Final Report
Computer Model of Farallon Seabird Populations

Contract: CX-8140-1-0019

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Preface and Acknowledgments

This report summarizes the computer model developed by the Point Reyes Bird Observatory (PRBO), per contract CX-8140-1-0019 for the Gulf of the Farallones National Marine Sanctuary (GFNMS). Please refer to the accompanying software (Farallon Seabirds 1.4) and User’s Manual. We thank Bill Sydeman for valuable assistance in data compilation and synthesis and thank Jan Roletto and Ed Ueber for comments on earlier versions of this report. This is PRBO Contribution No. 615.
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Introduction

This report summarizes and provides relevant background information regarding *Farallon Seabirds 1.4*, the computer model of Farallon seabird demography and population change developed by the Point Reyes Bird Observatory for the Gulf of the Farallones National Marine Sanctuary. The seabird model is actually three separate models, each with similar structure, one for each of three seabird species: Common Murre (*Uria aalge*), Brandt’s Cormorant (*Phalacrocorax penicillatus*) and Western Gull (*Larus occidentalis*). These three species were chosen from among seabirds breeding on the Farallon Islands on the basis of availability of demographic data, especially data collected from the Farallon populations themselves, coupled with interest in management of these species. Relevant background material on these three species (regarding population trends on the Farallones and in the California Current and causal factors thought to influence these trends) is included in the Appendix (especially Figure 2 of that document).

The model is intended, above all, as a management tool. We summarize the important features or capabilities of the computer model as follows: First, the model can predict the future course of population levels for the three seabird species, extrapolating current conditions into the near future (next several years, up to 20 years). Secondly, the model can predict the long-term recovery of each species from the effects of a toxic spill (such as an oil spill), over a period of a decade or more. A third feature of the model is that it can predict mortality from an oil spill given characteristics of the spill, when used in conjunction with NOAA’s On-Scene Spill Model (OSSM). A fourth feature is that it can predict the consequences of a one-time catastrophe (e.g. die-off due to red tide) and predict recovery of the population. Fifth, the model can project the effects of changes in food (fish) availability, for example, due to changes in fishing practice, as well incorporate differences in food availability resulting from wide-spread oceanographic anomalies, such as occur in conjunction with the El Niño Southern Oscillation. The final feature to mention is that these scenarios can be combined (e.g., oil spill occurring during a poor food year). These features are discussed in detail below.

An important component of the model is that it incorporates unpredictability or stochasticity (i.e., random variation) that is characteristic of the natural world. Stochasticity is incorporated in several ways. First, environmental (especially food) conditions cannot be precisely predicted from one year to another. Secondly, even if environmental conditions or food levels were known precisely there is still some unpredictability regarding the demographic response of the seabirds. For example, under good environmental conditions fledging success tends to be high, but we can only provide an expected range of values. As a result of the two levels of
unpredictability, the computer model predicts, not a single value for a species, but an envelope of possibilities. Within this envelope there is a best estimate (given assumptions of the model and the scenario) and upper and lower bounds. The upper and lower bounds are defined with respect to the 10th and 90th percentile outcomes. That is, there is a 10% probability (given assumptions of the model) that a population will be at or below the lower 10% bound, and a 10% probability (given assumptions of the model) that the population will be at or exceed the upper, 90% bound.

Overview:
The overall model can be divided into three components: The first component is a toxic spill module. Given characteristics of an oil spill (time of year, size, direction of drift) this component predicts resultant mortality. The output of this component can then be passed to the second component, a demographic module, which is really the heart of the computer model. This module projects the appropriate population (Common Murre, Brandt’s Cormorant or Western Gull) into the future, one year at a time, keeping track of the total population and the age-structure of the population. The population projections are based on the best knowledge available regarding age-specific reproduction, fledging success, and survival of immature and mature birds. Reproductive success and survival of the three species are known to vary from year to year, and usually in relation to quality of the environment (Ainley & Boekelheide 1990). This intrinsic variation is incorporated into the demographic component. The last component is a "food" component, which allows one to specify changes in prey (fish) availability and/or changes in environmental (oceanographic) conditions that impinge on survival and reproduction of birds.

Model Components: Toxic Spill Module

The toxic spill component estimates direct mortality for designated populations on the basis of input from an oil-spill trajectory model (such as OSSM). The approach taken by the toxic spill module is to estimate the number of birds in the path of the spill and to assume (on the basis of empirical data) that some fraction of the birds at risk become oiled and die. This approach is especially suitable for risk assessment and evaluation of hypothetical scenarios. If, instead, the Farallon Seabirds model is to be used after a real spill occurs, this approach can still be adopted. However, if beached carcasses have been enumerated, one can, alternatively, estimate mortality from the oil spill by extrapolating from the number of beached carcasses (e.g., Page et al. 1990). In that case, an empirical mortality estimate would be fed into the demographic module instead of the estimate derived by the toxic spill module. We stress that the seabird computer model can be used with or without the toxic spill module. The approach adopted by the toxic spill module is to intersect the path of a
surface slick with the density distribution of a species of seabird, which provides an index of the number of birds at risk. By combining estimates of number of birds at risk with empirical data from studies of actual oil spills, the module derives an estimate of total mortality. Chronic oiling and/or sub-lethal effects of toxic spills are not included in the toxic spill module; instead these effects can be incorporated by altering life-table parameters in the demographic module.

**Estimation of mortality rates:**
Estimates of the proportion of seabirds, among all those at risk, that contact a slick and subsequently die are based on two detailed case studies, the *T/V Puerto Rican* and the *Nestucca* (Dobbin et al. 1986, Ford et al. 1991). The *T/V Puerto Rican* spill was a 35,000 barrel (bbl) spill that occurred in the Gulf of the Farallones on November 3, 1984. The *Nestucca* spill was a 5,500 barrel spill that began at the mouth of Grays Harbor in Washington on December 22, 1988. A total of 1,269 oiled seabirds were recovered following the *T/V Puerto Rican* incident; a total of 13,473 oiled seabirds were recovered following the *Nestucca* incident.

These two cases represent interesting differences in terms of their effects on seabirds. In the case of the *T/V Puerto Rican*, only 0.036 oiled birds were recovered per barrel of spilled oil, whereas in the case of the *Nestucca*, 2.45 birds were recovered per barrel of spilled oil. The magnitude of this difference is related primarily to the behavior of the slicks themselves. The slick from the *T/V Puerto Rican*, composed primarily of light refined hydrocarbons, traveled only about 150 km and had largely dissipated within about 10 days after the spill occurred. The crude oil from the barge *Nestucca*, on the other hand, was more persistent and traversed over 500 km of coastline, over a period of about 20 days. The constituency of the oil, size of the slick and movement are more reliable indicators of spill impact on seabirds than is volume. The aerial extent of a surface slick, which is explicitly incorporated by the toxic spill component, is a composite of the persistence of the spilled material, the volume spilled, and the wind and current factors that control its movement.

During the *T/V Puerto Rican* incident, aircraft-based surveys of bird densities were carried out concurrently with the spill, providing an accurate assessment of the seabird densities in the area impacted by the spill. The oil slick was tracked from aircraft, and the path of the oil slick was later reconstructed by connecting sequential observations to form a single continuous polygon. Based on these data, estimates were made of the numbers of murres, loons, and other seabirds that were in the region through which the slick passed, thus providing estimates of the number of birds at risk. The total number of birds that died were estimated by extrapolation
from the numbers of beached oiled birds, taking into account loss at sea and on the beach. For Common Murres, it was estimated that 4,255 birds encountered the slick, of which 1,787 or 42% died.

In the Nestucca incident, aerial overflights were made during the following year, at the same time of year. Transects were run at 22 km intervals from the Columbia River to about half way up Vancouver Island. Rates of carcass loss at sea were studied using carcasses equipped with radio transmitters; loss rates on the beach face were studied by placing lines of carcasses out on the shoreline and checking them at intervals. In this incident, it was estimated that 252,070 murres were at risk, of which about 30,000 or 12% died.

Integration with the On-Scene Spill Model:
The On-Scene Spill Model (OSSM) is an oil spill trajectory model written and maintained by the Modeling and Simulations Studies Group (NOAA/HAZMAT/MASS) at Sandpoint, Seattle. This group provides real-time support for spills of oil and other toxic substances, and they are present at all major spills where trajectory modeling is needed. OSSM is an interactive program written for the Apple Macintosh. In its current formulation, effective use of OSSM requires training and familiarity with trajectory modeling and we recommend that this part of any simulation be carried out with the assistance of the Modeling and Simulations Studies Group. We stress that the seabird computer model can be used without OSSM, e.g., if one estimates oil spill mortality on the basis of beached carcasses. The User’s Manual describes how the Farallon Seabirds computer model can accept OSSM output (see section 2.2.1 therein).

