

RH: Seabird Demography at the Pribilofs

MODELING THE INFLUENCE OF PRODUCTIVITY, SURVIVAL, AND META-
POPULATION DYNAMICS ON TRENDS OF KITTIWAKES AND MURRES AT THE
PRIBILOF ISLANDS, ALASKA

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ABSTRACT.— Populations of Red-legged (*Rissa brevirostris*) and Black-legged Kittiwakes

(*R. tridactyla*) and Common (*Uria aalge*) and Thick-billed Murres (*U. lomvia*) have been monitored since 1976 at St. George and St. Paul islands in the Pribilof Island group. Prior analysis of population trends (Byrd 1989, Hunt and Byrd 1999) indicated declines in all species at one or both of these islands. Declines in Red-legged Kittiwakes are of particular conservation concern as the majority of the world's population of this species nests at the Pribilof Islands. We synthesized demographic data for these populations to evaluate to what extent are population trends driven by variations in productivity (defined as number of fledged young per nesting pair). This evaluation included a reassessment of population trends during 1976-2002 that now incorporates measures of sampling error and explicitly tests whether population growth rates are stable, increasing or decreasing at a constant rate, or exhibit variable rates over time.

Productivity was directly estimated by observation in 15 to 27 years during 1975–2002, depending on species and island. We indirectly estimated productivity in the other years during this time period by quantifying correlations in productivity with congeneric populations (kittiwakes) or with May weather parameters (murre). Survival of adult Red-legged Kittiwakes at St. George Island was 0.930 (SE = 0.009), based on resightings of color-banded individuals. Other demographic parameters were derived by reference to other populations. We compared 10 pairs of matrices of demographic parameters using a life table response experiment to evaluate how much of the variation in population growth rate was contributed by variation in productivity. Productivity accounted for a fourth or less of the variation in population growth. The large majority of variation in population growth rate was thus attributable to mortality and emigration or dispersal, but distinction between these two demographic processes was not possible for most species due to lack of data. However, census data from other islands for the

geographically restricted Red-legged Kittiwake allowed us to construct meta-population models to evaluate the relative contributions of survival and dispersal. These models indicated that natal dispersal rates of 2 to 10% from St. George Island were sufficient to account for the early increase in numbers at Buldir Island and the recent increase at St. Paul Island. However, this emigration from St. George Island constituted only a minor part of this large population's decline, and thus increased mortality was the principal contributor to the decline. These results collectively suggest that seabird monitoring programs, which commonly measure productivity, should increase efforts to enable estimation of survival and dispersal.

Seabirds generally have some of the longest life spans in class Aves, and high survival rates can be viewed as an adaptation to low and variable rates of recruitment (Weimerskirch 2002). Productivity of seabirds, which we define as the number of fledged young produced per pair of nesting adults at a colony, is a major component of recruitment. Productivity among seabirds in the north Pacific has varied substantially over time and space (Byrd et al. 1993, Hatch et al. 1993a). This variability may be driven by ecosystem shifts in food availability (Anderson and Piatt 1996, Hunt and Byrd 1999).

On an evolutionary time scale, survival and recruitment processes are expected to have approximately equal effects on fitness (Pfister 1995). High adult survival rates have high "elasticities," meaning that a proportionate change in this demographic parameter has a large effect on population growth rate as compared to comparable changes in other demographic parameters, such as those involved in recruitment (Lebreton and Clobert 1991). Life-history

theory predicts that natural selection would reduce variation in those parameters with high elasticities (Pfister 1995, Roff 2002). Consequently, adult survival in seabirds is generally high and fairly invariant, while productivity is low and highly variable (Nur and Sydeman 1999). The net effect of a given demographic parameter on population trends is a function of both its elasticity and its variation, and thus the expectation that survival and recruitment contribute equally under long-term evolutionary equilibria. However, conservation concerns operate on a much shorter time scale, and perturbations of a species' environment and its demography can imperil populations by shifting either survival or recruitment rates from evolved long-term averages.

The largest concentration of nesting seabirds in the north Pacific is located at the Pribilof Islands (Byrd et al. 1985). The majority of the world's Red-legged Kittiwakes (*Rissa brevirostris*) breed there, as well as large numbers of Black-legged Kittiwakes (*R. tridactyla*), Common Murres (*Uria aalge*), and Thick-billed Murres (*U. lomvia*), and other Laridae and Alcidae. In some or most years since 1976, indices of abundance and productivity of these four species have been estimated at the two principal islands, St. George and St. Paul (Byrd et al. 1985, 1997). Declines in several populations have generated concerns about whether the carrying capacity of the Bering Sea ecosystem has shifted (Hunt and Byrd 1999). Notably, reduced numbers of Red-legged Kittiwakes and its restricted distribution led to a class 2 categorization on the Endangered Species List (Byrd et al. 1997).

Central to understanding the causes of population change at the Pribilof Islands is to determine to what extent declines are driven by changes in seabird productivity. We here synthesize the available demographic data on these 4 species at St. George and St. Paul islands to

estimate the proportional contribution of productivity to differences among species and island populations in observed trends. This investigation entails providing estimates for all demographic parameters for a population and then comparing these sets, or matrices, of parameters between populations in the quantitative context of a life-table response experiment (LTRE; Caswell 2001). The utility of a comparative approach is apparent when one considers what inference can be made in the absence of comparison. Consider Black-legged Kittiwakes at St. George Island, which have monotonically declined since monitoring began in 1976 (see Results). Some values for survival and recruitment rates (including productivity) existed to mathematically result in the observed trend, but we do not know if survival, recruitment, or both are lower than what would be observed in a stable or increasing population, nor whether dispersal was relevant to these population changes. Because we observed variation in population trends among species, islands, and time during 1976–2002, we thus had the possibility of ascribing differences in trends to differences in productivity vs differences in other demographic parameters (i.e., survival and dispersal). For Red-legged Kittiwakes, other census data from the species' limited geographic distribution (Byrd et al. 1997) allowed us to more clearly identify the respective roles of survival and dispersal in their demography.

METHODS

The ultimate objective of estimating the contribution of productivity to observed population trends requires several steps. First, we need to estimate population growth rate for each of the four species on each of the two islands. Prior studies have provided some information on trends (Byrd 1989, Hunt and Byrd 1999), and thus the genesis of some conservation concern (Byrd et al. 1997). Nonetheless, we present an analysis of trends as this

represents recent additional data through 2002, and we provide the first empirically rigorous evaluation of the magnitude and shape of these trends, which also account for sampling variation. Second, we need estimates of each demographic parameter in the species' life history. Productivity has been estimated in most years for these species at St. George and St. Paul islands, and we generate some estimates for the other years via correlations with weather or productivity in conspecifics. Little other demographic data is available for kittiwakes and murre from the Pribilof Islands, other than adult survival rates for Red-legged Kittiwakes at St. George since 1991. We therefore derived estimates for other demographic parameters by reference to studies on these species in other areas. Third, we then synthesized these demographic parameters in matrix population models and contrast pairs of matrices. Because inherent species (phylogenetic) differences in demography may obscure differences due to environmental variation (which we are primarily interested in), we limited our contrasts to those between congeneric populations. For instance, demography of Red-legged Kittiwakes at St. George Island was contrasted with Black-legged Kittiwakes at St. George Island and to both Red- and Black-legged Kittiwakes at St. Paul Island.

Population trends.— A set of plots for monitoring population trends was established in 1976 on St. George and St. Paul islands. These plots were distributed throughout colonies at each island and are described by Hickey and Craighead (1977) and Byrd et al. (1985). In 1976, 1982, and 1984 numbers of each species of kittiwake and murre with adult plumage were counted once, whereas in subsequent years when counts occurred, replicate counts were done. Most counts in all years occurred between 1300 and 1900 hours and between the initiation of incubation and chick fledging to minimize variability due to attendance patterns (Byrd et al.

1985, Hatch and Hatch 1988, 1989). Because of weather and logistical constraints, not all plots were sampled within each replicate count. Thus, we did not have a set of multiple complete counts within a year to enter directly into the analysis. Instead, we computed a mean and variance for each individual plot and summed these to arrive at the overall mean count and its variance for that year.

