CHAPTER 11

RESTORATION TECHNIQUES: MODELS

INTRODUCTION

Models can be useful tools in designing restoration programs because they can often detect signals in noisy systems. Properly used, they can assist in understanding the fundamental processes of seabird biology, in evaluating the progress of a restoration program, and in eliminating management or restoration activities that would result in biologically improbable scenarios. For example, analysis by Nur *et al.* (1993) revealed that adult survival of Brandt's cormorants was positively correlated with a well-established index of prey availability. This information was then incorporated into a population-dynamic model of this species by Nur *et al.* (1994), who demonstrated that if food availability could be improved, both adult survival and reproductive success might be enhanced.

Population models have the advantage of not relying on intuition, which can lead a restoration planner astray. For example, increasing the reproductive success of breeding birds may seem like a useful restoration action, but in many cases the effect will be negligible because other factors have overriding effects on population growth. A population model can explicitly demonstrate and quantify this point.

There are several caveats that must be expressed with regard to the use of models. Because models are an attempt to describe and account for the interrelationships in extraordinarily complex systems that have no physical boundaries, there will be instances in which predictions from models are incorrect. It is appropriate to trust model results in order to understand fundamental processes and to gain insights into how ecosystems operate. However, when results and predictions are used for management decisions, they should be verified or "ground-truthed" whenever possible with direct observations. In addition, any model used to design restoration programs should be readily available so that the public can make independent analyses. This should not pose a problem. There are several age-structured population models, for example, that are readily available either commercially or as shareware or freeware, such as RAMAS/age (Ferson and Akcakaya 1990) and RAMAS/metapop (Akcakaya 1994).

One use of models is to compare a variety of restoration techniques to help select the most cost-effective restoration option. With any specific set of parameters, models can assist in evaluating the relative "restorative value" of possible approaches. By running models on competing options, managers can evaluate potential projects and avoid those with little promise. For example, some models suggest that survival (adult, subadult, and/or juvenile) may be the key to population regulation, thus focusing restoration projects on increasing survival.

Models can guide research to help form testable hypotheses, identify areas where more data would be useful, and interpret results. Models can also assist in identifying what information is needed, although experienced restoration managers often will not need model results for this purpose.

PREREQUISITES FOR USING MODELS

In order for a model to be useful, it must be well designed, with adequate data used as model inputs. For many seabird species injured by EVOS, essential data from that vicinity are limited or unavailable. Occasionally a colony is difficult to access, so that obtaining high-quality data from that location is impossible. This obstacle can be overcome by using biological information from other regions or conducting a study at a convenient location within the spill area. For example, the life history and demographics of double-crested cormorants are well known from locations in Washington and California, even although they are poorly studied in Alaska.

The common murre is one of the few EVOS-impacted species of seabirds for which sufficient data seem to be available to run demographic models. However, this species, in many respects, has been poorly studied at the EVOS area. The drawback of using substituted data is that demographic characteristics may vary significantly with distance from the injured population. Thus, the validity of the model's results may ultimately hinge on the assumption that different colonies have similar demographic profiles. The sensitivity of conclusions to the assumptions being made can itself be, and should be, explicitly modeled. With respect to common murres, the available data from distant colonies are quite variable. Thus, demographic models may not be useful in assessing how the EVOS spill affected common murres because demographic data for common murres from the region are sparse, and we may not have confidence in results derived from substituted data.

For many species, density-dependence (i.e., demographic parameters, such as fecundity, survival, or recruitment, are functions of population size or density) must be incorporated into the model in order to make accurate predictions. For example, where nest-site availability is limited, this limitation acts as a negative density-dependent factor and reduces recruitment (Birkhead and Furness 1985). High population density may result in saturation of high-quality sites, thus forcing new recruits to take up lower-quality sites where reproductive success is reduced. Positive density-dependence is an important factor in a wide range of species at low population densities. In the common murre, reproductive success increases with density at the colony (Birkhead 1977), apparently due to better protection from predators at high density than at low density. Thus, density-dependence is an important factor that should be incorporated into a model.

ASSUMPTIONS UNDERLYING USE OF A MODEL

Models require many assumptions. Central to the use of any model is the assumption that the model inputs are applicable to the situation. As noted above, using demographic data for common murres from the Farallon Islands or Scotland in a model for the EVOS area assumes that those data are appropriate for murres in the Gulf of Alaska. The modeler must constantly be aware of the maxim "garbage in garbage out," although models lend themselves to evaluation of assumptions.