In general, oil or any comparable material moves with the surface current plus about 3% of the wind speed in a downwind direction. OSSM simulates oil spill trajectories by tracking the paths of a large number of independently moving points (Lagrangian elements). The movement of the Lagrangian elements is determined by the combined effects of wind and current vector fields plus a random factor that simulates the process of spreading. The composite of the paths of all the elements forms an approximation of the movement of a surface slick. At specified model time intervals, OSSM can be made to write lists of the latitude/longitude coordinates of the Lagrangian elements. These lists can then be used by other programs, and this is what the toxic spill module of the Farallon Seabirds computer model is designed to do.

Estimation of Mortality:
Estimation of the number of birds killed by a given oil spill scenario, using the toxic
spill module, requires three basic steps:

1) Simulate an oil spill using a trajectory model such as OSSM. Positions of the Lagrangian elements are outputted at intervals in standard OSSM format, and the output is reformatted using the utility REFORM (see User's Manual 3.1).

2) Using the output from step 1 and the distribution of the number of seabirds in the region affected by the spill, estimate the number of birds at risk.

3) Multiply the result from step 2 by the appropriate mortality rate and pass the results to the demographic module.

Step 1 must be carried out externally, using OSSM. The simulation may be either for a real or hypothetical spill scenario. Step two involves intersecting the simulated spill trajectory with the appropriate seabird distribution. Step three is straightforward once estimates of the mortality rate have been made. Furthermore there is provision for modifying the mortality rate (fraction of birds that become oiled and die, among those at risk) if one has information on this point (see User’s Manual section 2.2.2). We stress that if other estimates of toxic spill mortality are available, such results can be used with the demographic module, thus by-passing OSSM (see User’s Manual section 2.3).

Calculating the number of birds at risk is carried out by dividing the study area, from Pt. Sur to Fort Ross, into a large number of rectangular regions (pixels) about 5 km on each side. Each pixel is characterized on the basis of bird density for each of the study species for each season of the year. This characterization is based on the studies carried out by the Mineral’s Management Service between 1980 and 1985 (Briggs et al. 1983; Briggs et al. 1986; ECI 1992). The number of birds at risk is estimated as the product of the density and the area of each pixel, summed over all pixels containing Lagrangian elements.

Integrating the toxic spill and demographic components:
The estimated mortality resulting from a toxic spill scenario is used to modify the known or assumed population size (and each age class within the population) at the time of the spill. In the absence of information to the contrary, we make the following assumptions:

(1) The spatial distribution of the study species is similar for all age classes. We investigated the possibility of differential distributions for different age classes, but the original data on seabird distribution in the Gulf of the Farallones (collected by Mineral’s Management Service) are not sufficient to permit this.

(2) Within the specified region (Fort Ross to Point Sur), Farallon birds make up a constant fraction of birds of a given species, throughout the region. However, the
model requires no assumption of what that fraction is. For example, if the density of all Common Murres (irrespective of origin) is twice as great at Point Reyes as at Año Nuevo, then by assumption 2, the density of Farallon Common Murres is also twice as great at Point Reyes as at Año Nuevo.

(3) Farallon Island birds (of the three study species) are year round residents. These assumptions are supported by observations of PRBO biologists. These assumptions are the default assumptions. If one has reason to believe that one age class was at greater risk in a spill, and thus suffered greater mortality, this can be incorporated into the scenario (see User's Manual 2.8).

Based on assumptions 1 through 3, the proportion of the population in the study area, Fort Ross to Point Sur, killed by a toxic spill will be equal among resident and migrant birds, and across all age classes. Interaction between the toxic spill and demographic components involves multiplying the initial values of the population size in each age class by the proportion which survived the spill.

Simulation of the impact of a toxic spill: Common Murres:
As an example of the model application, we modeled the effect of a crude oil spill on populations of Common Murres, Brandt’s Cormorants and Western Gulls in the study area. We started by simulating a 100,000 bbl spill of crude oil occurring along the westbound vessel traffic lane about 5 km southeast of Farallon Island (Figure 1). The spill occurred during the passage of a small storm front (based on real time winds from March 1990) and outflow continued over a 24 hour period. Oil initially moved northward oiling the Farallon Islands and brushing the tip of Point Reyes. At this time, however, the wind turned and came around from the northwest, driving the slick back across the Farallon basin toward Half Moon Bay. Heavy oiling occurred from Point San Pedro to Año Nuevo. Light oiling occurred on the southern side of Monterey Bay near Pt. Lobos.

At this time of year, the Common Murre populations have not yet begun to coalesce at their colonies (Figure 2; see below for discussion of Brandt’s Cormorants and Western Gulls). Concentrations of murres north of Pt. Reyes peninsula, near Bolinas, and in Monterey Bay were not seriously impacted. High density areas between Pillar Point and Pigeon Point, however, suffered extensive mortality. Approximately 84,000 murres were present in the area affected by the spill (i.e., at risk), of which 42% or 35,280 were killed. The mortality rate of 42% is that observed for murres in the T/V Puerto Rican incident. Only about 12% of murres were thought to have died in the Nestucca incident, but we use the first-mentioned incident because of greater accuracy and precision attached to that mortality estimate. The death of 35,280 murres
Figure 1. The cumulative track of a simulated 100,000 bbl oil spill. Wind conditions are based on records from March 1990. The spill is simulated as a cluster of independently moving Lagrangian elements. The stippled area, representing the extent of the spill, was generated by mapping the position of each Lagrangian element at 6 hour intervals and drawing a 1,000 meter radius circle around the position of each element. The map is included for information purposes only; the *Farallon Seabirds* model does not produce such a map, though OSSM does.
Figure 2. Distribution of Common Murres in the study area in March. Data are based on Mineral’s Management studies carried out between 1980 and 1985 (see text for references; also BCI 1992). Data were recorded in 5’ latitude/longitude boxes and contoured using a standard linear interpolation algorithm. Contour levels were selected automatically so that each contour band contains about twice as much area as the next highest band. The map was drawn with CAMRIS, commercial software available from Ecological Consulting Inc. The toxic spill module uses the same database that has been used to draw the map.
represents about 15.3% of the population in the study area. Wind and current conditions prevailing at this time would probably have beached about half of these of these birds, resulting in the recovery of 15,000 - 20,000 dead and dying murres between Pillar Point and Año Nuevo and south from Point Lobos to Point Sur. The long-term consequences of such a spill are considered below (see Example 2, Figure 11).

**Impact on Brandt's Cormorants:**
Although their diving habits, wettable plumage, and low buoyancy would seem to suggest a high vulnerability to the effects of spilled oil, in fact, cormorant deaths from oil spills are not numerous; Brandt's Cormorants made up only 1% of the recovered birds in the 1971 San Francisco oil spill (Smail et al. 1972), <1% in the T/V Puerto Rican spill (Dobbin et al. 1986), and <1% in the Apex Houston spill (Page et al. 1990). In some spill incidents the proportion has been higher: 13% shags in the case of the Amoco Cadiz (Hope Jones et al. 1978) and 2.2% cormorants in the case of the Exxon Valdez (ECL, unpublished data). The exact conditions under which larger numbers of cormorants die are unclear.

In March, some adult Brandt's Cormorants are present on the breeding colonies at the Farallon Islands but many are still scattered along the coast to the east and south (Figure 3). Egglaying has not yet begun. The oil slick passed through an area of low to moderate densities, with the largest number of birds affected near the mainland coast (around Pigeon Pt.). Nearly all oiled cormorants would probably have been found on island or mainland beaches, as cormorants typically return to shore when stressed (Dobbin et al. 1986).

The mortality rate used in this example is based on data for the T/V Puerto Rican incident, because it is the best studied oil spill incident in the region. Because so few cormorants were killed in this incident, we have chosen the rate for loons because loons and cormorants are of a similar size and buoyancy. In the T/V Puerto Rican case, 201 loons died out of an at-risk population of 7,238, for a mortality rate of 2.8% (Dobbin et al. 1986). We have used this mortality rate (as the default value) for Brandt's Cormorants in the Farallon Seabirds model, but the mortality rate can be adjusted up or down by the user, as such information becomes available. Since approximately 3,709 cormorants were at risk in the path of the slick, we estimate that 2.8% of that number, or 103 Brandt's Cormorants, were killed. Thus, 0.67% of the entire population in the study area died.
Figure 3. Distribution of Brandt's Cormorants in the study area in March. Legend as in Figure 2. Densities are shown as birds per square kilometer.
Impact on Western Gulls:
Western Gulls are widespread in March and are present on the breeding colonies year-round (Figure 4). The oil slick passed through the area of greatest concentration of this species, including particularly dense areas near Southeast Farallon Island. Most debilitated oiled gulls would probably have been found on island or mainland beaches, since they typically return to shore when stressed. A considerable proportion of oiled gulls would not be impaired sufficiently for easy capture. Many gulls survive oiling (Dobbin et al. 1986).

