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Density dependence and changes in the carrying capacity of Alaskan seabird populations

Holly F. Goyert [a,*], Edward O. Garton [a], Brie A. Drummond [b], Heather M. Renner [b]

[a] Idaho Cooperative Fish & Wildlife Research Unit, University of Idaho, College of Natural Resources, Dept. of Fish and Wildlife Sciences, Moscow, ID 83843, United States
[b] Alaska Maritime National Wildlife Refuge, U.S. Fish and Wildlife Service, Homer, AK 99603, United States

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ABSTRACT

Evidence for regulation of animal populations by negative density dependence is ubiquitous across the animal realm, and yet the dynamics of carrying capacity (K) are often overlooked. K acts as a threshold below which population size tends to increase and above which it tends to decrease. Documenting changes in this threshold is particularly important to population viability analysis (PVA). We reconstructed the population sizes of five long-lived seabird species in Alaska, USA, and analyzed their population dynamics from the past four decades: Black-legged (*Rissa tridactyla*) and Red-legged Kittiwakes (*R. brevirostris*), Common (*Uria aalge*) and Thick-billed Murres (*U. lomvia*) and Tufted Puffins (*Fratercula cirrhata*). We evaluated a set of models that allowed for either density independence or density dependence, with or without a time trend in K. The best approximating models indicated that these seabird populations behaved in a negative density-dependent fashion. K increased significantly for murres, and remained relatively stable for Red-legged Kittiwakes. It decreased significantly (>40%) for Black-legged Kittiwakes and Tufted Puffins, particularly in the Gulf of Alaska, following the 1989 Exxon Valdez oil spill. Although we have less confidence in the puffin data, our PVA suggests that, in the next 100 years, Tufted Puffins may become extirpated from the few colonies that are monitored in the Gulf of Alaska. Negative density dependence can help to prevent population crashes, but time lags and serial correlation in rates of change could suppress the recovery of contracted populations. Therefore, estimating the magnitude of population fluctuations around a changing carrying capacity is essential to managing and conserving declining populations.

1. Introduction

Negative density dependence (hereafter just ‘density dependence’) has long been recognized as a driving force of population regulation, where carrying capacity (K) limits growth rates (May, 1981; Turchin, 1999). Unfortunately, the widespread use of ceiling models (Morris and Doak, 2002) has led to the misinterpretation of K as a static upper bound to population size. More accurately, K acts as a negative feedback threshold around which population size fluctuates. When below K, populations tend to increase, and when above K they tend to decrease. We define K as a quasi-equilibrium under density dependence, at which population growth rate is 0 (Conroy and Carroll, 2009; Dennis and Taper, 1994; May, 1981; Mills, 2012). The factors that drive population dynamics around K include competition, predation, disease, and resource limitation, which act on vital rates (e.g., birth and death). Just as habitat quality can change through time, so, too, can the number of individuals that it supports (i.e., K; May, 1981). Ignoring density dependence can lead to uncertain and erroneous inference in population projections (Morris and Doak, 2002). Accommodating a dynamic K is crucial to estimating the extinction risk of imperiled animal populations.

Marine birds are long-lived K-selected colony-breeders, and their populations are regulated primarily by density-dependent processes (Hunt et al., 1986; Wooller et al., 1992). The USA supports the largest number of seabird species of any other nation, and is thus ranked highest in global seabird conservation priority (Croxall et al., 2012). Alaska (AK) contains over one third of the US shoreline, including several Important Bird Areas, and hosts approximately one fifth of seabird species worldwide (>70 species; Smith et al., 2014). Of the 19 breeding species that are monitored at colonies in AK (Dragoo et al., 2015), we evaluated the population dynamics of five focal species: Black-legged (*Rissa tridactyla*) and Red-legged Kittiwakes (*R. brevirostris*), Common (*Uria aalge*) and Thick-billed Murres (*U. lomvia*) and Tufted Puffins (*Fratercula cirrhata*). Black-legged kittiwakes and murres have circumpolar distributions, while Tufted Puffin populations are restricted to the North Pacific. The global distribution of Red-legged Kittiwakes is almost exclusively found within the range of this study (apart from the Commander Islands, Russia). They are listed as “Vulnerable” according to the Red List of the International Union for Conservation of Nature (IUCN; BirdLife International, 2015a). This is in contrast to the four

* Corresponding author.
E-mail address: hgoyert@uidaho.edu (H.F. Goyert).

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other study species, which are listed as "Least Concern". Baseline information on these species' trends is of high conservation need, particularly to provide context for a U.S. Fish & Wildlife Service (USFWS) review of tufted puffins, in response to a 2014 petition for their listing under the Endangered Species Act (ESA).

Our objective was to characterize the status of seabird populations in AK at a regional scale, based on colony-scale surveys dating back to the 1970s. We hypothesized that (1) density dependence drives the population dynamics of all five species (Hunt et al., 1986), and (2) tufted puffins project low probabilities of persistence (given documented declines; Gaston et al., 2009; Piatt and Kitaysky, 2002). We implemented an information-theoretic approach to test for both density independence and density dependence, the latter of which allowed us to estimate K. It was important that we measure changes in K across the 40-year time-series, for the purpose of explaining observed population fluctuations around estimated trends. This suite of stochastic models fed into a population viability analysis (PVA) to estimate probability of persistence and determine whether declines in K are likely to result in extinction.