We assessed population trends for kittiwakes and murre by evaluating the fit of various least squares regression models to the observed population histories for each species on each island ($4 \text{ species} \times 2 \text{ islands} = 8 \text{ histories}$). The natural log of population size was used (Eberhardt 1985), and we evaluated the fit of 4 models which represent 4 different hypotheses for population change. The 4 model types are simple linear, quadratic, joint linear, and a null model of a stable population. A simple linear model connotes a constant rate of population growth, whereas a quadratic model implies a constantly changing rate of growth. A joint linear model is a joining of two time periods of linear population growth, thus depicting constant population growth rates within each time period but different growth rates between periods. The null model of no trend is simply the mean population size over time and its variance. Because of variation in oceanographic conditions over time to which seabirds may be responding (Jones et al. 2002, Jenouvrier et al. 2003), we felt that a contrast of both quadratic and joint linear models should be examined. Some physical and biological oceanographic parameters change abruptly during climate regime shifts (Mantua et al. 1997), which could lead to joint-linear population dynamics. However, trends in some species may only gradually respond to even abrupt ecosystem changes, and their trends depicted most closely by quadratic models.

We used the Akaike information criterion, adjusted for sample size (AICc; Burnham and

Anderson 1998), to evaluate which of the four models best fit each population history. The AICc selects models to optimize the balance between bias and parameter precision. A model with many parameters will explain much of the variation in the data, and thus be relatively unbiased. However, the precision with which each parameter is measured declines as more parameters are included in a model (Burnham and Anderson 1992). In these regression models, the number of estimated parameters equals the number of coefficients representing slope (0 for a null model, 1 for a linear model, and 2 for quadratic and joint-linear models) plus a parameter each for the intercept and variance of the model (Burnham and Anderson 1998:48). For the joint linear models, which depict a discrete point in time when population growth rate changes, we used AICc to objectively determine when the change in population trend occurred. Because we are, in essence, estimating this temporal change point in a joint linear model, we include this change point in our count of parameters. However, if one had an *a priori* belief that population trend changed at a specific time (e.g., a recorded climate shift), then that expected change point could be used in all joint linear models and not included in the parameter count. In this case, quadratic and joint linear models would differ only by how much variation in the data they explained. Because of these contrasting philosophies in how to count parameters, we contrasted results for when K, the number of estimated parameters, equals four versus five for the joint linear models.

We incorporated sampling error into estimation of population growth rates and selection of appropriate regression models by iteratively simulating population histories according to the mean and standard deviation (SD) in population size for each year's count. Thus, for each species at each island, we iteratively created 2000 population histories and for each we evaluated

which of the four regression models best fit the data. The frequency with which each of these four models was selected as the best model represents the probability that a given model is the best model of the four considered and equates to an AICc weight (Burnham and Anderson 1998). Incorporating these measures of sampling error resulted in models with fewer parameters (null models and ones with a single, constant slope) being selected more often than for an analysis where sampling error is ignored (unpublished data). We accounted for uncertainty about which model best fit the data by computing population trends that were weighted averages among the four model types in accordance to the values of the AICc weights. Specifically, we used the back-transformed yearly predicted values of population size from each model, computed a weighted mean for each year, and then computed the mean rate of change for a time period of interest. If the model with the highest AICc weight was a model with constant population growth, we computed this mean rate of change for the whole span of years of the study (1976-2002), whereas if a joint-linear or quadratic model had the highest AICc weight, we computed a mean rate of population change for each of two discrete periods suggested by the joint-linear model.

Counts were not replicated in 1976, 1982, and 1984. To include some cautionary conservatism to our estimation of population growth rates, we included an assumed level of sampling error for these years. Specifically, we calculated the coefficient of variation (CV) for each year in which counts were replicated, and then calculated what the SD of population counts for 1976, 1982, and 1984 would be when applying the mean CV to these years.

Productivity.— Productivity of kittiwakes is defined as the number of young fledged from a constructed nest, and thus includes kittiwakes that built nests but did not lay eggs. Productivity

of murres is defined as the number of young fledged per nest site that contained an egg. Murres, which have a clutch size of one, do not build nests *per se*, thus the restriction to only birds seen with an egg. Some murres will lay a second egg if the first is destroyed, but in these cases clutch size was still considered one for calculating productivity.

Productivity was estimated from a series of plots distributed around each island, beginning in 1975 at St. Paul Island and 1976 at St. George Island (Byrd et al. 1985). Within each plot, nest sites were visually monitored. Plots were treated as sample units as the fate of nests within a plot were not independent (Byrd 1989), and we calculated mean productivity among plots to represent annual productivity.

Productivity was estimated from these direct observations in the majority of years for all species. We derived indirect estimates of productivity for years without direct estimates by using predictive equations from regression analysis. For kittiwakes, productivity was directly estimated for at least one island in every year, thus all indirect estimates were derived from correlations established within species between islands. For murres, there were some years when productivity was not measured at either island. Because productivity of murres at another colony in Alaska was related to spring weather parameters (Murphy et al. 1986), we evaluated whether productivity of murres at the Pribilof Islands was related to snow fall, depth of snow on the ground, and maximum temperatures observed in May, using both linear and quadratic parameters for each of these three weather variables. We used AICc values to select the best fitting models for each species, and then used the predictive equations from these models and the appropriate weather data to estimate productivity in years without direct estimates. We accounted for model selection uncertainty by producing a productivity estimate for each model

and then computing a weighted average among these predicted values using AICc weights.

For a subset of years with direct estimates of productivity, additional data were collected to allow estimation of components of productivity. These components were the proportion of nests into which eggs are laid, the proportion of nests with eggs that hatch eggs, and the proportion of hatched young that fledge. We examined correlations among components of productivity for a population using regression models and comparing AICc values to that from a null model of no correlation. Coefficients of variation (CVs) were also calculated to assess which components varied most.

Adult survival of Red-legged Kittiwakes.— Beginning in 1991, adult Red-legged Kittiwakes were captured at nest sites and marked with unique color band combinations. Resighting effort occurred every year throughout the breeding period in defined plots within which the kittiwakes were marked. These mark-resight data were used in a Cormack-Jolly-Seber model (Lebreton et al. 1992) in program MARK to estimate annual probabilities of apparent survival and resighting (White and Burnham 1999) from 311 individuals. We examined several models that may potentially explain annual variation in these rates, and used AICc statistics to evaluate which models best fit the data. A goodness-of-fit test of the most general model (median \hat{c} method; Cooch and White 2004) revealed that a variance inflation factor was needed, which we estimated as 1.78. Both quasi-likelihood AICc statistics (i.e., adjusted for variance inflation) and parameter estimates were adjusted as described by Burnham and Anderson (1998).

Competing models with respect to variation in survival included a null model with no variation, a model with significant but unexplained annual variation, and models with annual

variation (i to $i+1$) attributed to productivity in summer i or the August to April mean value of the North Pacific Index (NPI). We examined the relationship between productivity and survival probability because Black-legged Kittiwakes that raise chicks incur future survival costs (Golet et al. 2004). The NPI is a climatic index that represents the area-weighted sea level atmospheric pressure over the region 30°-65°N, 160°E-140°W, and for which low values are generally related to high oceanic primary productivity (Mantua et al. 1997). We included a survival model with the NPI because a recent study of Least Auklets (*Aethia pusilla*) in the southern Bering Sea found a relationship between NPI and annual survival of that species (Jones et al. 2002). We estimated the amount of variation in the data explained by these productivity and NPI covariates using an analysis of deviance (Skalski et al. 1993).

Other demographic parameters.— Our strategy was to compile a complete set of demographic parameters for one kittiwake and one murre population from the Pribilof Islands, and use these as “reference” matrices to derive demographic parameters for the other populations. For each of the four populations in which a joint-linear or quadratic model of trend fit best (see Results), we derived two sets of demographic parameters - one for each of two time periods (early and late) identified by the change point from the joint linear model. Our two reference matrices were Red-legged Kittiwakes at St. George Island in the later period and Common Murres at St. George Island. Our choice of kittiwake population was based on the greater amount of data-based estimates (adult survival rates), and we chose St. George Island Common Murres because they were the most stable and least variable of the murre populations at the Pribilof Islands.