The mortality rate used in this analysis is based on data for the T/V Puerto Rican incident, because it is the best studied oil spill incident in the region. In the T/V Puerto Rican case, 20 gulls died out of an at-risk population of 9,966, for a mortality rate of 0.2%. In this example, approximately 35,653 Western Gulls were at risk in the path of the simulated slick, and thus we estimate that 0.2%, or 66 gulls were killed by the spill. This represents about 0.06% of the population in the study area.

Model Components: Demographic Module
Overview:
The demographic component of the model is based on extensive Farallon data collected for all three species, supplemented with data from the literature as necessary. The demographic component is essentially an age-structured Leslie matrix (Leslie 1945, Ainley et al. 1990, McDonald & Caswell 1993). This type of population matrix is also known as a projection matrix because it can be used to project the population one year into the future, or if applied repeatedly, any number of years into the future. The projection matrix includes as elements survival and fecundity parameters. Survival and fecundity are treated as age-specific in the population matrix. The Leslie matrix actually models net-fecundity, which is to say, for each age class (1-yr-olds, 2-yr-olds, etc.), the top element of each column is the number of female chicks produced per female of that age class that survive to age one year (12 months). The net-fecundity is thus a product of three components: chicks fledged per breeding female x probability a fledged chick survives to one year x probability a female of that age class attempts to breed. Furthermore, unlike standard Leslie matrices, the elements of this Leslie matrix (a different one for each species) vary from year to year. The variation in these parameters is partly in relation to food availability and partly is unpredictable. Thus, if a population experiences several poor-food years in succession, population growth will be less positive (and more likely the population will shrink) than if a sequence of years are all food-rich. Such annual and stochastic variation is an important component of the model, reflecting the fact that the environment and the response of seabirds to the environment are not
Figure 4. Distribution of Western Gulls in the study area in March. Legend as in Figure 2. Densities are shown as birds per square kilometer.
easy to predict. As shown below, the best estimates for future growth of Farallon Western Gulls and Brandt’s Cormorants are similar, assuming current conditions hold, but the variability concerning projected growth of the cormorants is much greater than that concerning projected growth of the gulls.

Below we summarize the demographic parameters, considering each species in turn. The basic structure of each species’ demographic module is the same, but the parameter values differ. For all three species, population parameters of the demographic matrix were refined so that the expected population dynamics of the model population conformed with recent and current population trends, in other words, each species’ model has been validated using historical data. We defer discussion of “food” effects until the subsequent section.

**Common Murre:**
For this species we have modeled females (the conventional sex to be modeled, on the assumption that reproductive potential of a species is limited by females, which is consistent with observations on this population). Because murres are strictly monogamous (and thus reproductive success is the same for the two sexes) and because the sexes are similar in survival, there is essentially no difference between using one sex or the other for the modeling. For the first parameter, adult survival, recent data for Farallon Common Murres indicate 93.3% of adults (those aged four and older) survive (Sydeman 1993) and that is what we have used (Table 1). In the absence of data to the contrary, we assume no age-specificity in adult survival, except that maximum life span for murres is assumed to be 35 years (approximate maximum life span for any seabird of equivalent size). Annual adult survival also varies between years, in conjunction with food availability (Sydeman 1993), and we have incorporated this annual variation into the model (see below).

The second parameter is subadult survival. We have no Farallon data on this point, but have assumed that survival of 1 yr olds, 2 yr olds, and 3 yr olds is 0.80, 0.87 and 0.933, on the basis of data from band recoveries of Common Murres (Mead 1974), a pattern of survival among sub-adults and adults that is consistent with that seen for Farallon Western Gulls (Spear et al. 1986). We assume that subadult survival varies from year to year as does adult survival. Specifically we assume that subadult mortality is directly proportional to adult mortality; thus, if adult mortality should double, so would subadult mortality.

The third parameter is age of first breeding. Data from the Farallones are meager and indicate that some individuals breed at age 5, and that no murres have been seen
breeding at age 4. Birkhead & Hudson (1977) established that Common Murres in their population first bred at ages 4, 5 and 6, with a mode at 5. Combining these two data sources we assume that some murres begin breeding at age 5, the others at age 6, with a majority attempting to breed at age 5 (specifically, the probability that a 5 yr old attempts breeding is 60%). There are no data indicating year-to-year variation in age of first breeding, and so we have assumed no such variation (i.e., in every year 60% of 5 yr olds attempt breeding).

The fourth parameter is probability of breeding (among those who have ever bred). Observations of marked murres indicate that all attempt to breed except in very poor food years (such as in 1983 and 1992). In 1983 only about half attempted breeding (Ainley & Boekelheide 1990); in 1992, approximately 70% attempted to breed (PRBO, unpublished). In the model, we use a value of 60% of experienced birds attempting to breed in a very poor food year (defined below), mid-way between the estimates of 50% and 70%; otherwise 100% are assumed to breed. We note that predictions of the model are not sensitive to the exact proportion assumed breeding in a very poor food year (in the model, 60%). We could have used values of 50% or 70% breeding probability in very poor food years and still obtained similar output. This is because in such a year, reproductive success and post-fledging survival are very low; hence very few surviving chicks will be produced irrespective of the assumed breeding probability.

The fifth parameter is chicks fledged per breeding pair. We have 21 years of data in this regard (Ainley & Boekelheide 1990, PRBO unpublished). On average, 0.78 chicks are raised per pair, but this parameter fluctuates with food conditions (see below). Furthermore, there is likely a correlation between age and reproductive success, if only because breeding experience influences reproductive success in every seabird species thus far studied (reviewed in Newton 1989, Sydeman et al. 1991, Pyle et al. 1991). There are no direct data on the relationship of age to reproductive success in Common Murres (from any population that we know of) but on the basis of observations on other Farallon seabirds (including alcids) we assume that age-specific reproductive success is 0.42, 0.62, 0.81, and 0.84 chicks per breeding pair for individuals aged 5, 6, 7, and 8 or more years old. We arrived at these numbers by assuming that a first-time breeder is half as successful and a second-time breeder is 90% as successful as an individual breeding for the third time or more. We then combined this relationship with the fact that 5 yr olds are all inexperienced (see above), that 6 yr olds are a mixture of first-time and second-time breeders, that 7 yr olds are second-time and third-time breeders, and that 8 yr olds are all breeding for the third or fourth time.

The sixth and final parameter used is post-fledging survival (survival to 12 months). Two points to keep in mind are: (1) There are no Farallon data on this point (to date), and yet the literature indicates great variability in results from study to study,
ranging from less than 30% to more than 60% (Mead 1974, Hudson 1985). Variation in this parameter has a strong impact on the projected population growth. With 30% post-fledging survival, the Farallon population would be shrinking, with 60% survival, it would be growing rapidly, at about 8% per year (just as it did in the 1970’s; see Appendix, Figure 2 therein). We have used a middle, fairly typical figure of 40% post-fledging survival, because that produces a slowly growing population (1.1% per year assuming constant, average environmental conditions), just as has been observed on the Farallones between 1984 and 1991 (Figure 2 in Appendix). Our own observations suggest annual variation in post-fledging survival. We have assumed that post-fledging survival was proportional to survival of one-year olds.

Western Gull:
For this species, we modeled males, rather than females, because the former appears to be the sex that limits population growth (Spear et al. 1986). That is, it appears that female compete for mates, as a result of a sex ratio imbalance favoring females (Spear et al. 1986). The first parameter to be considered is adult survival. Data from the Farallon population indicates (1) age-specificity and (2) annual variation in average adult survival (Sydeman and Nur, unpublished). We have used actual values obtained for age-specific survival of males (PRBO unpublished data), and then smoothed out the bumps (Table 2). Survival is maximal for adults aged three to six then slowly declines until age 17, at which point it declines more quickly (Table 2). Few gulls live to age 20 and none have been seen to survive past age 21; the demographic matrix is consistent with these observations. In addition, adult survival varies between years, but not in a way that is correlated with food availability (PRBO unpublished). Thus, in each year we randomly chose (from a normal distribution) an average adult survival value with a mean and standard deviation matching the observed inter-annual mean and standard deviation.

Subadult survival was estimated from band recovery data (Spear et al. 1986): on average, 75% survival for one-year olds and 82% survival for two-year olds. As with Common Murres, we assumed that subadult survival in a given year varied in concert with adult survival.

The third parameter is probability of breeding. Detailed observations demonstrate that once having bred, all adults (or more than 99%) attempt to breed in subsequent years (Pyle et al. 1991), even in poor food years.

