Projecting Long-term Impacts of Mortality Events 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 on the Farallon Islands National Wildlife Refuge.

Firstly, we conducted a population viability analysis based on over 20 years 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 especially low

reproductive success, as was observed from 2009 to 2011. We modeled population trends under

three environmental scenarios defined by the probability of future breeding failure: "Optimistic"

(probability of failure, p = 0.0), "Realistic" (p = 0.115), or "Pessimistic" (p = 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 the "no additional mortality"

scenario after 20 years (defined as 95% overlap in frequency distributions). We determined that

threshold, *C*, 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 stochastic variation in population outcome, the

greater *C* must be to be able to discriminate a long-term effect of the mortality event against the

backdrop of environmental variability. *C* is not the actual estimate of anticipated mortality but

provides a threshold of detectability to evaluate prospective or retrospective mortality events.

The approach presented here can have broad applicability when evaluating the population level

effects of mortality events. We demonstrate that consideration of stochasticity is critical for

population projections given the high degree of variability characterizing many ecosystems;

deterministic projections alone may provide poor guidance. Finally, we suggest that managers

need to plan for both "best case" and "worst case" scenarios when evaluating impacts of

mortality events.

KEYWORDS: Impact Assessment; Mortality; Population Recovery; Population Viability

Analysis; Stochastic Modeling; Western gull.

1. 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, Martinez-Abrain 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). Even with accurate event-related mortality assessments, other processes

such as compensatory mortality and/or density-dependence make it difficult to translate

individual mortality events into long-term population impacts (Gascoigne et al. 2008). For

example, under compensatory mortality, net survival and/or reproduction for the population may

actually increase, relative to baseline rates, after a mortality event as a result of density-dependent processes (Gascoigne et al. 2008), which may, in turn, compensate for the direct mortality due to the event.

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) of the Western gull (*Larus occidentalis*) population on the Farallon Islands, California (Nur and Sydeman 1999a), contrasting scenarios with and without additional mortality due to a proposed 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 & 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, less than 0.15 chicks fledged per pair in each of the three years (Warzybok et al. 2014). In the 23 years preceding, 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, oil spill, etc. The demographic modeling presented here relies on detailed observations and statistical analysis of the Farallon breeding population, covering the period 1986 to 2011 (Spear & 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 be applied in a retrospective analysis as well.

While stochastic population models have been used to address long-term impacts due to chronic sources of mortality in fish (see review by Maunder and Punt 2013), birds (e.g., Francis and Sagar 2012, Cook and Robinson 2017), and marine mammals (e.g., Brandon and Punt 2013), this approach has not, to our knowledge, been used to address the potential long-term impact of an acute mortality event, as we do here.

We specifically address the question: At what magnitude of a mortality event, can the signal still be discerned after 20 years, against the backdrop of stochastic population fluctuations? 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.

2. METHODS

2.1. Study Site

The data used in our population models were collected 48 km west of San Francisco on Southeast Farallon Island, CA, USA, part of the Farallon Islands National Wildlife Refuge (37˚42' N, 123˚00' W) (Ainley and Boekelheide 1990; Appendix A, Figure A1). 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).

2.2. Field Methods and Relevant Previous Studies

A marked population of Western gulls on Southeast Farallon Island has been the subject of numerous studies on life-history and the relationships between life-history and environmental variables (Spear et al. 1987, Sydeman et al. 1991, Pyle et al. 1991, Spear and Nur 1994, Spear et al. 1995, Pyle et al. 1997, Spear et al. 1998, Sydeman et al. 2001). Specific methods for determining Western gull fecundity and survival can be found in these references, also summarized in Appendix A.

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 (c. 95%) surviving individuals attempt to breed in the following year (Spear et al. 1987, Pyle et al. 1991, this study), (3) reproductive success and survival vary with age early in life (Sydeman et al. 1991, Pyle et al. 1991, Pyle et al. 1997), (4) there has been high annual variability in reproductive success, but no overall trend since 1990 (this study), and (5) the size of the breeding population has shown a decreasing trend from the mid-1980s to the mid-2000's with a slight increase since then (Ainley et al. 1994; Figure 1).
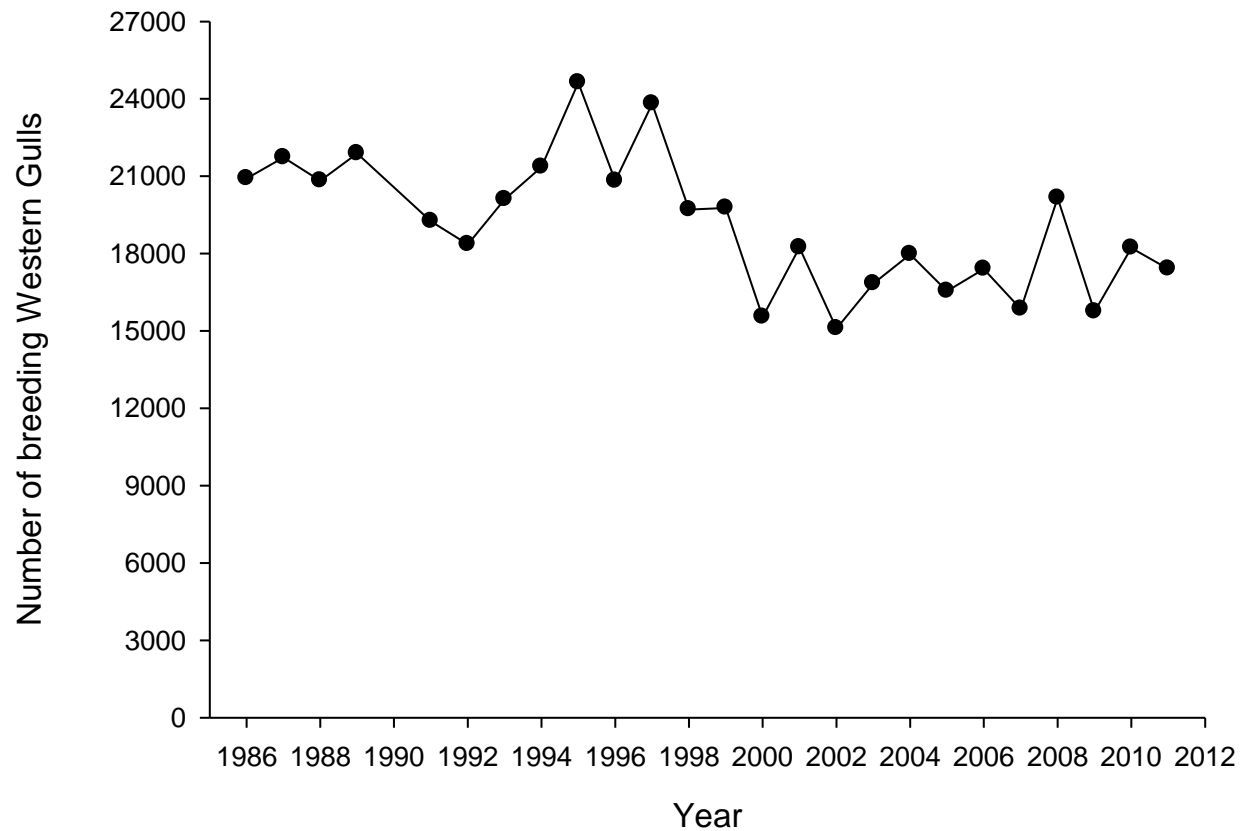
Figure 1. Western gull breeding population variation for the South Farallon Islands, 1986–2011 (source Warzybok et al. 2014). Note, no census was conducted in 1990.

2.3. 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 & Nichols 1998) for each of

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 variance were incorporated into the stochastic demographic model (Appendix B).

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 years. We then compared those

simulation results (i.e., no additional mortality), to a comparable set of simulations in which a

one-time additional mortality event 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 modelled population size can be discerned 20 years later, when compared to no additional

mortality. We define an ecologically distinguishable impact as <95% overlap in the distributions

of population size after 20 years. 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%.

2.4. 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 & Sydeman

1999a, Caswell 2001). Variation in demographic parameters with respect to both age and

environmental conditions were estimated (Appendix B). Mean and variance in survival (for all

age-classes), reproductive success (RS), and probability of breeding were incorporated into the

population dynamic model, as described in Appendix B.

