

Projecting long-term impacts of a mortality event on vertebrates: incorporating stochasticity in population assessment

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Abstract. Wildlife managers must be able to assess the long-term, population-wide impacts of mortality events on long lived vertebrates, taking into account the stochastic nature of population fluctuations. Here, we present a case study of the potential impacts on Western gulls (*Larus occidentalis*) of a single, non-target mortality event, potentially resulting from exposure to rodenticide directed at eradicating house mice (*Mus musculus*) on the Farallon Islands National Wildlife Refuge. Firstly, we conducted a population viability analysis based on over 25 yr of Farallon Western gull demographic data to model future population trends under varying environmental conditions. Future population trends for Farallon Western gulls, independent of any potential mouse eradication-related mortality, depend on the frequency of years with near-failure in reproductive success, as was observed in 2009, 2010, and 2011. We modeled population trends under three environmental scenarios defined by the probability of near-failure in future breeding: optimistic (probability of near-failure = 0.0), realistic (probability = 0.115), or pessimistic (probability = 0.25). Secondly, we determined the maximum level of additional mortality, C , that would result in a population outcome distribution that cannot be effectively distinguished from a no additional mortality scenario after 20 yr (defined as 95% overlap in the two frequency distributions). We determined the threshold of detection to be an additional mortality of 3.3% beyond normally observed levels under the realistic scenario, 2.8% under the optimistic scenario, and 4.2% under the pessimistic scenario. Results demonstrate that the greater the background stochasticity, the greater C must be to be able to discriminate a long-term effect of the mortality event against the backdrop of environmental variability. We demonstrate that incorporation of stochasticity is critical for evaluating one-time mortality events given the high degree of variability characterizing many ecosystems; deterministic projections alone may provide poor guidance. While the need to account for stochasticity in Population Viability Analysis models is well established, this study is innovative in addressing how to evaluate a future or retrospective one-time mortality event in the context of stochasticity. Our approach can help resource managers' plan for both best-case and worst-case scenarios when evaluating impacts of mortality events.

Key words: impact assessment; mortality event; population recovery; population viability analysis; stochastic modeling; Western gull.

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INTRODUCTION

It is common for wildlife to experience acute mortality events due to weather, disease, oil

spills, or other contaminant exposure, culling, or other events (Peterson et al. 2003, Sutherland et al. 2004, Fey et al. 2015). Wildlife managers must be able to assess the short-term and

long-term population-wide impacts of these events in order to be able to pursue management actions that can best maintain or recover affected populations (Morris and Doak 2003). The long-term significance of a mortality event will ultimately depend on the ability of the population to recover (Monson et al. 2000, Peterson et al. 2003, Martínez-Abraín et al. 2006). However, assessment of population recovery is difficult given the stochastic nature of the environment and resulting variation in demographic parameters which will influence future population trends (Burgman et al. 1993).

One approach used to assess population impacts from mortality is to quantify the observed population trend subsequent to the event (Heubeck et al. 2003). However, this can be difficult to interpret due to impacts of other environmental influences which may confound attempts to discern a signal due to the mortality event. For example, a population may display a downward trend in abundance following an event because environmental conditions, independent of the mortality event, have depressed survival and/or productivity. Conversely, a favorable change in environmental conditions may obscure what otherwise would have been a decline in abundance due to a mortality event.

To provide insight and planning guidance for wildlife managers confronted with these issues, we present a case study of a stochastic population projection to assess potential impacts and recovery following a mortality event. We conducted a population viability analysis (PVA; Beissinger and McCullough 2002) of the Western gull (*Larus occidentalis*) population on the Farallon Islands, California, contrasting scenarios with and without additional mortality due to a proposed house mouse (*Mus musculus*) eradication project (USFWS 2019). Proposed Farallon mouse eradication methods include the island-wide application of bait pellets containing rodenticide (USFWS 2019). This method has proven effective for other island eradication projects worldwide (Howald et al. 2007, Keitt et al. 2011, Mackay et al. 2011, Raymond et al. 2011) but carries the risk of non-target exposure from the ingestion of toxic bait pellets or scavenging of affected mice, as documented in previous rodent eradications, such as Rat Island, Alaska (Paul and Salmon 2010, USFWS 2019). The Farallon Islands harbor

the world's largest known colony of Western gulls (Penniman et al. 1990), a generalist predator, and opportunistic scavenger, which may be susceptible to non-target mortality during the proposed mouse eradication.

An important strength of PVA is that it incorporates stochasticity, the unpredictable variation in demographic parameters that reflects underlying environmental variability (Burgman et al. 1993, Beissinger 2002). This allows for a probabilistic assessment of future populations and evaluation of actions that may reduce or increase risk (Nur and Sydeman 1999a, Akçakaya et al. 2004). Reproductive success for Farallon Western gulls exhibits high stochasticity in response to environmental perturbations such as El Niño. Additionally, reproductive success during 2009, 2010, and 2011 was extremely low, <0.15 chicks fledged per pair in each of the three years (Warzybok et al. 2014). In the 23 yr preceding 2009, reproductive success had never been less than 0.30 chicks fledged per pair and was usually much higher (mean = 0.84 chicks/pair). The cause of this near-failure in the three years has not been identified, but it may be linked to reduced food availability for this species, possibly reflecting marine and/or human influences (Pierotti and Annett 1990).

Here, we present an assessment of long-term population impacts from a potential mortality event given substantial environmental stochasticity observed for the Farallon population. We evaluate three scenarios that make different assumptions about future Western gull productivity, reflecting variation in underlying environmental conditions. For each scenario, we provide a criterion for the assessment of a one-time mortality event, such as might occur with rodenticide ingestion, and oil spill. The demographic modeling presented here relies on detailed observations and statistical analysis of the Farallon breeding population, covering the period 1986–2011 (Spear and Nur 1994, Nur et al. 1994, Pyle et al. 1997). We draw on this extensive time series of demographic parameter estimates to develop a stochastic population model, which we then present as a case study demonstrating the value of this approach. Here, we apply the method to a prospective analysis, but the approach can equally be applied in a retrospective analysis.

While stochastic population models have often been used to address long-term impacts due to chronic sources of mortality in fish (see review by Maunder and Punt 2013), birds (Francis and Sagar 2012, Cook and Robinson 2017), and marine mammals (Brandon and Punt 2013), a stochastic approach has not, to our knowledge, previously been implemented to address the potential long-term impact of an acute mortality event, as we do here. However, to do so requires specifying a threshold by which to discern the mortality signal against the background of variable mortality, and, below, we provide an operational threshold.

