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Regionalizing indicators for marine ecosystems: Bering Sea-Aleutian Island seabirds, climate, and competitors



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ABSTRACT

Seabirds are thought to be reliable, real-time indicators of forage fish availability and the climatic and biotic factors affecting pelagic food webs in marine ecosystems. In this study, we tested the hypothesis that temporal trends and interannual variability in seabird indicators reflect simultaneously occurring bottom-up (climatic) and competitor (pink salmon) forcing of food webs. To test this hypothesis, we derived multivariate seabird indicators for the Bering Sea-Aleutian Island (BSAI) ecosystem and related them to physical and biological conditions known to affect pelagic food webs in the ecosystem. We examined covariance in the breeding biology of congeneric pelagic gulls (kittiwakes Rissa tridactyla and R. brevirostris) and auks (murres Uria galge and U. lomvia), all of which are abundant and well-studied in the BSAI. At the large ecosystem scale, kittiwake and murre breeding success and phenology (hatch dates) covaried among congeners, so data could be combined using multivariate techniques, but patterns of response differed substantially between the genera. While data from all sites (n = 5) in the ecosystem could be combined, the south eastern Bering Sea shelf colonies (St. George, St. Paul, and Cape Peirce) provided the strongest loadings on indicators, and hence had the strongest influence on modes of variability. The kittiwake breeding success mode of variability, dominated by biennial variation, was significantly related to both climatic factors and potential competitor interactions. The murre indicator mode was interannual and only weakly related to the climatic factors measured. The kittiwake phenology indicator mode of variability showed multi-year periods ("stanzas") of late or early breeding, while the murre phenology indicator showed a trend towards earlier timing. Ocean climate relationships with the kittiwake breeding success indicator suggest that early-season (winter-spring) environmental conditions and the abundance of pink salmon affect the pelagic food webs that support these seabirds in the BSAI ecosystem.

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1. Introduction

Ecological indicators play an important and growing role in understanding and managing terrestrial and aquatic ecosystems. In marine ecosystems, indicators are used to provide key information for assessments of ocean productivity and 'health' (Halpern et al., 2012). Ecosystem indicators play a role in ecosystem-based fisheries management (Cury et al., 2008; Einoder, 2009; Levin et al., 2009). Developing appropriate indicators, however, is a challenge.

In contrast to many large-scale physical indicators (Mantua et al., 1997; Sydeman et al., 2014), most biological indicators are developed at relatively small spatial scales, such as islands or single points along coastlines. Local indicators of ecosystem structure or functions are appropriate for investigating the dynamics of populations and communities within small-scale management units – such as marine protected areas or areas of special fisheries closures – but are often not appropriate to address questions pertaining to large marine ecosystems (Levin et al., 2009). Large-scale indicators are needed for understanding the complexity and regulation of large-scale pelagic food webs, and the effects of climate variability and change on pelagic ecosystem productivity and functions.

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Many, if not most, upper trophic level marine predators, such as piscivorous fish, birds, and mammals, demonstrate greater responses to ocean climate variability than do mid trophic level organisms (Kirby and Beaugrand, 2009; Chust et al., 2014). For this reason, these species may be well-suited as large-scale indicators, especially when parameters co-vary in space and time, and may be combined using multivariate statistical techniques such as Principal Component Analysis (PCA; Jolliffe, 2002). Fisheries landings have often been used as input variables for PCA-derived ecosystem-state indicators (Hare and Mantua, 2000; Beaugrand, 2004; Osterblom et al., 2007), but these data may be compromised by fishing effort, which can explain as much or more of the variability than climate or food web variability (Litzow and Mueter, 2014). Seabirds, on the other hand, are rarely the target of direct human harvest and have been put forth as reliable, nearreal-time indicators of the distribution and abundance of pelagic food supplies (Cairns, 1987; Frederiksen et al., 2006; Piatt et al., 2007; Sydeman et al., 2017) and changes in marine ecosystems more generally (Durant et al., 2009; Parsons et al., 2008; Sydeman et al., 2012). As secondary and tertiary consumers, seabirds forage on mesozooplankton, such as krill and large calanoid copepods (e.g., Neocalanus spp.), and larger nekton such as cephalopods (e.g., squids and octopuses), small epipelagic and mesopelagic fishes (e.g., sand lance Ammodytes spp., capelin Mallotus villosus, lanternfish Myctophidae), and age-0 and age-1 forms of piscivorous fishes (e.g., pollock Gadus chalcogrammus, salmon Oncorhynchus spp., cod Gadus macrocephalus). Therefore, seabirds may provide information on the availability of these prey species. Multivariate seabird indicators of marine ecosystem health and dynamics have been developed (e.g., Sydeman et al., 2001; Frederiksen et al., 2007a; Lahoz-Monfort et al., 2013; Zador et al., 2013) and are now integrated into annual ecosystem monitoring programs such as the Commission for the Conservation of Antarctic Marine Resources (CCAMLR) ecosystem monitoring program (CCAMLR, 2014) and the Ecosystem Considerations chapter of the Stock Assessment and Fishery Evaluation Report of the North Pacific Fishery Management Council (Zador, 2014; see also http://access.afsc.noaa.gov/ reem/ecoweb/index.php).