Estimates of annual variation (specifically process variation) were based on the most recent

period available to us, 1999 to 2011. We consider the relatively recent time period to be most

relevant for this exercise as demographic data from the earlier period, 1986 to 1998, showed

higher abundance, lower recapture probability and survival rates, and higher RS (this study). In

addition, there was a substantial change in the oceanographic conditions after 1998 (Peterson and

Schwing 2003, Bestelmeyer et al. 2011) which may have had an important influence on Western

gull demography. Therefore, we believe that the relatively recent period will likely be more

representative of expected conditions over the next 20 years than the period before 1999.

2.5. Estimation of Demographic Parameters and Calibration of Model

Annual adult survival was determined through capture/recapture analysis of banded gulls from

1986-2011 (Appendix B). 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 & Sydeman 1999a). Age-specific survival, recapture, and transition to

breeding state were modeled as described in Appendix B (see Lee et al. 2012). Finally, we

assume no net immigration or emigration, i.e., that any emigration is balanced by immigration

(see Appendix B).

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 and Appendix

B). 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 to 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 utilizing supplementary food resources during recent field studies (Cassell 2016,

Point Blue unpublished data). Full justification for demographic parameter estimates and

assumptions are detailed in Appendix B, as are details regarding model calibration.

2.6. 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 B (Akçakaya 2005).

Annual adult survival and fecundity were sampled independently as they displayed no significant

covariance ($P > 0.2$).

   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 to

2011). In the period between 1986 and 2008, annual RS ranged from 0.30 to 1.55 fledged young

per pair (Figure 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 years previous to that (1999

to 2008), indicated a reduction of 86% in mean RS (Figure 2). Such recent "bad years" could

significantly impact the population trajectory if it were to recur in the future, and thus affect
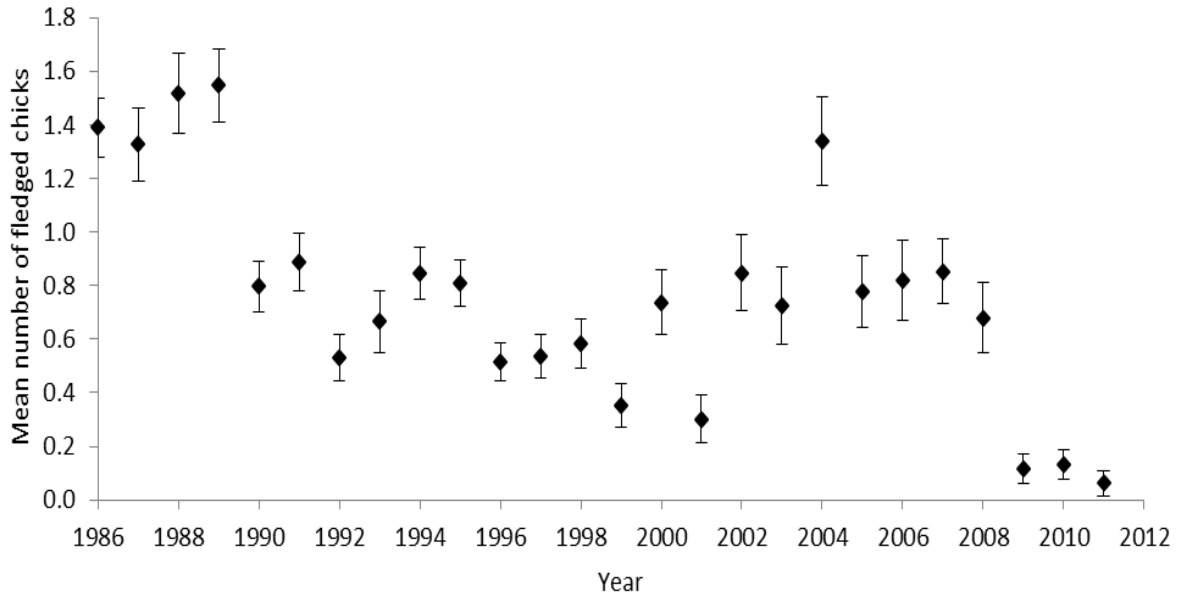
Figure 2. Annual estimates (± SE) for mean number of chicks fledged per female Western

gull breeding in C, H, and K plots combined on Southeast Farallon Island, California 1986–

2011.

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 to 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

to 2008 are presumed to apply in the future. In this case, fecundity was modeled based on

analysis of 1999 to 2008 results only. In contrast, under the "Realistic Scenario," bad years

occur with a frequency of 3 years every 26 years (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 years

(probability of 0.25 per year) as observed during the most recent 12 years 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.

2.7. 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. Statistical analyses provided no evidence that survival or reproductive rates vary in relation to population size or density for this population (Point Blue unpublished); therefore, we assumed population parameters to be density-independent (Nur & 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 (Warzybok et al. 2014). Assuming average breeding probability (Appendix B) and the long-term stable age structure implied by the elements of the Leslie matrix (Caswell 2001), and given 17,400 breeding individuals, we infer an additional 14,800 juveniles, sub-adults, and non-breeding adults in the population.

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.

To determine the value of *m* such that two distributions (with and without additional

mortality) overlap by 95%, which we define as *C*, we first identified the median of the no

mortality distribution, m_{no}. We then analyzed the distribution of outcomes under the same

conditions except that *m* gulls were removed at the outset. We took an iterative approach,

varying *m* in increments of 50 birds and identifying the value at which, with *m* gulls removed,

the distribution of outcomes had been shifted by 5% (i.e., 55% of outcomes were now below the

original median) when compared with the "no mortality" scenario. A displacement in the

distribution by 5%, specifically from 50% below m_{no} with no mortality to 55% of outcomes

below m_{no} with mortality of *m*, is equivalent to an overlap of 95% between two distributions,

assuming the two distributions differ only in their location and have the same shape and spread

(which we confirmed). The value of *m* which produced a displacement of 5% in the distribution

of outcomes defined the threshold value, *C*.

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, giving us a total of 20,000 simulations to analyze.

Simulation results were in terms of the cumulative distribution function for population size,

which we then converted into a probability distribution function.

In summary, we report the value of C such that any mortality exceeding C will result in ecologically distinguishable differences in two probability distributions of Western gull population size 20 years into the future.


3. RESULTS

3.1. Demographic Summary for the Period 1986-2011

There was substantial annual variation in the estimated size of the breeding population calculated from peak incubation censuses during the period 1986-2011 (Figure 1). However, during the focal period, 1999 to 2011, variability was reduced, and there was a slight increasing trend of 0.74% (SE = 0.70%) per year, based on linear regression of ln-transformed abundance.

RS displayed high variability during the period 1986 to 2008, but with no clear trend from 1990 to 2008 (trend not significant, P = 0.46, Figure 2). RS varied approximately four-fold between the most successful year (equal to 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.

Recapture probability was variable for females from 1986-2009, though less so in the period 1999-2009 (Figure 3a); recapture probability was consistently high for males (Figure 3c). Female adult survival was variable, but less so for the period 1999-2009, varying from 0.82 to 0.94 during the latter period (Figure 3b). Male adult survival was also variable (Figure 3d), but, again, less so for 1999-2009, varying from 0.85 to 0.93, during the latter period.