The fourth parameter is age of first breeding. Three cohorts of gulls were closely followed from birth to recruitment age (Spear, Sydeman, Pyle, unpublished). These data indicate that age of first breeding varied mainly from 3 to 6 years, with a mode at age 4 and median at age 5. We used the observed frequency distribution of age of first breeding, combined with adult survival, to infer the age-specific probability that a gull that had never bred would attempt to breed at that age (see Table 2 for these
Table 2. Demographic parameters for Western Gulls

<table>
<thead>
<tr>
<th>Age</th>
<th>Reproductive Success, i.e. Chicks fledged/Pair</th>
<th>Survival</th>
<th>Breeding Prob. if nulliparous&lt;sup&gt;1&lt;/sup&gt; (Per cent)</th>
<th>Breeding Prob. if experienced&lt;sup&gt;2&lt;/sup&gt; (Per cent)</th>
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<sup>1</sup> - Probability that an individual attempts to breed, if it has never bred before.

<sup>2</sup> - Probability that an individual attempts to breed, if it has bred earlier in its life.
probabilities). Age-specific probability of breeding did not vary from cohort to cohort, and so this distribution was considered fixed.

The fifth parameter, chicks fledged per breeding pair was determined from PRBO’s extensive data (21 years). On average, 1.29 chicks are raised per pair per year, but this parameter varies with age of the (male) parent (Pyle et al. 1991, PRBO unpublished); reproductive success also varies from year to year depending on food conditions (Sydeman et al. 1991; see below). Age-specific reproductive success is shown in Table 2, based on PRBO observations and after smoothing out the pattern. The number of chicks fledged per pair increases substantially from age 3 to age 9, then declines until age 16. Three year olds thus make little contribution to future population growth.

The sixth parameter, post-fledging survival, was derived from band recovery data (estimate of 50%, Spear et al. 1986) and direct observation of individually marked gulls (estimate of 61%, Spear & Nur 1994). An average of both estimates yielded first-year survival of 55.5%. This figure, in conjunction with other parameter values enumerated above, produces a slowly declining gull population (on average), consistent with observations of the last several years (see Appendix, Figure 2). In other words, we have validated the model using recent, historical data. There is no evidence of annual variation in post-fledging survival (Spear & Nur 1994), but because post-fledging survival is not known with certainty we allowed this to vary randomly in each year, between 50 and 61% (the lower and upper estimates).

**Brandt’s Cormorant:**
For this species, we have modeled females, the conventional sex for Leslie matrix modeling. Our reasoning is the same as that stated for Common Murres, i.e., we assume that reproductive potential of a species is limited by females, which is consistent with observations on this population. Because cormorants are strictly monogamous (and thus reproductive success is the same for the two sexes) and because the sexes are similar in survival, there is little difference in predictions based on using one sex or the other for the modeling.

With regard to adult survival, we have extensive observations (from 15 years) on marked individuals of the Farallon population. These data indicate a lack of age-specificity of survival (Nur et al. 1993), except that old Brandt’s Cormorants (like old Western Gulls) show reduced survival rates. The data also indicate substantial between-year variation in adult survival (averaged over all ages), which we have incorporated into the model (see below). The best estimate of female survival, based strictly on our observations of marked individuals, is 72%, compared to 76% for males (Nur et al. 1993). These estimates take into account the fact that adult Brandt’s Cormorants often skip breeding between years (Boekelheide & Ainley 1989), and thus, that some birds, who may have been alive in a given year, might have been
missed that year. The estimates do not, however, take into account dispersal from one colony to another, either within the Farallon Islands or between the Islands and colonies elsewhere. *Phalacrocorax* spp. (the genus that includes cormorants and shags) show a considerable amount of dispersal of breeders, as documented by Carter et al. (1992, pages 120-126). Thus, our survival estimate is biased downwards. Consequently, in the model, we have used an average adult survival of 82%, the same as reported by Potts et al. (1980) in a study of another cormorant, the European Shag (*Phalacrocorax aristotelis*). Adult survival of less than 82% (using parameter values listed below) would result in a declining population, contrary to observations of 1984 - 1991. In other words, we have validated the model (and use of this parameter value) using recent, historical data. Age-specific survival used in the model is shown in Table 3. Few individuals (and no females) have been observed at ages beyond 15, hence, we assume none survive past this age (Table 3).

For the survival of subadults (one-year olds) we used an estimate obtained from the European Shag, 75% (Potts et al. 1980). This is about 90% that of the adult figure, just as was the case among one-year old Western Gulls. As with Common Murres and Western Gulls, we assumed subadult survival in a given year varied in concert with adult survival. Additionally, observations on Brandt’s Cormorants marked as chicks demonstrated that apparent survival to age 2 and beyond does vary markedly between cohorts.

The third parameter is probability of breeding, given that an individual has bred earlier in its life. In the first place, adult Brandt’s Cormorants often skip breeding (if they have bred before) and secondly, the probability they do so varies between years (Nur, Sydeman & Ainley 1993), being related to food conditions (see below). From our data we estimated that 33% of previous breeders did not attempt breeding in a given year, but we modified this to 23% in the model, on the assumption that females might have dispersed and bred elsewhere (see above). That is we assumed that 30% [= (.33-.23)/.33] of all experienced individuals not observed breeding in a given year, but thought to be alive, may have bred elsewhere, either because they dispersed or because we failed to identify them. We justify the use of 23% for that fraction that skip breeding in a given year because this parameter, when used in the model in conjunction with other parameter values, replicates observed population behavior of this species. In other words, we have validated the model using recent, historical data. We have assumed that the probability of breeding is not age-specific, with one exception: Because all females who bred at age 2 and survived to age 3 were observed breeding as 3 yr olds (i.e., none were known to have skipped, PRBO unpublished), we assumed that breeding probability was 100% for 3 yr olds with breeding experience (Table 3).

The fourth parameter is age of first breeding. Observations on 14 cohorts of banded Brandt’s Cormorants indicated that females commonly first breed at ages 2, 3, 4 and 5
Table 3. Demographic parameters for Brandt’s Cormorants

<table>
<thead>
<tr>
<th>Age</th>
<th>Reproductive Success, i.e. Chicks fledged/Pair</th>
<th>Survival</th>
<th>Breeding Prob. if nulliparous(^1) (Per cent)</th>
<th>Breeding Prob. if experienced(^2) (Per cent)</th>
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<tbody>
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<td>N/A</td>
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</tbody>
</table>

\(^1\) Probability that an individual attempts to breed, if it has never bred before.

\(^2\) Probability that an individual attempts to breed, if it has bred earlier in its life, averaged over all years. This probability varies from year to year depending on food availability (see text).
(Boekelheide & Ainley 1989; Nur, Sydeman & Ainley unpublished). On the basis of our data we inferred that 20% of breeders first bred at age 2, 30% at age 3, 32% at age 4, and 17% at age 5. This parameter was incorporated into the demographic matrix (Table 3). Because of lack of data on year-to-year variation, this distribution was assumed fixed in each year (as was done for the other two species).

The fifth parameter, chicks fledged per breeding pair was determined with reference to PRBO’s extensive data (21 years; Ainley & Boekelheide 1990; PRBO unpublished). Only two-year olds showed lower reproductive success than older adults: their reproductive success was set at 0.75 compared to 1.50 for all older adults, this being the mean value observed for three and four year old females. Furthermore, reproductive success varied from year to year depending on food conditions (see below).

The sixth parameter, post-fledging survival was derived from the literature, based on band recovery data (Potts 1969); we used an average value of 59% (the same as reported for the European Shag on Farne Islands), but allowed this to vary between years, in proportion to variation in survival of one-year olds. Furthermore, our data demonstrated that variation in apparent survival of chicks to age 2 is significantly related to food conditions in the year of hatching (Nur, Sydeman, Ainley, unpublished).

Density dependence:
Though food is thought to limit population numbers in many seabird species, including Farallon seabirds at present (see Appendix, pages 14-16), this does not necessarily imply density dependence. Nevertheless, there are likely to be limits on population size in the foreseeable future for at least one species, the Western Gull. For Western Gulls, the primary limitation is nesting space. Currently, Western Gulls have saturated all available nesting space on Southeast Farallon Island. Even if additional breeders are able to insert themselves into the breeding population they would likely only obtain territories of poor quality, and hence have low breeding success. Breeding numbers have actually declined in recent years, due possibly to encroachment by pinnipeds and murres (see Appendix, page 12 therein). The demographic model predicts that on average, Western Gull numbers will continue to decline, if current conditions hold. If breeding numbers should increase, however, a ceiling is set with respect to the reproductive output of the entire island, that ceiling corresponding to the output of 22,000 breeders (the maximum observed in recent years and 16% greater than the 1992 level). The ceiling is assumed to be an output of 14,190 chicks (=11,000 pairs x 1.29 chicks per pair, the average reared per pair). In
other words, in the model, if the number of breeders should increase by 30% (relative to the present), resulting in 24,600 breeders the reproductive success per pair, all else being equal, would have to decrease by a percentage such that no more than 14,190 chicks are reared, on average. In this case, reproductive success per pair would have to decrease by 10.6%. Likewise, if the number of breeders should increase by 50% (relative to the present), resulting in 33,000 breeders, reproductive success per pair, all else being equal, would decrease by 33%. Any increase in breeding population size less than 16% would have no effect on per pair reproductive success.