The reference matrix for Red-legged Kittiwakes at St. George Island, and other

populations, is symbolically shown in Figure 1. The age of first breeding was set at five years. Although poorly studied in Red-legged Kittiwakes, age of first breeding in an Alaskan colony of Black-legged Kittiwakes exhibited variation among individuals and averaged five years of age (Suryan et al. 2000). Survival rates of these breeding-aged Red-legged Kittiwakes at St. George was 0.930 (see Results). Survival from fledging to breeding age is also poorly studied in Red-legged Kittiwakes, but 57% of fledgling Black-legged Kittiwakes in Prince William Sound, Alaska, survived to breed (Suryan et al. 2000). We approximated this value for Red-legged Kittiwakes at St. George and split this value into survival rates for the different age classes. How to split this value among age classes of pre-breeding aged birds is immaterial from a demographic perspective. Nonetheless, we assigned values using the general knowledge that post-fledging birds less than one year of age have the lowest survival and birds two to four years of age may survive at approximately the rate of breeding adults (Nur and Sydeman 1999, Table 1).

In our construction of this pre-breeding matrix (Caswell 2001) of demographic parameters, fecundity is the product of natal fidelity, breeding propensity, productivity, and post-fledging (juvenile) survival to one year of age (Fig. 1). Productivity and juvenile survival were already described above. Breeding propensity, the probability that a five-year or older kittiwake will breed (make a nest), has not been studied for Red-legged Kittiwakes, so we used the value of 0.894 estimated for Black-legged Kittiwakes in Prince William Sound (Golet et al. 1998, 2004). We note that numbers of Red-legged Kittiwakes during this later period at St. George Island were stable (see results), and the literature-based parameter estimates used here were from North Pacific Black-legged Kittiwakes studied concurrently and also with a stable to slowly

increasing population (Suryan and Irons 2001). The final parameter to identify for this kittiwake reference matrix is natal fidelity. This term represents the average rate of immigration and emigration by juvenile birds with respect to their eventual breeding status at St. George Island. This value would be greater than one if juvenile birds produced at other colonies immigrated to this colony at a greater rate than the emigration rate by juvenile birds produced at St. George Island. Because Red-legged Kittiwakes at St. George Island were stable at this time, we used a value of 1.0 for fidelity. Collectively, these estimates for demographic parameters resulted replicated the observed rate of population growth of Red-legged Kittiwakes at St. George in this later period (Tables 1 and 2).

Our reference matrix for murre (Common Murres at St. George Island) has less empirical support than for kittiwakes because we do not have adult survival rates estimated from either island population. We used an adult survival rate of 0.905, which represents the average of rates estimated for 2 colonies in the Gulf of Alaska (Piatt unpublished data) and a colony in central California (Sydeman 1993). We set average age of first breeding at 5 years (Birkhead and Hudson 1977). Survival from fledging to first breeding is poorly studied in murre as compared to kittiwakes. We therefore used values that approximated the survival to 3 years in Thick-Billed Murres (Gaston et al. 1994). We used values of breeding propensity for Common and Thick-billed Murres as estimated by Hatch and Hatch (1990) in the Semidi Islands, Alaska, which represented the percent of site holders at a colony that laid an egg. Because the colony of Common Murres at St. George Island was approximately stable, we set natal fidelity to 1.0. Collectively, this set of demographic parameters (Table 1) resulted in the population growth rate observed for Common Murres at St. George Island.

For each species at each island, we had estimates of productivity and population growth rate (Tables 1 and 2). The remaining components of the demography for each population can be viewed as two sets of parameters - those related to survival (juvenile, subadult, and adult survival) and those related to temporary or permanent dispersal from the local breeding population (breeding propensity and natal fidelity). We do not here consider dispersal (but see Discussion) of breeding adults as it is generally much lower than juvenile dispersal (Greenwood and Harvey 1982, Huyvaert and Anderson 2004). Data-based estimates for these parameters do not exist for these populations, so we derived estimates from the reference matrices in a process described below. In one analysis, we left the values for breeding propensity and natal fidelity equal to the reference matrix values for congeneric populations, but altered the survival rates such that the resultant population growth rate from these parameters equaled the one independently observed from plot data. In a second analysis, we did the reverse in that we left survival rates consistent among congeneric populations but altered values of breeding propensity and natal fidelity to equal observed population growth rates. Thus, the first of these two analyses identifies how much survival rates may have varied among populations and the second identifies how much non-breeding and dispersal processes may have varied.

We did not alter survival rates of all age classes by similar amounts as that would not be expected from life history theory (Pfister 1995). Among long-lived birds, adult survival varies less than juvenile and subadult survival (Weimerskirch et al. 1997, Nur and Sydeman 1999), but for adults a given amount of variation has a much greater relative effect (elasticity) on population growth rate (Lebreton and Clobert 1991, Schmutz et al. 1997). The generic demography of seabirds is such that the elasticity of adult survival is about 2.5 times greater than

the summed elasticity for the younger age classes. Thus, we altered adult survival rates by a certain percentage and then multiplied that percentage by 2.5 to denote the alteration in survival for younger age classes. In our second analysis, we altered natal fidelity and breeding propensity by equal amounts because these two parameters have identical elasticities, as they are both components of fecundity (see Fig. 1).

The contribution of productivity to observed trends.— Our goal is to look retrospectively at a series of data and assess how variation in productivity and other vital rates affected population change. Such a goal is frequently sought by population biologists, and analysis methods first focused on key factor analysis (Varley and Gradwell 1960). However, Vickery (1991) summarized many of the statistical problems with this approach. Alternatively, an analytical method that overcomes such problems, such as treatment of age-structure in long-lived animals with overlapping generations, is the life table response experiment (LTRE; Sibly and Smith 1998, Caswell 2001, Cooch et al. 2001). This approach uses Leslie-style matrix population models (Caswell 2001) and compares sets of matrices to examine how differences in projected population growth rate is a function of the variation in each vital rate among matrices, and thus is heuristically analogous to analysis of variance (Cooch et al. 2001).

We used the LTRE by comparing matrices of demographic parameters between pairs of congeneric populations. If a population exhibited two different periods of population growth, we parameterized a matrix for each of these periods. Thus, in sum we compared 10 pairs of matrices to quantify how variation in productivity versus variation in survival (or breeding propensity and natal dispersal) of various age classes contributed to variation in population growth during 1976–2002. Within each matrix, productivity was represented by the mean

productivity value for the span of years represented in the trend data. However, we did not use the last year of productivity in the time span in calculating this mean as that year's productivity could not influence the observed population trend. We conducted two LTREs to correspond to the two ways in which we altered parameters (either survival or dispersal) to produce a set of demographic parameters that produced the observed trend. In our first LTRE, we used the matrices of demographic parameters where survival rates were altered, and thus were asking the question how much does survival vs productivity affect population growth. In the second LTRE, we altered breeding propensity and natal fidelity, keeping survival constant, and thus were asking the question how much do dispersal processes vs productivity affect population growth.

We were concerned that whereas survival and recruitment related parameters in a matrix describe demography of an overall population, counts at colonies (from which population growth rate is estimated) may include only a portion of the population if subadult birds do not attend the colony (Murphy et al. 1986). We therefore conducted an analysis similar to the one above for examining contributions of productivity and survival, except that we offset the years of productivity data to account for the lag in time it potentially takes for chicks to return to the colony as subadults or adults and be counted. More specifically, we calculated population growth rates for each population for 1982–2002 and then conducted five sets of LTREs where productivity was based on the following five sets of years: 1982–2001, 1981–2000, 1980–1999, 1979–1999, and 1978–1997.

Meta-population dynamics of Red-legged Kittiwakes.— The global population of Red-legged Kittiwakes is distributed among only six colony areas in the southern Bering Sea. Amak Island, Bogoslof Island, and Koniuji Island are small colonies (< 1,000), the Buldir Islands'

colony is moderately larger (~10,000), the Commander Islands collectively contain about 32,000, and numbers at the Pribilof Islands are large and predominantly at St. George Island (220,000 in 1976), with only 2,200 at St. Paul during the same counting period (Byrd et al. 1997). We used a meta-population model to evaluate the extent to which natal dispersal to Buldir Island could explain the decline in numbers at St. George Island. We focused on these islands for this model because the Buldir Islands had a documented increase in numbers of nests from 4,400 in 1976 to 9,350 in 1993 (Byrd et al. 1997), which was coincident with a decline in numbers at St. George Island (see Results). Further, numbers at St. Paul Island and apparently also the Commander Islands declined during this time period at rates not too disparate from St. George Island (Byrd et al. 1997), and thus would not likely be recipients of immigrants from St. George Island. The other colonies are too trivial in numbers to consider here.