It is also important to use the correct model. In recent years population models that incorporate stochasticity (i.e., variation due to chance effects) have become common, resulting in a model that is probabilistic rather than deterministic. The reasons for developing stochastic, probabilistic models are manifold. The first is that nature is stochastic; not only is the environment unpredictable, but so are demographic responses to the environment. More realistic and accurate predictions can be made if stochasticity is incorporated. A second reason is that without a probabilistic framework, no sense of variability of outcome is possible.

A modeler should always state explicitly the assumptions in the model. This allows others to evaluate the reasonableness of the assumptions and to test the sensitivity of predictions to changes in model assumptions. For example, a model may assume the presence (or absence) of density-dependence. A different type of assumption may relate to the efficacy of restoration action. For example, following an oil spill, even if one has good estimates regarding the number of oiled birds that are treated and released alive, little is known about the subsequent fate of these "rehabilitated" birds. One can compare predictions regarding impact and subsequent recovery from a spill assuming that (1) some or all rehabilitated birds die within a specified period, (2) a fraction of rehabilitated birds survive but never successfully breed, (3) a fraction of rehabilitated birds survive, and their breeding is impaired only for the immediate breeding season, or (4) some combination of these possibilities. Finally, for some oil spills (e.g., *Apex Houston, Nestucca, Exxon Valdez*), models have been developed to estimate total injury to seabird populations resulting from the spilled oil. Because restoration activities may be based on these estimated or modeled injuries, any evaluation of the efficacy of a particular restoration activity should also include an evaluation of the model's assumptions.

TYPES OF MODELS

Restoration managers can select many types of models as tools in restoration planning or implementation. This section briefly discusses (1) demographic models to predict population changes, (2) stochastic/deterministic/probabilistic models, and (3) sensitivity analysis. Several other types of models could be used depending on the specific situation, including economic models (cost-effective approaches to demographics), statistical models, models of marine trophic systems, and conceptual models.

Demographic Models to Predict Population Growth or Decline

Population dynamics takes a central role in formulating and evaluating a restoration plan. For restoration to succeed, some change in population dynamics must be achieved, either at the level of an entire population or at the level of a subpopulation. Consequently, demographic models can be a useful tool for predicting population growth or decline.

The number of adults is a function of seven population parameters or variables: (1) adult survival, (2) subadult survival, (3) juvenile survival, (4) reproductive success per breeder, (5) probability that an adult will breed, (6) age of first breeding, and (7) net immigration. The significance of this formulation for restoration is that a program will attempt to increase one or more of these parameters, except age at first breeding (which might be decreased). The program can then be judged by considering which parameter or combination of parameters is targeted and the efficacy of the program in altering that parameter.

One difficulty with this approach is that knowledge of subadult and juvenile survival is fragmentary for most seabird species. There is little information about whether subadult survival varies from year to year, and whether there is a correlation between adult and subadult survival. Estimates of survival based on capture and recapture-resighting are biased because of dispersal. Because subadults and breeding adults are usually found in separate areas, different mortality influences may be at work. Juvenile survival seems to vary greatly among populations. Four different population estimates for first-year survival in common murres varied from 0.47 to 0.67 (Nur 1993). In addition, Hudson (1985) provided a list of survival-to-breeding age for Atlantic common murres that ranged from 0.17 to 0.41. Such a large variation in first-year survival or survival-to-breeding age will impact population growth trajectories. Population modeling for common murres on the Farallon Islands showed that 40% juvenile survival results in average population growth of 1.1%, whereas 60% juvenile survival results in a population rapidly growing at the rate of 8% per year (N. Nur, unpubl. data). Hatchwell and Birkhead (1991) modeled the Skomer population of common murres and concluded that a change in juvenile or subadult survival was the major factor explaining why the population grew in the 1980s but not in the 1970s.

Population growth of seabird colonies is undoubtedly influenced by immigration and emigration. Models of single populations have de-emphasized the role of immigration and emigration because it is difficult to incorporate into the usual age-structured or unstructured models. In contrast, immigration and emigration are an explicit part of metapopulation models, so these parameters cannot be ignored (Burgman *et al.* 1993). Emigration is difficult to study because individuals are leaving the study colony and death is hard to distinguish from emigration. The number of immigrants can sometimes be quantified, but the pool from which they come is much harder to identify. A review of population recovery of marine birds shows that immigration played a role in many growing populations (Nur and Ainley 1992).