We used a case study to determine the environmental sensitivity of each species' population dynamics. The Exxon Valdez oil spill was a dramatic anthropogenic disturbance that occurred in March 1989, at the start of the pre-breeding season in Prince William Sound. We quantified its effect on the vulnerability or resilience of species in the region. The three study genera were differentially exposed to the oil slick, due to their distinct foraging niches. All are primarily piscivorous but kittiwakes are surface feeders whereas murres and puffins are divers, and the latter forage closer to shore (Denlinger, 2006; Smith et al., 2012). After the oil spill, murres showed higher carcass recovery rates and greater population-level impacts than other species (Piatt and Ford, 1996; Piatt et al., 1990). By incorporating the novel perspective of a dynamic K into our 40-year time-series, we were able to estimate the magnitude of such impacts on K. This is important in maintaining the population thresholds necessary to buffer catastrophes in the conservation of declining populations. Our analysis offers insight into where future management efforts should be directed to promote population persistence and connectivity of circumpolar seabird species breeding in the North Pacific.

2. Methods

2.1. Data

Alaskan seabirds inhabit four large marine ecosystems (Fig. 1; lme.noaa.gov; Koeppen et al., 2015): the Aleutian Islands (AI), Arctic (ARC), Eastern Bering Sea (EBS), and Gulf of AK (GOA). Seabird monitoring data have been collected by a number of organizations (Appendix A) at over 30 sites within these ecoregions, some datasets now reaching 40 years. Until now, these data had not been synthesized across the entire state (Byrd et al., 2008; Byrd et al., 2005; Slater and Byrd, 2009). This is due, at least in part, to the exhaustive methods required to standardize variability in the portion of each population sampled by the monitoring programs. Murres and Black-legged Kittiwakes are relatively common species that breed in conspicuous aggregations on coastal ledges at numerous colonies (Byrd, 1989). As such, monitoring data exist for a significant proportion of these species' Alaskan populations (Table 1). In contrast, Tufted Puffins nest in burrows and are difficult to count on colonies, hence they are monitored at only 8 sites that comprise just one tenth of their Alaskan populations. Our sampling protocols include the use of permanent index plots across years and are designed to reduce uncertainty in the detectability of population trends (see Appendix A and Section 4.4 for further discussion).

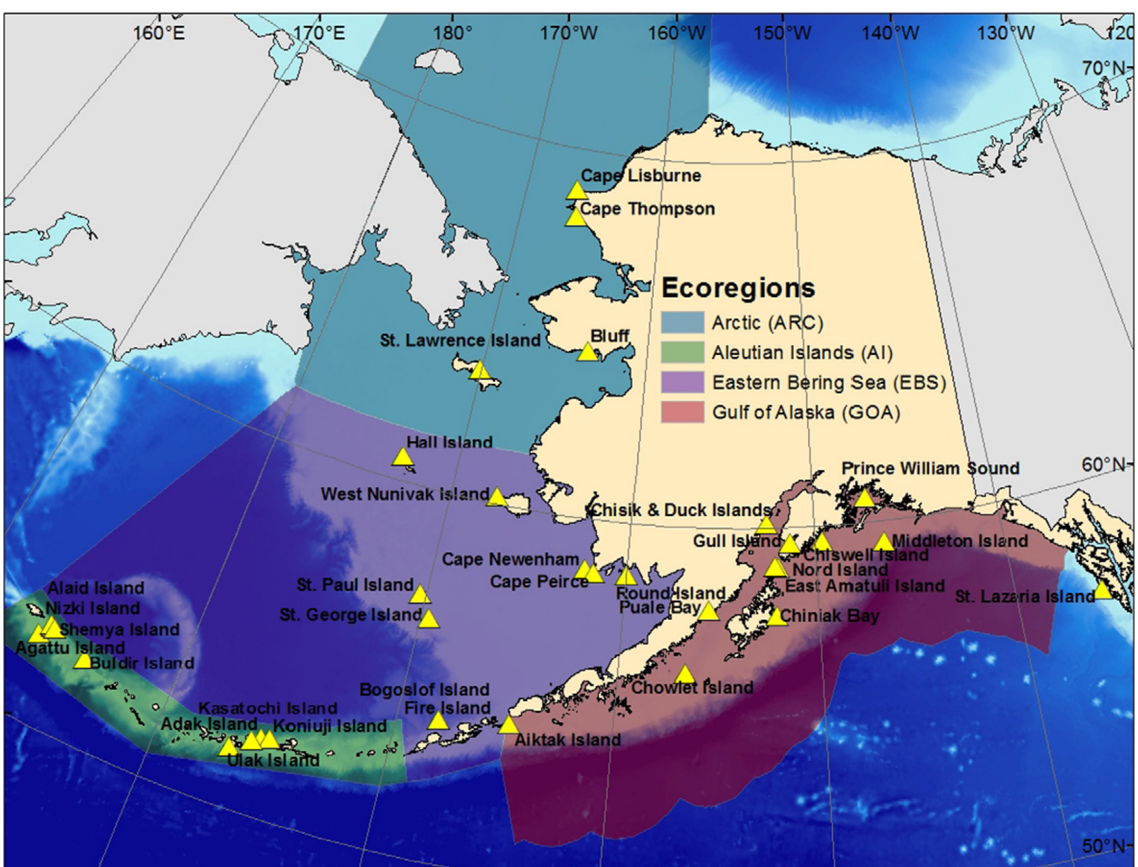

Fig. 1. Sites of monitored seabird colonies in Alaska (yellow triangles), and their corresponding ecoregions.