Parameters for the projection matrix from St. George Island in the early period are shown in Table 1. We first set survival parameters to that in the reference matrix, and breeding propensity and natal fidelity were equally reduced from the reference matrix by the proportion necessary to reproduce the observed growth rate of 0.955 (see last row of Table 1). We then projected for each year how many dispersing 1-year old kittiwakes St. George Island produced by using the age structure projected by this matrix, the initial population size of 220,000, and the rate of natal dispersal of one year-old kittiwakes, which is $(1 - \text{the fidelity rate}) \times N_{1,i}$, where $N_{1,i}$ is the number of one year-old kittiwakes in year i . These dispersing one year-old kittiwakes then became part of the Buldir population, where they then adopted the demographic parameters of that local, *in situ* population. The matrix of parameters for the *in situ* Buldir population were the same as the reference matrix except with a slightly lower value for productivity (0.28). This

lower productivity value for Buldir than St. George Island has empirical basis (Dragoo et al. 2001), plus it resulted in an *in situ* population growth rate of 1.0. Constructed in this manner, any increase in this modeled Buldir population over time must be from immigrants. We re-ran this meta-population model with three reduced levels of dispersal but increased levels of mortality. In one model the proportionate reductions in survival, relative to the reference matrix, were equal to those on fidelity and breeding propensity. In the other two models the proportionate reductions in survival were three and four times that of for breeding propensity and natal fidelity.

We similarly constructed a meta-population model to evaluate whether the recent rapid increase in numbers of Red-legged Kittiwakes at St. Paul Island could be a function of dispersal from St. George Island. Because the colony at St. George Island is two orders of magnitude larger, geographically very close, and has recently had a slightly positive growth rate, it is a logical and likely source of emigrants to St. Paul Island. We ran three iterations of this model that similarly reflected the ability of dispersal processes to account for this colony's rapid growth. The source population was the kittiwake reference matrix, St. George Island in the late period. However, instead of natal fidelity (NF) equally 1.0, as in Table 1, we reduced it to allow some dispersal ($1 - NF$). To maintain the observed growth rate for St. George Island, we increased juvenile survival by a comparable portion that we reduced NF . The three iterations of this meta-population model then are where $NF = 0.98$, $NF = 0.95$, and $NF = 0.92$. The vital rates for the *in situ* population at St. Paul Island were those of the reference matrix, except for the site-specific information on productivity at St. Paul Island. These vital rates for this *in situ* population produced a growth rate of 1.001, and thus virtually all increases to the population

must come from immigrants.

RESULTS

Population trends.— Four of the eight populations exhibited rates of population growth that changed over time; that is, a quadratic or joint linear model fit best (Table 2). For Red-legged Kittiwakes at St. Paul Island, a joint-linear model with a change point at 1996 had the highest AICc weight, regardless of whether a joint-linear model was considered to have $K = 4$ versus $K = 5$ (number of estimated parameters). For the other three populations with temporally changing trends, AICc model weights for joint-linear models were nearly equal or higher than that for quadratic models when $K = 4$, but quadratic models had higher weights when $K = 5$ for the joint linear models. Although we present trend results and LTRE results (see below) for both $K = 4$ and $K = 5$, we here emphasize the results from $K = 4$ for the remainder of this paper based upon the following. Complete island censuses of Red-legged Kittiwakes at St. George Island occurred in 1976 (220,000) and 1992 (123,000) (Byrd et al. 1997). Applying the model-averaged estimates of population growth from Table 2, which are derived from counts at plots scattered around the island, to the 220,000 count and projecting it to 1992 resulted in an estimate of 122,734 for $K = 4$ and 134,153 for $K = 5$. Given that the sample plots accurately reflect the trends of the whole island, then the joint-linear model was appropriately weighted when $K = 4$ but under-weighted when $K = 5$. However, we acknowledge that these unreplicated entire island counts lacked any measure of sampling variation, and thus the unknown inaccuracy of these counts may equal or exceed the difference between projected population sizes when $K = 4$ and $K = 5$. All four of these populations with growth rates that changed over time experienced increases in population growth rates, and these increases occurred in the late 1980s or mid 1990s

(Fig. 2).

Of the other four populations, only Common Murres at St. George Island was stable. Black-legged Kittiwakes at both islands and Thick-billed Murres at St. Paul Island declined at a virtually constant rate throughout the study period (Fig. 2, Table 2). Among all populations, except the recent increase in Red-legged Kittiwakes at St. Paul Island (see Meta-population results), population growth rate was lower at St. Paul than St. George island, averaging 2.5% less across species.

Productivity.— Direct measures of productivity were highly variable among years, ranging from 0 to 0.67 for kittiwakes and 0.15 to 0.75 for murres, with respective averages of 0.26 and 0.52 (Table 1, Fig. 3). Annual variation in productivity (CV) in murres (average CV = 26) was less than for kittiwakes (average CV = 72). Productivity of kittiwakes was positively correlated within and between islands, with an average r^2 of 0.578 among pairs of populations (Table 3). For murres the average r^2 among populations was 0.384. Approximately one-quarter to half the annual variation in productivity of Thick-billed Murres could be explained by its correlation with May weather (Table 4). The correlation of Common Murre productivity with weather was much weaker ($r^2 < 0.06$). We used predicted values from these statistical relationships as indirect estimates of productivity for years when direct estimates were not available (173 and 51 direct and indirect estimates, respectively). Twenty (8.9%) estimates of productivity were based on correlations with May weather. Mean values of direct estimates of productivity were similar to mean values of combined direct and indirect estimates (1.1% average difference among populations; Fig. 3). We therefore proceeded to use all estimates for the below LTRE analysis.

Part of the difference in annual variability (CV) of productivity between kittiwakes and murrelets may be due to a subtle difference in definition of productivity. Kittiwakes that nest but do not lay eggs contribute zero values to productivity, whereas murrelets that remained on site at the colony but did not lay eggs did not contribute to productivity measures. These murrelets without eggs would alternatively contribute to reduced measures of breeding propensity, as measured by Hatch and Hatch (1990). However, when looking at individual components of productivity, it is clear that a substantive part of the CV differences between species groups is real and not simply a function of definitions. The CV of components in common between species groups (egg and chick success) were much larger for kittiwakes than for murrelets (Table 5). Further, there were strong correlations between egg and chick success for kittiwakes, but not for murrelets, which further magnifies annual variability in overall productivity for kittiwakes.

Adult survival of Red-legged Kittiwakes.— Annual survival of Red-legged Kittiwakes was 0.930 (SE = 0.009). The model that best fit the data contained no annual variation in apparent survival or resighting probability (Table 6). Models where survival varied in relation to either productivity during the previous summer or the overwinter mean value of the North Pacific Index fit nearly as well ($\Delta AICc < 1.0$), although they explained only 15% of the year-specific variation in survival. The similar fit of models with either productivity or the North Pacific Index was coincidental, as these two covariates were unrelated to each other ($r^2 = 0.04$, $\Delta AIC = 26.8$ of model denoting relation, relative to null model of no relation). Resighting rate was very high and averaged 0.953 (SE = 0.008).

LTRE and the contribution of productivity.— We compared 10 pairs of matrices, and for 9 of these 10 were able to estimate the proportional contribution by productivity by perturbing

either survival parameters or breeding propensity and natal fidelity from values in reference matrices. For these 9 paired comparisons and when $K = 4$ for joint-linear models, the average proportional contribution of productivity to the difference in population growth was 0.232. For the analysis where breeding propensity and natal fidelity, rather than survival parameters, were perturbed the average proportional contribution of productivity was 0.195. *A priori*, one might think these two values should be equal, and the reason for their difference, albeit small, relates to mathematics of partitioning fecundity into its individual components, which is elaborated in the Discussion. In contrasting these two analyses (perturbing either survival or breeding propensity and natal fidelity), breeding propensity and natal fidelity had to be perturbed by a much larger proportional amount than did survival parameters (Table 1) to produce the observed trend, which is reflective of the much higher elasticity of adult survival relative to that for other parameters. When $K = 5$, these two respective estimates of the contribution of productivity to productivity were 0.252 and 0.223, indicating that the LTRE results are robust regardless of whether the number of parameters in a joint-linear model are considered to be four versus five. In sum, across these nine pairs of comparisons, variation in productivity accounted for only a quarter or less of the variation in population growth. Differences between kittiwakes and murrelets in this average contribution of productivity were minimal (0.242 vs. 0.225); differences between St. George Island were slightly larger than for St. Paul Island (0.265 vs. 0.207; for the LRTE analysis with survival perturbations and $K = 4$). There was no clear relationship between how much variation in productivity contributed to variation in population growth and the absolute magnitude of variation in population growth (Fig. 5).

