Reproductive success of kittiwakes and murres in sequential stages of the nesting period: Relationships with diet and oceanography

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ABSTRACT

Reproductive success is one of the most easily-measured and widely studied demographic parameters of colonial nesting seabirds. Nevertheless, factors affecting the sequential stages (egg laying, incubation, chick-rearing) of reproductive success are less understood. We investigated the separate sequential stages of reproductive success in piscivorous black-legged kittiwakes (*Rissa tridactyla*) and thick-billed murres (*Uria lomvia*) using a 36-year dataset (1975–2010) on the major Pribilof Islands (St. Paul and St. George), which have recently had contrasting population trajectories. Our objectives were to evaluate how the proportion of successful nests varied among stages, and to quantify factors influencing the probability of nest success at each stage in each island. We modeled the probability of nest success at each stage using General Linear Mixed Models incorporating broad-scale and local climate variables, and diet as covariates as well as other measures of reproduction such as timing of breeding and reproductive output in the previous year and previous stage. For both species we found: (1) Success in previous stages of the breeding cycle and success in the prior year better explained overall success than any environmental variables. Phenology was also an important predictor of laying success for kittiwakes. (2) Fledging success was lower when chick diets contained oceanic fish found farther from the colonies and small invertebrates, rather than coastal fish species. (3) Differences in reproductive variables at St. Paul and St. George islands did not correspond to population trends between the two islands. Our results highlight the potential importance of adult condition and annual survival to kittiwake and murre productivity and ultimately, populations. Adult condition carrying over from the previous year ultimately seems to drive annual breeding success in a cascade effect. Furthermore, condition and survival appear to be important contributors to population dynamics at each island. Therefore, adult condition and survival prior to breeding, and factors that influence these parameters such as foraging conditions in the non-breeding season, may be important datasets for understanding drivers of seabird demography at the Pribilof Islands.

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1. Introduction

Seabirds are widely touted as "indicator species" for the state of the marine ecosystem (Furness and Camphuysen, 1997; Montevecchi, 1993; Piatt et al., 2007). Several characteristics are proposed to make them useful indicators: they are top predators, they are conspicuous central place foragers during the breeding season, many species are widespread and common, and as a group they exploit different aspects of the marine system (i.e., fish vs. plankton, surface vs. depth, nearshore vs. offshore) (Einoder, 2009).

Reproductive success (chicks fledged per nest start) is one of the most easily-measured and widely studied demographic parameters of colonial nesting seabirds (e.g., Dragoo et al., 2012; Mavor et al., 2008) even though for long-lived species, its relative contribution to population trends is often minimal (Schmutz et al., 1997; Schmutz and Byrd, 2004). Variation in seabird breeding success is often used as an indicator of changes in the marine environment because success is widely assumed to be "mediated through the food web" (e.g., Ainley et al., 1995; Byrd et al., 2008a; Frederiksen et al., 2005). Proximate causes of success or failure during different stages of seabird nesting cycles differ, however, because these cycles extend over several months and energetic constraints vary over this period (Shaffer et al., 2003).

Reproductive failure may occur during any one of three separate sequential stages: the nest building period (for those species that build nests), the incubation period, and the chick-rearing period. Prior to egg laying, seabirds are not tied to the nest site and have only themselves to feed. Laying failure may be related to breeding experience of the individual (Coulson, 1966),

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climate conditions prior to incubation (Quillfeldt, 2001), or nutritional condition of the adult (Kitaysky et al., 2010), which could theoretically be influenced by either reproductive expenditure during the previous breeding season or foraging conditions leading up to egg production in the current season [or unavailability of habitat – e.g., auklets (Bedard, 1969); gannets (Nelson, 1980)]. During incubation and chick-rearing, in contrast, adult birds are constrained by incubation or chick-feeding duties and have both decreased foraging range and increased energetic demands to raise young (Golet et al., 2000). Egg loss can result from predation or abandonment by the parent, either because the egg was not viable or because of food supply limitations during the laying or incubation period (e.g., Hatch and Hatch, 1990; Wanless and Harris, 1992). Finally, chick loss may result from storm events, predation, or the adult's inability to provide sufficient food resources to the chick during this energetically intensive period (e.g., Baird, 1990; Gill and Hatch, 2002; Hatch and Hatch, 1990). Given success or failure during each nesting stage may be affected by different aspects of the marine environment, understanding when breeding loss occurs and how each stage of reproduction relates to environmental factors are crucial to using seabirds as bioindicators.