For Common Murres, there is not likely a limit to population size in the foreseeable future. In 1982, when the murres were hit hard by gill-netting and El Niño, the population was nearly three times its current level (Appendix, Figure 2) and was showing no signs of density dependence (PRBO unpublished). It would take the population about 53 years just to double its size, under current conditions (assuming environmental constancy) and assuming no additional mortality. Since population levels at least three times present number would be required before any density dependence might be credibly invoked, and since the time horizon of the Farallon Seabirds model is 20 years, we have not included density dependence in the model for Common Murres.

In the 1970’s, the population of Brandt’s Cormorants was twice or even three times its current level (see Appendix, Figure 2). Current population levels are low (a breeding population of 12,000 or less) and the population shows no sign that it is capable of much growth, a point that is confirmed by the demographic model (see Examples 1, 3, and 4, discussed below). Because it is extremely improbable that Brandt’s Cormorants would be able to double or triple their numbers in the near future (and because survival and reproductive success showed no density dependence during the higher population levels of the 1970’s), we have not incorporated any density dependent limits on population size for this species, either.

Inter-annual variation of food and environmental conditions

This section describes the “food” component of the computer model. Earlier sections of this document reported that reproductive success for all three species varied annually and was related to environmental conditions, which affect prey availability; as expected, greater prey availability resulted in better reproductive success (Ainley & Boekelheide 1990; PRBO unpublished). Additional demographic parameters that have been found to be related to prey availability include: survival of adult Common Murres, survival and breeding probability of adult Brandt’s Cormorants, and survival
of juvenile Brandt's Cormorants (Nur et al. 1993; PRBO unpublished).

**Indices of prey availability and environmental conditions:**
We have access to three distinct indices of prey availability in each year: abundance of juvenile rockfish (*Sebastes* spp.), the preferred prey item for chick-feeding (Ainley & Boekelheide 1990), as sampled by National Marine Fisheries Service (NMFS) trawls in each spring (Adams 1992); the number of juvenile rockfish in king salmon (*Oncorhynchus tshawytscha*) stomachs, these data collected by NMFS as well (Adams 1992); and the percent of prey items fed to murre chicks that were rockfish (Ainley & Boekelheide 1990; Ainley et al., unpublished). All three indices correlated with each other, providing validity to each index, and indicating that each was, in part, sampling some common environmental variation. For example, a 1 unit change in the log juvenile rockfish trawl index is approximately equal to a 12.44 unit change in the murre diet index (Figure 5).

In the model we have used "murre diet" as our index of prey availability, both because we have the longest time series for this index and because this index generally correlated best with demographic parameters of the three seabird species (Nur et al. unpublished). Further information about the use of murre diet as an index of food availability is provided in Ainley et al. (1993) and Sydeman et al. (1991). Murre diet is well-correlated with reproductive success of each study species, as would be expected if murre diet provides a good index of overall food availability. One reason for the success of murre diet at predicting reproductive success of other seabird species is that, during the chick-rearing period, Farallon seabirds show high diet overlap (Ainley & Boekelheide 1990: Appendix 3.5 therein).

Prey availability was in turn related to oceanographic conditions. El Niño-like conditions in the Gulf of the Farallones lead to reduced prey availability (Ainley & Boekelheide 1990). (Some years in which local conditions were El Niño-like, e.g., 1978, were not officially deemed El Niño years, and other years [e.g., 1976] that were official El Niño years did not manifest themselves as anomalous in the Gulf of the Farallones [Ainley & Boekelheide 1990, Chapter 2].) Two indices of oceanographic conditions are sea surface temperature (SST) at the Farallones in March and sea level in February (Ainley & Boekelheide 1990:36-44). Use of these indices of oceanographic conditions is also discussed in Ainley et al. (1993). The two indices are highly correlated and we have used SST in March as the model's oceanographic index; there is a strong statistical relationship between SST and prey availability (murre diet index). Use of February sea level, in addition to March SST, does not appreciably improve our predictive power. SSTs at other times of year do not correlate with
Figure 5. Murre diet in relation to estimates of juvenile rockfish abundance as determined by NMFS trawls (Adams 1992, PRBO unpublished); see text. The statistical relationship shown is significant ($P = 0.046$; regression analysis). The relationship is approximately linear, such that murre diet index increases 12.44 units with a one unit increase in the juvenile rockfish index.
measures of prey availability nor do they correlate with seabird demographic variables.

**Structure of the model:**
In the model, SST is chosen for each year from a probability distribution based on the past 22 years of data (1971-1992; see also User’s Manual, Figure 6 therein). As a result, SST varies randomly from one year to the next and one year’s SST does not influence the next year’s SST. This aspect of the model is justified since there was no indication of autocorrelation among SSTs or sea level or among murre diet scores (P > 0.3 for lags of one, two or three years); that is, knowing SST (or murre diet) in one year did not help one predict what next year’s SST (or murre diet) would be. Next, the model chooses a murre diet value for that year, based on the regression relationship between murre diet index and SST, incorporating random variation about the regression line. Then each of one to three demographic parameters (depending on the seabird species) is derived from the observed statistical relationship between that parameter and two independent variables: SST and murre diet index (see below). Figure 6 provides one example, reproductive success of Common Murres in relation to SST and murre diet index. For each demographic variable, random variation in the model is incorporated about the predicted multiple-regression equation, as determined by the observed variation of that parameter about the regression line. For example, when murre diet index is low we expect reproductive success to be low, too, but there will still be some random variation about any predicted value of reproductive success. The same holds for the effect of SST on demographic variables.

Thus, in the model, SST influences demographic parameters in two ways: indirectly, by influencing prey availability (as measured by murre diet index), which in turn influences demographic parameters, and directly, by a second pathway, independent of SST’s effect on murre diet. As a result, demographic parameters in the model exhibit (1) correlation with food and environment, (2) covariation among the parameters (survival and fecundity both tend to increase when conditions are good), and (3) additional, unpredictable variation. We believe that these are important features for a predictive population model. In addition, it is important to distinguish between the effect of prey availability, as measured by murre diet index, and the more widespread effects (in time and space) of ENSO events. Murre diet index reflects availability of one prey type (juvenile rockfish) at one time of year (spring) whereas SST measures oceanographic anomalies that have more diffuse consequences. In any case, the multiple regression analyses indicate that both murre diet and SST make significant, independent contributions to explaining annual variation in seabird demographic variables.
Figure 5. Common Murre reproductive success in relation to murre diet index and March Sea Surface Temperature (SST; PRBO unpublished). Murre diet index is the proportion of prey fed to murre chicks that is juvenile rockfish, measured in percent. March SST is measured in degrees, Celsius. Both murre diet and SST, considered individually, are significantly correlated with murre reproductive success (n = 20 years, \( P < 0.01 \)). Taken together the two variables explain 52% of the annual variation in murre reproductive success (\( P = 0.01 \)). Part A shows the influence of murre diet on reproductive success, while controlling for the effect of SST on both variables. Part B shows the converse, the effect of SST on murre reproductive success, while controlling for the effect of murre diet index. Thus this figure shows partial regressions, analogous to partial correlations, for two variables while controlling for a third. Data points (triangles) are from individual years; also shown are regression lines of best fit.
The demographic parameters that are generated using the multiple regression approach are: reproductive success for each species, adult survival of murres, and adult survival and breeding probability of Brandt’s Cormorants. On the basis of observations at the Farallones, we assume that when conditions are poor (murre diet value is less than 16, for a scale that varies between 0 and 100, with 100 being the best possible score), only 60% of murres attempt to breed (see above). Western Gulls always attempt breeding (Pyle et al. 1991; see above). For Brandt’s Cormorants, breeding probability varies with SST and murre diet index (Nur et al. 1993; see above). Post-fledging survival (to age 1) and subadult survival are assumed to fluctuate in parallel with adult survival for all species (see above).

Perturbation of food and the environment:
With the food component of the model, prey availability can be altered and the consequences observed in one of two ways. Examples 3 and 4 (see below) demonstrate the two types of perturbation. In the first type of perturbation, there is a change in prey availability itself, as indicated by a change in the murre diet index.

In the example discussed (Example 3) we assume a drop in the murre diet index of 12.44 units, corresponding to a drop in the log rockfish trawl index of 1 unit overall (Figure 5). Since the trawl index measures abundance of juvenile rockfish on a \( \log_{10} \) scale (Adams 1992), this scenario corresponds to a ten-fold drop in abundance of juvenile rockfish in NMFS trawl nets, which may or may not correspond to a ten-fold drop in actual abundance of juvenile rockfish. Example 3 tracks the consequences of a persistent drop in prey availability of this magnitude for the three seabird species.