The contrast of Red-legged Kittiwakes at St. Paul Island in recent years (1996-2002) to

the reference matrix, Red-legged Kittiwakes at St. George Island in the later period, was the one comparison not included above. For these kittiwakes at St. Paul Island, even with survival rates set at the unrealistic level of 1.0, productivity was insufficient to produce the observed trend in the absence of dispersal, and thus the missing estimate for the contribution of productivity for this population in Fig. 4. When we instead perturbed breeding propensity and natal fidelity from reference matrix values, we were able to produce the observed trend when breeding propensity was at its maximum (1.0) and natal fidelity was 4.95. For natal fidelity this means that among 1-yr old kittiwakes that become part of the St. Paul Island population, 3.95 of them are immigrants for every 1 such kittiwake that is a local, *in situ*, recruit. Because productivity of Red-legged Kittiwakes at St. Paul Island in this later period was less than that at St. George Island, productivity clearly was not a contributor to the difference in population trend for these two populations.

Offsetting years of productivity estimates with trend data, to account for variation in when sub-adult birds begin attending colonies, had negligible effects on LTRE results (< 5% average absolute change in contribution of productivity to population growth). This result was not surprising as all data sets contained both high and low years of productivity and thus mean values of productivity among sets of offset years were similar.

Meta-population dynamics of Red-legged Kittiwakes.— Our model indicated that much of the population decline at St. George Island in the early period was due to reduced survival and not dispersal. Nonetheless, dispersal was adequate to account for the increase in numbers at Buldir Island (Table 7). Specifically, a natal dispersal rate (1 - natal fidelity) from St. George Island of 0.08 - 0.10 (meaning 1 in every 10 to 12 one-year old kittiwakes disperses) was

adequate to produce the observed rate of population growth at Buldir Island. This dispersal rate is only one-fifth the rate required for the decline at St. George Island to have been a function of just dispersal processes and not reduced survival (Table 7), thus indicating that mortality was the larger contributor to the population decline.

Similarly, dispersal from St. George Island could account for the recent rapid increase in numbers at the nearby, small colony at St. Paul Island (Table 8). A dispersal rate from St. George Island of only 0.02 was sufficient for St. Paul Island to increase at 15% per year, despite having survival and productivity rates that were equal to or less than that at St. George Island.

DISCUSSION

Productivity is the most frequently estimated vital rate in seabird demography (Dragoo et al. 2001, Nur and Sydeman 1999). Behavior and productivity are profoundly influenced by food supply and foraging conditions during summer (Kitaysky et al. 2000, Gill and Hatch 2002), and thus measurement of productivity provides some indirect assessment of ecological conditions in these ocean environments (Hunt and Byrd 1999). Our poor ability to predict productivity of Common Murres at the Pribilof Islands using May snow and air temperature data, despite success in this regard for Common Murres on the southern Seward Peninsula, Alaska (Murphy et al. 1986), is perhaps not unsurprising because the Pribilof Islands are proximal to the edge of the continental shelf (in great contrast to the Seward Peninsula site). This proximity magnifies oceanic influences such as ocean temperatures and behavior of nutrient upwellings (citation). Within the Pribilof Islands, murres (pursuit-divers) and kittiwakes (surface feeders) exhibit different feeding ecologies (Kitaysky et al. 2000), which leads to the prediction that some variations in foraging conditions will impact foraging success and productivity of one but not

both genera. This is consistent with our findings that murre and kittiwakes exhibited different degrees of correlation and variation among components of productivity (Table 5) and that overall productivity of murre and kittiwakes were uncorrelated (unpublished data). Despite these differences between murre and kittiwakes, overall productivity for both genera exhibited approximately equal effects on population trends.

Across all populations in this study, productivity explained approximately a fourth, or less, of the variation in population trends. Consequently, variation in one or more rates of survival (all age classes following fledging) or dispersal (natal dispersal or breeding propensity) must account for the remainder of variation in population growth. For all populations except Red-legged Kittiwakes at St. Paul since 1996, we demonstrated how either survival or dispersal processes could possibly account for the large amount of trend variation not explained by variation in productivity. We noted that much larger variations in natal dispersal or breeding propensity were needed, relative to survival of breeders (Table 1), to account for the variation not explained by productivity. That is not to say that such large variations in temporary or permanent dispersal processes are not possible. Kittiwakes elsewhere in Alaska (Suryan and Irons 2001) and in Europe (Coulson and Nève De Mévergnies 1992, Danchin and Monnet 1992, Cadiou 1999) demonstrate a propensity to emigrate from colonies where conditions are poor and immigrate to new sites or colonies where reproductive success may be higher. Our meta-population models indicate that growth of several small colonies of Red-legged Kittiwakes is likely the result of low level natal dispersal from a much larger source population at St. George Island. Recent genetic work suggests that gene flow among Red-legged Kittiwakes from St. George and Buldir islands is sufficient to consider these birds collectively within a single

evolutionary significant and management unit (Patirana et al. 2002). Importantly, however, these same meta-population models indicated that most of the decline in Red-legged Kittiwakes at St. George Island was due to reduced survival and not due to reduced productivity or dispersal to other islands. Given that the large majority of the global population for this species resides on this island, understanding the amounts of and causes for such survival variation is important.

We note that Black-legged Kittiwakes, one of the most well-studied seabirds, exhibits distinct life history differences between Pacific and Atlantic populations (Hatch et al. 1993b, Coulson 2002, Weimerskirch 2002). Kittiwakes in the north Pacific ocean have high adult survival and low recruitment rates, whereas in the north Atlantic survival rates are lower but recruitment higher. These life history differences likely exist due to differences in how environments vary in these two broad ecoregions (Weimerskirch 2002), and thus for North Pacific colonies such as those at the Pribilof Islands, extended periods of poor or no reproductive success may be normal on an evolutionary time scale. Such a life history pattern means that North Pacific seabirds would be particularly vulnerable to perturbations of adult survival rates. We have argued that changes in survival of Red-legged Kittiwakes are principally responsible for variations in population growth rate. Further, mass mortality of murrelets in Alaskan waters have been noted several times (Piatt and Van Pelt 1997). Mass mortalities in seabirds may be less infrequent than previously assumed, are speculated to be related to food availability, and have relevance to population dynamics (Piatt and Van Pelt 1997, Camphuysen et al. 1999). Our models in this paper demonstrate that small perturbations to adult survival, whether naturally or anthropogenically driven, could be the primary demographic force for variations in population trends witnessed among murrelets and kittiwakes at the Pribilof Islands.

One component of demography that we have thus far ignored is permanent emigration of adult breeders. One reason for having done so is that breeding dispersal is thought to be much lower than natal dispersal (Greenwood and Harvey 1982), and natal dispersal seems to already be low for Red-legged Kittiwakes. Second, for most sampling methods, permanent emigration cannot be distinguished from mortality, and credible estimates of such emigration are largely lacking. We note that a recent mark-resighting effort with Red-legged Kittiwakes at Buldir Island indicates an adult survival rate of 0.96. Given the high elasticity of adult survival, this 3% greater survival rate than that at St. George Island would be expected to create a significant difference between islands in population trends, if all other vital rates were generally comparable. However, both recent productivity and trends are similar between islands (Dragoo et al. 2001). One hypothesis to explain this apparent incongruence is that survival of Red-legged Kittiwakes at St. George Island is really ~0.96 as well, and that the estimate of 0.93 includes a 3% bias due to permanent emigration from the sampled area. Importantly, in this example, we are hypothesizing dispersal within an island colony and not between islands. This hypothesis seems tenable as the Buldir Island colony is small and logistically accessible and all kittiwakes can be examined for the presence of bands, thus little opportunity for dispersal within the colony but away from previous nesting ledges to go undetected. In contrast, the huge population at St. George Island predates that mark-resight efforts occur within finite, delimited areas and thus there is the real possibility that birds could permanently move to another part of the colony and their subsequent lack of detection then effectively contribute towards a biased survival estimate. Such a pattern of dispersal, if true, does not invalidate our previous results. It principally would mean that some of the assumed levels for other demographic parameters in the species' life

history are in error. The consequence of such error would be some quantitative, but not qualitative, differences in the results presented here. Because survival and dispersal processes account for the large majority of variation in population trends, this example of possible permanent emigration primarily serves to further underscore the need to design effective sampling protocols to measure these demographic parameters.