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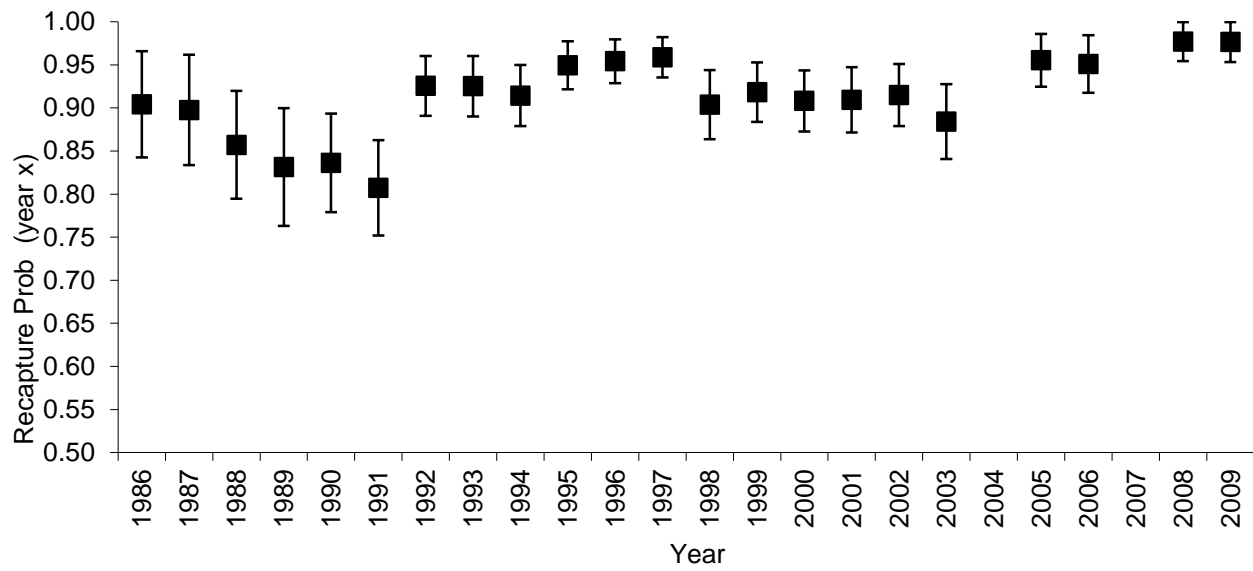
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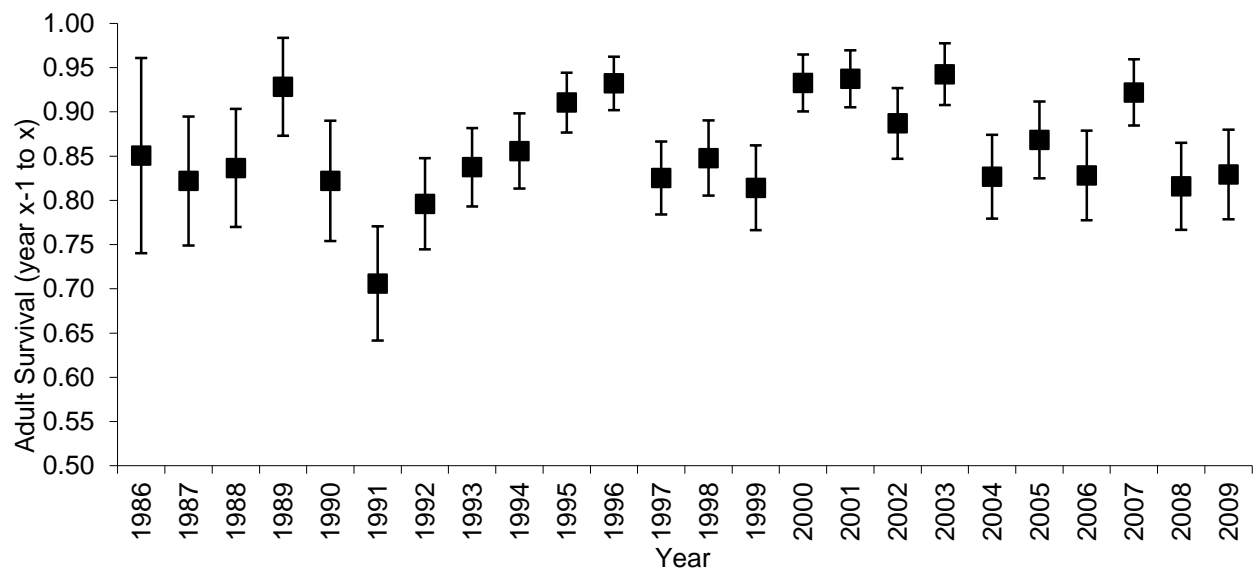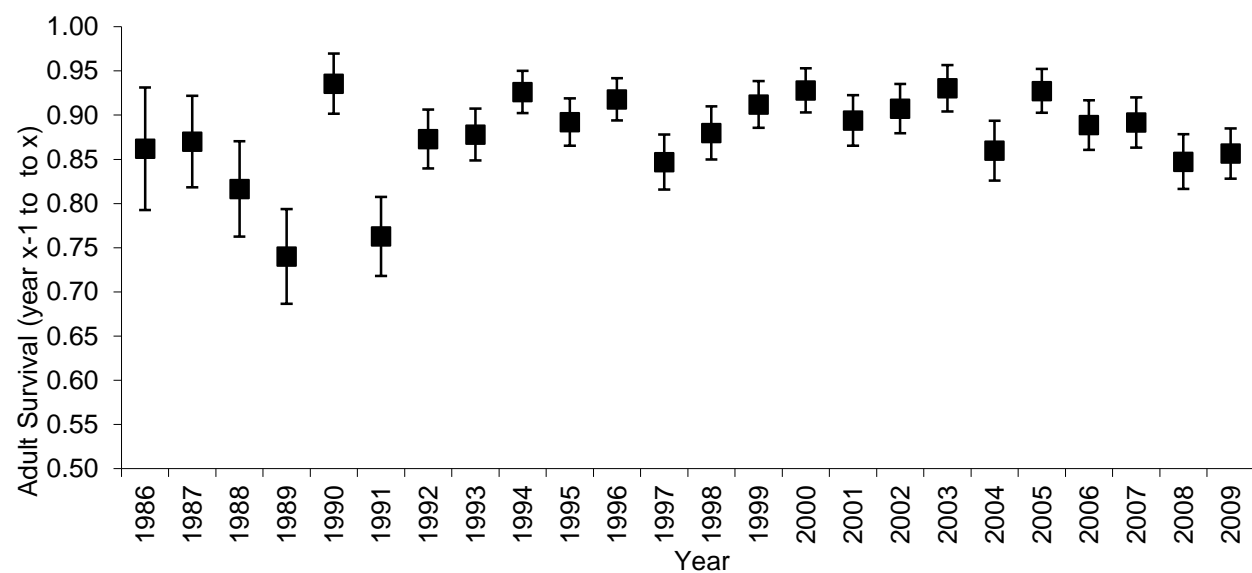
C)
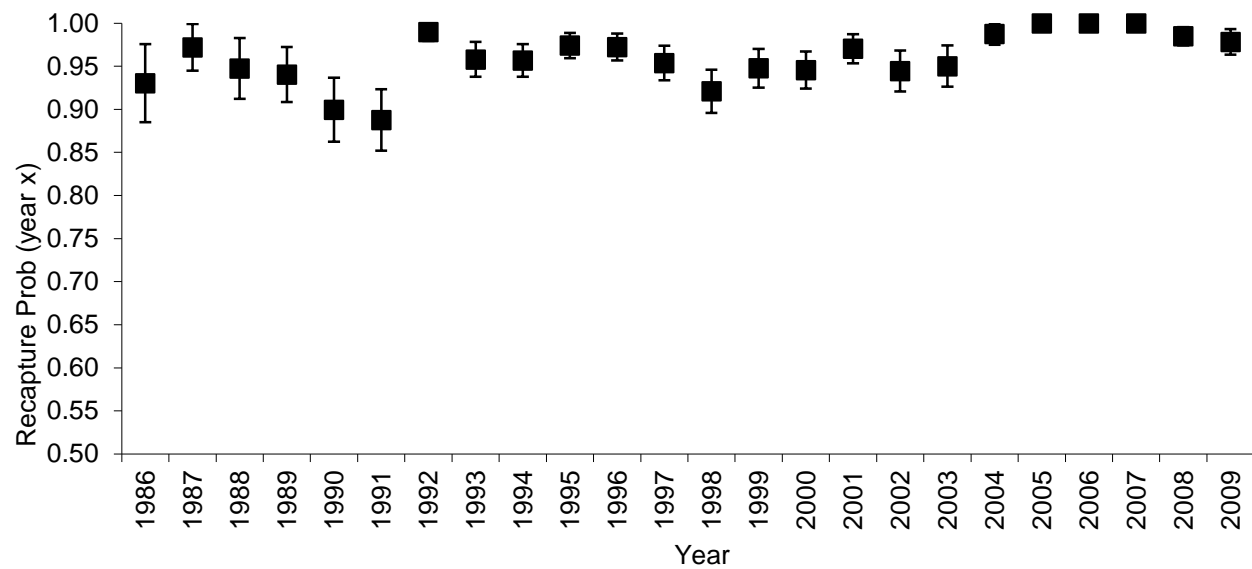
D)

Figure 3. Annual variation in recapture probability (panels a and c) and survival (panels b

and d) (± 1 SE) for Farallon Island Western gulls from long-term study plots, 1986 to 2009,

for females (panels a and b) and males (c and d), as estimated from year-specific models

with program MARK (Appendix B). Survival shown for year x refers to survival from year

x to x+1. Missing value for female recapture probability in 2004 could not be estimated in

program MARK.