Species vary in the tendency of young and adults to disperse. Terns and cormorants, for example, show much dispersal, even among breeding adults, while storm-petrels and fulmars have high degrees of philopatry. Within a species the possibilities include (1) a complete absence of interchange between neighboring colonies, (2) wide dispersal so that all colonies in a geographical area are completely mixed and function as a single population, and (3) an intermediate situation between the two extremes. In order to define the boundaries of a population, analysis of DNA or of morphometric characteristics of a population may be feasible (see Chapter 3a). For some species, color phases can help define the boundaries between populations.

In sum, demographic models may be useful because they can set bounds around possible outcomes when population parameters are manipulated and can provide insight into fundamental demographic relationships. However, demographic models are useful only when input parameters are sufficiently well known to allow reasonable bounds to be set for possible outcomes. Unfortunately, for many seabird populations, such input parameters are not sufficiently well known.

Stochastic/Deterministic/Probabilistic Models

Population dynamics models consider all population parameters together. A variety of such models are available (Emlen 1984, Caswell and Macdonald 1993). Whether to use a deterministic model, which ignores chance effects, or to include stochasticity to develop a model that is probabilistic depends on the question that is being asked. One problem with deterministic models is that they do *not* accurately predict average response. Instead, greater environmental and demographic variability depresses population growth rates (Boyce 1992). Moreover, the deleterious effects of random events are strongest for the smallest populations, such as those colonies that are just forming, have been decimated, or are being restored. Where a large population is being modeled, the additional complications of including genetic and random demographic events in a model may not be warranted.

The stochastic population model for the Farallon common murre by Nur *et al.* (1994) predicted that on average the population would grow by 1.1% per year. However, as a result of "error" associated with the stochasticity, the model also predicted that in the face of a very variable, unpredictable environment, there was a 10% chance the population would shrink by 21% or more, or would grow by 53% or more, after 10 years.

The effects of stochasticity on populations have been categorized in four parts (Shaffer 1981, Lande 1993). First, even in identical environments the genetic makeup of two populations will differ due to genetic drift and founder effects, which affect vital rates. Second, random demographic events will affect the number of adults surviving in a finite population from year to year. Random events can skew any population, especially small ones. Third, demographic parameters can vary in any one year due to environmental fluctuation such as excellent or poor feeding conditions. Fourth, environmental catastrophes, while rare and drastic, can occur.

Probabilistic analyses that incorporate demographic and environmental stochasticity form the basis for population viability analysis (Boyce 1992). These analyses can be useful tools for a restoration manager.

Sensitivity Analysis

Sensitivity analysis should be conducted in most modeling exercises. When the modeler varies the assumptions in a model to learn the effect on the model's predictions, it will become apparent which assumptions are critical to the outcome of the model. This evaluation allows the modeler to decide whether particular assumptions drive the model results and helps to evaluate the efficacy of the model.

USING A DEMOGRAPHIC MODEL TO COMPARE RESTORATION TECHNIQUES

This section provides an example of how demographic models can be used to compare restoration techniques. Under this approach, a restoration manager can select between two projects. For example, the first project, if successful, will increase the reproductive success of common murres by 10%. The second project will increase the survival rate of adult common murres by 1%.

A population model for common murres developed by Nur *et al.* (1994) determined that a 2.8% increase in common murre survival produced population growth of about 1.0-1.1%. In contrast, a 10% increase in murre reproductive success resulted in a population growth of only 0.8%. In this instance, the model's comparison of the efficacy of the two techniques would lead a restoration manager to concentrate efforts on small improvements in adult survival instead of moderate improvements in reproductive success. However, the restoration manager should also be aware of the fact that the model is more sensitive to changes in adult survival than to changes in reproductive success. That is, a relatively small error in estimating survival (e.g., survival is actually 0.93 instead of 0.94) will cause a wider range in the estimated population growth than a larger error in estimating reproductive success (e.g., 0.75 instead of 0.85). Comparisons such as this will vary depending on the relative importance of the demographic parameter being compared and the life history of the species whose demography is being modeled.

Where models show that adult survival is the key factor in restoring an injured seabird species, restoration managers can then focus on how to increase adult survival. Depending upon the specific circumstances, fisheries management practices could be changed to lessen bycatch of the injured population. For example, state or federal regulations could restrict the type, location, or season available to gillnet gear or longlines. In addition, Congress could establish a marine sanctuary that might close key areas to activities that decrease adult survival of an injured species.