Most previous studies of seabird survival have estimated just survival or survival and a detection, or resighting, probability (reviewed by Nur and Sydeman [1999]). However, several relatively recent developments in mark-recapture theory allow one to appropriately quantify movement and dispersal processes, which are of interest themselves and also allow for less biased estimates of survival. Some of these methods are now seeing use for seabirds. Multi-state models (Nichols et al. 1993) have been used to estimate movement of Roseate Terns (*Sterna dougallii*) among colonies (Spendelov et al. 1995) and to estimate transition probabilities among breeding states in Black-legged Kittiwakes (Golet et al. 2004). Combining mark-resight data with band recovery data in a combined model (Burnham 1993) allowed for estimation of permanent emigration of Great Cormorants (*Phalacrocorax carbo*, Frederiksen and Bregnballe 2000). Adding robust design methods (Pollock 1982) onto basic mark-resight approaches, which principally means adding iterative resampling of the population over short time periods when no mortality or immigration is thought to occur, allows for estimation of temporary emigration (Kendall and Nichols 1995). For seabirds a common cause for temporary emigration from the sample population is non-breeding, which often severely limits their detectability (Nur and Sydemen 1999). There are real concerns about how logistically tractable these methods are to employ for some large colony populations, but they clearly should be

contemplated.

Another recent innovation in mark-resight methods has particular relevance to our primary objective of determining the relative contributions of different demographic parameters to population change. A simple analytical twist to typical Cormack-Jolly-Seber survival models allows one to estimate both survival and recruitment in a population (Pradel 1996). Because in this analytical model, survival includes emigration and recruitment includes immigration, estimation of population growth is also possible. Thus, the respective contributions of survival and recruitment to population growth can be directly estimated and for any explicit time interval desired (e.g., annually; Nichols et al. 2000). This direct estimation is in contrast to the LTRE approach used in this study, which is an indirect method and is reliant on asymptotic statistical behavior. Indirect asymptotic methods are expected to perform well when projecting the demographic consequence of an extended future with a given set of vital rates. In contrast, the direct estimation approach should generally perform better for retrospective examinations because it estimate parameters well while undergoing transient dynamics and other aspects of short time-scale variation that are not consistent with asymptotic behavior (Fox and Gurevitch 2000, Nichols et al. 2000). Some sampling issues related to this direct estimation approach must be forethought and designed (e.g., Drietz et al. 2002, Hines and Nichols 2002), but it should be readily applicable to most situations where a Cormack-Jolly-Seber model has been historically applied. That said, this approach alone does not distinguish among the various components of survival or recruitment and thus combinations of sampling approaches will be needed to allow estimation of the suite of demographic parameters addressed in this study.

We identified how estimates of proportional contribution of productivity to population

change differed slightly between when survival parameters were perturbed and when breeding propensity and natal fidelity were perturbed, despite an intuitive expectation that they would be the same. Recall that natal fidelity, breeding propensity, productivity, and juvenile survival collectively constitute a single cell in the projection matrix in Figure 1 and their product represents fecundity. When conducting a LTRE, computations rely in part on the sensitivity (closely related to elasticity) associated with each cell, not the individual components of each cell. However, the differences between pairs of matrices are due to just a subset of the components (termed lower-level parameters; Caswell 2001) of fecundity being different from one another, which sets up some non-additive relationships when calculating proportional contributions (detailed in Cooch et al. [2001]). Because the two LTREs involved different subsets of these lower-level parameters, different degrees of non-additivity arose, which led to differences in the final estimates of proportional contributions. This scenario creates some bias, which in this study is apparently small given the minor differences among the two LTREs. However, in some other matrix formulations (e.g, stage based) biases may be large, and identification of probable bias should be addressed through simulation.

Our results indicate that variation in survival and dispersal processes strongly influence the dynamics of kittiwakes and murrelets at the Pribilof Islands. For Red-legged Kittiwakes at their largest colony, the influence of survival was particularly dominant. Other recent studies have also identified dispersal processes to also be important to these (Parrish 1995, Suryan and Irons 2001) and related species (Frederiksen and Petersen 2000). These results provide incentive for monitoring programs to incorporate sampling that will allow estimation of these important parameters. However, we do not intend to undervalue the continued monitoring of productivity.

This paper has not attempted to address all the possible factors influencing variation in productivity or survival, but food supply for piscivorous seabirds in the southeast Bering Sea has been implicated as a governing influence on the dynamics of these birds (Hunt and Byrd 1999). Productivity is responsive to this (Gill and Hatch 2002), which in turn may influence breeding propensity, survival, and dispersal (Golet et al. 2004).

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Annual Survival - 1 yr olds	0.843	0.900	0.867	0.900	0.846	0.895	0.852	0.900	0.829	0.761	0.860	0.859
Annual Survival - 2, 3, and 4 yr olds	0.871	0.930	0.896	0.917	0.860	0.910	0.879	0.930	0.855	0.773	0.875	0.874
Annual Survival - 5+ yr olds	0.906	0.930	0.916	0.917	0.893	0.913	0.908	0.930	0.899	0.858	0.899	0.898
Proportional Change in Survival from St. George RLKI or COMU	-0.032 ^c	N/A ^d	-0.019	N/A	-0.060	-0.005	-0.053	^e	-0.079	-0.155	-0.044	-0.045
Proportional Change in Natal Fidelity and Breeding Probability from St. George RLKI or COMU	-0.207	N/A	-0.113	N/A	-0.268	-0.020	-0.335	4.80 ^f	-0.485	-0.760	-0.192	-0.197

a RLKI = Red-legged Kittiwake, BLKI = Black-legged Kittiwake, COMU = Common Murre, TBMU = Thick-billed Murre.

^b These values represent numbers of fledglings per breeding pair, as described in the text. For input to our matrix projection

models, we divided this number by two to represent number of fledglings per breeding individual.

^c The upper value in this row is the proportional change in post-fledging survival and survival of one to four year-olds. The lower value is that for breeding-aged adults (five years and older) and is 2.5 times less than upper value. The rationale for this difference is based on life-history theory and elasticity differences, as elaborated in the text.

^d N/A = Not applicable. This is because these are the reference matrices for all congeneric populations.

^e Change in all survival parameters to 1.0 insufficient to replicate observed population growth rate.

^f Breeding propensity set at 1.0, whereas natal fidelity may exceed 1.0 to reflect immigration vs emigration (see text).

Table 2. Evaluation of population trends of kittiwakes and murre nesting at the Pribilof Islands, 1975–2002. For each species for each island, a Monte Carlo procedure was used (2000 iterations) that incorporated sampling error (SD) associated with each year's population estimate. Thus, for each species for each island, 2000 different population histories were created and each was analyzed with regression models to see if a trend was detectable. For each population history, we compared the fit of four models: no trend, linear trend (constant rate or increase or decrease), quadratic trend (changing rate of population growth), and a joint linear model indicating two time periods of differing linear trend. The fit of models was evaluated with the Akaike information criterion corrected for sample size (AICc; Burnham and Anderson 1998). Shown below are the frequencies with which each of these 4 models was selected out of a set of 2000 population histories. These frequencies (shown on a 0 to 1 scale) represent AICc weights and function as a weight of evidence for determining whether a trend exists. We used these AICc weights to derive weighted mean estimates of each year's predicted population size, with predictive values coming from each model's regression equation. Using these weighted mean estimates of population size, we then calculated a mean rate of population growth for the whole time period, except for when a joint-linear model best fit the data, in which case we calculated mean rates of population growth for two time periods. Estimation of population growth by these methods accounts for sampling error within years and lack of certainty in which model best represents the data. For each population, we present results from two trend analyses - one where the number of estimated parameters (K) in a joint-linear model is considered to be four, and one where it is five.