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; the between-year SD in fecundity based

on the process variance was 0.122 for prime-age adults.

3.2. Population trends in relation to environmental variability

Each scenario incorporated variability in the three key demographic parameters, based on data

from the 1999-2011 period (survival, recapture probability) or the 1999-2008 period (RS; Table

1). 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 (Figure 4a). The median result under this scenario was

a 12.4% increase after 20 years; however, the first quartile (25th percentile) was a 9% decline,

while the third quartile was a 38% increase (Figure 4a). The probability of any decline at all after

20 years was 36%.

Under the "Realistic" Scenario, the population is expected to decline by 6.6% after 20 years

(Figure 4b), assuming no additional mortality (shown in gray). 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 years is 58%.

Under the "Pessimistic" Scenario, the population is expected to decline by 26% after 20

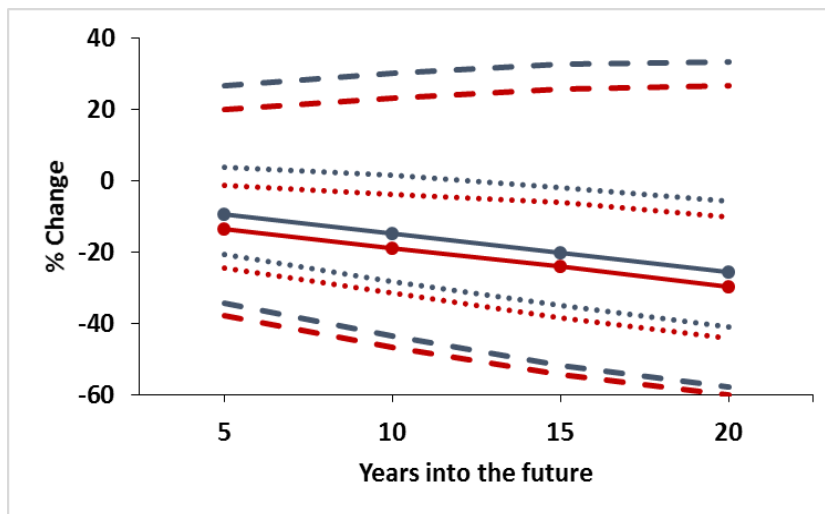years (Figure 4c). There is a 25% probability that the population will decline by 41% or more,

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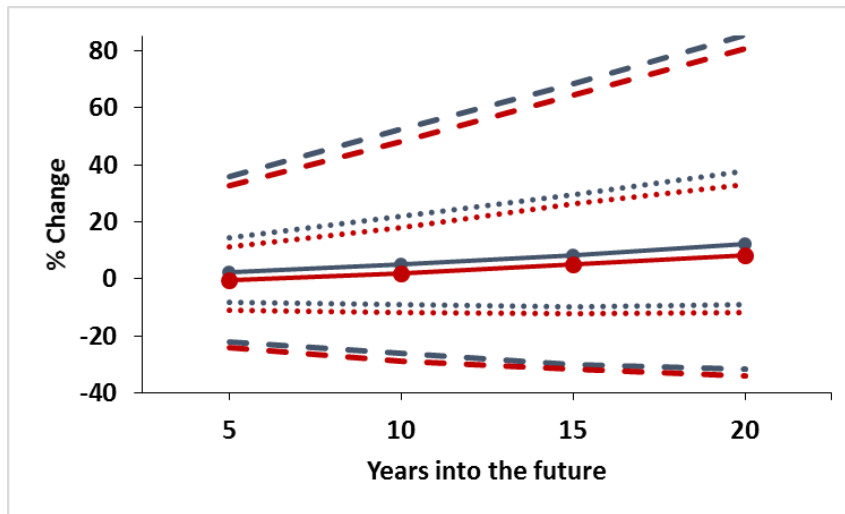
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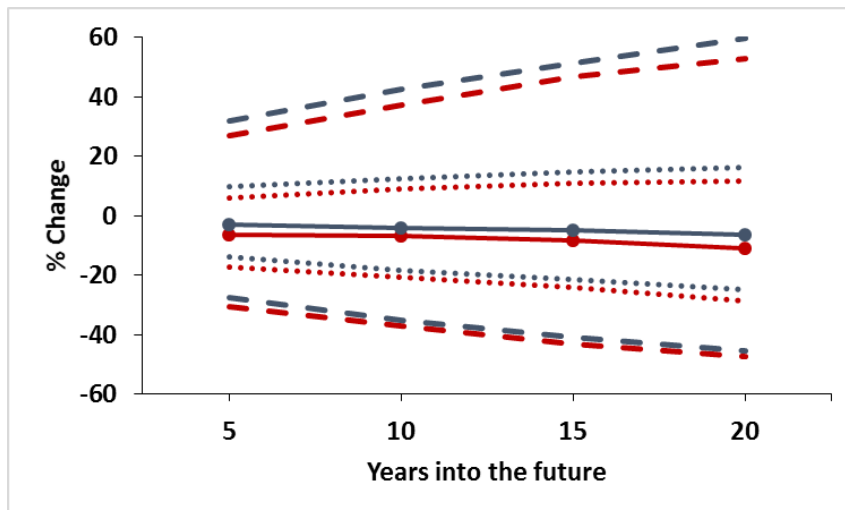
C)

Figure 4. Estimated percent change in the Farallon Island Western gull population over 20 years, with (red) and without (black) 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 at historic frequency of, on average, 3 times per 26 years), or C) "Pessimistic" conditions: re-occurrence of near-failure years at recent frequency (on average, 3 times per 12 years). Solid lines with circles are the median predicted values. Dotted lines represent the 25th and 75th percentile of predictions. Dashed lines represent the 25th and 75th percentile of predictions. Note results are from independent sets of 10,000 simulations for each 5-year time period. Assumes a starting population in year 0 of 32,200 individuals in the absence of any additional mortality.

whereas there is a 25% probability that the decline will be less than 6% (i.e., population will increase, stay the same, or if there is any decline it will be less than 6%). The probability of any decline after 20 years 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.

3.3. 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) results in a shifting of the

probability distribution of population size after 20 years by 5% and thus represents 95% overlap

between the "mortality" and "no additional mortality" scenarios (Figure 5). What had been the

50th percentile under "No additional mortality" (6.6% decline) becomes the 55th percentile under

assumption of "Mortality of 1050 gulls" at year 0 of the simulation. Using the same methods,

we determined that *C* for the "Optimistic" Scenario was 900 (2.8% of the population), and for

the "Pessimistic" Scenario was 1350 (4.2%). The 95% CI for the calculations of *C* in each

scenario was approximately ± 130 individuals. Thus, *C* increased as the proportion of "bad"

years increased in the simulations.