In the Bering Sea-Aleutian Islands (BSAI) ecosystem, Alaska, seabirds are abundant and diverse. Previously-developed multivariate seabird indicators for the Pribilof Islands (Fig. 1), host to one of the largest and most diverse seabird communities in the Bering Sea and the world, identified two modes of variability (Zador et al., 2013). One, which includes change in the phenology (timing of breeding) and breeding success (production per unit effort) of a suite of locally-breeding surface-feeding and diving seabirds, was linked to water column properties. The other represents change in the breeding success of surface-feeding kittiwakes only, was linked to sea ice conditions, and was hypothesized to fluctuate in relation to the abundance of pink salmon (Oncorhynchus gorbuscha), a potential competitor for prey resources. In more recent work, Springer and van Vliet (2014) demonstrated an inverse relationship between pink salmon abundance and Alaskan seabird breeding success, and suggested a role for competitive top-down control of

In this study, we extend upon these studies to investigate whether temporal patterns in seabird breeding parameters are coherent across the entire BSAI ecosystem (Fig. 1), and assess whether broad-scale abiotic and biotic conditions explain modes of variability in these parameters. The breeding biology of seabirds, as upper trophic level predators, may be controlled by two processes: bottom-up climatic factors that affect primary production and food availability (Ware and Thomson, 2005), and biotic factors such as predation or competition that may also alter food webs and prey availability (Cury et al., 2000; Frederiksen et al., 2007b). In the North Pacific, recent work suggests that both of these mechanisms

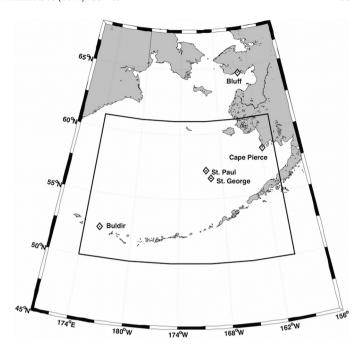


Fig. 1. Map of the Bering Sea–Aleutian Islands study area from Buldir Island in the west to Cape Peirce in the east, and Bluff to the north. The Pribilof Islands (St. Paul and St. George) are on the outer Bering Sea shelf. Monthly environmental data were obtained for the domain 50–60°N and 174°E–160°W (delineated by thin black line). All four seabird species were studied at Buldir and each of the Pribilof Islands, while only common murre and black-legged kittiwakes were studied at Bluff and Cape Peirce. Phenology and productivity were measured at all sites with the exception of Bluff, where only phenology was studied.

operate and may occur simultaneously or out of phase (Hunt et al., 2002, 2011; Litzow and Ciannelli, 2007). Our study area extends from Buldir Island in the western Aleutians, east to Cape Peirce, and north to Bluff, a coastal site in the north-eastern domain of the Bering Sea. The study area does not include the Russian coastline of the western Bering Sea. While the study sites cover a diversity of marine habitats (Piatt and Springer, 2007) affected by regional processes, we hypothesize that common variability in seabird indicators reflects large-scale physical and biological factors that cross regional boundaries. To test this idea, we 1) developed multivariate indicators of seabird reproductive parameters using murres (Uria spp.) and kittiwakes (Rissa spp.) from five sites, and 2) investigated if interannual variation in these indicators can be attributed to multivariate ocean climatic and/or biological factors. Relative to a previous study (Zador et al., 2013), we test if the apparent effects of pink salmon on seabird indicators described by Springer and van Vliet (2014) are independent or contemporaneous with climatic effects. Zador et al. (2013) also showed that the kittiwake breeding success indicator exhibited quasi-biennial variability, and that murre and kittiwake data could be combined. Here, we test whether the modes of variability described by Zador et al. (2013) are applicable across sites in the BSAI ecosystem.

2. Methods

2.1. Biological data

The U.S. Fish and Wildlife Service's (USFWS) Alaska Maritime National Wildlife Refuge (AMNWR) collects and compiles data annually on seabird populations at sites scattered throughout the Gulf of Alaska, Aleutian Islands, Bering Sea, and Arctic Ocean, including information on reproductive biology, phenology (timing of breeding), and food habits (e.g., Dragoo et al., 2014). Using data from the AMNWR program and compiled by Dragoo et al. (2014),

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