Herein, we address the question: At what magnitude of a mortality event can its signal still be discerned after 20 yr, against the backdrop of stochastic fluctuations in populations in the wild? We use empirical data from long-term studies of the population of interest to construct a realistic population model, incorporating information on demographic parameters and their temporal variability, and then use the model to address the question of significance of a mortality event of specified magnitude.

METHODS

Study site

The data used in our population models were collected 48 km west of San Francisco on the South Farallon Islands, California, USA, part of the Farallon Islands National Wildlife Refuge (37°42' N, 123°00' W; Ainley and Boekelheide 1990; Appendix S1: Fig. S1). The local marine environment is characterized by large annual variation in productivity and within-season changes in food availability (Ainley and Boekelheide 1990, Sydeman et al. 2001). Annual food availability depends, in part, upon wind-driven seasonal upwelling and advection (Santora et al. 2017).

Field methods and relevant previous studies

A marked population of Western gulls on the South Farallon Islands has been the subject of numerous studies on life-history and the relationships between life-history and environmental variables (Spear et al. 1987, 1995, 1998, Sydeman et al. 1991, 2001, Pyle et al. 1991, 1997, Spear and Nur 1994). Specific methods for determining

Western gull fecundity and survival can be found in these references and are also summarized in Appendix S1.

Studies of this marked population have demonstrated that (1) individuals in this population are apparently monogamous (Gilbert et al. 1998), (2) once having bred, nearly all (~95%) surviving individuals attempt to breed in the following year (Spear et al. 1987, Pyle et al. 1991, this study), (3) reproductive success varies with age (Sydeman et al. 1991, Pyle et al. 1991, 1997), (4) there has been high annual variability in reproductive success (this study), and (5) the size of the breeding population has shown a decreasing trend from the mid-1980s to the mid-2000s with a slight increase since then (this study, Fig. 1).

Overview of approach

We developed a population dynamic model for the South Farallon Islands population of Western gulls using the best available information (published and unpublished) that incorporates stochasticity in the demographic parameters. We estimated demographic parameters for the population model based on analyses of the time series 1986–2011, as described below. For the model, we determined annual variation, age-specific variation, and degree of stochasticity. We estimated process variance as a subset of the total variance (Gould and Nichols 1998) with respect to three demographic parameters: survival, breeding probability, and reproductive success, following the approach outlined by Cooch and White (2019). Process variance is the variance in a demographic parameter once sampling error has been removed. The resulting estimates of annual process variance were incorporated into the stochastic demographic model (Appendix S2).

We then simulated three environmental scenarios, in which the frequency of years with high reproductive failure differed. Reproductive failure either did not re-occur in the future (optimistic); occurred at low, historic frequency (realistic); or occurred at the elevated frequency seen in more recent years (pessimistic), as detailed below. We projected future population change under these three scenarios over 20 yr. We then compared those simulation results (i.e., no additional mortality), to a set of simulations in which a one-time additional mortality event

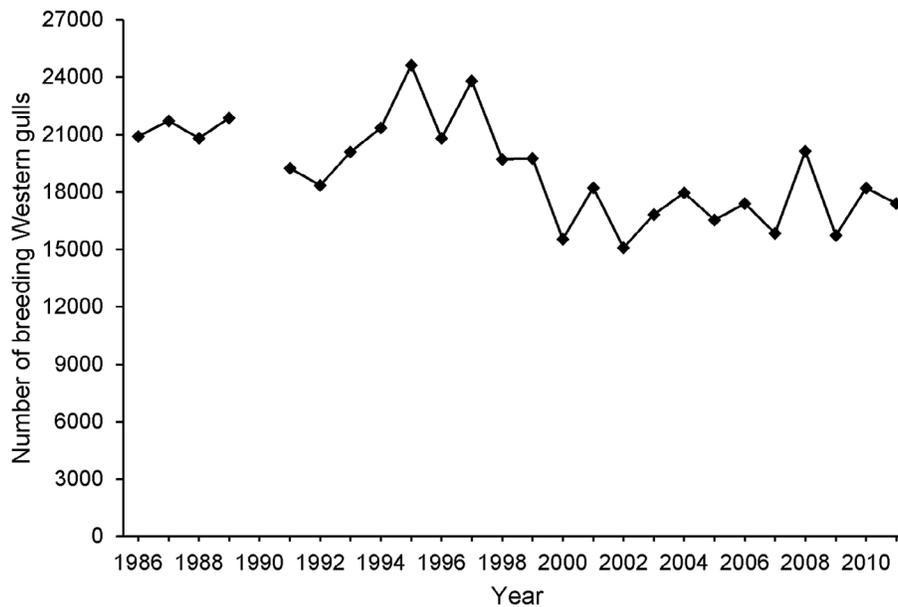


Fig. 1. Western gull breeding population variation for the South Farallon Islands, 1986–2011 (source Warzybok et al. 2014). *Note:* No census was conducted in 1990.

occurred in Year 0. We define the mortality threshold C , as the maximum level of gull mortality in year 0 for which no ecologically distinguishable impact in modeled population size can be discerned 20 yr later, when compared to no additional mortality. We define an ecologically distinguishable impact as $< 95\%$ overlap in the distributions of population size after 20 yr. That is, for each of the three scenarios (optimistic, realistic, or pessimistic), we determined the magnitude of C such that the two frequency distributions (with and without mortality of C) overlapped by 95%. To provide context, we also consider an example of a larger mortality event, one that results in only 90% overlap after 20 yr.

Population model

We conducted a Population Viability Analysis (PVA) using a Leslie matrix whose elements are allowed to fluctuate in relation to variation in future environmental conditions (Nur and Sydesman 1999a, Caswell 2001). Variation in demographic parameters with respect to both age and environmental conditions were estimated (Appendix S2). Mean and variance in survival (for all age classes), reproductive success (RS),

and probability of breeding (bp) were incorporated into the population dynamic model, as described in Appendix S2.