In the second type of perturbation, oceanographic conditions can be altered by specifying a change in the distribution of SST values. We have categorized oceanographic conditions as "good" (low SST, characterized by cold water), "poor" (high SST, corresponding to strong El Niño events), and "moderate" (intermediate between "good" and "poor") (Figure 7). For each of the three oceanographic states there is a corresponding range of SST values (e.g., poor years are those with SST greater than or equal to 13.6\(^\circ\)). Rather than allowing SST to vary randomly across the entire spectrum, the user can specify a specific combination of good, poor or moderate years. Example 4 gives examples of such perturbations and their consequences for seabird species.

Four Examples

To illustrate the use of the model, we present several different scenarios. Each of the
Figure 7. Frequency distribution of March sea surface temperature (SST) used by the model. Years have been classified into "cold water" ("good" years from the point of view of seabird demography, symbolized "N" in the Farallon Seabirds user interface), "severe" (symbolized "S" in the user interface, corresponding to very poor years in terms of environmental conditions for seabirds), and "moderate" (symbolized "M", years that are intermediate between N and S).
first three examples considers each species in turn and uses the same time scale, extrapolating ten years into the future. The first example is a simulation assuming that current conditions are maintained but allowing for typical environmental variation from year to year. In the second example, we consider the effects of a large oil spill, near the Farallones, in March. This example was treated earlier, with regard to the toxic spill module. The toxic spill module predicted that 15.3% of Common Murres, 0.67% of Brandt’s Cormorants and 0.06% of Western Gulls in a specified region (between 36° and 38°30’, from Fort Ross to Point Sur) would be killed by the simulated spill. Therefore, the demographic module for each species tracks the recovery of the population assuming 15.3%, 0.67% or 0.06% of the Farallon population, respectively, has died just before the breeding season. The third example is of a sustained drop in prey availability (i.e., reduction in the murre diet index) during the breeding season, such as might occur either with a change in fishing pressure or change in environmental conditions (see Appendix, pages 14-16, 19-21). The fourth, and final example, considers changes in the pattern of ENSO events for Brandt’s Cormorants (the species most sensitive of the three to ENSO perturbation) and Western Gulls (the species least sensitive of the three).

**Status Quo, Example 1:**
The population trajectory from Example 1 (Status Quo) is shown in Figures 8, 9, and 10, for each species in turn. The best estimate (median outcome) for each year is shown as well as upper 10% (90th percentile) and lower 10% (10th percentile) bounds. The starting total population size for Common Murres at present (1993) is estimated to be 59,200 on the basis of trends in breeding numbers between 1984 and 1991. (The 1992 breeding numbers were unusually low, presumably because of reduced breeding effort, see above; it is not clear yet whether the 1993 breeding censuses for the three species provide an unbiased basis for estimating total population size and so, for the time being, we have not used the 1993 data to estimate total population size.) In the simulation, the population size in year 0 is 59,200. Figure 8 indicates a wide variation of possible outcomes: there is a 10% chance murre numbers would decrease to 46,700 or less (that figure marking a 21% decline over a ten-year period), and an equal probability of an increase to 90,400 or more (a 53% increase over 10 years). The best estimate of future growth is provided by the median outcome: population growth greater than the median is as likely (by definition) as population growth less than the median. The model can also provide a mean estimate of future population growth, in this case the geometric mean, but for simplicity we have omitted mean values from Figures 8 - 20 and only present 10th percentile, median and 90th percentile outcomes. The median outcome in this scenario (population of 66,000) is a 12% increase over 10 years, representing an
Figure 8. Example 1: Common Murres. Population trajectories under the status quo. Shown are the the 10th, 50th and 90th percentile outcomes for total population size during the breeding season, in each of ten years subsequent to year 0. Population size for year zero (present) is assumed to be 59,200 on the basis of trend data 1984 - 1991.
average increase of 1.1% per year. The variation in results is in part due to unpredictability of food (environmental) conditions. The model is most useful when used to contrast this scenario (Status Quo) with others, as discussed below.

For Brandt’s Cormorants there is also a wide variation of possible outcomes (Figure 9): there is a 10% probability that the population would increase to at least 39,300 (97% greater than the current level of 19,900), and an equal probability that the population would decrease to 8,700 or fewer, less than half current level (i.e., a decline of 56%). The best estimate, however, is of a gradual decrease to 19,300 individuals, or a decrease of 3.0% over ten years, i.e., 0.3% per year. As with murres, the great variability in results is due, in part, to unpredictability of food.

Western Gulls show considerably less variation in outcome (Figure 10). The best estimate is that the gull population will decrease to 36,700 compared to a current level of 38,900 (a 5.7% drop over 10 years, or 0.6% decline per year). There is a 10% probability that the population will increase to at least 46,200 (a 19% increase over 10 years), and a 10% probability that it will decrease to 29,300 or fewer (a decrease of 25%). Thus we have reasonable confidence that the Western Gull population will number between 29,000 and 46,000 over the next ten years. Gull population size is more predictable than the other two species because Western Gull demography is less sensitive to annual variation in food: only reproductive success has been shown to be related to environmental conditions for this species.

Observations of breeding numbers of Western Gulls over the past two decades confirms that population size is apparently quite stable (Appendix, Figure 2) thus validating predictions of the model. In contrast, numbers of Brandt’s Cormorants and Common Murres have fluctuated widely over the past two decades (Appendix, Figure 2), these observations also confirming predictions of the model.

**Impact of a simulated oil spill, Example 2:**
The population trajectory resulting from the simulated oil spill is shown in Figures 11, 12 and 13. The best estimate (median outcome) for each year is shown as well as upper 10% (90th percentile) and lower 10% (10th percentile) bounds. The spill was assumed to occur in March of year 1 (i.e., just before the breeding season). In the breeding season of year 1 (i.e., soon after the spill) murre numbers average about 49,600 (Figure 11). As can be seen, though, there is great variability about population size even after a spill of fixed mortality (among murres alive in March of year 1, 15% died). On average, the population recovers to 56,000 (95% of the pre-spill level) by year 10. What is worth noting is that murre numbers would have been about 66,000 (on average) without the spill (see Status Quo, Example 1), hence the population in
Figure 9. Example 1: Brandt’s Cormorants. Population trajectories under the status quo. Shown are the 10th, 50th and 90th percentile outcomes for total population size during the breeding season, in each of ten years subsequent to year 0. Population size for year zero (present) is assumed to be 19,900 on the basis of trend data 1984 - 1991.
Figure 10. Example 1: Western Gulls. Population trajectories under the status quo. Shown are the 10th, 50th and 90th percentile outcomes for total population size during the breeding season, in each of ten years subsequent to year 0. Population size for year zero (present) is assumed to be 38,900 on the basis of trend data 1984 - 1991.
Figure 11. Example 2: Common Murres. Population trajectories assuming a major oil spill in March of year 1 (see text). Shown are the 10th, 50th, and 90th percentile outcomes for total population size during the breeding season, in each of ten years subsequent to year 0. Population size for year zero (present) is assumed to be 59,200 on the basis of trend data 1984 - 1991.
year 10 is about 15% below what it would have been in the absence of a spill. There is also a 10% chance of 39,600 or fewer murres after 10 years, i.e., no recovery at all, and instead a decline of 33% compared to pre-spill numbers.

The impact of the simulated oil spill on Brandt's Cormorants or Western Gulls is negligible and is easily swamped by natural variability in numbers (Figures 12 and 13). This is because less than 1% of Brandt's Cormorants died in the spill and only 0.06% of Western Gulls died. Thus in year 1, the model predicts about 20,500 Brandt's Cormorants soon after the spill (Figure 12), but about 20,700 in the absence of a spill (status quo; Figure 9). In contrast, the 10th percentile and 90th percentile outcomes in year 1, in the absence of a spill, are much broader: 14,000 and 26,000, respectively. By comparing Figure 9 with Figure 12 and Figure 10 with Figure 13, one can see that the trajectories with or without a spill are very similar. The simulated oil spill was off-shore, but we can expect that a near-shore simulated spill would kill more Brandt's Cormorants than in this example, since this species is concentrated near to the shore, at least in March (Figure 3). In summary, of the three species considered, murres are likely to suffer the greatest mortality in absolute and relative terms, but, according to parameters of the demographic model, they have reasonably good recovery prospects.

