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Patterns of distribution, abundance, and change over time in a subarctic marine bird community

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ABSTRACT

Over recent decades, marine ecosystems of Prince William Sound (PWS), Alaska, have experienced concurrent effects of natural and anthropogenic perturbations, including variability in the climate system of the northeastern Pacific Ocean. We documented spatial and temporal patterns of variability in the summer marine bird community in relation to habitat and climate variability using boat-based surveys of marine birds conducted during the period 1989–2012. We hypothesized that a major factor structuring marine bird communities in PWS would be proximity to the shoreline, which is theorized to relate to aspects of food web structure. We also hypothesized that shifts in physical ecosystem drivers differentially affected nearshore-benthic and pelagic components of PWS food webs. We evaluated support for our hypotheses using an approach centered on community-level patterns of spatial and temporal variability. We found that an environmental gradient related to water depth and distance from shore was the dominant factor spatially structuring the marine bird community. Responses of marine birds to this onshore-offshore environmental gradient were related to dietary specialization, and separated marine bird taxa by prey type. The primary form of temporal variability over the study period was monotonic increases or decreases in abundance for 11 of 18 evaluated genera of marine birds; 8 genera had declined, whereas 3 had increased. The greatest declines occurred in genera associated with habitats that were deeper and farther from shore. Furthermore, most of the genera that declined primarily fed on pelagic prey resources, such as forage fish and mesozooplankton, and few were directly affected by the 1989 *Exxon Valdez* oil spill. Our observations of synchronous declines are indicative of a shift in pelagic components of PWS food webs. This pattern was correlated with climate variability at time-scales of several years to a decade.

1. Introduction

Patterns of species distribution, abundance, and composition are often associated with gradients, along which multiple environmental characteristics change in tandem (Whittaker 1956, 1967). Ecological communities are also shaped, however, by biotic interactions and by disturbance (Beals, 1984). Marine ecosystems of the northern Gulf of Alaska (GoA) have experienced major natural and anthropogenic perturbations over recent decades (Spies, 2007). Over that period, dramatic population changes have occurred in numerous marine taxa (Anderson and Piatt, 1999). In this paper, we asked whether temporal patterns of change in abundance and community composition differed along environmental gradients in a GoA marine bird community.

Coherence between climate variability and fluctuations in marine populations have been observed across vast spatial scales in the Pacific Ocean (Francis et al., 1998; Chavez et al., 2003). Climate forcing and ecosystem response can operate at different time-scales, however, making the resulting time-series out of phase. One proposed explanation for low-frequency fluctuations in marine biological time-series is cumulative integration of stochastic climate variability (Di Lorenzo and Ohman, 2013). Oceanic integration of high-frequency atmospheric variability over time can produce physical ocean time-series characterized by low-frequency fluctuations (Hasselmann, 1976; Hsieh et al., 2005). In biological time-series, such low-frequency variability can be further enhanced, if the rate of population change is forced by the environment, but damped across the time-scale (such as generation time) over which the population responds to the environmental forcing (Di Lorenzo and Ohman, 2013). This damped, autoregressive forcing-response relationship is expected to result in stronger and smoother fluctuations in the biological time-series (i.e. greater low-frequency

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power), relative to the fluctuations of the physical environmental drivers themselves.

Two primary modes of low-frequency atmospheric-oceanic variability have been characterized in the northeastern Pacific Ocean (Chhak et al., 2009). The Pacific Decadal Oscillation (PDO; Mantua et al., 1997; Zhang et al., 1997) is in part related to variability in the Aleutian Low pressure system (Graham, 1994; Bond et al., 2003). In the coastal GoA, the positive phase of the PDO corresponds to warm coastal water column temperatures, increased runoff, and increased alongshore advection (Royer, 2005). The North Pacific Gyre Oscillation (NPGO) corresponds to atmospheric forcing by the North Pacific Oscillation (Di Lorenzo et al., 2008). The positive phase of the NPGO is associated with strengthening of the Alaska Coastal Current and associated fluctuations in sea surface temperature (Di Lorenzo et al., 2008). Physical forcing influences the coastal ecosystems of the northern GoA in several ways. Variability in temperature affects growth and development of invertebrates and fish (Mackas et al., 1998; von Biela et al., 2016a). Freshwater runoff and advection of low-salinity water along the coast by the Alaska Coastal Current influences water column stability, which in turn affects the amount and timing of primary production by phytoplankton (Royer et al., 2001; Eslinger et al., 2001). Variable exchanges of both surface and deep waters (including nutrients and organisms) occur between fjord systems such as PWS and the adjacent GoA, and these processes are influenced by variability in physical forcing (Cooney et al., 2001; Halverson et al., 2013).

The 1989 *Exxon Valdez* oil spill (EVOS) was a notable anthropogenic perturbation of ecosystems in the northern GoA, especially in PWS where the spill originated. The EVOS had immediate acute effects on marine organisms, as well as biological effects that persisted for a decade or more (Peterson et al., 2003; Esler et al., this issue). Some species associated with nearshore sediments have experienced chronic oil exposure (Trust et al., 2000; Golet et al., 2002; Esler et al., 2010), which affected population recovery from losses due to acute mortality (Iverson and Esler, 2010). PWS marine communities have thus experienced concurrent effects of anthropogenic disturbance and a variable physical environment.