For projecting into the future, we used parameter estimates from the period 1999 to 2011, the most recent period for which we had estimates for all our demographic parameters, as our focal period. We note that there was a substantial, well-documented change in the oceanographic conditions in 1998/1999 (Peterson and Schwing 2003, Bestelmeyer et al. 2011) which likely had had an important influence on Western gull demography, as it did on other seabirds of the South Farallon Islands (Nur et al. 2019). Population trends differed in the two time periods, with a relatively stable trend in the more recent period (1999–2011) compared with greater fluctuation in earlier period (up to 1999). For the purposes of population projection, we chose the latter period (1999–2011) for modeling as being representative of future conditions, especially since the variance in reproductive success in recent years (2012–2019) was more similar to the latter period (0.088 vs. 0.082, respectively) than it was to the period up to and including 1998 (0.151; Point Blue, unpublished data).

Estimation of demographic parameters and calibration of model

Annual adult survival was determined through analysis of capture histories of banded gulls from 1984 to 2011 (Appendix S2). RS was defined as the average number of young reared to fledging per breeding pair per breeding season, conditional on an individual attempting to breed. Net fecundity, a component of the Leslie matrix, was defined as the product of RS \times breeding probability \times 0.5 (Nur and Sydeman 1999a). Age-specific survival, recapture, and transition to breeding state were modeled as described in Appendix S2 (see also Lee et al. 2012). Finally, we assume no net immigration or emigration, that is, that any emigration is balanced by immigration (see Appendix S2).

For survival, RS, and breeding probability, we determined age-specific variation as well as process variation with respect to annual variation in the three parameters (Table 1; Appendix S2). An important feature of our study was that we calibrated the demographic parameter values used so that the model we developed reproduced the observed population trend data during the more recent time period, 1999–2011. We assume that all age classes are considered equally at risk to any mortality associated with the proposed project, due to extensive observations of Western gulls of all age classes being present on the Farallon islands during the fall and winter. Moreover, field studies do not indicate any differences among age classes in the exploitation of supplementary food resources (Cassell 2016; Point Blue. *unpublished data*). Additional justification for demographic parameter estimates and assumptions are detailed in Appendix S2, as are details regarding model calibration.

Stochastic modeling under three environmental scenarios

Stochastic population modeling was carried out with RAMAS GIS version 5 (Akçakaya 2005). The primary outcome variable was the number of individuals in each age class of the population in each year of the simulation, as a function of environmental variability and starting population size in the year 0 of the simulation. Demographic parameter values for survival and fecundity for each time step (i.e., year), in a given simulation, are randomly chosen from a

distribution whose mean and variance were determined as described in Appendix S2 (Akçakaya 2005). Annual adult survival and fecundity were sampled independently as they displayed no significant covariance ($r = -0.261$, $n = 24$, $P > 0.2$).

A critical feature of the Farallon Western gull population, for the purposes of this modeling, was the unusually low RS observed in the last three years of the data set analyzed (2009–2011). In the period between 1986 and 2008, annual RS ranged from 0.30 to 1.55 fledged young per pair (Fig. 2). However in 2009, 2010, and 2011, between 0.06 and 0.13 fledged young were produced on average per pair. Comparing 2009–2011 to the 10 yr previous to that (1999–2008), indicated a reduction of 86% in mean RS (Fig. 2). Such recent bad years could significantly impact the population trajectory if it were to recur in the future, and thus affect population recovery following a mortality event. Therefore, to model baseline RS (i.e., without bad years), we used the mean value for the years 1999–2008, using the between-year estimate of process variance for the same period. We then examined three environmental scenarios that differ with respect to probability of bad years reoccurring. We assume that environmental conditions, broadly considered, are responsible for recurrence of bad years.

Under the optimistic scenario, bad years do not recur. Thus, conditions observed in 1999–2008 are presumed to apply in the future. In this case, fecundity was modeled based on analysis of 1999–2008 results only. In contrast, under the realistic scenario, bad years occur with a frequency of 3 yr every 26 yr (probability of 0.115 per year), which corresponds to the rate observed during the entire study period (1986–2011). Finally, the pessimistic scenario assumes bad years recur with a frequency of 3 in every 12 yr (probability of 0.25 per year) as observed during the most recent 12 yr of the relevant time series (2000–2011). Thus, the optimistic and pessimistic scenarios bookend a reasonable range of values to consider for the future. The realistic and pessimistic scenarios effectively lower mean fecundity and increase fecundity variance relative to the optimistic scenario.

Table 1. Summary of final demographic parameters for Western gull in relation to age.

Age	Reproductive success	Breeding probability	Calibrated survival	SD survival	Net fecundity	SD fecundity
1	0	0	0.610	0.041	0	0
2	0	0	0.810	0.033	0	0
3	0	0	0.875	0.028	0	0
4	0.436	0.191	0.890	0.026	0.042	0.012
5	0.436	0.524	0.890	0.026	0.114	0.033
6	0.649	0.81	0.890	0.026	0.263	0.076
7	0.882	0.953	0.890	0.026	0.420	0.122
8	0.882	0.953	0.890	0.026	0.420	0.122
9	0.882	0.953	0.890	0.026	0.420	0.122
10	0.882	0.953	0.890	0.026	0.420	0.122
11	0.882	0.953	0.890	0.026	0.420	0.122
12	0.882	0.953	0.890	0.026	0.420	0.122
13	0.882	0.953	0.890	0.026	0.420	0.122
14	0.882	0.953	0.890	0.026	0.420	0.122
15	0.882	0.953	0.890	0.026	0.420	0.122
16	0.882	0.953	0.890	0.026	0.420	0.122
17	0.718	0.953	0.890	0.026	0.342	0.099
18	0.718	0.953	0.890	0.026	0.342	0.099
19	0.718	0.953	0.890	0.026	0.342	0.099
20	0.718	0.953	0.890	0.026	0.342	0.099
21+	0.535	0.953	0.890	0.026	0.255	0.074

Notes: Mean calibrated survival and net fecundity values and the respective standard deviations (SDs) were directly input into the Population Dynamic Model Matrix. "SD" refers to estimated process variation among years used in the stochastic modeling. Fecundity estimates shown exclude "near-failure" years of 2009–2011, which were modeled separately (see text). All parameter estimates from Appendix S2; see text therein for explanation.