   Figure 4b depicts results under "Realistic" conditions, bad years occurring at the historic

frequency of 3 times per 26 years, with and without additional mortality. If the population incurs

mortality of *C* in year 0, after 20 years its median value is expected to be 28,730 gulls. This

represents a decline of 10.8% compared to 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 to the pre-mortality

population size. However, there is also a 25% probability that after 20 years, under this scenario,

the population will have grown to 35,960 or more individuals, an 11.7% or greater increase

compared to the pre-mortality level. Thus, despite a one-time mortality event that kills 3.3% of

the gull population, there is still a 25% probability that the population would have grown by
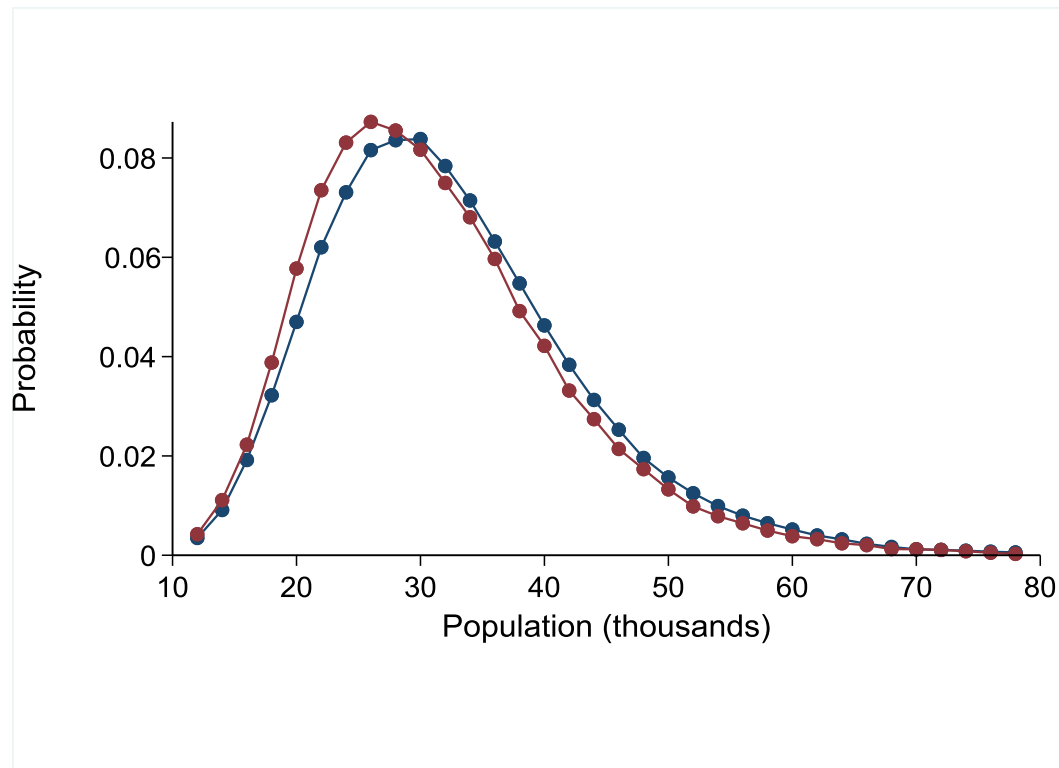
Figure 5. Probability distribution with respect to total population size, in thousands, for "no additional mortality" (blue) and "additional mortality of 1050 gulls" (red) scenarios, after 20 years, under "Realistic" Environmental Scenario. Results of 30,000 simulations for each scenario, with or without mortality, C. Initial population size, with no mortality, is 32,200 individuals. Results binned into bins of 2,000; results shown display 3-value running mean. The two probability density functions overlap by approximately 95% (see text).

11.6% after 20 years, compared to a 25% probability that the population would have grown by 16.2% or more without such a mortality event.

4. DISCUSSION

4.1. Stochasticity of population trajectory

Our modeling results indicate that, under "no additional mortality" scenarios, the Farallon 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 with 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 years. Furthermore, under all three scenarios, there is high variability in outcome (Figure 4). 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 the Southern Oscillation Index (SOI) (Nur & Sydeman 1999b, Lee et al. 2007). However, an analysis of reproductive success, breeding probability, and adult survival for the Western gull population for the full period analyzed here, 1986 to 2011, revealed no significant correlation with any of six principal indicators of marine condition: SST, SOI, Sea Surface Salinity, Pacific Decadal Oscillation, Northern Pacific Gyre Oscillation, or upwelling index (N. Nur, et al. unpublished; see Nur et al. 2011 for data sources).

Reproductive success varied among years, and among decades (Figure 3). 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 2012-2018, the mean and between-year SD of RS was 0.84 and

0.30, respectively, similar to that observed in 1990-2008, 0.74 and 0.29, respectively (Johns and

Warzybok 2018). Thus, the three years, 2009 to 2011, were indeed anomalous and their

reoccurrence in the future is difficult to predict.

   The near-failure of breeding during the 2009 to 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 2000's and was observed extensively in the

three years of near-failure described here (Warzybok et al. 2014).

4.2. 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, i.e. 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. 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. We also 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 shift the outcome distribution by 5% under "Optimistic" conditions, compared to 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 the observed Glaucous-wing gull 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 years, swamp the effects of a mortality event such as loss of 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 broad 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 lead to modifications of the precise estimates of C, but not of our overall findings and conclusions. We note in this regard that both reproductive success and abundance estimates for this population in 2012-2018 were consistent with what was observed in 1986-2011.

In our modeling we did not consider age-specificity or sex-specificity of mortality. In our case, field observations and the timing of the proposed management action, in late fall and early winter, well outside the breeding season, supported this approach. Attendance of non-breeding Farallon gulls of all sex and age classes has been noted during this time period (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 (Weilgus et al. 2001, Fa and Brown 2009). For example, the *Prestige* oil spill resulted in sex-specific mortality of European shags (*Phalacrocorax aristotelis*), which Martinez-Abrain 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, cautions 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, Weilgus 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 most important implication of this study is that, given that population 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 & 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, Peterson et al. 2003, Coulson et al. 2001).

The framework for which we are advocating has been used to assess fish stocks (review in Maunder & Punt 2013); in addition, there are examples of applications to birds and mammals (Breen et al. 2003, Lebreton 2005, Francis & 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 probabilistic distributions by more than 5%.

The assessment of long-term mortality can be both prospective and retrospective. In our case we chose 20 years 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, e.g., 10 years might be chosen.

4.3. Conclusion

The long-term intensive study of Western gulls on Southeast Farallon Island 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 years 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, and the recognition 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.

5. ACKNOWLEDGMENTS

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

Calibrated Survival and Net Fecundity values and the respective Standard Deviations (SDs) were

used in the Population Dynamic Model Matrix. "Standard Deviation" refers to estimated process

variation among years used in the stochastic modeling. Fecundity estimates exclude "Near-

Failure" Years of 2009-2011 (see text). Parameter estimates from Appendix B; see Methods text

therein for explanation.

| Age	Reproductive Success	Breeding Probability	Calibrated Survival	SD Survival	Net Fecundity	SD Fecundity
1	0	0	0.61	0.041	0	0
2	0	0	0.81	0.033	0	0
3	0	0	0.875	0.028	0	0
4	0.436	0.191	0.89	0.026	0.042	0.012
5	0.436	0.524	0.89	0.026	0.114	0.033
6	0.649	0.81	0.89	0.026	0.263	0.076
7	0.882	0.953	0.89	0.026	0.420	0.122
8	0.882	0.953	0.89	0.026	0.420	0.122
9	0.882	0.953	0.89	0.026	0.420	0.122
10	0.882	0.953	0.89	0.026	0.420	0.122
11	0.882	0.953	0.89	0.026	0.420	0.122
12	0.882	0.953	0.89	0.026	0.420	0.122
13	0.882	0.953	0.89	0.026	0.420	0.122
14	0.882	0.953	0.89	0.026	0.420	0.122
15	0.882	0.953	0.89	0.026	0.420	0.122
16	0.882	0.953	0.89	0.026	0.420	0.122
17	0.718	0.953	0.89	0.026	0.342	0.099
18	0.718	0.953	0.89	0.026	0.342	0.099
19	0.718	0.953	0.89	0.026	0.342	0.099
20	0.718	0.953	0.89	0.026	0.342	0.099
21+	0.535	0.953	0.89	0.026	0.255	0.074

SUPPLEMENTARY MATERIALS

APPENDIX A.

REPRODUCTIVE SUCCESS AND POPULATION COUNT FIELD METHODS

Although general methods for this study have been previously described (Sydeman et al. 1991),

herein we summarize our protocol for determining Western gull survival and fecundity. Our

standard protocol has remained relatively unchanged since the start of the time series in 1986.