Impact of reduced prey availability, Example 3:
The population trajectories after a chronic (ten-year) decrease in prey availability are shown in Figures 14, 15 and 16. The change in prey availability is implemented in the model by specifying a change in the murre diet index but this can be equated with a corresponding change in fish abundance. In this scenario, we have assumed a one-unit decrease in log abundance of short-belly rockfish (the "trawl index," derived from the work of NMFS trawls [Adams 1992, see above], over each of the next ten years. Over a nine-year period (Adams 1992) the trawl index varied from -1.45 to 2.96 ($\bar{X} = 1.08$); thus the reduced-fish scenario is equivalent to the index ranging from -2.45 to 1.96 ($\bar{X} = 0.08$). A one unit change in the trawl index, in turn, is equivalent to a change in the murre diet index by 12.44 units (the murre index varies from 0 to 100; Figure 6). The best estimate (median outcome) is shown for each year, for each species, as well as upper 10% (90th percentile) and lower 10% (10th percentile) bounds.

For Common Murres, the expected outcome after 10 years of reduced food availability is 55,100 murres, almost the same as ten years after a major oil spill (Figure 14). That is, instead of a 12% increase over the course of a decade (status quo), we would expect a 6.9% decrease. There is also a 10% chance that numbers
Figure 12. Example 2: Brandt’s Cormorants. Population trajectories assuming a major oil spill in March of year 1 (see text). Shown are the 10th, 50th, and 90th percentile outcomes for total population size during the breeding season, in each of ten years subsequent to year 0. Population size for year zero (present) is assumed to be 19,900 on the basis of trend data 1984 - 1991.
Figure 13. Example 2: Western Gulls. Population trajectories assuming a major oil spill in March of year 1 (see text). Shown are the 10th, 50th, and 90th percentile outcomes for total population size during the breeding season, in each of ten years subsequent to year 0. Population size for year zero (present) is assumed to be 19,900 on the basis of trend data 1984 - 1991.
Figure 14. Example 3: Common Murres. Population trajectories assuming reduction of prey availability starting in the beginning of year 1 (see text). Shown are the 10th, 50th, and 90th percentiles for total population size during the breeding season, in each of ten years subsequent to year 0. Population size for year zero (present) is assumed to be 59,200 on the basis of trend data 1984 - 1991.
would be 37,800 or fewer (36% decrease compared to numbers in year 0). On the other hand, there is a 10% chance that despite an overall reduction in prey availability, the population might still increase to 77,000 after 10 years (a 30% increase over this time period).

Brandt’s Cormorants also show a strong effect of reduced prey availability (Figure 15). After 10 years, we would expect a population size of 14,500, a 27% decrease in numbers compared to the numbers in year 0, and a 25% decrease compared to the status quo predictions. At the same time, there is a 10% probability that Brandt’s Cormorant numbers would increase to 30,000 or more (an increase of 46% over a ten year period), despite the overall reduction of food availability. This outcome can be compared to the 90th percentile outcome under status quo conditions, 39,300. There is a 10% probability that with reduced prey availability, Brandt’s Cormorants would decrease to 6,600 or fewer in year 10, a 67% decrease compared to their numbers in year 0, and 2,100 fewer individuals than the 10th percentile outcome under the status quo.

Finally, for Western Gulls, reduced prey availability (as indexed by murre diet) is predicted to have a weak effect on their population trajectory (Figure 16). The best estimate is that of 34,400 gulls in year 10, a decrease of 12% over a ten year period, compared to the estimated decrease of 6%, under assumptions of the status quo. Similarly, the upper and lower bounds (90th and 10th percentile outcomes) are 2,000 to 3,000 lower than respective values under the status quo. The fact that the predicted population size of Western Gulls is only weakly depressed by reduction in fish abundance reflects the fact that Western Gull demography is not strongly related to a single prey type (juvenile rockfish) or to oceanographic conditions, the way the other two species are.

**Change in oceanographic conditions (El Niño), Example 4:**
The default condition is for SST, the index of oceanographic condition, to be selected from the natural range of SST values observed over a 22 yr period. The user can specify, instead, that a given year is "good", "poor" or "moderate"; this can be done for any sequence of years, as well. Within each category, if so designated, there is still stochastic variation in the SST value for a year, but that variation is constrained. For example in "good" years, SST varies between 9.8°C and 11°C, compared to the total, natural range of 9.8°C to 14.3°C. As a result of such a change in SST, the index of prey availability will be affected as well (see above). Figures 17 and 18 show the predicted population trajectory of Brandt’s Cormorants and Western Gulls, respectively, if each of ten years is moderate (no good or poor years; Example 4A).
Figure 15. Example 3: Brandt’s Cormorants. Population trajectories assuming reduction of prey availability starting in the beginning of year 1 (see text). Shown are the 10th, 50th, and 90th percentiles for total population size during the breeding season, in each of ten years subsequent to year 0. Population size for year zero (present) is assumed to be 19,900 on the basis of trend data 1984 - 1991.
Figure 16. Example 3: Western Gulls. Population trajectories assuming reduction of prey availability starting in the beginning of year 1 (see text). Shown are the 10th, 50th, and 90th percentiles for total population size during the breeding season, in each of ten years subsequent to year 0. Population size for year zero (present) is assumed to be 38,900 on the basis of trend data 1984 - 1991.
Figure 17. Example 4A: Brandt’s Cormorants. Population trajectories assuming all years are “moderate” (see Figure 7), i.e., environmental variability is reduced. Shown are the 90th, 50th and 10th percentile outcomes for total population size during the breeding season, in each of ten years subsequent to year 0. Population size for year 0 is assumed to be 19,900 on the basis of trend data 1984 - 1991.
Figure 18. Example 4A: Western Gulls. Population trajectories assuming all years are "moderate" (see Figure 7), i.e., environmental variability is reduced. Shown are the 90th, 50th and 10th percentile outcomes for total population size during the breeding season, in each of ten years subsequent to year 0. Population size for year 0 is assumed to be 38,900 on the basis of trend data 1984 - 1991.
The effect of such a change in oceanographic conditions is to reduce variability in outcome without affecting the median outcome much, as can be seen by comparing Figure 17 with that of Figure 9 and Figure 18 with Figure 10. For example, under the status quo, Brandt’s Cormorant population size varies between 38,600 (90% outcome) and 8,800 (10% outcome), whereas in the absence of good and bad years, the 90% and 10% outcomes are not nearly so divergent, 29,400 and 13,300, respectively. The trend is the same for Western Gulls, i.e., to display reduced variability of outcome when all years are moderate, but the effect is not nearly so marked (cf. Figures 10 and 18).

Figures 19 and 20 display the projected population trajectories of Brandt’s Cormorants and Western Gulls, respectively, if good and bad years alternate, with no moderate years at all (Example 4B). Comparison of Figures 19 and 20 indicates that Brandt’s Cormorants track oceanographic conditions very closely, whereas Western Gulls do so to a less marked degree. In a bad food year, the 10%, 50%, and 90% outcomes for Brandt’s Cormorants all decrease sharply compared to the previous year, whereas in a good food year, the same set of outcomes all increase sharply. For Brandt’s Cormorants, the overall trend, for a sequence of alternating good and bad years is a long-term decline. This result should not be taken to imply that environmental variability is less conducive for maintaining Brandt’s Cormorant numbers than environmental stability. Rather, "poor" years in the model represent an extreme: only four out of 22 years (18%) were classified as poor (see Figure 7). Good years were represented in seven out of 22 years (32%). Thus Figures 19 and 20 indicate the long-term effects of "very poor" years (worst 18% in the historical record) alternating with "relatively good" years (best 32% in the historical record).

Uses/applications of the model

The following is an outline of possible uses and applications of the model. The range of applications is very broad; the authors would be happy to consult with GFNMS staff on specific applications. Example 1, above, provides one application of the model: to project future population trends for the three species, assuming no overall change in conditions. A second application is to predict the short-term and long-term consequences of an oil spill, as in Example 2. Different scenarios can be simulated in which characteristics of the spill are varied (size of spill, location of spill, type of oil, season). Also, more than one oil spill can be modeled by the demographic module. Alternatively, one can model the long-term consequence of an oil spill where the mortality is precisely known (or assumed). This leads to a third application: one can specify a one-time mortality event of known or unknown cause. The mortality, for example, may be a result of red tide or gill-netting. Here "one-time" refers to a
Figure 19. Example 4B: Brandt's Cormorants. Population trajectories assuming "good" and "poor" years alternate (see Figure 7 and see text), i.e., the environment varies between two extremes. Shown are the 90th, 50th and 10th percentile outcomes for total population size during the breeding season, in each of ten years subsequent to year 0. Population size for year 0 is assumed to be 19,900 on the basis of trend data 1984 - 1991.
Figure 20. Example 4B: Western Gulls. Population trajectories assuming "good" and "poor" years alternate (see Figure 7 and see text), i.e., the environment varies between two extremes. Shown are the 90th, 50th and 10th percentile outcomes for total population size during the breeding season, in each of ten years subsequent to year 0. Population size for year 0 is assumed to be 38,900 on the basis of trend data 1984 - 1991.
relatively short period of time (confined to part of one year).