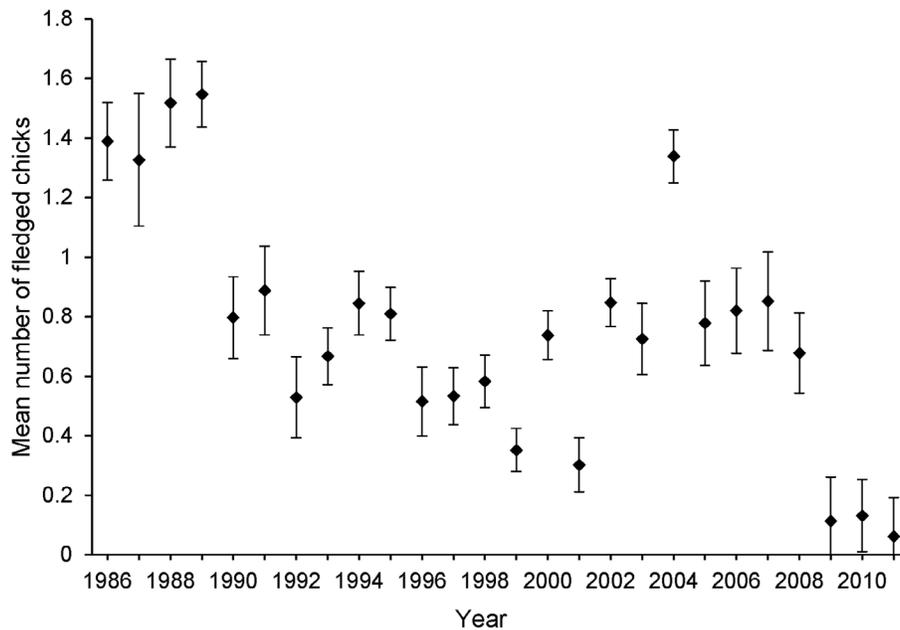


Fig. 2. Annual estimates (\pm standard deviation [SE]) for mean number of chicks fledged per female Western gull breeding in C, H, and K plots combined on the South Farallon Islands, California 1986–2011.

Starting population size, mortality scenarios, and simulations

The Leslie matrix population model was implemented using a post-breeding census (Caswell 2001, Akçakaya 2005). Hence, the youngest age class in the simulations refers to juvenile individuals who have just fledged. The simulations were of the entire population, including juveniles, sub-adults, and adults. There was no evidence that adult survival or reproductive success varied in relation to population size or density for this population (Prais-Winsten time series regression analysis of adult survival and RS in relation to current population size or previous year's population size: $P > 0.2$ for all analyses). Hence, we assumed population parameters to be density-independent (Nur and Sydeman 1999a).

The starting total population size for the simulations was 32,200 individuals, including all age classes. To obtain this value, we started with the estimate for initial breeding population size, 17,400 breeding birds, based on an all island census conducted in 2011 (Appendix S1; Warzybok et al. 2014). Though there is some uncertainty regarding estimates for any given year, the three year-moving average for 2011 was similar to the single year estimate, that is, 17,200 breeding birds. Assuming average annual breeding probability (Table 1) and the long-term stable age structure implied by the elements of the Leslie matrix (Caswell 2001), and given the 2011 estimate of 17,400 breeding individuals, we infer an additional 14,800 juveniles, sub-adults, and non-breeding adults in the population (see Appendix S2).

In scenarios with additional mortality, the starting population size in year 0 was $32,200 - m$ where m represents the number of gulls removed from the population as a result of a mortality event (e.g., rodent eradication or oil spill) immediately before the first year of the simulation. For these scenarios, we assumed that m gulls were removed in proportion to the age distribution of the total population, as there is no evidence to suggest the risk of mortality differs between age classes with regard to bait ingestion. The presence of all age classes of Western gulls on the island in fall and winter was noted above (see *Methods: Estimation of demographic parameters and calibration of model*).

To determine the value of m such that two distributions (with and without additional mortality) overlap by 95%, which we define as C , we took an iterative approach. We varied m in increments of 50 individuals and compared the distribution of final population size after 20 yr without additional mortality to distributions with mortality of m in year 0. Simulation results were in terms of the cumulative distribution function for population size at year 20, which we then converted into a probability distribution function for final population size grouped into bins of 1000 individuals. We then identified the threshold, C , as that value of m , for which the two probability distributions, with and without additional mortality, overlapped by 95%.

We carried out this exercise for each of the three environmental scenarios, optimistic, realistic, and pessimistic. All scenario summaries depict results based on 10,000 simulations, the maximum for the RAMAS program. However, to more precisely calculate the degree of overlap in distributions (so as to determine C), we combined the results of two different runs of 10,000 simulations each, thus yielding a total of 20,000 simulations to analyze. To illustrate the consequences of a mortality event of magnitude C , we display graphically the two expected distributions (with and without additional mortality).

The value of C under each scenario is such that any additional mortality exceeding C will result in ecologically distinguishable differences in the two probability distributions of population size 20 yr into the future. We also used the same approach to illustrate the consequences of a larger mortality event, such that the overlap in probability distributions is 90%.

RESULTS

Demographic summary for the period 1986–2011

There was substantial annual variation in the estimated size of the breeding population during the period 1986–2011, as calculated from breeding season censuses (Fig. 1). However, during the focal period, 1999–2011, inter-annual variability was less marked (SD reduced by 16%), and there was a slight increasing trend of $0.74 \pm 0.70\%$ (mean \pm SE) per year, based on linear regression of ln-transformed abundance.

Reproductive success (RS) displayed high variability during the period 1986–2008, but with no clear trend from 1990 to 2008 (trend not significant, $P = 0.46$, Fig. 2). RS varied approximately fourfold between the most successful year ($RS = 1.34$) and the least successful year (0.30) during the period 1990–2008. However, during the three year period 2009–2011, RS was below 0.15 chicks fledged per pair in each year.

Female adult survival was variable, but less so for the period 1999–2009 (range 0.81–0.94) than the earlier period (range 0.71–0.93; Fig. 3A). Male adult survival was also variable and, again, less so for the period 1999–2009 (range 0.85–0.93) than for the preceding period (range 0.74–0.94; Fig. 3B). Recapture probability was variable for females from 1986 to 2009, though markedly less so in the period 1999–2009 (Fig. 4A). In contrast, for males, recapture probability was relatively high throughout the time series (Fig. 4B).