		AICc weights derived from Monte Carlo simulation								Model-weighted	
		Saint George Island				Saint Paul Island				population growth rate ^a	
		No	Quad-	Joint	No	Quad-	Joint			St.George	St. Paul
Species	K	Trend	Linear	ratic	Linear	Trend	Linear	ratic	Linear		
Red-legged										1976–1989	1976–1996
Kittiwake	4	0.000	0.034	0.520	0.446	0.011	0.025	0.000	0.964	0.955	0.942
										1989–2002	1996–2002
										1.005	1.150
										1976–1989	1976–1996
	5	0.000	0.31	0.968	0.001	0.089	0.128	0.048	0.735	0.962	0.948
										1989–2002	1996–2002
										1.003	1.125
Black-legged										1976–2002	1976–2002
Kittiwake	4	0.000	1.000	0.000	0.000	0.000	0.979	0.004	0.017	0.974	0.955
										1976–2002	1976–2002
	5	0.000	1.000	0.000	0.000	0.000	0.997	0.003	0.000	0.974	0.955

										1976–1988	
Common										1976–2002	0.928
Murre	4	0.479	0.471	0.002	0.048	0.000	0.281	0.053	0.666	1.004	1988–2002
											0.980
											1976–1988
										1976–2002	0.942
	5	0.493	0.492	0.012	0.003	0.000	0.329	0.655	0.016	1.004	1988–2002
											0.974
											1976–1987
Thick-billed										0.975	1976–2002
Murre	4	0.000	0.000	0.332	0.668	0.078	0.869	0.000	0.053	1987–2002	0.985
										1.025	
											1976–1987
										0.980	1976–2002
	5	0.001	0.000	0.945	0.054	0.084	0.914	0.001	0.001	1987–2002	0.985
										1.023	

COMU	--	0.355	0.598	0.638
	18	18	13	13
	--	0.953	0.991	0.995
TBMU		--	0.159	0.012
		22	15	16
		--	0.555	0.283
St. Paul				
COMU			--	0.541
			16	16
			--	0.995
TBMU				--
				18
				--

Table 4. Relationship between weather at the St. Paul airport in May and productivity of murres and kittiwakes at St. Paul and St. George islands during 1975–2002. Linear and quadratic terms for daily snowfall, depth of snow on the ground, and maximum temperature were used in regression models, and the best fitting model selected by AICc values.

	Common Murre		Thick-billed Murre	
	St. George	St. Paul	St. George	St. Paul
Variables in best fitting model	Snowfall	Snowfall	Temperature,	Snowfall ²
r^2 of this model	0.058	0.029	0.500	0.220
Deviation of AICc from null model	-1.19	-0.433	-12.57	-4.60

Table 5. Means and coefficients of variation (CV) for components of productivity for eight populations of murre and kittiwakes nesting at the Pribilof Islands, 1975–2001. Components are the proportion of nests in which eggs are laid (Lay), the proportion of eggs laid that hatch (Egg), and the proportion of chicks hatched that fledge (Chick). These data were collected only during a subset of the years for which productivity were gathered. Thus, in this table mean productivity is the product of the components and was calculated just for the years with data on components. Also shown are correlations (r) among components for each population.

	RLKI at St. George Island ($n = 18$)			BLKI at St. George Island ($n = 17$)			RLKI at St. Paul Island ($n = 18$)			BLKI at St. Paul Island ($n = 13$)		
	○	CV	r : AICc weight ^a	○	CV	r : AICc weight	○	CV	r : AICc weight	○	CV	r : AICc weight
Lay	0.668	32.9	0.484 : 0.811	0.621	39.7	0.795 : 0.999	0.574	43.6	0.469 : 0.784	0.733	20.7	0.558 : 0.770
Egg	0.526	38.1	0.395 : 0.614	0.436	0.646	0.730 : 0.990	0.593	33.6	0.785 : 1.000	0.562	37.7	0.812 : 0.997
Chick	0.719 ^b	18.2	0.554 : 0.894	0.561 ^c	47.8	0.574 : 0.872	0.585	59.6	0.536 : 0.892	0.599	25.9	0.417 : 0.507
Productivity	0.280	60.5		0.214	88.2		0.258	77.5		0.279	63.1	
	COMU at St. George Island ($n = 17$)			TBMU at St. George Island($n = 21$)			COMU at St. Paul Island ($n = 15$)			TBMU at St. Paul Island ($n = 17$)		
	○	CV	r : AICc weight	○	CV	r : AICc weight	○	CV	r : AICc weight	○	CV	r : AICc weight
Egg	0.646	22.4	-0.035 : 0.275	0.667	10.9	-0.312 : 0.553	0.657	24.4	-0.145 : 0.286	0.590	26.2	0.316 : 0.479
Chick	0.818	18.7		0.816	20.8		0.792	10.2		0.767	8.2	
Productivity	0.528	29.0		0.541	22.7		0.519	25.6		0.455	29.1	

^a The correlation coefficient (r) and the AICc weight of a linear model relating two components of productivity. The AICc weight for the null model of no correlation between these components equals $1 - (\text{AICc weight shown in table})$. For kittiwakes, the first r within a column is the Lay-Egg correlation, the second r is the Egg-Chick correlation, and the third r is the Lay-Chick correlation. For murre, we could only calculate an Egg-Chick correlation.

^b Sample size for the chick component of productivity was $18 - 1 = 17$ because in one year no eggs hatched young from which to calculate chick productivity.

^c Sample size for the chick component of productivity was $17 - 2 = 15$ because in two years no eggs hatched young from which to calculate chick productivity.

Table 6. Models of apparent survival of color-banded Red-legged Kittiwakes based on resightings at St. George Island, Alaska, 1991-2002. Survival (N) and resighting (D) probabilities varied according to the indicated subscripts; a dot (.) indicates an invariant probability. The second model relates productivity (as shown in Fig. 3) at time i to survival from i to $i+1$. The third model relates the mean value of the North Pacific Index for August to April between time i and $i+1$ to survival from i to $i+1$.

Model	AICc ^a	AICc weight	Number of parameters	Deviance
N, D	0.00	0.42	2	189.41
$N_{productivity}, D$	0.86	0.27	3	188.36
N_{NPI}, D	0.86	0.27	3	188.36
N, D_{year}	4.93	0.04	12	175.38
N_{year}, D	11.81	0.00	12	181.70
N_{year}, D_{year}	18.20	0.00	21	170.67

^a Quasi-likelihood AIC values and weights were calculated to account for the variance inflation factor of 1.78, as estimated by the median c-hat method described by Cooch and White (2004).

Table 7. Meta-population dynamics of Red-legged Kittiwakes at St. George and Buldir islands during 1976–1993. A total island count for the source population of dispersers (St. George Island) was 220,000 in 1976. Total island counts of nests at the Buldir Islands was 4,400 in 1976 and 9,350 in 1993. Our meta-population model used vital rates for St. George Island in the early period that produced the observed colony growth rate (Table 1), except that the four different model runs depicted below reflect different allocations of decremented survival or decremented breeding propensity and natal dispersal. Thus, below we indicate what proportions of the decrements indicated in the last two rows of Table 1 that we used as inputs to this meta-population model, and we then show here the actual values for these vital rates, which are breeding propensity (BP), natal fidelity (NF), survival of adults (S_A), survival of one year-olds (S_1), and juvenile survival (S_J). The far right column represents the case where the entirety of vital rate differences between St. George in the early and late periods are reflected in NF , BP , and the observed productivity differences.

	Proportional decrements to vital rates relative to that indicated in last 2 rows of Table 1			
	0.8 Survival, 0.2 NF and BP	0.75 Survival, 0.25 NF and BP	0.5 Survival, 0.5 NF and BP	0.0 Survival, 1.0 NF and BP
Model predictions of number of nests at Buldir	9013	10094	15262	22032
	Values for subset of vital rates in the source population (St. George Island)			
NF	0.922	0.902	0.800	0.610
BP	0.824	0.807	0.715	0.545
S_A	0.911	0.912	0.918	0.930

S_I	0.855	0.857	0.872	0.900
S_J	0.736	0.738	0.751	0.775

Table 8. Meta-population dynamics of Red-legged Kittiwakes at St. George and St. Paul islands during 1996–2002. We used three different levels of natal dispersal from St. George to St. Paul island. In this model, the first dispersing individuals were born in 1996, and thus they are reflected in the 1999 prediction of total birds, but do not contribute to the predicted nest count until 2002, due to age of first breeding being specified as five years.

Year	Predicted total birds from trend analysis	Predicted numbers based on vital rates in a meta-population model ^a					
		Natal fidelity = 0.98		Natal fidelity = 0.95		Natal fidelity = 0.92	
		Total birds	Nests	Total birds	Nests	Total birds	Nests
1996	666	666	444	666	444	666	444
1999	1013	1213	444	2072	444	2987	444
2002	1540	1671	693	3248	1084	4929	1501

^a To compensate for different levels of fidelity used in the model and still maintain the same *in situ* population growth rate for St. George Island (1.005), we altered levels of juvenile survival from the 0.775 value in the reference matrix. In the three sets of model runs represented above, juvenile survival was 0.791, 0.816, and 0.842.

