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Biogeography of seabirds within a high-latitude ecosystem: Use of a data-assimilative ocean model to assess impacts of mesoscale oceanography

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ABSTRACT

We assessed the biogeography of seabirds within the Bering Sea Large Marine Ecosystem (LME), a highly productive and extensive continental shelf system that supports important fishing grounds. Our objective was to investigate how physical ocean conditions impact distribution of seabirds along latitudinal gradients. We tested the hypothesis that seabird biogeographic patterns reflect differences in ocean conditions relating to the boundary between northern and southern shelf ecosystems. We used a grid-based approach to develop spatial means (1975–2014) of summertime seabird species' abundance, species' richness, and a multivariate seabird assemblage index to examine species composition. Seabird indices were linked to ocean conditions derived from a data-assimilative oceanographic model to quantify relationships between physics (e.g., temperature, salinity, and current velocity), bathymetry and seabirds along latitudinal gradients. Species assemblages reflected two main sources of variation, a mode for elevated richness and abundance, and a mode related to partitioning of inner/middle shelf species from outer shelf-slope species. Overall, species richness and abundance increased markedly at higher latitudes. We found that latitudinal changes in species assemblages, richness and abundance indicates a major shift around 59–60°N within inner and middle shelf regions, but not in the outer shelf. Within the middle shelf, latitudinal shifts in seabird assemblages strongly related to hydrographic structure, as opposed to the inner and outer shelf waters. As expected, elevated species richness and abundance was associated with major breeding colonies and within important coastal foraging areas. Our study also indicates that seabird observations supported the conclusion that the oceanographic model captured mesoscale variability of ocean conditions important for understanding seabird distributions and represents an important step for evaluating modeling and empirical studies. Biogeographic assessments of LMEs that integrate top predator distributions resolve critical habitat requirements and will benefit assessment of climate change impacts (e.g., sea-ice loss) predicted to affect high-latitude marine ecosystems.

1. Introduction

Macroecology provides a framework for assessing relationships between marine organisms and ocean-climate conditions to understand the biogeography of Large Marine Ecosystems (LMEs; Sherman, 1991). As global climate change is predicted to impact marine biodiversity patterns and food web interactions in LMEs (Willig et al., 2003; Tittensor et al., 2011), investigating the biogeography of potential indicator species and how they reflect latitudinal gradients in the physical and biological components of the coastal ocean will improve our ability to predict future range shifts of species and key ecosystem services (e.g., fisheries; Meuter and Litzow, 2008). This is especially important in high-latitude, sea-ice-dominated ecosystems, where conditions are predicted to change rapidly, thereby possibly denying presently resident species of habitat qualities essential for survival (Arrigo et al., 2008; Wang et al., 2012). However, to reveal key processes underlying the spatial organization of LMEs, macroecological investigations require large, long-term data sets of species distributions and climatic

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conditions. Upper trophic level predators (i.e. seabirds and marine mammals) integrate the influences of hydrography and lower trophic levels (i.e., zooplankton and fish) via changes in their distribution, abundance or species composition.

Large data sets of seabird species' distribution and abundance patterns are available for assessing seabird biogeography in the eastern Bering Sea (e.g., Renner et al., 2013; Hunt et al., 2014). Living at the interface between land, sea and air, seabirds are highly mobile and conspicuous in marine ecosystems, and may be useful indicators of ocean-climate conditions and fishery resources (Piatt et al., 2007). In this study, we investigated the biogeography of seabird species' abundance, richness, and assemblages using a 40-year dataset of pelagic seabird distribution and abundance. We assessed the co-occurrence of seabird assemblages and hydrographic features of the eastern Bering Sea and tested hypotheses about the differences in seabird responses to hydrographic clines and latitudinal variability. Through this approach, we also assessed the utility of seabirds as indicators of the macro-ecology of a high-latitude LME, the eastern Bering Sea shelf region.

The eastern Bering Sea shelf ecosystem is a vast and highly productive ecosystem that sustains a diverse array of micronekton, fish, shellfish, seabirds and marine mammals (Piatt and Springer, 2003), and is one of the most important fishing grounds in the world (Meuter and Litzow, 2008; Baker and Hollowed, 2014). Stretching from the Alaska Peninsula to Bering Strait (Fig.1), the Bering Sea represents a 1200 km gradient of sub-Arctic to Arctic environmental conditions within a 600 K km^2 continental shelf that is 500 km wide (Stabeno et al., 1995; Piatt and Springer, 2007; Danielson et al., 2011a, 2011b). Biological productivity and its fate in this marine ecosystem are strongly influenced by the latitudinal extent, concentration, and timing of retreat of seasonal sea-ice cover (Stabeno et al., 2012). Substantial environmental gradients in ocean conditions and bathymetry exist in both the cross-shelf and along-shelf directions, and interact to influence the structure of benthic, mid-water and surface biological communities (Coachman, 1986; Danielson et al., 2014; Stabeno et al., 2016; Sigler et al., 2011, 2017). Environmental gradients in the cross-shelf direction are similar to many continental shelf ecosystems (Levin and Dayton, 2009), with well-mixed coastal waters inshore, stratified waters offshore, and a hydrographic front marking the boundary between oceanic and shelf waters (Schumacher et al., 1979; Kachel et al., 2002; Ladd and Stabeno, 2012). The spatial structure of the southeastern Bering Sea shelf ecosystem is organized according to hydrographic conditions related to the bathymetry of the inner (< 50 m), middle (50–100 m) and outer shelf regions (100–200 m), each separated by fronts (Coachman, 1986), along with centers of rich biological productivity associated with submarine canyon systems and islands (Hunt et al., 2008). In the southeastern Bring Sea, the southern extent of cold bottom temperatures (i.e., cold pool) within the middle shelf is a defining characteristic of the ecosystem's biogeography and impacts regional fisheries (Meuter and Litzow, 2008; Baker and Hollowed, 2014).