Averaged over the two sexes, process variance for survival was 28.6% of the total variance; the between-year SD in survival based on the process variance was 0.026 for adults (Table 1). Process variance for fecundity was 20.4% of the total variance; the between-year SD in fecundity based on the process variance was 0.122 for prime-age adults (Table 1).

Population trends in relation to environmental variability

Each scenario incorporated variability in the three key demographic parameters (see *Methods: Stochastic modeling under three environmental scenarios*, above). The three scenarios differed only with respect to the recurrence of bad years. Under the optimistic scenario, population size showed a large spread in results due to stochasticity with respect to the three principal parameters (Fig. 5A). The median result under this scenario was a 12.4% increase after 20 yr, corresponding to a median growth rate of $\lambda = 1.006$ (90% CI 0.982–1.031). However, the first quartile (25th percentile) was a 9% decline, while the third quartile was a 38% increase (Fig. 5A). The probability of any decline at all after 20 yr was 36%.

Under the realistic scenario, the population is expected to decline by 6.6% after 20 yr assuming no additional mortality (Fig. 5B), a median growth rate of $\lambda = 0.997$ (90% CI = 0.970–1.024).

There is a 25% probability that the population will decline by 25% or more, whereas there is a 25% probability the population will increase by 16% or more. The probability of any decline at all after 20 yr is 58%.

Under the pessimistic scenario, the population is expected to decline by 26% after 20 yr (Fig. 5C), corresponding to a median growth rate of $\lambda = 0.985$ (90% CI = 0.958–1.014). There is a 25% probability that the population will decline by 41% or more, whereas there is a 25% probability that the population will not decline or if it does, the decline will be less than 6%. The probability of any decline at all after 20 yr is 80%. In other words, even with relatively high probability of near-failure, there is still a 20% probability that the population will be stable or increase.

Determination of mortality threshold, C

By simulating results with different mortality levels, we determined that, for the realistic scenario, removal of 1050 gulls (i.e., 3.3% of the population) shifts the probability distribution of outcomes, thus resulting in 95% overlap between the mortality and no additional mortality scenarios (Fig. 6A), that is, $C = 1050$. What had been the median outcome after 20 yr (30,100; a decline of 6.6%), assuming no additional mortality, is now the 55th percentile outcome 20 yr after a mortality event killing 1050 individuals. Fig. 6A illustrates the high degree of overlap between the two distributions, for $m = 0$ and $m = 1050$.

Using the same methods, we determined that C for the optimistic scenario was 900 ($m = 2.8\%$ of the population) and for the pessimistic scenario was 1350 ($m = 4.2\%$). The 95% CI for the calculations of C in each scenario was $\sim \pm 130$ individuals. Thus, C increased as the proportion of bad years, that is, stochasticity, increased in the simulations.

Although we believe that there is high value for examining the 95% overlap distribution, the approach we have used can also demonstrate overlap of distributions for other levels of mortality, m . Fig. 6B depicts the overlap in population outcomes after 20 yr under the realistic scenario, with and without a one-time mortality event, $m = 2400$. This level of mortality results in 90% overlap of the two distributions.

The large spread in terms of outcome after 5, 10, 15, and 20 yr is illustrated in Fig. 5 for all

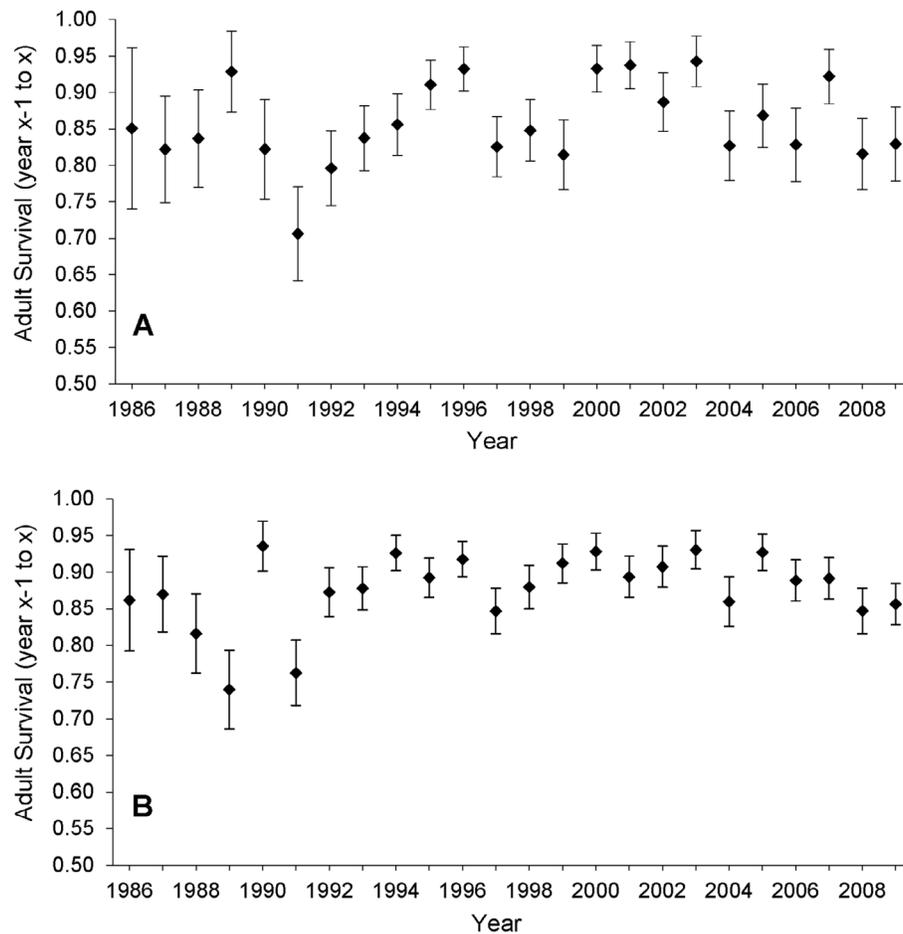


Fig. 3. Annual estimates of survival (Φ) ± 1 standard deviation (SE) for Farallon Island Western gulls from long-term study plots, 1986–2009, for females (A) and males (B), as estimated from year-specific models with program MARK (capture histories from 1984 to 2011, Appendix S2). Survival shown for year x refers to survival from year $x - 1$ to x .

three stochasticity scenarios. For example, Fig. 5B depicts results under realistic conditions, bad years occurring at the historic frequency of 3 times per 26 yr, with and without additional mortality. If the population incurs mortality of 1050 individuals in year 0, after 20 yr its median value is expected to be 28,730 gulls. This represents a decline of 10.8% compared with the pre-mortality population size of 32,200. Under the same set of assumptions, there is a 25% probability that there will be 23,030 individuals or fewer, which represents a population decline of 28.5% or greater compared with the pre-mortality population size. However, there is also a 25% probability that after 20 yr, under this scenario, the population will

have grown to 35,960 or more individuals, an 11.7% or greater increase compared with the pre-mortality level. Thus, despite a one-time mortality event that reduces the gull population by 3.3%, there is still a 25% probability that the population would have grown by 11.7% or more after 20 yr, compared with a 25% probability that the population would have grown by 16.2% or more without such a mortality event.