Fig. 1. Structure of pre-breeding population projection matrices (Caswell 2001) used to model demography of kittiwakes and murrelets nesting at the Pribilof Islands. The top row represents fecundity and columns indicate age classes (shown as subscripts). First breeding occurs at five years of age, and fecundity is represented by the product of natal fidelity (F), breeding propensity (BP), productivity (P), and survival of juveniles from fledging to one year of age (SJ). Survival of immature birds prior to first breeding (SP) and breeding adults (SA) are shown on the second to fifth rows.

$$\begin{bmatrix} 0 & 0 & 0 & 0 & F_{5+} \times B_{5+} \times P_{5+} \times SJ_{5+} \\ SP_1 & 0 & 0 & 0 & 0 \\ 0 & SP_2 & 0 & 0 & 0 \\ 0 & 0 & SP_3 & 0 & 0 \\ 0 & 0 & 0 & SP_4 & SA_{5+} \end{bmatrix}$$

Fig. 2. Population trends of kittiwakes and murrelets at the Pribilof Islands during 1976-2002.

Trend lines are derived from weighted averages of predicted values from four different models: stability (population growth rate = 1.0), constant increase or decrease (linear), constantly changing rate of increase (quadratic), or a joint-linear model with two different time periods of constant increase (or decrease).

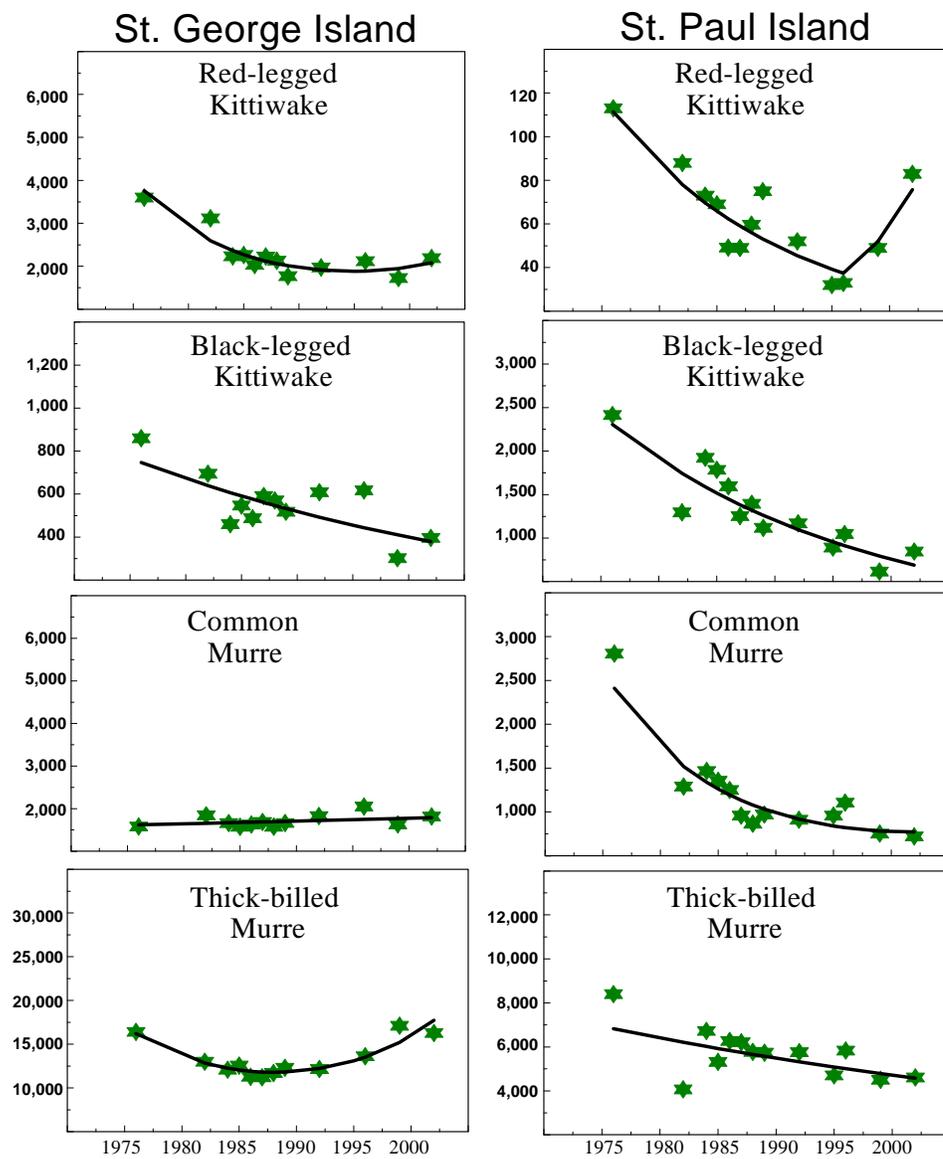


Fig. 4. Proportionate contribution of each demographic parameter to variation between pairs of matrices in projected population growth rate, *sensu* a life table response experiment (Caswell 2001, Cooch et al. 2001). For kittiwakes, one matrix in each pair of compared matrices was that for Red-legged Kittiwakes at St. George Island during the later period of population growth (the “reference matrix”). For murre, the reference matrix was Common Murres at St. George Island. Within each graph, the left and right sides of the dotted line respectively portray results from the analysis where survival or dispersal parameters were perturbed.

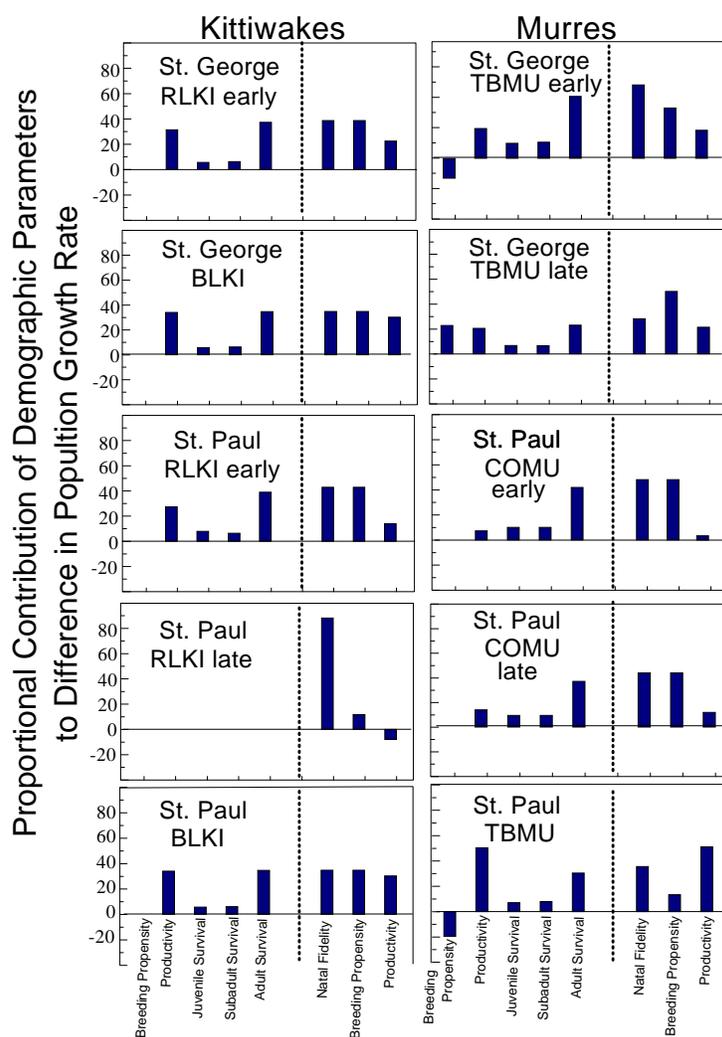


Fig. 5. The contribution of productivity to differences in population growth rate in relation to the magnitude of differences in population growth rate among pairs of matrices. Matrix pairs were comprised of a reference matrix (St. George RLKI for kittiwakes, St. George COMU for murre) and a congeneric population. Squares indicate the life table response experiment where survival parameters were perturbed, and diamonds indicate the one where natal fidelity and breeding propensity were perturbed.