Western gull chicks were marked each year with unique 8-9 digit engraved incoloy metal

bands. In addition, each chick received a single plastic leg band, the color and position of which

signified a unique cohort (i.e., hatch year). Daily resighting of banded gulls to determine survival

and recruitment began by April 1st of each year, approximately three weeks prior to earliest

possible egg-laying. Positive identification of individuals was achieved by reading the metal

band number using binoculars or a scope and comparing it to previous banding records. In this

way, we were able to obtain resighting data and map birds to their individual breeding territories,

which were then marked with a wooden stake placed within 1 m of their nest. From 1986 until

1993, the reproductive success of banded individuals was monitored in 12 study plots which

Ficovered most of the accessible areas of the island. In 1994, efforts were reduced to three main

study plots (C, H, and K) which have been monitored annually ever since, and are the focus in

this study (see Figure A1). Previously followed birds were confirmed present in these 3 long-

term nest plots, as established breeding birds seldom move their nest sites more than 10 m (Pyle

et al. 1991). Potential new recruits were also noted and added to the study.

Starting on April 22nd of each year, prior to egg laying, gull study plots were surveyed every

three days to observe nest status, record nest contents, and determine laying dates of eggs. Birds

resighted during the previous month were confirmed with regard to specific nest sites and their

eggs were marked to keep track of order and hatching success. As per Sydeman et al. (1991),
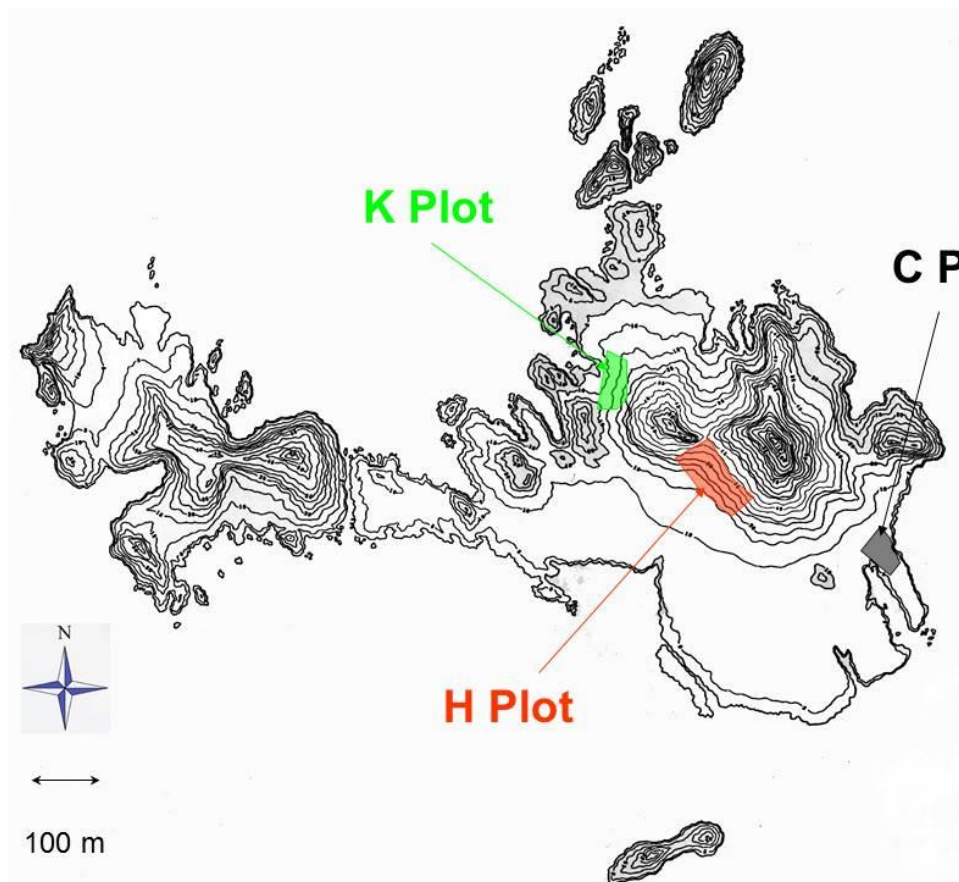
Figure A1. Map of South Farallon Islands depicting Southeast Farallon Island on the right of the Figure, with gull study plots marked with shading (C, H, and K); on the left of the Figure is West End Island. Elevation contours shown.

nests were left undisturbed during incubation once the clutch was complete. We returned to nest sites just prior to hatching (approximately 24 days later) to determine hatching dates and temporarily mark chicks. All surviving chicks at a nest were banded at approximately 15 days old and then left alone again until mid-July when they were nearing fledging age. At this time, each chick was resighted every three days, and its feathering status and development noted. Chicks were classified as fledged when they were fully feathered (i.e. flight and body feathers

fully emerged and almost all down has been shed) and capable of sustained flight, at

approximately six to seven weeks of age (Spear and Nur 1994). Numbers of fledged chicks were

used as our metric of reproductive success, one component of fecundity.

Western gull population counts were conducted annually during the peak breeding season,

typically late May to early June depending on the timing of breeding in any given year. To

facilitate counting, the island is sub-divided into plots in which all birds gulls were individually

counted. Because not all breeding birds are present at the time of the census, we calculate a

correction factor to convert counts of individual birds into an estimate of breeding pairs. The

correction factor is derived by carefully counting all the nests in each of the three main study

plots (C, H, and K). On the day of the census, we conduct 3 replicate counts of individual birds

within those plot boundaries. We then calculate the plot-specific correction factor by multiplying

the number of nests by 2 (to account for both adults) and dividing by the mean number of adults

present in the plots during the 3 replicate counts. Finally, the mean correction factor derived

from the three plots is applied to the all island census to estimate the whole island population.

SUPPLEMENTARY MATERIALS

APPENDIX B.

DEMOGRAPHIC PARAMETER ESTIMATION FOR POPULATION MODELING

To estimate demographic parameters of survival, recapture, and transition to breeding state (age of first breeding) for this species with delayed maturity, we used a particular case of multi-state capture-mark-recapture modeling with two states, juvenile pre-breeders (*J*) and adult breeders (*B*) of which one (*J*) was unobservable except when banded and released just prior to fledging (Kendall and Nichols 2002, Crespin et al. 2006, Lee et al. 2012).   We generally followed the methods described in Lee et al. (2012) to structure our models for estimating age-specific survival, recapture, and transition to breeding state, using program MARK. We ranked models of survival, recapture and transition probabilities as age-specific (i.e., categorical), constants, and with linear, quadratic, and cubic age trends. We then ranked models of annual variation in survival and recapture (year-specific, constant, and annual linear trend) while holding transition rate in its most parsimonious, age-parameterized form. Sample size limitations did not permit model structures with both age and time effects in the same parameter (e.g., S(age+year)). Data from each sex were analyzed separately and estimates from the two sexes were then combined as appropriate. Preliminary analyses revealed no large plot effects, so data from the 3 plots (C, H, and K; see above, Figure A1) were pooled.

The top 10 models for each sex are presented in Tables B1 (females) and B2 (males). Age-specific estimates of survival and recapture probability are presented in Tables B3 (females) and B4 (males). Year-specific estimates of recapture and survival probabilities, and their SEs, are presented in Figures 3A and 3B for females, and Figures 3C and 3D for males.

Annual adult survival was determined through capture/recapture analysis of banded gulls caught from 1986-2011, with respect to age- and year-specific variation. Survival of juveniles

and subadults refers to annual survival of first-year, second-year, and third-year individuals. By

the fourth year of life, Western gulls have reached adult levels of survival (Spear & Nur 1994,

Pyle et al. 1997). Farallon Western gulls generally disperse widely during the first one to three

years of life (Spear & Nur 1994), therefore it was not possible to derive accurate estimates of

juvenile survival from capture/recapture analyses using only island-based observational data.

Instead, we relied on previous empirical and statistical studies of age-specific juvenile and

subadult survival of this population (Spear & Nur 1994, Pyle et al. 1997).