DISCUSSION

Stochasticity of population trajectory

Our modeling results indicate that, under no additional mortality scenarios, the Farallon

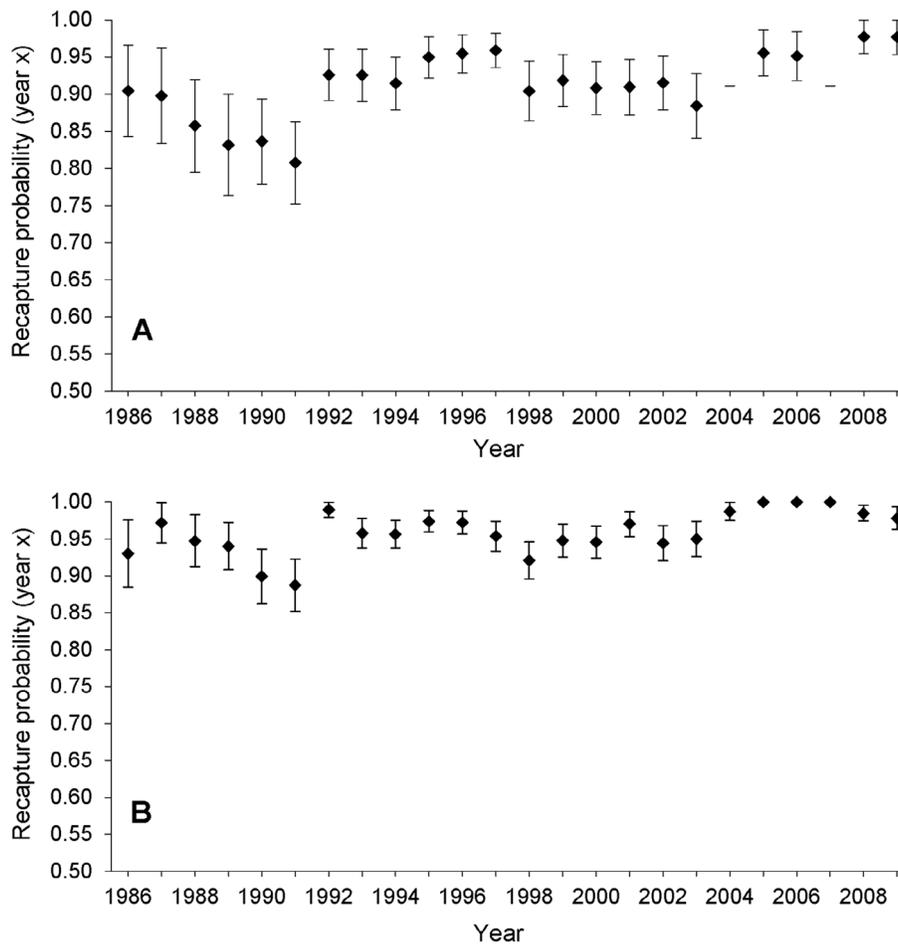


Fig. 4. Annual estimates of recapture probability (P) \pm 1 standard deviations (SE) for Farallon Island Western gulls from long-term study plots, 1986–2009, for females (A) and males (B), as estimated from year-specific models with program MARK (capture histories from 1984 to 2011, Appendix S2). Missing value for female recapture probability in 2004 and 2007 (panel A) could not be estimated in program MARK.

Western gull population has a 64% chance of increasing over the next twenty years given optimistic productivity estimates. However, the population will more than likely decline under the assumption of realistic productivity, and likely decline at a much steeper rate if the incidence of bad years were to occur with probability of 0.25 per year. It is not surprising that variation in the incidence of near-failure in breeding (from not occurring at all to occurring with probability 0.25) is reflected in the median expected outcome after 20 yr and in the median expected growth rates (ranging from 1.006 to 0.985). Furthermore, under all three scenarios, there is high variability

in outcome (Fig. 5). Thus, even without considering the effects of variation in the frequency of bad years, there is substantial uncertainty of the population's trajectory. When we add projections regarding future probability of near-failure in breeding, this adds more uncertainty to the population's ultimate trajectory.

The factors causing variation in demographic rates for this population of Western gulls are largely unknown. For other seabird species breeding on the Farallones, reproductive success, adult survival, and/or breeding probability have been shown to be related to oceanographic conditions as reflected in Sea Surface Temperature (SST) or

