m). The domains differ in stratification, which intensifies from winter to summer and breaks down in the fall. To examine seabird distributions with respect to these domains in multiple seasons, we quantified the cross-shelf distribution of species with respect to water depth using a 37-year database. We then used a multivariate tree analysis to group species with similar depth-use distributions, and mapped these clusters against the hydrographic domains. There were three patterns of seabird depth use: an inshore, shallow-water group in summer and fall, but not winter and spring, which conformed roughly to the Inner Shelf Domain; a group of species that were distributed widely across the Middle and Outer Shelf Domains, and a third group of species that occupied the outer portion of the Outer Shelf Domain and the Shelf-Slope Domain. The multivariate tree analysis revealed close correspondence between the seabird-derived domains and the bathymetrically-defined Outer Shelf and Shelf-Slope domains in spring and to a lesser extent in summer. In summer and fall, and to a lesser extent in spring, the seabird groupings showed a differentiation between the Inner Shelf Domain and the Middle Shelf Domain. Seabird-derived differentiation between the Shelf-Slope Domain and the Outer Shelf Domain was strongest in spring and summer. These seasonal patterns likely reflected the seasonal variation in the hydrographic differentiation of the bathymetrically-defined domains. Cross-validation of the multivariate tree analysis showed that the portion of seabird distribution patterns explained by the tree analysis was smallest in winter (when there is no stratification on the middle and inner shelves) and greatest in summer (when stratified water columns result in hydrographically defined domains), as would be expected under our hypothesis. We also examined hypotheses predicting why pursuit diving seabirds most often forage in shallow water whereas surface-foraging (surface-seizing) seabirds are more common over deep offshore waters. The hypothesis for regionally enhanced primary production as a driving factor was not supported for the inshore foraging seabirds but was supported for those foraging over shelf-slope waters.

1. Introduction

The distribution and abundance of seabirds have been linked to a wide variety of marine phenomena at spatial scales from those of ocean basins to small-scale tidal fronts a few hundred meters in width. Hunt and Schneider (1987) reviewed the marine ornithological literature available, and found that the examples of the distribution and abundance of seabirds at the scale of 100 km to 1000 km (meso-scale) were mostly drawn from upwelling systems during those seasons known for calm weather. Much less attention had been paid to how seabird communities might vary across broad expanses of continental shelf, or in winter, spring, or fall, when inclement weather may be a challenge (but see Renner et al., 2008).

Studies of seabird use of continental shelf ecosystems have taken two tacks. In the one, there has been an emphasis on the depth of water in which different foraging types prefer to seek prey. For example, Wynne-Edwards (1935), Joiris (1978, 1983), and Stone et al. (1995) suggested that seabirds that pick their prey from the surface (surface-seizing) forage farther offshore than do species that dive and pursue their prey underwater (pursuit-divers) in northwestern Atlantic and North Sea shelf systems. In the other, seabird foraging habitats have been related to waters with different mixing regimes, which in turn were tied to different depth ranges (Iverson et al., 1979; Kessel, 1979; Hunt et al., 1981b). The seasonally changing

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conditions in the Bering Sea allow the separation of depth effects from oceanographic effects on seabird habitat use. Schneider (1997) explored some of the reasons why these foraging preferences might exist, and we address these hypotheses in Section 4.

In the eastern Bering Sea, early analyses showed that seabird species tended to be associated with specific depth ranges; over the outer shelf and slope, surface-seizing species predominated whereas in relatively shallow waters, pursuit-diving species predominated (Iverson et al., 1979; Kessel, 1979; Hunt et al., 1981b). The depth ranges corresponded to the then recently described hydrographic structure of eastern Bering Sea shelf waters (Kinder and Schumacher, 1981). Later work showed that there were significant spatial differences in the amount of surface-caught and sub-surface-caught prey obtained by seabirds over the southeastern Bering Sea shelf, with more subsurface-prey consumed in shallow waters and more surface-prey consumed in the outer portion of the shelf and shelf-slope (Schneider and Hunt, 1982; Schneider et al., 1986).