Relationships between seabird demography and local and regional climate variables are largely affected by life history traits and colony location (review by Sydeman et al., 2012). Accordingly, the degree in climatic responsiveness of seabirds may reflect different tradeoffs between survival and reproduction (Coulson, 2002). For instance, although many studies have found relationships between climate variables and seabird productivity (Sydeman et al., 2012), others are weak (Satterthwaite et al., 2012), and population trajectories do not necessarily match patterns in reproductive success (Murphy et al., 1991). Some seabird species are more flexible in that they can adapt foraging in response to changes in the environment, masking effects on some breeding parameters (Piatt et al., 2007). For instance, kittiwakes can compensate for low food supply by increasing foraging range and effort, resulting in low interannual variation in chick growth rates despite variable foraging conditions (Kitaysky et al., 2000). Similarly, murres can increase foraging effort or feeding rates to maintain relatively constant levels of fledging success when facing low prey density (Harding et al., 2007) or a handicapped mate (Paredes et al., 2005). Of course, seabirds' ability to compensate for low food availability is limited; in extremely poor food years (i.e., El Nino events in the Southeastern hemisphere; Duffy, 1990), nest failure can occur at any stage of reproduction, leading to very low or zero reproductive success.

In general, though, changes in ocean conditions often correlate with seabird productivity and prey availability in a variety of marine habitats (Byrd et al., 2008a; Wolf et al., 2009; Watanuki and Ito, 2012); therefore changes in climatic variables (e.g., SST, PDO) are expected to affect seabird demography via food supply. Studies examining the relationships between prey availability and seabird productivity can use concurrent measures of foraging effort and prey abundance and distribution, but this is logistically a difficult task. Alternatively, seabird diets, which are a function of both prey availability and foraging effort, may be useful for exploring how the marine food web mediates seabird population processes (Connan et al., 2008).

We investigated the separate sequential stages of reproductive success in piscivorous black-legged kittiwakes (*R. tridactyla*) and thick-billed murres (*U. lomvia*) using a 36-year dataset (1975–2010) on the Pribilof Islands in the Bering Sea, Alaska. We had two primary objectives: (1) evaluate whether the proportion of successful nests varied among nesting stages and between islands, and (2) quantify factors influencing the probability of nest success at each stage. For the latter, we hypothesized that different stages would be responsive to different cues in the environment; we

modeled three stages of nest success using (a) previous nesting stage reproductive output (assumed to be related to body condition which was not measured), (b) climate variables (broad-scale and local indices) likely to influence foraging conditions, and (c) seabird diet.

2. Study area and species

The Pribilof Islands are located in the Southeastern Bering Sea (~57°N, 169°W) near the edge of the continental shelf. St. Paul Island is approximately 65 km north of St. George Island and is closer to the southern extent of the winter sea ice, whereas St. George Island is closer to the edge of the continental shelf than St. Paul Island. The area along the shelf break is a region of high productivity that supports large numbers of forage fishes, marine mammals, and seabirds (Springer et al., 1996).

St. George and St. Paul Islands together comprise one of the largest breeding concentrations of marine birds in the North Pacific, estimated to exceed 2 million individuals (Hickey and Craighead, 1977). Both islands are approximately equal in size but St. George Island has more extensive cliff nesting habitat and an order of magnitude more ledge-nesting seabirds than St. Paul Island (Hickey and Craighead, 1977). Black-legged kittiwakes and thick-billed murres are the most abundant species of piscivorous seabirds on the Pribilofs, where they nest in mixed colonies with red-legged kittiwakes (*Rissa brevirostris*) and common murres (*Uria aalge*). The total population of black-legged kittiwakes at St. Paul (~15,000 individuals) and St. George (~72,000 individuals) for 2005 was calculated based on Hickey and Craighead (1977) counts and trend rates reported by Byrd et al. (2008b). The two islands also support substantially different numbers of breeding thick-billed murres: St. George=1,500,000, St. Paul=57,000 (Hickey and Craighead, 1977; modified using Byrd et al. (2008b)). Reproductive success of kittiwakes and murres at the Pribilof Islands is presumed to be related mostly to prey availability, as nest predation for ledge-nesting birds at both islands is minimal (Byrd et al., 2008a).

3. Materials and methods

3.1. Data collection

Reproductive success was estimated each year on St. Paul and St. George islands, 1975–2010, by recording the status (i.e., presence of nest structure, egg or chick) of nests on systematically-selected plots within the viewable population (see Byrd, 1989; Byrd et al., 2008a; Hunt et al., 1981). Prior to 1989 (except in 1984), nests monitored were not grouped into plots or plot-specific data were not available, and nests were treated as a simple random sample. In subsequent years plots were used as single-stage cluster samples, to more accurately represent the variance. Data collection consisted of photographing or drawing each plot and numbering nest sites on the photograph or drawing so individual sites could be identified and followed throughout the nesting cycle. For kittiwakes, nest sites were considered active only when new plant material was added within that season. Since murres do not build nests, the appearance of an egg constituted an active site (therefore, laying success could not be estimated for murres as it was for kittiwakes). Numbered sites typically were checked every three to five days throughout the incubation and chick-rearing periods to estimate loss of reproductive potential during the laying (kittiwakes only), egg, and chick stages of the nesting cycle. Nests were monitored until chicks departed the cliffs (fledged). Hatch dates were estimated as the mid-points between the date the egg was last seen and the date the chick was first observed. Nests were monitored in the same areas each year, with substantial overlap in individual nests and plots, but