At about 59–60° north, there is a transition between the northern (Arctic) and southern (sub-Arctic) shelf ecosystems (Sigler et al., 2011; Stabeno et al., 2012). The hydrographic differences north and south of this transition zone are influenced by winter sea ice conditions (e.g., approximate location of the maximum sea ice extent in March), and persist throughout the summer (Danielson et al., 2011a, 2011b). North of the transition zone, there are major differences in the hydrography of the inner (< 40–50 m) and middle (50–100 m) shelf regions compared to the southeastern shelf (Ladd and Stabeno, 2012). In winter the inner and middle shelf regions are well mixed from the Alaska Peninsula to Bering Strait (Stabeno et al., 2012). In summer in the southeastern Bering Sea (south of the transition zone), the inner shelf remains well mixed due to the interaction of wind and tidal mixing (Danielson et al., 2014), while, the middle shelf is stratified by solar heating (Ladd and Stabeno, 2012). The pycnocline of the summer southern middle shelf is

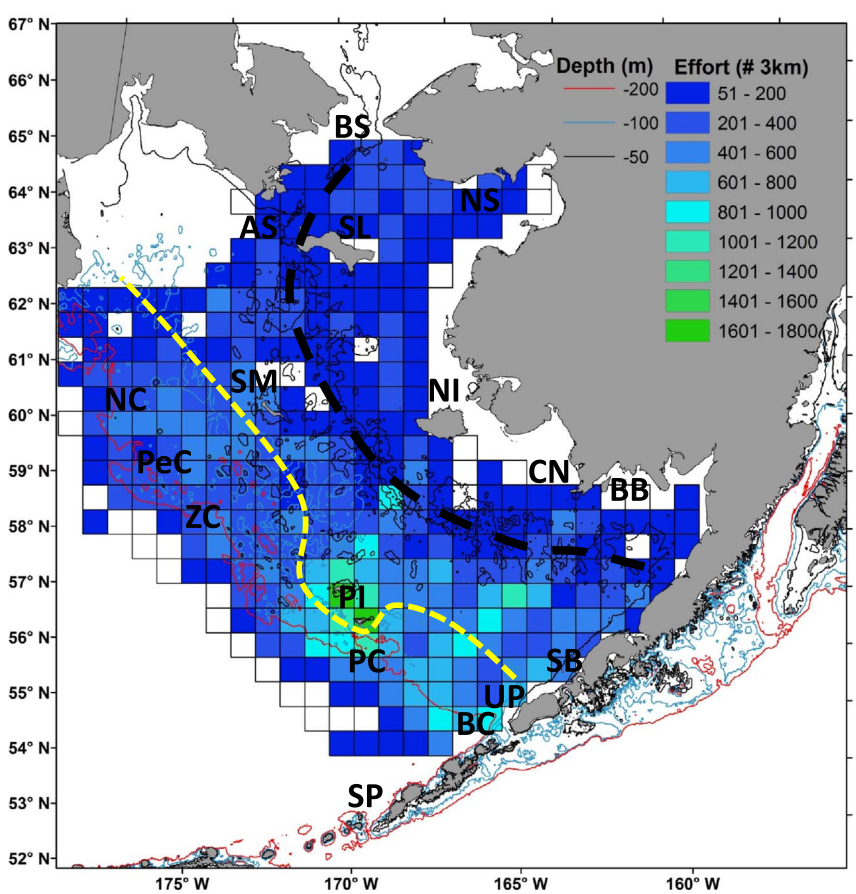

Fig. 1. Eastern Bering Sea shelf study domain, extent of the seabird grid (50 × 50 km) and summarized survey effort (# 3 km survey segments); a cut off of 50 segments was applied (UTM 2 map projection). Empty cells are effort < 50. AS is Anadyr Strait, BB is Bristol Bay, BC is Bering Canyon, BS is Bering Strait, CN is Cape Newenham, NC is Navarin Canyon, NI is Nunivak Island, NS is Norton Sound, PC is Pribilof Canyon, PeC is Pervenets Canyon, PI is Pribilof Islands, SB is Slime Bank region, SL is St. Lawrence Island, SM is St. Matthews Island, SP is Samalga Pass, UP is Unimak Pass, ZC is Zhemchug Canyon. Depth contours correspond to the 50 m (black), 100 m (light blue) and 200 m (red) isobaths. Black-dashed line is the approximate position of the 50 m isobaths, yellow-dashed line is approximate position of the 100 m isobaths, which partitions the shelf into inner, middle and outer regions. (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)