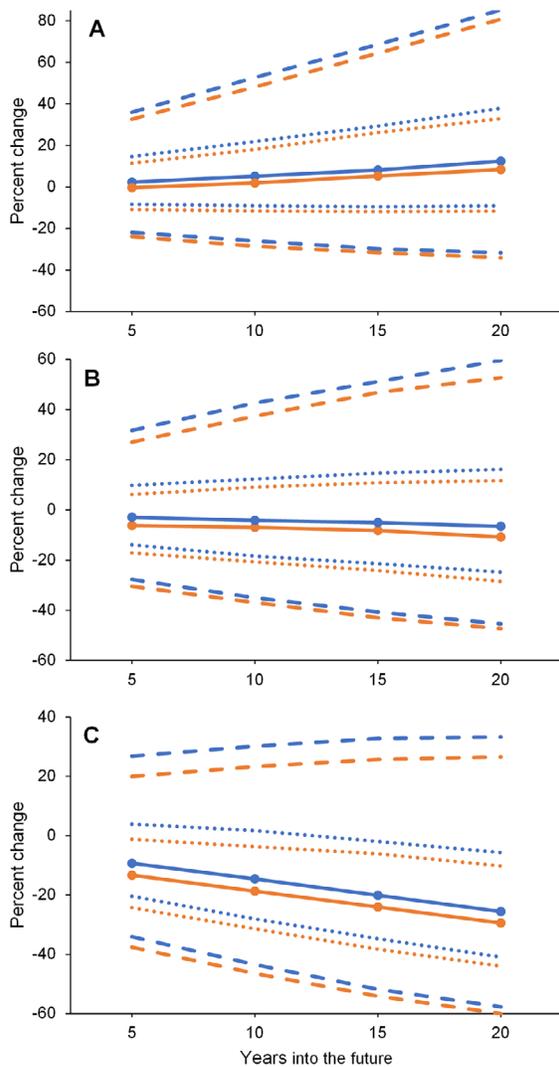


Fig. 5. Estimated percent change in the Farallon Island Western gull population over 20 yr, with (orange) and without (blue) additional mortality of *C*. Results assume (A) optimistic conditions (no re-occurrence of bad years), (B) realistic environmental scenario (re-occurrence of near-failure years with probability, $P = 0.115$), or (C) pessimistic conditions (re-occurrence of near-failure years with $P = 0.25$). Solid lines with filled circles are the median predicted values. Dotted lines below and above the median values represent the 25th and 75th percentile of predictions, respectively. Dashed lines below and above the median values represent the 5th and 95th percentile of predictions, respectively. Note results are from independent sets of 10,000 simulations for each 5-yr time period.

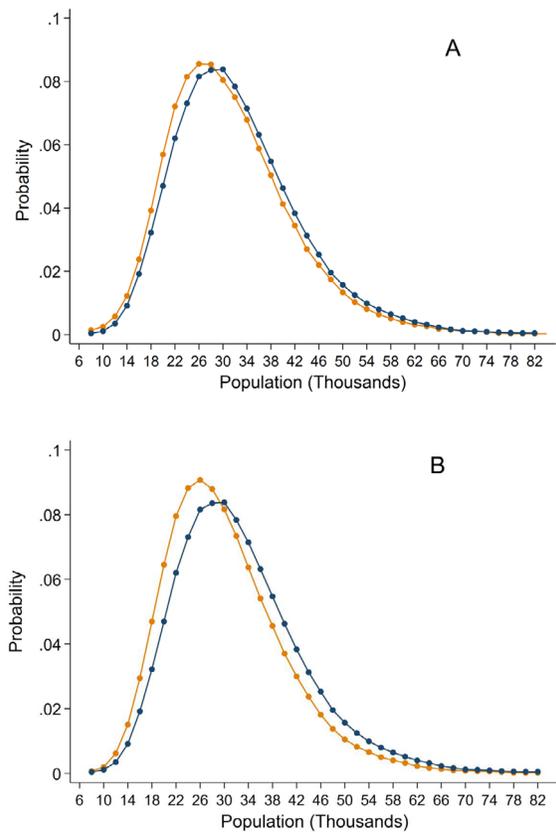


Fig. 6. (A) Probability distribution with respect to total population size, in thousands, for additional mortality of 1050 gulls (orange) and no additional mortality (blue) scenarios, after 20 yr, under realistic environmental scenario. Results of 20,000 simulations for each scenario, with or without mortality, *C*. Initial population size, with no mortality, is 32,200 individuals. Results binned into bins of 2000; results shown display 3-value running mean. The two probability density functions overlap by 95% (see text). (B) As in (A) but depicting additional mortality of 2400 gulls (orange) compared with no mortality scenario (blue). The two probability density functions overlap by 90%.

the Southern Oscillation Index (SOI; Nur and Sydeman 1999b, Lee et al. 2007, Schmidt et al. 2015). However, no indices of oceanographic condition have yet been shown to correlate with reproductive success, breeding probability, or adult survival for this species.

Reproductive success varied among years, and among decades (Fig. 2). While, near-failure in RS

was observed for 2009, 2010, and 2011, the years since then have shown a return to that observed prior to 2009. In 2012–2019, the mean and between-year SD of RS was 0.850 and 0.277, respectively, similar to that observed in 1999–2008, 0.743 and 0.286, respectively (Johns and Warzybok 2019). Thus, the three years, 2009–2011, were indeed anomalous and their re-occurrence in the future is difficult to predict.

The near-failure of breeding during the 2009–2011 seasons was likely due to multiple compounding factors, previously found to influence this population's reproductive success, including food depletion, intraspecific predation, and weather (Sydeman et al. 1991). Notably, intraspecific predation on gull chicks varies among years and can occur at high rates (Warzybok et al. 2014). Predation rates may in turn reflect success at feeding chicks whereby adults that are unable to locate food may increase their predation on other chicks. High rates of failed breeding may also facilitate intraspecific predation and thus lower reproductive success even further. Such predation appears to have occurred regularly in the 2000s and was observed extensively in the three years of near-failure described here (Warzybok et al. 2014).

Long-term mortality impacts and the mortality threshold, C

Given our estimates of the total Farallon population of 32,200 birds in 2011, we determined that the mortality threshold, C , was 1050 gulls, that is, 3.3% of the total, under the realistic scenario. We acknowledge uncertainty in estimating the total population of Western gulls on the Farallones, and thus in estimating C in absolute terms, but the relative level of mortality represented by C , 3.3%, was robust to assumptions of the starting population size. That is, under the Realistic scenario, a one-time mortality event would need to exceed 3.3% to be detectable after 20 yr, within a reasonable range of starting population sizes. These results are independent of any assessment of actual risk to this Western gull population from rodenticide exposure in a proposed eradication effort; rather, results obtained apply to any mortality event of relatively short duration. We emphasize that 1050 represents a threshold of detection, not an estimate of anticipated mortality resulting from mouse eradication.

This value reflects the substantial stochasticity associated with the three demographic parameters, especially for reproductive success. Furthermore, we found that C varied with environmental scenario; C was 900 (2.8%) under the optimistic scenario and was 1350 (4.2%) under the pessimistic scenario. While it might seem counterintuitive that a lower level of mortality is sufficient to result in a detectable shift in the distribution of outcomes under optimistic conditions, compared with the realistic and pessimistic scenarios, these results are consistent with our finding that the CV of population outcome was greatest for the pessimistic scenario (0.41) and lowest for the optimistic scenario (0.36). In other words, the greater the variability in population outcome, the greater C must be to result in a long-term effect of the mortality event that can be discriminated against the backdrop of environmental variability.