A fourth application is to predict the consequences of a long-term change in survival or fecundity parameters. For example, survival might be decreased or increased by 10% relative to its baseline value. Such a change in parameters might be warranted if a persistent mortality factor arose (or disappeared) or a current factor increased or decreased in severity. For example, one might project the consequences of a 10% reduction in murre reproductive success due to an increase in gull predation. In addition, this provides a mechanism to alter predictions of the model if more recent information becomes available regarding survival and fecundity parameters.

A fifth application is illustrated by Example 3, predicting the consequences of a change in prey (fish) availability, such as might result from a change in fishing practice or change in environmental conditions. The sixth area of application that we mention concerns modeling the effects of oceanographic anomalies, e.g., predicting the consequences of a given year being a strong ENSO event. This can be done for any number of years (up to 20). Examples 4A and 4B presented other patterns of oceanographic anomaly. Finally, these applications can all be combined, e.g., the effect of an oil spill, together with a chronic decrease in reproductive success due to gull predation, and a strong ENSO event, all in the same year.

Management Implications

The seabird computer model indicates the future course of each species, assuming current conditions hold, and gives, as well, an indication of variability around the best estimate. Thus, for Brandt’s Cormorants we expect that on average numbers for this species will remain stable, yet there is a 10% chance that, with no perturbations, population size will decrease to less than half what it is now. With oil spills or reduction in fish stocks, the decrease would be even greater. This result should be incorporated into any management plans for this species. To a lesser degree, Common Murres show variability in their population trajectory, whereas Western Gulls show the greatest predicted stability.

Population size of Western Gulls on the Farallon Islands is of some concern since gulls have an adverse impact on other breeding seabirds. The model indicates that, if current conditions hold, it is unlikely that Western Gulls will increase much beyond 45,000 gulls, which corresponds to a breeding population of 22,000, the maximum observed between 1987 and the present (Appendix, Figure 2).

The model also indicates the great sensitivity of Common Murres to oil spills,
whereas Western Gulls are quite insensitive. The apparent insensitivity of Brandt’s Cormorants to an oil spill is due in part to our simulating an off-shore oil spill. The model can be used to show that Brandt’s Cormorants are very sensitive to a large one-time mortality event, that is, they would not likely be able to recover from a die-off. This was not evident in any of our scenarios because in none was there any large-scale mortality of this species. Brandt’s Cormorants lack the ability to recover because, on average, the production and survival of young does not exceed that required to balance mortality. To enhance the ability of Brandt’s Cormorants to recover would require improving fecundity or survival of individuals.

The model indicates to what extent Brandt’s Cormorants and Common Murres are sensitive to changes in food availability. Such information should be considered with respect to any future fisheries, especially rockfish fisheries. We note that even with a drop in the overall level of food available (as in Example 3), there is a 10% chance Brandt’s Cormorants would increase by 46% over a ten-year period. An implication of this result is that a short-term increase in the population size (due to several favorable years occurring in a row) does not give an indication of what the long-term impact of a perturbation will be. We feel this is an important result indicating limitations on the use of short-term changes in seabird populations to indicate the health of that population, or of the underlying resource. Conditions may actually deteriorate (e.g., a decline in prey availability) yet the population may show a positive response over the near-term. For instance, an oil spill may kill thousands of seabirds of a species, yet the population may still increase from one year to the next. Therefore, the mere evidence of a population increase over a short period of time cannot be taken to indicate the lack of mortality attributable to an oil spill or other die-off; as shown in Example 2 (above), substantial mortality may be masked by population increases, especially due to favorable environmental conditions.

Caveats and Limitations

The model is intended to project into the near future (the next decade or two), assuming current conditions hold (except as explicitly modified by the user). It would not be suitable for modeling Farallon seabird populations in the past, e.g. the 1970’s, unless one modified demographic parameters appropriately. This caveat is especially applicable to murres, which until 1982 were growing at a fast rate, 8 to 10% per year, but currently are growing at a slow rate (less than 2% per year; see Appendix, Figure 2). Modifying demographic parameters, so as to model the population in the 1970’s, is no simple matter, however, because we have no information on murre survival or age of first breeding during the 1970’s. At the same time, it would not be possible for a murre population to grow at 8 to 10% per
year--unless some of the parameters values used in the model were altered.

At the same time, excessive extrapolation into the future is unwarranted. One can, in theory, project 30, 50, or even 100 years into the future, but it is very unlikely that all demographic parameters will remain constant during that time. In fact, Farallon seabird species have demonstrated that demographic parameters are likely to change over a period of 10 to 20 years. For example, Western Gull reproductive success is lower in recent years than in the 1970’s (Sydeman, et al. unpublished). Common Murre survival and/or age of first breeding have undoubtedly changed between the 1970’s and the late 1980’s. Similarly, Hatchwell & Birkhead (1991) observed changes in survival and reproductive success of the Skomer population of Common Murres between the mid 1970’s and the late 1980’s.

An important limitation of the model is that the oil spill module only considers lethal effects of a spill. Due to the absence of adequate data on sublethal effects on seabirds, no such effects are explicitly included in the model. Sublethal effects can be included by altering breeding probability or chicks fledged per pair accordingly, as discussed in the User’s Manual. Effects of chronic oiling are not included either; such effects can be incorporated by altering life-table parameters.

**Updating and Revising the Model**

We distinguish between updating the model and revising it; the latter would involve a substantial revision of the model, utilizing new data as they become available.

With regard to updating the model, all that would be required, to keep the model current, is to input up-to-date estimates of total population size for each species. Alternatively, one can provide an updated estimate of breeding population size (as discussed in the User’s Manual, sections 2.7.1 and 3.2); however, such an estimate should be based only on years in which the proportion of breeders is typical for that species. The reason for this limitation is that the seabird computer model follows the fate of the entire population and breeding census estimates are used only to infer total population size. If breeding numbers in a given year are unrepresentative of the total population (as was the case in 1983 and 1992, for instance, years in which many Common Murres and Brandt’s Cormorants did not attempt breeding), then a poor estimate of total population size will result. PRBO biologists, including the senior author, can provide guidance in updating population size.

Even if additional data become available indicating that some of the life-table parameters (survival, reproductive success, breeding probability) should be altered, such a change can be accommodated within the model as it now stands, without
having to revise the software (see section 2.7.1 of the User's Manual). A similar point applies to the oil spill module: if new data indicate that the mortality rate for a species exposed to oil should be higher or lower than the current default value, such a change can be introduced without requiring a software revision (see section 3.3 of the User's Manual).

Nevertheless, we anticipate, and recommend, that in the future, the computer model be revised, making more substantial changes. Three areas of revision or further work are outlined below:

(1) We recommend a revision of the environmental database (including both oceanographic and food indices) and its relationship to demographic parameters of individual seabird species, as such data become available. We think such a revision would be appropriate in late 1995 or 1996, and about every four to five years thereafter. The environmental database is current through 1992, with a few exceptions. One exception is that Common Murre survival from 1991 to 1992 could not be reliably estimated because many adult murres were not occupying breeding sites in 1992. Resightings of individuals in 1993 (seen in 1991) will help establish the 1991 to 1992 survival rate. Enough individuals were identified in 1992 to allow estimates of survival from 1992 to 1993. By the end of the 1995 breeding season, survival from 1991 to 1992, 1992 to 1993, 1993 to 1994, and 1994 to 1995 can be estimated for Common Murres, thus increasing the number of years of data relating adult survival to environmental variables, from 5 to 9. The computer model for Brandt's Cormorants and Western Gulls will also be improved with the addition of three or four years of survival data. Improving estimates of adult survival and its relationship to environmental variables will improve estimates of chick and subadult survival, too, since these parameters are linked in the computer model.

(2) As additional data on spatial distribution of seabirds become available, this information can be incorporated by revising the appropriate computer files (*.grd files in the computer model). Such information may be forthcoming from efforts of the Oil Spill Response (OSPR) program, of the California Department of Fish & Game, to improve the knowledge of at-sea and offshore distributions of various seabird species.

(3) The model can be fine-tuned using additional population data for the three seabird species in Central California and the Gulf of the Farallones to compare observed population dynamics and predicted trajectories. This exercise can be carried out by using census data from the mid-1990's, as they become available. In addition, accurate census data (from aerial surveys) may become available from
earlier years, at least for Common Murres, as part of anticipated efforts of the OSPR program (see above). If observed population dynamics and predicted trajectories (using current parameters) match well, no further changes would be required; otherwise, demographic parameters would be revised using all available information. We suggest such a comparison be conducted in late 1995 or 1996.
List of References


Appendix

The following is a draft of a paper to be published in a Symposium Proceedings volume (N. K. Johnson and J. Jehl, Editors), as part of the Centennial Meeting of the Cooper Ornithological Society. We include this as an appendix because it presents valuable information on trends in numbers of breeding Farallon seabird species, as well as a discussion of factors that may influence these population trends.