In this paper we test the hypothesis that seabird communities vary across the broad expanse of the southeastern Bering Sea shelf as a function of the location of the different hydrographic domains there. As these domains are seasonal phenomena, driven by thermal stratification built up by insolation in the warmer months, we predicted that seabird communities would also show stronger cross-shelf patterns during summer, when stratification is stronger, than during winter, when the water column over much of the shelf is well mixed (Stabeno et al., 2001; Hermann et al., 2002). Using a broader range of species than Schneider and Hunt (1982) and Schneider et al. (1986), we also examined the hypothesis that pursuit-diving seabirds prefer shallower waters and that surface-seizing seabirds prefer deeper waters. Ornithological studies have continued over the southeastern Bering Sea Shelf and have provided a rich data set. We take advantage of these new data to ask a series of new questions:

1) Do seabird species differ by bathymetry in their use of the southeastern Bering Sea shelf?
2) If one clusters seabird species by the depth intervals over which they forage, do these clusters define "domains" across the southeastern Bering Sea shelf that are similar to the bathymetrically-defined hydrographic domains?
3) Does the relationship of seabird distributions to bathymetry vary seasonally depending on stratification?
4) Is there a consistent pattern of surface-seizing seabirds predominating in the outer shelf and slope regions and the pursuit-diving seabirds occurring predominately in the Inner Shelf Domain?

We sought answers to these questions by using a 37-year data set of pelagic observations of seabirds obtained in the southeastern Bering Sea between 1975 and 2012.

2. Methods

2.1. Study area

2.1.1. The southeastern Bering Sea shelf

The southeastern Bering Sea continental shelf stretches from the shores of western Alaska to the shelf edge (depth ~200 m), which is almost 500 km distant. In summer, the shelf is characterized by

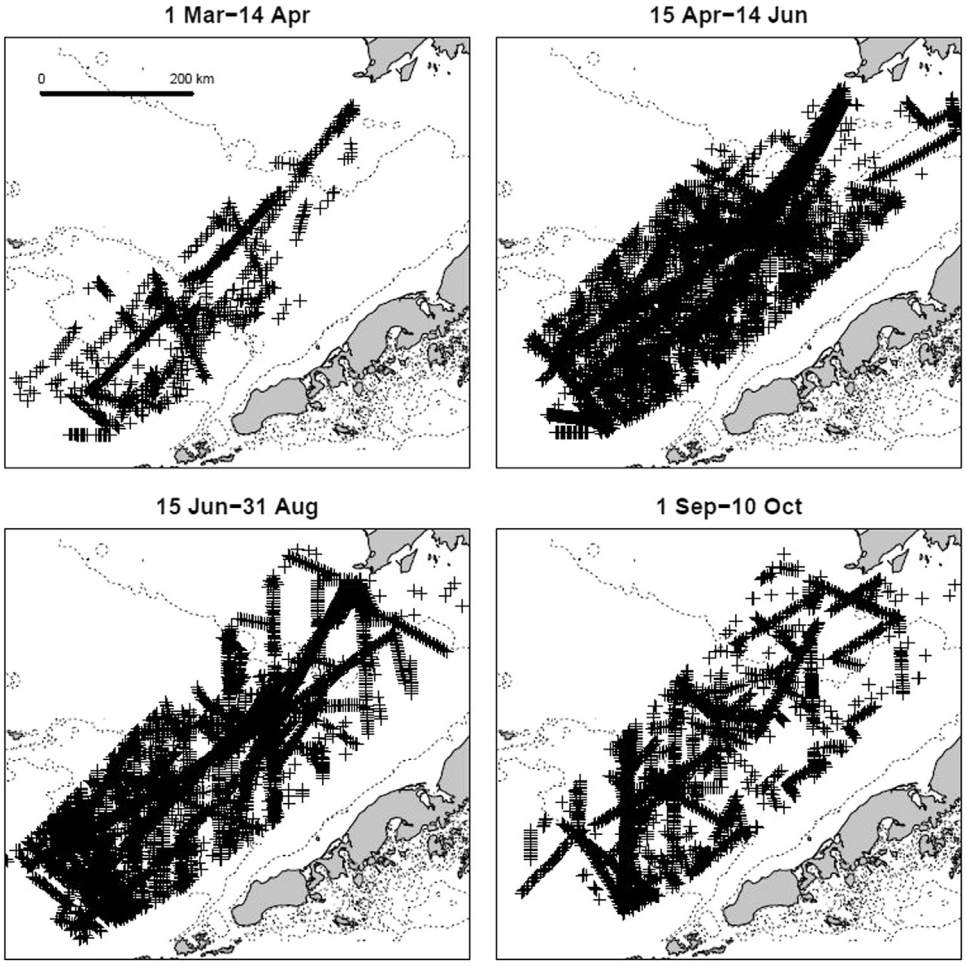

Fig. 1. Distribution of seabird counts, by season, on the southeast Bering Sea shelf. Each cross represents a 3 km-long transect segment.

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