We do not claim that a one-time mortality event of 1050 gulls is not significant, as this value is substantially more than, for example, the observed Glaucous-winged gull (*Larus glaucescens*) mortality observed post eradication on Rat Island, Alaska (Paul and Salmon 2010). We support all efforts to minimize non-target mortality with regard to any proposed management action. Moreover, the current plan for mouse eradication details steps to be taken to ensure that non-target mortality of Western gulls is much less than the levels identified in this exercise, such as hazing of gulls (USFWS 2019). Nevertheless, our results indicate that environmental variability due to normal variation in demographic parameters as well as the incidence of near-failures of reproductive success will, after 20 yr, swamp the effects of a mortality event of magnitude 3.3% or less of the gull population.

To arrive at our estimates, we drew on an extensive time series of demographic data, from 1986 to 2011, which enabled us to capture both typical variation among years as well as markedly anomalous years such as 2009–2011. Predicting the future mean and variance of demographic parameters is inherently uncertain, but the range of years analyzed provides a robust basis for examining the impact of stochastic variation on population trajectory. Adding additional years of data to the time series analyzed may well lead to modifications of the

precise estimates of C , but not, we maintain, of our overall conclusions.

Extending the modeling approach

In this case study, we based our projections on estimates from the time period 1999–2009, when the population trend was relatively stable, but other applications of this approach may need to consider, instead, declining or growing populations. The approach outlined here can incorporate anticipated trends over time, and doing so would affect the estimate of C . While analyses to date do not provide evidence of density dependence in this population, consideration of density dependence may be applicable in other situations.

The modeling approach can be extended to consider age-specificity or sex-specificity of mortality. However, in this case study, field observations and the timing of the proposed management action did not provide a basis for considering age-specificity or sex-specificity of mortality. Attendance of non-breeding Farallon gulls of all sex and age classes has been noted during this time of year (USFWS 2019). This is not generally the case with regard to mortality events, whether due to accidental spills (Rice et al. 1996, Golet et al. 2002) or due to activities such as hunting (Wielgus et al. 2001, Fa and Brown 2009). For example, the *Prestige* oil spill resulted in sex-specific mortality of European shags (*Phalacrocorax aristotelis*), which Martínez-Abraín et al. (2006) argue resulted in greater reduction of the population in subsequent years than would have been the case with mortality affecting the two sexes equally. Milner et al. (2007), too, caution against ignoring sex-specificity of population impacts when modeling the impacts of mortality sources.

Mortality due to oil spills, hunting, or other sources can adversely affect components of reproductive success, such as numbers of animals alive to breed, mating success, or survival of offspring, over the long-term (Walton et al. 1997, Wielgus et al. 2001, Milner et al. 2007, Fa and Brown 2009). The modeling approach we have taken can be utilized to incorporate these long-term fecundity effects with readily available software packages. Thus, even without specific information on long-term fecundity effects, one can evaluate the potential role they may play.

The approach we outline here can be used to evaluate additional levels of mortality. While here we focused on identifying the magnitude of mortality, C , that produces a 95% overlap in distributions after 20 yr, we also illustrate application of this approach to evaluate a mortality event which yields an overlap of 90% between distributions. The flexibility in the modeling approach allows resource managers to consider specific characteristics of impacted species and choose the level of overlap among distributions that is used in the impact assessment.

Stochastic assessment of a one-time mortality event

The most important implication of this study is that, given that dynamics of wild populations are strongly stochastic (Boyce 1977, Burgman et al. 1993, Higgins et al. 1997), a stochastic approach to mortality assessment is required. In contrast, Heubeck et al. (2003), when recommending an approach for what they term Oil Spill Impact Assessment, only consider a retrospective assessment of changes in population over the short term, without explicitly considering that other environmental factors may confound attempts to quantify the impact of an oil spill. We argue that a more comprehensive modeling approach be used (Schaub and Abadi 2010). Opportunities to apply such a framework in the future include evaluating impacts of tiger poaching (Kenney et al. 1995), and that of oil spills and other mortality events on seabirds and mammals (Harris et al. 1998, Monson et al. 2000, Coulson et al. 2001, Peterson et al. 2003).

The framework for which we are advocating has been used to assess fish stocks (review in Maunder and Punt 2013); in addition, there are examples of applications to birds and mammals (Breen et al. 2003, Lebreton 2005, Francis and Sagar 2012). However, such previous studies have examined effects of chronic sources of mortality (such as bycatch), whereas here we apply a stochastic framework to evaluating long-term impacts of a single event and propose a metric for assessment: divergence of two probabilistic distributions by at least 5%.

The assessment of long-term mortality can be both prospective and retrospective. In our case, we chose 20 yr as the appropriate timeline and this choice, related to the longevity of our study

species, will influence the specific level of C . For shorter-lived species, a shorter timeframe, for example, 10 yr might be chosen.

CONCLUSION

The long-term intensive study of Western gulls on the South Farallon Islands reveals strong stochasticity of demographic parameters, with future reproductive success especially unpredictable, resulting in uncertainty in future population trajectories. Such stochasticity applies to all wildlife populations and thus must be adequately incorporated into impact and risk assessment studies. While a stochastic framework has been used to evaluate mortality impacts for chronic mortality sources, it has not previously been applied to an acute, one-time event. To provide a quantitative basis for such an assessment, we have identified a threshold of mortality, C : mortality at this level or below is not expected to result in an ecologically distinguishable impact 20 yr after the event. Thus, environmental stochasticity can be expected to swamp the effects of a mortality event unless the loss exceeds 3.3% of the gull population, assuming the probability of near-failure of breeding to re-occur at historic frequency.

We emphasize that it is not the value of C that is most important to focus on, but rather the approach that we illustrate, recognizing that unpredictability of population trajectory must be embraced in evaluating mortality events. Our results demonstrate the challenges of assessing the long-term impact of an acute mortality event given the stochastic nature of environmental conditions and associated demographic parameters. The stochastic framework we present will assist managers in identifying best-case scenarios as well as worst-case scenarios, and providing probabilistic assessments of the range of outcomes. The strength of this approach is that one can not only factor in variation in demographic parameters, but also incorporate and assess the efficacy of management actions that are intended to address or compensate for the mortality source.

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CONFLICT OF INTEREST.

None.

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