Reproductive success (RS) was determined for each nest as the number of chicks fledged

per breeding pair per year (Appendix A). For the purposes of the PVA, the population-wide RS

was modeled using a generalized linear mixed effects model with negative binomial error

structure and breeding attempt as the sample unit. Individual was treated as a random effect,

because the same individual appears multiple times in the dataset. The number of chicks fledged

was the response variable (0-3), and year and age were categorical explanatory variables (fixed

effects). Model selection was not performed to find the most parsimonious age or year

polynomial curve in RS, instead only year-categorical and/or age-categorical models were fit,

and these estimates used in the population model. To maintain independence of the outcome

variable, RS was modeled with females only.

Breeding probability refers to the likelihood that an individual that has survived to the

beginning of the breeding season actually attempts to breed in that season, which may vary with

the age of the individual (Nur & Sydeman 1999a). In this study, almost all adults were resighted

only when attempting to breed, hence recapture probability, as determined from capture-

recapture analyses (Lebreton et al. 1992), was used as an estimate of breeding probability.

Breeding probability was calculated as a combination of the conditional probability that, in a

given year: 1) an individual that has never bred before breeds for the first time at age x; and 2)

the probability that an individual that has previously bred, breeds again in a given year (Nur and

Sydeman 1999a). The first component, was determined from age-specific estimates of transition

probability, as modeled for each sex separately (Table B5). These were calculated for adults of

ages 4, 5, 6, and 7, and then averaged across the two sexes. No females bred before age 4, and,

since 1993, no males have been observed to breed at age 3 (Point Blue unpublished), hence for

the purposes of the model we assumed age 4 was the earliest age of breeding for adults. Whereas

the most common ages of first breeding are 4, 5, 6, and 7 for both sexes (Pyle et al. 1997, D. Lee,

unpublished), a small number of individuals are first observed breeding at ages 8 and older.

Rather than assuming that this small number of older individuals are breeding for the first time,

we make the more parsimonious assumption that they may have initially bred outside the

boundaries of the three study plots (Figure A1), and then subsequently moved their nest location

into the plot (see Pyle et al. 1997). Hence, we assume that by age 7, all gulls have reached the

full level of breeding probability displayed by gulls that have previously bred, 0.953 (Table B5).

Age-specific Estimation of Parameters

Survival by age was estimated using the program MARK (Cooch and White 2019) for

individuals banded as chicks and subsequently captured or identified at the South Farallon

Islands. For adults, age 4 and older, annual survival showed no clear pattern with respect to age,

for either females or males (Tables B3 and B4). Therefore the population dynamic model

assumed that all adults had the same survival value (Table 1). Survival prior to age 4 could not

be directly estimated from these capture-recapture analyses since only a very small number of

marked subadult gulls are identified at the colony before breeding. Therefore, we relied on prior

analyses for this population based on intensive field observations and statistical analysis by

Spear & Nur (1994) and Pyle et al. (1997). We used mean values for females and males (see

Tables B3 and B4), calculated over all ages, for the initial survival values in the model, prior to

calibration (Table 1).

The first component of fecundity, age-specific RS, was directly estimated from females of

known-age. We assumed that values for males were similar to that of females as justified by

Pyle et al. (1997). We found that RS increased with age up to age 7, then was fairly level

through age 16, and then declined subsequently. Based on this analysis, we grouped adults into

four categories with respect to variation in RS: 1) Young adults (ages 4-5 yrs), 2) transitional

adults (age 6), 3) prime-age adults (ages 7 to 16 yrs), and 4) old adults (ages 17 and older); age-

by-age estimates are shown in Table 1.

Recapture probability (p; Cooch and White 2019) was used to estimate breeding probability.

Age-specific estimates of p were obtained as part of the survival modeling described above.

Results indicated that p differed little with age for either sex and remained high throughout life

(mean = 0.953 averaging across the two sexes). Therefore we assumed that once an individual

bred, it bred in subsequent years with probability = 0.953 (Table 1), and further assumed that if

an individual bred its resighting probability was 1.

Age-specific breeding probability in the population model includes a second component, the

probability an individual breeds for the first time. Capture-recapture analyses provided estimates

of the transition probability (ψ) from pre-breeder (never having bred before) to breeder. The

population model assumed that the earliest age of breeding was 4 years, with the probability of

breeding at age 4 being 19%. For 5 year olds, 52% attempt to breed, composed of individuals

that bred the year before and have survived to age 5, as well as an additional fraction that are

breeding for the first time as 5-year olds (as estimated from the pre-breeder to breeder transition probability). Similar calculations apply to age 6, at which age 81% are attempting to breed. By age 7, we assume that individuals reach the full-adult value of 95.3% breeding probability. Age-specific breeding probability was summarized in Table 1.

Estimation of Variation in Demographic Parameters

Survival (symbolized Φ) and recapture probability (symbolized p) were estimated for each year during the period 1986 to 2009, for both males and females (Figure 3), based on capture histories compiled for field seasons spanning the period 1986 to 2011. It was not possible to estimate year-specific survival beyond 2009-2010 while simultaneously estimating year-specific recapture probability due to limitations of capture-recapture analysis (Cooch and White 2019). For the initial parameter values in the population model, we used mean survival estimates, averaged across both sexes, based on the most recent 11 years available, 1999 to 2009 (i.e., 1999/2000 to 2009/2010).

To determine year-to-year variation in the demographic parameters, we followed Cooch and White (2019) to estimate process variance of each parameter (i.e., year-to-year variance not due to sampling error). For survival and breeding probability, we estimated process variance separately for each sex, and then averaged the two values, just as we averaged mean survival and breeding probability across the two sexes. For RS, we only analyzed females (see above), and thus only estimated process variance for them.

In the Leslie matrix, fecundity is the product of RS x breeding probability (bp), hence we calculated process variance of fecundity as the variance of a product of two random variables (Mood et al. 1974), assuming no covariance between RS and bp .

For the calculations of between year variance in survival and fecundity, as well as mean

fecundity, we restricted our analysis to the more recent period, from 1999 to 2011, for the

reasons described above. Note that year-specific survival from 2010 to 2011 and year-specific bp

in 2011 could not simultaneously be estimated, hence we only used annual estimates through

2009/2010. Mean and SD of annual survival and fecundity with respect to process variance were

then included in the stochastic modeling conducted in RAMAS (Akçakaya 2005).

In addition, for juvenile and subadult survival, we scaled the between year SD relative to

that of adults given that survival was a binomially distributed random variable and its variance =

$\Phi \times (1-\Phi)$ (Mood et al. 1974). That is, the closer survival was to 0.50, the greater its variance.

See Table 1 for SD values used in the modelling.

We quantified the mean annual recapture probability (p), which we use as a measure of

breeding probability (bp) for individuals that have bred before. We also incorporated the between

year variation observed for this parameter as a component of fecundity. Recapture probability

was defined as the likelihood that an individual that has bred before (prior to year x), breeds in

year x, given that it has survived to year x. This assumes that all breeding individuals were

resighted and identified each year (i.e., resighting probability is effectively equal to 1). This

assumption is justified because breeding birds were highly site-tenacious and, once having bred,

nearly all surviving individuals returned to the same territories each year to attempt reproduction

(Pyle et al. 1991, 1997, Spear et al. 1987). In addition to breeding probability, the demographic

model must also consider the transition probability (symbolized ψ), that is the probability that an

individual that has never bred before, breeds in a given year (Nur & Sydeman 1999a). We were

not able to explicitly estimate how ψ varied on a year by year basis over the full time series due

to data limitations. However, we were able to estimate how ψ varies with age using program

MARK, and supplemented by intensive field studies of age of first breeding in this population

(Pyle et al. 1997).

Net fecundity was defined as the product of RS $\times$ breeding probability $\times$ 0.5 (Nur &

Sydeman 1999a). We calculated variance in net fecundity based on the product of variance in

the individual parameters (Mood et al. 1974), assuming no covariance between RS and *p*.

Calibration

We calibrated the performance of the population model such that the set of demographic

parameter values used produced a population whose median trajectory corresponded to the

observed population behavior. The first step in this calibration process was to determine the

observed population trajectory. We estimated the annual constant rate of change by conducting a

linear regression on ln-transformed whole colony counts of Western gulls on the South Farallon

Islands at the time of peak incubation for the period 1999 to 2011 (Nur et al. 1999). This resulted

in a small increasing trend of 0.74% ($\pm$ 0.70 [SE]) per year (Figure 1). Therefore, the population

model was calibrated to reproduce this growth rate by adjusting different parameters. .