Studies of top marine consumers can provide insights into processes of ecosystem change (Reid and Croxall, 2001; Fredericksen et al., 2006). Marine birds are a relatively conspicuous group of species in ocean environments, where many organisms are difficult to observe because they are underwater (Piatt et al., 2007a). While they possess adaptations to buffer moderate variability in their food supply, vital rates of marine birds are sensitive to large fluctuations in prey availability (Cairns, 1987; Piatt et al., 2007b; Cury et al., 2011). Marine birds are relatively long-lived organisms, with delayed maturity, low reproductive rates, and high adult survivorship (Lack, 1967). Fluctuations in marine bird populations are therefore expected to most directly correspond to environmental variability over response time-scales from several years to decades. As long-lived upper-trophic consumers that can buffer moderate variability, changes in marine bird populations can be indicative of important ecosystem perturbations (Irons et al., 2008). For example, Agler et al. (1999) concluded that, coincident with climate fluctuations that affected forage fish abundance, abundance of piscivorous taxa of marine birds declined more than non-piscivorous taxa in PWS between the early 1970s and the early 1990s.

Marine birds of PWS constitute an ecologically diverse group of species that are adapted to habitats ranging from the intertidal to the open ocean, habitats that differ dramatically in food web structure (Lack, 1967; Isleib and Kessel 1973; Schreiber and Burger, 2001). In offshore waters, for example, primary production is generated by phytoplankton (Parsons, 1986), while in intertidal and shallow nearshore waters, most intrinsic primary production is generated by macrophytes, sea grasses, and benthic microalgae (Mann, 2000). Pelagic and nearshore-benthic food webs are linked, however, via consumption of phytoplankton by benthic filter-feeders (Newell and Shumway, 1993), and by consumption of macroalgae-derived suspended particulate matter by organisms feeding in the water column (Kaehler et al., 2006; von Biela et al., 2016b). In nearshore areas, both kelp- and phytoplankton-derived carbon are assimilated by benthic invertebrates and fish, as well as by avian consumers of both prey types (Duggins et al., 1989; Fredriksen, 2003; von Biela et al., 2016b). The strength of benthic-pelagic coupling weakens along a spatial gradient from the coast to offshore (Fredriksen, 2003; Kopp et al., 2015).

While physical environmental drivers clearly affect organisms in both nearshore-benthic and pelagic systems, we expected that environmental fluctuations would result in greater variability in the pelagic food web for several reasons. First, the primary autotrophs in the offshore pelagic system (phytoplankton) are characterized by low biomass and high annual turnover (Mann, 2000), with each year's production strongly linked to physical processes in the atmosphere and ocean (Eslinger et al., 2001). In addition, the crucial role played by a small number of species of schooling planktivorous fishes in transferring energy to higher trophic levels makes the pelagic food web vulnerable to sudden shifts (Bakun, 2006). In contrast, in the nearshore-benthic system, the primary autotrophs (macrophytes and seagrasses) are characterized by high biomass and relatively low annual turnover (Mann, 2000). Nearshore-benthic systems exist at an ecological boundary, and receive allochthonous carbon inputs from pelagic, terrestrial, and riverine sources (Tallis, 2009; von Biela et al., 2013). We considered that these diverse pathways of energy flow may increase stability of the nearshore-benthic food web.

Here, we investigate the relationship between spatial and temporal patterns of variability within a diverse group of marine bird taxa using boat-based surveys of marine birds conducted in PWS during the summers of 1989–2012. We hypothesized that a major factor structuring marine bird communities in PWS would be proximity to the shoreline, which is theorized to relate to aspects of food web structure, and was incorporated into our sampling design (via stratification) at the onset of our study. We also hypothesized that shifts in physical ecosystem drivers such as the PDO and the NPGO differentially affected nearshore-benthic and pelagic components of PWS food webs. Given their ecological diversity, we predicted that responses of regionally sympatric marine bird taxa to environmental perturbations would vary based on their use of resources and habitats.

We evaluated support for our hypotheses using an approach centered on community-level patterns of spatial and temporal variability. First, we examined spatial patterns of community composition and the relationship between community composition and habitat. Our use of the term "community" follows the concrete community concept (McCune and Grace, 2002), and refers to the organisms that occur within a specific location in space and time. By "community composition" we refer to the abundances of taxa in a location. Second, we evaluated population- and community-level changes over time, and determined whether community-level changes correlated with climate variability. Third, we evaluated the relationship between temporal changes and spatial patterns of marine bird community composition. Synchronous population changes among co-occurring taxa would suggest common extrinsic agents of change, linked to the same factors that spatially structure the community.

2. Methods

2.1. Marine bird surveys

PWS is a subarctic estuarine fjord system (~9000 km^2) that is separated from the northern GoA by several large islands (Niebauer et al., 1994; Fig. 1). We conducted boat-based surveys of marine birds throughout PWS in 12 different years within the period of 1989–2012. Surveys were conducted during the breeding season, in July, and were originally designed to assess effects of the EVOS on marine birds in PWS (Klowsiewski and Laing, 1994). Our study employed a stratified-randomized sampling design, based on proximity to the shoreline (Agler