For example, while we assume that emigration equals immigration for the purpose of our

models, we know that estimates of survival often underestimate true survival due to permanent

emigration of individuals from the study area, regardless whether or not it is balanced by

immigration (Clobert and Lebreton 1991).   So, to replicate the behavior of the observed

population trajectory, we increased survival for all age classes by a small amount. For first-year

survival, we increased the value from 0.582 to 0.610. We feel this is a reasonable adjustment

since female survival was estimated by Spear & Nur (1994) at 0.61, so this corresponds to using

the higher of the two sex-specific values available. For second-year survival, we increased the

value from 0.794 to 0.810, again noting that female survival was estimated by Spear & Nur

(1994) at 0.81.   For third-year survival, we increased the value from 0.854 to 0.875, but note

that female survival was estimated by Spear & Nur (1994) at 0.89, so 0.875 reflects a value that

was in between the previous male and female estimates. For survival in the fourth-year of life,

we assumed the same value as adults (i.e., 4 years and older, see below), following Pyle et al.

(1997). For all individuals four years old and older, we increased the value from 0.884 to 0.890

to allow for some, presumably low, emigration. Note that extensive evidence for gulls in

general, and for this population specifically, indicates that adult dispersal was less than that of

juveniles and subadults, consistent with a smaller adjustment (Pyle et al. 1997, Nur & Sydeman

1999a).

We had no reason to expect over- or under-estimation of age-specific fecundity values,

therefore we made no adjustments to this parameter. All the simulations used the survival values

adjusted through the calibration process (Table 1).

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Appendix Table B1. Model selection results from program MARK for female Western gulls for survival (S), recapture probability (p), and transition probability (Psi). $year_{cat}$ refers to year as a categorical variable, $year_{lin}$ refers to year as a linear variable. AIC_c is the Akaike Information Criterion corrected for finite sample sizes. Top 10 models of those analyzed are shown.

Model	AICc	Δ AICc	AICc Weights	Number of Parameters	Deviance
$\{S(year_{cat})\ p(year_{lin})\ Psi(age^3)\}$	3023.84	0.00	1.00	35	1606.05
$\{S(year_{lin})\ p(year_{cat})\ Psi(age^3)\}$	3036.00	12.16	0.00	36	1616.13
$\{S(year_{cat}\ p(year_{cat})\ Psi(age^3)\}$	3043.34	19.50	0.00	59	1574.93
$\{S(year_{lin})\ p(year_{lin})\ Psi(age^3)\}$	3089.32	65.49	0.00	10	1722.84
$\{S(constant)\ p(age)\ Psi(age^3)\}$	3091.71	67.87	0.00	9	1727.25
$\{S(age^2)\ p(age)\ Psi\ (age^3)\}$	3091.86	68.03	0.00	11	1723.36
$\{S(constant)\ p(age^2)\ Psi(age^3)\}$	3092.83	68.99	0.00	10	1726.35
$\{S(constant)\ p(age^3)\ Psi(age^3)\}$	3092.98	69.15	0.00	11	1724.48
$\{S(age^3)\ p(age)\ Psi(age^3)\}$	3093.10	69.26	0.00	12	1722.56
$\{S(age^2)\ p(age^2)\ Psi(age^3)\}$	3093.41	69.58	0.00	12	1722.88

Appendix Table B2. Model selection results from program MARK for male Western gulls for

survival (S), recapture Probability (p), and transition probability (Psi). $year_{cat}$ refers to year as a

categorical variable, $year_{lin}$ refers to year as a linear variable. age^a refers to age as a categorical

variable, values calculated for age 3 years through 22 years. AIC_c is the Akaike Information

Criterion corrected for finite sample sizes. Top 10 models of those analyzed are shown.

Model	AICc	Delta AICc	AICc Weights	Number of Parameters	Deviance
$\{S(year_{cat})\ p(year_{lin})\ Psi(age^3)\}$	4592.03	0.00	1.00	36	2011.72
$\{S(year_{cat})\ p(year_{cat})\ Psi(age^3)\}$	4606.11	14.08	0.00	62	1972.24
$\{S(year_{cat})\ p(constant)\ Psi(age^3)\}$	4617.07	25.04	0.00	35	2038.80
$\{S(year_{lin})\ p(year_{lin})\ Psi(age^3)\}$	4821.12	229.10	0.00	10	2293.55
$\{S(age^2)\ p(constant)\ Psi(age^3)\}$	4851.84	259.81	0.00	10	2324.26
$\{S(age)\ p(constant)\ Psi(age^3)\}$	4853.39	261.36	0.00	9	2327.83
$\{S(age^3)\ p(constant)\ Psi(age^3)\}$	4853.82	261.79	0.00	11	2324.23
$\{S(constnt)\ p(constnt)\ Psi(age^3)\}$	4855.88	263.85	0.00	8	2332.33
$\{S(constant)\ p(year_{lin})\ Psi(age^3)\}$	4857.31	265.28	0.00	9	2331.75
$\{S(age^a)\ p(constant)\ Psi(age^3)\}$	4860.78	268.75	0.00	28	2296.78

Appendix Table B3. Age-specific recapture and survival estimates, with standard errors, for

female Western gulls on Southeast Farallon Island, from captures, 1986 – 2011, $n = 280$

individuals.

Recapture Age	Recapture Probability	SE Recapture Probability	Survival Age	Survival Probability	SE Survival
4	-	-	4-5	0.793	0.100
5	0.891	0.059	5-6	0.834	0.039
6	0.948	0.025	6-7	0.790	0.033
7	0.934	0.024	7-8	0.885	0.027
8	0.936	0.023	8-9	0.866	0.029
9	0.937	0.023	9-10	0.867	0.031
10	0.920	0.027	10-11	0.850	0.033
11	0.976	0.017	11-12	0.879	0.033
12	0.929	0.028	12-13	0.845	0.038
13	0.942	0.028	13-14	0.838	0.044
14	0.870	0.043	14-15	0.818	0.050
15	0.886	0.043	15-16	0.833	0.052
16	0.906	0.044	16-17	0.918	0.053
17	0.838	0.061	17-18	0.853	0.068
18	0.846	0.068	18-19	0.797	0.078
19	0.860	0.073	19-20	0.809	0.083
20+	0.881	0.038	20-21+	0.798	0.042

Appendix Table B4. Age-specific recapture and survival estimates, with standard errors, for

male Western gulls on Southeast Farallon Island, from captures, 1986 – 2011, *n* = 493

individuals.

Recapture Age	Recapture Probability	SE Recapture Probability	Survival Age	Survival Probability	SE Survival
3	-	-	3-4	0.830	0.079
4	0.975	0.025	4-5	0.835	0.030
5	0.967	0.016	5-6	0.906	0.019
6	0.939	0.017	6-7	0.851	0.021
7	0.953	0.016	7-8	0.826	0.023
8	0.945	0.017	8-9	0.846	0.023
9	0.950	0.016	9-10	0.887	0.022
10	0.957	0.016	10-11	0.885	0.024
11	0.961	0.016	11-12	0.924	0.025
12	0.933	0.025	12-13	0.812	0.032
13	0.960	0.019	13-14	0.857	0.034
14	0.938	0.026	14-15	0.884	0.032
15	0.963	0.021	15-16	0.873	0.036
16	0.940	0.029	16-17	0.836	0.044
17	0.974	0.026	17-18	0.789	0.052
18	0.969	0.030	18-19	0.800	0.059
19+	0.962	0.037	19-20+	0.742	0.071

Appendix Table B5. Estimation of Breeding Probability, First Time and Repeat. We assume that all individuals that have not bred by age 7, do so at that age. Thus, 7 yr olds breed with the same probability as older adults (0.953). A small number of 3 year old males have attempted to breed, but none in recent years (Point Blue, unpublished), hence we consider this probability to be zero.

Age	Probability Breeding For First Time			Compound Probability of Breeding First-time or Repeat
	Male	Female	Mean	
3	c. 0	0	0	0
4	0.313	0.069	0.191	0.191
5	0.536	0.342	0.439	0.524
6	0.577	0.489	0.533	0.810
7+	NA	NA	NA	0.953